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Influence of environmental and spatial variables on the distribution of surface sediment diatoms in an upland loch, Scotland

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The spatial distribution of surface sediment diatoms was analyzed using ArcGIS in the Round Loch of Glenhead, an acid upland lake in south-west Scotland. The assemblages were composed almost entirely of benthic species. *Tabellaria quadriseptata* was fairly evenly distributed across the loch but some species (*Navicula madumensis*, *Brachysira brebissonii*, *Aulacoseira perglabra* and *Eunotia vanheurckii* var *1*) showed rather patchy distributions. Ordination analysis was performed to assess the influence of environmental and spatial variables on the diatom composition of the samples. Loss of ignition was significantly negatively correlated with redundancy analysis species axis 1 (r = –0.77), indicating the influence of substrate on the diatom assemblages. The positive relationship between theoretical bottom shear stress resulting from wind stress and redundancy analysis (r = 0.31) suggests wind stress also influences the spatial distribution of diatoms within the loch. Spatial variables [(principal coordinates of neighbour matrices (PCNM 1 and PCNM3) positively correlated with redundancy analysis axis 2], indicated that spatial variables, ignored in former studies, are a further influence on diatom distribution. Unique environmental and spatial variables explained 27.3% and 8.6% of diatom variability respectively. Environmental and spatial interactive variables combined explained 4.8% of variation. Although the pure contribution of spatial variables was only 8.6%, the study highlighted the importance of differences in the spatial distribution of different benthic diatom species in this upland lake.

Keywords: Diatom, distribution, composition, benthic, substrate, wind, lake, Scotland

Abbreviations: **DCA** – detrended correspondence analysis, **GAM** – generalizes additive models, **I** – downward irradiance, **Kd(PAR)** – diffuse attenuation coefficient for downward irradiance, **LOI** – sediment organic matter content, **PAR** – photosyntheticall active radiation, **RDA** – redundancy analysis, **TBSS** – theoretical bottom shear stress

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Introduction

It is often assumed that sediment deposition below a certain water depth is conformable and representative. However, the complexity of diatom deposition in lake basins is receiving increasing attention as a result of multicore studies (ANDERSON 1989, 1990a, b; ANDERSON 1998; ADLER and HUBENER 2007). In these studies, research focused on the selection of a representative core site from multiple cores collected from a range of water depths and locations within a lake. Studies of transects across lakes from littoral to pelagic zones also demonstrated the variability in surface sediment diatom composition (MERILÄINEN 1971, BRADBURY and WINTER 1976, KINGSTON et al. 1983, KAUPPILA 1998). The majority of sites investigated spatially have been lowland lakes.

In upland lakes, the spatial variability of living benthic diatom communities has been surveyed, but only from samples spatially limited to the littoral zone (JONES and FLOWER 1986) or, in the case of surface sediment diatom assemblages, from samples collected along transects (ALLOTT 1991). However, transect sampling is an imperfect method of capturing whole-lake distributions (WATTS and HALLIWELL 1996). A stratified random sample (SRS) method that ensures good area coverage and preserves the advantage of randomness is preferred (WATTS and HALLIWELL 1996).

Diatom samples collected according to the SRS method can be analysed using multivariate statistical techniques to identify the principal factors that explain the distribution. Until now, only environmental variables have been included in such analyses (KAUPPILA 1998). Here we also consider the importance of spatial variables. Spatial patterns in the abundance and distribution of organisms are inherent properties of ecological systems (FORTIN and DALE 2005), and therefore need to be included (LEGENDRE and FORTIN 1989, BORCARD et al. 1992). Consequently, we use principal coordinates of neighbour matrices (PCNM) a technique introduced by BORCARD and LEGENDRE (2002) and now used to construct spatial models in various fields of ecology (BORCARD et al. 2004, CRIST et al. 2006). The respective contributions of environmental and spatial variables to the variability of surface sediment diatom can then be calculated using the variation partitioning technique (BORCARD et al. 1992). Here we use this approach to analyse the spatial patterns of benthic diatoms in a Scottish upland lake, the Round Loch of Glenhead.

