The effect of nutrient enrichment and changes in the weather on the abundance of *Daphnia* in Esthwaite Water, Cumbria

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SUMMARY

1. A simple counting technique has been used to produce a long-term (1956–1991) record of the seasonal variations in the abundance of *Daphnia* in Esthwaite Water, a productive lake in the English Lake District. For most of this period, there was a progressive increase in the winter concentration of phosphorus and a gradual increase in the temperature of the lake.

2. The seasonal variations in the abundance of *Daphnia* followed the same pattern throughout the period with a strong cohort (C1) produced in early summer and a weaker cohort (C2) in late summer.

3. The main factors regulating the strength of the C1 cohort were the trophic status of the lake and the physical stability of the water column. The gradual decline in the strength of this cohort is attributed to the combined effects of enrichment and warming on the growth of the edible algae that follow the *Asterionella* decline. The timing of the *Asterionella* decline has advanced in recent years, but there has been no comparable change in the timing of the *Daphnia* maximum.

4. The only factors to have a significant effect on the strength of the C2 cohort were the stability of the water column and the depth of the thermocline. The *Daphnia* were never abundant when the lake was strongly stratified since these conditions favoured the growth of the cyanobacteria *Microcystis* and *Aphanizomenon*.

5. The ultimate factor regulating the strength of the C2 cohort was the year-to-year variations in the weather type that dominates the U.K. during the summer. *Daphnia* numbers were low when the synoptic situation was dominated by high pressure i.e. when there was a marked increase in the frequency of calm, anticyclonic days.

6. The results are discussed in relation to the climatic changes projected for the area at the end of the 21st century. The greatest uncertainties are those connected with mesoscale changes in the circulation of the atmosphere and the consequent shift in the trajectory of storms across the Atlantic.

Keywords: climate, *Daphnia*, eutrophication, phenology, Schmidt stability

Introduction

Plankton in lakes are strongly influenced by year-to-year variations in the weather. Changes in the intensity of mixing have a profound effect on the succession of phytoplankton (Reynolds, 1984, 1993), whilst variations in water temperature influence both the growth and reproductive rates of the zooplankton (Vijverberg, 1980; Straile, 2000). Quantifying the impact of these weather-related effects is, however, difficult since most lakes are either being enriched with nutrients or recovering from previous periods of enrichment (O'Sullivan & Reynolds,

2005). Studies that consider the combined effects of variations in the weather and changes in the availability of nutrients on the dynamics of lake plankton are still rare. The best examples are those from Lake Constance and the Muggelsee in Germany (Straile & Geller, 1998; Adrian, Wilhelm & Gerten, 2006; Huber, Adrian & Gerten, 2010), two lakes that are still recovering from earlier periods of enrichment. The biological changes associated with re-oligotrophication are very different from those expected in a warmer world. They include a delay in the timing of some seasonal events and a general reduction in the biomass of phytoplankton (Anneville, Gammeter &

Straile, 2005). In contrast, the changes associated with an increase in the supply of nutrients are very similar to those expected in a warmer world. They include an advance in the spring growth of diatoms (Thackeray, Jones & Maberly, 2008), an increased risk of cyanobacterial blooms (Jöhnk *et al.*, 2008; Nõges *et al.*, 2009; Wagner & Adrian, 2009; Elliott, 2012) and changes in the life history traits and survival of zooplankton (Adrian *et al.*, 2006; George & Hewitt, 2006).

In this paper, I use a statistical approach to quantify the effects of a long-term increase in the supply of nutrients and more recent changes in the weather on the abundance of *Daphnia* in Esthwaite Water, a small lake in the English Lake District. When Pearsall (1921) classified the English Lakes, he described Esthwaite Water as the most productive lake in the area. Since then, nutrient loading has increased, and there has been an associated change in the composition of the phytoplankton (Lund, 1972; Heaney, Smyly & Talling, 1986). The data analysed cover the period between 1956 and 1968 when these loads were relatively low, and the period between 1969 and 1991 when they increased progressively. Previous studies (e.g. George *et al.*, 1990; George & Hewitt, 2006) have shown that the main factor regulating the dynamics of the *Daphnia* in the period before this phase of enrichment was the intensity of wind-induced mixing. Here, I examine the extent to which the continued enrichment of the lake has modified these responses or produced a fundamental change in the dynamics of the *Daphnia*. The paper includes an analysis of the synoptic situations (weather types) that influence the summer characteristics of the lake and considers the potential impact of future changes in the weather on the dynamics of the phytoplankton and zooplankton.

Description of site and methods

Esthwaite Water (54°18′N; 2°54′W) covers an area of about 1 km^2 has a mean depth of 6.9 m, a maximum depth of 16 m and an average residence time of *c*. 90 days (Mackay *et al.*, 2012). The period of stable stratification typically extends from the beginning of June to the end of September, but there are large year-to-year variations in the depth of the seasonal thermocline. The productivity of the lake is largely determined by the quality of the effluent discharged from a local sewage treatment plant and, from the early 1980s, by the operation of a fish farm on the lake. In the 1950s, the average winter concentration of dissolved reactive phosphorus (DRP) in the lake was 1.5 μg L^{-1}, but this increased to an average of 8.2 μg L^{-1} in the 1980s. The seasonal succession of the phytoplankton

follows the pattern commonly reported in temperate lakes (Reynolds, 1984). The spring community is dominated by diatoms, the early summer community by flagellates and the late summer community by blooms of cyanobacteria. The crustacean plankton is typical of a deep lake and consists of a few species from a small number of genera. In winter and spring, the most abundant species is the calanoid *Eudiaptomus gracilis* (Sars), but the summer community is dominated by Cladocera of the *Daphnia hyalina-galeata* complex. Genetic studies (Reid, Carvalho & George, 2000) suggest that the dominant form is *D. galeata*, but Christie (1983) noted that some forms were very similar to *D. longispina* O.F. Muller. Since the lake is privately owned, no scientific sampling of the fish is permitted. The most important pelagic species is the trout (*Salmo trutta* Linn), but small numbers of rainbow trout (*Oncorhyncus mykiss* Wal) have been introduced for the benefit of anglers. Further details of the physical, chemical and biological characteristics of the lake can be found in papers by Lund (1972), Heaney *et al.* (1986), Talling & Heaney (1988) and George & Allen (1994).

