Meteorological and climatic impacts on the phytoplankton community of a small meso-eutrophic lake

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Declaration

I declare that this thesis has not been submitted in support of an application for another degree at this or any other university. It is the result of my own work and includes nothing that is the outcome of work done in collaboration except where specifically indicated. Many of the ideas in this thesis were the product of discussion with my supervisors; Ian Jones, Eleanor Mackay, Alex Elliott and Andrew Folkard.

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Statement of authorship

Chapters 4-7 are presented in the style of papers, two of which have been published and are presented as the final copy before journal editing. The papers have multiple authors and their contributions are identified below.

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Data Statement

Original data collected during this thesis is stored in NERC's Environmental Information Data Centre (EIDC) hosted by the Centre for Ecology & Hydrology under the title Blelham Tarn: Ecological and chemical lake profiles, and inflow and outflow chemistry 2016-17.

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Abstract

Climate change is having long term impacts on the physical structure of lakes including potential shallower surface mixing, increases in stratification strength and increases in surface water temperature. It is therefore vital that lake thermal dynamic properties, like the depth of surface mixing, are quantified in a robust way. Comparing methods of mixed depth estimation in this thesis, however, found that values were highly inconsistent leading to disparate interpretations of ecological and chemical water quality parameters. Future limnological studies using the mixed depth should be vigilant to this issue and test multiple methods to ensure that findings are not dependant on the choice of method.

Long term changes in lake water temperature and surface mixing as a result of climate change occur concurrently, but they have separate consequences for phytoplankton growth. Using a phytoplankton model, water temperature and mixed depth were changed independently. Increases in water temperature led to an increase in phytoplankton growth at most mixed depths. Contrary to previous research, mixed depth shallowing did not always lead to increases in cyanobacteria biomass, with shallowing from deep to intermediate depths resulting in a reduction in cyanobacteria.

The magnitude and frequency of episodic weather events such as storms are also expected to increase as a result of climate change. It is therefore becoming increasingly likely that extreme events will occur at a time of heightened stratification strength, but the interaction of these two extremes have not yet been explored in detail. Despite concerns that episodic weather events will push lakes into more extreme states, evidence here suggests that in some cases storms can return the thermal stability and seasonal phytoplankton community succession to conditions more typical for the time of year. This highlights the importance of setting the responses of episodic weather events in the context of long term averages.

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Contents

1 INTRODUCTION 1

1.1 Overview 1
1.2 Thesis focus 2
1.3 Aims and objectives 5
1.4 Thesis structure 7

2 LITERATURE REVIEW 8

2.1 Overview 8
2.2 Lake physical processes 8
2.2.1 Lake Heat Budget 8
2.2.1 Temporal changes in heat budget 12
2.2.2 Thermal Stratification 15
2.2.3 Surface mixing 18
2.2.4 Defining the depth of surface mixing 20
2.3 Vertical distribution of resources for phytoplankton growth 24
2.3.1 Light 24
2.3.2 Nutrients 25
2.4 Phytoplankton 27
2.4.1 Morphology and motility 28
2.4.2 Classifying phytoplankton 30
2.4.3 Mixing vs sinking 33
2.4.4 Phytoplankton interactions with lake physics 37
2.4.5 Seasonal succession 38
2.5 Climate Change 39
2.5.1 Physical impacts of long term climatic change 39
2.5.2 Nutrient impacts of long term climatic change 43
2.5.3 Phytoplankton responses to long term climatic change 44
2.5.4 Physical impacts of storm events 48
2.5.5 Nutrient impacts of storm events 50
2.5.6 Phytoplankton responses to storm events 50
2.5.7 Summary 53

3 SITE DESCRIPTION AND METHODOLOGY 54

3.1 Site description 54
3.1.1 Location 54
3.1.2 Climate 56
3.1.3 Geology and morphometry 57
3.1.4 Catchment land use 59
3.1.5 Long term monitoring and previous research 60
3.1.6 Water quality and nutrient status 61
3.2 Methodology 64
3.2.1 High resolution monitoring 64
3.2.2 Fieldwork Campaign 69

3.2.3 Phytoplankton community modelling: Phytoplankton RespOnses To Environmental CHange (PROTECH) model 81

4 WIDE-SPREAD INCONSISTENCY IN ESTIMATION OF LAKE MIXED DEPTH IMPACTS INTERPRETATION OF LIMNOLOGICAL PROCESSES . 83

4.1 Highlights 83
4.2 Abstract 83
4.3 Graphical Abstract 84
4.4 Introduction 85
4.5 Materials and methods 91
4.5.1 Site description 91
4.5.2 Field methods and data collection 91
4.5.3 Methods for estimating mixed depth, z_{mix} 92
4.5.4 Comparison of mixed depth method estimates 96
4.5.5 Determining the homogeneity of ecological and chemical parameters within the mixed depth 97
4.5.6 Calculation of example metrics using different mixed depth estimates 97
4.6 Results 97
4.6.1 Comparing mixed depth estimates 97
4.6.2 Using the density-derived estimate as a predictor for ecological and chemical derived estimates of mixed depth 100
4.6.3 Determining the homogeneity of limnological variables within the mixed layer 104
4.6.4 The impact of using different mixed depth estimates when calculating example metrics 107
4.7 Discussion 111
4.8 Conclusions 113

5 MODELLING LAKE CYANOBACTERIA BLOOMS: DISENTANGLING THE CLIMATE-DRIVEN IMPACTS OF CHANGING MIXED DEPTH AND WATER TEMPERATURE 115

5.1 Summary 115
5.2 Introduction 116
5.3 Methods 120
5.3.1 Site description 120
5.3.2 PROTECH model 121
5.3.3 Driving data 126
5.3.4 Model validation 127
5.3.5 Model Experiment 128
5.4 Results 130
5.4.1 Validation 130
5.4.2 Impacts of temperature change before and after stratification 133
5.4.3 Impacts of temperature and mixed depth change during the stratified period 135
5.4.4 Comparing experimental methods 143
5.5 Discussion 146

6 FROM ONE EXTREME TO ANOTHER: THE IMPACT OF A STORM EVENT ON PHYSICAL AND CHEMICAL LAKE PROCESSES AT A TIME OF ATYPICAL STRATIFICATION STRENGTH 152

6.1 Abstract 152
6.2 Introduction 153
6.3 Materials and Methods 157
  6.3.1 Site description 157
  6.3.2 High Resolution Monitoring 158
  6.3.3 Statistical analysis 158
6.4 Results 162
  6.4.1 The characteristics of the 2016 event 162
  6.4.2 Additional high flow events 170
  6.4.3 Storm impacts on nutrient levels 176
6.5 Discussion 178

7 THE IMPACT AND RECOVERY OF A PHYTOPLANKTON COMMUNITY IN RESPONSE TO A STORM EVENT IN A SMALL MESO-EUTROPHIC LAKE 182

7.1 Abstract 182
7.2 Introduction 184
7.3 Materials and Methods 188
  7.3.1 Site description 188
  7.3.2 Determining the ‘typical’ phytoplankton seasonal succession 190
  7.3.3 Determining the short term responses to the storm event 191
7.4 Results 194
  7.4.1 The seasonal succession 194
  7.4.2 Vertical responses of the phytoplankton community to the storm event ... 198
7.5 Discussion 208

8 DISCUSSION 214

8.1 Overview 214
8.2 Methodological approaches to monitoring and disentangling processes occurring on multiple timescales 215
  8.2.1 High resolution monitoring 216
  8.2.2 Traditional lake sampling 219
  8.2.3 Modelling 221
  8.2.4 A combined approach to water quality research 223
8.3 The mixed depth concept 223
8.4 Impacts of long term climate change 225
  8.4.1 Importance of surface mixing 226
  8.4.2 Importance of increasing temperature 227
  8.4.3 Importance of stratification strength and stability 228
8.5 Impacts of short term weather events 232
8.6 Interaction of long term climatic impacts and short term weather impacts .. 235

9 CONCLUSIONS 238

9.1 Thesis conclusions 238
9.1.1 Investigating the consistency of a commonly used limnological concept: ‘the mixed depth’ *238*
9.1.2 Distinguishing the impacts of long term changes in water temperature and mixed depth for phytoplankton *239*
9.1.3 Determining the importance of antecedent conditions for physical and chemical responses to extreme storm events *240*
9.1.4 Identifying the impact of a storm event on the seasonal succession and vertical structure of the phytoplankton community *240*
9.1.5 Summary *241*
9.2 Suggested areas for future research 242
9.2.1 Application of mixed depth recommendations *242*
9.2.2 Distinguishing the relative impacts of multivariate storm events on phytoplankton communities *242*
9.2.3 Identifying how the importance of antecedent conditions prior to storm events differs with location, lake type and storm characteristics *243*

List of Tables

Table 2.1 Types of lake mixing regime with examples (Lewis, 1983) 17

Table 2.2 Phylogenetic groups (some are non-planktonic) (Cox and Shubert, 2016). .. 31

Table 2.3 Characteristics of the three functional groups of phytoplankton groups according to Reynolds (2006). 33

Table 3.1 Summary of data sources used in this thesis. 64

Table 4.1 Examples of temperature and density thresholds and gradients used in existing literature to calculate the mixed layer depth. 90

Table 4.2 The mean difference, root mean square error (RMSE) and range in mixed depth estimates as calculated using Methods 1a, 1b, 2 & 3. Negative values indicate that the latter mixed depth estimates are deeper. 99

Table 4.3 Statistical model coefficients and adjusted R^2 values for the depth of the density-derived mixed depth compared with the mixed depth calculated from chlorophyll a, oxygen, specific conductivity and pH as well as the depth of the chlorophyll a and oxygen maxima for Method 2 and Method 3. The significance level is denoted as ***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1, ns- not significant. Quadratic models were used for oxygen and specific conductivity whereas linear models were used for chlorophyll a, chlorophyll a maxima, oxygen maxima and pH, 2016 n=23; 2017 n=23. 103

Table 4.4 The coefficient of variation (COV) and the range of temperature, oxygen, chlorophyll a, concentration of hydrogen ions (exponential of pH) and specific conductivity values in the water column (WC) and the mixed layer for Method 1a (M1a), Method 2 (M2) and Method 3 (M3), percentage values in brackets depict the percentage variation in the mixed layer relative to the whole water column variation. 106

Table 5.1 Morphometric characteristics of the 12 phytoplankton taxa........................124

Table 5.2 Summary of phytoplankton movement characteristics at different light thresholds within PROTECH. 125

Table 5.3 Seasonal mean phytoplankton biomass (chlorophyll a mg m^{-3}) during the stratified period for water column integrated and 5 m integrated results using the fixed mixed depth method...144

Table 5.4 Seasonal mean phytoplankton biomass (chlorophyll a mg m^{-3}) during the stratified period for water column integrated and 5 m integrated results using the percentage mixed depth method. 145

Table 6.1 Number of breakpoints identified during June-October and the day of the year identified as a breakpoint for the storm event for within lake physical metrics. ..164

Table 6.2. Long term and 2016 means for the periods before (16/08/16-20/08/16), during (21/08/16-25/08/16) and after (26/08/16-30/08/16) the event and T-test results to test if 2016 conditions were significantly different compared to the long term mean ***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1, ns- not significant, df =8 and n=5 for each test. 168

Table 6.3. T-test to test if values of physical drivers and within lake physical metrics five days before the event (16/08/2016-20/08/2016) and five days after the event (26/08/2016-30/08/2016) were statistically significant during the 2016 event and tests to determine if the differences between before and after time periods are significantly different from the long term mean differences for the same time period

***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1, ns- not significant, df =12 and n=7. 169

Table 6.4. Long term and 2010 means for the periods before (06/07/10-15/07/10), during (16/07/10-25/07/10) and after (26/07/10-04/08/10) the event and T-test results to test if 2010 conditions were significantly different compared to the long term mean ***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1, ns- not significant, df =18 and n=10 for each test. 173

Table 6.5 Long term and 2012 means for the periods before (21/05/12-15/06/12), during (16/06/12-11/07/12) and after (12/07/12-06/08/12) the event and T-test results to test if 2012 conditions were significantly different compared to the long term mean ***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1, ns- not significant, df =50 and n=23 for each test. 175

Table 7.1 Mean percentage of each phylogenetic and functional group for fortnights prior to and following the event for the long term average and 2016. 195

Table 7.2 The percentage change in biovolume at each depth in the water column before, during and after the event. 200

Table 7.3 The coefficient of variation for each phylogenetic and functional in the water column based on mean abundance values before (10/08/16 and 17/08/16), during (22/08/2016 and 24/08/2016) and after the event (31/08/16 and 07/09/16). 201

List of Figures

Figure 1.1 Flow diagram outlining the overall thesis structure. 7

Figure 2.1 Diagram showing the exchanges of heat, Q_s is solar radiation, Q_{sr} is reflected solar radiation, Q_{lin} is the incoming long wave radiation, Q_{lout} is the outgoing long wave radiation, Q_h is the sensible heat flux and Q_e the latent heat flux. Made using BioRender...9

Figure 2.2 Diagram showing the conceptual temperature profile of a lake during the stratified period including an isothermal epilimnion, a metalimnion marked by a steep gradient of decreasing temperature and a cool isothermal hypolimnion. 16

Figure 2.3 A modified version of Figure 2.2 showing the epilimnion being split into an upper actively mixing layer and the depth of recent mixing as marked by the isothermal layer. 23

Figure 2.4 The conceptual idea of critical depth and critical turbulence for sinking phytoplankton in fully mixed and stratified systems according to Huisman et al., (2002). 34

Figure 2.5 Schematic of fully mixed and stratified system. T is temperature (red), N is nutrients (blue) and PAR is photosythetically active radiation (yellow) adapted from Ross and Sharples, (2008). 37

Figure 3.1 Map of Blelham Tarn, catchment and tributaries. 55

Figure 3.2 Monthly averages for (a) air temperature (b) relative humidity (c) solar radiation and (d) wind speed taken from the automated monitoring buoy 2008-2018 and (e) rainfall recorded at the Ambleside weather station 1985-2010 (Met Office, 2019). 57

Figure 3.3 The bathymetry of Blelham and location of the monitoring buoy (triangle) at the deepest point of the lake (14.5m) bathymetry from Ramsbottom (1976). Photo credit: E.Gray. 58

Figure 3.4 Monthly mean nutrient concentrations for (a) silica, (b) soluble reactive phosphorus (black) and total phosphorus (grey) and (c) nitrate (black) and ammonia (grey) sampled fortnightly from Blelham Tarn 2008-2018. 63

Figure 3.7 Discharge of Blelham Beck calculated u*sing the Blelham and Leven discharge in 1974 (Black line) and discharge calculated from the rating curve derived in this study (grey line).* 69

Figure 3.8 Nutrient concentrations of (a) total phosphorus, (b) soluble reactive phosphorus, (c) total nitrogen, (d) nitrate and (e) silica collected monthly during June-October 2016. 72

Figure 3.9 Relationship between (a) chemically measured and fluorescence measured chlorophyll a for measurements at depth 0.5-0.9 m, (b) chemically measured and fluorescence measured chlorophyll a for measurements at depth 0.5 m and 1 m and (c) chemically measured (black) and fluorescence (grey) measured chlorophyll a for measurements at depth 0.5 m and 1 m with date. 78

Figure 3.10 Example profiles where a sub-surface chlorophyll a maxima occurs in both the chemically determined (black) and fluorescence profiles (grey) for (a) 12/07/2017, (b) 19/07/2017 and (c) 26/07/2017. 79

Figure 4.1 Diagram of density profiles marking the mixed depth (X) for (a) a theoretical mixed depth; (b) estimating the mixed depth using a 0.1 kg m^{-3} or 1 ^{o}C difference from the surface (Surface ρ or T) (Methods 1a and b); (c) estimating the mixed depth using Method 2 where lines are extended from the depth of the maximum gradient (Δρ/Δz max), the density minimum (ρ min) and the density maximum (ρ max) with the upper intersection of the lines marking the top of the pycnocline or base of the mixed depth and (d) estimating the mixed depth using Method 3 were the upper and lower values of the section of the profile containing the depth of the maximum gradient (Δρ/Δz max) and a change in the density gradient (Δρ grad) significantly different from zero marking the mixed depth and the top of the hypolimnion, respectively, the grey shading marks the profile confidence intervals. 93

Figure 4.2 Mixed depth estimates using Method 1a (density threshold; black square) and Method 1b (temperature threshold; grey circle) in (a) 2016 and (b) 2017. 98

Figure 4.3 Density-derived mixed depth estimates using Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) (a) 2016 and (b) 2017. 100

Figure 4.4 Depth of the mixed layer calculated from density (✳), chlorophyll a (●), oxygen (▲), pH (◆) and specific conductivity (■) for (a) 2016 using Method 2, (b) 2016 Method 3 (c) 2017 Method 2 and (d) 2017 Method 3...102

Figure 4.5 The coefficient of variation in the mixed layer for temperature (✳), chlorophyll a (●), oxygen (▲), concentration of hydrogen ions (pH) (◆) and specific conductivity (■) for (a) 2016 Method 1a, (b) 2016 Method 2 , (c) 2016 Method 3, (d) 2017 Method 1a, (e) 2017 Method 2 and (f) 2017 Method 3...105

Figure 4.6 The percentage of chlorophyll a and oxygen within the mixed layer using mixed depth estimates calculated using Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) for (a) chlorophyll a in 2016, (b) oxygen in 2016, (c) chlorophyll a in 2017 and (d) oxygen in 2017. 108

Figure 4.7 The difference in the concentration of oxygen within the mixed layer compared to the concentration in the layer 0.5 m below using mixed depth estimates calculated from Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) for (a) 2016 and (b) 2017. 109

Figure 4.8 The z_{mix}:z_{eu} ratio calculated using density derived mixed depth estimated using Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) for (a) 2016 and (b) 2017. Values below the horizontal y intercept line at 1 z_{mix}:z_{eu} mark when mixed depths are shallower than the euphotic depth and vice versa for values above. 110

Figure 5.1 Blelham Tarn is located in the lake district in North West England (square), with the monitoring buoy (triangle) located at the deepest point in the lake (14.5 m) bathymetry from Ramsbottom (1976). 121

Figure 5.2 Observed (black line) and simulated (grey line) mean fortnightly (a) total chlorophyll a biomass, (b) C strategists biomass, (c) CS strategist biomass and (d) R strategist biomass for Blelham Tarn for the three year period simulated with the range of fortnightly values for that period being depicted by the error bars. 132

Figure 5.3 (a) Chlorophyll a concentrations with temperature in fully mixed spring prior to stratification (black square) and fully mixed autumn following stratification (grey circle) and (b) average day of the year when chlorophyll a first exceeded (black square) and dropped below (grey circle) 5 mg m^{-3} with temperature change. 133

Figure 5.4 Percentage of C (dark grey triangle), CS (light grey circle), and R (black square) strategists in (a) fully mixed spring and (b) fully mixed autumn. 134

Figure 5.5 Shannon diversity index with temperature change for fully mixed spring (black squares) and fully mixed autumn (grey circles). 135

Figure 5.6 Mean chlorophyll a concentrations at each mixed depth and temperature change for (a) annual mean (b) stratified spring, (c) stratified summer and (d) stratified autumn, the black circle marks the baseline mixed depth and temperature for Blelham Tarn. 137

Figure 5.7 Percentage of (a,d,g,j) C (b,e,h,k) CS (c,f,I,l) and R strategists in (a,b,c) annual average, (d,e,f) stratified spring, (g,h,i) summer, (j,k,l) stratified autumn, black circle marks the baseline mixed depth and temperature for Blelham Tarn. 139

Figure 5.8 Percentage of total cyanobacteria at each mixed depth and temperature change for (a) Dolichospermum in stratified summer (b) Planktothrix in stratified summer, (c) Dolichospermum in stratified autumn and (d) Planktothrix in stratified autumn, black circle marks the baseline mixed depth and temperature for Blelham Tarn. 141

Figure 5.9 Shannon diversity index for each mixed depth and temperature change for (a) annual average (b) stratified spring (c) stratified summer, (d) stratified autumn black circle marks the baseline mixed depth and temperature for Blelham Tarn. 142

Figure 6.1 Map of Blelham Tarn, catchment and tributaries. 157

Figure 6.2 The long term mean (solid black line), standard deviation (grey shading) and 2016 mean values with the blue, green and orange shading marking the five days prior to the event (16/08/2016-20/08/2016), the five days during the event (21/08/2016-25/08/2016) and the five days following the event (26/08/2016-

30/09/2016), respectively for (a) outflow discharge, (b) cubed wind speed, (c) outflow discharge compared to the water residence time and (d) the total heat flux (Q_{tot}). 163

Figure 6.3 The long term mean (solid black line), standard deviation (grey shading) and 2016 mean values with the blue, green and orange shading marking the five days prior to the event (16/08/2016-20/08/2016), the five days during the event (21/08/2016-25/08/2016) and the five days following the event (26/08/2016-30/09/2016), respectively for (a) Schmidt stability, (b) surface water temperature (0.5 m) and (c) the depth of recent mixing. The vertical dashed line marks the breakpoint. 165

Figure 6.4 The long term mean (solid black line), standard deviation (grey shading) and 2010 mean values with the blue, green and orange shading marking the 10 days prior to the event (06/07/10-15/07/10), the 10 days during the event (16/07/10-25/07/10) and the 10 days following the event (26/07/10-04/08/10), respectively for (a) outflow discharge, (b) cubed wind speed, (c) total heat flux (Q_{tot}), (d) Schmidt stability, (e) surface water temperature and (f) mixed depth using method 1. 172

Figure 6.5. The long term mean (solid black line), standard deviation (grey shading) and 2012 mean values with the blue, green and orange shading marking the 23 days prior to the event (21/05/12-15/06/12), the 23 days during the event (16/06/12-11/07/12) and the 23 days following the event (12/07/12-06/08/12), respectively for (a) outflow discharge, (b) cubed wind speed, (c) total heat flux (Q_{tot}), (d) Schmidt stability, (e) surface water temperature and (f) mixed depth using method 1. 174

Figure 6.6 The long term mean (solid black line), standard deviation (grey shading) and event values (dashed black line) with the horizontal red line marking the limiting value for each nutrient for (a) SRP 2010, (b) DIN 2010, (c) silica 2010, (d) SRP 2012, (e) DIN 2012, (f) silica 2012, (g) SRP 2016, (h) DIN 2016 and (i) silica 2016. 177

Figure 7.1 Map of Blelham Tarn, its tributaries and its location in the UK and the English Lake District. 189

Figure 7.2 The percentage of each phylogenetic group based on (a) fortnightly means from the long term average and (b) fortnightly data for 2016. The results of the BLR analysis are depicted in c-h which contain samples from 2008-2015 and 2017-2018 (grey points) and 2016 (black points) with confidence intervals of the LOESS fit (dashed grey lines) and a solid black line showing the 2016 LOESS model fit for (c) Bacillariophyta, (d) Chlorophyta, (e) Cryptophyta, (f) cyanobacteria, (g) Miozoa and (h) Ochrophyta. 196

Figure 7.3 The percentage of each functional group based on (a) fortnightly means from the long term average and (b) fortnightly data for 2016. The results of the BLR analysis are depicted in c-f which contain samples from 2008-2015 and 2017-2018 (grey points) and 2016 (black points) with confidence intervals of the LOESS fit (dashed grey lines) and a solid black line showing the 2016 LOESS model fit for (c) S strategists, (d) C strategists, (e) CS strategists and (f) R strategists. 197

Figure 7.4 (a) The total biovolume at each depth for each date and (b) the depth of the biovolume maximum (solid black line), the euphotic depth (light grey line) and the mean (grey dashed line) and range (grey shading) of the mixed depth. 199

Figure 7.5 The total biovolume for each phylogenetic group for each sample day for (a) 1 m, (b) 2m, (c) 3m, (d) 4m and (e) 5m depths in the water column. Vertical dashed lines mark the start (21/08/2016) and end (25/08/2016) of the storm event. 202

Figure 7.6 The total biovolume for each CSR functional group for each sample day (a) 1 m, (b) 2m, (c) 3m, (d) 4m and (e) 5m depths in the water column. Vertical lines mark the start (21/08/2016) and end (25/08/2016) of the storm event.......................... 204

Figure 7.7 Diversity metrics at depths 1-5 m for (a) species turnover, (b) species richness, (c) species diversity, (d) phylogenetic diversity and (e) functional diversity. 206

Figure 7.8 Pielous evenness at depths 1-5 m for (a) species evenness, (b) phylogenetic evenness and (c) functional evenness. 207

Figure 8.1 Conceptual diagram of (a) the potential physical, chemical and ecological impacts of atypically stable stratification strength as a result of long term climate change and (b) the potential physical, chemical and ecological impacts of a storm event occurring at a time of atypically high stratification strength...................... 237

1 Introduction

1.1 Overview

Lakes are globally important and provide several ecosystem services such as drinking water, fisheries, flood regulation and recreation (Millennium Ecosystem Assessment, 2005). Lakes are also a vital component of global carbon (Cole *et al.*, 2007; Tranvik *et al.*, 2009) and nutrient cycles (Vitousek *et al.*, 1997; Moss, 2012) and support a diverse range of plant and animal species (Dudgeon *et al.*, 2006). With climate change, global mean air temperatures are increasing which is altering long term climatic baselines and seasonal weather patterns (IPCC, 2013) with further evidence that climate change is also increasing the frequency and magnitude of extreme events such as heatwaves, storms, floods and droughts (Beniston *et al.*, 2007; Coumou and Rahmstorf, 2012; Hov *et al.*, 2013).

Lakes and climate are closely coupled (Winder and Schindler, 2004). Climatic changes therefore have the potential to profoundly impact the physical structure of lakes. These impacts include warmer surface water temperatures, stronger and longer periods of stratification and consequently shallower surface mixing. Coupled with nutrient enrichment and eutrophication, these climatic impacts are resulting in widespread water quality problems. One concern is that this combination of factors is leading to the proliferation of cyanobacteria blooms. Cyanobacteria blooms have a number of associated water quality implications including increased turbidity, oxygen depletion and toxin production as well as changes in phytoplankton community biodiversity (Paerl and Huisman, 2009; Paerl and Paul, 2012; Huisman *et al.*, 2018). Blooms have a number of socio-economic and environmental implications including a reduction in the number of available water bodies for commercial uses, increased drinking water treatment and clean-up costs, reduced recreational and amenity value, losses from the tourist industry and potential health costs to humans, livestock and pets (Pretty *et al.*, 2003). The estimated damage costs of eutrophication as a whole are £75-114.3 million yr^{-1} in England and Wales (Pretty *et al.*, 2003) and $2.2 billion yr^{-1} in the USA (Dodds *et al.*, 2009).

In addition to the impacts of long term changes, the increase in frequency of extreme events such as storms can significantly impact the physical structure of the lake which in turn impacts the phytoplankton community composition and water quality (e.g. Jennings *et al.*, 2012). The impact of storm events on lake systems are complex, and will vary according to lake type, catchment land use and event timing, amongst other factors. Storms associated with heavy rainfall can result in negative water quality consequences such as an increased delivery of pollutants and nutrients through catchment runoff and sewer overflows which can lead to increased phytoplankton growth (Whitehead *et al.*, 2009). Conversely, increased flushing can reduce water residence times and flush phytoplankton blooms out of the system which may be beneficial for water quality (Whitehead *et al.*, 2009).

1.2 Thesis focus

In order to understand how changes in the physical structure of lakes, as a result of changes in meteorology, impact chemical and ecological processes several physical metrics (e.g. Wedderburn number, lake number and Schmidt stability) and concepts have been devised (see Read *et al.*, 2011 for a summary). One of these widely used concepts is the depth of surface mixing, which is commonly referred to as the epilimnion, mixed depth or mixed layer. The depth of surface mixing depends on the balance between stratifying (vertical density gradient induced by surface heating) and mixing forces (convective cooling and wind mixing), which change seasonally and in response to weather (Spigel and Imberger, 1980; Imberger and Hamblin, 1982). The depth of surface mixing is important as it determines the vertical distribution of particles and proportion of the water column that is directly in contact with the atmosphere (Imberger, 1998). At present there is no universal method of defining the mixed depth which has resulted in the development and application of a range of different methods (e.g. thresholds or gradients of temperature or density). The consistency and comparability between these methods has not been tested, nor have the implications of using different methods to calculate ecological and chemical metrics. This needs to be addressed as the mixed depth is often used as an explanatory or predictive variable when attributing ecological and chemical changes to mixed depth change as a result of long term climatic shifts, seasonal shifts or episodic weather events (e.g. Winder and Sommer, 2012; Giling, Nejstgaard, *et al.*, 2017).

Climate change has been linked to increases in lake surface water temperature (O’Reilly *et al.*, 2015), increases in stratification strength and length (Woolway and Merchant, 2019), and potential shallower surface mixing (Livingstone, 2003). Increases in lake water temperature is a driver of shallower surface mixing. Although these drivers are intrinsically linked, they have separate consequences for phytoplankton growth. Increases in temperature directly impact the growth rates of phytoplankton whereas shallower surface mixing impacts the light and nutrient climate phytoplankton are exposed to

(Winder and Sommer, 2012). Disentangling these impacts would help understand the relative importance of these two drivers for phytoplankton growth and community composition, particularly as mixed depth and temperature will change at different rates in different lakes. This is particularly relevant for understanding the mechanisms behind the dominance of problematic phytoplankton such as cyanobacteria species which are a significant water quality problem for many lakes and reservoirs across the world (Huisman, *et al*., 2018). It is suggested that combined increases in water temperature and shallower surface mixing promote surface blooms of cyanobacteria due to favourable traits such as buoyancy (e.g. Carey *et al*., 2012). Low light adapted cyanobacteria species such as *Planktothrix,* which can form sub-surface biomass maxima, are also thought to benefit from increases in water temperature and shallower surface mixing (Posch *et al*., 2012). Recent research suggests, however, that cyanobacteria responses to multiple stressors are variable amongst lake type and nutrient gradients (Richardson *et al*., 2018). This suggests that a "one size fits all" generalisation for predicting cyanobacteria responses to climate change is not appropriate (Richardson *et al*., 2018; Richardson *et al*., 2019).

With the projected long term change towards increased stratification stability in many lakes, it is likely that extreme meteorological events such as storms, will occur at a time of unusually high lake stability. The interaction between this within lake and meteorological extreme has not yet been explored, but is it is likely that the within lake antecedent conditions prior to a storm event will influence the physical, chemical and ecological response. Much of the previous research into extreme events has focussed on extreme meteorological events which induce an extreme within lake response (Harris and

Baxter, 1996; Jennings *et al.*, 2012; Giling, Nejstgaard, *et al.*, 2017). The trend towards increased lake stability, however, may mean that extreme storm events will result in heat loss and induce wind mixing which will return lake stability to conditions which are closer to the average for the time of year. Furthermore, vertical gradients of density during stratified periods results in the vertical heterogeneity of resources for phytoplankton growth which can lead to vertical niche partitioning (Ouellet Jobin and Beisner, 2014). Storms can significantly alter the physical structure of lakes and therefore the vertical distribution of resources. Previous research has not yet addressed how a phytoplankton community vertically restructures in response to a storm event and how this might differ at different depths.

1.3 Aims and objectives

This thesis uses a combination of high resolution meteorological and within-lake monitoring, phytoplankton community modelling and field data collected from a small monomictic lake (Blelham Tarn, UK) to address the following research gaps: (1) to investigate the consistency of a commonly used limnological concept ‘the mixed depth’, (2) to distinguish the impacts of long term changes in water temperature and mixed depth for phytoplankton; (3) to determine the importance of antecedent conditions for physical and chemical responses to extreme storm events and (4) to identify the impact of a storm event on the seasonal succession and vertical structure of the phytoplankton community. To address these aims the thesis has the following objectives:

i. To identify the methods currently used to calculate the mixed depth and evaluate their consistency;

ii. To evaluate how the choice of mixed depth definition may influence the calculation and interpretation of chemical and ecological metrics calculated from vertical profiles collected in the field;
iii. To develop alternative methods of estimating mixed depth which can be applied to profiles of physical, chemical and ecological variables;
iv. Use a phytoplankton community model to disentangle the separate climate driven impacts of water temperature and mixed depth change on phytoplankton communities, with a focus on cyanobacteria;
v. Use high resolution data to determine the importance of physical within lake antecedent conditions prior to an extreme storm event;
vi. To analyse the phytoplankton community before and after a storm event in the context of the long term average to examine deviations from the usual seasonal succession;
vii. To analyse phytoplankton community biomass and composition collected at different water column depths before and after a significant storm event.

1.4 Thesis structure

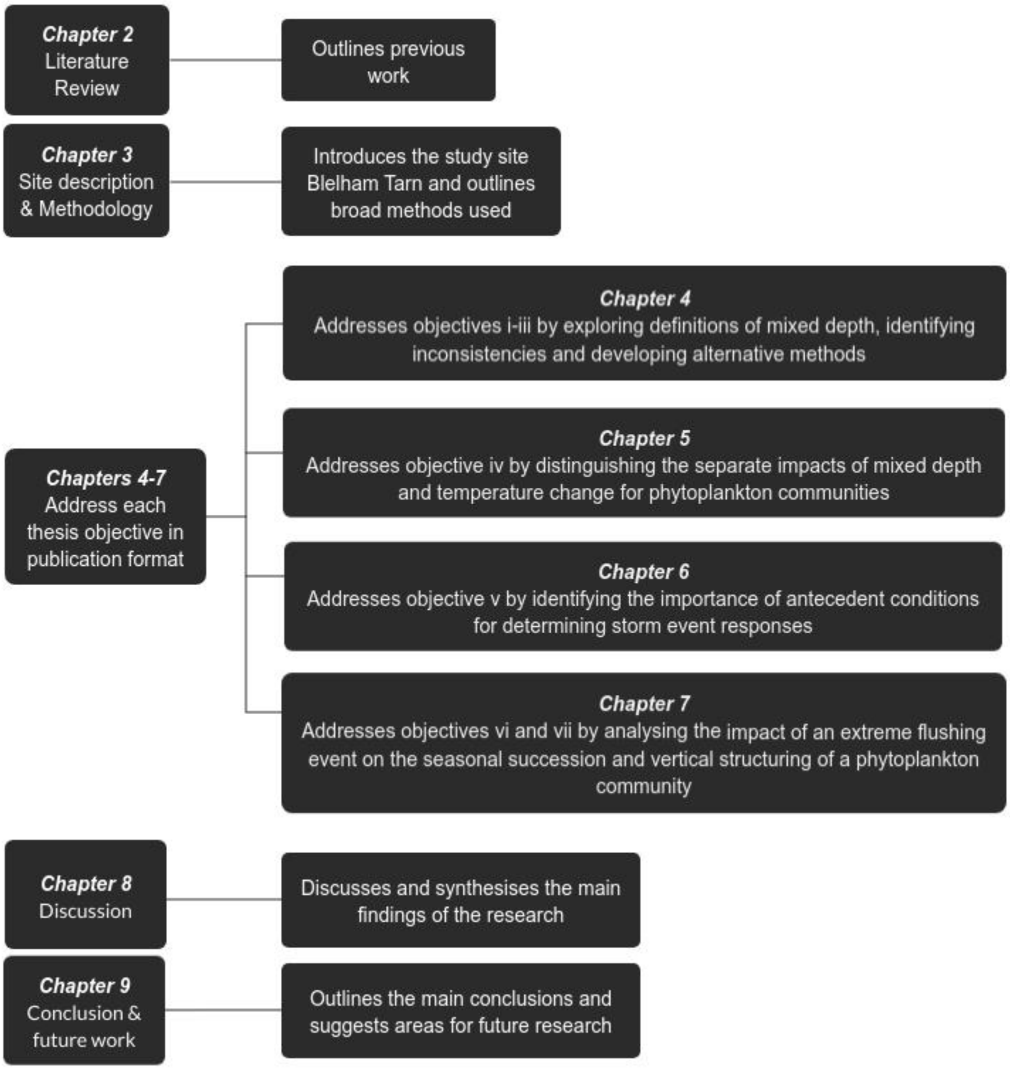

Figure 1.1 Flow diagram outlining the overall thesis structure.

2 Literature Review

2.1 Overview

The primary aim of this project was to investigate different impacts of climate change and weather events on the physical structure and phytoplankton community of a small, monomictic, meso-eutrophic lake. This literature review will begin by providing an overview of the physical drivers that control lake stratification and surface mixing as well as outlining the current caveats and methods used to define the surface mixed layer. The importance of vertical gradients of nutrients and light for phytoplankton growth will also be explored, along with phytoplankton adaptations to different environmental conditions. Current research investigating the impacts of long term climate change on the physical structure of lakes and phytoplankton communities will be discussed, along with the consequences of short term episodic weather events for physical, chemical and ecological processes.

2.2 Lake physical processes

2.2.1 Lake Heat Budget

The heat budget of a lake is dependent on climate and weather systems, lake morphometry (depth and surface area) and the attenuation of light in the water column (Wiegand *et al.*, 1982; Gorham and Boyce, 1989). The majority of a lake's heat exchange occurs at the air-water interface and is dependent on a number of variables including air temperature, wind speed, relative humidity and cloud cover (Wetzel, 2001). Ultimately, heating or cooling of lake surface waters depends on the balance between net short wave and net long wave radiation as well as the fluxes of sensible and latent heat (**Error! Reference source not found.**).

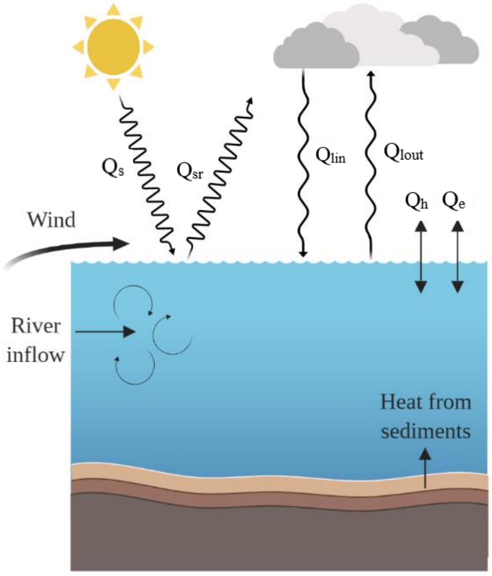

Figure 2.1 Diagram showing the exchanges of heat, Q_s *is solar radiation,* Q_{sr} *is reflected solar radiation,* Q_{lin} *is the incoming long wave radiation,* Q_{lout} *is the outgoing long wave radiation,* Q_h *is the sensible heat flux and* Q_e *the latent heat flux. Made using BioRender.*

Solar radiation has a latitudinal gradient, with lakes in equatorial regions receiving relatively constant solar radiation whereas in temperate and polar regions the sun's angle changes with the seasons. Incoming short wave radiation can be reflected from clouds before it reaches the water surface. When short wave radiation does reach the water surface some is reflected, the amount of which depends on the angle of the sun and wave action at the surface (Kirk, 1994). When the light energy enters the water the depth of light penetration will depend on the amount of energy absorbed by water molecules and suspended matter as well as the amount of scattering (Kirk, 1994). Long wave radiation is emitted by terrestrial objects and clouds and is exchanged between the lake and the atmosphere, usually having a net cooling effect (Wetzel, 2001). Outgoing long wave radiation from the lake depends on the temperature of the water, while incoming longwave radiation is influenced by air temperature and relative humidity (Wetzel, 2001).

Turbulent heat exchange occurs via the latent and sensible heat fluxes. Sensible heat transfer is a convective heat flux which varies according to the temperature gradient between the air and lake surface as well as wind speed. The latent heat flux is the heat lost (gained) from the lake via evaporation (condensation), which depends on the moisture gradient between the air and water surface. The magnitude of this varies according to the temperature difference between the lake surface and the atmosphere and the wind speed. The high specific heat capacity of water in comparison with air often means that the latent heat flux has a net cooling effect on the lake (Laird and Kristovich, 2002). The efficiency of the transfer of heat from the lake surface to the atmosphere by sensible and latent heat partly depends on the stability of the atmospheric boundary layer (Woolway, Verburg, *et al.*, 2017). In general, the higher the lake surface water temperature is compared to the temperature of the overlying air, the more unstable the atmospheric boundary layer is which can increase heat loss from the lake surface. Woolway, Verburg *et al.*, (2017) found that the instability of the atmospheric boundary layer increased in lakes closer to the tropics and that the frequency of unstable conditions decreased with an increase in lake size during summer.

River inflows can be an additional source of heat gain or loss. The impact of river inflows on the heat budget of a lake depends on the temperature of the inflowing water relative to the lake as well as the retention time and volume of the lake (Strasškraba and Hocking, 2002). This mechanism tends to have the largest impact on lakes with lower volumes and short retention times. The large inflow from Thompson River into Kamloops Lake, British Columbia, for example, has a net cooling effect on the heat budget for the majority of the year, and the inflowing water redistributes heat throughout the water column (Carmack *et al.*, 1979).

The depth of heat penetration in the water column depends on lake turbidity. Turbid lake waters with a large amount of suspended sediments in the water column (Stefan *et al.*, 1983) or a high concentration of phytoplankton in upper surface waters (Eloranta, 1978; Lind *et al.*, 1992; Jones *et al.*, 2005) can reflect or absorb incoming solar radiation therefore preventing it from reaching deeper waters and resulting in excess surface heat loss (Jones, George and Reynolds, 2005; Houser, 2006). Highly turbid surface waters that dissipate a large amount of light at the surface have been associated with warmer surface waters and shallower epilimnion thicknesses or thermocline depths (De Stasio *et al.*, 1996; Pérez-Fuentetaja *et al.*, 1999), but the relative impact of this changes with season (Persson and Jones, 2008) and is also dependent on lake size (Mazumder and Taylor, 1994; Fee *et al.*, 1996). For example, Persson and Jones (2008) found that larger extinction coefficients during summer led to the surface waters of lakes becoming warmer, but in late summer, mixing into the cool hypolimnion outweighed the warming effect. When comparing the effects of lake surface area and water clarity in lakes in northwestern Ontario, Canada, Fee *et al*., (1996) found that lake surface area had the largest influence on epilimnion thickness but water clarity was important in small lakes. Furthermore, a study by Houser (2006) found that in small coloured lakes, the mixed layer was shallower and cooler and the heat accumulation during the stratified period was significantly lower in comparison to similar clear lakes.

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2.2.1 Temporal changes in heat budget

The heat budget of a lake changes according to daily, seasonal and long term climatic cycles in addition to short term changes in weather. Heating and cooling is driven by seasonal climatic cycles. The seasons are caused by the tilt of the Earth's rotational axis as it orbits the sun, in the Northern Hemisphere the tilt towards the sun is maximised on the summer solstice (21st June) resulting in the longest number of day light hours (shortest in the southern hemisphere). During the winter solstice (21st December) the Earth's tilt away from the sun is maximised resulting in the shortest day length in the northern hemisphere (longest in the southern hemisphere). In temperate monomictic lakes during spring the increase in solar radiation means that water at the surface warms at a faster rate compared with water below which sets up a density gradient, inhibiting the full water column from mixing. The strength of stratification and depth of surface mixing in summer will then be modulated by changes in weather during summer, with warm weather strengthening the density gradient and cooler or windier weather resulting in the weakening of stratification. The decrease in day length following the summer solstice will mean that eventually the lake will begin to lose heat which will weaken stratification strength until the lake overturns in the autumn and will remain fully mixed and isothermal in winter.

Due to the non-linear relationship between water temperature and density fresh water is most dense at 3.94 ^{o}C. This means that inverse stratification can occur in dimictic lakes during winter if the surface water temperatures drop below 3.94 ^{o}C (Bertilsson *et al.*, 2013). Lakes located at more northerly latitudes, high altitudes or continental interiors are often ice covered during winter which reduces the exchange of heat between the lake surface and the atmosphere, depending on the ice thickness and transparency (Bengtsson and Svensson, 1996). During the early stages of winter in particular, heat fluxes from the sediment can become an important source of heat. Lake sediments retain heat gained during summer warming and slowly release this to the bottom of the lake water during winter. The overall impact of this on the lake water temperature depends on the water depth. Sediments overlain by a shallow water column contain more heat than sediments underneath deeper water columns (Bengtsson and Svensson, 1996). In late winter when the ice layer thins and transparency increases solar radiation becomes a major heat source again (Bengtsson and Svensson, 1996).

The differences in heating and cooling between night and day can result in large daily differences in surface water temperature (Frempong, 1983; Woolway *et al.*, 2016). These differences in temperature are primarily controlled by changes in solar radiation (Frempong, 1983). Diel changes in solar heating change the energy storage of the lake, being the lowest at night and highest during the day (Frempong, 1983). The size of the diel temperature range depends on the season with summer having the largest daily range and winter the lowest (Woolway *et al.*, 2016). The diel range is dependent on lake area with daily ranges increasing with decreasing lake area (Woolway *et al.*, 2016). This is due to the higher wind speeds experienced by lakes with a larger surface area which increase the depth of mixing meaning that heat is distributed over a larger layer of water which leads to lower diel temperature ranges (Woolway *et al.*, 2016).

Inter-annual variations in heating and cooling are driven by weather and climatic cycles such as the North Atlantic Oscillation (NAO) (Gerten and Adrian, 2001; George *et al.*, 2004; Dokulil *et al.*, 2006; Blenckner *et al.*, 2007) and the El Niño Southern Oscillation (ENSO) (Bai *et al.*, 2012). The North Atlantic Oscillation (NAO) is a weather phenomenon caused by fluctuations in sea level pressure between areas above (Icelandic low) and below (Azores high) 55°N (Hurrell, 1994). These fluctuations in pressure influence weather systems in Europe and North America depending on the phase of the oscillation (Hurrell, 1994). A strong NAO occurs when Arctic sea level pressures are anomalously low and pressures south of 55°N are anomalously high, causing strong westerly weather fronts (wet and windy) in winter across Europe (Hurrell, 1994). When the pressure differences are weak winters tend to be drier and colder (Hurrell, 1994). The changes in phase of the NAO therefore result in a large decadal and inter-annual variability in precipitation, wind speed, storminess and air temperature (Hurrell and Deser, 2010).

The NAO therefore has detectable impacts on lake water temperatures (Gerten and Adrian, 2001; George *et al.*, 2004; Dokulil *et al.*, 2006; Blenckner *et al.*, 2007). For example, George *et al*., (2004) found that lake water temperatures and mild wet winters were positively correlated with the NAOI (NAO Index) for four lakes in the English Lake District. The formation of ice on Windermere, UK, is also strongly related to the phase of the NAO (George, 2007). On a larger scale, a meta-analysis of the effects of the NAO on European lakes identified that lake water temperatures were strongly related to the NAO (Blenckner *et al.*, 2007). The effects of the NAO can differ depending on the lake mixing regime. Gerten and Adrian, (2001) found that the effects of the winter NAO on lake water temperatures in polymictic lakes in Germany only persisted until spring, whereas in a deep dimictic lake the impact on the hypolimnion water temperature remained until the following winter. Warming hypolimnetic waters in twelve deep lakes across Europe have also been attributed to the NAO affecting deep lakes in spring before the onset of thermal stratification (Dokulil, 2014).

2.2.2 Thermal Stratification

The predominant exchange of heat at the surface of lakes and the seasonal and diurnal heating cycles can result in thermal stratification in lakes of sufficient depth. During this process the surface waters warm at a faster rate than water below which results in a vertical density gradient. The vertical thermal structure of a lake depends on the balance between stratifying (buoyancy) and mixing forces (turbulence) (Boehrer and Schultze, 2008). During stratification the water column has been conceptualised as having three distinct layers (Figure 2.2). The upper layer directly in contact with the atmosphere is the epilimnion, or mixed layer, which is traditionally defined as being isopycnal (isothermal) with relatively uniform mixing rates (Robertson and Imberger, 1994). The metalimnion lies below the epilimnion and is characterised by a steep density (temperature) gradient called the pynocline (thermocline). The bottom layer of the water column, the hypolimnion, is directly in contact with the lake bed and is the densest (coolest) layer (Figure 2.2). The strength of stratification weakens as the lake loses heat and the number of wind events increases until turbulent forces dominate resulting in full water column mixing (Churchill and Kerfoot, 2007).

There are different types of thermal stratification, with lakes around the world having different mixing patterns, determined by climate and lake morphometry. The frequency in which lakes stratify and mix has been classified, first by Hutchinson (1956) and revised later by Lewis (1983) to create eight mixing regimes (amictic, cold monomictic, continuous cold polymictic, discontinuous cold polymictic, dimictic, warm monomictic, discontinuous warm polymictic and continuous warm polymictic) (Table 2.1).

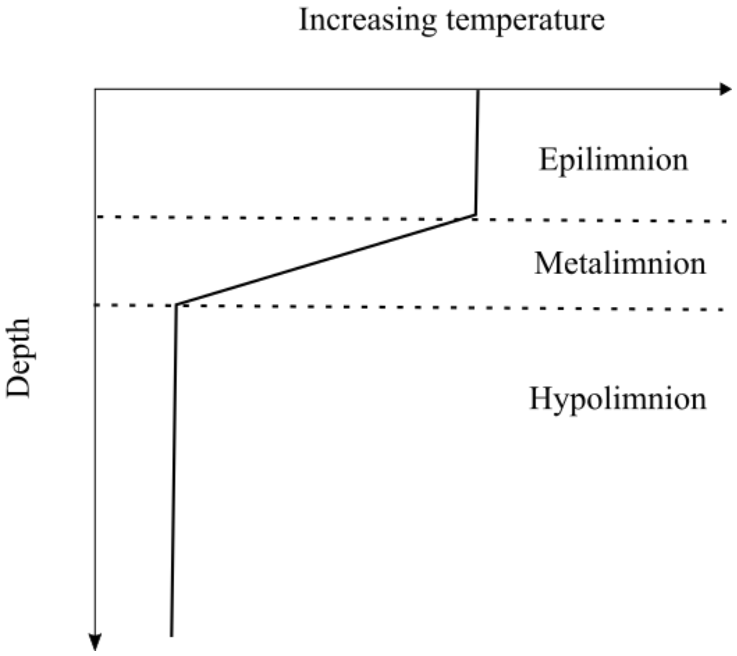


Figure 2.2 Diagram showing the conceptual temperature profile of a lake during the stratified period including an isothermal epilimnion, a metalimnion marked by a steep gradient of decreasing temperature and a cool isothermal hypolimnion.

Table 2.1 Types of lake mixing regime with examples (Lewis, 1983)

Mixing Regime	Frequency	Description	Lake example
Amictic	Never mixes	Permanently ice covered lakes which are rare and confined to the Antarctic. These lakes have a permanent inverse stratification.	Fryxell, Antarctic (Smith *et al.*, 1993)
Cold monomictic	Mixes once	Ice covered for most of the year but mix in ice free periods in summer. Temperatures remain below 4°C.	Char, Canada (Schindler, 1974)
Continuous cold polymictic	Mixes many times	Ice covered for part of the year, ice free above 4°C in warm periods and stratify on a daily basis in warm season.	Smokey Hollow , Canada (Harvey and Coombs, 1971)
Discontinuous cold polymictic	Mixes many times irregularly	Ice covered some of the year, ice free above 4°C and stratified in warm periods but this is interrupted by mixing events.	Tobacco, Canada (Harvey and Coombs, 1971)
Dimictic	Mixes twice	Inverse stratification during ice covered periods and stable stratification in warmer periods with mixing occurring between the two periods.	Baikal, Russia (Hutchinson, 1957)
Warm monomictic	Mixes once	Has stable stratification once a year and mixes once a year (no ice cover).	Windermere, UK (Jenkin, 1942)
Discontinuous warm polymictic	Mixes more than once irregularly	Mixes and stratifies irregularly.	Leven, UK (Bindloss, 1974)
Continuous warm polymictic	Mixes more than once	Stratifies and mixes for a few hours at a time.	Sonachi, Kenya (MacIntyre and Melack, 1982)

2.2.3 Surface mixing

During the stratified period the depth of surface mixing will change according to meteorological drivers. Wind blowing over the surface of a lake generates an area of shear stress at the water surface which results in surface waves and the transfer of energy from the atmosphere to the lake resulting in turbulent mixing (Wetzel, 2001). The depth of surface mixing will therefore depend on the wind speed and the resistance of the lake to mixing forces due to density gradients. Lake surface area and fetch are strongly related to the wind speed that lakes experience, with lakes with a larger surface area and fetch generally experiencing higher wind speeds and therefore tend to have deeper surface mixed depths (Spigel and Imberger, 1980; Gorham and Boyce, 1989; Oswald and Rouse, 2004).

Any factors that modify wind speed can therefore influence the depth of surface mixing. Wind sheltering by surrounding forests is important for small lakes as the increased surface roughness provided by the tree canopy reduces wind speeds before they reach open water (Venäläinen *et al.*, 1998). Deforestation on lake shorelines can therefore have a significant effect on lake water temperatures and the wind received by the lake surface (France, 1997; Steedman *et al.*, 1998). The removal of trees from the shorelines of selected Canadian Shield lakes resulted in higher daytime and lower night time shoreline water temperatures in comparison to nearby forested lake shorelines (Steedman *et al.*, 1998). Furthermore, reduced sheltering from shoreline trees in lakes in north-western

Ontario, Canada resulted in a tripling of the wind speed above the lake surface and thermocline deepening (France, 1997).

Wind blowing across the surface of lakes can also induce internal waves as surface water pushed downwind results in the tilting of the thermocline (Shintani *et al.*, 2010). Thermocline tilting causes a storage of energy at the downwind end of the lake which is compensated by an internal wave (seiching) along the thermocline boundary and upwelling of cool hypolimnetic water at the upwind end (Shintani *et al.*, 2010). This wave causes turbulence and redistributes energy to the rest of lake with the extent of the thermocline tilt determining the amount of energy available to mix the water column (Shintani *et al.*, 2010).

Convection is another important source of mixing and is driven by temperature differences between the air and water surface (Gunkel and Casallas, 2002; MacIntyre *et al.*, 2002; Heiskanen *et al.*, 2015). During periods of lower air temperatures, water at the surface of the lake will cool and will therefore become dense and sink, in its place warm buoyant water will rise to the surface, resulting in a mixing cycle. When the cool dense water sinks it can sometimes reach the metalimnion and can therefore deepen the surface mixed later (MacIntyre *et al.*, 1999). It has been suggested that convective cooling may be more important than wind mixing in tropical lakes, for example Macintyre *et al.*, (2002) found that over 70% of the energy for surface layer deepening in an embayment in Lake Victoria, resulted from convective heat losses for the majority of the time (82% of instances). Further to this, Gunkel and Casallas, (2002) found that nocturnal cooling by convection currents were a source of heat loss and partial lake destratification for Lago San Pablo, Ecuador. In this case convective cooling may be more important than wind mixing during the evening due to significant decreases in air temperature at night creating a greater difference between the lake surface water temperature and the air temperature (MacIntyre *et al.*, 2002). Convection can also be an important mixing mechanism in small sheltered lakes which are exposed to low wind speeds (Heiskanen *et al.*, 2014).

2.2.4 Defining the depth of surface mixing

The surface mixed layer of a lake (also known as the mixed depth or epilimnion), is a physical concept referring to the depth of homogenous active turbulence at the surface of a lake (Robertson and Imberger, 1994). The mixed depth concept is commonly associated with a number of features and assumptions: (1) it is isopycnal (or isothermal); (2) mixing rates are relatively homogenous and (3) the distribution of particles are relatively homogenous. This concept is used ubiquitously in limnology due to the importance of surface mixing for physical, chemical and ecological processes. The most accurate way to determine the depth of mixing is to measure turbulence directly using microprofilers such as a Self Contained Autonomous Micro-Profiler (SCAMP) (Folkard *et al.*, 2007) or an Acoustic Doppler Current Profiler (ADCP) (Woolway and Simpson, 2017). Turbulence is not, however, routinely measured within lakes therefore a variety of alternative techniques have been developed to estimate the mixed depth. These include: temperature (Coloso *et al.*, 2008) or density gradients (Staehr *et al.*, 2012), temperature (Wilhelm and Adrian, 2007), or density differences (Winder *et al.*, 2009), turbulence thresholds (MacIntyre *et al.*, 1999, 2009), and isotopic (Imboden *et al.*, 1983) or chemical tracers (Maiss *et al.*, 1994). In oceanographic studies further methods have been developed to estimate the mixed depth including using buoyancy frequency (Carvalho *et* *al.*, 2017) and statistical methods such as the maximum angle technique (Chu and Fan, 2011).

The widespread routine measurement of water column temperatures means that temperature or density values are most commonly used to estimate the mixed depth with methods falling into two categories: (1) using a threshold of density or temperature change from the surface or (2) using a threshold gradient of change in density or temperature. Studies of oceanographic profiles suggest that gradient thresholds are more susceptible to anomalous changes in temperature or density and therefore require highly resolved vertical profile measurements (Brainerd and Gregg, 1995; Thomson and Fine, 2003; Dong *et al.*, 2008). Threshold changes in temperature or density from the surface therefore provide a more stable means of estimating the mixed depth, particularly if vertical profiles are of a low resolution (Brainerd and Gregg, 1995; Thomson and Fine, 2003).

The mixed depth concept has a number of caveats. In the first instance, there is no universal method for estimating the mixed depth with a range of temperature and density thresholds and gradients currently being used in the literature. Examples of these include: 0.2 ^{o}C (Yang *et al.*, 2018), 1 ^{o}C (Mackay *et al.*, 2011), or 0.8 ^{o}C (Zhao *et al.*, 2018) change in temperature from the surface; a 0.1 kg m^{-3} (Andersen *et al.*, 2017) change in density from the surface; a 1 °C m^{-1} (Kasprzak *et al.*, 2017), 0.5 ^{o}C m^{-1} (Yankova *et al.*, 2016) or 0.25 ^{o}C m^{-1} (Özkundakci *et al.*, 2011) temperature gradient; or a 0.07 kg m^{-3} m^{-1} (Staehr *et al.*, 2012), 0.03 kg m^{-3} m^{-1} (Tonetta *et al.*, 2016) or 0.5 kg m^{-3} m^{-1} (Lamont *et al.*, 2004) density gradient. Studies have also used the depth of the maximum temperature or density gradient to define the depth of the mixed layer (e.g. Wilhelm and Adrian, 2007), which is incorrect as this includes portions of the metalimnion where density (or temperature) changes rapidly which inhibits the fluxes of variables of interest. It is unclear whether a universal method should be adopted in order to aid cross-comparison between lakes (e.g. Woolway *et al*., 2016) or whether the definition should be adapted to each individual lake (e.g. Giling, Staehr *et al*., 2017). There is also a lack of guidance in the literature on how researchers should choose the arbitrary threshold or gradient of change from the surface for their studies.

The assumption of homogenous mixing within the mixed layer is also flawed as mixing rates within isopycnal (or isothermal) regions are not homogenous. When temperature measurements have been compared with mixing rates it has been found that the actively mixed region is substantially shallower than the isothermal layer (MacIntyre, 1993; Brainerd and Gregg, 1995; Tedford *et al.*, 2014). Direct measurements of turbulence show that mixing rates can differ with temperature differences as little as 0.02 ^{o}C (MacIntyre, 1993) which is below the accuracy of some temperature sensors. Based on these findings the surface mixed layer or epilimnion can be subdivided into an actively mixed upper layer and a region below which is defined by the depth of recent or potential mixing (Brainerd and Gregg, 1995) (Figure 2.3).

