

The contribution of epipelton to total sediment microalgae in a shallow temperate eutrophic loch (Loch Leven, Scotland)

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Abstract Benthic microalgae are known to perform important ecosystem functions in shallow lakes. As such it is important to understand the environmental variables responsible for regulating community structure, positioning and biomass. We tested the hypothesis that the positioning (across a depth gradient of 2–22 m overlying water depth) and relative biomass (determined using bulk and lens tissue harvested chlorophyll (Chl) *a* concentrations) of the epipelton community would vary independently with season (12 monthly samples) and across natural gradients of

light and habitat disturbance relative to the total benthic algal community (i.e. all viable microalgae in the surface sediments) in a shallow eutrophic loch. Total sediment microalgal Chl *a* concentrations (TS-Chl; range: 5–874 $\mu\text{g Chl } a \text{ g}^{-1} \text{ dw}$) were highest in winter and in the deepest site (20 m overlying water depth), apparently as a result of phytoplanktonic settling and sediment focussing processes. Epipellic Chl *a* concentrations (Epi-Chl; range: <0.10–6.0 $\mu\text{g Chl } a \text{ g}^{-1} \text{ dw}$) were highest in winter/spring, a period when water clarity was highest and TS-Chl lowest. Principal components analysis highlighted strong associations between Epi-Chl and sites of intermediate depths (2.5–5.5 m) in all seasons except autumn/winter. Autumn/winter represented the season with the highest average wind speeds preceding sampling, during which the highest Epi-Chl concentrations were associated with the deepest sites. Epi-Chl was associated with intermediate light and habitat disturbance during spring/summer and summer/autumn and varied positively with habitat disturbance, only, in autumn/winter and winter/spring. The epipelton community structure also varied with depth; diatoms dominated shallow water sediments, cyanobacteria dominated deep water sediments, and sediments at sites of intermediate depth returned the highest biovolume estimates and the most diverse communities. This study has strengthened the hypothesis that the structure and biomass of benthic microalgal communities in lakes are regulated by habitat disturbance and water clarity, both of which are

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expected to respond to climate change and eutrophication. The degree to which these structural responses reflect functional performance requires clarification.

Keywords Benthic algae · Epipelon · Community structure · Depth · Sediment disturbance · Lake · Chlorophyll *a*

Introduction

Recent attention has been paid to the performance of ecosystem functions by sediment microalgae in shallow lakes (e.g. Woodruff et al., 1999; Bartoli et al., 2003; Spears et al., 2006). The driving force behind much of this study has been the extensive research conducted on estuarine mudflats in which benthic microalgal ecosystem functioning has generally been attributed to the epipelon (Admiraal, 1984; Paterson, 1989; Perkins et al., 2004), those microalgae capable of repositioning themselves in the sediment (Poulickova et al., 2008). Our understanding of the role of biodiversity in driving specific ecosystem functions in lake sediments is limited by a lack of knowledge regarding the regulation of microalgal community composition by environmental factors (Aberle & Wiltshire, 2006; Poulickova et al., 2008). There is, therefore, a requirement to assess the spatial and temporal variation in the epipelon community structure and to identify the environmental drivers of this variation.

The microalgal community of shallow eutrophic lake sediments (i.e. with high light attenuation and high phytoplanktonic settling rates) is likely to be dominated by settled phytoplankton with cells from other habitats (e.g. epipelon, epipsammon, epiphyton, metaphyton and resting stages/spores) also present in variable amounts (Round, 1981; Stevenson, 1996). Taken collectively this community is referred to in this study as the ‘total (sediment) microalgal community’.

Operational separation of the total microalgal community into groups based on taxonomy or habitat preference is difficult (Poulickova et al., 2008). The use of high performance liquid chromatography (HPLC) pigment analysis has been widely used to separate microalgal communities into groups based on pigment profiles (Bonilla et al., 2005; Buchaca & Catalan, 2007). Additionally, the use of lens tissue separation methods has been reported as an efficient

(~90% efficiency; Eaton & Moss, 1966; Round, 1981) method of selectively isolating the epipelon community from the total microalgal community and has been effectively used for taxonomic investigations of freshwater epipelon (Eaton & Moss, 1966; Round & Eaton, 1966; Happey-Wood, 1988). Although these methods have been used to further the understanding of sediment microalgal ecology, much still remains to be learned about the factors driving seasonal and spatial variation in the epipelon community and its relative contribution to the total sediment microalgal community in eutrophic lakes.

Light conditions, habitat disturbance and nutrient limitation have all been identified as drivers of spatial and seasonal variation in sediment microalgal biomass (Hoagland & Peterson, 1990; Borchardt, 1996). In shallow eutrophic lakes nutrient limitation may be less important than light limitation (Vadeboncoeur & Lodge, 2000). Additionally, in large shallow lakes, the effects of local environmental drivers (e.g. light, nutrient limitation and grazing) may be superseded by the redistribution of sediments and associated microalgae via wave and current-induced re-suspension and relocation processes to deeper sediment habitats (Hilton et al., 1986; Cattaneo, 1987). Although these deeper habitats are commonly aphotic and are rarely included in studies of the epipelon, the associated sediment microalgal community may still perform important functions (e.g. food source for benthic invertebrates (Armitage et al., 1995), phytoplanktonic ‘seed bank’ (Head et al., 1999); and the production of extra-cellular polymers (Spears et al., 2007b; Gerbersdorf et al., 2008)) and is, therefore, still of interest.

This study was designed to investigate the factors responsible for shaping the distribution of epipelon and total microalgal communities in a shallow eutrophic loch (Loch Leven, Scotland). We tracked epipelon and total sediment microalgal communities over natural gradients of light, habitat disturbance, and nutrient concentrations in order to: (1) quantify the relative seasonal contribution (monthly samples for 1 year) of the epipelon to total benthic microalgal biomass and (2) assess the environmental factors (i.e. light, habitat disturbance and nutrient supply) driving the vertical distribution of epipelon in the surface sediments. The specific hypothesis tested was that the epipelon community would vary across gradients of habitat disturbance, light and nutrients independently of the total microalgal community.