Samples of water for chemical analyses and plankton counts have been collected from the lake at regular intervals since the 1940s. The data analysed here cover the period between January 1956 and December 1991. In the 1950s and 1960s, these samples were collected at weekly intervals, but winter sampling was reduced to fortnightly intervals in 1979. Samples have always been collected from a fixed station near the deepest point in the lake using methods that have changed little over the years. Measurements of the vertical variations in the temperature and oxygen content of the water were also taken at the same station using some form of profiling instrument. In the 1950s, 1960s and 1970s, this instrument was a Mackereth temperature/oxygen probe (Mackereth, 1964) but this was replaced by a Yellow Springs Instruments sonde in the 1980s. The stability of the water column was estimated using the procedure described by Schmidt (1928) and the depth of the thermocline determined by inspection. Tests showed that the most reliable estimates of this depth were those based on an inspection of contour plots of the temperature gradient. Samples of water for chemical analyses, chlorophyll determinations and phytoplankton counts were collected by lowering a 5-m-long weighted hose of the type described by Lund & Talling (1957) into the water column. The only chemical results reported here are the winter concentrations of DRP and the summer concentrations of nitrate-nitrogen. DRP concentrations were measured by the method of Proctor & Hood (1954) until 1964 and then by the method of Stephens (1963). Nitrate-nitrogen was measured by the

procedure described by Mackereth (1963) until 1964 and then by the cadmium reduction method of Morris & Riley (1963). The phytoplankton samples were preserved in Lugol's iodine and counted using the inverted microscope technique described by Lund, Kipling & Le Cren (1958). In previous papers, I have used these counts to estimate the amount of food available to the *Daphnia*. Since no comparable estimates are available for the 1980s, I have used the timing of the *Asterionella* decline as a 'marker' for the growth of these edible species. This approach is based on the results summarised in George *et al.* (1990) which include plots of the 'average' seasonal periodicity of *Asterionella*, *Cryptomonas* and a variety of microalgae. When these edible species decline, the phytoplankton community is dominated by large, slow-growing species of cyanobacteria, such as *Aphanizomenon flos-aquae* Ralfs *ex*. Born *et* Flah. and *Microcystis aeruginosa* Kütz. emend. Elenkin.

The methods used to collect and count the zooplankton changed in the 1970s. Until 1972, samples were collected by lowering a Rodhe trap to successive depths and counting all the animals caught. In 1967, this method was supplemented by the simple 'filter paper' method described by Talling (2003). In this procedure, the animals collected by the 5-m tube were counted when the water was filtered for the extraction of chlorophyll. A hand lens was used to count all the animals trapped by the GF/C filters and a note made of the number of *Daphnia* and copepods present. The efficiency of this method depends on the number of animals caught which varied from less than five individuals per sample in winter to more than twenty individuals per sample in summer. In 1974, the Rodhe trap sampling ceased, so the time series analysed here is based on a harmonisation of the results produced by two methods (see Results).

Standard statistical techniques were used to identify the factors responsible for the observed variation in the abundance of *Daphnia*. Each time series was organised into a weeks versus years matrix and averages calculated for the periods when the *Daphnia* were most abundant. The physical variables used were: the surface temperature of the lake, the week of thermal stratification, the depth of the thermocline in late summer and the stability of the water column. The onset of thermal stratification was estimated from the Schmidt stabilities and was deemed to have occurred when these values exceeded a 'threshold' of 20 J m^2. The chemical variables used were: the average winter concentration of DRP and the average summer concentration of nitrate-nitrogen. The biological variables used were the average number of *Daphnia* present in early and late summer, the timing of the *Daphnia* maximum, the timing of the *Asterionella* decline and the late summer concentrations of *Aphanizomenon* and *Microcystis*. 'Early summer' was defined as the period between weeks 16 and 25 and 'late summer' the period between weeks 31 and 40. The timing of the *Asterionella* decline was based on the procedure described by Maberly *et al.* (1994) and was defined as the first week when an exponential decline in the cell numbers was deemed to have occurred. The only other variable used was the number of days in late summer when the U.K. was dominated by calm, anticyclonic weather. These situations are known to increase the risk of cyanobacterial blooms (George *et al.*, 2009) which then limit the performance of the *Daphnia* (George *et al.*, 1990). These frequencies were downloaded from a database maintained by the Climate Research Unit at the University of East Anglia (http://www.cru.uea.ac.uk/cru/dat/lwt/). The original frequencies (Lamb, 1950) were based on a subjective analysis of daily weather maps, but the new frequencies are based on the automated procedure described by Jenkinson & Collison (1977).

All the meteorological and limnological time series were examined for evidence of temporal autocorrelation and the residuals checked for departures from normality. These checks demonstrated that none of the climatic variables were autocorrelated, and the number of autocorrelations noted in the limnological time series was sufficiently low (<5%) to be attributed to chance.

