ECOLOGY OF FRESHWATER PLANKTON IN CONTRASTING HYDRAULIC ENVIRONMENTS

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by

Rory J. Sanderson B.Sc. (Hons) M.Sc.

Department of Biology
University of Leicester

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ABSTRACT

The effects of contrasting water residence time on the planktonic community of three water bodies was studied. The sites were Rutland Water, Covenham reservoir and the River Nene, in order of decreasing retention time. The river was the only site where the residence time was sufficiently short to directly impact upon planktonic populations.

The importance of physical mechanisms of control in the river was indicated by the dominance of r-selected phytoplankton, namely diatoms and green algae, and zooplankton, namely rotifers. This pattern was in contrast to that of the reservoirs in which slower-growing cyanobacteria and cladocerans dominated. Riverine rotifers were found to have rapid population turnover, due to a combination of short pre-adult duration and high maximum growth rates. Some species also showed a shift in reproductive behaviour to the constant production of resting eggs. This was assumed to convey benefits in a system where resting stages may be less susceptible than adults to downstream displacement.

The total chlorophyll 'a' concentration achieved per unit phosphorus was significantly lower in the river than either of the reservoirs. Algal density was negatively associated with discharge in the Nene, suggesting the importance of physical control. The relationship was not a simple one, however, as periods of increased retention time during the summer were associated with low algal density. The absolute density of rotifers was found to be constrained by discharge. Animals were rare above a threshold flow velocity of 0.08 ms⁻¹.

Simple models of water flow in open channels were insufficient to account for the continued persistence of a plankton in the Nene given the level of advection. It was assumed that the overall retention time of the system was increased by the presence of dead zones within the channel (Reynolds, 1988) which 'held' planktonic organisms for sufficient time for populations to develop. This behaviour was important during the spring when population density increased in the main channel. It was less important, and even potentially detrimental, to main channel populations during the summer.

Biotic control within the plankton community was more important in the reservoirs than in the river, with evidence of 'top-down' control of phytoplankton, and food limited zooplankton growth. Cladocerans were found to suppress rotifers via a combination of mechanical interference and exploitative competition for food, especially when the phytoplankton was dominated by edible forms. The two groups coexisted when the competitive advantage of the cladocerans was reduced.
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# CONTENTS

## CHAPTER 1
OVERVIEW .................................................................................................................................1

## CHAPTER 2
LONG-TERM TRENDS IN PHYTOPLANKTON DEVELOPMENT IN THE NENE .............................................. 5

### 2.1 Introduction
- Patterns of phytoplankton development in lakes ..................................................................... 5
- Patterns of phytoplankton development in rivers ...................................................................... 6
- Nutrient availability and predicted algal biomass ....................................................................... 7
- Aims ........................................................................................................................................... 8

### 2.2 Methods
- Calculation of predicted algal biomass from nutrient concentration ........................................... 8

### 2.3 Results
- Phytoplankton Biomass .................................................................................................................. 11
- Annual patterns of algal development in the Nene ..................................................................... 12
- Analysis of factors controlling algal development in the Nene .................................................... 16

### 2.4 Discussion

### 2.5 Summary

## CHAPTER 3
THE PHYTOPLANKTON OF THE RIVER NENE .................................................................................. 25

### 3.1 Introduction
- River form and function ............................................................................................................... 25
- Longitudinal patterns of plankton development ......................................................................... 25
- Can models of fluvial geomorphology explain the presence of a potamoplankton? ...................... 27
  - Plug flow ................................................................................................................................. 27
  - Turbulent flow ....................................................................................................................... 28
  - Turbulent flow plus aggregated dead-zone model .................................................................. 29
  - Which model applies in nature? ......................................................................................... 30
- Dead-zone function ..................................................................................................................... 30
- Dead-Zones as potential sources of river plankton ..................................................................... 30
- River Phytoplankton .................................................................................................................. 31
- Shifting zones of dominance ....................................................................................................... 33
- Objectives ................................................................................................................................... 34
- Study River ................................................................................................................................ 34
  - Geology ................................................................................................................................. 36
  - Physical features .................................................................................................................... 36
  - Water Quality ......................................................................................................................... 36
  - Flow Characteristics ............................................................................................................. 37
  - Study Sites ............................................................................................................................ 37

### 3.2 Methods
- Chlorophyll 'a' analysis .................................................................................................................. 38
- Methods used in the analysis of plankton dynamics .............................................................. 41
  - Estimation of flow velocity from discharge data .................................................................. 41
  - Calculation of non algal turbidity from water transparency and algal density .................... 43
  - Estimation of euphotic depth ................................................................................................. 44
  - Calculation of flow generated turbulent force at Wansford .................................................. 45
- Models of algal loss processes at Wansford during 1994 .......................................................... 46
  - Sedimentation loss rates ........................................................................................................ 46
  - Calculation of grazing losses ............................................................................................... 54
  - Estimation of hydraulic removal loss rates ........................................................................... 55
  - Estimation of main channel imports to the Wansford stretch of the river during 1994 ............ 58
- Estimation of maximum algal growth rates from cell morphology ......................................... 59

### 3.3 Results
- Characteristics of Flow Regime at Wansford ........................................................................... 61
  - Flow rate ................................................................................................................................. 61
  - Flow velocity ......................................................................................................................... 65
  - Flow related habitat types in the main channel at Wansford station .................................... 65
- Physical Characteristics of the Lower River Nene .................................................................... 65
- Potential Light Limitation ........................................................................................................... 67
3.3.4 Plant nutrient concentrations.........................................................................................68
3.3.5 Chlorophyll 'a' abundance at Wansford station, Nassington and Wansford backwater...........................................................................................................69
3.3.6 Riverine Phytoplankton Composition.............................................................................71
3.3.7 Cell Density and Seasonal Succession...............................................................................74
3.3.8 Potential sources of phytoplankton loss at Wansford Station...........................................77
  3.3.8.1 Algal settlement losses.................................................................................................77
  3.3.8.2 Grazing losses...............................................................................................................80
  3.3.8.3 Hydraulic losses............................................................................................................81
3.3.9 Comparison of maximum and observed phytoplankton growth rates...........................83
3.3.10 Grazing losses imposed by littoral zooplankton...............................................................84

3.4 Discussion..........................................................................................................................87
  3.4.1 Flow characteristics of the River Nene.........................................................................87
  3.4.2 Fluvial habitat characterisation in the Nene.................................................................88
  3.4.3 Seston concentration and light limitation.......................................................................89
  3.4.4 Nutrient levels ...............................................................................................................90
  3.4.5 Phytoplankton composition...........................................................................................91
  3.4.6 Temporal distribution of blue-green bacteria..................................................................92
  3.4.7 Estimated loss rates and algal dynamics.......................................................................94
  3.4.8 The source of imports to the main-channel community...............................................97
  3.4.9 Littoral grazers..............................................................................................................98

3.5 Summary...........................................................................................................................100

CHAPTER 4
THE ZOOPLANKTON OF THE RIVER NENE........................................................................102

4.1 Introduction.........................................................................................................................102
  4.1.1 River zooplankton..........................................................................................................103
  4.1.2 Modes of reproduction..................................................................................................105
    4.1.2.1 Rotifera....................................................................................................................103
    4.1.2.2 Cladocera................................................................................................................104
    4.1.2.3 Copepoda................................................................................................................105
  4.1.3 Zooplankton life history strategies................................................................................106
  4.1.4 Selection of suitable life history strategies for rivers.......................................................108
    4.1.4.1 Which zooplankton groups are expected to dominate in rivers?.........................108
    4.1.4.2 Are all rotifers equally suited to life in rivers?......................................................109
    4.1.4.3 Selection within a single species.............................................................................110
  4.1.5 The zooplankton of river systems................................................................................111
  4.1.6 Potential sources of main-channel populations..............................................................112
    4.1.7 Objectives....................................................................................................................113

4.2 Methods............................................................................................................................114
  4.2.1 Field methods..............................................................................................................114
  4.2.2 Laboratory Methods......................................................................................................115
  4.2.3 Analysis of the precision and accuracy of the sample methods used...............................116
    4.2.3.1 Concentration by filtration......................................................................................116
    4.2.3.2 Spatial distribution of animals and the precision of the sampling regime..............116
    4.2.3.3 Effect of variable sample volume of filtration efficiency......................................117

4.3 Results...............................................................................................................................117
  4.3.1 Wansford station zooplankton.........................................................................................117
    4.3.1.1 Density....................................................................................................................117
    4.3.1.2 Zooplankton composition.........................................................................................118
    4.3.1.3 Rotifer composition..................................................................................................118
    4.3.1.4 Comparison of the spring rotifer development during 1992-1994..........................120
    4.3.1.5 Riverine algal palatability.......................................................................................122
  4.3.2 Explaining rotifer population dynamics - multiple regression models..........................123
    4.3.2.1 Growing season (Feb-Oct, 1994)........................................................................123
    4.3.2.2 Spring period (April - May, 1994)......................................................................127
    4.3.2.3 Spring period 1992-1994....................................................................................127
    4.3.2.4 Average monthly rotifer density...........................................................................130
  4.3.3 Keratella cochlearis population dynamics, 1992-1994......................................................130
  4.3.4 Potential food limitation of River Nene zooplankton.....................................................133
  4.3.5 Theoretical dilution rates from the Wansford section of the river.................................135
  4.3.6 Level of importation required to maintain the observed population development at Wansford ..........................................................................................................................137
  4.3.7 Longitudinal survey of River Nene rotifer populations................................................138
4.3.8 Zooplankton of River Nene retention zones ................................................................. 139
  4.3.8.1 Nassington .......................................................... 140
  4.3.8.2 Wansford Backwater ......................................... 141
  4.3.8.3 Factors controlling rotifer dynamics in backwater habitats ................................. 142
  4.3.8.4 Potential food limitation at Wansford backwater .................................................. 144
  4.3.9 Comparison of system stability using zooplankton dynamics as an indicator ......... 145
4.4 Discussion ....................................................................................................................... 146
  4.4.1 River Nene zooplankton composition ................................................................. 146
  4.4.2 Factors controlling zooplankton dynamics in the Nene ....................................... 149
  4.4.3 River Nene rotifer dynamics .............................................................. 152
  4.4.4 Resting eggs ......................................................................................... 154
  4.4.5 The potential for food limitation in the Nene ............................................................. 156
  4.4.6 River function ................................................................. 158
  4.4.7 Retention zones of the Nene ............................................................... 161
4.5 Summary ......................................................................................................................... 163

CHAPTER 5
THE LIFE-HISTORY CHARACTERISTICS OF ZOOPLANKTON FROM THE RIVER NENE AND RUTLAND WATER .......................................................................................................................................166
5.1 Introduction ....................................................................................................................... 166
  5.1.1 Selection for life-history traits .............................................................................. 166
  5.1.2 River habitat templets .......................................................................................... 167
  5.1.3 Typical riverine plankton .................................................................................... 168
  5.1.4 Typical lacustrine plankton ................................................................................. 169
  5.1.5 How can the dominance of rotifers in river systems be explained? ......................... 169
  5.1.6 Aims .............................................................................................................. 170
5.2 Methods ......................................................................................................................... 171
  5.2.1 Rotifer cultures ............................................................................................... 171
    5.2.1.1 Collection and isolation of animals ................................................................. 172
    5.2.1.3 Rotifer food source ...................................................................................... 173
  5.2.2 Cladoceran cultures ............................................................................................ 174
    5.2.2.1 Collection and isolation of animals ................................................................. 174
    5.2.2.2 Individual growth rate experiments ............................................................... 174
    5.2.2.3 Reproductive output ..................................................................................... 175
    5.2.2.4 Cladoceran food source .............................................................................. 176
5.3 Results ......................................................................................................................... 176
  5.3.1 Rotifer culture ....................................................................................................... 176
    5.3.1.1 Rotifer population growth rates ................................................................. 176
    5.3.1.2 Sexual reproduction in the Nene population .................................................. 180
    5.3.1.3 Threshold food concentration .................................................................... 183
  5.3.2 Cladoceran cultures ............................................................................................. 184
    5.3.2.1 Individual growth rates ................................................................. 184
    5.3.2.2 Reproductive output of mature females ......................................................... 186
  5.3.3 Modelled potential rates of increase ....................................................................... 187
    5.3.3.1 Model derivation ....................................................................................... 188
    5.3.3.2 Simulated competition between a riverine rotifer and a riverine cladoceran .......... 191
5.4 Discussion ...................................................................................................................... 193
  5.4.1 Rotifer life-histories ............................................................................................. 193
  5.4.2 Cladoceran life-histories ..................................................................................... 195
  5.4.3 Temporal heterogeneity and grazer competition .................................................... 196
  5.4.4 Spatial heterogeneity and the role of dead zones ..................................................... 198
5.5 Summary ......................................................................................................................... 198

CHAPTER 6
THE ZOOPLANKTON OF TWO LOWLAND RESERVOIRS IN THE EAST OF ENGLAND ................................................................. 199
6.1 Introduction ..................................................................................................................... 199
  6.1.1 Seasonal changes in the physical structure of temperate lakes ................................ 199
  6.1.2 Ecological consequences of thermal stratification .................................................. 200
  6.1.3 Seasonal succession of planktonic communities in temperate lakes ....................... 202
  6.1.4 The role of competition in structuring zooplankton communities ............................ 204
    6.1.4.1 Zooplankton size and competitive ability - Why large Daphnia dominate .... 204
LIST OF FIGURES

CHAPTER 2

Figure 2.1 Relationship of Rast and Lee (1978) (modified slightly from Vollenweider, 1979) between mean annual lake chlorophyll 'a' concentration and annual P-loading in a selection of North American lakes, corrected for hydraulic loading and residence.................................................................8

Figure 2.2 Relationship between phytoplankton cell density and chlorophyll 'a' concentration in the Nene at Wansford, 1994 .........................................................................................................................10

Figure 2.3 Seasonal incidence of chlorophyll 'a' concentration and discharge in the Nene between 1975-1995. Some years excluded due to the lack of a continuous data set........................................................................................................................................13

Figure 2.4 Relationship between mean annual chlorophyll 'a' concentration and mean annual discharge, River Nene, 1975-1995........................................................................................................................................15

Figure 2.5 Relationship between mean discharge (Jan - Apr) and mean chlorophyll 'a' during the growing season of 1975-1995.........................................................................................................................16

Figure 2.6 Frequency histogram of mean monthly chlorophyll 'a' biomass at Wansford, 1975-1995......17

Figure 2.7 Cumulative distribution of monthly mean chlorophyll 'a' biomass plotted as normal quantile plot......................................................................................................................................................17

Figure 2.8 Frequency histogram of mean monthly chlorophyll 'a' biomass below 50 µg l⁻¹, showing similar bimodal distribution to figure 2.6........................................................................................................................................18

Figure 2.9 Scatter plot of mean monthly chlorophyll 'a' and discharge at Wansford. Inset shows stylised relationship. Any value is possible within the shaded zone below the line describing maximum chlorophyll 'a' per unit discharge...............................................................................................................................................19

Figure 2.10 Mean monthly chlorophyll 'a' concentration related to temperature and discharge in the Nene. Points surface smoothed by negative exponential interpolation........................................................................................................................................20

CHAPTER 3

Figure 3.1 Schematic representation of plankton development in low gradient, nutrient rich rivers, showing the spatial displacement of predator / prey cycles along the river during the growing season. After Garnier et al., (1995)........................................................................................................................................26

Figure 3.2 Physical characteristics of laminar plug flow and turbulent flow in rivers.................................................27

Figure 3.3 The River Nene................................................................................................................................................35

Figure 3.4 Sample sites................................................................................................................................................39

Figure 3.5 Power relationship between average velocity and discharge at Wansford.........................................................42

Figure 3.6 Relationship between algal cell number and Secchi depth at low discharge.................................................43

Figure 3.7 Calculation of the potential loss rates of suspended particles from fully mixed water columns....................................................................................................................................................48

Figure 3.8 Physical properties of particles and their associated sinking rates at 15°C...........................................................52

Figure 3.9 Schematic representation of loss of particles from a river section (N) that received variable concentrations from upstream........................................................................................................................................59

Figure 3.10 Discharge at Orton gauging station (line) and rainfall (bar), 1992 to 1995.................................................62

Figure 3.11 Duration curve of daily flow rates throughout 1994 at Orton Lock.................................................................63

Figure 3.12 Duration curve of daily flow rates during 1992-1994 at Orton Lock............................................................64

Figure 3.13 Distribution of shear stress produced by daily discharge through the River Nene at Wansford, 1994, assuming the average height of bed projections to be 1 mm..............................................................................65

Figure 3.14 Physical characteristics of the River Nene at Wansford, 1994.............................................................................66

Figure 3.15 Algal contribution to turbidity at Wansford, 1994....................................................................................................67

Figure 3.16 Percentage of river depth below the euphotic depth at Wansford, 1994...............................................................68

Figure 3.17 Plant nutrient concentrations at Wansford, 1994...................................................................................................69

Figure 3.18 Chlorophyll 'a' concentration at three sample sites on the River Nene, 1994.......................................................71

Figure 3.19 Phytoplankton and bacterial density in the River Nene at Wansford, 1994.......................................................74

Figure 3.20 Phytoplankton and bacterial composition at Wansford, 1994, expressed as percentage of total cell density...........................................................................................................................................75

Figure 3.21 Seasonal development of the two dominant algal groups related to discharge in the River Nene at Wansford, 1994 ...........................................................................................................................................6

Figure 3.22 Algal size groups expressed as percentage of total cell number. Group 1, <250 µm²........76

Figure 3.23 Temporal distribution of blue-green bacteria at Wansford during 1994, and their association with fluctuating discharge.......................................................................................................................................78

Figure 3.24 Daily exponential loss rate of particles with known sinking velocities from mixed columns of different depth...........................................................................................................................................79

Figure 3.25 Daily exponential loss rate of suspended particles through hydraulic removal from the Wansford stretch of the river......................................................................................................................................82
CHAPTER 4

Figure 4.1 Typical rotifer life history.................................................................104
Figure 4.2 Typical cladoceran life history.........................................................105
Figure 4.3 Maximum daily population growth rates of rotifers. After Stemberger and Gilbert (1985). ...109
Figure 4.4 Threshold food concentration for population growth of selected rotifers. After Stemberger and Gilbert (1985). ..........................................................110
Figure 4.5 Filtration apparatus used to concentrate river zooplankton samples. .................................................115
Figure 4.6 Seasonal variation in total zooplankton density at Wansford during the growing season of 1994. .................................................................117
Figure 4.7 Seasonal variation in the relative abundance of planktonic groups at Wansford, 1994. ........118
Figure 4.8 Abundance of dominant rotifer taxa at Wansford station during the growing season of 1994. ........120
Figure 4.9 Total rotifer density, chlorophyll 'a', temperature and discharge during spring 1992-1994 at Wansford station. .................................................................121
Figure 4.10 Composition of algal palatability groupings at Wansford, 1994. .................................................................123
Figure 4.11 Regression line predicting log rotifer density from log chlorophyll 'a' concentration at Wansford, 1994. ........................................................................124
Figure 4.12 Single regressions of Brachionus sp. density against chlorophyll 'a' and discharge at Wansford, 1994. ........................................................................125
Figure 4.13 Single regressions of Keratella sp. density against chlorophyll 'a' and discharge at Wansford, 1994. ........................................................................125
Figure 4.14 Relationship between rotifer community diversity and discharge at Wansford, 1994. ........126
Figure 4.15 Relationship between log chlorophyll 'a' concentration and log rotifer density during the spring development, 1992-1994. ........................................128
Figure 4.16 Relationship between discharge and rotifer density during the spring development, 1992- 1994. (a. log-log plot, b. untransformed plot). ........................................128
Figure 4.17 Relationship between rotifer density and temperature at Wansford during the spring development 1992-1994. .................................................................129
Figure 4.18 Population characteristics of K. cochlearis during April-May, 1992-1994. ........................................131
Figure 4.19 Food availability at Wansford related to specific parameters of rotifer population growth. ....134
Figure 4.20 The percentage of food limited carrying capacity reached by grazing rotifers at Wansford, 1994. ........................................................................135
Figure 4.21 Correlation between observed chlorophyll 'a' density and rotifer density during the spring development 1992-1994. ........................................................................135
Figure 4.22 Estimated loss rate of Keratella cochlearis via dilution (white bars) during May 1992 (left), 1993 (middle), 1994 (right). Birth rate (stippled bars) and actual death rate (opaque bars) are presented for comparison. ........................................................................136
Figure 4.23 Observed density of K. cochlearis (stippled) at downstream sites on the River Nene against expected density (grey), calculated from observed birth rates and transit times between sites. ............................139
Figure 4.24 Abundance of dominant rotifer taxa at Nassington during the growing season of 1994. 140
Figure 4.25 Seasonal variation in the relative distribution of planktonic groups at Nassington, 1994. 140
Figure 4.26 Seasonal variation in the relative distribution of planktonic groups at Wansford backwater, 1994. ........................................................................141
Figure 4.27 Total rotifer density at Wansford backwater during the growing season of 1994. Chlorophyll 'a' also shown. ........................................................................141
Figure 4.28 Abundance of dominant rotifer taxa at Wansford backwater during the growing season of 1994. ........................................................................142
Figure 4.29 Simple linear regressions of chlorophyll 'a' concentration and rotifer density, and discharge and rotifer density, at Nassington during the spring development period, 1994. 143
Figure 4.30 The potential grazing loss rate of algae in Wansford backwater, 1994, and algal density expressed as chlorophyll 'a' concentration. ........................................................................145
Figure 4.31 The effective food concentration available to rotifiers at Wansford Backwater, 1994. 145
Figure 4.32 Regression relationship between discharge and chlorophyll 'a' abundance in the River Nene during spring 1992-1994. ........................................................................151
Figure 4.33 Graphic representation of the population threshold food concentration under different loss rates. ........................................................................157
CHAPTER 5

Figure 5.1. Conceptual representation of potential river systems based on the two habitat template axes of temporal and spatial heterogeneity, after Townsend and Hildrew (1994). ................................................168
Figure 5.2. Numerical growth of *K. cochlearis* populations from the River Nene at different food concentration. ..................................................................................................................................................177
Figure 5.3. Rate of cultured *K. cochlearis* increase during the exponential growth phase (River Nene). .........................................................................................................................................................177
Figure 5.4. Numerical growth of *K. cochlearis* populations from Rutland Water at different food concentration. ..................................................................................................................................................178
Figure 5.5. Rate of cultured *K. cochlearis* increase during the exponential growth phase (Rutland Water). .........................................................................................................................................................178
Figure 5.6. Instantaneous rates of change in culture *K. cochlearis* populations from the River Nene. .........................................................................................................................................................179
Figure 5.7. Instantaneous rates of change in culture *K. cochlearis* populations from Rutland Water. .........................................................................................................................................................180
Figure 5.8. Egg production (expressed as egg ratio) of the riverine *K. cochlearis* population. a. resting eggs. b. amictic eggs. .........................................................................................................................................................181
Figure 5.9. The proportion of total *K. cochlearis* egg production accounted for by resting eggs. ..........182
Figure 5.10. Male production expressed as a proportion of total animals in riverine *K. cochlearis* cultures. .........................................................................................................................................................182
Figure 5.11. Food dependent daily instantaneous growth rates of *K. cochlearis* cultures from the River Nene. .........................................................................................................................................................183
Figure 5.12. Food dependent daily instantaneous growth rates of *K. cochlearis* cultures from Rutland Water. .........................................................................................................................................................184
Figure 5.13. Growth of juvenile *D. curvirostris* from the River Nene. .................................................................................................................................................................185
Figure 5.14. Growth of juvenile *D. galeata* from Rutland Water. ......................................................................................................................................................................................185
Figure 5.15. Individual growth rate of cultured *D. curvirostris* and *D. galeata*. .................................................................................................................................................................185
Figure 5.16. Individual growth rates of *Daphnia* at two different food concentrations. ..................186
Figure 5.17. Relationship between food concentration and the daily rate of neonate production of *D. curvirostris*. a. normal plot. b. log-normal plot showing threshold for reproduction (x-intercept). ........................187
Figure 5.18. Potential population development model for *D. curvirostris* at 20°C. a. normal plot. b. log-normal plot........................................................................................................................................................................189
Figure 5.19. Potential population development model for *D. galeata* at 20°C. a. normal plot. b. log-normal plot .................................................................................................................................................................189
Figure 5.20. Effect of temperature on the numeric development of *D. curvirostris*. Populations started with a single newly hatched animal. ..................................................................................................................190
Figure 5.21. Effect of temperature on the exponent of *D. curvirostris* population increase. ..........191
Figure 5.22. Potential population development of *D. curvirostris* and *K. cochlearis* at 20°C and non-limiting food concentration. Both populations started with a single animal. .........................192
Figure 5.23. Figure showing the competitive advantage of rotifers over cladocerans in the short-term. 192

CHAPTER 6

Figure 6.1 An example of activity curves for different species of *Polyarthra* ...........................................201
Figure 6.2 Site map of study reservoirs ........................................................................................................216
Figure 6.3 Temperature (A.) and percentage oxygen saturation (B.) profiles from Rutland Water, 1991-1992. ..................................................................................................................................................219
Figure 6.4 Temperature (A.) and percentage oxygen saturation (B.) profiles from Covenham reservoir, 1991-1992. ..................................................................................................................................................219
Figure 6.5 Error associated with different sampling effort from the two reservoirs. ........................222
Figure 6.6 Bogorov trough counting chamber ............................................................................................224
Figure 6.7 Chemical characteristics of Rutland Water, 1991-1992. ................................................................................................................................................................................228
Figure 6.8 Chlorophyll 'a' concentration and water clarity in Rutland Water, 1991-1992. .................229
Figure 6.9 Water temperature in Rutland Water, 1991-1992. ................................................................................................................................................................................229
Figure 6.10 Chemical characteristics of Covenham reservoir, 1991-1992. .............................................230
Figure 6.11 Chlorophyll 'a' concentration and water clarity in Covenham reservoir, 1991-1992. ........231
Figure 6.12 Water temperature in Covenham, 1991-1992. .............................................................................231
Figure 6.13 Rutland Water algal community composition, 1991. .............................................................232
Figure 6.14 Rutland Water algal community composition, 1992. .............................................................232
Figure 6.15 Covenham reservoir algal community composition, 1991. .................................................233
Figure 6.16 Covenham reservoir algal community composition, 1992. ...................................................233
Figure 6.17 D. longispina density in Rutland Water 1991-1992. ................................................................237
Figure 6.18 Rotifer fauna of Rutland Water .................................................................................................238
LIST OF TABLES

CHAPTER 2

Table 2.1 Mean annual statistics for the River Nene at Wansford for the period 1995-1995. Values represent annual means with standard error................................................................. 14

CHAPTER 3

Table 3.1 Variables used when calculating sinking rates of particles with typical freshwater algal characteristics....................................................................................................................... 51
Table 3.2 Sinking velocity categories into which individual values were arranged................................................................. 51
Table 3.3 Exponential loss rates of particles from the River Nene at Wansford during typical flow conditions of 1994................................................................................................................................. 57
Table 3.4 Wilcoxon’s signed rank test of chlorophyll 'a' concentration from three habitats of the River Nene during 1994.......................................................................................... 71
Table 3.5 Algal and bacterial taxa recorded at Wansford during 1994.................................................................................. 74
Table 3.6 Estimated daily loss rate of palatable algal groups due to rotifer grazing in the River Nene..... 81
Table 3.7 Zooplankton taxa found in the littoral habitats of the River Nene, with some reference to the ecology of the taxa.......................................................... 85
Table 3.8 Density of littoral crustaceans in the River Nene during the summer (July - August) of 1993................................................................. 85
Table 3.9 Potential loss rate of algal cells due to the grazing activity of littoral populations of the River Nene................................................................. 86
Table 3.10 Estimated loss rates of phytoplankton cells from the main river at Wansford during 1994..... 95

CHAPTER 4

Table 4.1 Selected life-history parameters of freshwater zooplankton...............................................................107
Table 4.2 General characteristics of different potential source habitats in river systems.............................................112
Table 4.3 River Nene rotifers...........................................................................................................................119
Table 4.4 Extent of imports required to balance the K. cochlearis population development observed at Wansford during May 1992-1994.................................................................138

CHAPTER 5

Table 5.1 Results of t-tests between the production of amictic eggs (expressed as the egg ratio) during the exponential and plateau growth phase of K. cochlearis cultures...............................................................181
Table 5.2 Results of t-tests between the production of mictic eggs (expressed as the egg ratio) during the exponential and plateau growth phase of K. cochlearis cultures. Negative results indicate an increase in the production of resting eggs during the plateau growth phase...............................................................181
Table 5.3 Effect of temperature on life-history parameters of D. curvirostris. EDT and PDT represent egg development time and post-embryonic development time respectively...............................................................190

CHAPTER 6

Table 6.1 Some statistics of Rutland Water and Covenham reservoirs..........................................................................................................................218
Table 6.2 Efficiency of sedimentation procedure for rotifer concentration.........................................................................................223
Table 6.3 Selected annual mean characteristics of Rutland Water 1991-1992 .................................................................................226
Table 6.4 Selected annual mean chemical characteristics of Covenham 1991-1992. .................................................................227
Table 6.5 Log algal cell density predicted from TP for different types of freshwater system (after Søballe and Kimmel, 1987). ....................................................................................234
Table 6.6 Rotifer species collected from the two study reservoirs..........................................................................................235
Table 6.7 Crustacean species collected from the two study reservoirs..........................................................................................236
Table 6.8 Pearson product-moment correlations among parameters expected to have an effect on rotifer density during spring (Mar-Jun) 1991 - 1992. n=22..........................................................................................240
Table 6.9 Pearson product-moment correlations among parameters expected to have an effect on rotifer density during summer (Jul-Oct) 1991 - 1992. .................................................................241
Table 6.10 Pearson product-moment correlations among parameters expected to have an effect on rotifer density during the growing season (Mar-Oct) 1991........................................................................256
Table 6.11 Pearson product-moment correlations among parameters expected to have an effect on rotifer density during the growing season (Apr-Oct) 1992.................................................................257
CHAPTER 7

Table 7.1 Species richness, diversity, evenness, and percentage abundance of dominant groups of pelagic rotifers in Rutland Water, Covenham, and the Nene ................................................................. 293

Table 7.2 Percentage composition of the dominant rotifer groups in Rutland Water, Covenham (1991-1992), and the Nene (1993-1994) .................................................................................................................. 294
CHAPTER 1

OVERVIEW

The following definition of plankton, after Reynolds (1984), is used in this thesis:

'The community of plants and animals adapted to suspension in the sea or in freshwaters and which is liable to passive movement by wind and current'.

These organisms, be they plants (phytoplankton) or animals (zooplankton), are therefore distributed throughout their environment with some degree of chance, depending on the movement of water in which they are entrained.

Water is almost constantly in motion. Its movement is described as either laminar or turbulent depending on the degree force applied, be it gravitational, wind or tidal, and the resistance of its molecules. Laminar flow occurs when the external force applied is insufficient to shear bonds between layers of water molecules which slip over one another in an ordered fashion as a result. Many planktonic organisms experience laminar flow in their immediate surroundings owing to their small size, but they may be freely suspended by large scale turbulent movements.

Turbulent flow results when the energy applied to the water increases sufficiently to shear the layers of molecules. This changes the direction of the flow path to produce a series of recoiling eddies which are propagated through the medium until they are overcome by viscous forces and flow returns to laminar. The direction of mass water movement may be the same as with laminar flow, but a single molecule may travel in any direction at any one time with turbulent flow. Turbulent motion is common in freshwaters, especially shallow systems subject to wind or gravitational mixing, and is essential to the plankton as it helps to keep organisms in suspension.

A number of groups, especially within the phytoplankton, have adopted morphological and physiological characteristics to increase the chances of entrainment in turbulent mixed columns (Hutchinson, 1967). These same adaptations, however, may create difficulties in advective environments such as rivers, where flow, albeit turbulent, imposes a dilution loss rate which is greatest for easily entrained organisms.

The definition of plankton given above suggests a lack of ability to maintain position in the face of a constant and unidirectional flow. Zooplankton may be better adapted than most phytoplankton to oppose this movement, yet rotifers and cladocerans are known
to be relatively poor swimmers (Hynes, 1970; Winner, 1975; Walz, 1993) and are therefore at risk unless they adopt behaviours to avoid flow (Richardson, 1992). *Daphnia pulex*, for example was unable to maintain position against a velocity of >2.5 cm s\(^{-1}\), whereas copepods withstood velocities of up to 7.5 cm s\(^{-1}\) (Richardson, 1992).

Reynolds (1989) described the persistence of a river plankton (potamoplankton) as a paradox, as there seemed to be no obvious explanation for the retention of organisms which have such limited ability to counter the movement of water. The fact that an apparently self-perpetuating planktonic community has been recorded from the middle/lower reaches of a number of rivers world-wide including the Severn (Reynolds and Carling, 1991), Thames (Bowles and Quennell, 1971), Rhine (Admiraal et al., 1994), Meuse (Descy, 1987; Marneffe et al., 1996), Seine (Gamier et al., 1995), Po (Ferrari et al., 1989), and Orinoco (Saunders and Lewis, 1989), indicates that conditions were suitable for population development.

Planktonic population growth rates must exceed loss rates, assumed to be dominated by hydraulic removal (Pace et al., 1992), for such development to occur *i.e.* the retention time of water exceeds the generation times of the species found. Reynolds and Glaister (1993), however, found that the retentive capacity of a stretch of the River Severn was insufficient to explain the extent of algal growth observed assuming turbulent mixing. They concluded that retention was increased by the inclusion of dead zones which are areas of slow flowing water linked to the main channel in which the physical conditions are more commensurate with plankton development (Young and Wallis, 1987; Reynolds, 1988). This idea was not in itself original, as Hynes (1970) had previously suggested that most river plankton originated within the confines of the channel, but it did provide a theoretical mechanism by which these areas could constantly seed the river community. This 'dead zone' model remains largely untested, but provides the best solution to the problem of river plankton persistence to date.

Simple models of plankton regulation in rivers have managed to predict algal population dynamics in downstream sections of the River Seine without recourse to the dead zone model (Billen et al., 1994; Garnier et al., 1995). Such slow-flowing sections of lowland rivers may develop a dense plankton which is more similar to that of lakes (De Ruyter van Steveninck et al., 1992) owing to increased physical stability and similar mechanisms of control.

Relatively little work has been performed on the dynamics and limiting factors of river plankton compared to lakes and reservoirs (Pace et al., 1992). There is, however, a generally accepted theory that variations in physical forces exert a greater influence over
community structure than chemical, biotic competitive, or trophic interactions, which have been investigated at length in standing waters (Carpenter, 1988; Reynolds et al., 1994). Many of the critical controlling factors in rivers relate to the physical properties of flow (Reynolds, 1992), including light limited photosynthesis resulting from increased turbidity (Reynolds 1994a), turbidity related shifts in the feeding efficiency of zooplankton grazers (Kirk and Gilbert, 1990), as well as the direct removal of animals (Hynes, 1970).

Chemical and biotic interactions are not unimportant in river systems, rather their expression is masked by the overwhelming constraints imposed by physical factors. Biotic mechanisms may become more obvious when the flow rate is reduced, or flow stabilised during summer, especially in riverine reservoirs, dead zones, and slow flowing lowland river reaches. The planktonic community may become more similar to that of lakes under these conditions (Rzoska et al, 1955; Brook and Woodward, 1956; Threkeld, 1982; Shiel and Walker, 1984; Reynolds and Carling, 1991) as noted above.

The level of control displayed by physical advection is dependant on the relative timescales of water turnover and population processes within the plankton. The fact that most river plankton is dominated by what are generally considered to be $r$-selected species (MacArthur and Wilson, 1967; Pianka, 1970) at the expense of $K$-selected species implies that physical control is dominant over biotic control in systems with rapid water renewal. The lower biomass attained by both phytoplankton (Søballe and Kimmel, 1987) and zooplankton (Pace et al., 1992) in river systems compared to lakes and reservoirs also suggests that physical forces limit growth rather than nutrients or food.

**Project rationale**

The work reported in this thesis builds upon the existing knowledge of what remains a relatively poorly understood topic in freshwater ecology. Although many studies have documented the presence of a potamoplankton, far fewer have attempted to explain the factors which control population dynamics in river systems, especially over prolonged periods of time. Chapters 2 - 4 assess how temporal and spatial variability in flow regime, and therefore retention time, affect the plankton of the River Nene, a eutrophic lowland river in the east of England. Emphasis is placed on elucidating the factors which have the greatest degree of control over plankton development throughout the year, as these remain poorly understood (Reynolds et al., 1994). Chapters 2 and 3 concentrate solely on the phytoplankton while chapter 4 considers the zooplankton. Comparisons of potential population growth rates with estimated loss rates are used to
assess the 'viability' of the plankton, and address the question; should a plankton exist at all given the specific physical characteristics of the Nene?

Chapter 5 examines the life-history traits of zooplankton species adapted to the river, and offers a plausible explanation for the dominance of rotifers over cladocerans in the grazing community, which is the opposite pattern to that expected in systems with longer retention time. Chapter 6 describes the plankton ecology of two reservoirs in eastern England, Rutland Water and Covenham reservoir, both of which have similar water quality but longer water residence time than the Nene. The grazing zooplankton, and in particular the competitive balance between rotifers and cladocerans, was used to assess the impact of changed hydraulic stability on system function.
CHAPTER 2

LONG-TERM TRENDS IN PHYTOPLANKTON DEVELOPMENT IN THE NENE

2.1 Introduction

2.1.1 Patterns of phytoplankton development in lakes

Phytoplankton populations from standing waters in temperate zones are known to display relatively predictable seasonal cycles of development (Reynolds, 1984; Sommer et al., 1986). In the past, these cycles were thought to be controlled by predominantly physical forces, but the synthesis of Sommer et al., (1986) showed the importance of biological interactions in forcing the autogenic succession of community structure throughout the year. The exact species composition, periodicity, and biomass attained by different groups varies from year to year but the pattern of development is 'generally' reproducible, and constitutes 'one of the most striking examples of pattern conformation in freshwater communities' (Reynolds, 1984).

A typical seasonal succession of phytoplankton development in eutrophic lakes, after Sommer et al., (1986), is summarised below. The actual biomass attained is dependent on the nutrient availability of the water body, as described by Vollenweider (1968).

A spring crop of fast-growing algal species may develop towards the end of winter when the light climate improves and water temperature increases. This is often dominated by diatoms owing to their efficient growth in mixed water columns at low light levels (Reynolds, 1984). A chlorophyll 'a' maxima is often reached in spring which subsequently declines owing to nutrient limitation and zooplankton grazing pressure (Vyhnálek, 1989), leading to a pronounced 'clear-water' phase of variable duration (Komárková, 1989) though usually less than one month in eutrophic systems liable to stratification.

The clear-water phase gives way to summer phytoplankton crops when suitable levels of nutrients have been recycled through the zooplankton and grazer population density has reduced as a result of food limitation (Seda, 1989). The summer phytoplankton is characterised by a structural diversification into small 'undergrowth' species which are suitable food for zooplankton grazers and 'canopy' species which are larger, better competitors for limiting resources, and relatively more resistant to grazing (Vyhnálek et al., 1991). Net-algal species may become dominant during the summer (Reynolds,
1984; Komárková, 1989). The autumnal overturn is usually associated with a peak in algal density owing to the release of nutrients from deeper water layers, which is dominated by species adapted to cope with mixing, such as large unicells and filamentous forms. Algal density generally decreases towards the winter as growth conditions become unfavourable, and remains at low biomass until late winter.

Phytoplankton dynamics from nutrient rich lakes are therefore generally typified by a peak in biomass during spring, followed by variable summer standing crops, and an autumnal peak at overturn. There are, however, significant variations to this model. For example, lakes with high flushing rates tend not to suffer from nutrient limitation, and therefore develop populations throughout the growing season. The predictability of the flushing is important though, as irregular events can 're-set' the seasonal succession to an earlier state, or even back to the spring state if sufficiently disturbed. Shallow lakes are also prone to sporadic re-setting events owing to 'optical winters' (Sommer et al., 1986) in which high abiogenic shading effectively reduces primary production back to winter levels.

2.1.2 Patterns of phytoplankton development in rivers

Algal development patterns in rivers are likely to be somewhat different from those of lakes owing to the over-riding control displayed by physical factors such as discharge, turbidity and temperature regime (Descy, 1987; Gosselain et al., 1994; Garnier et al., 1995). Nutrient limitation of plankton is rarely evident in rivers (Reynolds, 1994a) and so has limited potential to control algal dynamics. Annual patterns are also less likely to be as predictable as those of lakes, whose volume acts as a buffer against large-scale discharge-related perturbations. This variability was shown in the Rhine, whose mean seasonal chlorophyll 'a' concentration ranged from 80 µg l⁻¹ to 20 µg l⁻¹ over a ten year study period, predominantly as a function of mean discharge (Tubbing et al., 1994).

The natural variability of rivers makes it difficult to describe a 'typical' seasonal succession of phytoplankton. Generalisations are therefore limited, but in most large rivers within the temperate zone, a bloom dominated by diatoms occurs after a decrease of discharge in the spring, whereas a mixed population of green algae and diatoms comprises the summer phytoplankton (Reynolds, 1988). This pattern was shown in the Rhine, where a marked spring peak in chlorophyll 'a' was followed by a series of short-lived peaks during the summer and low autumn / winter biomass (van Dijk and van Zanten, 1995). A similar pattern was also found in the Vistula (Kowalczewski et al., 1985), where four to six peaks were recorded throughout the growing season.
Other rivers have a different seasonal pattern of algal development. Rivers of the Seine drainage network often showed a rapid decline of the spring peak, after which algal densities remained relatively low throughout the summer (Billen et al., 1994; Garnier et al., 1995). Both the initial decline of the spring peak and the prolonged summer trough were difficult to explain as nutrient levels were high and grazer biomass was low. The authors finally concluded that the combined effects of grazing, parasitism and silica depletion were responsible for lowering algal density, although little quantitative evidence was offered.

2.1.3 Nutrient availability and predicted algal biomass

The density of algae expected to develop in the River Nene is related to some extent to the nutrient concentrations of the water (Søballe and Kimmel, 1987). A number of quantitative relationships between chlorophyll 'a' biomass and phosphate concentration exist for standing water systems. These relationships can be applied to the Nene to see if the river is as productive per unit phosphorus concentration as predicted by these lake models. If this is not the case, then there is a strong possibility that some factor, or combination of factors, other than nutrient limitation dictates algal development in the river.

Vollenwieder (1968) first formulated quantitative relations between nutrient loading, of both nitrogen and phosphorus, and lake primary productivity. Further relationships concentrated more on phosphorus, as this nutrient was considered limiting in freshwater systems. The relationship of Rast and Lee (1978), (presented in Wetzel, 1983) was based on a number of North American lakes and showed how mean annual chlorophyll 'a' concentration increased with phosphorus loading of the water body. This regression is presented in figure 2.1 along with a generalised classification of lake trophic state from Reynolds (1984).

Søballe and Kimmel (1987) also showed a general increase in algal density with total phosphorus concentration for over 600 rivers, reservoirs and lakes in the USA. They found that the algal density attained per unit phosphorus was dependant on the type of water body. A parallel response occurred between water body type, i.e. the slopes of the regression lines were not significantly different, but orthogonal comparisons of the intercepts indicated that, on average, the ratio of algal biomass to total phosphorus followed the sequence: rivers < reservoirs < natural lakes (p < 0.001). The division was not obvious when rivers and reservoirs with similar retention times were compared forcing the authors to conclude that the algal abundance attained per unit phosphorus was dependant on the residence time of the system.
Figure 2.1 Relationship of Rast and Lee (1978) (modified slightly from Vollenweider, 1979) between mean annual lake chlorophyll 'a' concentration and annual P-loading in a selection of North American lakes, corrected for hydraulic loading and residence (from Reynolds, 1988).

2.1.4 Aims

Chlorophyll 'a' measurements from Wansford have been taken as part of the DoE 'Harmonised Monitoring' sampling programme since 1976, now maintained by the Environment Agency (EA). These data were kindly supplied along with temperature, total oxidised nitrate, soluble reactive phosphorus and discharge for the period 1976 to 1996.

The following analysis aims to identify 'typical' annual patterns of phytoplankton development in the Nene (measured as chlorophyll 'a'), thereby placing the study years into context. The analysis also allows the identification of some of the dominant factors which control seasonal abundance patterns. The algal biomass attained per unit phosphorus concentration can also be used to indicate the position of the Nene within the classification of Søballe and Kimmel (1987), and hence indicate if this impounded river system acts as a river or more as a series of reservoirs bound by lock-gates.

2.2 Methods

2.2.1 Calculation of predicted algal biomass from nutrient concentration

Three separate methods were used to predict the development of algal biomass from the measured phosphorus concentration of the Nene.

Annual mean chlorophyll 'a' concentration at Wansford was calculated from weekly sample data. Phosphorus loading to this stretch of water was calculated from annual average SRP concentration and an estimate of the average retention time from the formula of Vollenwieder and Kerekes (1980), presented in Reynolds (1984)

\[
P_a = \frac{[P]_q}{(1 + \sqrt{\tau_w})}
\]

where \([P]_q\) is the average SRP concentration in the inflow (\(\mu g l^{-1}\)) and \(\tau_w\) is the mean retention time of water in the Wansford stretch of the river. The Wansford ‘stretch’ was taken to be the length of river bounded by lock gates immediately upstream and downstream of the sample station. The total volume was estimated as 2.7 x 10^3 m^3 (sd ± 6 x 10^3, n=16) from a 16 year dataset, assuming a length of 6.5 km, an annual mean river depth of 2.1 m (sd ± 0.1 m, n=16) and constant channel width of 20m. The average retention time of water within this section of river was 0.4 days (sd ± 0.2, n=16).

The regression of Rast and Lee (1978) was used to predict the concentration of chlorophyll 'a' (\(\mu g l^{-1}\)) from the phosphorus loading, assuming that their relationship holds for rivers with high phosphate content. The formula is:

\[
[chl.a] = 0.55([P]_q)^{76}
\]

The nutrient loading concept was designed primarily for use in lakes and may not be directly applicable to most rivers. Uptake of nutrients by algae tends to reduce concentrations within lakes such that in-flowing nutrients are diluted throughout the whole volume of the lake. Loading estimates therefore aim to take account of this dilution factor when estimating nutrient availability to primary producers. Rivers, however, have a much shorter retention time than lakes. Nutrient concentrations also tend to increase along the length of rivers, especially as a result of anthropogenic pollution, so there is less chance of any depletion in any single stretch. Considering these characteristics of rivers, nutrients are not diluted with passage from one area of a river to the next and so the actual measured concentration at any point in the catchment may therefore be a more realistic measure from which to base a prediction of the annual mean chlorophyll 'a' concentration.

The concentration of total phosphate during winter / spring may also be used to predict the average summer algal biomass (Dillon and Rigler, 1974). This relationship was developed for stratified lakes in which the spring concentrations before stratification dictate the potential algal development in the epilimnion during summer. The regression equation relating the two quantities is:

$$\log [chl]_w = 1.449 \log [P_A]_w - 1.136$$

where $[chl]_w$ is the mean summer chlorophyll 'a' concentration and $[P_A]_w$ is the mean winter / spring concentration of available phosphorus.


Søballe and Kimmel (1987) produced a relationship between algal cell density and total phosphorus specifically for rivers of Northern America. Chlorophyll 'a' concentrations from the Nene had to be converted to cell densities to use this relationship with the present dataset. This was performed using a regression derived from 1994 data set when both chlorophyll 'a' and algal counts were available from the river (figure 2.2). A general chlorophyll 'a' content per cell had to be assumed to apply this relationship to the other years.

![Figure 2.2 Relationship between phytoplankton cell density and chlorophyll 'a' concentration in the Nene at Wansford, 1994.](image-url)
The chlorophyll 'a' derived estimates of annual cell density in the Nene were compared to the predicted values from the regression equation of Søballe and Kimmel (1987).

\[
\log[\text{cells / ml}] = 0.69 \log[TP] + 4.27
\]

SRP was used instead of TP in the Nene. The predicted algal density will therefore be slightly lower than if TP was used, although SRP accounted for the majority of TP in the Nene.

2.3 Results

2.3.1 Phytoplankton Biomass


The average annual phosphate concentration (soluble reactive phosphate) for the period 1975-1995 estimated from loading (section 2.2.1) was 146 μg P l\(^{-1}\) (se ± 8, n=17) which was predicted to support an average chlorophyll 'a' concentration of 80 μg chl 'a' l\(^{-1}\) (se ± 4, n=17) according to the formula of Rast and Lee (1978) (see section 2.2.1).

The annual mean concentration of 1132 μg P l\(^{-1}\) (se ± 90, n=17), not derived from loading, was predicted to support 114 μg chlorophyll 'a' l\(^{-1}\) (se ± 7, n=17). This phosphorus concentration was higher than those used to construct the original regression so care is needed as linearity cannot be assumed.

The observed annual mean chlorophyll 'a' concentration of 38 μg chlorophyll 'a' l\(^{-1}\) (se ± 3, n=17) was significantly lower than that predicted from both the loading estimate and measured phosphorus concentration (p<0.001).


The average spring SRP concentration from the 1975-1995 data set was 796 μg P l\(^{-1}\) (se ± 87, n=17) which was expected to support an average summer concentration of 1167 μg chlorophyll 'a' l\(^{-1}\) (se ± 194, n=17), after Dillon and Rigler (1974). This estimate, which was of a similar magnitude to that obtained from the regression of Rast and Lee (1978) ignoring the loading component of the procedure, was well above that attained in the Nene (54 μg chlorophyll 'a' l\(^{-1}\); se ± 4.2, n=17) during summer. The observed low summer density cannot therefore be attributed to nutrient limitation.

The mean SRP concentration during the growing season 1975-1995 was 1,132 μg P l⁻¹ (se ± 88, n=17). The predicted mean algal density from the river relationship of Søballe and Kimmel (1987) was 20,088 cells ml⁻¹. The observed mean algal cell density in the Nene was 14,473 ml⁻¹ between 1975-1995 with a standard error of 943 cells ml⁻¹ (n=17). The estimated cell density of Søballe and Kimmel (1987) was not significantly different to the actual density in the Nene (p > 0.05, t-test of single observation against annual mean for Nene). The Nene therefore acted in a similar way to the rivers of the USA, rather than a more lentic system.

A similar analysis was performed on a thirteen year data set from the lower Rhine at Lobith sampling station (river km 850), presented in Tubbing et al., (1994). This large lowland river is highly regulated and was found to have substantially more algal biomass than expected from the river relationship of Søballe and Kimmel (1987). The observed mean algal cell density was 24,335 cells ml⁻¹ (se ± 1791, n=13) compared to a predicted density of 11,530 from an average TP concentration of 499 pg P l⁻¹. The actual density was more similar to that expected in lakes (28,240 cells ml⁻¹, Søballe and Kimmel, 1987). The Rhine phytoplankton biomass was therefore more indicative of a standing water body than a river. This conclusion was strengthened by the relationship of Rast and Lee (1978) (assuming measured TP concentration as loading) which showed no significant difference between the measured and predicted chlorophyll 'a' biomass for lakes.

2.3.2 Annual patterns of algal development in the Nene

Figure 2.3 shows the periodicity of algal development in the Nene at Wansford during 1975-1995. The patterns are variable but tend to fall into two general categories, those years with a clearly defined spring peak followed by a low summer density, and those years when the spring development was maintained throughout the growing season albeit at fluctuating biomass.

Years within the first category included 1985, 1987, 1989, and 1990 - 1995. The spring development generally lasted for approximately three months prior to the summer crash. The timing of the peak was relatively similar among years, starting in April and ending during June. The reason for the decline was not always obvious, and on only two occasions (1987 and 1992) was it coincident with increased discharge.
Figure 2.3 Seasonal incidence of chlorophyll a concentration and discharge in the Nene between 1975-1995. Some years excluded owing to the lack of a continuous data set.
Years within the second category included 1975, 1976, 1978, 1980, 1981, 1982, and 1986. Peaks occurred during the summer months but were usually separated by troughs when chlorophyll 'a' biomass decreased to near zero. The last peaks generally occurred during October / November.

The annual average chlorophyll 'a' biomass was significantly different between these two groups of years (t-test; p < 0.05). The second category had a greater mean chlorophyll 'a' concentration (46 se±1 μg chlorophyll 'a' l⁻¹, n=7) as opposed to the first (34 se ± 3 μg chlorophyll 'a' l⁻¹, n=9). This was not surprising considering the extended period over which algal populations occurred in this category. Annual average SRP, nitrate, temperature and discharge were calculated to ascertain if they had an effect on annual algal density (table 2.1). The two year groups were again tested with a simple t-test but no significant results were returned, i.e. none of the environmental variables considered had significant, sole, control over algal density at this scale of measurement. The use of annual mean values may, however, be too insensitive to determine potential relationships between algal density and independent variables at a finer time-scale (see next section).

<table>
<thead>
<tr>
<th>Year</th>
<th>Chlorophyll 'a' (μg l⁻¹)</th>
<th>Temperature (°C)</th>
<th>SRP (mg l⁻¹)</th>
<th>TON (mg l⁻¹)</th>
<th>Discharge (m³ s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>90.3 ± 22.6</td>
<td>13.3 ± 1.9</td>
<td>1.0 ± 0.2</td>
<td>7.1 ± 0.5</td>
<td>9.3 ± 2.0</td>
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<tr>
<td>1976</td>
<td>65.5 ± 16.7</td>
<td>12.0 ± 2.1</td>
<td>1.2 ± 0.1</td>
<td>9.5 ± 1.3</td>
<td>4.1 ± 1.5</td>
</tr>
<tr>
<td>1977</td>
<td>40.8 ± 13.6</td>
<td>10.6 ± 1.5</td>
<td>0.8 ± 0.1</td>
<td>11.7 ± 0.9</td>
<td>12.5 ± 2.9</td>
</tr>
<tr>
<td>1978</td>
<td>38.3 ± 11.7</td>
<td>10.7 ± 1.5</td>
<td>1.1 ± 0.2</td>
<td>10.3 ± 0.4</td>
<td>9.3 ± 2.2</td>
</tr>
<tr>
<td>1979</td>
<td>34.3 ± 12.1</td>
<td>10.4 ± 1.8</td>
<td>1.0 ± 0.2</td>
<td>10.6 ± 0.5</td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>51.1 ± 13.6</td>
<td>11.1 ± 1.6</td>
<td>0.9 ± 0.1</td>
<td>8.8 ± 0.6</td>
<td>12.6 ± 1.9</td>
</tr>
<tr>
<td>1981</td>
<td>42.3 ± 14.7</td>
<td>11.3 ± 1.6</td>
<td>1.0 ± 0.1</td>
<td>8.4 ± 0.4</td>
<td>12.4 ± 2.5</td>
</tr>
<tr>
<td>1982</td>
<td>41.2 ± 10.7</td>
<td>12.0 ± 1.6</td>
<td>1.1 ± 0.1</td>
<td>9.3 ± 0.7</td>
<td>12.2 ± 3.0</td>
</tr>
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<td>1985</td>
<td>49.8 ± 18.5</td>
<td>10.4 ± 1.7</td>
<td>1.6 ± 0.2</td>
<td>9.9 ± 0.8</td>
<td>8.9 ± 1.8</td>
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<tr>
<td>1986</td>
<td>40.5 ± 9.8</td>
<td>11.1 ± 1.7</td>
<td>1.3 ± 0.2</td>
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<td>12.3 ± 2.3</td>
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<td>1987</td>
<td>27.5 ± 12.3</td>
<td>11.4 ± 1.5</td>
<td>1.3 ± 0.2</td>
<td>10.8 ± 0.6</td>
<td>12.3 ± 2.0</td>
</tr>
<tr>
<td>1990</td>
<td>45.9 ± 18.5</td>
<td>11.8 ± 1.6</td>
<td>1.8 ± 0.3</td>
<td>8.6 ± 0.8</td>
<td>6.1 ± 2.3</td>
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<td>1991</td>
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<td>1.8 ± 0.2</td>
<td>10.0 ± 0.8</td>
<td>3.6 ± 0.5</td>
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<td>1992</td>
<td>35.9 ± 11.0</td>
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<td>1.0 ± 0.1</td>
<td>10.9 ± 0.8</td>
<td>11.6 ± 3.2</td>
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<td>1993</td>
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<td>0.7 ± 0.1</td>
<td>10.3 ± 0.5</td>
<td>11.6 ± 2.5</td>
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<tr>
<td>1994</td>
<td>14.8 ± 5.5</td>
<td>11.7 ± 1.5</td>
<td>0.6 ± 0.1</td>
<td>9.4 ± 0.4</td>
<td>11.2 ± 2.6</td>
</tr>
<tr>
<td>1995</td>
<td>27.1 ± 11.4</td>
<td>11.7 ± 1.7</td>
<td>1.1 ± 0.2</td>
<td>8.7 ± 0.6</td>
<td>8.3 ± 2.5</td>
</tr>
</tbody>
</table>

Table 2.1 Mean annual statistics for the River Nene at Wansford for the period 1975-1995. Values represent annual means with standard error.
Discharge is known, however, to have an effect on riverine algal abundance (Hynes, 1970; Descy, 1987). Figure 2.4 shows a plot of annual average discharge against annual average chlorophyll 'a'. Discharge did not account for a significant amount of the residual variation in chlorophyll 'a' as shown by the low coefficient of determination and general scatter about the regression line.

\[
y = -1.323x + 51.902 \\
\tau = 0.347
\]

![Figure 2.4](image)

**Figure 2.4** Relationship between mean annual chlorophyll 'a' concentration and mean annual discharge, River Nene, 1975-1995.

The level of discharge during spring was hypothesised to have an important effect on the size of the algal population that developed during the growing season, as discharge has an indirect effect on algal growth rates through temperature and light climate modifications, and a direct effect on loss rates through settlement, dilution and the removal of resting eggs. Figure 2.5 shows the association between mean chlorophyll 'a' concentration for the growing season and mean discharge during the first four months of the year in the Nene.

The relationship was not significant (p>0.05) when all years were considered together. There seemed, however, to be two distinct year groups each with a different algal response to discharge. The individual regression lines for the two groups were highly significant. The regression equation for the upper year group was:

\[
[M_a] = 91.489 - 1.656[Q]
\]

where \([chla]\) is mean chlorophyll 'a' concentration for the growing season and \([Q_s]\) is average discharge during Jan - Apr. The equation for the lower year group was:
\[
\begin{align*}
\text{[chl}_a] & = 56.975 - 1.471Q_i
\end{align*}
\]

Discharge accounted for 75% of variation in chlorophyll 'a' concentration in the upper group, and 82% of variation in the lower group. The slopes of the two lines were not significantly different from each other (p>0.05, test for colinearity), i.e. discharge had a similar effect on the two groups. The intercepts of the two lines were, however, significantly different (p < 0.05, ANCOVA).

![Figure 2.5](image)

Figure 2.5 Relationship between mean discharge (Jan - Apr) and mean chlorophyll 'a' during the growing season of 1975-1995.

The upper group was dominated by years that attained a higher chlorophyll 'a' concentration irrespective of the length of time that algal populations developed (i.e. the upper group contained all years with a continued summer development plus four years with no summer development). There was, however, no reason to divide the years into these groups apart from their obvious difference in response to discharge. T-tests performed showed no significant difference between the groups when SRP, nitrate and temperature were considered.

2.3.3 Analysis of factors controlling algal development in the Nene

Mean monthly statistics were calculated to offer information at a finer temporal scale. These data were used in regression analyses to assess how discharge, temperature, SRP and nitrate concentration affected chlorophyll 'a' biomass. The chlorophyll 'a' data were manipulated prior to the analysis to ensure that they conformed to a normal
distribution as they were initially non-normally distributed \( p < 0.001 \), Kolmogorov-Smirnov test for goodness of fit).

The initial distribution resembled an extreme Poisson (figure 2.6). This type of distribution was not unexpected considering the predominance of months with low chlorophyll 'a' biomass especially during the winter. The distribution was not, however, described by a simple Poisson model, as a square root transformation did not normalise the data. In fact, no single transformation could be applied to this data set owing to its bimodal nature.

![Histogram](image)

**Figure 2.6** Frequency histogram of mean monthly chlorophyll 'a' biomass at Wansford, 1975-1995.

There were two distinct distributions within the data set, as shown by figure 2.7.

![Quantile plot](image)

**Figure 2.7** Cumulative distribution of monthly mean chlorophyll 'a' biomass plotted as normal quantile plot.
The first followed a simple poisson distribution (below 50 µg/l chlorophyll 'a') which was normalised by square root transformation, the second (above 50 µg/l chlorophyll 'a') was already normally distributed and required no transformation. The former was dominated by low densities during winter months, whereas the latter was dominated by higher densities during the growing season. The two distributions were treated separately for regression analysis. This was considered appropriate as the winter months offered little to the general understanding of algal control in the Nene.

**Chlorophyll 'a' concentration < 50 µg/l**

The distribution of this data set was again bi-modal (figure 2.8). A single square root transformation was not adequate to ensure normality. Winter months (October - February) were removed from the dataset. This removed the majority of data points with low biomass. The remaining data set was normally distributed after log transformation.

A general linear multiple regression model was performed on this data set using mean monthly discharge, temperature, SRP and nitrate as independent variables. SRP and nitrate both described a significant proportion of variation in chlorophyll 'a' concentration (P < 0.05). The coefficient of determination was, however, low (r² = 0.18) indicating that there was considerable residual variation. Nutrients were considered unlikely to be limit algal growth at the measured concentrations, and both independent variables were negatively correlated with chlorophyll 'a' which made little ecological sense. Little confidence was therefore placed in this model.

![Chlorophyll 'a' concentration < 50 µg/l](image)

**Figure 2.8** Frequency histogram of mean monthly chlorophyll 'a' biomass below 50 µg/l, showing similar bimodal distribution to figure 2.6.

**Chlorophyll 'a' concentration > 50 µg/l**
No significant predictors of chlorophyll 'a' biomass were found when the > 50 μgl⁻¹ dataset was analysed by multiple regression, but this was no doubt influenced by the summer periods when low density was associated with low discharge. The inclusion of many more independent factors, such as light intensity, turbidity, grazing intensity and parasitism might give the model more predictive power.

The potential controlling effect of discharge on chlorophyll 'a' concentration became clearer when mean monthly chlorophyll 'a' and mean monthly discharge were plotted against each other (figure 2.9). No correlation was present owing to the large degree of scatter, but a general pattern emerged as indicated by the stylised inset. The biomass of chlorophyll 'a' attained was highly variable below a maximum 'ceiling' density defined as the maximum biomass attainable at a set discharge. This 'ceiling' was described by the negative linear relationship:

\[
[chla] = -6.25[Q] + 250
\]

where \([chla]\) is mean monthly chlorophyll 'a' concentration (μgl⁻¹) and \([Q]\) is mean monthly discharge (m³s⁻¹). No appreciable algal development was expected above a discharge of 40 m³s⁻¹, relating to a flow velocity of 0.51 ms⁻¹.

![Figure 2.9 Scatter plot of mean monthly chlorophyll 'a' and discharge at Wansford. Inset shows stylised relationship. Any value is possible within the shaded zone below the line describing maximum chlorophyll 'a' per unit discharge.](image)

The combined effects of temperature and discharge on algal development are shown in figure 2.10. The majority of high algal densities were confined to periods when
temperature was above 10°C and discharge below 20 m$^3$s$^{-1}$. Within these limits, the development was rather variable, but outside it was severely restricted.

![Figure 2.10](image)

**Figure 2.10** Mean monthly chlorophyll 'a' concentration related to temperature and discharge in the Nene. Points surface smoothed by negative exponential interpolation.

Multiple regression models attempting to describe weekly fluctuations in chlorophyll 'a' biomass were non-significant. The regressions would have been better if other variables known to affect algal development were included, but the conclusion to be drawn from this analysis is that river plankton populations are extremely dynamic, and subject to a range of control measures linked to the physically dynamic nature of river flows themselves.

Physico-chemical parameters had a much closer relationship with discharge than chlorophyll 'a', indicating the potential role of biotic interactions as important controls on algal development. Discharge was negatively correlated with temperature and SRP and positively correlated with nitrate and turbidity. Pearson correlation coefficients were -0.740, -0.836, 0.658 and 0.800 respectively during 1994 (n=34, all significant at p < 0.01) while the value for discharge and chlorophyll 'a' was -0.040 (not significant).

### 2.4 Discussion

Chlorophyll 'a' concentrations in the Nene were significantly lower than those predicted by the relationships of Rast and Lee (1978) and Dillon and Rigler (1974) derived for lakes. This discrepancy is a product of the different nature of lake and river systems. Lakes are relatively stable and often allow phytoplankton to develop until nutrients become limiting. Rivers, on the other hand, are more prone to disturbance and tend to
be limited by physical parameters rather than nutrients (Descy, 1987). The Rhine, however, established substantial algal populations, somewhere intermediate between those expected from a river and a lake according to the Søballe and Kimmel (1987) classification. The Rhine is a much larger river than the Nene, and may behave more like a ponded lake system than a river. The size of the river and nature of flow regulation measures are therefore likely to be of importance to plankton development as they dictate the flow regime of the river.

Nutrient levels in the Nene were well above those characteristic of eutrophic waters (Wetzel, 1983). Algal density during summer was not correlated with phosphate levels indicating a lack of nutrient limitation. In fact, low chlorophyll 'a' concentrations during the summer were associated with the highest SRP levels, indicating that other factors were responsible for low algal density at these times.

The algal biomass attained per unit phosphorus concentration in the Nene was found to be more similar to the rivers of N. America than the lakes studied by Søballe and Kimmel (1987). The authors concluded that rivers attained a lower chlorophyll 'a' biomass per unit phosphorus than reservoirs and lakes owing to their shorter retention time. The net negative influence of rapid water renewal was attributed to decreased time available for algae to interact with transported material, namely plant nutrients, before their removal from the system.

Other flow related factors with the potential to decrease algal development included a poor light climate associated with abiogenic turbidity, physical abrasion, and settlement from shallow water columns. Countering these negative impacts were factors which tended to promote algal growth in rivers, including high nutrient concentrations, a low density of herbivorous zooplankton, and decreased sedimentation rates owing to turbulent mixing. The overall impact of decreased water residence time on algal development was, however, considered to be negative by Søballe and Kimmel (1987).

The limitations of applying published relationships between algal biomass and phosphorus concentration to the Nene dataset are recognised. One cannot assume that the physical, chemical, and biological conditions in this study fall within the range used to construct the original relationship.

Their use, however, was crucial in the present study to allow a broad understanding of system function, and was considered valid owing to the wide range of conditions found in the water bodies used to construct the relationships. The range of physico-chemical parameters cited in Søballe and Kimmel (1987) encapsulated those found in the Nene.
From a management point of view, the physical limitation of riverine algal communities may be favourable. Rivers are well suited for carrying high phosphate loads without incurring the excessive algal production expected in lentic systems. This is important as many of the world’s rivers have high anthropogenic phosphate loading as a result of domestic, industrial and agricultural effluents. The lower residence time of water is likely to be the major factor reducing the level of algal response (in terms of biomass accumulation) below those predicted for lakes.

Two distinct annual patterns of phytoplankton development were apparent in the Nene during the period 1975-1995. Some years resembled the patterns described for the Rhine (van Dijk and van Zanten, 1995) and Vistula (Kowalczewski et al., 1985) with phytoplankton population development continuing throughout the growing season while other years resembled that described for the rivers of the Seine catchment (Billen et al., 1994) which had little development after the crash of the spring peak.

The river Nene has very high nutrient levels and should therefore be able to support a summer phytoplankton community assuming no other factors limit growth. The fact that over half of the years for which data was available had no such development indicates the action of some 'over-riding' influence which prevented algal growth. It is not clear from the present study what this influence was, but it was certainly not due to reduced nutrient levels during the years in question. It is possible that all such rivers can exist in both states depending on the environmental cues received during the early part of the year. In the few longer-term studies that exist, no generalised seasonality has been described, presumably owing to the highly stochastic nature of river function which makes this a difficult task.

The reasons for the rapid decline of spring populations and the maintenance of low summer algal densities have not been adequately described in the literature, and will be discussed in the following chapters. The pelagic zooplankton of the river showed a similar seasonality to the phytoplankton. Garnier et al., (1995) proposed that biotic control dominated by grazing and parasitism caused the spring decline. The low pelagic zooplankton grazing pressure in the Nene during the summer months cannot explain the low phytoplankton density (section 3.3.8.2) in years with low summer biomass. De Ruyter van Steveninck et al., (1992) also had trouble describing the natural loss rates in terms of predicted grazing and settlement loss.

The effect of discharge on the extent of plankton development in rivers is well documented. There was, however, no direct correlation between mean annual discharge and chlorophyll 'a' concentration in the Nene. It is possible that there was insufficient
difference between annual mean discharge to detect such an influence, i.e. a plankton can develop under a relatively wide range of discharge as long as other environmental conditions are favourable. It is also possible that the use of annual means missed important relationships that occurred over a finer time-scale, for example, weeks or months.

It was hypothesised in section 2.3.2 that the discharge during the early part of the year may have a more pronounced influence on the average algal density attained throughout the growing season, by removing resting stages with sediment at high flows and delaying the important spring peak. This idea was primarily based on the observation that the average chlorophyll 'a' concentration of 1994 was the lowest for the sample period, and was associated with the highest winter / spring discharge. Highly significant correlations were found between spring discharge and the mean algal density in the following growing season, but there appeared to be two independent groups of years which differed in their response. Garnier et al., (1995) also noted the importance of discharge during the early part of the year on the dynamics of algae in the following growing season. High spring discharge tended to delay the spring development which reached a lower peak biomass as a result.

The reason for the differentiation into two annual groups in the Nene was somewhat of a mystery as there was no obvious physical or chemical basis for the separation. It was noted that the group with lower biomass accumulation per unit discharge contained all years from 1991 to 1995, with the inclusion of 1987. The reason for the low algal biomass of this latter year was the poor weather conditions during the summer which led to high discharge and low solar irradiation. The same was true in the Rhine, when the lowest algal biomass over a ten year study period was attained in 1987 (de Ruyter van Steveninck et al., 1990). A possible reason for the lower biomass in 1991-1995 was the impact of phosphate stripping measures in the Nene catchment which were started in 1993. Phosphate stripping may have been influential in reducing algal levels post 1991, but the mechanism was not a simple one as no significant reduction in SRP was found between groups when the residuals from the discharge / SRP regression were analysed by t-test.

It is also possible that the low biomass attained in these years was owing to a poor recruitment of resting stages from the sediments. The size of the innocula available depends on two parameters, firstly the size of the standing population in the previous season, and secondly the discharge during the winter. It is feasible that if the density is reduced in a single year owing to high winter flow rates removing a significant number of resting propagules, then the effects will cascade throughout subsequent years. This
may partly explain the low density during the 1991-1995 period.

The upper limits to algal biomass development in the Nene seemed to be set by discharge as shown by the 'ceiling' density achieved at different flow rates (figure 2.9). Temperature and light intensity were also likely to be of importance as these factors influence growth rates when nutrients are plentiful. Algal populations only developed when temperature was above 10°C and discharge below 20 m³s⁻¹ (figure 2.10). Outside these limits the loss rates imposed by dilution may to be too great to be matched by growth rates. Within this 'zone of development', however, there was substantial variation in the density achieved presumably as a result of variable growth rates and biotic interactions.

The complex nature of phytoplankton regulation in rivers reduced the power of the relatively simple regression analyses which described relatively little residual variation in algal density as a result, whether at the weekly, monthly or annual scale of measurement. Another reason for the poor predictive power of the models stemmed from treating all algae as a single taxonomic unit, when in reality it was composed of many species each with different tolerance ranges to the vast diversity of potential controlling factors. This gross simplification undoubtedly disguised many significant patterns, but was necessary considering the use of chlorophyll 'a' as a surrogate measure of algal density.

2.5 Summary

The biomass of phytoplankton in the Nene was below that predicted from phosphate concentration using regressions derived from lakes. This indicates that phosphate does not limit algal growth in the river as is often the case in lentic waters, rather some other suite of limiting factors are involved. The importance of discharge was shown by the presence of a distinct relationship between maximum chlorophyll 'a' per unit discharge. Below this 'ceiling' level, the density attained was highly variable, controlled by such factors as light intensity, temperature, sedimentation rate, and biotic interactions.