Materials and methods

Study site

Loch Leven (latitude 56°10'N, longitude 3°30'W) is a shallow (mean depth 3.9 m; maximum depth 25 m) eutrophic loch with a surface area of 13.3 km² (Fig. 1). Intermittent stratification usually occurs during summer/autumn in two deeper water basins that together constitute <5% of the total loch surface area. Six sample sites were included in this survey selected to represent a gradient of depth (2, 2.5, 3.5, 5.5, 10, 22 m overlying water depth; Fig. 1). Water and sediment chemistry during the study period were assessed and are discussed in Spears et al. (2007a). Water column chlorophyll *a* (Chl *a*) concentrations were extracted from the Loch Leven Long Term Data Set (Carvalho et al., 2007) and determined according to APHA (1992) following filtration (Whatman GF/C filters) and extraction of pigments in cold methanol. Cross-comparisons between methanol extraction and acetone extraction following acidification at Loch Leven returned a significant linear regression (methanol Chl *a* = 1.1277 × acetone Chl *a* + 0.5322; $R^2 = 0.94$). Bailey-Watts et al. (1974, 1990) have previously reported on the structure and seasonal variation in the phytoplankton community of Loch Leven.

In general, the loch bed is composed of sandy substrata in water depths of less than 2 m with organic matter, silt and clay content increasing with depth (Calvert, 1974). Benthic microalgae have been

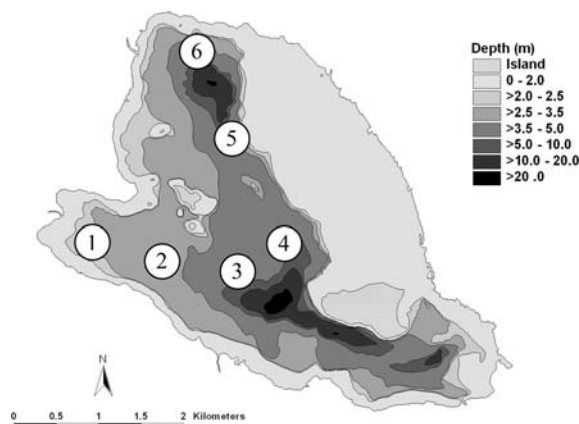


Fig. 1 Bathymetric map of Loch Leven showing the six sample sites

shown to perform important functions in Loch Leven including biostabilisation of sediments via the production of extra-cellular polymers (Spears et al., 2007b) and the regulation of benthic-pelagic nutrient cycling via the maintenance of pH and dissolved oxygen conditions in surface sediments (Spears et al., 2008).

Field measurements

We measured light levels using a Macam quantum radiometer/photometer Q101 (Macam Photometrics Limited, Livingston, Scotland) and calculated monthly light attenuation coefficients (April 2004–April 2005) and the percentage incident light reaching the sediment surface from vertical light profiles (taken at the 20-m site only) according to Fee et al. (1988). Bottom water (~30 cm above lake bed) temperature and dissolved oxygen saturation were quantified at each site on each date using a Quanta probe (Hydrolab Water Quality Monitoring System, Hydrolab Corporation, Colorado, USA). The Loch Leven Estates provided daily wind speed measurements recorded using a cup counter on the western edge of the loch from which average wind speeds over the week preceding each sample date were calculated.

Sample collection, processing and pore water chemical analyses

We collected sediment cores from the six sites monthly (April 2004–April 2005) from a boat using a Jenkin surface-sediment sampler (core internal diameter of 6.7 cm). An additional six cores (one from each site) were collected on the 30th June 2005 for the microscopic assessment of epipelton community composition. All cores were sealed and transported to the laboratory where water overlying the sediment surface was carefully syphoned off using a syringe to leave exposed sediment. Subsamples of the bottom water were retained for chemical analyses as outlined below. The upper 3 cm of sediment was sectioned and homogenised to facilitate subsampling for analyses. The depth of 3 cm represents the estimated depth to which viable microalgal cells may be quantified in Loch Leven (Fig. 2). Although photosynthesis will be restricted to the upper few hundred microns of surface sediments (Admiraal,

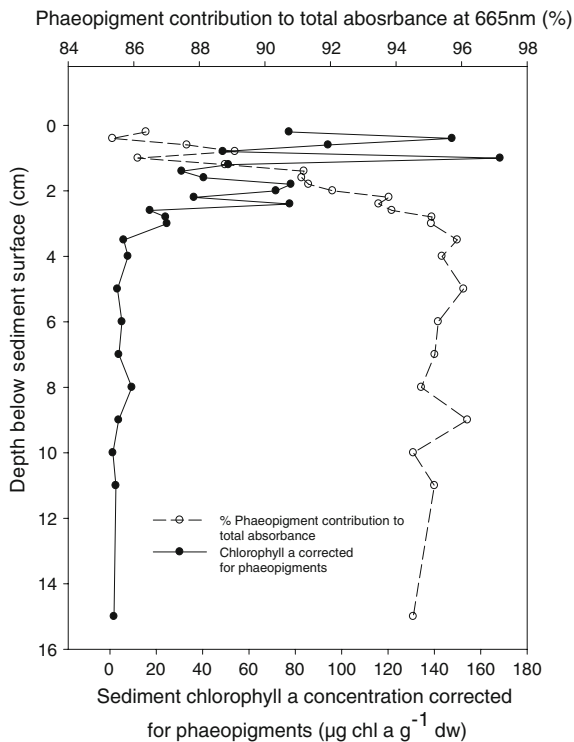


Fig. 2 Distribution of microalgal pigments with depth below the sediment surface (site 3 on 22 March 2004) including chlorophyll *a* concentration corrected for phaeopigments and the contribution to the absorbance at 665 nm by phaeopigments expressed as a percentage of total absorbance

1984; Paterson, 1989), viable microalgae may extend several centimetres into aphotic sediment layers (e.g. Fig. 2; up to 6 cm; Cyr, 1998) with vertical migration reported to occur at depths of centimetres (Palmer & Round, 1965; Round, 1966; Burkholder, 1996; Stevenson, 1996). As such, when considering the contribution of epipelton to the total sediment microalgal community it is important to ensure that the depth of surface sediment sampled reflects the depth of the viable community in the habitat of interest (Cyr, 1998; Aberle & Wiltshire, 2006).