Results

The 'filter paper' method of counting Daphnia

The filter paper method of counting zooplankton was introduced in 1968 but did not replace the Rodhe trap counts until 1973. Talling (2003) used the data acquired during this period of 'overlap' to compare the total number of animals caught but not the number of *Daphnia* in the samples. Figure 1a compares the number of *Daphnia* caught by the two methods between 1969 and 1972. The fitted regression is statistically significant ($r = 0.78$, d.f. = 139, $P < 0.001$) and explains 61% of the observed variation. Figure 1b is a log-log plot to show that the method still works when the *Daphnia* numbers are low. It should be noted that since the hose only collects water from the top 5 m, the number of animals caught is *c.* 30% higher than those caught by the trap. Once the filter paper counts have been adjusted to account for this bias, there is good agreement between the two population estimates. Figure 1c compares the week-to-week variations in the number of *Daphnia* caught by the hose and trap in 1970. The numbers caught in each week are closely correlated
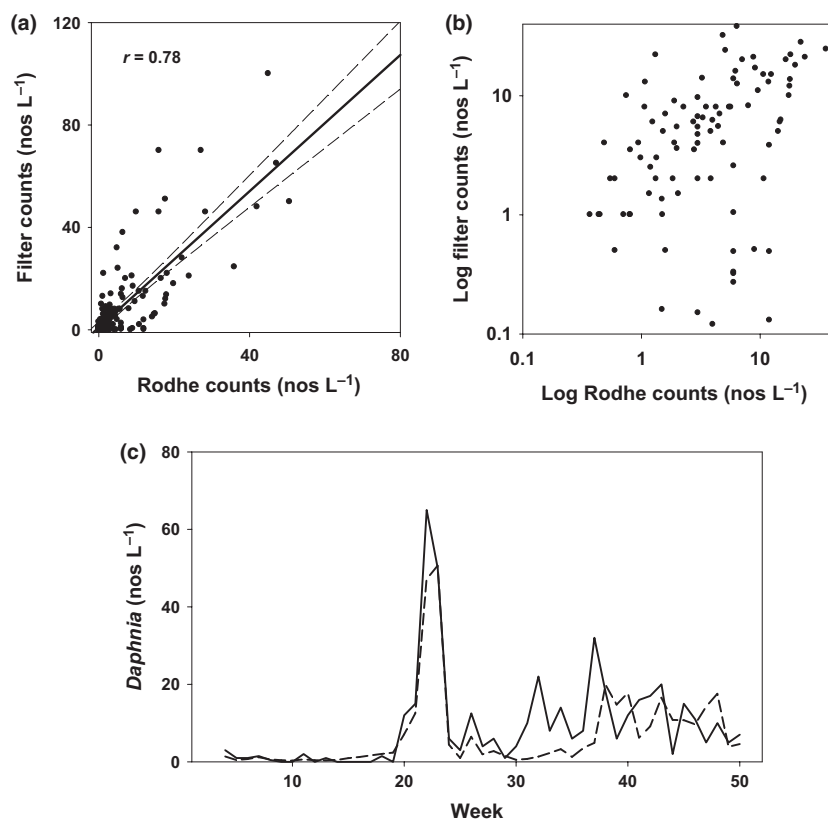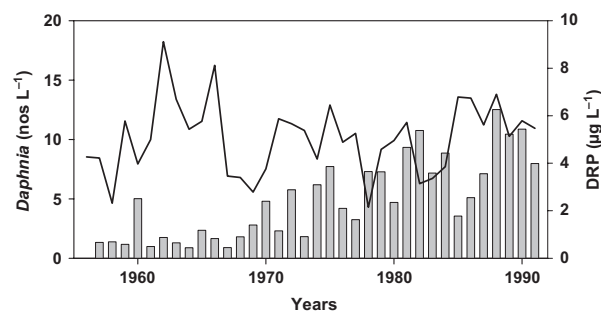
Fig. 1 (a) The relationship between the filter paper and the Rodhe Trap counts (1969–1972). (b) Logarithmic plot to show the effectiveness of the method at low population densities. (c) A comparison of the filter paper and Rodhe Trap counts for 1970. The broken line shows the filter paper counts (after correction for the sampling bias).

($r = 0.84$, d.f. $= 50$, $P < 0.001$), and the filter paper method even provides a reasonable measure of the annual maximum.

The relationship between the abundance of Daphnia and the trophic status of the lake

In the English Lakes, the winter concentration of DRP provides a reasonable measure of their trophic status (Sutcliffe *et al.*, 1982). In winter, the concentrations leached from the surrounding land are high, but there is little biological uptake in the open water. Figure 2 compares the long-term change in the annual abundance of *Daphnia* with the observed variations in the winter DRP. The results demonstrate that, whilst the DRP concentrations increased by a factor of five between the 1960s and the 1980s, there was no corresponding increase in the abundance of *Daphnia*. The main factor responsible for the post-1970 increase in the DRP was the deterioration in the quality of the effluent discharged from the sewage treatment works and the establishment of the fish farm in 1981. By the mid-1980s, this problem had become so severe that phosphate stripping was introduced at the

Fig. 2 The relationship between the annual abundance of *Daphnia* (line) and the winter concentrations of dissolved reactive phosphorus.

sewage treatment works during the summer. This treatment was extended to cover the full year in 1989, but the DRP concentrations remained high and there was no obvious improvement in the performance of the *Daphnia*.

