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ORIGINAL PAPER

Seasonal Patterns of Phytoplankton Taxon Richness in Lakes: Effects of Temperature, Turnover and Abundance

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Species richness is a key ecological characteristic that influences numerous ecosystem functions. Here we analyse the patterns and possible causes of phytoplankton taxon richness in seasonal datasets from twenty contrasting lakes in the English Lake District over six years and near-weekly datasets over 33 years from Windermere. Taxon richness was lowest in winter and highest in summer or autumn in all of the lakes. Observed richness was very similar to richness estimated from coverage and sampling effort, implying that it closely reflected true seasonal patterns. Summer populations were dominated by Chlorophyta and functional groups X1, F, N and P (*sensu* Reynolds). In Windermere, weekly taxon richness was strongly positively correlated with surface water temperature, as was the number of functional groups and the number of taxa per functional group. Turnover in richness of taxa and functional groups were positively correlated and both were related to surface temperature. This suggests that high taxon richness in summer is linked to higher water temperature, promoting a turnover in richness of taxa and functional groups in these lakes. However, since the number of taxa per unit concentration of chlorophyll *a* decreased with increasing concentration of chlorophyll *a*, competition might occur when abundance is high.

Key words: English lake district; phytoplankton; seasonal change; species richness; turnover of richness; Windermere.

Introduction

Species diversity is fundamental to ecosystem productivity, their resilience to perturbation and their efficiency of resource use (Gunderson 2000; Ptacnik et al. 2008; Tilman et al. 2014; Tilman and Pacala 1993). Most studies of the causes and

consequences of species richness on ecosystems have been carried out on terrestrial plants, but there has been a large recent increase in studies on phytoplankton in fresh waters and the oceans (Borics et al. 2021). Early research was triggered by a paper of Hutchinson's (Hutchinson 1961) who coined the term 'the paradox of the plankton' in reference to the co-existence of more species at one time than would be expected from competition theory. Hutchinson suggested possible reasons for this, including extrinsic temporal (e.g. Descamps-Julien and Gonzalez 2005) and spatial (e.g. Longhi and Beisner 2010) variation in niches and the lack of the community reaching equilibrium under rapidly changing conditions. Subsequently, a range of other explanations has been proposed including intrinsic chaotic fluctuations produced by interactions among multiple species (Huisman and Weissing 2002; Scheffer et al. 2003) and the diversity of characteristics of species from different phylogenetic groups (Kléparski et al. 2022).

A given lake experiences a repeatable seasonal pattern of physical and chemical conditions, driven by the climate, overlain by stochastic events, driven by local weather. Lakes at high latitude experience particularly large seasonal changes in daylength and surface light and also surface temperature (Maberly et al. 2020) that alter stratification, availability of potentially limiting resources, including light and nutrients, growth rates and the components of the planktonic food web (Reynolds 1984). As a result there are often repeatable seasonal patterns of phytoplankton abundance and composition in a given lake (Sommer et al. 2012), especially for the dominant species (Maberly et al. 1994). Seasonal patterns and species composition of phytoplankton differ among lakes depending on their physical and chemical characteristics, such as area and depth as well as local weather, propensity to flush, and inputs of material from their catchment, particularly nutrients, alkalinity and coloured dissolved organic carbon (Borics et al. 2021; Feuchtmayr et al. 2019; Interlandi and Kilham 2001). For long-lived organisms, diversity is the result of selection, drift, mutation and gene flow from a regional species pool (Vellend 2010) and to a lesser extent this may be the case for phytoplankton (Ptacnik et al. 2010a). However, seasonal patterns of phytoplankton species richness are much less constrained by drift, mutation and gene flow. Instead, given the short timescale and the propensity of phytoplankton to disperse, produce dormant stages and grow rapidly,

seasonal patterns will largely depend on selection from a local species pool (Finlay 2002; Finlay and Clarke 1999).

Here we analyse seasonal patterns of phytoplankton taxon richness in relation to lake conditions in 20 contrasting sites within one geographical region, the English Lake District, and complement this with near-weekly analyses of phytoplankton from one of the lakes, the South Basin of Windermere, over 33 years.

Results

Seasonal Numbers of Phytoplankton Taxa in 20 Lakes (1991 to 2015)

The studied lakes vary in area from 0.07 km^2 (Louhrigg Tarn) to 8.94 km^2 (Ullswater) and in mean depth from 3.3 m (Elterwater) to 39.7 m (Wastwater) (Maberly et al. 2016) (Supplementary Material Table S1). The lakes cover a range of productivities from ultraoligotrophic Wastwater (average concentration of total phosphorus (TP) and chlorophyll a of 3.8 and 0.9 mg m^{-3} respectively) to eutrophic Blelham Tarn (average concentration of TP and chlorophyll a of 29.3 and 18.6 mg m^{-3} respectively (Supplementary Material Table S1). Over the six years and four seasons in the Lakes Tour samples (see Methods), 348 taxa were identified by light microscopy, of which 198 were identified at least to species, 136 were identified to genus, seven were identified to a group such as 'pennate diatom' and seven were unidentified and given a form description. The total number of phytoplankton taxa identified in each of the twenty lakes varied between 83 in Wastwater and 159 in the North Basin of Windermere. Across the lakes there was a significant positive relationship between total taxon number and the natural log of the concentration of total phosphorus (Table 1). Consistent with phosphorus being the overall limiting nutrient in these lakes (Maberly et al. 2016), there was also a similar strong positive relationship with the natural log of the concentration of chlorophyll a and also alkalinity. Alkalinity was strongly correlated with both log TP and log chlorophyll a (adjusted R^2 values of 0.66 and 0.65 respectively). When a stepwise regression was performed on these data with backward elimination (that gave slightly higher adjusted R^2 values than the other options), lake area and the natural log of chlorophyll a were retained as variables that explained the total taxon number at each lake (Table 1).

Table 1. Relationship between total number of taxa and lake characteristic for the 20 lakes for individual variables (in order of decreasing P value) and following a stepwise regression with backward elimination. Standard errors are given in parentheses.

Variable	Regression equation	Adj R^2	P
Stratification (S, temperature difference, °C)	y = 114.6 (28.1) + 1.00 (2.31)S	0.00	0.67
Volume (V, Mm^3)	y = 124.8 (5.8) + 0.032 (0.067)V	0.00	0.64
Area (A, km^2)	y = 120.2 (6.3) + 2.15 (1.54)A	0.05	0.18
Mean depth (D, m)	y = 136.8 (7.5) −0.71 (0.43)D	0.08	0.12
Natural log [TP] (P, ln mg m^{-3})	y = 112.9 (7.0) + 0.88 (0.38)P	0.19	0.03
Natural log Chl a (C, ln mg m^{-3})	y = 113.0 (5.8) + 1.68 (0.57)C	0.29	0.008
Alkalinity (K, mequiv m^{-3})	y = 106.3 (6.7) + 0.10 (0.03)K	0.37	0.003
Stepwise regression	y = 89 (6) + 3.0 (0.9)A + 17 (3)C	0.71	0.000