We estimated the sediment water content by weighing sediment subsamples before and after a 24-h drying period at 40°C in an oven. Subsamples were also retained for pore water chemical analysis following centrifugation and filtration (Whatman GF/C filters). The soluble reactive phosphorus (SRP) and ammonium-nitrogen (NH₄-N) concentrations in the pore water and bottom water were determined spectrophotometrically following the methods of Wetzel & Likens (2000).

Quantification of total microalgal Chl *a* concentration

We used sediment Chl *a* as a proxy for total microalgal community biomass (TS-Chl; µg Chl *a* g⁻¹ dry weight sediment (dw)). Wet homogenised sediment was weighed into an acid-washed 15-ml centrifuge tube and pigment extraction in 90% cold acetone was allowed to continue for 24 h in the dark. Phaeophyton corrected Chl *a* concentrations were quantified following spectrophotometric analyses and using standard equations (Wetzel & Likens, 2000).

Pigment content and ratios can change as part of photoacclimation to either high or low light (Falkowski & LaRoche, 1991). In general, high light results in a decrease in light harvesting pigments and an increase in the ratio of reaction centre pigments to light harvesting pigments (Perkins et al., 2006). As a result, Chl *a* concentration per cell is a function of the light environment (i.e. a light dose/intensity response). However, within this dataset we assume that the magnitude of Chl *a* change used to indicate change in biomass is qualitative as a comparison of biomass as a function of season and depth.

Quantification of epipellic Chl *a* concentration

We separated the epipelton from the total microalgal community using glass Petri-dish traps. Five grams wet weight of homogenised sediment (from each site and on each date) was poured into an upturned Petri-dish top (10 cm internal diameter) within 4 h of sediment collection. A sheet of lens tissue was then placed over (although in contact with) the sediment slurry before being overlain by the upturned Petri-dish bottoms (9 cm internal diameter). The traps were incubated near a window under room conditions overnight and harvested at 11 a.m. the following day. This time was chosen following a pilot study in which no increase in trapped epipelton was observed between 11 a.m. and 1 p.m. (unpublished data) the following day. The upturned Petri-dish bottom was removed and thoroughly washed through a filtration system (GF/C filter) to ensure the collection of harvested cells. Photosynthetic pigments (Epi-Chl) were then extracted from algae on the filters and quantified as outlined above. Round (1981) critically discussed similar harvesting techniques and reported a harvesting efficiency of around 90%.

Epipelon community composition

We assessed the variation in epipelon community composition across the six sites on 30th June 2005. This was achieved by harvesting epipellic algae as outlined above with glass cover slips used in place of the upturned Petri-dish bottoms. Cover slips were mounted onto slides and the harvested live cells were counted using a Vickers M41 Photoplan microscope (Vickers Limited, UK) with 10× eyepiece. Counts were terminated following enumeration of 200 individual live cells or 55 fields using a 25× objective lens. Cell biovolumes were estimated using the equations outlined by Hillebrand et al. (1999).

Statistical analyses

We assessed the similarity in the temporal variation in mean loch (i.e. average of six sites on each sample date) TS-Chl ($n = 12$) and Epi-Chl ($n = 12$) values using correlation analysis ($\alpha = 0.05$). The samples were allocated to season based on the variables described in Table 1. The variation in the average seasonal (Degrees of Freedom (df) = 3) values of TS-Chl and Epi-Chl between the four seasons (Table 1) and between the six depth classes (df = 5) were assessed using two-way analysis of variance (ANOVA: total df = 71, $\alpha = 0.05$). Principal components analysis (PCA) using correlation was used to produce the two synthetic axes that best captured the variation in the data (Epi-Chl, % water content of surface sediments, % incident light reaching the sediment surface, bottom water temperature, pore

water SRP and $\text{NH}_4\text{-N}$, and bottom water SRP and $\text{NH}_4\text{-N}$ concentrations) averaged across each season. The ordination of the six sites across PC 1 and 2 and the corresponding distribution of the environmental variables were used to highlight the conditions under which Epi-Chl concentrations were highest during each season. All statistical analyses were carried out using Minitab statistical software, version 14 (Minitab Ltd., Coventry, UK).

Results

Variation in environmental conditions

Water column Chl *a* concentrations were characterised by a strong summer/autumn peak (dominated by cyanobacteria) with a secondary peak (dominated by diatoms) occurring in spring (Fig. 3a). Light attenuation was highest in autumn/winter and lowest in spring/summer (Table 1). The average values of wind speed during the week preceding sampling, pore water SRP and pore water $\text{NH}_4\text{-N}$ are shown (Table 1). The average annual depth gradients of the percent water content of surface sediments and the percent of incident light reaching the sediment surface increased and decreased with depth, respectively (Fig. 4).