The seasonal variation in the abundance of Daphnia

In a typical year, the growth of the *Daphnia* population follows a diacmic pattern with a strong (C1) cohort produced in early summer and a much weaker (C2)
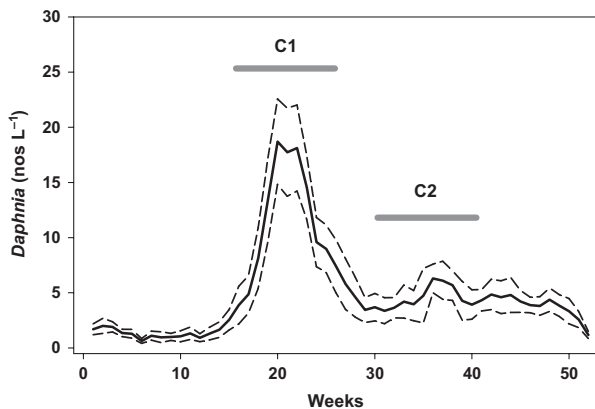
Fig. 3 The seasonal variation in the abundance *of Daphnia*. The solid line shows the weekly average and the broken line the 95% confidence intervals. The bars show the averaging periods for the early summer (C1) and the late summer (C2) cohorts.

cohort in late summer (Fig. 3). In previous publications (e.g. George & Hewitt, 2006), we have used a series of 10-week blocks (quintiles) to summarise the seasonal variations in the dynamics of the lake. Here, the limits of

the third quintile have been changed from weeks 21–30 to 16–25 to produce a better match to the timing of the early summer cohort. The timing of the fourth quintile remains the same and covers weeks 31–40, i.e. the period described as 'late summer'. This approach has proved effective at identifying the drivers of change in a number of Cumbrian lakes (George, Talling & Rigg, 2000) since it avoids the problems posed by averaging variables over short time scales. In the following section, I describe some of the internal and external factors that have influenced the strength of the two cohorts.

Factors influencing the strength of the early summer (C1) cohort

Figure 4a shows the year-to-year variations in the strength of the early summer (C1) cohort. The fivefold increase in the supply of nutrients recorded between the late 1960s and the 1980s had little effect on the abundance of *Daphnia.* In the 1960s, the average strength of this cohort was 11.1 individuals L^{-1}, but this only increased to 11.7 individuals L^{-1} in the 1980s. The most conspicuous
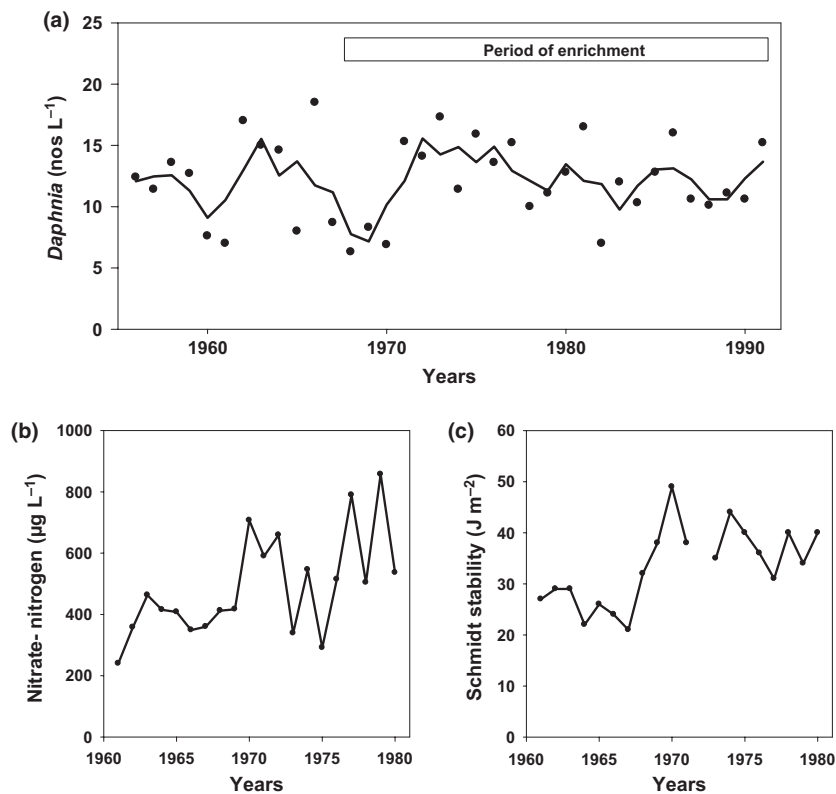

Fig. 4 (a) The long-term change in the strength of the early summer (C1) cohort in relation to the trophic status of the lake. The horizontal bar shows the period of enrichment, the points show the values and the line the three-point running mean. (b) The change in the early summer (C1 period) concentration of nitrate-nitrogen (1960–1980). (c) The change in the early summer stability of the water column (1960–1980). In 1972, the lake stratified rather late in the year.

feature of the time series is the decline and partial recovery noted between the mid-1960s and the early 1970s. A detailed analysis of the data acquired during this period suggests that this 'check' was the result of two different factors: a marked increase in the supply of nutrients and a subsequent increase in the stability of the water column. In 1968, a motorway linking the Lake District to the cities of the north-west was completed and resulted in a sharp increase in the number of people visiting the area. This led to problems at the Hawkshead sewage treatment works and a substantial increase in the concentration of nutrients reaching the lake. Since any phosphorus entering the lake during the growing season is rapidly assimilated, the most appropriate measure of this increase was the early summer concentration of nitrate-nitrogen (Fig. 4b). The variations in these concentrations suggest that 1969 was a pivotal year in the trophic history of Esthwaite. Between 1961 and 1969, the average concentration of nitrate-nitrogen was 380 μg L^{-1}, but this increased to an average of 580 μg L^{-1} between 1970 and 1979. At around the same time, there was a marked change in the stability of the water column (Fig. 4c) which increased from an average of 27 J m^{-2} between 1961 and 1969 to an average of 39 J m^{-2} between 1970 and 1979. Taken together, these changes had a direct effect on the composition of the phytoplankton and an indirect effect on the dynamics of the *Daphnia*. In a previous publication, George *et al.* (1990) showed that the main factor influencing the abundance of *Daphnia* in early summer was the availability of edible algae. These edible forms always appear when the spring diatoms are in decline. If there is a good match between the reproductive potential of the *Daphnia* and this 'window of opportunity', the early summer cohort is strong. If there is a poor match between the reproductive potential of the animals and the appearance of the edible algae, these numbers tend to be low. In