Commonly, lake temperature data are measured at 0.5 m or 1 m intervals or less and the accuracy of the temperature sensors are usually 0.1-0.2 ^{o}C. Therefore, mixed depths calculated using temperature or density differences or gradients do not capture the actively mixed upper layer but rather the depth of recent or potential mixing. This means that when the mixed depth is defined in this way one of the underlying assumptions of the mixed depth, that there is a homogenous distribution of particles within the mixed layer, cannot be assumed. This is not universally recognised and introduces a point of confusion when relating the depth of recent mixing to changes in ecological and chemical variables both within limnology and oceanography (Carranza *et al.*, 2018). Measuring temperature at a coarse resolution of 0.5 m or 1 m may also be insufficient to accurately determine the depth of recent mixing as the thermocline is often a sharp boundary which may not be adequately captured at this resolution.

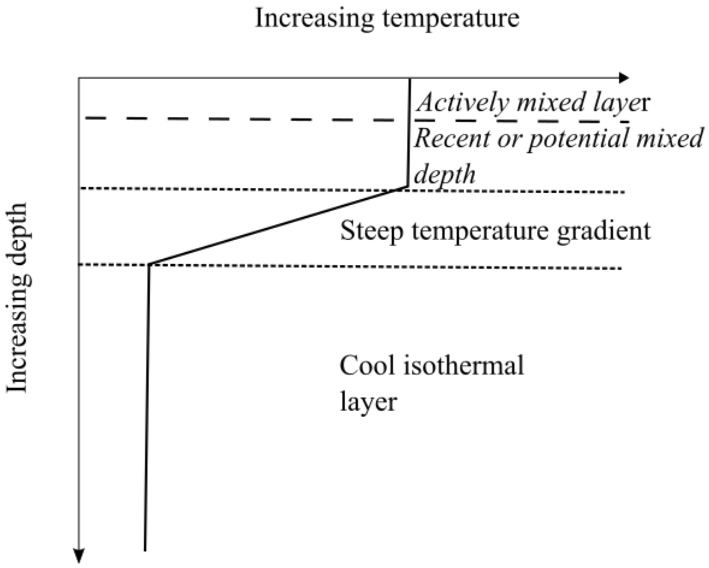


Figure 2.3 A modified version of Figure 2.2 showing the epilimnion being split into an upper actively mixing layer and the depth of recent mixing as marked by the isothermal layer.

2.3 Vertical distribution of resources for phytoplankton growth

The depth of light penetration and the physical structure of a lake has important controls on chemical and ecological processes resulting in vertical gradients of nutrients and light. Shifts in the depth of surface mixing and changes in seasonal stratification can therefore have significant impacts on the vertical structuring and composition of the phytoplankton community.

2.3.1 Light

Photosynthesis depends on the interception and absorption of photons. The amount of photosynthetically active radiation (PAR; wavelengths 400-700 nm) reaching a phytoplankton cell depends on fluctuations in solar radiation reaching the surface of the lake as well as surface waves, water clarity and the depth of surface mixing (Kirk, 1994). Incoming radiation that is not reflected at the surface can be absorbed or scattered by water molecules and suspended particles (Kirk, 1994). Light declines steeply and exponentially with increasing depth and can be approximated using the extinction coefficient (Kirk, 1994).

Lakes also contain a number of dissolved and suspended particles which also impact the extinction coefficient, including dissolved humic substances, inorganic particulate matter (tripton) and phytoplankton (Kirk, 1994; Carpenter *et al.*, 1998; Nürnberg and Shaw, 1998). The concentration of humic substances and particulate matter in a lake will depend on the catchment land use and the underlying geology. Nutrient rich lakes are more likely to support a higher phytoplankton biomass where a proportion of light will be absorbed by photosynthetic pigments and prevented from reaching deeper depths in the water column (Kirk, 1994).

2.3.2 Nutrients

Nutrients can be sourced allochthonously from catchment runoff or autochthonously during within-lake biogeochemical processes. The availability of nutrients within lake systems determines the amount of phytoplankton biomass a lake can support. The ratio of nutrients required for phytoplankton growth differs with taxa (Klausmeier *et al.*, 2008), but phytoplankton principally require carbon, nitrogen and phosphorus (along with trace elements); silica is also a necessity for Bacillariophyta (Reynolds, 2006).

Phosphorus can be sourced naturally through the weathering of rocks. Inputs into the lake will therefore vary with catchment geology. Small amounts of phosphorus are also contained in rainfall (Kalff, 2002). Phosphorus is readily available to phytoplankton in dissolved form as orthophosphate (soluble reactive phosphorus or SRP). Particulate phosphorus can also be made bioavailable if they are transformed into a soluble form (Kalff, 2002). Despite the abundance of nitrogen gas in the atmosphere, nitrogen cannot be obtained readily by most phytoplankton due to its inertness (nitrogen fixing cyanobacteria are the exception to this) (Reynolds, 2006) but the deposition of reactive nitrogen from the atmosphere has increased with the burning of fossil fuels (Elser *et al.*, 2009). Nitrogen is also relatively scarce within the earth’s crust, therefore the main sources of nitrogen are via runoff or internal recycling (Kalff, 2002). Dissolved inorganic nitrogen comprising of nitrate (NO_3^-), nitrite (NO_2^-) and ammonia (NH_4^+) are bioavailable to phytoplankton. Silica is abundant in the earth’s crust, but it is relatively unreactive and often forms compounds with oxygen, aluminium, potassium and hydrogen (Reynolds, 2006). Hydrolysis of silicates can occur during weathering, forming monosilicic acid which is bioavailable to Bacillariophyta (Reynolds, 2006).

The nutrient budgets of many lakes have been considerably modified by anthropogenic activities leading to the eutrophication of many lake systems (e.g.Vollenweider, 1970; Smith, Joye and Howarth, 2006; Moss, 2011; Battarbee *et al*., 2012; McGowan *et al*., 2012). Agriculture and urbanisation have significantly increased the concentrations of nitrogen and phosphorus being delivered into lake systems (Daniel *et al.*, 1998; Jeppesen *et al.*, 2009). This has occurred diffusely through the catchment erosion of agricultural soils containing fertilizer and manure, and through runoff from urban areas (Whitehead *et al.*, 2009). Phosphorus and nitrogen can also enter the system directly via sewage wastewater treatment works or industrial waste which can become concentrated at times of low flow (Whitehead *et al.*, 2009).

A significant amount of phosphorus, nitrogen and silica are stored in lake sediments due to the accumulation of sinking organic and inorganic matter. Nitrogen and phosphorus can therefore be re-released back into the water column via internal loading. This means that eutrophication can continue to have negative consequences on the system even if external sources of nutrients have been reduced (Jarvie *et al.*, 2013; Sharpley *et al.*, 2013). During stratification the hypolimnion is isolated from the atmosphere and the respiration of microbes during the decomposition of organic matter results in oxygen depletion and eventually anoxia. Phosphorus is bound to ferric iron oxyhydroxides ($FeOOHPO_4$) and during anoxic conditions sulphide (S^{2-}) reacts with iron to form iron sulphide and dissolved sulphide which is thought to release phosphorus from the compound (Kalff, 2002). Under oxic conditions microbial respiration can release phosphorus into the overlying water, but microbes can also reduce phosphorus release by oxidising organic matter using NO_3^- and SO_4^- as electron acceptors. A high pH during oxic conditions can also induce the release of phosphorus from FEOOH compounds as it is replaced by OH^-. The biggest source of NH_4^+ is from the breakdown and mineralisation of organic matter in the sediments under aerobic and anaerobic conditions (Kalff, 2002). During oxic conditions NH_4^+ is oxidised to NO_3^-. Nitrogen can then be lost to the system by the reduction of NO_2^- and NO_3^- to NO and N_2O and then finally to N_2 gas (Kalff, 2002). When Bacillariophyta sink through the water column a small proportion of monosilicic acid can be re-released but the silica frustules from Bacillariophyta remain largely intact when they reach the sediments (Reynolds, 2006).

2.4 Phytoplankton

Phytoplankton contribute 1-2 % of global plant carbon (Falkowski, 1994) but they are responsible for 40-50 % of global net primary production (Falkowski, 1994; Basu and Mackey, 2018) and are therefore an important component of global biogeochemical cycles. Phytoplankton are a primary source of energy for pelagic lake food webs and have important controls on water quality. Phytoplankton are morphologically, phylogenetically and functionally diverse with size classes differing by orders of magnitude (0.2 µm to > 2 mm) (Reynolds, 2006). This means phytoplankton species are non-uniform in their resource requirements with different species being adapted to different environmental conditions.

2.4.1 Morphology and motility

Phytoplankton species have different morphologies (Reynolds *et al.*, 2002; Naselli-Flores *et al.*, 2007; Kruk *et al.*, 2010; Naselli-Flores and Barone, 2011), sinking rates (Reynolds, 1994; Huisman *et al.*, 2001, 2002; Padisák, Soróczki-Pintér, *et al.*, 2003) and levels of motility (Naselli-Flores *et al.*, 2007; Kruk *et al.*, 2010). Phytoplankton can be broadly categorised as non-motile and negatively buoyant, neutrally buoyant and motile (Reynolds, 2006). Extrinsic features such as mucilage, spines and cilia can reduce sinking rates by increasing friction, and flagella can allow directed movement (Reynolds, 2006). The composition of phytoplankton cells typically make them denser than water, though oils and lipids can increase buoyancy (Reynolds, 2006). Non-motile negatively buoyant species with rigid outer walls and a spherical shape will fall through the water column according to Stokes Law, where the sinking velocity is dependent on the size of the particle, gravity and the viscosity of the fluid (Reynolds, 2006). Many negatively buoyant phytoplankton, however, are not spherical and can be prolate, disc shaped or oblate, for example. These shapes maximise the surface area to volume ratio thereby increasing the frictional drag and reducing the sinking rates. Colonial phytoplankton cells can be held within mucilage which can slow sinking rates as long as the reduction in density outweighs the increase in size (Reynolds, 2006).

Motile species can move using one or more flagella or by regulating buoyancy. Larger phytoplankton species for example dinoflagellates such as *Ceratium* and *Peridinium* require flagella to prevent them from sinking and have faster movement rates in comparison to smaller flagellated species (Reynolds, 2006; Ross and Sharples, 2008; Durham *et al.*, 2013). This ability can lead to the vertical heterogeneity of flagellate distribution which can enable daily migration or rapid responses to changes in mixing (Bergström *et al.*, 2003; Clegg *et al.*, 2007).

Some species of cyanobacteria can lower their density as they contain gas filled vesicles, which allow them to float to the surface and maintain their position in a favourable light climate (Walsby, 1975; Reynolds *et al.*, 1987). Buoyancy can be regulated via a number of mechanisms. One way is through growth, if buoyancy is to be maintained the resource allocation to gas vesicle production needs to keep pace with growth, whereas if a reduction in buoyancy is required gas vesicles can be diluted out by directing cell resources elsewhere (Walsby, 1975, 1992). In other taxa, such as *Dolichospermum*, cells float to the surface to high light intensities which allow them to photosynthesise rapidly which raises the turgor pressure and eventually results in the collapse of the vesicles (Reynolds, 2006). An alternative buoyancy regulation mechanism used by *Microcystis* is to regulate the production of glycogen (heavy molecule) (Chu *et al.*, 2007). A higher production results in downward movement and a reduction in production results in a neutral or upward motion (Chu *et al.*, 2007). The ability to regulate buoyancy can lead to the formation of problematic surface blooms by species such as *Dolichospermum* (Salmaso, 2000; Salmaso *et al.*, 2015; Recknagel *et al.*, 2016) and *Microcystis* (Ibelings *et al.*, 1991; Chu *et al.*, 2007; Yang and Jin, 2008). Narrow bands of cyanobacteria species such as *Planktothrix* can also accumulate at depth (Jacquet *et al.*, 2005; Ernst *et al.*, 2009; Dokulil and Teubner, 2012; Wentzky *et al.*, 2019).

2.4.2 Classifying phytoplankton

There are thousands of freshwater phytoplankton species, therefore predicting the responses of individual phytoplankton species to environmental change is difficult (Benincà *et al*., 2008). By grouping phytoplankton in terms of their phylogenetic groups it is thought that important ecological differences will be expressed (Webb *et al*., 2002) (Table 2.2). Species within phylogenetic groups, however, often respond in different ways to changing physical drivers owing to the diversity of morphologies and traits (Salmaso *et al.*, 2012). This led to the development of morpho-functional classification techniques (Reynolds, 1984; Kruk *et al.*, 2002, 2010, 2011; Reynolds *et al.*, 2002), which are thought to better explain phytoplankton responses to environmental change. This was supported by a comparison of taxonomic and functional groupings by Kruk *et al*., (2002) who found that functional classifications had a higher discriminatory power.

Table 2.2 Phylogenetic groups (some are non-planktonic) (Cox and Shubert, 2016).

Phylogenetic Group	Description
Bacillariophyta	Eukaryotic Autotrophic Unicellular or colonial Generally non-motile but can be motile Possess turgor resisting walls consisting of organic and siliceous components (siliceous valves)
Charophyta	Eukaryotic Autotrophic Unicellular or colonial Motile or non-motile Cellulose cell walls
Chlorophyta	Eukaryotic Autotrophic Unicellular or colonial Motile or non-motile Cellulose cell walls
Cryptophyta	Eukaryotic Autotrophic Unicellular Motile (2 flagella of slightly unequal length) No cell wall but proteinaceous plates
Cyanobacteria	Prokaryotic Autotrophic Colonial or unicellular Buoyancy regulating Cell wall like bacteria (4 layers)
Euglenozoa	Eukaryotic Around 66 % are heterotrophic Unicellular or colonial Motile (usually 2 flagella 1 shorter than the other) Cell walls lacking
Haptophyta	Eukaryotic Autotrophs Unicellular Motile or non-motile Some produce calcium carbonate scales
Miozoa	Eukaryotic Some are heterotrophic Unicellular Motile (2 dissimilar flagellates) Plated surface
Ochrophyta	Eukaryotic Autotrophs Unicellular Motile (2 differing flagella 1 with hairs) Cell coverings include siliceous scales

One alternative to phylogenetic groupings is to classify phytoplankton according to their functional traits such as the ability to acquire nutrients and light, susceptibility to grazing and sinking velocities (Litchman and Klausmeier, 2008). An example of this is the 31 groups developed by Reynolds *et al.*, (2002) which was based on the typical habitats of species as well as tolerances and sensitivities for light, nutrients, flushing, stratification and pH. This method of grouping, however, requires specialist knowledge of these specific requirements for individual species. This information is difficult to obtain and unknown for many species making it difficult to apply this system (Reynolds *et al.*, 2002; Salmaso and Padisák, 2007; Naselli-Flores and Barone, 2011; Salmaso *et al.*, 2015). Phytoplankton morphology is strongly related to phytoplankton function. Size and morphology characteristics such as the maximum linear dimension and surface area are more obtainable and directly measurable compared to identifying specific phytoplankton traits (Reynolds, 2006; Kruk *et al.*, 2010). One example of this is the CSR method, which is based on the relationship between phytoplankton morphology and function (Reynolds, 2006). Using the maximum linear dimension, volume and surface area of phytoplankton cells, species can be grouped into categories (summarised in Table 2.3). Some species express intermediate characteristics such as CS strategists which have morphologies and traits spanning the separate C and S group. CS strategists include *Dinobryon*, *Eudorina* and *Dictyosphaerium* (Reynolds, 2006).

Table 2.3 Characteristics of the three functional groups of phytoplankton groups according to Reynolds (2006).

Strategist	Description	Representative species
C 'Competitors'	'Invasive opportunists' Mostly unicellular Low growth thresholds for light Low sinking rates Susceptible to grazing	*Chlorella*, *Chlamydomonas*, *Rhodomonas*
R 'Ruderals'	'Attuning or acclimating' A mix of colonial and unicellular phytoplankton Very low growth threshold for light Most are non motile (sinking rates variable) Some species are susceptible to grazing	*Asterionella* *Aulacoseira* *Planktothrix*
S 'Stress tolerant'	'Acquisitive' A mix of colonial and unicellular phytoplankton Mostly motile Can exploit alternative resources e.g. nitrogen fixation or mixotrophy (can obtain carbon via phagotrophy or particulate organic matter as well as via photosynthesis)	*Dolichospermum* *Ceratium* *Uroglena*

2.4.3 Mixing vs sinking

Nutrients and light are vertically heterogeneous, the light and nutrient climate that phytoplankton experience therefore depends on the depth of surface mixing. Vertically, there are narrow bands of space that are suitable for phytoplankton growth with the suitable space fluctuating with changes in physical drivers. This led to the development of the “critical depth” hypothesis whereby phytoplankton growth can only be maintained if the surface mixed layer is shallower than some critical depth (Sverdrup, 1953; Figure 2.4). This theory suggested that if mixing was sufficiently shallow then the light conditions will be favourable for photosynthesis and therefore phytoplankton growth can be maintained. This did not explain, however, how phytoplankton blooms can form in the absence of stratification or during times of weak stratification which led to the idea of “critical turbulence” (Huisman *et al.*, 1999; Huisman and Sommeijer, 2002; Huisman *et al.*, 2002). If turbulent mixing was less than a critical value then phytoplankton populations can be maintained as growth exceeds sinking losses (Huisman *et al.*, 1999; Huisman and Sommeijer, 2002; Huisman *et al.*, 2002; Figure 2.4).

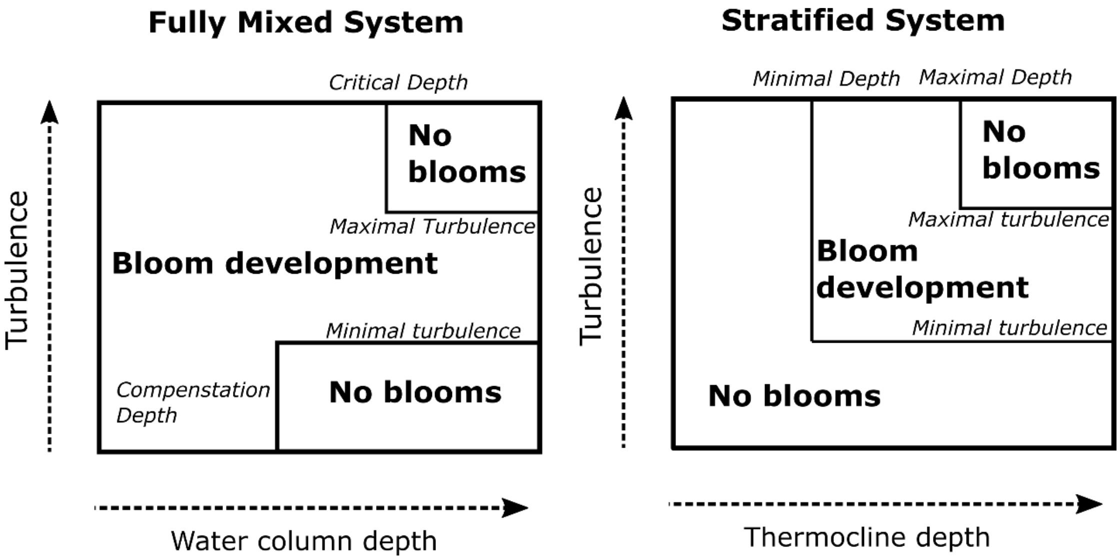


Figure 2.4 The conceptual idea of critical depth and critical turbulence for sinking phytoplankton in fully mixed and stratified systems according to Huisman et al., (2002).

Phytoplankton are subject to continuous turbulent mixing which can push phytoplankton towards or away from favourable light or nutrient levels (Huisman *et al.*, 1999; Huisman and Sommeijer, 2002; Huisman *et al.*, 2002). In a fully mixed water column individuals will be roughly exposed to the same fluctuations in nutrients and light. The depth of surface mixing, however, changes seasonally and in response to weather variations. Deeper mixed layers can create a lower light environment, reduce sinking losses and increase nutrient availability, whereas shallow mixed layers provide light enrichment but have high sinking losses and reduce nutrient availability (Diehl *et al*., 2002; Diehl, 2002; Berger *et al*., 2006). Shifts in the depth of surface mixing can therefore result in large community shifts. An artificial mixing experiment found that at time of low mixing the community became dominated by flagellates and times of high mixing pennate diatoms dominated (Jäger *et al.*, 2008). Low turbulence enclosures also demonstrated vertical niche partitioning (Jäger *et al.*, 2008). Phytoplankton with high sinking velocities such as diatoms and chlorophytes that are adapted to low light conditions, tend to dominate in deeper layers whereas buoyant or motile phytoplankton (buoyant cyanobacteria and flagellates) often dominate in shallow mixed layers (Reynolds *et al.*, 1983; Visser *et al.*, 1996; Ptacnik *et al.*, 2003; Jäger *et al.*, 2008). The turbidity of the water column influences the type of phytoplankton that lakes can sustain (Huisman and Sommeijer, 2002). Clear waters are able to sustain phytoplankton with high sinking rates and turbid waters are only able to sustain phytoplankton with low sinking rates.

The depth of mixing (which determines light and nutrient availability) in relation to the euphotic depth controls the vertical distribution of phytoplankton (Ross and Sharples, 2008; Longhi and Beisner, 2009) (Figure 2.5). Phytoplankton can aggregate in thin layers at the surface (typically buoyant cyanobacteria), at depth forming a deep chlorophyll maximum (DCM, chlorophyll being a proxy for phytoplankton biomass), or at the sediment surface (Litchman and Klausmeier, 2001; Mellard *et al.*, 2011). Phytoplankton can also be homogenously mixed in the epilimnion. Deep chlorophyll maxima form due to the balance between light availability, surface mixing and nutrient availability (Hamilton *et al.*, 2010; Leach *et al.*, 2018). In clear water oligotrophic lakes, light can penetrate to deeper depths compared with turbid or eutrophic systems, therefore phytoplankton may aggregate at depths where nutrient availability is generally higher (Hamilton *et al.*, 2010; Mellard *et al.*, 2011; Leach *et al.*, 2018). At times of low mixing, neutrally buoyant cells may rise or sink to the depth of neutral buoyancy, alternatively motile phytoplankton or phytoplankton with the ability to regulate buoyancy may position themselves at a depth with higher nutrient availability (Reynolds, 2006). For example, the low light adapted cyanobacteria *Planktothrix* is often associated with DCM in deep lakes (Reynolds *et al.*, 1983; Nürnberg *et al.*, 2003; Selmeczy *et al.*, 2018). Sub-surface maxima can also occur in eutrophic systems, particularly when the depth of surface mixing is shallower than the euphotic depth (Simmonds *et al.*, 2015; Brentrup *et al.*, 2016; Leach *et al.*, 2018).

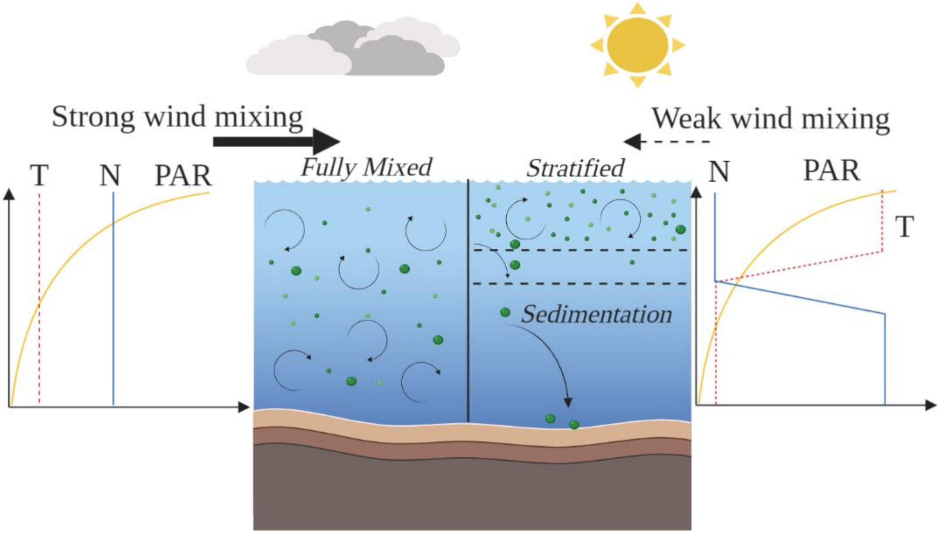


Figure 2.5 Schematic of fully mixed and stratified system. T is temperature (red), N is nutrients (blue) and PAR is photosythetically active radiation (yellow) adapted from Ross and Sharples, (2008).

2.4.4 Phytoplankton interactions with lake physics

Phytoplankton can also modify the physical environment of a lake through a number of positive feedback mechanisms (Kahru *et al.*, 1993; Kumagai *et al.*, 2000; Ibelings *et al.*, 2003; Jones *et al.*, 2005; Rinke *et al.*, 2010). Increased absorption of heat in the surface mixed layer can lead to mixed depth shallowing and increased heat loss (Jones *et al.*, 2005). A limnetic enclosure experiment in Blelham Tarn, UK, found that increases in absorption of solar radiation by phytoplankton in surface waters increased the surface water temperature resulting in the emittance of long wave radiation and sensible heat from the lake to the atmosphere (Jones *et al.*, 2005). Water temperatures in areas covered by surface cyanobacteria blooms are often higher compared to surrounding bloom free waters due to the absorption of light energy by photosynthetic pigments (Paerl *et al.*, 1985; Kahru *et al.*, 1993; Ibelings *et al.*, 2003). This was demonstrated by a mesocosm experiment which found that blooms of *Microcystis* and *Dolichospermum* reduced the depth of surface mixing and enhanced stratification strength, which in turn helped them out compete other species (Kumagai *et al.*, 2000).

2.4.5 Seasonal succession

Studies of eutrophic, monomictic temperate lakes have found that phytoplankton typically follow a seasonal change in community composition due to changes in light, nutrients and thermal stratification (Lund, 1965). The spring phytoplankton bloom is triggered by changes in temperature and light and in deep lakes this usually coincides with the onset of thermal stratification (Salmaso, 2000; Winder and Schindler, 2004; Reynolds, 2006). Although diatom blooms can sometimes occur prior to the onset of stratification (Bartone and Schelske, 1982). During the spring bloom low light adapted diatom species dominate, with light availability being the main factor determining the replication rates (Reynolds, 2006). The diatom population tends to rapidly decrease due to silica depletion and may be replaced by small fast-growing flagellates (C strategists) in the first instance followed by colonial chlorophytes (CS strategists). In summer, as stratification strengthens, slower growing S strategists tend to dominate. As stratification strength begins to weaken in late summer, dominance may then switch back to diatoms (R strategists) or flagellates (CS or C strategists) (Reynolds, 1976, 1988, 2006). This pattern is a generalisation, with the timing and exact composition varying annually in response to meteorological events and nutrient availability.

2.5 Climate Change

Increased emissions of greenhouse gasses since the industrial revolution is resulting in a net uptake of energy by the climate system. More than half of the observed global average temperature increase 1951-2010 is attributed to the increase in anthropogenic greenhouse gas emissions (IPCC, 2013). Combined land and ocean surface temperatures have increased by 0.85 ^{o}C on average (0.65-1.06 ^{o}C) globally between 1880-2012 (IPCC, 2013). Temperatures are expected to continue to increase under most regional climate projections and are likely to exceed +1.5 ^{o}C by the end of the 21st century compared to 1850-1900 (IPCC, 2013). In addition to this long term warming trend, changes in extreme climate events have been observed since 1950 (IPCC, 2013). The frequency of heatwaves in Europe, Asia and Australia appears to have increased and the number of heavy precipitation events in North America and Europe also appear to be increasing (IPCC, 2013). Lakes and climate are closely coupled so these climatic changes have the potential to profoundly impact physical, chemical and ecological processes within lake ecosystems, with significant changes being detectable within long term monitoring records of lakes around the world (e.g. Maberly and Elliott, 2012; O'Reilly *et al.*, 2015).

2.5.1 Physical impacts of long term climatic change

2.5.1.1 Increases in water temperature

Many lakes are experiencing increases in surface water temperature (Adrian *et al.*, 2009; Schneider and Hook, 2010; O'Reilly *et al.*, 2015; Sharma *et al.*, 2015). The average rate of warming is variable globally and inconsistent regionally, with some lakes exhibiting a cooling trend (O'Reilly *et al.*, 2015). This variability is due to interactions between climate and individual lake characteristics (Butcher *et al.*, 2015; Kraemer *et al.*, 2015;

Winslow *et al*., 2015, 2017; Woolway *et al*., 2016). Deep lakes and lakes with high average water temperatures appear to be responding more significantly to climatic change even though the rate of warming they experience is generally slower (Kraemer *et al.*, 2015). Increases in summer surface water temperatures have also been found to be amplified in deep and cold lakes (Woolway and Merchant, 2017). In contrast, Torbick *et al*., (2016) found that small lakes were warming more rapidly than larger lakes in the north-eastern United States.

In small lakes (<0.5 km^2) warming is restricted to surface waters, whereas large lakes (>0.5 km^2) also experience deepwater warming (Winslow *et al.*, 2015). This difference has been attributed to the sheltering of small lakes which reduces turbulent wind mixing and therefore contains warming close to the surface (Winslow *et al.*, 2015). Increases in lake surface water temperatures are also spatially variable within large lakes. Water clarity also determines the vertical distribution of heat in the water column and therefore the vertical extent of warming (Persson and Jones, 2008; Butcher *et al.*, 2015; Richardson *et al.*, 2017; Ptak *et al.*, 2018). Increases in water clarity can induce deep water warming (Stefan *et al.*, 1996; Butcher *et al.*, 2015), whereas increases in turbidity can prevent light penetrating to deeper waters due to increased heat absorption at the surface (Hocking and Straškraba, 1999; Butcher *et al.*, 2015; Heiskanen *et al.*, 2015; Richardson *et al.*, 2017). The impact of this on summer surface water temperatures will also depend on cooling induced by the entrainment of cold hypolimnetic water (Persson and Jones, 2008).

Climatically induced water warming rates are also temporally heterogeneous, differing on seasonal and sub-seasonal timescales (Carvalho and Kirika, 2003; Winslow *et al*., 2017; Woolway *et al*., 2017). Much of the previous research into increasing lake water temperatures have focussed on summer warming rates (Schneider and Hook, 2010; O'Reilly *et al.*, 2015), but there is increasing evidence that this is insufficient for understanding annual and global heating trends (Winslow *et al.*, 2017; Woolway *et al.*, 2017). Carvalho and Kirika (2003) for example, found that winter and spring water temperature increases in Loch Leven, Scotland were higher than annual mean increases. Lakes elsewhere in the UK and Ireland have also been found to be warming most in winter (Woolway *et al.*, 2016). Central European lakes are generally warming most in spring (Dokulil, 2014; Schmid and Köster, 2016; Woolway *et al.*, 2017), whereas a study of a small mountain lake (Piburger See, Austria) found that significant warming only occurred between August-December at all lake depths (Niedrist *et al.*, 2018). In contrast, Lake Superior, North America is warming most in the summer season (Austin and Colman, 2008). Analysis of monthly surface water temperature warming rates in lakes situated in Wisconsin, USA found that temperature increased at the highest rate in September and October (Winslow *et al.*, 2017).

2.5.1.2 Changes to lake stratfication and mixing

Long term changes in water temperature are impacting the stratification and mixing regime of lakes (Kraemer *et al.*, 2015; Woolway and Merchant, 2019). Given the spatial and temporal intricacy of the warming trends, the changes in lake stratification as a result of climatic warming are complicated. The lack of regional consistency in the response of lakes to warming means that average warming rates are an unreliable predictor for changes in stratification, but rather lake morphometry and the average temperature of lakes should be taken into account (Kraemer *et al.*, 2015).

Analysis of long term lake water temperature data has demonstrated that many lakes are experiencing an increase in the strength and length of stratification. Much of the previous research has focussed on the advancement of the onset of stratification in spring rather than the delay in overturn in autumn, which may be partly due to the higher warning rate in spring in many regions (Carvalho and Kirika, 2003; Dokulil, 2014; Schmid and Köster, 2016; Woolway *et al*., 2017). Examples of observed earlier onset of stratification include 28 ± 6 days for Blelham Tarn, UK, (1968-2008) (Foley *et al.*, 2012), 16 days earlier in Lake Washington, USA (1962-2002) (Winder and Schindler, 2004), 3 weeks earlier in Heiligensee, Germany (1975-1992) (Adrian *et al.*, 1995) and 2-3 weeks earlier in Lake Zurich (1947-1998) (Livingstone, 2003). For many lakes, the increase in the length of stratification is due to warmer spring time temperatures (Adrian *et al.*, 1995) and increased warming of the upper water column layers which enhances stratification stability and therefore resistance to mixing (Livingstone, 2003; Foley *et al.*, 2012). In contrast, the observed increase in the length and strength of stratification in Lake Kinneret, Israel (1969-1991) is due to the long term decline in mean winter air temperatures resulting in cooler hypolimnetic water temperatures which increases the vertical density gradient and therefore the resistance to mixing (Hambright *et al.*, 1994).

The impact of warming water temperatures on the depth of surface mixing and the depth of the thermocline will differ with lake size and morphometry (Kraemer *et al.,* 2015). Small sheltered lakes with short fetch lengths are likely to experience shallower mixing with increases in surface water temperatures as they are more sheltered from wind mixing (Kraemer *et al.,* 2015). In lakes with larger surface areas the depth of the thermocline is strongly determined by lake fetch (Gorham and Boyce, 1989; Mazumder and Taylor, 1994; Boehrer and Schultze, 2008), therefore the position of the mixed depth and the thermocline may be more resistant to change even if the surface waters warm (Kraemer *et al.*, 2015).

In addition to the warming trend, there has also been an observed decrease in wind speeds (atmospheric stilling) (Vautard *et al.*, 2010). This may decrease wind mixing energy in some regions and contribute to thermocline shallowing (Woolway *et al.*, 2019). The application of this to lake ecosystems is still in the early stages, but decreases in wind speeds were found to have a substantial impact on the stratification dynamics of polymictic Lake Võrtsjärv, Estonia (Woolway *et al.*, 2017) and enhanced stratification strength in Lake Taihu, China (Deng *et al.*, 2018).

Climate change also has the potential to change the mixing regime of a lake (Woolway and Merchant, 2019). Numerical lake model simulations of 635 lakes worldwide found that around 100 lakes were projected to change mixing regime (Woolway and Merchant, 2019). A proportion of these lakes changed from monomictic to permanently stratified and others changed from dimictic to monomictic (Woolway and Merchant, 2019).

2.5.2 Nutrient impacts of long term climatic change

Efforts to reduce nutrient sources from the catchment (Gerten and Adrian, 2000; Jeppesen *et al.*, 2002) and the lack of precipitation events during long periods of clement weather could lead to a reduction in external nutrient loading from the catchment during summer (Köhler *et al.*, 2005; Weyhenmeyer *et al.*, 2007). This could lead to nutrient limitation of nitrogen and phosphorus during the summer growing season. Increases in lake stratification strength and stability can also lead to prolonged anoxia in the hypolimnion of lakes (Jankowski *et al.*, 2006; Foley *et al.*, 2012). This can lead to greater accumulation of nutrients such as phosphorus in the hypolimnion which are released into the epilimnion during mixing (Mackay *et al.*, 2014). This form of internal loading is likely to become more important in a changing climate and may compensate for reductions in external loading (Köhler *et al.*, 2005; Mackay *et al.*, 2014).

2.5.3 Phytoplankton responses to long term climatic change

A significant water quality concern is that the direct and indirect impacts of warming surface waters will create conditions favourable for cyanobacteria blooms, particularly in nutrient-rich systems (Dokulil and Teubner, 2000; Jöhnk *et al.*, 2008; Paerl and Huisman, 2008, 2009; Carey *et al.*, 2012; Elliott, 2012; Huisman *et al.*, 2018). This is due to a number of favourable traits that cyanobacteria possess. These include the ability to grow in high temperatures, buoyancy, a high affinity and high storage capacity for phosphorus, nitrogen fixation, akinete production (dormant cells) and the ability to harvest light at low intensities (Carey *et al.*, 2012). Cyanobacteria blooms increase turbidity at the surface of lakes which can shade macrophytes and competitors. The decomposition of the organic material created by blooms can lead to oxygen depletion in the water column which can lead to fish kills in severe cases (Lawton and Codd, 1991; Paerl and Huisman, 2008). Some species also produce toxic by-products which can be harmful to aquatic life and human health (Carmichael, 1992, 2001; Svrcek and Smith, 2004; van Apeldoorn *et al.*, 2007; Wood *et al.*, 2017). Due to these negative impacts, a significant amount of research has focussed on the mechanisms of bloom formation and the drivers behind the proliferation of cyanobacteria blooms (Dokulil and Teubner, 2000; Jöhnk *et al.*, 2008; Paerl and Huisman, 2008, 2009; Carey *et al.*, 2012; Elliott, 2012; Huisman *et al.*, 2018).

Cyanobacteria responses to climatic drivers and other stressors, however, cannot be generalised with cyanobacteria abundance varying amongst lake type (Richardson *et al*., 2018) Increases in water temperature, changes in the depth of mixing and changes in the length of stratification can impact the growth of phytoplankton species and although these drivers are interlinked they have separate consequences for phytoplankton growth (Winder *et al.*, 2012).

2.5.3.1 Phytoplankton responses to increasing temperatures

Changes in water temperature directly impact the rate of cellular processes such as photosynthesis. In general, phytoplankton will experience an increase in growth rate with increasing temperatures up to a temperature limit which will differ between species (Butterwick *et al.*, 2004; Reynolds, 2006). There is some evidence that increases in temperature will favour the growth of smaller phytoplankton cells due to their faster growth rates and increased efficiency of nutrient uptake at higher temperatures (Winder *et al.*, 2009; Rasconi *et al.*, 2015). This is particularly evident amongst certain species of diatoms, with palaeological records and within lake experiments suggesting that increases in temperature and shallower mixing may result in shifts to smaller cell sizes (Rühland *et al.*, 2008, 2015; Saros *et al.*, 2016). Concurrently, temperature increases will also increase grazing, at a faster rate compared to the increase in primary productivity (Allen *et al.*, 2005; Sommer and Lewandowska, 2011) which will affect phytoplankton biomass and species composition.

Periods of enhanced lake stability and high stratification strength can result in the dominance of few phytoplankton species resulting in an uneven community lacking in diversity (Sommer, 1993; Padisák, Borics, *et al.*, 2003). In particular, it is posited that temperature increases directly favour the growth of cyanobacteria species due to them having faster growth rates at higher temperatures compared to their competitors (Reynolds, 1989, 2006; Jöhnk *et al.*, 2008; Paerl and Huisman, 2009). Recent evidence has suggested, however, that growth rates of cyanobacteria at higher temperatures are not significantly different from the growth rates of chlorophytes (Lürling *et al.*, 2013). Cyanobacteria species also have highly variable growth rates due to their different morphologies so their responses to environmental changes should not be simplified or generalised (Carey *et al.*, 2012). Nevertheless, cyanobacteria appear to be prevalent in lakes with warmer surface waters which is likely due to the indirect effects of warming (Wagner and Adrian, 2009; Carey *et al.*, 2012). For example, Moss *et al*., (2003) found that increases in temperature in mesocosm experiments did not lead to an increase in cyanobacteria. This is likely due to the absence of the indirect impacts of water temperature increases such as a shallower surface mixed layer (Moss *et al.*, 2003).

2.5.3.2 Phytoplankton responses to shallower surface mixing

Increased stratification strength and shallower surface mixing results in increased light availability for phytoplankton in the upper mixed layer but also leads to a reduction in available nutrients due to increased separation from the nutrient rich hypolimnion (Livingstone, 2003; O'Reilly *et al.*, 2003). It is therefore suggested that climatic warming will favour species adapted to low turbulence environments (Findlay *et al.*, 2001; Diehl *et al.*, 2002; Ptacnik *et al.*, 2003; Jäger *et al.*, 2008). Cyanobacteria species have a number of traits that make them suited to these conditions (Carey *et al.*, 2012; Mantzouki *et al.*, 2016). In the first instance, many species are buoyant which allow them to rise to the surface of the water column where light conditions are favourable (e.g. *Dolichopspermum* and *Microcystis*). In shallow lakes (<12 m) there is evidence that cyanobacteria species such as *Microcystis* and *Dolichopspermum* can migrate quickly, exploiting both the nutrient rich hypolimnion and the illuminated surface layers (Ganf and Oliver, 1982; Wagner and Adrian, 2009). Buoyancy can also be facilitated further at higher water temperatures due to reduced water viscosity (Reynolds *et al.*, 1987). There is also evidence that low light adapted cyanobacteria genera such as *Planktothrix*, which can accumulate biomass at deep water column depths, will also be favoured with warming and reduced surface mixing (Posch *et al*., 2012) Cyanobacteria also have adaptations to allow them to overcome nutrient scarcity. In the first instance, species such as *Dolichospermum* have heterocysts which allow them to fix nitrogen gas when ammonium and nitrate are lacking (Wood *et al.*, 2010). Cyanobacteria can also overcome phosphorus limitation as some species contain enzymes which breakdown organic compounds containing phosphorus and others can store excess phosphorus in cells (Whitton *et al.*, 1991; Reynolds, 2006).

2.5.3.3 Changes in the length of the growing season

Changes in the timing of the onset of stratification can lead to phenological changes in the seasonal succession of the phytoplankton (Adrian *et al.*, 2006; Thackeray *et al.*, 2008, 2016; Feuchtmayr *et al.*, 2012). Many studies have reported that the timing of the spring bloom is advancing as a result of climatic warming and the earlier onset of stratification; this is evidenced in both observed (Gerten and Adrian, 2001; Winder and Schindler, 2004; Thackeray *et al.*, 2008, 2010; Meis *et al.*, 2009; Winder *et al.*, 2012) and modelling studies (Elliott *et al.*, 2005; Peeters, Straile, Lorke and Ollinger, 2007). The timing of the spring bloom has been found to differ amongst phytoplankton species. Feuchtmayr *et al*.,

(2011) found that the peak of *Asterionella formosa* (Bacillariophyta) advanced during a 58-year period (1945-2003) but peaks of *Aulacoseira* spp. (Bacillariophyta) and *Cryptomonas* spp. (Cryptophyta) were delayed. This study also found that soluble reactive phosphorus was a better predictor than temperature for the timing of the spring bloom which suggests that climatically induced changes may also be modulated by local factors (Feuchtmayr *et al.*, 2012). In addition, Winder *et al.*, (2012) found that higher water temperatures advanced the timing of the spring bloom for most functional groups, but the bloom magnitudes were highly variable amongst taxa depending on the light and nutrient climate of the individual lake systems. Increased stratification strength can lead to increases in the accumulation of nutrients in the hypolimnion. When these nutrients are mixed into the upper layers of the water column during the breakdown of stratification in autumn they can stimulate further blooms of phytoplankton and extend the growing season into autumn (e.g. Nürnberg *et al.*, 2013).

Changes in the timing and the length of the phytoplankton growing season can have implications for higher trophic levels. One consequence is trophic asynchrony due to shifts in the timing of life history events (Adrian *et al.*, 2006). These impacts can desynchronise predator-prey relationships such as those between phytoplankton, zooplankton and fish (Thackeray *et al.*, 2010; Ohlberger *et al.*, 2014).

2.5.4 Physical impacts of storm events

Storms can be comprised of short term changes in a number of physical drivers most notably, increases in wind speed, decreases in air temperature and increases in rainfall. Increases in wind stress (Klug *et al.*, 2012) and surface cooling are likely to decrease stratification strength and increase the depth of surface mixing (Wüest and Lorke, 2003). The depth of surface mixing induced by increases in wind speed will depend on the strength of the wind as well as the size and fetch of the lake (Spigel and Imberger, 1980). The timing of the storm event in relation to seasonal stratification strength will also partially determine the depth of surface mixing. If events occur at times of year when stratification is weak it may result in full water column mixing (e.g. Jones *et al.*, 2008). Increases in wind speed can also induce internal waves in stratified lakes (Imberger, 1998; Woolway *et al.*, 2018) which can interact with basin topography causing further mixing and turbulence (Saggio and Imberger, 1998).

Storm events accompanied with heavy precipitation can increase inflow discharge and decrease water residence time (Strasškraba and Hocking, 2002; Havens *et al.*, 2016; Zwart *et al.*, 2017). The impact of the inflowing water on the heat budget and stratification of the lake will depend on the difference in temperature between the inflowing water relative to lake water temperatures (Carmack *et al.*, 1979; Rueda and MacIntyre, 2010; Fink *et al.*, 2014). Inflowing water that is cooler than the epilimnion may enter the lake into the metalimnion (James *et al.*, 2008; Jung *et al.*, 2016), whereas water of a similar temperature to the epilimnion may result in the flushing of the upper layer of the water column.

Jennings *et al.*, (2012) identified two types of storm event, short lived events that have a temporary impact on the vertical structure of a lake and events associated with heavy rainfall that have prolonged impacts. The prolonged impacts of storm events are due to the delivery of dissolved organic matter (DOM) and dissolved organic carbon (DOC) which have long lasting effects on water clarity with severe, less frequent events having the largest impacts (Jennings *et al.*, 2012). The delivery of DOC into lakes during storms can therefore enhance the light limitation which may already be light limited due to epilimnetic deepening with increased wind speeds (von Einem and Granéli, 2010).

2.5.5 Nutrient impacts of storm events

Storm events can incorporate nutrients in the surface mixed layer through increases in external loading (Vanni *et al.*, 2006; Coloso *et al.*, 2008; Crockford *et al.*, 2015; Norris *et al.*, 2017) and through the re-distribution of internal sources of nutrients (James *et al.*, 2008; Mackay *et al.*, 2014; Crockford *et al.*, 2015). Heavy precipitation and increases in catchment runoff from agricultural and urban areas can increase nutrient loading into lakes during storm events (Vanni *et al.*, 2006; James *et al.*, 2008; Crockford *et al.*, 2015; Norris *et al.*, 2017; Morabito *et al.*, 2018). Heavy precipitation events can also overwhelm drainage systems which can lead to uncontrolled discharges of nutrient rich untreated wastewater into lakes (Whitehead *et al.*, 2009). Mixed depth deepening into the nutrient rich hypolimnion can also entrain and re-distribute nutrients into the surface mixed layer (James *et al.*, 2008; Mackay *et al.*, 2014; Crockford *et al.*, 2015).

2.5.6 Phytoplankton responses to storm events

Storms can impact the phytoplankton community directly through biomass loss due to physical flushing and indirectly by altering the vertical distribution of resources for growth (Vanni *et al.*, 2006). The impacts of storm events on phytoplankton communities are often more prolonged compared to the recovery of the physical structure (Jennings *et al.*, 2012) and the impacts will vary according to interactions between meteorological (Jennings *et al.*, 2012), catchment (De Eyto *et al.*, 2016; Kasprzak *et al.*, 2017) and within lake factors (Beaver *et al.*, 2013; Havens *et al.*, 2016; Giling, Nejstgaard, *et al.*, 2017; Ji *et al.*, 2018).

The impact of storm events on overall primary productivity is conflicting and is related to the balance between an increase in light limitation, an alleviation of nutrient limitation and the magnitude of the biomass losses through flushing (Vanni *et al.*, 2006). Storm events can alter the light climate in two ways, in the first instance, increases in wind speed and reductions in air temperature lead to reduced stratification strength and deeper surface mixing which exposes phytoplankton to lower light levels (Huisman, van Oostveen and Weissing, 1999; Diehl, 2002). The second way is through the increase in the delivery of organic matter through increased catchment runoff during heavy rainfall events which can lead to an increase in turbidity and a shallower euphotic depth (De Eyto *et al.*, 2016; Kasprzak *et al.*, 2017; Perga *et al.*, 2018). Storm events are often associated with a decline in biomass, particularly if they are associated with heavy rainfall and flushing (Jacobsen and Simonsen, 1993; Harris and Baxter, 1996; Vanni *et al.*, 2006). The increase in nutrient delivery from catchment runoff and potential mixing into the nutrient rich hypolimnion, however, can result in an increase in productivity post-storm due to the alleviation of nutrient limitation (James *et al.*, 2008; Crockford *et al.*, 2015; Yang *et al.*, 2016; Norris *et al.*, 2017).

Storm events can lead to significant impacts on the composition of phytoplankton communities. Events occurring in summer have been associated with a decrease in cyanobacteria (Jacobsen and Simonsen, 1993; Harris and Baxter, 1996; Beaver *et al.*, 2013; Isles *et al.*, 2015; Srifa *et al.*, 2016; Blottière *et al.*, 2017) due to the breakup of surface blooms by wind mixing and flushing. The increased water pressure at deeper mixed depths can also burst gas vesicles which can remove the buoyancy advantage of some cyanobacteria species (Walsby, 1994). Following storms it is common for cyanobacteria and slow growing eukaryotic phytoplankton to be outcompeted initially by small fast growing species such as cryptomonads (Jacobsen and Simonsen, 1993; Padisák *et al.*, 2009; Cardoso *et al.*, 2019) followed by slower growing low light adapted diatoms (Harris and Baxter, 1996; Beaver *et al.*, 2013) which are better adapted to stronger mixing and low light climates (Kunz and Diehl, 2003). This pattern is not ubiquitous amongst lakes, with increases in cyanobacteria being associated with the increase in nutrient delivery during extreme storm events (Yang *et al.*, 2016). In clear water systems, storms can also entrain deep chlorophyll *a* maxima of cyanobacteria in the surface mixed layer which exposes them to a more favourable light climate (Giling, Nejstgaard, *et al.*, 2017; Kasprzak *et al.*, 2017). This coupled with increased nutrient availability due to catchment runoff, can lead to an increase in primary productivity of cyanobacteria (Giling, Nejstgaard, *et al.*, 2017; Kasprzak *et al.*, 2017).

Depending on the timing, storms can advance the seasonal succession of phytoplankton. A storm occurring late in the growing season advanced the seasonal succession of phytoplankton from cyanobacteria to eukaryotic phytoplankton in Lake Champlain, due to an advance in the weakening of stratification (Isles *et al.*, 2015). Similarly large shifts in the community biomass can also occur in spring and advance the seasonal succession (Barbiero *et al.*, 1999). In contrast, Znachor *et al.*, (2008) found that although a storm event in the spring advanced the seasonal succession, a similar event in the summer led to a regression of the phytoplankton community which was comparable to a community that normally occurred earlier in the season. The community resistance to storms can also differ with season, for example Barbiero *et al*., (1999) found that the biggest impacts on the community occurred in spring whereas summer communities were more resistant to storm events with the dominant species remaining despite increases in species richness.

2.5.7 Summary

This review has highlighted the importance of lake stratification and surface mixing for chemical and ecological processes within lakes. There are currently however, multiple ways to define the mixed depth but the consistency of these definitions when calculating ecological and chemical metrics is so far untested. Changes in water temperature and surface mixing as a result of long term climate change are intrinsically linked but this review has highlighted that they have separate consequences for phytoplankton growth, which have not yet been disentangled. This review has also highlighted that there is a wealth of knowledge about the long term impacts of climate change on physical, chemical and ecological lake processes. There are also many examples of phytoplankton responses to storm events in the existing literature. The interaction between how long term changes in climate might influence the response of a lake to short term episodic events, however, is relatively unexplored.

3 Site Description and Methodology

3.1 Site description

3.1.1 Location

Blelham Tarn is a small, monomictic, lake (0.1 km^2) located in the Lake District, North West England (Figure 3.1). Blelham Tarn (Lat:54.3959, Long:-2.9780) is situated in the Windermere catchment to the west of the North Basin of Windermere.

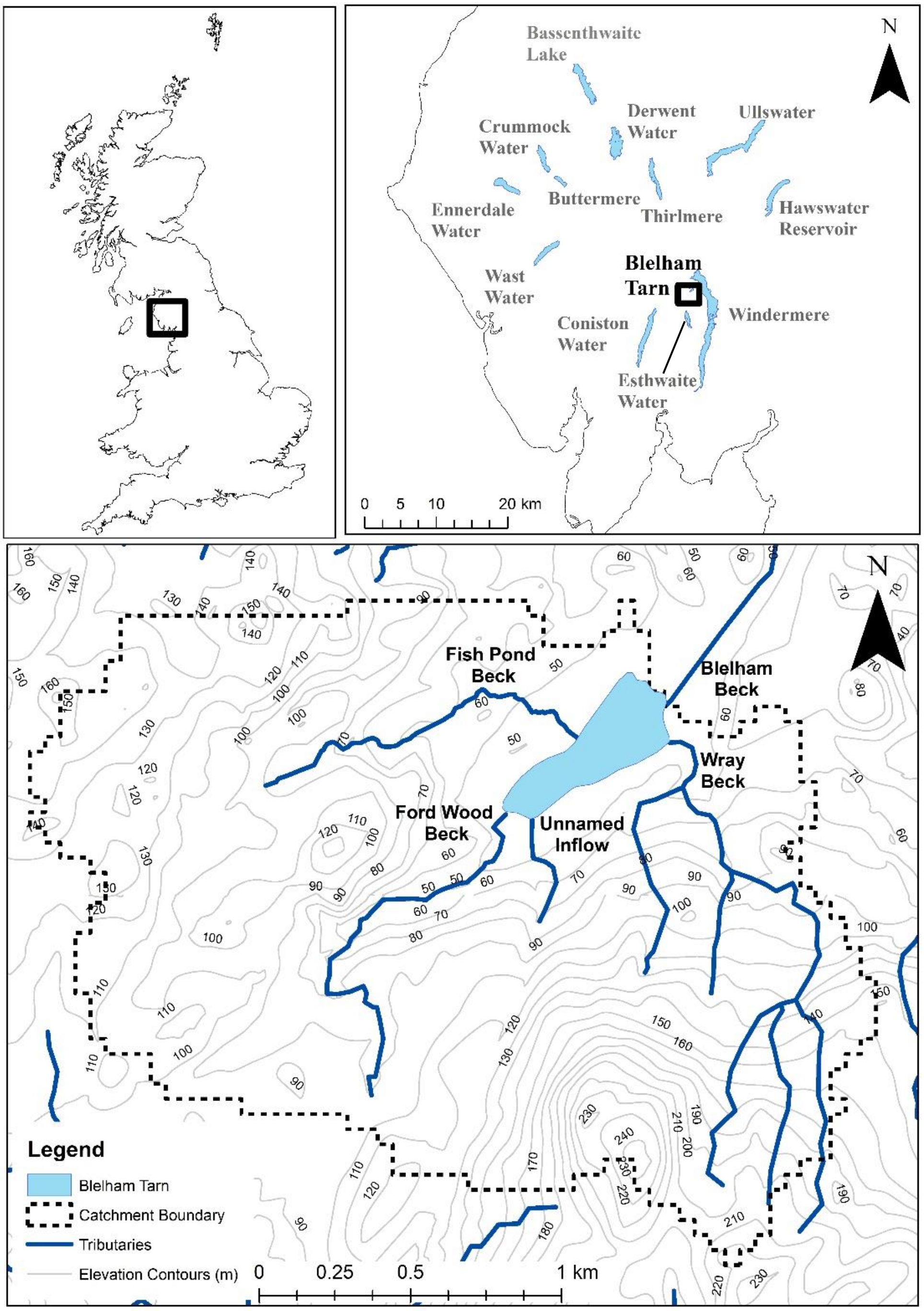


Figure 3.1 Map of Blelham Tarn, catchment and tributaries.

3.1.2 Climate

The English Lake District experiences a wet, mild climate and its proximity to the west coast means that the area is exposed to prevailing westerly winds from the Atlantic Ocean. The westerly winds contain a large amount of moisture which falls as orographic rainfall as the air hits the mountainous areas of the region (Barker *et al.*, 2004; Malby *et al.*, 2007). The mountainous topography means that rainfall is highly varied across the region; at Ambleside (the closest weather station to Blelham Tarn) the average annual rainfall is quite high at 2005.1 mm yr^{-1} (Figure 3.2). As a result of the temperate climate, Blelham Tarn is rarely ice-covered in winter and is stratified for a large proportion of the year. The onset of stratification has ranged between 13th March-1st May based on data from 2008-2018, with overturn occurring between 4th October-8th November over the same time period.

Blelham Tarn is also impacted by climatic cycles including the North Atlantic Oscillation (NAO) and Rossby Waves (George *et al.*, 2000, 2004; Strong and Maberly, 2011). The NAO particularly impacts the winter season of the lake, with wet and mild winters being associated with positive values of the NAO index (NAOI). Surface and bottom water temperatures of Blelham Tarn are also strongly correlated with the NAOI (George *et al.*, 2004). Changes in rainfall associated with the NAO have an impact on the chemistry and ecology of the lake; the NAO was positively correlated with dissolved phosphorus and negatively correlated with nitrate and wet winters resulting in lower phytoplankton biomass and delayed onset of phytoplankton growth (George *et al.*, 2004). Tropospheric Rossby Wave Breaking (RWB) bringing warm moist air or cool dry air is also linked to the surface temperatures of Blelham Tarn in all seasons (Strong and Maberly, 2011).

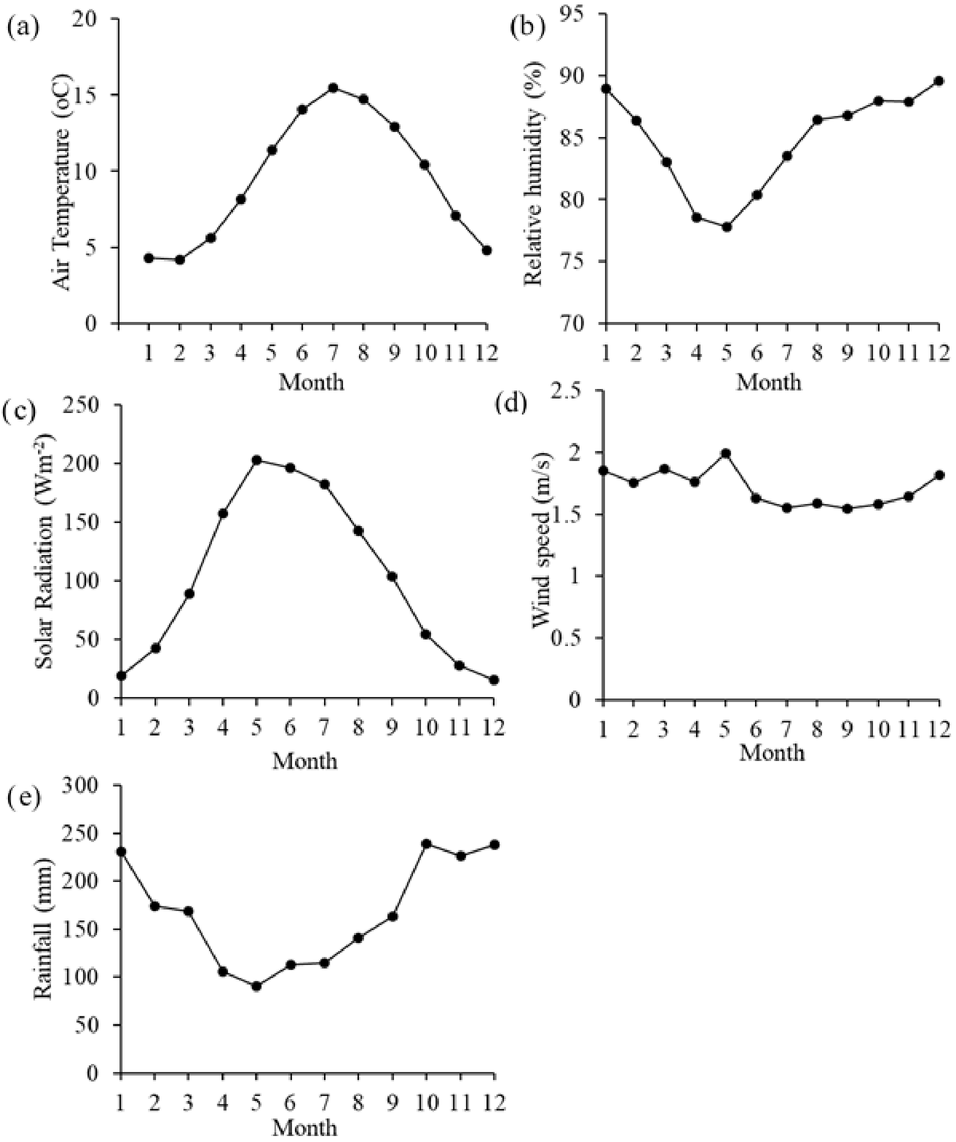


Figure 3.2 Monthly averages for (a) air temperature (b) relative humidity (c) solar radiation and (d) wind speed taken from the automated monitoring buoy 2008-2018 and (e) rainfall recorded at the Ambleside weather station 1985-2010 (Met Office, 2019).