Monthly variations in total microalgal and epipellic Chl *a* concentrations

Average TS-Chl across the six sites was highest in December 2004 and lowest in February 2005

Table 1 Average values across both season and depth of bottom water temperature and dissolved oxygen saturation (DO %), weekly average wind speed preceding the sample

Season	Sample period	Bottom water temperature (°C)	Weekly average wind speed (km h^{-1})	Kd (m^{-1})	Bottom water DO % saturation	Pore water SRP (mg l^{-1})	Pore water $\text{NH}_4\text{-N}$ (mg l^{-1})
Spring/Summer	14/04/09–29/06/04	12.16 (0.32)	11.74 (5.44)	0.67 (0.18)	103 (0.42)	0.13 (0.03)	2.87 (0.81)
Summer/Autumn	29/07/04–07/10/04	13.95 (1.99)	13.32 (6.11)	1.46 (0.47)	97 (1.04)	0.11 (0.01)	3.16 (1.03)
Autumn/Winter	02/11/04–20/12/04	6.79 (1.29)	15.44 (1.67)	1.60 (0.33)	90 (4.15)	0.30 (0.06)	3.58 (1.19)
Winter/Spring	09/02/05–14/04/05	4.78 (1.56)	8.43 (1.72)	1.07 (0.16)	97 (6.14)	0.32 (0.03)	2.60 (0.84)

Values in parenthesis represent the standard error of the mean

dates, light attenuation coefficients (Kd) and pore water soluble reactive phosphorus (SRP) and ammonium-nitrogen ($\text{NH}_4\text{-N}$) concentrations

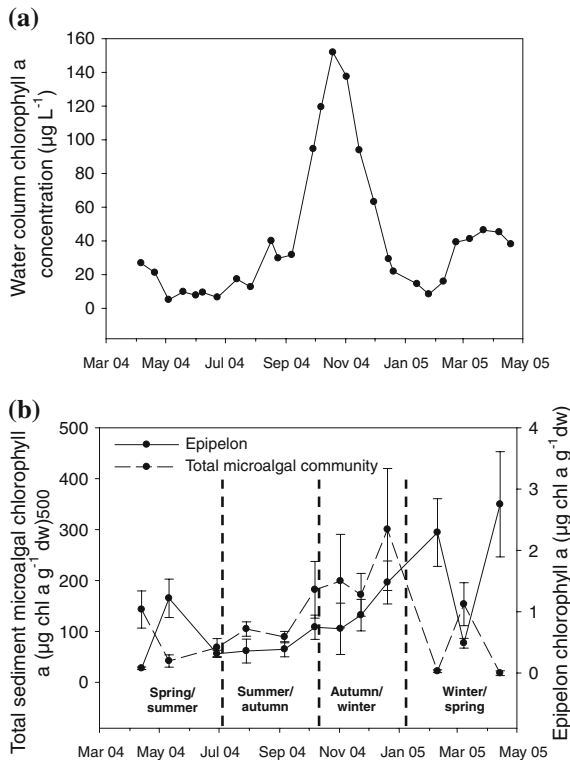


Fig. 3 **a** Water column Chl *a* concentrations between April 2004 and April 2005 extracted from the Loch Leven Long Term Monitoring Dataset (Carvalho et al., 2007). **b** Average ($n = 6$) monthly variation in total microalgal Chl *a* (TS-Chl) and epipellic Chl *a* (Epi-Chl) concentrations. Error bars represent standard error of the mean of six replicate sites

(Fig. 3b). Epi-Chl was lowest in April 2004 and highest in April 2005 (Fig. 3b). No significant correlation was observed between TS-Chl and Epi-Chl monthly mean loch values ($P = 0.296$).

Variation in total microalgal Chl *a* with season and depth

The variation in TS-Chl with season and depth is shown (Fig. 5a). Average seasonal concentrations ranged between $24 \mu\text{g Chl } a \text{ g}^{-1} \text{ dw}$ (2 m site in winter/spring) and $617 \mu\text{g Chl } a \text{ g}^{-1} \text{ dw}$ (22 m site autumn/winter). We found significant effects of season (two-way ANOVA; $df = 3$; $F = 9.4$; $P < 0.01$), depth ($df = 5$; $F = 7.31$; $P < 0.01$) and an interaction between the two ($df = 15$; $F = 2.25$; $P = 0.02$) on TS-Chl. TS-Chl was significantly lower in winter/spring than in all other seasons and was significantly higher in autumn/winter than in all other

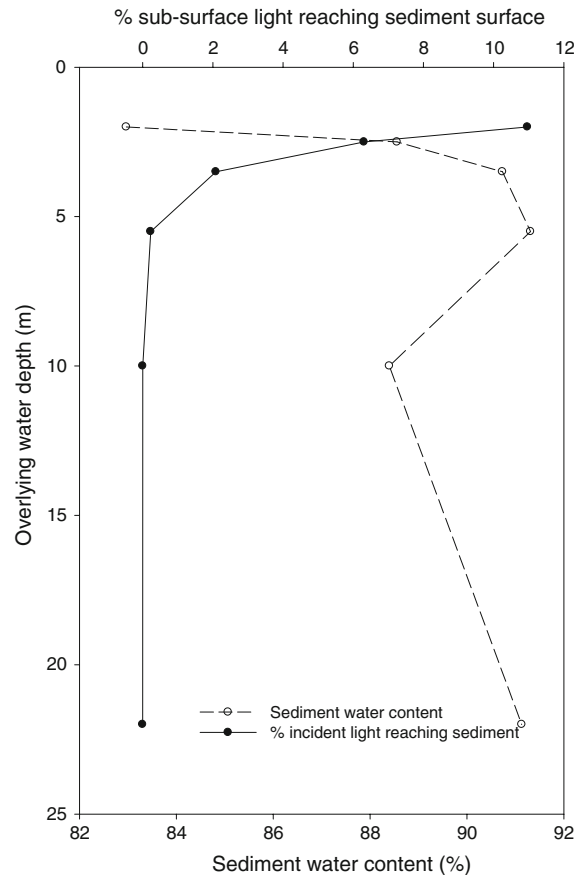


Fig. 4 Average water column depth gradients of the percentage of incident light reaching the sediment surface and the percent water content of surface sediments at each site during the study period

seasons. Additionally, TS-Chl was significantly higher at 22-m water depth than it was in all other sites. The range of TS-Chl over all sites and dates ($n = 72$) was $5\text{--}874 \mu\text{g Chl } a \text{ g}^{-1} \text{ dw}$.