Materials and methods

Study site

The Round Loch of Glenhead (British National Grid reference NX 450 804, 55°5' N, 4°25' W) is a small lake located in the Galloway hills of south-west Scotland (Fig. 1). The climate of Galloway is mild oceanic with an annual average precipitation of ca. 2500 mm yr^{-1} and an average temperature 8.5 °C with a range from –6 °C to 27 °C (YANG 2009). Soils in the catchment are mainly deep peats and peaty podsols; skeletal soils and bare rock occur on the steepest slopes (JONES et al. 1989).

The lake itself is situated within a rugged moorland landscape at 295 m altitude and has an open water area of 12.5 ha with a mean water depth of 4.3 m (maximum depth is 14.0 m). The average pH of the lake (04/2005–03/2006) is 5.2 and dissolved organic carbon is 362.5 μmol L^{-1} (for more details of water chemistry, see SHILLAND et al. 2006).

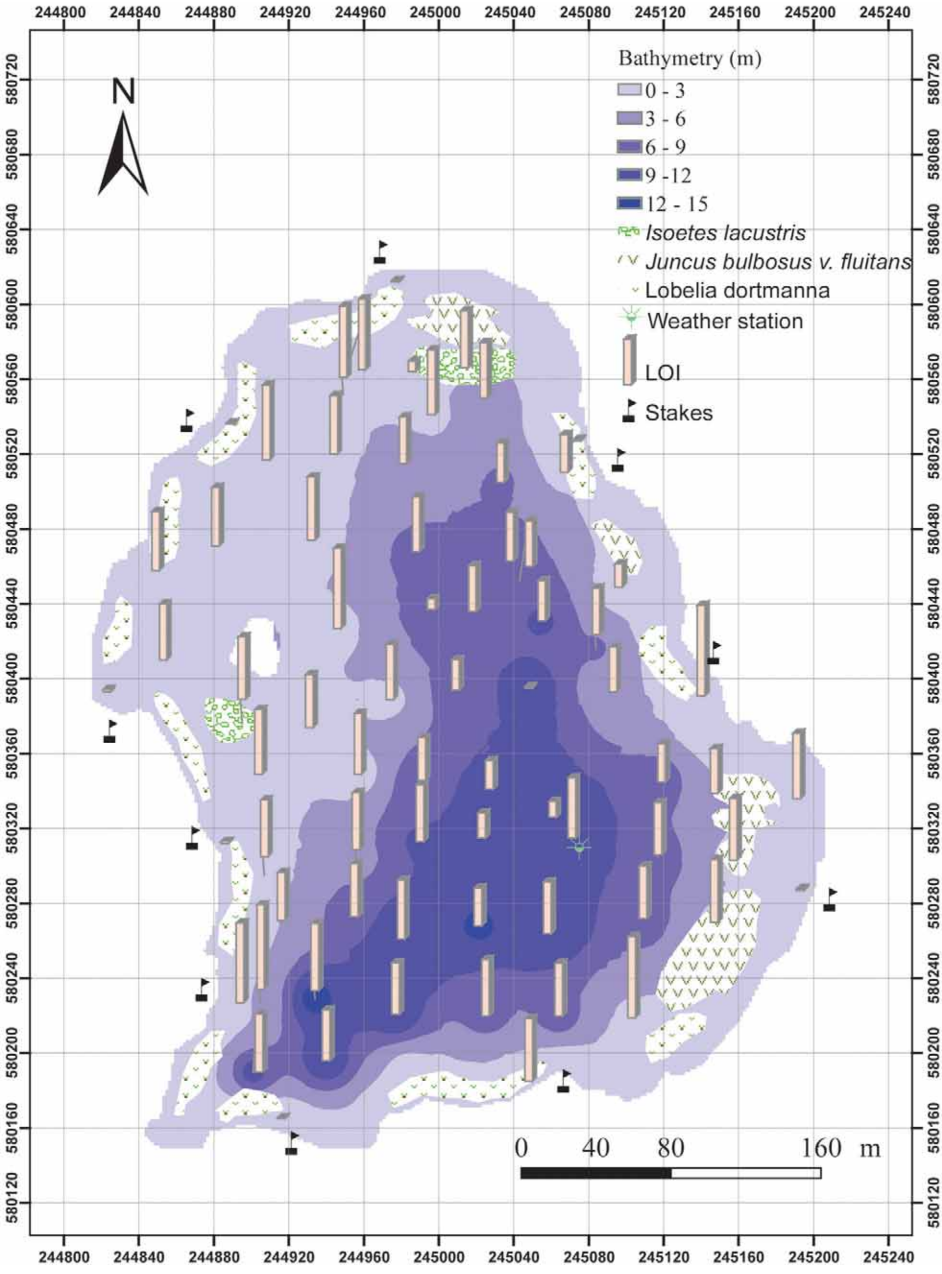

Fig. 1. Location and map of the Round Loch of Glenhead, south-west Scotland, UK, showing lake bathymetry, the main distribution areas of the dominant aquatic macrophytes (*Isoetes lacustris*, *Juncus bulbosus* var. *fluitans*, *Lobelia dortmanna*), loss on ignition (as histograms), the location of the weather station and the position of the ten stakes. Note that , which occurs sporadically in the loch, is not shown because its main growth period was after the main diatom sampling in April 2007.

Diatom habitats in the lake are confined to the littoral zone. They are dominated by the epilithon growing on stones and boulders that occur around the whole perimeter of the lake and the epiphyton growing principally on submerged plants. The dominants are *Juncus bulbosus* var. *fluitans*, *Lobelia dortmanna*, and *Isoetes lacustris* (SHILLAND et al. 2006). *Juncus bulbosus* var. *fluitans* is abundant in sandy bays, especially in the eastern littoral areas, whereas *Lobelia dortmanna* occurs around almost all the margins of the lake and *Isoetes lacustris* grows on mud surfaces with water depths of up to 3 m (YANG 2009). The photic depth is about 6 m deep and epipsammic and epipelic diatoms can be found down to 6 m (YANG 2009).

Sampling