3.1.3 Geology and morphometry

Blelham Tarn is classed as small (< 1 km^2) with an area of 0.1 km^2, and a moderate depth (maximum depth of 14.5 m and mean depth of 6.8 m) (Ramsbottom, 1976) (Figure 3.3). The tarn was glacially formed by an ice stream which branched off the larger Windermere ice stream to excavate Blelham Tarn and Esthwaite Water (Fryer, 1991). As a result of its glacial formation the superficial deposits underlying Blelham Tarn consist of till (Devensian- diamicton), with the bedrock geology comprising of Wray Castle formation-mudstone (hemipelagic, laminated) (BGS, 2019). The total volume of the lake is 0.693 $m^3 \times 10^6$ and it is fed by four main inflows with one outflow (Blelham Beck) (Ramsbottom, 1976) (Figure 3.3). The outflow has been artificially straightened and flows into the North Basin of Windermere (Natural England, 2014). The annual mean residence time of the lake is 33.8 days (Jones and Elliott, 2007).

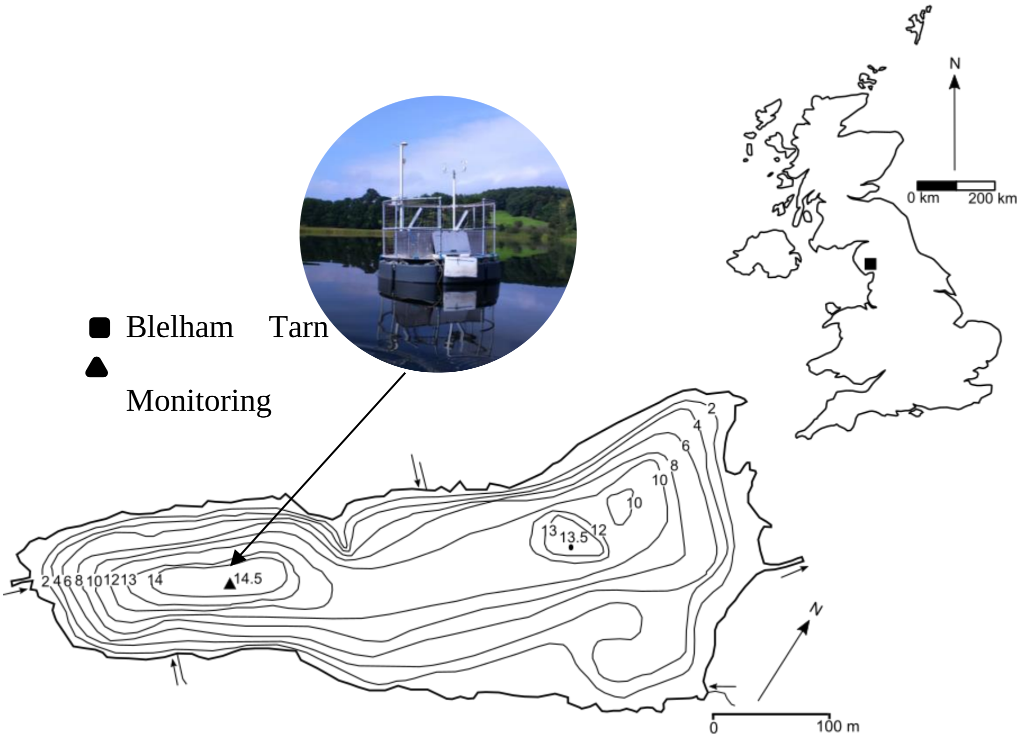


Figure 3.3 The bathymetry of Blelham and location of the monitoring buoy (triangle) at the deepest point of the lake (14.5m) bathymetry from Ramsbottom (1976). Photo credit: E.Gray.

3.1.4 Catchment land use

The surrounding catchment is predominantly used for livestock grazing (42.6% improved grassland land cover) but the catchment also contains forested areas (26.6% broad-leaved/mixed woodland land cover), with a section of broad-leaved forest surrounding much of the lake perimeter up to the shore edge sheltering the lake (UK Lakes Portal, 2019). The remaining 30.8% land cover comprises of neutral grass (7.0%), arable horticulture (5.4%), bracken (5.2%), calcareous grassland (4.4%), acid grassland (3.5%) and coniferous woodland (2.3%) (UK Lakes Portal, 2019). The catchment contains a small number of settlements including Outgate to the south-west of the lake which discharges treated wastewater into Ford Wood Beck which flows directly into the lake (

Figure 3.1). Blelham Tarn and Bog are classed as a Site of Special Scientific Interest (SSSI) and the Blelham Bog is a National Nature Reserve as it provides a habitat for rare invertebrates as well as rare mosses, grasses and sedges (UK Lakes Portal, 2019).

3.1.5 Long term monitoring and previous research

Blelham Tarn has been extensively monitored since 1945 initially by the Freshwater Biological Association (FBA) and later by the Institute of Freshwater Ecology and then the Centre for Ecology & Hydrology since 1989. In addition to routine fortnightly monitoring of ecological (phytoplankton counts), chemical (nutrient concentrations) and physical data (temperature and oxygen profiles), the lake also contains an automated monitoring buoy which was installed during 2007 and records meteorological variables, surface levels of ecological, physical and chemical parameters as well as temperature at metre depth intervals in the water column (Figure 3.3). Long term monitoring nutrient and phytoplankton data from 2008-2018 have been used in Chapters 6 & 7.

Some of the first studies from the lake detail the long term changes in the catchment land-use and erosion by analysing bed sediments from the lake (Harmsworth, 1968; Pennington *et al.*, 1977). Later, the site contained a series of experimental tubes which were used to investigate seasonal cycles of phytoplankton development and the impacts of changing phosphorus, grazing and mixing on the seasonal growth of phytoplankton (Reynolds, 1986). Data from the experiments were later used to investigate the impacts of phytoplankton growth on the heat budget of lakes (Jones *et al.*, 2005). Analysis of the long term data from the site has provided a record of shifts in lake processes in response to climatic change including lengthening stratification duration and an increase in the number of days with hypolimnetic anoxia (Foley *et al.*, 2012). Data from the lake have contributed to various multi-site studies investigating the response of lake variables to changes in climatic cycles and meteorological drivers on a local (Woolway *et al.*, 2015), regional (George *et al.*, 2004; George, 2007; Feuchtmayr *et al.*, 2012) and global scale (Bruce *et al.*, 2018). Data from the lake have also been used as an experimental system within the Phytoplankton RespOnses To Environmental CHange model (PROTECH) to investigate the intermediate disturbance hypothesis (Elliott *et al.*, 2001), the impacts of changing retention times on phytoplankton communities (Jones and Elliott, 2007) and the impacts of changes in mixing and background extinction on phytoplankton communities (Bernhardt *et al.*, 2008) amongst others.

3.1.6 Water quality and nutrient status

Blelham Tarn lies on the meso-eutrophic boundary (eutrophic for chlorophyll *a* concentrations and secchi depth; mesotrophic for total phosphorus) (Maberly *et al.*, 2016). The lake has suffered a deterioration in water quality which has been associated with the surrounding agricultural land use (Moorhouse *et al.*, 2014). A large proportion of the nutrients (e.g. two thirds of phosphorus) entering the lake are therefore sourced from agriculture (Gasca *et al.*, 2015). The lake also suffers with severe oxygen depletion during the stratified period (Foley *et al.*, 2012), as a result, a proportion of the phosphorus concentrations come from internal loading (Gasca *et al.*, 2015). Overall, according to WFD standards, the lake is of a moderate status for chlorophyll *a* and phosphorus concentrations and would fail oxygen concentration targets (Maberly *et al.*, 2016).

Monthly average values for nutrient concentrations show a depletion of silica in late spring due to the spring diatom bloom with silica accumulating in the following months (Figure 3.4). Total phosphorus increases during the growing season due to the phosphorus contained within the phytoplankton. Concentrations of soluble reactive phosphorus, however, remain low and decrease throughout the growing season due to uptake by phytoplankton (Figure 3.4). Nitrate also decreases during the growing season and ammonium remains low throughout year, but increases in concentration during the overturn period in autumn (Figure 3.4).

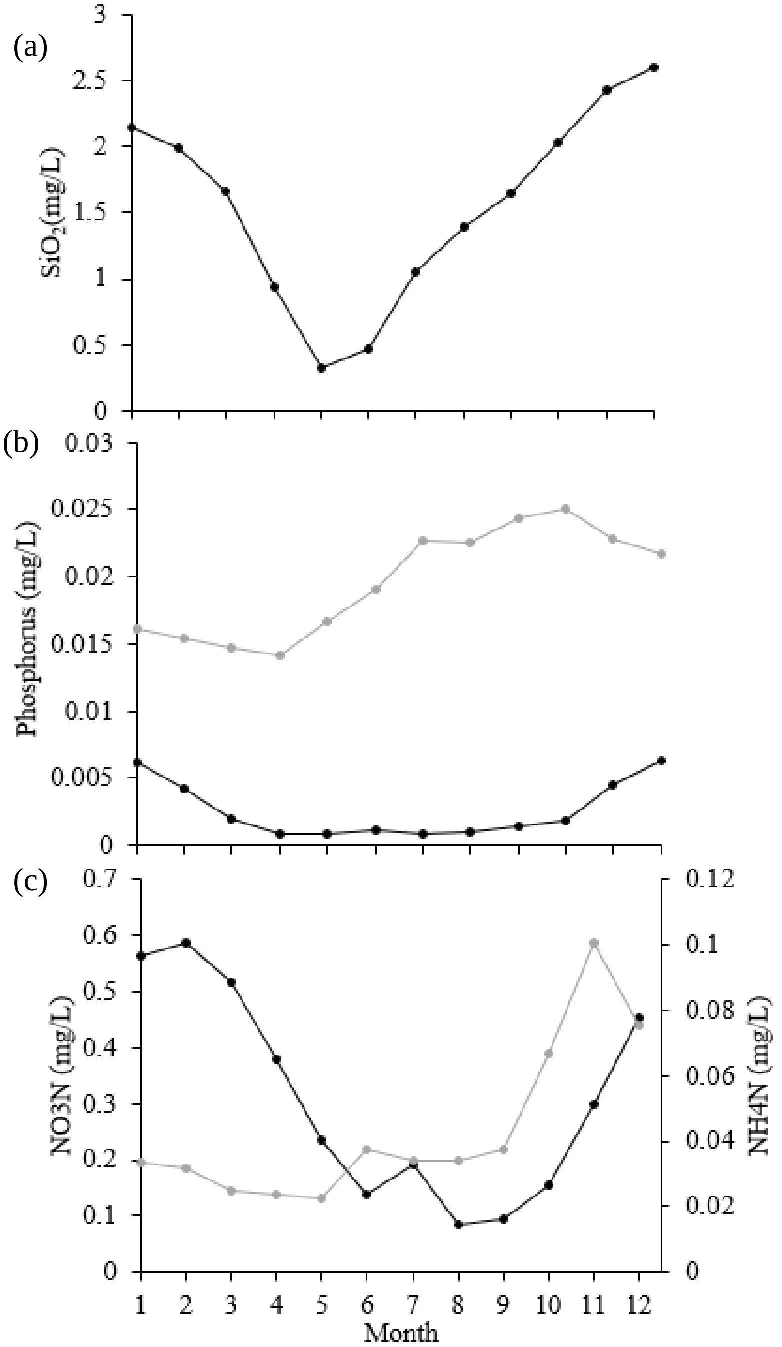


Figure 3.4 Monthly mean nutrient concentrations for (a) silica, (b) soluble reactive phosphorus (black) and total phosphorus (grey) and (c) nitrate (black) and ammonia (grey) sampled fortnightly from Blelham Tarn 2008-2018.

3.2 Methodology

In order to determine the interactions between lake physics and phytoplankton dynamics a combination of methodologies was used. These included high resolution monitoring of meteorological and within-lake variables, a two-year fieldwork campaign and phytoplankton community modelling using the Phytoplankton RespOnses To Environmental CHange model (PROTECH). Specific methodologies have been included in each results chapter but broader methodological details are outlined in this section (Table 3.1).

Table 3.1 Summary of data sources used in this thesis.

Data source	Chapter 4	Chapter 5	Chapter 6	Chapter 7
Long term monitoring				
Phytoplankton				x
Nutrients			x	
High resolution Monitoring				
Meteorological data		x	x	
Water temperature		x	x	
Fieldwork data				
Chemical chlorophyll *a*	X			
Phytoplankton				x
Sonde profiles	X			
Light profiles	X			x
Stream nutrients		x		
Secondary data				
River Leven discharge		x	x	

3.2.1 High resolution monitoring

Blelham Tarn contains an *in situ* automated monitoring buoy located at the lake's deepest point (14.5 m) which records meteorological and within-lake ecological and physical parameters at a four minute frequency (Figure 3.3). Meteorological variables recorded include: air temperature, wind speed, relative humidity and solar radiation. Water temperature is measured at a depth of 0.5 m and then at metre intervals 1-10 m with the final temperature sensor being located at a depth of 12 m. Data collected from the automated monitoring buoy have been used in two chapters in the form of daily averaged data to drive the PROTECH model (Chapter 5) and to calculate heat fluxes, mixed depth and measures of lake stability when assessing the impact of storm events (Chapter 6). The data were quality checked at the hourly scale for each variable and gaps were identified. Causes of the data gaps included sensor errors or data relay errors, in general these errors were identified and resolved quickly over a time period of days rather than weeks. A large data gap of 27 consecutive days occurred in January 2015 due to the replacement of the monitoring buoy infrastructure. Gaps in the meteorological data exceeding three hours were infilled using relationships between the data recorded at Blelham Tarn and data recorded by the nearby buoy located on Esthwaite Water (Lat:54.3593, Long:-2.9858). Gaps in the data less than three hours were infilled using a linear interpolation.

The outflow from Blelham Tarn is not continuously gauged, but discharge data were required in order to calculate nutrient loading (Chapter 5; 2012-2014) and changes in residence time (Chapter 6; 2008-2018). Prior to this study a relationship between daily outflow discharge from Blelham Tarn and the River Leven was established in 1974, when daily measurements were available for both sites. Data from the nearby River Leven (Lat:54.273913, Long:-2.954740; Figure 3.6) were therefore obtained from the Environment Agency and a power law relationship was applied to the River Leven data to convert it into Blelham Tarn outflow (Blelham Beck) data ($R^2=0.92$; $p<0.05$),

Equation 3.1

$$Q_{BB} = 0.0076{Q_{RL}}^{1.253}$$

where Q_{BB} is the outflow discharge of Blelham Tarn and Q_{RL} is the discharge from the River Leven. This relationship was used to calculate discharge in Chapters 5 and 6, but in order to check this relationship new measurements of discharge were also taken.

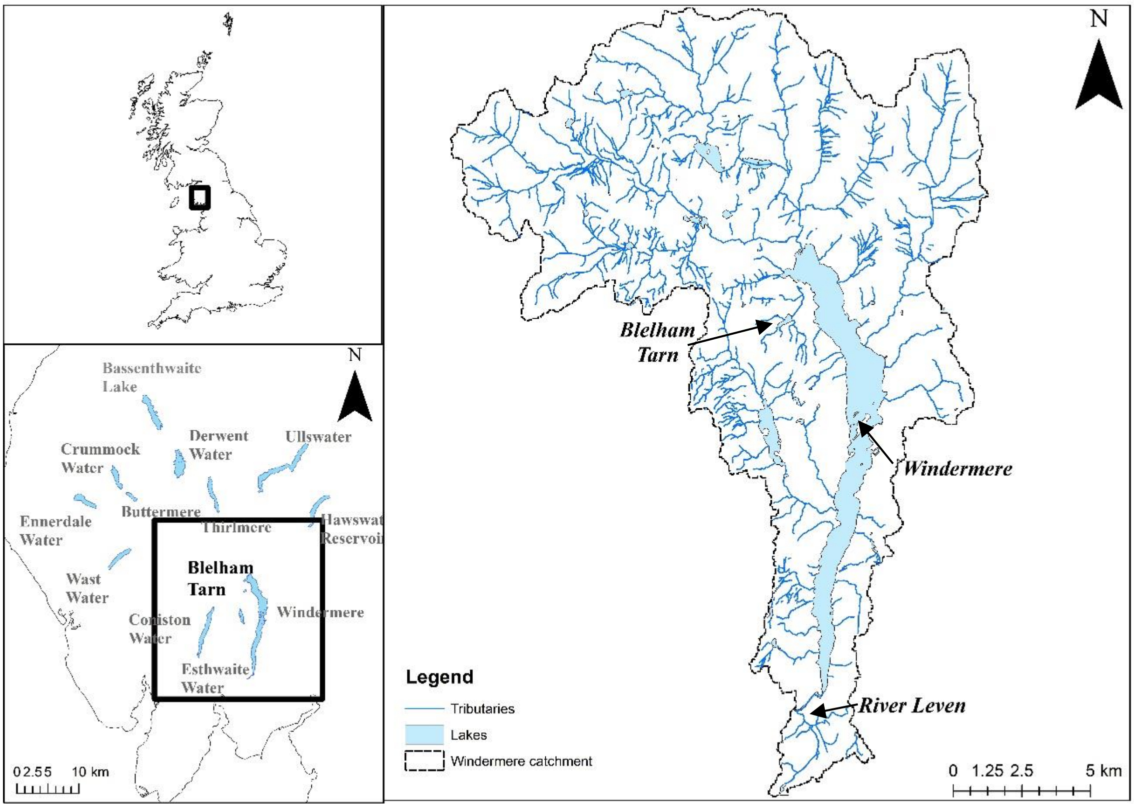


Figure 3.5 The Windermere catchment area showing the position of the River Leven relative to Blelham Tarn.

Blelham Tarn has four main inflows, three of which were accessible (Figure. 3.1). Water level loggers were installed into the outflow (Blelham Beck) and into one inflow (Wray Beck), with water level, depth and water temperature being recorded every 15 minutes. An additional logger located on the bank of Wray Beck recorded air temperature and atmospheric pressure which was later used to adjust the water level pressure recorded at Wray Beck and Blelham Beck. Data from the loggers were downloaded and quality checked every month. Stream surveys were carried out at the inflows and outflow to determine the bed bathymetry of each stream with the depth of the stream at bank full level being recorded every 10 cm. Using a Sontek handheld Acoustic Doppler Velocimeter (ADV), flow speed measurements were taken at three or four equally spaced locations across each inflow and the outflow depending on the wetted width, recording the water depth and the location relative to the bathymetry survey. Using the flow speed and cross sectional area of the flow measurement the stream discharge was calculated using the 'Mean-Section Method'(Shaw, 2005),

Equation 3.2 $Qseg = 0.5(v1+v2) \times 0.5(d1+d2) \times b,$

where v is the flow velocity, d is depth and b is the number of segments. The mean discharge (Q) for the stream was calculated by adding up each Qseg and dividing by the number of Qseg's. Separate rating curves were then plotted between discharge and water level for the inflow and outflow. The rating curve from the inflow was inadequate and the stream was dredged part way through the measurement period with may have altered the water level and discharge relationship, therefore only the rating curve from the outflow was used (Figure 3.6).

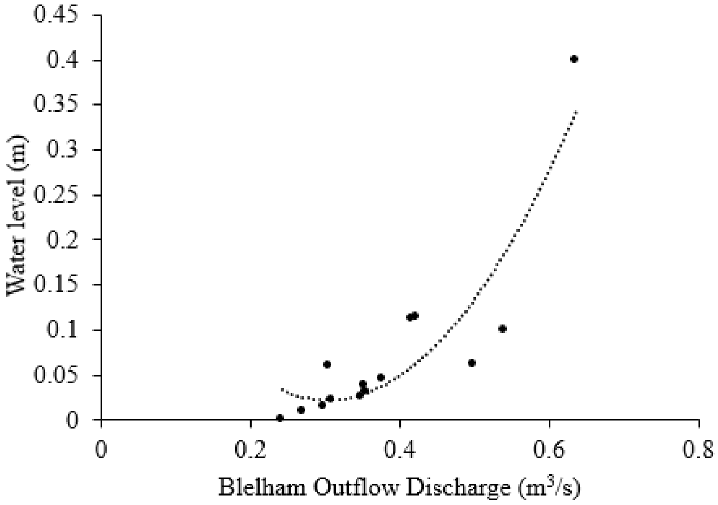


Figure 3.6 Rating curve derived from the relationship between the outflow discharge and water level.

This rating curve equation was used to convert the remaining water level values from the outflow into daily discharge using a polynomial relationship equation (R^2=0.8162),

Equation 3.3 $$y=2.9011x^2 -1.7618x + 0.2899$$

where, y is discharge and x is water level.

The discharge values calculated using equations 3.1 and 3.2 were compared (Figure 3.7). Discharge values derived using both methods compared well, with discharge peaks occurring at similar times and magnitudes (Figure 3.7). The higher baseline flow calculated using the River Leven dataset is likely due to the higher volume of water in the Leven compared to the outflow of Blelham Tarn (Figure 3.7). This comparison confirms that deriving discharge using the River Leven relationship is appropriate.

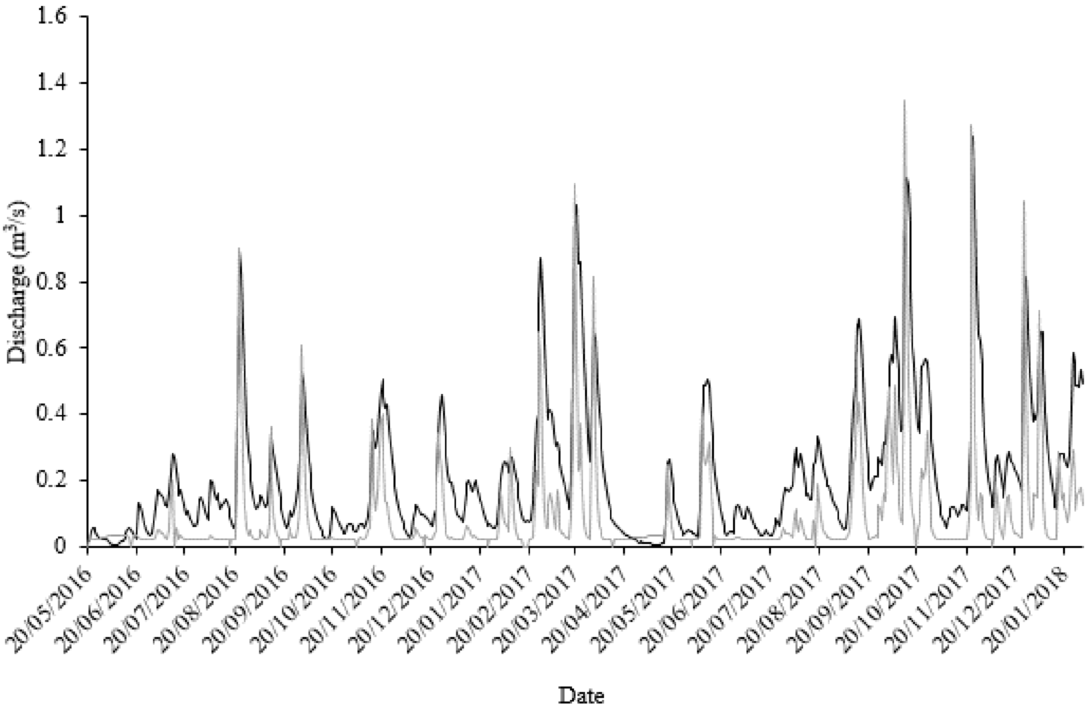


Figure 3.5 Discharge of Blelham Beck calculated u*sing the Blelham and Leven discharge in 1974 (Black line) and discharge calculated from the rating curve derived in this study (grey line).*

3.2.2 Fieldwork Campaign

A two-year fieldwork campaign was carried out at Blelham Tarn during 2016 and 2017. In 2016 fortnightly sampling occurred during April and May with weekly sampling starting in June and ending on 10/11/2016. During 2017 fortnightly sampling occurred during April which increased to weekly from 10/05/2017 and ended on 08/11/2017. In addition to routine sampling, additional targeted fieldwork days were carried out to capture the impacts of significant storm events. Monthly sampling for lake and stream nutrient concentrations was also undertaken.

3.2.2.1 Nutrient analysis

3.2.2.1.1 Soluble reactive phosphorus (SRP)

Samples were filtered in the field through a 47 mm GF/C filter paper and were analysed on the day of sampling. The concentration of SRP was determined colourmetrically. Ammonium molybdate and antimony potassium tartrate react in an acid medium (sulphuric acid) with phosphorus in the water samples to form an antimony-phospho-molybdate complex, this is reduced to a blue coloured complex with ascorbic acid and read colourmetrically at 880 nm using a spectrophotometer. A standard containing a known concentration of SRP (50 µg/L) was prepared and diluted into samples containing 10, 20, 30 40, 50 µg/L and 100 µg/L in order to create a calibration curve. In order to quality check the measurements an additional stock of 50 µg/L was made and diluted to a concentration of 10 µg/L. This was the working analytical quality control solution (AQC) which was compared to the 10 µg/L absorbance value obtained from the calibration curve.

Total phosphorus (TP), total nitrogen (TN), nitrate and silica were analysed by members of the CEH Lancaster Chemistry Laboratory, according to the following methods.

3.2.2.1.2 Total Phosphorus (TP)

TP was determined using potassium persulphate digestion and colourmetric analysis using molybdenum blue. Unfiltered water was digested in $K_2S_2O_8$ and H_2SO_4 and heated. The samples were allowed to cool then measured using a SEAL AQ2 discrete analyser. Samples for a calibration curve were prepared and digested in the same way and the data were corrected by the mean of the blanks.

3.2.2.1.3 Total Nitrogen (TN)

To determine TN the sample was acidified in HCL and then purged with zero grade air to remove inorganic carbon. Samples were then measured using a Shalar Formacs CA16 analyser with an attached ND25 to measure the TN.

3.2.2.1.4 Nitrate

Nitrate concentrations were determined using ion chromatography. Samples were filtered through Whatman cellulose acetate filters (0.45 µm) and then run through a Dionex ICS2100 Ion Chromatograph. Precision and reproducibility were checked using QC samples at 10 sample intervals.

3.2.2.1.5 Silica

Silica was determined with a colourmetric method using a Seal AQ2 analyser. The reactive silica combines with ammonium molybdate which is then reduced with ascorbic acid to form silicomolybenun blue complex. The colour was then measured using a spectrophotometer at 880 nm and blank measurements were used to correct for background colour in the samples.

3.2.2.1.6 Preliminary nutrient findings

Identifying the nutrient status and nutrient dynamics within the lake was not the main focus of this thesis. The findings are, however, relevant to the overall water quality of the lake and provide context for the following results chapters and so the results are therefore presented here. The collection of SRP data at metre intervals in the water column during June-October in 2016 revealed an accumulation of phosphorus during the stratified period supporting previous findings from Gasca *et al*., (2015), the majority of which was in the form of soluble reactive phosphorus (Figure 3.8). There was also an accumulation of total nitrogen (TN) at depth, and the concentration of silica increased with time.

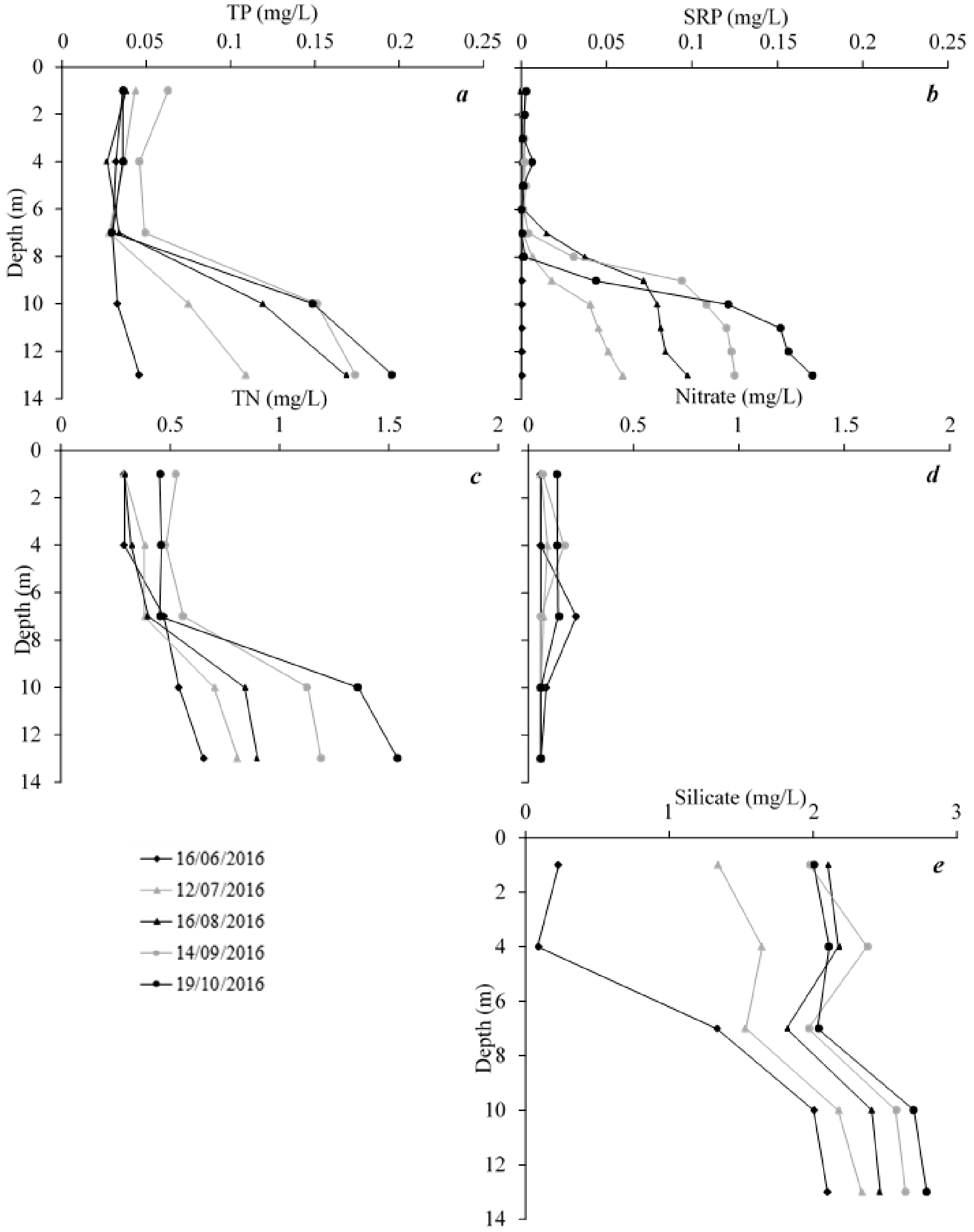


Figure 3.6 Nutrient concentrations of (a) total phosphorus, (b) soluble reactive phosphorus, (c) total nitrogen, (d) nitrate and (e) silica collected monthly during June-October 2016.

3.2.2.2 Water quality parameters

Using a Yellow Springs Instrument (YSI) EXO sonde, temperature, pH, specific conductivity, oxygen and chlorophyll a fluorescence were measured in the water column. During 2016 measurements were taken from a depth of 1 m to a depth of 13 m and in 2017 measurements were taken at a depth of 0.5 m to 13 m in half metre intervals. The sonde was held at the surface of the water column to stabilise for three minutes prior to sampling and was then lowered at half metre intervals and left for two minutes to stabilise at each depth during the winter and for five minutes during the stratified period. Data from each sample day were downloaded and quality checked prior to the following sample day and the sonde was calibrated at least every six weeks according to manufacturer specifications.

3.2.2.3 Light

A LI-COR underwater quantum cos-corrected sensor was also used to measure photosynthetically active radiation (PAR); measurements were taken just below the surface and then at one metre intervals from 1 m to 9 m. The natural logarithm of the PAR measurements were regressed with depth and the slope of the equation was used to estimate the extinction coefficient (k) for each sample day. The euphotic depth (z_{eu}) was then defined as the depth where only 1 % of the surface measurement of PAR remained,

Equation 3.1 $$z_{eu} = ln(100)\,/k.$$

3.2.2.4 Phytoplankton

3.2.2.4.1 Biomass: chemical determination

Chemical analysis for chlorophyll a provides an overall indication of phytoplankton biomass. Water samples (500 mL) were collected at metre intervals in the water column from 1 m to 10 m during 2016 and 0.5 m then 1 m to 9 m during 2017. Samples were filtered immediately after each sample day through a 5.5 cm diameter GF/C filter paper. The filter paper was frozen and the sample was analysed within a month of collection using the method detailed in Talling (1974). Chlorophyll *a* was extracted using methanol and measured for colour using a spectrophotometer. The spectrophotometer was set to the absorbance wavelength 750 nm for background turbidity and 665 nm for the red absorbance maximum of chlorophyll a,

Equation 3.2 $Chlorophyll\ a\ concentration = \left(13.9 *\ A_{corr665} * \frac{1}{d}\right) * v/V$

where, 13.9 approximates the reciprocal of the specific absorption coefficient at 665 nm for chlorophyll *a* in this solvent, *V* is the volume of sample filtered (ml), *v* is the volume of extract (ml), $A_{corr\ 665}$ corrected absorbance at 665 nm (= A_{665} - A_{750}) and *d* is the path-length of cuvette (cm).

3.2.2.4.2 Biomass: fluorescence

An alternative way of determining chlorophyll *a* biomass is to measure the fluorescence using the YSI multi-parameter sonde. By exposing phytoplankton to a known wavelength of light and measuring the amount re-emitted at longer wavelengths a relative measure of the chlorophyll *a* content in the water can be gained (Abbott *et al.*, 1982; Gregor and Maršálek, 2004; Beardall *et al.*, 2009). Measuring phytoplankton biomass in this way is beneficial as it provides high temporal and spatial resolution datasets using a non-destructive, rapid sampling technique (Bilger *et al.*, 1995). This is in contrast to taking chemical chlorophyll *a* samples in lake waters which can be time consuming, expensive and of a low spatial and temporal resolution (Bilger *et al.*, 1995). There are, however, some methodological issues when measuring phytoplankton biomass using this method.

The amount of solar radiation reaching a phytoplankton cell depends on fluctuations in solar radiation reaching the surface of the lake and therefore cloud cover as well as surface waves, water clarity and the position of phytoplankton in the water column. Fluctuations in light received by photosynthetic pigments can increase photosynthesis whereas constant exposure to high light results in photo-inhibition (Abbott *et al.*, 1982). Not all of the energy received by photosynthetic pigments can be used for photosynthesis with the remaining energy being dissipated as heat or re-emitted as light at a longer wavelength to that used in electron excitation (Maxwell and Johnson, 2000). Photosynthesis, heat dissipation and fluorescence occur in competition so the increase in efficiency of one will decrease the yield of another with total chlorophyll fluorescence being only 1-2% of the total light absorbed (Maxwell and Johnson, 2000).

Photosynthesis is comprised of two systems: photosystem one (PSI) and photosystem two (PSII). PSII is the first protein in the light dependent reactions of photosynthesis and is most effected by environmental stressors such as high photon fluxes or temperatures (Bilger *et al.*, 1995). Fluorescence fluctuations occur due to a decrease in the amount of electron acceptors in the photosynthetic pathway downstream of PSII; once PSII absorbs light and accepts an electron it cannot accept another electron until this has been passed onto another electron carrier. This results in a decrease in the efficiency of photochemistry and an increase in the yield of chlorophyll *a* fluorescence (Maxwell and Johnson, 2000).

The changes in fluorescence yield due to these processes are termed ‘quenching’ of which there are two main types. ‘Photochemical quenching’ is an increase in the rate at which electrons are transported away from PSII by the activation of enzymes by light. ‘Non-photochemical quenching’ (NPQ) is the change in fluorescence due to the increase in efficiency of energy being emitted as heat (Maxwell and Johnson, 2000). In practice the effect of these two quenching mechanisms on fluorescence is distinguished by making the effect of photochemical quenching zero using a ‘light doubling’ technique or by taking measurements in the dark. There are three types of NPQ however, photoinhibitory quenching is the most relevant and damaging and occurs under extreme light stress when phytoplankton are close to the surface of the water column (Müller *et al.*, 2001).

Quenching can therefore reduce the fluorescence emitted by phytoplankton close to the surface of lakes resulting in a potential under-estimation of biomass. Comparative measures were not taken at night time therefore there was no quantitative estimation of NPQ. To determine if estimates from the fluorescence method were underestimating biomass, fluorescence results were compared to the biomass results gained using the chemistry method (Figure 3.9). Comparing the results from the two methods demonstrate a reasonably good relationship between results from the two methods (R^2=0.56 p-value <0.05) at all depths (Figure 3.9) and most importantly at the shallowest depths in the water column (R^2=0.57, p-value <0.05) (Figure 3.9). Comparing the fluorescence and chemical phytoplankton biomass estimates at the shallowest depths over time demonstrate that the biomass pattern for the two estimates is very similar (Figure 3.9).

This suggests that quenching is not a methodological issue for this lake. It would be very unlikely for the chemistry and fluorescence results to produce the same concentration value as they estimate biomass in different ways. Further visual inspection of chlorophyll *a* profiles containing a sub-surface peak show that the sub-surface peaks occur in both the chemistry and fluorescence datasets. If quenching was impacting the surface chlorophyll *a* biomass readings, you would only expect the sub-surface chlorophyll *a* peak to form in the fluorescence data rather than both datasets (Figure 3.10). Based on this evidence it is unlikely that quenching is an issue in this lake. This is probably due to the high cloud cover on many sample days and lower intensity of the sun at this latitude compared to equatorial regions.

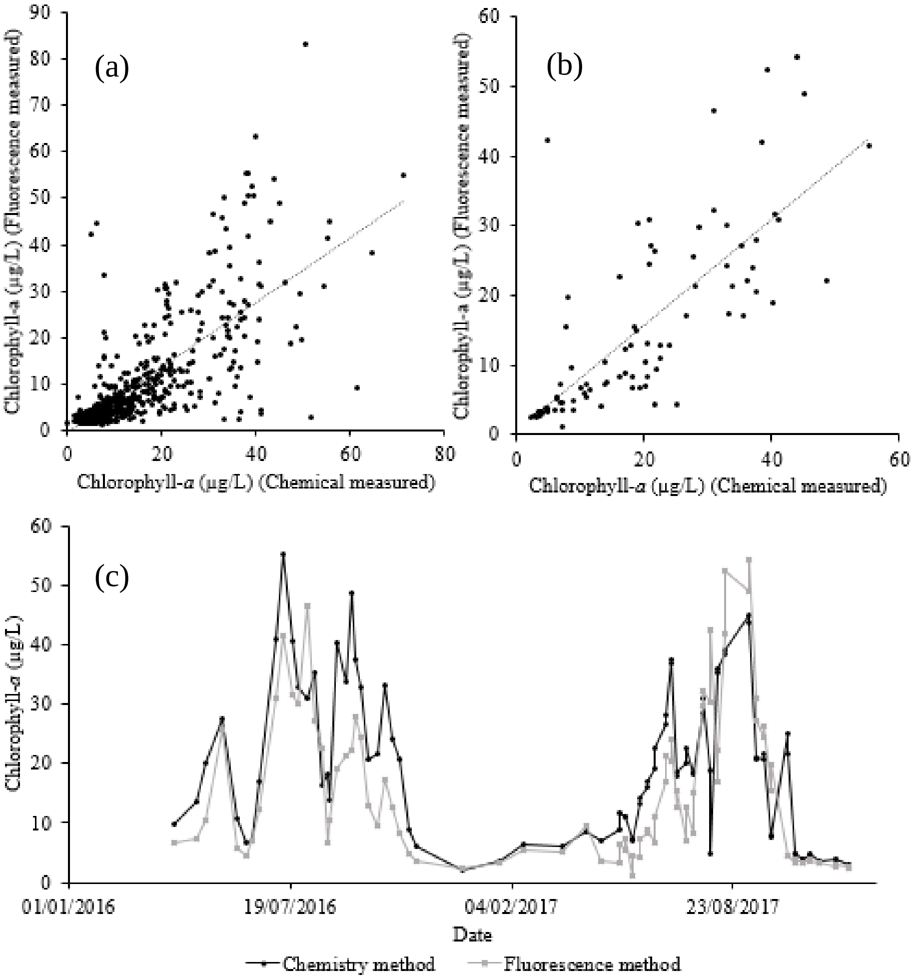


Figure 3.7 Relationship between (a) chemically measured and fluorescence measured chlorophyll a *for measurements at depth 0.5-0.9 m, (b) chemically measured and fluorescence measured chlorophyll* a *for measurements at depth 0.5 m and 1 m and (c) chemically measured (black) and fluorescence (grey) measured chlorophyll* a *for measurements at depth 0.5 m and 1 m with date.*

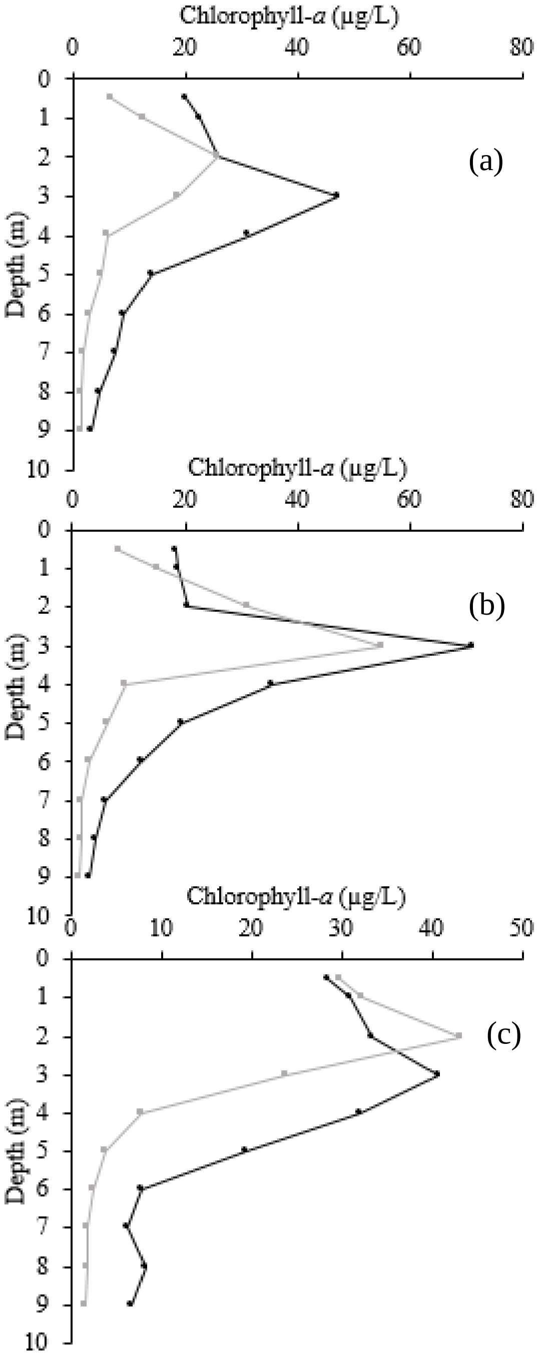


Figure 3.8 Example profiles where a sub-surface chlorophyll a *maxima occurs in both the chemically determined (black) and fluorescence profiles (grey) for (a) 12/07/2017, (b) 19/07/2017 and (c) 26/07/2017.*

3.2.2.4.3 Phytoplankton taxonomy

Phytoplankton samples for taxonomic identification were collected from the lake at metre intervals in the water column from 1 m to 10 m during 2016 and 0.5 and 1 m to 9 m during 2017. The water samples were added to 2.5 ml of the preserving agent Lugols iodine in dark bottles prior to sampling. In the laboratory, the sample was left to settle resulting in a 5 ml final supernatant. Samples were stored in a cool room at a constant temperature and stored to avoid exposure to light, the samples were also checked periodically for evaporation losses and topped up with Lugols and/or water if necessary. Analysis of the meteorological data, multi-parameter sonde data and chemically determined chlorophyll *a* concentrations were used to determine which phytoplankton samples to count (Chapter 7).

Phytoplankton samples were counted using the PlanktoMetriX (PMX) software (Zohary *et al.*, 2016). PMX is an image analysis system designed for counting and measuring organisms in the size range of 1-1000 µm using a microscope. PMX is the first programme to allow the counting and measuring of phytoplankton and the instantaneous calculation of biovolumes and biomass. Prior to analysis, a database was created within PMX using phytoplankton count data from 2011-2015 to identify the species common to Blelham Tarn. In total 142 different species of phytoplankton were identified, the CEN, (2014) guidance was then used to identify the geometric shape and equations needed to calculate the biovolume for each species. The appropriate equations were then assigned to each species within the database.

Having analysed chemically determined chlorophyll *a* data and chlorophyll *a* fluorescence data from the same sample days it was decided that only samples collected in the top 5 m of the water column were to be counted, as below 5 m there was very little chlorophyll *a* biomass. To increase counting efficiency a sub-sample taken from 1 m was used to identify the species present and to accumulate ten measurements for each species. These measurements were averaged and the biovolumes were applied to samples 1-5 m.

Phytoplankton populations were counted using an Olympus BX45 inverted microscope with the sample being contained within a Lund chamber and cover slip (Lund, 1959). The counting of the phytoplankton is based on the number of individuals observed in a known number of random fields of view in a chamber of known area and volume. Larger phytoplankton were counted at a magnification of x100 whereas nanophytoplankton were counted at a magnification of x400. A random position in the chamber was selected and all phytoplankton in the field were counted, if a phytoplankton was positioned in between fields it was counted if at least 50 % of the cell or colony was inside the field of view and excluded if less than 50 % of the cell or colony was visible inside the field of view. When counting, 100 fields of view were examined at a magnification of x100 and 100 fields of view were examined at x400. The preferences were set to limit the phytoplankton counts to 100 individuals, after this number, individuals were no longer counted.

3.2.3 Phytoplankton community modelling: Phytoplankton RespOnses To Environmental CHange (PROTECH) model

PROTECH is a process-based phytoplankton community model that simulates the growth of selected phytoplankton within a given lake (Elliott *et al.*, 2010). PROTECH is a well-established model that has been successfully used in numerous studies of lakes and reservoirs within the UK, Europe and beyond (Elliott *et al.*, 2010). Previously, the model has successfully simulated Blelham Tarn, to investigate the intermediate disturbance hypothesis (Elliott *et al.*, 2001), the impacts of changing retention times on phytoplankton communities (Jones and Elliott, 2007) and the impacts of changes in background extinction on phytoplankton communities (Bernhardt *et al.*, 2008) amongst others. The model can simulate the growth of up to 18 species in 0.1 m layers, however the model is typically run with 8-12 species.

The model is unique as the growth of the phytoplankton is species specific and determined by the morphometry of the phytoplankton. The daily growth rates of phytoplankton within the model vary depending on temperature, light, and nutrients (phosphorus, nitrate and silica) as well as losses due to sinking and grazing. The model assumes that each phytoplankton species will grow at its maximum rate provided that there are no environmental constraints. Species are also assigned specific movement characteristics such as non-buoyant and non-motile, neutrally buoyant and non-motile, buoyancy regulating or swimming flagellates (Elliott *et al.*, 2010).

The depth of mixing within PROTECH can be fixed (as in Chapter 5), pre-determined using high resolution water temperature data or calculated from thermal structure models within PROTECH (Elliott *et al.*, 2010). The depth of mixing within the model determines the light and nutrient environment that phytoplankton are exposed to and within PROTECH the phytoplankton are actively mixed throughout the defined mixed layer.

4 Wide-spread inconsistency in estimation of lake mixed depth impacts interpretation of limnological processes

(Gray, E., Mackay, E. B., Elliott, J. A., Folkard, A. M., & Jones, I. D. (2020). Wide-spread inconsistency in estimation of lake mixed depth impacts interpretation of limnological processes. Water Research, 168, 115136; doi: https://doi.org/10.1016/j.watres.2019.115136).

4.1 Highlights

- Different definitions of the mixed depth produce highly inconsistent estimates
- Interpretation of ecological processes can be shaped by the mixed depth definition
- Studies should assess the robustness of their findings to mixed depth definition

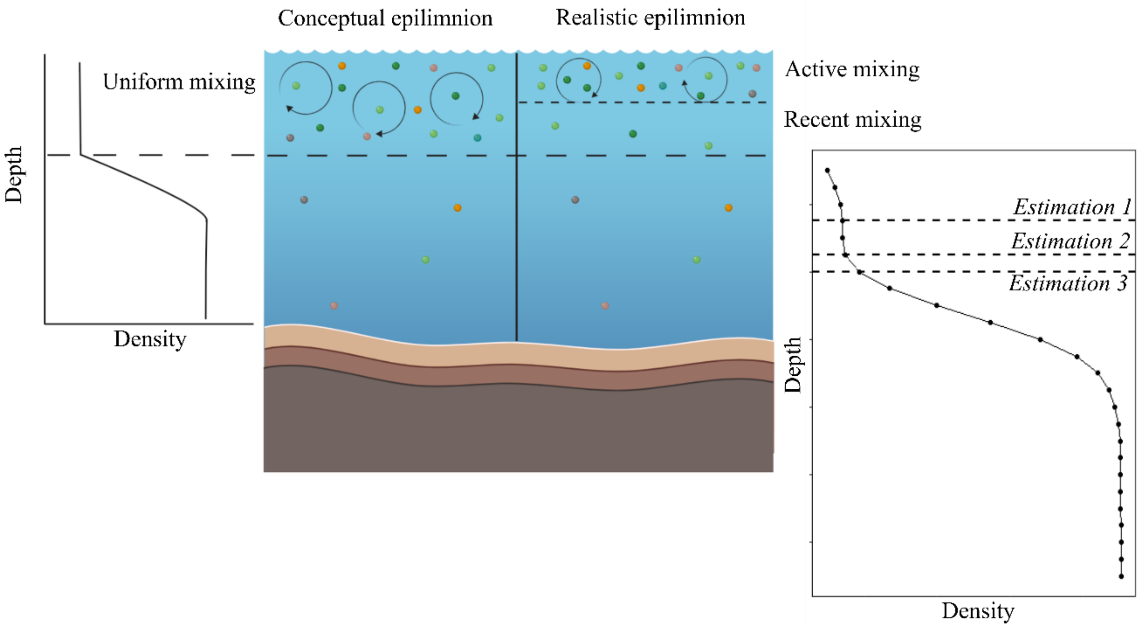
4.2 Abstract

The mixed layer, or epilimnion, is a physical concept referring to an isothermal layer at the surface of a water body. This concept is ubiquitous within limnology, is fundamental to our understanding of chemical and ecological processes, and is an important metric for water body monitoring, assessment and management. Despite its importance as a metric, many different approaches to approximating mixed depth currently exist. Using data from field campaigns in a small meso-eutrophic lake in the UK in 2016 and 2017 we tested whether different definitions of mixed depth resulted in comparable estimates and whether variables other than temperature could be assumed to be mixed within the layer.

Different methods resulted in very different estimates for the mixed depth and ecologically important variables were not necessarily homogenously spread through the epilimnion. Furthermore, calculation of simple ecologically relevant metrics based on mixed depth showed that these metrics were highly dependent on the definition of mixed depth used. The results demonstrate that an idealised concept of a well-defined fully mixed layer is not necessarily appropriate. The widespread use of multiple definitions for mixed depth impairs the comparability of different studies while associated uncertainty over the most appropriate definition limits the confirmability of studies utilising the mixed depths.

Keywords: mixed depth, lake, phytoplankton, oxygen, euphotic depth

4.3 Graphical Abstract



4.4 Introduction

The “mixed layer” of a lake is a physical concept referring to a layer at the surface of a lake within which temperature is uniform (Sverdrup, 1953; Robertson and Imberger, 1994). The depth of the mixed layer, or epilimnion, depends on the balance between stratifying and mixing forces, with deepening being driven by wind mixing and convective cooling and shallowing being driven by warming (Wüest and Lorke, 2003). In stratified lakes, this layer typically overlies water in which the mixing rates are significantly smaller, enabling vertical gradients to develop in variables of interest, including temperature, particulate matter and dissolved gasses. This concept is used extensively and underpins our understanding of limnological processes. It is therefore fundamental for monitoring and assessment purposes (Schauser *et al.*, 2003; Peter *et al.*, 2009; Jaša *et al.*, 2019) and studies on the restoration of lakes (Hoyer *et al.*, 2015; Hupfer *et al.*, 2016; Stroom and Kardinaal, 2016) as well as the limnology of lakes (Brainerd and Gregg, 1995; Diehl, 2002; Wüest and Lorke, 2003).

There are, though, many practical problems generated by the concept of an idealised mixed depth. The layer is mixed by turbulence, but turbulence itself is not commonly measured directly. Furthermore, where turbulence has been directly measured it has shown the actively mixing layer can be substantially shallower than the isothermal layer (MacIntyre, 1993; Tedford *et al.*, 2014). These measurements have indicated that temperature differences as little as 0.02 ^{o}C can delineate regions with different mixing rates (MacIntyre, 1993). The “mixed layer” can therefore be sub-divided into two regions; an actively mixed upper layer and a region below whose depth is determined by recent mixing, and characterised as “mixed” by its homogeneity in terms of one or more variables, most commonly temperature or density (Brainerd and Gregg, 1995). As temperatures are frequently only measured to an accuracy of 0.1 or 0.2 ^{o}C, and at only 0.5 m or 1 m vertical resolution or less, the most commonly collected limnological temperature profiles cannot identify this actively mixing layer. It is even questionable whether this depth of recent mixing can be accurately determined using relatively coarse resolution measurements, as sharp changes in gradient can become smeared, blurring the boundary between epilimnion and metalimnion. Furthermore, temperature profiles can be complicated by the presence of secondary thermoclines developing during the daytime, enhancing the potential for confounding results arising from different mixed depth definitions. Such diurnal thermoclines can affect gas fluxes (MacIntyre *et al.*, 2002) and the vertical distribution of nutrients and phytoplankton (MacIntyre and Melack, 1995). These secondary thermoclines can complicate the estimation of a systematically defined mixed depth. Each ecological variable is also subject to different source and sink terms operating at different timescales. Thus, physical mixing within the epilimnion might be sufficient for homogenising a variable with slow rates of production or loss, but the same mixing may be insufficient for homogenising a variable with faster production and loss.

The necessity to infer the mixed depth without direct turbulence measurements has led to a vast array of methods being developed for defining the depth of the mixed layer, typically exploiting the notion of a vertical limnological profile being generated by rapid vertical mixing in the surface waters of a lake and much diminished mixing beneath. A Web of Science search using terms ‘lake’ AND ‘mix* depth’ AND ‘layer’ followed by removal of non-lake references or those referring to sediment mixed depths or chemoclines identified at least 313 research papers explicitly referring to a mixed layer.

Often references to the mixed depth were descriptive (24 %) or theoretical (16 %) rather than quantitative and in 10 % of papers the mixed depth was arbitrarily or visually defined. The remaining studies determined the mixed depth using a variety of methods which included being calculated within lake models (11 %), fixed within mesocosm or laboratory experiments (8 %), directly measured through turbulence (8 %) or calculated using a secondary variable (23 %). The latter method could be categorised into temperature (Coloso *et al.*, 2008) or density gradients (Staehr *et al.*, 2012), temperature (Wilhelm and Adrian, 2007), or density differences (Winder *et al.*, 2009) and isotopic (Imboden *et al.*, 1983) or chemical tracers (Maiss *et al.*, 1994). Temperature gradients were most commonly used to define the mixed depth, followed by density gradients, temperature thresholds and density thresholds. There are, however, at least 20 different thresholds and gradients of temperature or density currently being applied to estimate the mixed depth (Table 4.1).

Implicitly, the common usage of such a wide variety of methods suggests that each one is assumed to define approximately the same depth of mixed layer. If the vertical profiles of a lake match the idealised concept, then this should be true, but any discrepancies from an idealised profile could lead to different methods producing different estimates for the mixed depth. This would make a cross comparison of mixed layer depths between different studies meaningless and poses difficulties for the understanding and quantification of linkages to biological or chemical processes.

These methodological caveats are of particular concern when using the mixed depth as an explanatory or predictive variable in chemical and ecological studies. For example, the mixed depth can control the vertical distribution of phytoplankton and therefore the light climate to which they are exposed (Diehl *et al.*, 2002). The ability for a phytoplankton community to grow and maintain biomass depends on the ratio of the mixed depth to the euphotic depth (Huisman, van Oostveen and Weissing, 1999) in addition to the loss of cells due to sinking and the motility and light affinity of the species in the community (Diehl *et al.*, 2002; Huisman *et al.*, 2002; Jäger *et al.*, 2008). Mixing that encroaches into the hypolimnion during stratification can also incorporate nutrients into the mixed layer increasing their availability for phytoplankton near the surface (Kunz and Diehl, 2003) and mix oxygen into the hypolimnion potentially reducing future internal loading (Mackay *et al.*, 2014). Having a robust estimate of mixing is therefore required to understand the vertical positioning and composition of phytoplankton taxa within a lake, along with the mechanisms of bloom formation (Cyr, 2017) and the associated water quality impacts (Dokulil and Teubner, 2000; Jaša *et al.*, 2019).

Similarly, the vertical pattern of productivity in the water column is influenced by the mixed depth and water clarity (Obrador *et al.*, 2014); therefore lake metabolism studies require a robust mixed depth estimation. The depth of surface mixing determines how much of the water column has regular contact with the atmosphere, influencing the depth of oxygen penetration. This is particularly important in stratified, productive systems where incomplete mixing can result in anoxia in the hypolimnion due to the oxidisation of organic matter by bacteria (Nürnberg, 1995). The direction of the flux of oxygen into and out of the mixed layer will also vary depending on the vertical distribution of primary producers in the water column relative to the mixed depth (Staehr *et al.*, 2010, 2012; Obrador *et al.*, 2014; Peeters *et al.*, 2016).

Despite the widespread use of the mixed depth concept and the large number of methods used to estimate mixed depth, there is a lack of research evaluating the consistency among methods of mixed depth estimation and the implications of using different estimates when interpreting ecological and chemical data. This study therefore aims to: (1) determine if different methods of calculating the mixed depth produce comparable estimates; (2) evaluate the extent to which ecological and chemical parameters are homogenously distributed throughout the mixed depth; (3) evaluate how the choice of mixed depth definition may influence the calculation of simple example metrics relevant to studies of phytoplankton dynamics and metabolism. Analysis of vertical profiles of physical, chemical and ecological parameters collected from a small meso-eutrophic lake in the UK were used to address these aims.

Table 4.1 Examples of temperature and density thresholds and gradients used in existing literature to calculate the mixed layer depth.