The taxon number changed seasonally in the 20 lakes. Total taxon number was lowest in winter (all lakes) and highest in summer (12 lakes) or autumn (8 lakes) (Fig. 1A). The ratio of the maximum number of taxa to the minimum number of taxa (y), representing the magnitude of seasonal variability, increased with the concentration of total phosphorus (x): (y = 1.43 (0.11) + 0.025 (0.006)x, adjusted
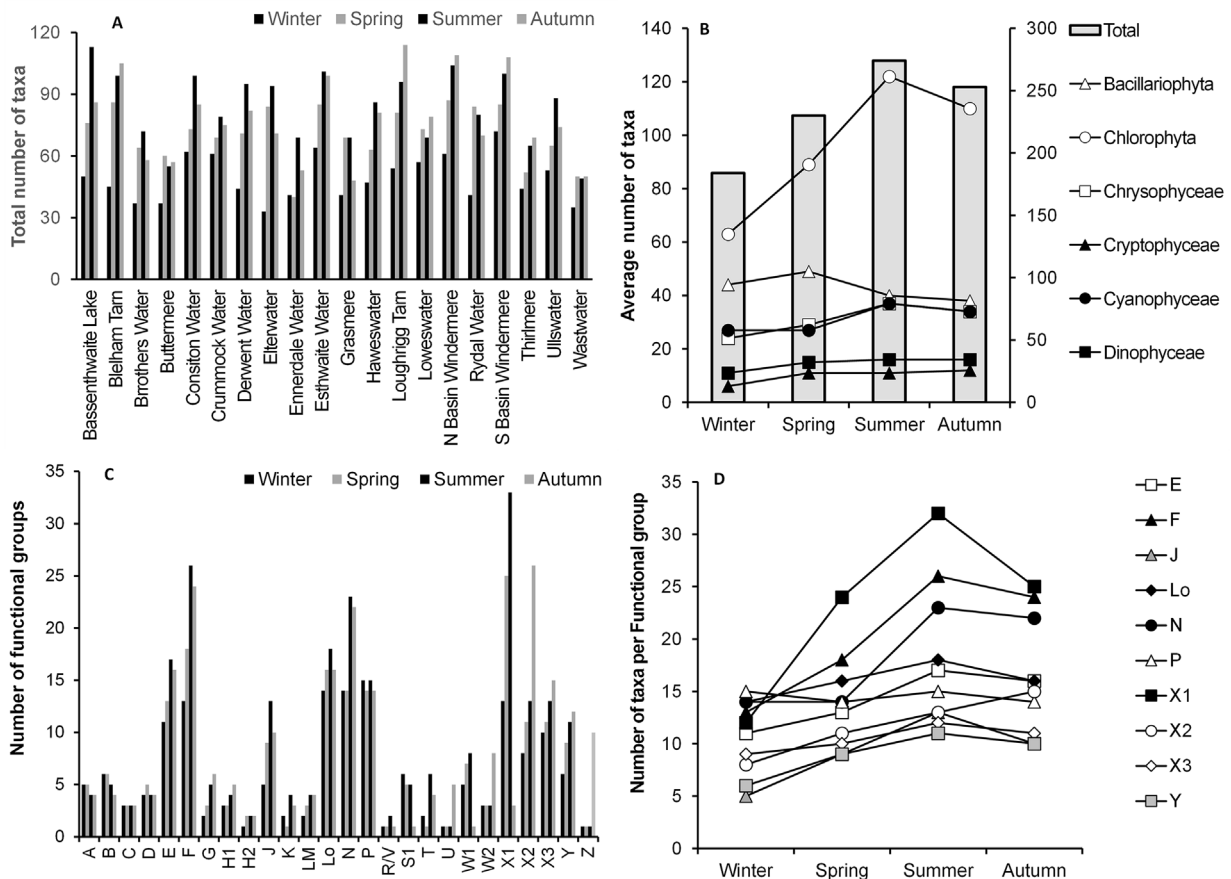
Figure 1. Seasonal changes in total phytoplankton taxon number and number per phylogenetic and functional group in twenty lakes sampled four times each year in six years (1991 to 2015). (**A**) Total number of recorded taxa. (**B**) Average number of taxa per phylogenetic group and average taxon numbers (columns). (**C**) Total number of taxa per functional group. (**D**) Average numbers of taxa for the ten most abundant functional groups, following Reynolds et al. (2002).

$R^2 = 0.46$, P < 0.001, SE in parentheses). There were similar, but less strong, relationships between the normalised numbers of taxa (y) and the concentration of chlorophyll a (x); (y = 1.54 (0.11) + 0.035 (0.011)x, adjusted $R^2 = 0.33$, P < 0.01) but the correlation with the strength of summer stratification was not significant (P > 0.05). However, when the seasonal change in taxon number was expressed as the ratio of the maximum to the minimum calculated as a percentage of the maximum number, there was only a weak significant relationship with lake area (P = 0.04, Table 2) but no other single variable was significant. A backwards elimination stepwise regression produced a significant relationship with positive effects of the natural log of total phosphorus and negative effects of lake area and the concentration of chlorophyll a (Table 2). These analyses suggest that there is a relatively small effect of lake characteristics (Supplementary Table S1) on the seasonal magnitude of phytoplankton taxon richness.

On average across the 20 lakes, taxon number was highest in summer, and the Chlorophyta was the dominant group (Fig. 1B). Twenty-seven of the thirty-one functional groups of Reynolds et al. (2002) were recorded. The absent groups were M, R, S_N and S2, although the lack of identification to species might have prevented unambiguous classification for some taxa. There were seasonal changes in the abundance of different functional groups (Fig. 1C, D). Summer communities were dominated by taxa in genera from Groups X1 (habitat template from Padisak et al. (2009): shallow, eu-hypertrophic environments) such as *Ankyra*, *Chlamydomonas*, *Chlorella*, *Crucigenia* and *Monoraphidium*), group F (habitat template: clear, deeply mixed meso-

eutrophic lakes) such as *Botryococcus*, *Coenochloris*, *Dictyosphaerium*, *Elakatothrix*, *Oocystis*, *Paulschulzia* and *Pseudosphaerocystis*), group N (habitat template: continuous or semi-continuous mixed layer of 2–3 m in thickness) such as *Coenocystis*, *Cosmarium*, *Staurodesmus* and *Tabellaria*) and group L_o (habitat template: deep and shallow, oligotrophic to eutrophic, medium to large lakes) such as *Gymnodinium*, *Peridinium*, *Snowella* and *Woronichinia*. Notably, many of these genera are from the Chlorophyta, corresponding to the phylogenetic analysis.
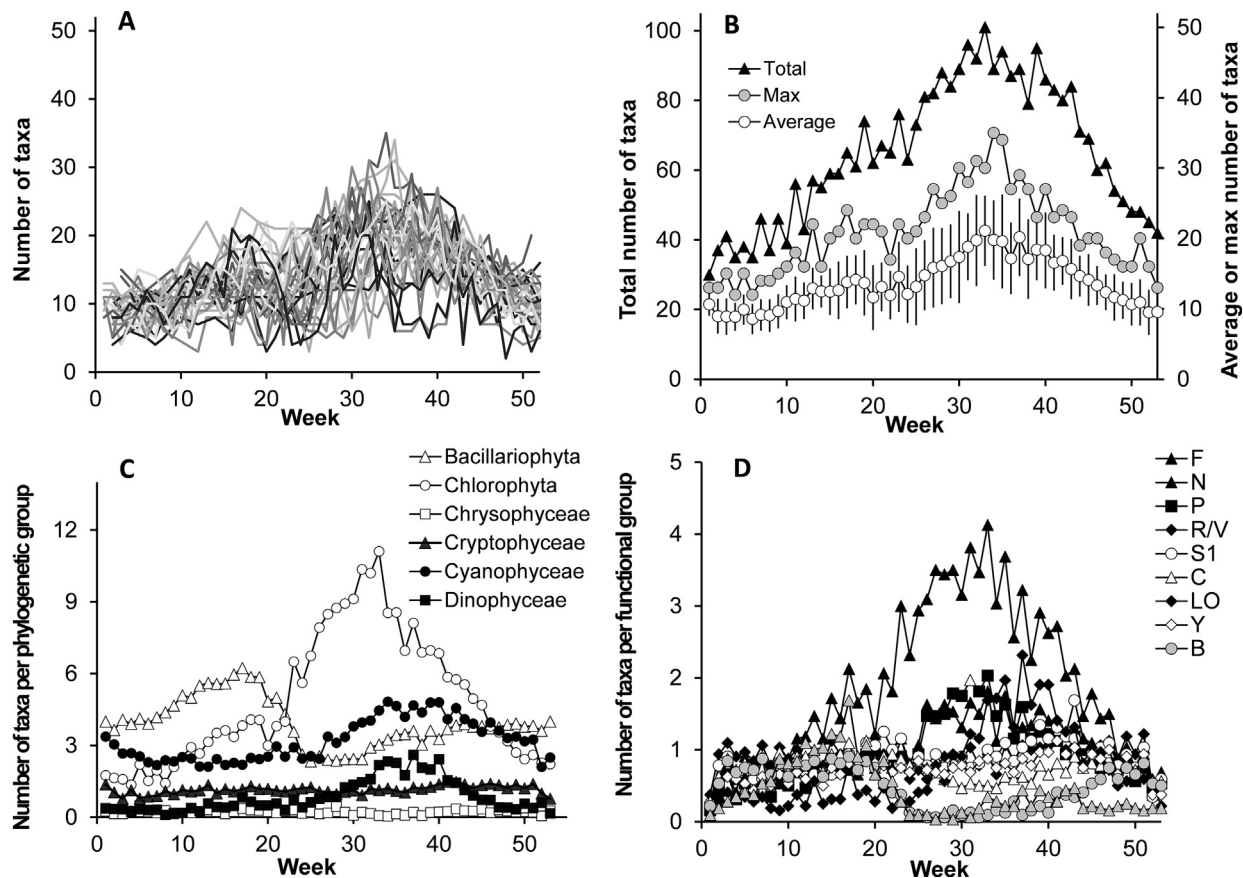
Weekly Numbers of Phytoplankton Taxa in the South Basin of Windermere (1945 to 1977)