The stratified random sampling (SRS) method was used to collect the surface sediment samples in the loch from 22nd to 28th April 2007. The loch area was divided into 40 × 40 m grids (Fig. 1) and GPS positions (as OSGB 36) of the centre points of each grid were set up on a GARMIN GPS III. The boat was navigated according to the waypoints and anchored at the centre of each grid square. When the boat stopped drifting, one surface sample was collected randomly within each grid using either an epipelic sampler (YANG and FLOWER 2009), when the water depth was less than 1.5 m, or a Renberg corer (RENBERG 1991) when water depth was more than 2.0 m. The top 1 cm sediment was removed for surface sediment samples. Shallow water samples (from ca. 0.5 m depth) were collected using the epipelic sampler at ten georeferenced points (Fig. 1) around the lake shore. All samples were transported back to the laboratory and stored at 4 °C.

Diatom analysis

Each sample was treated in the same way with no attempt to separate live and dead cells. Subsequently the samples were oxidised using hydrogen peroxide (H_2O_2) by heating in a water bath (RENBERG 1990). Microspheres were added to calculate the diatom concentration (BATTARBEE and KNEEN 1982). All samples were mounted on microscope slides using Naphrax as a mountant. Diatom valves were identified and counted using a Leitz research microscope under oil immersion at 1000 times magnification and phase contrast. A minimum of 500 valves was identified and counted for each sample.

The abundance contours of the dominant taxa were analysed using the IDW method in ArcGIS 9.0.

Environmental data

Environmental variables used in the analysis included photosynthetically active radiation (PAR), wind speed and direction, bottom shear stress and sediment organic matter content (LOI).

PAR was measured using a LICOR LI-250 underwater light meter at 0.5 m depth intervals between 10 am and 2 pm in the loch centre. Diffuse attenuation coefficients for downward irradiance Kd (PAR) were calculated from the slope of the linear regression of the natural logarithm of downward irradiance (I) versus depth (Z), and values only from a fit $r^2 > 0.95$ were accepted (KIRK 1994):

$$Kd(PAR) = -1/z \ln(Iz/I0)$$

where Kd(PAR) is the diffuse attenuation coefficient for downward irradiance, Iz is the PAR measurement at depth z, and I0 is the PAR measurement at the water surface. The kd(PAR) and surface PAR (I0) were used to infer the PAR at different water depths.

The temperatures at different water depths (1–12 m), wind speed and direction data were monitored by the weather station installed on a platform floating in the lake centre in October 2005. Data were provided by D. Monteith.