the following section, I explore the extent to which the relatively poor performance of the C1 cohort in the 'enrichment' years can be explained by a mismatch between this 'window of opportunity' and the development of the *Daphnia*. At one time, the collapse of the spring diatom bloom was thought to be a direct result of nutrient limitation and that the critical factor was the supply of silica (Lund, 1950). We now know that a number of other factors are involved and that the rate of decline can be enhanced by the early onset of thermal stratification (Huisman & Sommeijer, 2002). The physical factors regulating the phenology of the *Daphnia* are, in contrast, much simpler. Here, the key variable is the temperature of the water which regulates both the brood size and the rate at which eggs are laid.

Figure 5a,b show the year-to-year variations in the timing of the *Daphnia* maximum and the timing of the *Asterionella* decline. In the case of the *Daphnia* maximum (Fig. 5a), there was a tendency for the peak to appear rather earlier in the year but the long-term trend was not statistically significant. In the case of the *Asterionella* decline (Fig. 5b), this trend was statistically significant ($r = -0.38$, d.f. = 35, $P < 0.05$) and the average rate of advance was 0.42 days per year. The reasons for this differential response become clear when we consider the factors influencing the growth of the two populations. In the case of the *Daphnia* (Fig. 6a,b), the most influential factor was the temperature of the water ($r = -0.43$, d.f. = 35, $P < 0.01$) but there was also a weak positive correlation ($r = 0.37$, d.f. = 35, $P < 0.05$) with the timing of the *Asterionella* decline. In contrast, the timing of the *Asterionella* decline (Fig. 6c,d) was determined by the combined effects of the change in temperature and the increase in the supply of nutrients. The most influential factor was the winter concentration of DRP ($r = -0.51$, d.f. = 35, $P < 0.01$), but there was a weak negative
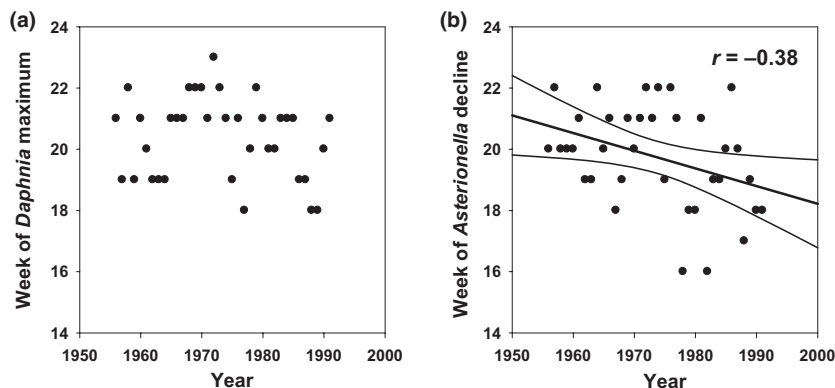

Fig. 5 The year-to-year variation in the timing of (a) the *Daphnia* maximum and (b) the *Asterionella* decline. A linear regression ($P < 0.05$) has been fitted to the timing of the *Asterionella* decline.
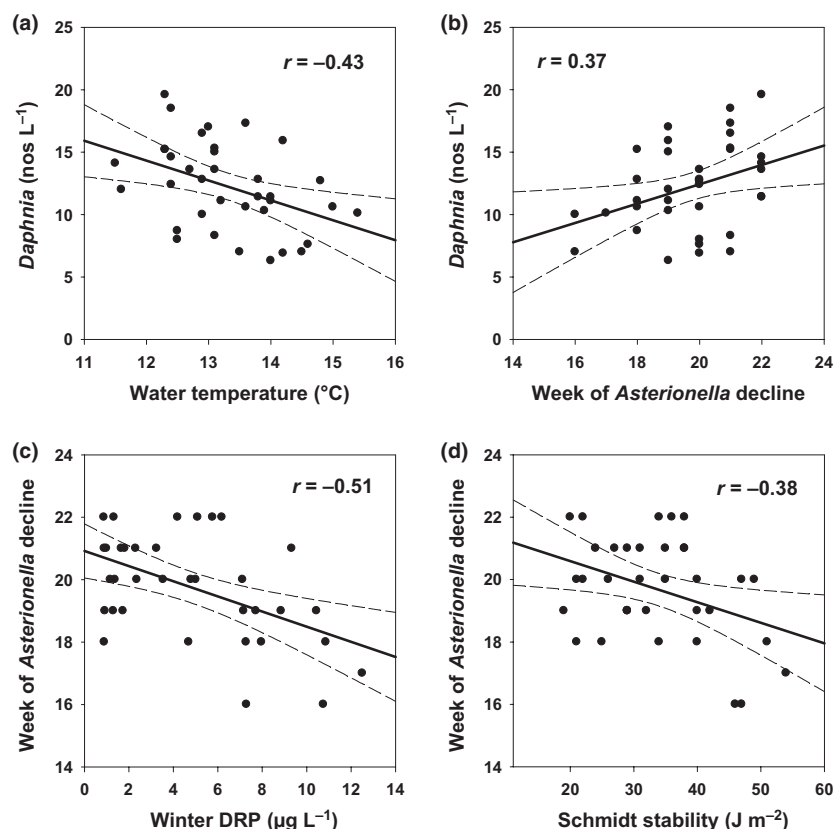
Fig. 6 The relationship between the strength of the C1 cohort of *Daphnia* and (a) surface temperature and (b) timing of the *Asterionella* decline. The relationship between the timing of the *Asterionella* decline, and (c) winter dissolved reactive phosphorus and (d) stability of the water column.