Reference	Method
Temperature thresholds	
(Augusto-Silva and MacIntyre, 2019)	0.02 °C from the surface
(Yang *et al.*, 2018)	0.2 °C from the surface
(Zhao *et al.*, 2018)	0.8 °C from the surface
(Mackay *et al.*, 2011)	1 °C from the surface
(Vidal *et al.*, 2010)	0.04 °C from the surface
Temperature gradients	
(Kasprzak *et al.*, 2017)	1 °C m^{-1}
(Coloso *et al.*, 2008)	1 °C /0.5 m
(Xie *et al.*, 2017)	0.01 °C m^{-1}
(Yankova *et al.*, 2016)	0.5 °C m^{-1}
(Özkundakci *et al.*, 2011)	0.25 °C m^{-1}
(Hamilton *et al.*, 2010)	0.225°C m^{-1}
(McCullough *et al.*, 2007)	0.05 °C m^{-1}
(Whittington *et al.*, 2007)	0.02 °C m^{-1}
(Wilhelm and Adrian, 2007)	Depth of the maximum temperature gradient
Density thresholds	
(Andersen *et al.*, 2017)	0.1 kg m^{-3} from the surface
Density gradients	
(Staehr *et al.*, 2012)	0.07 kg m^{-3} m^{-1}

(Giling, Staehr, *et al.*, 2017)	0.03 kg m^{-3} m^{-1} - 0.18 kg m^{-3} m^{-1}
(Tonetta *et al.*, 2016)	0.03 kg m^{-3} m^{-1}
(Zwart *et al.*, 2016)	0.1 kg m^{-3} m^{-1}
(Lamont *et al.*, 2004)	0.5 kg m^{-3} m^{-1}

4.5 Materials and methods

4.5.1 Site description

Blelham Tarn is a small (surface area 0.1 km^2), moderate depth lake (mean depth 6.8 m, maximum depth 14.5 m) (Ramsbottom, 1976), which stratifies typically for seven to eight months each year between spring and autumn. It is located in north-west England, UK (54°24’N, 2°58’W) and lies on the meso-eutrophic boundary (mean total phosphorus 24.5 mg m^{-3}) (Maberly *et al.*, 2016).

4.5.2 Field methods and data collection

Vertical profiles of oxygen, chlorophyll *a* (measured via fluorescence as a proxy for phytoplankton biomass), temperature, specific conductivity and pH were measured using a YSI EXO2 multi-parameter sonde. Given the limitations of chlorophyll *a* fluorescence profiles (Gregor and Maršálek, 2004), water samples for chemical determination of chlorophyll *a* were taken at metre intervals in the water column (1-10 m) using standard methods (Mackereth *et al.*, 1979). Vertical profiles of chlorophyll *a* obtained using both methods were compared visually and statistically using linear regression (R^2=0.53, $p<0.001$). The probes were calibrated every six weeks according to manufacturer specifications. Profiles were measured weekly between 9:30 am and 11 am during the stratified period (46 sample days), defined here as when the density difference from the surface to the bottom was greater than 0.1 kg m^{-3}, at 0.5 m intervals in the water column from 1 m to 13 m (2016) and 0.5 m to 13 m (2017).

A LI-COR underwater quantum cos-corrected sensor was also used to measure photosynthetically active radiation (PAR); measurements were taken just below the surface and then at one-metre intervals from 1 m to 9 m. The natural logarithm of the PAR measurements were regressed with depth and the slope of the equation was used to estimate the extinction coefficient (k) for each sample day. The euphotic depth (z_{eu}) was then defined as the depth where only 1 % of the surface measurement of PAR remained,

Equation 4.1 $$z_{eu} = ln(100)\,/k.$$

4.5.3 Methods for estimating mixed depth, z_{mix}

Four methods of mixed depth estimation were tested for consistency, the first two methods used threshold changes in density (Method 1a) and temperature (Method 1b) from surface values to determine the depth of the mixed layer whereas Methods 2 and 3 determined the depth of the mixed layer statistically (Figure 4.1).

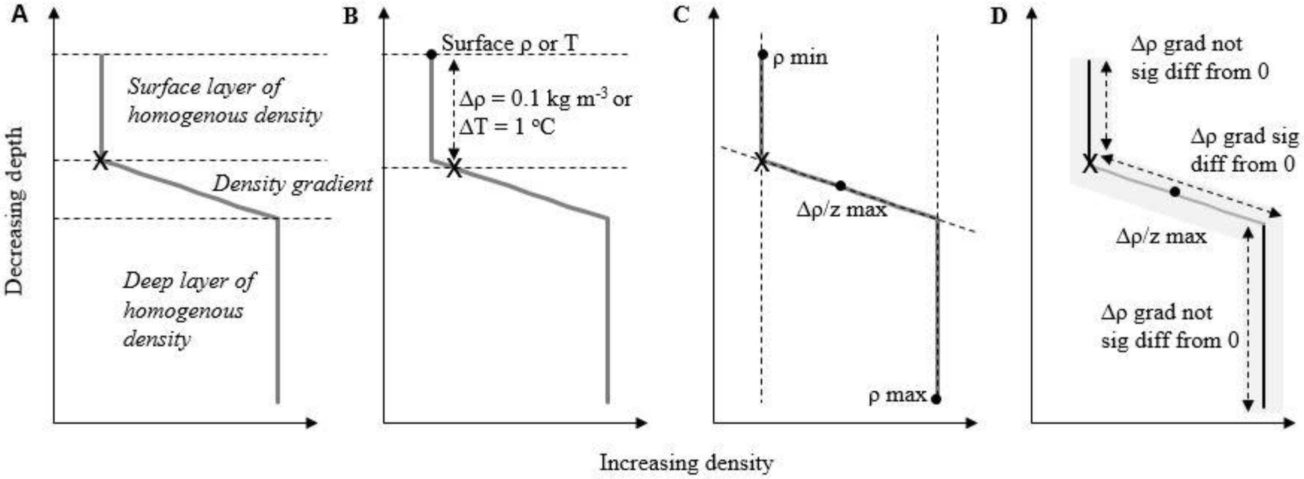


Figure 4.1 Diagram of density profiles marking the mixed depth (X) for (a) a theoretical mixed depth; (b) estimating the mixed depth using a 0.1 kg m^{-3} or 1 °C difference from the surface (Surface ρ or T) (Methods 1a and b); (c) estimating the mixed depth using Method 2 where lines are extended from the depth of the maximum gradient (Δρ/Δz max), the density minimum (ρ min) and the density maximum (ρ max) with the upper intersection of the lines marking the top of the pycnocline or base of the mixed depth and (d) estimating the mixed depth using Method 3 were the upper and lower values of the section of the profile containing the depth of the maximum gradient (Δρ/Δz max) and a change in the density gradient (Δρ grad) significantly different from zero marking the mixed depth and the top of the hypolimnion, respectively, the grey shading marks the profile confidence intervals.

4.5.3.1 Method 1a: Density threshold

The baseline mixed depth for this study was calculated as the depth at which the density first became 0.1 kg m^{-3} greater than the density at the surface (e.g. Andersen *et al.*, 2017) (Figure 4.1). Water density was calculated using water temperature and salinity from equations within Lake Analyzer (Read *et al.*, 2011). Salinity was calculated from conductivity using the GibbsSeaWater (GSW) Oceanographic Toolbox (McDougall and Barker, 2011).

4.5.3.2 Method 1b: Temperature threshold

Temperature is frequently used instead of density to define the mixed layer, therefore a 1 ^{o}C difference in temperature from the surface was used, roughly equating to a 0.1 kg m^{-3} density difference at moderate water temperatures. Below these temperatures the density difference will be smaller and vice versa for higher temperatures (Figure 4.1).

Equivalent and directly comparable threshold methods cannot be applied to chemical and ecological variables due to their different units of measure. Therefore, two statistical methods were used which avoid the use of an arbitrary threshold or gradient and could therefore be applied to profiles of chlorophyll *a* fluorescence, oxygen, pH and specific conductivity, as well as density profiles. If the idealised concept of the stereotypical shape of the vertical density profile holds true then both these statistical methods should provide estimates of mixed depth which are reasonably consistent with each other and with the mixed depth estimated by a density threshold (Figure 4.1). Similarly, if the epilimnion is truly mixed then applying these methods to other limnological variables should also estimate a comparable depth for the bottom of the mixed layer.

4.5.3.3 Method 2: Intersection of the plane of maximum gradient with the plane of the profile minimum (or maximum)

A Generalised Additive Model (GAM) with a gamma error distribution and logarithm link function was fitted to every profile for each variable collected (46 sample days, 6 variables = 276 profiles in total) using the mgcv package (version 1.8-26) (Wood, 2011) within the R programming language (RCoreTeam, 2018). The number of knots used in the GAM were optimized and fixed for each variable and the fitted values were predicted at 0.5 m depth intervals. Using the fitted predictions, the first derivative was calculated using forward differences to find the depth of the maximum gradient. At the depth of the maximum gradient the plane was extrapolated to all depths using the intercept and slope. Vertical lines were then drawn corresponding to the mean of three maximum and minimum values from each profile. The depth where the vertical lines intersected the extended maximum gradient line marked the top and bottom of the thermocline, or equivalent for other variables, that is, the mixed layer depth and the top of the hypolimnion, respectively (Figure 4.1).

4.5.3.4 Method 3: Depth of statistically significant deviation

Using the confidence intervals from the first derivative of the fitted GAM, the sections of the profile where changes in the gradient were significantly different from zero were calculated (Simpson, 2018). The section of the profile that contained the depth of the maximum gradient was identified, with the upper and lower values of this section being the mixed depth and the top of the hypolimnion, respectively (Figure 4.1).

4.5.4 Comparison of mixed depth method estimates

To compare the differences in mixed depth estimates, the mean difference (including the directional sign of the difference i.e. shallower or deeper), mean absolute difference (not including the directional sign), root mean square error and the range were calculated for the different estimates of mixed depth for each sample day. The relative shift in the mixed depth (shallowing, deepening or no change) was calculated between sample days as well as the percentage of instances in which the methods were consistent. Initial comparisons were made between temperature and density thresholds (Methods 1a and 1b), followed by comparing Method 1a with the two statistical methods (Methods 2 and 3).

Statistical models were then used to determine if the depth of the mixed layer calculated from density using Method 2 was a good predictor for the depth of the mixed layer calculated by Method 2 from the other variables. A similar assessment was carried out using Method 3. This was initially assessed by linear regression of the density-derived mixed depth against the depth of the mixed layer derived from chlorophyll *a*, oxygen, pH and specific conductivity profiles. The residuals from each regression were visually inspected for normality, homoscedasticity, autocorrelation, and the influence of outliers with no issues found. Non-linearity was initially assessed visually and then each model was fitted with a quadratic density-derived mixed depth term to optimise the model fit. The density-derived mixed depth as a predictor of the mixed depth calculated from oxygen and specific conductivity profiles was better described using a quadratic model whereas the equivalent for chlorophyll *a* and pH were best described using a linear model based on the F-test.

4.5.5 Determining the homogeneity of ecological and chemical parameters within the mixed depth

The coefficient of variation (expressed as a percentage) and the range of values for temperature, chlorophyll *a*, oxygen, specific conductivity and pH within the mixed layer were calculated for each method of mixed depth estimation and compared to the equivalent variation for the whole water column.

4.5.6 Calculation of example metrics using different mixed depth estimates

The following metrics were calculated for each sample day using mixed depth estimates for Method 1a, Method 2 and Method 3: (a) the percentage of oxygen and chlorophyll *a* within the mixed layer and whether more than 50% of chlorophyll *a* and oxygen were contained within the mixed layer, (b) the directional flux of oxygen, that is, the sign of the difference in the mean concentration of oxygen in the mixed layer compared to the concentration 0.5 m below and, (c) the ratio between the mixed depth and euphotic depth.

4.6 Results

4.6.1 Comparing mixed depth estimates

4.6.1.1 Methods 1a and 1b

Mixed depth estimates calculated using temperature were on average 0.7 m deeper than estimates calculated from the density baseline, equivalent to an increase of 70 %. The RMSE was 1.1 m. The differences differed temporally (Figure 4.2) with the maximum daily range in values being 5.5 m.

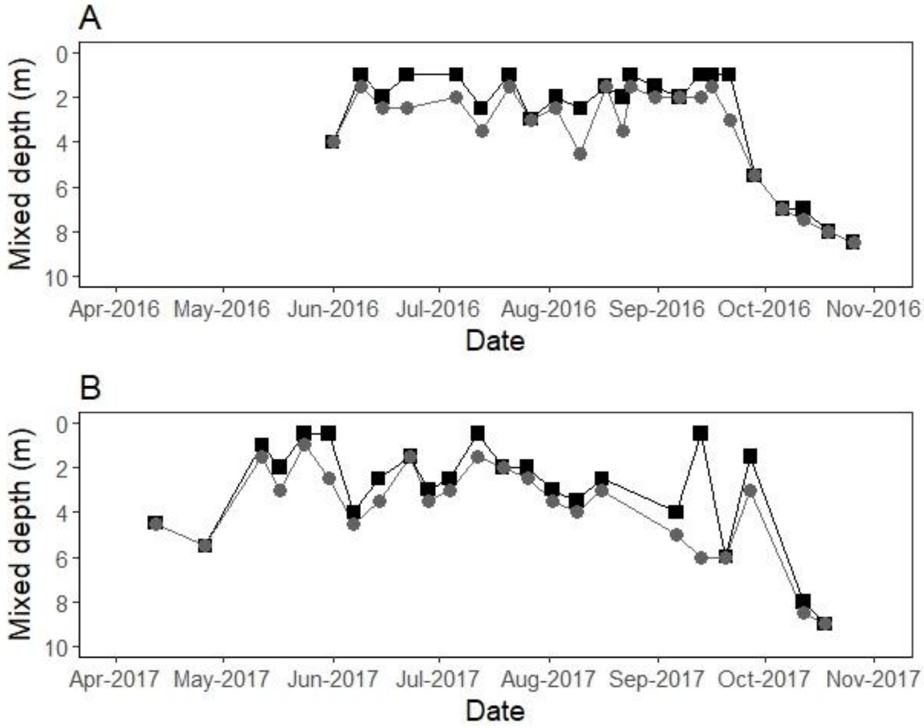


Figure 4.2 Mixed depth estimates using Method 1a (density threshold; black square) and Method 1b (temperature threshold; grey circle) in (a) 2016 and (b) 2017.

4.6.1.2 Methods 1a, 2 and 3

There were large differences between the density-derived estimates of mixed depth calculated using the three different methods (Figure 4.3). Method 2 estimates were shallower than Method 1a by 0.8 m on average, whereas Method 3 estimates were deeper by 0.6 m (Table 4.2). The daily differences in the estimates had no consistent systematic pattern (Figure 4.3), with the largest daily range in values (5 m) occurring between Method 1a and Method 2. The methods were also inconsistent on whether there was shallowing, deepening or no change in the mixed depth between sample days with methods only being directionally consistent for 51 % of sample days (one method disagreed for 42 % of sample days and three different answers occurred for 7 % of sample days).

Table 4.2 The mean difference, root mean square error (RMSE) and range in mixed depth estimates as calculated using Methods 1a, 1b, 2 & 3. Negative values indicate that the latter mixed depth estimates are deeper.

	M1a-M1b	M1a-M2	M1a-M3
Mean difference (m)	0.7	0.8	-0.6
Mean absolute difference (m)	0.7	1.2	1.3
Mean percentage difference (%)	70	108	77
RMSE (m)	1.1	1.7	1.6
Range (m)	5.5	5	4.5

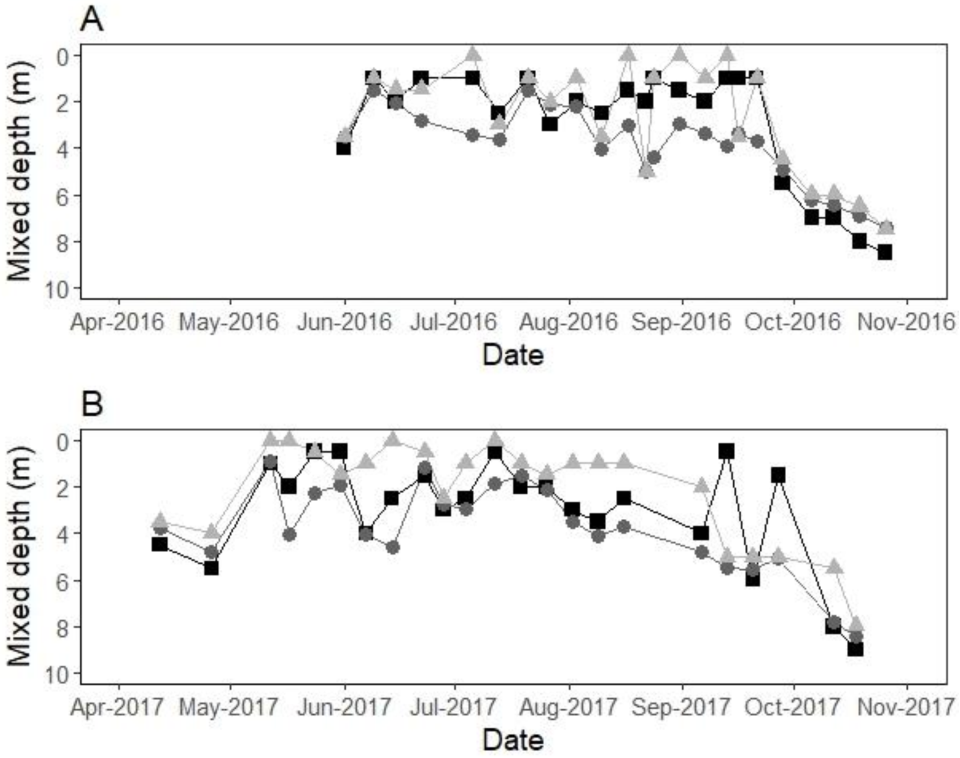


Figure 4.3 Density-derived mixed depth estimates using Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) (a) 2016 and (b) 2017.

4.6.2 Using the density-derived estimate as a predictor for ecological and chemical derived estimates of mixed depth

Mixed depths calculated using ecological and chemical parameters were varied and dissimilar from the estimates calculated from density (Figure 4.4). The density-derived estimate was found to be a poor predictor for the estimates using chlorophyll *a*, pH and specific conductivity profiles, with low *F*-statistic values and weak or insignificant r^2 and *p*-values (Table 4.3). A significant relationship was found between the depth of the oxygen derived mixed depth and the density derived mixed depth using a quadratic model. Further statistical testing, however, demonstrated that at depths shallower than

4.5 m the density derived mixed depth was a poor predictor for the equivalent oxygen derived mixed depth.

Mixed depth estimates were also a poor predictor of the chlorophyll *a* maxima for 2016 and 2017 and a good predictor for the depth of the oxygen maxima during 2016 using Method 3 but not during 2017 when no significance was found (Table 4.3).

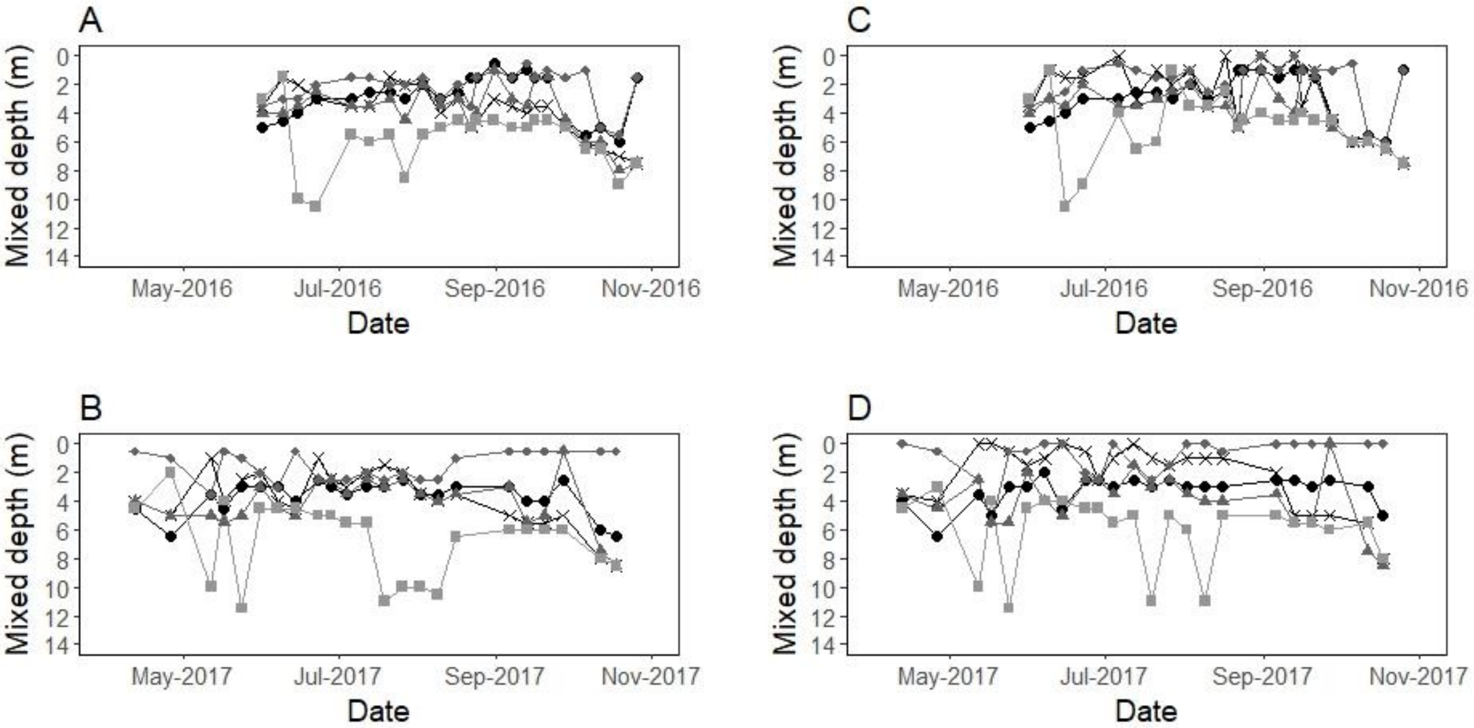


Figure 4.4 Depth of the mixed layer calculated from density (✕), chlorophyll a *(●), oxygen (▲), pH (◆) and specific conductivity (■) for (a) 2016 using Method 2, (b) 2016 Method 3 (c) 2017 Method 2 and (d) 2017 Method 3.*

Table 4.3 Statistical model coefficients and adjusted R^2 values for the depth of the density-derived mixed depth compared with the mixed depth calculated from chlorophyll a*, oxygen, specific conductivity and pH as well as the depth of the chlorophyll* a *and oxygen maxima for Method 2 and Method 3. The significance level is denoted as ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$, ·$p < 0.1$, ns- not significant. Quadratic models were used for oxygen and specific conductivity whereas linear models were used for chlorophyll* a*, chlorophyll* a *maxima, oxygen maxima and pH, 2016 n=23; 2017 n=23.*

	2016								**2017**							
	Residual SE		F-statistic		Adjusted R^2		p-value		Residual SE		F-statistic		Adjusted R^2		p-value	
	M2	M3	M2	M3	M2	M3	M2	M3	M2	M3	M2	M3	M2	M3	M2	M3
Chlorophyll a	1.57	1.58	1.50	4.64	0.02	0.14	ns	*	0.88	1.07	20.74	1.00	0.47	<0.01	***	ns
Oxygen	0.93	0.99	31.57	23.33	0.74	0.67	***	***	1.24	1.57	11.61	6.16	0.49	0.38	***	***
pH	1.25	1.45	1.84	7.29	0.04	0.26	ns	ns	0.75	1.27	18.18	4.67	0.44	0.14	***	ns
Specific Conductivity	2.07	2.23	1.46	1.17	0.04	0.02	ns	ns	2.51	2.47	2.2	1.07	0.1	<0.01	ns	ns
Chlorophyll a maxima	1.71	1.23	0.20	0.92	-0.04	<0.01	ns	ns	2.02	0.96	0.02	1.04	-0.05	<0.01	ns	ns
Oxygen maxima	1.59	1.46	3.77	15.87	0.11	0.40	.	***	2.02	1.22	0.03	0.28	-0.05	-0.03	ns	ns

4.6.3 Determining the homogeneity of limnological variables within the mixed layer

As expected, temperature had a small coefficient of variation and range of values within the mixed layer compared to the whole water column suggesting a homogenous distribution of heat within the mixed layer (Figure 4.5; Table 4.4). The coefficient of variation and range of values in the mixed layer for specific conductivity were also small relative to the whole water column suggesting homogeneity (Figure 4.5; Table 4.4). Though the coefficient of variation was relatively low for oxygen in the mixed layer, values could differ by up to 2.4 mg/L at times suggesting that oxygen concentrations were not always homogenous (Figure 4.5; Table 4.4). Chlorophyll *a* and the concentration of hydrogen ions demonstrated the largest coefficients of variation and range of values in the mixed layer relative to the water column (Figure 4.5; Table 4.4) and therefore had a heterogeneous distribution in the mixed layer for much of the stratified period (Figure 4.5).

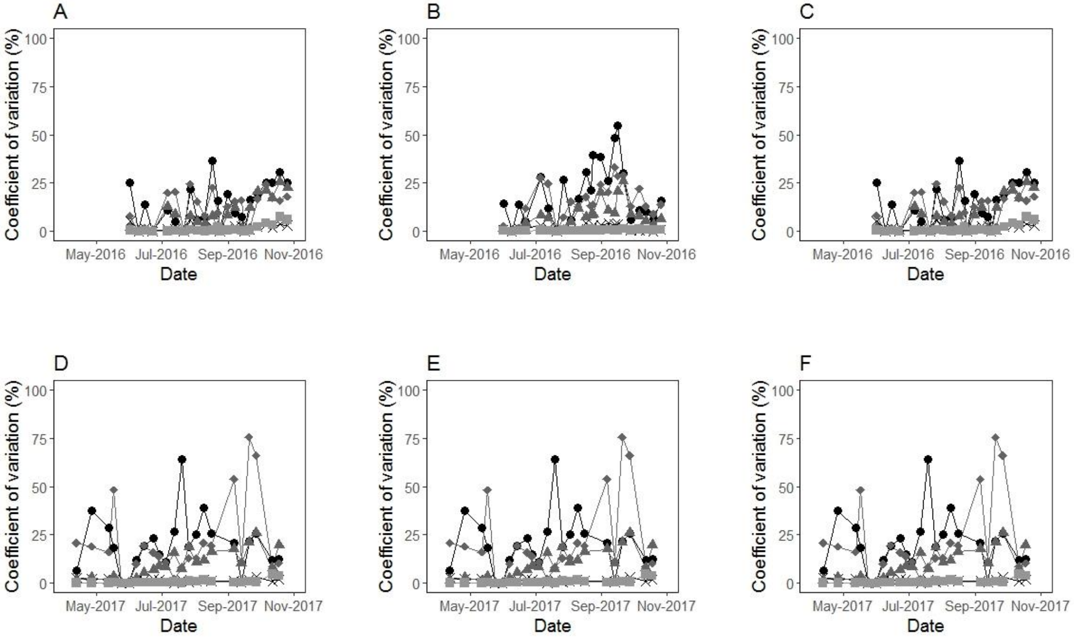
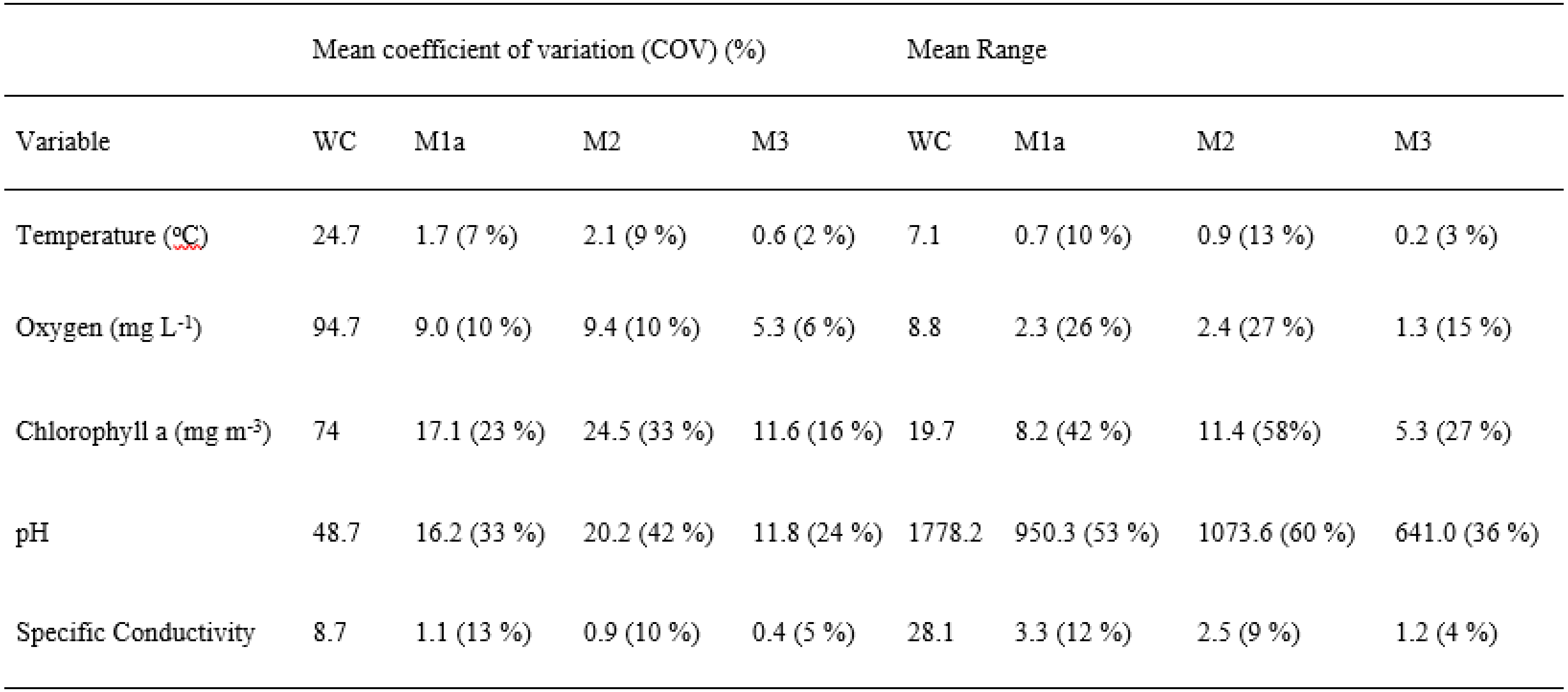


Figure 4.5 The coefficient of variation in the mixed layer for temperature (✳), chlorophyll a *(●), oxygen (▲), concentration of hydrogen ions (pH) (◆) and specific conductivity (■) for (a) 2016 Method 1a, (b) 2016 Method 2 , (c) 2016 Method 3, (d) 2017 Method 1a, (e) 2017 Method 2 and (f) 2017 Method 3.*

Table 4.4 The coefficient of variation (COV) and the range of temperature, oxygen, chlorophyll a, *concentration of hydrogen ions (exponential of pH) and specific conductivity values in the water column (WC) and the mixed layer for Method 1a (M1a), Method 2 (M2) and Method 3 (M3), percentage values in brackets depict the percentage variation in the mixed layer relative to the whole water column variation.*



	Mean coefficient of variation (COV) (%)				Mean Range			
Variable	WC	M1a	M2	M3	WC	M1a	M2	M3
Temperature (ºC)	24.7	1.7 (7 %)	2.1 (9 %)	0.6 (2 %)	7.1	0.7 (10 %)	0.9 (13 %)	0.2 (3 %)
Oxygen (mg L^{-1})	94.7	9.0 (10 %)	9.4 (10 %)	5.3 (6 %)	8.8	2.3 (26 %)	2.4 (27 %)	1.3 (15 %)
Chlorophyll a (mg m^{-3})	74	17.1 (23 %)	24.5 (33 %)	11.6 (16 %)	19.7	8.2 (42 %)	11.4 (58%)	5.3 (27 %)
pH	48.7	16.2 (33 %)	20.2 (42 %)	11.8 (24 %)	1778.2	950.3 (53 %)	1073.6 (60 %)	641.0 (36 %)
Specific Conductivity	8.7	1.1 (13 %)	0.9 (10 %)	0.4 (5 %)	28.1	3.3 (12 %)	2.5 (9 %)	1.2 (4 %)

4.6.4 The impact of using different mixed depth estimates when calculating example metrics

4.6.4.1 The percentage of chlorophyll *a* and oxygen within the mixed layer

The mean percentage of chlorophyll *a* in the mixed layer during the stratified period differed between methods. Even the proportion of days when the majority (>50 %) of chlorophyll *a* was contained within the mixed layer varied greatly depending upon the mixed layer estimation method (Figure 4.6). For 2016 the proportion of days when the majority of chlorophyll *a* was contained within the mixed layer was 35 %, 74 % and 39 % for Methods 1a, 2 and 3 respectively, whereas for 2017 the values were 48 %, 65 % and 30 %. The methods only all agreed for 50 % of sampling days on whether the majority of chlorophyll *a* was contained within the mixed layer (Figure 4.6). The mean percentage of oxygen in the mixed layer for the whole of the stratified period also differed depending on the definition used for mixed depth (Figure 4.6). The proportion of days when the percentage of oxygen in the mixed layer was greater than 50 % varied between methods (Figure 4.6). For 2016 the proportion of days when the majority of oxygen was contained within the mixed layer was 43 %, 83 %, and 43 % for Methods 1a, 2 and 3 respectively whereas for 2017 the values were 61 %, 74 % and 35 %. The methods all agreed on whether the majority of oxygen in the water column was in the mixed layer for less than half (46 %) of the sampling days (Figure 4.6).

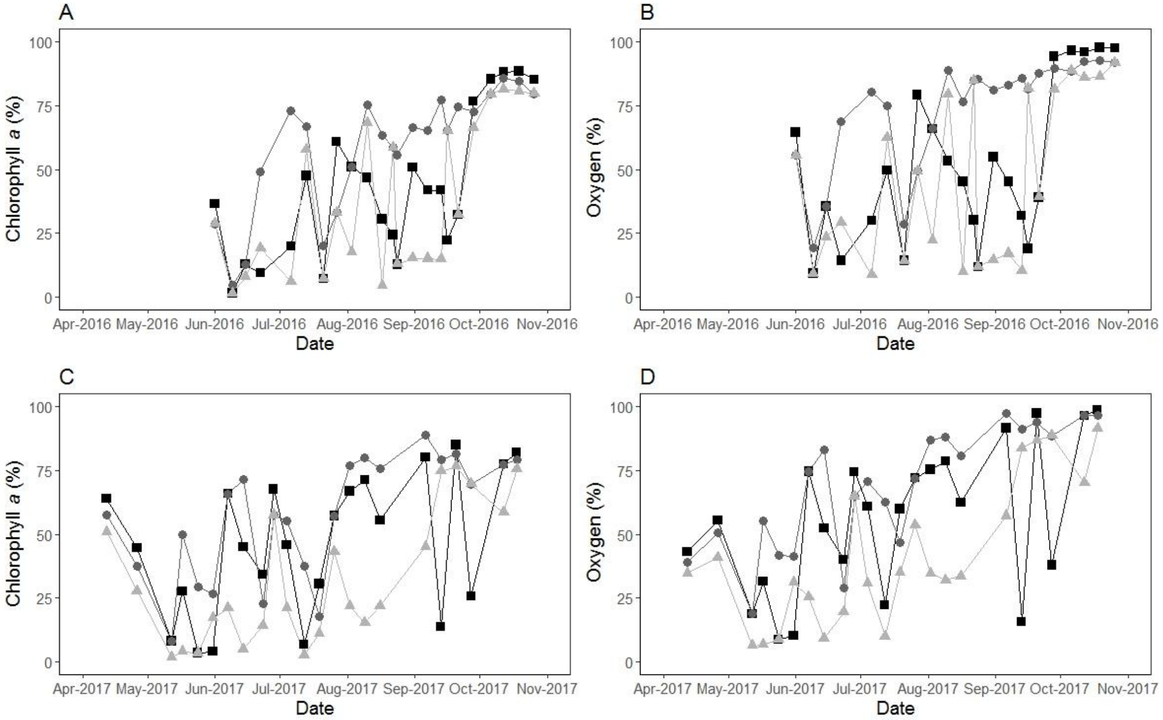


Figure 4.6 The percentage of chlorophyll a *and oxygen within the mixed layer using mixed depth estimates calculated using Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) for (a) chlorophyll* a *in 2016, (b) oxygen in 2016, (c) chlorophyll* a *in 2017 and (d) oxygen in 2017.*

4.6.4.2 The directional flux of oxygen

The direction of the flux of oxygen between the mixed layer and the layer below, as determined by whether concentration was greater within or beneath the mixed layer, was not always consistent between methods with contradictory results occurring 24 % of the time (Figure 4.7). Even when the direction of the oxygen flux was consistent between methods the size of the gradient between the mixed layer and the water directly underneath was markedly different (Figure 4.7). Thus, both the direction and magnitude of the flux of oxygen between the mixed layer and the thermocline were highly dependent on how the mixed layer depth was defined.

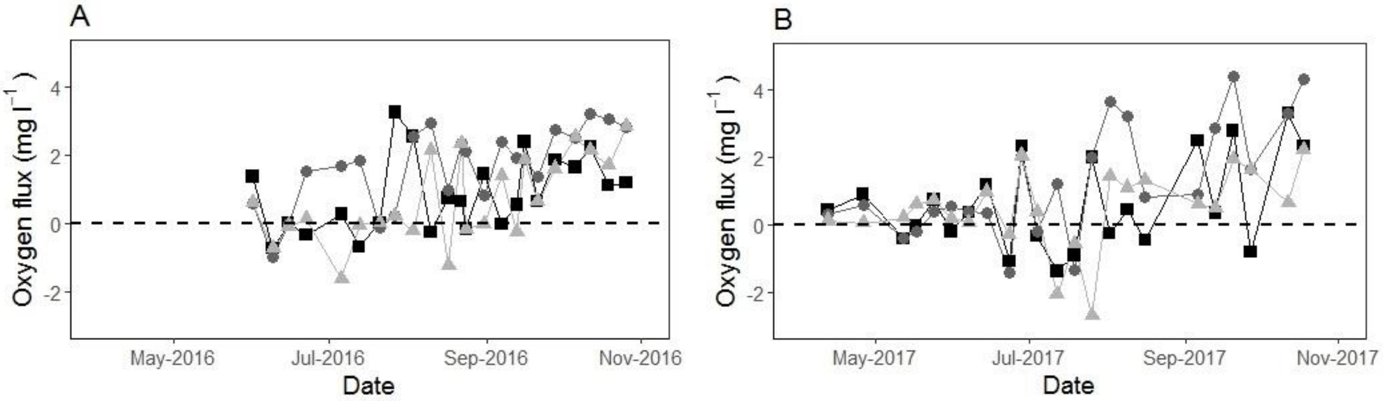


Figure 4.7 The difference in the concentration of oxygen within the mixed layer compared to the concentration in the layer 0.5 m below using mixed depth estimates calculated from Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) for (a) 2016 and (b) 2017.

4.6.4.3 Mixed layer to euphotic layer depth ratio

The ratio of mixed depth to euphotic depth was very different depending on which method was used to calculate mixed depth (Figure 4.8). The mean ratio calculated using Method 2 (0.9) was typically greater than that using Method 1a (0.7), which was itself greater than that using Method 3 (0.6). As well as the systematic differences there was also a lot of temporal variation between the consistency of the estimates (Figure 4.8). The mean difference between the mixed depth to euphotic depth ratio between Method 1a and Method 2 was 0.32 and between Method 1a and Method 3 was 0.90, with methods being contradictory as to whether the euphotic or the mixed depth was deeper for 20 % of sample days (Figure 4.8).

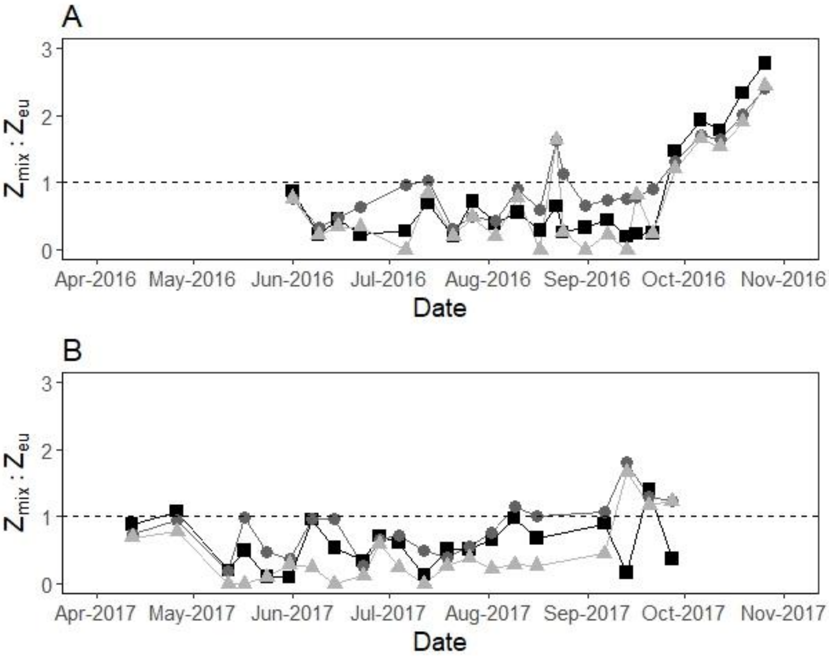


Figure 4.8 The z_{mix}:z_{eu} ratio calculated using density derived mixed depth estimated using Method 1a (black square), Method 2 (grey circle) and Method 3 (light grey triangle) for (a) 2016 and (b) 2017. Values below the horizontal y intercept line at 1 z_{mix}:z_{eu} mark when mixed depths are shallower than the euphotic depth and vice versa for values above.

4.7 Discussion

The results demonstrate that different approaches to mixed depth estimation are not necessarily comparable, even when those methods are underpinned by the same conceptual description of a mixed depth. This is the case when the same method is used with different variables (Figure 4.4) or when different methods are used with the same variable (Figure 4.3). It is particularly worth noting that, estimations of mixed depth from temperature profiles differ from estimations of mixed depth derived from density profiles (Figure 4.2). This is partly due to the non-linear relationship between temperature and density and partly due to the deviation of observed density profiles from an idealised profile, such as when both diel and seasonal pycnoclines are present. The functional role density gradients have in influencing mixing rates suggests that density be preferred to temperature as a variable for defining mixing length scales, despite the frequency with which temperature is still used (Table 4.1). The number of methods and variables examined here for estimating mixed depth is a relatively small sample compared with the vast array of mixed depth definitions in the literature (Table 4.1). Nevertheless, they indicate that even the direction of change in mixed depth over time can be dependent on the method chosen for its calculation. To some extent the development of automated tools for calculating mixed depth such as Lake Analyzer (Read *et al.*, 2011), offers a means to reduce the proliferation of definitions.

It is not necessarily the case though, that, a single definition of mixed depth estimation is always appropriate, as different definitions might be better suited to different conditions or different ecological questions. An example is the variety of mixed layer definitions used in a study comparing depth-related oxygen metabolism across disparate lakes

(Giling, Staehr, *et al.*, 2017), where it was considered that no one definition was suitable for all the lakes. It may also be sometimes appropriate, depending on the purpose of the study, to adopt a definition using a different variable than density or temperature, as the occurrence of a homogenous surface layer in one property does not guarantee that it will be homogenous in another property (Figure 4.5 and Table 4.4). Studies interested in identifying homogenous distributions of phytoplankton, for example, for which gradients of light and nutrients as well as turbulence are controlling their distribution (Huisman, van Oostveen and Weissing, 1999; Kunz and Diehl, 2003), could be inaccurate if a density definition of mixed layer was used. That the depth of the mixed layer is highly dependent on the definition, and that not all properties will be evenly distributed within it, necessitates caution when analysing vertically resolved limnological data. Even the analysis of simple metrics relating to the distribution of chlorophyll *a* and oxygen demonstrates that the choice of mixed depth definition could influence the interpretation of results (Figures 4.6-4.8). Thus, where phytoplankton samples are integrated over the epilimnion for assessing water quality (Noges *et al.*, 2010) the assessment could be influenced by the definition of mixed layer adopted. Similarly, whether phytoplankton maxima are within or beneath the mixed layer will depend on the definition chosen. The oxygen flux into and out of the mixed layer is important for metabolism studies (Obrador *et al.*, 2014), but the magnitude of the oxygen gradient between layers, and therefore the magnitude and direction of the oxygen flux, is highly dependent on the definition of mixed depth (Figure 4.7). Nutrient fluxes will be similarly dependent on definition, which may have consequences for water quality determination and restoration responses (Schauser *et al.*, 2003; Read *et al.*, 2014; Hupfer *et al.*, 2016). In general, the accuracy of flux estimated will be limited without turbulence measurements. The widely used ratio of the mixed depth to euphotic depth was also dependent on the definition of mixed depth used (Figure 4.8). This is consequential, when explaining the formation of sub-surface phytoplankton maxima, which are thought to occur in eutrophic systems when the euphotic depth is deeper than the mixed depth (Hamilton *et al.*, 2010; Mellard *et al.*, 2011; Leach *et al.*, 2018).

The interrogation and interpretation of vertical profiles is a fundamental and burgeoning area of limnological study (Hamilton *et al.*, 2010; Obrador *et al.*, 2014; Brentrup *et al.*, 2016; Leach *et al.*, 2018) and will require careful consideration of how best to use mixed depth as a predictive or explanatory variable or as a determinant of water quality monitoring. One approach is to assess the impact of using different mixed depth estimates when analysing results. For example, the Giling, Staehr *et al*., (2017) study on metabolism found that halving or doubling the threshold density gradient used to estimate the mixed depth changed the estimated thickness of the metalimnetic depth zone by 22 %. For the study, this inconsistency was deemed relatively insignificant to the findings, however the authors highlighted that this would become problematic when aggregating metabolic rates to the metalimnion and hypolimnion (Giling, Staehr, *et al.*, 2017). Another approach is to examine systematically which method or methods are more consistently useful than others for approximating a mixed depth.

4.8 Conclusions

By testing three methods of mixed depth and using them to calculate simple ecological and chemical metrics this study has demonstrated that methods of mixed depth estimation are inconsistent and influence the interpretation of chemical and ecological results. Based on these findings we recommend that future studies should:

- Favour density over temperature for estimating the mixed depth
- Not assume homogeneity of other variables within the mixed layer
- Assess the sensitivity of the findings of the study to mixed depth definition or
- Examine several methods to choose the most consistent and useful method for the study

Ultimately, any method adopted for estimating mixed depth from standard limnological data should be used cautiously and with awareness of the potential deviation of observed profiles from idealised ones.

5 Modelling lake cyanobacteria blooms: disentangling the climate-driven impacts of changing mixed depth and water temperature

(Gray, E., Elliott, J. A., Mackay, E. B., Folkard, A. M., Keenan, P. O., & Jones, I. D. (2019). Modelling lake cyanobacterial blooms: Disentangling the climate-driven impacts of changing mixed depth and water temperature. *Freshwater Biology*. doi: https://doi.org/10.1111/fwb.13402)

5.1 Summary

1. Climate change is already having profound impacts upon the state and dynamics of lake ecosystems globally. A specific concern is that climate change will continue to promote the growth of phytoplankton, particularly blooms of toxic cyanobacteria, via lake physical processes including warming surface waters and shallowing of the mixed layer. These two mechanisms will have different impacts on lake phytoplankton communities, but their inter-connectedness has made it difficult to disentangle their independent effects.
2. We fill this knowledge gap by performing 1666 numerical modelling experiments with the phytoplankton community model, PROTECH, in which we separated the independent effects on lake phytoplankton of temperature change and changes in the depth of the surface mixed layer. Given the large global abundance of small lakes (< 1 km^2) and the importance of their ecosystems in global processes and

budgets, we used a small meso-eutrophic lake as an example study site for the modelling experiments.

3. Increasing the lake temperature and positioning the mixed layer at a shallower depth had different ecological impacts, with warming typically resulting in more biomass and a dominance of cyanobacteria.
4. The response to mixed depth shallowing depended on the original depth where mixing occurred. As anticipated, where the original mixed depth was moderate (4–6 m) and there was a simultaneous increase in water temperature, cyanobacterial biomass increased. However, when the same absolute difference in shallowing and temperature increase were applied to a deeper mixed depth (9–13 m), lower cyanobacterial biomass resulted, owing to poorer conditions for low-light tolerant cyanobacteria.
5. Our study shows that the response of cyanobacterial blooms to climate-induced warming and shallowing of mixed layers in lakes around the world will not be universal, but rather will be system-specific, depending upon the average mixed layer depth of the lake in question and the light affinity of the dominant cyanobacteria species.

5.2 Introduction

Climate change is impacting phytoplankton communities in lakes across the world through direct and indirect effects of temperature change (Winder and Sommer, 2012; Huisman *et al.*, 2018). Though intrinsically linked, water temperature, the duration of lake stratification and the depth of the surface mixed layer have independent and separate consequences for phytoplankton growth (Winder and Sommer, 2012). Phytoplankton are a key part of lake food-webs, therefore shifts in community composition in response to changing physical drivers can have consequences for higher trophic levels and water quality (Winder and Sommer, 2012; Huisman *et al.*, 2018). The increase in the magnitude and frequency of cyanobacteria blooms associated with climatic warming are a global water quality concern because they can increase water turbidity, cause oxygen depletion during bloom die back, and certain species produce toxins (Michalak, 2016; Paerl and Huisman, 2008). It is therefore important to understand how phytoplankton growth will respond to changing physical drivers.

Lake water temperatures are increasing with climatic warming, as lakes and climate are closely coupled (Winder and Schindler, 2004). The pattern of warming is complex and varies globally (O'Reilly *et al.*, 2015), seasonally (Winslow *et al.*, 2017), with lake size (Woolway *et al*., 2016) and vertically within lakes (Winslow *et al.*, 2015). On average, surface summer water temperatures are warming at a global mean of 0.34 ^{o}C decade^{-1} which is likely to significantly change the physical structure of lakes (O'Reilly *et al.*, 2015). Higher spring and autumn temperatures are increasing the duration of lake stratification (Livingstone, 2003; Peeters *et al*., 2007), whilst periods of sustained high temperatures and low wind speeds also strengthen stratification, inhibiting mixing, resulting in shallower surface mixed layers (Livingstone, 2003; Winder and Sommer, 2012). These changing physical drivers have separate consequences for phytoplankton growth.

The first driver, water temperature, directly affects phytoplankton growth because it influences the rate of important cellular processes such as photosynthesis. Most phytoplankton will exhibit an exponential increase in growth rate with temperature from 0 ^{o}C to 25-35 ^{o}C provided they are not limited by any other resource (Reynolds, 2006). The range of maximum temperatures for exponential growth reflects that growth rates are species specific, varying with cell size, indicating that different species will respond to warming at different rates (Reynolds, 2006). Research suggests that increasing water temperatures will favour the dominance of smaller phytoplankton due to their faster growth rates and greater nutrient uptake efficiency at higher temperatures compared with larger cells (Rasconi *et al.*, 2015). Cyanobacteria are also likely to increase at higher water temperatures owing to some species having higher optimal temperatures for growth compared to some species in other taxa (Carey *et al.*, 2012; Paerl and Paul, 2012).

The depth of the mixed layer is a fundamental driver of phytoplankton growth because it affects the light and nutrient environment they are exposed to and thus their vertical distribution and the rate of sinking losses (Diehl, 2002; Huisman *et al.*, 2004; Ptacnik *et al.*, 2003). Deeper mixed layers can create a lower light environment, reduce sinking losses and increase nutrient availability, whereas shallow mixed layers may increase light availability and sinking losses and reduce nutrient availability (Diehl *et al.*, 2002; Huisman *et al.*, 1999). Phytoplankton have different affinities for light and levels of motility, therefore changes in the mixed depth can result in large shifts in taxonomic composition (Lehman *et al.*, 1998; Huisman *et al.*, 2004). Generally, sinking phytoplankton, such as diatoms and Chlorophytes that are adapted to low light conditions, tend to dominate in deeper layers whereas buoyant or motile phytoplankton (buoyant cyanobacteria and flagellates) often dominate in shallow mixed layers (Reynolds *et al.*, 1983; Visser *et al.*, 1996; Ptacnik *et al.*, 2003; Jäger *et al.*, 2008). Increased surface water temperature with climatic warming may result in shallower mixed depths for many lakes which may then increase cyanobacteria abundance (Paerl and Huisman, 2009). Many species of cyanobacteria have traits suited to shallow mixed layers (Carey *et al.*, 2012) including gas vesicles that allow them to control and maintain their position and exploit optimal light conditions (Walsby *et al.*, 1997). Buoyancy can also be facilitated further at higher water temperatures due to reduced water viscosity (Reynolds *et al.*, 1987). Other cyanobacteria, such as *Planktothrix,* are well adapted to low light conditions and thrive in lakes where the mixed depth is deeper (Ernst *et al.*, 2009; Dokulil and Teubner, 2012).

Although not the focus of this study, the duration of stratification is also influenced by climate warming and can affect the length of the phytoplankton growing season, with warmer spring air temperatures being associated with earlier onset of stratification and spring phytoplankton blooms (Peeters, Straile, Lorke and Livingstone, 2007; Berger *et al.*, 2010; Winder *et al.*, 2012). Persistent high temperatures during autumn can also delay overturn (Hondzo and Stefan, 1993; Peeters *et al.*, 2013) although the impact of this on the phytoplankton growing season is uncertain.

The impacts of temperature change, stratification and mixing have previously been studied in combination using observed data, models and experiments (Berger *et al.*, 2006; Bernhardt *et al.*, 2008; Berger *et al.*, 2010). These studies, however, did not disentangle the impacts of these separate physical drivers on phytoplankton communities throughout the stratified period. Using a phytoplankton community model, PROTECH (Reynolds *et* *al.*, 2001), we systematically and independently changed the water temperature and mixed depth of a model experimental lake system. We chose a small lake (<1 km^2) for the experiment due to the worldwide abundance and significance of small lakes in global budgets and processes (Downing *et al.*, 2006; Verpoorter *et al.*, 2014). The experiment therefore aimed to separate the impacts of the depth of mixing and temperature change on phytoplankton communities whilst keeping the length of stratification constant. We hypothesised that: (1) increases in temperature during fully mixed periods will extend the length of the growing season; (2) changes in water temperature alone will have different impacts on the phytoplankton community than changes in the depth of mixing alone; (3) together, changes in mixed depth and temperature will have greater impacts on phytoplankton than changes in either factor alone; (4) shallower mixing depths and increases in temperature will lead to an increase in cyanobacteria abundance; (5) phytoplankton taxa within the same phylogenetic group may respond differently to changes in physical drivers due to differences in morphology. Though the model runs were based on morphometry of a single lake, they were designed so that the results would be relevant to monomictic, nutrient-rich lakes across the globe.

5.3 Methods

5.3.1 Site description

Blelham Tarn is the modelled lake for the experiment, using three consecutive years of *in situ* driving data (2012-2014). Blelham Tarn is a small (surface area 0.1 km^2), shallow (mean depth 6.8 m, maximum depth 14.5 m) (Ramsbottom, 1976) lake located in the English Lake District (54^{o}24’N, 2^{o}58’W) (Figure 5.1). The trophic status of Blelham Tarn lies on the meso-eutrophic boundary (mean total phosphorus 24.5 mg m^{-3}) (Maberly *et al.*, 2016) and it is monomictic, typically stratifying from spring to late autumn.

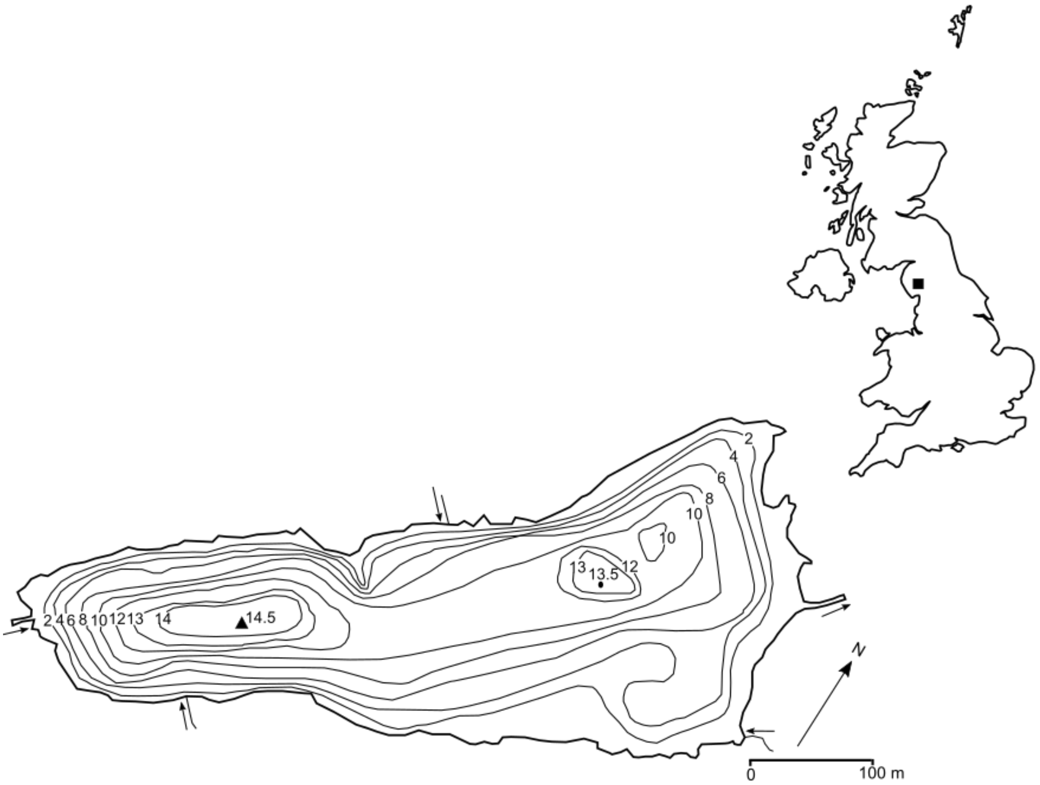


Figure 5.1 Blelham Tarn is located in the lake district in North West England (square), with the monitoring buoy (triangle) located at the deepest point in the lake (14.5 m) bathymetry from Ramsbottom (1976).

5.3.2 PROTECH model

PROTECH is a process-based phytoplankton community model that simulates the daily growth of selected phytoplankton taxa within a lake. PROTECH is a well-established model that has been successfully used in numerous studies of lakes and reservoirs within the UK, Europe and beyond (Elliott *et al.*, 2010) including successful simulations of Blelham Tarn (Reynolds *et al.*, 2001; Jones and Elliott, 2007; Bernhardt *et al.*, 2008).