The theoretical bottom shear stress (TBSS) τ was calculated as the following formula (JAMES et al. 2004):

$$\tau = H\left[\frac{\rho(\upsilon(2\pi / T)^3)^{0.5}}{2\sinh(2kh)}\right]$$

where τ is the calculated bottom shear stress, H is the wave height, ρ is the density of water, T is the wave period, υ is the kinematic viscosity, k is the wave number ($2\pi/L$ where L = wavelength, cm), and h is the water depth. Wave characteristics (H, T and L) were calculated from wind speed, water depth and fetch distance using wave models according to the Coastal Engineering Research Center (1984). Wind speed was measured from weather station located near the loch centre and the one point measurement was cautiously extrapolated to the whole loch.

For LOI, the percentage dry weights (DW) of sediment samples were calculated after drying a known weight of sample overnight at 105 °C and then combusting in a muffle furnace at 550 °C for 2 hours.

Spatial data

In the field, BNG (British National Grid) coordinates of each sampling site were recorded. The original coordinate values were z-score transformed and these standard coordinates were used to create the dataset of spatial variables derived from PCNM using the program Spacemaker2 (Borcard and Legendre 2004, http://www.bio.umontreal.ca/legendre/). A matrix of Euclidean distances between samples was created and subsequently truncated based on truncation distance, which was equal to or larger than the largest distance between neighbours.

Data analysis

All environmental data were z-score transformed (LEGENDRE and GALLAGHER 2001) if the normality criteria were not satisfied. Species data were Hellinger transformed, because this method minimises the effects of the large number of zeros common in species abundance data (LEGENDRE and GALLAGHER 2001). Species with percent abundance of less than 3% per single sample were considered as »rare« taxa and were excluded from further ordination analysis. Preliminary detrended correspondence analysis (DCA) was performed using the program CANOCO 4.5 to measure the patterns of compositional variation and the biological species turnover (the gradient length) (ter BRAAK and PRENTICE 1988). Redundancy analysis or canonical correspondence analysis was selected based on gradient length to explore the relationships between diatom assemblages and environmental variables (TER

BRAAK and PRENTICE 1988). To reduce the possible effects of the difference in the number of variables included in each set of explanatory variables, we only used those environmental variables that were significant based on a forward selection ($p \leq 0.05$ after 999 random permutations) (ØKLAND and EILERTSEN 1994). To explore the relationship between single species distribution and environmental variables, GAM (HASTIE and TIBSHIRANI 1990) were performed using the R-language (R Development Core Team 2006) mgcv package (WOOD 2008). With respect to the spatial variables, the coordinates were created using PCNM and those eigenvectors with positive eigenvalues were retained for inclusion in the subsequent ordination analysis. Variation partitioning was used to quantify the proportion of the variation in diatom assemblage explained by variation in each of the combinations of environmental, and spatial variable sub-models (BORCARD et al. 1992). The unadjusted R^2 value was biased (PERES-NETO et al. 2006) and therefore they were adjusted into R^2_a. Based on the proportion of variation explained (R^2_a) in the analyses, the contributions of every component to the total variation in the diatom assemblages were calculated (BORCARD et al. 1992). The significances of fractions were tested by means of 999 permutations under a reduced model. All the analyses were performed using the R-language (R Development Core Team 2006) function varpart in the vegan package (OKSANEN et al. 2008).

Results

Distribution of surface sediment diatoms

A total of 18 genera and 94 species were collected during the study. The mean diatom abundance was 5.802×10^3 valves DW mg^{-1} with a SD of 4.766×10^3 valves DW mg^{-1}. Most species (80%) belonged to the genera *Eunotia*, *Navicula*, *Frustulia* or *Tabellaria*. The most abundant species were *Navicula leptostriata* Jørgensen, *Frustulia rhomboides* var. *saxonica* (Rabenhorst) de Toni, *Eunotia incisa* W. Sm. ex Greg., *Tabellaria quadriseptata* Knudson, *Brachysira brebissonii* R. Ross in Hartley, *Aulacoseira perglabra* Østrup and *Eunotia vanheurckii* var. 1 R.J.Flower. The environmental variables are summarised in table 1. GAM models that fitted the distribution of *Navicula leptostriata* abundance included LOI, PAR and TBSS and they were able to account for 54.8% of the variance. The selected models for *Frustulia rhomboides* var. *saxonica* and *Eunotia incisa* both included LOI and PAR, amounting to 35.9% and 24.9% of the total variance, respectively. Although the models that fitted *Tabellaria quadriseptata* and *Eunotia vanheurckii* var *1* only included LOI,

Tab. 1. Summary Statistics for environmental variables. LOI=loss of ignition, PAR = photosynthetically active radiation, and TBSS= theoretical bottom shear stress.