Variation in epipellic Chl *a* with season and depth

Two-way ANOVA results indicated significant effects of season ($df = 3$; $F = 6.11$; $P < 0.01$) but not depth on Epi-Chl (Fig. 5b). Epi-Chl was significantly higher in winter/spring than in all other seasons. In general, Epi-Chl increased from shallow sites to sites of intermediate depth (i.e. 2.5–5.5 m) and declined with increasing depth thereafter. Epi-Chl peaked at 3.5-m water depth in autumn/winter and winter/spring and at 5.5-m water depth in spring/summer and summer/autumn. The percent

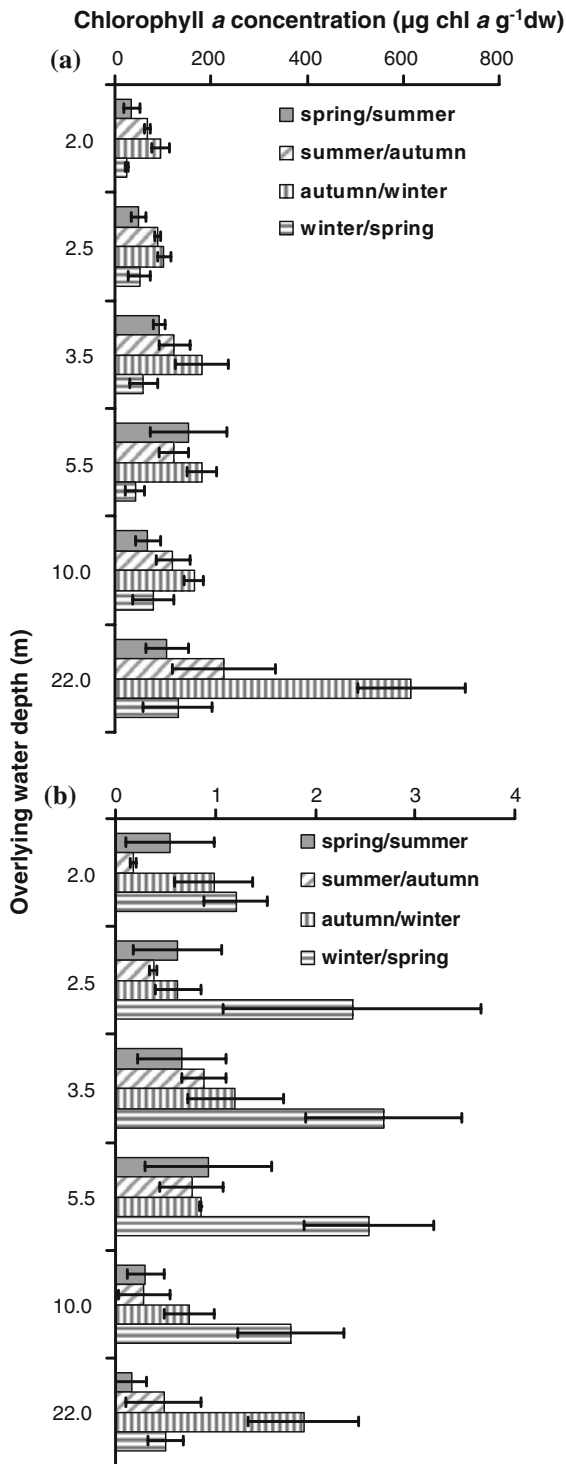


Fig. 5 Variation in (a) benthic microalgal (TS-Chl) and (b) epipellic (Epi-Chl) Chl *a* concentration with season and depth. Error bars represent the standard error of the mean ($n = 3$)

contribution of Epi-Chl to TS-Chl never exceeded 31% (10-m site, 14 April 2004). The range of Epi-Chl over all sites and dates ($n = 72$) was <0.10 (i.e. below detection) to $6.0 \mu\text{g Chl } a \text{ g}^{-1} \text{ dw}$.

The PCA results (Table 2; Fig. 6) indicate a general increase in water depth with PC 1. In spring/summer Epi-Chl was positively associated with the sites of intermediate depth (3.5 and 5.5 m) and varied negatively with pore and bottom water SRP and $\text{NH}_4\text{-N}$ concentrations, positively with bottom water temperature and was equi-distant to both the percent incident light at the sediment surface and the percent water content of the surface sediments. In summer/autumn the two sites of intermediate depth (3.5 and 5.5 m) were strongly and positively associated with Epi-Chl, pore water SRP concentration and % water. In autumn/winter Epi-Chl was positively associated with the deepest site and varied positively with % water and pore and bottom water $\text{NH}_4\text{-N}$ concentration and negatively with temperature and % light. In winter/spring Epi-Chl varied positively with % water, negatively with % light and bottom water SRP concentration and was positively associated with sites of intermediate depth.

Spatial variation in epipelton community composition

The epipelton community composition varied with overlying water depth (Fig. 7). Diatoms (mainly *Navicula* sp.) were most abundant in the shallowest sites (Fig. 7a–c) with cyanobacteria (*Oscillatoria* sp.) dominant in the deeper sites (Fig. 7d–f). The total epipelton biovolume was highest ($426 \mu\text{m}^3 \text{ m}^{-2}$) at 3.5 m overlying water depth, decreasing to $13.5 \mu\text{m}^3 \text{ m}^{-2}$ at 20 m overlying water depth (Fig. 8).