Phytoplankton growth rates within the model are based on morphological characteristics including the surface area to volume ratio and maximum linear dimension as defined by Reynolds, (1989) (Table 5.1). The overall growth rate, ($\Delta X/\Delta t$), is also determined by losses due to sinking and grazing using the equation (

Table 5.2),

Equation 5.1 $$\Delta X/\Delta t = (r' - S - G - D)X,$$

where r' is the proportional growth rate over 24 hours, *S* represents the losses due to settling, *G* the losses due to grazing, *D* the losses due to dilution, and X is the chlorophyll *a* concentration (mg

Phytoplankton	Light condition (µmol photon m^{-2} s^{-1})	Movement (m day^{-1})
Nonbuoyant nonmotile diatoms		
Asterionella & Synedra	≤ 500	Sink 0.2
	> 500	Sink 1.0
Stephanodiscus	All	Sink 0.2
Aulacoseira	≤ 500	Sink 0.8
	> 500	Sink 1.0
Buoyancy-regulating cyanobacteria		
Dolichospermum	> 100	Sink 0.3
	≤ 100 but > 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
Planktothrix	> 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
Swimming flagellates		
Cryptomonas & Dinobryon	> 100	Rise 0.1
	≤ 100	Rise 0.2
Ceratium	> 100	Sink 0.1
	≤ 100	Rise 0.1
Plagioselmis	> 150	Sink 0.5
	≤ 100 but > 30	No move
	≤ 30	Rise 0.5
Nonbuoyant nonmotile chlorophytes		
Coenochloris & Sphaerocystis	All	Sink 0.1

m^{-3}). The growth rate changes with water temperature, light levels and nutrient limitation of phosphorus, nitrate or silica defined by,

Equation 5.2 $$r' = min\{r'_{(\theta I)}, r'_P, r'_N, r'_{Si}\},$$

where $r'_{(\theta I)}$ is the growth rate due to temperature and daily photoperiod, and r'_P, r'_N, r'_{Si} are the growth rates determined by phosphorus, nitrate and silica concentrations, respectively. In addition to morphology, each phytoplankton is given appropriate movement characteristics as well as any additional abilities such as nitrogen fixation (Table 5.1 and Table 5.2). Further details about the model set up including mortality and respiration rates can be found in Reynolds, Irish & Elliott (2001) and Elliott, Irish & Reynolds (2010).

The phytoplankton chosen to be included in the model set up represented common taxa observed in Blelham Tarn during a fortnightly monitoring programme carried out from 2012-2014 (Table 5.1). These phytoplankton also covered a range of phylogenetic (diatoms, flagellates, chlorophytes and cyanobacteria) and CSR-functional groupings. The use of the CSR classification, developed by Reynolds (1988), helps us understand phytoplankton responses in terms of their traits and morphology, which cut across taxonomical groups (Reynolds, 2006).

Table 5.1 Morphometric characteristics of the 12 phytoplankton taxa.

Phytoplankton	Surface area (μm^2)	Volume (μm^3)	SA:V	Maximum dimension (μm)	Phylogentic grouping	Competitors (C), stress tolerant (S), ruderals (R)	Grazed	Nitrogen fixer
Plagioselmis	108	72	1.5	11	Flagellate	C	Yes	No
Stephanodiscus	404	280	1.4	11	Diatom	C	Yes	No
Dinobryon	629	848	0.7	40	Flagellate	C	Yes	No
Cryptomonas	1030	2710	0.4	21	Flagellate	CS	Yes	No
Synedra	4100	7900	0.5	110	Diatom	R	No	No
Aulacoseira	4350	2970	1.5	240	Diatom	R	No	No
Dolichospermum	6200	29000	0.2	75	Cyanobacteria	CS	No	Yes
Coenochloris	6430	17200	0.4	64	Chlorophyte	S	No	No
Asterionella	6690	5160	1.3	130	Diatom	R	No	No
Planktothrix	7350	13970	0.5	300	Cyanobacteria	R	No	No
Sphaerocystis	7850	65500	0.1	50	Chlorophyte	S	Yes	No
Ceratium	9600	43700	0.2	201	Flagellate	CS	No	No

Table 5.2 Summary of phytoplankton movement characteristics at different light thresholds within PROTECH.

Phytoplankton	Light condition (µmol photon m^{-2} s^{-1})	Movement (m day^{-1})
Nonbuoyant nonmotile diatoms		
Asterionella & Synedra	≤ 500	Sink 0.2
	> 500	Sink 1.0
Stephanodiscus	All	Sink 0.2
Aulacoseira	≤ 500	Sink 0.8
	> 500	Sink 1.0
Buoyancy-regulating cyanobacteria		
Dolichospermum	> 100	Sink 0.3
	≤ 100 but > 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
Planktothrix	> 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
Swimming flagellates		
Cryptomonas & Dinobryon	> 100	Rise 0.1
	≤ 100	Rise 0.2
Ceratium	> 100	Sink 0.1
	≤ 100	Rise 0.1
Plagioselmis	> 150	Sink 0.5
	≤ 100 but > 30	No move
	≤ 30	Rise 0.5
Nonbuoyant nonmotile chlorophytes		
Coenochloris & Sphaerocystis	All	Sink 0.1

5.3.3 Driving data

A three year period (2012-2014) of daily averaged solar radiation data recorded by a Kipp Zonan CMP6 Pyranometer (sensitivity 5 to 20µV/W/m²) attached to an *in situ* automated monitoring buoy (Figure 5.1) was used to calculate the photosynthetically active radiation available to the phytoplankton within the model. The buoy also measured lake water temperatures every 4 minutes at 1 m depth intervals in the water column from 1-10 m with additional temperature sensors at 0.5 m and 12 m. Whilst PROTECH can estimate temperature from external physical drivers in this study, the buoy data were linearly interpolated into the equivalent 0.1 m PROTECH layers (0.1 m to 14.5 m) to provide a daily water temperature structure to drive the PROTECH model over the simulated three year period.

To calculate daily nutrient loading to the lake, daily average discharge (m^3 s^{-1}) from the nearby River Leven was obtained from the Environment Agency. As the outflow from Blelham Tarn is not continuously gauged, a relationship between this daily data and Blelham Tarn outflow was established for 1974, when daily measurements were available for both sites. A power law relationship provided the best regression fit between the two discharges (R^2=0.92; p<0.05),

Equation 5.3
$$Q_{BB} = 0.0076 {Q_{RL}}^{1.253},$$

where Q_{BB} is the outflow discharge of Blelham Tarn and Q_{RL} is the discharge from the River Leven. Daily discharges for each inflow were then calculated based on the proportion of discharge that each inflow contributed to the outflow discharge for 2017 based on monthly spot samples. Monthly concentrations of nitrate and silica in three of the inflows into Blelham Tarn were also sampled during 2017. The calculated daily discharges were averaged for each month and multiplied by the monthly spot concentration for nitrate and silica, assuming that the nutrient load was the same for each day in the sample month, following Walling and Webb (1981). The monthly pattern for nutrient load calculated for 2017 was repeated for each year in the sample period (2012-2014) therefore daily variations in discharge resulted in different daily nutrient concentrations. The same monthly nutrient loading pattern was used here as the analyses focusses on changes in mixed depth and temperature rather than nutrients. Daily nutrient concentrations for phosphorus were based on estimates modelled from land use type using an export coefficient approach previously calculated by Gasca, Maberly & Mackay (2015).

Monthly sampling of nutrients has been reported to underestimate nutrient loading by up to 50-60 % (Cassidy and Jordan, 2011), therefore an extra 50% was added onto the calculated values for nitrate, silica and phosphorus to account for this. The nutrient loading for phosphorus was also increased by a further 50% to account for the internal phosphorus release from the sediments during anoxic conditions in the hypolimnion during stratification (Foley *et al.*, 2012).

5.3.4 Model validation

In PROTECH, phytoplankton are actively mixed throughout the mixed layer, therefore changes in the depth of mixing determine the light and nutrient availability for phytoplankton. The average mixed depths used as a baseline during the stratified period were: 5 m for the entire stratified period, 4 m in spring, 4.5 m in summer and 7 m in autumn. They were derived, from water temperature profiles measured in 2012-2014, using Lake Analyzer (Read *et al.*, 2011) and defined as the depths at which the vertical gradient of water density first exceeded 0.1 kg m^{-3} m^{-1} . These baseline mixed depths and the control water temperature profiles measured at the monitoring buoy were used in the model validation run. The benchmark of acceptability for the model was that it produced, on average, a reasonable seasonal pattern of phytoplankton chlorophyll *a* and functional groupings compared to observed data from recent years. Therefore, for comparison, fortnightly means were calculated for both the simulated and observed chlorophyll *a* and functional groupings from the whole period. These were then compared both visually and by calculating the coefficient of determination for the data (Figure 5.2).

5.3.5 Model Experiment

The validated model was run in a series of experiments in which the mixed depth was systematically changed by 0.5 m intervals from 0.5 m to 14.5 m. These depths were fixed for each model run during the identified period of stratification determined in the baseline run. It is not expected that the mixed depth of Blelham Tarn will fluctuate through this full range, rather the experiment is seen as a template for similar monomictic lakes with naturally different starting depths of mixing. Furthermore, for each mixed depth, the baseline water temperatures (which remain fixed according to the observed buoy data) were systematically changed in 0.5 ^{o}C intervals from -2 to +6 ^{o}C in the top 5 m of the water column throughout the year. Temperature was changed at the surface rather than through the whole water column because analysis of long term temperature trends from Blelham Tarn suggests that warming is accelerated in surface waters only, with little change in deep water temperature (Foley *et al*., 2012). This means that in scenarios when mixing occurred deeper than 5 m, phytoplankton will not be exposed to warming at those depths, where temperatures will remain at baseline values. Overall, this gave a total of 493 model simulations. The phytoplankton concentrations were integrated over the top 5 m of the water column so the model could be validated against the observed data.

In addition to the main experiment a series of extra runs were performed to check some of the methodological assumptions made. To determine if changing the water temperature in the top 5 m of the water column only influenced the results, the experiment was repeated by applying the water temperature change to the whole water column, producing an additional 493 model simulations. Furthermore, fixing the mixed depth in defined intervals throughout the stratified period meant that short term fluctuations in light and nutrient availability were lost. To determine if the absence of this variability impacted the results, additional model runs were completed in which the baseline mixed depth was shifted in 10 % intervals from 10 % to 200 %, again keeping the baseline duration of stratification the same. This was repeated for both a top 5m water temperature change and a whole water column temperature change, resulting in 680 more model simulations. To determine whether sampling depth had an impact on the results, all results from each experiment were also calculated for the whole water column. Results from these additional runs have been summarised in Tables 5.3 and 5.4.

The model outputs from the experiments analysed were daily total chlorophyll *a* (mg m^{-3}) concentrations, individual phytoplankton taxa chlorophyll *a* (mg m^{-3}) concentrations, the percentage abundance of each taxonomic group (diatoms, flagellates, chlorophytes and cyanobacteria) and the percentage abundance of each C, S, R and CS functional group. The diversity (H') of the twelve phytoplankton species was calculated using the Shannon index according to the following equation,

Equation 5.4 $$H' = -\sum \left(\frac{b_i}{B}\right) log_2(\frac{b_i}{B}),$$

where B is biomass measured as the total concentration of chlorophyll a (mg m^{-3}) and i is the biomass (chlorophyll a (mg m^{-3})) of the ith phytoplankton taxon. For each of the resulting variables, overall annual means were calculated. Seasonal averages were calculated with spring being defined as March, April and May, summer as June, July and August, autumn as September, October and November and winter as December, January and February. Spring and autumn were split into their respective stratified and fully mixed periods of time and analysed separately. The *stratified* seasons, that is the period when the *in situ* temperature data showed there had been a surface mixed layer were: spring beginning on 01/03/2012, 11/04/2013, 31/03/2014 and ending on the last day of May; summer as June, July and August; and autumn as the beginning of September until lake overturn on 07/10/2012, 03/11/2013 and 07/11/2014. Outside of these periods, the mixed depth of the model was set at the full depth of the lake irrespective of water column temperatures.

5.4 Results

5.4.1 Validation

The intention of the experiments was not to create an exact reproduction of Blelham Tarn’s phytoplankton community but to simulate an experimental community with a realistic biomass, seasonal growth pattern and morphological and taxonomic diversity. The model performed well in terms of biomass, capturing both the amount and seasonal pattern of mean observed total chlorophyll *a* (Figure 5.2). In terms of the community, annual observed and modelled means for C (modelled = 2.7 ± 2.8 mg m^{-3}, observed = 2.0 ± 3.2 mg m^{-3}), R (modelled = 9.1 ± 7.1 mg m^{-3}, observed = 8.9 ± 8.0 mg m^{-3}) and CS (modelled = 3.2 ± 4.2 mg m^{-3}, observed = 3.1 ± 6.0 mg m^{-3}) strategists were very similar (Figure 5.2). The model performed less well for S strategists (modelled=1.2 ± 0.6 mg m^{-3}, observed= 4.2 ± 7.9 mg m^{-3}); this group was therefore not considered in the analysis.

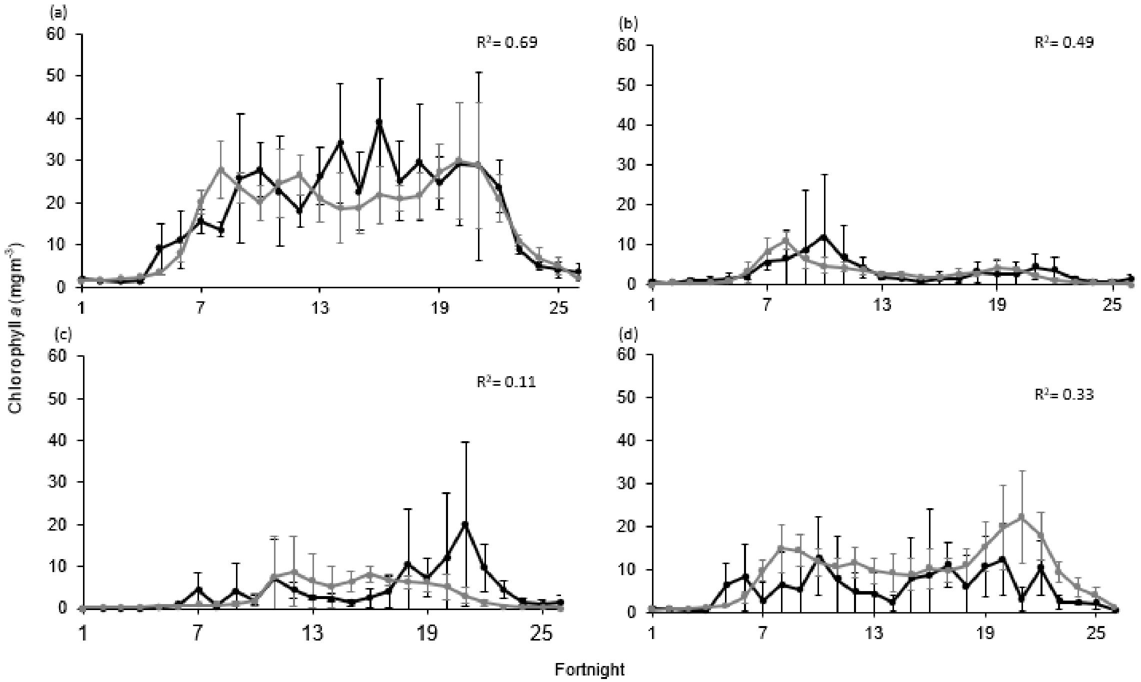


Figure 5.2 Observed (black line) and simulated (grey line) mean fortnightly (a) total chlorophyll a *biomass, (b)* C *strategists biomass, (c)* CS *strategist biomass and (d)* R *strategist biomass for Blelham Tarn for the three year period simulated with the range of fortnightly values for that period being depicted by the error bars.*

5.4.2 Impacts of temperature change before and after stratification

5.4.2.1 Phytoplankton Biomass

Prior to stratification in spring, chlorophyll *a* concentrations increased at an average rate of 1.2 mg m^{-3} ^{o}C^{-1}, leading to elevated concentrations at higher temperatures (17.5 mg m^{-3} at +6 ^{o}C compared to 9.6 mg m^{-3} at +0 ^{o}C) (Figure 5.3). Post-stratfication, in autumn, chlorophyll *a* concentrations remained slightly higher at the highest temperature increases (12.8 mg m^{-3} at +6 ^{o}C, cf. 10.6 mg m^{-3} at -2 ^{o}C) (Figure 5.3). Higher temperatures also advanced the onset of the spring bloom; at +6 ^{o}C chlorophyll *a* concentrations reached 5 mg m^{-3} eleven days earlier than at -2 ^{o}C (Figure 5.3). The end of the growing season, defined as the first day when chlorophyll *a* < 5 mg m^{-3}, was extended by seven days at +6 ^{o}C compared to -2 ^{o}C (Figure 5.3).

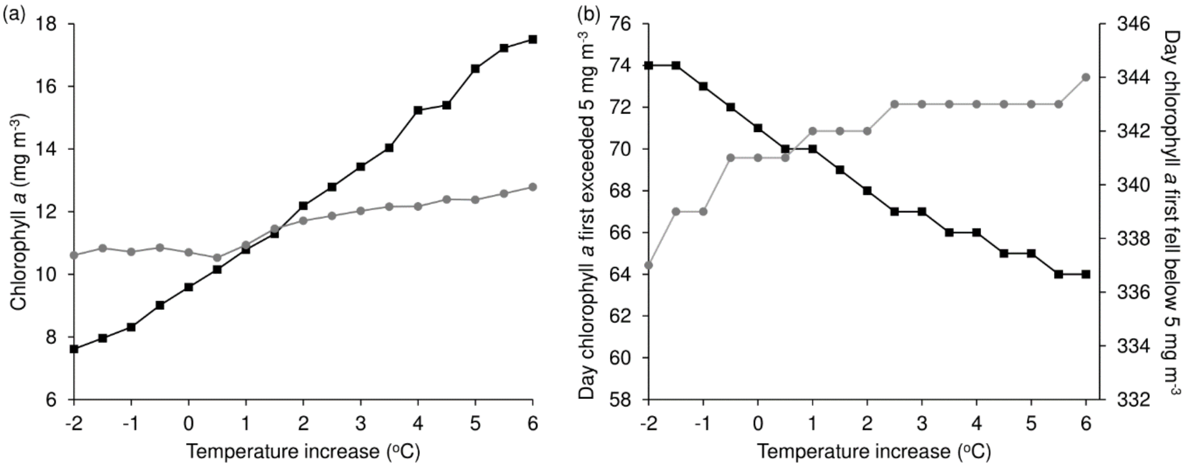


Figure 5.3 (a) Chlorophyll a *concentrations with temperature in fully mixed spring prior to stratification (black square) and fully mixed autumn following stratification (grey circle) and (b) average day of the year when chlorophyll* a *first exceeded (black square) and dropped below (grey circle) 5 mg m^{-3} with temperature change.*

5.4.2.2 Phytoplankton community

Increasing temperature prior to stratification also resulted in community shifts with the percentage of R strategists increasing by 32 % (from -2 ºC to + 6 ºC) at the expense of CS and C strategists (Figure 5.4). In comparison, increases in temperature had very little impact on the functional composition of the post-stratification fully mixed community in autumn (Figure 5.4). There was also a decrease in diversity with warming (from H' = 3.0 at -2 ºC to H' = 2.3 at +6 ºC) in spring, but only a small change in diversity of the post-stratification community in autumn (Figure 5.5).

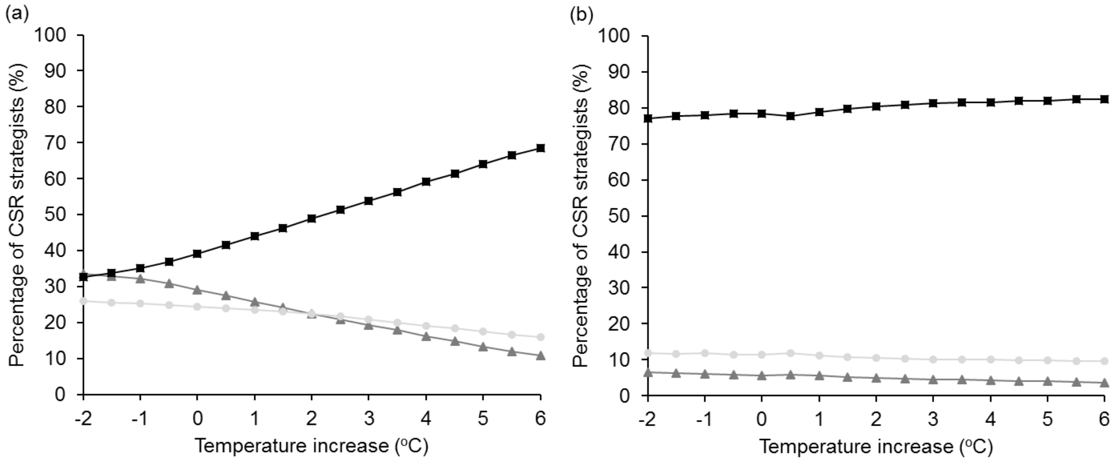


Figure 5.4 Percentage of C (dark grey triangle), CS (light grey circle), and R (black square) strategists in (a) fully mixed spring and (b) fully mixed autumn.

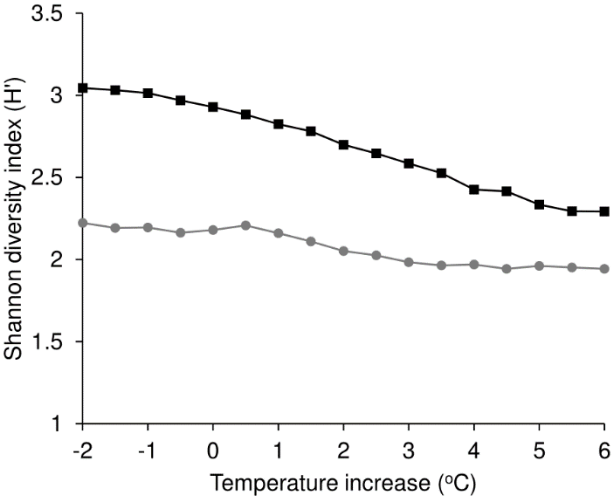


Figure 5.5 Shannon diversity index with temperature change for fully mixed spring (black squares) and fully mixed autumn (grey circles).

5.4.3 Impacts of temperature and mixed depth change during the stratified period

5.4.3.1 Phytoplankton biomass

Reducing the mixed depth (to 0.5 m) and increasing the temperature (to + 6 °C) relative to the baseline increased the annual average chlorophyll *a* biomass (+ 7.2 mg m^{-3}) by over three times compared to changes in temperature (+ 3.0 mg m^{-3}) or mixed depth (+ 2.2 mg m^{-3}) alone (Figure 5.6). However, deepening the mixed depth from the baseline led to greater increases in phytoplankton biomass (e.g. + 3.1 mg m^{-3} from the baseline to 11 m) compared to mixed depth shallowing. This was further enhanced by increases in temperature. Increasing the temperature by 6 °C at a mixed depth of 11 m, for example, led to an increase in phytoplankton biomass of 10.4 mg m^{-3} compared to baseline conditions (Figure 5.6).

The impact of changing temperatures and depths of mixing varied with season. In spring, increases in phytoplankton biomass were driven by increases in temperature with smaller variations in biomass with changing mixed depth (e.g. + 8.5 mg m^{-3} increase from +0 ^{o}C to +6 ^{o}C at the spring baseline mixed depth) (Figure 5.6). There was a strong bimodal pattern in summer, with the greatest increases occurring with combinations of high temperatures and both shallower (< 4 m) (increase of 19.1 mg m^{-3} from baseline conditions to +6 ^{o}C at 0.5 m mixed depth) and deeper mixed depths (> 8.5 m). The largest summer chlorophyll *a* concentration (43.9 mg m^{-3}) occurred at a mixed depth of 11 m at + 5 ^{o}C (Figure 5.6). For autumn, the peak in chlorophyll *a* occurred at depths between 10-12 m (Figure 5.6).

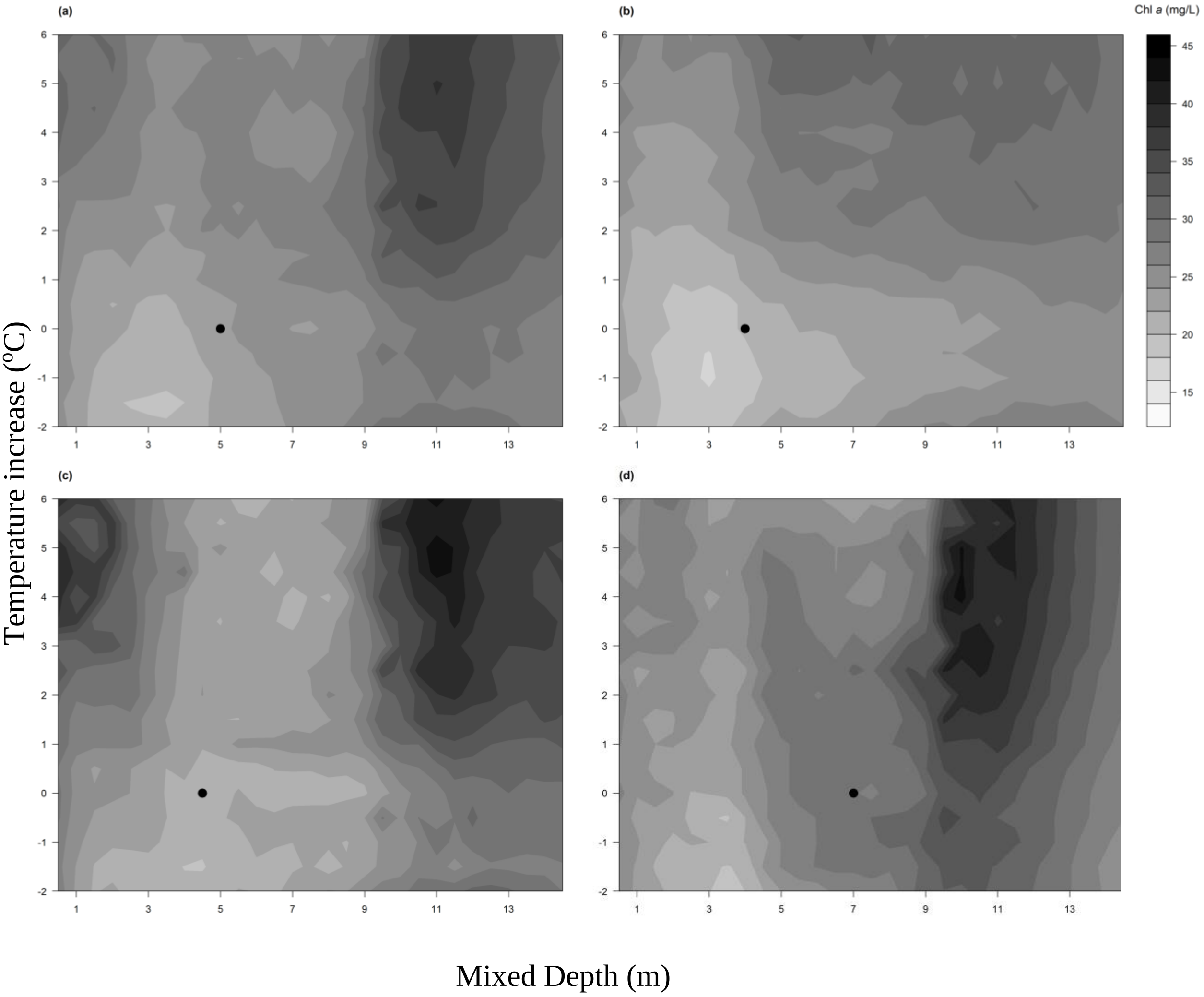


Figure 5.6 Mean chlorophyll a *concentrations at each mixed depth and temperature change for (a) annual mean (b) stratified spring, (c) stratified summer and (d) stratified autumn, the black circle marks the baseline mixed depth and temperature for Blelham Tarn.*

5.4.3.2 Phytoplankton Community

The annual average phytoplankton biomass was dominated by CS and R strategists, with C strategists occurring only in notable concentrations at lower temperatures (below + 0.5 ^{o}C) and mixed depths shallower than 6.5 m (Figure 5.7). R strategists increased at the expense of CS strategists when the mixing deepened (e.g. a decrease in CS strategists of 11 % from the baseline mixed depth to 14.5 m) (Figure 5.7). Shifts in functional groups followed a broad seasonal pattern, which was modified by changes in mixing and temperature.

Spring was dominated by R-types at most mixed depths and temperatures, C-types increased at the expense of R-types for mixed depths shallower than 6.5 m and temperatures below +0.5 ^{o}C and CS-types contributed 20-40 % of the community when mixing was shallower than 9 m and temperature higher than the baseline (Figure 5.7). In summer, contrasting functional types occupied different mixed depth ranges. CS-types dominated at shallow mixed depths (< 8 m at temperatures greater than the baseline) and R-types with deep mixing (> 8 m), C-types contributed a negligible amount to the community (Figure 5.7). The stratified autumn community reverted back to R-type dominance at the expense of CS-types, with C-types occurring at temperatures below +0.5 ^{o}C and mixed depths shallower than 6 m (Figure 5.7).

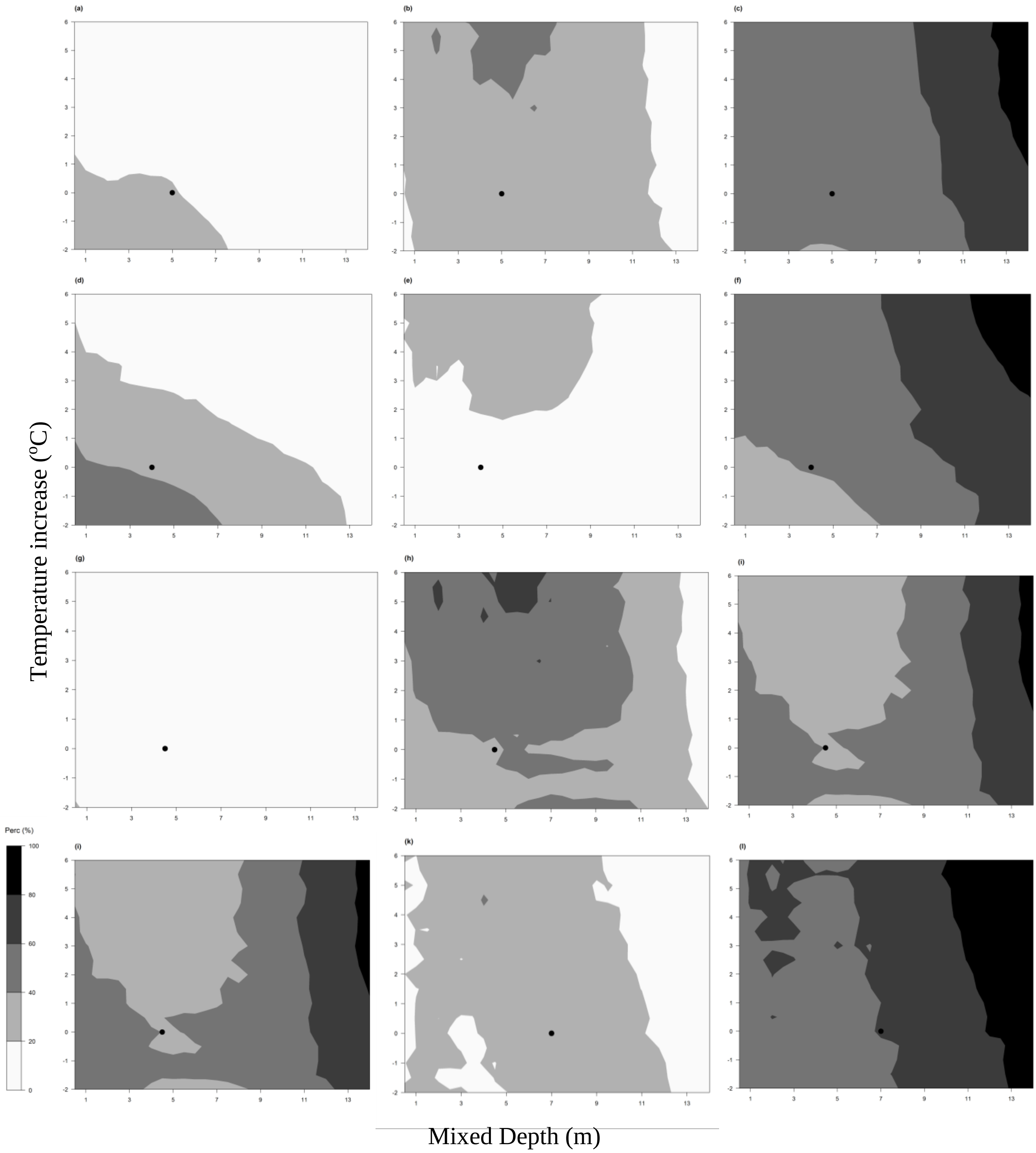


Figure 5.7 Percentage of (a,d,g,j) C (b,e,h,k) CS (c,f,I,l) and R strategists in (a,b,c) annual average, (d,e,f) stratified spring, (g,h,i) summer, (j,k,l) stratified autumn, black circle marks the baseline mixed depth and temperature for Blelham Tarn.

The responses of the CS- and R-types during summer and stratified autumn were primarily due to the contrasting responses of the two cyanobacteria taxa: *Dolichospermum* dominated with shallow mixing and *Planktothrix* with deep mixing (Figure 5.8). In summer *Dolichospermum* dominated when mixing was shallower than 10 m and *Planktothrix* at depths deeper than 10 m (Figure 5.8). Stratified autumn was dominated by *Planktothrix* at most mixed depths and temperatures, although *Dolichospermum* contributed more to the cyanobacteria biomass at shallower mixed depths (Figure 5.8). The annual average and seasonal diversity decreased with deeper mixing (Figure 5.9). Low diversity values occurred at mixed depths shallower than 10.5 m and high temperatures (above +2°C) in summer compared to stratified spring and autumn (Figure 5.9).

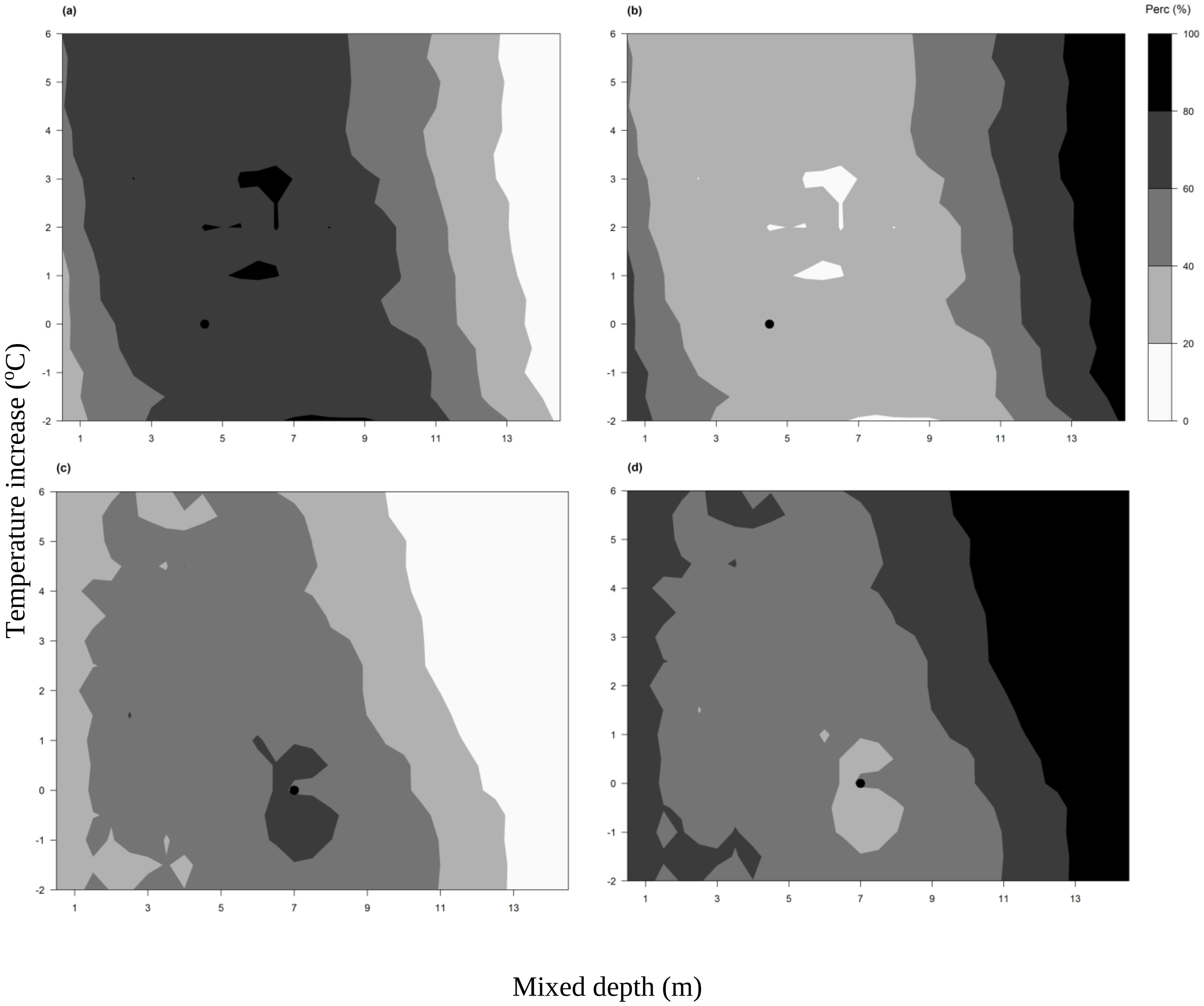


Figure 5.8 Percentage of total cyanobacteria at each mixed depth and temperature change for (a) Dolichospermum in stratified summer (b) Planktothrix in stratified summer, (c) Dolichospermum in stratified autumn and (d) Planktothrix in stratified autumn, black circle marks the baseline mixed depth and temperature for Blelham Tarn.

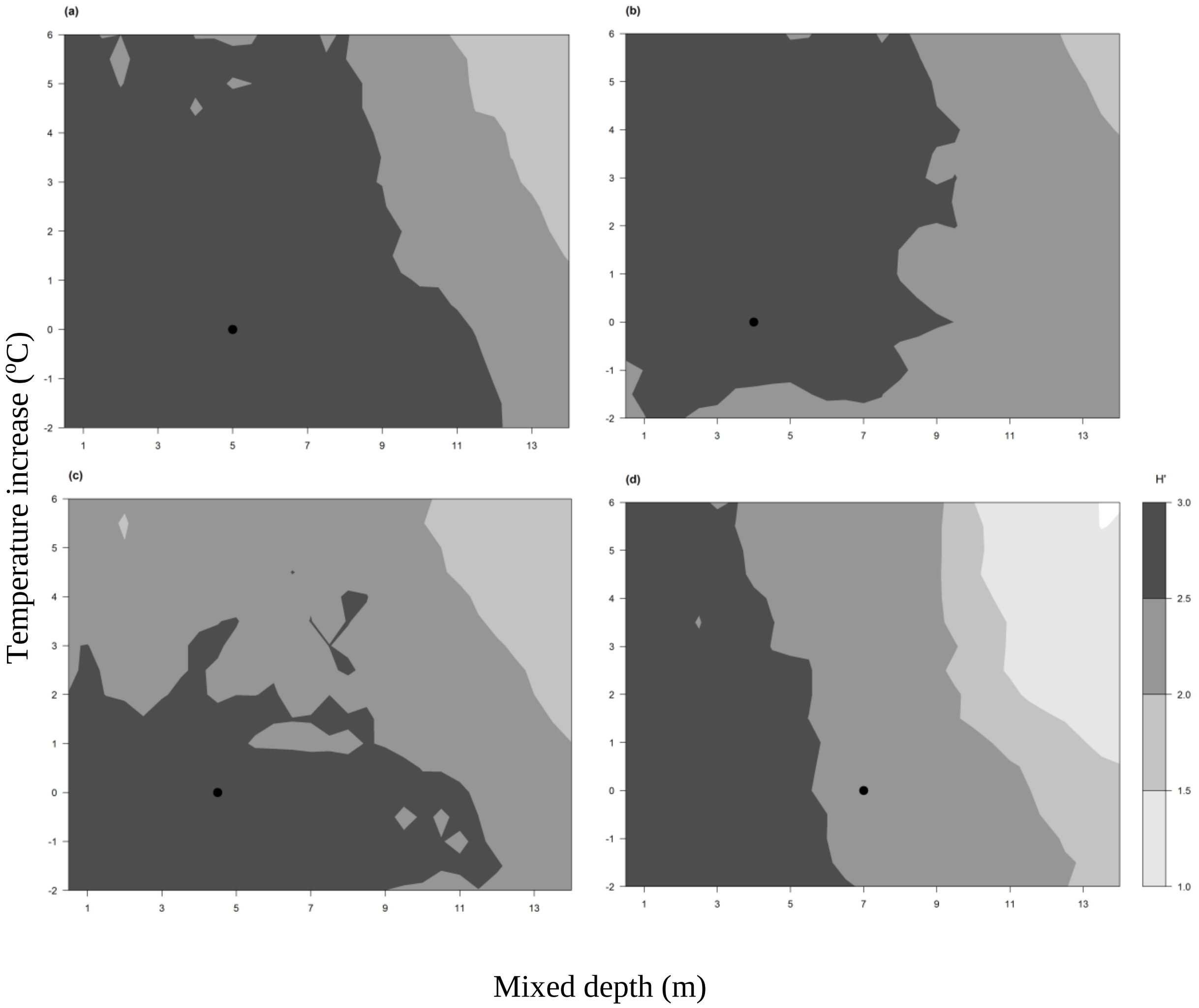


Figure 5.9 Shannon diversity index for each mixed depth and temperature change for (a) annual average (b) stratified spring (c) stratified summer, (d) stratified autumn black circle marks the baseline mixed depth and temperature for Blelham Tarn.

5.4.4 Comparing experimental methods

Full analyses of the results were performed for each method of temperature change (top 5 m of the water column and whole water column), mixed depth method (fixed mixed depths and percentage shifts) and sampling depth (top 5 m and whole water column). The different methods of mixed depth change (fixed and percentage shifts) produced very similar seasonal mean chlorophyll a concentrations (Table 5.3 and Table 5.4). Applying the change in water temperature to the top 5 m of the water column or the whole water column made very little difference to seasonal mean chlorophyll a concentrations for both mixed depth methods (Table 5.3 and Table 5.4). Integrating the results over the top 5 m of the water column consistently produced slightly higher chlorophyll a values compared to whole water column integrations for both mixed depth methods, but the seasonal patterns were consistent (Table 5.3 and Table 5.4).

Table 5.3 Seasonal mean phytoplankton biomass (chlorophyll a *mg m^{-3}) during the stratified period for water column integrated and 5 m integrated results using the fixed mixed depth method.*

	Spring chlorophyll *a* (mg m^{-3})		Summer chlorophyll *a* (mg m^{-3})		Autumn chlorophyll *a* (mg m^{-3})	
	5 m integrated	Water column integrated	5 m integrated	Water column integrated	5 m integrated	Water column integrated
Temperature change in the top 5m	27.0	23.8	29.1	24.0	28.1	25.9
Temperature change in the whole water column	26.2	24.3	28.4	24.3	29.4	26.2

Table 5.4 Seasonal mean phytoplankton biomass (chlorophyll a *mg m^{-3}) during the stratified period for water column integrated and 5 m integrated results using the percentage mixed depth method.*

	Spring chlorophyll *a* (mg m^{-3})		Summer chlorophyll *a* (mg m^{-3})		Autumn chlorophyll *a* (mg m^{-3})	
	5 m integrated	Water column integrated	5 m integrated	Water column integrated	5 m integrated	Water column integrated
Temperature change in the top 5m	25.5	23.1	28.5	22.6	28.3	24.5
Temperature change in the whole water column	26.1	23.6	28.9	22.8	28.5	24.8

5.5 Discussion

Regarding the first hypothesis, we found that the timing of the spring bloom advanced with increases in water temperature. This extension of the growing season has also been observed in field studies (Thackeray *et al.*, 2008, 2010; Meis *et al.*, 2009) and previous modelling experiments (Peeters, Straile, Lorke and Livingstone, 2007). In these studies, however, spring warming was accompanied by earlier onset of stratification, obfuscating whether changes in water temperature or changes in stratification were the key driver. As our study kept the length of stratification the same for all model runs, it demonstrated that advance in the spring bloom can be solely due to temperature accelerating growth rates rather than the higher light availability that ordinarily accompanies changes in stratification and shallower mixed depths. At this time of year nutrients are plentiful after being replenished during the winter, therefore, the growth rate of the R-strategist diatoms, which are adapted to low light conditions in the fully mixed layer, accelerated with increasing temperature. The growing season in autumn was also extended by temperature increases alone, although for a shorter length of time than in the spring. By independently changing mixed depth and temperature, model outcomes have also highlighted that temperature changes had different impacts on this modelled phytoplankton community compared to mixed depth changes, supporting hypothesis two. Increases in temperature increased phytoplankton biomass and increased the proportion of the community made up of cyanobacteria consisting of two functional groups (CS and R) for most mixed depths. This result was expected due to accelerated growth rates at higher temperatures and the favourable morphologies of the cyanobacteria taxa (Carey *et al.*, 2012). However, the experimental results showed that shallower mixed depths could have contrasting impacts on the phytoplankton community depending on the typical current position of the mixing layer. If the original depth of mixing was located at intermediate depths (4-9 m), shallowing could increase biomass and the proportion of the community made up of the CS cyanobacteria. However, if the original depth of mixing was naturally deeper (9.5-14.5 m), shallowing to intermediate depths could decrease biomass and reduce the percentage of R strategist cyanobacteria, particularly if sizeable temperature increases also occurred (Figure 5.6).

Mixed depth and water temperature change do not necessarily occur in isolation and this modelling study has found that combined increases in water temperature and shallower depths of mixing (from baseline conditions) had a synergistic effect on phytoplankton biomass, supporting hypothesis three. The magnitude of the synergistic response varied with season. Modelled increases in biomass and community change in spring were primarily driven by temperature increases as opposed to combined mixed depth and temperature changes. The highest temperature increases in spring led to cyanobacteria dominance, consistent with previous findings from other modelling studies (Elliott *et al.*, 2005; Markensten *et al.*, 2010) and observed data (Weyhenmeyer, 2001; Jacquet *et al.*, 2005; Dupuis and Hann, 2009). In contrast, summer demonstrated the largest synergistic response (+19.0 mg m^{-3} chlorophyll *a* with rising temperature and mixed depth shallowing from the baseline) with large changes in community composition and phytoplankton biomass occurring when both the depth of mixing and water temperature changed.

Previous work has suggested that warming and shallower mixed depths combined will create conditions favourable for cyanobacteria (Paerl and Huisman, 2009; Paerl and Paul, 2012). In this experiment, they did produce an increase in phytoplankton biomass overall and an increase in the biomass of the buoyant cyanobacteria *Dolichospermum*. Faster growth rates at high temperatures and the ability to regulate buoyancy at shallow mixed depths meant that *Dolichospermum* was able to outcompete other CS-strategists within the model. This suggests that lakes with shallow surface mixed layers similar to Blelham Tarn (4 m annual average), which are experiencing accelerated warming in surface waters (increase of 1.1 ± 0.3 ^{o}C in Blelham Tarn 1968-2008) (Foley *et al.*, 2012), may experience a deterioration in water quality with warming and shallower surface mixing. This finding is in agreement with expectations and predicted trends (Paerl and Huisman, 2009; Paerl and Paul, 2012), supporting hypothesis four.

The largest cyanobacteria biomass in the model experiments, occurred at deeper mixed depths due to the low light adapted *Planktothrix*. Therefore, contrary to hypothesis four, when the mixed layer moved from deep to intermediate depths there was a reduction in the biomass of phytoplankton and R strategist cyanobacteria (*Planktothrix*). This suggests that for lakes with naturally deeper mixed depths than Blelham Tarn, shallowing and warming of the mixed layer may reduce phytoplankton biomass and biomass of low light adapted cyanobacteria. These experimental findings indicate that shallower mixed depths and increases in temperature may not always lead to increases in cyanobacteria biomass, providing evidence against hypothesis four. This is also relevant when considering artificial mixing to mitigate against surface cyanobacterial blooms. Indeed, previous artificial mixing experiments have found it to be ineffective at reducing *Planktothrix* populations (Reynolds *et al.*, 1983; Visser *et al.*, 2016).

Dolichospermum and *Planktothrix* are both genera of cyanobacteria but they have different morphologies and affinities for light (Table 5.2) and therefore responded differently to changes in mixing depth in this modelling experiment. The contrasting responses of two phytoplankton taxa belonging to the same phylogenetic group supports hypothesis five, that phytoplankton responses in these modelled results would differ depending on their morphology and traits (Reynolds *et al.*,

Phytoplankton	Light condition (μmol photon m^{-2} s^{-1})	Movement (m day^{-1})
Nonbuoyant nonmotile diatoms		
Asterionella & Synedra	≤ 500	Sink 0.2
	> 500	Sink 1.0
Stephanodiscus	All	Sink 0.2
Aulacoseira	≤ 500	Sink 0.8
	> 500	Sink 1.0
Buoyancy-regulating cyanobacteria		
Dolichospermum	> 100	Sink 0.3
	≤ 100 but > 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
Planktothrix	> 30	Sink 0.1
	≤ 30 but > 10	No move
	≤ 10	Rise 0.1
Swimming flagellates		
Cryptomonas & Dinobryon	> 100	Rise 0.1
	≤ 100	Rise 0.2
Ceratium	> 100	Sink 0.1
	≤ 100	Rise 0.1
Plagioselmis	> 150	Sink 0.5
	≤ 100 but > 30	No move
	≤ 30	Rise 0.5
Nonbuoyant nonmotile chlorophytes		
Coenochloris & Sphaerocystis	All	Sink 0.1

1983). *Dolichospermum* dominated in shallow mixed layers as its ability to regulate buoyancy allowed it to maintain its position in a favourable light climate whereas non-motile or negatively buoyant species would be lost from the mixed layer through sedimentation (Huisman *et al.*, 2004). These findings are consistent with previous observations of *Dolichospermum* being associated with problematic surface blooms in lakes with shallow surface mixing (Salmaso *et al.*, 2015). In contrast, deeper mixed layers were dominated by *Planktothrix*, a cyanobacteria adapted to low light conditions (Dokulil and Teubner, 2012). *Planktothrix* has been associated with persistent blooms in deep mixed layers in observed data (Ernst *et al.*, 2009) and experimental systems, often forming a sub-surface peak or a deep chlorophyll *a* maxima (Reynolds *et al.*, 1983; Nürnberg *et al.*, 2003; Selmeczy *et al.*, 2018). Studies in Lake Zurich and Lake Geneva have suggested that *Planktothrix* will benefit from warming in extremely deep lakes due to a reduction in full water column mixing, which contrasts with the reduction in *Planktothrix* for shallow lakes found in this study (Posch *et al.*, 2012; Gallina *et al.*, 2017).

This modelling experiment made a number of assumptions and simplifications in order to disentangle the separate impacts of complex physical drivers. Here we have modelled only twelve phytoplankton taxa, including two cyanobacteria taxa. While these were chosen to represent a wide range of morphological traits, real lakes typically contain a richer phytoplankton community than this. Similarly, we simplified the modelling by keeping a fixed nutrient pattern between years. The model itself also contains a number of assumptions and simplifications in order to represent complex biological processes (Elliott *et al.*, 2010; Reynolds *et al.*, 2001). Nevertheless, the model is mechanistic and has been widely tested on many systems around the world and the results allow an understanding of the separate impacts of mixed layer and temperature change on a phytoplankton community which cannot be achieved using observed data alone (Elliott *et al.*, 2010).

This study has highlighted the important role of temperature as a driver for increasing spring biomass and extending the length of the growing season. By modelling the depth of surface mixing and temperature independently we have shown that they have different impacts on phytoplankton growth; increases in temperature accelerate growth rates but changes in the mixed layer depth have contrasting impacts depending on the baseline depth, but also on the traits of the extant cyanobacteria. Mixed depth and temperature change are intrinsically linked, both being functions of warming processes, and these experimental findings show that combined changes have a synergistic impact on phytoplankton biomass. Furthermore, shallower surface mixing and temperature increases may lead to an increase in buoyant cyanobacterial taxa such as *Dolichospermum* if the original depth is relatively shallow. On the other hand, mixed layer shallowing from deep to intermediate depths could lead to a reduction in cyanobacterial biomass by removing the competitive advantage of low-light adapted taxa, such as *Planktothrix*. Thus the response of cyanobacteria blooms to climate warming in small lakes around the world should not be a universal increase, but rather, will depend on the current depth of mixing and light tolerance of the dominant cyanobacteria species.

6 From one extreme to another: the impact of a storm event on physical and chemical lake processes at a time of atypical stratification strength

(Gray, E., Mackay, E.B., Folkard, A.M, Elliott, J.A., and Jones, I.D. (2019) From one extreme to another: the impact of a storm event on physical and chemical lake processes at a time of atypical heightened stratification strength. In preparation for submission)

6.1 Abstract

Surface water temperatures and stratification strength are increasing in many lakes. In addition to this long term trend there is a projected increase in the frequency and magnitude of extreme events such as storms. It is therefore becoming more likely that extreme storm events will occur at times of extreme stratification stability. Given this, we investigated the importance of within-lake antecedent conditions for determining the physical responses to extreme storm-driven flushing events. Using high resolution meteorological and within-lake data, we analysed the physical response of a small monomictic lake to an extreme flushing event which occurred in the summer of 2016 at a time of atypically high stratification strength. We compared the responses found here to two additional extreme summer flushing events with contrasting antecedent conditions (atypically unstable and typical conditions). The results demonstrate antecedent lake conditions strongly influence the impact of a storm on a lake. In particular, storm events occurring at a time of extreme lake stability may return the lake to conditions that are

typical for the time of year rather than push it into a more extreme state and may shift nutrient concentrations from limiting to non-limiting levels.

6.2 Introduction

There is growing evidence that the magnitude and frequency of extreme events such as storms, are increasing as a result of climate change (Beniston *et al.*, 2007; Coumou and Rahmstorf, 2012; Hov *et al.*, 2013). In the UK and areas of North-Eastern Europe there is a projected increase in the frequency of heavy precipitation events in summer (Beniston *et al.*, 2007; Kendon *et al.*, 2014). Storms accompanied with heavy precipitation can have substantial impacts on physical, chemical and ecological processes within lakes (Robson and Hamilton, 2003; Tsai *et al.*, 2008; Jennings *et al.*, 2012; Kasprzak *et al.*, 2017; Ji *et al.*, 2018; Woolway *et al.*, 2018). It is therefore important to understand the potential consequences of these events for the socio-economic and environmental ecosystem services that lakes provide (Scheffer *et al.*, 2001; Delpla *et al.*, 2009; Whitehead *et al.*, 2009; Pace *et al.*, 2015; Michalak, 2016).

Global atmospheric warming is also leading to an increase in air temperatures (IPCC, 2013) and consequently an increase in lake surface water temperatures (Schneider and Hook, 2010; O’Reilly *et al.*, 2015; Woolway and Merchant, 2017). Increasing water temperatures and atmospheric stilling (Vautard *et al.*, 2010) have been attributed to increases in the strength and length of stratification (Peeters, Straile, Lorke and Livingstone, 2007; Kraemer *et al.*, 2015; Woolway, Meinson, *et al.*, 2017; Woolway *et al.*, 2019) and potential shallower surface mixing in many lakes (Livingstone, 2003; Winder and Sommer, 2012). It is therefore becoming increasingly likely that extreme storm events will occur at times of extreme stability within lakes, resulting in interactions between two extremes that have not been explored in detail.

Given the importance of a lake’s physical structure for its chemical (Mackay *et al.*, 2011; Foley *et al.*, 2012; Peeters *et al.*, 2016; Giling, Nejstgaard, *et al.*, 2017) and ecological processes (Diehl *et al.*, 2002; Ptacnik *et al.*, 2003; Jäger *et al.*, 2008) and water quality (Michalak, 2016), it is important to understand the potential impacts of extreme events. This is particularly relevant as it has been suggested that short term episodic events such as storms could be as important as long term changes for physical, chemical and ecological processes (Jennings *et al.*, 2012; De Eyto *et al.*, 2016; Giling, Nejstgaard, *et al.*, 2017; Kasprzak *et al.*, 2017; Perga *et al.*, 2018). Determining the impact of a storm event on the physical structure of a lake is complex and will depend on the magnitude and nature of the storm itself (Jennings *et al.*, 2012), the morphometry (von Einem and Granéli, 2010; Read *et al.*, 2014) and mixing regime of the lake and the timing of the event in relation to seasonal stratification (Spigel and Imberger, 1980).

Storms are multivariate events consisting of any combination of increases in wind speed, decreases in air temperature and heavy precipitation. Increases in wind stress (Klug *et al.*, 2012) and surface cooling are likely to decrease stratification strength and increase the depth of surface mixing (Wüest and Lorke, 2003). The impact of increased wind stress will depend on the wind strength, the size and fetch of the lake and the strength of stratification at the time of the event (Spigel and Imberger, 1980). Increases in wind speed can also induce internal waves in stratified lakes (Imberger, 1998; Woolway *et al.*, 2018) which can interact with basin topography causing increased mixing and turbulence

(Saggio and Imberger, 1998). An increase in inflow discharge as a result of heavy rain will decrease water residence time and deliver material into the lake from the catchment, potentially increasing turbidity (Jennings *et al.*, 2012; De Eyto *et al.*, 2016; Havens *et al.*, 2016). This is exacerbated in some regions when storms follow periods of warm, dry weather (Perga *et al.*, 2018). Increases in turbidity following high precipitation events have also been found to have more prolonged impacts compared to those of wind-driven storm events (Jennings *et al.*, 2012).

Storm events can also lead to changes in the concentration and vertical distribution of nutrients in the water column. Heavy precipitation and subsequent increases in catchment runoff from agricultural or urban areas can increase nutrient loading into lakes during storm events (Vanni *et al.*, 2006; James *et al.*, 2008; Crockford *et al.*, 2015; Norris *et al.*, 2017). Heavy precipitation events can also overwhelm drainage systems which can lead to uncontrolled discharges of nutrient rich untreated wastewater into lakes (Whitehead *et al.*, 2009). Furthermore, weakening of stratification and consequent deeper surface mixing that encroaches into the hypolimnion can also re-distribute nutrients into the mixed layer (James *et al.*, 2008; Mackay *et al.*, 2014; Crockford *et al.*, 2015).

A disproportionate amount of the existing literature has focussed on extreme events which induce extreme responses in physical (Woolway *et al.*, 2018), chemical (Vachon and del Giorgio, 2014; Giling, Nejstgaard, *et al.*, 2017) or ecological (Isles *et al.*, 2015; De Eyto *et al.*, 2016; Kasprzak *et al.*, 2017) variables in lakes. The knowledge gained from these events is vital for our understanding, but climatic extremes may not always induce an extreme response and understanding why and when this occurs is also important (Perga *et al.*, 2018). The importance of antecedent conditions prior to extremes has been investigated in relation to the impact of previous rainfall on soil dryness in the catchment and consequent sediment loading into lakes (Perga *et al.*, 2018). There is a lack of research, however, that has explored whether the meteorological and within-lake conditions prior to an extreme event are typical or extreme for that time of year and how this influences the physical response. This is important due to the long term trend towards higher surface water temperatures (O'Reilly *et al.*, 2015), potential shallower surface mixing (Livingstone, 2003) and longer water residence times (Whitehead *et al.*, 2009). The aim here, is to investigate the effects of within-lake antecedent conditions on a lakes' physical responses to storm events. There are many different types of extreme events but storm induced flushing events are of interest as they can impact a lake through changes in thermal stability and water residence time (Carmack *et al.*, 1979; Vanni *et al.*, 2006). Flushing events can also deliver external nutrients and redistribute internal nutrients. River flow is also known to be changing as a result of climate change (Milly *et al.*, 2005; Fowler and Kilsby, 2007). Using high resolution meteorological and within-lake data, the physical and nutrient impacts of an extreme flushing event on a lake occurring at a time of extreme stratification strength in the summer of 2016 were investigated and the responses compared with two additional flushing events (occurring in 2010 and 2012) which had contrasting antecedent conditions.