In order to investigate seasonal patterns at a near-weekly resolution, based on phytoplankton taxa that had been identified consistently, taxon richness was analysed for the South Basin of Windermere (basin details in Supplementary Material Table S1, Maberly et al. 2016; Talling 1999). A total of 165 taxa were recorded, of which 118 were identified at least to species and 47 were identified to genus. There was a large year-to-year variation in the number of taxa in a particular week (Fig. 2A), but a strong underlying pattern (Fig. 2B). The average seasonal pattern of taxon richness, was consistent with the pattern seen in the seasonal data from the Lakes Tour at lower temporal resolution. Taxon richness was at a minimum at the start and end of the year and at a maximum in weeks 33 or 34, for the average, maximum and total number of taxa. (Fig. 2B). In week 33, a total of 101 different taxa were recorded over 33 years, which represents 61% of the 165 taxa of phytoplankton recorded at this site (Finlay et al. 2002). On average, only 21 taxa were

Table 2. Relationship between the magnitude of seasonal change in taxon number (expressed as the ratio of the seasonal maximum to the minimum number of taxa as a percentage of the maximum) and lake characteristics for the 20 lakes for individual variables (in order of decreasing P value) and following a stepwise regression with backward elimination. Standard errors are given in parentheses.

| Variable	Regression equation	Adj R^2	P
Mean depth (D, m)	y = 2.22 (0.20) − 0.006 (0.011)D	0.00	0.63
Stratification (S, temperature difference, °C)	y = 2.50 (0.69) − 0.03 (0.06)S	0.00	0.60
Natural log [TP] (P, ln mg m^{-3})	y = 2.41 (0.44) − 0.11 (0.17)P	0.00	0.53
Area (A, km^2)	y = 2.38 (0.14) − 0.08 (0.04)A	0.17	0.04
Natural log Chl a (C, ln mg m^{-3})	y = 2.43 (0.22) − 0.16 (0.11)C	0.06	0.16
Alkalinity (K, mequiv m^{-3})	y = 2.42 (0.20) − 0.001 (0.000)K	0.08	0.12
Volume (Mm^3)	y = 2.29 (0.13) − 0.003 (0.002)V	0.09	0.10
Stepwise regression	y = 1.42 (0.64) − 0.07 (0.03)A + 0.91 (0.41)P − 0.80 (0.28)C	0.44	0.006

Figure 2. Weekly changes in total phytoplankton numbers of taxa, and taxa per phylogenetic or functional group in the South Basin of Windermere (1945–1977). (**A**) Number of taxa for each year. (**B**) Taxon numbers: total (▲, left-hand axis), maximum (●, right-hand axis) average (○, right-hand axis), with error bars showing one standard deviation. (**C**) Average number of taxa per phylogenetic group. (**D**) Average number of taxa for the ten most abundant functional group, following Reynolds et al. (2002).

present in week 33, representing 13% of the total recorded taxa and the maximum number, in week 34, 35 taxa, represents 21% of the total. The seasonal pattern for the three different measures of taxon number were highly correlated, with Pearson's correlation coefficients between 0.91 and 0.95.

Relationship Between Phytoplankton Taxon Richness and Abundance

Since there was a seasonal variation in phytoplankton abundance (Supplementary Material Fig. S1), we checked the reliability of our observed data in representing taxon richness using the analytical methods described by Chao and Jost (2012) for the more detailed data from Windermere. The estimated coverage (a measure of sample completeness) varied between 0.89 and 0.97. Apart from lower coverage in the first week and the last two

weeks; the overall average was 0.93 (Fig. 3A). Q1, the number of taxa that were only detected on one occasion for a particular week over the 33 years, varied between 9 and 32 indicating that there were undetected taxa in every week. However Q1 increased roughly in proportion to taxon richness so that the quotient of Q1 to the observed number of taxa was relatively constant over the weeks. Apart from week 1, the number of sampling days with data (sampling units) was between 18 and 31. Estimated taxon richness for 20 and 40 sampling units followed a very similar seasonal pattern to the observed data (Fig. 3B). Similarly, the more meaningful estimate of taxon richness based on sample completeness (coverage, Chao and Jost 2012) also showed very similar seasonal patterns to the observed data (Fig. 3C). The validity of the observed data is further shown in Supplementary Material Figure S2. Based on monthly data (to increase stability in data and to clarify the resulting plots), we plot the rarefaction
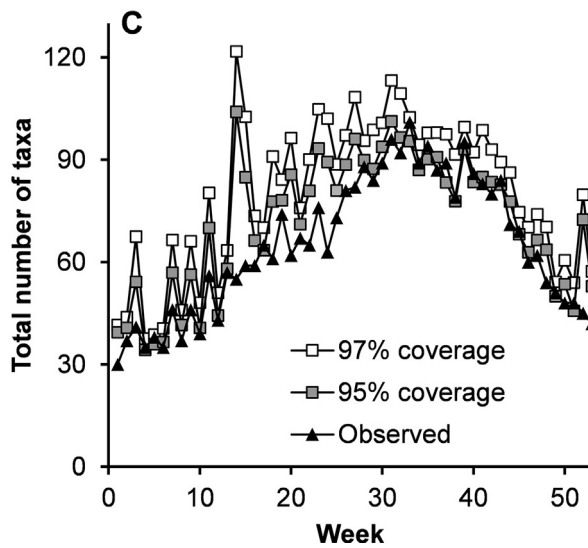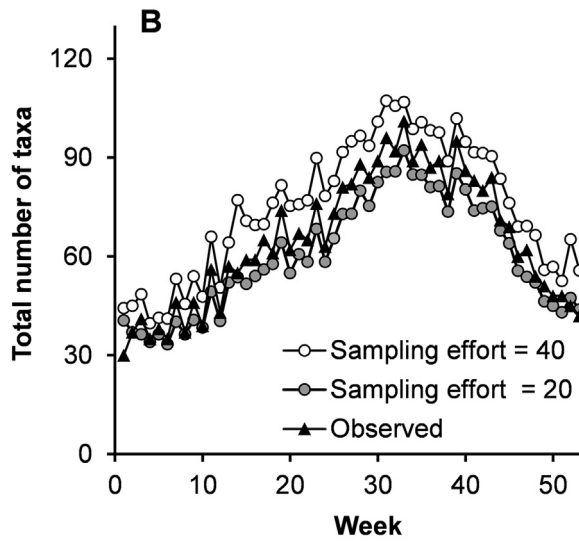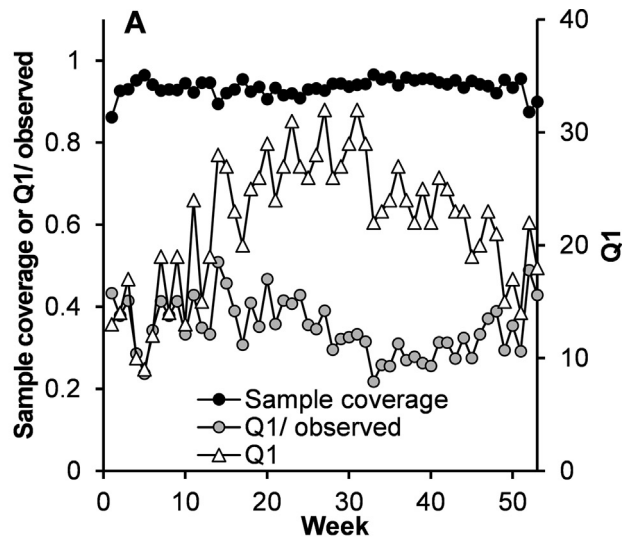
and extrapolation sampling curves (Supplementary Material Fig. S3), where standardized richness estimates are depicted for a continuum of sampling effort and sample coverage. The sampling curves show that taxon richness in summer and autumn (months 6, 7, 8, 9, 10 in figures) is higher than the other months. Moreover, seasonal patterns for abundant taxa and dominant taxa follow generally consistent patterns.