correlation with the stability of the water column ($r = -0.38$, d.f. = 35, $P < 0.05$). These results suggest that the relatively poor performance of the *Daphnia* in the 1970s and 1980s can best be explained by the gradual development of a mismatch between the decline of the *Asterionella* and the reproductive potential of the *Daphnia*. By the end of the study, there was a 2–3 week difference between the timing of the *Daphnia* maximum and the timing of the *Asterionella* decline i.e. the *Daphnia* maximum was recorded some weeks after the collapse of the diatoms had provided a 'window of opportunity' for the edible algae. Further support for this mismatch hypothesis can be gained by relating the long-term change in the strength of the C1 cohort to the observed variations in the trophic and physical characteristics of the lake (Table 1). Trials with a variety of multiple regression models showed that a model that included the winter concentration of DRP, the stability of the water column and the week of the *Asterionella* decline as the regressor variables explained 31% of the observed variation and was statistically significant at the 95% level. All three variables had an effect on the early summer performance of the *Daphnia*, but the most significant factor was the stability of the water column.

Table 1 The results of a multiple regression analysis where the dependent variable was the strength of the early summer (C1) cohort of *Daphnia* and the regressor variables were the winter dissolved reactive phosphorus (DRP), the stability of the water column during the C1 period and the week of the *Asterionella* decline

Variable	Coefficient	Standard error	t	P
Intercept	2.27	8.45	0.26	0.79
Slope (DRP)	0.30	0.16	1.78	0.08
Slope (stability)	−0.13	0.16	−2.04	0.05
Slope (*Asterionella*)	0.65	0.36	1.78	0.07
			$R^2 = 31\%$	
			$P < 0.05$	

Factors influencing the strength of the late summer (C2) cohort

Figure 7 shows the year-to-year variation in the strength of the late summer (C2) cohort. These results demonstrate that there has been a general decline in the strength of this cohort from an average of 5.2 individuals per litre in the 1960s to an average of 3.4 individuals per litre in the 1980s. The main factor responsible for this decline was the increased dominance of the bloom-forming cyanobacteria.
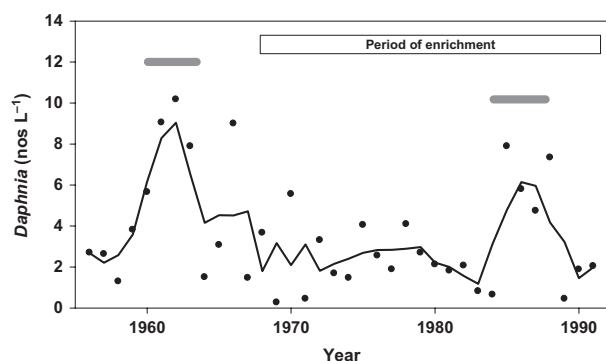
Fig. 7 Year-to-year variation in the strength of the late summer (C2) cohort. The points show the annual values and the line the three-point running mean. The horizontal bars show the years when the late summer stability of the water column was <30 J m^{-2}.

The seasonal development of these species is influenced by a variety of factors, but dense 'blooms' only appear during warm periods when there is little wind-induced mixing (George & Heaney, 1978). Surface blooms of cyanobacteria interfere with the development of the *Daphnia* in two different ways: their colonies interfere with the animal's food selection mechanism (Gliwicz & Lampert, 1990) and they produce toxins that may be a direct threat to life. Figure 8a shows the relationship between the strength of the C2 cohort and the Schmidt stabilities calculated for the same period. The greatest *Daphnia* numbers were always recorded when mixing was most intense ($r = -0.60$, d.f. = 35, $P < 0.001$) and the lowest when the stability exceeded *c.* 60 J m^{-2}. The relationship between the strength of the C2 cohort and the average concentration of either *Microcystis* or *Aphanizomenon* (Fig. 8b) was less clear-cut. *Daphnia* numbers were low when these numbers were high, but low numbers were also recorded when there were few cyanobacteria. The most likely explanation for the poor

performance of the *Daphnia* in these 'bloom-free' years is the effect that calm summers have on the regrowth of edible algae (George & Hewitt, 2006). The flagellates that are the preferred food of the *Daphnia* require regular inputs of DRP to support their development. In windy summers, substantial quantities of DRP are entrained from the anoxic hypolimnion to support the regrowth of edible algae (Heaney *et al.*, 1986). In calm summers, entrainment of nutrients from depth is of much lower magnitude, and these fast-growing forms then have to rely on the flux of nutrients from the surrounding land. Despite these complications, the main factor regulating the strength of the C2 cohort during the period of study was the mixing characteristics of the water column, not the trophic status of the lake. Trials with a variety of multiple regression models showed that a model that included the stability of the water column and the depth of the seasonal thermocline as the only significant drivers (Table 2) explained more than 40% of the observed variation in the strength of the C2 cohort and was statistically significant at the 99% level.