Discussion

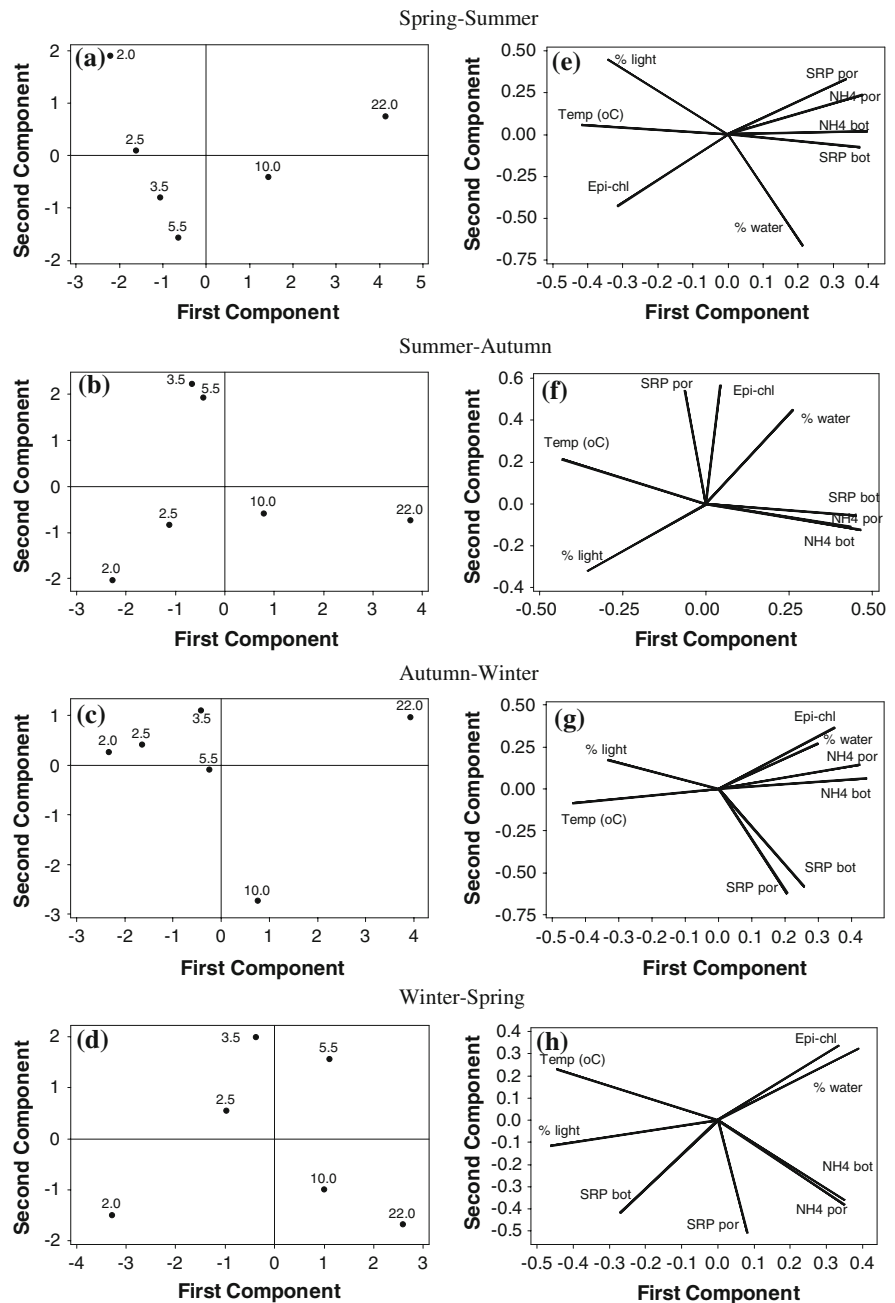
Variation in the benthic microalgal community with season

We observed significant seasonal variation in TS-Chl. The autumn/winter TS-Chl peak corresponded with the season of highest light attenuation, driven mainly by the shading effects of phytoplankton in Loch Leven (Bailey-Watts, 1974), and appeared to result from

Table 2 The eigenvalues (EV) and cumulative proportions (CP) of the variance over depth explained by principal component 1 (PC1) and 2 (PC2), for each season

	Spring–Summer		Summer–Autumn		Autumn–Winter		Winter–Spring	
	EV	CP	EV	CP	EV	CP	EV	CP
PC1	5.64	0.705	4.37	0.547	4.87	0.610	4.17	0.522
PC2	1.49	0.892	2.86	0.905	1.98	0.857	2.56	0.842

Fig. 6 Results of principal components analysis showing the ordination of the six sites along principal components 1 (first component) and 2 (second component) and the loading plots showing relative weightings and ordination of each environmental variable measured along both principal components. Depths are given for each site in the ordination plots. Plots are shown for Spring/Summer (a, e); Summer/Autumn (b, f); Autumn/Winter (c, g) and Winter/Spring (d, h). Variables included in the analysis were the percentage of incident light reaching the sediment surface (% light); bottom water temperature (temp (°C)); soluble reactive phosphorus (SRP bot) and ammonium-nitrogen (NH₄ bot) concentrations; pore water SRP (SRP pore) and NH₄-N (NH₄ pore) concentrations; the water content of the surface sediments (% water) and the epipelonal Chl *a* concentration (Epi-Chl)