6.3 Materials and Methods

6.3.1 Site description

Blelham Tarn is a small, meso-eutrophic lake (mean total phosphorus 24.5 mg m^{-3}) (Maberly *et al.*, 2016) located in the Lake District National Park in the north-west of England (Figure 6.1). It is monomictic and typically stratifies between April and late October. The lake has a moderate depth (mean depth 6.8 m, max depth 14.5 m) (Ramsbottom, 1976) and an average annual residence time of c. 35 days (Jones and Elliott, 2007). The lake has one outflow, Blelham Beck, and four main inflows (Figure 6.1).

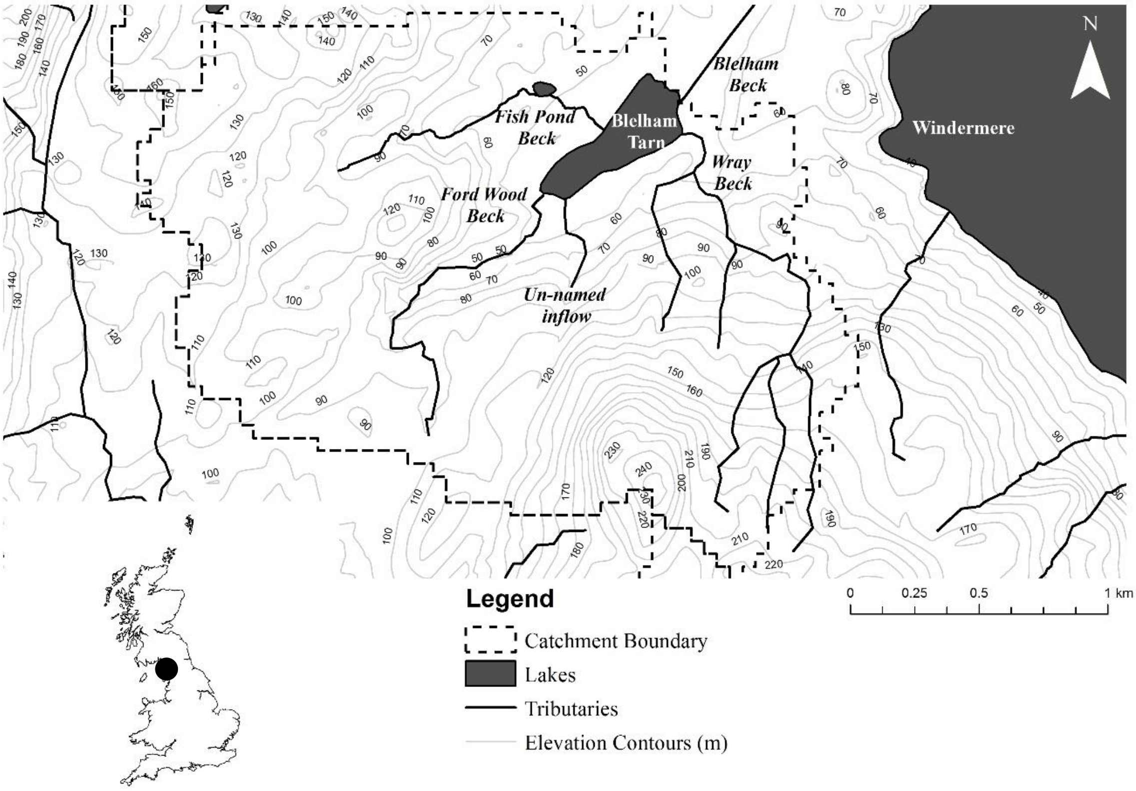


Figure 6.1 Map of Blelham Tarn, catchment and tributaries.

6.3.2 High Resolution Monitoring

An automatic water quality monitoring station (AWQMS) is located at the lake's deepest point (14.5 m). The AWQMS records meteorological variables including air temperature, wind speed, solar radiation and relative humidity. A series of platinum resistance thermometers (PRT) recording temperature are located at one metre intervals in the water column from 1-10 m with additional PRTs located at 0.5 m and 12 m. They record data at four-minute intervals, which have been averaged to daily values for the purposes of this study for an eleven year time period (2008-2018).

Flow has been gauged continuously at a nearby point on the River Leven by the Environment Agency between 1939-2018. A relationship derived in 1974 between the daily discharge recorded in the River Leven, and the daily discharge recorded at the Blelham Beck outflow from Blelham Tarn was used to allow the discharge in Blelham Beck to be calculated for the full period of the River Leven dataset (Gray, Elliott, *et al.*, 2019).

6.3.3 Statistical analysis

6.3.3.1 Calculation of physical metrics

Daily values of Schmidt stability (*St*) for 2008-2018 were calculated from the lake bathymetry (Ramsbottom, 1976), and the water temperature profile from the AWQMS, using Lake Analyzer v3.4.0 (Read *et al.*, 2011). Daily values of the total heat flux at the lake surface (Q_{tot}) were also calculated for this period using the meteorological and water temperature data from the AWQMS, using Heat Flux Analyser (Woolway *et al.*, 2015). Water density was calculated within Lake Analyzer v3.4.0 (Read *et al.*, 2011) and the depth of recent surface mixing (Z_{mix}) was then determined using two methods to ensure that the findings were not dependent on the mixed depth method being used (Gray, Mackay, *et al.*, 2019b). The first method determined the mixed depth using a 0.1 kg m^{-3} change in density from the surface. The second method determined the depth of recent mixing statistically by applying a Generalised Additive Model (GAM) to each density profile and identifying the depth of the maximum gradient using the fitted values (Gray, Mackay, *et al.*, 2019b). The depth of the maximum gradient plane was extrapolated to all depths using the intercept and slope. A vertical line was then drawn corresponding to the mean of three minimum density values from each profile. The depth where the minimum line intersected the extended maximum gradient line marked the mixed depth (Gray, Mackay, *et al.*, 2019b).

The daily instantaneous residence time (T_{res}) was also calculated, as

Equation 6.1

$$T_{res} = (V/Q)/t$$

where V is the volume of Blelham Tarn (693000 m^3) (Ramsbottom, 1976), Q is the daily mean discharge of Blelham Beck (m^3 s^{-1}) and t is number of seconds in a day (86400 s).

6.3.3.2 Defining an extreme event

Three significant flushing events were found in the eleven-year study period, occurring in July 2010, June 2012 and August 2016. Examination of the long term flow record (1939-2018) from the National River Flow Archive (National River Flow Archive, 2019) revealed that the peak discharges for these events were all in the top 10 recorded discharges for summer (June, July and August) in the entire long term flow record. The percentile of the peak discharge value for the full record and for summer were calculated.

The mean and standard deviation discharge values for each day of the year over the entire record period were calculated to determine the long term mean annual discharge pattern. The length of each flushing event was then determined as the number of consecutive days when the outflow discharge exceeded the long term mean plus two standard deviations. Once the event length had been calculated, time periods of equal length prior to and after the event were selected to determine the immediate antecedent and recovery conditions, respectively.

6.3.3.3 Defining the timing of the event response

To determine the timing of the response for the physical metrics, and to test if the event timing was consistent amongst lake physical indicators (Schmidt stability, mixed depth and surface water temperature) statistical breakpoint analysis was applied using the ‘strucchange’ package in the statistical software package R (Zeileis *et al.*, 2003). This method applies piecewise linear regression models to the dataset and finds breakpoints that minimise the residual sum of squares. The Bayesian Information Criterion (BIC) is then used to find the optimal number of breakpoints as a compromise between the number of parameters and the residual sum of squares (Zeileis *et al.*, 2003). The analysis was applied to data June-October 2016 and in this case the breakpoint should extract the day of the year (and confidence intervals) where there are marked changes within the lake physical metrics.

6.3.3.4 Determining the magnitude of the event compared to the long term average

To assess the impact of the storm on the physical structure of the lake, a series of t-tests were performed within R on the differences between the values of outflow discharge, wind speed cubed, total heat flux, Schmidt stability, the mixed depth and the surface water temperature from the time periods before and after each event. Additional t-tests were performed on the values of each physical driver parameter (outflow discharge, wind speed cubed, total heat flux) and each lake physical response parameter (Schmidt stability, mixed depth and surface water temperature) from the time periods before, during and after the event and the equivalent days from the long term average data. These were used to test whether the antecedent conditions were typical for the time of year prior to the event, whether the event was extreme compared to the long term average, and whether the event had detectable lasting impacts on the system.

6.3.3.5 Nutrient impacts

The impacts of the storm events on lake nutrient concentrations (dissolved inorganic nitrogen, silica and soluble reactive phosphorus) were also investigated. Fortnightly data collected by the UK Centre for Ecology & Hydrology during 2008-2018 were linearly interpolated from fortnightly to daily values, the mean and standard deviations were then calculated for each day of the year to provide the seasonal baseline pattern. The nutrient concentrations were compared to limitation levels in order to identify any shifts in the nutrient regime. These limitation levels were defined as: 100 mg/L for dissolved inorganic nitrogen (DIN) (Reynolds, 2006), 500 mg/L for silica (Lund, 1950) and 0.003 mg/L for soluble reactive phosphorus (Reynolds, 1998).

6.4 Results

6.4.1 The characteristics of the 2016 event

6.4.1.1 Physical drivers

The 2016 event was primarily a flushing event as the cube of the wind speed remained within one standard deviation of the long term mean and the total heat flux was higher than the long term average during the event (Figure 6.2). Blelham Beck outflow discharge exceeded the long term mean plus two standard deviations for five consecutive days 21/08/16-25/08/16 which subsequently led to a decrease in the residence time below the long term average (Figure 6.2). The peak flow of 0.9 $m^3 s^{-1}$ occurred on 22/08/2016 which was in the 98th percentile for the entire flow record (1939-2018) and in the 99.9th percentile for summer. The immediate antecedent conditions were therefore defined as the five day period prior to the event (16/08/16-20/08/16), and the impact on the recovery was assessed using the five days immediately after the event (26/08/16-30/08/16).

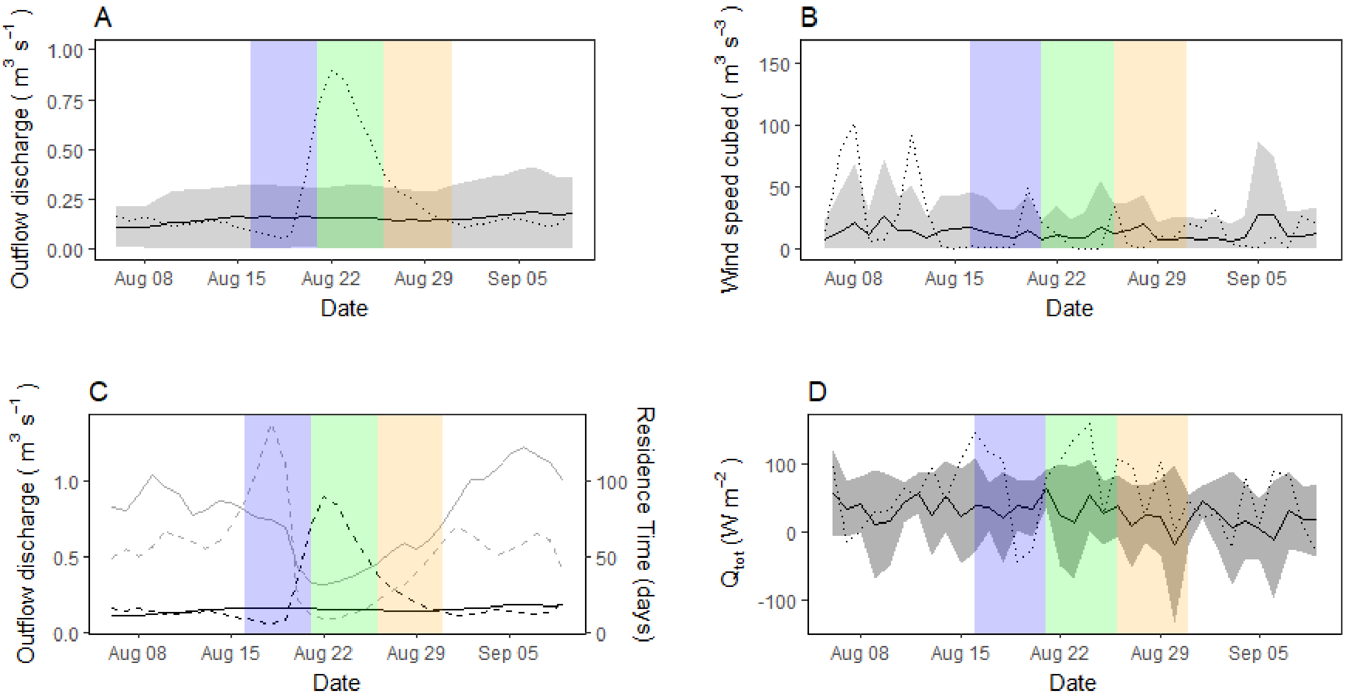


Figure 6.2 The long term mean (solid black line), standard deviation (grey shading) and 2016 mean values with the blue, green and orange shading marking the five days prior to the event (16/08/2016-20/08/2016), the five days during the event (21/08/2016-25/08/2016) and the five days following the event (26/08/2016-30/09/2016), respectively for (a) outflow discharge, (b) cubed wind speed, (c) outflow discharge compared to the water residence time and (d) the total heat flux (Q_{tot}).

6.4.1.2 The timing of the event response

The breakpoint analysis identified 4-5 breakpoints between June-October depending on the physical metric (Table 6.1). For the flushing event, a consistent breakpoint at day 230-231 (19/08/16-20/08/16) was identified in each of the physical response parameters (Table 6.1; Figure 6.3). This breakpoint was located on either the first day of the flushing event or the day prior to it, marking a period of significant change within the lake.

Table 6.1 Number of breakpoints identified during June-October and the day of the year identified as a breakpoint for the storm event for within lake physical metrics.

Variable	Number of breakpoints identified (June-October)	Day of the breakpoint and confidence intervals for the storm event
Schmidt stability	4	230 ± 1
Mixed depth (method 1)	5	230 ± 1
Mixed depth (method 2)	4	231 ± 1
Surface water temperature (0.5 m)	5	230 ± 1

6.4.1.3 Physical Response

In the five days prior to the event, the mean Schmidt stability and mean surface water temperatures were both higher than the long term mean plus one standard deviation and the mixed depth was shallower than the long term mean (Figure 6.3). During the event the mean Schmidt stability and surface water temperature decreased and the mixed layer deepened to values similar to the long term mean and therefore more typical for the time of year (Figure 6.3). This decrease was short-lived however as the Schmidt stability, surface water temperature and mixed depth recovered to values exceeding the long term mean plus one standard deviation in the five days following the event (Figure 6.3).

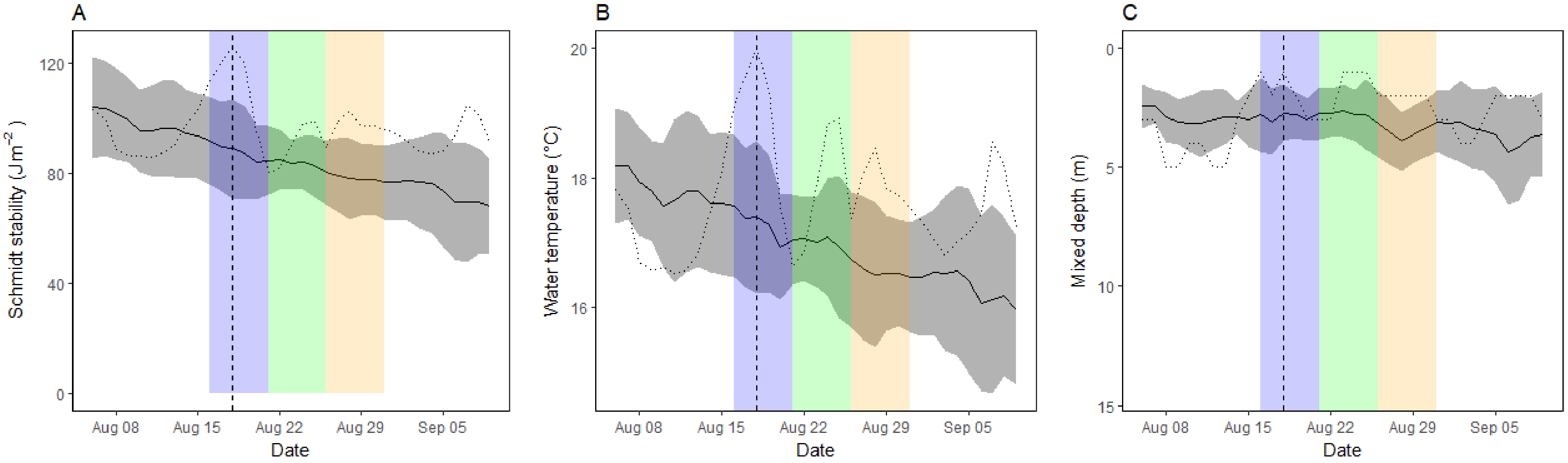


Figure 6.3 The long term mean (solid black line), standard deviation (grey shading) and 2016 mean values with the blue, green and orange shading marking the five days prior to the event (16/08/2016-20/08/2016), the five days during the event (21/08/2016-25/08/2016) and the five days following the event (26/08/2016-30/09/2016), respectively for (a) Schmidt stability, (b) surface water temperature (0.5 m) and (c) the depth of recent mixing. The vertical dashed line marks the breakpoint.

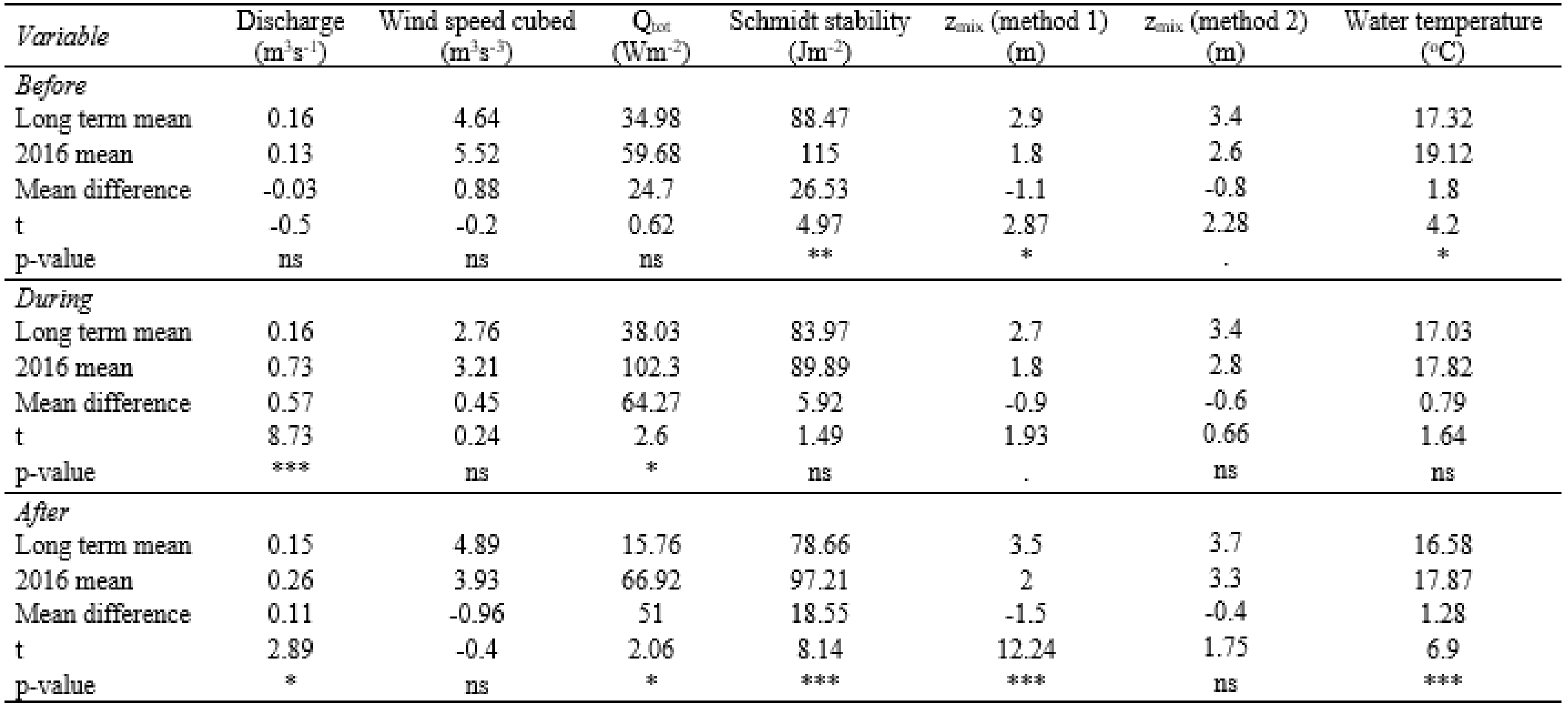
6.4.1.4 Comparisons with the long term mean

Values of the driving and response variables from before, during and after the event were compared to the corresponding long term mean values. The driving variables immediately prior to the storm event in 2016 were not significantly different from the long term mean, although the outflow was smaller than usual and the heat flux noticeably higher than usual (Table 6.2). All within-lake stability variables were significantly different from the long term mean (Table 6.2). This suggests that at the time of the flushing event the lake was already in a state of atypically high stability.

During the storm, as expected, the outflow discharge was significantly high, which led to a reduction in the water residence time (Table 6.2). Despite the total heat flux remaining high for the time of year, the Schmidt stability and surface water temperature reduced and went from being significantly high before the event to not being significantly different from the long term mean during the event, the mean difference between the 2016 values and the long term mean also reduced (Table 6.2). Similarly the significance of the shallowness of the mixed depth for the time of year also reduced and the difference between the 2016 values and the long term mean decreased (Table 6.2). This meant that the storm event shifted the lake from being atypically stable to normal levels of stability for the time of year. In the five days following the event, flow remained significantly high, but was much lower compared to during the event (Table 6.2). As the total heat flux remained significantly high, the Schmidt stability and surface water temperature returned to being significantly high for the time of year resulting in the lake becoming atypically stable again (Table 6.2).

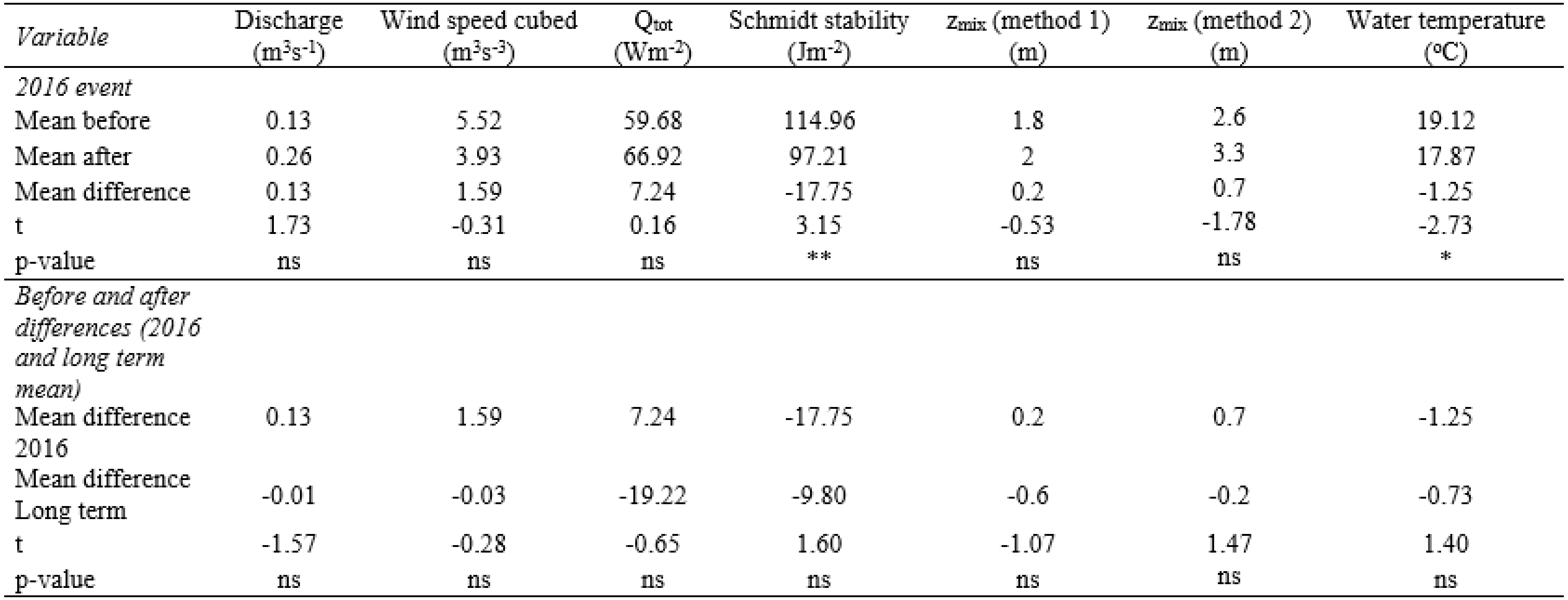
Although the Schmidt stability and surface water temperature were both significantly lower after the event compared to before it, by 17.79 Jm^{-2} and 1.25 °C respectively (Table 6.3), and the mixed depth deeper, by 0.2-0.7 m, depending on method used, there is normally a decline at this time of year in these variables. Therefore, although the decline in the Schmidt stability and surface water temperature, and the deepening of the mixed depth, were slightly larger than normal none of these changes were statistically different from the typical changes in the long term mean at this time of year (Table 6.3).

Table 6.2. Long term and 2016 means for the periods before (16/08/16-20/08/16), during (21/08/16-25/08/16) and after (26/08/16-30/08/16) the event and T-test results to test if 2016 conditions were significantly different compared to the long term mean ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$, ·$p < 0.1$, *ns- not significant, df =8 and n=5 for each test.*



Variable	Discharge (m^3s^{-1})	Wind speed cubed (m^3s^{-3})	Q_{tot} (Wm^{-2})	Schmidt stability (Jm^{-2})	z_{mix} (method 1) (m)	z_{mix} (method 2) (m)	Water temperature (°C)
Before							
Long term mean	0.16	4.64	34.98	88.47	2.9	3.4	17.32
2016 mean	0.13	5.52	59.68	115	1.8	2.6	19.12
Mean difference	-0.03	0.88	24.7	26.53	-1.1	-0.8	1.8
t	-0.5	-0.2	0.62	4.97	2.87	2.28	4.2
p-value	ns	ns	ns	**	*	.	*
During							
Long term mean	0.16	2.76	38.03	83.97	2.7	3.4	17.03
2016 mean	0.73	3.21	102.3	89.89	1.8	2.8	17.82
Mean difference	0.57	0.45	64.27	5.92	-0.9	-0.6	0.79
t	8.73	0.24	2.6	1.49	1.93	0.66	1.64
p-value	***	ns	*	ns	.	ns	ns
After							
Long term mean	0.15	4.89	15.76	78.66	3.5	3.7	16.58
2016 mean	0.26	3.93	66.92	97.21	2	3.3	17.87
Mean difference	0.11	-0.96	51	18.55	-1.5	-0.4	1.28
t	2.89	-0.4	2.06	8.14	12.24	1.75	6.9
p-value	*	ns	*	***	***	ns	***

Table 6.3. T-test to test if values of physical drivers and within lake physical metrics five days before the event (16/08/2016-20/08/2016) and five days after the event (26/08/2016-30/08/2016) were statistically significant during the 2016 event and tests to determine if the differences between before and after time periods are significantly different from the long term mean differences for the same time period ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$, ·$p < 0.1$, *ns- not significant, df =12 and n=7.*



Variable	Discharge (m^3s^{-1})	Wind speed cubed (m^3s^{-3})	Q_{tot} (Wm^{-2})	Schmidt stability (Jm^{-2})	z_{mix} (method 1) (m)	z_{mix} (method 2) (m)	Water temperature (°C)
2016 event							
Mean before	0.13	5.52	59.68	114.96	1.8	2.6	19.12
Mean after	0.26	3.93	66.92	97.21	2	3.3	17.87
Mean difference	0.13	1.59	7.24	-17.75	0.2	0.7	-1.25
t	1.73	-0.31	0.16	3.15	-0.53	-1.78	-2.73
p-value	ns	ns	ns	**	ns	ns	*
Before and after differences (2016 and long term mean)							
Mean difference 2016	0.13	1.59	7.24	-17.75	0.2	0.7	-1.25
Mean difference Long term	-0.01	-0.03	-19.22	-9.80	-0.6	-0.2	-0.73
t	-1.57	-0.28	-0.65	1.60	-1.07	1.47	1.40
p-value	ns	ns	ns	ns	ns	ns	ns

6.4.2 Additional high flow events

The outflow discharge exceeded the long term mean plus two standard deviations for 10 consecutive days in 2010 (16/07/10-25/07/10) and 23 consecutive days in 2012 (16/06/12-11/07/12). Time periods of equal length were used to determine the antecedent and post-event conditions for each event. The peak discharge during the events reached 1.2 $m^3 s^{-1}$ and 1.3 $m^3 s^{-1}$ for 2010 and 2012, respectively, both of which are above the 99th percentile for discharge from the entire 1939-2018 record.

Prior to the 2010 event, the outflow discharge was significantly high and the total heat flux (-21.24 Wm^{-2}) was significantly low (Table 6.4; Figure 6.4). Within the lake, the mixed depth was significantly deeper (1.1-1.6 m deeper) and the surface water temperature significantly lower (-1.04 ^{o}C) (Table 6.4; Figure 6.4) than the long term mean. The extreme event therefore occurred at a time when the lake was unusually unstable in comparison with the long term mean conditions. During the 2010 event, discharge was significantly high and the Schmidt stability and surface water temperature decreased even further during the event, remaining significantly low and therefore increasing instability (Table 6.4; Figure 6.4). The mixed layer also deepened slightly and remained deeper than the average for the time of year (Table 6.4; Fig. 4). Following the event, the discharge recovered to become similar to the long term mean for the time of year (Table 6.4; Fig. 4) whereas the Schmidt stability and surface water temperature, remained significantly low and therefore the lake remained atypically unstable for the time of year (Table 6.4; Fig. 4).

Prior to the 2012 event, meteorological conditions were largely typical for the time of year, although discharge was lower than normal (Table 6.5; Figure 6.5). Schmidt stability was a little lower than normal, indicating decreased stability, while mixed depths were a little shallower, indicative of increased stability, and surface water temperature about the same as normal. Collectively these conditions suggest the lake was relatively normal for the time of year. During the event, the outflow discharge was significantly high and the Schmidt stability and water temperature were significantly low meaning that the storm caused the lake to become more unstable (Table 6.5; Figure 6.5). This instability continued following the event as the discharge remained significantly high and the Schmidt stability and water temperature remained significantly low (Table 6.5; Figure 6.5).

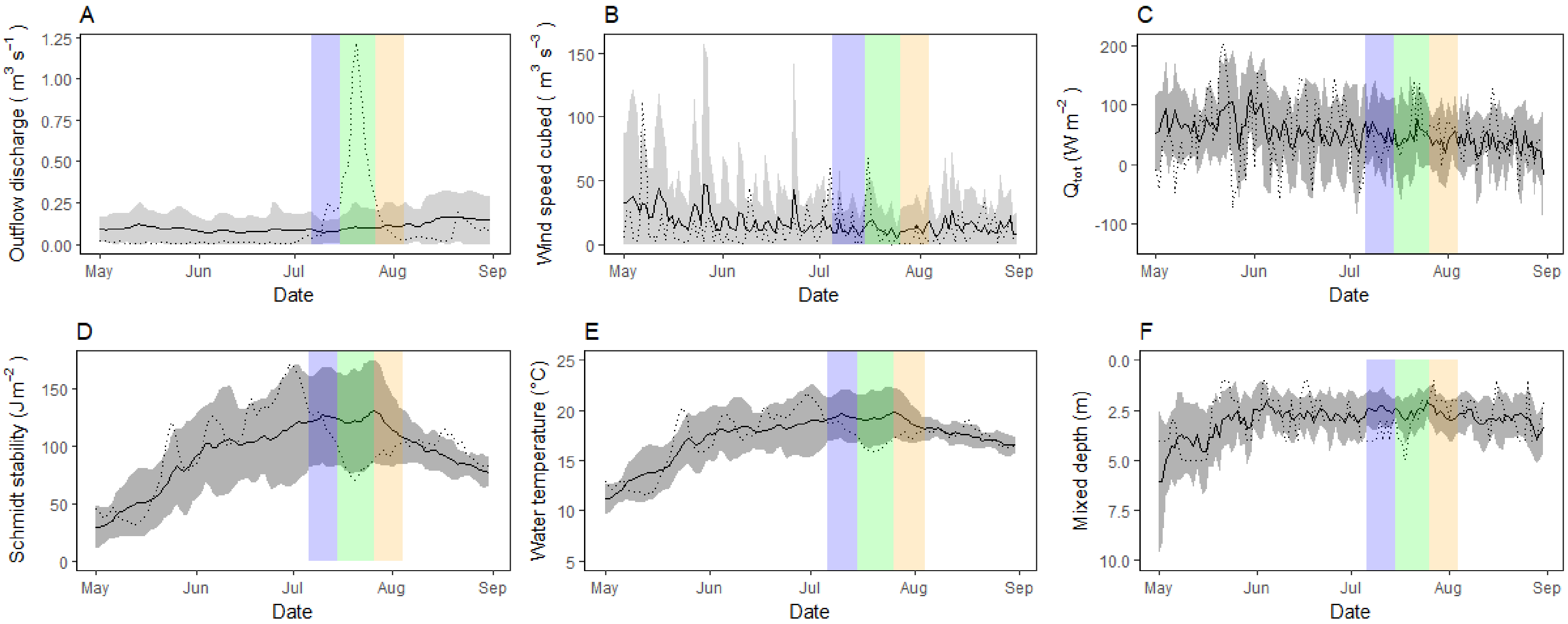
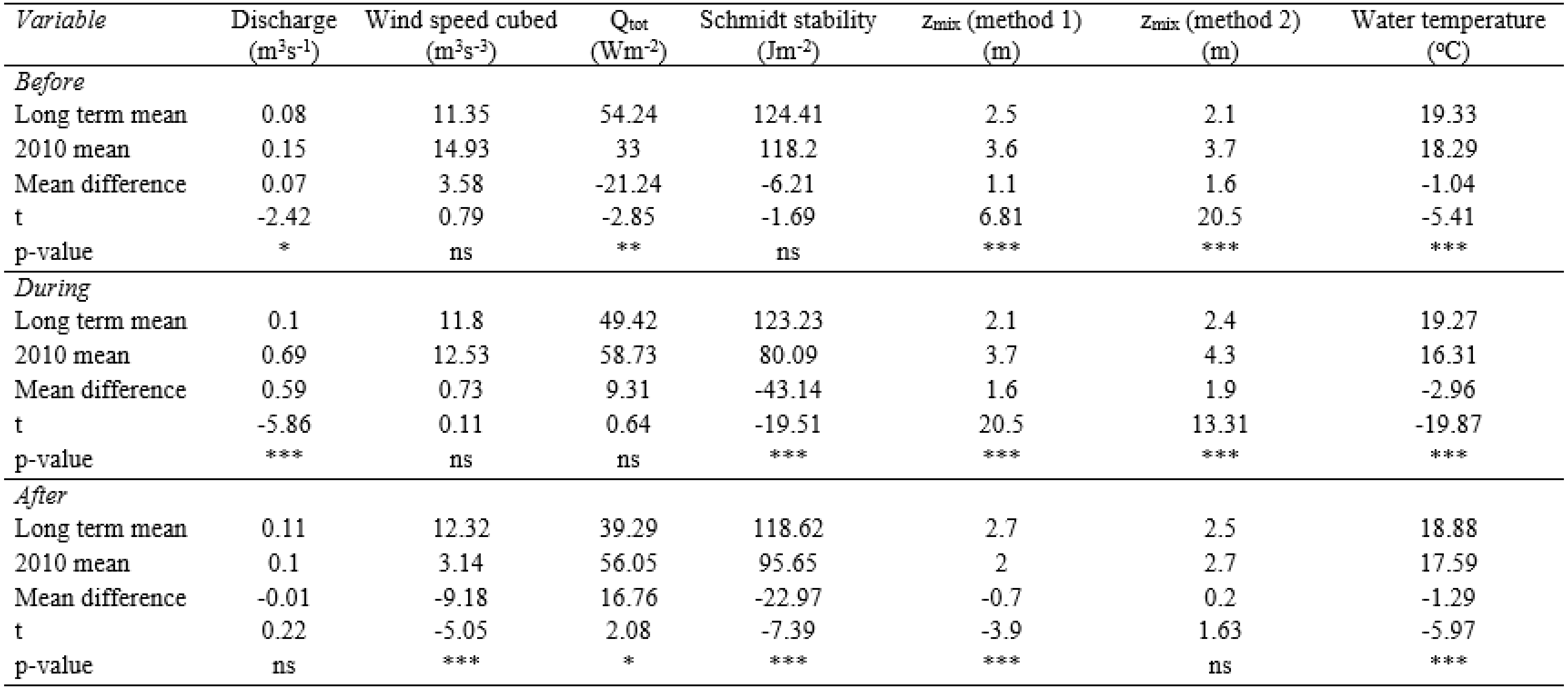


Figure 6.4 The long term mean (solid black line), standard deviation (grey shading) and 2010 mean values with the blue, green and orange shading marking the 10 days prior to the event (06/07/10-15/07/10), the 10 days during the event (16/07/10-25/07/10) and the 10 days following the event (26/07/10-04/08/10), respectively for (a) outflow discharge, (b) cubed wind speed, (c) total heat flux (Q_{tot}), (d) Schmidt stability, (e) surface water temperature and (f) mixed depth using method 1.

*Table 6.4. Long term and 2010 means for the periods before (06/07/10-15/07/10), during (16/07/10-25/07/10) and after (26/07/10-04/08/10) the event and T-test results to test if 2010 conditions were significantly different compared to the long term mean ***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1, ns- not significant, df =18 and n=10 for each test.*



Variable	Discharge (m^3s^{-1})	Wind speed cubed (m^3s^{-3})	Q_{tot} (Wm^{-2})	Schmidt stability (Jm^{-2})	z_{mix} (method 1) (m)	z_{mix} (method 2) (m)	Water temperature (ºC)
Before							
Long term mean	0.08	11.35	54.24	124.41	2.5	2.1	19.33
2010 mean	0.15	14.93	33	118.2	3.6	3.7	18.29
Mean difference	0.07	3.58	-21.24	-6.21	1.1	1.6	-1.04
t	-2.42	0.79	-2.85	-1.69	6.81	20.5	-5.41
p-value	*	ns	**	ns	***	***	***
During							
Long term mean	0.1	11.8	49.42	123.23	2.1	2.4	19.27
2010 mean	0.69	12.53	58.73	80.09	3.7	4.3	16.31
Mean difference	0.59	0.73	9.31	-43.14	1.6	1.9	-2.96
t	-5.86	0.11	0.64	-19.51	20.5	13.31	-19.87
p-value	***	ns	ns	***	***	***	***
After							
Long term mean	0.11	12.32	39.29	118.62	2.7	2.5	18.88
2010 mean	0.1	3.14	56.05	95.65	2	2.7	17.59
Mean difference	-0.01	-9.18	16.76	-22.97	-0.7	0.2	-1.29
t	0.22	-5.05	2.08	-7.39	-3.9	1.63	-5.97
p-value	ns	***	*	***	***	ns	***

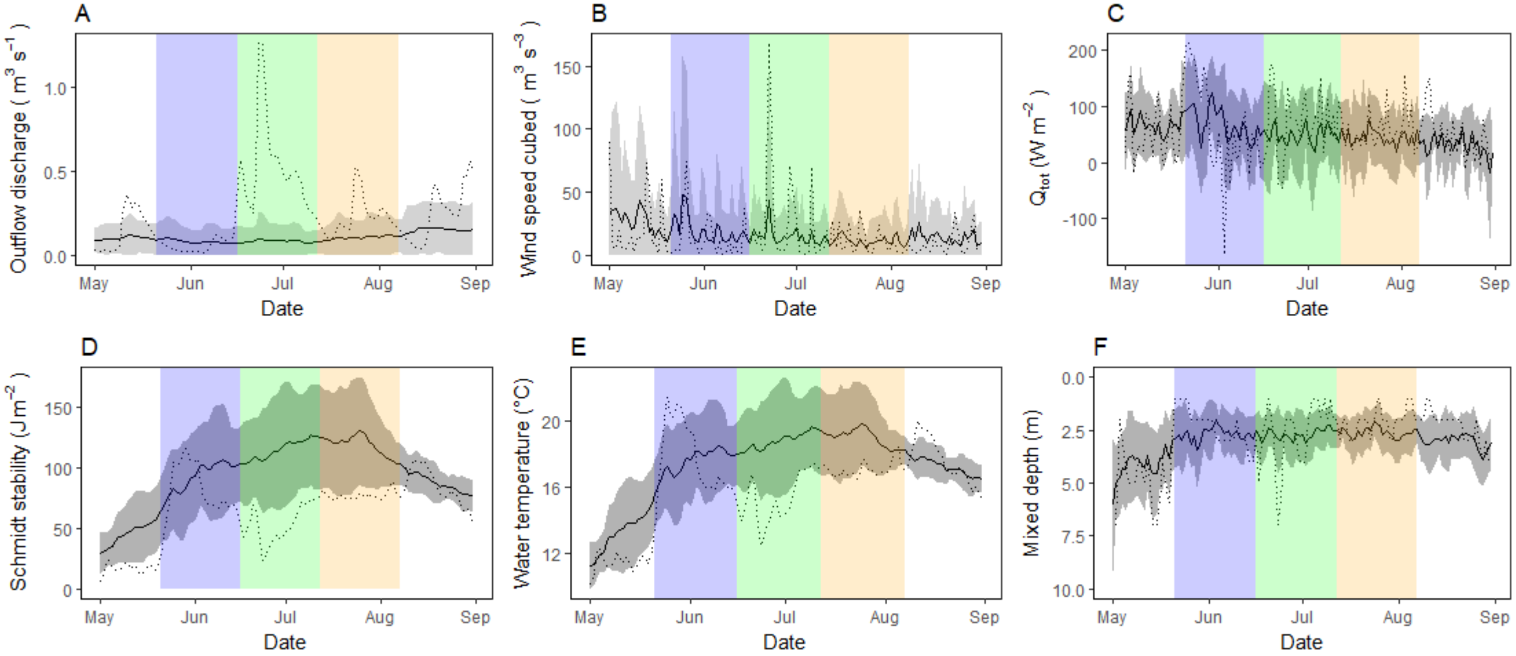
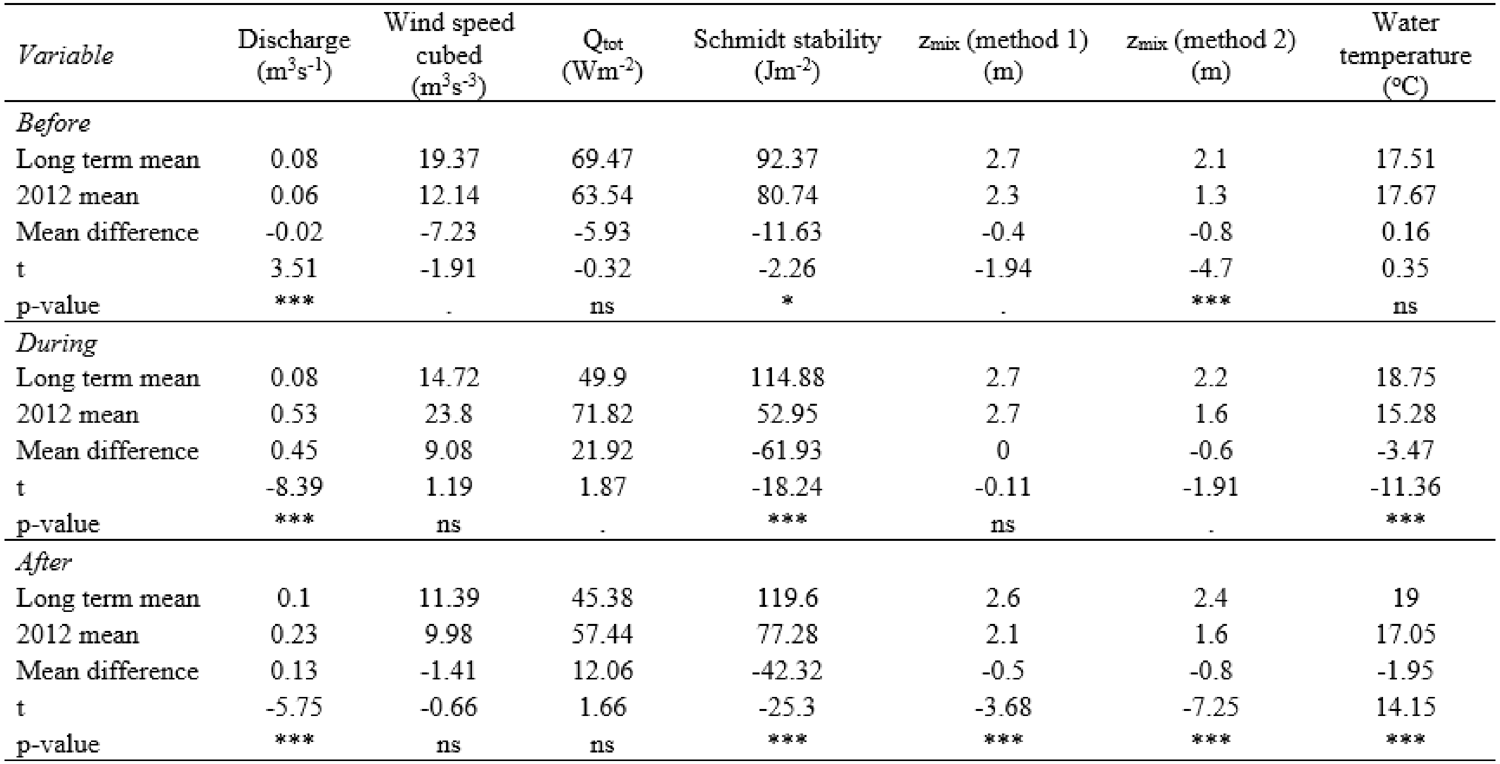


Figure 6.5. The long term mean (solid black line), standard deviation (grey shading) and 2012 mean values with the blue, green and orange shading marking the 23 days prior to the event (21/05/12-15/06/12), the 23 days during the event (16/06/12-11/07/12) and the 23 days following the event (12/07/12-06/08/12), respectively for (a) outflow discharge, (b) cubed wind speed, (c) total heat flux (Q_{tot}), (d) Schmidt stability, (e) surface water temperature and (f) mixed depth using method 1.

*Table 6.5 Long term and 2012 means for the periods before (21/05/12-15/06/12), during (16/06/12-11/07/12) and after (12/07/12-06/08/12) the event and T-test results to test if 2012 conditions were significantly different compared to the long term mean ***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1, ns- not significant, df =50 and n=23 for each test.*



Variable	Discharge (m^3s^{-1})	Wind speed cubed (m^3s^{-3})	Q_{tot} (Wm^{-2})	Schmidt stability (Jm^{-2})	z_{mix} (method 1) (m)	z_{mix} (method 2) (m)	Water temperature (°C)
Before							
Long term mean	0.08	19.37	69.47	92.37	2.7	2.1	17.51
2012 mean	0.06	12.14	63.54	80.74	2.3	1.3	17.67
Mean difference	-0.02	-7.23	-5.93	-11.63	-0.4	-0.8	0.16
t	3.51	-1.91	-0.32	-2.26	-1.94	-4.7	0.35
p-value	***	.	ns	*	.	***	ns
During							
Long term mean	0.08	14.72	49.9	114.88	2.7	2.2	18.75
2012 mean	0.53	23.8	71.82	52.95	2.7	1.6	15.28
Mean difference	0.45	9.08	21.92	-61.93	0	-0.6	-3.47
t	-8.39	1.19	1.87	-18.24	-0.11	-1.91	-11.36
p-value	***	ns	.	***	ns	.	***
After							
Long term mean	0.1	11.39	45.38	119.6	2.6	2.4	19
2012 mean	0.23	9.98	57.44	77.28	2.1	1.6	17.05
Mean difference	0.13	-1.41	12.06	-42.32	-0.5	-0.8	-1.95
t	-5.75	-0.66	1.66	-25.3	-3.68	-7.25	14.15
p-value	***	ns	ns	***	***	***	***

6.4.3 Storm impacts on nutrient levels

On average, soluble reactive phosphorus was below limiting levels during the growing season in each year, suggesting that the lake is persistently phosphorus limited (Figure 6.6). Dissolved inorganic nitrogen was generally above the level of limitation through the summer as was silica after June in each year (Figure 6.6). In 2016, though, dissolved inorganic nitrogen was systematically below limiting levels for the two months prior to the storm. The storm events did not appear to impact the nutrient balance except for during 2016 when the dissolved organic nitrogen concentrations were atypically low and limiting prior to the storm event but appeared to increase to non-limiting levels following the storm (Figure 6.6). This suggests that the system transitioned from being co-limited in nitrogen and phosphorus prior to the event to just phosphorus limited following the event (Figure 6.6).

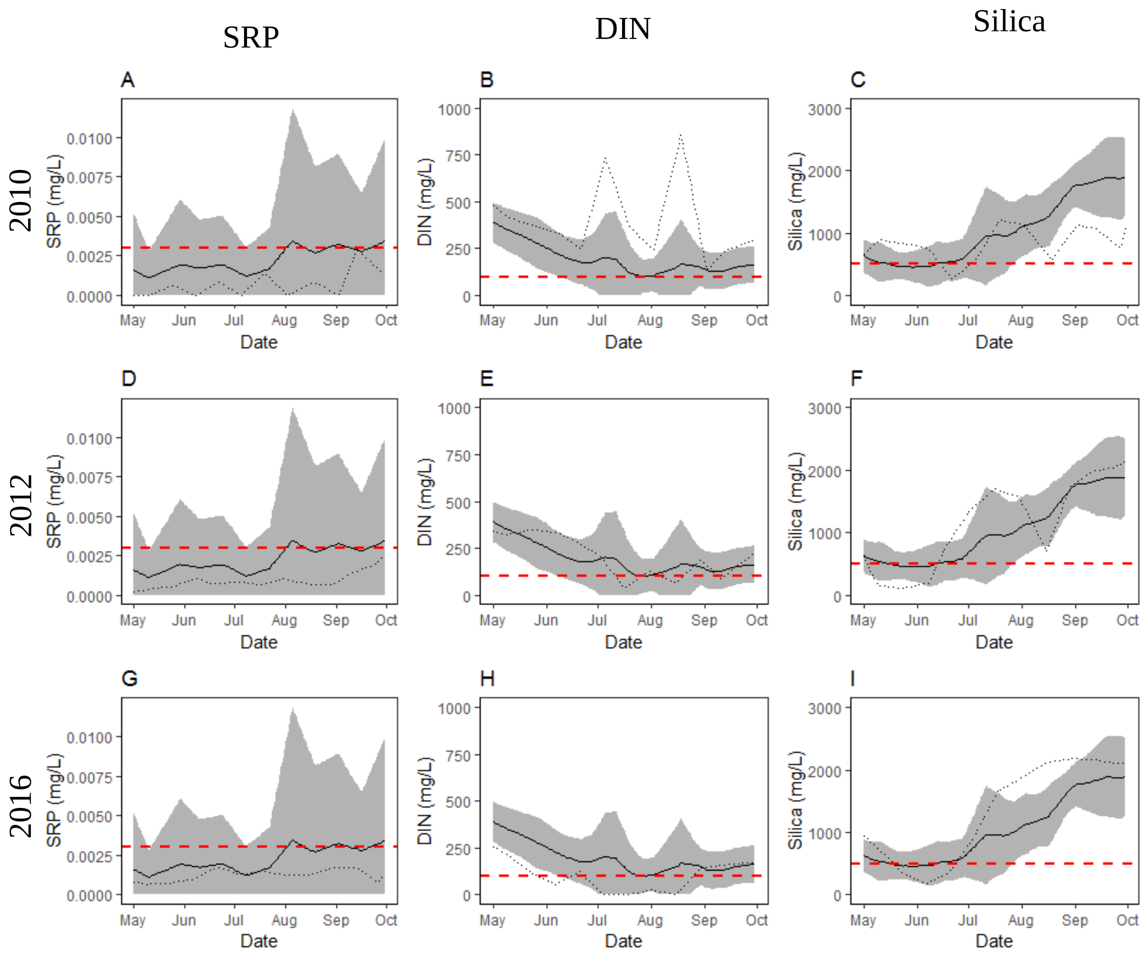


Figure 6.6 The long term mean (solid black line), standard deviation (grey shading) and event values (dashed black line) with the horizontal red line marking the limiting value for each nutrient for (a) SRP 2010, (b) DIN 2010, (c) silica 2010, (d) SRP 2012, (e) DIN 2012, (f) silica 2012, (g) SRP 2016, (h) DIN 2016 and (i) silica 2016.

6.5 Discussion

The importance of antecedent conditions for the physical response of a small monomictic lake to three summertime, storm-driven flushing events have been investigated. Each of the events investigated had peak daily discharge values that fell in the highest ten of all summer discharge values in a 79-year record (1939-2018). Each of the events had a destabilising impact on the water column but the impact of the response was dependent on the antecedent conditions prior to each event.

Much of the previous research into the impacts of extreme events has focussed on various lake variables being pushed to more extreme values (Jennings *et al.*, 2012; De Eyto *et al.*, 2016; Giling, Nejstgaard, *et al.*, 2017; Kasprzak *et al.*, 2017). Likewise, the July 2010 and June 2012 events studied here induced an extreme physical response. Prior to the July 2010 event the lake was already in an atypically unstable and cool state for the time of year, and the event weakened stratification further. During July, lake surface water temperatures are typically amongst the highest annually (~19 ^{o}C; Table 6.2) and if the event had occurred at a time of long term mean conditions then the lake structure may have been more resistant to the extreme event. The conditions prior to the June 2012 event were relatively typical for the time of year. At this time of year, the lake is usually gaining heat, leading to increases in stratification strength and surface water temperature, from ~ 17.50 ^{o}C to 19.00 ^{o}C, according to the long term means before and after the event, respectively (Table 6.5). The flushing event prevented this, such that surface water temperatures reduced to 15.28 ^{o}C during the event before recovering to 17.05 ^{o}C afterwards (Table 6.5).

In contrast, the August 2016 flushing event did not push the physical lake structure into a more abnormal state. Prior to the event the lake was atypically stable with high surface water temperatures and Schmidt stability. This is unusual, as the long term means of these variables usually start to decline by late August (Table 6.2).

Increased surface water temperatures (O'Reilly *et al.*, 2015) and strengthened stratification (Peeters, Straile, Lorke and Livingstone, 2007; Butcher *et al.*, 2015; Kraemer *et al.*, 2015; Woolway, Dokulil, *et al.*, 2017) are likely to become more common due to increases in air temperature (IPCC, 2013) and atmospheric stilling (Vautard *et al.*, 2010) which is reducing wind mixing (Woolway, Meinson, *et al.*, 2017; Woolway *et al.*, 2019). It is therefore becoming increasingly likely that extreme meteorological events such as storms will occur at a time of strong lake stability. During the storm event in 2016, the surface water temperature and Schmidt stability reduced to levels which were typical for the time of year (Table 6.2). This suggests that, as stratification in lakes is predicted to become more stable, there is an increased likelihood that extreme storm events will return lakes to conditions typical of the present day rather than push them to extreme states.

The physical structure of this small, monomictic lake responded quickly to changes in physical drivers so the impacts of these events on the physical structure of the lake were significant but relatively short-lived. This quick recovery of lake stability is likely due to the shallow mean mixed depth of the lake, such that only a relatively small volume of water needs to be heated in order to strengthen the vertical density gradient and reinstate stability. During the 2016 event the recovery of stability was helped due to the clement weather conditions following the event resulting in the incoming heat flux being larger than the norm for the time of year. This finding is analogous with other studies which have also found the physical impacts of storm events to be relatively short lived in comparison to chemical and ecological impacts (Jennings *et al.*, 2012; Perga *et al.*, 2018).

The impact of the 2016 event on the nutrient levels were more prolonged with evidence that the storm event shifted the nutrient regime of the lake from co-limitation in nitrogen and phosphorus before the event to just phosphorus limitation following the event. Limitation in dissolved inorganic nitrogen is relatively unusual for this lake and its occurrence may have been caused by the warm clement weather conditions which resulted in a lack of rain events delivering nutrients into the lake as well as the atypically strong lake stability. During times of stratification the bottom waters of the lake are isolated from the surface and the consumption of dissolved oxygen by microbial respiration can result in anoxia (Foley *et al.*, 2012). Anoxic conditions can lead to the release of phosphorus and ammonium from sediments which are isolated from the surface mixed layer (Mortimer, 1941; Nürnberg, 1988; Beutel, 2006; Mackay *et al.*, 2014). Warm stable weather and increases in stratification strength and length as a result of climatic warming can therefore reduce the amount of nutrients available in the surface mixed layer during the mid-summer and enhance hypolimnetic oxygen depletion (Jankowski *et al.*, 2006). Infrequent disturbances into this nutrient rich layer due to high stratification strength may have therefore led to nitrogen limitation. This limitation was then likely alleviated through increased nutrient loading from the catchment as a result of heavy precipitation and potentially due to the incorporation of nutrient rich water from the hypolimnion through deeper surface mixing.

Overall, the increased frequency of strong storm and flushing events predicted by climate change models (IPCC, 2013) may have the effect of returning lake temperature profiles to conditions normal for present day, rather than forcing them to more extreme conditions. This is because the stronger stratification also predicted by climate change models may resist the extent of mixing or flushing compared to if they were acting on lakes whose conditions were closer to long term means observed during the 20th and early 21st centuries. For lakes with relatively shallow mean mixed depths, these physical adjustments may be short-lived, but could, nevertheless, have profound long term impacts on ecological factors such as nutrient limitation within the lake. Such impacts could include returning lake nutrient dynamics to present day conditions.

7 The impact and recovery of a phytoplankton community in response to a storm event in a small meso-eutrophic lake

(Gray, E., Mackay, E.B., Elliott, J.A., Folkard, A.M, and Jones, I.D. (2019) The impact and recovery of a phytoplankton community in response to storm event in a small meso-eutrophic lake. In preparation for submission)

7.1 Abstract

1. Extreme meteorological events such as storms are expected to increase with climate change in certain regions. Abiotic disturbances like storm events can disrupt the structure and function of ecosystems through changes in biomass, species and functional diversity and evenness. Lake phytoplankton communities respond rapidly to storm events due to their fast generation times which can have impacts on the seasonal succession as well as the structure and function of the community.
2. This study in 2016 investigates the impact of a storm-driven flushing event on the phytoplankton community succession and on the vertical distribution and composition of the phytoplankton community within the water column of a small meso-eutrophic lake in the UK.
3. The phytoplankton community followed the typical phylogenetic seasonal succession, however the community had become abnormally dominated by a

disproportionate amount of Chlorophytes in comparison to the average for the period 2008-2018. The storm event over the 21-25th August appeared to reverse this dominance and return the community to a pattern more typical of that time of year.