There were highly significant correlations between estimates of taxon richness and the observed taxon number (x). For example, for a sampling effort of 40 (y): y = 9.36 (1.78) + 1.01 (0.03)x, adjusted R^2 = 0.97, P < 0.001). A coverage of 97% =19.53 (5.88) + 0.93 (0.09)x, adjusted R^2 = 0.69, P < 0.001. In weeks 14 and 15, the observed taxon richness was markedly lower than estimates based on coverage (Fig. 3C). This may be a result of the relatively low sample coverage, in week 14, in particular, and relatively many undetected species. This is the period when the dominant species in Windermere, *Asterionella formosa* Hass. (Finlay et al. 2002) is increasing in numbers rapidly (Maberly et al. 1994), possibly masking the presence of rare species. The regressions showed that both measures of estimated richness had a slope close to one so seasonal patterns of observed taxon richness will be closely related to the 'true' values; the positive intercept results from the taxa that were undetected. Among the total number of 1336 sampling days over 33 years, 12 taxa were only detected on one day, and 13 taxa were only detected on two days. Based on the Chao2 formula (Chao 1987), the minimum number of undetected taxa is at least (12 × 12)/(2 × 13) = 5.5.

Seasonal Changes in Composition of Phytoplankton Taxa and Functional Groups in the South Basin of Windermere (1945 to 1977)

As seen for the 20 lakes in the Lakes Tour, the summer phytoplankton in the South Basin of Windermere were dominated numerically by taxa from the Chlorophyta (Fig. 2C). The summer peak of taxon number was the result of large numbers of functional groups F (habitat template: clear, deeply mixed meso-eutrophic lakes) comprising species from the genera *Dictyosphaerium, Elakatothrix, Gemellicystis, Paulschulzia, Radiococcus* and *Sphaerocystis*), N (habitat template: continuous or semi-continuous mixed layer of 2–3 m in thickness) comprising species from the genera *Coelastrum, Coenococcus, Staurastrum* and *Tabellaria* and P (habitat template: similar to that of codon N but at higher trophic states) comprising species from genera such as *Closterium, Fragilaria, Spondylosium* and *Staurastrum*; Fig. 2D). These summer dominant functional groups are similar to those from the 20 lakes in the Lakes Tour except that functional group X1 was a less important component in Windermere.

There were strong correlations between total, maximum and average taxon numbers and the seasonal pattern of surface water temperature (Fig. 4A) and the strength of stratification (Fig. 4B) which is related to surface temperature, as this is the main cause of the temperature difference between the surface and water at depth (Supplementary Material Fig. S1). Regressions of average taxon number (x) against daylength as a proportion of 24 hours (x) were significant (x = 7.15 (1.55) + 12.75 (2.92)x, adjusted R^2 = 0.26, P < 0.001), but much weaker than against either temperature or stratification. The average number of taxa per week was correlated positively (r = 0.296) with the density of zooplankton, but the relationship was not statistically significant.

The average number of functional groups in each week (y) was correlated with the numbers of taxa (x) (y = 5.17 (0.28) + 0.35 (0.02)x, adjusted R^2 = 0.86, P < 0.001) (Fig. 5A). The average number of taxa per functional group (y) each week was slightly more highly correlated to the number of taxa (x) (y = 0.69 (0.04) + 0.05 (0.003)x, adjusted R^2 = 0.87, P < 0.001). The number of taxa, number of functional groups and number of taxa per functional group all increased significantly with water temperature (Fig. 5B). The turnover of taxon richness (x) and turnover of functional group richness (y) were also correlated (Fig. 5C; y = 2.45 (0.17) + 0.16 (0.02)x,

Figure 3. Seasonal patterns of taxon richness controlling for abundance and coverage. (**A**) Seasonal changes in sample coverage, Q1, the number of taxa that were detected in only one sampling unit and the quotient of Q1 to observed richness. (**B**) Total number of taxa per week from observation and estimated from a sampling effort of 20 and 40 sampling units. (**C**) Total number of taxa per week from observation and estimated from a coverage of 95% and 97%.
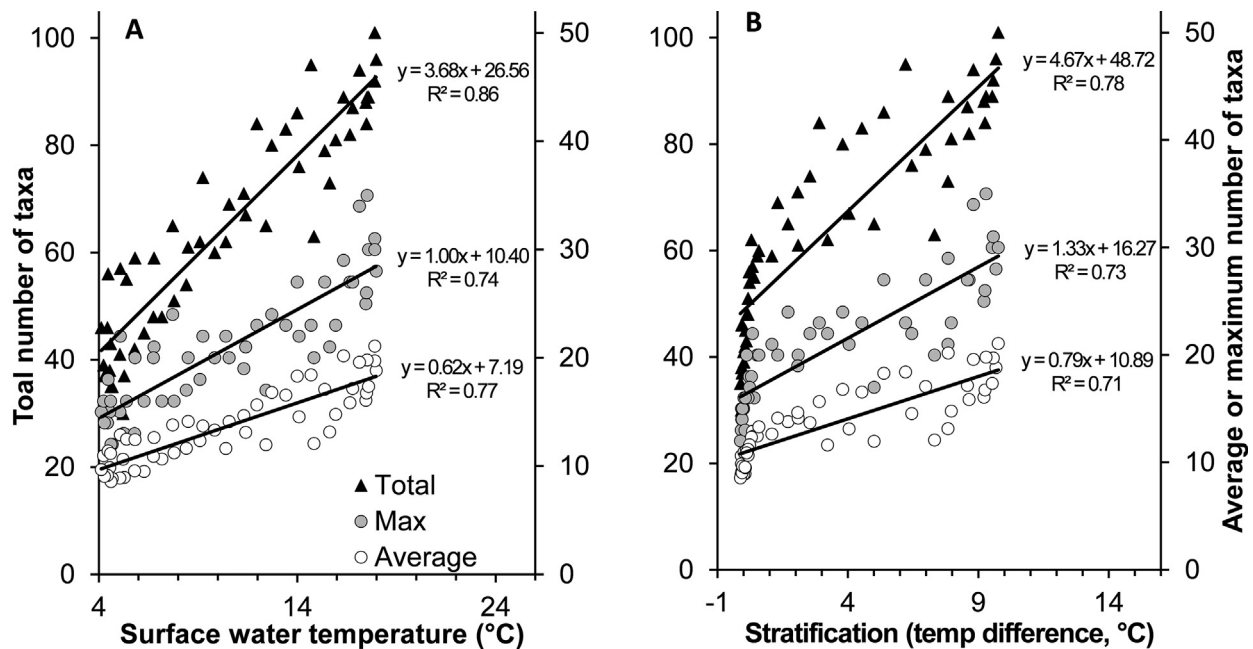
Figure 4. Relationships between taxon number and physical factors in the South Basin of Windermere (1945 to 1977). (**A**) Correlations between taxon number and surface water temperature. (**B**) correlations between taxon numbers and strength of stratification. Total number (▲, left-hand axis), maximum number (●, right-hand axis) average number of taxa (○, right-hand axis). All regressions are significant at P < 0.001.

adjusted R^2 = 0.61, P < 0.001). Turnover of the richness of taxa and functional groups increased significantly with water temperature (Fig. 5D).

In the South Basin of Windermere, phytoplankton chlorophyll *a* data overlapped with the species data analysed here between 1964 and 1977 (Talling 1993). Restricting the data to this time period, the total, maximum and average number of taxa increased significantly with the concentration of chlorophyll *a* (Fig. 6A). Average taxon number per concentration of chlorophyll *a* was greatest at low concentrations of chlorophyll *a* and this ratio declined with increasing concentration of chlorophyll *a* (Fig. 6B). The Lakes Tour sites showed a similar response as an annual mean among lakes and a seasonal mean for the 20 lakes. Given the evidence for a lack of effect of abundance on the number of taxa observed, this relationship appears to be real. A power regression was the best fit to the data from Windermere, while a logarithmic response was the best fit for the 20 lakes. The Lakes Tour sites had a greater number of taxa for a given concentration of chlorophyll *a* than the South Basin of Windermere. The reason is unclear and is likely to be caused partly by the exclusion of nanoplankton from the Windermere data but possibly also to changes, such as increased eutrophication, warming and food

web alteration that have occurred in the 38 years gap between the data from the South Basin of Windermere (1964 to 1977) and the Lakes Tour (1991 to 2015). Even in the period between 1945 and 1977, there was a statistically significant increase in total taxon number of 0.356 taxa per year in Windermere that did not appear to be linked to taxonomic acuity (data not shown).