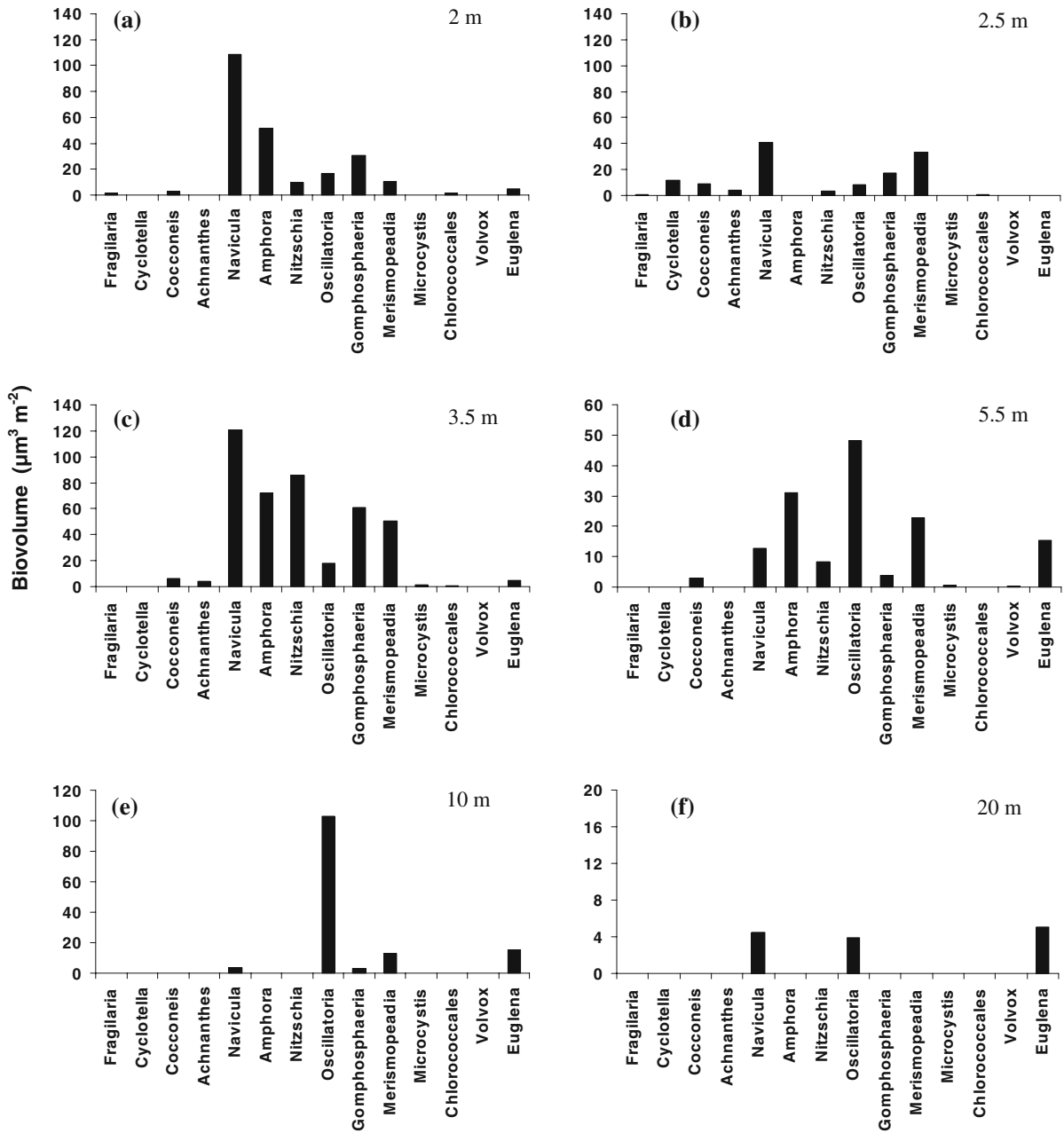


Fig. 7 Variation in epipelton community composition (expressed as biovolume) across the six sites (sampled 30th June 2005)

elevated rates of phytoplanktonic detritus following the characteristic summer/autumn bloom (Fig. 3a) as opposed to increased epipelton production at the sediment surface. This is in agreement with Lesen (2006) who reported lagged (2–3 month) coherence between total microalgal sediment Chl *a* concentrations and surface water concentrations. The lag time between the peak in phytoplankton in the water column and the

peak in total sediment microalgae in this study was about 2 months.

Significant seasonal variation in Epi-Chl was also observed. The winter/spring peak occurred during periods of lowest light attenuation apparently driven by a reduction in water column phytoplankton biomass. Similar seasonal peaks in the epipelton (although not expressed as pigment concentration) have been

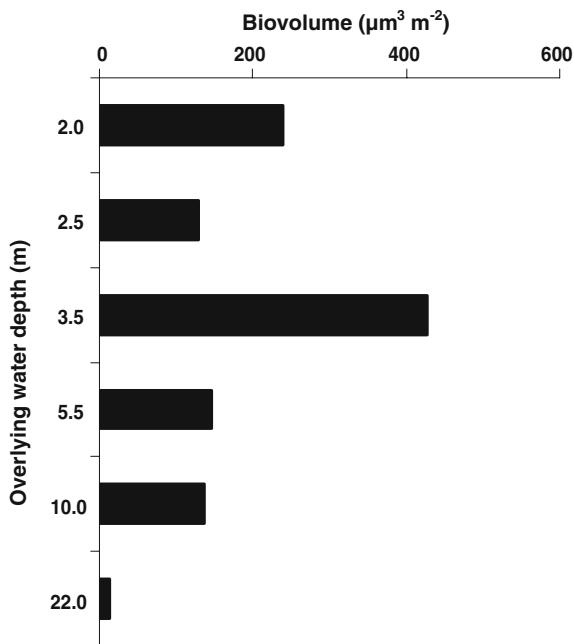


Fig. 8 Spatial (with depth) variation in total community biovolume across the six sites (sampled 30th June 2005)

reported in Blelham Tarn (April) and Lake Windermere (April and July) (Round, 1965). These peaks were attributed to high water clarity and temperature conditions and, in general, represented a build-up of the epipellic community through late winter–spring (Round, 1965). Bailey-Watts (1974) reported peaks, assumed to be related to high water clarity (i.e. low water column phytoplankton biomass), in total microalgal community biomass during May–July and August–November in shallow littoral zone sands and sediments (<1.9 m) in Loch Leven.