The behaviour of the river with respect to plankton development was very stochastic, and varied from year to year. Two major annual patterns were evident, those with development throughout the whole growing season (Mar-Oct) and those with a single period of development in spring. A similar dichotomy has been described from other European rivers, but rarely within the same river over a number years. No single environmental variable controlled the pattern of seasonal development.
CHAPTER 3

THE PHYTOPLANKTON OF THE RIVER NENE

3.1 Introduction

3.1.1 River form and function

The physical attributes of a 'natural' river, such as width, depth, flow rate, discharge and temperature are assumed to change in a predictable fashion with distance downstream, as described in the River Continuum Concept of Vannote et al., (1980). A relatively predictable continuum of habitats exists along the course of a river which are broadly divided into headwater reaches (stream order 1-3), middle order reaches (order 4-6), and large rivers (order >6). The biological communities associated with each reach are also thought to change in a typical manner so as to maximise the efficiency of energy utilisation lost from upstream compartments (Vannote et al., 1980). Planktonic productivity is usually confined to middle-lower order stretches of rivers where the physical impact of flowing water is reduced.

Many headwater streams have a relatively large proportion of their cross sectional area shaded by riparian vegetation which has two consequences for energy transfer. Firstly, allochthonous inputs from the canopy represent an important energy source, especially during autumn, and secondly, the level of irradiance reaching in-channel primary producers is reduced by shading. Headwater reaches are often heterotrophic (Production/Respiration <1) as a result, and rely on allochthonous material retained throughout the year by organic debris dams, as their primary energy source.

Middle order channels are less effected by riparian shading and direct allochthonous energy inputs. Primary production by rooted macrophytes and algae becomes a more important energy source, and an associated increase in the P/R ratio to >1 is typical.

High order sections of large rivers which are more sluggish and deeper than their upstream reaches may therefore develop a limnetic plankton community. Primary production may, however, be light-limited by high turbidity leading once again to P/R of <1 one.

3.1.2 Longitudinal patterns of plankton development

Billen et al., (1994) modelled the phytoplankton dynamics of the Seine river system
and found the distribution of communities loosely matched those predicted by Vannote et al., (1980). Low order reaches (1-4) had little algal development and were predominantly heterotrophic in nature while pelagic phytoplankton populations developed throughout the middle reaches (orders 5-6) leading to autotrophic conditions (P/R >1). High order channels were often heterotrophic owing to decreased photoautotrophic production rates in the turbid waters. A reduction in phytoplankton abundance towards the mouth of rivers was also noted in the River Rhine (De Ruyter van Steveninck et al., 1990) and the River Meuse (Descy and Gosselain, 1994); this may have been caused by a degree of loss through grazing and parasitism (Billen et al., 1994; Garnier et al., 1995) as well as light-limited growth rates. Biotic interactions may therefore be of importance in structuring riverine phytoplankton along with the more obvious physical control imposed by discharge, turbidity and temperature (Hynes, 1970; Søballe and Kimmel, 1987; Descy and Gosselain, 1994, Gosselain et al., 1994; Reynolds, 1994b).

The phytoplankton biomass of river sections in the Seine basin was found to alternate with stream order above seventh order i.e. high in seventh, low in eighth, high in ninth etc. (Garnier et al., 1995). This pattern was attributed to the spatial displacement of a typical predator-prey cycle, forced by the unidirectional flow. A refinement of the supposed algal development in River Continuum Concept (figure 3.1) can therefore be applied to the River Seine system.

![Figure 3.1](image-url)  
**Figure 3.1** Schematic representation of plankton development in low gradient, nutrient rich rivers, showing the spatial displacement of predator / prey cycles along the river during the growing season. After Garnier et al., (1995).
This pattern, however, is probably only applicable to certain seasons in temperate systems, and is also specific for rivers that have similar physical conditions and biotic interactions to the Seine. It does, however, show that, depending on the physical and biotic attributes of a river, the development of a planktonic community is quite possible in downstream reaches.

3.1.3 Can models of fluvial geomorphology explain the presence of a potamoplankton?

3.1.3.1 Plug flow

Laminar plug flow is the term used to describe the simultaneous movement of a single mass of water downstream without mixing (figure 3.2b). This type of flow may seem the most intuitive model for rivers, but is seldom realised in nature owing to the volume of the channel, the speed of flow and the effects of friction from the sides and bottom of the channel which induce mixing. The persistence of a 'true potamoplankton' would be unlikely, and at best, would rely on a constant inocula from an upstream source if the plug flow model were applicable to rivers.

![Plug Flow vs Turbulent Flow](image)

Figure 3.2 Physical characteristics of laminar plug flow and turbulent flow in rivers. A. Two dimensional representation of downstream movement in a flow rate of 0.25 m s\(^{-1}\), assuming a cell doubling time of 1 day. B. Two dimensional representation of the movement of a single 'parcel' of water.

With plug flow, the appearance of riverine algae would be manifest as a zone of increasing density, assuming a degree of \textit{in situ} reproduction, moving uniformly downstream towards the sea at a rate dependant on the discharge (figure 3.2a). The
appearance and density of populations drawn from a single station throughout the year would be sporadic and dependant on the timing, size, and subsequent growth of upstream inocula. Longitudinal surveys along the course of a river would likewise show a very heterogeneous distribution of planktonic organisms. The appearance of a population would simply be dependant on the chance of a plug passing the point when the sample was taken, and would not necessarily relate to the communities at other sites.

The distribution of phytoplankton and zooplankton populations in temperate rivers does not follow the patterns expected if laminar plug flow persists. Phytoplankton have been simultaneously recorded from many downstream reaches of the same river where they undergo synchronous population increase when conditions are favourable (Lack et al., 1978; Reynolds and Glaister, 1993; Köhler, 1994; van Dijk, 1995), indicating that the plankton is somehow retained within the system. The biomass of phytoplankton does, however, tend to increase downstream, indicating a degree of longitudinal transport (Lack et al., 1978; Søballe and Kimmel, 1987; De Ruyter van Steveninck et al., 1992; Reynolds and Glaister, 1993; Admiraal et al., 1994; Descy and Gosselain, 1994; Reynolds, 1994b; Stoyneva, 1994). The same applies to zooplankton density (Hynes, 1970; Winner, 1975; Saunders and Lewis, 1989; De Ruyter van Steveninck et al., 1990; Pace et al., 1992; De Ruyter van Steveninck et al., 1992; Tubbing et al., 1994; van Zanten, 1994; Marneffe et al., 1996).

The plug flow model therefore has obvious shortcomings when describing the occurrence and distribution of the potamoplankton and a more realistic model must be sought.

3.1.3.2 Turbulent flow

Laminar flow is only maintained if the force creating the flow is sufficiently small (gravitational force in the case of rivers), or the channel through which the water passes is sufficiently confined, to allow the layers of water molecules to slide over one another in an ordered fashion. If the energy is increased, or the channel widened, then layers of water are constantly sheared and entrained in turbulent eddies (figure 3.2.b). Irregularities in channel form will also increase eddy formation, as the layers of water that pass closest to the obstructions are slowed down in comparison to the main flow. The resulting turbulent flow is the dominant form of water motion in rivers (Carling, 1992; Reynolds, 1994b).
The overall movement of water with turbulent flow is still downstream, but the pockets of water entrained in eddies all have different flow rates and directions (figure 3.2b). The overall effect of this is to increase the retention time of water in a river reach and therefore decrease the rate at which particles are removed downstream (figure 3.2.a).

Reynolds (1988) showed that the loss of suspended particles from a fully mixed section of river occurred at an exponential rate, with 0.37 of the initial density remaining after the time taken to fully flush the section assuming plug flow. Turbulent flow therefore increases the retention capacity of the river over that of plug flow, but is this sufficient to account for the persistence of natural river populations?

The answer was no according to Reynolds (1988) who attempted to explain the apparent persistence of phytoplankton in the Thames as described by Lack et al., (1978). The exponential loss rates involved would have required impossibly high rates of reproduction (equivalent to cell doubling times in the order of 8-9 minutes) to maintain a static density of organisms over time. Even if one considers importation of sufficient cell numbers from immediately upstream, the problem of self maintenance is simply shifted up the river, rather than solved; i.e. "where did the inoculum to the first section that maintained a plankton originate?" The turbulent flow model, like the plug flow model therefore seems inadequate to explain the maintenance of a potamoplankton, and must be questioned as a suitable model for fluvial transport.

3.1.3.3 Turbulent flow plus aggregated dead-zone model

Many workers now believe that the aggregated dead-zone model described by Young and Wallis (1987) more adequately described the behaviour of flowing water in river channels. The model implies the presence of substantial regions of non-flowing water (dead-zones) within natural channels which are somehow protected from the main flow. Dead-zones vary in scale from small eddies caused by the frictional resistance of bed rocks, though embayments, to blind arms, but all act to increase the retentive properties of a river. The size and permanence of dead-zones is related to the rate of water exchange between the zone and the main flow. Reynolds (1994b) found that during low flow periods the aggregated dead-zone, i.e. all dead zones in the system irrespective of size and permanence, increased, whereas at higher discharge it decreased as some zones were lost, presumably overwhelmed by rising water.

Plankton populations should develop in dead zones as they offer a greater degree of physical stability than the main channel. Reynolds and Glaister (1993) showed that dead-zones of the River Severn, or retention-zones as they preferred to call them, could
be characterised by their increased algal density compared with the main flow. Typical retention-zones had a 1.5 - 43-fold increase in chlorophyll 'a' concentration (indicative of algal biomass) compared with the main body of the river. In one case, at Leighton Park, the conditions within the zone were sufficiently stable to allow the dominance of *Planktothrix agardhii*, a slow-growing species intolerant of rapid flushing rates (Reynolds and Carling 1991).

3.1.3.4 Which model applies in nature?

There is little doubt that turbulent flow exists in rivers but this alone cannot account for the maintenance of river plankton populations. The aggregated dead-zone model offers the most plausible explanation for the persistence of a potamoplankton to date. There has, however, been no rigorous test of the model, as the diversity of dead zones makes it very difficult to assess the overall function of any single stretch of river. When riverine plankton development is modelled, such as in the detailed work of Reynolds and Glaister (1993) on the River Severn, the turbulent flow model is often used as a first approximation, as the dead zone model is too complex to put into simple numeric terms.

3.1.4 Dead-zone function

The presence of non-flowing zones of high algal density obviously increases the overall retentive capacity of the channel, but they can only explain an increase in algal density mid-channel if a proportion of their plankton rich water is continually exported. In this sense, dead-zones may be considered as source areas (Pulliam, 1988) acting as "chemostats" with an input of nutrient-rich river water and an output of plankton-rich water. The extent of the exchange is determined by the shear stress across the boundary with the main flow, which is dependant on river discharge. The greater the difference in flow rates between the two areas, the greater the shear stress across the boundary, and the greater the fluid exchange. Reynolds and Glaister (1993) stated that for a dead-zone to be efficient at retaining algal populations in a reach, while at the same time supplying a constant inocula to the downstream flow, it is essential to think of a relatively large volume exchanging with the main flow over a time scale of days.

3.1.5 Dead-Zones as potential sources of river plankton

Dead-zones may explain the hitherto unresolved problem of the constant inocula needed to maintain a plankton in the face of a unidirectional flow. Hynes (1970) noted that much true river plankton actually originates in quiet bays and side arms of the river
itself, a view that has recently gained further acceptance through the observations of Reynolds and Glaister (1993); Billen et al., (1994); Descy and Gosselain (1994) and Stoyneva (1994). The role of the sediment, or more precisely the boundary layer dead-zone, has also been implicated as a source of plankton to the main flow either from resting stages (meroplankton) or simply after chance settlement and re-suspension (tychoplankton) (Brehm, 1911 in Hynes, 1970; Billen et al., 1994; Izaguirre and Vincour, 1994; Stoyneva, 1994).

The aggregated dead zone must act as both a store and a source of 'suitable' organisms if they are to aid the downstream enhancement of a river plankton. 'Suitable' in this case refers to species that are in some way adapted to life in rivers, for example by virtue of a high population growth rate (see section 3.1.6). Dead-zones that are particularly stable may develop a community which is dominated by lacustrine species (Rzőska et al., 1955; Brown et al., 1989; Richardson, 1991; Köhler, 1994; Neumann et al., 1994) which when washed into the river are ill-adapted to the physical conditions and are rapidly removed from the flow, especially if aquatic vegetation is present (Chandler, 1937; Reif, 1939; Hynes, 1970; Sandlund, 1982; Richardson, 1991). Plankton from such sources can only loosely be considered as part of the potamoplankton as they rarely reproduce in the main channel (Saunders and Lewis, 1988a; 1988b; 1989). Conversely, dead-zones that are frequently flushed may have such a similar structure to the main channel that they add little to the downstream enhancement of the potamoplankton. The natural diversity of flow regimes in river channels should lead to a wide spectrum of dead-zones, which when aggregated, form a suitable store and source of riverine plankton in lowland rivers, although a detailed analysis of the size, distribution and longevity of dead zones in plankton bearing rivers is still needed (Reynolds, 1988).

3.1.6 River Phytoplankton

The phytoplankton of low-gradient lowland rivers has been relatively well described (for reviews see Hynes, 1970 and Whitton, 1975). In all cases the species composition is rather similar, with two main groups of algae dominating the phytoplankton, the diatoms and the green algae. The uniformity is so striking, that it forced Reynolds (1994b) to write, 'unlike given phytoplankton from lakes, it is often difficult to identify the source of a collection, beyond that it is from a river'. The similarity between most river assemblages indicates that the phytoplankton is subject to exacting physical conditions. The life-history characteristics of the dominant species, such as high growth rates and small size, are those that are best adapted to the effects of flow.
The strongest selective agents in rivers result from the unidirectional flow (Hynes, 1970). The negative impacts of flow include the direct dilution of populations and reduced growth rates associated with a poor light climate. The positive effects of flow which promote growth include favourable nutrient gradients, reduced herbivorous grazer biomass owing to the lack of large grazers, and the constant removal of waste products (Søballe and Kimmel, 1987). The negative impacts are presumed to be strongest, as phytoplankton production is generally considered to be constrained by physical forces in rivers.

Turbidity in rivers is dependant on the erosive force of the flow with much of the suspended matter derived from non-living bed and bank material (Reynolds, 1992), although phytoplankton cells also contribute. The euphotic depth may be reduced to a fraction of the total river depth during periods of high flow. Any algae entrained within the flow will be subjected to full-depth mixing and a constantly changing light climate, including periods below the euphotic depth when light levels are insufficient to sustain net photosynthesis. Indeed, middle to low order rivers have been likened to shallow, turbid lakes owing to their high turbidity and constant mixing regimes (Reynolds, 1994a).

In light-limited systems the most successful species tend to be those with the fastest growth rates (Reynolds, 1994a). The potential growth rate of algae is related to their surface area / volume ratio (Reynolds, 1989), with those species achieving the highest ratios (small size or attenuated shape) generally growing the fastest. A further adaptive mechanism to life in intermittent light regimes is the ability to efficiently gather light when passing through the euphotic zone, which can be achieved by two methods. First, by increasing the amount of chlorophyll 'a' per cell, and second, by increasing the quantities of accessory pigments which absorb light in other areas of the visible spectrum. In both cases the most adapted species are either small or have an attenuated shape to ensure the pigments are in close contact with light. The most efficient light-harvesting species with fast growth rates are the small centric diatoms such as Cyclotella and Stephanodiscus and some pennates, including Nitzschia and Asterionella. These species are usually dominant in the turbid downstream portions of rivers where they out-compete other fast growing algae.

The other major selective agent in rivers is reduced retention time which also selects for species with rapid turnover times. Reynolds (1992) states that the overall residence time of flowing water in rivers can range from between a few hours to little more than a year or two, depending on the dimensions of the river and the discharge. Søballe and Kimmel (1987) showed that the retention time of North American rivers was
significantly less than that of reservoirs and lakes. Reduced retention time favours the development of $r$-selected species (MacArthur and Wilson 1967) with high rates of population increase that are more tolerant of high frequency disturbance (Reynolds, 1992), typically the small centric and pennate diatoms and members of the green algae in the order Chlorococcales and the flagellate cryptomonads. These species have a much higher capacity to increase population density during gradual downstream displacement or when entrained in dead zones. They also have the greatest capacity to recover after disturbance. Slower growing $K$-selected species, those that typically come to dominate north temperate lakes during the summer, are not generally selected for in rivers (Köhler, 1994), unless the residence time is sufficiently increased either spatially (stable dead-zones) or temporally (low flow periods of sluggish rivers).

3.1.7 Shifting zones of dominance

Two distinct zones of phytoplankton dominance have been observed along the axis of rivers. Chlorococcal algae are usually numerous in middle order sections of rivers whereas diatoms dominate in slower flowing, deeper reaches (Descy, 1987; Reynolds and Glaister, 1993). Reynolds (1994a) proposed a mechanism to explain this pattern. The diatoms with their rapid generation times and their light harvesting capacity might be expected to dominate along the whole of the river if they were not particularly prone to excessive sinking losses from shallower waters depths (Reynolds and Wiseman, 1982; Reynolds et al., 1990), where they are replaced by green algae. Even the smaller diatoms are sensitive to reduced water depth during periods of low discharge (i.e. during the summer), as sinking losses may exceed potential growth rates (Reynolds, 1994a). The boundary between the green algae and diatom dominated sections does not remain static throughout the year (Reynolds and Glaister, 1993; Schmidt, 1994). Low flows and decreased water depths in summer cause a downstream shift of the diatom zone to deeper waters, whereas higher flow rates during winter, with an associated increase in turbulent mixing and depth, shifts the zone of diatom dominance upstream.

The general effects of reduced residence time in river systems are manifest in their reduced algal density when compared to lentic systems of similar trophic status. Søballe and Kimmel (1987) compared the phytoplankton density of 149 lakes, 366 reservoirs and 126 river in North America, and found a positive association between retention time and algal abundance, expressed either as chlorophyll 'a' or cell density. Rivers, which had the shortest average retention time, attained the lowest average phytoplankton density per unit phosphate (8,487 cells ml$^{-1}$), while lakes which had a longer average retention time attained a significantly higher algal biomass per unit phosphate (16,812 cells ml$^{-1}$). The algal biomass of reservoirs was between lakes and
rivers, those systems with shorter residence times more closely resembling the species composition and density of rivers. Schmidt (1994) found a similar negative correlation between discharge and algal abundance in the River Danube. In both cases, however, it should be noted that the negative effects were probably owing to a combination of increased dilution and decreased growth rates due to poor light levels.

3.1.8 Objectives

The presence of a pelagic riverine phytoplankton community is well documented in lowland rivers, although the reason for its persistence remains an interesting problem given the potential scale of hydraulic losses. The restricted community composition, temporal patterns of abundance, and the degree of spatial variation in phytoplankton density give testament to the importance of flow-related control mechanisms. This chapter investigated the phytoplankton of a 'typical' eastern England river. Its aims were to:

- describe the physical nature of the River Nene, in terms of the turbulent force generated by flowing water throughout the season.
- describe and quantify the phytoplankton of the Nene at Wansford, and compare this to other lowland European rivers.
- test the potential for different models of fluvial geomorphology to explain the persistence of a plankton at Wansford.
- model the loss rates of phytoplankton cells under defined physical conditions and relate these to observed algal dynamics to gain an insight into river function.
- assess the potential impact of littoral grazers on pelagic riverine phytoplankton.

3.1.9 Study River

The River Nene rises in a group of hills in central England called the Northamptonshire Uplands, whose highest point of 224 m above sea level occurs near Daventry. These hills form the Southern boundary of the catchment which covers an area of 2,363 km². The river has three sources, Northern Water or Naseby Brook rising at Cromwell House between Naseby and Hazelbach (SP698778), Nenemore Springs between West Haddon and Watford (SP615726), and Hartwell Springs in Staverton Parish near the foot of Arbury Hill (SP540595) (Anon 1964). The river flows in a north-easterly direction from its source through Northampton, Peterborough and Wisbech to the North Sea at the Wash. The total length of the river is approximately 150 km over which distance it descends a total of 150 m. The river and its catchment area are shown in figure 3.3.
Figure 3.3 The River Nene

Catchment boundary

See figure 3.4

Dog in a Boublet Sluice: Tidal limit

Figure 3.3 The River Nene
3.1.9.1 Geology

The geology of the catchment is dominated by solid strata of Jurassic origin along with superficial deposits of recent and Pleistocene age (Anon, 1964). Alluvium deposits occur as a thin band along the river coarse above Peterborough but, along with peat deposits, almost completely obscure the underlying rock in the area of the fens. Groundwater sources are present in the catchment from porous rock strata and gravels.

3.1.9.2 Physical features

The hills from which the river rises soon give way to gently undulating countryside towards Oundle, after which come the flat plains around Peterborough and the fens towards the Wash. The river drops over 100 m during the first 30 km of its length, before reaching Northampton, the rest of the river having a much lower gradient. Some of the fen areas are actually below the level of high tides, having been reclaimed from the sea.

Downstream of Peterborough the river channel is artificially straightened and constricted by raised parallel flood banks. Habitat diversity is poor along this section of the river. Above Peterborough, the river follows a relatively natural meandering channel through a flood plain flanked by improved or semi-improved grassland, although it has been heavily constricted by navigation control since last century. Habitat diversity in this section is improved by the presence of marginal vegetation dominated by reed sweetgrass (*Glyceria spp.*), burreed (*Sparganium spp.*), common reed (*Phragmites australis*), club rush (*Scirpus spp.*), hard rush (*Juncus inflexus*) and yellow iris (*Iris pseudacorus*). The percentage vegetation cover of the main channel is between 10 - 20%, depending on time of year (Anon, 1993).

3.1.9.3 Water Quality

The river is tidal below the Dog in a Doublet sluice which is approximately 40 km upstream of the mouth. Water quality in this tidal section is poor with major effluent outfalls from West Walton Sewage Treatment Works (STW) in Wisbech and Sutton Bridge STW. Water quality problems also exist in the non-tidal river reaches above the sluice. For example, the biochemical oxygen demand at Wansford was higher than the F2 fishery target (6 mg/l) set down in the Lower Nene catchment management plan (Anon, 1993). Water quality above Northampton, the first major input of sewage to the Nene, is better.
3.1.9.4 Flow Characteristics

The average annual discharge, measured at Orton gauging station south of Peterborough, is in the order of $363 \times 10^6$ million m$^3$ yr$^{-1}$ (11.5 m$^3$s$^{-1}$). The average annual rainfall for the area is 625 mm, of which approximately 450 mm are lost through evapotranspiration. The major abstraction of river water to the pumped storage facility at Rutland Water occurs at Wansford. The pumps have the capacity to remove up to 8.8 m$^3$s$^{-1}$, although the amount taken is limited by the need to retain the recommended minimum residual river flow of 1.6 m$^3$s$^{-1}$ at Orton.

The flow characteristics of this lowland river are modified by the presence of locks and sluices along its length for navigation. A total of 37 locks are located downstream of Northampton to the Dog in a Doublet sluice, which are used by 1,300 registered pleasure boats and touring craft. Below Wisbech commercial vessels use the river. The locks may be used as sluices during winter to discharge flood waters. The flow rate and retentive capacity of the river is therefore highly modified by man to alleviate flooding in winter and maintain river levels during summer.

3.1.9.5 Study Sites

Three sites were sampled on a weekly basis during the growing season (March-October) during 1994.

The planktonic community of the main channel was sampled at Wansford. Samples were taken from a bridge in mid-channel away from any littoral influence and were therefore assumed to represent the true pelagic community with the possible inclusion of drift animals.

Two further sites were sampled on a weekly basis, a side channel at Nassington and a backwater upstream of the Wansford site. These samples were intended to allow a comparison between the main-channel community and that of two connected habitats with longer retention time. Both sites represented relatively defined areas of reduced flow compared to the river. No flow was detected at either site owing to the restricted nature of the connection with the river, although water quality was very similar, especially at Nassington. Nassington was considered to be a typical side-channel habitat, whereas Wansford backwater was representative of a floodplain lake.

**Site 1: Wansford station.** The main river channel was sampled at Wansford Station (TL094980). The river was approximately 20 m wide and 2 m deep at this point, with
dense marginal reed beds along the banks and emergent vegetation in the slack water behind the central support of the bridge during the summer. The section was typical of the navigable lowland portion of the river below Northampton, following a semi-natural meandering path. The river was sixth order at this point.

**Site 2: Nassington.** A side-channel habitat was sampled at Nassington (TL069965) approximately 6.5 km upstream of Wansford Station. The site was used for mooring boats and was connected to the main river at both ends, allowing free exchange of water with the river. The total length of the backwater was approximately 300 m and the water depth was approximately 2 meters. Flow rate was negligible, even when the river was in flood owing to the angle of the upstream connection. Dense stands of reeds grew on the far bank of the side-channel and floating mats of *Enteromorpha* appeared in summer. Samples were taken from a mooring platform approximately half way along the length of the channel.

**Site 3: Wansford backwater.** A backwater site was sampled near to the Wansford Station site (TL093982). This site had a single connection with the main river at its upstream end but no direct connection at the downstream end, and was separated from the river along its length by a levee. No records exist of the frequency of inundation, but consultations with local residents and the Environment Agency indicated that it was flushed by the river only at very high water levels. The site is owned by Sibson Fisheries, but has not been actively managed for some years. The total length of the backwater was approximately 400 meters, with a depth of between 0.5 to 3 meters. Both banks were covered with dense stands of reeds during summer and submerged macrophytes developed in the open water during summer. Samples were collected from the eastern bank away from any littoral influence.

### 3.2 Methods

Algal dynamics were assessed using chlorophyll 'a' as an indication of total algal density, and direct algal count data. The latter was supplied by the Environment Agency, Anglian Region.

#### 3.2.1 Chlorophyll 'a' analysis

A one litre sample for the determination of chlorophyll 'a' concentration was taken from the middle of the channel at all sample sites. Three replicate sub-samples were filtered through Whatman GF/C glass fibre filters and analysed by the solvent extraction using boiling ethanol. The absorbance of the extract was measured using a Hewlett Packard
Figure 3.4 Sample sites
B452 Diode Array Spectrophotometer at 665 nm and 750 nm, in order to compensate for background turbidity. Total pigment concentration was calculated from the following equation:

\[ Chla(\mu g l^{-1}) = \frac{k \cdot E_{665} \cdot v}{d \cdot V} \]

where
- \(k\) = specific absorption coefficient at 665nm for chlorophyll 'a' in ethanol (=12.0)
- \(E_{665}\) = turbidity corrected absorption at 665nm. \(A_{665} - A_{750}\) where A is the absorbance value.
- \(v\) = volume of extract in ml
- \(d\) = length of light path through cuvette in cm
- \(V\) = volume of water filtered in litres

The above procedure does not distinguish between the proportion of absorption owing to live or dead (degraded) pigment, as both forms have similar absorbance characteristics. Degraded pigments, however, have a lower absorbance capacity (Wetzel and Likens, 1991). Mild acidification of the extract causes the degradation of all pigment, so that the difference between turbidity corrected absorption at 665nm of unacidified and acidified extracts can be used to calculate the amount of undegraded pigment originally present. Acidification was achieved by adding 0.01 ml of 0.3M hydrochloric acid to the cuvette. The initial concentration of undegraded pigment was calculated from:

\[ Chla(\mu g l^{-1}) = \frac{k \cdot F \cdot (E_{665o} - E_{665a}) \cdot v}{d \cdot v} \]

and the initial concentration of phaeopigments from:

\[ Chla(\mu g l^{-1}) = \frac{k \cdot F \cdot [R(E_{665a}) - E_{665o}] \cdot v}{d \cdot v} \]

where
- \(F\) = factor to equate the reduction in absorbency to initial chlorophyll concentration, =2.43.
- \(E_{665o}\) = turbidity-corrected absorption at 665nm before acidification.
- \(E_{665a}\) = turbidity-corrected absorption at 665nm after acidification.
- \(R\) = maximum ratio of \(E_{665o}: E_{665a}\) in the absence of phaeopigments, = 1.7.
Chlorophyll 'a' concentration when assessed by the summation of degraded and undegraded forms (the last two equations) produces an estimate of algal abundance irrespective of the state of the cells when sampled. This measure was used in the analysis of results as it represents a more realistic approximation of the food available to many zooplankton grazers which cannot distinguish between live and dead food particles in suspension.

The coefficient of variation of replicate chlorophyll 'a' samples was assessed on 20 dates throughout the growing season of 1992. The average coefficient of variation of the mean concentration was 7%.

The temperature of the water was measured during routine sampling. pH was also measured using a Phillips PW 9420 meter and the oxygen content of the water was assessed with a YSI Model 57 oxygen field meter. Data on algal abundance at Wansford was supplied by the Environment Agency (formerly the National Rivers Authority) as was daily flow rate data from Orton gauging station, approximately 10 km downstream of the Wansford Station sampling site.

3.2.2 Methods used in the analysis of plankton dynamics

The following section gives details on the methods used to calculate certain parameters needed in the analysis of potamoplankton dynamics. Some of the methods relate equally to phytoplankton and zooplankton populations.

3.2.2.1 Estimation of flow velocity from discharge data

Discharge is a measure of the volume of water passing a fixed point in a river and in itself is not particularly relevant to the function of river plankton without some measure of channel area. If the cross sectional area of the channel is known, then the velocity of water flow can be calculated which is of more importance to planktonic communities than the discharge, as it governs the rate of transport through the system, and therefore the potential time available to complete life cycles within a given river stretch (Reynolds, 1988). Velocity can also be directly compared between rivers of different size.

Discharge, flow velocity and river dimensions are related according to the following mathematical relationship (Allen, 1995):

\[
Q = W.D.U
\]
where $Q$ is discharge ($m^3s^{-1}$), $W$ is stream width (m), $D$ is average stream depth (m) and $U$ is flow rate (ms$^{-1}$). Changes in the cross sectional area of the river with increasing stream order dampen the magnitude of discharge variations, resulting in a much smaller range of velocities compared to discharge. For example, a river with a cross sectional area of 60m$^2$ will have a velocity of 1 ms$^{-1}$ when discharge reaches 60 m$^3$s$^{-1}$, whereas a larger river with cross sectional area of 500 m$^2$ requires a discharge of 500 m$^3$s$^{-1}$ to reach the same velocity.

Reynolds (1988) produced a velocity-discharge relationship from the data of Bowles and Quennell (1971) on the River Thames, in which a twenty fold variation in discharge gave only a five fold variation in flow owing to changes in cross-sectional area. A similar relationship was derived for the River Nene at Wansford from channel velocity and discharge data taken concurrently during 1994 by the National Rivers Authority, Anglian Region. The data covered a wide spectrum of flow rates from baseline summer flows of less than 3 m$^3$s$^{-1}$ to spate events of over 50 m$^3$s$^{-1}$. Figure 3.5 shows the relationship between flow rate and velocity on a log-log plot. Mean velocity was significantly correlated with discharge ($p < 0.001$), the former being described by the following equation:

$$Q = 0.02 U^{0.88}$$

![Image of Figure 3.5](image)

Figure 3.5 Power relationship between average velocity and discharge at Wansford.

This relationship was used to estimate flow velocity from daily discharge values in the present study. An estimate of channel cross sectional area can also be made once both
the discharge and velocity are known. This is important as river depth, which has an influence on the settlement rate of algal cells from suspension, can be estimated.

Continuous daily discharge values were available from Orton gauging station which is situated approximately 10 km downstream of Wansford. These were assumed to be similar to those at Wansford as there were no major tributary inputs between the two sites and the abstraction point at Tinwell to Rutland Water pumped storage reservoir was upstream of the sample site.

3.2.2.2 Calculation of non algal turbidity from water transparency and algal density

The presence of silt in suspension causes a reduction in light penetration and therefore has the potential to limit algal primary production.

No direct measurement of non algal particle density was available, so an estimate was made by subtracting the light attenuation attributed to algal density alone from the total light attenuation, measured as Secchi depth. Algal light attenuation was estimated by regressing Secchi depth against algal cell number on ten occasions during the summer of 1994, when flow rate was below 3 m$^3$s$^{-1}$ (figure 3.6). It was assumed that the proportion of non algal suspended matter was minimal at low discharge and therefore that the majority of light attenuation was owing to algal particles.

![Figure 3.6 Relationship between algal cell number and Secchi depth at low discharge.](image)

\[ y = 9.61x^{-0.23} \quad r = 0.77 \]
Algal density and Secchi depth were significantly associated \((p<0.01)\). The regression is presented in figure 3.6. The Secchi depth associated with algal density alone was given by the equation

\[ Y = 9.613 \cdot X^{-0.23} \]

where \(Y\) is Secchi depth and \(X\) is algal density (cells ml\(^{-1}\)).

The relationship obtained is only a rough guide to algal light attenuation as the Secchi depth recordings were subject to operator error, and no account was made of the differential light scattering properties of the various taxonomic groups.

### 3.2.2.3 Estimation of euphotic depth

Photosynthesis may become directly limited at low light levels, for example when the intensity of solar radiation decreases below 100-200 \(\mu\)Em\(^{-2}\)s\(^{-1}\) (Reynolds, 1984). The intensity of light falling on the surface of water bodies usually exceeds this value for part of the day, even if overcast conditions persist, and therefore supports light-saturated photosynthesis near the surface. The intensity of solar radiation, however, is reduced during passage through the water column, owing to the combined effects of light absorbance and scattering by water, dissolved compounds, and suspended solids.

The result is a vertical profile of potential photosynthetic activity which is light saturated near the surface, then directly limited by falling light intensity (below 100-200 \(\mu\)Em\(^{-2}\)s\(^{-1}\) \(\left( I_0 \right)\)) until the compensation depth is reached where photosynthetic production exactly matches respiration. This depth is referred to as the euphotic depth which is commonly assumed to be the depth to which 1\% of surface irradiance penetrates. The euphotic depth can be measured directly by \textit{in situ} light recording, or estimated from the Secchi depth (the depth where light intensity is equivalent to 15\% of the surface intensity) by the following relationship:

\[ Z_{eu} = 1.7 \cdot Z_s \]

after Vollenweider (1974), where \(Z_{eu}\) is the euphotic depth and \(Z_s\) is the Secchi depth.

The euphotic depth was estimated at Wansford station from weekly Secchi depth recordings. The proportion of total depth below the euphotic depth was assumed to be directly related to the proportion of daylight hours that algal cells spent below the compensation point, assuming full mixing of the water column. For example, an algal
cell would spend on average 8 hours per day below the euphotic depth of a river section with a depth of 6 m and a euphotic zone of 4 m. The size of the euphotic zone compared to full mixed depth in rivers can therefore be used as a rough guide to potential light limitation of suspended algal populations, although the actual photosynthetic production cannot be predicted as no surface irradiance data was taken.

3.2.2.4 Calculation of flow generated turbulent force at Wansford

The type of flow generated by a river has important implications for plankton development as it affects the role played by dead zones, the potential to hold particles in suspension, and the rate at which these particles are lost through sedimentation. The characteristics of flowing water depend on the formation and force of eddy currents which mix the water in all directions. Reynolds (1994a) described all flowing water environments as 'kinetic', implying that the force produced by gravitational acceleration of water and the frictional resistance offered by the confines of the channel is usually sufficient to produce a constantly turbulent flow (Reynolds Number >2,000). Any particle entrained in such a flow is liable to redistribution throughout the mixed depth, at a rate set by the turbulent shear stress of the flow ($u^*$). In rivers, turbulent force increases with mean flow rate and the roughness of the bed via the following relationship (Reynolds, 1994b):

\[ U = 2.5 u^* \ln \left( \frac{12 h}{r_p} \right) \]

where $U$ is the mean flow velocity recorded at 0.4 of total average depth, $h$ is column depth and $r_p$ is an estimate of bed frictional resistance to water movement (height of projections from the bed).

The shear velocity encountered in the River Nene at Wansford was calculated from mean daily flow rates and depth assuming an average height of projections above the bed of 1 mm, a suitable estimate for a sluggish lowland river with a fine-silt substrate.

The reason for calculating shear velocity in the Nene was to ensure that turbulent flows were achieved. This was considered important as the degree of turbulence affects the retention time of water within a stretch, and therefore dictates potential rates of suspended particle dilution losses, and the capacity to fully entrain particles of different density. Both factors are critical to the development and maintenance of pelagic plankton communities.
3.2.3 Models of algal loss processes at Wansford during 1994

Algal population dynamics (indicated by total chlorophyll 'a' concentration) were calculated with the aid of the exponential growth model (Reynolds, 1984) in which the potential for increase was determined from the scale of rate processes acting on the population over finite periods of time. Population growth was expected when total rates of increase (importation and replication) exceeded total loss rates (death, sedimentation, grazing and export, or hydraulic removal), and vice versa. Loss rates associated with hydraulic removal, sedimentation and grazing were estimated for the range of conditions encountered in the River Nene at Wansford during 1994.

The aim of the analysis was to understand whether the mid-channel algal populations observed throughout the growing season were self-maintained, or whether they were constantly reliant on imports from other 'source' areas of the river basin, where net population increase was possible.

An assumed rate of intrinsic population increase was used throughout the analysis of population dynamics based on half the maximum potential growth rate of a typically small, $r$-selected, riverine taxa (see section 3.2.3.5). The obvious limitations of using a single estimate of growth rate throughout the spring and summer for all algal taxa should be borne in mind throughout the analysis but the supposed saturation of plant nutrients in rivers (De Ruyter van Steveninck et al., 1990) and the good water transparency at Wansford (figure 3.17) should have ensured that growth rates were not severely limited when temperatures were suitable for growth.

3.2.3.1 Sedimentation loss rates

The sedimentation of negatively buoyant, non-motile particles from water columns is hypothesised to cause a change in riverine algal composition from diatom dominance in the spring to chlorophyte dominance in the summer. Silica depletion may also be important (Gamier et al., 1995), but the dominant factor which drives this change is the preferential loss of the heavy diatoms from shallow, less turbulent waters associated with low flow rates in summer (Reynolds and Glaister, 1992). Reynolds et al., (1990) found that the loss rate of many phytoplankton groups from turbulent water columns of between 1 to 3 m depth exceeded growth rates and therefore excluded these species from such shallow habitats. Changes in the depth of water column accounted for over 90% of the variation in settlement rates of particles from fully turbulent flows. Variation in the water depth of rivers may therefore have an important impact on phytoplankton community composition.
The following section estimated the sedimentation loss rate of particles with different sinking velocities over the range of physical conditions encountered at Wansford during 1994, to assess the potential role of settlement in structuring algal community composition in the main channel.

The calculation of loss rates had three basic stages. The first was to ascertain if full turbulent mixing occurred throughout the year at Wansford, as the extent of physical mixing affects sedimentation rates (refer to section 3.2.3.4). The second stage was to estimate the sinking rates of particles with similar physical characteristics to the range of algae encountered in the river Nene. The last stage was the actual calculation of loss rates of a range of different particle forms from water columns of varying depth. Figure 3.7 shows the diagrammatic structure of the model derived to estimate loss rates of algae throughout the year in the River Nene at Wansford.

Stage 1: To assess the potential of turbulent mixing energy to fully entrain algal particles and thus derive the correct equation to describe loss rate.

The rate at which cells settle from the water column is dependant on the intensity of turbulence which randomly re-suspends particles throughout the full mixed depth. The minimum time required for full settlement of a population of cells (t') occurs from a static column in which all particles sink at a constant rate with no chance of re-suspension. Consider a population of homogeneously distributed particles of concentration N₀ in a static water column of height (h) metres. Particles settle at a range of times from t=0 to t' depending on their distance from the sediment surface, where t' represents the time taken for a particle to settle through the full depth of the column. For static columns with no turbulent mixing, this is defined as h / wₛ, where h is the column height in metres and wₛ is the sinking rate in m d⁻¹. For example, a population of randomly distributed cells sinking at a rate of 2 m d⁻¹ through a depth of 5m will all have settled by t'= 5/2 = 2.5 days. The number of cells remaining in suspension at any intermediate time (Nᵢ) will therefore be given by

\[ Nᵢ = N₀ - N₀ \left( wₛ * t / h \right) \]

after Reynolds (1984). If the column is mixed at t₁ before t' is reached then any particles remaining in suspension will be redistributed throughout the mixed depth, and the settlement time for the whole population will be extended to t₁ + t'. The settlement time continues to increase with further mixings until at ‘full turbulence’ the loss of particles to the boundary layer follows an exponential decay function. For a fully turbulent column the number of particles that remain in suspension at time t follows
\[ N_t = N_0 e^{-\frac{w}{t/h}} \]

After Reynolds et al. (1990). Any further increase in the intensity of mixing has no substantial effect on settlement rates once full turbulence is reached (Reynolds et al., 1990). Reynolds (1984) showed that the number of mixing events required to achieve full turbulence was relatively small, in the order of 5 events per time period \((t')\), which is usually surpassed in rivers even at low flows (Reynolds, 1992).

**Figure 3.7** Calculation of the potential loss rates of suspended particles from fully mixed water columns.
Similarly, the relationship between settling rate ($w_s$) and shear velocity generated by flow rate ($u^*$), dictates whether a particle is fully entrained and is therefore subject to exponential loss. Spigel and Imberger (1987) stated that the shear velocity must be at least 15 times the settling rate for 'full' entrainment to occur. This condition was satisfied in the River Nene even during the slowest flows of the summer when the lowest shear velocity produced was in the order of 0.001 m s$^{-1}$. A shear of this magnitude has the potential to fully entrain particles with a sinking velocity of up to 66.7 $\mu$m s$^{-1}$, whereas the sinking rate of one of the largest freshwater diatoms, *Stephanodiscus astraea*, was reported as 25 $\mu$m s$^{-1}$ (Reynolds, 1973, in Reynolds, 1984). Full entrainment of all algal species was therefore assumed in the river throughout the year and all settlement losses were therefore assumed to conform to the exponential decay model.

Stage 2: To estimate sinking velocities of algal 'type' particles under different physical conditions.

Any particle denser than water will inevitably sink. This can be a useful phenomenon for algal cells in some respects, for example, the maintenance of favourable nutrient concentration gradients with movement through the medium or the avoidance of dangerous surface sunlight intensities, but is also problematical for most cells that cannot actively regulate their position in the water column as they must remain in the mixed surface layer for photosynthesis. Algae that settle out of the mixed layer and enter the laminar flow boundary layer of rivers are effectively lost from the system and will not be re-suspended until the shear stress increases sufficiently to reduce the width of this layer. Cells may, however, be rapidly decomposed or grazed by the benthic community before re-entrainment can occur (Reynolds, 1994a).

All negatively buoyant particles sink through water at slightly different rates dictated by the difference in density between the particle and the water, the frictional resistance offered to movement and the viscosity of the fluid. Settling velocities (ms$^{-1}$) of small spheres are described by the Stokes equation, which assumes that the flow around the sinking particle is laminar. This assumption has been shown to be valid for most particles within the size range of freshwater algae. Stokes equation gives the settling velocity as

$$w_s = \frac{d^2 g (\rho' - \rho)}{18 \eta}$$

where $d$ is the diameter of the sphere ($\mu$m), $g$ is the constant of gravitational
acceleration (m s\(^{-2}\)), \(\rho'\) is the density of the particle and \(\rho\) is the density of water (kg m\(^{-3}\)), and \(\eta\) is the viscosity (kg m\(^{-1}\) s\(^{-1}\)).

Freshwater algae, as a whole, have developed a number of adaptations to reduce the speed with which they sink. These include reducing the density of cells by the inclusion of lipids, ionic regulation, mucilage secretion and gas vacuoles, and methods to increase the surface area to volume ratio, such as colony formation and increased form resistance. Form resistance relates to the deformation of shape from the basic sphere which increases the surface area to volume ratio and the frictional resistance to movement through a medium. Most algae, apart from the smallest unicells, have a morphology that is markedly non spherical, and thus benefit from reduced sinking rates. Form resistance can be accommodated in the Stokes equation to give a more realistic view of sinking velocity for natural algal populations thus:

\[
\begin{equation}
  w_i = \frac{d^2 g (\rho' - \rho)}{18 \eta \phi}
\end{equation}
\]

where \(\phi\) is the form resistance, a dimensionless coefficient derived from the difference between the observed sinking velocity of an algal cell and the theoretical sinking velocity of a sphere of the same volume.

Algal sinking rates are notoriously difficult to assess accurately, and are often variable even within single species owing to morphological and physiological differences between individual cells. Temperature also affects sinking rates as the density and viscosity of water are temperature dependant. Sinking rates of a range of 'algal types' under different temperatures were calculated. Algal types, in this context, refers to ranges of particles with typical freshwater algal volume, density and form resistance. The variables used in the calculation of sinking rates are given in table 3.1.

Sinking velocities were calculated according to the Stokes equation, modified for form resistance. Individual results are not presented but sinking velocities ranged from 0.18 \(\mu\)m s\(^{-1}\) for particles with low volume, low density and high form resistance, to 175.7 \(\mu\)m s\(^{-1}\) for the largest, most dense, spherical particle considered. This covered the measured range of sinking velocities found in the literature for natural algal particles (Round, 1981; Reynolds, 1984).
<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Water density (kg m⁻³)</th>
<th>Water viscosity (10⁻³ kg m⁻¹ s⁻¹)</th>
<th>Particle density (kg m⁻³)</th>
<th>Form resistance</th>
<th>Particle diameter (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>999.99</td>
<td>1.52</td>
<td>1050</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>10</td>
<td>999.73</td>
<td>1.31</td>
<td>1100</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>15</td>
<td>999.13</td>
<td>1.14</td>
<td>1150</td>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td>20</td>
<td>998.23</td>
<td>1.00</td>
<td>1200</td>
<td>4</td>
<td>30-40</td>
</tr>
</tbody>
</table>

Table 3.1 Variables used when calculating sinking rates of particles with typical freshwater algal characteristics. Note that temperature, density and viscosity are all dependant and are treated as a single variable in the calculations. Algal particle densities generally range from between below 1000 kg m⁻³ (positive buoyancy) to approximately 200 kg m⁻³ heavier than water (Reynolds, 1984). Form resistance is a unitless index of morphological attenuation, commonly ranging from one (spherical) to slightly above five (Reynolds, 1984). The full combination of densities and form resistance used should cover most freshwater algal forms. The range of volumes covered by spherical particles of between 5 and 40 μm diameter were 65.5 μm³ to 33,210 μm³.

Figure 3.8 shows the distribution of sinking velocities of algal particles with different combinations of size, density and form resistance. Form resistance is plotted on the vertical axis, while the horizontal axis shows the effect of changing density within a single size group, which is then repeated for the five size classes given in table 3.1. The figure assumes a water temperature of 15°C, although changing water temperature had a relatively minor effect on sinking velocity compared to the morphological differences considered.

Calculated settlement rates were placed into seven categories (table 3.2).

<table>
<thead>
<tr>
<th>Category</th>
<th>Sinking Velocity (μm s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>&lt; 2.0</td>
</tr>
<tr>
<td>II</td>
<td>2.0 - 3.99</td>
</tr>
<tr>
<td>III</td>
<td>4.0 - 7.99</td>
</tr>
<tr>
<td>IV</td>
<td>8.0 - 15.99</td>
</tr>
<tr>
<td>V</td>
<td>16.0 - 31.99</td>
</tr>
<tr>
<td>VI</td>
<td>32.0 - 63.99</td>
</tr>
<tr>
<td>VII</td>
<td>&gt; 64.0</td>
</tr>
</tbody>
</table>

Table 3.2 Sinking velocity categories into which individual values were arranged. See below for representative algal types in each category.

Sinking velocity increased with the size and density of the particle but decreased with attenuation of basic spherical shape. The particles with the lowest sinking velocities were therefore either small, attenuated, or light, and were congregated in the lower left of figure 3.8, whereas the fastest sinking velocities were achieved by the largest, densest, spherical particles (upper right corner of figure 3.8).
In reality it is difficult to place species into such artificial categories as natural sinking rates are so variable, but the generalisation made in figure 3.8 helps to predict the settlement loss rates for broad algal classes in rivers when water depth is reduced during the summer.

Each sinking rate category will contain a wide diversity of species of variable morphology and density, but it is possible to describe species with a morphology that is indicative of each category. In defining such species a constant density was assumed, as was a lack of motility, and non-coloniality. The species chosen were therefore designed to aid the reader to visualise the type of algae that fall within each category.

Category I is equally represented by small spherical algae such as *Chlorella vulgaris* (volume \(v = 65\ \mu\text{m}^3\), low form resistance) or attenuated forms with larger volume such as *Ankistrodesmus falcatus* \(v = 423\ \mu\text{m}^3\), high form resistance). Category I also contains most ultraplankton species <5 \(\mu\text{m}\) (Round, 1981). Category II is represented by *Elakthrothrix sp.* and single *Asterionella formosa* cells, both groups with a volume of approximately 200-250 \(\mu\text{m}^3\) and a slightly attenuated shape. Category III includes forms such as *Chrysococcus sp.*, a spherical algae \(v = 523\ \mu\text{m}^3\) and *Closteriopsis*...
longisima with a larger volume ($v = 2,000$) but highly attenuated shape. Category IV includes particles with dimensions similar to Chlamydomonas sp. ($v = 1,750 \, \mu m^{-3}$) and a slightly attenuated shape, and the larger pennate diatom Gyrosigma sp. ($v = 14,700 \, \mu m^{-3}$) which has a high form resistance. Category V includes large spherical forms such as Gymnodium sp. ($v = 15,000 \, \mu m^{-3}$, low form resistance) and larger attenuated forms like the diatom Cymbella helvetica ($v = 24,300 \, \mu m^{-3}$, high form resistance). Categories VI and VII include large spherical forms such as Cosmarium sp. which has a volume of approximately 22,500 $\mu m^{-3}$ but only slight attenuation of shape. Larger colonial forms are also likely to have sinking velocities that fall within these upper classes unless they have mechanisms to reduce density.

Certain algal groups do not adhere to the size based classification outlined above. Diatoms, in general, tend to have high sinking rates owing to increased density incurred by the opaline silica deposits in their frustules, and are therefore generally the first group to be lost when depth is reduced. Even considering this fact, sinking rates rarely rise above 30 $\mu m \, s^{-1}$ (Reynolds, 1984), indicating some form of adaptation not accounted for in this model.

Cyanobacteria may utilise gas vacuoles to modify buoyancy such that their sinking rates are unrelated to their shape and density and they remain in suspension for longer than their cell morphology alone predicts. A similar phenomenon may occur with flagellate algae such as Ceratium hirundinella which, although large, is motile and can therefore regulate its vertical position. These groups have sinking rates determined more by their ecology than by morphology alone.

Stage 3: To estimate daily exponential loss rates of phytoplankton from depths typically encountered at Wansford.

The calculation of daily exponential settlement loss rate from known depths is relatively simple given the level of turbulent mixing and the sinking rate of particles. Depth at Wansford was variable throughout the year and depended to a large extent on discharge, ranging from 2.61 m during the summer to 4.23 m during spates. The mixed layer was assumed to be total river depth, and turbulent velocity was considered sufficient to fully entrain all particles within the algal size range (refer to stage 1). Exponential loss rates $-(w_s t / h)$ were calculated according the second equation given in stage 1 (assuming full turbulent mixing) for the range of depths between 2.6 - 4.2 m and for particles with a range of sinking velocity. Daily loss rates were calculated to allow direct comparison to average daily exponential growth rates estimated from the methods given in section 3.2.4. Calculated rates are presented in section 3.3.8.1.
3.2.3.2 Calculation of grazing losses

Rotifers were the dominant zooplankton group found in the main channel of the River Nene at Wansford. The importance of rotifers as grazers of phytoplankton has often been overlooked owing to their small size, with more attention having been paid to their larger cladoceran competitors (Gilbert and Bogden, 1984). Rotifers may, however, have a larger impact on algal populations than their biomass would indicate owing to their high metabolic rates and low generation times. For example, Bogden and Gilbert (1982) found that the rotifer *Keratella cochlearis* dominated community grazing activity over extended periods in the shallow eutrophic Star Lake (Vermont). Much evidence also exists to suggest that algivorous rotifers are highly selective feeders (Dumont, 1977; Pourriot, 1977; Starkweather, 1980; Ross and Munawar, 1981; Gilbert and Bogden, 1984; Bogden and Gilbert, 1987) and may therefore have a high impact on certain species of algae, and in doing so change the structure of phytoplankton communities.

The volume of water cleared of particles per individual per unit time (individual filtration rate) is dependant upon grazer size, temperature, the palatability of algae, and the concentration of particles, with highest rates achieved below the incipient limiting level. Literature estimates of individual filtration rate for rotifers were variable but generally within the range 1 to 10 μl individual⁻¹ hour⁻¹ (Starkweather, 1980). Such estimates usually refer to generalist feeders such as *Keratella cochlearis* and *Brachionus sp.*

Community grazing rate (a) is defined by the following equation, after Reynolds (1984)

\[ a = N \times F \ (\mu l \cdot l^{-1} \cdot day^{-1}) \]

where \( N \) is the density of individuals per litre and \( F \) is the individual filtration rate. A single individual filtration rate of 5μl ind⁻¹ hr⁻¹ for all rotifers feeding on a palatable food source was used in the present analysis. Grazing losses will be lower for less palatable algae.

The use of a single filtration rate within the natural range for rotifers was considered appropriate in this instance, as a general estimate of grazing pressure was required. It would have been unjustified to utilise published relationships to gain more specific rate information without performing detailed feeding experiments with Nene animals and food sources. This was considered outside the scope of this project.
Exponential grazing loss rates of algae are expressed in ln units day$^{-1}$.

3.2.3.3 Estimation of hydraulic removal loss rates

Periods of high discharge in rivers are usually associated with decreased phytoplankton density as cells are washed through the system faster than they can reproduce. The following section calculates the loss rate of suspended algal particles from the Wansford stretch of the River Nene resulting from the hydraulic removal of cells under different flow conditions. The region considered was 6.5 km long with lock gates located at each end and was considered to act as a single entity in the following analysis, somewhat like a long shallow lake with variable retention time.

Three distinct models are available which describe the rate of water exchanged through a river stretch, each having a different effect on loss rates. The following section aims to assess the potential for each to describe the apparent persistence of phytoplankton in the Nene.

Models of water exchange

*Plug flow - 'first in, first out'*

Assuming a constant flow, the loss rate of suspended particles from a river section is dependant on the extent to which inflowing water is mixed into the standing volume of the section. Plug flow assumes that the incoming volume serially displaces water from the section. This results in a linear loss rate until the total concentration of particles within the section equals the concentration in the incoming water once the original volume has been replaced. No amount of cell replication can retain plankton within a stretch of river if plug flow operates and there is no constant inoculum from upstream. This model therefore does not fulfill the criteria for explaining the persistence of a potamoplankton.

*Full mixing*

The second model assumes that the incoming water is fully mixed with the main storage volume, such that the loss of particles from the section is slower and follows an exponential decay pattern (Reynolds, 1988). Exponential loss rate is defined by the function -(q.t / V) where q is the discharge through the section, t is the time and V is the volume of the section (after Reynolds, 1984). Particles will continue to be removed until the concentration within the section equals that of the inflowing water. In the case
where no particles are imported, the concentration will fall exponentially until all particles are removed, assuming no recruitment within the section. This, however, takes much longer than with plug flow, and may therefore allow persistence if rates of cell replication are of a suitable magnitude to equal losses.

Daily exponential loss rates of particles from the Wansford section during typical spate, spring and summer conditions, assuming full mixing and no recruitment, are presented in table 3.3. Note that these are the maximal potential loss rates for the discharge stated, as no plankton import to the section is assumed.

**Partial mixing**

Full mixing represents the lowest dilution rate of particles without recourse to the aggregate dead zone model. It is possible, however, that the frictional forces produced by flowing water in the Nene were not sufficient to fully mix inflowing water throughout the whole volume of the Wansford stretch. The loss rates from partially mixed sections fall between those associated with full mixing and plug-flow.

The extent of flow induced mixing is dependant on the turbulent shear stress produced by frictional resistance of water flow against the bed material. This stress sets up horizontal eddies, the size of which dictate the potential to mix water against the flow. The lateral coefficient of eddy diffusion ($K_x$) given by the following formula in Reynolds (1988) quantifies mixing potential

$$K_x = 11 u^* z$$

where $u^*$ is the shear velocity and $z$ is depth.

Eddy diffusion was calculated for the River Nene at Wansford assuming 'typical' physical characteristics associated with spate, spring and summer flow events and assuming an average height of bed projections of 1mm. The results are presented in table 3.3 and were used to calculate the daily loss rates of suspended particles from the Wansford stretch of the river assuming no particles were imported with incoming water. The physical characteristics associated with the different flow conditions and the loss rates assuming full mixing are also shown.

Daily exponential loss rates for the partial mixing model were calculated according to Margalef (1960), who stated that the resistance of plankton to downstream displacement was governed by
where $U$ is the average flow velocity, $K_x$ is the lateral coefficient of eddy diffusion, and $k$ is the growth rate needed to offset downstream loss. The inverse of $k$ was therefore taken to represent the daily loss rate assuming no internal population processes such as reproduction or death.

Rates associated with full mixing were calculated assuming an exponential loss rate of particles from the fully mixed section of the river (Reynolds, 1988). This loss rate was given by $-Q/V$, where $Q$ is the discharge (m$^3$s$^{-1}$) and $V$ is the volume of water in the section (m).

<table>
<thead>
<tr>
<th></th>
<th>Spate conditions</th>
<th>Spring conditions</th>
<th>Summer conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discharge (m$^3$s$^{-1}$)</td>
<td>43.0</td>
<td>11.0</td>
<td>2.7</td>
</tr>
<tr>
<td>Velocity (m s$^{-1}$)</td>
<td>0.5</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>4.0</td>
<td>3.4</td>
<td>2.81</td>
</tr>
<tr>
<td>Volume (m$^3$)</td>
<td>520000</td>
<td>438750</td>
<td>365430</td>
</tr>
<tr>
<td>Retention time (d)</td>
<td>0.1</td>
<td>0.5</td>
<td>1.6</td>
</tr>
<tr>
<td>Shear stress (ms$^{-1}$)</td>
<td>0.02</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>$K_x$ (m$^2$s$^{-1}$)</td>
<td>0.9</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Mixing length (m)</td>
<td>43.2</td>
<td>35.5</td>
<td>29.4</td>
</tr>
<tr>
<td><strong>Full mixing</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exp. loss rate (d$^{-1}$)</td>
<td>-7.1</td>
<td>-2.2</td>
<td>-0.4</td>
</tr>
<tr>
<td><strong>Partial mixing</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exp. loss rate (d$^{-1}$)</td>
<td>-7102.1</td>
<td>-2514.2</td>
<td>-855.4</td>
</tr>
</tbody>
</table>

Table 3.3 Exponential loss rates of particles from the River Nene at Wansford during typical flow conditions of 1994. Shear stress was calculated according to section 3.2.3.4. Mixing length relates to the horizontal distance taken to accommodate a single mixing through full depth and was calculated according to Reynolds (1988). 'Typical' river conditions were used rather than the range observed in 1994 as the analysis was more predictive that descriptive, aiming to describe the potential for plankton development under 'typical' flow conditions.

The daily exponential loss rates associated with the partial mixing model were extremely high, even during the summer when flow rate was low. Cells must double every 8.4, 23.8, and 70.0 seconds to equal the exponential loss rates of $-7102.1$, $-2514.2$ and $-855.4$ d$^{-1}$ respectively. Such rates are beyond the capability of even the fastest growing species. It is therefore unlikely that any plankton could develop in the river assuming the partial mixing model without importation from upstream. The partial mixing model, like plug flow, was therefore considered inadequate to explain the development of a potamoplankton in the River Nene. For example, discharge would have to fall to below
0.0045 m$^3$s$^{-1}$ for the rate of removal to be balanced by a daily exponential rate of increase of 2.0.

Hydraulic losses were reduced when full mixing was assumed, for example, the daily loss rate during 'typical' spring conditions was -2.17, but this is still higher than the maximum growth rate of most algae. This model was, however, used in subsequent calculations of hydraulic loss rates, as a simple model had to be adopted. Many of the conclusions drawn indicate that a more complex model of water retention is needed to fully describe fluvial dynamics in the Nene.

3.2.3.4 Estimation of main channel imports to the Wansford stretch of the river during 1994

The above analysis of loss rates assumed no importation of cells in the inflowing water. The net loss rate would, however, be lower if cells were imported to the section. It is reasonable to assume that some cells were imported from upstream of Wansford, as this was unlikely to be the first section to develop a plankton, given the similar morphology of upstream sections.

It is useful to think of the river as a series of long compartments acting independently of each other in order to visualise river function with regards to the hydraulic removal of phytoplankton downstream. The out-flowing water and its plankton from one section therefore acts as the in-flowing water to the next. Dilution within a section occurs if the inflowing water contains less plankton, the extent of which is defined by the difference in algal concentration between adjacent compartments and the volume of water exchanged per unit time.

Figure 3.9 shows a schematic river in which the loss rate of plankton from a section was calculated assuming different concentrations of imported material. In each case, (A to E) the daily exponential loss rate was calculated assuming a constant volume replacement of 0.05 per day (for example a discharge of 50 m$^3$d$^{-1}$ flowing through a section of 1000 m$^3$ volume). The example also assumes no recruitment of cells other than from upstream imports.

Loss rates decrease as the amount of imported material increases, and hence the rate of recruitment needed to maintain the concentration of the section is reduced. Any stretch of river that receives an import is therefore better able to maintain its plankton in the face of constant removal than a section that receives no upstream input.
Figure 3.9 Schematic representation of loss of particles from a river section (N) that received variable concentrations from upstream. In the example, the concentration of imports were 0, 0.25, 0.5, 0.75 and 1.0 times the concentration at N from A to E respectively. The associated daily exponential loss rates from N were -0.05, -0.0375, -0.025, -0.0125 and 0 through A to E respectively, assuming 0.05 of total volume at N was replaced per day.

The chlorophyll 'a' concentrations measured at Wansford and Elton Lock, 5 km upstream, were used to estimate the level of importation to the Wansford stretch of the river throughout 1994 (data for Elton Lock supplied by N.R.A). A total of 23 dates throughout the year, covering a diversity of flow conditions, were used. No overall pattern of downstream increase was apparent, and on a number of occasions, the density decreased with distance downstream. The lack of a downstream increase with distance was also evident over a longer stretch of river from Irthlingborough, approximately 50 km upstream to Wansford. The relative consistency of chlorophyll 'a' concentration along this section of the river indicated that dilution losses were negligible, as inflowing water contained a similar cell density to outflowing water.

There is a danger of over generalising, however, as there was considerable variation in the patterns of downstream increase depending on the flow conditions.

3.2.4 Estimation of maximum algal growth rates from cell morphology

An estimate of maximum potential growth rate for the algal groups recorded at Wansford was needed to assess the potential for net population development throughout
the year, taking account of estimated loss processes.

Maximum exponential rates of increase have been established for a number of algal species grown in laboratory cultures under optimal temperature, constant saturating illumination and excess nutrient concentrations. Daily exponential rates of increase obtained in this manner, expressed in natural logarithmic units, range from 0.21 for *Ceratium hirudinella* to 2.15 for *Chlorella pyrenoidosa* (Reynolds, 1984). Natural rates of increase are usually lower than these estimates owing to a combination of loss processes such as sedimentation, grazing and death, and sub-optimal growth conditions. *In situ* net rates of increase presented in Reynolds (1984) for a broad range of species were all below 1.0. The natural rate for *Ceratium hirudinella* measured during summer was found to be 0.13, approximately 40% of the maximum potential rate. This reduction is often even greater for smaller species. The average *in situ* growth rate in this study was assumed to be 50% of the maximum growth rate, defined by the following method.

Cell biovolume was used to estimate maximal potential growth rate, after the relationship of Reynolds (1984)

\[
    r = 1.855 - 0.226 \log_{10} V
\]

where \( r \) is the maximal exponential growth rate (ln units) and \( V \) is biovolume (\( \mu m^3 \)). The surface area (SA) to volume ratio was also be used to derive a separate estimate of maximum growth rate after Reynolds (1984).

\[
    r = 0.309 (SA/V) + 0.755
\]

Cell biovolumes and surface areas were calculated for River Nene algal groups, assuming simple geometric shapes. The final estimate of maximum growth rate was taken as the average of the two estimates.

Maximal growth rates determined in this manner are the product of a number of assumptions, and as such are not designed for rigorous analysis. They are only designed to give a rough estimate of potential rates of increase, as the level of confidence in the estimates is unknown. The major sources of error in the procedure are the use of literature derived sizes for each taxa, the estimation of volume from general geometric approximations of shape, and the use of published regressions relating growth rate to cell morphology.
3.3 Results

3.3.1 Characteristics of Flow Regime at Wansford

3.3.1.1 Flow rate

Figure 3.10 shows the average daily discharge and rainfall measured at Orton lock gauging station during the period 1992 to 1995 (data supplied by the Environment Agency, Anglian Region).

Annual discharge patterns, measured in cumecs \((\text{m}^3\text{s}^{-1})\), followed a typical pluvio-oceanic regime similar to the River Seine (Garnier et al., 1995), in which extended periods of low flows during the summer months were separated by higher flows during the winter.

There was substantial inter-annual variation in both discharge and rainfall between 1992 and 1995. 1994 had the highest spring discharge of the four year period, although low rainfall during the summer led to a stable and low summer discharge that was only broken by a spate event in September. The average daily discharge during 1994 ranged from between 66.8 \(\text{m}^3\text{s}^{-1}\) on the 7th January to 1.4 \(\text{m}^3\text{s}^{-1}\) on the 13th August, with an average of 11.4 \(\text{m}^3\text{s}^{-1}\) for the whole year. Annual average discharge for 1992, 1993 and 1995 was 11.52, 11.56 and 8.25 \(\text{m}^3\text{s}^{-1}\) respectively.

Figure 3.11 shows the discharge data for 1994 in the form of a duration curve which can be compared with figure 3.12, the duration curve for the period 1992-1995. Such figures are designed to show the cumulative proportion of days on which the flow reaches a particular discharge (Dingman, 1994). 1994 had the highest frequency of high flows, \(Q_{50}\) and \(Q_{95}\) values of 10.5 and 2.2 \(\text{m}^3\text{s}^{-1}\) respectively, compared to 4.8 and 2.01 \(\text{m}^3\text{s}^{-1}\) during 1992-1995. The early part of 1994 was responsible for the majority of the high flows.

The form of the curves showed that there were certain ranges of discharge that occurred more frequently than others (indicated by the horizontal sections of the plot). One was encountered at low flows less than 3 \(\text{m}^3\text{s}^{-1}\) during the summer / autumn period while another was associated with high flow events of over 40 \(\text{m}^3\text{s}^{-1}\). The third was within the range of 10 to 13 \(\text{m}^3\text{s}^{-1}\), and typified the average flow rate during the spring period. It is not immediately obvious why this level of discharge should be favoured over the intermediates, and may be a result of inaccurate gauging.
Figure 3.10 Discharge at Orton gauging station (line) and rainfall (bar), 1992 to 1995.
Figure 3.11 Duration curve of daily flow rates throughout 1994 at Orton Lock.
Figure 3.12 Duration curve of daily flow rates during 1992-1994 at Orton Lock.
3.3.1.2 Flow velocity

Daily average discharge throughout 1994 was converted to average flow velocity using the regression equation given in section 3.2.2.1. Flow velocity ranged from 0.03 to 0.79 m s\(^{-1}\) during 1994, a much narrower range than that of discharge.

3.3.1.3 Flow related habitat types in the main channel at Wansford station

The turbulent kinetic energy of the main channel flow was calculated according to section 3.2.2.4. The results are plotted as a histogram in figure 3.13.

![Figure 3.13: Distribution of shear stress produced by daily discharge through the River Nene at Wansford, 1994, assuming the average height of bed projections to be 1 mm.]

The majority of average daily shear velocities (estimated at 0.4 total depth) were below 0.01 m s\(^{-1}\). The lowest class interval (below 0.004 m s\(^{-1}\)) were those derived from the low flow periods during the summer with a discharge of approximately 3 m\(^3\)s\(^{-1}\). The next most abundant class (between 0.004 and 0.008 m s\(^{-1}\)) corresponded to flow rates that were between 6.7 and 14.9 m\(^3\)s\(^{-1}\) which can be broadly related to the winter / spring average flow during 1994, excluding spates. All shear velocities above 0.008 m s\(^{-1}\) were produced by relatively transient periods of high flows (above 14.9 m\(^3\)s\(^{-1}\)), hence the relatively low frequency within these intervals. The majority of flows throughout the year therefore produced relatively little turbulent energy. These levels are related to the classification of riverine habitat types in the discussion.

3.3.2 Physical Characteristics of the Lower River Nene
Figure 3.14 shows water temperature at Wansford during 1994. The temperature follows the expected seasonal pattern for north temperate rivers with mean daily values increasing from a winter minimum of 3°C to a summer maximum of 23°C. The temperature at the Nassington backwater and at Wansford backwater was not significantly different from that at Wansford during the growing season of 1994 (March - October) when tested with a Wilcoxon's signed-ranks test for paired observations (p>0.05).

![Graph showing temperature, suspended solids, and Secchi depth over the year 1994](image)

**Figure 3.14** Physical characteristics of the River Nene at Wansford, 1994.

The concentration of suspended solids at Wansford (figure 3.14) ranged from 0.5 to 99.7 mg l⁻¹ during 1994. Potential sources of seston included the resuspension of in-stream sediments, wash-in of terrestrial matter during heavy rainfall, transport from upstream degradation of CPOM, and planktonic productivity. High seston
concentrations during January, February, April and November coincided with periods of high discharge, and were considered to be predominantly the product of sediment carriage rather than autochthonous production.

Figure 3.15 shows that the proportion of non-algal turbidity was high at these times. Analysis of rotifer samples taken during these times also showed the majority of suspended matter to be a mixture of fine sediment and floculent decaying plant matter. The high seston concentration during May was associated with lower and less variable discharge and mainly comprised algal biomass, as indicated by low non-algal turbidity (figure 3.15).

\[\text{Figure 3.15 Algal contribution to turbidity at Wansford, 1994.}\]

Water transparency at Wansford is presented in figure 3.14. The pattern was inversely related to suspended solid concentration. Transparency was lowest (<0.5 m) when turbidity was dominated by non-algal particles, although reduced transparency in May was associated with high algal turbidity. Highest water transparency readings were associated with low suspended solid concentrations during the summer months.

No measurements of suspended solid concentration or Secchi disc depth were made at Nassington but the physical appearance of the water, noted during weekly sample visits, was very similar to that of the main channel. Wansford backwater had much clearer water than the true river habitats owing to minimal mixing of this water between the habitats.

3.3.3 Potential Light Limitation

The depth of the euphotic zone was estimated from Secchi depth using the method outlined in section 3.2.2.3. Figure 3.16 shows the proportion of total depth below the
compensation point during 1994, which equates to the proportion of time spent below this depth by suspended cells freely mixed throughout the full depth (refer to section 3.2.2.3).

The euphotic depth was less than full depth on a number of occasions, indicating that a proportion of the water column received inadequate light intensity to support net algal production. This occurred mainly during the winter and spring when suspended silt concentrations or algal density were highest. The euphotic depth reached the sediment surface from June to October, when flow rates were low, so that all entrained algae and benthic forms received adequate light to photosynthesise during daylight hours. Light conditions were good at the end of June when the phytoplankton density finally crashed to its summer low level.

3.3.4 Plant nutrient concentrations

Figure 3.17 shows the concentrations of plant nutrients in the River Nene at Wansford during 1994. Total phosphorus concentration (PO$_4$), including dissolved and inorganic forms, ranged from 0.02 to 4.35 mg l$^{-1}$, with an annual mean of 0.87 mg l$^{-1}$.

The seasonal pattern of total phosphorus concentration was related to river discharge. Low levels were apparent throughout the winter months when discharge was high, whereas high levels of total phosphorus coincided with consistently low flow rates during summer. This indicated that a relatively constant supply of the nutrient reached the river but was differentially diluted by a variable flow rate throughout the year. The
most likely source was sewage treatment plants as these are known to represent an important source of phosphorus-rich waste in populated catchments (Mason, 1991).