4. The event restructured the vertical distribution of the biomass in the water column from a biomass peak at 2 m prior to the event to a peak at 1 m following the event. The rate of biomass recovery following the event was highest at the surface and delayed with increasing depth.
5. There was an increase in species, phylogenetic and functional diversity and evenness following the event at all depths with the exception of 1 m, where there was a reduction in phylogenetic diversity and evenness in the week following the event. This was due to the dominance of Cryptophytes (C strategists) at 1 m, whereas the distribution of biomass was more even amongst phylogenetic and functional groups at 2-5 m depths.
6. With climate change it is projected that many lakes will experience increases in stratification strength. Findings here suggest that storm events occurring at a time of atypically high stratification strength may be beneficial for the phytoplankton community by reducing the dominance of one group, increasing diversity and evenness and returning the lake to a phytoplankton community more typical of the time of year.

7.2 Introduction

It is currently subject to debate whether the loss of biodiversity as a result of anthropogenic stressors and climate change will impair ecosystem function and the ability of a system to recover from disturbance events, or whether functioning can be maintained through the replacement of species that are more adapted to stress (McCann, 2000; Loreau *et al.*, 2001; Ho *et al.*, 2011; Soininen *et al.*, 2012; Oliver *et al.*, 2015). Biodiversity has two key components, the number of species in a community (species richness) and how the biomass is distributed amongst species (evenness) (Wilsey and Potvin, 2000; Soininen *et al.*, 2012). Diverse and even communities are often associated with being more resistant to disturbance (Naeem *et al.*, 1994; Naeem and Li, 1997; Kennedy *et al.*, 2002; Wittebolle *et al.*, 2009; Oliver *et al.*, 2015) with community evenness prior to a disturbance event being a key factor in preserving the functional stability of the ecosystem (Wittebolle *et al.*, 2009). Biomass, however, is often distributed unevenly between species (Passy, 2016) with systems with a lower species evenness tending to have a higher biomass (Mulder *et al.*, 2004). Species richness and evenness can respond differently to disturbance events (Mackey and Currie, 2001; Yeboah *et al.*, 2016). Immediately following an event there is often an initial increase in species diversity which then tends to decline during the recovery from the disturbance, whilst evenness increases with time from the disturbance (Yeboah *et al.*, 2016). This response is not universal across systems (e.g. Ho *et al.*, 2011; Mackey and Currie, 2001).

Understanding the response of ecosystems to disturbance events is becoming increasingly important as storms, along with other climatic extremes, are expected to increase in frequency and magnitude with climatic change (Coumou and Rahmstorf, 2012; Hov *et* *al.*, 2013; IPCC, 2013). Short term increases in wind speed and reductions in air temperature as a result of storms can significantly impact lake stratification leading to deeper surface mixing (Jennings *et al.*, 2012; Woolway *et al.*, 2018; Gray, Mackay, *et al.*, 2019a), while heavy precipitation can lead to reduced water residence times (Jacobsen and Simonsen, 1993; Klug *et al.*, 2012; Gray, Mackay, *et al.*, 2019a). These physical impacts of storm events can result in wider impacts on the whole pelagic lake ecosystem, through direct and indirect effects on phytoplankton communities, which are the main primary producers and a key influence on water quality (Winder and Sommer, 2012; Huisman *et al.*, 2018). Investigating the response of phytoplankton community biodiversity in the context of short term episodic events is also useful due to their fast generation times enabling short and longer term implications to be considered (Padisak, 1993; Sommer *et al.*, 1993; Reynolds, 2006).

Storm events can have long term impacts on phytoplankton communities by disrupting the typical seasonal succession (Barbiero *et al.*, 1999; Znachor *et al.*, 2008; Isles *et al.*, 2015). In general, storm events occurring early or late in the growing season have been found to advance seasonal succession through removing dominant groups (Barbiero *et al.*, 1999; Isles *et al.*, 2015). This advancement is not ubiquitous amongst lakes and events, with storm timing in relation to the growing season and within-lake factors such as nutrient availability and stratification strength also being important. The impact of storm events for community succession in summer in particular, is conflicting with some studies reporting a regression in the seasonal succession (Znachor *et al.*, 2008) whereas others found that summer communities were comparatively resilient to storm events with the dominant species recovering (Barbiero *et al.*, 1999). However, setting these seasonal changes in the context of year to year patterns has so far been predominantly descriptive, which can limit our understanding of how storms may impact the longer term ‘seasonal’ stability of the phytoplankton community. Establishing the typical seasonal pattern is becoming increasingly important in a changing climate as many lakes are experiencing increases in thermal stability (e.g. Livingstone, 2003). It is therefore becoming increasingly likely that storm events will occur at a time of atypically high stratification strength (Gray, Mackay, *et al.*, 2019a). The impacts of these long term changes in lake stability are likely to impact how phytoplankton communities respond to episodic events, which has not yet been explored.

The rapid response of phytoplankton species to disturbances can lead to a high species turnover and therefore considerable community shifts within a short period of time. During periods of strong and stable stratification, slower growing phytoplankton can dominate and exhibit organised population dynamics which can lead to decreases in species diversity and evenness (Padisák *et al.*, 1988; Jacobsen and Simonsen, 1993). Storm events can have different impacts on community composition, diversity and evenness depending on timing (Jacobsen and Simonsen, 1993; Harris and Baxter, 1996; Beaver *et al.*, 2013; Blottière *et al.*, 2014; Isles *et al.*, 2015; Srifa *et al.*, 2016). Events occurring in summer are often associated with a decrease in larger slower growing species typically belonging to cyanobacteria or chlorophyceae phylogenetic groups (Jacobsen and Simonsen, 1993; Harris and Baxter, 1996; Beaver *et al.*, 2013; Blottière *et al.*, 2014; Isles *et al.*, 2015; Srifa *et al.*, 2016) which are replaced initially by small fast growing species such as cryptomonads (Padisák *et al.*, 1988; Jacobsen and Simonsen, 1993; Cardoso *et al.*, 2019). If stronger mixing persists following the event, slower growing low light adapted phytoplankton often belonging to bacillariophyceae can dominate (Harris and Baxter, 1996; Beaver *et al.*, 2013). The response of biodiversity measures to storm events is variable, with both increases and decreases in diversity and evenness observed (Jacobsen and Simonsen, 1993; Hambright and Zohary, 2000; Figueredo and Giani, 2001).

When investigating phytoplankton responses to disturbance events, samples are commonly integrated over depth (Beaver *et al.*, 2013; Hambright and Zohary, 2000; Jacobsen and Simonsen, 1993; Padisák, 1993) or taken at the surface (Harris and Baxter, 1996; Isles *et al.*, 2015). The vertical distribution of phytoplankton communities within the water column, however, is often heterogeneous with depth (Longhi and Beisner, 2009; Hamilton *et al.*, 2010; Ouellet Jobin and Beisner, 2014; Leach *et al.*, 2018) due to the differing vertical gradients of light and nutrients in the water column (Diehl *et al.*, 2002; Diehl, 2002) which can lead to vertical niche partitioning, particularly during times of stable stratification (Olli and Seppälä, 2001; Longhi and Beisner, 2009; Beisner and Longhi, 2013). Samples have, in some instances, been taken at discrete depths, but only at a coarse temporal interval (Edson and Jones, 1988; Winder and Hunter, 2008) that may not detect short-term responses to the disturbance. The light and nutrient climate that phytoplankton are exposed to depends on the depth of surface mixing which can change rapidly and markedly in response meteorological drivers (Klausmeier and Litchman, 2001; Kunz and Diehl, 2003; Mellard *et al.*, 2011). Storm events therefore have the potential to disrupt the short term vertical structure and function of the phytoplankton community, which has not yet been investigated.

This research investigates the impact of a storm event on lake phytoplankton biodiversity through (1) quantifying how a storm event impacts the long term ‘typical’ seasonal succession of a phytoplankton community and (2) determining the short term impacts of the storm event on the vertical structure, function and diversity of the phytoplankton community. The event occurred 21-25 August 2016 at a time when lake stratification was atypically strong. The storm event led to a large reduction in water residence time and the impact of the storm on the physical structure of the lake was significant but relatively short lived (Gray, Mackay, *et al.*, 2019a). It is hypothesised that: (1) the storm event will impact the typical phytoplankton seasonal succession; (2) phytoplankton biomass, phylogenetic and functional groups will be more heterogeneous under stable thermally stratified conditions compared to a storm event and (3) changes in species turnover, diversity and evenness will differ vertically before, during and after the storm event.

7.3 Materials and Methods

7.3.1 Site description

Blelham tarn is a small (surface area 0.1 km^2) stratifying lake with a mean depth of 6.8 m and a maximum depth of 14.5 m located in the Lake District in north-west England (Figure 7.1), (54^{o}24’N, 2^{o}58’W) (Ramsbottom, 1976). The trophic status of the lake lies on the meso-eutrophic boundary (mean total phosphorus 24.5 mg m^{-3}) (Maberly *et al.*, 2016) and its mean annual retention time is c. 35 days (Jones and Elliott, 2007).

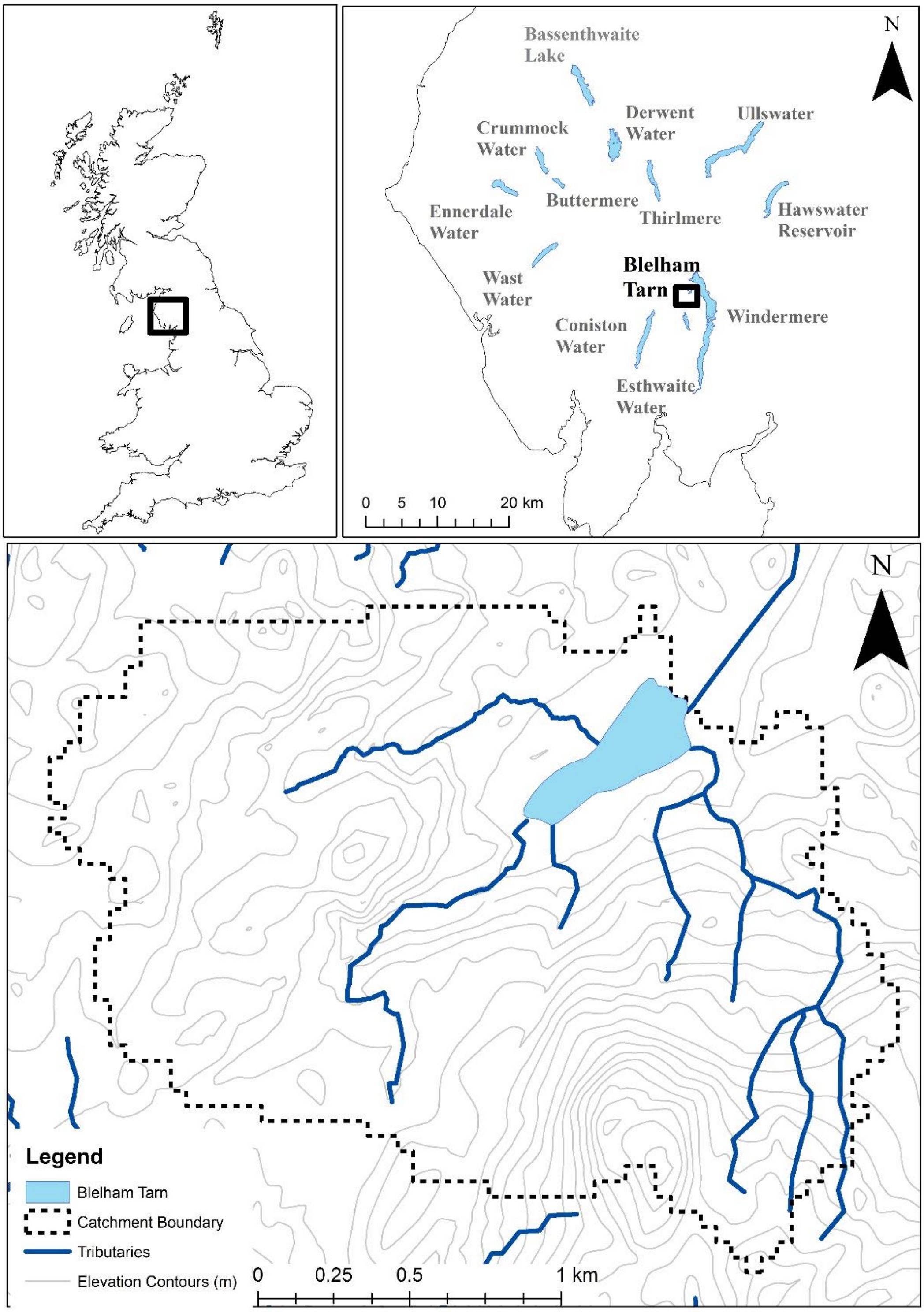


Figure 7.1 Map of Blelham Tarn, its tributaries and its location in the UK and the English Lake District.

7.3.2 Determining the 'typical' phytoplankton seasonal succession

Integrated samples from the top 5 m of the water column, collected fortnightly during UK Centre for Ecology & Hydrology long-term monitoring of Blelham Tarn (2008-2018), were used to determine the average seasonal pattern for the seasonal succession of the phytoplankton. Phytoplankton were enumerated in a Lund Chamber using the inverted microscope method (Lund *et al.*, 1958; Lund, 1959). In order to determine the 'typical' community baseline, mean biovolume values for the different taxa collected during 2016 were applied to taxa counts collected fortnightly in the long-term record (2008-2018). In total, estimations were present for 82 taxa leaving 43 taxa with missing biovolume values, the majority of which occurred in low abundances. In place of the missing values, biovolume measurements from Olenina, (2006) were used to obtain a taxa coverage of 95%. Once biovolume values had been assigned to each taxon in the long term record, the percentage of each phylogenetic (Bacillariophyta, Charophyta, Chlorophyta, Cryptophyta, cyanobacteria, Euglenozoa, Haptophyta, Miozoa and Ochrophyta) and CSR functional group ('Competitors', 'Stress tolerant' and 'Ruderals'; as defined by Reynolds (2016)) (Appendix One) were calculated for each sample day. In order to assess when the seasonal succession during 2016 deviated from 'typical' conditions, a bootstrapped LOESS regression (BLR) (Keith *et al.*, 2016) was applied to the eleven-year fortnightly dataset for the most abundant phylogenetic and functional groups. The dataset was re-sampled 1000 times by bootstrap with replacement with the number of data points equal to half the length of the dataset (Keith *et al.*, 2016). Each bootstrapped set was then modelled using LOESS regression to estimate a 95 % confidence interval, which represented the 'typical' seasonal pattern (Keith *et al.*, 2016). Finally, the 2016 data for each phylogenetic and functional group were modelled using LOESS regression and compared to the confidence intervals generated by the bootstrapped data. Sections of the data that fell outside of these confidence intervals were identified as periods of time when the 2016 succession significantly deviated from the ‘typical’ pattern.

7.3.3 Determining the short term responses to the storm event

7.3.3.1 Phytoplankton sampling and enumeration

To capture the changes in the vertical phytoplankton community structure during the growing season and in response to a storm event, weekly sampling was carried out during June-October 2016, which captured a significant storm induced flow event 21/08/2016-25/08/2016 (Gray, Mackay, *et al.*, 2019a). Prior to the event, a sample was taken 17/08/2016, with two samples being taken during the event (22/08/2016 and 24/08/2016) and then returning to a weekly frequency (31/08/2016). Water samples for phytoplankton counts were collected at discrete one metre depth intervals from 1 m to 5 m and were immediately preserved in Lugol’s solution and allowed to settle for at least 72 hours before enumeration. Phytoplankton samples were transferred to a Lund chamber and examined with an Olympus BX45 inverted microscope using the method as detailed in Lund *et al*., (1958). Phytoplankton sample enumeration and biovolume calculations were performed within the PlanktoMetrix software (Zohary *et al.*, 2016) which contains the appropriate geometric shape of each phytoplankton taxa according to CEN, (2014). To determine phytoplankton cell measurements for each sample day, a sub-sample from 1 m depth was taken and 10 individuals for each species were measured. The mean of the species dimensions were used to calculate the biovolume of the species which were then applied to each phytoplankton count for that sample day (1 m - 5 m). Phytoplankton were identified to species where possible or to genus level.

7.3.3.2 Phytoplankton metrics: community composition, turnover, diversity and evenness

Phytoplankton community responses to the storm event were first analysed in terms of the change in the total biovolume for each sample day, as well as the depth of the biovolume maxima. The mean percentage abundance of phylogenetic and functional groups were calculated for the two sample days before (10/08/16 and 17/08/16), during (22/08/16 and 24/08/16) and after the event (31/08/16 and 07/09/16). The coefficient of variation (CV) was calculated for each phylogenetic and functional group before, during and after the event in order to determine which groups were most variable with depth. The species exchange ratio (SER_a) was calculated to measure the turnover of species between earlier and later sample days based on the species proportional abundance (Hillebrand *et al.*, 2018);

Equation 7.1

$$SER_a = \frac{\sum_i(\rho_i - \rho'_i)^2}{\sum \rho_i^2 + \sum \rho'^2_i - \sum \rho_i \rho'_i},$$

where ρ_i is the proportional abundance of species i at time one and ρ'_i at time two. If SER_a approaches zero then the species identity and dominance does not change and if it approaches one then all species are replaced. Diversity was determined using species richness and then by calculating species, phylogenetic and functional diversity using the Shannon-Weaver diversity index (*H*’) within the ‘vegan’ package in the R statistical programming language (Oksanen, 2019);

Equation 7.2

$$H' = -\sum_{i=1}^{S} pi \, log_b \, pi,$$

where pi is the total biovolume for each species, phylogenetic or functional group i, and S is the number of species, phylogenetic or functional groups and b is the base of the logarithm. Species, phylogenetic and functional evenness was determined by calculating Pielou's evenness (J');

Equation 7.3 $$J' = \frac{H'}{H'_{max}},$$

where, H' is Shannon-Weaver diversity, with values of one indicating a high community evenness.

7.3.3.3 Physical metrics: euphotic depth and mixed depth

A cos-corrected LI-COR underwater quantum sensor was used to measure light, measurements were taken just below the surface and then at one-metre intervals from 1 m to 9 m. The natural logarithms of the light measurements were regressed with depth and the slope of the equation was used to estimate the extinction coefficient (k) for each sample day. The euphotic depth (z_{eu}) was then defined as the depth where only 1 % of the surface measurement of PAR remained;

Equation 7.4 $$z_{eu} = ln(100)\,/k.$$

Vertical profiles of temperature collected at the same time as the phytoplankton samples were converted into density within Lake Analyzer (Read *et al.*, 2011). The depth of recent mixing (z_{mix}) was calculated from the density profiles using three methods according to (Gray, Mackay, *et al.*, 2019b). Method 1 used a 0.1 kgm^{-3} threshold change in density from the surface to define the depth of recent mixing. The other methods used a Generalised Additive Model (GAM) fitted to each profile, with the depth of the maximum gradient identified using the model fit. For Method 2, the depth of the maximum gradient plane was extrapolated to all depths using the intercept and slope of the plane. A vertical line was then drawn corresponding to the mean of three minimum density values from each profile. The depth where the minimum line intersected the extended maximum gradient line marked the mixed depth. Finally, method 3 used the confidence intervals from the first derivative of the fitted GAM to identify sections of the profile where changes in the gradient where significantly different from zero. The upper section of the profile that contained the depth of the maximum gradient was determined as the depth of recent mixing (Gray, Mackay, *et al.*, 2019b).

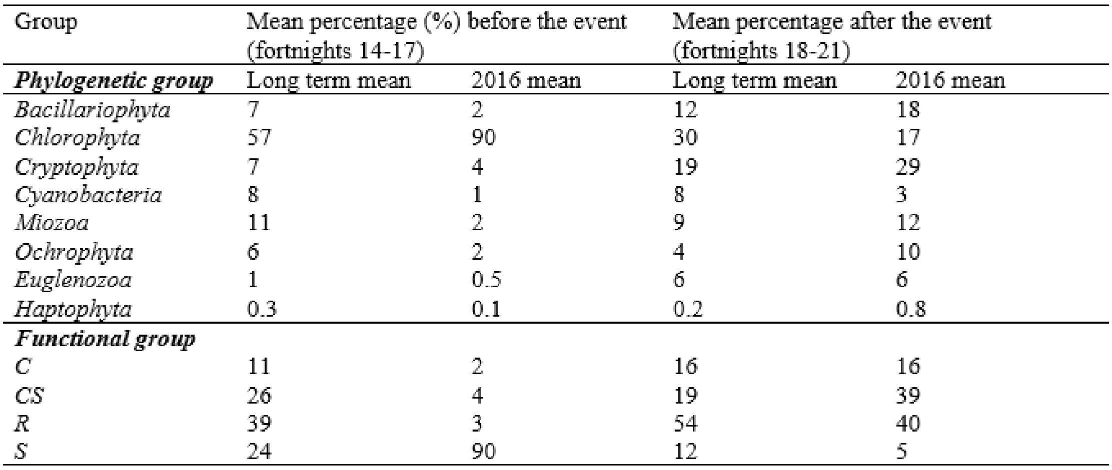
7.4 Results

7.4.1 The seasonal succession

The long-term average seasonal succession of the phytoplankton progresses from a community dominated by Bacillariophyta in spring to dominance by Chlorophyta in the summer season (Figure 7.2). During 2016 the phytoplankton appeared to be following this pattern, however, the dominance of Chlorophytes (90 %) was significantly greater than the eleven-year average (57 %) during fortnights 14-17 (Table 7.1; Figure 7.2) exceeding the confidence intervals for the typical seasonal succession (Figure 7.2). The Chlorophyte *Coenochloris fotti* contributed a mean of 90 % of the total biovolume to the overall phytoplankton community for fortnights 14-17. As a result, the other phylogenetic groups had proportionally lower abundance for the time of year (Table 7.1; Figure 7.2) with Bacillariophyta, Cryptophyta and cyanobacteria proportions falling below the confidence intervals (Figure 7.2). Following the storm event, which occurred between fortnights 17 and 18, the dominance of the Chlorophyte ended (Table 7.1; Figure

7.2). There was an initial increase in the proportion of Cryptophyta, Miozoa and Ochrophyta during fortnight 18 (Figure 7.2) which meant their proportions were now more typical of the seasonal succession (Table 7.1; Figure 7.2). The response of the Bacillariophyta was more lagged, with abundances not reaching levels typical for the time of year until the following fortnight (19) (Table 7.1; Figure 7.2).

Table 7.1 Mean percentage of each phylogenetic and functional group for fortnights prior to and following the event for the long term average and 2016.



Group	Mean percentage (%) before the event (fortnights 14-17)		Mean percentage after the event (fortnights 18-21)	
Phylogenetic group	Long term mean	2016 mean	Long term mean	2016 mean
Bacillariophyta	7	2	12	18
Chlorophyta	57	90	30	17
Cryptophyta	7	4	19	29
Cyanobacteria	8	1	8	3
Miozoa	11	2	9	12
Ochrophyta	6	2	4	10
Euglenozoa	1	0.5	6	6
Haptophyta	0.3	0.1	0.2	0.8
Functional group				
C	11	2	16	16
CS	26	4	19	39
R	39	3	54	40
S	24	90	12	5

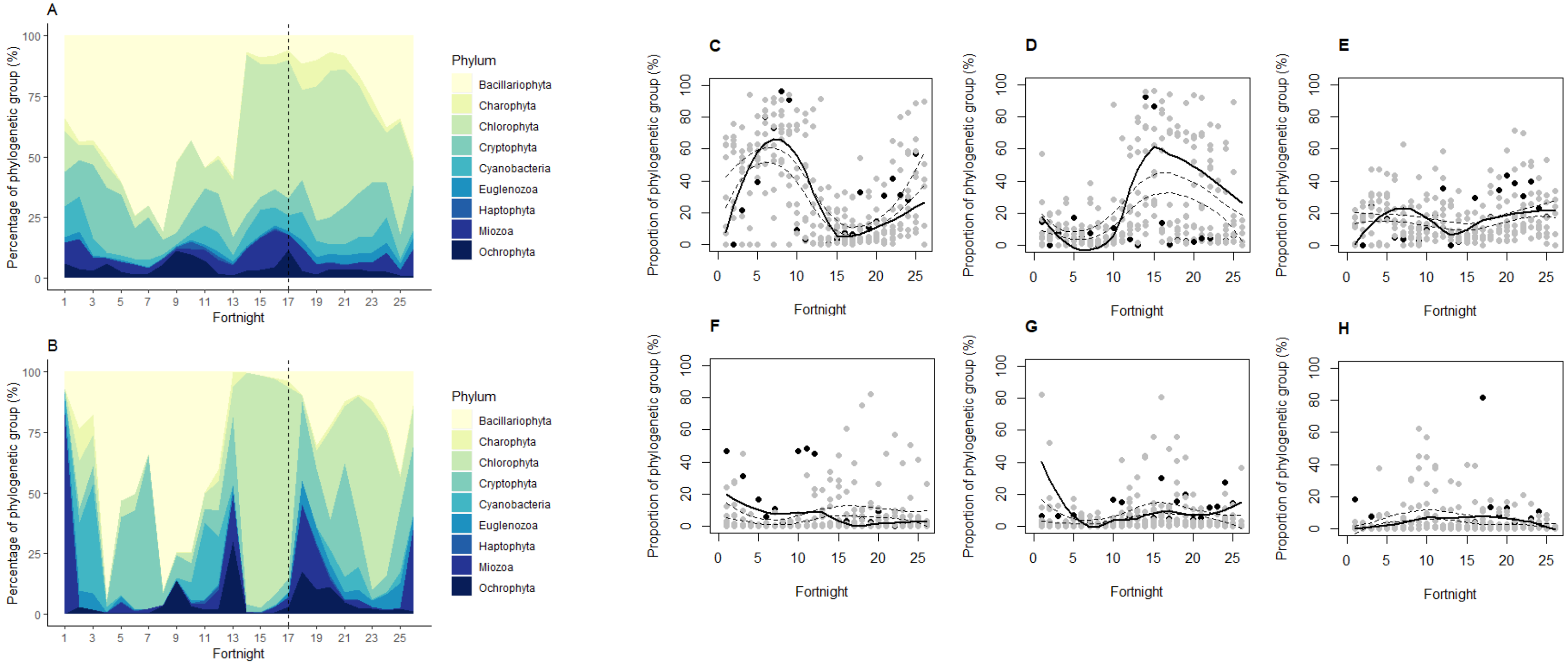


Figure 7.2 The percentage of each phylogenetic group based on (a) fortnightly means from the long term average and (b) fortnightly data for 2016. The results of the BLR analysis are depicted in c-h which contain samples from 2008-2015 and 2017-2018 (grey points) and 2016 (black points) with confidence intervals of the LOESS fit (dashed grey lines) and a solid black line showing the 2016 LOESS model fit for (c) Bacillariophyta, (d) Chlorophyta, (e) Cryptophyta, (f) cyanobacteria, (g) Miozoa and (h) Ochrophyta.

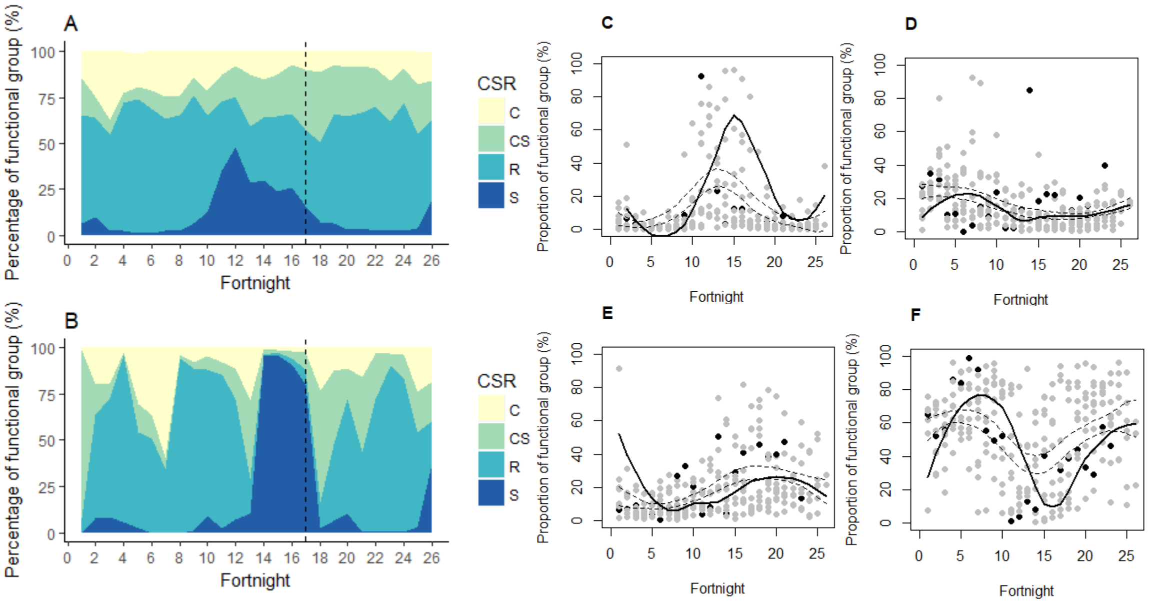


Figure 7.3 The percentage of each functional group based on (a) fortnightly means from the long term average and (b) fortnightly data for 2016. The results of the BLR analysis are depicted in c-f which contain samples from 2008-2015 and 2017-2018 (grey points) and 2016 (black points) with confidence intervals of the LOESS fit (dashed grey lines) and a solid black line showing the 2016 LOESS model fit for (c) S strategists, (d) C strategists, (e) CS strategists and (f) R strategists.

7.4.2 Vertical responses of the phytoplankton community to the storm event

7.4.2.1 Biovolume

Before the storm event, the total biovolume was already beginning to decline at most depths (Figure 7.4). However, the rate of this decline increased at most depths at the time of the event (22/08/16), with 2 m and 3 m experiencing the greatest percentage reduction in biovolume at 83 and 88 % respectively, whilst 1 m experienced the lowest percentage reduction at 40 %. Following this reduction, the total biovolume began to recover at most depths. This increase was greatest at 1 m, where the biovolume increased by 90 % in just two days (22/08/16 to 24/08/16). The level of increase declined with increasing depth and there was a 10 % reduction in biovolume at 5 m during the same time period (Table 7.2). The increase in biovolume therefore appeared to be delayed with increasing water column depth (Table 7.2). The highest percentage increase immediately after the event (22/08/16 to 24/08/16) occurred at 1 m, in the following week the highest increase was at 3 m (24/08/16-31/08/16) and a week after this the highest percentage increase was at 4 m (31/08/16-07/09/16) (Table 7.2).

The vertical distribution of the total biovolume shifted from a maximum at 2 m in the four weeks prior to the event to 1 m during and in the three weeks following the event (Figure 7.4). The euphotic depth shallowed during the event and the mixed depth deepened below the euphotic depth, depending on the definition of the mixed depth used (Figure 7.4).

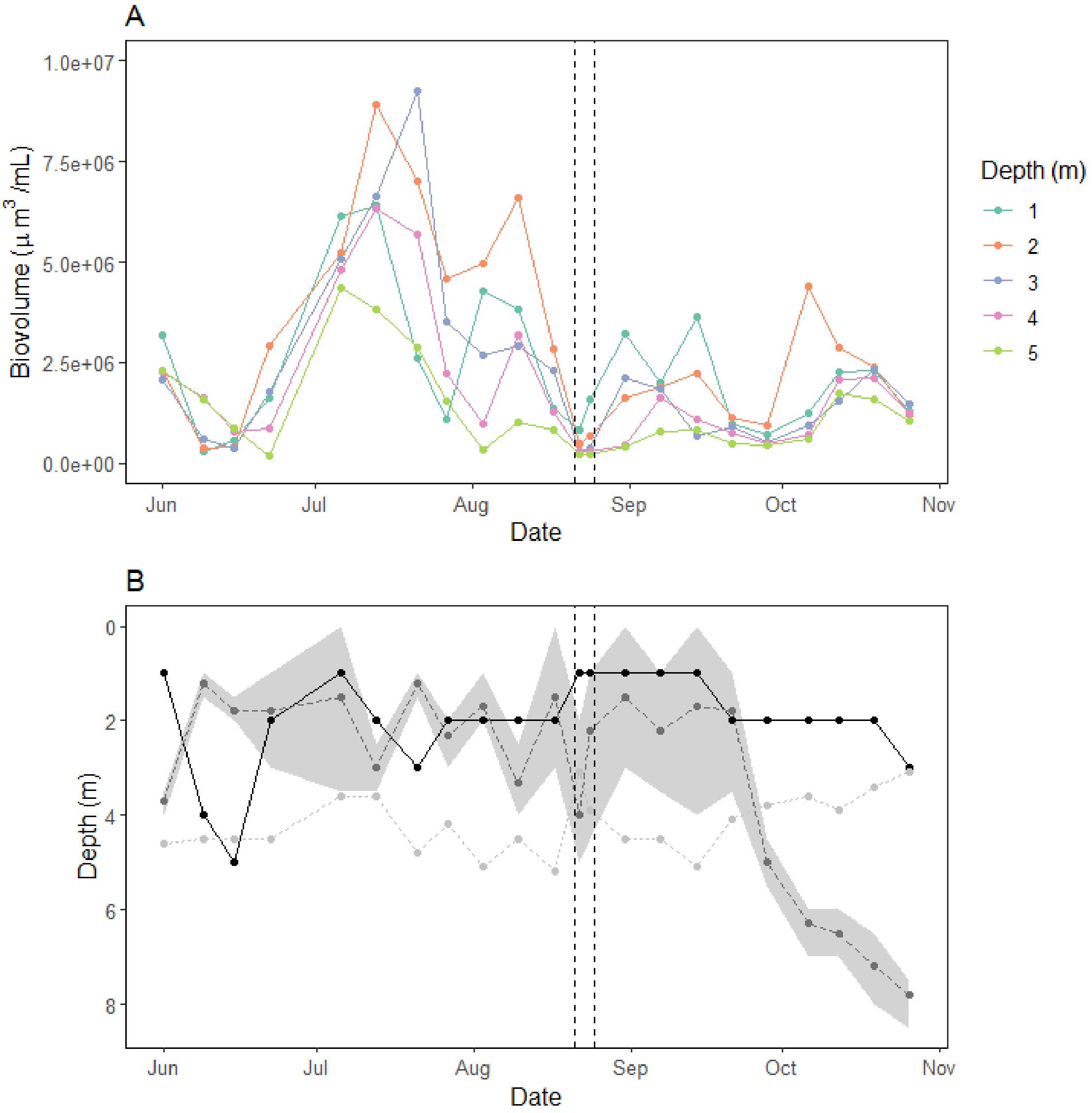


Figure 7.4 (a) The total biovolume at each depth for each date and (b) the depth of the biovolume maximum (solid black line), the euphotic depth (light grey line) and the mean (grey dashed line) and range (grey shading) of the mixed depth.

Table 7.2 The percentage change in biovolume at each depth in the water column before, during and after the event.

	Percentage change (%) at each depth				
Before	1 m	2 m	3 m	4 m	5 m
10/08/16-17/08/16	-64	-57	-21	-60	-19
During					
17/08/16-22/08/16	-40	-83	-88	-78	-72
22/08/16-24/08/16	90	43	34	10	-10
After					
24/08/16-31/08/16	106	139	472	48	89
31/08/16-07/09/16	-38	15	-14	255	99

7.4.2.2 Phylogenetic groups

In the four weeks prior to the storm event, chlorophytes dominated at all depths in the water column and had a relatively similar distribution with depth (CV= 19 %) (Table 7.2; Figure 7.5). In the two weeks prior to the event the mean percentage of Chlorophytes was 70-75 % at 1-4 m and 52 % at 5m. This dominance was due to the Chlorophyte *Coenochloris fotti* which contributed a mean percentage biovolume of 69-75 % at 1-4 m and 50 % at 5 m. In contrast, Cryptophytes contributed only 8-16 % of the biovolume at 1-4 m and 24 % at 5 m prior to the event. During the event, there was a large reduction in Chlorophytes at all depths (Figure 7.5): the percentage contribution to the total of *Coenochloris fotti* decreased from a mean (across depth) of 61 % in the week prior to the event to 32 % and 5 % during the event (22/08/16 and 24/08/16, respectively) and then <1 % in the week following the event (31/08/16). Cryptophytes responded quickly at 1 and 2 m contributing 55 % and 35 % of the total biovolume respectively, during the event but their relative proportion decreased with depth (CV= 59 %) (Table 7.3; Figure 7.5). In the 2-3 weeks following the event the composition of the community differed with depth, with Cryptophytes continuing to dominate at 1 m (Figure 7.5), while at 2, 3 and 4 m the biovolume appeared to be distributed more evenly between Bacillariophyta, Cryptophyta and Miozoa (07/09/16 and 14/09/16).

Table 7.3 The coefficient of variation for each phylogenetic and functional in the water column based on mean abundance values before (10/08/16 and 17/08/16), during (22/08/2016 and 24/08/2016) and after the event (31/08/16 and 07/09/16).

Phylogenetic group	CV (%) before event	CV (%) during event	CV (%) after event
Bacillariophyta	29	22	9
Charophyta	23	38	61
Chlorophyta	13	19	40
Cryptophyta	39	59	37
Cyanobacteria	29	51	52
Euglenozoa	Low abundance	Low abundance	86
Haptophyta	66	32	54
Miozoa	70	107	64
Ochrophyta	16	50	19
Functional group			
C	52	22	15
CS	18	36	16
R	26	26	17
S	13	22	36

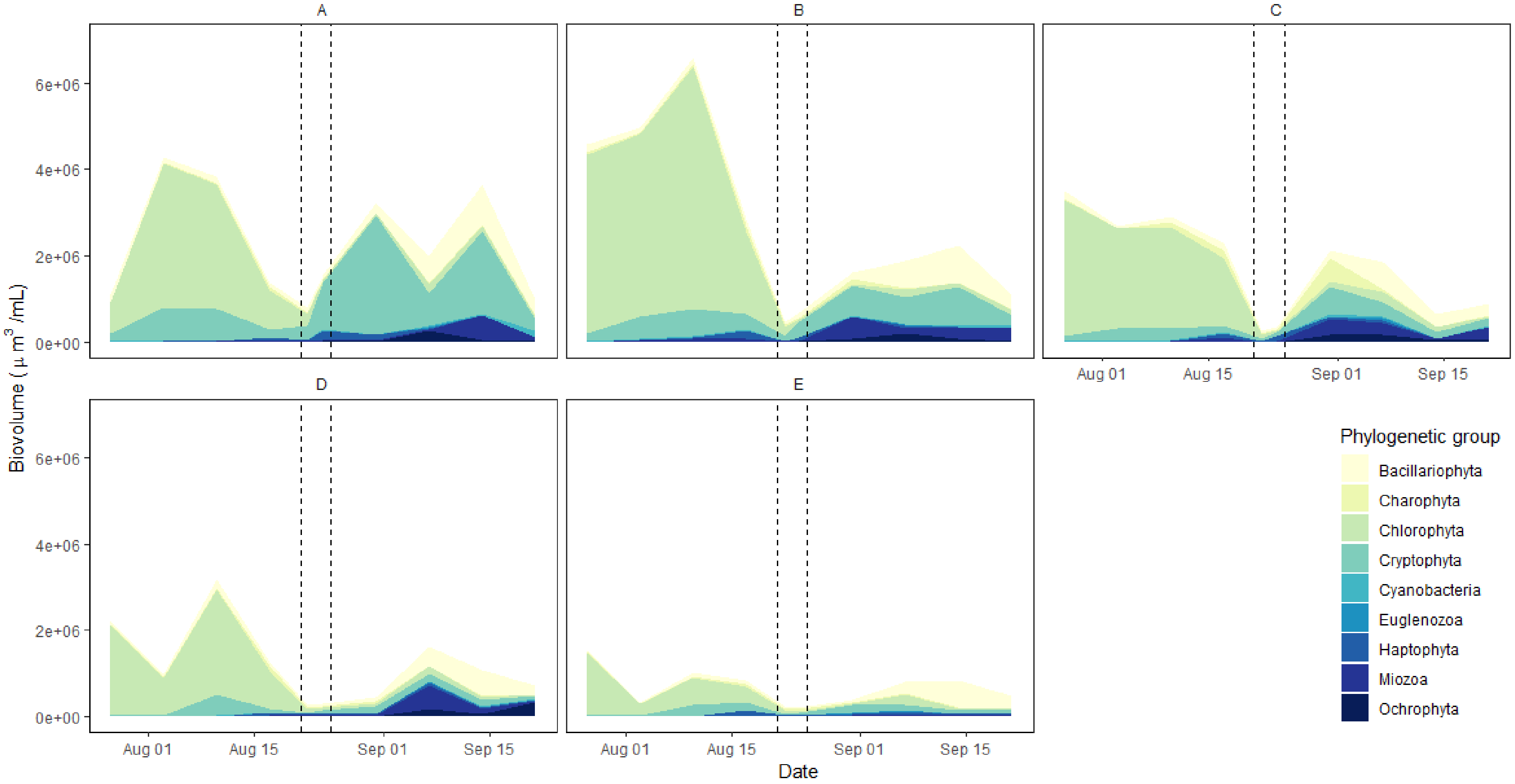


Figure 7.5 The total biovolume for each phylogenetic group for each sample day for (a) 1 m, (b) 2m, (c) 3m, (d) 4m and (e) 5m depths in the water column. Vertical dashed lines mark the start (21/08/2016) and end (25/08/2016) of the storm event.

7.4.2.3 Functional Groups

Prior to the storm event the community was dominated by S strategists at all depths in the water column, the mean proportion of S strategists in the two weeks prior to the event at 1-4 m was 70-75 % and 50 % at 5 m (Figure 7.6). The proportion of S strategists was relatively similar across depth with the coefficient of variation being low at 13 % (Table 7.2; Figure 7.6). There was a marked reduction in the biovolume of all strategists during the event, but C strategists recovered quickly at 1 m in particular, contributing 60 % of the biomass (Figure 7.6). In the two weeks following the event the proportion of C, CS and R strategists, which contributed the majority of the biovolume, had a relatively similar distribution with depth (CV= 15-17 %) (Table 7.3; Figure 7.6)

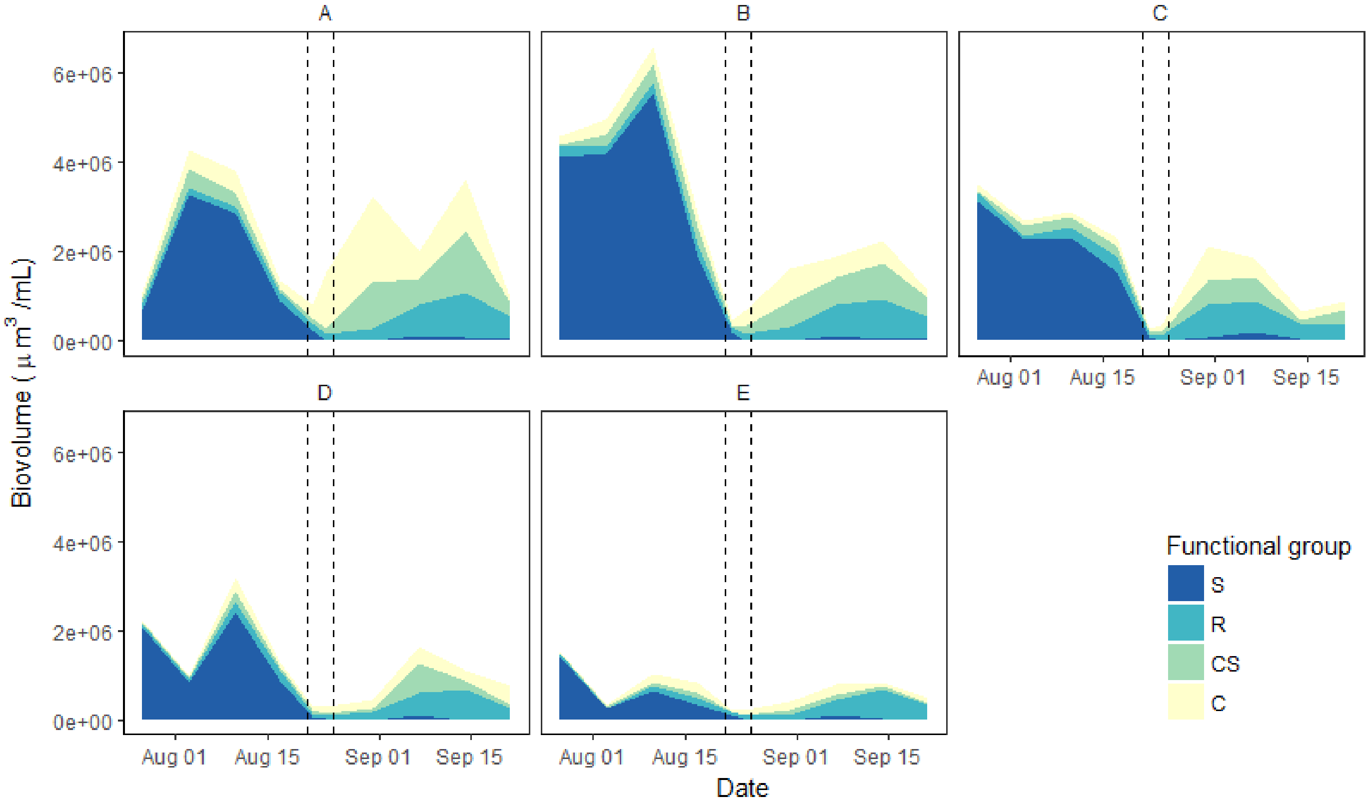


Figure 7.6 The total biovolume for each CSR functional group for each sample day (a) 1 m, (b) 2m, (c) 3m, (d) 4m and (e) 5m depths in the water column. Vertical lines mark the start (21/08/2016) and end (25/08/2016) of the storm event.

7.4.2.4 Species turnover, diversity and evenness

Species turnover was low at all depths prior to the storm event (Figure 7.7). During and following the event there was an increase in species turnover at most depths, with the largest turnover value occurring at the depth with the greatest biovolume (2 m) (Figure 7.4; Figure 7.7). Species turnover at 2-5 m depth followed a similar pattern, but species turnover at 1 m depth was generally lower and decreased in the week following the event (31/08/16) (Figure 7.7).

Species richness was declining at most depths prior to the event (Figure 7.7). In the following two weeks (31/08/16 and 07/09/16), there was a marked increase in species richness at all depths which then plateaued at the end of September (14/09/16 and 21/09/16) (Figure 7.7). Species richness was highest at 1 m for the majority of the weeks following the event (Figure 7.7). Species diversity was increasing at most depths prior to the event (Figure 7.7) and the response following the event differed with depth. For example, in the two weeks following the event species diversity at 1 m was lower than at other depths. Similarly to species diversity, functional and phylogenetic diversity were increasing prior to the storm event and continued to increase at most depths in the first day during the storm event (Figure 7.7). In the weeks following the event functional and phylogenetic diversity plateaued at 2-5 m (Figure 7.7). Again, the response at 1 m was different compared to other depths. Phylogenetic and functional diversity decreased in the second day during the event (24/08/16) and remained lower than other depths in the week following the event (31/08/16) (Figure 7.7).

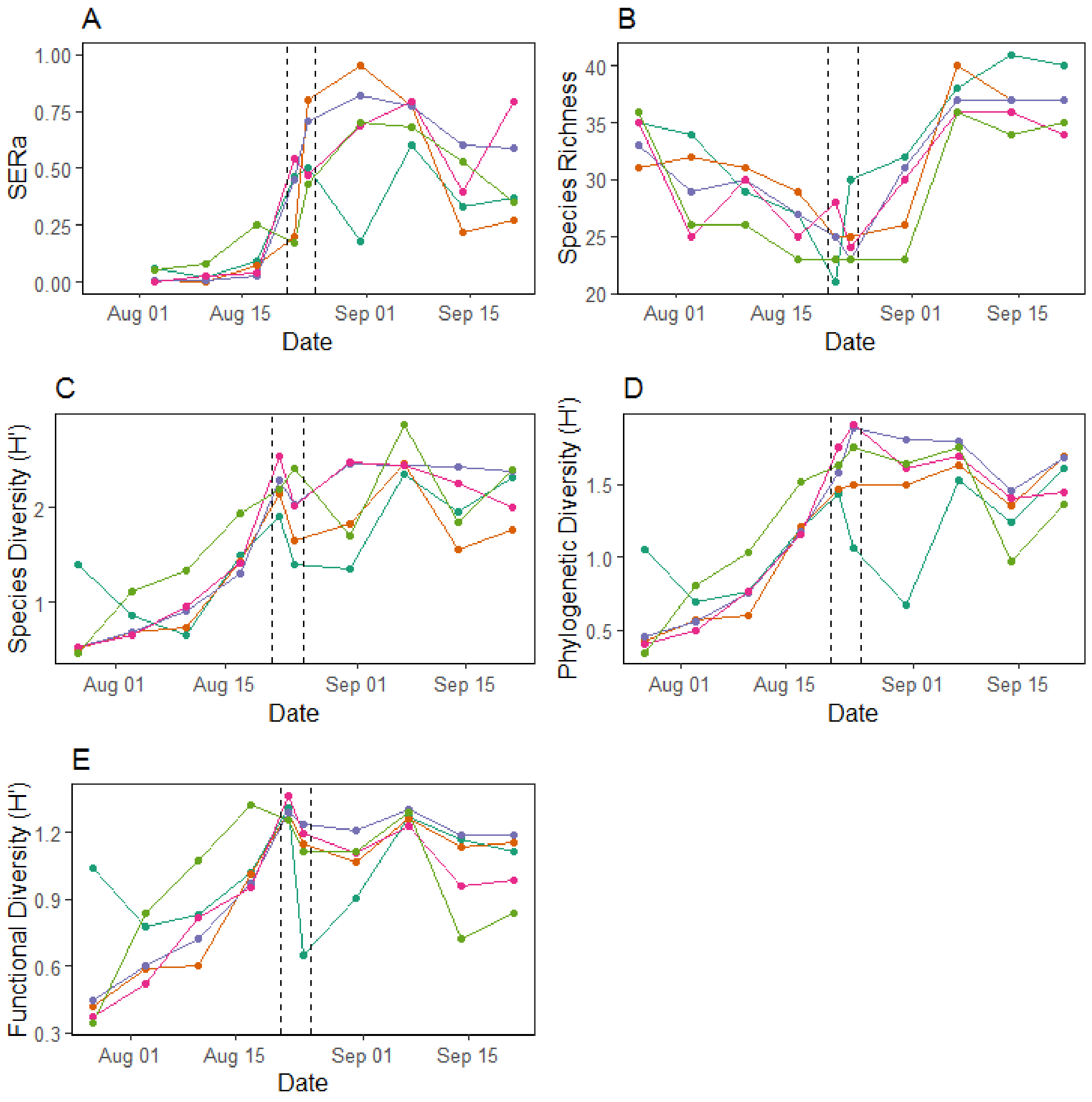


Figure 7.7 Diversity metrics at depths 1-5 m for (a) species turnover, (b) species richness, (c) species diversity, (d) phylogenetic diversity and (e) functional diversity.

In the four weeks prior to the event, species, phylogenetic and functional evenness were increasing (Figure 7.8). Following the event evenness plateaued at most depths but again the response at 1 m differed compared to the other depths (Figure 7.8). Species, phylogenetic and functional evenness at 1 m started to decline from the second sample day of the event, continuing this decline in the following week (31/08/16) until reaching levels similar to other depths a week later (Figure 7.8).

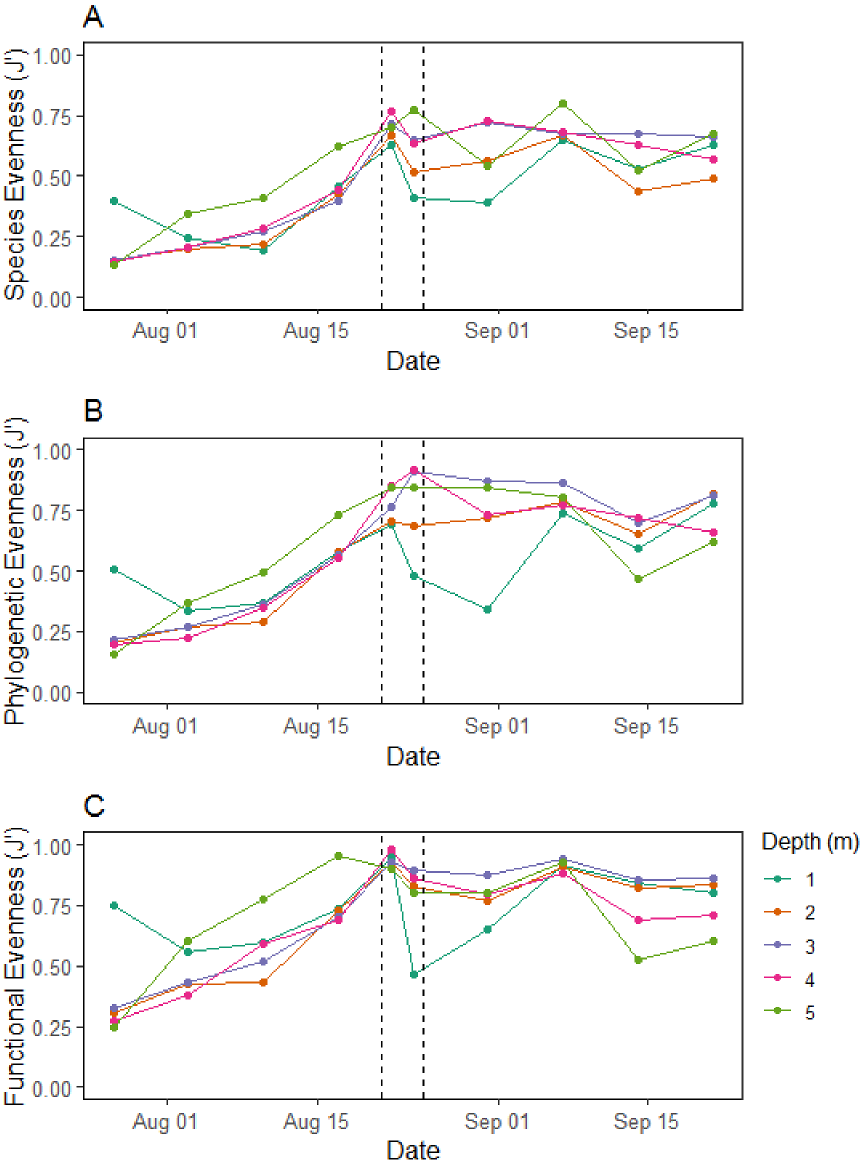


Figure 7.8 Pielous evenness at depths 1-5 m for (a) species evenness, (b) phylogenetic evenness and (c) functional evenness.

7.5 Discussion

This study investigated the impact of a storm-induced flushing event on the seasonal succession of a phytoplankton community and the vertical structure and composition of the community. The storm occurred at a time of atypically strong stratification strength and the storm appeared to switch the nutrient regime from co-limitation of nitrogen and phosphorus to solely phosphorus limitation (Gray, Mackay, *et al.*, 2019a).

Prior to the storm event the community had an atypically high dominance of Chlorophytes and S strategists. Although these groups typically contribute a large proportion of the biomass at this time of year, the large magnitude of the dominance was unusual. The heightened physical stability of the lake would have been favourable for slower growing S strategists to gradually outcompete other species and dominate, leading to low contributions of other phylogenetic and functional groups. Sommer *et al.*, (1993) suggested that phytoplankton communities can reach a form of equilibrium if 1-3 species comprise over 80 % of the biomass, this occurred prior to this event because *Coenochloris fotti* comprised 90 % of the biomass. This usually happens when there is stress, such as from nutrient limitation, with the dominant species being the most adapted to the conditions and therefore outcompeting others (Sommer *et al.*, 1993; Padisák, Borics, *et al.*, 2003). This may have been the case here as *Coenochloris sp* are known to be tolerant to low nutrient concentrations (Reynolds *et al*., 2002) and nitrogen and phosphorus were limiting (Gray, Mackay, *et al.*, 2019a). The dominance of slow growing larger taxa during periods of strong physical stability is not uncommon and has been observed in other lakes (Jacobsen and Simonsen, 1993; Isles *et al.*, 2015).

The storm event appeared to occur at a time when Chlorophytes and S strategists usually start to decline in the typical seasonal succession. The storm event therefore advanced the seasonal succession by removing the dominance of Chlorophytes and S strategists and creating a community which was more typical in terms of composition and relative abundances for that time of year, which supported hypotheses one. It is likely that the community composition would have naturally changed in this way but the transition had been accelerated by the storm event, reflecting the importance of these disturbances in regulating community succession. These findings are similar to that of Isles *et al.*, (2015) where a storm event occurring in late summer removed the dominance of cyanobacteria and advanced the seasonal succession.

In the weeks prior to the storm event, under thermally stable conditions, the distribution of phytoplankton biomass was heterogeneous with depth, with the depth of the biomass maxima occurring at 2 m. The system was co-limited by nitrogen and phosphorus from early July (Gray, Mackay, *et al.*, 2019a), which roughly coincided with the seasonal biomass maxima suggesting that dissolved nutrients were being rapidly utilised by the growing phytoplankton community prior to the peak (Figure 7.4). Following the biomass peak and prior to the storm event, phytoplankton biomass began to decline due to a combination of high sinking losses and low nutrient concentrations. Nevertheless, the storm event did lead to a marked decrease in biomass at all depths and likely accelerated this decline. This enhanced decline can be anticipated, since during the event a large proportion of the lake surface water would have been replaced (Jacobsen and Simonsen, 1993; Harris and Baxter, 1996; Vanni *et al.*, 2006). The rate of biomass recovery following the storm event was depth dependent. Biomass recovered particularly quickly at 1 m but was delayed with increasing depth (Table 7.2). The short term shallowing of the euphotic depth following the storm event, potentially from an increased delivery of terrigenous material from the catchment (Perga *et al.*, 2018), may have been why the biomass recovered closer to the surface in a more favourable light climate. There was also an indication that the mixed depth deepened below the euphotic depth, producing conditions that are unlikely to support deeper maxima of phytoplankton biomass (Hamilton *et al.*, 2010; Brentrup *et al.*, 2016; Leach *et al.*, 2018).

During times of high thermal lake stability phytoplankton communities have been observed to separate with depth resulting in vertical niche partitioning (Klausmeier *et al.*, 2001; Clegg *et al.*, 2007; Jäger *et al.*, 2008) and reduced spatial overlap between phytoplankton groups (Beisner and Longhi, 2013). This separation can also lead to more diverse communities (Jäger *et al.*, 2008). Conversely, increased thermal stability (Padisák *et al.*, 1988; Jacobsen and Simonsen, 1993) and infrequent disturbances (Barbiero *et al*., 1999; Padisak, 1993; Reynolds *et al*., 1993; Sommer *et al*., 1993) have been observed to result in the dominance of one to a few species. This apparent contradiction may be due to differences in sampling methodologies as frequently, phytoplankton samples are typically integrated over depth rather than taken as discrete intervals. Differences in community composition and diversity with depth may, therefore, have been missed in studies using the integrative sampling techniques. Other explanations for these differences may also be important such as lake morphology, nutrient status or phytoplankton community composition. Nevertheless, the findings from this study were analogous with the latter theory, with increased thermal stability leading to the dominance of one species, *Coenochloris fotti*. The rapid change in the physical conditions from strong and stable stratification to relative instability did, however, instigate a prominent change in community composition at all depths in the water column with community composition becoming heterogeneous with depth following the event. This therefore provides evidence against hypothesis two.