Discussion

Reliability of Observed Species Richness in Representing True Richness

The meaning of species richness is intuitive and easily interpreted, but can be affected by effects of abundance and sampling effort (Cermeno and Falkowski 2009; Gotelli and Colwell 2001). Using the more detailed data from Windermere, we showed that the observed richness estimates were very similar to estimates that controlled for abundance and coverage. We did not make similar estimates for the less detailed data from the Lakes Tour, but the overall agreement between the seasonal patterns in this dataset and Windermere suggests that they are reliable, particularly since the number of identified data from the South Basin of
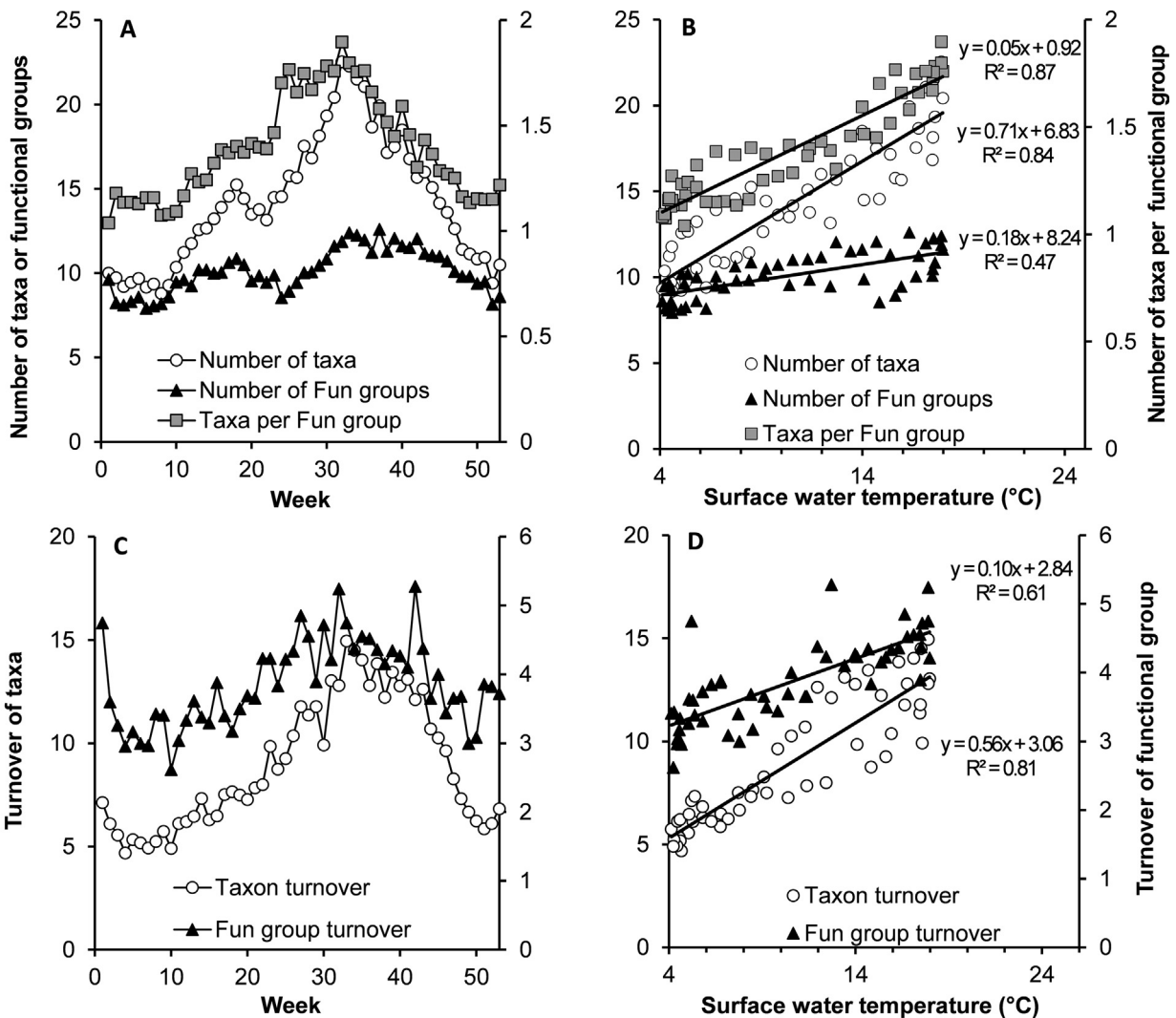
Figure 5. Weekly changes in number and turnover of taxon richness and functional groups in the South Basin of Windermere (1945 to 1977). (**A**) Weekly changes in functional groups and taxa per functional group with average taxon number for comparison. (**B**) Relationships with surface water temperature for numbers of taxa, functional groups and taxa per functional group. (**C**) Weekly changes in turnover of taxa and functional groups. (**D**) Relationships with surface water temperature.

Windermere from the Lakes Tour was only slightly lower than for the detailed dataset (153 vs 165). Finlay (Finlay 2002; Finlay and Clarke 1999) argued that for microbes the large number of propagules, relative ease of dispersal and rapid growth will mean that the environment selects which species are abundant in a given environment to a much greater extent than for other types of organism. The corollary to this argument is that many more than the 165 identified taxa in Windermere will potentially be present but at extremely low densities and possibly in resting stages that are not in the open water and may emerge if suitable conditions arise. In addition, these data are based on morpho-species and

genetic analysis would undoubtedly uncover even greater diversity. The Lakes Tour data recorded 348 taxa, a measure of the gamma-diversity of large non-acidic lakes in the region. Of these, 268 taxa were present in seven lakes within the Windermere catchment and so are likely to be present in the South Basin of Windermere given their hydrological connectance.

Variations in Seasonal Taxon Richness Among Lakes

The primary purpose of this analysis was to compare seasonal taxon richness across lakes of differ-
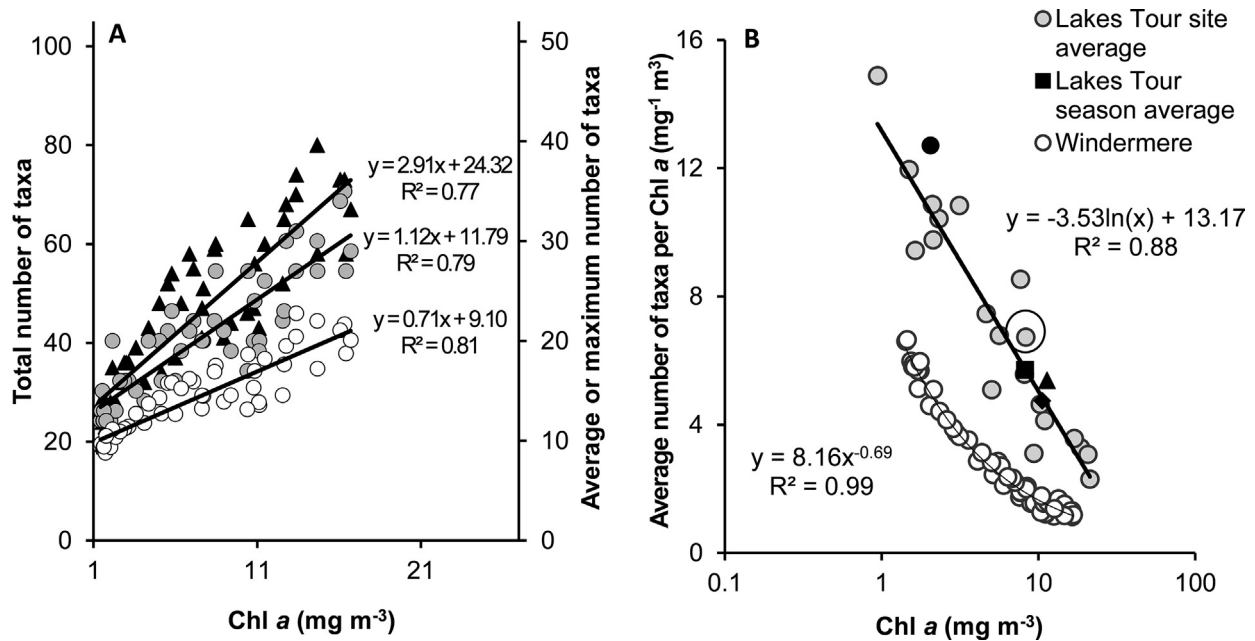
Figure 6. Taxon richness and concentration of chlorophyll *a* (1964 to 1977). (**A**) Taxon number from the South Basin of Windermere and the ratio of concentration of chlorophyll *a* to total number (▲, left-hand axis), maximum number (●, right-hand axis) average number of taxa (○, right-hand axis). (**B**) Average taxon number per concentration of chlorophyll *a vs* concentration of chlorophyll *a* (on a log scale) for weekly averages for the South Basin of Windermere (○) with power regression, annual site averages for the Lakes Tour lakes (●) with logarithmic regression and superimposed season averages (closed symbols: ●, winter; ◆, spring; , summer and ■, autumn). The large circle shows the data for the South Basin of Windermere from the Lakes Tour. All regressions are significant at P < 0.001.