Figure 3.17 Plant nutrient concentrations at Wansford, 1994.

A further potential source of particulate phosphorus was from eroded soil transported to the river during periods of overland flow as shown by the sharp peak in total phosphorus during September that coincided with increased discharge. This relationship was the opposite to that described above. Total phosphorus may also have been supplemented by the re-suspension of in-stream sediments which adsorbed phosphate during the long summer low flow period when soluble reactive phosphate levels in the surrounding water were high (Dorioz, 1995).

The majority of phosphorus in the Nene, as in most rivers with moderate flow rate, was
in the soluble reactive state (S.R.P.), which is most efficiently utilised by primary producers (figure 3.17). The annual mean concentration during 1994 was 0.615 mg l\(^{-1}\), approximately 70% of mean total phosphorus. S.R.P. dynamics in the River Nene were also related to discharge. Concentration increased when flow rate declined in April and remained high throughout the summer, but decreased sharply in September with high flows, and were similarly reduced with subsequent spates in November and December. Concentrations remained above limiting levels indicating that algal production was not constrained by phosphorus concentration.

Figure 3.17 shows the concentration of total organic nitrogen (\(\text{NO}_3\)) during 1994. The annual mean concentration was 9.38 mg l\(^{-1}\). The seasonal pattern of abundance was opposite to that of phosphorous, with the highest concentrations found during winter and the lowest concentrations during the summer. This type of association indicates that the major source of nitrogen to river water was via run-off from terrestrial sources which entered the river during high flows.

Figure 3.17 also shows the concentration of silicon dioxide (SiC\(^2\)) in the river water during 1994. There was a one hundred fold difference between the minimum silicon dioxide concentration of less than 0.10 mg l\(^{-1}\) and maximum of 10.10 mg l\(^{-1}\). The concentration remained above limiting levels for diatom growth for most of the year, assuming a half-saturation concentration of 0.06 mg l\(^{-1}\) (Paasche, 1980). Seasonality partially mirrored that of stratifying lakes with a reduction in concentration during May when diatoms were abundant. The minimum level reached in May was potentially low enough to limit diatom growth (Klapper, 1991; De Ruyter van Steveninck \textit{et al.}, 1992), but only persisted for a very short time. Short-term silica depletion in spring was also a common phenomenon in sixth and seventh order rivers in the River Seine catchment (Garnier \textit{et al.}, 1995) after which levels were rapidly regained, as in the Nene.

3.3.5 Chlorophyll 'a' abundance at Wansford station, Nassington and Wansford backwater

Total chlorophyll 'a' concentration throughout the growing season of 1994 at Wansford station, Nassington and Wansford backwater is shown in figure 3.18. Wansford station and Nassington had similar temporal patterns, with a major spring peak of chlorophyll 'a' of over 100 \(\mu\)g l\(^{-1}\) during May, following a smaller initial peak in April. Levels then declined to a summer minimum of around 5 \(\mu\)g l\(^{-1}\) with no subsequent recovery later in the year. The chlorophyll 'a' levels of Wansford backwater were different to those of the river habitats. There was no spring peak and levels were generally lower than in the river during the spring and early summer. The maximum chlorophyll 'a' concentration
in the backwater was 14 µg l⁻¹, an order of magnitude lower than that of the river habitats.

Figure 3.18 Chlorophyll 'a' concentration at three sample sites on the River Nene, 1994.

Statistical analysis of weekly chlorophyll 'a' concentrations was performed using the non-parametric Wilcoxon's Signed Rank Test. All sites were compared in a pairwise manner. The result of the test are shown in table 3.4.

<table>
<thead>
<tr>
<th></th>
<th>Wansford station</th>
<th>Nassington</th>
<th>Wansford backwater</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wansford station</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nassington</td>
<td>93</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Wansford backwater</td>
<td>39*</td>
<td>38*</td>
<td>X</td>
</tr>
</tbody>
</table>

Table 3.4 Wilcoxon's signed rank test of chlorophyll 'a' concentration from three habitats of the River Nene during 1994. * represents a significant difference at p=0.05 level.

No significant difference was apparent between the chlorophyll 'a' concentration of Wansford station and Nassington, but there was a significant difference between both of these sites and Wansford backwater.

3.3.6 Riverine Phytoplankton Composition
Phytoplankton population dynamics are presented as either total cell number or biovolume calculated from suitable geometric formulae applied to each taxon. Both of these measures were significantly related to total chlorophyll 'a' concentration ($r^2 = 0.73$ and $0.82$ respectively). The seasonal pattern of chlorophyll 'a' concentration is often used in the following analysis to describe algal dynamics, but the conclusions drawn could equally apply to cell density or biovolume. Algal density data from Wansford was kindly supplied by the National Rivers Authority, Anglian Region.

Figures 3.19 and 3.20 show that the phytoplankton of the River Nene was dominated by two groups, the Chrysophyta (predominantly diatoms) and the Chlorophyta (green algae), which accounted for 39% and 36% respectively of the 120 taxonomic units recorded during 1994. Chlorophytes were the dominant group in terms of cell number, representing 61% of the annual total. The Cryptophytes were a ubiquitous group, but often present in only small numbers (5% of total cell number). Cyanobacteria were similarly abundant, but members of the Euglenophyta and Pyrrophyta were rarely present and never abundant, both groups representing less than 1% of the total cell number.

A full list of taxa is given in table 3.5. The level to which various groups were identified was variable. Algae with obvious diagnostic characteristics were identified to species whereas species which could not be confidently separated were placed within an 'umbrella classification,' such as 'small green cells' or 'centric diatoms'. The total number of species present during 1994 was therefore likely to be higher than 120, as each 'umbrella' grouping consisted of a potential multi-species assemblage.

### CYANOBACTERIA

- Anabaena flos-aquae
- Anabaena sp.
- Aphanizomenon flos-aquae
- Gomphosphaeria sp.
- Lyngbya sp. < 2um
- Merismopedia sp.
- Microcystis sp.
- Oscillatoria agardhii
- Oscillatoria limnetica
- Oscillatoria redekii
- Oscillatoria sp. < 2um
- Oscillatoria sp. 3-4um
- Oscillatoria sp. 4-8um
- Oscillatoria sp. 8-16um

### CHLOROPHYCEAE

- Actinastrum sp.
- Ankistrodesmus acicularis
- Ankistrodesmus angustatus
- Ankistrodesmus falcatus
- Ankistrodesmus subcapitatus
- Botryococcus sp.
- Chlamydomonas sp.
- Chlorella sp.
- Chlorella vulgaris
- Koliella sp.
- Lagerheimia sp.
- Micractinium sp.
- Oocystis sp.
- Pediastrum duplex
- Pediastrum sp.
- Pediastrum tetra
- Pediastrum boryanum
- Scenedesmus acuminatus

72
<table>
<thead>
<tr>
<th>Chlorogonium sp.</th>
<th>Scenedesmus bijuga</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chodatella sp.</td>
<td>Scenedesmus quadricauda</td>
</tr>
<tr>
<td>Closteriopsis sp.</td>
<td>Scenedesmus sp.</td>
</tr>
<tr>
<td>Coelastrum sp.</td>
<td>Schroederia sp.</td>
</tr>
<tr>
<td>Crucigenia quadrata</td>
<td>Sphaerocystis sp.</td>
</tr>
<tr>
<td>Crucigenia rectangularis</td>
<td>Stichococcus sp.</td>
</tr>
<tr>
<td>Crucigenia sp.</td>
<td>T. staurogeniaeforme</td>
</tr>
<tr>
<td>Crucigenia tetrapedia</td>
<td>Tetraedron sp.</td>
</tr>
<tr>
<td>Dictyosphaerium sp.</td>
<td>Tetrastrum sp.</td>
</tr>
<tr>
<td>Elakatothrix sp.</td>
<td>Tetrastrum staurogen.</td>
</tr>
<tr>
<td>Eudorina sp.</td>
<td>Ulothrix sp. &lt; 10um</td>
</tr>
<tr>
<td>Gloeotile sp.</td>
<td>Ulothrix sp. 11-20um</td>
</tr>
<tr>
<td>Kirchneriella sp.</td>
<td></td>
</tr>
</tbody>
</table>

**BACILLARIOPHYCEAE**

<table>
<thead>
<tr>
<th>Amphora sp.</th>
<th>Navicula sp. 21-30um</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asterionella formosa</td>
<td>Navicula sp. 31-40um</td>
</tr>
<tr>
<td>Centric diatom &lt; 5um</td>
<td>Navicula sp. &gt; 40um</td>
</tr>
<tr>
<td>Centric diatom 11-20um</td>
<td>Nitzschia acicularis</td>
</tr>
<tr>
<td>Centric diatom 21-30um</td>
<td>Nitzschia sigmoidea</td>
</tr>
<tr>
<td>Centric diatom 31-40um</td>
<td>Nitzschia sp. 11-20um</td>
</tr>
<tr>
<td>Centric diatom 6-10um</td>
<td>Nitzschia sp. 21-30um</td>
</tr>
<tr>
<td>Centric diatom 6-10um</td>
<td>Nitzschia sp. 31-40um</td>
</tr>
<tr>
<td>Centric diatom &gt;40um</td>
<td>Nitzschia sp. &gt; 40um</td>
</tr>
<tr>
<td>Cocconeis sp.</td>
<td>Pennate diatom 6-10um</td>
</tr>
<tr>
<td>Cosmarium sp.</td>
<td>Pennate diatom 11-20um</td>
</tr>
<tr>
<td>Cymatopleura sp.</td>
<td>Pennate diatom 21-30um</td>
</tr>
<tr>
<td>Cymbella sp.</td>
<td>Pennate diatom 31-40um</td>
</tr>
<tr>
<td>Diatoma sp.</td>
<td>Pennate diatom 41-50um</td>
</tr>
<tr>
<td>Diatoma vulgaris</td>
<td>Pennate diatom &gt; 50um</td>
</tr>
<tr>
<td>Fragilaria sp.</td>
<td>Rhizosolenia sp.</td>
</tr>
<tr>
<td>Gomphonemia sp.</td>
<td>Rhoicosphenia sp.</td>
</tr>
<tr>
<td>Gyrosigma sp.</td>
<td>Stephanodiscus hantzschii</td>
</tr>
<tr>
<td>Melosira granulata</td>
<td>Surirella sp.</td>
</tr>
<tr>
<td>Melosira varians</td>
<td>Synedra sp.</td>
</tr>
<tr>
<td>Meridion sp.</td>
<td>Synedra ulna</td>
</tr>
<tr>
<td>Navicula sp. &lt; 10um</td>
<td>Tabellaria fenestrata</td>
</tr>
<tr>
<td>Navicula sp. 11-20um</td>
<td>Tabellaria sp.</td>
</tr>
</tbody>
</table>

**CRYPTOPHYCEAE**

<table>
<thead>
<tr>
<th>Cryptomonas - A</th>
<th>Cryptomonas - E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cryptomonas - B</td>
<td>Rhodomonas sp.</td>
</tr>
</tbody>
</table>

**CHRYSOPHYCEAE**

<table>
<thead>
<tr>
<th>Dinobryon sp.</th>
<th>Mallamonas sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mallamonas akrokomos</td>
<td>Synura sp.</td>
</tr>
</tbody>
</table>

**CONJUGATOPHYCEAE**

<table>
<thead>
<tr>
<th>Closterium acutum</th>
<th>Closterium sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closterium parvulum</td>
<td>Staurastrum sp.</td>
</tr>
</tbody>
</table>

**EUGLENOPHYTA**

| Euglena sp.                  | Phacus sp.                            |

**DINOPHYTA**
Table 3.5 Algal and bacterial taxa recorded at Wansford during 1994.

3.3.7 Cell Density and Seasonal Succession

Total cell density ranged from a minimum of 124 cells ml\(^{-1}\) during the winter, to 219 x 10\(^3\) cells ml\(^{-1}\) during a bloom at the end of May (figure 3.19). Highest cell densities occurred during the spring and early summer period, followed by a lower density during the summer and autumn broken only by periodic increases during September and December. No corresponding autumnal peaks were observed in the chlorophyll 'a' concentration (figure 3.18) or total biovolume of algae, indicating that these peaks were dominated by small cells.

Chrysophyta were dominant during the spring of 1994 (figure 3.20). Centric diatoms were by far the most abundant group representing 94% of total Chrysophyta cell density, with *Stephanodiscus hantzschii* dominating the main peak during May. Regularly recorded pennate diatoms included *Nitzschia sp.* and *Navicula sp.*, although densities were never high. These pennate groups may have been tychoplanktonic *i.e.* washed from the sediment surface by high discharge. Diatoms became less abundant at the end of May when flow rates fell to approximately 3 m\(^3\)s\(^{-1}\).

Figure 3.19 Phytoplankton and bacterial density in the River Nene at Wansford, 1994.
Chlorophytes began to increase in abundance slightly after the diatoms at the end of March. Characteristic taxa of this early period were *Tetrastrum staurogeniaeforme*, *Ankistrodesmus angustatus*, *Kirchneriella sp.*, *Crucigenia sp.*, *Lagerheima sp.*, and unidentified spherical cells. Cell density fell during May, when *Stephanodiscus hantzschii* dominated the phytoplankton, prior to the development of the main chlorophyte peak at the start of June, which was dominated by unidentified curved cells, *Ankistrodesmus angustatus* and *Chlorella sp.* Density crashed at the end of June and remained low until September when the abundance of unidentified spherical cells increased along with discharge. A similar peak occurred at the end of November shortly after a spate event, this time dominated by unidentified elliptical cells.

One of the most notable features of the phytoplankton was the change in dominance from diatoms in the spring months to green algae in the early summer (figure 3.21). A similar pattern has been recorded from a number of lowland river studies and was attributed to the suite of changes associated with declining discharge. Most other studies had a reversal of the dominance again in the autumn, somewhat like that associated with the autumnal overturn in lakes (Sommer *et al.*, 1986), but this was lacking in the River Nene.

Cryptophytes were relatively abundant during the summer months when total cell number was low (figure 3.20). The group was dominated by *Rhodomonas sp.* and *Cryptomonas sp.* but actual cell densities rarely rose above 800 cells ml^{-1}. These
groups are motile and so were less liable to settlement losses from the shallow depths of the summer. They are also considered to be highly palatable groups for zooplankton filter feeders indicating a low grazing pressure during summer. The small size of the phytoplankton (figure 3.22) indicates that rapid rates of replication were favourable in the Nene.

![Figure 3.21](image1.png)

**Figure 3.21** Seasonal development of the two dominant algal groups related to discharge in the River Nene at Wansford, 1994.

![Figure 3.22](image2.png)

**Figure 3.22** Algal size groups expressed as percentage of total cell number during 1994. Group 1, <250 μm³; group 2, 250 - 500 μm³; group 3, 501 - 5000 μm³; group 4, 5001 - 25000 μm³; group 5, >25000 μm³.
A number of cyanobacterial taxa were recorded from the main channel of the river, although cell numbers were rarely high. Two distinct groups were apparent with regards to temporal distribution. The first group, represented by Oscillatoria limnetica, was present throughout the spring period at Wansford when flows were relatively high but stable i.e. little daily change in magnitude (figure 3.23). Total cell densities were variable but reached 2,500 cells ml\(^{-1}\) during May.

The second group was predominantly found over a restricted period of approximately ten days in September which coincided with high discharge after a long period of low flow (note the high positive change in discharge at the time, figure 3.23). This second group consisted of species such as Oscillatoria agardhii, O. redekii, Microcystis sp. Merismopedia sp., Anabaena flos-aquae, and Aphanizomenon flos-aquae. The dominant group in terms of cell number was O. agardhii, which reached in excess of 6,000 cells ml\(^{-1}\) during mid-September. Some groups were recorded sporadically throughout other times, but rarely at high density. Figure 3.23 shows that cell numbers were highest during the first few days of increased discharge and then proceeded to decline indicating that they were rapidly removal from the flow and were therefore considered as 'drift' organisms.

3.3.8 Potential sources of phytoplankton loss at Wansford Station

3.3.8.1 Algal settlement losses

Estimated exponential daily loss rates owing to settlement into the boundary layer at Wansford are presented in figure 3.24 for particles with sinking rates from zero (neutral buoyancy) to 40 μm s\(^{-1}\), from fully mixed columns of different depth. Loss rates were lowest for the slowest sinking species but increased with a reduction of the mixed depth, as expected. Sinking velocity had more effect on estimated loss rates than depth over the range of values considered. Daily loss rates ranged from a minimum of zero to a maximum of -1.38 for the combination of physical conditions and sinking velocities considered in this model, although this could be expanded to include any algal particle in any theoretical water column.

Settlement losses were assumed to be restrictive (losses > growth) for the fastest sinking species considering the maximum rates of increase of most large algal species (section 3.2.4). Restrictive combinations of sinking velocity with depth can be roughly assessed by imagining a line drawn horizontally across the graph at a loss rate of -0.80. All combinations with a loss rate above this line will generally be too high to allow populations to develop considering the maximum rates of increase for small algae.
fluctuating discharge.

We see...
Figure 3.24 Daily exponential loss rate of particles with known sinking velocities from mixed columns of different depth.
Small algae with low sinking velocity had loss rates lower than their potential maximum rates of replication, calculated from cell dimensions according to section 3.2.4. For example, a cell with the dimensions of *Chlorella vulgaris* (category I, section 3.2.3.1) had a daily loss rate of less than -0.10 even at the shallowest summer depths, while it's estimated maximum daily growth rate was 1.30. Small fast growing species were therefore more capable of off-setting sedimentation losses throughout the year, while favourable growth conditions persisted, and were therefore more suited to the shallow water depths of between 2.5 to 3.0 metres encountered during the summer months.

Algae with category V sinking rates may have had prohibitively large loss rates from shallow columns during the summer, and this may have been partly responsible for the lack of diatom dominance throughout this period (see figure 3.21). During the spring, when water depth was deeper, between 3.0 - 3.5 metres, the loss rates of group V species were less prohibitive. It seems quite possible from the figures generated, that the critical settlement loss rate (that which is just balanced by the rate of increase) could occur at a depth between those of the spring and those of the summer, and therefore helped to force the change in dominance from diatoms to green algae. For example, a population of *Stephanodiscus astraea* with a sinking rate of 25 μm s⁻¹ would be lost at a rate of -0.83 from a column of 2.7m depth (typical of the summer period), whereas at a depth of 3.5m (typical of the spring period) the loss rate would be reduced to -0.62. The *in situ* maximum rate of increase for this species was estimated as 0.90, so it is not impossible that the reduction in depth between spring and summer had an important effect on diatom populations.

One problem encountered with this model was that neutrally buoyant particles had no loss rate at all when simply considering sedimentation alone. Death rates owing to other factors are needed to increase the predictive power of this model, and should be addressed in future work.

### 3.3.8.2 Grazing losses

The potential role of pelagic grazing zooplankton should not be dismissed as a control mechanism of algal populations during the summer (Garnier *et al.*, 1995). Increased retention times associated with the low flow rates of the summer, should have provided an ideal habitat for the development of grazing rotifer populations. Mean monthly grazing rates were calculated from monthly average rotifer density throughout 1994, assuming an average filtration rate of 5 μl ind⁻¹ hr⁻¹ (refer to section 3.2.3.2). The results are presented in table 3.6.
<table>
<thead>
<tr>
<th>Month</th>
<th>Daily loss rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>-0.0013</td>
</tr>
<tr>
<td>February</td>
<td>-0.0017</td>
</tr>
<tr>
<td>March</td>
<td>-0.0020</td>
</tr>
<tr>
<td>April</td>
<td>-0.0075</td>
</tr>
<tr>
<td>May</td>
<td>-0.0546</td>
</tr>
<tr>
<td>June</td>
<td>-0.0056</td>
</tr>
<tr>
<td>July</td>
<td>-0.0013</td>
</tr>
<tr>
<td>August</td>
<td>-0.0014</td>
</tr>
<tr>
<td>September</td>
<td>-0.0010</td>
</tr>
<tr>
<td>October</td>
<td>-0.0013</td>
</tr>
<tr>
<td>November</td>
<td>-0.0013</td>
</tr>
<tr>
<td>December</td>
<td>-0.0013</td>
</tr>
</tbody>
</table>

Table 3.6 Estimated daily loss rate of palatable algal groups owing to rotifer grazing in the River Nene.

Grazing losses were largest during the spring, and especially in May, when members of the genus *Synchaeta* were dominant. These species are selective feeders, preferring diatoms and so may have had a larger impact on this group than the generalised grazing loss model of table 3.6 predicts. Grazing losses were, however, much smaller than potential rates of increase under favourable conditions and were therefore expected to have little effect on phytoplankton dynamics.

3.3.8.3 Hydraulic losses

Figure 3.25 shows the loss rates owing to hydraulic removal of plankton from the Wansford stretch of the river exposed to the range of conditions experienced during 1994. The dominant controlling factors were assumed to be the discharge through the system and the concentration of imported material. Discharge ranged from between 1.4 to 66.8 m³ s⁻¹ and the assumed import ranged from between zero to 100% of the concentration at Wansford. The loss rate was calculated from the volume displaced per day, taking into account the degree of importation (refer to section 3.2.3.3), and assuming full mixing within the section.

An exponential rate of cell replication of 0.80 d⁻¹ was assumed as the maximum rate of increase of small algae in optimal growth conditions. Loss rates above this level were considered to be non-sustainable and liable to cause a reduction of plankton density.
Figure 3.25 Daily exponential loss rate of suspended particles through hydraulic removal from the Wansford stretch of the river.
The predicted loss rates presented in figure 3.25 indicate that plankton development at Wansford was unlikely to occur without substantial importation when discharge was above 4 m\(^3\) s\(^{-1}\). At 8 m\(^3\) s\(^{-1}\) a constant importation of 52% was required to achieve a minimum loss rate of -0.80. This value increased to 74% at a flow rate of 16 m\(^3\) s\(^{-1}\), 86% at a flow rate of 32 m\(^3\) s\(^{-1}\), and 92% at 64 m\(^3\) s\(^{-1}\).

Discharge rarely rose above 4 m\(^3\) s\(^{-1}\) during the summer months of 1994, and the average size of the inoculum from upstream was approximately 100% (section 3.2.3.4). Hydraulic loss rates were expected to be at a minimum during this period, with each section of river acting as a shallow lake in an interconnected series. The lack of biomass development (figure 3.18) therefore poses an interesting question. Phytoplankton density was either affected by other loss processes or was growth limited.

Discharge generally exceeded 4 m\(^3\) s\(^{-1}\) in the Nene except during the summer and autumn period of 1994, so the main river channel was theoretically acting as a sink for plankton for the rest the year, with natural rates of increase insufficient to offset hydraulic losses. Any plankton development, at these times must therefore have been reliant on imports from other sources. The average discharge during March, April and May when phytoplankton populations reached maximum biomass was 15.2 m\(^3\) s\(^{-1}\), 15.4 m\(^3\) s\(^{-1}\), and 8.3 m\(^3\) s\(^{-1}\) respectively. The loss rate of cells associated with the high discharge of first two months could only be theoretically maintained by replication if there was a constant and substantial import of cells with inflowing water.

3.3.9 Comparison of maximum and observed phytoplankton growth rates

The growth rate required to obtain observed weekly chlorophyll 'a' densities at Wansford is presented in figure 3.26.

The values refer to net growth and therefore take into account all loss processes between each sample occasion. The maximum growth rate of a spherical algae of 10 \(\mu\)m diameter is also shown. This rate was estimated from surface area and volume relations according to section 3.2.4. It represents an assumed upper limit of cell replication rate under optimal conditions in the field, indicating that any elevated rates of increase were the product of algal importation from other sources. Figure 3.26 indicates that during the spring the mid-channel habitat acted as a sink for algal populations (Pulliam, 1988), in that importation was required to maintain the observed growth rate. Allowing for errors in cell density calculation, the net rates of increase in summer were of a similar magnitude to maximum growth rates, indicating that a population may maintain itself
providing growth conditions were favourable.

![Graph showing net growth rates and replication rates](image)

**Figure 3.26** Net rate of increase required to obtain observed chlorophyll 'a' concentrations at Wansford during 1994.

### 3.3.10 Grazing losses imposed by littoral zooplankton

Table 3.7 lists the species collected from the littoral habitats of the River Nene between July - August, 1993. The potential for horizontal migrations and specific feeding ecology of each taxa was indicated as these factors dictate whether grazing will impact on pelagic phytoplankton.

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Diel horizontal migration</th>
<th>Food preference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Simocephalus vetulus</em></td>
<td>non-migratory^1,2^</td>
<td>phytoplankton^7^</td>
</tr>
<tr>
<td><em>Ceriodaphnia spp.</em></td>
<td>migratory^1,2,4^</td>
<td>phytoplankton^2,7,8^</td>
</tr>
<tr>
<td><em>Scaphaloberus mucronata</em></td>
<td>migratory^3^</td>
<td>phytoplankton^3^</td>
</tr>
<tr>
<td><em>Sida crystallina</em></td>
<td>migratory^5^</td>
<td>phytoplankton^2,5^</td>
</tr>
<tr>
<td><em>Chydorus sphaericus</em></td>
<td>migratory^1,6^</td>
<td>phytoplankton^6,8^</td>
</tr>
<tr>
<td><em>Chydorus globosus</em></td>
<td>migratory^6^</td>
<td>detritus^2,7^</td>
</tr>
<tr>
<td><em>Pleuroxus striatus</em></td>
<td>non-migratory^1^</td>
<td>detritus^5^</td>
</tr>
<tr>
<td><em>Pleuroxus aduncus</em></td>
<td>non-migratory^1^</td>
<td>detritus^5^</td>
</tr>
<tr>
<td><em>Pleuroxus trigonellus</em></td>
<td>non-migratory^1^</td>
<td>detritus^5^</td>
</tr>
<tr>
<td><em>Pleuroxus unincatus</em></td>
<td>non-migratory^1^</td>
<td>detritus^5^</td>
</tr>
<tr>
<td><em>Alona guttata</em></td>
<td>non-migratory^6^</td>
<td>detritus^5^</td>
</tr>
<tr>
<td><em>Alona costata</em></td>
<td>non-migratory^6^</td>
<td>detritus^5^</td>
</tr>
<tr>
<td><em>Alona rectangula</em></td>
<td>non-migratory^6^</td>
<td>detritus^5^</td>
</tr>
</tbody>
</table>
Table 3.7 Zooplankton taxa found in the littoral habitats of the River Nene, with some reference to the ecology of the taxa. The likelihood of each taxon performing horizontal migrations is shown, as are the general feeding preferences for each group. For those groups with no reference cited, the group was assumed to be non-migrating and reliant on detritus or periphytic food. These were chosen as they were assumed to be the most likely combination of characters for littoral groups. Where only a single citation was found for a particular species, this was applied to all other species of the genus, as in the case of *Pleuroxus* spp. In some cases conflicting accounts were found in the literature, as with the feeding preferences of *Chydorus sphaericus*. References cited were: 1 Lauridsen et al., (1996); 2 Fairchild (1981); 3 De Meester et al., (1993); 4 Scourfield and Harding (1966); 5 Vuille (1991); 6 Paterson (1993); 7 Lair (1991) 8. Geller and Müller (1981).

Littoral crustacean density is presented in table 3.8. Total density was divided between taxa that were likely to have an effect on mid-channel phytoplankton density, *i.e.* those that filter feed and undergo migrations, and those taxa that were unlikely to impact upon phytoplankton owing to their feeding ecology.

<table>
<thead>
<tr>
<th>Site</th>
<th>Number of animals per litre</th>
<th>Sampling occasions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Impacting</td>
<td>Non-impacting</td>
</tr>
<tr>
<td>Wansford mid-channel</td>
<td>0.14 (0.18)</td>
<td>0.05 (0.03)</td>
</tr>
<tr>
<td>Wansford bridge</td>
<td>4.66 (4.49)</td>
<td>1.38 (0.82)</td>
</tr>
<tr>
<td>Wansford littoral</td>
<td>185.7 (85.58)</td>
<td>12.38 (7.63)</td>
</tr>
<tr>
<td>Nassington</td>
<td>617.0</td>
<td>124.0</td>
</tr>
<tr>
<td>Ferry Meadows</td>
<td>8.0</td>
<td>0.40</td>
</tr>
<tr>
<td>Fotheringhay</td>
<td>18.90</td>
<td>17.70</td>
</tr>
</tbody>
</table>

Table 3.8 Density of littoral crustaceans in the River Nene during the summer (July - August) of 1993. Numbers in brackets are standard deviations.

Large standard deviations indicate that the distribution of littoral animals was heterogeneous in both space and time. The average was, however, used to gain a broad insight into the potential grazing impact of the littoral community on the main channel algal populations. The grazing rates given in table 3.9 were calculated assuming that migrating animals spent an average of 8 hours per day in the main channel and the rest of the time in the littoral zone. Non-migrating animals were assumed to feed exclusively

85
in the littoral zone.

The community grazing rate was calculated assuming a maximum clearance rate of 400 μl l⁻¹ hr⁻¹ for cladoceran filter feeders and a clearance rate of 100 μl l⁻¹ hr⁻¹ for cyclopoids feeding raptorially on algae, although advanced stages may be predominantly predatory on other plankters (Schriver et al., 1995). These rates were derived from literature estimates given in Zankai & Ponyi (1986) and Lair (1991; 1992). All mid-channel algae were assumed to be filtered optimally due to their small size. The rough guide to littoral grazing impact produced by this method would benefit from a more thorough treatment of individual species filtration capacity.

<table>
<thead>
<tr>
<th>Littoral Site</th>
<th>Exponential loss rate (ln units day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Littoral zone</td>
</tr>
<tr>
<td>Wansford bridge</td>
<td>-0.038</td>
</tr>
<tr>
<td>Wansford littoral</td>
<td>-1.417</td>
</tr>
<tr>
<td>Ferry Meadows</td>
<td>-0.061</td>
</tr>
<tr>
<td>Fotheringhay</td>
<td>-0.136</td>
</tr>
<tr>
<td>Nassington</td>
<td>-5.448</td>
</tr>
</tbody>
</table>

**Table 3.9** Potential loss rate of algal cells owing to the grazing activity of littoral populations of the River Nene.

The lowest grazing rates occurred at Wansford bridge. This may have resulted from the small size of the macrophyte bed at this site and the fact that it was probably less stable in terms of hydraulic permanence than the larger sites. The loss rates in the fringing habitats were highly variable despite the similarity in their physical structure from site to site. Nassington fringe had the highest grazing potential, primarily owing to the high density of Simocephalus vetulus, Ceriodaphnia pulchella and Chydorus sphaericus. All littoral sites, however, had a higher crustacean grazing potential than the mid-channel habitat, and so had the potential to increase grazing losses above those calculated for pelagic rotifers alone (section 3.3.8.2).

The results given in table 3.9 may underestimate the grazing impact of non-migrating animals on open-water phytoplankton populations as water exchange across the littoral / pelagic ecotone allows a greater interface between littoral grazers and phytoplankton than expected in lentic systems. The relative area of the two zones, rate of exchange between the two, and the type and density of littoral grazers dictates the grazing loss rate of pelagic phytoplankton.

The average proportion of the lowland section of the River Nene channel that was
dominated by macrophyte cover during the summer was estimated as 0.2 of total volume. The rate of water exchange between the two habitats was dependant on the flow rate and the frictional shear across their interface. This was difficult to measure, but similar measurements between retention zones and open water on the River Severn were between 0.7 - 2.0% of dead zone volume per hour (Reynolds and Glaister, 1993). These values were used to model the impact of littoral grazers in the Nene.

The littoral volume was assumed to be 20% of total river volume in the section around Wansford station, and the exchange rate was taken as 1.05% of total volume per hour. The phytoplankton exponential daily rate of change in the littoral zone at Wansford was assumed to be approximately -1.4 (table 3.9). This value was only intended as a rough estimate as it did not account for reproduction or loss rates owing to sedimentation in the littoral. The impact of grazers on pelagic phytoplankton dynamics was assessed in terms of the change in their net rate of increase, given the above conditions.

The rate of increase in the pelagial was assumed to be 0.35 d⁻¹ for a small alga during summer (optimal growth rate of 0.8, sedimentation and hydraulic loss rate of -0.45). This rate was reduced to 0.10 d⁻¹ by the impact of non-migratory littoral grazers, assuming a mixing rate between the zones of 1.05% of dead zone volume per hour. This reduction in net rate of increase was substantial and, although based on a number of assumptions, may aid the description of the lack of summer phytoplankton development given the apparent absence of alternative loss processes.

### 3.4 Discussion

#### 3.4.1 Flow characteristics of the River Nene

The annual discharge observed at Orton lock ranged from 1.4 m³s⁻¹ to 66.8 m³s⁻¹ during 1994. This was low compared to other rivers in which the plankton community has been studied. For example, discharge ranged from 28 to m³s⁻¹ 480 in the River Meuse (Gosselain et al., 1994), 28 to 50 m³s⁻¹ in the middle reaches of the River Severn (Reynolds and Glaister, 1993), 300 to 1200 m³s⁻¹ in the River Po during July and August (Ferrari et al., 1989), and 1000 to 8000 m³s⁻¹ in the River Rhine (van Zanten and van Dijk, 1994). One might therefore have expected a denser phytoplankton to develop in the Nene considering the general assumption that flow rate controls algal development in rivers (Søballe and Kimmel, 1987). This was not the case, as the density and species composition of the Nene phytoplankton was similar to other studies.
Most of the river sections noted above have larger channels than the River Nene at Wansford, so the flow velocities, the important characteristic when considering planktonic travel times and replication rate (Reynolds, 1988), were probably much more similar to those encountered at Wansford. This would explain the similarities in community composition between the rivers.

The flow velocity at Wansford ranged from 0.03 to 0.78 m s\(^{-1}\) during 1994. This cannot be directly compared to the majority of published studies as no velocities, or channel dimensions from which velocity could be back-calculated from discharge, were quoted. Bowles and Quennell (1971), however, found the critical velocity above which a potamoplankton would not develop was 0.48 m s\(^{-1}\) in the River Thames. A similar threshold of 0.51 m s\(^{-1}\) is suggested for phytoplankton development in the Nene, as chapter 2 found that cell density was rarely high when discharge exceeded 40 m\(^3\)s\(^{-1}\). (figure 2.10). This suggests that the Nene and the Thames functioned in a similar manner with regards to the effect of flow velocity on phytoplankton regulation.

The flow velocity of the Nene was below this threshold for much of the growing season, especially between mid April to mid September when no spate events occurred, and one would therefore expect the development of a planktonic community. Rather surprisingly, phytoplankton density remained low during much of the summer of 1994 when flow velocity was at its lowest. This indicates that flow mediated population regulation was not the only factor which determined the development of planktonic populations in the River Nene.

3.4.2 Fluvial habitat characterisation in the Nene

Reynolds (1992) produced a broad classification of river habitats with reference to flow velocity, relative roughness of the bed, and the shear force generated. In this classification lowland stretches of rivers were grouped into three classes depending on the level of turbulence encountered. The first were termed 'fluvial dead zones' which had a shear velocity below 0.001 m s\(^{-1}\), the second were termed 'pools' which had a shear velocity of between 0.001 ms\(^{-1}\) and 0.01 ms\(^{-1}\), and the third were termed 'flooding rivers' which had a shear velocity of over 0.1 ms\(^{-1}\).

The range of turbulent velocities encountered in the main channel of the River Nene (figure 3.13) corresponded with those of Reynolds' classification. The lowest flows produced a shear stress equivalent to the dead zone/pool type habitat, while the highest recorded flow rate during 1994 produced a shear stress associated with a river in flood. The physical characteristics of the main channel during the growing season are
described below.

**Spring**

The main channel of the river was characterised by shear velocities of between 0.004 and 0.008 ms\(^{-1}\) during spring, 1994. This level of turbulence was considered to produce 'pool' type habitats according to the classification of Reynolds (1992). Under this classification pools, with a shear velocity of between 0.001 - 0.1 ms\(^{-1}\), resembled slow flowing, often deep stretches of water, where the shear velocity was relatively low owing to the depth of the water, slow flow rate or smoothness of bed. Reynolds (1994b) associated such habitats with a plankton dominated by small diatoms. The phytoplankton of the Nene was indeed dominated by this group during spring.

**Summer**

The majority of shear stress created by summer flow rates were below 0.001 ms\(^{-1}\) and therefore produced conditions which resembled 'dead zone' habitats, after Reynolds' (1992). Reynolds (1994b) stated that such habitats were likely to develop a phytoplankton dominated by large S-selected species (Grime, 1979) such as dinoflagellates and blue-green bacteria. The phytoplankton of the Nene remained dominated by smaller forms, however, during the summer, indicating that species with fast-growth rates were more adapted even under low-flow conditions. Reynolds' classification may therefore not adequately describe the physical conditions observed in the Nene during summer. The relative scarcity of the plankton during the summer remains a mystery, as the physical conditions seemed ideal for growth owing to increased retention time, high nutrient levels and high transparency. The analysis of potential loss rates (section 3.4.7) should aid the understanding of this phenomenon.

3.4.3 Seston concentration and light limitation

Seston concentration in the Nene increased with discharge indicating the importance of abiogenic sediment carriage rather than algal production. Figure 3.15 showed that the low Secchi depths recorded in the winter and early spring were predominantly the product of light scattering by non-algal particles. Suspended sediment concentrations were sufficient to restrict the euphotic zone to less than the river depth during the winter and spring of 1994. Phytoplankton growth was therefore potentially light-limited at these times, but unlikely later in the growing season.

Reduced light attenuation is expected to favour diatoms, as they are more adapted to
growth at low light intensity than green algae (Reynolds, 1984). This may help to explain the observed shift in dominance from diatoms in the spring to green algae in the summer, when the euphotic zone reached full depth.

The light climate may be of importance in dictating phytoplankton production and community composition in rivers. For example, Reynolds et al., (1994) argued that the similarity between shallow lake and riverine phytoplankton assemblages was owing primarily to the constraints imposed by a similar light climate, often dominated by high and fluctuating sediment content. Reduced retention time may therefore not be the only factor which constrains the phytoplankton of river habitats.

3.4.4 Nutrient levels

Total phosphorus concentrations in the Nene were indicative of a eutrophic system able to support algal blooms during favourable conditions of flow and turbidity (Kiss, 1987). The Clyde RPB considered a monthly mean value of 0.30-0.40 mg l\(^{-1}\) during the vegetative season as a tentative standard, above which eutrophication effects in rivers were expected. This value was exceeded in the River Nene at Wansford, as was the limiting concentration of 0.10 mg l\(^{-1}\) for plant growth in rivers (Mackenthun, 1973).

Soluble reactive phosphorus concentrations remained above the half saturation concentration (0.001 to 0.05 mg P l\(^{-1}\) (Pöhlmann et al., 1989 in De Ruyter van Steveninck et al., 1992)) for algal growth throughout 1994, and above 0.20 mg l\(^{-1}\) S.R.P., the annual mean S.R.P. concentration expected to produce communities typical of eutrophic systems within rivers. No phosphate limit to algal growth was therefore expected at any point throughout the year.

Nitrogen does not usually limit phytoplankton production in freshwater systems, and was unlikely to be limiting at the levels recorded in the River Nene which were above those associated with eutrophic conditions in lakes (Wetzel, 1983). Nitrogen is more soluble than phosphorus, and is readily leached into rivers, especially from agricultural land that has been subject to fertiliser application (Moss, 1988; Haslam, 1990). The catchment of the lower River Nene is heavily farmed, and so the high nitrogen levels in the water are not particularly surprising.

Seasonal changes in the N:P ratio may have forced community level responses (Reynolds, 1984). The falling ratio in summer, 1994 (figure 3.17) was expected to favour the growth of nitrogen fixing cyanobacteria if nitrogen was limiting. This did not occur in the river, thus indicating that non-limiting levels were present.
The high nutrient concentrations often found in rivers result from the degree of association with terrestrial nutrient sources (De Ruyter van Steveninck et al., 1990). Elevated nutrient concentrations are, however, seldom converted to increased algal biomass in rivers as shown by chapter 2.

3.4.5 Phytoplankton composition

Diatoms, especially Stephanodiscus spp., were the dominant algae in the Nene during spring. These species have rapid life history and good light gathering apparatus which make them particularly successful when discharge is relatively high but light climate poor. They became less abundant towards the end of spring when discharge decreased, presumably owing to increased sinking rates from shallow, less turbulent waters.

Small green chlorococcan algae became the dominant group in the summer as they were less susceptible to settlement loss but maintained high growth rates in unlimiting nutrient concentrations. This seasonal shift from one fast-growing group to another was also noted by Descy (1987) in the Meuse. He noticed that the diatoms became abundant once again during the autumn as discharge increased and the light climate deteriorated. This did not happen in the Nene, as discharge remained low until the end of the year, except for short-lived spate events.

The importance of discharge mediated control of river phytoplankton was shown by the diatom / green shift, and the size-structure of the phytoplankton, as the majority of cells had an estimated biovolume of less than 5,000 μm³, indicating that a small size was a favourable trait of riverine forms. This feature relates to the ability to remain in suspension in shallow columns as shown by the dominance of group 1 cells during the summer, and also the ability to replicate rapidly. The larger volume cells that may come to dominate summer periods in standing waters (Sommer et al., 1986) were largely absent from the river plankton, presumably because their growth rates were too low to match the losses from downstream removal and settlement.

The persistent dominance of small r- selected species (MacArthur and Wilson, 1967), or scramble competitors, required that conditions were disturbed on a regular basis to maintain their advantage over contest competitors (K- selected species). If conditions remained relatively undisturbed, as in deep lakes, the latter group would become dominant as resources became limiting. The intermediate disturbance hypothesis of Connell (1978) was cited by Padisák and Dokulil (1994) as the mechanism whereby r-selected species maintained prolonged periods of dominance in shallow mixed lakes. This hypothesis is equally valid in rivers as they are not only disturbed by frequent...
degeneration in light climate (optical winters, Reynolds et al., 1994) but also frequent physical removal owing to high-flow events, both of which may 're-set' the natural biological succession back to an early spring level.

Constantly fluctuating discharge maintains the desired level of disturbance required to favour the fast growing species typical of lowland rivers. The level of disturbance is important, as too much will preclude any development (even the fastest growing species require a number of hours to complete a life cycle under favourable conditions), while too little would lead to the development of contest competition and the dominance of 'net' species typical of oligotrophic lakes during the summer (Sommer et al., 1986), assuming an undisturbed low discharge.

The River Nene phytoplankton composition was similar to that described by Descy (1987) as typical of large lowland, nutrient-rich rivers such as the Meuse (Descy, 1987; Gosselain et al., 1994), the Rhine (De Ruyter van Steveninck et al., 1990; De Ruyter van Steveninck et al., 1992; Admiraal et al., 1994; Tubbing et al., 1994), the Thames (Lack, 1971), the Spree (Köhler, 1994), the Vistula (Kowalczowski et al., 1985), the Danube (Kiss, 1987; Schmidt, 1994), the Seine (Billen et al., 1994; Garnier et al., 1995) and the Severn (Reynolds and Glaister, 1993). These rivers all developed a phytoplankton dominated by centric diatoms (genera Stephanodiscus and Cyclotella) and Chlorophyceae (mostly Chlorococcales). Maximal densities during peaks were usually between 10,000 to 100,000 cells ml⁻¹, which corresponded to a chlorophyll 'a' concentration of between 50 and 200 μg l⁻¹. The similarities in the density and composition of river plankton from such diverse sources once again indicates the importance of physical control, mediated by discharge, in these systems.

3.4.6 Temporal distribution of blue-green bacteria

A number of studies of nutrient rich lowland rivers have found blue-green bacteria in the potamoplankton. It is generally considered that such slow-growing species favour slow flowing areas of the river which have little connection with the main channel (Reynolds, 1992) or riverine reservoirs (Gosselain et al., 1994). Such conditions usually occur when low flow rates dominate, hence the presence of most cyanobacterial taxa during late summer in the River Nene.

The most abundant cyanobacterial taxa was Oscillatoria sp., (now referred to the genera Limnothrix and Planktothrix) a relatively disturbance-tolerant taxa. This group possesses adaptations that equip it for development in shallow riverine habitats, where the light climate may be poor. Firstly, it has a large surface area to volume ratio, and a
relatively high maximum growth rate of 0.8 at 20°C (Reynolds, 1984). Secondly, it has
the ability to increase its growth efficiency by raising cell-carbon-specific chlorophyll
'\textit{a}' and accessory pigment content when the light climate dictates (Reynolds, 1994a).
Thirdly, zero buoyancy reduces the chances of settlement loss from shallow water,
while constant mixing ensures that cells are quickly moved from inhibiting light
concentrations.

Two distinct groupings of cyanobacteria were noted in the Nene, those that were
abundant throughout the spring, namely \textit{O. limnetica}, and those that were transient
during summer spates, for example \textit{O. agardhi} and \textit{O. redekei}.

The presence of \textit{O. limnetica} for protracted periods during the spring indicated that this
species was more capable of development under riverine conditions than either \textit{O. agardhi} or \textit{O. redekei}. It most likely developed in dead zones with increased retention
times and better light climate than the main channel, from which cells were constantly
imported to the main channel via water exchange. The persistence of this species
indicated a degree of pre-adaptation to riverine conditions not found in other species of
the genera.

The late summer taxa quickly disappeared from the mid-channel plankton, indicating
that they were washed from stable dead zones, into the main channel, and then rapidly
removed downstream without significant reproduction. The long period of low flows
during the summer of 1994 presumably provided suitably stable conditions in certain
dead zones for their development. It was noteworthy that they were not recorded in
significant numbers during spate events after September, presumably because there was
insufficient time, or physical stability within the dead zones, to allow populations to
develop. The presence of such typically lacustrine blue-green bacteria in the
potamoplankton may be partly dependant on the stability of dead zone habitats and their
frequency of flushing.

Schmidt (1994) considered blue-green bacteria that were washed into the main channel
of the River Danube to be of allochthonous origin, even though they originated from
small side-arm habitats, because they showed no increase in cell number once in the
open river habitat. Köhler (1994) found a similar rapid downstream decrease in cell
density of cyanobacteria that were washed into the River Spree from impoundments.
He proposed that these 'summer' species were ill-adapted to life in rivers, as they
developed in stable conditions (see also Stoynева, 1994). They were therefore unlikely
to be able to adapt to the exacting conditions imposed by flowing waters which
necessitated a rapid life-history and efficient light harvesting capabilities.
It is therefore conceivable that dead zones act in two distinct ways during spring and summer depending on their physical structure. In the spring, when dead zones have a similar structure to the river and a considerable exchange of water with the main flow, the conditions are more suitable for the development of fast growing, 'riverine type' algae, which may increase in number in the main channel. Under such circumstances, the dead zones act as a source of riverine algal populations to the main flow.

In the summer, however, the majority of dead zones may be more stable owing to reduced water exchange with river flows and therefore develop $K$-selected species in favour of typical riverine forms. Any $r$-selected algae transported into dead zones are therefore lost as conditions are not favourable for their growth, whereas any algae exported from dead zones into the river are similarly lost as the true river habitat is not suitable for their growth. In terms of the mid-channel populations, the dead zones therefore act as a sink for truly $r$-selected species during the summer. This hypothesis may help in the explanation of the low algal levels in the Nene during the summer, when hydraulic, settlement and grazing losses did not seem to balance net losses.

### 3.4.7 Estimated loss rates and algal dynamics

The potential daily loss rates of phytoplankton cells from the Wansford section of the river owing to settlement, grazing, and hydraulic removal were estimated on a monthly basis during 1994 and presented in table 3.10. This type of analysis was intended to allow a better overall understanding of the control mechanisms influencing riverine algal abundance.

Hydraulic removal represented the greatest source of loss throughout the year, and was therefore assumed to have a major influence on riverine plankton development. A similar view is held by Gosselain *et al.*, (1994) in the River Meuse and Schmidt (1994) in the River Danube who noted a decrease in plankton abundance with increased discharge. It should be noted, however, that this relationship may also have been the product of reduced growth rates owing to increased turbidity.

Settlement losses were relatively low compared to hydraulic losses for most of 1994, but may have had an impact during the summer period, especially on larger cells, when water depth and turbulent flow decreased. The loss rates presented in table 3.10 were calculated assuming a small particle with a low sinking velocity typical of the river phytoplankton. Particles with higher velocities would have been subject to increased loss rates, and may have been significantly disadvantaged during the summer months. Figure 3.22 showed that the dominant algae during the summer, in terms of cell
number, were the small chlorophytes which had a sinking velocity of less than 4 μm s⁻¹ (categories I and II by the definition given in section 3.2.3.1) and *Rhodomonas sp.* a motile group with the ability to offset settlement by active movement. The lack of larger groups potentially indicates that settlement loss represented a control mechanism of phytoplankton composition in the River Nene, especially as the higher retention times of summer should have favoured the development of larger, slower growing species.

<table>
<thead>
<tr>
<th>Month</th>
<th>Hydraulic removal</th>
<th>Settlement</th>
<th>Grazing</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>-5.74 (-3.03)</td>
<td>-0.11 (-0.006)</td>
<td>-0.001</td>
<td>-5.848</td>
</tr>
<tr>
<td>February</td>
<td>-3.91 (-2.29)</td>
<td>-0.11 (-0.006)</td>
<td>-0.001</td>
<td>-4.024</td>
</tr>
<tr>
<td>March</td>
<td>-2.88 (-0.90)</td>
<td>-0.12 (-0.004)</td>
<td>-0.002 (-0.001)</td>
<td>-3.000</td>
</tr>
<tr>
<td>April</td>
<td>-2.92 (-1.71)</td>
<td>-0.12 (-0.006)</td>
<td>-0.008 (-0.006)</td>
<td>-3.046</td>
</tr>
<tr>
<td>May</td>
<td>-1.70 (-0.42)</td>
<td>-0.13 (-0.005)</td>
<td>-0.055 (-0.045)</td>
<td>-1.883</td>
</tr>
<tr>
<td>June</td>
<td>-0.75 (-0.16)</td>
<td>-0.14 (-0.004)</td>
<td>-0.006 (-0.004)</td>
<td>-0.899</td>
</tr>
<tr>
<td>July</td>
<td>-0.62 (-0.12)</td>
<td>-0.15 (-0.003)</td>
<td>-0.001 (-0.0002)</td>
<td>-0.768</td>
</tr>
<tr>
<td>August</td>
<td>-0.50 (-0.09)</td>
<td>-0.15 (-0.003)</td>
<td>-0.001 (-0.001)</td>
<td>-0.653</td>
</tr>
<tr>
<td>September</td>
<td>-1.68 (-1.65)</td>
<td>-0.13 (-0.008)</td>
<td>-0.001 (-0.001)</td>
<td>-1.809</td>
</tr>
<tr>
<td>October</td>
<td>-0.87 (-0.49)</td>
<td>-0.14 (-0.005)</td>
<td>-0.001</td>
<td>-1.011</td>
</tr>
<tr>
<td>November</td>
<td>-1.92 (-1.11)</td>
<td>-0.13 (-0.007)</td>
<td>-0.001</td>
<td>-2.046</td>
</tr>
<tr>
<td>December</td>
<td>-2.45 (-1.55)</td>
<td>-0.12 (-0.006)</td>
<td>-0.001</td>
<td>-2.571</td>
</tr>
</tbody>
</table>

Table 3.10 Estimated loss rates of phytoplankton cells from the main river at Wansford during 1994. Hydraulic removal assumed no importation of cells from upstream. Settlement losses assumed a particle with sinking rate of 4.8 μm s⁻¹. Grazing rate calculated from average rotifer density assuming an individual filtration rate of 5 μl l⁻¹ hr⁻¹ and a density of 11 rotifers per litre during winter months. Standard deviations in brackets.

The removal of phytoplankton cells by pelagic grazers had the smallest impact on phytoplankton populations of all loss processes considered. This was owing to the low density and small individual size of the zooplankton, which was dominated by rotifers. The magnitude of the losses were unlikely to impact on populations with even a modest growth rate unless grazing was concentrated on specific groups. This may have occurred in the Nene during May when *Synchaeta* were dominant, as these animals are known to be specialist feeders on small diatoms (Dumont, 1977). Grazing losses were probably concentrated on this group and may have played a role in forcing the reduction of diatoms (notably *Stephanodiscus hantzschii* and other small centric forms) during the spring, although silica depletion may also have been involved (Gamier et al., 1995).

The lack of an efficient pelagic grazing community was implied by the size distribution of algal groups, the majority of which had an effective diameter of less than 5 μm, and were assumed to be generally suitable for ingestion by rotifers, although the influence
of short residence time, favouring fast growing small species, would also produce a similar result.

Pelagic grazing losses are usually considered to outweigh sedimentation losses during summer in both lakes (Reynolds, 1984) and in rivers (Billen et al., 1994; Descy and Gosselain 1994; Garnier et al., 1995). The findings of this study are therefore in direct contradiction to previous work, principally as a result of low grazing zooplankton density. The lack of an obvious form of top-down control, and the high nutrient concentrations, indicate that other factors were involved in suppressing algal populations during the summer. De Ruyter van Steveninck et al., (1992) found similarly low grazing impacts in the River Rhine, but stated that rates may be increased by the inclusion of benthic filter feeders. No data were available on the density of this group of animals in the Nene.

The dominant loss process considered was the potential for downstream displacement of algae by flowing water. No inputs were assumed when calculating these rates, so they relate to the absolute dilution loss that must be balanced via replication or importation if a population is to be maintained. The loss rates were found to be too high to be maintained by natural rates of replication alone for most of the year. The maintenance of a self-perpetuating population was considered possible during June, July and August when the daily exponential loss rates were below -1.0, but unlikely to occur at any other time of the year without substantial inputs from other sources.

The only period when algal populations in the Nene showed a marked increase in density was during spring. The assumed maximum rates of algal replication (section 3.2.4) were much smaller than those required to maintain the observed rates of increase at this time. This indicated that a substantial importation was received during the spring period, as was described in section 3.2.3.4. Without this constant inoculum from upstream, or imports from dead zones within the section, plankton development would have been an impossibility owing to high loss rates.

The role of dead zone imports was assumed to be critical to the maintenance of a potamoplankton at this time. The relatively high discharge should have allowed a significant exchange of water between such zones and the main channel, while the physical similarity caused by the exchange should have ensured that dead zones developed a phytoplankton suited to, and therefore able to reproduce in, riverine conditions. This may not have been the case in summer when many dead zones may have been suitably stable to develop a phytoplankton dominated by cyanobacteria.
**Low summer density**

The summer / autumn period of 1994 had the lowest estimated loss rates (table 3.10) and hence the lowest net rate of increase required to maintain a plankton. It does not seem unreasonable to expect mid-channel chlorophyll 'a' levels to develop under such conditions, assuming that growth rate was not severely limited by another factor. No nutrient limitation was obvious during the summer (figure 3.17), light penetration was good (figure 3.16) and there was little grazing impact from pelagic zooplankton (table 3.6). The lack of chlorophyll 'a' development during the summer therefore poses an interesting question.

Chlorophyll 'a' concentration did not increase with downstream transport during the summer months (section 3.2.3.4). This indicated that there was no net algal increase in the main channel, a fact that was confirmed by the lack of development at Wansford from week to week. Net loss rates in the section were therefore considered to equal net growth rates. The actual loss rates were lower than those given in table 3.10, because no hydraulic loss was encountered as a result of a similar concentration of chlorophyll 'a' being imported with inflowing water, as described in section 3.2.3.4. The lack of biomass development indicates that algal growth was limited by some, as yet unidentified factor. Alternatively, the analysis may have overlooked a further source of loss such as the effect of littoral or benthic grazers (see below), or even less obvious causes such as UVB damage.

**3.4.8 The source of imports to the main-channel community**

A constant supply of cells to the main channel from dead zones seems vital to plankton development in the River Nene (Reynolds, 1988; Reynolds, 1994b; Reynolds and Glaister, 1994). The extent of this input relies upon the discharge, which dictates the size and permanence of zones, the rate at which cells are washed into the main channel, and the density of cells in the zones. Considering the vast diversity of flow zones in semi-natural river channels, export from dead zones to the main channel may act as the constant source of cells needed to explain the development of river plankton during the spring. This source may only be viable as long as growth conditions and discharge remain within certain limits, *i.e.* the flushing time of the zone must be longer than algal generation times (allowing net growth) and the discharge must be sufficient to continually flush a portion of this production into the main channel.

The importance of constant dead zone exports during the spring becomes obvious when one considers the variable hydraulic loss rates encountered at Wansford over this
period. Discharge ranged from 2.7 to 40.0 m³s⁻¹, which corresponded to hydraulic loss rates of -0.63 to -7.67. No phytoplankton group has the ability to match these loss rates by *in situ* growth alone, therefore some level of importation was required to maintain a viable plankton population. If none was available, wide fluctuations in chlorophyll 'a' concentration at Wansford would have occurred, and this was generally not the case.

A number of authors have come to a similar conclusion *i.e.* that dead zones, or 'retention zones', play an important role in the maintenance of riverine plankton populations (Hynes, 1970; Jones and Barrington, 1985; Reynolds, 1988; Moss *et al.*, 1989; Reynolds and Glaister, 1993; Stoyneva, 1994). Padisák and Dokulil (1994) also noted the potential for littoral habitats to harbour dense algal populations which act as a source of plankton to open water habitats in shallow lakes. Quantitative evidence of dead zone function is still, however, lacking.

### 3.4.9 Littoral grazers

The grazing potential of littoral zooplankton should not be overlooked when estimating the losses of pelagic phytoplankton populations, especially when the littoral zone is well developed as was the case in the River Nene. It is therefore possible that littoral grazers had an impact on phytoplankton density in the summer.

The grazing losses within the littoral zones of the Nene were found to be between -0.04 to -5.45 which were above the potential growth rate of most algal species, indicating that the grazers could potentially force the decline of palatable species within the zone. These loss rates proved to be more influential than settlement losses which were approximately -0.15 during the summer of 1994.

The potential for littoral grazers to impact on pelagic phytoplankton populations depends on the degree of contact between the two. This contact may be attained by the horizontal migration of littoral species into the pelagial during the dark to feed on the relatively abundant algal food source with a reduced chance of being visually predated. Such horizontal migrations were described by Timms and Moss (1984), Davies (1985), Lauridsen and Buenk (1996), and Lauridsen *et al.*, (1996), whereby large crustaceans migrated into the littoral zone during daylight hours to avoid visual predators (Castonguay and FitzGerald, 1990; Vuille, 1991) and out into open water to feed at night.

Whether or not littoral forms undergo diel horizontal migrations seems to depend on the
ecology of the particular species. Taxa that are found freely swimming amongst macrophytes such as *Ceriodaphnia* spp. are more likely to undergo night-time migrations into open water, whereas those that are highly associated or physically attached to macrophytes such as chydorids, certain cyclopoid copepods, *Sida* spp. and *Simocephalus* spp. are less likely to migrate (Fairchild, 1981; De Meester *et al.*, 1993; Paterson, 1993).

The pelagic grazing losses associated with species that perform diel horizontal migrations in the Nene were generally less than -0.01 d⁻¹, and as such were considered to have relatively little impact on open water phytoplankton dynamics. The losses were more significant, however, when water exchange between the littoral and pelagic zones was considered as the mechanism allowing contact between grazers and open water phytoplankton.

The level of impact was dependant on the rate of exchange and the clearance rate within the littoral zone, with a predicted decline of palatable species growth rate from 0.35 to 0.10 d⁻¹ during summer. Few studies have previously considered the effects of littoral grazers when describing the spatial and temporal changes in phytoplankton concentration in rivers, probably owing to the fact that most low-flow areas are usually considered as source areas of riverine plankton (Reynolds, 1988). This may be the case when low-flow areas are dominated by open water, but when they are covered with dense macrophyte growths which harbour littoral grazers their role in river ecology may differ, acting as sinks for phytoplankton owing to the grazer loss rates imposed.

The River Nene has extensive littoral growth along its semi-natural banks between Northampton and Peterborough, sometimes reaching up to 4m in width. Such elongated structures provide a relatively large interface over which water exchange can occur, and as such, offer a relatively large potential sink for the small grazeable algae which dominate the main channel during the summer. Littoral vegetation only develops during late spring when conditions become favourable for growth. This source of loss may therefore only be apparent during the summer months and may contribute to the low phytoplankton density observed during the summer of 1994.

Schriver *et al.*, (1995) found clearwater conditions in macrophyte beds of Lake Stigsholm, Denmark, owing to the impact of littoral grazers. They concluded that the littoral zone had to cover between 15-20% of the lake area, and fish biomass had to be small (< 2 individuals m⁻²), for littoral zooplankton to have a significant top-down effect on pelagic phytoplankton abundance. The large littoral area and the degree of water exchange between open and littoral zones in rivers may increase the impact of
littoral grazers above that of lakes.

The methods used to model the potential loss rates were necessarily based on a number of assumptions, and as such were not intended in a strictly quantitative sense. This would require further work on the grazing preferences and clearance rates of littoral species and water exchange rates. The results do, however, indicate the potential for littoral grazers to influence the phytoplankton density of open waters.

3.5 Summary

The phytoplankton composition of the Nene was similar to other lowland European rivers. Small-celled species were dominant, especially diatoms and green algae, although motile forms were also present during the summer months when depth was decreased. Larger, slower growing species, such as the blue-green bacteria, were restricted to dead zones during the summer, and only appeared in the main channel after being 'washed-out' with rising water. Oscillatoria limnetica was slightly different as it was present in the plankton during spring.

Calculated loss rates showed that hydraulic dilution was the dominant limiting factor to plankton development, although high sinking rates of large, heavy cells may have also been restrictive in the relatively shallow river depths. Dilution losses were considered to be prohibitive without a constant importation of cells from upstream or from dead zones along the length of the river. They were assumed to be particularly important to the spring development which occurred at relatively high discharge. The situation was different in the summer as the combined loss rates were potentially lower than growth rates. The lack of biomass development indicated that either growth rates were inhibited, or the loss rates were higher than expected, possibly owing to the impact of littoral grazers.


1. Low temperatures and poor light climate preclude substantial algal growth in dead zones during the winter months. High discharge quickly moves algae downstream before biomass can accumulate mid-channel.

2. Increased temperature and light leads to algal development in dead zones. Hydraulic
loss rates associated with mid-channel habitats remain in excess of potential rates of increase unless substantial imports received.

3. Relatively high and fluctuating discharge leads to the 'cropping' of dead zone production in exchange for nutrient rich water. Dead zones may be considered as free flow chemostats when viewed in this light, with their output and internal biomass related to the rate of fluid exchange. They may not have substantially greater algal biomass than that recorded in the main channel as they are constantly having their production exported to the main channel.

4. Diatoms dominate in the spring when flow rate remains sufficient to mix water within dead zones and therefore reduce settlement losses.

5. Diatom dominance lost at end of spring when water depth decreases leading to higher settlement losses, preferential grazing losses from rotifers and possible silica depletion. Small green algae become dominant owing to their short life histories and lower sinking rates. 'Net' algae fail to develop in the main channel owing to slow rates of increase.

7. Chlorophyll 'a' levels remain low during the summer although growth rates may potentially exceed loss rates. The reasons for this lack of biomass accumulation deserve further study but could include further loss rates such as parasitic control (Garnier et al., 1995) or benthic / littoral grazing (Testard, 1993; De Ruyter van Steveninck et al., 1992; Garnier et al., 1995). The low algal biomass may also partly result from the functional separation of dead-zones from the main flow owing to decreased rates of fluid exchange across their boundary and the impact of littoral grazers.

8. The export of cyanobacteria to the main channel with increased flow after a long period of low discharge indicates that some dead zones become stable enough to support the development of blue-green bacteria. Such bacteria quickly decrease in abundance once washed in to the river.

9. The system returns to low chlorophyll 'a' abundance when the discharge increases sufficiently to raise loss rate above growth rate in the main channel, and temperature drops sufficiently to reduce growth in the dead zones.
CHAPTER 4
THE ZOOPLANKTON OF THE RIVER NENE

4.1 Introduction

The faunal component of the freshwater plankton is termed the zooplankton. Its main constituents are protozoans, rotifers and crustaceans. In general, body size increases from Protozoa (typically 10 - 100 μm) through Rotifera (50 - 500 μm) to Crustacea (300 - 5000 μm). Rotifers and crustaceans are considered to account for the majority of zooplankton productivity in fresh waters (Wetzel, 1983) although protozoans may become much more important under certain circumstances, for example in Lake Dalnee, USSR (Sorokin and Paveljeva, 1972).

Most rotifers are less than 1 mm in length, for example Keratella cochlearis which typically attains an adult size of less than 320 μm. There are over 1800 species of rotifer, the majority of which only occur in freshwater habitats. Their name is derived from the rotating 'wheel' of cilia around the mouth which induce feeding currents and aid locomotion. The cuticle may be thickened to form a lorica, or hard shell, which may be drawn out into projections that are useful as an anti-predator defence in some species. Approximately 30% of genera are planktonic, living constantly or occasionally in the open water. Most of the planktonic forms are members of the order Monogononta.

The crustacean zooplankton of freshwaters comprises cladocerans, cyclopoid and calanoid copepods. The majority have larger adult size than rotifers although some juvenile stages may be smaller. Cladocerans have a carapace that covers the body in most genera, although this is lacking in the predatory genera. The group includes herbivorous genera such as Bosmina and Daphnia, along with some carnivorous forms including Leptodora and Polyphemus, which are raptorial feeders. Copepods have a longer pre-adult development period than the predominantly parthenogenetic rotifers and cladocerans, and must undergo ten or eleven successive moults before reaching a sexually mature stage. The generation time of these animals is therefore far in excess of the other planktonic zooplankton groups.

4.1.1 River zooplankton

The same pressures which select 'successful' river phytoplankton will also act upon the pelagic zooplankton community, namely the reduced retention time of the system compared to that of most large standing waters.
A wide diversity in life history strategies and potential maximum rates of population increase exist within the zooplankton. The following section introduces the different reproductive strategies used by the Rotifera, Cladocera, and Copepoda.

4.1.2 Modes of reproduction

Three major groups of metazoans are found in the truly pelagic zooplankton of freshwaters; the rotifers and two subclasses of the Crustacea, the Cladocera and Copepoda.

4.1.2.1 Rotifera

The reproductive life history of typical planktonic rotifers is characterised by a large number of generations in which reproduction is parthenogenetic. With parthenogenesis, amictic (diploid) females produce genetically identical amictic eggs by mitosis which develop into further amictic females (clones). The eggs are usually large compared to females and the animals are born with the same number of cells as the adult (eutely). The development of the egg stage and juvenile stage (generation time) is rapid under favourable conditions (Walz, 1993a), and without the need for sexual reproduction, populations may develop in 2 to 5 days (Wetzel, 1983). There may be as many as 40 amictic generations before environmental conditions deteriorate sufficiently to cause the onset of sexual reproduction, and the development of resting eggs.

Mictic (sexual) females are produced under times of stress (often resulting from density dependent factors (Hutchinson, 1967)) which then produce mictic eggs via meiosis. Mictic eggs develop into males if unfertilised and rapidly reach maturity at a smaller size than females. They then begin to fertilise other mictic eggs. The small size of adult males increases their chance of reaching maturity by reducing their food requirements for growth, a feature that is of adaptive significance considering their appearance in the plankton at times when food supply is often limiting (this applies equally to male cladocerans, Romanovsky, 1984). Fertilised mictic eggs develop into thick walled encysted embryos which can lay dormant in sediments until conditions once again improve (May, 1987). Resting eggs always give rise to amictic females, leading to a pulse of parthenogenetic reproduction and a rapid increase in population numbers, a feature for which the rotifers as a group are noted (Walz, 1993d). Hatching from resting eggs may be a very important source of animals in spring and is characterised by a higher rate of increase than birth rate dictates (for a review see Sommer et al., 1986). The production of resting eggs may be more important for
populations that inhabit periodically inhospitable environments such as rivers.

Figure 4.1 Typical rotifer life history

4.1.2.2 Cladocera

Cladocerans have a similar parthenogenetic mode of reproduction to rotifers as long as conditions remain favourable. Females produce broods of eggs by mitosis which develop into further parthenogenetic females without the need for sexual reproduction. The brood size is usually larger than that of rotifers, up to 40 eggs in the larger Daphnia species, and is variable within a species (Hutchinson, 1967). The absolute size of the brood is controlled by food availability, with higher food densities supporting larger broods. Temperature controls the developmental rate of embryos and juveniles (Vijverberg, 1989) just like the rotifers, and so these two parameters, food and temperature, are primarily involved in determining the potential growth rate of populations (Threlkeld, 1987).

Parthenogenetic reproduction continues until males are produced, whether physically induced by temperature, drying, or day length changes, or biotically induced by crowding effects. Sexual females produce haploid eggs at such times which, if fertilised by a male, become enclosed in an ephippium of heavily melanised cuticular material protecting them through unfavourable periods. The ephippial eggs lay
dormant until conditions once again become favourable for development into parthenogenetic females after some period of freezing, drying or anaerobiosis (Threlkeld, 1987).

![Figure 4.2 Typical cladoceran life history](image)

Cladocerans have a longer pre-reproductive development period than rotifers. For example, *Daphnia* have an average of 8 distinct stages of egg development which may take upwards of 3 days to complete, and then a further 4-8 juvenile moults before becoming reproductive. The actual number of moults and the time between each varies greatly throughout the cladoceran group, for example *Bosmina* generally have two pre-adult moult compared to 4-8 in *Daphnia*. The greater generation time of the cladocerans compared to the rotifers reduces their ability to develop populations quickly, but their increased investment in reproduction once mature allows them to attain high growth rates.

4.1.2.3 Copepoda

Reproduction in both cyclopoid and calanoid copepods is obligatory sexual. Adult males transfer a spermatophore to the females during copulation which she carries until it is used to fertilise her eggs anything up to several months after the initial
transfer. Calanoids carry fertilised eggs in single sacs whereas cyclopoids carry double sacs attached to the abdomen. The number of eggs produced per brood is again dependant on food availability, with between 1 to 30 produced by calanoids and up to 72 by cyclopoids (Hutchinson, 1967; Wetzel, 1983). The pre-adult development period is much longer in the copepods than the parthenogenetic rotifers and cladocerans. There are six naupliar stages and then a further five copepodite stages before the sexually mature sixth stage copepodite is reached. Carter (1974, in Wetzel, 1983) found the shortest generation time of Diaptomus inhabiting a shallow pond was four weeks.

Adaptation to unfavourable conditions is via resting eggs in the calanoids, whereas the cyclopoids enter diapause at various developmental stages.

4.1.3 Zooplankton life history strategies

Most species of zooplankton have a limited ability to swim against a current and even if they were able to maintain a mid-channel position, their energetic needs would seriously reduce their fitness. A more plausible explanation for the existence of a riverine zooplankton is the utilisation of reduced flow dead zones in a similar way to that described for riverine phytoplankton above. Some zooplankton may show a level of behavioural adaptation to exploit such habitats, for example by locating in littoral areas (Brown et al., 1989; Richardson, 1991; Richardson, 1992) to minimise the chance of downstream movement, but there will also be a harsh selection pressure for those species with rapid life history characteristics, as with the phytoplankton.

Table 4.1 shows two life history traits of potential importance to riverine zooplankton, the maximum daily rate of population increase ($r_{\text{max}}$ d$^{-1}$) and the threshold food concentration for population growth. The values are taken from the literature and are by no means exhaustive, but the table serves to indicate the diversity of life histories present both between and within groups.