The response of diversity and evenness was complex and differed before and after the storm event as well as vertically. In general, the community had a relatively low species turnover and a low species, phylogenetic and functional diversity before the event. The low values of community evenness prior to the event agrees with previous research which suggests that systems with lower evenness have a higher biomass (Mulder *et al.*, 2004). The low evenness was due to the dominance of one species. This pattern was relatively similar with depth, with the response at 5 m being most distinct as it had the lowest biomass and species richness but the highest diversity and evenness. This meant that although there were a lower number of species at this depth, the biomass was more evenly distributed across the species, functional and phylogenetic groups. This may be because the environment at this depth is more variable in light, temperature and nutrients due to its proximity to the thermocline. Diversity and evenness however, were already increasing prior to the event because the dominance of *Coenochloris fotti* had begun to diminish.

Species turnover was high during and following the event due to the change from the dominance of one species prior to the event and the large reduction in biomass following the event, providing evidence in support of hypothesis three. Furthermore, diversity and evenness were relatively high at most depths post-storm and this is congruent with findings from other phytoplankton disturbance studies, where only integrated samples have been taken (Jacobsen and Simonsen, 1993; Padisak, 1993; Hambright and Zohary, 2000; Figueredo and Giani, 2001). The community recovery differed by depth, with the community at 1 m depth being the most distinct from the other depths, which provides supporting evidence for hypothesis three. C strategists (Cryptophytes), recovered quickly following the event and dominated the community at 1 m, resulting in lower evenness and diversity compared to other depths in the week following the event. The recovery of this phylogenetic and functional group is a typical response following a storm and has been observed in other systems (Padisák *et al.*, 1988; Jacobsen and Simonsen, 1993; Cardoso *et al.*, 2019). This is due to the fast replication rates of species in these groups as well as their flagella which allow these phytoplankton to position themselves in a favourable light climate close to the surface (Klausmeier *et al.*, 2001). The diversity and evenness responses to this disturbance event differ in comparison with terrestrial plant studies, where timescales are typically much longer. For example, Yeboah *et al.*, (2016) found that species richness and diversity declined whereas evenness increased with increasing time from a disturbance. Here, species richness, diversity and evenness were generally maintained at high levels in the weeks following the storm event.

These findings suggest that storm events coinciding with atypically heightened lake thermal stability may promote greater seasonal biodiversity in phytoplankton communities. In this case, the flushing event removed the dominance of one species and promoted the typical phytoplankton seasonal succession for the lake. The subsequent community was more diverse and even. Therefore, we observed here a possible mechanism whereby a storm event has “corrected” the succession course of the community away from a highly dominated structure and returned it to something more typical of the lake. The consequences of this are interesting because it might be expected that climate change will induce pronged periods of atypical weather such as warmer air temperatures, resulting in strong stratification, as was observed here. Furthermore, climate change is also expected to increase the frequency and change the seasonal occurrence of storms of the kind observed in this study. Thus, it is possible that climate change might provide a “corrective” pulse force (storms) for atypical seasonal community responses that formed over the preceding period.

8 Discussion

8.1 Overview

Climate change is leading to atmospheric warming and increases in the surface temperatures of the earth's surface (IPCC, 2013). Superimposed on this long term change is the increase in the magnitude and frequency of extreme events (Coumou and Rahmstorf, 2012; Hov *et al.*, 2013). Many lakes around the world are experiencing long term increases in surface water temperature (O'Reilly *et al.*, 2015) and shallower surface mixed layers (Livingstone, 2003) as a result of climate change. Short term weather events such as storms can also lead to abrupt changes in mixed depth (Jennings *et al.*, 2012; Woolway *et al.*, 2018; Chapter 6). The depth of surface mixing controls the vertical distribution of dissolved gases such as oxygen as well as the light and nutrient climate that phytoplankton are exposed to (Kunz, 2005; Wüest & Lorke, 2003). Changes in the mixed depth therefore have significant consequences for water quality. There is no universal way of defining the mixed depth which has led to the proliferation of methods which often use different arbitrary definitions making cross study comparisons difficult. The impact of using these different definitions when calculating chemical and ecological metrics were explored in Chapter 4. Alternative methods of mixed depth estimation were also presented which avoid the use of arbitrary definitions and may therefore facilitate cross study comparisons.

In addition to alterations in surface mixing, long term changes in climate are also resulting in warmer surface water temperatures (O'Reilly *et al.*, 2015), increased stratification strength (Butcher *et al.*, 2015) and increases in stratification length (Peeters, Straile, Lorke and Ollinger, 2007). These long term changes in climate are intrinsically linked but have separate consequences for phytoplankton growth (Winder and Sommer, 2012). The separate impacts of temperature and mixed depth change, on phytoplankton biomass and community composition were therefore distinguished in Chapter 5. Long term increases in lake surface water temperatures as a result of climate change and consequent increased stability means that it is becoming increasingly likely that storm events will occur at a time of atypically high stratification strength. The interaction between this long term trend and short term episodic events have been previously unexplored. This interaction was investigated in relation to the physical and chemical characteristics of the lake in Chapter 6, with Chapter 7 exploring the interactions of these opposing physical trends on the phytoplankton community. Episodic storm events can also alter the vertical gradients of resources available for phytoplankton growth (Jäger *et al.*, 2008) and are therefore likely to alter the vertical structuring of phytoplankton communities which was also explored in Chapter 7.

This discussion chapter evaluates the advantages and limitations of the different methodological approaches used in this thesis and explores the links between the findings of the different research chapters. The findings are related to relevant areas of limnology and the wider relevance of some of the findings to areas of climate change research and ecology are also discussed.

8.2 Methodological approaches to monitoring and disentangling processes occurring on multiple timescales

This thesis has investigated the impacts of different facets of climate change that are operating on different timescales. In order to achieve this, different methodological tools were implemented. This section of the discussion highlights the benefits and limitations of each tool and discusses the value in a combined approach to water quality research.

8.2.1 High resolution monitoring

The advancement of sensor technology has led to the widespread implementation of automated water quality monitoring stations (AWQMS) on lakes across the world (Hamilton *et al.*, 2015). This technology allows for the automated monitoring of meteorological variables and within-lake parameters including oxygen, water temperature and light at time scales that are not possible with conventional sampling techniques (Hamilton *et al.*, 2015). The integration and analysis of datasets from sites across the world has been facilitated by grassroots initiatives like the Global Lake Ecological Observatory Network (GLEON) (Weathers *et al.*, 2013; Hamilton *et al.*, 2015; Hanson *et al.*, 2016). The analysis of high resolution data has advanced the understanding of various aspects of limnology such as long term (O'Reilly *et al.*, 2015; Woolway & Merchant, 2017; Woolway, Weyhenmeyer, *et al.*, 2019) and short term changes in water temperature, lake metabolism (Staehr *et al.*, 2012), bloom development (Pomati *et al.*, 2011; Bowes *et al.*, 2016) and the responses to episodic events (Jennings *et al.*, 2012; Woolway *et al.*, 2018; Chapter 6). A number of tools have also been developed to standardise the calculation of physical and chemical metrics using high resolution datasets such as Lake Analyser (Read *et al.*, 2011), Lake Heat Flux Analyzer (Woolway *et al.*, 2015) and Lake Metabolizer (Winslow *et al.*, 2016).

Driving lake models with high resolution data collected from study sites is valuable as it provides accurate data from an optimal location and it provides a source of data for model validation. The accumulation of high resolution datasets over many years can therefore be modelled to investigate processes occurring over long timescales under different weather and climate conditions. An example of this was the three years of daily high resolution data (2012-2014) used to drive the PROTECH model in this thesis which was used to explore the potential impacts of mixed depth and temperature on phytoplankton communities in the context of climate change (Chapter 5).

The eleven-year (2008-2018) dataset of meteorological drivers and water temperature data used in Chapter 6 was a useful tool for determining both long term seasonal patterns as well as the short term response to storm events. The calculations of the total heat flux (using Lake Heat Flux Analyzer) and within lake stability measures such as Schmidt stability (using Lake Analyzer) and the mixed depth (using methods developed in Chapter 4) over the eleven-year period provided a record of the typical stability of the lake at different times of year. The record of this baseline pattern, enabled the identification of time periods where, lake stability and meteorological drivers, deviated from conditions that were typical for the time of year. This is important because the baseline conditions of many lakes (Adrian *et al.*, 2009; O'Reilly *et al.*, 2015; Woolway and Merchant, 2019), as well as other environmental systems, are shifting as a result of climate change and therefore instances of atypical conditions are likely to increase (Chapter 6). Few studies currently set their work in the context of deviations from the baseline using this type of data. Chapter 6 also demonstrated that the physical structure of the lake responds and recovers rapidly to changes in external physical drivers. These rapid changes could not be captured using traditional sampling techniques, which may result in events being missed or underestimated (Adrian *et al.*, 2012; Aguilera *et al.*, 2016).

However, there are limitations of automated high resolution monitoring. Whilst the monitoring of physical variables using sensors is relatively accurate and reliable, the automated monitoring of ecological variables such as phytoplankton biomass and species composition and chemical variables such as nutrients are not yet of the same standard. Sensors that measure chlorophyll *a* via fluorescence and other photosynthetic pigments such as phycocyanin (a cyanobacteria pigment) have associated caveats such as photochemical quenching, as discussed in Chapter 3. Although chlorophyll *a* fluorescence provides a good relative measure of phytoplankton biomass and continuous monitoring can provide useful insights into bloom development (Pomati *et al.*, 2011), it does not provide information on community composition and can only provide a spot measurement. Some sensors can distinguish between different spectral groups of phytoplankton, for example the FluroProbe provides separate biomass readings for browns (diatoms and dinoflagellates), greens (Chlorophytes), cyanobacteria and Cryptophytes (e.g. Beisner and Longhi, 2013). These sensors do not provide the same level of taxonomic detail gained using traditional methods of phytoplankton sampling such as that used in Chapter 7. Furthermore, sensors that measure concentrations of nutrients such as nitrogen and phosphorus are being developed and deployed in some freshwater systems but they are not currently widespread (Beaton *et al.*, 2012; Nightingale *et al.*, 2019). A current problem for lake studies is that many of these sensors do not have a sufficiently low limit of detection to measure the low concentrations of nutrients that can occur during times of high phytoplankton growth, reducing their utility in understanding mechanisms for short term change in phytoplankton dynamics.

The findings of Chapter 4 and Chapter 7, as well as many other studies, have demonstrated that lake variables such as chlorophyll *a*, oxygen and specific conductivity are heterogenous with depth (Hamilton *et al.*, 2010; Obrador *et al.*, 2014; Leach *et al.*, 2018). Often these variables are only recorded at the lake surface as these sensors are expensive compared with temperature sensors. For example, the chlorophyll *a* and oxygen sensors on the AWQMS at Blelham Tarn are both located at 1 m depth. Discrete sampling for profiles of chlorophyll *a* and oxygen used in Chapters 4, demonstrated that the peak in these variables were often below the surface at 2 – 3 m, therefore values recorded at the AWQMS may underestimate these variables at certain times of year. Automated vertical profilers are currently being implemented in some lakes to overcome this issue (e.g. Brentrup *et al.*, 2016) but they are expensive and not currently widespread.

8.2.2 Traditional lake sampling

Traditional lake sampling involves the manual data collection of physical, chemical and ecological variables, usually at one point from the lake at monthly, fortnightly or weekly intervals. Although data collected at monthly or fortnightly timescales may not capture the responses to episodic events, it can provide valuable insights into seasonal cycles and long term change. Manual data collection is also vital for obtaining levels of detail that cannot be captured with in situ sensors, such as vertical profiles of turbulent mixing rates, chemical and ecological variables, as well as the identification of phytoplankton species and nutrient concentrations (Mantzouki *et al.*, 2018). Long term monitoring datasets are an asset when studying the impacts of long term changes in climate and lake ecosystems. For example, Blelham Tarn, along with other Cumbrian Lakes, have been monitored at regular intervals (typically fortnightly) from 1945 until the present day. The long term monitoring of the Cumbrian Lakes has contributed to the understanding of long term changes in nutrient budgets (Reynolds *et al.*, 2012), ecosystem phenology (Thackeray *et al.*, 2008; Meis *et al.*, 2009), oxygen depletion (Foley *et al.*, 2012) and within-lake responses to climatic cycles such as the NAO (George *et al.*, 2004). In Chapter 7, eleven years (2008-2018) of phytoplankton data collected at Blelham Tarn were needed in order to identify the typical seasonal composition and abundance of phylogenetic and functional groups. This time period was chosen as it was most representative of the current climate conditions and it coincided with the time series of the AWQMS. By comparing the study period to this seasonal average, it was possible to identify how and when the community differed from the 'norm', which provided insights into the responses of phytoplankton communities to atypically high lake stability.

Sampling at fortnightly intervals, however, is inadequate for identifying phytoplankton community responses to episodic events such as storms, therefore sampling was carried out at weekly intervals prior to the storm event and sub-weekly intervals during the event in Chapter 7. This method did adequately capture the phytoplankton response in greater detail to that compared to the response captured in the fortnightly data, but as phytoplankton replication rates are fast (e.g. 0.21-1.84 r'_{20} d^{-1}) it is likely that some details in turnover and recovery rates were still missed (Reynolds, 2006). Phytoplankton samples in long term monitoring programmes are typically integrated over depth e.g. the top 5 m in Blelham Tarn. By sampling phytoplankton at discrete depths in the water column Chapter 7 identified that the phytoplankton community is frequently vertically heterogeneous, in terms of community composition and biomass.

The temporal resolution of temperature profiles collected in Chapter 4 (weekly) were also insufficient to capture diurnal heating and cooling. It was therefore difficult to distinguish whether seasonal or daily thermoclines were captured during the measurements. This is a common issue for long term monitoring field campaigns where temperature is often collected at infrequent sampling intervals. The continuous monitoring of temperature by AWQMS's at depth intervals in the water column can overcome this. The spatial resolution of temperature measurements collected by both an AWQMS and by manual data collection during fieldwork are too coarse to capture active turbulent mixing (Brainerd and Gregg, 1995). Therefore, mixed depth estimations used in Chapters 4, 6 and 7 only estimate the depth of recent mixing rather than the depth of active mixing.

8.2.3 Modelling

There are a large number of lake ecosystem models which represent and simulate lake processes in different ways (Mooij *et al.*, 2010). Models are a useful tool in environmental systems for projecting long term changes in climate (IPCC, 2013) and its impacts (Elliott *et al.*, 2005; Jeppesen *et al.*, 2009; MacKay *et al.*, 2009; Jones *et al.*, 2011; Elliott, 2012), as well as exploring and testing hypotheses and concepts (Elliott *et al.*, 1999; Elliott *et al.*, 2001), testing water quality management scenarios (Carpenter *et al.*, 1999; Reynolds *et al.*, 2001; Hamilton *et al.*, 2015; Page *et al.*, 2018) and for disentangling complex or synchronous processes (Huisman and Weissing, 1994; Huisman, van Oostveen and Weissing, 1999; Huisman and Sommeijer, 2002; Chapter 5).

Some climatic impacts on lakes are intrinsically linked such as water temperature and mixed depth change, but they have separate impacts for phytoplankton growth (Winder and Sommer, 2012). It is very difficult to disentangle the separate impacts of these effects using observed data alone, hence models can be a useful complementary approach to data collection. By changing mixed depth and temperature independently in Chapter 5 the separate impacts of these two drivers on phytoplankton growth were disentangled. This improved our mechanistic understanding of phytoplankton community responses to changing physical drivers. These findings were also applicable to similar lakes around the world as the experiment covered different combinations of mixed depth and temperature change. Other forms of experimental approaches include mesocosms (e.g. Feuchtmayr *et al.*, 2009), within-lake tubes (e.g. Jones *et al.*, 2005) and whole lake experiments (e.g. Schindler, 1974). Although these alternative experimental conditions can have advantages such as a larger community diversity, they are often more expensive and time consuming to run in comparison to models. Models can also iterate through a large number of scenarios in a small amount of time (e.g. 1666 simulations in Chapter 5) which would be difficult to achieve using an alternative experimental approach.

Models, however, are limited representations of the real world, as they simplify complex physical, chemical and ecological processes. The PROTECH model, for example, can only simulate a small number of phytoplankton taxa in comparison to the large number of species that occupy lake systems (Chapter 7; Appendix one). The PROTECH model also contains a number of assumptions and simplifications in order to represent complex biological processes (Elliott *et al.*, 2001; Elliott *et al.*, 2010). Also, the data used to drive models is not always available at the timescale being modelled. For example, the nutrient data used in Chapter 7 was only collected on monthly intervals whereas the model was simulating a daily timescale, requiring the nutrient data to be interpolated to daily values.

8.2.4 A combined approach to water quality research

A combined approach to water quality research is still needed to answer questions about the physical, chemical and ecological processes in lake ecosystems at the appropriate timescale (Hampton *et al.*, 2018; Mantzouki *et al.*, 2018). To some extent the limitations of each method can be covered using complimentary techniques and methods. For example, high resolution data to investigate short term changes in lake dynamics, is often used in conjunction with fieldwork campaigns which can collect data that cannot be automatically monitored. High resolution data and ecological models are also becoming increasingly used in conjunction in order to forecast near real-time water quality and ecological conditions (Li *et al.*, 2014; Persaud *et al.*, 2015; Page *et al.*, 2018).

8.3 The mixed depth concept

Reducing environmental processes to simplified concepts is a useful methodological tool as they provide a means of understanding and explaining complicated systems. One example of a widely used concept in limnology and oceanography is that of the mixed depth. The mixed depth has been defined as the upper portion of the water column that is in direct contact with the atmosphere, has relatively uniform mixing rates and a homogenous distribution of particles (Sverdrup, 1953; Robertson and Imberger, 1994). The mixed depth concept is used ubiquitously within limnology and has underpinned the understanding of chemical and ecological processes such as gas and nutrient distribution (e.g. Staehr *et al.*, 2012; Mackay, Folkard and Jones, 2014; Giling, Staehr, *et al.*, 2017) and phytoplankton dynamics (Huisman and Sommeijer, 2002; Sebastian Diehl, 2002; Leach *et al.*, 2018).

Chapter 4 highlighted that the mixed depth concept has perhaps become confused or unclear overtime. Most of this confusion stems from how the mixed depth is being measured and whether this provides us with the depth of the 'actively mixed layer' or the depth of 'recent or potential mixing' (Brainerd and Gregg, 1995). The actively mixed layer can only be directly measured using turbulence measurements, therefore, using thresholds or gradients of temperature or density change to estimate mixed depth only captures the depth of recent mixing. As turbulence is not routinely measured, the mixed depth is more commonly determined using secondary variables. The assumptions of the mixed depth definition such as a homogenous distribution of particles and uniform mixing rates can be applied to the 'actively mixed layer' as defined by measuring turbulence, but cannot be applied to the depth of 'recent mixing' as defined using secondary variables. Although this issue was raised by Brainerd and Gregg in 1995 incorrect assumptions about the depth of recent mixing persist in limnological (Tedford *et al.*, 2014) and oceanographic studies (Thomson and Fine, 2003; Carranza *et al.*, 2018). Previous research (MacIntyre, 1993; Tedford *et al.*, 2014), and the findings of Chapter 4 have demonstrated that a homogenous distribution of chemical and ecological variables cannot be assumed when the depth of recent mixing has been defined using secondary variables.

An additional issue with the mixed depth concept is the large number of arbitrary thresholds and gradients of temperature and density change to define the mixed layer (Chapter 4; Table 4.1). This large number of definitions makes cross comparison between studies difficult, which may be overcome by using the alternative statistical methods presented in Chapter 4. The results of Chapter 4 also demonstrated that the choice of mixed depth definition can change the outcome of simple ecological and chemical metrics. The framework and methods developed in Chapter 4 were directly implemented in Chapters 6 and 7 which also highlighted some inconsistencies. In Chapter 6, the strength of statistical tests differed according to the mixed depth definition in a small number of cases. The relative position of the mixed depth (shallower or deeper) in relation to the euphotic depth was also inconsistent during the storm event in Chapter 7. This is concerning if changes in the mixed depth are being attributed to either a long term change in climate or a short term episodic event, because the answer may differ depending on the method of estimation used. There is, therefore, a need for limnologists to be more rigorous when applying and defining key components of lake thermal dynamics, especially in a changing climate.

It is hoped that by illustrating the large differences in mixed depth estimation using simple examples in Chapter 4 clarity will be added to this issue and may encourage future studies to test multiple methods of mixed depth estimation. It may also be helpful if there is a subtle change in language when referring to the mixed depth in future by using the ‘depth of recent mixing’ when the mixed depth has been determined using a secondary variable and the ‘actively mixing layer’ when turbulence has been directly measured. This may help to reinforce and clarify what exactly is being measured and what can be inferred directly from this measurement.

8.4 Impacts of long term climate change

The long term effects of climate change are having a number of long term impacts on the physical structure of lakes including potential changes in surface mixing (e.g. Livingstone, 2003), increases in surface water temperatures (e.g. O’Reilly *et al.*, 2015) and increases in the strength (e.g. Elo, Huttula and Peltonen, 1998; Verburga and Hecky, 2009) and length of stratification (e.g. Peeters, Straile, Lorke and Ollinger, 2007). This thesis has investigated different aspects of these changes and their impacts, with the exception of changes in stratification length.

8.4.1 Importance of surface mixing

Many lakes are expected to experience shallowing in the mixed depth as a result of increases in air temperature (O'Reilly *et al.*, 2015) and atmospheric wind stilling (Woolway, Meinson, *et al.*, 2017; Woolway *et al.*, 2019). Previous research has demonstrated the importance of the depth of mixing for phytoplankton biomass and community composition by controlling the light and nutrient climate that phytoplankton are exposed to (Diehl *et al.*, 2002; Huisman and Sommeijer, 2002; Diehl, 2002). In a changing climate, many lakes are experiencing an increase in cyanobacteria blooms which are a major water quality concern for lakes around the world (Paerl and Huisman, 2008; Paerl and Paul, 2012; Huisman *et al.*, 2018). It has been suggested that shallower surface mixing is one factor that may be contributing to increases in cyanobacteria blooms (Paerl and Paul, 2012). This is due to the favourable traits and morphologies of cyanobacteria such as buoyancy and superior nutrient acquisition and storage (Carey *et al.*, 2012).

Recent research has demonstrated that the responses of cyanobacteria to environmental change are not ubiquitous and differ with lake type, season and stressor gradients (Richardson *et al.*, 2018) as well as between cyanobacteria taxa (Carey *et al.*, 2012; Lofton *et al.*, 2019; Chapter 5). These findings suggest that cyanobacteria responses to environmental change should be generalised with caution, as a one size fits all approach cannot be applied to all lakes (Richardson *et al.*, 2018). The findings of Chapter 5 contributed to this area of research by demonstrating that the cyanobacteria *Dolichospermum* and *Planktothrix* responded differently to changes in mixed depth. *Dolichospermum* increased in abundance with shallowing from moderate depths, which supports the general idea of cyanobacteria dominance increasing with mixed depth shallowing. At deeper mixed depths, however, low light adapted *Planktothrix* dominated and mixed depth shallowing from deep to intermediate depths resulted in a reduction of *Planktothrix* and therefore overall cyanobacteria abundance. Therefore, lakes with naturally deeper mixed depths may benefit from mixed depth shallowing through the reduction of low light adapted *Planktothrix*. This was in contrast to findings by Posch *et al*., (2012), where warming and mixed depth shallowing in Lake Zurich led to an increase in *Planktothrix*. This contradiction may be due to the difference in the maximum mixing depth of the modelling study (14.5 m) compared to Lake Zurich (120 m) as Planktothrix populations have been recorded at depths of 74 m in Lake Zurich (Posch *et al.*, 2012). This illustrates the complexities in phytoplankton responses to environmental change.

8.4.2 Importance of increasing temperature

An additional impact of long term climate change is the increase in surface water temperature that is being experienced by many lakes (O’Reilly *et al.*, 2015), including Blelham Tarn (Foley *et al.*, 2012). Increases in surface water temperature have a number of potential indirect impacts such as shallower surface mixing and increases in stratification strength but increases in surface water temperature can also directly impact phytoplankton growth rates (Reynolds, 2006). Previous research suggested that increases in temperature lead to increases in cyanobacteria due to their higher temperatures for optimal growth (Reynolds, 2006). Recent research suggests that cyanobacteria growth rates differ between species and that cyanobacteria have similar optimum growth rates compared to some Chlorophytes (Lürling *et al.*, 2013). Findings from Chapter 5 demonstrated that isolated increases in temperature led to increases in phytoplankton biomass at most mixed depths, and an increase in cyanobacteria biomass at most mixed depths in each season. As PROTECH models phytoplankton growth rates based on the morphology rather than predetermined optimal temperatures for growth, this result was purely as a result of the morphology of different taxa. Furthermore, although this thesis did not explicitly explore the impacts of changes in stratification length, isolated increases in temperature in Chapter 5 advanced the spring bloom. At this time of year nutrients are plentiful after being replenished during the winter and diatoms dominate the spring bloom which are adapted to low light conditions experienced at this time of year when stratification is weak. As diatoms would not be light or nutrient limited they could therefore increase in biomass in response to increases in temperature.

8.4.3 Importance of stratification strength and stability

The final long term climatic change impact explored in this thesis was that of increased stratification strength and stability. The atypically high stratification strength that occurred in mid to late summer in 2016 in Blelham Tarn (Chapter 6) may become a more common occurrence with future climate change, which will have consequences for chemical and ecological processes within lakes.

Prolonged stratification strength and infrequent abiotic disturbances can lead to stable population dynamics in phytoplankton communities (Passarge and Huisman, 2002; Padisák, Borics, *et al.*, 2003; Passarge *et al.*, 2006). Under these conditions there is potential for the community to reach an equilibrium or steady state, whereby the biomass is dominated by a few species (Trifonova, 1993; Padisák, Borics, *et al.*, 2003). The resulting community is therefore highly uneven and of a low diversity, and often has a high biomass (Naselli-Flores *et al.*, 2003; Padisák, Borics, *et al.*, 2003). A steady state can be attained via two mechanisms; through competitive exclusion or as a result of specific traits such as mixotrophy, motility and buoyancy regulation and superior growth rates (Naselli-Flores *et al.*, 2003).

One concern of increased stability is that it provides conditions suitable for cyanobacteria growth, which is partly due to the ability of some species to regulate buoyancy (Carey *et al.*, 2012). Indeed, the findings of Chapter 5 demonstrated that lakes like Blelham Tarn may experience an increase in the dominance of the buoyant cyanobacteria *Dolichospermum* as a result of combined warming and mixed depth shallowing. Furthermore, stratification stability can also lead to nutrient limitation due to reduced inputs from the catchment during periods of low rainfall and reduced mixing into the nutrient rich hypolimnion (Köhler *et al.*, 2005; Weyhenmeyer *et al.*, 2007). This may have been a contributing factor for causing the nutrient limitation during mid-summer 2016 in Blelham Tarn (Chapter 6). As some species of cyanobacteria can also fix nitrogen this may provide them with an additional competitive advantage in stable stratified systems. Prolonged stratification can also lead to increased build-up of nutrients in the hypolimnion (Mackay *et al.*, 2014), which may promote a secondary autumn bloom of phytoplankton as stratification weakens and mixing encroaches into the hypolimnion (Winder and Cloern, 2010).

Warm and stable conditions do not necessarily equate to cyanobacteria dominance, however with the Chlorophyte, *Coenochloris fotti* contributing > 90 % of the biomass at its peak during the summer of 2016 in Blelham Tarn (Chapter 7). Functionally, this type of phytoplankton shares similarities with some cyanobacteria taxa because it is an S strategist and tolerant to low nutrient concentrations (Reynolds *et al.*, 2002). Again, this emphasises that generalisations about an increase in cyanobacteria in warm stable conditions may not always be the case. Predicting precisely which phytoplankton taxa are going to succeed under certain conditions is near impossible due to the chaotic interactions between individuals as well as within lake and abiotic variations (Benincà *et al.*, 2008). Conversely, predicting which functional types are most likely to succeed under certain environmental conditions is more achievable.

Strongly stratified systems are also vertically heterogeneous in terms of density and temperature, light and nutrients. This can create a heterogeneous distribution of phytoplankton biomass (Hamilton *et al.*, 2010; Mellard *et al.*, 2011; Leach *et al.*, 2018) as well as vertical niches with different phytoplankton occupying their most suitable light and nutrient climates within this vertical gradient, which can create vertically diverse communities (Olli and Seppälä, 2001; Clegg *et al.*, 2007; Longhi and Beisner, 2009; Beisner and Longhi, 2013; Ouellet Jobin and Beisner, 2014). Phytoplankton samples are commonly integrated over depth, it is therefore unclear how often this phenomenon occurs and whether it is more common for lakes of a certain morphology or nutrient status or phytoplankton community. Chapter 7 found that during the thermally stable conditions of summer 2016, the distribution of biomass was vertically heterogeneous but the composition of species was relatively homogenous with the same functional and phylogenetic group dominating at each depth, contrary to the above findings. During periods of heightened thermal stability it is not unusual for the community to be dominated by flagellated or buoyancy regulating species, which are capable of regulating their vertical position and can therefore occupy favourable vertical niches. Flagellates have also been observed to perform daily vertical migrations by moving to deeper, nutrient rich waters during the night and migrating to illuminated surface waters during the day (e.g. Jones, 1988). The sampling frequency in this thesis, however, was not set up to capture this diel processes.

In the case of Chapter 7, however, the community was dominated by a non-motile Chlorophyte, therefore the subsurface maxima of the population at 2 m during stable conditions was probably due to a positive balance between sedimentation losses and net growth. The within lake conditions may have also been unsuitable to support vertical separation because favourable nutrient concentrations were below the euphotic depth. Integrated nutrient samples from the surface 5 m of the water column demonstrated that the lake was co-limited in nitrogen and phosphorus from late June - early July (Chapter 6) and the euphotic depth was 4.5-5 m (Chapter 7). Therefore, migration to deeper depths for favourable nutrient concentrations would be light limited and vice versa for migration to shallower depths. Previous instances of niche separation have generally occurred in lakes where the euphotic depth extends to deeper depths in the water column forming deep chlorophyll *a* maxima (e.g.Olli and Seppälä, 2001). For example, in a mesocosm study the euphotic depth was 9 m compared to a maximum depth of 12 m (Olli and

Seppälä, 2001), whereas in Blelham Tarn only 4.5-5 m out of 14.5 m were illuminated at times of high thermal stability in 2016 (see further examples in Beisner and Longhi, 2013).

8.5 Impacts of short term weather events

Positive feedback mechanisms as a result of long term climatic change are projected to increase the frequency and magnitude of extreme weather events such as heatwaves and storms (e.g. Coumou and Rahmstorf, 2012). Previous research into the impacts of these events on aquatic (e.g. Morabito *et al.*, 2018) and terrestrial (Gutschick and BassiriRad, 2003) ecosystems have demonstrated the potential extreme and long-lasting impacts that these events can have. Within lakes, episodic weather events can significantly impact physical, chemical and ecological processes within a short period of time (Jennings *et al.*, 2012; Klug *et al.*, 2012; De Eyto *et al.*, 2016; Giling, Staehr, *et al.*, 2017; Kasprzak *et al.*, 2017). It is therefore becoming increasingly important for the impacts of extreme events to be incorporated into climate change projections (Perga *et al.*, 2018). The ecological response of phytoplankton communities to abiotic disturbances are useful to capture due to their fast replication rates and their rapid response and recovery compared to studies of larger terrestrial plant or tree communities (e.g. Yeboah *et al.*, 2016).

In many ways the bulk ecological response of the phytoplankton community to the storm event analysed in Chapter 7 was analogous to findings observed in previous phytoplankton disturbance studies. Diversity and evenness increased and slower growing species were replaced by small fast-growing flagellates following the storm (Padisák *et al.*, 1988; Jacobsen and Simonsen, 1993; Cardoso *et al.*, 2019). Counter to expectations, the community composition was more vertically heterogeneous following the storm compared to the thermally stable conditions prior to the storm (Chapter 7). This may be because the community following the storm event was dominated by flagellates that appeared to position themselves in a more favourable light climate at the lake surface (Chapter 7). The vertical migration of these flagellates was likely facilitated by the relatively quick return to strong thermal stability and resistance to mixing (Chapter 6). Phytoplankton biomass recovery was also delayed with increasing depth. These findings are important as there is very limited previous research investigating the vertical restructuring of phytoplankton communities following storm events.

This thesis focussed on the physical, chemical and ecological impacts of storm events on one lake system (Chapter 6 and 7). In reality, each storm event is unique and the impact of a storm on physical, chemical and ecological lake processes will depend on complex interactions between storm type, magnitude, duration and frequency as well as lake morphology, location, catchment characteristics and antecedent conditions (Jennings *et al.*, 2012; De Eyto *et al.*, 2016; Perga *et al.*, 2018; Woolway *et al.*, 2018; Chapter 6). Storms are multivariate events consisting of any combination of changes in air temperature, wind speed and precipitation. This thesis only focussed on one type of storm event, where flow rates were extreme but changes in wind speed and air temperature were relatively small (Chapter 6). Capturing the responses to these events in the present day is important because flow regimes in north-west England (Fowler and Kilsby, 2007) and other areas of the world (Milly *et al.*, 2005) are expected to alter as a result of climate change.

The 2016 storm event described in Chapter 6 impacted both the thermal stability of the lake as well as reducing the residence time. The relative impact of these separate drivers is difficult to disentangle. Reductions in residence time directly remove phytoplankton biomass by flushing phytoplankton from the system whereas increased wind mixing redistributes phytoplankton over a greater proportion of the water column and alters the nutrient and light climate phytoplankton are exposed to (e.g. Vanni *et al.*, 2006). Due to the short lived impact on the thermal stability and longer lasting impact on residence time, it is likely that the flushing mechanism was the more important factor during this event.

The impact of the storm events investigated in Chapter 6 on the physical structure of the lake were significant but relatively short lived. This may be because Blelham Tarn is a relatively small lake and has a shallow average mixed depth and therefore only requires a small amount of heat to re-establish stability. Lakes with deeper average mixed depths, such as lakes with a larger fetch, may take longer to recover from disturbances. In contrast to the short term physical impact, the 2016 event appeared to have a longer lasting impact on nutrient concentrations (Chapter 6) and the seasonal succession and vertical structuring of the phytoplankton community (Chapter 7). The short lived impact of storm events on the physical structure of the lake relative to chemical and ecological impacts has also been found by Jennings *et al*., (2012).

Much of the previous research into extreme events, has focussed on events that have extreme physical, chemical and ecological responses (e.g. Klug *et al.*, 2012; Kasprzak *et al.*, 2017). The findings of Chapter 6 demonstrate that extremes in physical drivers like flow, may not always result in an extreme response. This was due to the importance of antecedent conditions (Chapter 6). The importance of antecedent conditions for determining the response of lake processes to storm events has received relatively little attention. Where antecedent conditions have been studied this has been in the context of catchment characteristics, whereby long periods of dry weather can increase the delivery of sediments into lake systems (Perga *et al.*, 2018). Chapter 6 demonstrated that stratification strength prior to the storm event was important for determining the event response and that extremes in flow may not always drive lakes into a more extreme state.

8.6 Interaction of long term climatic impacts and short term weather impacts

Long term changes in climate, are leading to increasing surface water temperatures, which are changing the baseline physical structure of lakes (e.g. Livingstone, 2003; O'Reilly *et al.*, 2015). This means that it is becoming increasingly likely that episodic events like storms will occur at a time of heightened stratification strength (Chapter 6; Figure 8.1). These long term changes are therefore likely to influence the responses of physical, chemical and ecological processes to episodic events (Chapters 6 and 7) but there is currently a lack of research exploring this interaction within limnology.

The occurrence of the storm event at a time of heightened stratification strength during the summer of 2016 in Blelham Tarn (Chapter 6) temporarily returned the lake to a stratification strength more typical for the time of year rather than pushing the system into a more extreme state (Figure 8.1). Therefore, increases in episodic events in the future may return the physical structure of lakes to conditions more typical to the present day. This thesis has only highlighted one example of this trend but Chapter 2 demonstrated that lakes respond in different ways to changes in physical drivers and climatic change due to variations in lake morphology and regional weather variations.

Periods of prolonged stratification strength can lead to the dominance of one or few species (e.g. Padisák *et al.*, 2003; Chapter 7). Research by Wittbolle *et al*., (2009) suggested that highly uneven communities are less resistant to external stress. Long term changes in climate that result in the dominance of few species may therefore make ecosystems more vulnerable to concurrent increases short term weather extremes. This concept is not just applicable to lakes, but could also be applied to other aquatic and terrestrial ecosystems. At a time of heightened thermal stability in Blelham Tarn (Chapters 6 and 7) 90 % of the phytoplankton community biomass was dominated by one species, making it highly uneven in terms of biomass distribution. The species richness values, however, remained relatively high with 25-35 species still being present in low abundance during these times of extreme biomass dominance (Figure 8.1). Therefore, when the system was disturbed during the storm event, species more suited to the new conditions recovered quickly (Chapter 6). Ecosystems with a lower species richness may find it more difficult to recover following a storm event.

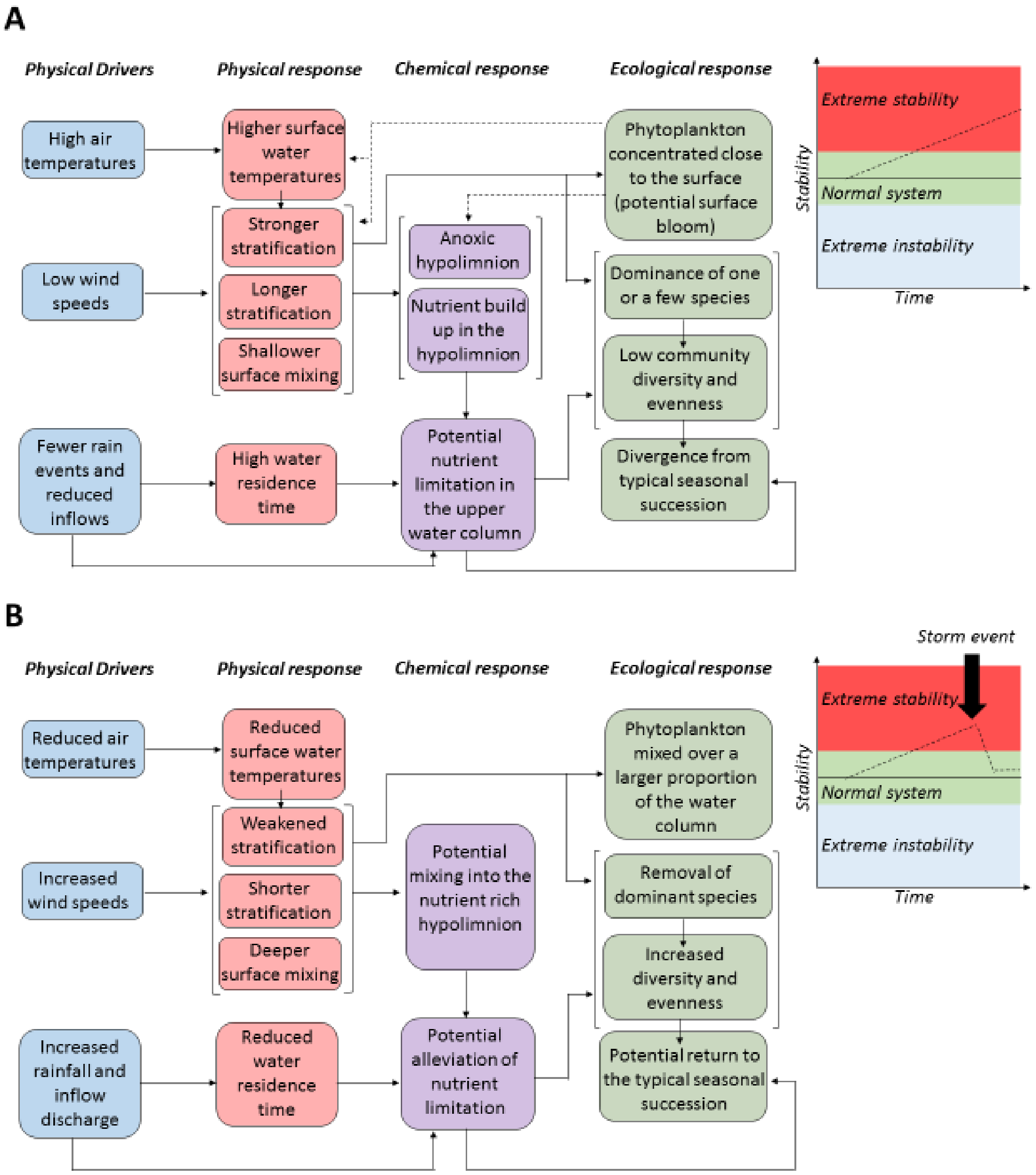


Figure 8.1 Conceptual diagram of (a) the potential physical, chemical and ecological impacts of atypically stable stratification strength as a result of long term climate change and (b) the potential physical, chemical and ecological impacts of a storm event occurring at a time of atypically high stratification strength.

9 Conclusions

This thesis has explored different facets of climate change impacts on physical, chemical and ecological processes within lakes. The following chapter revisits the aims and objectives defined in Chapter 1 and highlights the main conclusions in relation to each aim. The findings of this thesis have also prompted prospective areas for future research, outlined in this section.

9.1 Thesis conclusions

9.1.1 Investigating the consistency of a commonly used limnological concept: 'the mixed depth'

The mixed depth has been estimated using a number of methods. In the absence of direct turbulence measurements secondary variables such as temperature or density are often used. A systematic search of the existing literature found that there are at least 20 different thresholds and gradients of temperature and density currently being used to define the mixed depth. The lack of a universal definition for the mixed depth and the widespread use of multiple mixed depth definitions makes comparisons between studies difficult. The development of the two alternative statistical methods (Methods 2 and 3) for defining the mixed depth avoids the use of an arbitrary threshold and can be applied to physical, chemical and ecological variables. The comparison of three methods used to define the mixed depth demonstrated that different methods resulted in very different estimations. The calculation of ecological and chemical metrics such as the mixed depth to euphotic depth ratio, proportion of oxygen and chlorophyll *a* in the mixed layer and the direction of the oxygen flux differed markedly according to which mixed depth definition was used. Based on these findings it was concluded that studies should use several methods to estimate the mixed depth in order to assess the sensitivity of the findings to the mixed depth definition. The examination of multiple methods may also help determine the method which is most suited to the study.

9.1.2 Distinguishing the impacts of long term changes in water temperature and mixed depth for phytoplankton

Climate change is leading to an increase in surface water temperatures in many lakes, which is resulting in stronger density gradients. The depth of surface mixing is also expected to shallow in many lakes. Increases in water temperature and shallower surface mixing have separate consequences for phytoplankton growth. Increases in water temperature directly impact phytoplankton growth rates whereas changes in mixing impact the light and nutrient climate that phytoplankton are exposed to. These different impacts are difficult to distinguish from observed data, therefore a modelling experiment using the phytoplankton community model, PROTECH, was used to disentangle these impacts. Increases in lake water temperatures and shallower surface mixing had contrasting impacts on the phytoplankton community. Increases in water temperature generally led to more biomass and a shift in the phytoplankton community composition to the dominance of cyanobacteria. Changes in the mixed depth had contrasting impacts depending on the original mixed depth position and the light affinity of the dominant cyanobacteria species. Combined increases in water temperature and mixed depth shallowing from moderate depths (4-6 m) led to an increase in the biomass and dominance of buoyant cyanobacteria species (*Dolichospermum*). When shallowing and warming occurred from deeper depths (9-13 m), however, shallower surface mixing led to the reduction in the biomass of the low light adapted cyanobacteria (*Planktothrix*).

9.1.3 Determining the importance of antecedent conditions for physical and chemical responses to extreme storm events

Increases in lake surface water temperature are altering the baseline physical structure of lakes around the world. It is therefore becoming more likely that extreme episodic events such as storms will occur at times of heightened lake stability, therefore departing from the typical seasonal trend. A storm occurring at a time of atypically high stratification strength returned lake stability from being abnormally high to levels typical for the time of year. This finding has implications for the future, as many lakes are expected to be more stratified in comparison to current conditions. Storm events may therefore return the lake to conditions more typical for the time of year rather than push the system into a more extreme state. Evidence also suggested that levels of dissolved inorganic nitrogen went from limiting levels prior to the event to non-limiting during the event. This suggested that it is important to take antecedent conditions into account while analysing the impacts of storm events.

9.1.4 Identifying the impact of a storm event on the seasonal succession and vertical structure of the phytoplankton community

The increase in the magnitude and the frequency of extreme events such as storms also have implications for lake phytoplankton communities. A flushing event, which occurred at a time of atypically high stratification strength, had a marked impact on the composition and structure of the phytoplankton community of Blelham Tarn. The flushing event prevented the dominance of one species and restored the phytoplankton seasonal succession to one that was more typical for the time of year. The vertical structuring of phytoplankton community biomass and composition also differed before and after the event. The community had a sub-surface biomass peak prior to the event, but a relatively homogenous community composition, whereas following the event, the biomass peak was at the surface and the community composition was relatively heterogeneous with depth. As a result of climate change, many lakes may become more stably stratified for prolonged periods which could result in the dominance of one or few species and therefore deviate the community away from the typical seasonal succession. The concurrent increase in the magnitude and frequency of episodic events like storms, with the trend for higher thermal stability, may therefore restore phytoplankton communities to conditions more typical of the lake rather than push the community into an extreme state.

9.1.5 Summary

Climate change is having various impacts on the physical structure of lakes around the world. One consequence of this long term change is its influence on the depth of surface mixing. The concept of the mixed depth has perhaps become confused overtime and the definition of the mixed depth is inconsistent between studies. There is therefore a need for limnologists to improve their methodology for describing key components of lake thermal dynamics, especially in a changing climate. The impacts of long term changes in climate on the thermal structure of lakes will not have the same effects on the phytoplankton community nor the same effects on phytoplankton communities in different lakes. Despite the concern that increasing extreme episodic weather events will push lakes into more extreme states, some of these events may act to maintain lake ecosystems at levels closer to their inter-annual baseline.

9.2 Suggested areas for future research

9.2.1 Application of mixed depth recommendations

Chapter 4 made a number of recommendations on how multiple methods of mixed depth estimation should be tested and applied in order to determine the dependency of the results on the definition chosen. It is hoped that this will be applied to future studies in order to promote best practice and to see how the impact of the chosen definition differs with lake type and/or the subject of research. Chapter 4 also introduced two new statistical methods of mixed depth estimation and it is also hoped that these will be applied to future studies and different lake systems worldwide.

9.2.2 Distinguishing the relative impacts of multivariate storm events on phytoplankton communities

Storms are often multivariate events involving changes in wind speed, air temperature and rainfall. These can have different impacts on lake systems by changing the depth of surface mixing and the residence time and therefore have different implications for phytoplankton growth, which are difficult to distinguish using observed data. Therefore, using a similar approach to Chapter 5, a phytoplankton community modelling experiment could be performed which independently changes, air temperature wind speed and flushing in order to elucidate the relative importance of these drivers for community composition and recovery times. This experiment could also be performed in different seasons for different storm durations.

9.2.3 Identifying how the importance of antecedent conditions prior to storm events differs with location, lake type and storm characteristics

Chapters 6 and 7 explored the idea that extreme events such as storms are more likely to occur at a time of heightened stratification strength. There is a lack of previous research on the interactions between this long term trend and short term episodic events within limnology and in other areas of environmental science. This thesis provided evidence for one example of this, but future research could explore this relationship across multiple lake systems. Existing high resolution and long term datasets could be used to investigate the importance of antecedent conditions for determining physical, chemical and ecological storm responses for different types of lake (e.g size and mixing regime) in different locations around the world. Research could also look at the differences in the impacts of one storm event on different lake types, which are in close proximity to each other (e.g. Blelham Tarn, Esthwaite Water and Windermere). This research may indicate whether certain lake types are likely to be more vulnerable or resistant to storm events in a changing climate, which would be important for future water quality projections. Future research could also explore the relationship of storm timing in relation to antecedent conditions and season. This thesis also only focussed on flushing events and it is likely that other events, such as those that are primarily wind driven, could have different impacts which could also be distinguished and investigated further.

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Appendix One

Table detailing phylogenetic and functional groups of each phytoplankton taxa identified in Blelham Tarn.

Phytoplankton Species	Phylogenetic Group	CSR Functional Group
Achnanthes (Bory)	Bacillariophyta	R
Dolichospermum (Brébisson ex Bornet & Flahault)	Cyanobacteria	CS
Dolichospermum circinalis (Rabenhorst ex Bornet & Flahault)	Cyanobacteria	CS
Dolichospermum solitaria (Klebahn)	Cyanobacteria	CS
Dolichospermum spiroides (Klebahn)	Cyanobacteria	CS
Ankistrodesmus falcatus (Corda)	Chlorophyta	R
Ankyra judayi (G.M. Smith)	Chlorophyta	C
Aphanizomenon (Ralfs ex Bornet & Flahault)	Cyanobacteria	CS
Aphanizomenon flos-aquae (Ralfs ex Bornet & Flahault)	Cyanobacteria	CS
Aphanizomenon gracile (Lemmermann)	Cyanobacteria	CS
Aphanocapsa (Nägeli ex Kützing)	Cyanobacteria	S
Aphanocapsa elegans (Lemmermann)	Cyanobacteria	S
Aphanocapsa incerta (Lemmermann)	Cyanobacteria	S
Aphanothece clathrata (West & G.S.West)	Cyanobacteria	S
Asterionella formosa (Hassall)	Bacillariophyta	R
Asterococcus (Scherffel)	Chlorophyta	S
Aulacoseira granulata (Ehrenberg)	Bacillariophyta	R
Aulacoseira subarctica (O.Müller)	Bacillariophyta	R
Basichlamys sacculifera (Scherffel)	Chlorophyta	C
Bitrichia (Reverdin)	Ochrophyta	S
Botryococcus braunii (Kützing)	Chlorophyta	R
Carteria (Diesing)	Chlorophyta	C
Ceratium furcoides (Levander)	Miozoa	S
Ceratium hirundinella (O.F.Müller)	Miozoa	S
Characium (A.Braun)	Chlorophyta	CS
Chlamydocapsa planctonica (West & G.S.West)	Chlorophyta	S
Chlamydomonas (Ehrenberg)	Chlorophyta	C
Chlorella (Beyerinck)	Chlorophyta	C
Choricystis (Skuja)	Chlorophyta	C
Chromulina (L.Cienkowsky)	Ochrophyta	C
Chroomonas (Hansgirg)	Cryptophyta	C
Chrysochromulina parva (Lackey)	Haptophyta	C
Chrysococus (Klebs)	Ochrophyta	C
Closterium (kuetzingii Brébisson)	Charophyta	R

Closterium aciculare (T.West)	Charophyta	R
Closterium acutum (Brébisson)	Charophyta	R
Closterium ehrenbergii (Meneghini ex Ralfs)	Charophyta	R
Closterium gracile (Brébisson ex Ralfs)	Charophyta	R
Closterium kuetzingii (Brébisson)	Charophyta	R
Closterium parvulum (Nägeli)	Charophyta	R
Coccomyxa (Schmidle)	Chlorophyta	C
Coelastrum microporum (Nägeli)	Chlorophyta	R
Coelosphaerium (Nägeli)	Cyanobacteria	S
Coelosphaerium kutzingianum (Nägeli)	Cyanobacteria	S
Coenochloris fotti (Hindák)	Chlorophyta	S
Coenochloris ovalis (Korshikov)	Chlorophyta	S
Coenococcus (Korshikov)	Chlorophyta	S
Cosmarium (Corda ex Ralfs)	Charophyta	CS
Cosmarium abbreviatum (Raciborski)	Charophyta	CS
Cosmarium depressum (Nägeli)	Charophyta	CS
Cosmarium phaseolus (Brébisson ex Ralfs)	Charophyta	CS
Crucigenia tetrapedia (Kirchner)	Chlorophyta	R
Cryptomonas (Ehrenberg)	Cryptophyta	CS
Cyclotella (Kützing)	Bacillariophyta	R
Cyclotella comensis (Grunow in Van Heurck)	Bacillariophyta	R
Diatoma (Bory)	Bacillariophyta	R
Diatoma elongatum (Lyngbye)	Bacillariophyta	R
Dictyosphaerium (Nägeli)	Chlorophyta	R
Dictyosphaerium ehrenbergianum (Nägeli)	Chlorophyta	R
Dictyosphaerium puclhellum (H.C.Wood)	Chlorophyta	R
Dinobryon acuminatum (Ruttner)	Ochrophyta	R
Dinobryon bavaricum (Imhof)	Ochrophyta	R
Dinobryon crenulatum (West & G.S.West)	Ochrophyta	R
Dinobryon divergens (O.E.Imhof)	Ochrophyta	R
Dinobryon suecicum (Lemmermann)	Ochrophyta	R
Elakatothrix (Wille)	Charophyta	C
Euastrum (Ehrenberg ex Ralfs)	Charophyta	R
Eudorina (Ehrenberg)	Chlorophyta	S
Euglena (Ehrenberg)	Euglenozoa	C
Fragilaria (O.F.Müller)	Bacillariophyta	R
Fragilaria capucina (Desmazières)	Bacillariophyta	R
Fragilaria crotonensis (Kitton)	Bacillariophyta	R
Franceia ovalia (Francé)	Chlorophyta	R
Glenodinium berghii (Lernmennann)	Miozoa	CS
Gloeotila (Kützing)	Chlorophyta	R
Golenkinia radiata (Chodat)	Chlorophyta	R
Gonium pectorale (O.F.Müller)	Chlorophyta	S

Gonium sociale (Dujardin)	Chlorophyta	S
Gonyostomum semen (Ehrenberg)	Ochrophyta	C
Gymnodinium (Ehrenberg)	Miozoa	S
Gymnodinium helveticum (Penard)	Miozoa	S
Gyromitus (Skuja)	Chlorophyta	C
Kephyrion (Pascher)	Ochrophyta	C
Kirchneriella (Kirchner)	Chlorophyta	R
Kirchneriella obesa (West & G.S.West)	Chlorophyta	R
Koliella (Hindák)	Chlorophyta	R
Koliella longiseta (Vischer)	Chlorophyta	R
Koliella spiculiformis (Vischer)	Chlorophyta	R
Lagerheimia (Lagerheim)	Chlorophyta	C
Lagerheimia subsalsa (Lemmermann)	Chlorophyta	C
Lepocinclis (Ehrenberg)	Euglenozoa	C
Limnothrix redekei (Goor)	Cyanobacteria	R
Mallomonas (Perty)	Ochrophyta	C
Mallomonas akrokomas (Ruttner)	Ochrophyta	C
Mallomonas caudata (Iwanoff)	Ochrophyta	C
Meridion (C.Agardh)	Bacillariophyta	R
Merismopedia (Meyen)	Cyanobacteria	C
Micractinium (Fresenius)	Chlorophyta	R
Microcystis (Kützing)	Cyanobacteria	S
Monoraphidium (Nägeli)	Chlorophyta	C
Monoraphidium arcuatum (Korshikov)	Chlorophyta	C
Monoraphidium contortum (Thuret)	Chlorophyta	C
Monoraphidium dybowskii (Woloszynska)	Chlorophyta	C
Navicula (Kützing)	Bacillariophyta	R
Nephrocytium (Nägeli)	Chlorophyta	S
Nephrocytium agardhianum (Nägeli)	Chlorophyta	S
Nephroselmis (Stein)	Chlorophyta	C
Nephroselmis olivacea (Stein)	Chlorophyta	C
Nitzschia /Synedra (Ehrenberg/Ehrenberg)	Bacillariophyta	R
Ochromonas (Wysotzki, Wyssotzki)	Ochrophyta	C
Oocystis (Nägeli ex A.Braun)	Chlorophyta	S
Pandorina morum (O.F.Müller)	Chlorophyta	S
Paulschulzia pseudovolvox (P.Schultz)	Chlorophyta	S
Paulschulzia tenera (Korshikov)	Chlorophyta	S
Pediastrum boryanum (Turpin)	Chlorophyta	R
Pediastrum duplex (Meyen)	Chlorophyta	R
Pediastrum tetras (Ehrenberg)	Chlorophyta	R
Pelogloea (Lauterborn)	Cyanobacteria	S
Pennate diatoms	Bacillariophyta	R
Peridinium (Ehrenberg)	Miozoa	CS

Peridinium cinctum (O.F.Müller)	Miozoa	CS
Phacotus (Ehrenberg)	Chlorophyta	CS
Phacotus pyrum (Ehrenberg)	Chlorophyta	CS
Phacus (Ehrenberg)	Euglenozoa	CS
Pinnularia (Nitzsch)	Bacillariophyta	R
Planktothrix (Gomont)	Cyanobacteria	R
Planktothrix agardhii (Gomont)	Cyanobacteria	R
Planktothrix mougeotii (Anagnostidis & Komárek)	Cyanobacteria	R
Pleurotaenium (Ralfs)	Charophyta	R
Pseudanabaena (Lemmermann)	Cyanobacteria	R
Pseudanabaena limnetica (Lemmermann)	Cyanobacteria	R
Pseudosphaerocystis (Lemmermann)	Chlorophyta	S
Quadricoccus ellipticus (Hortobágyi)	Chlorophyta	S
Quadrigula (Bohlin)	Chlorophyta	R
Radiococcus (Schmidle)	Chlorophyta	C
Rhodomonas (G.Karsten)	Cryptophyta	C
Scenedesmus (Meyen)	Chlorophyta	R
Selenastrum (Reinsch)	Chlorophyta	R
Snowella lacustris (Chodat)	Cyanobacteria	S
Sphaerellopsis (Stein)	Chlorophyta	CS
Spondylosium (Wolle)	Charophyta	R
Spondylosium planum (Wolle)	Charophyta	R
Staurastrum (Meyen ex Ralfs)	Charophyta	CS
Staurastrum chaetoceras (Schröder)	Charophyta	CS
Staurastrum cingulum (West & G.S.West)	Charophyta	CS
Staurastrum lunatum (Ralfs)	Charophyta	CS
Staurodesmus (Teiling)	Charophyta	CS
Staurodesmus triangularis (Lagerheim)	Charophyta	CS
Stichococcus (Nägeli)	Chlorophyta	C
Syncrypta (Ehrenberg)	Ochrophyta	C
Synechococcus (Nägeli)	Cyanobacteria	S
Synedra (Nitzsch)	Bacillariophyta	C
Synedra acus (Kützing)	Bacillariophyta	C
Synedra ulna (Nitzsch)	Bacillariophyta	C
Synura (Korshikov)	Ochrophyta	C
Tabellaria (Ehernberg ex Kützing)	Bacillariophyta	R
Tabellaria flocculosa (Roth)	Bacillariophyta	R
Tabellaria flocculosa var. asterionelloides (Grunow)	Bacillariophyta	R
Tetraedron (Kützing)	Chlorophyta	C
Tetraspora (Vaucher)	Chlorophyta	C
Trachelomonas (Ehernberg)	Euglenozoa	CS
Trachelomonas hispedia (Perty)	Euglenozoa	CS
Trachelomonas volvocina (Ehernberg)	Euglenozoa	CS

Treubaria setigera (W.Archer)	Chlorophyta	R
Treubaria triappendiculata (C.Bernard)	Chlorophyta	R
Ulothrix (Kützing)	Chlorophyta	R
Uroglena (Ehernberg)	Ochrophyta	S
Urosolenia (H.L Smith)	Bacillariophyta	S
Woronichinia naegeliana (Unger)	Cyanobacteria	S