ent type. Additionally, patterns of total species richness were briefly compared among lakes. The 20 lakes in the Lakes Tour experience a similar climate but have very different morphometries and productivities but nevertheless had similar seasonal patterns of taxon richness. The link between nutrient availability and species richness in fresh waters (Interlandi and Kilham 2001; Ptacnik et al. 2010a; Stomp et al. 2011) at least at low nutrient availability, was also found here for the comparison of the 20 lakes. The published positive, but non-monotonic relationship between species richness and lake area (Stomp et al. 2011; Várbíró et al. 2017) contrasts with this study where there was no significant effect of lake area, albeit with only 20 lakes from one region and with a 120-fold variation in area. Meanwhile, the magnitude of seasonal variation in taxon number, normalised by the seasonal maximum number of taxa recorded, was not related significantly related to any of the investigated lake characteristics.

Seasonal Taxon Richness and Spatial Variation in Conditions

Variations in conditions with depth have been suggested to allow more species to co-exist than expected from competition theory. Light always declines with depth but stratification increases the underwater light availability for phytoplankton, by reducing mixing depth, and produces niches for varying physical, chemical and biological characteristics at different depths (Beisner and Longhi 2013; Finlay et al. 1997; Finlay and Esteban 1998). Although there were correlations between taxon richness and strength of stratification in Windermere, this was weaker than the relationship with surface temperature. Also, it does not appear to be directly linked to the seasonal pattern of taxon richness since the same pattern occurs in Bassenthwaite Lake that is weakly stratified and polymictic, unlike the other nineteen lakes, and there was no significant relationship between the normalised ratio

of the seasonal maximum to minimum number of species and strength of stratification. Furthermore, samples were collected from the epilimnion and thus represent a relatively uniform environment since the depth of the summer thermocline in the South Basin of Windermere at least, is usually below 10 m and averaged 12.9 m between weeks 22 and 46. It is possible, however, that even weak or intermittent stratification produces sufficient diversity of conditions over depth to support increased phytoplankton richness. Sub-surface chlorophyll maxima are widespread in lakes (Longhi and Beisner 2009). Species with flagellae can actively select particular depth zones if the rate of water movement does not exceed their swimming speed (Clegg et al. 2007) and cyanobacteria with gas vesicles can regulate their depth and form metalimnetic populations (Pomati et al. 2017). However, many of the summer dominant functional groups identified here comprise non-motile species. For example, of the 31 genera specifically mentioned as summer dominants in the two datasets, only three possess flagellae in their vegetative stages (*Chlamydomonas*, *Gymnodinium*, *Peridinium*) and one possesses gas vesicles (*Woronichinia*). This suggests that exploiting the different conditions at depth is not the primary cause of high summer taxon richness.

Seasonal Diversity, Temperature and Turnover of Richness and Functional Groups

The similar seasonal patterns of high taxon richness in the summer and autumn, in all lakes, suggests that seasonal taxon richness is controlled by factors linked directly to seasonal weather or indirectly to the evolution of conditions during the growing season. The decline in taxon diversity with latitude is ubiquitous across different groups of organisms and strongly linked to a positive response to temperature (Allen et al. 2002; Hillebrand 2004; Stomp et al. 2011). For aquatic organisms, for example, diversity declined with latitude for ocean foraminfera (Rutherford et al. 1999) and copepods (Rombouts et al. 2009) and this was associated with declining surface temperature. Marine phytoplankton may (Righetti et al. 2019) or may not (Rodríguez-Ramos et al. 2015) also show this pattern. These significant relationships with temperature were attributed to increased vertical niche-differentiation during stratification which is more marked in regions with higher surface temperature or to effects of temperature, at longer time scales, on rates of speciation or extinc-

tion (Allen et al. 2002; Allen and Gillooly 2006). Similarly to these spatial studies, our temporal study on Windermere also found an increase in taxon richness with seasonal temperature. This did not appear to be caused by exploitation of vertical niches, as discussed above. Instead, we interpret the seasonal relationship with water temperature to be linked, at least in part, to the temporal dynamics of the phytoplankton population and niche-assembly. Turnover of taxa richness, measured here simply as the number of species that have appeared or disappeared from one sampling date to the next, increased seasonally in a similar way to species number and consequently there was a high correlation between the two features. The pattern of this measure agreed well with turnover calculated using Jaccard's and Sorensen's indices as implemented by Baselga and Orme (2012) (Supplementary Material Fig. S4). The data indicate that increasing temperature increases the rate of species turnover of richness, in an analogous way to turnover based on speciation and extinction over longer time periods. Turnover of richness, calculated from Jaccard dissimilarity turnover, was implicated in latitudinal variation in marine phytoplankton diversity (Righetti et al. 2019) but here the opposite pattern was found: high species richness was associated with a low species turnover. This difference is perhaps the result of the different nature of the data: near-weekly temporal patterns here and one degree spatial patterns in the marine example. Clearly, more work is required to investigate the causes and implications of this, however temporal turnover appears to be an important mechanism that affects species diversity and ecosystem function (Magurran and Henderson 2010).

Functional and Taxonomic Groups

Phytoplankton functional groups, can provide more powerful insights into ecosystem functioning than taxonomic groups (Borics et al. 2021). The reason for the predominance of groups F, P, N, X1, and Lo in the summer is unclear. Summer dominant in other lakes may differ. For example in large, shallow, sub-tropical Lake Okeechobee in Florida, different functional groups were present in winter and summer (Ma et al. 2022). The dominant groups, H1, J, X2 and Y in the two seasons differed from the dominant groups reported here which is perhaps not surprising given the large differences in area, depth, nutrient content and climate between Okeechobee and the lakes studied here.

In Windermere, for functional group F in particular, the relatively large colonies of green algae may not be easily filtered by zooplankton and this group starts to dominate just after the early summer peak in zooplankton (Supplementary Material Fig. S1). Different phylogenetic groups also have a different stoichiometric requirement for mineral resources. Chlorophyta have a lower requirement for phosphorus on a carbon basis than Dinophyceae and Bacillariophyta (Quigg et al. 2003) that might provide them with an ecological advantage during summer phosphate depletion. Temperature can also affect algal stoichiometry (Yvon-Durocher et al. 2015). Stoichiometry, however, does not explain why the number of taxa per functional group increases in the summer.

Abundance

The positive relationship between the number of plant species or functional groups and the biomass of terrestrial plants (e.g. Loreau et al. 2001) is analagous to the strong increase in number of taxa and the concentration of chlorophyll *a* reported here. However it is an open question as to whether abundance or diversity is driving the relationship (Gross and Cardinale 2007). The strong decrease in numbers of taxa per unit chlorophyll *a* as the concentration of chlorophyll *a* increases might suggest that competition for resources is greatest during the summer, but it might also reflect complementarity between taxa in supporting phytoplankton biomass (Ptacnik et al. 2010b). Experiments and process-based models are needed to disentangle these factors.

Conclusions

Despite their different characteristics, a consistently greater number of phytoplankton taxa were present in the summer than at other times of the year in the twenty lakes. The extensive, long-term dataset for Windermere resulted in the observed seasonal changes in richness to be a close representation of true richness. The temporal changes were linked positively to surface water temperature but not obviously to stratification and vertical niche separation. Instead, taxon number was correlated with high rates of turnover and temperature. In the summer, the Chlorophyta and specific functional groups were dominant. The number of species per functional group was larger in the summer and contributed to the high number of summer taxa. In contrast, the

number of taxa contributing to a given concentration of chlorophyll *a* was lowest in the summer, possibly reflecting competition for resources but also perhaps complementarity.