There is a diversity of $r_{\text{max}}$ values within all three groups, although substantial overlap occurs between the rotifers and cladocerans. The average $r_{\text{max}}$ value for rotifers, cladocerans and copepods is 0.52, 0.31 and 0.25 respectively. The difference between the three groups is not particularly high, these values correspond to doubling times of 1.33, 2.24 and 2.77 days respectively, but indicates that, in general, the rotifers have the greatest potential to maintain populations in the face of constant dilution by unidirectional flows.
<table>
<thead>
<tr>
<th>Species</th>
<th>Max. growth rate (in units day(^{-1}))</th>
<th>Threshold food level (mg C l(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rotifers</strong></td>
<td></td>
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<tr>
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</tbody>
</table>

The highest $r_{\text{max}}$ value recorded for any metazoan was for the rotifer *B. calyciflorus* (Bennet *et al.*, 1993) of 1.85, which translates into a doubling time of 0.38 days, a similar value to $r$-selected algal species. The highest $r_{\text{max}}$ for a cladoceran found in the literature was that of *Moina brachiata* with an $r_{\text{max}}$ of 0.86 (Romanovsky, 1985) (doubling time of 0.81 days). This comparison indicates that rotifers have the greatest potential for rapid population development, but does not preclude the development of certain cladocerans in slow flowing rivers or dead zones. Calanoids should not be neglected simply because of their slow rates of development, as they have increased ability to swim against a current and have been recorded in number from many rivers (Reif, 1939; Richardson, 1991; 1992).

4.1.4 Selection of suitable life history strategies for rivers

4.1.4.1 Which zooplankton groups are expected to dominate in rivers?

Cladocerans generally possess more $K$-selected life-history characteristics compared to rotifers, including lower threshold food concentrations for development, lower maximum growth rates, and increased resistance to starvation (Romanovsky, 1984; 1985). Under the $r/K$ classification of MacArthur and Wilson (1967), cladocerans are the superior competitors when conditions are stable (contest competitors) as they can deplete food levels below the higher thresholds of the rotifers. The rotifers however have the advantage of rapid population growth rates under favourable conditions and so may develop in numbers before the cladocerans, (scramble competitors). This pattern has been observed in the zooplankton seasonal dynamics of a number of temperate lakes (Sommer *et al.*, 1986), where rotifers were the first group to respond to the spring diatom peak, but rapidly became displaced by larger cladocerans in a matter of weeks.

$R_{\text{max}}$ strategists are particularly successful in frequently disturbed habitats where equilibrium conditions are seldom achieved such as rivers. Townsend and Hildrew (1994) described rivers as highly disturbed habitats with little temporal stability. The intermediate hypothesis of Connell (1978) has also been used to describe the continued dominance of $r$-selected species in rivers, where fluctuating discharge constantly re-sets any moves to a sub-climax community structure, except perhaps during extended periods of low flows in large lowland rivers.

The adaptive strength of rotifers in disturbed habitats is a product of their short development times and high growth rates. Species with short generation times are able to increase in number even in the face of rapid dilution losses. *Brachionus*
angularis, for example, was able to maintain a population in a habitat with a flushing time of 2.8 days (Walz, 1993b; 1993c). This fact alone allowed the rotifers to attain rapid population development under favourable conditions (high saturating food levels), not the ultimately reached growth rate of the group. The cladocerans can attain high $r_{\text{max}}$ through the production of large broods later in life, but this takes longer to achieve owing to their extended juvenile development period. The minimum residence time required for cladocerans to maintain a population was found to be between 8-14 days, substantially longer than rotifers (Walz, 1995). They are therefore more likely to be washed downstream before completing a generation, and are therefore less suited to life in rivers than rotifers.

4.1.4.2 Are all rotifers equally suited to life in rivers?

A continuum of life history strategies exists within the Rotifera which is generally correlated with body size. Stemberger and Gilbert (1985) described the log-log least squares regression line for the relationship between $r_{\text{max}}$ and individual dry mass of eight rotifer species as $r_{\text{max}} = 1.019 \cdot M^{0.381}$ (where $M$ was rotifer body mass as $\mu g$ ind.$^{-1}$) (figure 4.3). There was a similar relationship for threshold food concentration and mass, described by $T = 1.824 \cdot M^{0.832}$ (where $T$ is the threshold as $\mu g$ ml.$^{-1}$) (figure 4.4). Larger species tended to have higher $r_{\text{max}}$ at the expense of higher food requirements (higher thresholds for development) and were therefore able to develop populations more rapidly when food was abundant, but become displaced by smaller, slower growing $K_S$-selected species when food was limiting. This is the same pattern as already described for rotifers and cladocerans, but on a finer scale than when all rotifers were considered as $r_{\text{max}}$-strategists.

![Figure 4.3 Maximum daily population growth rates of rotifers. After Stemberger and Gilbert (1985).](image)
Figure 4.4 Threshold food concentration for population growth of selected rotifers. After Stemberger and Gilbert (1985).

The competitive superiority of different rotiferan life-histories has been shown under experimental conditions (Rothhaupt, 1993a; 1993b; Walz, 1993a; 1993c), but is also expected in situ, where environmental conditions vary. It seems likely that the exacting conditions which select for algal r-strategists in rivers will also select for rotiferan r-strategists. The selecting agent is again expected to be the shortened retention times encountered in most river systems and the relative frequency with which the system is disturbed by elevated flows, both of which should favour fast growing species, especially in productive waters where food is abundant.

4.1.4.3 Selection within a single species

Specific clones with favourable life-history traits may be selected for in river systems, shifting the genetic composition of the population. For example, Bennet et al., (1993) showed that $r_{\text{max}}$ varied between individuals of a single species, and that under high dilution rates in turbidostat culture, those individuals with the highest $r_{\text{max}}$ were selected for, changing the kinetics of the whole population. They were able to increase the $r_{\text{max}}$ of a Brachionus calyciflorus population by 51% over a matter of months, from 1.23 d$^{-1}$ to 1.85 d$^{-1}$. The mechanism for this shift was a simple demographic change to individuals with faster production of smaller eggs and an associated reduction in life span. The changes were however genetically fixed, as clones removed from the experimental conditions did not lose their biotic potential for increase.

A similar selection for high $r_{\text{max}}$ clones could occur in rivers as long as the selecting agent was suitably strong and constantly applied as in the experiments of Bennet et
al., (1993). The stochasticity of natural systems will, however, constantly reduce the strength and direction of the selection pressure, especially the periodic decreases in food levels which limit r-selected growth, so that selection is likely to be less strict than the laboratory derived results.

4.1.5 The zooplankton of river systems

The zooplankton of rivers, like the phytoplankton, is dominated by species with rapid generation times, namely the rotifers. A number of studies have shown rotifers to be numerically dominant over crustaceans in the main channel, *i.e.* River Canard, N. America (Winner, 1975), River Loire, France (Lair, 1980), River Darling, Australia (Geddes, 1984; Shiel and Walker, 1984), River Guadalquivir, Spain (Guisande and Toja, 1988), River Po, Italy (Ferrari and Mazzoni, 1989), Rhode River, N. America (Dolan and Gallegos, 1992), River Potomac, N. America (Sellner *et al.*, 1993), River Rhine, Germany and the Netherlands (Admiraal *et al.*, 1994; van Zanten and van Dijk, 1994), River Meuse, France, Belgium and the Netherlands (Descy and Gosselain, 1994; Marneffe *et al.*, 1996), Ohio River, N. America (Thorpe *et al.*, 1994), and River Danube, Slovakia (Vranovsky, 1995). These rivers share a ubiquitous community structure, like that of the algae, including truly planktonic rotifers of the genera *Brachionus, Keratella, Synchaeta, Polyarthra, Asplanchna, Filinia* and *Trichocerca* (Hynes, 1970). Tan and Shiel (1993) found a similar composition in Australian billabongs (highly disturbed, low retention time habitats) and attributed the success of rotifers to their life history characteristics, in particular their rapid generation times.

Pace *et al.*, (1992) also stated that the zooplankton of many rivers was dominated by small species with short generation times. These species had the added advantage of being less effected by the presence of suspended silts which reduced the feeding efficiency of larger cladocerans.

Zooplankton density is generally considered to be lower in rivers than in lakes (Chandler, 1937; Pace *et al.*, 1992; Phillips, 1995; van Dijk and van Zanten, 1995) and reproductive populations only tend to develop in the slower, deeper waters of downstream reaches (Winner, 1975; Richardson, 1992; Tubbing *et al.*, 1994), below 4th or 5th order (Richardson, 1991), and particularly in tidal portions where copepods may become more abundant (Pace *et al.*, 1992; Admiraal *et al.*, 1994; van Zanten and van Dijk, 1994). A true zooplankton, consisting of ‘non-drift’ organisms was considered to be virtually absent from fast flowing low order sections (Hynes, 1970; Vannote *et al.*, 1980), and Tubbing *et al.*, (1994) found that the density of rotifers
increased from <100 individuals litre\(^{-1}\) in the middle reaches of the River Rhine at Koblenz (590 km from source), to >1000 individuals litre\(^{-1}\) in the downstream reaches at Bimmen (865 km from source).

Downstream sections of regulated rivers where flow rate is impaired may develop a potamoplankton dominated by small cladocerans, as was reported for the River Meuse, at Hermalle-sous-Argenteau (river km 620) (Marneffe et al., 1996). Riverine reservoirs or naturally occurring deep pools may also shift the balance of dominance from rotifers to cladocerans as conditions become more lacustrine in nature, for example in pools of the Illinois River, N. America (Brown et al., 1989), impoundments of the Murray River, Australia (Shiel and Walker, 1984) and the White Nile below the Gebel Aulya dam (Rzoska et al., 1955), also (EjsmontKarabin et al., 1993; Carter et al., 1995). The composition of riverine zooplankton is therefore influenced by the physical conditions in the main channel, the presence of source areas (dead zones), and their frequency of flushing.

4.1.6 Potential sources of main-channel populations

The origin of zooplankton in rivers raises the same theoretical problems already discussed for the algae, namely, where does the zooplankton originate in the first place, and are there inocula constant enough to maintain the downstream densities observed? Hynes (1970) stated that all zooplankton must originate in lentic areas within the river channel itself such as embayments, similar to the aggregated dead zone model of Reynolds (1988). Saunders and Lewis (1989) stated that suitable lentic habitats existed along the periphery of most river channels, and could be divided into three broad categories: channel habitats, side-channel habitats, and flood plain habitats (table 4.2).

<table>
<thead>
<tr>
<th>Morphology</th>
<th>1. Channel habitats</th>
<th>2. Side-channel habitats</th>
<th>3. Floodplain habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Retention Time</td>
<td>Low</td>
<td>Medium</td>
<td>Flooiplain lakes. Separated by levee at low water</td>
</tr>
<tr>
<td>Flushing frequency</td>
<td>High</td>
<td>Medium</td>
<td>High</td>
</tr>
<tr>
<td>Source areas during Low water</td>
<td>Rising water</td>
<td>High water</td>
<td></td>
</tr>
<tr>
<td>Stability</td>
<td>Low</td>
<td>Medium</td>
<td>High</td>
</tr>
<tr>
<td>Dominant animals</td>
<td>Rotifers</td>
<td>Dependent on flushing rate.</td>
<td>Crustaceans</td>
</tr>
<tr>
<td>Life history strategy</td>
<td>(r_{\text{max}})-selected</td>
<td>(r_{\text{max}} + K_s)</td>
<td>(K_s)-selected</td>
</tr>
<tr>
<td>Fate in channel</td>
<td>Increase</td>
<td>Dependent on species</td>
<td>Decrease</td>
</tr>
<tr>
<td>Chemistry</td>
<td>Riverine</td>
<td>Riverine</td>
<td>Variable</td>
</tr>
</tbody>
</table>

Table 4.2 General characteristics of different potential source habitats in river systems
Channel habitats and side-channels together make-up the dead zone habitats of rivers and are expected to develop a rotifer dominated community owing to the riverine influence on water quality and retention time. The dead zones are expected to function in exactly the same manner as was described for algae above, acting as a source of animals to the main flow. Their major potential for internal development is expected during low flow periods when their functional area is maximal, but their export to the river may be low owing to reduced water exchange between compartments. Side arms, which have longer retention times (owing to their volume or small interface with the river) and the flood plain waters are expected to have their main influence at rising and high water, when their zooplankton are flushed into the river. The appearance of crustaceans in rivers is often sporadic and increases with discharge as sequential lentic sources are flushed (Saunders and Lewis, 1988; 1989).

A number of river studies have noted a negative correlation between the abundance of rotifers and discharge, for example animals were washed from side-channels of the Danube at velocities above 1 cm s$^{-1}$ by (Vranovsky, 1995), also Rzoska et al., (1955); Threlkeld and Choiniski (1985); Ferrari et al., (1989); Pace et al., (1992); Thorpe et al., (1994); van Zanten and van Dijk (1994); Telesh (1995); van Dijk and van Zanten (1995) indicating that as water level rises, more in-channel dead zones are washed-out, the retention time of the section is decreased, and the number of animals is reduced as a consequence. Relatively still conditions are considered optimal for the development of a riverine zooplankton. Rotifer densities were usually highest during spring and summer (Hynes, 1970; De Ruyter van Steveninck et al., 1992; Admiraal et al., 1994; Marneffe et al., 1996) and lowest during winter, however, the influence of other variables such as water temperature and food abundance are also strongly involved in controlling seasonal cycles in rivers (Winner, 1975; van Dijk and van Zanten, 1995).

4.1.7 Objectives

The dominance of rotifers in riverine zooplankton communities is considered to be a product of the selective pressure for short generation times imposed by the action of flowing water. Their location in lowland reaches and the degree of temporal and spatial variability also indicates the strength of physical control on the community. This chapter investigated the zooplankton of the lowland section of a 'typical' eastern England river. Its aims were to:

- describe the zooplankton community structure of the River Nene, and relate this to the life-history traits of the dominant groups.
• assess the relative importance of growth limitation and loss processes to zooplankton dynamics throughout the growing season.
• estimate the potential hydraulic losses associated with the flow regime of the Nene and use this to assess the potential for planktonic development given the accepted models of water flow in open channels.
• comment on the role of dead zones in the ecology of river zooplankton.
• suggest reasons for the observed low summer zooplankton density when flow rate was low.

4.2 Methods

4.2.1 Field methods

Sample collection

Refer to section 3.1.9.5 for a description of sample site location. All zooplankton samples were taken with a 10 litre cuboidal perspex sampler (Patalas/Schindler trap) from a depth of one metre, taking care to avoid any littoral influence. The sample volume varied from between 20 litres to 40 litres, depending on the silt load of the water and the expected density of animals. Settlement was not a practical means of concentrating animals from samples of this volume and so filtration through a 53μm mesh was adopted. The 10 litre samples were pooled and filtered through the apparatus detailed in figure 4.5. The force of water passing the mesh was kept to a minimum to avoid damage to delicate forms, and the mesh was constantly bathed in a water bath to avoid desiccation. The mesh was carefully removed, after the whole sample had been filtered, and its contents thoroughly rinsed with filtered water into the water bath. Care was taken to ensure that all surfaces that were in contact with the concentrated sample were also rinsed.

Samples were preserved in 4% formaldehyde, the recommended long term preservative for zooplankton (Steedman, 1973; Pontin, 1978). The concentrated sample was transferred to a 200 ml sample bottle and 20 ml of 40% formaldehyde was added, giving a preservative concentration of 4%. The volume was made up to 200 ml with filtered river water and the contents inverted to ensure equal distribution of preservative. 4% formaldehyde causes rapid death of rotifers, with an associated distortion of illoricate species which makes identification to species difficult. Live net hauls were therefore taken to aid identification. A type-species reference collection was also developed by isolating known species and preserving them as above.
4.2.2 Laboratory Methods

Rotifers were identified and counted at x 100 magnification using a Zeiss Axiovert 100 inverted microscope and following the method described by Lund (1958). Subsamples of 5 ml or 10 ml volume were drawn from thoroughly mixed samples with a wide bore automatic pipette, introduced into settlement chambers, and left to settle for a minimum of 30 minutes prior to analysis. Samples were not left for more than 90 minutes as the settlement of low-density silt particles over rotifers reduced the precision of counts. A count of over 100 animals of the dominant taxon was aimed for to ensure an adequate level of accuracy, but this was not always achieved owing to low rotifer density at certain times of the year. The whole chamber was always analysed, as random settlements were not achieved.

Animals were identified to species level where possible but some illoricate species, such as Synchaeta sp., could only be identified to genus. The number of eggs was also recorded to allow birth rates to be assessed. Total density of animals and eggs per litre was calculated from

\[ \text{density} = \left[ \frac{v_1}{v_2} \right] \times \text{count} \times \left( \frac{1}{v_3} \right) \]

where \( v_1 \) is the concentrated sample volume in ml, \( v_2 \) is the subsample volume in ml, and \( v_3 \) is the initial volume of water sampled in litres.
Population dynamics were analysed according to the methods of Edmondson (1960), refer to Appendix A.4.8. Instantaneous birth rates were calculated from field data and published embryonic development rates after Herzig (1983).

4.2.3 Analysis of the precision and accuracy of the sample methods used

4.2.3.1 Concentration by filtration

Filtration was used to concentrate zooplankton samples owing to the need to sample large volumes as animal density was often low. Filtration may lose some small, delicate species which either pass through the mesh or become damaged beyond recognition. An experiment was undertaken to assess the capture efficiency of filtration compared to settlement. Details are given in appendix A.4.1.

Capture efficiency was variable between rotifer groups indicating that the size and morphology of the animal affected its liability to loss during filtration. Loricate species such as *Keratella quadrata* were retained with the greatest efficiency whereas small illoricate forms such as *Synchaeta oblonga* were subject to higher filtration losses. The capture efficiency of single species was also variable between samples, indicating that filtration was neither fully efficient or precise.

The accuracy and precision of density data from filtered samples is therefore prone to variation caused by factors such as the size, morphology and density of animals, the speed of filtration, and the presence of other particles such as filamentous algae which might block the filter. No single transformation was considered applicable to correct for filtration losses, so this inherent variability must be recognised when analysing the data from the river samples. The low density of animals in the river system, however, necessitated the use of filtration, but errors were minimised by adopting as controlled a filtration procedure as possible.

4.2.3.2 Spatial distribution of animals and the precision of the sampling regime

The spatial distribution of animals at Wansford was assessed on 12/5/94 to assess the level of contagion inherent in river populations. This was important as the distribution affects the accuracy of results and dictates a suitable sampling strategy. The methods used and the results of the study are given in appendix A.4.2.

Results indicated that the pelagic rotifer populations of the Nene were randomly distributed and that a single 10 litre sample was sufficient to give an 'acceptable'
accuracy (95% confidence limits of ± 40% of the mean) for the numerically dominant groups (Appendix A.4.3).

The sample regime adopted for the river study utilised composite sampling and a large sample volume (Appendix A.4.4). Replicate 10 litre Patalas samples were pooled to achieve a final volume of either 20 litres or 40 litres. Final sample volume was governed by the silt load in the river and the expected density of animals. 20 litres were sampled when the silt load was high, as the presence of silt in samples tended to make subsequent laboratory enumeration and identification of zooplankton difficult. This type of composite sampling gave results with a greater accuracy than that described as 'acceptable' by Elliot (1973).

4.2.3.3 Effect of variable sample volume of filtration efficiency

It was considered possible that the use of different sample volumes effected filtration efficiency. An experiment was conducted to test for this effect which compared the capture efficiency from 40 l and 10 l samples. Details are given in appendix A.4.5.

No significant difference in filtration efficiency from samples of different volume was found, indicting that this had no impact on the accuracy of results. This aspect of the methodology was therefore considered justified.

4.3 Results

4.3.1 Wansford station zooplankton

4.3.1.1 Density

Weekly zooplankton abundance, expressed as number per litre at Wansford, is shown in figure 4.6.

![Figure 4.6](image)

**Figure 4.6** Seasonal variation in total zooplankton density at Wansford during the growing season of 1994
Total density was low throughout much of the growing season except during the spring. Numbers were very low during the summer, except for a small increase in September which coincided with an increase in discharge (refer to figure 3.10).

4.3.1.2 Zooplankton composition

The zooplankton of the Nene was dominated by rotifers (figure 4.7). Rotifers accounted for 95% of total density, with copepod nauplii the next most abundant group. Very few copepodites or cladocerans were found in the main channel of the river.

4.3.1.3 Rotifer composition

A full list of species collected from the main-channel of the Nene is presented in table 4.3. The majority of species were poorly represented in terms of density, and only occurred sporadically. Many of these species, such as *Lepadella patella*, *Colourella unicatus*, *Cephalodella gibba*, and *Lecane sp.*, were of littoral origin. These and other low density species were probably the result of drift from littoral habitats along the river edges.

![Graph](image)

**Figure 4.7** Seasonal variation in the relative abundance of planktonic groups at Wansford, 1994.

The main-channel community was dominated by species of the genera *Keratella*, *Brachionus*, and *Synchaeta*, which together accounted for 83% of total rotifer numbers throughout 1994. *Synchaeta oblonga* was the most abundant species of all, accounting for 57% of total density. All species attained their greatest density during spring, after which numbers fell and remained low throughout the summer (figure 4.8). The community remained relatively diverse throughout the study period with many species represented at low density.
<table>
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<tr>
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<th>Genus</th>
<th>Species</th>
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</table>

Table 4.3 River Nene rotifers. Asterisk represents littoral or periphytic species (Pontin, 1978).
4.3.1.4 Comparison of the spring rotifer development during 1992-1994

The rotifer community was studied during the spring development period of 1992, 1993 and 1994. Figure 4.9 shows total rotifer density with water temperature, chlorophyll 'a' concentration, and discharge, three of the most important variables thought to control zooplankton development (van Dijk and van Zanten, 1995), during the spring period.

Total rotifer density differed between the three years. The highest rotifer density was achieved in 1992 with a maximum of over 9,000 animals per litre. The maximum density of 1993 was somewhat lower at approximately 2000 rotifers per litre, and that of 1994 was the lowest at approximately 950 animals per litre.

The community composition was also different between years. 1992 was dominated by *K. cochlearis* which accounted for 65% of total rotifers during spring. The next most dominant taxa was *Synchaeta sp.* with 12% of total numbers, and then *B. angularis* with 9%. Community composition was similar during 1993. *K. cochlearis* accounted for 42%, *B. angularis* 20% and *Synchaeta sp.* 13% of total rotifer density. *Synchaeta sp.* was the dominant taxa during the spring of 1994 accounting for 65% of total density. *K. cochlearis* was the next most abundant group with 8%.

![Figure 4.8 Abundance of dominant rotifer taxa at Wansford station during the growing season of 1994.](image)
Seasonal dynamics were similar each year. Population development was initiated at the end of April and lasted for approximately one month before densities fell to summer low levels. Low abundance was maintained throughout much of the summer of 1993 and 1994, but no data were available for 1992 after the initial crash at the end of May.

Water temperature increased steadily until reaching a plateau at approximately 20°C by the end of June in 1993 and 1994. The temperature was higher during May 1992 when rotifer numbers achieved their maximum recorded level. No obvious pattern was apparent with regards to the degree-day requirement from the start of the year for the initiation of the spring development (920, 1,122 and 904 for 1992, 1993 and 1994 respectively), indicating that accumulated temperature had only a minor role on community development.

The chlorophyll 'a' concentration in the river was used as an estimate of food availability to filter feeding zooplankton (figure 4.9), although this assumed all algal
species were equally palatable. The levels recorded during 1994 were generally lower than the other years and were thought to be a consequence of the high spring discharge. Levels did rise, however, at the end of April, closely followed by rotifer density. Algal populations developed during March in 1992 and 1993. A slight decline was noted during April of 1993 which coincided with a rise in discharge, but levels began to increase again at the end of April. This second increase was concurrent with the development of rotifer populations. 1992 had a relatively high and stable chlorophyll 'a' concentration from March until June. An early summer crash was evident at the end of May each year. Its cause was uncertain, but grazing pressure and changing discharge patterns are suspected as having an influence.

Discharge, measured at Orton gauging station, showed high annual variability. The highest discharge was recorded during the early part of 1994 when values remained above 10 m$^3$s$^{-1}$ until the start of May. The short period of low discharge that followed was coincident with increased rotifer density, but this ended when the discharge rose again to approximately 10 m$^3$s$^{-1}$. Discharge was generally lower during 1993 but briefly peaked during March, April and June. 1992 had the lowest discharge of the three years with levels rarely rising above 5 m$^3$s$^{-1}$ except at the end of May during a short lived spate event.

4.3.1.5 Riverine algal palatability

Chlorophyll 'a' may not always be a viable indicator of food availability to filter feeding zooplankton owing to the presence of unpalatable algae. Figure 4.10 shows the number of algal cells recorded at Wansford during 1994 that were palatable to rotifers.

Algae were divided into four palatability groupings relevant to generalist rotifer feeders for figure 4.10. The first group contained all species with an average cell / colony diameter less than 5μm. The second group contained species with a diameter of between 5 and 20μm. These two groups were considered to represent a high quality food resource to generalist feeders such as *K. cochlearis*. Group three species included naked flagellates and cryptomonads with a diameter of between 20μm and 45μm which act as a high quality food source for *Synchaeta sp.* and *Polyarthra sp.* Group four species represented all unpalatable cells with a diameter of over 20 μm and all resistant green algae and cyanobacteria.

The majority of algal cells fell within the first two groups apart from sporadic peaks of group 4 cells in May and November. The results indicate that most algae in the
river were small enough to act as a food source to rotifers.

![Graph showing algal palatability groupings at Wansford, 1994](image)

Figure 4.10 Composition of algal palatability groupings at Wansford, 1994

4.3.2 Explaining rotifer population dynamics - multiple regression models

4.3.2.1 Growing season (Mar-Oct, 1994)

This section of work aims to identify the dominant control parameters for rotifer dynamics in the River Nene at Wansford during the growing season (March-October) of 1994 using multiple linear regression models.

Simplified models containing only the independent variables that accounted for a significant degree of residual variation in the dependant variable were produced following the methods outlined in Appendix A.4.7. The full models are also presented in the appendix. The following results describe simplified regression models only.

Rotifer density

Regression equation for simplified model: \( Y = -0.280 + 1.403 \cdot X \)

where \( X \) is chlorophyll 'a' concentration (\( \mu g/l \))

The simplified model contains only chlorophyll 'a' as a predictor variable of rotifer abundance in the River Nene (figure 4.11). 66% of the variation in total rotifer density was described by chlorophyll 'a' concentration. All other independent variables were responsible for relatively little of the residual variation (see appendix A.4.7). Discharge had little control over rotifer abundance during the growing season.
Figure 4.11 Regression line predicting log rotifer density from log chlorophyll 'a' concentration at Wansford, 1994.

**Brachionus sp. density**

A similar regression was performed on the total density of all members of the genus *Brachionus*, as the numerical dominance of *Synchaeta sp.* had the potential to mask trends in sub-dominant taxa.

Regression equation for simplified model: \( Y = -1.182 + 1.088.X_1 + 0.561.X_2 \)
where \( X_1 \) is chlorophyll 'a' concentration and \( X_2 \) is discharge.

The subset model included two independent variables, chlorophyll 'a' and discharge. Both variables accounted for a significant amount of variation (appendix A.4.7). The two variables together accounted for 64% of the total variation in *Brachionus sp.* density during 1994, but chlorophyll 'a' described more variation than discharge as shown by the magnitude of their standard partial regression coefficients (0.614 and 0.332 respectively). Log discharge (figure 4.12) had little direct affect on *Brachionus* density and was only included in the model because it accounted for a significant portion of the residual variation around the chlorophyll 'a' regression line as indicated by figure 4.12.

**Keratella sp. density**

*Keratella cochlearis* and *Keratella quadrata* densities were amalgamated for this analysis.

Regression equation for simplified model: \( Y = -1.024 + 1.192.X_1 + 0.363.X_2 \)
where $X_1$ is chlorophyll 'a' concentration and $X_2$ is discharge.

The results were similar to those documented for *Brachionus sp.* Chlorophyll 'a' and discharge were the only variables that described a significant amount (85%) of variation in total *Keratella sp.* density.

It is worth noting again that the discharge was only left in the model because it described a significant amount of residual variation from the chlorophyll 'a' regression line. It had no significant effect on *Keratella* density alone (30% residual variation explained) (figure 4.13).
Community diversity

The Shannon-Wiener index of community diversity was calculated for each sampling occasion at Wansford during 1994 and used as the dependant variable in the following regression. This index takes into account both species richness and abundance and is calculated from the following equation

\[
diversity = - \sum_{i=1}^{S} P_i \ln P_i
\]

where \( S \) is the total number of species and \( P_i \) is the proportion of individuals that each species contributes to the total.

The aim of the analysis was to assess the effect of flow rate on community structure to ascertain if physical disturbance influenced the plankton composition.

Regression equation for simplified model: \( Y = 0.178 + 0.544.X \) where \( X \) is the discharge.

Community structure varied as a function of discharge during the growing season of 1994 (figure 4.14). 58% of the total variation in diversity was accounted for by variations in the discharge. Diversity tended to be greatest when discharge was high.

The number of species present on each sample occasion was also found to be positively related to discharge and chlorophyll 'a' (\( P = 0.06 \) and 0.03 respectively) indicating the potential for species addition with rising water.

![Figure 4.14 Relationship between rotifer community diversity and discharge at Wanford, 1994.](image-url)
4.3.2.2 Spring period (April - May, 1994)

The persistently low number of rotifers during the summer may have disguised important relationships during the spring development. The regression models were therefore repeated during the eight week period April-May when rotifers populations were generally more abundant.

Chlorophyll 'a' concentration was the only independent variable that described a significant amount of residual variation in total rotifer density during the period. Chlorophyll 'a' was responsible for 63% of residual variation compared to 66% for the whole growing season. This was also the only important predictor of Keratella sp. abundance, describing 68% of residual variation compared to 85% over the whole growing season. Non of the independent variables measured had a significant influence on Brachionus sp. populations during the spring.

4.3.2.3 Spring period 1992-1994

Simple linear regressions for total rotifer density

Weekly rotifer data were available for the April-May spring development period of 1992, 1993 and 1994. The three periods were subject to very different environmental conditions. This therefore offered the chance to assess the effects of environmental variables on rotifer development over a wider range than was available during 1994. Regressions were repeated using discharge, chlorophyll 'a' concentration and temperature as the independent variables.

Total rotifer density was related to chlorophyll 'a' concentration (figure 4.15) and discharge (figure 4.16) during the spring period, as shown by simple linear regressions. Both relationships were similar to those found for rotifer populations in the River Rhine (vanDijk and vanZanten, 1995).

Chlorophyll 'a' and rotifer density were positively associated during the spring period, indicating that either both variables were influenced by similar physical conditions, or that food limited rotifer development. There was more variation in rotifer density at high chlorophyll 'a' levels which indicated that when food was plentiful other parameters controlled rotifer abundance.

Rotifer density was negatively associated with discharge through a linear logarithmic function (figure 4.16a). High rotifer density was precluded by high flows, as was the
case during 1994. Figure 4.16b shows the same relationship plotted on the actual scales of measurement. The relationship was described by a negative exponential, similar to that found by Vranovsky (1995) in the River Danube. High variability at low discharge is clearly seen in this plot. There seemed to be a threshold flow rate of approximately 5 m$^3$s$^{-1}$, or 0.08 ms$^{-1}$, above which rotifer development was suppressed.

Figure 4.15 Relationship between log chlorophyll 'a' concentration and log rotifer density during the spring development, 1992-1994.

Figure 4.16 Relationship between discharge and rotifer density during the spring development, 1992-1994. (a. log-log plot, b. untransformed plot).

Multiple linear regressions for total rotifer density

The multiple regression for the spring development period, 1992-1994 is presented in
appendix A.4.7. The equation for the simplified model is presented below.

Regression equation for simplified model: \[ Y = -0.085 + 0.737X_1 + 0.090X_2 \]
where \( X_1 \) is chlorophyll 'a' density and \( X_2 \) is temperature.

![Graph showing the relationship between rotifer density and temperature at Wansford during the spring development 1992-1994.](image)

**Figure 4.17** Relationship between rotifer density and temperature at Wansford during the spring development 1992-1994.

Chlorophyll 'a' and temperature described a significant amount of variation in rotifer density during spring (60% of variation). Both variables were positively associated with high rotifer density, and both are known to have an important role in defining rotifer birth rates (Sarma and Rao, 1991). The temperature and chlorophyll 'a' levels during spring may therefore be of great importance for riverine populations, especially when high discharge has the potential to limit development (figure 4.17). Discharge was not included in the model as it was itself negatively correlated with chlorophyll 'a'. This does not mean that discharge had no effect on rotifer populations, more that discharge affected both riverine phytoplankton and zooplankton communities in a similar manner *i.e.* high discharge tended to reduce plankton density in the main channel.

*Keratella sp.* density was also dictated by chlorophyll 'a' levels and temperature during the spring period for the same reasons described above. *Brachionus sp.* density was only significantly associated with chlorophyll 'a' level. This may have been the result of amalgamating counts from four different species, each with slightly different optimum growth conditions.
4.3.2.4 Average monthly rotifer density

A multiple linear model was produced using monthly averages during the growing season, from the 1992, 1993 and 1994 data sets. The simplified model contained discharge, chlorophyll 'a' and temperature as significant predictor variables (p<0.05). Temperature described the highest proportion of variance, followed by chlorophyll 'a' and discharge (partial correlation coefficients of 0.71, 0.66 and 0.52 respectively). The model described 92% of variation in total rotifer number at this scale of measurement. The regression line was described by the following equation:

\[ Y = -1.519 + 0.114X_1 + 0.18X_2 + 0.77X_3 \]

where \( X_1 \) is temperature, \( X_2 \) is chlorophyll 'a' density and \( X_3 \) is discharge (d.f =9).

The high proportion of residual variance explained gives this model high predictive power. It should therefore be possible to predict mean monthly rotifer abundance during the spring from the mean temperature, chlorophyll 'a' concentration and discharge. The fact that all three variables had a significant effect indicates that a particular combination of these factors are required to allow the development of river populations. Discharge had a negative impact on chlorophyll 'a', but chlorophyll and temperature were unrelated. Temperature may be an important cue for the development of the rotifer community in the Nene, although the failure of any one factor may inhibit this development.

The low density found during the summer, when temperature was high and discharge low, may therefore have been effected by the low density of suitable food items. The timing of the spring development may also be dependant on the temporal alignment of all three factors. The natural variability in the timing and magnitude of rotifer plankton development from year to year is not surprising considering the variability of its controlling variables.

4.3.3 Keratella cochlearis population dynamics, 1992-1994

The population dynamics of riverine rotifers were analysed using Keratella cochlearis as a model organism. This species was the most suitable in this respect as it was the dominant egg carrying taxa recorded from the river over the three year period and its eggs were relatively easy to identify when detached from the animals. Population parameters estimated from the egg ratio (the ratio of eggs per adult female) were therefore considered to be reliable.
*K. cochlearis* population dynamics during the spring of 1992-1994 are presented in figure 4.18. Density mirrored the pattern shown for total rotifers in figure 4.9. The timing of the peaks was similar each year although total densities were much higher in 1992 and 1993 than in 1994, reaching 8280, 1020 and 75 animals per litre respectively. Numbers increased at the end of April during 1993 and 1994 and reached a peak within a two week period, after which they declined back to low densities at the end of May.

![Figure 4.18](image_url)

**Figure 4.18** Population characteristics of *K. cochlearis* during April-May, 1992-1994. A. density. B. egg ratio, C. instantaneous birth rate and growth rate, D. instantaneous death rate, E, proportion of potential development realised. Birth, death and intrinsic rates of increase were derived using the methods of Edmondson (1960, 1965) as modified by Paloheimo (1974) (details in appendix A.4.8). The proportion of the potential development realised relates to the difference between the density expected from a given birth rate and the observed density.

*K. cochlearis* dynamics were slightly different in 1992, with development initiated later (during May) and populations building more slowly to a peak at the end of May. No quantitative data were available after May 1992, but qualitative sample analysis
showed the number of *K. cochlearis* was low at the start of June, indicating a rapid crash in numbers similar to the other years.

The egg ratio during 1994 was high during May, and remained high prior to the crash in numbers. The egg ratio was low prior to the initiation of the 1993 development which reached peak density within a seven day period. Egg ratios remained high throughout the peak but the actual number of animals declined after the initial pulse of growth. Egg ratio was high prior to the 1992 development and remained high throughout May until the last sampling date prior to the crash.

Birth rate was high during May 1994 owing to high egg production and warm temperature, but the actual rate of population increase (r) was generally lower. This resulted in high positive death rates and a low proportion of the potential development being realised. This pattern is indicative of a system that is controlled by loss processes, whether they be dominated by death or export. A similar pattern occurred during May 1993. High potential birth rates were not matched by actual development of numbers after the initial increase on the 14th of May.

The instantaneous birth rate of May, 1992 was higher than the other years, as a result of a high egg ratio combined with higher water temperature (figure 4.9). The actual population growth rate (r) was still some way below the potential rate, as indicated by the high death rates and the relatively low proportion of potential development realised.

The instantaneous rate of increase was highest during the first week of the population development each year and actually exceeded the birth rate during 1994 and 1993, as indicated by a negative death rate. The explosive nature of the development, especially during 1993 and 1994 indicates a source of importation, as natural birth rates were insufficient to explain the development observed. The consistent timing of the initial development each year, and the fact that the highest rates of increase occurred at the onset of the development, leads to the conclusion that hatching of resting eggs formed a significant part of the spring development.

*Resting egg production*

The number of *K. cochlearis* resting eggs was greatest in 1992, when 29% and 53% of all eggs were mictic on the 13th and 22nd May respectively. They were usually found as part of a pair carried by single females, the other being a standard amictic egg. The density of resting eggs was much lower in 1993 and 1994 when they
comprised only 5% and 10% of total eggs production respectively on a single sample date during May. Resting eggs were also produced by *K. quadrata*, *Brachionus angularis* and *B. calyciflorus*, and may represent a life history strategy adaptation to life in systems with short retention times.

*Temperature as a potential hatching cue for resting eggs*

Temperature was assumed to be a potential cue for the hatching of resting eggs. Spring temperatures were relatively similar each year (figure 4.9) which may explain the synchronous timing of rotifer development during 1992-1994 when other environmental variables (especially discharge and chlorophyll 'a' density) varied considerably. The temperature of river water increased from below 10°C (when minimal and sporadic release was expected (May, 1987)) at the beginning of April to above 15°C by the end of the month. Degree days above 10°C prior to population development were, however, rather variable (349 for 1992, 304 for 1993 and 190 for 1994).

*Termination of K. cochlearis development*

*K. cochlearis* density peaked at the end of May 1992 along with the chlorophyll 'a' concentration (142 µg l⁻¹). Numbers declined rapidly after this date, until on 3rd of June, animals were scarce. This period coincided with a notable increase in discharge to 23.87 m³s⁻¹.

The major decline in *K. cochlearis* density during 1993 occurred between the 20th to 28th May when discharge increased from approximately 3.24 m³s⁻¹ to 7.48 m³s⁻¹. *K. cochlearis* density declined in the latter half of May, 1994 when discharge decreased to low levels. Increased loss rates were thought to be important at the time, as high egg production indicated that food was not limiting.

4.3.4 Potential food limitation of River Nene zooplankton

The potential for food limited growth in riverine rotifer populations was established at Wansford by estimating the concentration of food available to individual animals on each sample occasion, and relating this to an estimate of the threshold food level of a typical 'small' rotifer. Food levels above this threshold were assumed to be adequate to promote population growth. The methods used for these calculations are presented in appendix A.4.9.
The effective food concentration exceeded the level required to promote maximum rates of increase in rotifer populations throughout the whole of the 1994 growing season, and was therefore not considered to be limiting at any time. With this in mind, dense populations were expected to develop, though they were rarely realised as shown by figure 4.19, which details the percentage of food limited carrying capacity actually reached at Wansford.

**Figure 4.19** Food availability at Wansford related to specific parameters of rotifer population growth. A single value of threshold (food concentration for zero population growth), Ks (food concentration for half maximum population growth rate) and r<sub>max</sub> (concentration required for maximum population growth) was estimated from values cited in Stemberger and Gilbert (1985) for *Keratella cochlearis* and *Synchaeta oblonga*, the two dominant rotifer groups in the River Nene. The effective food concentration is that experienced by the animal. If the density exceeded one animal per ml then the total available food was shared accordingly.

The carrying capacity was calculated according to appendix A.4.9 and relates to the point at which population growth equals zero (Begon *et al.*, 1990). Under stable environmental conditions, one may expect the density of grazing animals to approach the food limited carrying capacity, but as figure 4.20 shows, the density of grazing rotifers remained well below the potential carrying capacity of the system, indicating that some factor other than food limited rotifer development.

The proportion of carrying capacity reached during the spring development of 1992 and 1993 was slightly higher than that of 1994 owing to the fact that larger rotifer populations were formed in the presence of a similar algal concentration. The proportions attained were still only a fraction of the potential carrying capacity, 2% (st. ± dev. 2.0, n=13) and 6% (st. dev. ± 5.3, n=9) during May 1993 and 1992 respectively.
Figure 4.20 The percentage of food limited carrying capacity reached by grazing rotifers at Wansford, 1994.

Figure 4.21 is a plot of total rotifer density against chlorophyll 'a' concentration during April-May 1992-1994. There was a great deal of variation in the density achieved at high food levels indicating that other factors influenced population development when food was abundant, and reduced the likelihood of populations reaching their food dependant carrying capacity.

Figure 4.21 Correlation between observed chlorophyll 'a' density and rotifer density during the spring development 1992-1994.

4.3.5 Theoretical dilution rates from the Wansford section of the river

In view of the apparent abundance of food, an assessment of the hydraulic loss rates affecting fully entrained rotifer populations from the Wansford section of the river was made. This was intended to address the question, Is a rotifer population likely to
develop in the main channel of the river given the constant removal of animals downstream? This was best answered by comparing the potential birth rates of figure 4.22 with the potential physical loss rates with flow. These were calculated assuming full turbulent mixing, no appreciable capacity for rotifers to swim against a current (Richardson, 1992) and no importation of animals from upstream sources or dead zones.

The exponential loss rate was calculated as \(-\frac{q \cdot t}{V}\) according to Reynolds (1984) where \(q\) is the discharge through a section of known volume \(V\) and \(t\) is the number of days between samples. The volume of the Wansford section of the river was calculated for average bed dimensions of 6.5 km (length), 20 m (width) and 3.24 m (depth), yielding a total volume of 421 200 m\(^3\). Discharge was taken to be the average daily flow rate during the inter-sample period. Estimated dilution rates for the month of May, 1992-1994 are presented in figure 4.22.

![Graph showing estimated loss rate of Keratella cochlearis via dilution (white bars) during May 1992 (left), 1993 (middle), 1994 (right). Birth rate (stippled bars) and actual death rate (opaque bars) are presented for comparison.](image)

**Figure 4.22** Estimated loss rate of *Keratella cochlearis* via dilution (white bars) during May 1992 (left), 1993 (middle), 1994 (right). Birth rate (stippled bars) and actual death rate (opaque bars) are presented for comparison.

The estimated loss rate was much larger than the birth rate during May 1993 and 1994. Populations were therefore considered unlikely to develop unless supplemented by imports. There was a much smaller difference between the estimated loss rate and potential rate of population increase in 1992, indicating that populations may at least be maintained. Importation was however needed to allow the high density of rotifers which developed during the spring of this year to occur, otherwise births would simply have covered those animals lost downstream. The high dilution loss rate at the end of May, 1994 was the product of a short-lived but substantial increase in discharge (figure 4.22).
4.3.6 Level of importation required to maintain the observed population development at Wansford

The estimated loss rates calculated in section 4.3.5 assumed no importation from upstream sections of the river. This was a highly unlikely scenario as all sections of the river around Wansford had a similar morphology, and were therefore likely to develop a similar plankton. Discharge through the section was therefore likely to import animals from upstream.

The level of external importation required to allow the observed population development during May 1992 - 1994 was calculated from the following formula

\[
\frac{(d'_{\text{potential}} - d'_{\text{actual}})}{d'_{\text{potential}}} \times 100
\]

to yield a value expressed as a percentage of the population density at Wansford. It is important to note that the only source of animal loss was assumed to be through dilution. This assumption was necessary as no direct death rate data was available.

The best way to view this statistic is to imagine that in cases where the expected death rate was greater than the observed rate, it was assumed that imports to the section accounted for the difference. The level of importation required therefore depended on the disparity between the two death rates, the larger the difference, the larger the importation needed.

Actual death rates were usually smaller than potential death rates indicating a general reliance of populations on imported animals (table 4.4). For example, *K. cochlearis* populations needed on average 76% (proportion of 0.76, standard deviation 0.9, n=4) of the density at Wansford to be added with incoming water to maintain the observed density during May, 1994. *Brachionus sp.* required an even higher level of input, averaging 90% (standard deviation of proportion 0.41, n=4) during May.

These results were as expected considering the high discharge of 1994, and were in relatively good agreement with the high concentration of algal chlorophyll 'a' imported to Wansford from upstream during the spring of 1994. Populations were considered unlikely to develop without such inputs given the extent of potential discharge related loss rates. The importation requirement of over 100% that occurred on a limited number of occasions was the product of negative deaths rate which indicated the need for importation of a higher density of animals than were present at Wansford, and may have been supplemented by the hatching of resting eggs.
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</tbody>
</table>

Table 4.4 Extent of imports required to balance the *K. cochlearis* population development observed at Wansford during May 1992-1994.

The importation required to maintain the *K. cochlearis* population of May 1993 were variable (table 4.4) but still relatively high with an average of 59% (st. dev. from table 17). The first value was ignored as it was the product of a negative death rate with a degree of resting egg development adding to population development.

1992 had lower hydraulic loss rates owing to lower spring discharge. The proportion of importation required to maintain the observed population development was therefore lower than that of the following years, 22% (st. dev. ± 11, n=4) for *K. cochlearis*, 9% (st. dev. ± 0.4, n=4) excluding the start of development where the hatching of resting eggs was assumed to lower instantaneous loss rates. The actual level of importation from upstream was however not likely to be significantly lower than other years and this no doubt allowed a greater proportion of births to be realised and therefore a larger biomass to accumulate during 1992.

4.3.7 Longitudinal survey of River Nene rotifer populations

The longitudinal survey aimed to quantify the scale of imports from upstream sections of the river, and also to estimate the potential role of dead zones in the development of a potamoplankton.

A survey of rotifer populations was performed on 16.6.96 from four sites along the lower River Nene. Rotifer density (again using *K. cochlearis* as a model population) was compared to that expected to develop at subsequent downstream sites (assuming no deaths), given the discharge derived transit time and the recorded birth rate (see
appendix A.4.10 for details). Four sites were chosen along a 39 km stretch of the river. Fotheringhay was situated 16 river km above Wansford, Ferry Meadows was 8 river km below Wansford and North Side was 15 km below Ferry Meadows. The density of *K. cochlearis* at each site is presented in figure 4.23.

The observed population density varied significantly between all four sites (as tested by ANOVA *p*<0.001). Actual densities were always some way below the expected values and showed no obvious pattern of downstream increase. The River Nene had a very slow flow rate during the sampling period (transit time of 5.0, 2.5 and 4.7 days between successive downstream sites), and high chlorophyll 'a' levels (an average concentration of 122 µg/l, st. dev. ± 38), giving the appearance of a stable ponded system.

![Figure 4.23 Observed density of *K. cochlearis* (stippled) at downstream sites on the River Nene against expected density (grey), calculated from observed birth rates and transit times between sites. Error bars plotted on observed densities too small to be shown with scale used.](image)

### 4.3.8 Zooplankton of River Nene retention zones

Two potential source habitats (Pulliam, 1988) of the River Nene were sampled on a weekly basis during the growing season of 1994 to test the effect of increased retention time on the development of zooplankton communities in riverine habitats. Nassington was a backwater channel of the river with no measurable flow rate. It was connected to the river at both ends and had a very similar water quality as a result of water exchange. Wansford backwater was a floodplain lake next to the river separated by a levee.
4.3.8.1 Nassington

The zooplankton community structure at Nassington was similar to that of Wansford station with rotifers numerically dominant while cladocerans were rare (figure 4.24). The dominant species were similar and occurred with a similar periodicity to those of the main channel. Total rotifer density was, however, significantly higher (p<0.05) at Nassington than Wansford station (Wilcoxon's Signed Rank test for paired observations).

![Figure 4.24](image)

**Figure 4.24** Abundance of dominant rotifer taxa at Nassington during the growing season of 1994.

The number of crustaceans at Nassington (dominated by copepod nauplii), expressed as a percentage of total zooplankton density, was higher in summer than that of Wansford station (figure 4.25). This difference was significant (p<0.05) when tested by a Wilcoxon's Signed Rank test for paired observations.

![Figure 4.25](image)

**Figure 4.25** Seasonal variation in the relative distribution of planktonic groups at Nassington, 1994.
4.3.8.2 Wansford Backwater

The zooplankton of Wansford backwater were numerically dominated by rotifers for much of the year (figure 4.26). The proportion of cladocerans and copepodites was small throughout the growing season of 1994, while the number of nauplii was high, especially during the summer. Nauplii density was significantly higher (p<0.001, Wilcoxon's signed rank) than at the riverine sites.

![Graph showing seasonal variation in the relative distribution of planktonic groups at Wansford backwater, 1994.](image)

**Figure 4.26** Seasonal variation in the relative distribution of planktonic groups at Wansford backwater, 1994.

Rotifers were generally more abundant at Wansford backwater than at the riverine sites. The difference was significant (p<0.001, Wilcoxon's signed rank test). Their temporal distribution was more typical of a lacustrine system, with two distinct peaks in density during spring and autumn (figure 4.27). This was different to the river, which lacked the autumnal peak.

![Graph showing total rotifer density at Wansford backwater during the growing season of 1994. Chlorophyll 'a' also shown.](image)

**Figure 4.27** Total rotifer density at Wansford backwater during the growing season of 1994. Chlorophyll 'a' also shown.
The rotifer community composition was somewhat different to that of the river sites. Figure 4.28 shows the density of the major rotifer groups. *Keratella quadrata* and *Polyarthra sp.* (mainly *P. dolichoptera* and *P. remata*) were the dominant groups in terms of density, while *K. cochlearis* and *Synchaeta sp.*, which were dominant in the river, were proportionally much less abundant.

![Graphs showing rotifer abundance](image)

**Figure 4.28** Abundance of dominant rotifer taxa at Wansford backwater during the growing season of 1994.

Wansford backwater had significantly more *Polyarthra sp.* than the river sites (*p<0.001*, Wilcoxon's signed rank) while *Brachionus sp.* were significantly less abundant (*p<0.010)*.

Rotifer community diversity was significantly lower in the backwater than that of the river when tested with a Wilcoxon's signed rank test (*p<0.05*). This was partly owing to the lower number of littoral taxa recorded in the backwater plankton.

### 4.3.8.3 Factors controlling rotifer dynamics in backwater habitats

Multiple regressions were used to identify variables expressing some control over rotifer population dynamics at Wansford backwater and Nassington. The tests were similar to those described in section 4.3.2.

*Regression model for total rotifers (Nassington)*
The similarity of the rotifer communities and water quality parameters of Wansford station and Nassington led to similar results for the regression analysis. 73% of the variation in total rotifer abundance was described by chlorophyll 'a' concentration. No other independent variable, including discharge, had a significant effect (p>0.05).

The equation of the line was

\[ Y = -0.319 + 1.494X \]

where \( X \) is chlorophyll 'a' density (\( \mu g l^{-1} \)).

The relationship between chlorophyll 'a' concentration and total rotifer density at Nassington during the spring development period of 1994 is presented in figure 4.29. It also shows what appears to be a significant negative relationship between rotifers and discharge. This parameter was not included in the final model, however, owing to its interaction with chlorophyll 'a'. The regression model was not able to show the individual effect of discharge on rotifers alone, as it seemed to affect both algae and zooplankton alike. A significant positive relationship between algae and rotifers may therefore be a result of discharge controlled development of plankton in general, rather than a food limited control of rotifers. This fits with the other data which indicate no food limitation of populations.

![Figure 4.29](image)  

**Figure 4.29** Simple linear regressions of chlorophyll 'a' concentration and rotifer density, and discharge and rotifer density, at Nassington during the spring development period, 1994. Both lines significant at \( p=0.05 \) level.

*Regression model for total rotifers (Wansford backwater)*
The independent variables used in the Wansford backwater regression analysis were the same as for the river sites except that they did not include discharge owing to its minimal impact on the system. The model describing total rotifer density was less predictive than for the river sites. Chlorophyll 'a' concentration and temperature described 58% of the variation in total rotifer number over the whole growing season. Chlorophyll 'a' concentration was the most important parameter found to influence rotifer density, with temperature describing a lesser proportion of variability. The importance of chlorophyll 'a' may lead us to suspect some level of food limited growth in Wansford backwater, especially as total rotifer density was so much higher than at the river sites.

The full regression model is given in appendix A.4.7. The resulting regression line describing rotifer density is given below.

\[ Y = 1.559 + 1.812X_1 - 0.034X_2 \]

where \( X_1 \) was log chlorophyll 'a' concentration (\( \mu g l^{-1} \)) and \( X_2 \) was temperature (°C).

4.3.8.4 Potential food limitation at Wansford backwater

The chlorophyll 'a' concentration at Wansford backwater was significantly lower than that of the river sites (\( p=0.002 \), Wilcoxon's signed rank test). Peak rotifer densities were usually short lived and associated with a fall in chlorophyll 'a' indicating a degree of 'top-down' control of the algae (figure 4.27). The daily loss rate owing to rotifer and nauplii grazing was calculated assuming an average individual filtration rate of 0.12 ml d\(^{-1}\) and 40 ml d\(^{-1}\) respectively multiplied by animal density (Thompson et al., 1982, in Reynolds, 1984). These losses were potentially large enough to reduce algal biomass especially during spring, assuming a maximum growth rate of 0.35 (Reynolds, 1984) (figure 4.30).

Although food limitation seemed likely from the periodicity shown in figure 4.27, no conclusive evidence was obtained from the pattern of egg ratio development in \( K. cochlearis \), \( K. quadrata \) and \( Brachionus sp. \) i.e. ratios often remained high despite falling numbers.
Figure 4.30 The potential grazing loss rate of algae in Wansford backwater, 1994, and algal density expressed as chlorophyll 'a' concentration.

Figure 4.31 shows the effective food concentration available to rotifers at Wansford backwater. The levels were above the limiting levels for maximum growth rate of small rotifers.

Figure 4.31 The effective food concentration available to rotifers at Wansford Backwater, 1994.

4.3.9 Comparison of system stability using zooplankton dynamics as an indicator

The proportion of potential development realised each week was calculated from the difference between the population density expected to develop and the actual development observed. The potential increment to the population was calculated from the birth rate assuming exponential growth, no egg loss or failure to develop, and that egg ratio and temperature remained constant throughout the inter-sample period.
The aim of the analysis was to compare the proportion of potential development achieved at the riverine sites with the backwater, the hypothesis being that losses were lower in the backwater system where discharge had minimal dilution effect. Only data from samples with a suitable density of animals and eggs were used. This meant that only egg bearing species, and only certain periods of the year were compared. Data for *K. cochlearis* and *K. quadrata* (n=6) were amalgamated from Wansford station and Nassington and compared with data for *K. quadrata* from Wansford backwater (n=7). A preliminary test showed there to be no significant difference in the proportions of potential development attained by the different species (Kruskal-Wallace test), so amalgamation was considered viable.

The difference between the proportion of potential development attained in the two habitats was tested with a Mann-Whitney U test. Wansford backwater achieved a significantly higher proportion of potential development (p<0.01) than the river sites.

4.4 Discussion

4.4.1 River Nene zooplankton composition

Rotifers accounted for 95% of total zooplankton density in the main channel of the Nene throughout the growing season (Feb.-Oct.) of 1994. This was a similar figure to that of the Rhine which had a zooplankton that comprised 97% rotifers (van Dijk & van Zanten, 1995), Apure with 90% (Saunders and Lewis, 1989), Hudson with over 75% on occasions (Pace *et al*., 1992) and the Po with 98% (Ferrari & Mazzoni, 1989). Cladocerans by comparison were very poorly represented in the Nene. The only crustacean group present in numbers were the copepod nauplii. This group may become abundant in running waters (van Dijk & van Zanten, 1995) owing to their ability to resist and avoid flowing water (Richardson, 1992).

Cladocerans are known to out-compete rotifers in more stable systems when resources becomes limiting (Brooks and Dodson, 1965; Hall *et al*., 1976), so the numerical dominance of rotifers in the Nene indicated a reversal in the normal competitive balance between the two groups. Rotifers were presumably favoured by the physical instability and short retention times associated with the river habitat. Rotifers have the capacity for more rapid population development than cladocerans owing to their shorter pre-reproductive development period, and are therefore more likely to complete reproduction before they are washed out of the system.

The high biotic potential of certain rotifer species is well established in lakes, where
their numbers closely follow those of edible algae during the spring (Sommer et al., 1986), while cladocerans take longer to appear in the plankton. Such species often require high food concentrations to maintain their growth rates, and may be replaced by slower growing species when the food resource is depleted. Food levels were generally high in the Nene, especially during the spring, when chlorophyll 'a' concentration reached over 200 μg l⁻¹. This concentration was considered adequate to sustain high rotifer density, whereas the lower concentrations of the summer period were expected to be associated with cladoceran dominance according to simple competitive theory. The lack of cladocerans was therefore assumed to be driven by physical processes in the river system, even during the slow-flow conditions during the summer.

Other factors may have also favoured rotifers in the Nene. The water was often turbid, as indicated by the low Secchi depths during periods of moderate to high flow, the high levels of abiogenic turbidity (figure 3.15), and the presence of silt / floculent matter in rotifer samples. Small grazers may benefit in turbid environments as they can graze between large inedible particles (Dumont, 1977; Pourriot, 1977; Starkweather, 1980; Bogden and Gilbert, 1982; Gilbert and Bogden, 1984; Walz, 1995) whereas Daphnia are generally considered to have little ability to feed selectively (DeMott, 1982; Lampert, 1987), and therefore suffer decreased feeding efficiency when the medium contains particles poor food quality (Kirk and Gilbert, 1990). Small species also tend to feed more efficiently when the phytoplankton contains high densities of filamentous or toxic algae (Fulton and Pearl, 1987; Gilbert, 1990; Fulton and Jones, 1991) as is often the case in rivers (Hynes, 1970), although blue-green bacteria were poorly represented in the main-channel of the Nene. Predation by planktophagous fish may also favour the dominance of small species by the selective removal of larger animals (Ferrari and Mazzoni, 1989; Telesh, 1993). This may have been important in the Nene, where plankivorous fish density was in the order of 19.7 gm⁻², during 1992 (Balbi, pers. comm.).

The rotifer community of the Nene was dominated by K. cochlearis during 1992 and 1993. Synchaeta oblonga was the dominant species during 1994, accounting for 65% of total rotifer number. Synchaeta are known for their high specific growth rates (Berner-Frankhauser, 1987; May et al., 1993; Walz, 1995) and are therefore adapted to highly disturbed habitats with low retention times. The switch from Keratella to Synchaeta dominance in 1994 may have resulted from the high spring discharge imposing a strong selection pressure on rotifers with high biotic potential.

Species of the genus Keratella and Brachionus are were dominant in the rivers Rhine
(Admiraal et al., 1994) and Meuse (Gosselain et al., 1994). Species of these genera are particularly adapted to life in rivers, owing of their high specific growth rates. *K. cochlearis* may be specifically suited to life in rivers owing to its cosmopolitan nature and tolerance of fluctuating conditions (Ruttner-Kolisko, 1977). Indeed, Ferrari and Mazzoni (1989) considered it as a rheophilous species, becoming relatively more abundant with flow. Zonfal (1989), however, found the plankton of the River Danube was dominated by *S. oblonga*, with *Keratella* and *Brachionus* sub-dominant. The inter-annual variation in community composition in the Nene may have been driven by inter-annual variation in spring discharge.

The rotifer density of the Nene during spring varied widely between study years. The maximum density during 1992 was above 9,000 animals per litre, lower in 1993 at approximately 2,000 animals per litre, and even lower still during 1994 at around 950 animals per litre. The average discharge during April-May, when rotifer populations developed, was 3.37 m³s⁻¹, 7.38 m³s⁻¹, and 11.47 m³s⁻¹ in 1992-1994 respectively. An inverse relationship between population size and discharge was therefore apparent. Other river studies have described a similar relationship for both phytoplankton (Spballe and Kimmel, 1987) and zooplankton (Ferrari and Mazzoni, 1989; Pace et al., 1992).

The maximum rotifer density of the Nene was similar to published values for other rivers including 12,000 l⁻¹ in the Vistula (Kowalczewski et al., 1985), 6,500 l⁻¹ in the Po (Ferrari and Mazzoni, 1989), 4,000 l⁻¹ in the Meuse (Mameffe et al., 1996) and 1,500 l⁻¹ in the Rhine (van Dijk & van Zanten, 1995). The density found during 1994 was, however, lower than most other lowland European rivers, for which data are available.

The low density during 1994 indicated that rotifer population development was restricted in some way. The total zooplankton density of rivers is usually lower than from lakes of similar trophic status (van Dijk and van Zanten, 1995) owing to the advective effects of flow constantly removing animals from the system (Pace et al., 1992), and it would seem that discharge had an effect on annual rotifer density from the above observation. Food limitation may also have been involved during the summer, as the chlorophyll 'a' concentrations were generally low, although further analysis indicated adequate food for development throughout the year, *i.e.* the food-limited carrying capacity of the system was not reached (figures 4.19 and 4.20).

Cladocerans accounted for less than 1% of total zooplankton density during 1994, so the potential for mechanical interference (Gilbert, 1985; 1988; May and Jones, 1989;
Urabe, 1992, Walz, 1995) to limit rotifer abundance was considered to be minimal in the Nene.

Invertebrate predator density was rarely high in the River Nene and so this was also considered to be of minimal impact. The only predators found were the occasional *Asplanchna sp.*, known to have an effect on vulnerable species such as *K. cochlearis* (Gilbert, 1980) and copepods, which may predate species such as *Polyarthra spp.*, *Keratella cochlearis*, and *K. quadrata* (Brandl and Fernando, 1978; Zankai, 1984; Walz *et al*., 1987). Neither were recorded at high density during 1994 (both had a maximum density of less than 5 individuals per litre) and were therefore assumed to have little impact on rotifer population dynamics.

The Environment Agency reported a mean fish biomass of 19.7 g m⁻² and a mean density of 0.38 fish m⁻² from the Nene between Northampton and Peterborough, during the period April to October, 1989. The dominant fish were roach, bream, chub and dace, all of which may take small zooplankton prey during their development (Hammer, 1985; Telesh 1993). The rapid decline in rotifer density at the end of May, especially considering that food was abundant (high *K. cochlearis* egg ratio during decline phase, figure 4.18) may have been hastened by the activity of 0+ predation in the Nene.

The potential for vertebrate predators, namely planktivorous fish, to limit rotifer numbers has, however, been the subject of some debate. Rotifers were generally considered too small to be a viable prey item for mature visual predators by Stenson (1982) but were considered suitable for the young larvae of fish such as carp, roach and perch during their early development by Hammer (1985) and Kogan *et al*., (1980). The rotifer *Brachionus plicatilis* is widely used in aquaculture as the sole food source of many marine fish larvae such as mullet (*Mugil cephalus*) and sole (*Solea solea*) (Lubzens *et al*., 1989; Lubzens *et al*., 1993). The impact of young of the year predation on pelagic rotifers was, however, thought to be of small ecological importance as larvae live in littoral or near benthic habitats (Walz, 1995) or forage around the emergent vegetation / open water ecotone (Garner, 1996). An assessment of the impact of these animals on rotifer populations would be extremely useful in understanding the population dynamics of susceptible rotifer species.

4.4.2 Factors controlling zooplankton dynamics in the Nene

Multiple linear regression analyses were performed on the Nene data-set to assess the level of control displayed by discharge, chlorophyll 'a' and temperature on
zooplankton dynamics. Oxygen, pH and turbidity were also used in some of the analyses as they may influence zooplankton dynamics (Radwan, 1984; Mikschi, 1989, Kirk and Gilbert, 1991), but none were found to be significant in the Nene models, indicating that the other factors were more influential.

Regressions for the whole growing season of 1994 showed that chlorophyll 'a' was the only independent variable which described a significant proportion of the variation in rotifer density. Similar results were found for total *Keratella* density and *Brachionus* density, although discharge was also included in the model. Discharge was, however, of secondary importance as the majority of residual variation was described by chlorophyll 'a' concentration.

The lack of a positive association between rotifer density and temperature throughout the whole growing season of 1994 was not surprising considering that density was low during summer when temperatures were high. Similarly, the negative relationship between discharge and density was not as strong as expected, as low density was often associated with low discharge during the summer months when rotifers were expected to flourish if simply controlled by flow rate.

Chlorophyll 'a' was the only variable found to significantly predict rotifer density during the spring of 1994 and also during the spring period of 1992-1994, when temperature was also included in the model. Discharge was not included in any of the spring models.

In all cases, the association of rotifer density and chlorophyll 'a' was a positive one. High rotifer density was precluded at low food levels indicating possible food limitation. Care must be taken, however, if assuming a trophic link between the two variables, as physical control may have had a similar effect on the two variables, thereby forcing a significant regression without any true causation (covariation, see below). Indeed, such a close relationship between the food resource and rotifer grazers was unexpected if food limited population growth, as there were no examples of 'grazer-overshoot', when the rotifer population remained high for a short period after a fall in algal density. This was taken as a sign that both rotifer and algal density were controlled in a similar manner by other forces *i.e.* planktonic 'organisms' were controlled as a single group, irrespective of whether they were animal or plant in origin. Zooplankton food limitation was shown to be unlikely in the Nene, as the carrying capacity of the system was rarely reached. A similar conclusion was drawn by Pace *et al.*, (1992) in the Hudson river, who considered physical control to be of primary importance.
The omission of discharge from the majority of the Nene regression models was unexpected considering the fact that it is generally thought to be of primary importance in defining the zooplankton structure of river systems (Hynes, 1970). This was thought to be owing to an interaction between chlorophyll 'a' and flow rate. Figure 4.32 shows that the two variables were themselves negatively correlated, i.e. high discharge was associated with reduced algal concentration during spring.

When two independent variables covary the one which describes the greatest residual variation remains in the model. In the case of the Nene models, this was chlorophyll 'a' concentration, although it makes very little biological sense to ignore discharge as figure 4.16 shows. It is much more likely that discharge had a similar effect on both the suspended algal and zooplankton populations controlling potential population loss rates i.e. when conditions were favourable for algal development, they were suitable for rotifer development, and vice versa. This would describe the synchronicity of the two parameters.

\[ y = -0.655x + 2.288 \quad r = 0.676 \]

Figure 4.32 Regression relationship between discharge and chlorophyll 'a' abundance in the River Nene during spring 1992-1994.

The form of the negative exponential relationship between discharge and rotifer density (figure 4.16) was similar to that found by Vranovsky (1995) in the Danube. Rotifer density was highly variable at flow rates less than 5 m³s⁻¹, indicating that other forms of control were important when physical control mechanisms associated with flow were minimal. These may have been more akin to biotic interactions which influence planktonic communities in more stable systems. Flow rates above 5 m³ s⁻¹ were all associated with low rotifer density. A flow rate of approximately 5 m³ s⁻¹ or 0.08 ms⁻¹ is proposed as a threshold for rotifer development in the Nene, above which a plankton cannot develop to great density. Vranovsky (1995) proposed a lower
velocity of 0.01 \text{ m s}^{-1} \text{ as the flow-threshold for the Danube.}

The model with the greatest power to predict rotifer density in the Nene used monthly average values for both dependant and independent variables over the spring period 1992-1994. This model may have been more successful in describing rotifer variation because it used a less detailed scale of measurement which smoothed the effects of short term fluctuations to which rivers are vulnerable. Discharge, chlorophyll 'a' and temperature were all significant predictors of rotifer density. These variables were considered to be of primary importance as they have the ability to control the balance between growth and loss rates, and thereby dictate the capacity for survival of any population (van Dijk and van Zanten, 1995).

4.4.3 River Nene rotifer dynamics

Detailed population parameters were calculated for \textit{Keratella cochlearis} to gain an understanding of how riverine zooplankton were developed and maintained in the Nene. The temporal distribution of this species was very similar to that of total rotifiers, especially during 1992 and 1993 when it was the dominant species, and was therefore considered to act as a suitable 'model' organism for riverine rotifers.

The obvious limitations of applying the classic method of population analysis to an inherently unstable river population must be recognised. The analysis is dependant on a number of assumptions, one of which is that there is no immigration to, or emigration from, the population between observations. The weekly sample regime and the highly mobile nature of river plankton is likely to cause this assumption to be violated, and therefore weakens this analysis. The following discussion should therefore be viewed with these limitations in mind. Some indication of the degree immigration/emigration, and a shorter inter-sample duration would increase the validity of results.

The egg ratio, which can act as an indication of food limited population growth, was high throughout most of the spring development period, leading to high birth rates especially during May. The instantaneous population growth rate was, however, usually below the birth rate, as indicated by the high death rates and the low proportion of birth rate actually realised. This was most noticeable during 1993 and 1994 when total densities declined after a relatively explosive period of increase in spite of constant egg production. The pattern was somewhat different in 1992 as density increased steadily throughout May, although the population was still subject to constant high death rates. The high birth rates (and egg ratios) indicated that rotifer
growth was not food limited during the spring, even when populations fell at the end of May.

The high death rates imposed on the *K. cochlearis* populations imply that the system was driven by loss process. There was also the possibility that some eggs failed to develop to maturity owing to selective predation on fecund females or the production of resting eggs for 'seeding' next years population.

Negative death rates were observed during April of 1993 and 1994. They have previously been viewed as a shortcoming of this method of population analysis (Bosch and Ringleberg, 1985; Andrew and Fitzsimons, 1992; Urabe, 1992), although they can result from a significant importation or the hatching of resting eggs. The consistent timing of the initiation of the spring peaks and the fact that negative rates occurred at the start of development led to the conclusion that the development of individuals from resting eggs formed a significant part of the spring increase in the Nene. This was probably also the case in 1992 when death rate was low, but not negative. Importation of animals from other sources such as dead zones, was unlikely to cause this phenomenon as discharge was low during the period and had little potential to crop excess productivity from these zones into the main-channel.

The change in temperature during April, from below 10°C at the start of the month to 15°C at the end, may have cued the hatching of resting eggs from the sediment of the Nene. This would help to explain the synchronisation of population development between the three years, as the temperature of the water during April was similar. May (1987) showed that temperature controlled the hatching of nine species of rotifer resting eggs including *K. cochlearis*. Hatching was maximal at temperatures between 10 - 15°C, and all eggs hatched within a 14 day period. Similar pulsed release was shown by Nipkow (1961, in Gilbert, 1974) for 30 species of rotifer, all of which hatched within 8 days of a shift in temperature from 4-6°C to 12-14°C. Other environmental parameters may also illicit release of resting stages such as photoperiod (Pourriot, 1965 in Scott, 1977), chemical composition of bathing water (Ruttner-Kolisko, 1964, in Scott, 1977) and salinity (Pourriot and Snell, 1983), all of which may have been influential in the Nene.

Once the population had reached a peak in 1993 and 1994, the density declined quite rapidly. It is therefore possible that the spring development was initially reliant on the hatching of resting eggs, after which time the reproductive output was insufficient to offset losses, hence the decline. This hypothesis gains strength when one considers that birth rates are reduced by the production of resting eggs, which do not develop
until after a period of dormancy, and may therefore hasten the decline of standing populations that are subjected to high loss rates in rivers. For example, *Keratella cochlearis* from the river Nene were found to produce resting eggs at a constant rate and hence suffered lower intrinsic rates of increase compared to a reservoir population.

The overall periodicity of rotifer development in the Nene was somewhat different to the normal pattern expected in lowland rivers. The dynamics in these rivers are characterised by a typical seasonal pattern: low densities in winter followed by a spring peak and relatively high density during the summer (van Dijk and van Zanten, 1995). Low densities were recorded in the Nene, followed by a defined spring peak after which numbers crashed. The density never recovered during 1993 and 1994, remaining low through to October when sampling was terminated. This lack of a plankton during summer was rather mysterious considering the fact that discharge was low, and therefore dilution loss rates were also low.

The reasons for the rapid spring crash and summer low density are difficult to assess without further data, and this is an area that deserves further work. Hypotheses regarding the rapid decline in density that deserve consideration include the action of 0+ vertebrate predators during the spring and the change in algal composition from diatom dominance to green algae, although the latter is unlikely to have an impact on general feeders such as *K. cochlearis*. The production of resting eggs may also decrease birth rates sufficiently to cause problems to extant populations. The role of dead zones may also change with flow conditions from source habitats when flow rate is sufficient to 'crop' internal production to isolated habitats when flow rates are reduced. Under such conditions certain zones may develop a plankton dominated by lacustrine species that are poorly adapted to riverine conditions when finally flushed into the main channel.