Expressed as aerial values, the range of total microalgal and epipellic Chl *a* concentrations in this study were 6–653 mg Chl *a* m⁻² and <0.1–6.2 mg Chl *a* m⁻², respectively. Reported concentrations of total microalgal Chl *a* concentrations in other lakes range from 4 to 240 mg Chl *a* m⁻² (Wasmund, 1984; Cyr, 1998) with epipellic Chl *a* concentrations ranging from 2 to 30 mg Chl *a* m⁻² (Hickman & Round, 1970; Happey-Wood et al., 1988).

Effects of habitat disturbance, light and nutrients on the benthic microalgal community

In general, TS-Chl concentration increased with overlying water depth with the highest concentrations

corresponding with the deepest site (22-m water depth) and the lowest concentrations being observed in the shallowest site (2-m water depth). This trend was consistent across the seasons. Similar trends have been observed in other shallow eutrophic lakes (Cariou-Le Gall & Blanchard, 1995; Cyr, 1998) and are generally attributed to turbulence-induced ‘sediment focusing’ of shallow water sediments to deeper areas of the lake bed (Håkanson, 1982; Hilton et al., 1986). Sediments in Loch Leven are expected to be particularly sensitive to such processes due to having a relatively large fetch for a shallow lake (Smith, 1974). Wave mixing is also known to be significant in Loch Leven (Spears & Jones, 2010), and deep water currents have been reported to reach 1.15 km h⁻¹ (Smith, 1974). Thus, shallow water sediments may be easily disturbed and efficiently translocated by currents to deeper areas of the loch bed.

The PCA showed that Epi-Chl was highest in sites of intermediate depth during all seasons except winter/spring in which Epi-Chl increased towards the deepest site. This latter observation suggests that sediment disturbance processes may, at least sporadically, override any local environmental drivers (e.g. light, temperature, nutrients, etc.) and result in the translocation of epipellic biomass from shallow waters to deeper waters in winter/spring. This is inconsistent with the low wind conditions observed in the weeks preceding sampling during this season (Table 1). However, winter/spring is generally the windiest season in Loch Leven and the reported wind values may not accurately represent average conditions during this season (Spears & Jones, 2010).

Sites of intermediate depth corresponded with intermediate levels of light and habitat disturbance (%water content) across all seasons and a positive variation between Epi-Chl and light was not observed in any season. However, we did observe positive variation between % water (i.e. habitat disturbance) and Epi-Chl in autumn/winter and winter/spring highlighting the importance of habitat disturbance in regulating biomass accrual in Loch Leven. Although photoinhibition may regulate benthic algal biomass (e.g. Vinebrooke & Leavitt, 1999) in shallow water sediments, on average the observed light levels (i.e. ~10% incident light at sediment surface) did not appear to support this hypothesis. Instead, it is likely that the high biomass observed in sites of intermediate depth was the result of a trade-off between habitat disturbance in shallow water sediments and light

limitation in deeper water sediments (Fig. 4). Hoagland & Peterson (1990) reported similar observations for microalgae grown on artificial substrata.

Epi-Chl varied positively and negatively with SRP and $\text{NH}_4\text{-N}$ concentrations measured at the loch bed. These concentrations were never below 42 and $487 \mu\text{g l}^{-1}$ for SRP and $\text{NH}_4\text{-N}$, respectively, suggesting that nutrient limitation is not responsible for the observed positive covariation. Nutrient concentrations and Epi-Chl are both likely driven by the disturbance regime described above. The negative covariation observed between Epi-Chl and pore water SRP may be the result of photosynthetic processes responsible for stripping SRP from pore water (e.g. direct P uptake (Borchardt, 1996); formation of Fe–P complexes driven by dissolved oxygen production (Dodds, 2003); and the formation of apatite–P complexes driven by the maintenance of pH (Carlton & Wetzel, 1988)). These processes may also be responsible for the creation of ‘microzones’ in which nutrients are depleted (Burkholder, 1996). The methodology used here to quantify pore water nutrient concentrations represents the average conditions over the upper 3 cm of sediment and will be too coarse to allow observation of such fine-scale processes.

Spatial variation in epipelon community composition

The epipelon community composition changed with increasing water depth as expected with high light-requirement species, such as the diatom *Navicula* spp. being more abundant in shallow water sediment and low light tolerant species, such as *Oscillatoria* spp. being dominant in deeper water sediment. These changes in community structure are in agreement with a number of studies that have observed a lower light dose acclimation in filamentous cyanobacteria when compared to epipellic diatoms (Ploug et al., 1993; Kromkamp et al., 1998). The biovolume estimates are also in agreement with the Chl *a* estimates and again indicate peak epipellic biomass at sites of intermediate depth. These optimum conditions also appeared to support more diverse epipelon communities.

Conclusions

We observed changes in the structure of the benthic microalgal community as a result of environmental

drivers. This was manifest within non-coherent variation in epipellic Chl *a* concentrations relative to the total benthic microalgal community Chl *a* concentration across seasons and water depth. The epipelon responded seasonally to changes in the water column light climate whereas the total benthic microalgal community appeared to be responding to phytoplanktonic detritus and translocation processes. We observed an apparent trade-off between wave-induced sediment disturbance and light limitation where epipellic Chl *a* concentration was highest at intermediate depths. However, these local habitat preferences appeared to be easily overridden by habitat disturbances. Distribution of the total benthic microalgal community appeared to be driven by sediment translocation/focussing to deeper water zones at all times.

The patterns of community positioning may have significant implications with respect to the performance of key ecosystem functions. The performance of functions attributed to the epipelon (e.g. biostabilisation, oxygenation of sediment surface and the reduction of phosphorus release) is expected to be strongest at intermediate depths. Other functions performed by the benthic microalgal community (e.g. replenishment of sediment nutrients and food supply for other benthic organisms) will dominate in deeper water sediments. The extent of these two functionally contrasting zones will likely be driven by environmental change.

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