Methods

Study sites and water collection: The lakes of the English Lake District in North West England, UK, are among the best studied in the world. They comprise numerous small and larger lakes with very different physical and chemical properties (Fryer 1991). Twenty of these have been studied seasonally, at roughly-five-year intervals, in the so-called 'Lakes Tour' (Kadiri and Reynolds 1993). The lakes data from the Lakes Tour used here derive from Winter (January), Spring (April), Summer (July) and Autumn (October) in 1995, 2000, 2005, 2010 and 2015. In 1991, the winter samples were also collected in February at two sites and early March at two sites and in summer, only one site was sampled in July, the remainder being sampled in early to mid August. Water was collected at the deepest point using an integrated water sampler to a depth of 5 m (apart from the two basins of Windermere, 0–7 m) at the deepest point on each lake. One of these lakes, the South Basin of Windermere, has been the subject of an intensive, ongoing monitoring programme since 1945 (Pickering 2001). The main limnological features of the lake are described in Talling (Talling 1999). Here, water samples were collected approximately weekly (on average 40 samples per year) between 28 February 1945 and 20 December 1977 at the deepest point using a sampling tube that integrated water from the top 0–5 m (1945–1962), 0–10 m (1962–1964) and 0–7 m (1964 onwards) (Heaney et al. 1988).

Analyses: Phytoplankton samples were preserved in Lugol's iodine in the field and a 300 mL sample was concentrated by sedimentation to 5 mL before analysis. For the samples from the Lakes Tour, a sub-volume was transferred to a counting chamber and the algae were identified and enumerated as described by Lund (Lund 1959). Microplankton and nanoplankton were counted at x100 magnification and x400 magnification respectively. Counts were made by several different people over the years. At the South Basin of Windermere, samples were collected and prepared in the same way but all counts were made by J.W.G. Lund, personally or under his close supervision, making the database unusually coherent. In the early years phytoplankton were identified and enumerated using the (Utermöhl 1931) method but from 1965 onwards the counting slide described above was used. This allowed nanoplankton to be identified and quantified: these taxa were removed from the analysis as these data were not available over the whole time-period. On some dates only certain taxa, typically diatoms, were counted and these data were also removed from the analysis. With both counting methods, typically a number of fields equivalent to producing 100 counts for each taxon were enumerated.

Based on sampling data, observed counts of taxa typically underestimate true taxon richness and strongly depend on sampling effort and sample completeness. To remove or control for a sampling effect, we used a non-asymptotic approach to compare taxon richness via rarefaction and extrapolation on the basis of standardized sampling effort or sample coverage (an objective measure of sample completeness). Sample coverage is defined as the fraction of individuals (for abundance data) or incidences (for detection/non-detection data) in the entire assemblage that belong to detected taxa. This measure can be very efficiently estimated directly from sampling data. The concept of sample coverage was originally developed by Alan Turing and I. J. Good in their cryptographic analysis during World War II. Sample-effort-based standardization represents the traditional comparative approach in ecology. Chao

and Jost (2012, their table 1) showed that traditional richness estimates for samples with a standardized size generally results in the compression of the magnitude of differences in richness among assemblages. Chao and Jost (2012) advocated the use of sample-coverage-based standardization to compare unbiased taxon richness estimates based on equally complete samples.

Taxa were classified into phylogenetic groups using the phylogeny in AlgaeBase (Guiry 2022) and also into functional groups following Reynolds et al. (2002). Other types of character-based phytoplankton functional groups- (Kruk et al. 2011; Salmaso and Padisák 2007) and functional traits (Litchman and Klausmeier 2008) are available. The original Reynolds classification, not updated with the refinements of (Padisak et al. 2009), was used for the practical reasons that an extensive list of taxa matched to functional groups were available thanks to the work of the late Colin Reynolds with the first author. Less than 8% of taxa were unable to be classified to a functional group, which was largely because of a lack of taxonomic resolution or because taxa were judged not to be primarily planktonic.

Concurrent with the collection of the phytoplankton samples, temperature depth-profiles were measured with a thermistor. Stratification strength was quantified here as the difference in temperature between the water at the surface and the bottom of the lake (about 40 m). The depth-integrated water samples were analysed for total phosphorus (TP) and alkalinity following (Mackereth et al. 1989). After filtering, phytoplankton chlorophyll *a* was extracted in boiling methanol and measured spectrophotometrically (Talling 1974). Data were available from 1964. The number of zooplankton on the filter papers were counted and converted to density using the volume of water filtered. Data were available from 1968.

Turnover of phytoplankton taxa richness in the South Basin of Windermere was calculated from the number of taxa on each sample date that had either appeared or disappeared between two adjacent sampling dates. These were then averaged for each week over the 33 years. Turnover of each functional group was calculated in the same way. Taxon richness turnover was also calculated following Baselga and Orme (2012).

Statistics: Stepwise regressions were performed in Minitab 21.2 (64-bit). The R package iNEXT (interpolation/extrapolation) from CRAN (cran.r-project.org), and software (iNEXT-online available at https://chao.shinyapps.io/iNEXTOnline/) were used to make all computations and graphics.

Author Contributions

SCM and BJF initiated the work, SCM and AC performed the analyses and wrote the manuscript.

Conflict of Interest Statement

The authors declare that there are no conflicts on interest connected with this work.

Data availability

Data will be made available on request.

Acknowledgements

Funding

Appendix A. Supplementary Material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.protis.2022.125925.

References

Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science **297**:1545–1548

Allen AP, Gillooly JF (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecol Lett **9**:947–954

Baselga A, Orme CDL (2012) betapart : an R package for the study of beta diversity: *Betapart package*. Methods Ecol Evol **3**:808–812

Beisner BE, Longhi ML (2013) Spatial overlap in lake phytoplankton: Relations with environmental factors and consequences for diversity. Limnol Oceanogr **58**:1419–1430

Borics G, Abonyi A, Salmaso N, Ptacnik R (2021) Freshwater phytoplankton diversity: models, drivers and implications for ecosystem properties. Hydrobiologia **848**:53–75

Cermeno P, Falkowski PG (2009) Controls on diatom biogeography in the Ocean. Science **325**:1539–1541

Chao A (1987) Estimating the population size for capture-recapture data with unequal catchability. Biometrics **43**:783

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology **93**:2533–2547

Clegg MR, Maberly SC, Jones RI (2007) Behavioral response as a predictor of seasonal depth distribution and vertical niche separation in freshwater phytoplanktonic flagellates. Limnol Oceanogr **52**:441–455

Descamps-Julien B, Gonzalez A (2005) Stable coexistence in a fluctuating environment: an experimental deomonstration. Ecology **86**:2815–2824

Feuchtmayr H, Pottinger TG, Moore A, De Ville MM, Caillouet L, Carter HT, Pereira MG, Maberly SC (2019) Effects of brownification and warming on algal blooms, metabolism and higher trophic levels in productive shallow lake mesocosms. Sci Total Environ **678**:227–238

Finlay BJ (2002) Global dispersal of free-living microbial eukaryote species. Science **296**:1061–1063

Finlay BJ, Clarke KJ (1999) Ubiquitous dispersal of microbial species. Nature **400**, 828–828.