### 4.4.4 Resting eggs

The adaptive significance of resting egg production may stem from the fact that these eggs settle into the boundary flow layer and are less liable to downstream movement than entrained particles. They can therefore act as the 'seed' for next years population growth along the length of the plankton bearing stretch of the river. Whether this strategy is widespread among other riverine species is an interesting question that deserves further work. The development of the, as yet, undocumented strategy of constant sexual reproduction in the Nene *K. cochlearis* population provides evidence of the strength of the selecting agents acting in rivers which may illicit similar
responses from other riverine species.

Resting eggs from *K. cochlearis*, *K. quadrata*, *Brachionus sp.* and *Synchaeta oblonga* were all recorded in the plankton of the Nene. They tended to be produced prior to population decline, when food levels were high, as indicated by the presence of females carrying two eggs. They were therefore not the product of a density dependant cue, but were probably a specific life history trait adapted to cope with life in unpredictable, short-retention time systems, where the chances of being permanently lost downstream were reduced by 'seeding' the sediment with eggs for development in the next season.

Pontin (1989) found that the colonist species *Keratella valga* and *Brachionus urceolaris* produced resting eggs prior to reaching their peak abundance before food became limiting. The production was therefore not related to density dependant stresses, the often cited reason for sexual reproduction in rotifers (Gilbert, 1974, Hofmann, 1977), but was a direct adaptation to life in ephemeral water bodies.

The size of the resting egg bank, and hence the population that develops from this source when conditions are favourable for hatching, is dependant on the density of animals achieved in the preceding season (May, 1987). The high density of *K. cochlearis* in 1992 may therefore have left many resting eggs which contributed to the initial, explosive, development of 1993 which was associated with negative death rates (figure 4.18). The initial development of 1994 was associated with a smaller negative death rate, and reached a much lower biomass than 1993. The resting egg bank may have been smaller than that of the previous year, as the maximum density of *K. cochlearis* was smaller in 1993 than 1992, and the number of resting eggs observed in samples was also smaller.

It is difficult to predict whether the development of the 1992 population was similarly supplemented by a significant hatching of resting eggs, although the two highest rates of increase were associated with the first two weeks of the development when hatching was expected.

Reynolds (1994a) showed that slower growing species could dominate short retention time habitats for an extended period of time as long as their starting population numbers were high. The initial size of the inoculum from resting eggs may therefore have had a profound effect on the persistence and size of *K. cochlearis* populations, and may be important to the ecology of riverine species.
4.4.5 The potential for food limitation in the Nene

Food limited growth was one possible reason for low rotifer abundance throughout 1994 and especially during the summer periods of 1993 and 1994 when densities were low. Stemberger and Gilbert (1985) stated that food limitation, defined by the population threshold, was as important as predation, competition and abiotic factors in controlling species populations. This factor was therefore investigated to test the potential for 'bottom-up' control of riverine zooplankton populations in the Nene.

Food availability is also important as it partly dictates the rate at which a species reproduces by controlling the rate of egg production (Sarma and Rao, 1991) and the duration of juvenile development (Walz, 1995) along with temperature. Maximum rates of increase are achieved at a food concentration some way above the threshold for development, termed the incipient limiting level (ILL).

The extant food levels at Wansford were in excess of the incipient limiting level for 'small rotifers' typical of those found in the Nene (figure 4.19). This implied that food limitation was unlikely, even during the summer months when chlorophyll 'a' levels were relatively low. The carrying capacity of the system, in terms of the number of rotifers sustained when population growth is zero, was calculated from the individual threshold concentration for a typical rotifer, assuming no losses other than those of senility (figure 4.19). The results showed that the total rotifer density never reached the carrying capacity, even when environmental conditions were favourable, again indicating that the system was not strictly controlled by food or density dependant factors, but more likely by loss mediated processes.

Two major assumptions, both of which relate to the use of literature derived estimates of threshold food concentration, were made during the calculation of the carrying capacity which may have led to its overestimation from field data. These are discussed below.

The first was that the threshold food concentration (minimum concentration of food required to meet an individual's metabolic costs) were invariably defined under strictly controlled laboratory conditions, including the use of a high quality food source (Stemberger and Gilbert, 1985). Natural algal assemblages are much more diverse than this and contain a range of taxa, most of which are of reduced nutritive value to rotifers. The absolute concentration of food (measured as chlorophyll 'a') required to offset metabolic losses will therefore be higher under natural conditions, as the assimilation efficiency per unit weight of algae will be less than with a high
quality source alone. The extent to which this occurs depends on the composition of the algal community and cannot easily be defined. The algae found at Wansford were, however, dominated by the smaller size ranges which should have constituted a relatively palatable food resource (refer to section 4.3.1.5).

The second problem with the calculated carrying capacity is that it was originally derived from a literature estimate of individual threshold food level. This cannot be directly applied to populations with a loss rate above that owing to senility alone as increased food is required to allow lost animals to be replaced through increased rates of reproduction. This assumption is therefore of some importance in the Nene where loss processes were presumed to be large (high death rates). For example, when a population is subject to losses \((d')\), but the instantaneous rate of increase \((r)\) is zero, the individual threshold energy required is increased, owing to the need to increase birth rate \((b')\) to replace lost animals so that the equation \(r = b' - d'\) equals zero.

The 'utilisable harvest' of chemostat cultures works under a similar principle. More food is required by steady state populations to offset increased rates of export, until \(r_{\text{max}}\) is achieved at the ILL (see figure 4.33). After this point, if losses continue to rise, the population declines to extinction. If the loss rate from river populations is greater than the maximum rate of increase under saturating food levels, the population will have a similar fate unless numbers are supplemented by imports.

Figure 4.33 Graphic representation of the population threshold food concentration under different loss rates. \(C_0\) represents individual threshold concentration, \(R_1\) is the population threshold when mortality rate \(m_1\) applied. \(R_{\text{ILL}}\) (incipient food level) is the food concentration required when the loss rate, \(m_2\), is equal to maximum growth rate. Modified from Rothhaupt (1993b).
The threshold concentration of river populations, which are subject to continual export downstream, will therefore be greater than the individual threshold value used in the production of figure 4.19 (R as opposed to Co in figure 4.33). As a result of this, the carrying capacity of the system will be smaller than estimated, reducing confidence in the initial conclusion that food did not limit growth in the Nene. The fact that the extant food concentration was in excess of that required for maximum growth rates of small rotifers does, however, indicate that food was probably in abundant supply, and that population density was curtailed by some other factor than reduced growth rates.

4.4.6 River function

Estimated loss rates owing to dilution from the Wansford stretch of the river, assuming no imports, were much higher than the potential birth rates during the spring of all three years, raising the question of how a plankton developed at all. The fact that it was able to develop implies that the estimated loss rate was too high, either owing to an inadequacy of the simple flow model used to predict losses or the fact that plankton was imported with flowing water, thus reducing dilution losses. These two explanations are not mutually exclusive as increased hydraulic retention will aid the maintenance of a plankton which will be imported to downstream sections with flow.

The calculated loss rate may have been higher than that in reality as it was based on a purely physical model of water movement through the section. It took no account of the holding nature of dead zones (Young and Wallis, 1987) which increases the overall retention time of a river stretch, and therefore reduces loss rates accordingly (Reynolds and Glaister, 1993). No attempt was made to estimate the extent of the aggregate dead zone in the Wansford section owing to their diverse nature and the problems associated with estimating the rates of fluid exchange across their boundaries. A survey of potential dead zones in the Nene did, however, show different zooplankton structure and density in certain areas of the river compared to the main channel, thus proving the existence of these zones. Dead zone imports from within the Wansford section may therefore have introduced organisms to the main channel thus helping to reconcile the discrepancy between estimated loss rates and actual loss rates.

Loss rates were overestimated by ignoring importation to the section. In reality, imports from the river section directly upstream of Wansford were expected, as there was no reason to believe that Wansford was the first section to develop a plankton.
This importation was likely to be a significant proportion of the population at Wansford owing to the physical similarity of the river along its lower reaches. The level of importation required to balance the population dynamics of *K. cochlearis* at Wansford, assuming dilution rates were the dominant loss process, was found to be approximately 76% of the standing population during May, 1994.

This importation may come from a mixture of sources, including the hatching of resting eggs, cropping of dead zone productivity, and wash-in from upstream sections. The estimation of importation required was, however, rather subjective owing to the assumption that all deaths were the result of dilution. In reality, no correlation was found between observed death rate and discharge in the Nene, indicating that other sources of death may also be important. If other death rates had been accounted for, the level of importation required may have been even greater. It would therefore be extremely useful to obtain data on predation rates and natural death rate to strengthen this part of the analysis. The over-riding conclusion from this piece of work, however, was that the river section at Wansford was reliant on external importation to maintain a population.

The actual level of importation from upstream sections was found to be variable along the length of the lower Nene, based on a single sampling occasion during the summer of 1996 (section 4.3.10). Each section had a relatively similar plankton density which added to that of the next with the movement of water, and therefore provided evidence that actual losses were well below those calculated assuming no imports. In some cases the level of importation was > 100% of the density in the section itself, implying a net hydraulic gain, although it must be stressed that these results applied to a summer period when flow rate was low.

Rotifer density did not increase with downstream transit in the Nene as expected from other river studies as a result of the 'age' of the water (Hynes, 1970; Saunders and Lewis, 1989; Reynolds and Glaister, 1993; Admiraal *et al.*, 1994)). Crustacean density increased towards North Side, where the number rose to 686 animals per litre, and included *Bosmina longirostris* and *Daphnia galeata* (accounting for 23% and 8.2 of the total respectively). The chlorophyll 'a' density also decreased from above 100 μg l⁻¹ at Ferry Meadows to 80 μg l⁻¹ at North Side. The reason for the reduction of rotifers is somewhat unclear as food limitation was not expected at these algal densities, although competition from cladocerans and potential shifts in the composition of the algae may have made this more likely. Predation by adult copepods may also have had an influence (Walz *et al.*, 1987; Williamson and Butler, 1986). The downstream decrease may also have been owing to conditions resembling
the 'sedimentation zone' of other lowland rivers such as the Rhine in which a
downstream decrease in rotifer density was also noted (de Ruyter van Steveninck et

In such cases the decrease was often accompanied by an increase in crustacean
density, usually dominated by copepods and their nauplii (van Zanten and van Dijk,
1994) but also including *Bosmina longirostris* and *Daphnia sp.* (de Ruyter van
Steveninck et al., 1992; Admiraal et al., 1994; Tubbing et al., 1994). The area of the
river where this transition occurred was termed the 'sedimentation zone', as algal
density also declined owing to increased rates of settlement from less turbulent water.
The longer retention times and reduced food level in such regions favours crustacean
development with lower thresholds for growth than rotifers (Walz, 1995). The area of
maximum rotifer density is usually situated just above this zone but differs according
to the flow regime in the river. The River Meuse, which is highly modified and
subject to low summer discharge, had a maximum plankton density (up to 4000
rotifers) somewhat further upstream than the less regulated River Rhine which had a
more constant discharge (Gosselain et al., 1994).

Rotifers were considered unlikely to be affected by sedimentation themselves until
after death, as they are motile. Balbi (pers. comm.), however, found large quantities of
rotifers in sedimentation traps around Wansford which indicates that natural death
rates may have been high during the summer. The downstream reduction of rotifers
after Wansford during the summer may therefore have been owing to a combination
of food limited growth with the sedimentation of algal particles (the egg ratio
decreased from 0.792 at Fotheringhay, to 0.589 at Wansford, to 0.562 at Ferry
Meadows and finally 0.220 at North Side) and high death rates followed by
sedimentation.

The results of 16.6.96 showed that it was feasible to obtain importation from upstream
sections of similar magnitude to the losses with flow during the summer. During such
periods the river acted as a long reservoir, each section undergoing population cycles
presumably driven more by environmental forces than physical loss processes.

The actual source of losses remains somewhat of a mystery if upstream sections
import plankton at high density and further work in this area is needed to fully
understand the functioning of the Nene throughout the year, as it seems the river acts
in different ways depending primarily on the flow rate.

The picture may have been somewhat different during the spring when flow rates
were higher. The role of dead zones in the maintenance and downstream enhancement of populations was probably more important than biotic control during these periods. The analysis would therefore benefit from similar sample transects at other times of the year.

4.4.7 Retention zones of the Nene

Nassington side-channel and Wansford backwater both had a denser plankton community than the main channel of the Nene, and therefore had the potential to act as source areas when water was exchanged between them. The relative difference between source areas and main channel depends on the frequency with which they are flushed. The zooplankton of backwaters is more likely to differ in terms of density and composition than the zooplankton of channel habitats, as backwaters are generally more stable. This was shown by the respective community structures of Nassington and Wansford backwater.

Nassington had a similar zooplankton community structure to that of the main channel. The only difference between the two was the significantly higher density of rotifers and copepod nauplii. Conditions were not sufficiently different, however, to force a more pronounced change in the community composition, e.g. to one dominated by cladocerans, even though retention time was increased. This may have been owing to the frequency with which the side-channel was disturbed, which would tend to favour rotifer dominance, but may also have been contributed to by high abiogenic turbidity and planktivorous predation (Telesh, 1993), both of which decrease the likelihood of cladoceran development. A similar conclusion was found by Threkeld (1982) who proved that the physical condition of river water entering a reservoir precluded cladoceran development rather than the advective movements themselves.

Other side-channel habitats had a plankton composition that differed more markedly to that of the main channel. For example, a channel 800m upstream of Wansford station, sampled during September 1994, had a plankton dominated by *D. pulicaria*. This backwater differed from Nassington in that it had only a single connection with the river and therefore had a reduced rate of water exchange. The longer retention time allowed cladoceran development as did decreased turbidity. Large stands of submerged macrophytes, dominated by *Elodea*, were present which may have acted as a refuge from visual predators.

The zooplankton composition of Wansford backwater was somewhat different to that
of the main channel. The density of rotifers was significantly higher than Nassington or the main channel, and there were noticeable differences in the dominant species. Rotifers were still dominant even though the longer retention time and lower chlorophyll 'a' concentration of this system should have suited cladoceran development. The lack of *Daphnia* was therefore probably owing to 'top-down' predation pressure from planktivorous fish. No fish data were available to back-up this assumption but the small size-structure of the plankton is strong circumstantial evidence.

Notable changes to the rotifer community structure included the lack of *Brachionus*, the reduction in the dominance of *K. cochlearis*, and the increased density of *Polyarthra*. *Brachionus* were considered well adapted to river habitats owing to their r-selected life-history traits, but less well adapted to the backwater site with its lower food concentration. *K. cochlearis* was classified as a rheophile by Ferrari and Mazzoni (1989), ideally suited to flowing habitats owing to its hydrodynamic shape and thick lorica. It is therefore not surprising that this species was relatively less abundant in the lentic waters of Wansford backwater. Similarly, *Polyarthra*, classified as a taxa prevalent in slower flows by Ferrari and Mazzoni (1989), was the dominant rotifer in the backwater, but was virtually absent from the river habitats. The community structure therefore mirrors the difference in physical structure between the river and the backwater.

Community diversity at Wansford backwater was generally lower than that of the river, reflecting the greater stability of the backwater. Stability was also inferred from the greater proportion of potential development actually realised. Loss rates were generally less than in the river and hence larger populations were able to develop.

Food levels were lower in the backwater than in the river but much larger rotifer densities were supported. Some degree of food limitation was expected as shown by the relationship between rotifer density and chlorophyll 'a' peaks, but the proportion of carrying capacity attained was still relatively low. This was, however, greater than that attained in the river habitat, again indicating that this system was more stable. The presence of higher rotifer density at this site is important indirect evidence of the lack of food limited growth during spring in the river, where chlorophyll 'a' levels were much higher. High loss rates were therefore a much more likely reason for the low rotifer density in the river during 1994, compared to the backwater habitats.

The potential for the two backwaters to add to the river plankton differed. The relatively large connection between Nassington and the river ensured a constant
exchange of water between the two habitats. The similarities between community structure also ensured that plankton from Nassington had a degree of 'pre-adaptation' to life in flowing water. In this sense, Nassington had a degree of similarity with in-channel retention zones under the classification of Saunders and Lewis (1989). Wansford backwater was expected to have a different influence on the river. The levee between the two habitats ensured that plankton only entered the river during high flows, when they were likely to be washed downstream quickly. The abundant non-rheophillic species were also less likely to fare well in high flows, especially the soft bodied attenuated forms such as *Polyarthra sp.* (Ferrari and Mazzoni, 1989). Therefore even though Wansford Backwater had a high rotifer density, the species composition and timing of importation to the river decreased the potential for this dead zone to influence the potamoplankton.

Inputs of this type were apparent on 16.9.94 when water level was rising and flushing out plankton from such habitats. The density of animals showed a definite increase, as did community diversity and species richness, both of which were the highest recorded throughout the study period, indicating the diverse origin of the animals. The increased density of rotifers was short-lived as numbers declined to low levels within seven days of the peak.

Rotifer community diversity was significantly associated with discharge during 1994. Ferrari and Mazzoni (1989) came to a similar conclusion in the Po River where spate events destabalised the zooplankton structure causing a reduction in the density of dominant taxa and the introduction of new taxa at a low density. Species richness was also positively associated with discharge in the Nene. High flow rates were therefore responsible for the importation of a number of species to the main channel from source habitats either within the channel or connected habitats. The presence of littoral species in the plankton also strengthens this conclusion, as they were only present as migrants, washed from their more natural habitats by variable flow rate, and never attained high density in mid-channel. The plankton of the Caura River was almost exclusively dominated by 'drift' animals washed into the main channel from connected source habitats (Saunders and Lewis, 1989). Zooplankton diversity and density was positively correlated with discharge in this case, as the river itself was too fast flowing to allow the development of any pelagic rotifer community.

4.5 Summary

The following list presents the dominant features of zooplankton development in the river Nene based on the 1994 growing season, and the spring period of development

1. The zooplankton was dominated by rotifers irrespective of differences in flow regime between years.

2. Rotifers were at low abundance during the winter owing to slow growth rates and high dilution rates.

3. Phytoplankton density increased prior to zooplankton which required a higher temperature to raise birth rates above dilution rates.

4. Development of resting eggs, cued by an increase in temperature from 10°C to 15°C, was an important feature of the initial spring development. Populations reinvested part of their growth to re-seed the resting egg bank for next year. The conditions which dictated the onset of sexual reproduction are not known, but they were not density dependant as populations remained well above the food limited carrying capacity.

5. The maximum rotifer density attained during the spring was determined by the balance between population growth rates and loss processes. The highest density occurred in 1992 when discharge was lowest, while the lowest density was associated with the highest spring discharge in 1994, indicating the importance of discharge for riverine zooplankton development.

6. Rotifer populations declined rapidly approximately one month after the initial development. The reason for this was unclear as the environmental controls seemed to differ from year to year. An increase in discharge was apparent at the same time as rotifers declined in 1992 and 1993 which may have increased loss rates and hastened their decline. Chlorophyll 'a' concentrations also crashed at the same time indicating the effect of flow rate was felt by all planktonic organisms. The crash of 1994 was not concomitant with increased discharge indicating that other loss processes were involved.

7. Populations did not recover over the summer of 1993 and 1994. This seems puzzling as discharge was low (reduced loss rates), and temperatures were high. Low summer chlorophyll 'a' levels may have been involved, but little potential food limitation was found.

8. The periodic increase in rotifer density and diversity during September 1994,
showed the potential importance of dead zones in the Nene system, although imported animals were rapidly removed from the main channel owing to high flow rates which initially washed them into the river.

9. The over-riding influence of discharge on the river system was shown by the threshold discharge for rotifer development which was approximately $0.08 \text{ ms}^{-1}$ in the Nene, at Wansford. Little zooplankton development was expected at flow velocities above this level.
CHAPTER 5

THE LIFE-HISTORY CHARACTERISTICS OF ZOOPLANKTON FROM
THE RIVER NENE AND RUTLAND WATER

5.1 Introduction

Chapter 4 introduced the diversity of life-history strategies found within the pelagic
filter-feeding zooplankton. The strong selective pressures acting in river habitats should
restrict this diversity to a small number of optimally adapted strategies. The following
chapter introduces these selective agents, predicts the optimal life-history traits for river
species, and tests these predictions by comparing traits of species from a riverine and a
lacustrine environment.

5.1.1 Selection for life-history traits

Life-histories can be defined as a set of co-adapted reproductive traits, resulting from
historic selection events in a particular environment (Brown, 1983). This line of
thinking follows that described by Stearns (1977) who attributed the evolution of
similar strategies in a wide range of organisms to the selective power of environmental
conditions acting on animals. Similar life-history traits are therefore expected to be
displayed by animals living in similar environments, especially if the environment is
perceived as ‘harsh’ in terms of the constraints placed on growth and reproduction.
Such environments are usually subject to high, and unpredictable disturbance
(Reynolds, 1992; Townsend and Hildrew, 1994).

The concept of life-history selection is often summarised in terms of $r$ and $K$- selection
(MacArthur and Wilson, 1967; Pianka, 1970) as this is the generally accepted theory
concerning physiological / morphological adaptation to environment (Barclay and
Gregory, 1980; Romanovsky 1985). Examples of specific life-history traits that can be
selected for include:

a) the allocation of energy to reproduction or somatic growth once mature
b) post embryonic development time
c) relative egg size
d) number of eggs produced per unit time
e) threshold food concentration for development
f) longevity
g) the production of resting stages.
Variation in such characters determines the position of a particular individual along the $r$ / $K$ continuum and identifies the type of habitat in which the animals will be successful (Townsend and Hildrew, 1994).

5.1.2 River habitat templates

The idea that certain combinations of life-history traits develop under different environmental stimuli, or 'habitat template axes', can be used to predict the optimal strategies for particular habitats. The axes used as a framework for river habitat templates (features of the environment that exert the greatest selective pressure) were defined by Southwood (1977). One axis represented temporal heterogeneity of the habitat, i.e. the frequency and predictability of disturbance, the second axis represented spatial habitat heterogeneity.

Sections of a river that are subject to frequent disturbance of low predictability should theoretically favour species with $r$-selected traits which are geared towards rapid population development under non-limiting growth conditions. These species were termed scramble competitors or ruderal species under the classification of Grime (1977; 1979). Stress-tolerators ($K$-selected species) have a distinct disadvantage in such conditions owing to their slower individual growth rates and lower reproductive potential once mature. Such species generally come to dominate planktonic communities in more stable systems of lower trophy (Romanovsky, 1984; 1985), where resource-limited competitive ability is a more advantageous characteristic.

Spatial heterogeneity may modify the effects of temporal disturbance. Diverse habitats are more likely to include areas in which the disturbance is less intense, for example the side channels of a river. These areas have a more stable structure and may therefore act as refugia for $K$-selected species. A natural river system with high habitat diversity may thus contain organisms displaying a number of life-history strategies, each adapted to the specific environmental conditions to which they are exposed.

The combined effects of the two template axes on life-history adaptation are represented in figure 5.1.

The most important temporal disturbance in river systems is that of flow (Townsend and Hildrew, 1994), although the importance of changes in water quality associated with altered discharge cannot be discounted (Threkeld, 1982). This level of disturbance is maximal in the mid-channel pelagic zone where spatial heterogeneity is low. Under such conditions, the combination of life-history traits expected to predominate are those
associated with r-selected species (figure 5.1, zone 4), such as a short pre-reproductive period, high reproductive output once mature, and short life-span which convey a degree of resilience to disturbance.

![Conceptual representation of potential river systems based on the two habitat templet axes of temporal and spatial heterogeneity, after Townsend and Hildrew (1994). Italicised text refers to habitat characteristics, bold text refers to suitable life-history traits. Stable habitats include reservoirs or summer periods in impounded rivers, disturbed habitats refer to unregulated rivers. K-selected traits dominate in stable systems owing to their competitive advantages, although r-strategists may dominate initially owing to their high biotic potential. r-selected traits are favoured in disturbed habitats, although spatial heterogeneity may allow K-strategists to become locally abundant. Zone 4 is typical of the pelagic environment of many rivers. Only r-selected traits are adapted to this habitat type, where rapid reinstatement through reproduction is the only method to offset the losses caused by disturbance.](image)

**Figure 5.1**

**5.1.3 Typical riverine plankton**

The dominant life-histories of potamoplankton fit with the general predictions outlined above. The pelagic environment of most rivers is dominated by groups which express some r-selected traits. The phytoplankton is usually dominated by diatoms and small green algae which have rapid intrinsic rates of increase (Reynolds, 1984; 1994b), while slower growing species, such as the cyanobacterial species *Oscillatoria aghardii*, are confined to slow flowing 'dead zones' during the summer months (Reynolds and Carling 1991). The dominant zooplankton group of rivers is the Rotifera (Winner, 1975; Pace et al., 1992; Descy, 1994; Thorpe et al., 1994; van Zanten & van Dijk, 1994). These animals have limited ability to avoid flows but are resilient to disturbance owing to their parthenogenetic mode of reproduction, short generation times and high
potential rates of increase (van den Brink et al., 1994). Those species with the highest growth rates, for example Brachionus spp., and Synchaeta spp., typify the plankton of rivers (Hynes, 1970) and were termed ‘fugitives’ by Hutchinson (1951) owing to their dominance in highly disturbed habitats.

5.1.4 Typical lacustrine plankton

Lake zooplankton communities are often dominated by cladoceran grazers with more K-selected life-history traits suited to competition for limiting resources rather than ‘explosive’ growth. These traits include low rates of individual growth, prolonged time to maturity and the production of few large eggs. The greater competitive ability of species with these characteristics, compared to rotifers, stems from their larger individual size and the metabolic benefits which this conveys, according to the ‘size efficiency hypothesis’ of Brooks and Dodson (1965). Larger animals also benefit from the greater starvation resistance of adults (Romanovsky, 1985) and young (Gliwicz and Guisande, 1992) and the lower threshold food concentration for development (Gliwicz, 1990) which allows them to survive periods of low food availability which are fatal to rotifers. Indeed, the threshold food concentration was considered one of the most important life-history characteristics of zooplankton which defines their temporal and spatial distribution in waters of different trophic status (Romanovsky, 1984; 1985).

r-selected species are not precluded from more stable habitats, but are temporally restricted to periods of the year when competition for resources is low such as early in the spring prior to cladoceran development (Sommer et al., 1986).

5.1.5 How can the dominance of rotifers in river systems be explained?

A degree of overlap exists between the life-history characteristics of rotifers and cladocerans, so the division between the two groups is 'not clear-cut'. Rotifer dominance in rivers may be explained by the speed with which they respond to environmental change (Walz, 1993d) via a combination of short development times and high birth rates. The duration of juvenile development is influenced by temperature and food level but can be as little as two days under optimal conditions (Walz, 1993c).

Some cladocerans may have birth rates equal to those of rotifers, but they have relatively longer generation times of 8-14 days (Porter et al., 1983) owing to an extended period of pre-adult development which acts as a time lag to population development. Cladocerans have to complete a number of molts prior to reaching maturity which takes upwards of six days, depending on the temperature and extant
food concentration (Porter et al., 1983; Orcutt and Porter, 1984; Threkeld, 1987). These animals are therefore more susceptible to dilution losses in rivers before reaching a reproductive age (Brook and Woodward, 1956).

The natural distribution of cladoceran populations in river systems is usually restricted to backwater habitats, regulated stretches with longer retention times than the main channel (Rzoska et al., 1955; Shiel and Walker, 1984; Saunders and Lewis, 1989; Thorpe et al., 1994), or riverine reservoirs (Threkeld and Choinski, 1985; Dirnberger and Threkeld, 1986; Esmontkarabin et al., 1993; Descy, 1994). They may also become more abundant in downstream reaches of large rivers (Pace et al., 1992; Admiraal et al., 1994; Mameffe et al., 1996) where conditions become more lentic. Walz (1993b) noted that rotifers dominated Lake Postmünster, an impounded river, during periods when the residence time was below 3.6 days, whereas crustaceans dominated at higher residence times.

5.1.6 Aims

The use of published life-history characteristics was considered insufficient to accurately assess the ability of different species to survive in the Nene, as the literature estimates show wide variation depending on experimental conditions and the potential plasticity of certain traits within a species. This plasticity may lead to 'directed' shifts in the ecology of a species, depending on the environmental selective agents to which the species was subjected. An example of this was given by Bennet et al., (1993) for the rotifer Brachionus angularis, which increased birth rate as a response to increasing dilution rates in a flow through chemostat.

Species from two habitats of different retention time, the River Nene and Rutland Water, were therefore directly compared in an attempt to imply that the actual environmental stimuli in the river favoured the selection of r-selected traits which conveyed a greater degree of adaptation to life in unstable habitats. The work also aimed to imply that a 'typical' riverine rotifer was more adapted to unstable physical conditions than a 'typical' riverine cladoceran. This may seem obvious, but was considered a suitable objective given the strength of selective agents in rivers which may elucidate 'extreme' adaptations, possibly not fully explored in previous work.

The specific hypotheses tested in this part of the study were:

a) That rotifers from the study sites displayed more r-selected life-history traits than Daphnia, and were therefore more adapted to life in rivers.
b) That a *Keratella cochlearis* population from the River Nene had more *r*-selected life-history traits than a population from Rutland Water, reflecting the selective pressures imposed by the riverine habitat.

c) That a *Daphnia* population from the River Nene had more *r*-selected life-history traits than a population from Rutland Water.

d) That the chlorophyll 'a' concentration of the river was sufficient to support species with high population growth rates.

5.2 Methods

5.2.1 Rotifer cultures

Relatively few species of planktonic rotifer have been successfully cultured in the laboratory (Stemberger, 1981). The type of culture vessel, culture medium, food source, and temperature can all affect the results. Defining ideal conditions can be a very time consuming procedure that was considered beyond the scope of this study, so a more pragmatic approach was favoured which used a simple monospecific food source (*Rhodomonas lacustrus*) and a static culture system. Fortunately this system provided good growth conditions for the cosmopolitan rotifer *Keratella cochlearis*, which was considered a model organism for study as it was abundant in both the River Nene and Rutland Water.

5.2.1.1 Collection and isolation of animals

Rotifers from both habitats were collected using a plankton net (53 μm diameter pore). A number of samples from different horizontal and vertical strata were amalgamated to ensure an unbiased sample of all genotypes was attained. The samples were then transferred to a watch glass under low power magnification from which *K. cochlearis* individuals were removed with the aid of a capillary pipette. Animals were serially washed through clean Whatman GFC filtered river/lake water a total of ten times prior to establishing batch cultures with 50 animals which were maintained in 150 ml conical flasks at 20°C with a 14:10 hour day : night cycle and abundant food. The two species isolated were *K. cochlearis* var. *tecta* form *macrocantha* from the river and *K. cochlearis* var. *tecta* form *typica* from the reservoir.
5.2.1.2 Experimental cultures

Design and maintenance

Growth rates were analysed by direct counts of static 4 ml cultures raised at five food levels. The food concentrations used were 0.05 μg R. lacustrus dry weight ml⁻¹, 0.30 μg dry weight ml⁻¹, 1.20 μg dry weight ml⁻¹, 4.80 μg dry weight ml⁻¹, and 9.60 μg dry weight ml⁻¹, which spanned a range from near the threshold food level to the incipient limiting level for K. cochlearis (Stemberger and Gilbert, 1985).

Animals were chosen at random from the batch cultures, serially washed through clean medium, and acclimated to the experimental food level for four days prior to starting trials. Care was taken not to introduce any visual bias when choosing animals to ensure that all potential genotypes in the culture had an equal chance of starting an experiment. This was considered important as the 'natural' rates of increase were the parameter under study. Ten non-gravid females were selected after four days acclimation and placed into 4 ml cultures. Each food density was replicated three times giving a total of fifteen experimental trials per water body. These were arranged in a random block design to minimise the effects of any uncontrolled variables.

The culture medium used was Whatman GFC-filtered water from the rotifers' home site with a small volume of the algal culture medium added with the food source. This was used rather than a synthetic medium to gain a more accurate representation of natural growth rates (May, 1987). Experimental cultures were maintained at 20°C with a 14:10 hour light : dark cycle in a Vinden Scientific constant environment cabinet. Culture medium and food were changed every two days (Stemberger and Gilbert, 1985) when the density of animals, amictic eggs, resting eggs, males and dead animals was assessed.

Algal counts from experimental cultures proved that R. lacustrus remained viable during the 2 day period between each medium change.

Enumeration

Density was assessed by placing the contents of each culture in a watch glass under a dissecting microscope and removing all animals and eggs individually with a micro pipette before transferring them into fresh medium. This method ensured accurate counts and also decreased the extent of bacterial cross-contamination, as very small volumes of old culture were transferred along with the animals. Males, resting eggs and
dead animals were discarded after enumeration.

Cultures with a high density of animals were sub-sampled to aid enumeration. This was achieved by thoroughly mixing the culture contents immediately before removing a fixed volume (usually 1 ml or 0.5 ml) with an automatic pipette. This procedure was assumed to sample females, males, eggs and moribund/dead animals equally and so maintained the consistency of the data set. The sub-sampling procedure was tested prior to general use. Twenty replicate sub-sample counts (with replacement) from a culture of known density were made. The distribution of counts was tested with a chi-squared test for randomness (Elliot, 1973). The result was non-significant at the p=0.05 level indicating that samples were drawn from a random distribution.

5.2.1.3 Rotifer food source

The cryptomonad flagellate *Rhodomonas lacustrus* var. *nannoplanttica* was chosen as the sole rotifer food source. Cryptomonads have been reported as providing adequate nutrition for a number of pelagic species including *K. cochlearis* (Stemberger, 1981; Vancil, 1983; May, 1987). This unicellular motile algae is a common component of pelagic phytoplankton communities and can occur at high density throughout the year. The culture was obtained from the Culture Collection of Algae and Protozoa at the Freshwater Biological Association (ref. no. CCAP 995/3). No attempt was made to produce axenic cultures as the initial cultures were not bacteria free themselves.

Algae were grown in Diatom Medium (Beakes *et al.*, 1988) in 150 ml conical flasks at 20°C under constant illumination. All cultures were capped with foil to reduce airborne contamination. The cultures were maintained in a constant growth phase by regular sub-culturing into fresh autoclaved solution. Analysis of population development of sub-cultures showed growth was linear rather than exponential. Microscopic analysis, however, proved cells were highly motile and in good condition.

The dry weight of *R. lacustrus* was estimated as 40 pg cell⁻¹. This figure was derived from Reynolds’ (1984) published regression of cell volume against cell dry weight, using average algal volume from the formula given by Wetzel and Likens (1991) for measured cell dimensions. Experimental food concentrations were obtained by adding the correct volume of algal culture to yield the desired dry weight of algae per unit volume of culture. The density of algal cells in the stock solution was assessed by performing ten replicate counts from three randomly drawn sub-samples. Counts were made using a Whipple graticule at x100 magnification. The average coefficient of variation from 35 replicate counts was 0.22, with a standard deviation of 0.08.
5.2.2 Cladoceran cultures

Cladoceran cultures were designed to give accurate estimates of the age at first reproduction and age specific fecundity under different food conditions, as these two parameters influence population growth rates. Results were fed into a population growth model (see section 5.3.3 for model details) to obtain an estimate of the daily instantaneous growth rate which could be compared to the rates observed in rotifer trials.

5.2.2.1 Collection and isolation of animals

*D. galeata* from Rutland Water and *D. curvirostris* from a backwater approximately 400 m upstream of Wansford station were collected using a 140 μm mesh plankton net. Animals were taken from a number of localities and then pooled to ensure a broad cross-section of genotypes were sampled. Animals were removed individually using a Pasteur pipette and transferred to Whatman GFC-filtered 'home' water before being placed into batch culture which were maintained in one litre glass beakers filled with filtered water plus algal food at 20°C with a 14:10 hour light : dark cycle. These cultures were observed at approximately weekly intervals and sub-cultured when overcrowding was imminent, as indicated by falling egg ratio or ephippia production.

5.2.2.2 Individual growth rate experiments

A repeated measures design in which all measurements were made on the same animals was used to obtain data on the egg development time and post-embryonic development time of *Daphnia*, which together represent the generation time (Lei and Armitage, 1982). Experimental animals were obtained from mature *Daphnia* acclimated to experimental food concentrations for six days. First instar offspring were placed into individual sterilin plastic vials (total culture volume of 30 ml) filled with Whatman GFC-filtered water from the home site and a known concentration of *Scenedesmus obliquus*.

Five replicates at two food levels, 0.1 mg C l⁻¹ and 1.0 mg C l⁻¹, representing naturally occurring high and a low food concentration (Lampert, 1977; Taylor, 1985), were run, giving a total of 20 trials which were arranged in a randomised block design. All experiments were maintained at a constant 20°C. As *Daphnia* only increase in size during moults, size measurements were only made after a moult occurred to minimise handling stress. Cultures were scanned for the presence of moult cases twice daily at roughly twelve hour intervals and when one was found, the animal was removed from
the culture and its length, from the tip of the head to the base of the tail spine, was measured under a dissecting microscope using a ocular micrometer. These measurements were made as quickly as possible to reduce handling as this may affect growth and reproductive output (Infante and Litt, 1985; Vivjerberg, 1989). The animals were observed for some time after their return to the culture to ensure that they did not become trapped in the meniscus. If this happened the animal was gently ‘sunk’ by dropping water from a Pasteur pipette on the culture surface.

The chances of becoming trapped between observations was minimised by covering the upper surface of cultures with black card to reduce direct overhead lighting, as *Daphnia* may exhibit positive phototaxis (Ringelberg, 1987). All cultures were stirred at each observation to ensure that algae remained in suspension. Animals were transferred to clean cultures every other day to ensure a relatively stable food concentration was maintained and algal toxins did not inhibit growth. No significant food depletion occurred over the two day period between medium exchange indicating that algal growth was maintained in the filtered water. Cultures were terminated when animals produced their first brood.

5.2.2.3 Reproductive output

Five animals of a similar age were randomly assigned to 100 ml cultures in pyrex glass beakers and raised at experimental food concentrations until they became mature. The food concentrations used were 0.1 mg C l⁻¹, 1.0 mg C l⁻¹, and 2.5 mg C l⁻¹ although owing to bacterial and protozoan contamination, high birth rates were observed at all three concentrations. Lampert (1987) states that most protozoa are of a suitable size to supplement the diets of *Daphnia*, and so these may have acted as a supplementary food source. The results of these cultures were therefore only considered useful for estimating the maximum potential birth rate. Further experiments were performed, however, that minimised contamination by rinsing animals through clean medium during transfers. These cultures had the same experimental set-up but were carried out at slightly lower food levels of 0.025 mg C l⁻¹, 0.1 mg C l⁻¹, 0.25 mg C l⁻¹, and 1.0 mg C l⁻¹ of *Scenedesmus obliquus*. Axenic cultures were not used as antibacterial rinsing has been associated with decreased reproduction (Peters, 1987).

The cultures were checked twice daily when the number and average size of neonates produced was assessed (mean of 5 measurements). All neonates were removed to maintain constant food conditions for experimental animals. The number of neonates was divided by the number of adults to yield an estimate of egg production per female
per day. Cultures were mixed at each observation and animals were transferred to clean culture medium every other day. Minimal handling stress ensured a representative estimate of reproductive output. The cultures were kept at 20°C with a 14:10 hour light: dark cycle.

The results of a pilot study in which the reproductive output of 20 replicate animals was assessed showed that the analysis of egg production from 2 animals gave an error of less than 20% of the mean (Elliot, 1973). Five animals per food concentration was therefore considered sufficient to gain an accurate estimation of egg production rates.

5.2.2.4 Cladoceran food source

*Daphnia* cultures were fed a xenic culture of *Scenedesmus obliquus* supplied by the University of Barcelona. This algae is known to be a high quality monospecific food source for *Daphnia* (Vijverberg, 1989), especially when combined with bacteria (Peters, 1987). Cultures were maintained in 1000 ml conical flasks in autoclaved Diatom Medium at 20°C in a 14:10 hour light: dark cycle with a low flow air supply to keep cells in suspension. All cultures were capped with a cotton wool bung to reduce contamination and kept in a constant growth phase by regular sub-culturing.

The average dry weight of *Scenedesmus* cells (33 pg cell\(^{-1}\) (sd ± 5)) was calculated according to a suitable geometric approximation (two cones, base-to-base (Wetzel and Likens (1991)) applied to cell dimensions taken from a healthy culture. This was then converted to cellular carbon assuming a carbon content of 53% of the ash free dry weight (Reynolds, 1984). Ten replicate cell counts from each of three sub-samples of the stock solution were performed to calculate the volume of stock solution required to achieve the final experimental food density.

5.3 Results

5.3.1 Rotifer culture

5.3.1.1 Rotifer population growth rates

Population growth of the Nene animals is presented in figure 5.2. Growth was initially exponential as indicated by the straight line plots on a log scale, but declined as food became limiting nearer the carrying capacity. Final density and rates of increase were both influenced by food concentration.
Exponential rates of increase over the first sixteen days were calculated from the slopes of the regression lines presented in figure 5.3. Analysis of variance showed that all slopes were significantly different to each other (Tukey's *a posteriori* test) except those of the two highest food concentrations which were assumed to be above the incipient limiting level for this species of rotifer. The highest rate, an exponential daily increase of 0.291, was achieved at the highest food concentration and there was therefore no sign of growth rate inhibition at this concentration. The slope of the line at the lowest food level was not significantly different from zero, indicating that the food level was near the threshold for population growth.

![Figure 5.2](image)

**Figure 5.2.** Numerical growth of *K. cochlearis* populations from the River Nene at different food concentration.

![Figure 5.3](image)

**Figure 5.3.** Rate of cultured *K. cochlearis* increase during the exponential growth phase (River Nene). Figure in brackets relates to the rate, unbracketted figure relates to food concentration (µg dwt.)
ml$^{-1}$). All slopes significantly different from zero (p<0.001) except at 0.05 µg dwt. ml$^{-1}$.

Figure 5.4 shows the numerical development of the Rutland Water *K. cochlearis* population. The pattern observed was similar to that of the River Nene. Exponential growth rate increased with food concentration, as did the carrying capacity. Figure 5.5 shows the rates of increase over the exponential phase of growth. All rates were significantly different from each other except for those of the two highest food levels which were assumed to be above the incipient limiting concentration. The highest daily exponential rate of increase (0.349) was observed at 4.80 µg ml$^{-1}$. This rate was significantly higher than that of the river population (p>0.05).

![Figure 5.4](image1.png)

**Figure 5.4.** Numerical growth of *K. cochlearis* populations from Rutland Water at different food concentration.

![Figure 5.5](image2.png)

**Figure 5.5.** Rate of cultured *K. cochlearis* increase during the exponential growth phase (Rutland Water). Figure in brackets relates to the rate, unbracketted figure relates to food concentration (µg dwt.
ml⁻¹. All slopes significantly different from zero (p<0.001) except at 0.05 µg dwt. ml⁻¹.

The instantaneous growth, birth and death rates of the river species at 4.8 µg dwt. ml⁻¹ are presented in figure 5.6. The rate of egg production was maintained at a uniform high rate for approximately 12 days. This 'potential increment to population density' was realised by the high daily growth rate which closely matched birth rate and was possible owing to the low death rates at the start of the cultures. The birth rate started to decline after 14-16 days in culture when density dependant factors reduced egg production. Growth rate fell below zero for a short time once the carrying capacity was reached. One interesting feature of this culture was that after day 18 the birth rate stayed higher than the death rate at a time when population increase was static. This was explained by the production of resting eggs.

![Figure 5.6. Instantaneous rates of change in culture K. cochlearis populations from the River Nene. Error bars equal one standard deviation. r is the instantaneous rate of increase, b' is the instantaneous birth rate, and d' is the instantaneous death rate.](image)

Figure 5.7 shows the same growth parameters for the Rutland Water population at 4.8 µg dwt. ml⁻¹. The two graphs appeared similar at first glance but there were some important differences. The rate of increase up until day 16 was higher in this population, although the egg ratio was approximately the same as the Nene culture. This was presumably the result of an egg development time slightly less than the two day observation interval causing an underestimation of the instantaneous birth rate. It also indicated that the River Nene population was probably producing resting eggs throughout the culture, as the same rates of numerical increase observed in figure 5.7 were not achieved, although it was also possible that the egg development time of the river population was longer than that of the reservoir.
The birth rate gradually decreased after day 10, presumably as a result of the food level falling below the incipient limiting level. Population growth rate soon followed and crashed to zero on day 18 when the carrying capacity of the system was reached. At this point the birth rate roughly equalled the death rate, and the population growth rate oscillated around zero. The equality of birth and death rates indicates that no other losses in the form of resting egg production occurred from this population and no resting eggs were observed throughout the duration of the study.

5.3.1.2 Sexual reproduction in the Nene population

Sexual resting eggs and males were observed in the River Nene cultures at all food concentrations. Figure 5.8a shows the resting egg production expressed as the number per adult female. Resting eggs were rare before the twelfth day of culture, after which time they were produced at a relatively constant rate until the end of the culture period. There was little observable trend between the level of production and food concentrations except for the lowest concentration in which all egg production was minimal. The production of asexual eggs followed a different temporal pattern (figure 5.8b). Egg ratios were highest at the start, but decreased towards the end of the culture period when food became limiting.

Figure 5.7. Instantaneous rates of change in culture K. cochlearis populations from Rutland Water. Error bars equal one standard deviation, r is the instantaneous rate of increase, b' is the instantaneous birth rate, and d' is the instantaneous death rate.
Figure 5.8. Egg production (expressed as egg ratio) of the riverine *K. cochlearis* population. a. resting eggs. b. amictic eggs.

T-tests between the egg ratios observed during the periods of exponential increase and the plateau growth phases showed that amictic egg production was significantly lower during the second growth phase at all food concentrations with positive growth (table 5.1). This was expected as food became limiting (Stemberger and Gilbert, 1985). Mictic egg production was not significantly different after the twelfth day (table 5.2) indicating a relatively constant rate of resting egg production irrespective of the influence of declining food levels.

<table>
<thead>
<tr>
<th>Food concentration (µg dwt ml⁻¹)</th>
<th>Growth phase</th>
<th>mean egg ratio</th>
<th>variance</th>
<th>t statistic</th>
<th>probability</th>
</tr>
</thead>
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<td>0.30 exponential</td>
<td>0.368</td>
<td>0.014</td>
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<td></td>
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<tr>
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<td>0.011</td>
<td>9.961</td>
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<td>0.001</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>9.60 exponential</td>
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</tbody>
</table>

Table 5.1. Results of t-tests between the production of amictic eggs (expressed as the egg ratio) during the exponential and plateau growth phase of *K. cochlearis* cultures.

<table>
<thead>
<tr>
<th>Food concentration (µg dwt ml⁻¹)</th>
<th>Growth phase</th>
<th>mean egg ratio</th>
<th>variance</th>
<th>t statistic</th>
<th>probability</th>
</tr>
</thead>
<tbody>
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<td>0.0007</td>
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<td>0.525</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>1.20 exponential</td>
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<td>0.0028</td>
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<td>plateau</td>
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<td>0.0011</td>
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<tr>
<td>4.80 exponential</td>
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<td>0.0003</td>
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</tr>
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<td></td>
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</tr>
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<td></td>
</tr>
<tr>
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<td>0.060</td>
<td>0.0004</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5.2. Results of t-tests between the production of mictic eggs (expressed as the egg ratio) during the exponential and plateau growth phase of *K. cochlearis* cultures. Negative results indicate an increase in the production of resting eggs during the plateau growth phase.

The decline of amictic egg production whilst resting egg production remained constant...
is highlighted in figure 5.9 which shows the proportion of all eggs which were mictic. There was a general increase in the proportion of sexual eggs produced with time in culture, although at the lower food concentration this happened slightly earlier as a result of a food limited drop in amictic egg production.

Figure 5.9. The proportion of total *K. cochlearis* egg production accounted for by resting eggs.

The production of mictic resting eggs relies on fertilisation by male rotifers. These are only usually produced in response to some environmental stress. Continuous male production was, however, a common feature of the river population. Males appeared after four days in culture, even at high food concentrations, proving that food limitation did not cue their production (figure 5.10).

Figure 5.10. Male production expressed as a proportion of total animals in riverine *K. cochlearis* cultures.
They remained a relatively high proportion of total animal density until cultures were terminated. There was no significant difference (p>0.05) between male production during the exponential and plateau phase of growth at any food level, proving that this was a constant population characteristic rather than a density dependant feature. The delay in resting egg production was presumably a result of the need for male fertilisation of haploid eggs.

5.3.1.3 Threshold food concentration

The slope of instantaneous growth rate from both populations was not significantly different from zero at the lowest food level (0.05 μg dwt ml⁻¹), indicating that this was very near to the threshold for population growth, i.e. sufficient to meet the metabolic costs of the animals but not to cover the costs of reproduction. A better estimate was obtained by calculating the food availability per individual when the population was at carrying capacity. This was done for the two populations, using each food concentration as a replicate sample. The average threshold for the river population was 0.031 μg dwt ml⁻¹ (sd ± 0.015, n=4) while that of the reservoir population was lower at 0.012 μg dwt ml⁻¹ (sd ± 0.05, n=4). The two were significantly different (p<0.05) when tested by a t-test.

Figures 5.11 and 5.12 show the effect of increased food concentration on the instantaneous growth rate of the two rotifer populations. This was most pronounced at relatively low levels, between 0.05 and 1.50 μg dwt ml⁻¹, above which growth rate changed little as the incipient limiting level was approached.

![Figure 5.11. Food dependent daily instantaneous growth rates of K. cochlearis cultures from the River Nene.](image)

183
Both populations showed a rapid response to increased food levels at low concentration as shown by the close proximity of the threshold and Ks concentration (half maximum growth rate). The Ks concentration for the river population was estimated as 0.483 µg dwt ml\(^{-1}\) while that of the reservoir population was 0.374 µg dwt ml\(^{-1}\).

### 5.3.2 Cladoceran cultures

*Daphnia* population growth rates from river and reservoir were modelled from estimates of generation time and egg production per adult female taken from laboratory cultures.

#### 5.3.2.1 Individual growth rates

This rate is important as it defines the post-embryonic development time of an individual. Figures 5.13 and 5.14 show the typical growth characteristics of the two species grown at high food level. *D. curvirostris* rapidly reached adult size (mature at fifth instar after an average of 6 days), after which time there was little subsequent increase in size. *D. galeata* took longer to reach adult size (mature at seventh instar after an average duration of 8 days), and showed more tendency to increase in size after this as shown by the wide standard deviation after day nine. This species had a significantly smaller adult size (1.47 mm; sd ± 0.03, n=10) than that of the river population (1.64 mm; sd ± 0.05, n=10), (p < 0.001).

Individual growth rate during pre-adult development at non-limiting food concentration is presented in figure 5.15. Both species had a similar length at first instar but the daily rate of increase in size was significantly higher for *D. curvirostris* (0.15) than *D. galeata* (0.11), (p<0.05).
Figure 5.13. Growth of juvenile *D. curvirostris* from the River Nene

Figure 5.14. Growth of juvenile *D. galeata* from Rutland Water.

Figure 5.15. Individual growth rate of cultured *D. curvirostris* and *D. galeata*. 
The effect of food concentration on these rates is presented in figure 5.16. Rates measured at 0.1 mg C l\(^{-1}\) were lower than those recorded at 1.0 mg C l\(^{-1}\) for both species.

![Graph showing individual growth rates of Daphnia at two different food concentrations.](image)

**Figure 5.16.** Individual growth rates of *Daphnia* at two different food concentrations.

The mean egg development time was estimated as 2 days for both species from direct observation of cultures at 20°C. The total generation time for the two species was therefore estimated as 8 days for *D. curvirostris* and 10 days for *D. galeata* grown at high food density.

5.3.2.2 Reproductive output of mature females

The number of eggs produced per adult female per day, was calculated as a function of food density. The most reliable data set for the estimation of maximum egg production rates was from the trials which were infested with protozoans, as these were assumed to provide the highest food availability. There was no difference between egg production rates within the species from these experimental food concentrations (0.20, 1.0 and 2.5 mg C l\(^{-1}\)) when tested by ANOVA, indicating that all were above the incipient limiting level, owing to protozoan infestation. A further ANOVA showed there to be no age specific change in egg production rates. This finding was unexpected (Vivjerberg, 1976; Lei and Armitage, 1982; Taylor and Aiken, 1985) but allowed a single mean adult rate to be used in the population growth model. Non-infected cultures were used to assess the effect of variable food concentration on egg production rates below the incipient limiting level.
The mean number of eggs produced per day under non-limiting conditions by *D. curvirostris* (4.0, sd ± 2.1, n=30) was significantly higher (p<0.05) than that of *D. galeata* (3.0, sd ± 1.4, n=30), but was ultimately dependant on the experimental food concentration as shown by figure 5.17a. The number of neonates produced per day increased with food concentration towards an asymptote at the incipient limiting level. The point at which this line crosses the horizontal axis signifies the threshold food concentration for reproduction. This was calculated from the log relationship of figure 5.17b as 0.021 mg C l⁻¹, which was similar to 0.044 μg dwt ml⁻¹ cited by Reynolds (1984).

\[ y = 1.701 \log(x) + 2.862 \]

*Scenedesmus obliquus* (mgCl⁻¹)

**Figure 5.17.** Relationship between food concentration and the daily rate of neonate production of *D. curvirostris*. a. normal plot. b. log-normal plot showing threshold for reproduction (x-intercept).

The relative size of neonates (measured from the tip of the head to the base of the tail spine) compared to maternal length was estimated from cultures as this can offer further information on the type of life-history adopted by the two species. *D. curvirostris* neonates were on average 0.34 of the adult length (sd ± 0.05, n=50) while *D. galeata* neonates were larger at 0.39 of adult length (sd ± 0.08, n=50). The difference was significant at the 0.001 probability level when tested by a t-test.

**5.3.3 Modelled potential rates of increase**

Population growth is more complicated in cladocerans than rotifers owing to the longer generation times involved. Exponential increase is only achieved once a population has achieved a stable age structure. Prior to this, assuming the population is begun from juvenile animals, for example after ephippial hatching, there is time lag before exponential growth is achieved. The length of this lag, and its effect on population development in short retention time systems, was investigated by the following work in which the generation time and egg production rate once mature was used to model potential rates of population increase starting with a single first instar animal.
5.3.3.1 Model derivation

The model was constructed from basic principles in Microsoft Excel. The starting point was a single first instar animal which remained immature for a known period of time, after which it reproduced at a constant daily rate. This rate was maintained each day until the animal became senescent and died. Longevity was estimated from published data for *D. parvula* (Orcutt and Porter, 1984). The population then increased by a daily factor which was equivalent to the number of animals in the population at time 't'-generation time' multiplied by the daily egg production value. The reproductive output of all mature animals was accounted for by this method. This value was then amended for senescence, but this had little overall effects on results.

A number of assumptions were made when developing the model.

a) The daily reproductive rate was assumed to remain constant throughout adult life
b) No death rate was assumed except that owing to senescence.
c) All eggs were assumed to develop to maturity.
d) No male production was assumed.
e) No food limitation was assumed.

The last point is very important as resource depletion owing to grazing is expected at high animal density, leading to reduced fecundity and decreased population growth rates (Sommer *et al.*, 1986). The model was therefore intended to describe the maximum 'potential' population growth rates assuming no food limitation or predation. This was considered appropriate for this study which aimed to describe the lack of cladocerans from river habitats in terms of their slower growth.

Figure 5.18a shows the modelled numerical increase of a *D. curvirostris* population initiated with a single newly hatched animal (generation time of 8 days, reproductive rate of 3.75 eggs female$^{-1}$ day$^{-1}$). The population growth exponent was 0.360, which was higher than that observed from both rotifer populations, and stems from the large broods produced by mature females. There was, however, a long period prior to this exponential increase which stretched over approximately 16 days, or two times the generation time.

The reason for this long delay is better shown in the log plot of figure 5.18b. Here the effect of the initial pre-adult eight day period can be seen where there was no change in population size, followed by a further eight day period where the population increases at a linear rate. This area of the curve derives from the initial animal reproducing at a
constant daily rate. After this period, the numeric development is supplemented by
reproduction of the first generation animals which now begin to mature. As the
population begins to assume a stable age structure the growth form becomes more
exponential, but as noted above, this takes at least a duration of two times the
generation time.

Figure 5.18. Potential population development model for *D. curvirostris* at 20°C. a. normal plot. b. log-normal plot.

Figures 5.19a and 5.19b show the same model for the cultured *D. galeata* population
(generation time of 10 days, reproductive rate of 2.65 eggs female⁻¹ day⁻¹). The form
of the curve is very similar but the slope of the exponential increase is somewhat
shallower at 0.260. The time lag prior to attaining near exponential growth is also
longer, at approximately 20 days. This is clearly seen in figure 5.19b where the lack of
linearity of the log plot is highlighted.

Figure 5.19. Potential population development model for *D. galeata* at 20°C. a. normal plot. b. log-normal plot.

Temperature has an important influence on the life-history parameters which affect
population growth rate. Published temperature relations (Bottrell *et al.*, 1976; Orcutt
and Porter, 1984) were used to estimate the resulting shift in generation time and egg production in the *D. curvirostris* population. It was necessary to assume the published relationships applied across the genus (Bottrell et al., 1976), although it is recognised that for increased accuracy, further work is needed with the experimental population. The data used to construct figure 5.20 are presented in table 5.3.

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<tr>
<th>Temperature (°C)</th>
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<th>EDT (days)</th>
<th>PDT (days)</th>
<th>mature lifespan (days)</th>
<th>eggs / female / day</th>
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</thead>
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**Table 5.3.** Effect of temperature on life-history parameters of *D. curvirostris*. EDT and PDT represent egg development time and post-embryonic development time respectively (from Orcutt and Porter, 1984).

Figure 5.20 uses data from table 5.3 to show how temperature effects the numerical development of model populations. As expected, the highest exponential rate of increase was found at the highest temperature. The relationship between temperature and the exponent of increase in a population of stable age distribution is shown in figure 5.21.

![Figure 5.20. Effect of temperature on the numeric development of *D. curvirostris*. Populations started with a single newly hatched animal.](image)

The increase in growth rate with temperature was adequately described by an exponential relationship. Rates were higher than those of *K. cochlearis* at 25 °C and 20°C but the time lag associated with juvenile development may still be sufficient to disadvantage populations in river systems with low retention times, and hence explain the scarcity of these animals in river systems.
5.3.3.2 Simulated competition between a riverine rotifer and a riverine cladoceran

A model simulation of the competitive ability of *K. cochlearis* and *D. curvirostris* was run to test the overall ‘suitability’ of each form to life in environments with short retention time. The simulation was performed assuming a temperature of 20°C (within the natural range of the Nene) and assuming a non-limiting food concentration (the Nene chlorophyll 'a' values peak at over 200 µg l⁻¹).

Figure 5.22 shows the results of the simulation over a relatively extended period of time. The eventual ‘winner’ of the competition in terms of their ability to increase their density was the cladoceran, owing to its high birth rate once mature. The time scale of the simulation was, however, much longer than the retention time of the main channel of the river, and may therefore not be directly applicable to the river environment.

The outcome was changed when a reduced timescale was analysed. Figure 5.23 shows that within the natural range of main channel retention times in the Nene (see section 5.4.3), the rotifer was likely to be the better adapted because of its much shorter generation time which allows exponential growth to be achieved more rapidly. This ability also makes it more able to reinstate populations after a disturbance.

The model suggests a reason for the competitive superiority of rotifers in disturbed systems. This, however, is only a first attempt at understanding a very complex set of factors which control river zooplankton populations. It does not make allowance for
changes in food concentration, either through grazing or abiotic control, which can dramatically redefine the competitive outcome. Mechanical interference competition (Gilbert and Stemberger, 1985) was not considered, nor were the effects of invertebrate or vertebrate predation. The starting density of the populations may also have an effect on the outcome of the competition, as shown by Sarma et al., (1996). The larger the initial density, the higher the probability of retaining a population in a particular stretch of the river. The historic distribution of a species, and its ability to leave resting eggs may therefore alter the competitive balance shown in figure 5.23.

Figure 5.22. Potential population development of *D. curvirostris* and *K. cochlearis* at 20°C and non-limiting food concentration. Both populations started with a single animal.

Figure 5.23. Figure showing the competitive advantage of rotifers over cladocerans in the short-term.
All of the factors mentioned above interact to produce the observed dominance of rotifers throughout the majority of unregulated river systems of the world. The purely physical effect of short retention time on the zooplankton, however, remains of primary importance to the development of river populations, as shown by the model results.

5.4 Discussion

5.4.1 Rotifer life-histories

The rates of increase achieved by the two rotifer populations were dependant on the experimental food concentration of the cultures. Food availability and temperature are known to dictate potential rates of increase (King, 1967; Herzig, 1983; Walz, 1995) and will be of great importance in disturbed systems where high growth rates are required to maintain population density in the face of constant loss (Townsend and Hildrew, 1994).

The chlorophyll 'a' concentration in the River Nene (used as an estimate of algal biomass) was higher than that of Rutland Water during the spring. The high food availability in the river for at least part of the year, was considered an important prerequisite for the development of the \( r \)-selected species which dominated the zooplankton community. The average dry weight of algae during March-June when zooplankton populations usually reached peak density was 5.1 \( \mu \text{g ml}^{-1} \) (sd ± 2.01, \( n=75 \)) from 1979 to 1995. This food concentration was above the incipient limiting level of \( K. \text{cochlearis} \), and should have supported a high population growth rate.

The maximum growth rates achieved in the cultures (0.29 in the Nene and 0.34 in Rutland Water) were very similar to previously-cited estimates. Stemberger and Gilbert (1985) quoted the \( r_{\text{max}} \) of cultured \( K. \text{cochlearis} \) as 0.28 at 19°C, while Walz (1993a) quoted a value of 0.30 at 20°C. The two populations studied here, however, had significantly different growth rates from each other. The initial hypotheses that the river population would have the higher rate was disproved and suggested that the river population was the more \( K \)-selected of the two.

This conclusion was questioned when it was found that the river population produced resting eggs at a constant rate throughout the duration of the experiment. These eggs, along with males, did not add to the numerical increase of the cultures and so helped to account for the lower instantaneous rate of increase. Resting egg production was also assumed to require more energy than amictic egg production (Gilbert, 1977). The pattern of resting egg production proved that the onset of sexual reproduction was not
reliant on any density dependant cue such as food limitation or crowding, as described by Gilbert (1963) for *Brachionus calyciflorus*, and led to the conclusion that the life-history trait was adopted by this species to give some selective advantage in temporally unpredictable habitats. A similar phenomenon was noted in *Keratella valga* and *Brachionus urceolaris* populations from ephemeral water bodies (Pontin, 1989) which favoured a constant rate sexual reproduction rather than depending on density dependant cues, as the onset of unfavourable environmental conditions was unpredictable and more under physical than biotic control. Girdner and Larson (1995) showed a similar adaptation by crustacean taxa which encyst as draught resistant stages in temporary high-mountain ponds.

The selective advantage of maintaining a constant rate of resting egg production may stem from the fact that mictic eggs have increased ability to withstand downstream removal, as they sink onto the sediment and therefore become protected from the effects of flow to a degree by the boundary layer. Resting stages may therefore help to 'retain the innoculum' (Reynolds et al., 1994) in a suitable area of the river for growth (Pace et al., 1992). Reynolds and Descy (1996) stressed the importance of benthic stages for the maintenance of river phytoplankton, and this idea may equally apply to river zooplankton. Indeed, Townsend and Hildrew (1994) quoted the development of resistant stages as an *r*- selected life-history strategy, as they can aid the rapid reinstatement of populations after disturbance.

The reservoir population produced no resting eggs throughout the duration of the study. This species was adapted to living in an environment with a substantially higher residence time and environmental stability. Sexual reproduction may be expected in this population, but only when cued by some specific combination of environmental stimuli (Pilarska, 1972; Gilbert, 1974; Hofmann, 1977) which were obviously not mimicked by the culture conditions.

The threshold food concentration for population development was significantly higher in the river rotifer species and reflected the persistent production of resting eggs. The high threshold indicated that the river species was more *r*- selected, requiring higher food levels to maintain positive population growth than the reservoir species. The *K*, food level (food concentration required to support half-maximum growth rate) was also higher for the river population, indicating the reliance of high growth rate on high food concentration.

The river species appeared to be the more *r*- selected of the two, when considered in terms of the *r* / *K* continuum, indicating that the physical nature of the river imposed a
selective force on this population that was not as apparent in the reservoir. Selection at this intra-specific level indicates some degree of plasticity in life-history traits (Bennet et al., 1993).

Which rotifers are expected to thrive in river habitats

It is an oversimplification to classify all rotifers as $r$-selected animals as some authors have done before (Allen, 1976). *K. cochlearis* is considered to be a relatively $K$-selected species when compared to other rotifers. Its occurrence in the river may therefore be somewhat surprising, although it may gain some advantage from its generalist feeding behaviour and cosmopolitan distribution which allows it to thrive under a wide range of conditions (Hutchinson, 1967; Bogden and Gilbert, 1987). This may be especially useful in disturbed habitats where environmental conditions are liable to unpredictable change.

*K. cochlearis* was the dominant species throughout 1992 and 1993 in the Nene, but was replaced by *Synchaeta* in the spring of 1994. 1994 had a particularly wet spring which resulted in high discharge and reduced residence time of water in the river. It is therefore possible that under these conditions the growth rate of *K. cochlearis* was unable to offset the level of losses imposed. *Synchaeta* are more $r$-selected than *K. cochlearis*, having a recorded $r_{max}$ of 0.80 (Stemberger and Gilbert, 1985; Berner-Frankhauser, 1987; May et al., 1993). This genus may therefore have been more able to thrive under such conditions especially in the absence of potential ($K$-selected) competitors. Zonfal (1989) noted the dominance of *Synchaeta* over other rotifers in systems with short retention times.

5.4.2 Cladoceran life-histories

The riverine species, *Daphnia curvirostris*, attained a larger adult size than *D. galeata* and was therefore expected to display more $r$-selected traits according to the size-based classification of Romanovsky (1984). The present culture experiments showed that *D. curvirostris* had a significantly higher individual growth rate and a shorter time to maturity than *D. galeata*. The generation time of the riverine species was on average two days shorter than that of the reservoir species at 20°C, although this was dependant on food availability. The food concentration of the river during spring was usually above the incipient limiting level of cladocerans and should therefore have supported rapid rates of development.

The rate of egg production was significantly higher in the river population which
produced a higher number of smaller neonates than the reservoir population. The strategy adopted by the reservoir population was typically *K*-selected whereby each juvenile was allocated more resources, as indicated by the significantly larger size of juveniles compared to adults (section 5.3.2.2), to allow a better chance of survival under poor food conditions. Smaller animals tend to adopt this trait, at the cost of reduced population growth rates (Gliwicz and Guisande, 1992; Guisande and Gliwicz, 1992).

The differences in birth rate, time to maturity, and the pattern of energy allocation to neonate production once mature indicated that *D. curvirostris* was the more *r*-selected species of the two. This is in agreement with the initial hypothesis that the species found in the river would display more *r*-selected traits than the reservoir population.

Modelling population development showed the competitive superiority of *D. curvirostris* over *D. galeata* when food was unlimiting. The river species was therefore considered more suited to living in habitats with shorter retention times.

The actual ability of cladoceran populations to offset the scale of losses associated with the main channel of rivers was questioned by Hynes (1970). This was reflected in the spatial distribution of cladocerans in the Nene which was restricted to side-channel habitats with longer water residence time or downstream tidal reaches where the 'age' of the water was more commensurate with longer cladoceran generation times. Spatial heterogeneity was also considered very important to the ecology of rivers by Garner (1996), as areas of lower flow acted as a zooplankton refuge and feeding ground for juvenile fish.

Reduced water residence time was unlikely to be the only factor determining the selection of riverine cladoceran species' life-history traits, although it was likely to be of great importance (Townsend and Hildrew, 1994). The type and intensity of predation may also influence the distribution of species with different traits (Brandl and Witteringová, 1991). For example, early maturation may be selected in environments with a high degree of size-selective predation.

### 5.4.3 Temporal heterogeneity and grazer competition

The reason for rotifer domination of disturbed habitats is not immediately obvious if one simply considers the maximum rates of increase achieved under optimal growth conditions. Certain rotifers, including species of the genus *Synchaeta* and *Brachionus* have higher growth rates than cladocerans, but other rotifers, including *K. cochlearis,*
have lower growth rates than some of their cladoceran competitors (Walz, 1995). *Daphnia* may therefore appear the more *r*-selected group of animals if this life-history trait is considered alone. The modelled population development of the two riverine groups showed that over an extended period (at least two times the generation time of the cladoceran) *D. curvirostris* was likely to attain numerical dominance owing to its higher birth rate, and therefore appeared more adapted to the riverine environment. This was in direct contradiction to the rotifer dominance observed in the Nene.

The adaptive advantage of the rotifers was found to stem from their short generation times which allowed them to reach exponential growth in a shorter period of time than *Daphnia*. Walz (1987, 1993d) also considered this trait to be more important than the maximum growth rate of a species for life in habitats with short retention times. For example, the number of young produced once mature is unimportant if the animal cannot reproduce before being removed from the habitat. Precocious maturation may therefore be at least as important as fecundity (Gould, 1977).

The generation time of the river *K. cochlearis* population was calculated from population doubling time to be 2.4 days at 20°C. The average generation time of *D. curvirostris* was 8 days while that of *D. galeata* was 10 days at 20°C. If the residence time of water in the system was longer than the generation time of cladocerans, they may be expected to dominate the plankton. If the water residence time is lower than the cladoceran generation time, but above that of the rotifers, the advantage will switch to the latter group. This is a necessarily simplistic view of river systems as the retention capacity of dead zones will constantly readdress such relationships.

The water residence time of rivers is usually short enough to influence zooplankton dynamics (Aksnes *et al.*, 1989; Pace *et al.*, 1992). The total residence time of water in the River Nene above Wansford (*i.e.* the average 'age' of the water reaching Wansford) was estimated as 5.14 days (sd ± 0.37, n=16) during spring, following the methods of Leopold *et al.*, (1964) in Søballe and Kimmel (1987), which falls below the generation time of *Daphnia* at average spring temperatures. Cladocerans would therefore not be expected to reach reproductive age before being washed below Wansford, and were therefore unlikely to form a substantial part of the pelagic zooplankton community of this site. This was not the case for *K. cochlearis*, which was able to complete at least a single generation before reaching Wansford, and therefore maintain a riverine population. The size of the population would, however, be expected to increase downstream as the 'age' of the water increased (Marneffe *et al.*, 1996).
5.4.4 Spatial heterogeneity and the role of dead zones

Spatial heterogeneity, which according to Townsend and Hildrew (1994) reduces the effect of temporal disturbance, may increase the potential for cladoceran development in areas with longer residence time along channel margins (Reynolds, 1988). Populations without the ability to rapidly recoup numbers after a disturbance event may therefore benefit by locating in such areas. These areas may also be extremely important for providing innocula for the recolonisation of the main channel after high flow events. Water exchange between the main channel and dead zones will also increase the effective retentive capacity of rivers, allowing a denser plankton to develop than would otherwise be expected.

5.5 Summary

The hypotheses set-out in the introduction were confirmed. The river species displayed more *r*-selected life-history traits than reservoir species. These were supposed to convey competitive superiority in a habitat with a high degree of temporal variability. Suitable adaptations included short generation times and high birth rates. These were attained at the expense of higher food requirements which were indicated by higher thresholds for development.

*K. cochlearis* was more adapted to the river environment than *D. curvirostris*, as a result of its relatively high growth rate and short generation time. The cladoceran also had a high growth rate, but suffered as a result of taking longer to reach a reproductive age. This reduced the ability to rapidly respond to favourable growth conditions after disturbance events or to complete reproduction before being washed downstream.