Discussion

In their study of the dynamics of *Daphnia* in Esthwaite Water between 1956 and 1972, George *et al.* (1990) made a number of predictions regarding the changes expected in a warmer world. They predicted that the growing season would start earlier and continue for longer and that there would be an increased risk of prolonged cyanobacterial blooms. Here, I have used a simple method to extend these historical records to see whether these expectations have been confounded by the progressive increase in the productivity of the lake. The results demonstrate that most of the changes noted in the 1970s and 1980s were still being driven by the observed year-to-year variations in
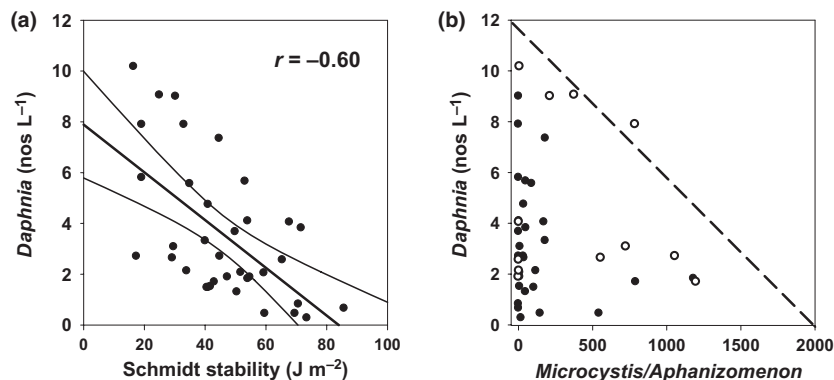

Fig. 8 (a) The relationship between the strength of the C2 cohort and (a) the stability of the water column. (b) The abundance (cells per mL) of *Microcystis* (open circles) and *Aphanizomenon* (closed circles).

Table 2 The results of a multiple regression analysis where the dependent variable was the strength of the late summer (C2) cohort of *Daphnia* and the regressor variables were the winter dissolved reactive phosphorus (DRP), the stability of the water column during the C2 period and the depth of the thermocline during the C2 period

Variable	Coefficient	Standard error	t	P
Intercept	2.27	3.08	0.74	0.47
Slope (DRP)	−0.11	0.10	−1.09	0.28
Slope (stability)	−0.06	0.02	−2.47	0.02
Slope (thermocline)	0.53	0.26	1.98	0.05
			$R^2 = 45\%$	
			$P < 0.01$	

the weather. The only exception was the nutrient-related advance in the decline of the *Asterionella* population which amplified the phenological shift associated with the early onset of stratification.

There is now mounting evidence that the timing of many limnological events has advanced in recent years (Maberly *et al.*, 1994; Gerten & Adrian, 2002; Nõges *et al.*, 2009; Thackerey *et al.*, 2012). One consequence is the tendency for the dynamics of some grazers to become uncoupled from the growth of their phytoplankton food (Winder & Schindler, 2004; Berger *et al.*, 2007). Cushing (1982) was one of the first to recognise the importance of these trophic 'mismatches', but comparable losses of synchrony have since been reported in a number of lake systems (George & Taylor, 1995; Wagner & Benndorf, 2007; Thackeray *et al.*, 2010). Most of these shifts have been attributed to changes in the climate, but systematic increases in the supply of nutrients can produce very similar results (Thackeray *et al.*, 2008; Feuchtmayr *et al.*, 2012).

The schematic diagram in Fig. 9 explains how the 'mismatch' noted for the C1 cohort appears to have been produced by the combined effects of an increase in
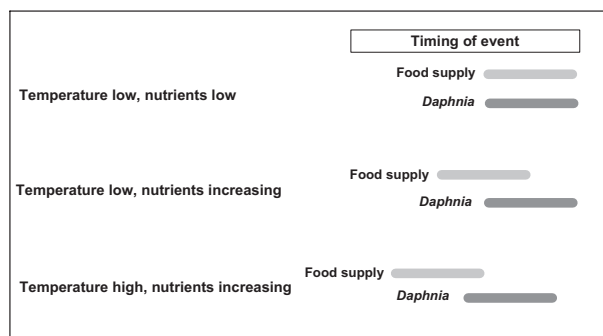
Fig. 9 Schematic diagram showing the combined effects of temperature and the supply of nutrients on the periodicity of the *Daphnia* and their food supply.

temperature and the supply of nutrients. In the 1960s, when nutrient inputs were relatively low and the summers were cooler, there was a good match between the reproductive potential of the *Daphnia* and the availability of edible algae. The first factor to disrupt this synchrony was the increase in the supply of nutrients that followed the rapid growth of tourism in the late 1960s. These increases allowed the spring diatoms to reach their silica-determined maximum earlier in the year (Reynolds, 1990) and led to the earlier growth of the flagellates that are the preferred food of *Daphnia*. The second factor to disrupt this synchrony was the early onset of thermal stratification. Diatoms grow best in a well-mixed water column so, when a lake stratifies early, more of the spring bloom is lost by sedimentation (Huisman & Sommeijer, 2002). Very similar shifts in the timing of the spring diatom bloom have recently been reported for the *Asterionella* population in the North Basin of Windermere (Thackeray *et al.*, 2008; Feuchtmayr *et al.*, 2012). Here, the statistic used as a measure of this advance was the week of the *Asterionella* maximum, but this was again influenced by increases in the temperature as well as the supply of nutrients. If summer temperature continues to increase, the timing of the *Daphnia* maximum could change to reduce the effect of this mismatch. In the late 1980s, there was a suggestion that the timing of this maximum had changed, but this shift was not sufficient to counter the observed shift in the timing of the *Asterionella*.