Finlay BJ, Esteban GF (1998) Planktonic ciliate species diversity as an integral component of ecosystem function in a freshwater pond. Protist **149**:155–165

Finlay BJ, Maberly SC, Cooper JI (1997) Microbial diversity and ecosystem function. Oikos **80**:209–213

Finlay BJ, Monaghan EB, Maberly SC (2002) Hypothesis: The rate and scale of dispersal of freshwater diatom species is a function of their global abundance. Protist **153**:261–273

Fryer G (1991) A Natural History of the Lakes, Tarns and Streams of the English Lake District. Freshwater Biological Association; Ambleside, 368 p

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett **4**:379–391

Gross K, Cardinale BJ (2007) Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. Am Nat **170**:207–220

Guiry MD (2022) AlgaeBase Guiry, M.D. and Guiry, G.M. world-wide electronic publication, National University of Ireland, Galway. http://www,algaebase.org

Gunderson LH (2000) Ecological resilience—in theory and application. Annu Rev Ecol Syst **31**:425–439

Heaney SI, Lund JWG, Canter HM, Gray K (1988) Population dynamics of *Ceratium* spp. in three English lakes, 1945–1985. Hydrobiologia **161**:133–148

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. Am Nat **163**:192–211

Huisman J, Weissing FJ (2002) Oscillations and chaos generated by competition for interactively essential resources: Competitive chaos. Ecol Res **17**:175–181

Hutchinson GE (1961) The paradox of the plankton. Am Nat **95**:137–145

Interlandi SJ, Kilham SS (2001) Limiting resources and the regulation of diversity in phytoplankton communities. Ecology **82**:1270–1282

Kadiri MO, Reynolds CS (1993) Long-term monitoring of the conditions of lakes: the example of the English Lake District. Arch Hydrobiol **129**:157–178

Kléparski L, Beaugrand G, Kirby RR (2022) How do plankton species coexist in an apparently unstructured environment? Biol Lett **18**:20220207

Kruk C, Peeters ETHM, Van Nes EH, Huszar VLM, Costa LS, Scheffer M (2011) Phytoplankton community composition can be predicted best in terms of morphological groups. Limnol Oceanogr **56**:110–118

Litchman E, Klausmeier CA (2008) Trait-based community ecology of phytoplankton. Annu Rev Ecol Evol Syst **39**:615–639

Longhi ML, Beisner BE (2009) Environmental factors controlling the vertical distribution of phytoplankton in lakes. J Plankton Res **31**:1195–1207

Longhi ML, Beisner BE (2010) Patterns in taxonomic and functional diversity of lake phytoplankton: Taxonomic and functional diversity of lake phytoplankton. Freshw Biol **55**:1349–1366

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science **294**:804–808

Lund JWG (1959) A simple counting chamber for nannoplankton. Limnol Oceanogr **4**:57–65

Ma C, Li Z, Mwagona PC, Rabbany A, Bhadha JH (2022) Spatial and seasonal dynamics of phytoplankton groups and its relationship with environmental variables in Lake Okeechobee, USA. J Freshw Ecol **37**:173–187

Maberly SC, Hurley MA, Butterwick C, Corry JE, Heaney SI, Irish AE, Jaworski GHM, Lund JWG, Reynolds CS, Roscoe JV (1994) The rise and fall of *Asterionella formosa* in the South Basin of Windermere - analysis of a 45-year series of data. Freshw Biol **31**:19–34

Maberly SC, De Ville MM, Thackeray SJ, Ciar D, Clarke M, Fletcher JM, James JB, Keenan P, Mackay EB, Patel M, Tanna B, Winfield IJ, Bell K, Clarke R, Jackson A, Muir J, Ramsden P, Thompson J, Titterington H, Webb P (2016) A Survey of the Status of the Lakes of the English Lake District: The 2015 Lakes Tour. (Report to United Utilities No. LA/NEC05369/1), 149 p

Maberly SC, O'Donnell RA, Woolway RI, Cutler MEJ, Gong M, Jones ID, Merchant CJ, Miller CA, Politi E, Scott EM, Thackeray SJ, Tyler AN (2020) Global lake thermal regions shift under climate change. Nat Commun **11**:1232

Mackereth FJH, Heron J, Talling JF (1989) Water analysis: Some revised methods for limnologists, Scientific Publication. Freshwater Biological Association; Titus Wilson, Kendal, 120 p

Magurran AE, Henderson PA (2010) Temporal turnover and the maintenance of diversity in ecological assemblages. Philos Trans R Soc B Biol Sci **365**:3611–3620

Padisak J, Crossetti LO, Naselli-Flores L (2009) Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. Hydrobiologia **621**:1–19

Pickering AD (2001) Windermere: Restoring the Health of England's Largest Lake. Freshwater Biological Association Special Publication No. 11. Titus Wilson, Kendal, 126 p

Pomati F, Matthews B, Seehausen O, Ibelings BW (2017) Eutrophication and climate warming alter spatial (depth) co-occurrence patterns of lake phytoplankton assemblages. Hydrobiologia **787**:375–385

Ptacnik R, Solimini AG, Andersen T, Tamminen T, Brettum P, Lepistö L, Willén E, Rekolainen S (2008) Diversity predicts stability and resource use efficiency in natural phytoplankton communities. Proc Natl Acad Sci USA **105**:5134–5138

Ptacnik R, Andersen T, Brettum P, Lepistö L, Willén E (2010a) Regional species pools control community saturation in lake phytoplankton. Proc R Soc B Biol Sci **277**:3755–3764

Ptacnik R, Moorthi SD, Hillebrand H (2010b) Hutchinson reversed, or why there need to be so many species. Adv Ecol Res **43**:1–43

Quigg A, Finkel ZV, Irwin AJ, Rosenthal Y, Ho TY, Reinfelder JR, Schofield O, Morel FMM, Falkowski PG (2003) The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature **425**:291–294

Reynolds CS (1984) Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshw Biol **14**:111–142

Reynolds CS, Huszar V, Kruk C, Naselli-Flores L, Melo S (2002) Towards a functional classification of the freshwater phytoplankton. J Plankton Res **24**:417–428

Righetti D, Vogt M, Gruber N, Psomas A, Zimmermann NE (2019) Global pattern of phytoplankton diversity driven by temperature and environmental variability. Sci Adv **5**: eaau6253

Rodríguez-Ramos T, Marañón E, Cermeño P (2015) Marine nano- and microphytoplankton diversity: redrawing global patterns from sampling-standardized data: Phytoplankton diversity from sampling-standardized data. Global Ecol Biogeogr **24**:527–538

Rombouts I, Beaugrand G, Ibañez F, Gasparini S, Chiba S, Legendre L (2009) Global latitudinal variations in marine copepod diversity and environmental factors. Proc R Soc B Biol Sci **276**:3053–3062

Rutherford S, D'Hondt S, Prell W (1999) Environmental controls on the geographic distribution of zooplankton diversity. Nature **400**:749–753

Salmaso N, Padisák J (2007) Morpho-functional groups and phytoplankton development in two deep lakes (Lake Garda, Italy and Lake Stechlin, Germany). Hydrobiologia **578**:97–112

Scheffer M, Rinaldi S, Huisman J, Weissing FJ (2003) Why plankton communities have no equilibrium: solutions to the paradox. Hydrobiologia **491**:9–18

Sommer U, Adrian R, De Senerpont DL, Elser JJ, Gaedke U, Ibelings B, Jeppesen E, Lürling M, Molinero JC, Mooij WM, van Donk E, Winder M (2012) Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. Annu Rev Ecol Evol Syst **43**:429–448

Stomp M, Huisman J, Mittelbach GG, Litchman E, Klausmeier CA (2011) Large-scale biodiversity patterns in freshwater phytoplankton. Ecology **92**:2096–2107

Talling JF (1974) Photosynthetic Pigments: General Outline of Spectrophotometric Methods; Specific Procedures. In Vollenweider RA (ed) A Manual on Methods for Measuring Primary Production in Aquatic Ecosystems, IBP Handbook No. 12. Blackwell Scientific Publications; Oxford, pp 22–26

Talling JF (1993) Comparative seasonal changes, and inter-annual variability and stability, in a 26-year record of total phytoplankton biomass in four English lake basins. Hydrobiologia **268**:65–98

Talling JF (ed) Some English Lakes as Diverse and Active Ecosystems: A Factual Summary and Source Book. Freshwater Biological Association; Ambleside, 80 p

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. Annu Rev Ecol Evol Syst **45**:471–493

Tilman D, Pacala S (1993) The Maintenance of Species Richness in Plant Communities. In Schluter D, Ricklefs RE (eds) Species Diversity in Ecological Communities: Historical and Geographical Perspectives. The University of Chicago Press; Chicago IL, pp 13–25

Utermöhl H (1931) Neue Wege in der quantitativen Erfassung des Plankton. (Mit besonderer Berücksichtigung des Ultraplanktons.). Verh Int Ver Limnol **5**:567–595

Várbíró G, Görgényi J, Tóthmérész B, Padisák J, Hajnal É, Borics G (2017) Functional redundancy modifies species-area relationship for freshwater phytoplankton. Ecol Evol **7**:9905–9913

Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol **85**:183–206

Yvon-Durocher G, Dossena M, Trimmer M, Woodward G, Allen AP (2015) Temperature and the biogeography of algal stoichiometry. Global Ecol Biogeogr **24**:562–570