The riverine rotifer species produced sexual eggs at a constant rate irrespective of food concentration. This was viewed as a further adaptation to life in a habitat where the chances of being washed downstream were reduced in the resting stage.
CHAPTER 6
THE ZOOPLANKTON OF TWO LOWLAND RESERVOIRS IN THE EAST OF ENGLAND

6.1 Introduction

The fundamental physical and biotic processes of lakes, reservoirs and rivers are the same, but the scale and relative importance of these processes may differ between systems (Spøballe and Kimmel, 1986). Rivers are usually considered to be highly disturbed and temporally unpredictable compared to lakes and reservoirs (Townsend and Hildrew 1994). As a result, the dynamics of river plankton are more strongly influenced by the physical effects of water movement than by biotic interactions (Hynes, 1970). This was proven for the Nene (chapter 2), where algal productivity was controlled more by discharge and temperature than nutrient limitation.

Systems with longer retention time are buffered against such short-term disturbance. The increased physical stability allows biotic interactions to have a greater influence on plankton community structure, and these interactions, along with seasonally changing weather conditions initiate a relatively repeatable autogenic succession in the plankton (Sommer et al., 1986).

6.1.1 Seasonal changes in the physical structure of temperate lakes

Seasonal changes in the physical structure of deep temperate lakes may have an important effect on the development of planktonic communities (section 6.2.3). Some of these changes are described below for a 'typical' north temperate lake. Individual lakes or reservoirs may differ from the patterns described below, however, depending on factors such as basin morphology, flushing rate, degree of exposure, and management regime.

The surface of a lake may freeze during the winter, but owing to the physical properties of water which is at its most dense at 4°C, the ice acts as insulation and maintains liquid water below the surface. This is of great importance to animals that overwinter in an active state as they encounter a relatively stable and predictable set of environmental conditions.

The whole water column is of a relatively similar temperature and density after the ice melts, so little energy is needed to mix to full depth as there is little thermal resistance to
water movement. In most lakes, sufficient energy is derived from the action of wind on the water surface (Wetzel, 1983). This mixing period, referred to as the spring turnover, can last from a few days in small sheltered lakes, to weeks in larger exposed lakes. The temperature of the water column generally increases slowly during this period, depending on lake volume and weather conditions.

A calm period of sunny weather may be sufficient to heat the upper layers of deep lakes faster than the heat is redistributed by mixing, and this may result in a warm buoyant layer of water that 'sits' upon the cooler, deeper layers. The difference in density between layers now offers considerable resistance to further mixing and the effects of wind are therefore restricted to the warm surface layer, the epilimnion, which continues to be heated by solar radiation. The deeper layer, the hypolimnion, remains at a lower temperature owing to little interchange of water or heat between the layers. A third zone may be defined, the metalimnion, which is located between the epilimnion and the hypolimnion and is characterised by a marked thermal discontinuity between the warm epilimnetic waters and the cooler hypolimnion.

Thermal stratification may last throughout the summer until air temperatures fall and surface layers start to radiate heat back to the atmosphere and cool. This increases their density, and as they start to sink into the hypolimnion they set up internal circulations which are enhanced by wind action. The transition from weak summer stratification to full mixing, the 'autumn turnover', may occur in a matter of hours if associated with high wind velocities (Wetzel, 1983). Continued circulation ensures a homothermal water column which gradually cools to winter minimum temperatures.

### 6.1.2 Ecological consequences of thermal stratification

Temperature is known to have an important influence on the distribution of planktonic species as each has a defined tolerance range within which it can grow and reproduce. A narrower 'optimal' band exists within this tolerance range which supports maximum growth rates (Herzig, 1987), while outside the temperature does not support metabolic processes. Figure 6.1 is a schematic representation of the tolerance range of three species of planktonic rotifer in the genus *Polyarthra*. Stenothermal species are those with a restricted tolerance range, and are represented by *Polyarthra dolichoptera*, a cold stenotherm which reaches peak abundance below 10°C and *P. remata*, a warm stenotherm which requires temperatures above 10°C for growth and reproduction. Eurythermal species, represented by *P. vulgaris*, have a wider tolerance range which is portrayed by their cosmopolitan distribution in space and time.
The seasonal succession of thermal conditions in lakes is therefore of great importance to the development of planktonic communities. Thermal stratification may have wide ranging effects on this development. Not only is the temperature profile of the water changed, but other chemical changes take place. A similar stratification in oxygen concentration may exist with high oxygen concentrations in the epilimnion owing to atmospheric diffusion and algal photosynthesis, and lower concentrations in the hypolimnion where anoxic conditions may develop owing to the decomposition of organic matter produced in the epilimnion. A marked difference in the oxygen concentration between epilimnion and hypolimnion may lead to the development of an oxycline at the metalimnion.

The concentrations of nitrogen and phosphorus in different water layers are also changed as a result of stratification. Nitrate, ammonium and phosphorus concentrations decrease in the epilimnion throughout the stratified period owing to algal uptake and subsequent sedimentation to the hypolimnion. Nutrient recycling of soluble phosphorus and ammonia by grazers acts as a valuable source of nutrients to this upper layer during these times. Alternately, ammonium nitrogen and soluble phosphorus concentrations may increase in the hypolimnion as a result of organic matter decomposition and release from anaerobic sediments. These two nutrients are only made available to the euphotic zone after the autumn turnover, which often stimulates a peak of algal growth (Sommer et al., 1986). Prior to the turnover, algal production is usually nutrient limited in the epilimnion and light limited in the hypolimnion.
The physical and chemical differences between the two water layers may therefore have an effect on the spatial and temporal distribution of planktonic organisms. For example, the hypolimnion may be exploited by cold stenotherms with low oxygen requirements such as *Daphnia pulicaria* throughout the summer months, whereas the hypolimnion must be avoided by non-motile algae which would sink in the still waters.

### 6.1.3 Seasonal succession of planktonic communities in temperate lakes

The seasonal succession of planktonic communities in lakes of the temperate zone has been well documented by authors such as Hutchinson (1967), Lampert (1978), and Sommer et al., (1986), and is considered to be relatively predictable and repeatable from year to year. The patterns are broadly repeated in lakes of widely dispersed geographical location but similar morphologic, climatological and chemical properties. It may be assumed that a similar suite of factors influence the cycles observed in each of them (Reynolds, 1984).

The motivators of community change are acknowledged to be related to variations in the physical, chemical and biotic environment, usually initiated by allogenic drivers related to predictable seasonal climatic events. The planktonic community is assumed to continuously adapt to these changes, and in doing so may impact upon environmental conditions, thus forcing an aspect of autogenic succession. Each successive community is therefore more adapted to, and dependant on, the conditions produced by the previous (Sommer et al., 1986). Allogenic factors may be more important during the early spring and autumn when relatively large-scale disturbance events may initiate a rapid response, while autogenic factors may be more important during the relatively undisturbed period during spring and summer.

**Spring**

A bloom of fast-growing algae, especially diatoms, commonly develops during spring associated with an improved light climate and increased water temperature. The onset of stratification may aid this development as cells which circulate in the epilimnion remain in the euphotic zone for a longer period than they would if they were mixed to full depth. Small cells are abundant at this time but are subsequently reduced by grazing zooplankton whose populations closely follow those of the phytoplankton. Zooplankton density may develop to the extent that they exert a community grazing pressure in excess of algal growth rates, leading to a phytoplankton crash at the end of spring (Lampert and Taylor, 1984; Seda, 1989). This crash may lead to a period of increased water transparency which is generally referred to as the 'spring clearwater
phase' (Lampert, 1978; 1988a; Sommer et al., 1986). Nutrient limitation towards the end of spring may, however, also initiate the clearwater phase (Komárková, 1989; Vyhnálek, 1989; Vyhnálek et al., 1991) along with algal lysis (Vyhnálek et al., 1993). The phase is often short in eutrophic lakes compared to oligotrophic lakes (Gliwicz, 1990a), in which it can extend throughout the summer.

Zooplankton populations, which are often dominated by *Daphnia*, usually become food-limited during the clearwater phase as indicated by reduced fecundity (Seda, 1989) and increased length to weight ratios (Duncan et al., 1985). Population density and biomass decline as a result. This decline may also be hastened by the action of size-selective predators, particularly 0+ fish which were previously 'gape-limited' to smaller prey items (Gliwicz, 1985; McQueen and Post, 1988; Gliwicz and Pijanowska, 1989), (section 6.1.5.2).

**Summer**

The summer phytoplankton community of eutrophic lakes is usually more diverse than that of the spring and can be roughly divided into two categories based on cell / colony size; 'undergrowth' and 'canopy' species (Reynolds (1984). ‘Undergrowth’ is a term used to describe small algae that are suitable food items for the majority of filter feeding zooplankton, whereas ‘canopy’ refers to larger net algae which are unsuitable for most generalist feeders owing to their size and unpalatability (McQueen and Post, 1988; Dawidowicz, 1990; Gliwicz, 1990a). The summer community may become dominated by dinoflagellates and cyanobacteria as these species have low nutrient requirements compared to smaller forms and are therefore suited to nutrient depleted epilimnetic water. They also gain an advantage from their resistance to grazing and sedimentation, and their ability to migrate vertically to exploit favourable nutrient gradients.

The summer zooplankton community is usually more diverse than that of the spring as more species are able to coexist owing to the increased habitat diversity resulting from stratification, increased algal diversity leading to resource partitioning, and reduced competition from larger grazers (Pennak, 1957) (see section 6.15).

The autogenic succession of phyto and zooplankton communities is terminated by the physical destruction of stratification at the autumn turnover. Increased algal growth rates may result from nutrient replenishment of the euphotic zone and lead to an autumnal peak of species adapted to mixing, including large unicellular algae, filamentous forms, diatoms, and a variable biomass of small, edible species (Sommer et al., 1986). This latter group often supports an autumnal maxima of grazing.
Both algae and zooplankton populations decline with decreasing temperature. Some species of zooplankton set resting stages to aid rapid population growth when favourable conditions return to the lake.

6.1.4 The role of competition in structuring zooplankton communities

The argument as to the proximal control factors which structure zooplankton communities has been ongoing for over thirty years. Initially, differences in ecological tolerance to abiotic factors were thought to be of primary importance (Hutchinson, 1967), until during the early the 1960s when attention turned towards competition. Later in the same decade, attention focussed on the role of size-selective predation as a result of works by Hrbáček (1962) and Brooks and Dodson (1965). Today, the common view is that zooplankton community structure is influenced by both competition and predation (Rothhaupt, 1990). Predation, however, was considered unlikely to force actual extinctions itself, but rather initiate an interaction which causes a change in species’ competitive ability which then results in replacement (Gliwicz and Pijanowska, 1989; Gliwicz, 1994a) i.e. competitive ability is linked with susceptibility to predation (Rothhaupt, 1990).

An example of reduced competitive ability owing to predation occurs when large Daphnia are restricted to hypolimnetic waters which act as a refuge from visual predators during daylight hours (Threkeld, 1980; Tessier and Welser, 1991; Horppila, 1997). Daphnia must migrate into the upper productive layers to feed during the night, when the risk of predation is reduced. The migration itself, poor feeding conditions, and the low temperature in the hypolimnion exert a 'metabolic' cost on the migrating animals (Lampert, 1989) in terms of 'competitive fitness'. This 'cost' ultimately allows smaller species to coexist in the epilimnion that would otherwise be excluded through competitive interactions (Gliwicz and Pijanowska, 1989; Leibold, 1991).

6.1.4.1 Zooplankton size and competitive ability - Why large Daphnia dominate

Food limitation is widely known to be important in structuring planktonic communities. Pennak (1957) attributed the low momentary species richness of zooplankton in any single water body to competition for limiting food. Decreased fecundity associated with declining food levels (Gliwicz et al., 1981; Orcutt and Porter, 1984; Vanni, 1987; Seda, 1989) along with increased slopes of length / body mass relationships (Duncan 1985) and decreased lipid storage (Tessier and Goulden, 1982) all indicate the potential for
low food levels to control zooplankton community composition.

Suspension-feeding rotifers and cladocerans generally have similar food preferences, including algae, bacteria, and non-living particulate organic matter with maximum linear dimensions < 20 μm, and so run the risk of direct competition for food (Gilbert and Stemberger, 1985; Gilbert, 1988a). Large species, especially *Daphnia*, usually win this competition, although the reasons for this are not always simple. The following section details the current theories used to explain the competitive superiority of large *Daphnia*.

The size-efficiency hypothesis (Brooks and Dodson, 1965; Hall *et al.*, 1976) states that 'the larger the species, the better the competitor'. Cladocerans should therefore outcompete rotifers given sufficient time (Gilbert and Stemberger, 1985). The basis of the hypothesis stems from the fact that ability to collect food increases more rapidly than the per capita respiration rate with increasing body size. Small animals therefore have problems collecting sufficient food to offset energy expenditure, and have a higher threshold food requirement than larger animals as a result.

This mechanism was questioned by Romanovsky (1984; 1985) who found that thresholds for reproduction were lower for small cladoceran species whose juveniles required less energy to reach sexual maturity. A similar result was documented by Tessier and Goulden (1987) and Stemberger and Gilbert (1985) who found that small cladocerans and rotifers had lower thresholds than larger species, and argued that these smaller forms were therefore more adapted to food limited environments. The size efficiency hypothesis was therefore weakly supported until Gliwicz (1990b) provided conclusive evidence from laboratory studies that threshold food levels for growth decreased with cladoceran size as Brooks and Dodson (1965) predicted.

Further evidence may be called upon in support of the size-efficiency hypothesis. For example, large cladocerans may gain a competitive advantage from their ability to ingest and store surplus food as lipid reserves (Goulden and Hornig, 1980) and therefore survive periods of low food abundance better than small species (Threkeld, 1976). *Daphnia magna* and *D. galeata* can survive up to 25 days without food (Tessier *et al.*, 1983; Stuchlíková, 1991). *Daphnia* may also be able to 'assess' food conditions and alter reproductive investment to suit. Gliwicz (1992) found that large neonates were produced when food was scarce, as this gave the juveniles maximum starvation resistance and hence maximum probability of survival to maturity. This type of behavioural and physiological plasticity therefore conveys cladocerans with further competitive advantages when resources are scarce.
Rotifers, in contrast, have low starvation resistance owing to their small body size and lipid reserves. For example, *Keratella cochlearis* (a relatively *K*-selected rotifer (Walz, 1995)) had a starvation time of just 48 hours (Gilbert, 1985). This group is therefore unlikely to be competitive in situations when the food resource fluctuates, for example during the spring clearwater phase when large species usually dominate owing to their greater ability to resist prolonged periods of food shortage (Tessier and Goulden, 1987).

**Invertebrate predation**

Large cladoceran species may gain a further advantage over small filter feeders when invertebrate predators are present, as they preferentially select small prey items of < 1 mm including rotifers (Dodson, 1974a; Lynch, 1979; Williamson, 1983; Threkeld and Choinski, 1987; Vanni, 1988; Matveeva, 1989; Roche, 1990; Campbell, 1991; Herzig, 1995). Large cladocerans are generally unaffected by invertebrate predators, unless their juvenile stages are taken (Gliwicz and Umana, 1994; Herzig, 1995) or their egg sacs predated (Gliwicz and Stibor, 1993; Gliwicz and Lampert, 1994).

Many species of insects, cladocerans, copepods and rotifers are known to be obligate or facultative planktivores (Gliwicz and Pijanowska, 1989). Rotifers are the preferred prey items of predatory rotifers, copepods, and the young stages of many crustacean and insect predators (Williamson, 1983; Herzig and Auer, 1990). This type of predation may therefore cause changes in the balance between rotifer and cladoceran grazers in the zooplankton, and should be considered as a potential control of the zooplankton community structure of lakes.

Morin (1988) argued the significance of invertebrate predation to zooplankton community structure from the wide occurrence of morphological adaptations found which reduce susceptibility to such predation including the formation of neck teeth in *Daphnia pulex* (Jacobs, 1988; Lüning, 1992; Balaseiro and Vega, 1994; Herzig, 1995; Spaak, 1995; Brancelj et al., 1996; Repka and Pihlajamaa, 1996), helmets in *D. longispina* (Brett, 1992) and caudal spines in *Keratella cochlearis* (Conde-Porcuna et al., 1993) and *Brachionus calyciflorus* (Dumont, 1977). Some form of energetic cost is usually associated with such defence mechanisms, and this may decrease the competitive ability of species which are forced to adopt them (Repka et al., 1994).

Shifts in life-history characteristics such as increased size at first reproduction and the production of fewer, larger offspring (Lüning, 1992) are also seen as evidence of the impact of invertebrate predation (Vanni, 1987; Brett, 1992; Weider and Pijanowska,
1993; Repka and Pihlajamaa, 1996). Behaviour patterns may also be modified to reduce the temporal and spatial overlap of predator and prey populations. For example, diel vertical migration patterns may be altered by the presence of invertebrate predators (Herwig and Schindler, 1996; Nesbitt et al., 1996) along with horizontal migration patterns (Lysebo, 1995).

6.1.4.2 Indirect evidence for rotifer suppression by large cladocerans

A wealth of indirect evidence exists supporting the contention that large cladocerans suppress small filter feeding herbivores, especially rotifers (Gilbert, 1988a). Of the 30 studies reviewed by Gilbert (1988), 19 provided strong evidence of an inverse relationship between Daphnia biomass and rotifer biomass, while 8 more provided weak evidence. None of the papers provided evidence refuting the hypothesis that rotifers are suppressed by Daphnia.

Many examples of alternating Daphnia / rotifer dynamics come from seasonal patterns of replacement within a single water body (Ferguson et al., 1982; Orcutt and Pace, 1984; Threkeld and Choiniski, 1987; May and Jones, 1989; Lampert and Rothhaupt, 1991; Urabe, 1992; Conde-Porcuna et al., 1994) or displaced spatial patterns of abundance (Urabe, 1990). Rotifers usually develop large populations in the spring when food conditions are favourable, but then become displaced by larger cladocerans later in the season (Haberman, 1983; Sommer et al., 1986). Their initial advantage stems from a high reproductive potential and short generation times (Stemberger and Gilbert, 1985; Walz, 1993d), but they lose this edge when food becomes limiting owing to the lower thresholds of large cladocerans and their ability to resist prolonged periods of food shortage.

Further evidence for the competitive suppression of rotifers comes from studies which describe increased rotifer abundance in systems where Daphnia were rare (Gilbert, 1988a). A good example of this was given by Cryer et al., (1986) in Alderfen Broad where cladoceran numbers were depleted in years when there was strong recruitment of 0+ roach (Rutilus rutilus), as these fish fed preferentially on the larger zooplankton. Rotifers dominated the zooplankton during such years, but the pattern was reversed in years when roach recruitment was poor. Fussmann (1996) provided similar proof when Daphnia longispina were removed from an enclosure in the mesotrophic Schohsee (Germany), leading to exponential population growth of Synchaeta pectinata and Keratella cochlearis. No similar development was observed outside the enclosures, where Daphnia density remained high.
Still further evidence stems from studies in which planktivorous fish biomass was changed, leading to a cascading effect on the size structure of the pelagic zooplankton community (McQueen et al., 1986). The zooplankton community was typically dominated by large cladocerans when planktivorous fish biomass was low, but became dominated by smaller cladocerans and rotifers in systems when the planktivore biomass was high (Vanni, 1988; Gilbert, 1988a).

Lynch (1979) showed how the exclusion of fish from a section of Pleasant Pond led to the development of a community dominated by large *Daphnia pulex* which suppressed rotifer density. Two smaller cladocerans (*D. parvula* and *D. ambiguа*), along with an abundant rotifer fauna, developed in the section containing zooplanktivorous fish owing to the removal of the large cladocerans by size-selective predation, and the possible removal of invertebrate predators by a similar mechanism.

In a similar study Christoffersen et al., (1993) set up enclosures with and without planktivorous fish. In fishless enclosures, the biomass of macrozooplankton was significantly higher than those with fish present and the community structure was dominated by cladocerans at the expense of rotifers. Ronnenberger et al., (1993) noted a similar depression of rotifer density after biomanipulation of a German lake by planktivore removal and piscivore addition. The depression was again attributed to increased biomass of large cladocerans in the plankton which competitively suppressed smaller species.

6.1.4.3 Direct evidence for rotifer suppression by large cladocerans

Large cladocerans may exclude smaller forms and rotifers as a result of their competitive power to reduce shared food resources as discussed above. There is, however, another mechanism by which large *Daphnia* suppress rotifers. This was termed ‘mechanical interference competition’ by Gilbert and Stemberger (1985), who noted that *Keratella cochlearis* populations declined in the presence of *Daphnia* when food was plentiful, and therefore exploitative competition was unlikely. Direct observations showed that the rotifers were swept into the branchial chamber of *Daphnia* by feeding currents, and trapped there for some time before being rejected by the postabdomen. The risk of damage or death increased with time spent in the chamber, and was more likely to occur with young animals (Gilbert and Stemberger, 1985; Gilbert and MacIsaac, 1989). Gravid females could also become separated from their eggs once inside the branchial chamber although this didn’t seem to affect the hatching rate in experimental cultures, but may have a marked effect on natural populations if the eggs settle to the cold, anoxic sediments (Gilbert and Stemberger, 1985).
The size of the *Daphnia* had an important effect on the extent of mechanical interference. Burns and Gilbert (1986) found that rotifer death rates increased as a function of size with *Daphnia* over 1.2 mm long, irrespective of the species involved. The impact of mechanical interference was also increased at low food levels when *Daphnia* clearance rates were highest. *Daphnia* smaller than 1.2 mm were unable to interfere with adult rotifers, but were able to interfere with juveniles of some rotifer species (MacIsaac and Gilbert, 1989). Mechanical interference also increased with the density of *Daphnia*, although even quite low densities could impose high mortality rates on *K. cochlearis* populations (Burns and Gilbert, 1986; Gilbert, 1988b; Fradkin, 1995).

Not all species of rotifer are equally susceptible to mechanical interference (Gilbert, 1988b). The most susceptible are those that remain in the branchial chamber for a relatively long period (6-15 seconds) prior to rejection, and include small forms such as *Keratella cochlearis* and *Synchaeta oblonga*, or delicate species such as *Ascomorpha ecaudis*. Less susceptible species include those that are too large to enter the branchial chamber (e.g. *Conochilus unicornis*), those with a developed escape response (e.g. *Polyarthra remata*), and those which are rapidly rejected from the chamber once inside (e.g. *Asplanchna priodonta, Keratella crassa*). Rapid rejection was thought to be dependant on a large rotifer size or the presence of hard loricate projections (Gilbert, 1988b). Mechanical interference competition may therefore change the composition of rotifer communities by the selective removal of the most susceptible species (Gilbert, 1989).

The relative importance of the two mechanisms by which large cladocerans suppress smaller forms, exploitative competition and mechanical interference competition, has been the topic of some debate. Threkeld and Choinski (1987) along with May and Jones (1989) thought that exploitative competition was most important, whereas Burns and Gilbert (1986) and Gilbert (1989) thought mechanical interference was more important. It is most likely, however, that both mechanisms operate in natural systems (Gilbert, 1988a; 1988b; MacIsaac and Gilbert, 1990; Lampert and Rothhaupt, 1991), although the relative importance of each may be dependant on the size of *Daphnia* present (Jack and Gilbert, 1994). MacIsaac and Gilbert (1991) showed that large *Daphnia pulex* (> 1.2 mm) suppressed *K. cochlearis* primarily by interference whereas small species such as *Daphnia ambiguа* (< 1.2 mm) relied on exploitative competition alone.

Unlike large cladocerans, small cladocerans often coexist with rotifers in the absence of large *Daphnia* (Gilbert, 1988a; MacIsaac and Gilbert, 1989; Wickham and Gilbert, 1991). The inability of small cladocerans to exclude rotifers is somewhat of a mystery
considering the ‘size-efficiency hypothesis’ and their larger body size, but proof of long-term coexistence comes from both field studies (Lynch, 1979) and laboratory studies (MacIsaac and Gilbert, 1989). Lower clearance rates, lower resistance to starvation, and lower potential to interfere with rotifers may all reduce the competitive ability of small cladocerans, thus enabling this coexistence. MacIsaac and Gilbert (1989) found that low threshold food requirements of some small rotifers made them better competitors at constant low food levels, whereas small cladocerans were better competitors when food was pulsed owing to their resistance to starvation.

6.1.5 Under what conditions can small zooplankton dominate the plankton?

In spite of the competitive advantages displayed by large grazers, small species may dominate the plankton at certain times of year. Some rotifers may dominate during winter as a result of tolerance to low temperature (Haberman, 1983) or early in the spring before cladocerans become abundant (Sommer et al., 1866). They may also dominate in systems with short water residence time owing to their high potential population growth rates and short generation times (Pace et al., 1992).

Rotifers and small cladocerans are also known to increase in abundance during summer in eutrophic lakes (Sommer et al., 1986). Two hypotheses have been developed to explain this, food limitation and size-selective predation, both of which involve a reduction in the competitive fitness of larger cladocerans (Gliwicz, 1985; Lampert, 1988b).

Large cladocerans, which typically come to dominate the zooplankton of eutrophic lakes towards the end of spring, may be disadvantaged during the early summer clearwater phase. The juveniles of these species tend to have high food requirements (Romanovsky, 1985), and may be excluded at low food levels as a result, allowing smaller species to become more numerous. Algal community composition may also change towards the dominance of less palatable species during the summer (section 6.2.3).

6.1.5.1 Interference from ‘canopy’ algae during summer

Another explanation for the reduction in zooplankton size structure during summer is the size-specific differences in vulnerability to feeding interference from ‘canopy’ algae (Gliwicz, 1990a). These algae may become dominant in eutrophic lakes during the summer, and may even benefit from the presence of large cladoceran grazers which efficiently reduce the abundance of nanoplanktonic algae (Haney, 1987), thereby
recycling nutrients for canopy species growth (Dawidowicz and Gliwicz, 1987). This type of interaction is believed to cause the often observed association of *Daphnia* and large ‘grass-blade’ colonies of *Aphanizomenon flos-aquae* (Hrbácek, 1964; Lynch, 1980; Pecher and Fott, 1991).

Large grazers such as *Daphnia* are more affected by the presence of canopy species than smaller cladocerans, rotifers and copepods (Gliwicz, 1980; Edmondson and Abella, 1988). Much of the evidence for this statement stems from observations relating to the effects of filamentous blue-green algae on filter feeding communities. Negative effects stem from a number of ‘anti-herbivore defences’ employed by such algae (Lampert, 1987a), including toxin production which is known to decrease filtering rates (Porter and Orcutt, 1980; Lampert, 1981, Burns et al., 1987; Jungmann et al., 1991), poor nutritive value and ingestability (Lampert, 1981), and their potential to interfere with the normal feeding process (Burns et al., 1987; Henning et al., 1991), which leads to decreased growth rates and reproduction (Infante and Abella, 1985; Burns, 1987; Fulton and Jones, 1991).

Gliwicz (1977) formulated, and tested, a hypothesis to explain why large cladocerans were more disadvantaged by interference from net algae. He found that larger species had a wider gap between their carapace valves and were therefore more likely to ‘inhale’ filaments into their branchial chamber. Once inhaled, these filaments seriously disturbed the filtering process in daphnids (Gliwicz, 1990a) which were forced to clear their food groove by either post abdominal or labral rejections (Burns et al., 1987; Fulton and Jones, 1991). Energy was lost performing this action, and feeding efficiency reduced as food already in the groove was also ejected. The net result was decreased growth rate, survivorship and fecundity (Lampert, 1987b, deBernardi and Guissani, 1990).

The morphology of the filament may be important. Burns et al., (1987) found that single filaments of *Anabaena sp.* were more inhibitory to *Daphnia carinata* than large grass-blade colonies of *Aphanizomenon flos-aquae* which had little impact on *Daphnia pulicaria* populations as they were too large to be ingested (Pecher and Fott, 1991).

Smaller cladocerans with a reduced carapace gap, or selective feeders such as *Bosmina* (Bogden and Gilbert, 1982; DeMott, 1982; Kerfoot and Kirk, 1991), copepods and some rotifers (Dumont, 1977; Pourriot, 1977; Bogden et al., 1980; Starkweather, 1980; Bogden and Gilbert, 1982; Gilbert and Bogden, 1984) are much less affected by filamentous algae (Starkweather, 1981; Fulton and Paerl, 1987; Lampert, 1987b; DeMott, 1989; Gliwicz, 1990a), and often increase in density during periods of blue-green algal abundance (Burns et al., 1987; Gliwicz, 1990a; Hanazato, 1991; Kohl and
Lampert, 1991; Gulati et al., 1992; Sellner et al., 1993). Walz (1995) considered rotifers, including generalist feeders such as *Brachionus sp.*, to be remarkably uninhibited by the presence of blue-green bacteria, and may even gain nutritionally from their presence (Rothhaupt, 1991). For example, Dumont (1977) observed *Brachionus calyciflorus* individuals utilising *Aphanizomenon sp.* as a food source by 'nibbling' on the end of filaments. Rotifers may also benefit during bloom conditions owing to their resistance to some strains which are toxic to cladocerans (Walz, 1995). Gilbert (1990) showed that *Synchaeta pectinata* out-competed *Daphnia* when a toxic strain of *Anabaena affinis* was present in cultures, but was excluded when the toxic algae was absent.

The competitive superiority of smaller cladocerans during blooms was proven experimentally by Gliwicz and Lampert (1990) who showed that the normal pattern of decreased threshold food concentration with increased *Daphnia* size was reversed in the presence of *Cylindrospermopsis raciborski* filaments.

6.1.5.2 Size-selective predation

Small zooplankton may also be favoured during summer as a result of intense size-selective predation on large animals. The effect of vertebrate predation, particularly planktivorous fish, on the size-structure of zooplankton communities has been long recognised (Hrbáček et al., 1961; Brooks and Dodson, 1965). The reduced size structure results from the direct removal of the largest zooplankton individuals, especially fecund females (Morin, 1988), and the induction of morphological and behavioural changes in prey populations which lead to reduced overall fitness and therefore competitive ability. The diversity of zooplankton communities is generally increased in the presence of planktivorous fish (Gliwicz and Pijanowska, 1989, and section 6.1.4.2), as smaller grazers are able to coexist with larger forms.

Much evidence exists to support the notion that when vertebrate predators are abundant the size structure of the zooplankton community decreases. A number of studies have shown that the zooplankton community of lakes with low planktivorous fish biomass is dominated by larger forms than lakes with a high fish biomass (Hrbáček, 1962; Dawidowicz and Pijanowska, 1984; Rodriguez et al., 1993). Similar patterns occur in single water bodies when the fish density changes from year to year (Brooks and Dodson, 1965; Edmondson and Litt, 1982; Cryer et al., 1986; Prazáková, 1991; Seda and Kubecka, 1997), especially the density of 0+ fish (Johannsson and O’Gorman, 1991, Mehner et al., 1995). Some of the strongest evidence comes from studies in which the fish biomass was experimentally altered in either natural systems or enclosures. The addition of fish led to the exclusion of larger crustacea, allowing
smaller species and rotifers to become abundant, whereas the removal of fish led to the dominance of large forms and the competitive exclusion of many smaller species (Lynch, 1979; McQueen and Post, 1988; Eckartz-Nolden and Nolden, 1992; Jeppesen et al., 1992; Lazzerre et al., 1992; Meijer et al., 1994).

The effects of plantivorous fish predation on zooplankton communities are so well recognised that the size-structure and species composition of crustacean populations may be used to indicate fish biomass (Hrbácek et al., 1986; Seda et al., 1989; Kubecka and Duncan, 1994; Seda and Duncan, 1994; Seda and Kubecka, 1997), although they may not be very sensitive to small changes in planktivore biomass when predation levels are generally high (Johannsson and O’Gorman, 1991).

Vertebrate predation may also be important in forcing certain seasonal successions within the zooplankton community of lakes. Young fish, especially the 0+ cohort, are thought to have a major impact on their zooplankton prey owing to their feeding voracity, their high numbers, and the fact that most species are planktivorous at least during the juvenile stage (Gliwicz and Pijanowska, 1989). Synchronous spawning increases the predation intensity, as a high density of animals all start to feed together and undergo ontogenic shifts in prey choice at a similar time. For example, after hatching in May (perch) or June (roach), fry feed preferentially on rotifers and algae. As they grow, they begin to take larger prey items until in early summer, the greatest predation pressure is concentrated on large *Daphnia* (van Densen, 1985; Treasurer, 1990).

This sequential development of predation pressure is often associated with the decline in dominance of large cladocerans at the start of summer, that was previously described in terms of reduced food abundance (section 6.1.5). It is widely considered, however, that food limitation and predation pressure both interact to cause this seasonal reduction in zooplankton size-structure (Gliwicz, 1985; Tessier, 1986; Lammens, 1988; Lampert, 1988b; Moss et al., 1991). Summer zooplankton communities are often characterised by the presence of forms that have greater resistance to fish predation than those of spring. This resistance may result from decreased body size (Cerny and Bytel, 1991; Brett, 1992; Vonderbrink and Vanni, 1993), behavioural adaptations (Leibold, 1991; Ringelberg, 1991a; 1991b; Horppila, 1997), changed life-history characteristics (Machácek, 1991; Stibor, 1992; Weider and Pijanowska, 1993) and morphological adaptations (Dodson, 1974b; Tessier, 1986; Gliwicz and Pijanowska, 1989). Genotypes that adopt such 'defences' usually do so at a cost in terms of reduced fitness. Smaller less competitive species, are therefore more able to coexist with larger forms during the summer.
6.1.6 Phytoplankton density as a measure of system function

A number of authors have produced relationships which predict the algal density, or a surrogate measurement of algal density such as chlorophyll 'a', achieved per unit phosphorus in standing waters (Sakamoto, 1966; Dillon and Rigler, 1974). These relationships may be useful to water managers who can then use simple chemical standards to achieve desired biological targets. The relationship may, however, vary depending on the specific nature of the environment under study.

Søballe and Kimmel (1987) performed similar regressions for three specific system types which varied in a number of physical and chemical parameters: lakes, reservoirs and rivers. The data set was extensive, covering 149 lakes, 366 reservoirs and 126 rivers in North America. The regressions were significantly different from each other, with the highest algal density per unit phosphorus achieved in lakes, then reservoirs, and finally rivers. The low algal abundance of rivers was explained by their reduced water retention time leading to high hydraulic loss rates, and their higher turbidity which decreased algal growth rates owing to a poor underwater light climate. The relationship between algal density and phosphorus may therefore be used assess the level to which the planktonic community is physically restricted in different systems, assuming that phosphorus is the main limiting nutrient in fresh waters, although high grazing rates may also decrease the ratio.

6.1.7 Aims

The aims of the study described in this chapter were as follows:

1. To describe the community structure and function of the grazing zooplankton of two lowland reservoirs in the East of England, Rutland Water and Covenham reservoir.

2. To assess by correlation analysis the factors most closely associated with rotifer dynamics in these reservoirs, to test the hypothesis that biotic interactions have greater influence than physical control.

3. To assess the relative strength of competition imposed on rotifers from Daphnia of different size in the two reservoirs, to test the hypothesis that large animals have a greater negative impact on rotifer density.

4. To understand the relative importance of Daphnia exploitative and interference competition to rotifers dynamics to test the hypothesis that food limitation has greater influence than physical interference in the two reservoirs.
5. To assess the factors which reduce the competitive dominance of *Daphnia* to test the hypothesis that increased cyanobacterial density and vertebrate predation control *Daphnia* density and individual size.

6. To assess planktivorous fish density from the size structure of cladoceran fauna in the two reservoirs, and to propose reasons for differences.

7. To test the hypothesis that the reservoirs had a significantly higher algal production per unit phosphorus than the river as a result of the physical differences between the two habitat types, using the methods of Søballe and Kimmel (1986).

**6.2 Methods**

**6.2.1 Study Sites**

*Location*

Rutland Water, previously known as Empingham reservoir, is a pumped storage reservoir situated in twin valleys of the river Gwash between Leicester and Peterborough in the East of England (figure 6.2). The bedrock of the area is a marlestone, over which lay deposits of upper lias clay, sand ironstone, and limestone. The dam was mainly constructed from upper lias clay taken from borrow pits in the reservoir valley just upstream of the dam wall. The Welland and Nene river authority, which became the Anglian Water Authority in 1973, was granted Royal Assent for the reservoir in 1970. Construction work started in the following year and the dam was finally closed in 1975 after which it started to fill primarily by drainage from its own catchment. Pumped inputs from the rivers Nene and Welland commenced in 1976, but the reservoir did not reach top water level until 1979.

Covenham Reservoir is a pumped storage reservoir in the north-east of the Anglian Region of the Environment Agency, situated approximately 40 miles north-east of Rutland Water between Cleethorpes and Louth (figure 6.2). The underlying geology of the area is chalk with friable limestone, flint, marlestone, and boulder clay deposits. The reservoir was completed in 1970, the same year as it started to fill with water pumped from the Louth canal. This reservoir has no natural catchment of its own unlike Rutland Water as it was constructed above the level of the surrounding land.
Figure 6.2 Site map of study reservoirs showing sampling sites, littoral zone (area between reservoir boundary and dotted line), and positioning of destratification equipment (h = helixors).
Pumped inputs

Water is pumped into Rutland Water from two eutrophic lowland rivers, the river Nene at Wansford, approximately 20 km south-east of the reservoir, and the river Welland at Tinwell, approximately 10 km east of the reservoir. Maximum abstraction volume from the Nene is 5.3 m$^3$ s$^{-1}$, while that from the Welland is 7.9 m$^3$ s$^{-1}$. The choice of abstraction is based on the water quality and flow rate in each river at the time of pumping. The water enters the reservoir through west facing angled inlet pipes on the floor of the South arm (figure 6.2). The system was designed to induce column mixing to minimise the potential for thermal stratification in the south arm.

The Nene abstraction point was upstream of the Wansford Station sampling point, whereas the point at which discharge was measured was downstream of the sample point. This ensured that the residence time calculations used in the previous chapters were based on the true discharge through the section after any abstraction had taken place. The major abstraction tended to occur during the winter months when river levels are high. Any impact on the plankton should therefore have been minimal.

Water is abstracted from the eutrophic Louth canal to Covenham reservoir. This canal runs north from Louth to the southern bank of the Humber estuary. Water enters the reservoir through the Valve Tower, after passing through screens with a 5 mm mesh at the intake site. The screen is supposed to remove any large debris and fish, although it is possible that some fry and young elvers successfully enter the reservoir along with abstracted water.

Morphology

Table 6.1 presents some physical characteristics of the two reservoirs. Rutland Water is the larger reservoir with a total volume of 124 x 10$^6$ m$^3$. The natural catchment area is approximately 7,400 ha. The reservoir has a large surface area and a large shoreline development index owing to its irregular shape. The littoral zone of Rutland water is well developed (approximately 60% of surface area, figure 6.2) with high habitat diversity and macrophyte development, including Potamogeton pectinatus, Juncus effusus, and Elodea nutalli growths. Littoral vegetation was rarely cut in the early stages of reservoir management to encourage fish spawning and fry development (Knights, 1982).

The complex morphology of the reservoir may lead to differences in water quality, so there are two points from which water can be extracted to the Wing water treatment
works, one in the main basin at the south end of the dam wall, and one in the north arm at the Secondary Draw-off Tower.

Covenham reservoir occupies an artificially raised basin so the natural catchment of this reservoir is simply its surface area, which is approximately 0.8 km². The basin is nearly square in outline and the concrete lined banks slope down at a uniform angle of approximately 30°, resulting in a small littoral area (approximately 10% of the surface area, figure 6.2). The concrete banks and wind induced mixing make macrophyte colonisation difficult, so the littoral zone of this reservoir is relatively habitat poor compared to that of Rutland Water. The retention time of Covenham is lower than that of Rutland Water, but at 32 weeks it was still considered sufficiently long to have little impact on plankton dynamics.

<table>
<thead>
<tr>
<th></th>
<th>Rutland Water</th>
<th>Covenham</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Year of filling</strong></td>
<td>1975</td>
<td>1970</td>
</tr>
<tr>
<td><strong>Source</strong></td>
<td>Welland, Nene</td>
<td>Louth canal</td>
</tr>
<tr>
<td><strong>Natural catchment area (km²)</strong></td>
<td>74</td>
<td>0.8</td>
</tr>
<tr>
<td><strong>Volume (10⁶m³)</strong></td>
<td>124</td>
<td>10.9</td>
</tr>
<tr>
<td><strong>Surface area (km²)</strong></td>
<td>12.6</td>
<td>0.8</td>
</tr>
<tr>
<td><strong>Littoral surface area (km²)</strong></td>
<td>8.0</td>
<td>0.08</td>
</tr>
<tr>
<td><strong>Depth (maximum) (m)</strong></td>
<td>34</td>
<td>16</td>
</tr>
<tr>
<td><strong>Depth (mean) (m)</strong></td>
<td>10.7</td>
<td>14</td>
</tr>
<tr>
<td><strong>Circumference (km)</strong></td>
<td>35</td>
<td>3.6</td>
</tr>
<tr>
<td><strong>Shoreline development</strong></td>
<td>2.8</td>
<td>1.1</td>
</tr>
<tr>
<td><strong>Retention time (weeks)</strong></td>
<td>90</td>
<td>32</td>
</tr>
<tr>
<td><strong>Drawdown (m)</strong></td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 6.1 Some statistics of Rutland Water and Covenham reservoirs.

**Management**

The eutrophic nature of the two reservoirs led to the implementation of various management strategies to alleviate water quality problems during the planning stage. These included the use of angled inlet jets in the southern arm and compressed air 'helixor' air guns in the main basin of Rutland Water to promote destratification of the water column during the summer. Destratification reduces the chances of an anoxic hypolimnion developing which would otherwise create water quality problems with the release of iron, manganese, ammonia, silica and phosphate compounds from the sediments (Low, 1982). Destratification can also be a useful method of reducing algal
growth by making the light climate less favourable (Steel, 1976; McQueen and Story, 1986). Wind driven circulation patterns were also found to provide important mixing power in the reservoir, as the prevailing westerly winds had the greatest fetch down the length of the two arms. Ferric sulphate dosing of the inlet water has more recently been used as a nutrient control method to alleviate some of the problems associated with eutrophication.

The efficiency of the helixor air guns was questioned by Low (1982), but along with wind driven mixing, the two tended to be relatively effective at preventing thermal stratification as shown in figure 6.3. The presence of a summer oxycline does, however, indicate that mixing was only partially successful during periods of warm, still weather.

![Figure 6.3 Temperature (A.) and percentage oxygen saturation (B.) profiles from Rutland Water, 1991 - 1992.](image)

Covenham reservoir has similar mechanisms in place to encourage full depth mixing. The exposed nature of the elevated site encourages wind driven mixing, but there is also a 'bubble curtain' *in situ* to encourage mixing and aeration of the lower layers. Figure 6.4 shows that the mixing regime in this reservoir is also effective. Ferric dosing of inlet water is also practised at this site in an attempt to control excessive algal growth by reducing the concentration of available orthophosphate.
Figure 6.4 Temperature (A.) and percentage oxygen saturation (B.) profiles from Covenham reservoir, 1991 - 1992.

Neither of the reservoirs have used biomanipulation as a management tool. Rutland Water operates as a commercial 'put and take' trout fishery, and therefore minimises the potential for many methods to decrease the indigenous fish community which is dominated by the planktivorous roach (*Rutilus rutilus*). Covenham reservoir has been used as a 'stock reservoir' for fish in the past, but its ability to maintain indigenous cyprinid populations is questionable owing to the lack of littoral spawning sites.

**Sample sites**

Samples were provided by the Environment Agency for the study period. Rutland Water was sampled weekly from four sites (figure 6.2), two sites in the north arm (North buoy 1 and the Secondary Tower), one site in the south arm (south buoy 12), and one site in the main basin (Limnological Tower). Four sites were used as the zooplankton of Rutland Water were prone to heterogeneous horizontal patterns of distribution as a result of wind action and different water quality in the two arms (Harper and Ferguson, 1982).

Covenham was sampled fortnightly at two sites, the inlet Valve Tower and the Central draw-off point (figure 6.2). Two sites were assumed to give a representative estimate of plankton density from this reservoir owing to its simple morphology, although section 6.2.2 throws some doubt on this assumption.

**6.2.2 Field sampling methods**
Crustacean zooplankton were sampled with a ten litre clear perspex Patalas sampler. This apparatus was considered the most efficient volumetric sampler by Schindler (1969).

The box was lowered gently through the water column until the desired sample depth was reached. The hinged top and bottom faces remained open during the descent. Once the sample depth was reached a sharp tug on the rope ensured that both faces closed to give a quantitative sample from a fixed depth. The full Patalas was then raised to the surface and the contents poured through a zooplankton mesh (140 μm) and preserved in 70% IMS (industrial methylated spirit).

Samples were taken at a depth of 5m from all sites except for the Limnological tower at Rutland Water where a vertical profile of 0m, 2m, 4m, 8m, 12m, and 16m was performed. A vertical net haul was also taken at the Limnological Tower to provide a qualitative sample for size measurements and egg counts.

Rotifers were sampled with a 0-5m vertically integrated tube sample. The bottom of the tube was weighted and lowered to a depth of 5m. The upper end of the tube was then stoppered to retain the sample as the tube was raised to the surface. The contents were then evacuated into a large container and mixed thoroughly before removing a one litre sub-sample which was preserved with Lugol's iodine.

6.2.3 Sampling effort

The spatial distribution of zooplankton in Rutland Water was found to be patchy by Harper and Ferguson (1982). A similar pilot study of Daphnia density in Rutland Water during 1992 and Covenham reservoir in 1995 revealed contagious distributions in both, as sample variance was greater than sample mean density (20,030 and 247 respectively in Rutland Water and 5,633 and 242 in Covenham). This questioned the accuracy of the routine sampling methods adopted by the Environment Agency.

The number of samples required to obtain a specific degree of accuracy of the population mean estimate, assuming that the pilot study distributions were a fair representation of the usual degree of horizontal patchiness, was calculated using the formula of Zar (1984)

\[
n = \frac{s^2 r^2 (\alpha - 1)}{d^2}\frac{F_{\beta(1), (n-1,v)}}{s^2}
\]
where \( s^2 \) is the sample variance, \( d^2 \) is one half the width of the desired confidence interval about the mean, \( 1-\alpha \) is the confidence level for the confidence interval, and \( 1-\beta \) is the assurance that the confidence interval will be no larger than specified.

Iteration was used to estimate the approximate number of samples required to obtain a population mean which gives 90% certainty that the 95% confidence limits are within \( \pm 20\% \) of the value. This was found to be 55 samples from Rutland Water, and 19 samples from Covenham reservoir which were obviously much greater than the number of samples routinely collected, and prohibitive in terms of sampling effort. By rearranging the above formula, it was possible to calculate the likely scale of errors associated with the normal sampling regimes on these dates. This showed that \( d \) was 138% of the population mean in Rutland Water and 484% of the mean in Covenham reservoir. The precision of the sample data was therefore questionable, but this is, unfortunately, an unavoidable part of sampling any population liable to contagion. All one can do is adopt an optimal sampling strategy that gives the best return in terms of precision for sampling effort, and recognise the limitations of the data during further analysis.

Figure 6.5 shows the error of the population mean associated with taking an increasing number of samples from the pilot study distributions. Errors were highest for small sample numbers but quickly fell with increased sample effort. Little was gained in terms of precision by taking more than ten samples per water body.

**Figure 6.5** Error associated with different sampling effort from the two reservoirs. Error expressed as \( d \) (half the width of the 95% confidence interval) in terms of the percentage of the population mean.

### 6.2.4 Sample concentration

Crustacean zooplankton samples were concentrated using filtration through a 140 \( \mu \)m mesh. Rotifers were concentrated via sedimentation to avoid the losses associated with
filtration of these small, delicate animals (appendix A.4.1). The volumes treated in this way are usually small (1-2 litres) and so the method is only suitable if a high density of animals is present in the sample.

Samples were poured into one litre plastic settling chambers and allowed to settle for four days (Furet and Benson-Evans, 1982). The specific gravity of many rotifers is just above one, so rotifers sink slowly (Saunders-Davies and Pontin, 1987). A drop of detergent was added to reduce the number of animals adhering to the water surface, and the cylinder was capped to minimise the oxidation of iodine from solution. After four days, the supernatant was siphoned from the top of the column until approximately 80 ml remained. Care was taken not to disturb the surface of the sediment throughout the procedure. The remaining liquid was mixed and transferred to a new sample bottle and the volume made up to 100 ml with the rinsings of the settling chamber. Further Lugol's was added if the colour of the solution had faded significantly.

Most studies assume that the number of animals lost during supernatant removal is negligible. Analysis of these losses (table 6.2) showed that less than 5% of rotifers were lost during the procedure except for *Keratella quadrata*, which often became trapped in the meniscus, and may therefore be under-represented in the final population estimate.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. animals in 100 ml sample</th>
<th>No. animals in supernatant</th>
<th>No. animals in tube rinsings</th>
<th>Total losses</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Polyarthra sp.</em></td>
<td>4680</td>
<td>72 (1.5)</td>
<td>69 (1.5)</td>
<td>141 (3.0)</td>
</tr>
<tr>
<td><em>K. cochlearis</em></td>
<td>270</td>
<td>7 (2.6)</td>
<td></td>
<td>7 (2.6)</td>
</tr>
<tr>
<td><em>K. quadrata</em></td>
<td>670</td>
<td>9 (1.3)</td>
<td>50 (7.5)</td>
<td>59 (8.8)</td>
</tr>
<tr>
<td><em>Synchaeta sp.</em></td>
<td>1472</td>
<td>19 (1.3)</td>
<td>6 (0.4)</td>
<td>25 (1.7)</td>
</tr>
<tr>
<td>Nauplii</td>
<td>630</td>
<td>26 (4.1)</td>
<td>6 (1.0)</td>
<td>32 (5.1)</td>
</tr>
</tbody>
</table>

Table 6.2 Efficiency of sedimentation procedure for rotifer concentration. Figure in brackets represent standard deviations.

### 6.2.5 Enumeration and sub-sampling procedure

Crustacean zooplankton were enumerated under low magnification (x30 - x65) using a dissecting microscope. Samples were counted in a Bogorov trough which is a perspex block with a trapezoidal trough cut into its base (figure 6.6). The volume held was slightly above 10 ml. The sample is introduced at one end of the trough and disperses along its length. The distribution of animals is not usually random (larger organisms settle first) so the whole trough must be counted. Detailed identification was usually
made on isolated animals under higher power magnification.

Sub-samples were taken by pouring a sample of known volume between two beakers before removing a fixed volume with a wide mouthed pipette (approximately 4 mm in diameter). The mixing method was tested to ensure that a random distribution was achieved. A non-significant $\chi^2$ result ($p>0.05$) for goodness of fit to a Poisson distribution of replicated sub-sample counts (without replacement) indicated that the mixing achieved a random distribution.

The coefficient of variation associated with counts from a Poisson distribution is dependant on the size of the count (Elliot, 1973). Variance decreases with increasing effort until at a count of approximately 50 - 60, the increase in precision stabilises, and little benefit is gained from further effort (Bottrell et al., 1976). The present study aimed to count over 100 individuals of the dominant group in any sample to reduce the variation associated with population density estimates.

Size measurements of individual *Daphnia* were performed using a dissecting microscope with a calibrated eye-piece graticule. Measurements were made from the top of the head to the insertion point of the tail spine. Fifty animals, removed at random, were measured per sample. Egg counts, required for birth rate calculations, were performed at low magnification after the removal of broods with tungsten needles. Fifty gravid females were analysed when sample density permitted.

Rotifers were enumerated at x100 magnification using the inverted microscope method.
described by Lund et al., (1958). Sub-samples of 5 ml or 10 ml volume were taken from a thoroughly mixed sample of 100 ml (random distribution checked with \(\chi^2\) test, \(p>0.05\)) and introduced to the settlement chamber which was then left to settle for a minimum of 30 minutes. A pilot study showed that 100% of animals and eggs from a range of rotifer groups settled in this time. Silty samples were not left for more than 60 minutes as the count efficiency was impaired when the fine silt settled. Random settlement patterns could not be assumed so the whole chamber was counted. A density of 100 of the dominant animals per count was aimed for to minimise errors, although when rotifer density was low this was not possible. The limitations of the data from small counts were recognised and were therefore not used for strict statistical analysis. Identification to genus was possible with the above procedure, but identification to species within genera such as *Polyarthra* spp. and *Asplanchna* spp. required higher magnification.

### 6.2.6 Biomass and population dynamics

*Daphnia* spp. length measurements were assigned to size classes of 0.1 mm increments. The average dry weight of animals in each size class was calculated from published length / weight regressions for individual species (Dumont et al., 1975; Bottrell et al., 1976; McCauley, 1984). Biomass was calculated from the number of animals per litre in each class multiplied by the average dry weight of the class.

Rotifer dry weight was calculated from an estimate of individual volume converted to fresh-weights assuming a specific gravity of one and to dry weight assuming that this was 10% of fresh weight (Bottrell et al., 1976). Volume was estimated from simple linear measurements related to a suitable geometric formula describing the morphology of the species (Ruttner-Kollisko 1977; Bottrell et al., 1976; McCauley 1984).

Population dynamics were analysed according to the methods of Edmondson (1960) and Hall (1964). Instantaneous birth rates and instantaneous population growth rates were calculated from field data and published embryonic development rates (Bottrell et al., 1976; Herzig, 1983). Instantaneous death rates were calculated by difference.

### 6.2.7 Calculation of predicted algal density for different system types

The regression lines of Soballe and Kimmel (1987) were used to estimate the algal density expected in a 'typical' lake, reservoir and river, from the annual mean phosphorus concentration at the three study sites. The regressions are as follows
rivers: \[ \log \text{cells ml}^{-1} = (0.69 \times \log \text{TP}) + 4.27 \]
reservoirs: \[ \log \text{cells ml}^{-1} = (0.53 \times \log \text{TP}) + 4.30 \]
lakes: \[ \log \text{cells ml}^{-1} = (0.66 \times \log \text{TP}) + 4.65 \]

Comparing the actual algal density achieved per unit phosphorus at each site with the above predictions gives an indication of where they fit into Søballe and Kimmel's classification.

For the present analysis, chlorophyll 'a' concentrations were converted to cell density by the following equation which was derived from dates when both algal cell density and chlorophyll 'a' concentrations were available (data supplied by Environment Agency, Anglian Region)

\[ \log \text{cells ml}^{-1} = (1.028 \times \log \text{chl. 'a')} + 2.738 \]

The dataset for Rutland Water and Covenham reservoirs was increased to five years (1991-1995) to gain a more reliable estimate of mean annual TP and chlorophyll 'a' concentration. The data set used for the River Nene covered the years 1976-1995.

6.3 Results

6.3.1 Physical and chemical characteristics of the study reservoirs

6.3.1.1 Trophic status

Tables 6.3 and 6.4 give details of a number of chemical and physical parameters of the two reservoirs.

<table>
<thead>
<tr>
<th></th>
<th>pH</th>
<th>NH₄</th>
<th>TON</th>
<th>SiO₂</th>
<th>chl a</th>
<th>SRP</th>
<th>TP</th>
<th>SD</th>
<th>temp.</th>
<th>oxygen</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>mg/l</td>
<td>mg/l</td>
<td>mg/l</td>
<td>µg/l</td>
<td>µg/l</td>
<td>µg/l</td>
<td>m</td>
<td>°C</td>
<td>% satm</td>
</tr>
<tr>
<td>minimum</td>
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<td>3.14</td>
<td>0.20</td>
<td>0.30</td>
<td>3.0</td>
<td>25.0</td>
<td>1.25</td>
<td>1.3</td>
<td>80.0</td>
</tr>
<tr>
<td>maximum</td>
<td>8.44</td>
<td>0.18</td>
<td>7.04</td>
<td>4.38</td>
<td>37.4</td>
<td>243.0</td>
<td>640.0</td>
<td>5.5</td>
<td>20.2</td>
<td>135.0</td>
</tr>
<tr>
<td>average</td>
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<td>0.07</td>
<td>5.24</td>
<td>1.74</td>
<td>8.64</td>
<td>38.73</td>
<td>75.69</td>
<td>3.10</td>
<td>10.77</td>
<td>96.06</td>
</tr>
<tr>
<td>st.dev.</td>
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<td>0.04</td>
<td>1.13</td>
<td>1.31</td>
<td>8.61</td>
<td>41.15</td>
<td>74.30</td>
<td>1.04</td>
<td>5.45</td>
<td>10.25</td>
</tr>
<tr>
<td>n</td>
<td>98</td>
<td>87</td>
<td>87</td>
<td>88</td>
<td>98</td>
<td>90</td>
<td>97</td>
<td>82</td>
<td>98</td>
<td>66</td>
</tr>
</tbody>
</table>

Table 6.3 Selected annual mean characteristics of Rutland Water 1991-1992.
<table>
<thead>
<tr>
<th></th>
<th>pH</th>
<th>NH$_4$</th>
<th>TON</th>
<th>SiO$_2$</th>
<th>chl a</th>
<th>SRP</th>
<th>TP</th>
<th>SD</th>
<th>temp.</th>
<th>oxygen</th>
</tr>
</thead>
<tbody>
<tr>
<td>minimum</td>
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<td>0.03</td>
<td>2.65</td>
<td>0.46</td>
<td>2.10</td>
<td>3.0</td>
<td>21.0</td>
<td>1.25</td>
<td>3.0</td>
<td>80.0</td>
</tr>
<tr>
<td>maximum</td>
<td>8.62</td>
<td>0.233</td>
<td>8.44</td>
<td>7.39</td>
<td>56.30</td>
<td>126.0</td>
<td>335.0</td>
<td>7.75</td>
<td>19.8</td>
<td>230.0</td>
</tr>
<tr>
<td>average</td>
<td>8.16</td>
<td>0.08</td>
<td>6.04</td>
<td>4.42</td>
<td>13.0</td>
<td>23.09</td>
<td>76.02</td>
<td>3.60</td>
<td>10.51</td>
<td>108.97</td>
</tr>
<tr>
<td>st.dev.</td>
<td>0.05</td>
<td>0.05</td>
<td>1.31</td>
<td>1.70</td>
<td>11.76</td>
<td>31.45</td>
<td>67.35</td>
<td>1.16</td>
<td>5.30</td>
<td>27.16</td>
</tr>
<tr>
<td>n</td>
<td>46</td>
<td>41</td>
<td>41</td>
<td>41</td>
<td>46</td>
<td>28</td>
<td>46</td>
<td>34</td>
<td>39</td>
<td>34</td>
</tr>
</tbody>
</table>

Table 6.4 Selected annual mean chemical characteristics of Covenham 1991-1992.

Both reservoirs were eutrophic, with annual average TP concentrations of 76 $\mu$g l$^{-1}$. The average annual chlorophyll 'a' concentration of the two reservoirs was similar, 9 $\mu$g l$^{-1}$ in Rutland Water and 13 $\mu$g l$^{-1}$ in Covenham. The two means were not significantly different when tested by a t-test due to high variance within the datasets.

6.3.1.2 Seasonality

**Rutland Water**

The seasonality of major plant nutrients in Rutland Water are presented in figure 6.7. Soluble reactive phosphate followed a pattern typical for productive temperate lakes (Wetzel, 1983) with high levels during the winter as a result of sediment release, full depth mixing, input from rivers, and low rates of assimilation into algal biomass, but lower levels in spring and summer owing to algal growth. Levels may have been limiting to certain species during the summer, as concentrations fell below 5 $\mu$g l$^{-1}$ SRP.

Total oxidised nitrogen concentrations were high throughout the year and were considered unlikely to limit algal growth as the half saturation concentration (range between 0.17 - 0.76 mg N l$^{-1}$ for different species (Pöhlmann et al., 1989)) was exceeded throughout the study period. The decrease in nitrogen content during the summer may, however, have had an influence on algal dynamics through a changing N:P ratio.

Silicate concentration followed a seasonal pattern typical for stratifying lakes, high during the winter, decreasing in spring as a result of diatom uptake, low in summer, and increasing once again with the autumnal turnover. The half saturation concentration for diatom growth of 0.06 mg l$^{-1}$ (Paasche, 1980) to 0.08 mg l$^{-1}$ (Pöhlmann et al., 1989) was approached during the summer, indicating that diatom growth may have been nutrient limited.
Chlorophyll 'a' concentration and secchi disk depth from Rutland Water are presented in figure 6.8.

The seasonal pattern of chlorophyll 'a' development was similar to that predicted for eutrophic lakes (Hutchinson, 1967; Reynolds, 1984; Sommer et al., 1986). High levels were present in spring, but declined during a short-lived clearwater phase in May and June which corresponded to increased water transparency. Chlorophyll 'a' concentration increased in the summer and fluctuated until it fell in October to a winter minimum. The total algal density was generally lower in 1992 compared with 1991.

There was some indication of a negative association between chlorophyll 'a' concentration and secchi depth, although this was not statistically significant. High algal concentrations tended to depress Secchi depth more in spring than summer as the light scattering ability of the small species prevalent at this time was greater than that of the larger colonial species which may become more abundant in the summer (Horn, 1991).
Figure 6.8 Chlorophyll 'a' concentration and water clarity in Rutland Water, 1991-1992.

The water temperature of Rutland Water was as expected for a northern temperate water body and differed little between the study years (figure 6.9).

Figure 6.9 Water temperature in Rutland Water, 1991-1992.

**Covenham**

The seasonal pattern of SRP concentration in Covenham (figure 6.10) was different to
that of Rutland Water. Levels fell to potentially limiting concentrations at the end of May, 1991, and did not recover for the rest of the study period, although the annual average chlorophyll 'a' concentration did not seem to be severely affected as this was higher than that of Rutland Water. This lack of impact on algal biomass may reflect the fact that SRP is often rapidly recycled within the planktonic community. The reason for the continued low SRP levels is unknown but may have been the consequence of ferric sulphate dosing the incoming water by Anglian Water Services.

![Graph of chemical characteristics of Covenham reservoir, 1991-1992.](image)

**Figure 6.10** Chemical characteristics of Covenham reservoir, 1991-1992.

Total oxidised nitrogen and dissolved silicate concentrations were similar to those recorded from Rutland Water. Silicate may have limited diatom growth during summer 1992, but remained relatively high during 1991.

The chlorophyll 'a' concentration of 1991 was depressed between April - June in what was assumed to be a clearwater phase (figure 6.11). Levels then rose in the summer but were again depressed during September. An autumnal peak occurred in October and November before levels dropped in December to low levels. Concentration was generally lower in 1992 than 1991, possibly as a result of the lower SRP concentration, but the seasonal development was generally similar although the autumnal peak was
The water temperature of Covenham reservoir was as expected for a northern temperate water body (figure 6.12), and was similar to Rutland Water.

Figure 6.11 Chlorophyll 'a' concentration and water clarity in Covenham reservoir, 1991-1992.

Figure 6.12 Water temperature in Covenham, 1991-1992.
6.3.2 Phytoplankton community structure

The taxonomic composition of the Rutland Water algal community is presented in figures 6.13 and 6.14 for 1991 and 1992 respectively. The early part of 1991 was dominated by cryptomonads (Cryptomonas sp. and Rhodomonas sp.) and naked flagellates, both of which are considered to be a good food source for grazers. Diatom cell density was also high at this time but only accounted for a small proportion of biomass as small centric diatoms were the dominant group. A short-lived blue-green bloom of Anabaena spp. and Microcystis spp. developed during April, prior to the main summer peak which was dominated by Aphanizomenon flos-aquae and lasted from June to October. Cryptomonads became dominant once again during the winter period.

**Figure 6.13** Rutland Water algal community composition, 1991. bg. blue-greens; dg. digestible greens; cr. cryptomonads; dt. diatoms; nf. naked flagellates; rg. resistant greens.

1992 was similar to 1991 except that there was no spring development of blue-greens.
Cryptomonads and diatoms dominated the spring plankton but were replaced by cyanobacteria, mainly *Aphanizomenon flos-aquae*, which remained abundant until the end of the year. Blue-green bacteria accounted for less of the total biomass in the latter half of 1992 than 1991. Cryptomonads were more abundant as a result and probably offered a viable 'undergrowth' food source for grazing zooplankton at this time.

The algal community of Covenham reservoir (figures 6.15 and 6.16) was different to that of Rutland Water, and did not follow the typical pattern described by Reynolds (1984) and Sommer *et al.*, (1986) for eutrophic temperate lakes. The seasonal development was characterised by periods of blue-green dominance punctuated by periods when other groups were abundant, namely diatoms in the spring, and diatoms, digestible greens and cryptomonads in the late summer / autumn.

**Figure 6.15** Covenham reservoir algal community composition, 1991. bg. blue-greens; dg. digestible greens; cr. cryptomonads; dt. diatoms; nf. naked flagellates; rg. resistant greens.

**Figure 6.16** Covenham reservoir algal community composition, 1992. bg. blue-greens; dg. digestible greens; cr. cryptomonads; dt. diatoms; nf. naked flagellates; rg. resistant greens.
6.3.3 Phytoplankton density as a measure of system function

Annual mean TP was 55.5 µg l⁻¹ (st.dev. ± 23.3, n=5) in Rutland Water 1991-1995, 61.5 µg l⁻¹ (st.dev. ± 29.1, n=5) in Covenham 1991-1995, and 1, 132 µg l⁻¹ (st.dev. ± 351, n=17) in the River Nene 1976-1995. The estimated algal cell densities for the three system types, lakes, reservoirs and rivers, using the regression equations of section 6.3.6 are presented in table 6.5, along with the observed density (all values logged). Errors associated with the estimated densities were calculated from the residual variation around the original regression lines of Søballe and Kimmel (1987). The difference between observed density and that predicted for each system type was tested with a Welch’s approximate t-test (Sokal and Rolf, 1995). An asterisk indicates a significant difference at the p = 0.05 level.

<table>
<thead>
<tr>
<th></th>
<th>Rutland Water</th>
<th>Covenham</th>
<th>River Nene</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>cells ml⁻¹</td>
<td>st. error</td>
<td>cells ml⁻¹</td>
</tr>
<tr>
<td>'typical' river</td>
<td>3.40 *</td>
<td>0.12</td>
<td>3.43 *</td>
</tr>
<tr>
<td>'typical' reservoir</td>
<td>3.63</td>
<td>0.08</td>
<td>3.66</td>
</tr>
<tr>
<td>'typical' lake</td>
<td>3.82</td>
<td>0.10</td>
<td>3.85</td>
</tr>
<tr>
<td>observed density</td>
<td>3.60</td>
<td>0.01</td>
<td>3.91</td>
</tr>
</tbody>
</table>

Table 6.5 Log algal cell density predicted from TP for different types of freshwater system (after Søballe and Kimmel, 1987). Standard errors of estimates taken from original regression line. Significant departure of observed density from that predicted for each system type shown by an asterisk (p < 0.05).

The algal density achieved per unit TP in Rutland Water and Covenham was similar to that expected from standing waters, according to Søballe and Kimmel (1987). Rutland water most closely resembled a reservoir, whereas Covenham was most similar to a lake.

The algal density of the River Nene site was significantly lower than that of standing waters with a similar nutrient concentration, but was within the range of values expected from rivers. This indicated that algal development was limited by factors other than nutrient concentration at this site.

6.3.4 The zooplankton of Rutland Water and Covenham reservoirs

A list of rotifers from Rutland Water and Covenham reservoir is presented in table 6.6. The list is somewhat shorter than that from the River Nene, as it does not contain many of the littoral / benthic species that were sporadically found at this site.
Table 6.6 Rotifer species collected from the two study reservoirs. Site 1 represents Rutland Water. Site 2 represents Covenham Reservoir. Asterisk represents littoral or periphytic species after Pontin (1978).

The crustacean species list for the two reservoirs is presented in table 6.7. The cladoceran community of both reservoirs was dominated by Daphnia, almost exclusively D. longispina in Rutland Water, and a combination of D. magna, D. pulicaria, and D. galeata in Covenham. Bosmina longirostris was generally less abundant, as were the other cladocerans which were assumed to be migrants from benthic / littoral habitats. The predatory Leptodora kindtii was recorded from Rutland Water, but Covenham had no predatory cladocerans. Both reservoirs shared the same calanoid copepod species but there were some differences in the cyclopoid fauna of the two.

The copepod fauna of Rutland Water was previously described in detail by Smith (1988). Four species of cyclopoid copepod were present during 1991-1992, Cyclops abyssorum, C. vicinus, Mesocyclops leuckarti and Acanthocyclops robustus. C. abyssorum and M. leuckarti have been present since filling (Harper and Ferguson, 1982) but the others are more recent arrivals. C. vicinus was most abundant during the
winter and spring, whereas the other species were more prevalent during the summer and autumn. Total cyclopoid density remained below 30 animals l\(^{-1}\) for the majority of the year.

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Site</th>
</tr>
</thead>
<tbody>
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<td>Order - Cladocera</td>
<td>Daphnia</td>
<td>longispina</td>
<td>1, 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>pulicaria</td>
<td>1, 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>magna</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Ceriodaphnia</td>
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<tr>
<td></td>
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<td></td>
<td>Acanthocyclops</td>
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Table 6.7 Crustacean species collected from the two study reservoirs. Site 1 represents Rutland Water. Site 2 represents Covenham Reservoir.

Two species of calanoid copepods were found in Rutland Water, *Eudiaptomus gracilis* and *Eurytemora velox*, the same species recorded by Smith (1988). Both species were at their most abundant during the summer. *E. gracilis* reached a maximum density of 60 animals l\(^{-1}\) during June while *E. velox* reached 30 animals l\(^{-1}\), also in June.

The calanoid copepod fauna of Covenham consisted of the same two species, both of which occurred throughout the growing season (March - October). The density of *E. gracilis* was similar to that of Rutland Water, reaching a peak of 80 animals l\(^{-1}\) in August, 1991 and approximately 40 animals l\(^{-1}\) in April, 1992. *E. velox* were less numerous, reaching a peak density of below 15 animals l\(^{-1}\) during the summer.
Covenham's cyclopoid copepod fauna was represented by *Cyclops abyssorum*, *C. albidus*, *C. agilis speratus*, *Cyclops gigas*, and *Acanthocyclops robustus* (*C. vernalis americanus* Marsh). Only two of these species, (*C. abyssorum* and *Acanthocyclops robustus*), were considered as limnetic by Gurney (1931; 1933, in Smith, 1988). The others were associated with weedy waters, and may have been more representative of the fauna of the Louth canal, from which water was abstracted. Total cyclopoid density reached a peak a number of times during the growing season, typically reaching less than 30 animals l\(^{-1}\).

6.3.5 Zooplankton seasonality in Rutland Water

6.3.5.1 Cladocerans

*Daphnia longispina* was the dominant cladoceran in Rutland Water during the study period. *Bosmina longirostris* was occasionally present at low density, as was *D. pulicaria* but only from the deeper strata of the reservoir. These species never accounted for more than 5% of total cladoceran biomass.

Figure 6.17 shows the population fluctuations of *D. longispina* during 1991 and 1992. The general pattern was similar to that described by Harper and Fergusen (1980) for Rutland Water in which *D. hyalina* had three annual peaks during May, June and September between 1977-1980, although the magnitude of the peaks were variable. The first peak occurred at the end of April, and was followed by the second approximately one month later. A period of low density, associated with a grazing induced spring clearwater phase separated the two peaks, but this was more defined in 1991 than 1992. The third peak was ill-defined and lasted for a longer duration.

Figure 6.17 *D. longispina* density in Rutland Water 1991-1992.
6.3.5.2 Rotifers

The rotifer fauna of Rutland Water has not been described previously, but there seemed to be a reproducible annual pattern of development during the two year study period (figure 6.18). Rotifer density reached a peak early in the spring, prior to the development of the cladoceran biomass. A fall in density at the end of April coincided with the spring peak of *D. longispina*. The second rotifer peak occurred during May, once *Daphnia* numbers had declined. Rotifer density fluctuated throughout the summer months, but remained higher in 1992 than 1991.


*Polyarthra spp.* was the dominant rotifer group during the study period (figure 6.18) but actually comprised a number of different species, each with different optimum growth requirements. *P. dolichoptera* was dominant during the spring but was succeeded by *P. major*, *P. vulgaris* and *P. remata* in the summer. *Synchaeta spp.* was found throughout much of the year, but again, this taxonomic unit comprised a number of species, although preserved animals could not be identified accurately. *Keratella cochlearis* and *K. quadrata* were found throughout the warmer months, but *Asplanchna*
herricki was only present over a restricted period during the spring of both years.