The factors influencing the strength of the C2 cohort appear to have changed little over the years. The greatest *Daphnia* numbers are still recorded in years with more intense mixing and the lowest in summers with stable thermal stratification. The main factor responsible for this difference is the effect that warm, calm summers have on the development of cyanobacterial blooms. The factors regulating the seasonal periodicity of cyanobacteria are known to be complex (Reynolds *et al.*, 1981; Huisman, Matthijs & Visser, 2005), but dense blooms appear only when the weather is calm. Recent mixing experiments in a shallow lake in the Netherlands (Jöhnk *et al.*, 2008) have showed that just a few days of calm weather was enough to allow these species to float to the surface and accumulate downwind. That experiment was conducted during the hot summer of 2003 and also showed the extent to which global warming can accentuate the problems posed by high concentrations of nutrients. Wagner & Adrian (2009) reached very similar conclusions when they used a statistical approach to investigate the factors influencing the development of cyanobacteria in a productive German lake. Their analyses showed that once a certain 'threshold' concentration of nutrients has been reached, the key

determinants for cyanobacteria dominance were the duration and intensity of thermal stratification. In Esthwaite Water, the only variables to have a significant effect on the strength of the C2 cohort were the stability of the water column and the depth of the late summer thermocline. Despite a fivefold increase in the supply of nutrients, there were only two periods when the *Daphnia* were ever abundant at this time of year: the period between 1961 and 1963 and the period between 1985 and 1988. The strongest C2 cohort was recorded in 1962 when the stability of the lake was 17 J m^{-2} and the second strongest in 1985 when the stability was 19 J m^{-2}.

One of the key challenges faced by limnologists in the 21st century is the ability to distinguish between the 'local' and 'regional' factors that regulate the dynamics of lakes. The results presented here demonstrate that it is possible to identify clear climatic effects in systems that are still been impacted by cultural eutrophication. In Esthwaite Water, the most pronounced weather-related effects were those observed in late summer when the phytoplankton community was dominated by cyanobacteria. There is now mounting evidence that the weather patterns experienced in the U.K. during the summer are the result of global-scale changes in the atmosphere and the ocean (Strong & Maberly, 2011; Taylor, 2011). One way of highlighting these effects is to relate the changes observed in the lakes to the observed variation in the weather types that dominate the U.K. In summer, the weather type that has the most profound effect on the lakes is the anticyclonic type characterised by warm, calm conditions (George *et al.*, 2009). Figure 10a shows the extent to which the frequency of this weather type influenced the late summer stability of Esthwaite Water. The results demonstrate that summers dominated by high pressure can increase the stability of the water column by a factor of four ($r = 0.54$, $P < 0.001$), but the extremes reached during

spells of warm weather can be very much higher. Figure 10b shows the effect that these high-pressure conditions had on the strength of the C2 cohort. The relationship is very similar to that noted between the abundance of the *Daphnia* and the concentration of cyanobacteria. Thus, a low frequency of anticyclonic days does not necessarily result in a strong C2 cohort, but strong cohorts are never produced in summers when the atmospheric pressure is high.

The sensitivity of Esthwaite Water to these mesoscale variations in the atmospheric greatly complicates the task of predicting the possible effects of future changes in the climate. In 2009, the United Kingdom Climate Impacts Programme produced a report on the weather patterns expected in the U.K. at the end of the 21st century (http://www.ukcip.org.uk). This report contained probabilistic estimates of the likely changes in air temperature, rainfall and cloud cover but only a general indication of their effect on the atmospheric pressure and the wind speed. The temperature projections suggest that summers in the north-west of England will be at least 2 °C warmer by the end of the century. Increases in the magnitude will have a major effect on the thermal characteristics of the lakes, the dynamics of the plankton and the trophic mismatches discussed here. The biggest uncertainty is the extent to which mesoscale changes in the atmospheric circulation could either reduce or amplify the effects of a more general warming. If periods of low pressure become common, the limnological effects of the projected warming might be less severe. Conversely, if periods of high pressure become prolonged, there is the potential for cyanobacterial blooms to appear earlier and continue throughout the summer. The models currently used to simulate the climate cannot predict these mesoscale circulations with any degree of confidence. One of the hypothesised effects of global warming is a change in the
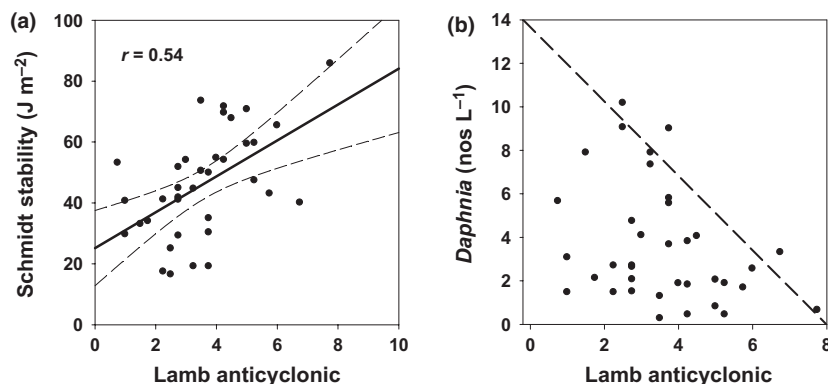
Fig. 10 (a) The relationship between the stability of the water column in late summer and the number of anticyclonic days recorded in the U.K. over the same period. (b) The relationship between the strength of the C2 cohort and the number of anticyclonic days.

frequency and intensity of extratropical cyclones. The analyses presented by McCabe, Clark & Serreze (2001) suggest that there has already been a significant decrease in the winter frequency of cyclones, but the patterns projected for the summer are less clear. In a review of some recent circulation model experiments, Brown concluded that shifts in the position of the Atlantic storm tracks are likely, but the changes noted varied from model to model (www.ukcip.org.uk/ukcp09). The results presented here demonstrate that shifts of this kind would have a major effect on the physical dynamics of Esthwaite Water, one of the most sensitive lakes in the Windermere catchment. The ecological impact of these shifts would, however, depend on the timing and frequency of the mixing events and the extent to which the management of the catchment can limit the supply of nutrients. In the 1990s, automatic monitoring stations were deployed in a number of lakes to explore their responses to short-term changes in the weather (Rouen *et al.*, 2005). Studies are now underway to quantify the impact of these 'episodic' events on the physical characteristics of the lakes as well as the seasonal succession of phytoplankton (Madgwick *et al.*, 2006).

Acknowledgments

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