6.3.5.3 *Daphnia* dominance

*Daphnia longispina* dominated the grazing zooplankton of Rutland Water (excluding copepods), accounting for 93% of the total biomass over the two year study period (figure 6.19). This was the opposite pattern to that found in the River Nene where rotifers were dominant. Rotifers were generally more prevalent early in the year before cladoceran biomass developed, and also later in the summer of 1992.

![Relative abundance in terms of biomass (µg l⁻¹) of rotifers (stippled) and *D. longispina* (filled) in Rutland Water, 1991-1992.](image)

6.3.6 Interactions within the grazing zooplankton of Rutland Water

The growing season was divided into spring and summer periods for the following correlation analysis, as the level and type of interactions were expected to differ between the seasons, primarily owing to a different phytoplankton community structure (figures 6.13 and 6.14).

6.3.6.1 Spring

The Product-Moment correlation coefficients for the spring period of both 1991 and 1992 are displayed in table 6.8. All variables were log-transformed prior to analysis to ensure normality.

Highly significant associations between chlorophyll 'a' concentration and *Daphnia* biomass, and *Daphnia* community filtration rate, were recorded during the spring. This indicated a level of grazing 'top-down' control on the small phytoplankton which were dominant at this time of the year (note the highly significant correlation between chlorophyll 'a' and edible phytoplankton groups).
<table>
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<th>temp.</th>
<th>e alg.</th>
<th>flag.</th>
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<th>CFR</th>
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<td>0.939</td>
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Table 6.8 Pearson product-moment correlations among parameters expected to have an effect on rotifer density during spring (Mar-Jun) 1991 - 1992. n=22. Values greater than 0.423 represent a significant relationship (p<0.05). All variables normally distributed after transformation (Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf, 1995)). CFR is the Daphnia community filtration rate, after Jones et al., (1979). Total CFR relates to Daphnia and rotifer grazing pressure.

Rotifer density was negatively associated with Daphnia biomass and measures of community filtration rate during the spring. The correlation coefficients were not as strong as those between Daphnia and chlorophyll 'a', but were still significant at the p<0.05 level. It is not clear from the data whether the rotifers were depressed indirectly by exploitative competition for food (via the negative impact of Daphnia on phytoplankton density) or directly by mechanical interference, or by a combination of both.

Predation may also have influenced rotifer population dynamics during the spring. The likelihood of this was estimated from an analysis of rotifer population dynamics in section 6.3.6.3.

6.3.6.2 Summer

The correlations of the summer were rather different to those of the spring period (table 6.9). Daphnia grazing had no negative impact on total chlorophyll 'a'. Higher temperature related algal growth rates may have been partly responsible for a lack of top-down control, but the lower biomass of Daphnia during the summer compared to spring, and the presence of colonial blue-green bacteria which impair the efficiency of Daphnia feeding were also probably involved in weakening the grazing impact on the algal community.
Rotifer density and \textit{Daphnia} community filtration rate were not significantly related during the summer. The potential for exploitative competition for food was reduced compared to spring as \textit{Daphnia} were not negatively associated with algal density. The potential for mechanical interference was also presumed to be lower, as \textit{Daphnia} individual size was smaller in the summer (see section 6.3.6.6).

### 6.3.6.3 Quantification of the community grazing pressure in Rutland Water

The negative correlation between community filtration rate (CFR) and chlorophyll 'a' concentration in Rutland Water during spring 1991 and 1992, was not proof of a causal relationship. It was therefore necessary to quantify the grazing pressure and relate this to potential algal growth rates, to ensure that \textit{Daphnia} filtration was of a magnitude capable of exerting a top-down influence.

The daily CFR of \textit{D. longispina} was calculated from published clearance rates by Jones \textit{et al.}, (1979), taking into account the size distribution of the population, temperature of the water, and food concentration. Rotifer grazing was estimated assuming an average clearance rate of 5 \( \mu l \) ind\(^{-1}\) hr\(^{-1}\). Figure 6.20 shows the exponential daily loss rate of edible algal particles attributed to \textit{Daphnia} and rotifer grazing.

Grazing pressure was dominated by \textit{Daphnia longispina} and had a seasonality roughly similar to that of \textit{Daphnia} biomass with only slight differences owing to changes in temperature and particle concentration which affect filtration rates. Rotifer community filtration rate was generally more important during early spring (March - April) prior to
Figure 6.20 Community filtration rate expressed as ml per litre cleared per day in Rutland Water, 1991-1992
Daphnia development, and during the summer, especially in 1992, when cyanobacteria were abundant.

The spring clearwater phase of 1991 (May - June) and 1992 (May - mid-July) occurred shortly after, or during, periods of peak filtration rate, indicating the importance of grazer influence on algal dynamics in Rutland Water. Community filtration rates in the order of 300 ml l$^{-1}$ d$^{-1}$, (equivalent to an exponential loss rate of 0.3 d$^{-1}$) may have exceeded algal replication rates of some species during the spring when water temperature was typically between 10 - 15 °C and may therefore have controlled algal biomass at this time. Loss rates would have been greater if sedimentation, parasitism, senescence, and losses owing to other grazers such as pelagic copepods were taken into account.

Chlorophyll 'a' concentration was not significantly reduced by Daphnia community filtration rate during the summer (section 6.3.6.2) irrespective of high community filtration rates in excess of 300 ml l$^{-1}$ d$^{-1}$. The high filtration rates were presumably founded on the undergrowth species, leaving the larger net algae relatively unaffected by comparison. Daphnia clearance rates were especially low during the summer of 1992 when blue-green bacteria were abundant. Rotifer community filtration accounted for over 50% of total filtration rate during this period.

An autumnal peak of Daphnia dominated community filtration during October was associated with decreased chlorophyll 'a' concentrations during both study years.

6.3.6.4 Analysis of the methods of rotifer suppression in Rutland Water

The following section aims to understand some of the factors which control rotifer populations in Rutland Water. Three methods of data analysis were used. These included an estimate of death rate owing to interference from Daphnia filtration, an analysis of birth rate fluctuation and food abundance, and a detailed analysis of the population dynamics of two rotifer groups. Keratella cochlearis and Polyarthra spp., were chosen because their eggs were relatively easy to identify when detached and they were relatively abundant. Information gained was useful for assessing the relative importance of food limitation, mechanical interference and predation to rotifer dynamics.

Death rate imposed by mechanical interference

The community filtration rate of large Daphnia (>1.2 mm body length) calculated for
palatable algal particles was converted to a *Keratella cochlearis* based clearance rate using the equation of Burns and Gilbert (1986) derived from laboratory observations

\[ y = 3.32x - 0.1 \]

where \( y \) is the *Keratella* based clearance rate (ml *Daphnia* \(^{-1}\) h\(^{-1}\)) and \( x \) is the effective algal filtration rate (ml *Daphnia* \(^{-1}\) h\(^{-1}\)). This equation was assumed to apply to the Rutland Water population as it was originally derived from a wide selection of species.

Figure 6.21 presents the measured instantaneous death rate of *Keratella cochlearis* (calculated as the difference between instantaneous birth rate and rate of increase) and the expected death rate owing to mechanical interference. Only those dates on which rotifer density exceeded 20 animals per litre were used as death rates are unreliable when based on small sample sizes (MacIsaac and Gilbert, 1989).

![Figure 6.21 A comparison of the natural death rates of *Keratella cochlearis* in Rutland Water (A) and estimated death rates owing to mechanical interference from large *Daphnia* (>1.4mm) (B).](image)

There was little association between the magnitude of measured death rates and estimated rates owing to interference. Estimated death rates were often higher than natural death rates, which makes little sense if mechanical interference competition (MIC) was important. The presence of negative death rates, however, may indicate some level of error in the data, probably resulting from sampling errors, or possibly the hatching of resting eggs which led to an underestimate of actual birth rate.

*Birth rate analysis*

Figure 6.22 shows that the instantaneous birth rates of *K. cochlearis* and *Polyarthra spp.* were negatively associated with *Daphnia* community filtration rate during the
Figure 6.22 Instantaneous birth rate of A. Keratella cochlearis and B. Polyarthra spp. in relation to the Daphnia community filtration rate in Rutland Water.
spring. Low birth rates could have resulted from egg separation whilst in the brood chamber of *Daphnia*, but as loose eggs were counted, this was considered to be an unlikely explanation. The low rates were more probably the product of food limitation. The pattern was less obvious in the summer when CFR was unrelated to chlorophyll 'a' concentration, and therefore food limitation was less likely.

*Rotifer population dynamics*

The mechanism by which population declines were brought about may be evident from the pattern of birth and death rates immediately preceding the crash. At high temperatures, rotifers initiate egg production within a few days of hatching, so that the population is likely to be comprised of mainly mature animals. Changes in the egg ratio of rotifers therefore tends to be a good indicator of extant food conditions (Urabe, 1992). A reduced birth rate (or egg ratio) prior to a population crash is usually considered the product of food limitation, whereas a high death rate associated with continued high birth rate signals the removal of adults from the population caused by for example, predation or mechanical interference competition.

Figure 6.23 shows the population characteristics of *Polyarthra spp.* in Rutland Water during 1991 and 1992.

The first spring peak of 1991 occurred before *Daphnia* became abundant, but subsided soon after. Egg production was high prior to, and during this first peak, but reduced before numbers crashed at the end of April in both years. Death rates were not high at this time. Reduced egg production and low death rates indicated that food limitation was the main cause of the early spring population decline. The pattern was similar during the second crash of *Polyarthra* density during July, although death rates were also high at this time. The last peak in August was founded on high egg production indicating that food was plentiful during this period (b' = 0.8). Density declined at the end of August, a matter of days after chlorophyll 'a' levels crashed. The decline followed a decline in fecundity, indicating that food was limiting.

*Polyarthra* dynamics during 1992 followed a similar pattern to that described for 1991. The first summer peak ended at the start of July when the egg ratio and birth rate fell to zero. The subsequent development which lasted until October was characterised by high birth rates and high death rates. Food was therefore considered to be in good supply at this time, but population development was checked by another factor. The final decline of *Polyarthra* at the end of September was preceded by a fall in egg production, indicating food limitation similar to 1991. Figure 6.11 showed that total chlorophyll 'a'
concentration declined a matter of days before the crash.

Figure 6.23 Population dynamics of *Polyarthra* spp. from Rutland Water 1991 - 1992. A. animal density (solid line) and egg density (broken line). B. egg ratio (eggs per female). C. instantaneous rate of increase (solid line) and instantaneous birth rate (hatched line). D. instantaneous death rate.

Figure 6.24 shows the population characteristics of *Keratella cochlearis* in Rutland Water during 1991 and 1992.

*Keratella cochlearis* birth rates and egg ratio fluctuated during the summer of 1991, indicating periods of food limited production. The effect of temperature on the birth rate was ignored as summer water temperatures were relatively high throughout the period. The major period of numerical development during August - September was terminated after a fall in egg production when chlorophyll 'a' concentration fell to below 5 µg l$^{-1}$, indicating that food limitation was involved.

Birth rate remained high during the summer of 1992 owing to constant egg production, indicating food was non-limiting, even though chlorophyll 'a' concentration was low at this time. High potential rates of increase (birth rates) were not realised owing to high death rates, similar to *Polyarthra* described above. *K. cochlearis* density crashed suddenly at the end of September. The cause of the decline may have been the result of poor food conditions, as the birth rate declined prior to the crash and the density of
animals followed a few days after a fall in total chlorophyll 'a', similar to 1991.

Figure 6.24 Population dynamics of *Keratella cochlearis* from Rutland Water 1991 - 1992. A. animal density (solid line) and egg density (broken line). B. egg ratio (eggs per female). C. instantaneous rate of increase (solid line) and instantaneous birth rate (hatched line). D. instantaneous death rate.

6.3.6.5 *Daphnia longispina* population dynamics

Figure 6.25 presents the population dynamics of *Daphnia longispina* in Rutland Water during 1991 and 1992. Peak densities were achieved during the spring, with the development of subsequent smaller densities until October. The first spring peak was founded on a high egg ratio (over 2.5 eggs per animal) indicating good food conditions early in spring, but declined when egg production fell, presumably owing to food limitation during the spring clearwater phase. The spring crash of 1992 was less obvious, and birth rates remained high throughout the spring and summer. Population density remained relatively stable, however, indicating that high birth rates were matched by deaths possibly resulting from predation of either eggs or adults. The only period of high death rate in 1991 was noted when populations declined rapidly during June.

The termination of the autumnal development at the end of September in both years was
the product of declining egg ratio, indicating the importance of food limited control.

Figure 6.25 Population dynamics of *Daphnia longispina* in Rutland Water. A. animal density (solid line) and egg density (broken line). B. egg ratio (number of eggs per individual). C. instantaneous rate of population increase (solid line) and instantaneous birth rate (broken line). D. instantaneous death rate.

The indication from the above analysis that *Daphnia* populations were food limited in spring was strengthened by figure 6.26 which shows the relationship between standardised brood size (SBS) and chlorophyll 'a' concentration in Rutland Water during spring. SBS was used as it is a better measure of fecundity than average brood size, as it accounts for differences in female size (Lampert, 1988b).

SBS was closely associated with food availability during the spring when the algae was dominated by small edible forms. The relationship between SBS and chlorophyll 'a' concentration was significant at the p<0.01 level. The slope of the relationship was significantly higher (P<0.01) during the spring of 1992, when chlorophyll 'a' levels were generally lower than in 1991, indicating that larger broods were produced per unit chlorophyll. It was therefore possible that the algal community of 1992 was more 'palatable' than during 1991. Indeed, figures 6.13 and 6.14 show that blue-green bacteria were present in spring 1991 but not in spring 1992.
The relationship was non-significant when the summer period was included, *i.e.* high chlorophyll 'a' did not lead to high SBS, presumably because of a reduction in food quality owing to the dominance of cyanobacteria. Figure 6.27 shows that low summer SBS coincided with a high proportion of blue-greens in the phytoplankton community.

6.3.6.6 Size-structure of the cladoceran community

The majority of *Daphnia longispina* individuals were smaller than 1.55 mm (figure 6.28). The median size of individuals in 1991 increased from 0.65 mm in January to 1.15 mm in August, and then remained at a similar level until December. The median size of 1992 fluctuated between 1.15 and 0.85 mm during spring but remained
Figure 6.28 Size distribution of *Daphnia longispina* from Rutland Water during 1991 (left) and 1992 (right). n=50 per month.
relatively stable at approximately 0.95 mm during July - September, after which time it increased 1.15 mm in December. The summer median size of 1992 was generally smaller than that of 1991.

Minimum size at maturity, calculated as the average length of the two smallest gravid females, can be a useful indicator of the level of predation acting on cladoceran populations. The size at maturity of *D. longispina* changed in a predictable manner throughout the year, as shown in figure 6.29. A large minimum size was typical during the spring compared to that of the summer. This was especially obvious in 1992, when the size at maturity fell to below 1.1 mm during July, and remained low until the start of October. Declining size is often taken as an indication of size-selective vertebrate predation, and was assumed to be related to the feeding action of planktivorous fish stock of this reservoir.

![Graph showing minimum size at maturity of *Daphnia longispina* and occurrence of *Leptodora kindtii*.](image)

**Figure 6.29** *Daphnia longispina* minimum size at maturity (line) and the occurrence of the invertebrate predator *Leptodora kindtii* (circles).

The presence of the invertebrate predator *Leptodora kindtii* was assumed to have little influence on the size structure of the *D. longispina* community, as they should cause an increase in the size at maturity when present, but as figure 6.29 shows the opposite was true.

6.3.7 Zooplankton seasonality in Covenham reservoir

6.3.7.1 Cladocerans

The grazing zooplankton of Covenham reservoir was dominated by three species of *Daphnia*: *D. magna* Straus, *D. pulicaria* Forbes, and *D. galeata* Sars in order of decreasing adult size. Figure 6.30 shows that one species was usually dominant at any
one time. *D. magna* almost exclusively accounted for the early peak of 1991 which lasted until July when *D. pulicaria* became abundant. Biomass remained low after the crash and did not develop until the spring of 1992, when *D. longispina* became dominant. This species remained dominant until October, when *D. magna* appeared in the plankton once again. Total cladoceran biomass was truncated early in the summer of 1991 but remained relatively high throughout the summer of 1992.

Biomass was used to represent species occurrence in Covenham, as density alone does not account for the size difference between *Daphnia* species. *D. magna*, however, reached a peak density of 29 animals per litre in the early summer of 1991, *D. longirostris* reached a peak density of 33 animals per litre in 1992, and *D. pulicaria* reached a peak density of 13 animals per litre in July, 1991.

![Graph of *Daphnia* spp. composition in Covenham reservoir, 1991-1992.](image)

**Figure 6.30** *Daphnia* spp. composition in Covenham reservoir, 1991-1992.

### 6.3.7.2 Rotifers

The rotifer fauna was somewhat impoverished in terms of abundance and diversity compared to Rutland Water. The mean number of species found per litre during the growing season was 2.35 (st.dev. ± 1.61, n=34) in Covenham as opposed to 3.91 (st.dev. ± 2.34, n=68) in Rutland Water. This difference was significant at the p<0.001 level when tested by the nonparametric Wilcoxon's signed rank test (Sokal and Rohlf, 1996). The density of rotifers was also lower in Covenham (figure 6.31). Peak densities during the two year study period remained below 300 animals per litre, whereas in Rutland they reached over 1000 animals per litre (figure 6.18). *Polyarthra spp.* was the dominant group in terms of density, accounting for 42.9% of all rotifers in 1991 and 58.5% in 1992. *Keratella cochlearis* was the next most abundant group accounting for 31.6 % and 27.9% of all rotifers in 1991 and 1992 respectively.

Total density reached a peak early in the spring prior to *Daphnia* development in both years but declined shortly after the cladocerans increased in density. This decline occurred earlier in 1992 than 1991 and lasted for longer, a similar pattern to that observed in Rutland Water.

6.3.7.3 *Daphnia* dominance

*Daphnia* species dominated the grazing zooplankton of Covenham (excluding copepods) in terms of biomass, as depicted in figure 6.32.

They represented over 95% of total biomass during the study period, a similar figure to Rutland Water where *D. longispina* accounted for 93% of total biomass. Rotifers were generally more common during the spring period, prior to the development of *Daphnia* populations, and again briefly during the summer.
6.3.8 Interactions within the grazing zooplankton of Covenham Reservoir

Correlation analysis was used to identify potential trophic interactions within the zooplankton community of Covenham reservoir. The whole growing season was analysed as too few data points were available to split the year between spring and summer like the Rutland Water analysis, and the lack of an obvious seasonal succession in the phytoplankton (figures 6.15 and 6.16) also made a seasonal split less applicable in this system. The two years were treated separately in the following analysis as the obvious difference in *Daphnia* community structure indicated a natural division, potentially driven by trophic interactions.

The data used in the correlation analysis were smoothed by applying a three point moving average as the original data were temporally variable but showed what seemed to be clear underlying patterns.

6.3.8.1 1991

*Daphnia* (expressed as either biomass or community filtration rate) were negatively correlated with algal density in 1991 (expressed as chlorophyll 'a' concentration) (table 6.10). Figure 6.33 shows that chlorophyll 'a' reached a peak early in the year but was depressed when *Daphnia* community filtration rate increased in the spring / early summer to a level that was considered sufficient to control algal development. Chlorophyll 'a' remained low until August, when an increased concentration coincided with decreased *Daphnia* abundance. A further early winter peak of chlorophyll 'a' occurred after *Daphnia* density had fallen to its winter minimum.
Table 6.10 Pearson product-moment correlations among parameters expected to have an effect on rotifer density during the growing season (Mar-Oct) 1991. n=14. Values greater than 0.532, in bold, represent a significant relationship (p=0.05). All variables normally distributed after log transformation (Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf, 1995)).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Daphnia (μg l⁻¹)</th>
<th>chl. 'a' (μg l⁻¹)</th>
<th>temp. (°C)</th>
<th>edible algae (pg ml⁻¹)</th>
<th>flagellates (pg ml⁻¹)</th>
<th>blue greens (pg ml⁻¹)</th>
<th>rotifers (no. l⁻¹)</th>
<th>DCFR (ml day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daphnia (μg l⁻¹)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>chl. 'a' (μg l⁻¹)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>temp. (°C)</td>
<td>-0.027</td>
<td>0.214</td>
<td>1.00</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>edible algae (pg ml⁻¹)</td>
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<td>0.585</td>
<td>0.819</td>
<td>1.00</td>
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<tr>
<td>flagellates (pg ml⁻¹)</td>
<td>-0.304</td>
<td>0.498</td>
<td>0.853</td>
<td>0.828</td>
<td>1.00</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>blue greens (pg ml⁻¹)</td>
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<td>0.537</td>
<td>0.680</td>
<td>0.900</td>
<td>0.784</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>rotifers (no. l⁻¹)</td>
<td>-0.688</td>
<td>0.578</td>
<td>0.181</td>
<td>0.352</td>
<td>0.499</td>
<td>0.350</td>
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</tr>
<tr>
<td>DCFR (ml day⁻¹)</td>
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<td>-0.755</td>
<td>-0.240</td>
<td>-0.392</td>
<td>-0.506</td>
<td>-0.215</td>
<td>-0.727</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Figure 6.33 Seasonal incidence of *Daphnia* community filtration rate and chlorophyll 'a' levels in Covenham, 1991-1992.

Figure 6.34 shows a similar antagonism between *Daphnia* filtration capacity and rotifer abundance. Rotifer density was low except for a brief period early in spring and during a period of low *Daphnia* abundance in August.

The negative correlation between *Daphnia* and rotifers is not proof of a causal relationship but could theoretically have been the product of food limitation caused by *Daphnia* grazing, or direct mechanical interference competition (MIC). The latter of the two may be more important in Covenham than it was in Rutland Water considering the increased size structure of the *Daphnia* population (figure 6.35).
Figure 6.34 Seasonal incidence of *Daphnia* community filtration rate and rotifer density in Covenham, 1991-1992.

A multiple regression with rotifer density as the dependant variable, and *Daphnia* community filtration rate (DCFR) and chlorophyll 'a' concentration as the independent variables, proved that DCFR described more residual variation in rotifer abundance than chlorophyll 'a' concentration, and therefore indicated that MIC may have been important in this water body during 1991. The lack of *Keratella cochlearis*, a rotifer known to be susceptible to MIC but with a low threshold food concentration for development, between April - August, 1991 also provides qualitative evidence that MIC may have suppressed rotifer populations in Covenham.

6.3.8.2 1992

*Daphnia* community filtration rates were not associated with chlorophyll 'a' concentration or edible algae during the growing season of 1992 (table 6.11).

<table>
<thead>
<tr>
<th></th>
<th>Daph</th>
<th>chl. a</th>
<th>temp.</th>
<th>e alg.</th>
<th>flag.</th>
<th>b.g.</th>
<th>rot.</th>
<th>DCFR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daphnia (µg l⁻¹)</td>
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<td></td>
<td></td>
</tr>
<tr>
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<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>edible algae (pg ml⁻¹)</td>
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<td>.099</td>
<td>.135</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>flagellates (pg ml⁻¹)</td>
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<td>.046</td>
<td>.025</td>
<td>.750</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>blue greens (pg ml⁻¹)</td>
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<td>.080</td>
<td>.027</td>
<td>.972</td>
<td>.623</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>rotifers (no. l⁻¹)</td>
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<td>.030</td>
<td>.125</td>
<td>.467</td>
<td>.823</td>
<td>.312</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>DCFR (ml day⁻¹)</td>
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<td>.143</td>
<td>.544</td>
<td>.420</td>
<td>.344</td>
<td>.479</td>
<td>.180</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Table 6.11 Pearson product-moment correlations among parameters expected to have an effect on rotifer density during the growing season (Apr-Oct) 1992. n=14. Values greater than 0.532, in bold, represent a significant relationship (p=0.05). All variables normally distributed after log transformation (Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf, 1995)).
Figure 6.35a Size distribution of Daphnia individuals in Covenham reservoir, 1991. n=50 per month.
Figure 6.35b Size distribution of *Daphnia* individuals in Covenham reservoir, 1992. n=50 per month.
Figure 6.33 shows that although low chlorophyll 'a' concentrations during June and July of 1992 coincided with high *Daphnia* CFR, this pattern was not repeated later in the summer when the two parameters reached a peak synchronously. No significant relationship was found between *Daphnia* and rotifer abundance in 1992 indicating a reduced level of both EC and MIC in this year, possibly resulting from a decreased individual *Daphnia* size (figure 7.35).

6.3.8.3 Estimated mechanical interference rates in Covenham Reservoir

Rotifer birth and death rates were not calculated with the Covenham data as the two week inter-sample period was considered too long to fulfil the assumptions of the method. The expected death rate of susceptible rotifers from mechanical interference with *Daphnia* over 1.2 mm long was, however, calculated according to section 6.3.

Figure 6.36 presents the estimated daily death rate of *Keratella cochlearis* from MIC alone. Exponential death rates during the population peak of *D. magna* reached -1.4 per day, indicating that the whole water volume was cleared of animals in less than one day. The maximum exponential growth rate of this species is between 0.3-0.4 d⁻¹ (Walz, 1995), so death rates in this order could have had significant effects on population density. The expected death rates of 1992 were much smaller as a result of the smaller body size of *Daphnia galeata* (figure 6.35).

![Figure 6.36](image)

**Figure 6.36** Daily death rates of rotifers susceptible to mechanical interference from large *Daphnia* in Covenham reservoir.

Estimated death rates during the growing season of 1991 in Covenham were significantly higher than those of Rutland Water (p < 0.05; Wilcoxon's signed rank test), as a result of the larger body size of *D. magna*. There was no significant difference between the estimated death rates of Rutland Water and Covenham during...
1992, when the dominant cladoceran was the small *D. galeata*. The persistence of rotifer populations throughout 1992, including *K. cochlearis*, indicated that MIC may have had little effect in this year, similar to Rutland Water.

6.3.8.4 Potential food limitation of *Daphnia* populations

The standardised brood size (SBS) of *D. magna* in the spring of 1991 did not exceed 6. This was low for what is generally considered to be an *r*-selected species (Romanovsky, 1984) that has been recorded with over 20 eggs per brood (Kleiven et al., 1992). It was possible that the larger gravid females were underestimated by epilimnetic sampling, as these animals are more likely to spend the daytime at greater depth to avoid visual vertebrate predation (Lampert, 1989). SBS decreased during the summer, but the lack of data points makes it difficult to draw any conclusions regarding food limitation during 1991.

SBS during 1992 was highest early in the spring (end of March - April) when a maximum of 30 eggs per brood were recorded from a single gravid *D. galeata* individual. The chlorophyll 'a' concentration was approximately 12 µg l⁻¹ at the time, although blue-green bacteria accounted for a large part of algal biovolume. Summer SBS was lower than in spring, with many animals found carrying only a single egg. This may be taken as a sign that food was limiting, but it was more likely that ballooning of the carapace, leading to egg loss, was the cause of low SBS estimates.

The high population density of *D. magna* in 1991 was associated with chlorophyll ‘a’ concentrations below 3 µg l⁻¹, which would not usually support such a high biomass. *D. magna* may therefore have been utilising detrital seston as an alternative food resource.

6.3.8.5 Size structure and predation

A notable feature of the zooplankton of Covenham was the annual shift in the size-structure of the *Daphnia* community. This was assumed to reflect changes in the intensity of planktivore fish predation (Hrbáček, 1987). Seda and Duncan (1994) proposed that the proportions of the three species of *Daphnia* could be used as a rough guide of vertebrate predation pressure on the zooplankton. Low predation was associated with a dominance of *D. magna* in the London reservoirs, whereas higher predation pressure was associated with a plankton dominated by the smaller *D. galeata*.

An ANOVA was used to test the average size at maturity of the three species in the
present study. The result was highly significant (P<0.001). *D. magna* was the largest species with an average mean size at maturity of 3.07 mm, *D. pulicaria* was next largest at 2.02 mm, and *D. galeata* was the smallest at 1.74 mm. The proportion of the three species may therefore be used to indicate annual changes in predation pressure in a similar fashion to that described by Seda and Duncan (1994).

Figure 6.37 presents the percentage contribution of different species to total cladoceran biomass from 1991 - 1995.

1991 and 1993 were dominated by the larger species, whereas the smaller species were more abundant in 1992, 1994 and 1995. It may be noteworthy that the smallest species, *Bosmina longirostris* was not recorded in years dominated by the large species. No further rotifer data was available but it would seem plausible that the density of rotifers was also higher in the years dominated by smaller cladocerans, as was the case in 1992. According to Seda and Duncan (1994) the dominance of *D. magna* in 1991 indicates that fish predation was low in this year, whereas the dominance of the small species in 1992 indicated a higher predation level.

The size of mature animals also changed throughout the growing season in a similar fashion to those described in Rutland Water. The mean size of mature *D. galeata* was lower in the summer of 1992 compared to that of spring. The difference, tested using a Wilcoxon's signed rank test, was significant at the p< 0.05 level. This reduction would be expected if there was a relatively strong recruitment of planktivores during 1992 which started to prey on *Daphnia* during the early summer, after an initial period of 'gape-limited' feeding.
6.3.9 Planktivorous fish density

Kubecka and Duncan (1994) described a relationship between the fish biomass and the biomass of 'large' Daphnia in a number of Czech and British reservoirs (figure 6.38). This method was used to estimate the fish density in Covenham reservoir during the study years.

The biomass of Daphnia over 1.25 mm long was calculated as protein nitrogen using the relationship of Kubecka and Duncan (1994)

\[ N = 0.625 \times (3 \times \text{length}^{2.5}) \]

where \( N \) is mg protein nitrogen and length is in mm. It was realised that the assumptions used when applying this method to the Covenham Daphnia community incorporated error into the calculation, but as it was only supposed to give a broad indication of fish biomass, it was considered adequate for the present study. Biomass calculated per unit volume in the present study had to be converted to an aerial unit of measurement \( (m^{-2}) \) assuming an average water column depth of 14m, for direct comparison with the relationship Kubecka and Duncan (1994).

**Figure 6.38** The relationship between the biomass of large Daphnia and fish stock in the Rimov, Jordon and three London reservoirs after Kubecka and Duncan (1994), showing predicted fish biomass in Covenham during 1991 and 1992.
The mean biomass of large cladocerans during the growing season of 1992 was approximately 50 mg protein N m\(^{-2}\), which corresponded to a fish biomass of approximately 100 kg ha\(^{-1}\). Mean biomass of large *Daphnia* during 1991 was approximately 150 mg protein N m\(^{-2}\), which corresponded to a fish biomass of approximately 15 kg ha\(^{-1}\), although an actual value could not confidently be given owing to the slope of the line.

The total fish biomass in the reservoir in 1994, when the cladoceran community structure was very similar to 1992, was less than 5 kg ha\(^{-1}\) (Brierly and Duncan, pers. comm.).

### 6.4 Discussion

#### 6.4.1 Algal community response to habitat type

The total phytoplankton density achieved per unit phosphorus concentration was a good indicator of overall system function in the present study. Neither the algal biomass achieved in Rutland Water or Covenham reservoir differed significantly to that expected for standing water bodies according to Søballe and Kimmel (1987), but both were significantly higher than that expected from river systems. Alternatively, the algal density per unit phosphorus of the River Nene was significantly lower than that expected from lakes or reservoirs, but was similar to that of river systems as was previously noted in chapter 2.

The observed algal cell density was higher in the river than either of the reservoir sites, but owing to the high phosphate levels, it was still lower than would be expected from a reservoir of similar phosphate concentration. This result indicates that the development of the river phytoplankton was restricted by some factor other than nutrient limitation which was unlikely to have been grazing because of the low density of cladocerans at this site. It was probably owing to a combination of enhanced rates of sedimentation from shallow depths, low growth rates resulting from poor light penetration, and high loss rates resulting from the hydraulic removal of cells. These mechanisms are mainly physical as opposed to the biotic interactions which limit growth in reservoirs during nutrient limitation.

The algal community structure at the different sites also indicated the physical differences between river and standing waters. Large, slow growing cells such as cyanobacteria, were predominantly absent from the river site, whereas they were the dominant group in the reservoirs during the summer, when they presumably out
competed smaller, faster growing species for limiting nutrients (Reynolds, 1984). This
type of competitive ability was not applicable to the river system where nutrients were
in plentiful supply, but fast growth-rates were an advantage owing to the physical
unpredictability of the environment.

6.4.2 The zooplankton of Rutland Water

6.4.2.1 Cladoceran dominance

The zooplankton structure of Rutland Water was different from that of the River Nene.
Cladocerans, predominantly *Daphnia longispina*, dominated the pelagic zooplankton
biomass for much of the growing season, while rotifer biomass was relatively low.
This result was not unexpected for a reservoir with relatively long water residence time,
as the size-efficiency hypothesis states that large filter-feeders which share a similar
food resource with smaller forms will dominate the plankton in the absence of
vertebrate predators (Brooks and Dodson, 1965; Hall *et al.*, 1976). *Daphnia spp.* tend
to be stronger competitors for limiting food than rotifers owing to their lower food
threshold requirements (Stemberger and Gilbert, 1985; Gliwicz, 1990b; Walz, 1995),
and increased resistance to starvation (Goulden and Hornig, 1980).

The threshold food concentration for *D. galeata*, a cladoceran of similar size to *D.
longispina*, is approximately 0.018 μg C l⁻¹ (Gliwicz, 1990b), whereas that of
*Polyarthra spp.*, the dominant rotifer group from Rutland Water, was 0.081 μg C l⁻¹
(estimated from the regression line of Stemberger and Gilbert (1985), assuming an
average individual dry mass of 0.06 μg). *D. galeata* should therefore theoretically be
able to reduce, and maintain, food levels below the critical threshold for rotifer
development in Rutland Water, and therefore suppress the smaller species through
exploitative competition.

Food limitation is essential for exploitative competition to have an impact on
zooplankton community structure. Evidence for food limitation in Rutland Water
stemmed from two sources, first was the negative correlation between *Daphnia*
fecundity and chlorophyll 'a' during spring (figure 6.26), and second was the often
observed declining egg production prior to rotifer population decline. Exploitative
competition was therefore assumed to operate in Rutland Water, and is suggested as a
mechanism of rotifer suppression.

6.4.2.2 The seasonal succession of the zooplankton community
The seasonal succession of grazing zooplankton in Rutland Water was similar to that described in the PEG model of plankton dynamics in temperate lakes (Sommer et al., 1986). Rotifers, dominated by *Polyarthra dolichoptera*, were the first group to develop at the end of March in both study years (figure 6.18) reaching a density of over 500 animals l$^{-1}$. Increased temperature was thought to be the proximal cue for this spring development as water temperatures began to increase in March, thus shortening egg development times. Rotifers declined as soon as *Daphnia longispina* populations developed at the end of April, and remained low until *Daphnia* numbers fell in May, 1991 and June, 1992, as indicated by the negative correlations of table 6.8. Rotifer density increased once again during the summer months.

Rotifers and cladocerans coexisted during the summer, indicating a possible relaxation of the competition which forced the reduction of rotifer numbers during the spring. The reasons for this relaxation in competition are discussed below, but were thought to be owing to the lack of top-down control of *Daphnia* grazing on phytoplankton density during summer, and therefore reduced exploitative competition between the groups. A reduction in potential mechanical interference may also have resulted from the smaller size structure of populations during the summer, as indicated by the reduced size at maturity (figure 6.29).

6.4.2.3 The nature of competition between rotifers and cladocerans in Rutland Water

**Spring**

The spring period was characterised by alternating cycles of rotifer and cladoceran abundance as indicated by the negative correlation between rotifer and *Daphnia* abundance (table 6.8). The reason for the antagonism in Rutland Water was not immediately evident, as *Daphnia* density was negatively associated with chlorophyll 'a' concentration during spring, indicating that either exploitative competition (EC) for food, or mechanical interference (MIC) from large *Daphnia* could have been involved. A similar antagonism between *Daphnia* and rotifers in a shallow European lake was observed by Lampert and Rothhaupt (1991), who believed that both exploitative competition for food and mechanical interference from large *Daphnia* were involved in the reduction of rotifer density.

Exploitative competition for food was thought to be the dominant method by which *Daphnia* suppressed rotifers during the spring. Evidence stems from three different sources. First, the calculated death rates associated with mechanical interference were unrelated to the actual death rates of *Keratella cochlearis* populations. Second, the birth
rates of *K. cochlearis* and *Polyarthra spp.* were depressed during periods of high community filtration rate, indicating that food resources were limiting as a result of high *Daphnia* grazing pressure. Third, *Polyarthra spp.* egg production fell prior to population declines during the spring, indicating that food limitation was the cause of the crash. In both study years, the declining egg ratios during April were coincident with falling chlorophyll 'a' levels rather than peak *Daphnia* community filtration rates. Rotifer populations were therefore already in decline before the peak of potential mechanical interference was reached.

The apparent lack of mechanical interference during the spring was surprising considering that large *Daphnia* were present in suitable numbers to inflict death rates on susceptible rotifers in the order of 0.3 - 0.4 day\(^{-1}\) (figure 6.21). Death rates of this magnitude are approximately equivalent to the maximum growth rate of species such as *Keratella cochlearis* (Walz, 1995) and may therefore have been expected to have a detectable influence on rotifer density, this, however, appeared not to be the case.

It was possible that the potential impact of MIC was overestimated in the spring by using *K. cochlearis* in the calculation of death rate. This species is known to be susceptible to interference, whereas *Polyarthra* the dominant genus in the spring, has a well developed escape response (Gilbert, 1988b) and is therefore less affected. An assessment of the differential susceptibilities of Rutland Water's rotifer fauna to MIC deserves further work, but the overall conclusion from this analysis remains the same, namely that MIC was of little importance to rotifer dynamics compared to EC during the spring.

May and Jones (1989) found a similar result from Loch Leven, Scotland where interference competition between *D. hyalina* var. *lacustrus* and *K. cochlearis* was not as prevalent as expected from the estimated filtration activity of large *Daphnia*. The authors concluded that exploitative competition was more influential in suppressing rotifer populations than interference competition, and that the laboratory derived estimates of interference were not applicable to their field situation. This may apply equally to Rutland Water. MacIsaac and Gilbert (1989), however, disagreed with their interpretation of the data, and suggested that interference was more important, after re-analysing the sequence of interactions. The main criticism levelled at the original work was that death rates estimated from small samples were prone to errors. This error was minimised in the current analysis by only using samples which contained a suitable animal density (at least 20 animals per litre).
Summer

Polyarthra spp. and K. cochlearis dynamics throughout the summer and autumn of 1991 also indicated that food limitation was more important than MIC during this period of the year, even though cladoceran and rotifer density were not significantly associated (table 6.9). Peak rotifer densities usually declined after a period of reduced fecundity, indicating food limitation. The same was true of the autumnal peak in 1992, which coincided with falling chlorophyll 'a' concentration at the end of September.

The summer of 1992 was somewhat different to that of 1991, in that a high birth rate was maintained without a significant increase in density. This pattern indicated that although food was in good supply, population development was arrested by some form of death rate.

The cause of rotifer deaths during the summer of 1992 remains somewhat of a mystery. The dominant predatory rotifer, Asplanchna spp., was not abundant (figure 6.18), and the potential for mechanical interference was low as Daphnia were of small individual size. The average density of animals above 1.4 mm between July - September in Rutland Water was 1.43 animals per litre (st. dev ± 1.32) and the average size was 1.53 mm (st. dev. ± 0.06). This was expected to produce an average summer Keratella based daily death rate of 0.02 (upper 95% C.L. 0.04, lower 95% C.L. 0, accounting for the error in the original regression line of Burns and Gilbert (1986) and the error in the estimate of mean size and density). This death rate was very small compared to potential rotifer growth rates and the actual death rates (figure 6.21).

Invertebrate predation may have been an important source of rotifer deaths during the summer of 1992. Cyclopoids are known to predate rotifers (Zankai, 1984) and may positively select certain species such as Polyarthra spp. (Brandl and Fernando, 1978). Cyclopoid copepods, Cyclops abyssorum, Acanthocyclops robustus, and Mesocyclops leuckarti, were abundant during the summer with an average density of 22.6 (st. dev. ± 17.1) animals per litre during 1992. Leptodora kindtii were also recorded during the summer of 1992 (figure 6.29). These predators generally feed on small cladocerans (Herzig, 1995) but may also select rotifers (Herzig and Auer, 1990). It is possible they had an effect on Keratella and Polyarthra populations in Rutland Water, but their low density, and the fact that death rates were comparatively low in 1991 when they were also recorded, indicated that they probably had little impact on rotifer dynamics.

One problem with estimating death rate from the difference between birth rates and rates of increase is that it is impossible to distinguish between the direct removal of adults,
and the failure of eggs to develop to adulthood (Edmondson, 1965). The production of resting eggs which develop after a period of dormancy, would have resulted in an overestimation of birth rate, and hence may partly explain the high death rates of summer 1992. It is generally accepted, however, that resting eggs are produced in response to a particular set of environmental cues, and it was therefore considered unlikely that their production would be continuous throughout the summer period. Further work on the potential control mechanisms of rotifer growth is needed to allow a thorough understanding of the observed differences between the summer of 1991 and 1992. This work should aim to assess the impact of resting egg production, parasitism, and predation on rotifer dynamics.

6.4.2.4 Daphnia grazing pressure

The role of Daphnia in the exploitative competition of rotifer populations in Rutland Water seems irrefutable. This interaction relies on the ability of Daphnia to control algal concentration, which in turn is dependant on the edibility of the phytoplankton, and the size and density of cladocerans. Phytoplankton was efficiently controlled during the spring as indicated by the negative correlation of table 6.8, but not during the summer of Rutland Water. The question remains as to why Daphnia were able to control algal biomass in spring but not in summer?

The spring phytoplankton community of Rutland Water was dominated by small edible forms which were assumed to be susceptible to Daphnia grazing. Figures 6.13 and 6.14 showed that naked flagellates, cryptomonads and diatoms were the dominant algae, all of which fall within the size range of the filter-feeding Daphnia (Gliwicz, 1977; Knisley and Geller, 1986; Lampert, 1987a), or were considered palatable owing to their 'soft' cell membranes (DeMott, 1995), although Sarnelle (1986) questioned the suitability of cryptomonads.

At times of maximum Daphnia filtration rate, the chlorophyll 'a' concentration declined to below 3 µg l⁻¹, and Daphnia populations became food limited, as indicated by falling standardised brood size (figure 6.26). Lampert (1988) stated that the 'critical' Daphnia biomass required to produce a spring clearwater phase in eutrophic waters was between 1.5 - 4.5 g dwt. m⁻². These aerial measurements are not strictly comparable to the volume derived estimates of Daphnia biomass in Rutland, but assuming an average depth of 20m at the Limnological Tower, the critical biomass was estimated as 2.12 g dwt. m⁻² in 1991 and 5.64 g dwt. m⁻² in 1992. These estimates were therefore of a suitable magnitude to cause the onset of the clearwater phase which lasted for approximately two weeks at the end of May in 1991, and ten weeks between May and

Summer *Daphnia* biomass achieved the critical level assumed to cause the onset of spring clearwater a number of times, but the overall chlorophyll 'a' concentration remained unaffected by grazing pressure, presumably as a result in a shift in algal species composition to more inedible forms (Dawidowicz, 1990) (figures 6.13 and 6.14).

6.4.2.5 The impact of cyanobacteria on the grazing community

Blue-green species dominated the phytoplankton of Rutland Water from June - October in 1991 (78.5% of algal biomass (st.dev. ± 15.1)), and from June - December in 1992 (56.6 % of the algal biomass (st.dev. ± 21.3)). These species typically increase in abundance during the summer as they have lower nutrient requirements (SRP declined to below 5 µg l⁻¹ during summer in Rutland Water) and they are relatively resistant to grazing.

*Daphnia* fecundity was low during the summer period, even when chlorophyll 'a' levels were high, for example during July, 1991 when it reached over 35 µg l⁻¹. This was presumably a consequence of the poor nutritive quality of cyanobacteria dominated algal community. Indeed, Sarnelle (1986) noted that *Daphnia* fecundity was more dependant on the 'quality' of the food resource rather than the 'quantity'. SBS during the summer of 1992 was higher than that of 1991, even though total chlorophyll 'a' concentration was lower. Food conditions were therefore assumed to be more favourable in 1992, probably as a result of the lower proportion of blue-greens present.

The role of filamentous cyanobacteria as a source of nutrition or a source of interference for *Daphnia* remains unresolved (section 6.1.5.1). There is a wealth of evidence which states that cladocerans are disadvantaged during blooms of colonial cyanobacteria (Gliwicz, 1977; Edmondson and Abella, 1988; Gliwicz, 1990a). Filamentous forms may physically interfere with the feeding process (Burns *et al.*, 1987; Henning *et al.*, 1991), while toxic forms similarly depress filtering rates (Porter and Orcutt, 1980; Burns *et al.*, 1987) leading to decreased growth and reproduction (Burns *et al.*, 1987; deBernardi and Guissani, 1990; Fulton and Jones, 1991). Contradictory evidence, however, has shown that various blue-green species may be ingested by cladocerans (Knisley and Geller, 1986; Fulton, 1988; Fulton and Paerl, 1988; Gliwicz, 1990c), although the assimilation efficiency may be low (Hartmann and Kunkel, 1991).

Susceptibility to interference increases with cladoceran body size as larger animals are
more likely to 'inhale' filaments which can block the food collecting apparatus (Gliwicz, 1977). This results in an increase in the threshold food concentration of large species which become less competitive as a result (Gliwicz, 1990c). Smaller cladocerans, copepods and rotifers are much less effected by filamentous algae (Dumont, 1977; Pourriot, 1977; Bogden and Gilbert, 1982; Gilbert and Bogden, 1984; Rothhaupt, 1991; Walz, 1995) and may increase in density during periods of blue-green abundance (Hanazato, 1991; Kohl and Lampert, 1991; Sellner et al., 1993). This was shown in Rutland Water by the increased rotifer abundance during the summer of 1992 when cladoceran density was lower than in 1991. The reduction in zooplankton size-structure, and the associated increase in the density of rotifers during summer, was assumed to be a product of a reversal of the usual competitive outcome.

The actual reason for the reduction of *Daphnia* density and average size during summer in Rutland Water, was not immediately obvious, as it could have been the product of food limitation or size-selective vertebrate predation, but irrespective of the mechanism the result was the same, the coexistence of rotifers and smaller cladocerans (Lynch, 1979; Gilbert, 1988a; Vanni, 1988; , 1991; Wickham and Gilbert, 1991).

If feeding inhibition from filamentous algae was the only factor limiting *Daphnia* individual size in Rutland Water, then the size-structure of the population was expected to be higher in 1992 than 1991 as the cyanobacterial density was lower in the latter year. The minimum size at maturity of *Daphnia* was, however, much smaller in 1992 than 1991, indicating that vertebrate predation was probably involved as well.

6.4.2.6 Potential impact of vertebrate predators on the *Daphnia* community

*Daphnia* size at maturity decreased during July in both study years, but was much more pronounced in 1992 (figure 6.29). The decline corresponded to a period with low blue-green abundance in 1992, indicating that the effects of physical interference were minimal, especially as SBS remained relatively high (figure 6.27). It was considered more likely that the feeding action of vertebrate predators caused the reduction, especially with the synchronous development of the 0+ fry community (refer to section 6.1.5.2).

Minimum size at maturity is often used as an indication of the predation pressure acting on a population (Stibor, 1992; Weider and Pijanowska, 1993; Gliwicz and Boavida, 1996). Size-selective vertebrate predators tend to cause a decrease in size at maturity and an increase in reproductive investment of *Daphnia* via larger broods of smaller offspring (Stibor, 1992), so that animals have a greater chance of reproducing before
reaching a suitable prey size. These changes may result from the direct removal of the larger egg bearing females from the population (Morin, 1988; Gliwicz and Boavida, 1996) or from the selection for phenotypically plastic life-history characteristics in the prey (Stibor, 1992). The second hypothesis has gained support from findings which showed that life-history traits were changed when Daphnia were exposed to fish kairomones alone rather than the fish themselves (Machácek, 1991). Other studies have also shown chemically induced shifts in prey species morphology without physical contact with the predator itself (Brönmark and Pettersson, 1994).

Annual differences in the strength of 0+ planktivore recruitment are common, and may lead to different zooplankton size-structure between years as described by Cryer et al., (1986). This may be a realistic explanation of the difference between the size at maturity in 1991 and 1992 in Rutland Water. Years with good recruitment were expected to coincide with a plankton community dominated by small sized individuals in the summer (van Densen, 1985). This may be manifest by a shift in species composition to smaller species (Prazáková, 1991; Seda and Kubecka, 1997) if the change in fish density is large, such as after a winter fish kill, or may simply involve a shift in the size distribution of the dominant species (Cryer et al., 1986), as was the case in Rutland Water. Long term changes in fish predation pressure in Rutland may however have been involved in the virtual replacement of D. pulex by D. hyalina shortly after the reservoir began to fill in 1975 (Harper and Ferguson 1982).

It is widely considered that food limitation, interference from 'net' algae, and size-selective vertebrate predation interact to cause the seasonal reduction of zooplankton size-structure from spring to summer (Gliwicz, 1985; Lampert, 1988b; Gliwicz and Pijanowska, 1989; Moss et al., 1991). It seems likely that the proximal mechanism for this shift in Rutland Water varies depending on the strength of 0+ predation. In the summer of 1992, when predation pressure was assumed to be strong, the size structure and density of the Daphnia population was low, irrespective of the density of blue-greens. The intensity of competitive interactions with rotifers was reduced which therefore allowed them to achieve a higher density than in 1991. The summer of 1991 was characterised by a greater size at maturity and higher Daphnia density. Competitive suppression of rotifers was therefore more likely, and may explain their lower abundance in this year as compared to 1992.

Gliwicz and Stibor (1993) also argued that a decrease in cladoceran population size-structure could be obtained by the action of small cyclopoids which can enter the brood pouches large Daphnia and predate on the eggs. The potential for this type of control was questioned in Rutland Water, however, owing to the relatively small size of
daphnids, as Gliwicz and Lampert (1994) stated that only animals over 2.25 mm long were effected.

6.4.3 The zooplankton of Covenham reservoir

*Daphnia spp.* were much more prevalent in terms of biomass than rotifers in Covenham Reservoir. Both rotifer density and community diversity were lower than those recorded from Rutland Water.

The major difference between the zooplankton communities of the two reservoirs was the presence of large *Daphnia* in Covenham, namely *D. magna* and *D. pulicaria*. *D. magna* is found throughout the temperate northern hemisphere, usually inhabiting temporary shallow pools rich in small algae, but may also occur in the plankton of lakes (Hrbáček, 1987). They are able to utilise detritus as a sole food source, and may be distributed just above the sediment surface of shallow waters during daylight hours (S. Lee, pers. comm.). *D. pulicaria* has often been miss-identified as *D. pulex* Linne emend., a closely related species which typically inhabits temporary rock pools and floodplain pools. *D. pulicaria* is more associated with the limnetic zone of larger lakes, especially when planktivorous fish biomass is low (Hrbáček, 1989). *D. galeata* is a common component of the limnetic zone of turbid ponds and reservoirs. The size structure of the population can indicate fish predation levels, as a continuum of morphological forms exists within this species (Seda and Kubecka, 1997).

The coexistence of more than one species of *Daphnia* in a single water body is a common phenomenon. Stella et al., (1972, cited in Hrbáček, 1987), found five co-occurring species in a number of temporary ponds and pools in north-eastern Sardinia. One to three co-occurring *Daphnia* species are common in lakes with multi-species fish stocks, such as the London water supply reservoirs (Seda and Duncan, 1994) and the Rimov Reservoir in the Czech Republic (Seda and Kubecka, 1997). The coexistence of such close competitors suggests differences in the spatial or sequential use of resources (Hrbáček, 1987). This may be related to differences in preference for seasonally variable abiotic factors, or may similarly be related to a changing food resource base or changing temperature.

6.4.3.1 Competition within the grazing plankton of Covenham

The presence of large *Daphnia* may have intensified the competitive interactions with rotifers and driven down their density as a result. It is well known that large *Daphnia* and rotifers rarely coexist at high density (section 6.1.4.2). The calculated death rates of
K. cochlearis resulting from mechanical interference were high in 1991 as a result of the presence of large D. magna individuals (figure 6.36, maximum size class 4.55 - 4.65 mm). According to Burns and Gilbert (1986), the density of animals of this size required to produce death rates in the order of maximum rotifer exponential growth rates (assumed to be 0.3 d⁻¹) were approximately 1.5 animals per litre. It was therefore quite possible that MIC was involved in reducing rotifer populations to nearly undetectable levels during the spring of 1991. This in direct contradiction to the situation in Rutland Water, where MIC was assumed to have a minimal influence.

The magnitude of estimated MIC induced losses during 1992 was much smaller, as the size-structure of the Daphnia community was lower than in 1991. Rotifer dynamics did not seem to be affected by Daphnia filtration during this year, much the same as during the summer months in Rutland Water, indicating that MIC was probably not important when the cladoceran community was dominated by smaller species.

Rotifer density was, however, low in Covenham during 1992 irrespective of reduced competition from Daphnia. The reason for this is not clear, and deserves further investigation, but may be partly owing to a low density of resting eggs available to initiate population growth as a result of the low standing stock of animals attained in the preceding year. Further work on the aerial density of resting eggs in the sediments of Covenham, and the potential for immigration through pumped input is needed to understand the dynamics of rotifers in Covenham. Weekly sampling would also be a minimum requirement considering the short generation times of these animals.

Mechanical interference was unlikely to be the only method by which rotifer density was depressed in Covenham. The significant negative correlation of chlorophyll 'a' concentration and Daphnia community filtration rate in 1991 indicated that grazing induced food limitation (EC) may also have been involved. Rotifer egg data was not considered suitable for quantitative analysis owing to low density, but from a qualitative standpoint, the number of eggs observed in samples was generally low, except during March, indicating that population growth may have been limited by low food levels rather than the intense predation of a highly productive community. 1992 was somewhat different in that Daphnia were not negatively correlated with algal density during the growing season. Exploitative competition for food was therefore less likely to affect rotifer populations.

A rough measure of average weekly rotifer egg production (per litre) between the growing seasons of the two years showed that 1992 had a higher density (12.71) compared to 1991 (6.78). It would be misleading to use this data as anything more than
qualitative evidence, but it acts as an indication that food conditions were, on average, more favourable for rotifer production in 1992, but the low numbers of animals achieved still remains an important feature worthy of further study. Some source of undetected deaths may have been involved, as was expected in Rutland Water during the summer of 1992.

6.4.3.2 Mechanisms regulating the size-structure of the zooplankton community

*Interference from cyanobacteria*

Cyanobacteria were present throughout the whole year, accounting for over 50% of total algal biomass on a number of occasions. These species usually only become abundant during warmer periods in eutrophic waters (Hutchinson, 1967), but were present during the winter and early spring of 1991. Certain features of Covenham's morphology may have aided the maintenance of high cyanobacteria densities, as they are generally favoured by high nutrient concentrations (Hutchinson, 1967), especially when full depth mixing decreases light availability.

The presence of blue-greens seemed to have less of an impact on the cladoceran community of Covenham compared to Rutland Water. For example, the highest *D. magna* densities occurred when blue-greens, dominated by *Aphanizomenon flos-aquae*, accounted for over 90% of algal biomass. In fact, the association of *Aphanizomenon flos-aquae*, with large *Daphnia* is not an uncommon one. This algae is known to form 'grass-blade' colonies as an anti-grazing defence in the presence of large cladocerans (Burns *et al.*, 1987; Pecher and Fott, 1991) which reduces the chances of ingestion and therefore the potential to impair *Daphnia* feeding (Lampert, 1987b). The dominance of *Aphanizomenon flos-aquae* may therefore explain the paradox of how *D. magna* dominated during the spring of 1991 when this algae was abundant, as grass-blade colonies were observed.

*Daphnia* grazing may have favoured cyanobacteria growth by removing small 'undergrowth' species from the community (Dawidowicz and Gliwicz, 1987; Haney, 1987; Fulton and Jones, 1991) and making nutrients available to these species (Dawidowicz, 1990).

It is difficult to speculate why large *Daphnia* declined at the end of July without reliable population dynamics data. The two main theories which are commonly used to explain the shift to smaller grazers in the summer; food limitation and predation, may both have been involved, but the apparent low density of small grazers in the summer remains a
mystery. For example, if the algal community became dominated by canopy species that interfered with the feeding of large grazers, or if vertebrate predation removed larger species, smaller forms would be expected to fill their niche. This was not the case in Covenham where rotifer and small cladocerans remained at low density. It was possible that a shift from *Aphanizomenon* dominance to *Anabaena flos-aquae* and *Microcystis aeruginosa* may have been involved, but it was considered unlikely that any ill effects caused by colony morphology or toxicity would affect all grazers equally.

The absence of large *Daphnia* in 1992 was not thought to be related to interference from 'net' algae for two reasons. First, there was no significant difference between the proportion of blue-greens in the algal community of 1991 and 1992 or the species composition which was dominated by *Aphanizomenon flos-aquae* in both years. Second, both *D. magna* density in 1991 and *D. galeata* density in 1992 were unrelated to blue-green abundance indicating that both cladocerans were mechanically unaffected by the cyanobacteria, although variable toxicity may have caused shifts in *Daphnia* community composition.

**Vertebrate predation**

The apparent immunity of large *Daphnia* to blue-green interference warrants an alternative explanation for the shift in body size observed between years. The most likely explanation revolves around the activity of size-selective vertebrate predators. The role of fish in regulating the size-structure of the zooplankton is widely recognised (refer to section 6.1.5.2), with the size-structure of zooplankton, but not necessarily the total biomass, suppressed in the presence of a high biomass of planktivorous fish (Seda and Kubecká, 1997). This is considered to be such a reliable relationship that a number of authors have developed a method for estimating planktivore biomass from the size-structure of the zooplankton community (Hrbáček *et al.*, 1986; Seda *et al.*, 1989; Kubecká and Duncan, 1994; Seda and Duncan, 1994; Seda and Kubecká, 1997).

The change in dominance from *D. magna* in 1991 to the smaller *D. galeata* in 1992 may therefore have been the result of a change in fish density. Similar short-term reversions in the size-structure and species composition of the grazing zooplankton community have been documented from carp-ponds in south-west Bohemia (Cerný and Bytel, 1991; Prazáková, 1991), which were managed on a two year rotation as a carp fishery. The first year after stocking was characterised by low fish predation pressure and a zooplankton dominated by the large cladoceran *D. pulicaria* Forbes. The high grazing rates imposed by this species led to low chlorophyll 'a' concentration and increased water transparency. Small *Daphnia*, rotifers and *Bosmina* were all relatively poorly
represented during this year. The second year was characterised by higher levels of planktivore predation and a switch to a zooplankton dominated by smaller grazers. D. pulicaria was usually absent during this year.

The high degree of top-down influence expressed in these ponds is not always apparent in more natural systems, where bottom-up control of algal density may be important (McQueen et al., 1986; Seda and Kubecka, 1997). The carp-ponds were, however, artificially fertilised to maintain high productivity and so had little potential for bottom-up control.

Pumped-storage reservoirs such as Covenham receive inputs of nutrient-rich water. Those with relatively short retention times are unlikely to become nutrient limited as a result of the high loading, but may be physically controlled by artificial circulation (Ridley et al., 1966; Steel, 1972; 1976; McQueen and Story, 1986). The effects of top-down control may therefore be more easily identified in such systems, as they are in the carp ponds. Indeed, a negative correlation was evident between zooplankton and chlorophyll 'a' during the growing season of 1991 when the zooplankton was dominated by large Daphnia, indicating a grazing effect on algal populations similar to the first year of carp stocking in the Bohemian ponds. No relationship was evident in 1992 when the smaller species of zooplankton were dominant. This situation was therefore similar to the second year of the carp-pond cycle and indicates that a shift in fish stock between years may drive changes further down the trophic cascade.

Unfortunately no fish stock data was available from Covenham for the study period, but a rough estimate from the biomass of large Daphnia indicated that the planktivorous fish density was at least five times higher in 1992 than 1991 (figure 6.38).

A similar analysis of the cladoceran species composition to that described by Seda and Duncan (1994) for the Thames Valley reservoirs (figure 6.39) was also used to indicate the difference between fish density in Covenham between 1991 and 1992.

The relative abundance of large Daphnia in the summer of 1991 (figure 6.37) indicated that the fish biomass was less than 6 kg ha\(^{-1}\), if the estimate of Wraysbury reservoir is used as a point of reference (figure 6.39). The pattern was different in 1992 when the dominance of small species indicated that fish biomass was higher than in 1991 and probably above the 46 kg ha\(^{-1}\) recorded from Queen Elizabeth II reservoir.
Figure 6.39 Schematic relationship between Daphnia species composition and the planktivorous fish biomass in the London reservoirs. Data from Covenham, 1991 and 1992 shown for comparison. QM, Queen Mary reservoir. Wr, Wraysbury reservoir. QEII, Queen Elizabeth II reservoir (after Seda and Duncan, 1994).

If size-selective predation causes the annual variation in Daphnia size-structure, as seems to be the case, it follows that the biomass of planktivores must be relatively unstable. The question remains as to whether the fish biomass of Covenham is likely to undergo such fluctuations, and why some years have such a low biomass? The answer may lie in the morphology of this reservoir, as described below.

6.4.4 Covenham reservoir morphology and fish stock

The importance of the littoral zone for the development of reservoir fish populations is unquestionable. One of the main limiting factors for lacustrine fish communities was considered to be the lack of littoral spawning sites by Zalewski et al., (1995). Most species which are found in reservoirs have a riverine origin and are therefore adapted to a system with a large land / water ecotone, relying heavily on the littoral zone for spawning (Duncan and Kubecka, 1995). The structural diversity of lake littoral zones, and especially the presence of macrophytes, is therefore considered essential for the spawning success of many phytophilous species such as pike and a number of cyprinids. Perciforms, such as perch and ruffe, are less dependant on a structurally complex littoral zone for spawning.

Juvenile and larval stages of phytophilous fish are also reliant on well vegetated littoral
shallows for survival as these habitats offer favourable feeding grounds and shelter from piscivorous fish. Mortality rates of larval fish are reduced in these areas compared to the open water, as indicated by the higher fry densities in the shallows during daylight hours (Jude and Pappas, 1992).

The littoral zone of Covenham Reservoir can be described as having a number of 'anti-fish' features similar to the London water supply reservoirs (Kubecka and Duncan, 1994; Duncan and Kubecka, 1995), as the steep sloping concrete banks and the wind driven mixing reduce the chances of macrophyte establishment in the littoral. Duncan and Kubecka (1995) found that reservoirs with this type of restricted littoral habitat were usually dominated by percids, as opposed to cyprinids which would otherwise be abundant owing to the high nutrient status of the water. Cyprinid density was kept low owing to the lack of spawning sites and the predation pressure of the piscivorous perciforms. It is more than likely that the fish community of Covenham reservoir was similar to the London reservoirs, owing to the physical similarity of the systems. A survey of fish stock conducted in the summer of 1994 found a biomass of less than 5 kg ha⁻¹, the majority of which comprised piscivorous eels.

These features can therefore explain years like 1991 when fish biomass was low, but what about the other years when predation was assumed to be more intense, i.e. 1992?

Large oscillations in the annual recruitment of fish may result from operational management of water supply reservoirs. Changes in the water level of as little as 50 cm may drastically affect spawning success during the spring. In fact, dropping the water level after spawning to strand fertilised eggs has been used as a biomanipulation tool to reduce the cyprinid stock of Rimov Reservoir (Kubecka, 1989). Water level fluctuations in Covenham during the spring may therefore have affected the spawning success in different years and, through trophic interactions, influenced the zooplankton community. The introduction of fry with pumped input may also vary depending on the density of fish in the Louth canal, the timing and the volume pumped during the spring. The mesh size on the input screens to Covenham was 5 mm, and therefore allowed small fry entry to the reservoir.

Another potential reason for large scale and rapid changes in the fish biomass of Covenham stems from the structural simplicity of the habitat. The stability of most freshwater ecosystems increases with habitat complexity, especially concerning the land/water ecotone (Coelho and Zalewski, 1995). Covenham, however, is likely to be vulnerable to short-term environmental changes as a result of the low habitat diversity, and these changes may be rapidly transferred through the food chain. For example, if a
high density of cyprinids were imported one year, they may quickly decimate cladoceran populations owing to the lack of visual refugia. The 0+ populations are unlikely to sustain this pressure as they will be predated by piscivores. The impact on the zooplankton may therefore be drastic, but only short-term.

The land/water ecotone of Rutland Water was more developed in terms of surface area and habitat diversity. The presence of a developed cyprinid fauna was not surprising considering the abundance of littoral spawning sites and visual refugia for fry development. The presence of a relatively high planktivore biomass was evident from the dominance of the small *D. longispina*, and the stability of the system was evident from the continued dominance of this species since the year after filling.

### 6.5 Summary

1. The development of chlorophyll 'a' concentration per unit phosphorus concentration was higher in the reservoirs, and the phytoplankton community had a greater abundance of *K*-selected species than in the river, indicating the physical stability of the reservoirs compared to the river.

2. Cladocerans dominated the grazing zooplankton of the reservoirs owing to their size-related competitive advantages under food limiting conditions. Rotifers were only abundant when the cladoceran populations were reduced in density and individual size. Biotic control was therefore more important to rotifers during the growing season, and the impact was dependant on the size structure of the cladocerans.

3. Top-down effects of cladoceran grazing caused a spring clearwater phase which was associated with a food limited crash of grazers.

4. Grazing pressure on nannoplanktonic algae during the spring and nutrient limitation led to a change in the phytoplankton community structure towards the dominance of larger 'net' algae including cyanobacteria during the summer. The detrimental effects of these algae on larger grazers allowed rotifers to become more abundant during the summer. This pattern was more obvious in Rutland Water where the phytoplankton community followed a more typical seasonal succession than in Covenham.

5. Vertebrate predation on larger cladocerans was also influential in the restriction of cladoceran size during the summer, and thus aided the observed coexistence of cladocerans and rotifers during the summer period as size-dependant competition was reduced.
6. Exploitative competition was the most influential mechanism by which cladocerans suppressed rotifer density in the study reservoirs except when the *Daphnia* community was dominated by the large *D. magna*, as was the case during early 1991 in Covenham reservoir.

7. The presence of large *Daphnia* in Covenham was related to the poorly developed littoral zone which reduced the potential for cyprinid spawning, and therefore reduced the potential for size selective predation on the pelagic zooplankton. The larger grazers did not however effectively control the abundance of 'nuisance' algae owing to the dominance of large colonial algae which have a degree of grazer resistance owing to their size.
CHAPTER 7

GENERAL DISCUSSION

7.1 Comparison of the physical attributes of the study sites

The three freshwater habitats considered in this thesis had markedly different physical characteristics, not least of which was their widely contrasting water retention time. The average retention time of water in Rutland Water was 96 weeks while that of Covenham reservoir was 30 weeks. These two systems were therefore considered to be relatively stable in terms of the time-scales required for planktonic life cycles. The River Nene had a much lower retention time of between 0.2 - 1.6 days, considering a single volume of water bounded by lock gates either side of the Wansford sample station. This habitat therefore offered much less physical stability. Retention times of this magnitude were likely to have two separate impacts on planktonic organisms. The first was at the community level; selecting for species with short generation times and high biotic potentials. The second was at the population level; dictating hydraulic loss rates and therefore impacting on temporal patterns of species density.

Physical control was assumed to have more influence over plankton ecology at the river site, whereas biotic interactions were likely to have a greater influence at the reservoir sites (Padisak and Dokulil, 1994). The lack of downstream development in algal density during 1994 in the Nene impied the potential for biotic control may have increased during the summer low flow period. This was a similar finding to workers such as Descy (1987) and Gosselain et al., (1994) who found that discharge controlled algal density during the spring, but reduced growth rates and grazing were responsible for poor algal development during summer in the River Meuse.

Short retention times are unlikely to be in any way 'sensed' by the organisms which achieve dominance in rivers, as true plankton are constantly subjected to water movements in the pelagial. They are unlikely to be able to detect the difference between circulatory movements in, for example, unstratified lakes and turbulent downstream movement in rivers and therefore probably do not avoid flows as a human may perceive them. This may not be strictly true for some of the larger crustacean plankton and nauplii which are known to be able to detect and avoid reservoir outflows (Richardson, 1992).

Typical potamoplankton species achieve dominance in rivers owing to certain favourable characteristics which in some way adapt them to the physical conditions
found in rivers. These may include short generation times which give animals a better chance of reproduction before being washed through the system, or include adaptations which equip them to cope with less direct effects of discharge such as increased turbidity and fluctuating light / temperature regimes. These factors are no less important than the ability to recoup dilution losses, as a failure to cope with one will preclude the organism from the river plankton.

7.2 Phytoplankton response to contrasting retention time

The difference between the algal response to nutrient concentration in the three habitats also gave an indication of system function. Algal density achieved per unit phosphorus at the river site was lower than that from the reservoirs. This evidence was important as it showed that the physical differences between the sites influenced plankton dynamics.

The algal density achieved per unit phosphorus in Rutland Water and Covenham between 1991-1995 was not significantly different to that of the 149 North American lakes and 366 reservoirs considered by Søballe and Kimmel (1987), but was significantly higher than the density expected to develop in river systems. The two study reservoirs therefore behaved as expected with respect to algal development. Conversely, the algal density of the Nene was significantly lower than that expected to develop in lakes and reservoirs, but insignificantly different to that expected from 126 North American rivers.

In fact, algal growth was much more likely to be physically limited in the river by abiotic factors related to the shortened retention time, for example increased loss rates, full turbulent mixing, physical abrasion, and poor light climate. Søballe and Kimmel (1987) suggested a 'threshold retention time' of 60 - 100 days below which significant changes in system structure and function are expected. The data from this study do not disagree with Soballe and Kimmel's findings, but neither do they offer a rigorous evaluation of their threshold owing to the limited number of study sites. It would, however, be interesting to add further sites to construct a similar threshold estimate of British systems.

Covenham reservoir developed greater algal density than Rutland Water indicating that the former was more stable than the latter, according to Søballe and Kimmel (1987). This result was unexpected considering the shorter retention time of Covenham, although at an average of 30 weeks this was well above the threshold required to affect system function. The reasons for Covenham's increased density may
have stemmed from the fact that there was no competition for nutrients from littoral vegetation, whereas Rutland Water has a well-vegetated littoral zone, or from the fact that water clarity was greater in Covenham, as indicated by higher Secchi depth. The presence of filamentous cyanobacteria throughout much of the year may have increased transparency, and thus improved the underwater light climate and conditions for algal growth by reducing the effects of self-shading similar to the cryptic clearwater described by Benndorf et al., (1988). Izzaguirre and Vincour (1994) noted that the lakes along the Salado river basin with little macrophyte cover were often dominated by cyanobacteria.

Inadequate reservoir mixing may also have allowed a greater biomass of algae to develop in Covenham if the 'bubble-curtain' used in Covenham was insufficient to circulate water fully. The preponderance of cyanobacteria, with their ability to regulate position in the water column to maximise vertical light and nutrient gradients, provides indirect evidence that column destabilisation was insufficient at this site.

With regards to river management, the physical limitation of algal growth via reduced retention times may make them suitable for the carriage of phosphate-rich and nitrate-rich waters which would otherwise cause excessive algal growth in lentic systems. Problems may, however, be encountered in lowland river sections or when polluted river water feeds into riverine reservoirs. For example, phytoplankton biomass has been shown to increase as a result of the long-term enrichment of rivers like the Rhine (van Dijk and van Zanten, 1995) and the Meuse (Descy, 1987), and has led to worries regarding the development of nuisance blooms in the backwaters of these rivers (Gosselain et al., 1994; Tubbing et al., 1994). Phosphate removal techniques have, however, failed to convert a decreased phosphorus concentration to reduced algal biomass, probably as a result of internal nutrient loading from sediments. There has been a similar lack of response since P-stripping began in the major sewage treatment works in the Nene catchment (Wray, pers. comm.).

The continued drive to reduce plant nutrient inputs to the Nene is, however, recommended, as the pulse of cyanobacteria recorded in the main channel of the Nene during a period of rising discharge late in the summer of 1994 showed the potential for nuisance algal development during clement weather. It may take some time before favourable results are noted, however, owing to internal release from nutrient-rich sediments and results are likely to be unpredictable owing to the naturally stochastic nature of river plankton development. Some degree of sediment 'flushing' downstream by opening lock gates during periods of high discharge may be encouraged to aid the
process. A similar technique is used periodically in the Meuse to 'flush' the system with relatively clean upland water during winter (Descy, pers. comm.).

7.3 Algal community structure

The difference in algal community structure from the three sites also indicated the over-riding influence of retention time on plankton ecology. The river site was dominated by small, fast-growing, \( r \)-selected species throughout most of the year, predominantly diatoms and green algae. The occasional appearance of cyanobacteria (which have been used as a model for \( K \)-selected species throughout this study) in the main-channel was usually associated with increased discharge, indicating that they were flushed from calmer areas within the catchment. This conclusion was strengthened by the fact that their numbers did not increase once in the flow, but rapidly declined owing to a lack of reproduction. These organisms were therefore considered to be ill-adapted to life in the true potamoplankton.

The phytoplankton community composition of the reservoir sites was different to that of the river, and was more typical of deep eutrophic lakes following a succession driven by seasonally predictable climatic and autogenic interactions (Sommer *et al.*, 1986). Rutland Water developed a dense spring phytoplankton dominated by small, fast-growing species, but this was reduced at the end of spring by the grazing action of a large population of *Daphnia*, a species which was virtually absent from the main-channel of the Nene. The summer phytoplankton was dominated by cyanobacteria, presumably owing to their competitive advantage at low nutrient concentrations and their resistance to grazing.

Covenham reservoir was slightly less predictable with regards to its phytoplankton composition. Cyanobacteria were sporadically dominant throughout the year, interspersed with periods of mainly diatom and green algae abundance. This seemed to indicate a fluctuation between conditions which favoured \( r \)- and \( K \)-selected species, similar to Rutland Water, but on a much less predictable temporal scale. The lack of predictability may have stemmed from the simplistic morphology of this reservoir, allowing allogenic perturbations to have a more direct impact than in Rutland Water. The presence of cyanobacteria species at high density does, however, indicate the increased stability of this system over the Nene.

Any prolonged period of cyanobacterial dominance was lacking in the Nene, presumably owing to the level of physical control displayed even during the low flow period in summer. The lack of grazers, lack of nutrient limitation and constant mixing
may have also favoured the continued dominance of species more typical of the early spring period in lakes, rather than the slower growing cyanobacteria.

7.4 Mechanisms of phytoplankton regulation

An analysis of the factors controlling phytoplankton abundance in the river, assessed as the amount of residual variation of chlorophyll 'a' accounted for in multiple regressions, gave relatively poor results when the whole growing season was considered. This was a similar situation to that described by Ruse and Hutchings (1996) who found that 80% of variation in phytoplankton taxa composition of the Thames could not be explained by the environmental data considered, which included measures of pH, biochemical oxygen demand, plant nutrient concentrations, temperature, transparency and discharge. They concluded that other measurements such as solar irradiation and light transmission in water should be included to increase the predictive power. Descy (1987), however, commented on the inherent difficulty of predicting riverine algal development in the Meuse, considering the wide variation in algal response to even the most rudimentary control measures, namely discharge, temperature and light intensity.

Abiotic parameters such as turbidity were much better predicted by discharge in the Nene than chlorophyll 'a', indicating that the impact of physical control was 'diluted' with increasing biotic complexity, i.e. algae were influenced by factors regulating not only loss processes, but growth processes also.

The poor results obtained from multiple regression models in the Nene did not disguise the importance of discharge as a regulating mechanism. Figure 2.10 showed the presence of a relatively consistent relationship which described the maximum algal density expected at any discharge in the Nene. The algal response to discharge was highly variable below this level, presumably as other factors such as light limitation, temperature, grazing and sedimentation losses imposed a greater degree of control during more lentic conditions. Discharge was also considered to be the most influential factor controlling algal density in the Meuse, and led Gosselain et al., (1994) to describe it as the primary 'forcing variable' of potamoplankton dynamics.

The importance of temperature was also shown in figure 2.11, in which plankton development only occurred above a certain temperature and below a certain discharge, indicating that algal density was dictated by the interaction between growth and loss processes (see also Gosselain et al., 1994). A similar relationship was described by Threkeld and Choinski (1985) who stated that the physiological
retention time, which considered the trade-off between temperature related growth rates and discharge related loss rates, offered a better predictor of plankton development in habitats with short retention time rather than discharge related losses alone.

The poor predictive power of phytoplankton regression models was influenced by the fact that low discharge was often associated with low chlorophyll 'a' concentration during the summer. This was also found by van Dijk van Zanten and (1995) in the Rhine in which significant correlations between discharge and chlorophyll 'a' were only achieved during the spring. This pattern made little sense if discharge was the most important predictor of algal density, as increased retention time and water clarity should have allowed greater plankton development. The fact that this was not the case indicated that other controls were influential during low flow periods.

Low summer chlorophyll 'a' concentration was also a feature of the rivers of Seine catchment (Garnier et al., 1995), as it was in a number of years in the Nene. The failure of plankton to develop in the Nene was especially puzzling as figure 3.26 showed that this was the only period when phytoplankton growth rates were high enough to offset loss rates without substantial importation from upstream.

The low summer biomass in European rivers could not be accounted for by alternative loss processes such as settlement and grazing, or by decreased growth rates, as light levels were high and nutrients unlimiting. Garnier et al., (1995) proposed high rates of cell lysis from viral, fungal, and bacterial attack as an explanation for both low summer density, and the abrupt termination of the spring peak.

These may have been important in the Nene, as the modelled loss rates presented in table 3.10 could not account for the lack of phytoplankton increase, especially considering that hydraulic losses were minimal owing to constant importation from upstream. De Ruyter van Steveninck et al., (1992) regarded sedimentation as a probable candidate for high losses from shallow summer depths, especially considering the reduced turbulent mixing associated with low flows, but were still only able to account for between 29 - 47% of the observed loss rates of summer phytoplankton populations in the Rhine. Sedimentation loss rates in the Nene would have been higher for larger cells than those modelled, but most of the cells in the plankton of the Nene were of small size and therefore subject to low sedimentation rates.

A more plausible explanation for low summer density in the Nene was increased
grazing pressure from littoral zooplankton. This idea has not been fully considered before, but calculations in the Nene at Wansford showed that exponential daily grazing loss rates were increased from approximately -0.001 owing to pelagic grazers alone to -0.35 by the inclusion of littoral grazers, and may therefore have been of a magnitude able to influence population processes. This calculation assumed that 25% of the littoral volume was exchanged with open water per day, although this could be varied for any rate of exchange. This area of analysis was only intended as a rough approximation of the impact of littoral grazers on pelagic algae, but it does imply the potential importance of the interaction.

This hypothesis may also be used to explain the spring decline in phytoplankton density, as the vegetation of the littoral zone only begins to develop in the spring. The littoral grazing losses may therefore be small prior to littoral zone development, but remain high during the summer as long as macrophyte cover remains. This area of work requires further investigation, focusing of the spatial and temporal distribution of littoral grazers, their feeding ecology and the extent of exchange between the open water and the littoral zones under various flow regimes.

Benthic filter feeders, and especially the zebra mussel *Dreissena polymorpha*, may have a grazing impact on phytoplankton populations and therefore aid the explanation of low summer density. Clearance rates vary with individual size (Kryger and Riisgård, 1988) but may reach upwards of $12 \times 10^6 \mu l \text{ individual}^{-1} \text{ day}^{-1}$, compared to approximately $11 \times 10^3 \mu l \text{ ind.}^{-1} \text{ d}^{-1}$ for *Daphnia* and $250 \mu l \text{ ind.}^{-1} \text{ d}^{-1}$ for rotifers, according to MacIsaac *et al.*, (1992). Clear water phases associated with *Dreissena* grazing at high density may therefore exceed in magnitude and duration those generated by zooplankton grazing (Bunt *et al.*, 1993; MacIsaac, 1996).

Mussel grazing has been shown to have a significant impact on phytoplankton standing stocks in a number of studies. For example, MacIsaac *et al.*, (1992) found that reef associated *Dreissena* populations in western Lake Erie had the capacity to filter $132 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$, and deplete local chlorophyll 'a' concentration to < 1 $\mu g l^{-1}$ as a result. Similarly, Ogilvie and Mitchell (1995) found that the freshwater mussel *Hyridella menziesi* was capable of filtering the whole volume of Lake Tuakitoto (New Zealand) every 32 hours, and may have accounted for the suppression of chlorophyll 'a' concentration to 10% that predicted from phosphorus / chlorophyll 'a' relationships. *Dreissena* grazing may also have a negative impact upon small zooplankton populations (MacIsaac, 1996), offering some explanation of the low rotifer density in the Nene during the summer. For example, Laurentyev *et al.*, (1995) noted significant changes in the protozoan community of Lake Huron as a result of *Dreissena* grazing.
Whether benthic grazers have a significant impact in the Nene deserves further study, including an assessment of density and size structure of populations, clearance rates and feeding ecology. *Dreissena* have been recorded in the Nene (Balbi, pers. comm.), but no veligers were found in the plankton during the study period. This indicates that adult density was relatively low, as each female can produce up to $10^6$ eggs year$^{-1}$, which should have been adequately sampled by the study methods as planktonic veligers range from between 70 - 250 μm long (MacIsaac, 1992). Such subjective evidence, however, should not be relied upon to dismiss the role of benthic grazers and further work on their impact is recommended in the Nene, as was concluded by de Ruyter van Steveninck *et al.*, (1990; 1992) in the Rhine and Garnier *et al.*, (1995) in the Seine.

**7.5 Do simple river function models account for plankton development?**

The scale of predicted hydraulic losses from the plankton of the Nene made it impossible for either a phytoplankton or zooplankton to develop assuming the turbulent mixing model of water movement. Constant importation to the pelagial was required to balance the observed population growth considering the size of downstream losses. The development, and maintenance, of a true potamoplankton during the growing season was therefore testament to the fact that simple fluvial models were inadequate to describe the behaviour of water flow in the Nene.

A high degree of importation was expected in the study reach of the Nene, as there was little evidence of overall downstream increase in plankton development during the spring and summer months, *i.e.* a relatively constant biomass was present above, within, and below the Wansford stretch. This means that hydraulic losses were much less than those predicted assuming no importation and therefore explains how a plankton developed at Wansford, but does not explain where the imported material originated. For example, somewhere upstream, the conditions must have been unfavourable for plankton development owing to high flow velocity. At a site downstream of this, however, a plankton developed which was then exported to the next section downstream. The process was presumably repeated, with each subsequent section gaining a slightly greater import, until in the lowland river reaches it appeared that a relatively constant biomass was maintained with distance downstream.

At the upstream sites which received less importation, however, the losses associated
with turbulent flow models would be too high to describe plankton development. The problem of explaining plankton development in the Nene was therefore simply moved to a section upstream of Wansford.

The aggregate dead-zone model of Young and Wallis (1987) with its application to river plankton (Reynolds, 1988) provides the best explanation of how a plankton is maintained in an essentially advective river environment. This theory was introduced in chapter 3 and shall not be covered in detail here, but suffice to say that it has the power to describe the retentive capacity needed to maintain a plankton at a higher discharge than that assuming turbulent mixing alone.

The model assumes that sufficient areas of low flow are maintained within, or connected to, the main channel. This was likely in the Nene which still follows a relatively natural channel, but may not be so in more channelised rivers. A survey of the plankton of low flow zones in the Nene showed differences in the community composition between areas of low flow and the main channel, but this area of work requires further study as my observations were merely intended as an overview.

The role of dead-zones, while being of primary importance to the maintenance of a river plankton, may vary depending on their physical structure, which is partly governed by the level of water exchange between themselves and the main channel. Zones with a much greater retention time than the main channel can develop a plankton that is unsuitable to growth in riverine conditions. For example, a dense population of *Daphnia curvirostris* was found in one quiet backwater of the Nene. This population would add little to the maintenance of a potamoplankton as they would be considered as drift animals once in the main channel, unable to reproduce at a suitable rate, and therefore rapidly lost downstream (Chandler, 1937). A similar scenario was described when a slow flowing section of the River Severn developed a cyanobacterial bloom during a period of low flow (Reynolds and Carling, 1991).

Planktonic organisms which develop within dead-zones must therefore possess suitable life-history characteristics to allow proliferation in the main channel. This means that the conditions in which they developed must be similar to those of the river itself. Fortunately, in semi-natural channels, there exists a wide diversity of dead zone structure, some of which will contain the correct parameters to allow typical riverine organisms to develop, and eventually feed into the flowing water as water is exchanged. Further work on the identification of these zones would be useful, as the dead zone theory as applied to plankton populations (especially zooplankton) remains relatively untested.
In the Nene, however, the action of dead zones may be two-fold. During spring, a number of zones are able to develop a plankton dominated by *r*-selected forms, owing to their physical similarity to the main channel. Export from these zones via water exchange would aid the development of the spring peaks of both phytoplankton and rotifers. During the summer, however, as flow rates diminish and a number of zones become more isolated from the main channel owing to reduced physical mixing, the plankton of these zones may become more lacustrine in nature and therefore add little to the development of typical riverine forms when washed into the river. The transient presence of cyanobacterial species and a number of littoral rotifers during the September spate of 1994 indicated that conditions had indeed become less riverine in a number of dead-zones.

The switch in the role of dead zones between spring and summer in the Nene may be taken a step further if one considers the impact of littoral grazers on pelagic phytoplankton populations. Exchange of water between the main channel and the littoral dead zone during summer, when these areas were known to house a grazer population, was hypothesised to cause the removal of phytoplankton cells rather than their addition. The littoral dead zone may therefore act as a sink, rather than a source habitat during summer months. The same may be true for pelagic rotifers as littoral vegetation is known to remove / filter animals from flowing water (Chandler, 1937).

7.6 Comparison of zooplankton community structure from the three study sites

Zooplankton community structure may be used to indicate system function, as community composition is strictly defined by ecological theory. Any deviations from this structure may therefore offer information on how a system is controlled.

Hardin (1960) stated in the principle of competitive exclusion, or ‘Gause’s Principle,’ that complete competitors should not coexist. Closely related species, or species with a similar ecology, should only coexist if they differ in their use of resources, that is, if they occupy a different niche hypervolume (Hutchinson, 1951 cited in Begon *et al.*, 1990). The structural simplicity of the pelagic environment offers little capacity for such differentiation, so plankton communities may be expected to be similarly simplistic in terms of species richness. This was found to be untrue with regards to the phytoplankton which is usually composed many species, and led Hutchinson (1961) to refer to the phenomenon as ‘the paradox of the plankton’.

Pelagic zooplankton community structure is much more simple than that of the phytoplankton, and therefore seems to adhere more strictly to the tenets of Gause’s
hypothesis. Pennak (1957), who drew upon information from 27 Colorado lakes and a further 42 world-wide, remarked on the simplicity of limnetic zooplankton communities. He found that there were generally only 1 - 3 species of copepod, 2 - 4 species of cladoceran, and 3 - 7 species of rotifer present at any one time. He also observed that it was very uncommon to find more than one species from any genus coexisting at any one time, and that when this occurred the dominant species was over 20 times more numerous than the subordinate. This was attributed to the increased likelihood of competitive exclusion between species with similar ecology, especially with regards to feeding preferences. In cases where congeneric coexistence was noted, as was often the case with *Daphnia*, a closer look at the interaction usually showed some form of niche separation, either temporally or spatially.

Another feature of pelagic zooplankton assemblages which adds to their simplicity is the dominance of a single species within each of the three groups mentioned above. Pennak (1957) described this dominance as a ‘valid and well defined generalisation’ of zooplankton communities. Very rarely did the dominant species account for less than 50% of all animals within the group. On average, this species represented 80% of all copepods, 78% of all cladocerans, and 78% of all rotifers, while the second most abundant species accounted for 17%, 17% and 20% of total density respectively. The superiority of these species was attributed to certain genetic, morphological, physiological and ecological features which gave them a competitive advantage at the time of sampling (Pennak, 1957).

The relatively simple community structure defined by Pennak (1957) has since been verified in a number of other lakes (Orcutt and Pace, 1984; Pant *et al*., 1985; Sprules and Munawar, 1991). Species richness may, however, be partly dependant on lake size, productivity and the proximity to other lakes (Dodson, 1992; Dodson and Silva-Briano, 1996).

Measures of the rotifer community structure from the two reservoirs and the river are presented in table 7.1 for comparison. The annual mean momentary species richness of Rutland Water (3.91) and Covenham reservoir (2.35) was at the lower end of the range defined by Pennak (1957). This was partly a result of using generic designations for single species, especially *Synchaeta* and *Polyarthra*, and the problems of identifying preserved animals accurately. The full species list of *Synchaeta* included *S. oblonga*, *S. kitina* and *S. pectinata*, while that of *Polyarthra* included *P. dolichoptera*, *P. vulgaris*, *P. remata* and *P. major*. There were a number of occasions when more than one species from the same genera coexisted, but they were treated as a single species for this analysis. The number of species coexisting at a single time
was, however, within the limits expected for lacustrine systems as defined by Pennak (1957), as were those of the cladoceran community (2.34 in Rutland Water and 2.11 in Covenham).

Rotifer diversity was also lower in the two reservoirs and the percentage dominance of the most abundant species higher than in the Nene, indicating a greater degree of physical and community stability in these habitats. The proportion of total density accounted for by the dominant and sub-dominant species in Rutland Water (67% and 21% respectively) and Covenham (74% and 17%) were similar to those described by Pennak (1957).

<table>
<thead>
<tr>
<th>Site</th>
<th>Parameter</th>
<th>Jan - Mar</th>
<th>Apr - Jun</th>
<th>Jul - Sept</th>
<th>Oct - Dec</th>
<th>Annual Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rutland Water</td>
<td>Species no.</td>
<td>2.12</td>
<td>5.69</td>
<td>5.27</td>
<td>2.29</td>
<td>3.91</td>
</tr>
<tr>
<td></td>
<td>Diversity</td>
<td>0.23</td>
<td>0.44</td>
<td>0.42</td>
<td>0.23</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>Evenness</td>
<td>0.69</td>
<td>0.60</td>
<td>0.59</td>
<td>0.67</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>Dominant %</td>
<td>72.79</td>
<td>58.48</td>
<td>61.98</td>
<td>79.05</td>
<td>67.11</td>
</tr>
<tr>
<td>Covenham Reservoir</td>
<td>Species no.</td>
<td>1.72</td>
<td>2.67</td>
<td>2.96</td>
<td>2.07</td>
<td>2.35</td>
</tr>
<tr>
<td></td>
<td>Diversity</td>
<td>0.26</td>
<td>0.24</td>
<td>0.28</td>
<td>0.25</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>Evenness</td>
<td>0.92</td>
<td>0.65</td>
<td>0.65</td>
<td>0.93</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>Dominant %</td>
<td>69.79</td>
<td>77.56</td>
<td>73.61</td>
<td>72.01</td>
<td>74.32</td>
</tr>
<tr>
<td>River Nene</td>
<td>Species no.</td>
<td>7.75</td>
<td>11.27</td>
<td>6.10</td>
<td></td>
<td>8.46</td>
</tr>
<tr>
<td></td>
<td>Diversity</td>
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<td>0.69</td>
<td>0.51</td>
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<td>0.61</td>
</tr>
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<td></td>
<td>Evenness</td>
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<td>0.70</td>
<td>0.82</td>
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<tr>
<td></td>
<td>Dominant %</td>
<td>32.82</td>
<td>50.29</td>
<td>52.19</td>
<td></td>
<td>49.42</td>
</tr>
</tbody>
</table>

Table 7.1 Species richness, diversity, evenness, and percentage abundance of dominant groups of pelagic rotifers in Rutland Water, Covenham, and the Nene. Diversity index used was the Shannon-Wiener index. Values represent means of two years data from the reservoirs and a single year from the river.

The momentary species richness of the Nene rotifer community (8.46) was above the upper limit cited for lacustrine pelagic communities by Pennak (1957), even considering the use of some genera as species designations. High species richness was assumed to result from the diversity of interconnected source habitats which import animals to the main-channel of the river with increased flow. Many of the species collected were of littoral origin and therefore constituted drift animals rather than a viable part of the pelagic community. Rotifer diversity and community evenness was higher in the Nene than in the two reservoirs as a result of this increased species richness and reduced numerical dominance of the two most abundant species. The
dominant rotifer accounted for only 49% of total abundance whereas the next most abundant taxa accounted for 34%. This again was assumed to be closely related to the physical nature of the river, which was vulnerable to rapid and unpredictable disturbance, and was therefore less likely to have a zooplankton community restricted by competitive forces than the reservoir sites. The dominance of rotifers over cladocerans in the Nene also indicates that competitive forces were less important in the river compared to the reservoir sites where cladocerans were by far the dominant group in terms of biomass.

The importance of physical disturbance, in the form of discharge, as a control of rotifer community diversity in the Nene was shown by the positive correlation between the two parameters (chapter 4). Periods of high discharge during the spring were associated with the wash-in of littoral species and a reduction in the dominance of a single species. Periods of reduced flow during the summer were associated with reduced species richness and diversity (table 7.1). It was assumed that the river community became slightly more similar to that of a lentic system during the summer low flow period, although conditions were not sufficiently stable to allow cladoceran development.

7.7 Comparison of rotifer composition between sites

The percentage composition of the main rotifer groups at each site are presented in table 7.2. Polyarthra spp. accounted for over 50% of rotifer density in the two reservoirs with Keratella spp. the next most abundant group. Synchaeta spp. were also relatively abundant in Rutland Water, but poorly represented in Covenham. Brachionus spp. were rare in both standing water bodies.

<table>
<thead>
<tr>
<th></th>
<th>River Nene</th>
<th>Rutland Water</th>
<th>Covenham</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>st.dev.</td>
<td>mean</td>
</tr>
<tr>
<td>Brachionus spp.</td>
<td>11.54</td>
<td>15.93</td>
<td>0.21</td>
</tr>
<tr>
<td>Polyarthra spp.</td>
<td>7.22</td>
<td>9.14</td>
<td>58.13</td>
</tr>
<tr>
<td>Synchaeta spp.</td>
<td>41.91</td>
<td>29.10</td>
<td>15.78</td>
</tr>
<tr>
<td>Keratella spp.</td>
<td>13.89</td>
<td>13.13</td>
<td>20.78</td>
</tr>
</tbody>
</table>


Synchaeta spp. were much more abundant in the river, as were Brachionus spp. The ubiquitous Keratella spp. were also well represented, but Polyarthra spp. were rather less abundant. The results suggest that Brachionus spp. and Synchaeta spp. were more
adapted to the riverine habitat, while *Polyarthra* spp. were less adapted.

Ferrari and Mazzoni (1989) found that *Polyarthra* spp. were often abundant in the Po River, Italy, but only during reduced flow phases. They were considered to be ill-adapted to high flows owing to their delicate form and the presence of external appendages which increase drag. In contrast, *Keratella* sp. were associated with periods of increased flow and were considered well adapted to river life owing to their thick loricas and hydrodynamic shape. *Keratella cochlearis* was the dominant rotifer during 1992 and 1993 in the Nene and were abundant in the 1994. In contrast, *Polyarthra* spp. were the most abundant group in the Wansford backwater. The species composition of a river may therefore give clues as to the type, and strength of selective forces acting in a particular environment.

### 7.8 Factors controlling zooplankton community structure in the study reservoirs

The grazing zooplankton of the reservoir sites was dominated by cladocerans. Rotifers accounted for less than 7% of grazer biomass in Rutland Water, and less than 5% in Covenham. This was expected in systems with long retention times, as cladocerans are generally considered to be better competitors for limiting resources than rotifers. Rotifers were usually more abundant early in the year, when competition was minimal. They were presumably reduced by food limitation during the spring clearwater phase which was initiated by cladoceran grazing. This was implied in Rutland Water by the negative association between *Daphnia* community grazing rates and rotifer birth rates, plus density, during the spring period, and declining *Polyarthra* density after a fall in egg production. The losses were therefore assumed to more a product of food limited growth rates (exploitative competition) than mechanical interference competition from increased cladoceran filtration activity, although the latter may have had more of an influence in Covenham reservoir during 1991 when the plankton was dominated by large *Daphnia magna*.

The association between rotifer and cladoceran density was not significant during the summer months in Rutland Water, indicating that the trophic link between the two components was weaker. This was probably owing to the presence of cyanobacteria which reduced *Daphnia* feeding efficiency, and therefore competitive ability, thus allowing the coexistence of the two groups. *Daphnia* density in the summer was still considered sufficient to reduce phytoplankton concentration to clearwater levels (Lampert, 1988a), but this did not occur, presumably as the algal community was dominated by relatively unpalatable species. A reduction of *Daphnia* brood size in association with an increase in cyanobacteria abundance was indicative of a poor
quality food resource in the summer.

Vertebrate predation in Rutland Water may also have decreased *Daphnia* competitive superiority in the summer of 1992 by reducing the density and individual size of the population, as indicated by the falling minimum size at maturity in July.

Rotifer density was negatively correlated with *Daphnia* grazing pressure in Covenham reservoir during 1991. The impact may have involved both exploitative competition for food (negative correlation of *Daphnia* community filtration rate and chlorophyll 'a') or direct mechanical interference, as the exponential daily death rate owing to interference was above -1.0 when the plankton was dominated by large *Daphnia magna*. No correlation between *Daphnia* and rotifers was found in 1992, possibly because the smaller *D. longispina* was dominant. This species imposed a lower grazing rate on algal populations and also a lower potential death rate through mechanical interference. The rotifer density still remained low, however, indicating that rotifer populations were either food limited or had a high death rate. This was a similar pattern to the summer of 1992, when rotifer dynamics indicated an undetected death rate acting on populations. 0+ fish predation may have been involved, as the *Daphnia* size structure in both reservoirs during 1992 indicated that fish predation was more intense than in 1991. More work is required on fish feeding efficiency and prey choice in the reservoirs to elucidate the potential death rates associated with vertebrate predation.

The two reservoir sites generally acted as expected with regards to the temporal patterns of rotifer and cladoceran development. The competitive superiority of cladocerans was evident from their dominance, but this was reduced as a result of mainly biotic interactions within the system, namely shifts in algal composition or the action of vertebrate predation. Without these cues, rotifers would probably have been less abundant.

7.9 Factors controlling zooplankton community structure in the Nene

The zooplankton of the Nene was considerably different to that of the two reservoirs. The main channel community was almost exclusively dominated by rotifers, whereas cladocerans were poorly represented. This pattern was consistent throughout the growing season and between years, and represented a clear reversal in the usual competitive outcome between the two groups.

Certain features of the river environment must therefore favour rotifer development at
the expense of cladocerans. A number of factors probably favour small species dominance in rivers, and these include their short generation times (Pace et al., 1992) which allow them to reduce the impact of advective losses and rapidly recolonise after disturbance events. Small species also tend to feed more efficiently than cladocerans in turbid environments (Kirk and Gilbert, 1990). Rotifers are also less affected by fish predation owing to their size (Brooks and Dodson, 1965), and may therefore gain an advantage in habitats with good fish recruitment. This may be especially important in rivers which have a high littoral area suitable for fish spawning compared to lakes. Rotifers may also be less susceptible to micropollutants than cladocerans (Hanazato and Yasuno, 1990).

Rotifer dominance is a common phenomenon from rivers around the world and was therefore not unexpected in the Nene, although a high degree of impoundment may favour crustacean dominance (Rzoska et al., 1955; Shiel and Walker 1984). Flow is restricted in the Nene by a series of sluices that maintain river height at a relatively constant level, thus extending retention time and allowing the development of a plankton density comparable with much larger rivers. These conditions did not, however, provide conditions conducive to cladoceran development even during the summer low flow period. *Bosmina longirostris* did, however, increase in density towards the tidal portion of the Nene during the summer of 1995, indicating that conditions became more lacustrine the further downstream one travelled, although the impact of tributary and standing water inputs may have had some effect on this pattern.

The factors which control rotifer development in the Nene were assessed using multiple regression models for the spring period 1992-1994, and the whole growing season of 1994. Rotifer density was significantly predicted by chlorophyll 'a' concentration during the growing season of 1994, but was unrelated to discharge. Food was not considered limiting to rotifer growth as proven by the low proportion of food limited carrying capacity realised and the lack of a fall in birth rate prior to the spring population crash. The association between rotifers and chlorophyll 'a' was therefore more likely to be a simple case of covariation with discharge rather than a causative relationship as indicated in the River Great Ouse by Bass *et al.* (1997) who assumed food limitation from a similar relationship.

Rotifer density was positively associated with chlorophyll 'a' and temperature during the spring period, but also negatively correlated with discharge. It was likely that discharge controlled loss rates, while temperature (Andrew and Fitzsimmons, 1992) and possibly food concentration (Duncan, 1989) influenced growth rates. Van Dijk
and van Zanten (1995) found similar results in the Rhine, with all three factors significantly correlated with rotifer density during the spring. Rotifer development in the spring did not follow chlorophyll 'a' concentration closely, but was delayed until temperature increased above 10°C when egg development times were reduced and resting eggs may have hatched. Bass et al., (1997) found a similar delayed development in the rotifer populations of the Great Ouse.

A simple flow related threshold was estimated for the Nene owing to the advective loss imposed by flowing water, above which rotifer development was minimal irrespective of the growth rate attained. This threshold was reached at approximately 0.08 ms⁻¹.

Discharge was considered to be the most important mechanism which controlled riverine zooplankton abundance in systems of low retention time by Pace et al., (1992). Advective losses were assumed to be the key to describing the generally low abundance of rotifers per unit chlorophyll 'a' in rivers and estuaries compared to reservoirs and lakes, in a relationship similar to the for phytoplankton density described by Søballe and Kimmel (1987). The importance of reduced retention time was also noted by many other workers including Brook and Woodward (1956), Hynes (1970), Winner (1975), Aksnes et al., (1989), van Dijk and van Zanten (1995), and Pourriot et al., (1997).

The impact of discharge on riverine zooplankton may not have been simply manifest through direct loss related processes. The association of water quality with discharge may have had a major impact on rotifer dynamics in the Nene, as shown by the close similarity of zooplankton dynamics between the main channel and the Nassington side-channel. The latter habitat had no recorded flow rate, and therefore a higher retention time than the former. The water quality was very similar, however, presumably as a result of a degree of exchange between the two habitats. The fact that rotifers were still dominant at Nassington, at the expense of cladocerans which utilise a very similar food resource, indicates that factors other than retention time influenced zooplankton dynamics. Threklaid (1982) came to a similar conclusion when he found that changes in water quality associated with inflowing water to reservoirs were more influential on zooplankton demographics than advective movements. This area of work requires further study to separate the direct effects of dilution from the indirect effects of water quality on the competitive balance within riverine zooplankton communities.

Rotifer populations from the Nene were, however, subject to constant high loss rates
as indicated by the low degree of potential birth rate realised as instantaneous growth. A large proportion of this loss was assumed to result from advective removal in flowing waters. The estimated loss rates, assuming full turbulent mixing, were higher than the measured birth rates, indicating that the system was reliant on population imports to maintain its number, and therefore was not viable without assuming the dead zone model of river dynamics (Reynolds 1988), a similar conclusion to that of the algal populations (see above).

Some of these imports may have originated from the hatching of resting eggs, but this seemed to occur over a relatively short period of time at the start of the spring development, as indicated by negative death rates of *Keratella cochlearis*. A riverine population of *K. cochlearis* was found to produce resting eggs at a constant rate irrespective of density dependant or food limited cues, whereas a reservoir population of the same species showed no similar behaviour (chapter 5). This was assumed to be a life-history trait adaptation to the riverine habitat to reduce the likelihood of downstream removal of populations. Whether all riverine species use resting eggs as a life-history strategy remains an interesting question that deserves further study. Care is needed if using this observation from a single population to describe a riverine zooplankton community response. Resting eggs from *Keratella cochlearis*, *K. quadrata*, Brachionids and *Synchaeta spp.* were, however, identified from river samples. Analysis of the density, species composition and the hatching cues are needed to fully understand the role of resting eggs from the river sediments in rotifer plankton dynamics.

Importation was, in fact, likely to occur from upstream sections as was described for the phytoplankton, considering the close relationship between these two parameters during the growing season as indicated by their significant correlation. The same problems then exist, as did for phytoplankton, in describing the reasons for the rapid population decline at the end of spring and the constant summer low biomass, especially as food seemed to be in excess of that needed to maintain maximum growth rates. Rotifer density declined abruptly after approximately one month in all three study years. The reason for the decline was assumed to be different in all three years, potentially resulting from increased loss rates associated with a period of high discharge in 1992 and 1993, but not in 1994.

The spring decline definitely deserves further investigation, as it represented a community response which must have been driven by an external factor. The fact that phytoplankton density also decreased around the same time may indicate a level of food related control, but the analysis of effective food concentration proved this was
not the case. It is possible that the changing role of dead zones also affected zooplankton in a similar manner to that already described for the phytoplankton, with a degree of physical 'isolation' induced at low flow rates leading to the development of more $K$-selected species which were rapidly lost when washed into the flow.

The role of 0+ fish cannot be ignored, as a synchronous hatching of these animals may have had a significant impact on mid channel and dead zone populations, as shown by Bass et al., (1997) in the River Great Ouse. In this study, rotifer numbers were observed to peak at over 2000 animals l$^{-1}$ during May, 1989, but declined rapidly to less than one twentieth of this by the end of the month. The similarity in the magnitude and timing of this spring decline, and the fact that this river is located close to the Nene, and has a relatively similar physical structure, indicates that fish predation was likely to have a similar impact on the Nene rotifer community. Further work on the timing and density of 0+ recruitment, and their feeding preferences in the Nene is required to ascertain an accurate predation rate to incorporate into the rotifer population models. This is an area of work that has often been ignored in the past, but is obviously of potential importance in river systems.

Bass et al., (1997) also found a continued low summer density in the main river channel during a number of years, as was the case in the Nene. The reasons for this can only be speculated, but again deserve further investigation. Continued predation by larval fish may be involved along with a lack of suitably $r$-selected imports from dead zones. Further work should also be carried out regarding the feeding ecology of riverine rotifers, as the effective food concentration may have underestimated the impact of food limitation when algal concentration was low.
Appendix A.4.1 Concentration by filtration

Filtration is the most common method used to concentrate zooplankton (Bottrell et al., 1976), even though settlement is the only truly accurate method. River studies have typically used filtration because of the need to take large volume samples (Kowalczewski et al., 1985; Ferrari and Mazzoni, 1989; De Ruyter van Steveninck et al., 1990), and this was considered as the optimal method for the present study. Filtration is not however without its problems. The following study into the accuracy and precision of filtration was deemed necessary considering the need to directly compare counts with settled reservoir samples.

Filtration may underestimate the density of certain rotifers, especially small and delicate species. For example, Polyarthra sp. was continually underestimated by filtration through netting of 20 μm and over (Likens and Gilbert, 1970). Matveyeva (1989) found the total density of rotifers was underestimated by a factor of between 1.4 - 3.4 when filtered through an 85 μm mesh compared with decanted samples. The final precision of filtration depends on the appropriate choice of mesh size, the volume of the sample, the density of seston, and the force applied during filtration. A mesh with 53 μm pore size was used in the present study as this allowed the removal of fine sediment from the sample and reducing net clogging, while avoiding the excessive losses of animals expected from using a mesh with pores of over 70 μm diameter (Bottrell et al., 1976).

A study was performed to assess the losses of different rotifer taxa and their eggs during filtration. The density of animals from 20 litre filtered samples (from Wansford Backwater) was compared to that gained from one litre sedimented samples which were assumed to capture 100% of the zooplankton. Both samples were drawn from a single composite sample and were therefore assumed to come from a random distribution. Three subsamples from each sample were enumerated to obtain a reliable mean density for various rotifer groups, and the relative efficiency of capture was calculated as the proportion of settled sample retained by filtration. The whole procedure was repeated on ten separate occasions throughout the growing season to gain an estimate of annual average filtration accuracy.

The abundance of rotifers from the two methods of concentration were compared with t-tests of log-transformed data to assess the significance of any losses with filtration. A significant difference at the p<0.05 level indicated that filtration lost significant numbers of animals compared to settlement. The results for most taxa were not significant except for Polyarthra sp. In general, however, the filtered samples retained
less animals than settled samples (only 5 comparisons out of a total of 58 had more animals in the filtered sample) indicating some level of loss in the filtrate.

The average annual efficiency of capture is presented in table A.4.1 for a number of different rotifer groups, encompassing a wide range of size and morphology. Not all groups were present in adequate numbers to make an estimate of retention from all ten sample occasions so the last column gives the number of comparisons used to derive the efficiency.

<table>
<thead>
<tr>
<th>Group</th>
<th>Length (μm)</th>
<th>Width (μm)</th>
<th>Filtration efficiency (%)</th>
<th>Lower C.L. (95%)</th>
<th>Upper C.L. (95%)</th>
<th>number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Keratella cochlearis</td>
<td>141</td>
<td>60</td>
<td>79</td>
<td>47</td>
<td>129</td>
<td>3</td>
</tr>
<tr>
<td>K. cochlearis eggs</td>
<td>60</td>
<td>40</td>
<td>67</td>
<td>29</td>
<td>115</td>
<td>5</td>
</tr>
<tr>
<td>Polyarthra sp.</td>
<td>100</td>
<td>70</td>
<td>57</td>
<td>26</td>
<td>81</td>
<td>8</td>
</tr>
<tr>
<td>Polyarthra sp. eggs</td>
<td>65-80</td>
<td>40-60</td>
<td>45</td>
<td>25</td>
<td>61</td>
<td>8</td>
</tr>
<tr>
<td>Nauplii</td>
<td>1000-100</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Synchaeta oblonga</td>
<td>150</td>
<td>90</td>
<td>77</td>
<td>51</td>
<td>101</td>
<td>7</td>
</tr>
<tr>
<td>S. pectinata</td>
<td>200</td>
<td>140</td>
<td>60</td>
<td>49</td>
<td>71</td>
<td>5</td>
</tr>
<tr>
<td>Keratella quadrata</td>
<td>217</td>
<td>90</td>
<td>80</td>
<td>49</td>
<td>115</td>
<td>5</td>
</tr>
<tr>
<td>K. quadrata eggs</td>
<td>75</td>
<td>60</td>
<td>70</td>
<td>47</td>
<td>95</td>
<td>5</td>
</tr>
<tr>
<td>Notholca squamula</td>
<td>120</td>
<td>110</td>
<td>85</td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>

Table A.4.1 The efficiency of rotifer capture using filtration compared to settlement as the method of sample concentration. Mean and confidence limits are derived from log transformed data.

The wide confidence limits indicate variation in the filtration efficiency between samples, probably as a result of different filtration speed and animal density. For example, high densities of animals may block the filter, reducing the effective pore size, and therefore increasing the number of animals retained.

The inherent variability of the method means that any single conversion factor applied to filtered counts to make them comparable to settled counts should only be used with caution. Similarly, the temporal series of samples concentrated by filtration should only be compared with caution, as the efficiency of retention of the different groups varies from week to week. This facet of concentration by filtration has often been ignored in previous river work, where precision was assumed to be constant.

Only those groups that were sufficiently abundant for statistical comparisons, were represented in the above table. To make the results generally applicable to the diversity of less abundant taxa that may appear in the plankton from time to time,
each taxa was assigned to one of four classes based on overall size and morphology. An average retention efficiency value was then calculated for each class allowing the density of similarly sized groups not represented in the study to be calculated from filtered samples. The four classes were defined as follows:

1. Small loricate species. Smallest axial dimension of less than 60 μm. *K. cochlearis* used to estimate retention efficiency of this group. Overall filtration retention efficiency estimated as 79%.

2. Small illoricate species. Smallest axial dimension of less than 80 μm. *Polyarthra sp.*, *S. oblonga*, rotifer eggs included. These groups more prone to deformation and variation in retention efficiency. Overall filtration retention efficiency estimated as 68%.

3. Large loricate species. Smallest axial dimension of more than 60 μm. *K. quadrata* and *N. squamula* included. Overall filtration retention efficiency estimated as 91%.

4. Large illoricate species. Smallest axial dimension of more than 80 μm. *S. pectinata* and nauplii used to estimate the retention efficiency of this group as no other abundant members present in the samples studied. Overall filtration retention efficiency estimated as 88%.

The results showed that large loricate species were retained with the greatest efficiency and small illoricate forms were most likely to be underestimated by filtration. The above classification is only for use as a rough guide, however, due to the use of a limited number of taxa to describe the behaviour of large arbitrary groups that include a wide diversity of animals with different morphology and the degree of variation between study taxa within a class. For example, the capture efficiency of the small illoricate class ranged from 57% to 77%, with the highest retention gained by the smallest group, rotifer eggs. This indicates that the morphology of the groups is also important feature, with the most delicate forms more likely to be underestimated by filtration.
Appendix A.4.2 Spatial distribution of animals

Ten replicate samples were taken on a single sample occasion from across the width of the river at the Wansford Station site on 12/05/94 to estimate the distribution of the zooplankton in the main channel. The spatial distribution of the dominant rotifer groups, *Synchaeta sp.*, *Notholca squamula*, *Keratella cochlearis*, was assessed using the variance to mean index of dispersion (Elliot, 1973), in which a ratio of one indicates that samples were drawn from a Poisson distribution. A ratio of less than one indicates a regular distribution whereas a ratio greater than one indicates that the data were drawn from a contagious distribution. The significance of any departure from unity was tested using the chi-squared distribution.

The variance to mean ratio is a good statistical test for agreement with a Poisson distribution, but is not a good measure of the degree of clumping in a population. Morisita’s index of dispersion was therefore also calculated (Morisita, 1959, in Elliot, 1973). The results were however in agreement with the former method.

All samples were drawn from a Poisson distribution (95% confidence level), indicating that the dominant rotifers species were randomly distributed throughout the open-water river channel. This discovery was initially surprising considering the high degree of contagion found in other plankton studies, but not unexpected, as Hynes (1970) states that an even distribution of riverine rotifers is likely due to the mixing effects of turbulent flow.

Marneffe *et al.*, (1996) found the distribution of zooplankton in the River Meuse to be homogeneous at flows of 50 m$^3$s$^{-1}$, but heterogeneous during lower flows when more lacustrine conditions prevailed. The flow rate in the River Nene on 12/05/94 was 9.39 m$^3$s$^{-1}$, much lower than that in the Meuse. The River Meuse is, however, a larger river with a more canalised structure than the Nene and will therefore require higher discharge to achieve the same mixing potential.
Appendix A.4.3 Precision of sampling regime

The constantly changing flow regime in rivers means that the potential mixing power of the water, and therefore the likely distribution of planktonic organisms, is stochastic. Results from pilot data taken on a single occasion should not be generally applied to all sample occasions, as conditions will never be the same. The pilot data does however give a 'broad' indication of the precision that can be expected from a sampling regime. The distribution found during the pilot survey can be used in the following equation to assess the precision gained, in terms of the ratio of confidence limits to arithmetic mean, by taking any number of replicate samples.

\[ D^2 = \frac{t^2 \cdot s^2}{n \cdot x^2} \]

Where \( D \) is the level of precision, \( t \) is Student's t (approximated to 2 for 95% probability level of \( D \)), \( s^2 \) is the variance, \( x \) is the mean of the counts and \( n \) is the number of replicate samples taken. Table A.4.2 shows the level of precision gained by taking different numbers of replicate samples from the distribution present on 19/05/94.

<table>
<thead>
<tr>
<th>Number of replicates</th>
<th>Synchaeta sp.</th>
<th>K. cochlearis</th>
<th>N. squamula</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.34</td>
<td>0.23</td>
<td>0.70</td>
</tr>
<tr>
<td>2</td>
<td>0.24</td>
<td>0.16</td>
<td>0.49</td>
</tr>
<tr>
<td>4</td>
<td>0.17</td>
<td>0.12</td>
<td>0.35</td>
</tr>
<tr>
<td>10</td>
<td>0.11</td>
<td>0.07</td>
<td>0.22</td>
</tr>
</tbody>
</table>

**Table A.4.2** The precision obtained from to different sampling effort. Precision is defined as \( D \), the proportion of arithmetic mean bounded by 95% confidence limits.

Precision increased (confidence limits become narrower) with sampling effort. Elliot (1973) stated that for most benthic studies, confidence limits of ± 40% of the arithmetic mean (\( D = 0.40 \)) were tolerable. These limits are surpassed by a single 10 litre sample for *Synchaeta sp.* and *K. cochlearis*. *N. squamula* counts, although conforming to a random distribution, had a higher variance than the other groups and therefore a lower precision. Four replicate samples were required to bring the precision within 'acceptable limits' for this group. The term 'acceptable limits' is only a guideline and cannot always be reached for all taxonomic groups, as their density and distribution fluctuates throughout the year.
Optimisation of sampling methods is necessary to gain the best possible precision per unit sampling effort. Increasing the number of replicates increases the accuracy of the data, but only at a cost in terms of time taken to process the samples. One method that increases the accuracy of samples without increasing subsequent laboratory analysis is that of composite sampling (Cassie, 1971; Prepas, 1984), where replicates are pooled in the field and then treated as a single sample. Two to four 10 litre samples (depending on the environmental conditions; see below) were pooled in the present study. This was expected to yield statistically viable data for the dominant taxa on each sampling occasion, assuming a similar spatial distribution of animals to when the pilot data was gathered. Confidence limits can be applied to single sample counts drawn from a random distribution as the variance is approximately equal to the mean (Zar, 1984). Replication of composite samples was therefore not performed as the pilot data showed that the Poisson distribution described riverine plankton distribution.
Appendix A.4.4 Sample size

The volume of the sample had to be adequate to yield suitable numbers of animals in a 5-10 ml subsample. Elliot (1973) stated that a minimum count of 25 animals was required to obtain confidence limits within 40% of the arithmetic mean if samples were drawn from a poisson distribution, while Bottrell et al., (1976) showed that the accuracy of replicate counts, represented as the coefficient of variation, levelled out at approximately 6-8% of the mean when counts exceeded 60 individuals. In the present study at least 100 animals of the dominant group were counted when possible. This level of accuracy could not always be guaranteed as the density of most rotifer species was strongly seasonal with a low density in the second half of 1994, but taking a large sample increased the likelihood that samples contained adequate numbers of animals (Resh, 1979).
Appendix A.4.5 Effect of sample size on filtration efficiency

The filtration of different sample volumes on different dates may introduce a further source of variation to the methods. For example, dense samples have the potential to clog filters, reducing the effective pore size, and therefore increase the density of small species retained compared to smaller samples. Samples concentrated from different volumes may therefore not be strictly comparable so a study was performed to compare the efficiency of rotifer capture from samples of 10 litres and 40 litres from Wansford Station. A single composite 40 litre sample taken on 12/05/94 was compared to ten replicate 10 litre samples taken at the same time from the main channel. The following formula (t-test for difference between a single observation and a population, (Sokal and Rohlf (1995)) was used to test the probability that the density of rotifers obtained from the 40 litre sample was not significantly different from that of the 10 litre samples.

\[ t_s = \frac{Y_1 - Y_2 - (\mu_1 - \mu_2)}{s_2 \sqrt{\frac{n_2 + 1}{n_2}}} \]

Where \( Y_1 \) and \( Y_2 \) are the means of the 40 litre and 10 litre samples respectively, \( \mu_1 - \mu_2 \) is equal to zero as testing for similarity, \( s_2 \) is the standard deviation of the 10 litre samples and \( n_2 \) is the number of replicate measurements. The procedure was repeated for a number of rotifer groups to ensure similar capture efficiency over a range of animal size and morphology. All data were transformed using a square route transformation as suggested by Elliot (1973) for counts from a Poisson distribution.

The results of the investigation are presented in table A.4.3. The mean number of animals per litre are given for each sample volume along with the 95% confidence limits of the 10 litre replicates. The \( t_s \) values obtained were compared with published values of the Student’s t-distribution for \( n-1 \) degrees of freedom to yield the probability that the two methods were sampling with equal accuracy.

There was no significant difference between the 40 litre sample and the 10 litre replicate samples at the \( p=0.05 \) level, indicating that sample volume had no significant effect on concentration efficiency. The morphological diversity of groups considered (illoricate species like \( S. oblonga \) and \( Polynarthra \) sp., the small spherical eggs of \( K. cochlearis \) and loricate species such as \( K. cochlearis \) and \( N. squamula \)) indicated that morphology had no effect on the results. In other words, the variation observed could easily have originated from sampling a random distribution rather than from an
obvious effect of sample size on the number retained.

<table>
<thead>
<tr>
<th>Group</th>
<th>length (nm)</th>
<th>Mean no. 1⁻¹. 10 l.</th>
<th>Upper C.L.</th>
<th>Lower C.L.</th>
<th>Mean no. 1⁻¹. 40 l.</th>
<th>ts</th>
<th>Probability level</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Synchaeta oblonga</em></td>
<td>150</td>
<td>279.63</td>
<td>314.75</td>
<td>248.43</td>
<td>352.12</td>
<td>1.33</td>
<td>P&gt;0.2</td>
</tr>
<tr>
<td><em>Keratella cochlearis</em></td>
<td>130</td>
<td>63.04</td>
<td>68.46</td>
<td>57.84</td>
<td>62.25</td>
<td>-0.10</td>
<td>P&gt;0.9</td>
</tr>
<tr>
<td>K. cochlearis eggs</td>
<td>70</td>
<td>48.83</td>
<td>62.08</td>
<td>37.78</td>
<td>63.38</td>
<td>0.29</td>
<td>P&gt;0.5</td>
</tr>
<tr>
<td><em>Notholca squamula</em></td>
<td>135</td>
<td>31.59</td>
<td>40.48</td>
<td>23.80</td>
<td>28.13</td>
<td>0.74</td>
<td>P&gt;0.4</td>
</tr>
<tr>
<td><em>Polyarthra sp.</em></td>
<td>90</td>
<td>7.06</td>
<td>9.75</td>
<td>4.81</td>
<td>14.25</td>
<td>1.73</td>
<td>P&gt;0.1</td>
</tr>
</tbody>
</table>

Table A.4.3 The difference between capture efficiency of rotifers from samples of different volume.

The use of different volumes to sample riverine rotifer populations in the present study did not introduce significant error.
Appendix A.4.6 Mode of preservation

The final strength of formaldehyde can affect the long term efficiency of preservation. Too low a concentration may allow bacterial attack of tissues, whereas too high a concentration may cause the loss of fragile groups, especially protozoans (Kimor, 1973).

The detrimental effects of formaldehyde preservation were tested on a number of rotifer taxa over a period of two months. The state of animals was visually checked under brightfield magnification (x 400) after a period of four and eight weeks. The following species were preserved in 4% formaldehyde with no signs of degradation (table A.4.4).

<table>
<thead>
<tr>
<th>Species</th>
<th>Morphology</th>
<th>Contraction</th>
<th>1 month</th>
<th>2 months</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polyarthra dolichoptera</td>
<td>Illoricate</td>
<td>Contracted</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Filinia longiseta</td>
<td>Illoricate</td>
<td>Contracted</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Synchaeta pectinata</td>
<td>Illoricate</td>
<td>Contracted</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>S. oblonga</td>
<td>Illoricate</td>
<td>Contracted</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Keratella cochlearis</td>
<td>Loricate</td>
<td>No contraction</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Keratella quadrata</td>
<td>Loricate</td>
<td>No contraction</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Brachionus calyciflorus</td>
<td>Loricate</td>
<td>No contraction</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Brachionus angularis</td>
<td>Loricate</td>
<td>No contraction</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Asplanchna priodonta</td>
<td>Illoricate</td>
<td>Contracted</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Testudinella patina</td>
<td>Loricate</td>
<td>No contraction</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Epiphanes senta</td>
<td>Illoricate</td>
<td>Contracted</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
<tr>
<td>Euchlanis dilatata</td>
<td>Loricate</td>
<td>No contraction</td>
<td>No degradation</td>
<td>No degradation</td>
</tr>
</tbody>
</table>

Table A.4.4 The effect of 4% formaldehyde preservation on different groups of rotifer.

All illoricate species contracted with fixation. The degree of contraction differed between groups, and made identification impossible to species with groups such as Synchaeta which have no distinguishing features other than surface structures. Identification to species was possible with Polyarthra due to the presence of ventral finlets and blades. Narcotics such as weak formaldehyde (Pontin, 1978) and procaine hydrochloride at a concentration of 0.04% (May, 1985) have been used during sample fixation to retain many of the morphological features required for accurate identification, but the method was rejected in this study as loricate forms also died in a relaxed state obscuring much of the lorica detail needed for their identification.
Appendix A.4.7 Regression models for riverine rotifer development

The independent variables used in the models were total chlorophyll 'a' concentration, water temperature, average daily discharge over a four day period prior to sampling, oxygen concentration, pH, and turbidity. All of the above independent variables may influence rotifer dynamics, but they do not represent an exhaustive list. No direct estimate of predation rate was available, and this may have a substantial impact on rotifer dynamics (Brandl and Fernando, 1978; Gilbert, 1980; Hammer, 1985), although high densities of invertebrate predators were never obtained from river samples.

Dependant variables were log-transformed when necessary to ensure normality. Independent variables were also log transformed if the original distribution of measurements were highly non-normal. All transformations were tested for normality with the Kolmogarov-Smirnov test prior to inclusion in the linear models. The residuals of all models were also tested for normality by plotting against a standard normal cumulative distribution. Log-transformations tended to reduce the presence of outliers, but where these had a significant weighting, the points were smoothed and the analysis re-run.

All independent variables were initially entered into the model. The model was then simplified by a stepwise removal of the predictor variable which accounted for the smallest degree of residual variation. The simplified model therefore contained only the dependant variables which were responsible for describing a significant amount (p<0.05) of residual variation (measured by F-ratio). The procedure was undertaken by the SYSTAT statistical package. The significance of each stepwise removal was tested by the F-ratio (MS due to independent variable removal / MS residual). If the F-statistic was not significant at the 5% level, then the variable was removed from the model.

The resulting simplified models were used to identify those variables with a significant influence on rotifer dynamics and to quantify the amount of variation explained. The use of simple regressions was avoided due to the potential interaction between some independent variables. Interaction of this sort can produce misleading results as the following example shows for the Wansford station data set. Single regressions of rotifer density on chlorophyll 'a' and pH were both positive and significant at the p<0.01 level (n=26). One may therefore conclude that both factors had a significant effect on rotifers. The two independent variables were, however, significantly correlated at the p<0.01 level i.e. they displayed a significant level of covariation. Multiple regression offers a tool to decide which of the covarying factors has the greater influence on the dependant variable.
The following result tables mimic the backwards removal of independent variables from the full model. The P value stated indicates the significance level associated with each removal. Variables with P values greater than 0.05 were removed from the model.

### A.4.7.1 Linear regression models for Wansford station during the growing season, 1994

#### Total rotifer density

<table>
<thead>
<tr>
<th></th>
<th>Multiple R</th>
<th>R²</th>
<th>F(removed)</th>
<th>P(removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FULL MODEL</strong></td>
<td>.861</td>
<td>.742</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Independent removed oxygen</td>
<td>.854</td>
<td>.729</td>
<td>.917</td>
<td>.350</td>
</tr>
<tr>
<td>temperature</td>
<td>.848</td>
<td>.718</td>
<td>.789</td>
<td>.385</td>
</tr>
<tr>
<td>discharge</td>
<td>.825</td>
<td>.680</td>
<td>2.837</td>
<td>.107</td>
</tr>
<tr>
<td>turbidity</td>
<td>.818</td>
<td>.669</td>
<td>.793</td>
<td>.383</td>
</tr>
<tr>
<td>pH</td>
<td>.812</td>
<td>.659</td>
<td>.696</td>
<td>.413</td>
</tr>
<tr>
<td><strong>SUBSET MODEL</strong></td>
<td>chlorophyll a</td>
<td>.812</td>
<td>.659</td>
<td>46.330</td>
</tr>
</tbody>
</table>

Regression equation for simplified model: \( Y = -0.280 + 1.403 \times X \)
where \( X \) is the chlorophyll 'a' concentration (\( \mu g l^{-1} \)).

#### Total Brachionus sp. density

<table>
<thead>
<tr>
<th></th>
<th>Multiple R</th>
<th>R²</th>
<th>F(removed)</th>
<th>P(removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FULL MODEL</strong></td>
<td>.804</td>
<td>.647</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Independent removed pH</td>
<td>.804</td>
<td>.646</td>
<td>.042</td>
<td>.840</td>
</tr>
<tr>
<td>turbidity</td>
<td>.803</td>
<td>.645</td>
<td>.039</td>
<td>.846</td>
</tr>
<tr>
<td>temperature</td>
<td>.801</td>
<td>.642</td>
<td>.214</td>
<td>.648</td>
</tr>
<tr>
<td>oxygen</td>
<td>.797</td>
<td>.635</td>
<td>.405</td>
<td>.532</td>
</tr>
<tr>
<td><strong>SUBSET MODEL</strong></td>
<td>chlorophyll a</td>
<td>.797</td>
<td>.635</td>
<td>20.607</td>
</tr>
<tr>
<td>discharge</td>
<td>.797</td>
<td>.635</td>
<td>6.041</td>
<td>.022</td>
</tr>
</tbody>
</table>

Regression equation for simplified model: \( Y = -1.182 + 1.088 \times X_1 + 0.561 \times X_2 \)
where \( X_1 \) is chlorophyll 'a' concentration (\( \mu g l^{-1} \)) and \( X_2 \) is discharge (\( m^3 s^{-1} \)).
### Total Keratella sp. density

<table>
<thead>
<tr>
<th></th>
<th>Multiple R</th>
<th>R²</th>
<th>F(removed)</th>
<th>P(removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FULL MODEL</strong></td>
<td>0.922</td>
<td>0.850</td>
<td>0.033</td>
<td>0.858</td>
</tr>
<tr>
<td>Independent removed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>temperature</td>
<td>0.922</td>
<td>0.850</td>
<td>0.012</td>
<td>0.915</td>
</tr>
<tr>
<td>oxygen</td>
<td>0.922</td>
<td>0.850</td>
<td>0.212</td>
<td>0.650</td>
</tr>
<tr>
<td>turbidity</td>
<td>0.921</td>
<td>0.848</td>
<td>0.155</td>
<td>0.698</td>
</tr>
<tr>
<td>pH</td>
<td>0.920</td>
<td>0.847</td>
<td>0.820</td>
<td>0.698</td>
</tr>
<tr>
<td><strong>SUBSET MODEL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>chlorophyll a</td>
<td>0.920</td>
<td>0.847</td>
<td>82.830</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>discharge</td>
<td>0.920</td>
<td>0.847</td>
<td>8.450</td>
<td>0.008</td>
</tr>
</tbody>
</table>

Regression equation for simplified model: \( Y = -1.024 + 1.192.X_1 + 0.363.X_2 \) where \( X_1 \) was chlorophyll 'a' concentration (\( \mu g l^{-1} \)) and \( X_2 \) was discharge (m\(^3\)s\(^{-1}\)).

### Community diversity

<table>
<thead>
<tr>
<th></th>
<th>Multiple R</th>
<th>R²</th>
<th>F(removed)</th>
<th>P(removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FULL MODEL</strong></td>
<td>0.823</td>
<td>0.677</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Independent removed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>temperature</td>
<td>0.820</td>
<td>0.672</td>
<td>3.7</td>
<td>0.580</td>
</tr>
<tr>
<td>oxygen</td>
<td>0.808</td>
<td>0.653</td>
<td>1.114</td>
<td>0.304</td>
</tr>
<tr>
<td>turbidity</td>
<td>0.785</td>
<td>0.616</td>
<td>2.289</td>
<td>0.145</td>
</tr>
<tr>
<td>pH</td>
<td>0.767</td>
<td>0.589</td>
<td>1.536</td>
<td>0.228</td>
</tr>
<tr>
<td>chlorophyll a</td>
<td>0.762</td>
<td>0.580</td>
<td>4.87</td>
<td>0.492</td>
</tr>
<tr>
<td><strong>SUBSET MODEL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>discharge</td>
<td>0.762</td>
<td>0.580</td>
<td>33.162</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>

Regression equation for simplified model: \( Y = 0.178 + 0.544.X \) where \( X \) is the discharge (m\(^3\)s\(^{-1}\)).

### A.4.7.2 Linear regression model for the April-May (spring development period), 1992-1994

### Total rotifer density

<table>
<thead>
<tr>
<th></th>
<th>Multiple R</th>
<th>R²</th>
<th>F(removed)</th>
<th>P(removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FULL MODEL</strong></td>
<td>0.778</td>
<td>0.606</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Independent removed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>discharge</td>
<td>0.775</td>
<td>0.601</td>
<td>0.258</td>
<td>0.617</td>
</tr>
<tr>
<td><strong>SUBSET MODEL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>chlorophyll a</td>
<td>0.775</td>
<td>0.601</td>
<td>5.194</td>
<td>0.033</td>
</tr>
<tr>
<td>temperature</td>
<td>0.775</td>
<td>0.601</td>
<td>7.981</td>
<td>0.010</td>
</tr>
</tbody>
</table>

Regression equation for simplified model: \( Y = -0.085 + 0.737.X_1 + 0.090.X_2 \) where \( X_1 \) is chlorophyll 'a' concentration (\( \mu g l^{-1} \)) and \( X_2 \) is temperature (°C).
A.4.7.3 Regression model for Nassington Backwater. Whole growing season

**Total rotifer density**

<table>
<thead>
<tr>
<th></th>
<th>Multiple R</th>
<th>R2</th>
<th>F(removed)</th>
<th>P(removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FULL MODEL</strong></td>
<td>.900</td>
<td>.811</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Independent removed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oxygen</td>
<td>.893</td>
<td>.797</td>
<td>.277</td>
<td>.627</td>
</tr>
<tr>
<td>pH</td>
<td>.892</td>
<td>.796</td>
<td>.042</td>
<td>.845</td>
</tr>
<tr>
<td>temperature</td>
<td>.889</td>
<td>.791</td>
<td>.728</td>
<td>.422</td>
</tr>
<tr>
<td>turbidity</td>
<td>.870</td>
<td>.757</td>
<td>1.143</td>
<td>.321</td>
</tr>
<tr>
<td>discharge</td>
<td>.853</td>
<td>.727</td>
<td>.965</td>
<td>.355</td>
</tr>
<tr>
<td><strong>SUBSET MODEL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>chlorophyll a</td>
<td>.853</td>
<td>.727</td>
<td>24.013</td>
<td>.001</td>
</tr>
</tbody>
</table>

Regression equation for simplified model: \( Y = -0.319 + 1.494X \)
where \( X \) is chlorophyll 'a' concentration (\( \mu g/l \)).

A.4.7.4 Regression model for Wansford Backwater. Whole growing season

**Total rotifer density**

<table>
<thead>
<tr>
<th></th>
<th>Multiple R</th>
<th>R2</th>
<th>F(removed)</th>
<th>P(removed)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FULL MODEL</strong></td>
<td>.785</td>
<td>.616</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Independent removed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oxygen</td>
<td>.785</td>
<td>.615</td>
<td>.024</td>
<td>.878</td>
</tr>
<tr>
<td>pH</td>
<td>.762</td>
<td>.581</td>
<td>1.984</td>
<td>.173</td>
</tr>
<tr>
<td>temperature</td>
<td>.762</td>
<td>.581</td>
<td>4.960</td>
<td>.047</td>
</tr>
<tr>
<td><strong>SUBSET MODEL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>chlorophyll a</td>
<td>.762</td>
<td>.581</td>
<td>24.045</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>

Regression equation for simplified model: \( Y = 1.559 + 1.812X_1 - 0.034X_2 \)
where \( X_1 \) was log chlorophyll 'a' concentration (\( \mu g/l \)) and \( X_2 \) was temperature (°C).
Appendix A.4.8 Calculation of Rotifer Population Dynamics

The instantaneous birth rate, $b'$, and intrinsic population growth rate, $r$, were calculated from field population data and published embryonic development rates. The instantaneous death rate was estimated by difference, $b' - r$. The death rate is the least reliable statistic in the population dynamics model (Prepas and Rigler, 1978 in Andrew and Fitzsimons, 1992), as it is not calculated directly but relies on two statistics which already have error associated with their estimates (Edmondson, 1960).

The instantaneous birth rate, $b'$, was calculated from

$$b' = \frac{\ln (e r_t +1) / D}{D}$$

where $e r_t$ is the egg ratio at time $t$, and $D$ is the embryonic development time estimated from the relationship described in Edmondson (1960) and the water temperature at the time of sampling. The instantaneous rate of increase was calculated from the exponential growth model

$$N_t = N_0 e^{rt}$$

where $N_0$ and $N_t$ are the recorded population densities at intervals 0 and $t$. The instantaneous death rate was estimated from

$$d' = b' - r$$

Instantaneous birth rate can be used to estimate the 'potential' increase in population numbers between two sampling occasions assuming growth follows the exponential model and there are no deaths or emigration. Other assumptions must hold, the most important of these being that immigration is negligible, all eggs hatch and grow to maturity, a uniform egg age distribution is present at the time of sampling, and the temperature and food reserves remain relatively constant between samples. Any reduction from the potential increase is evident from the actual increment measured in the field and can be attributed to either deaths, failure of all eggs to hatch, or departures from the assumptions of the model. The proportion of the potential development realised was calculated from the instantaneous birth rate and the observed rate of population increase. It is merely another method of presenting the death rate.
Appendix A.4.9 Calculation of the Food Limiting Carrying Capacity for Rotifers

The food limiting carrying capacity was calculated from chlorophyll 'a' concentration and a literature derived estimate of individual threshold food level for a 'typical' small rotifer. The population threshold is the concentration of food at which population growth rate equals zero. The population is expected to approach this carrying capacity if conditions are suitably stable and no other factor limits development. The aim of this analysis was therefore to assess the likelihood of food limitation to river rotifer populations.

Steps used in converting chlorophyll 'a' concentration to carrying capacity.

1. A threshold food concentration for 'small' rotifers was obtained from the literature. This was estimated at 0.1 μg ml⁻¹ dry weight of algae after Stemberger and Gilbert (1985) for a highly palatable food source. Not all algae in the natural environment will be of such high quality, so this estimate represents the absolute minimum food requirement for growth. The individual threshold was scaled up to population level by assuming that all rotifers feed equally efficiently on a general food source represented by chlorophyll 'a' concentration. This may be a gross oversimplification for a group of animals known to express considerable food preference.

2. My estimate of chlorophyll 'a' concentration was converted to an estimate of dry weight to allow the estimate of carrying capacity. This was done in two stages. First was a conversion from chlorophyll 'a' to an estimate of algal biovolume, second was a separate conversion from algal biovolume to dry weight. This converted the initial chlorophyll 'a' concentration to the same units used for the threshold estimate.

3. Reynolds (1984) regressed cell chlorophyll 'a' content against cell volume for a number of algal groups and came up with the following relationship

\[ \log \text{chl a} = 0.984 \log \text{vol} - 2.072 \]

which can be rearranged to

\[ \log \text{vol.} = 0.936 \log \text{chl a} + 2.174 \]

The suitability of this relationship which deals with single cells was questionable when applied to my data which deals with an algal community estimate of chlorophyll 'a'. A
A separate regression was therefore performed using my estimate of chlorophyll 'a' and a derived estimate of total algal biovolume (from E.A. supplied algal cell counts and estimated cell biovolumes for each taxa recorded). The results of this regression are presented in figure A 4.1 which also shows Reynolds' regression line.

\[
y = 0.803x + 3.098 \quad r = 0.781
\]

Figure A 4.1 The relationship between total cell volume and chlorophyll 'a' at Wansford, 1994 with 95% confidence limits. Reynolds' (1984) regression shown (dashed line).

An analysis of covariance was performed to test the significance of the difference between the two regression lines, both of which had no significant difference in their slope. A significant difference was found between the two lines at the \( p = 0.05 \) level. The relationship derived from community data was considered suitably \((r^2 \text{ of } 0.611 \text{ significant at } p<0.01 \text{ level})\) accurate to estimate algal volume from chlorophyll 'a' and so was used in preference to that of Reynolds (1984). The confidence of the estimate could also be calculated with the former method.

4. The estimate of total algal volume was then transformed to an estimate of dry weight using the regression relationship of Reynolds (1984) (figure A 4.2). This stage was needed as no dry weight data was available from chlorophyll 'a' samples. The relationship was re-drawn from Reynolds' (1984) original data to allow confidence limits to be applied to the relationship. Reynolds' regression used a single cell as the unit of measurement. This was 'scaled' to fit the range of total biovolumes obtained from samples at Wansford. This procedure did not affect the slope of the line.
5. The transformation of chlorophyll 'a' to dry weight was therefore completed in two stages, each of which had an associated error. The regression lines were combined to yield the following equation relating algal dry weight to chlorophyll 'a' concentration.

$$\log \text{dry weight} = 0.793 \cdot \log \text{chl a} + 2.772$$

The regression line and its 95% confidence limits are shown in figure A 4.3.

6. Algal concentration, expressed as dry weight (pgml\(^{-1}\)), was used as a direct estimate of available food to rotifers. The carrying capacity of the environment, expressed as the maximum number of animals sustained at a particular food level, was estimated by dividing the dry weight by the individual threshold food concentration. The carrying capacity is presented in figure 4.15 for the Wansford sample station.
Figure A 4.3 Relationship between chlorophyll 'a' and algal dry weight at Wansford, 1994.
Appendix A.4.10 Calculation of the expected development of rotifer populations with downstream transit

The expected increase in population size with downstream transit was calculated from an estimate of rotifer birth rate and the time taken for transit between sites. The following equation was used

\[ N_t = N_0 \cdot e^{(b' \cdot d \cdot t)} \]

where \( N_0 \) was the density of animals observed at a site, \( N_t \) was the expected density at a downstream site, \( b' \) the recorded birth rate at \( N_0 \), \( d \) (death rate) was assumed to be zero for this analysis, and \( t \) was the time taken for travel between sites.

The time taken for fully entrained particles to travel between sites was calculated from the simple formula (distance travelled / velocity of flow). The velocity of flow on the day of the study was 0.037 m s\(^{-1}\). The distance between sites is shown in the following table, along with the assumed time in transit.

<table>
<thead>
<tr>
<th>Site</th>
<th>km between sites</th>
<th>time (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fotheringhay</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wansford station</td>
<td>16</td>
<td>5.0</td>
</tr>
<tr>
<td>Ferry Meadows</td>
<td>8</td>
<td>2.5</td>
</tr>
<tr>
<td>North Side</td>
<td>15</td>
<td>4.7</td>
</tr>
</tbody>
</table>

Table A 4.5 The time taken for a fully entrained particle to travel between sites on the Nene.

Note the long transit times between sites due to low flow velocity. This may have an effect on the results of the analysis as no death rate between sites was assumed.

The relevant population statistics for *K. cochlearis* are presented in the following table. All data points were an average of three replicate samples from a single location.

This information was used in the formula outlined above to calculate expected animal density at downstream sites. The results of the analysis are presented in section 4.3.10.
<table>
<thead>
<tr>
<th>Site</th>
<th>density (no./l)</th>
<th>egg density (no./l)</th>
<th>egg ratio</th>
<th>temp (°C)</th>
<th>$b'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fotheringhay</td>
<td>1186.8</td>
<td>939.93</td>
<td>0.792</td>
<td>23</td>
<td>0.449</td>
</tr>
<tr>
<td>Wansford station</td>
<td>3945.27</td>
<td>2325.3</td>
<td>0.589</td>
<td>23</td>
<td>0.357</td>
</tr>
<tr>
<td>Ferry Meadows</td>
<td>2771.82</td>
<td>1556.82</td>
<td>0.562</td>
<td>23</td>
<td>0.343</td>
</tr>
<tr>
<td>North Side</td>
<td>2183.15</td>
<td>480.18</td>
<td>0.220</td>
<td>21</td>
<td>0.153</td>
</tr>
</tbody>
</table>

Table A 4.6 Statistics required for the calculation of *K. cochlearis* population birth rate.
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