	Min	Max	Mean	SD
Water depth	0.5	14.0	4.9	3.8
Dry weight	0.07	79.14	15.21	21.89
LOI	0.64	61.29	31.93	15.30
PAR	0.07	398.72	100.15	106.19
Temperature	9.7	11.3	10.7	0.5
TBSS	0	0.0221	0.0011	0.0041

the models accounted for 40.7% and 32.6% of the total variance, respectively. The models that fitted *Brachysira brebissonii* and *Aulacoseira perglabra* included PAR and TBSS and they amounted to 17.8 and 24.0% of the total variance, respectively.

The spatial distributions of the dominant taxa are shown in figures 2 and 3. *Navicula leptostriata* was common in the northern shallow water but was seldom found in the eastern and southern basin (Fig. 2). *Frustulia rhomboides* var *saxonica* and *Eunotia incisa* occurred mostly in the middle and southern parts of the lake basin. *Navicula madumensis* (=*Kobayasiella madumensis*, LANGE-BERTALOT 1999) JØRGENSEN (1948) occurred mostly

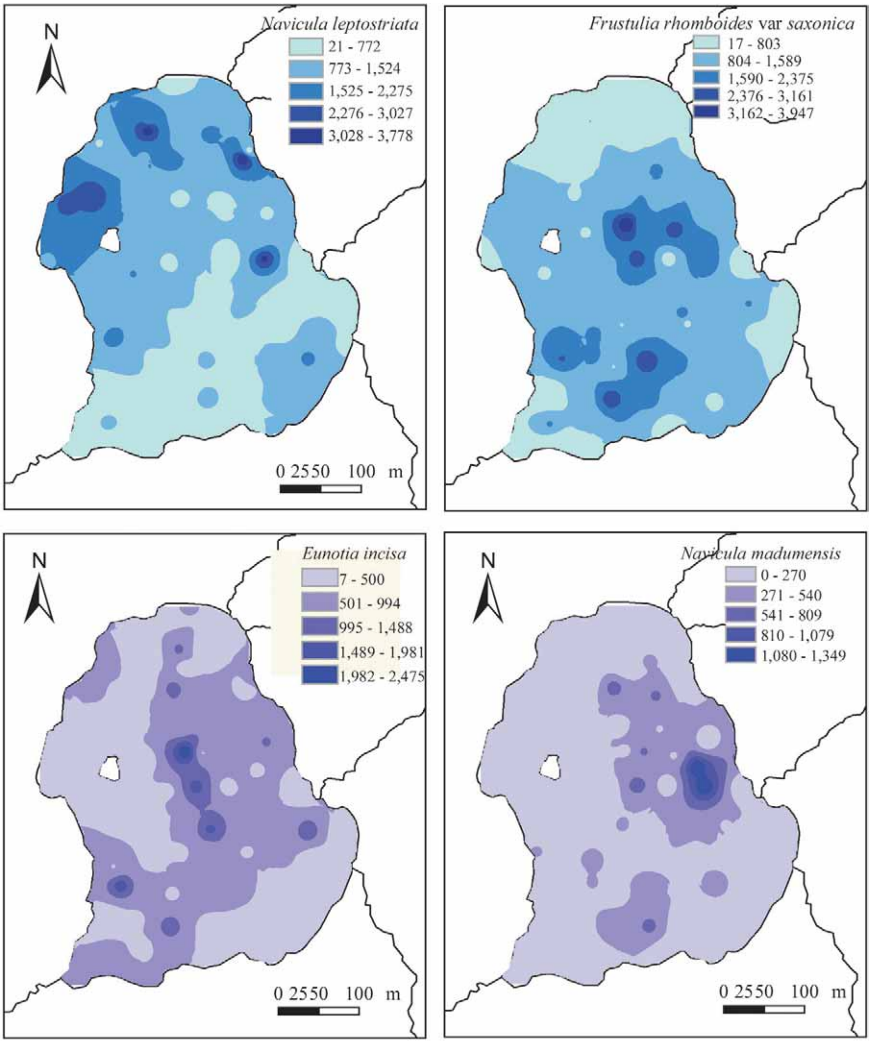

Fig. 2. Spatial distribution of surface sediment diatom concentrations (10^3 valves DW mg^{-1}) in the Round Loch of Glenhead in April 2007. Upper left, *Navicula leptostriata*; upper right, *Frustulia rhomboides* var. *saxonica*; bottom left, *Eunotia incisa*; botttom right, *Navicula madumensis*.

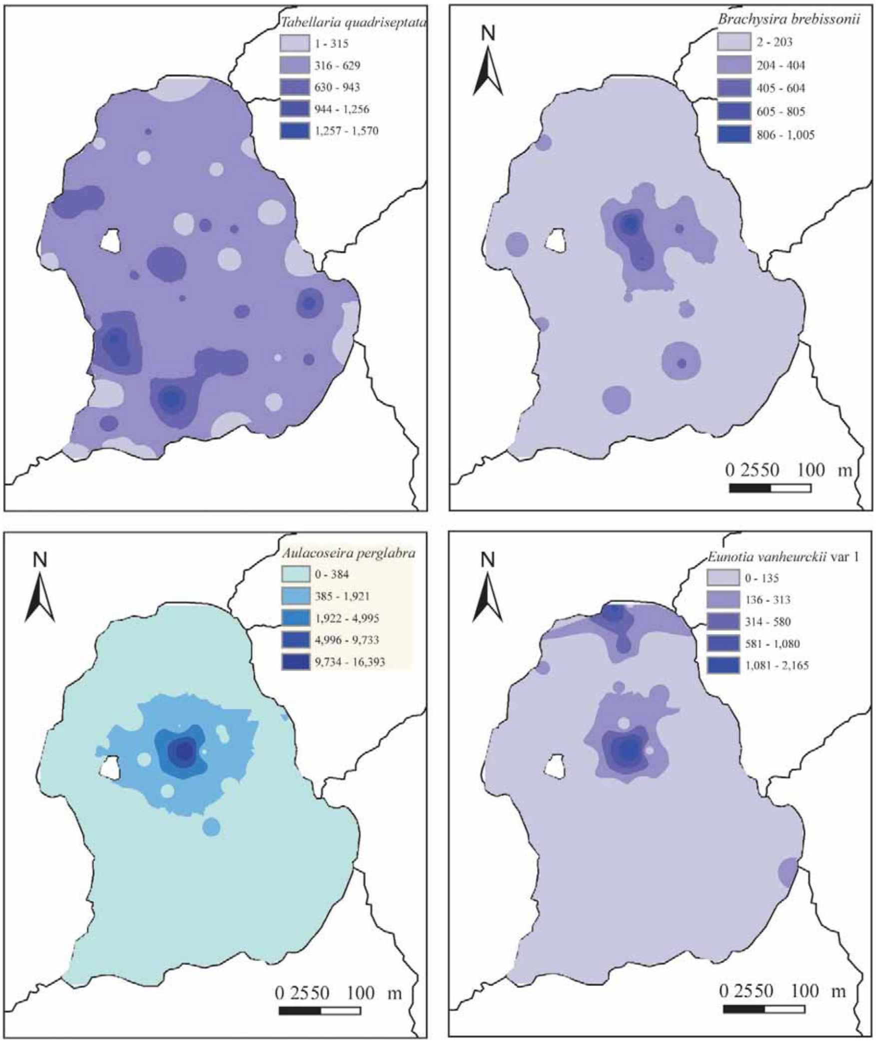

Fig. 3. Spatial distribution of surface sediment diatom concentrations (10^3 valves DW mg^{-1}) in the Round Loch of Glenhead in April 2007. Upper left, *Tabellaria quadriseptata*; upper right, *Brachysira brebissonii*; bottom left, *Aulacoseira perglabra*; botttom right, *Eunotia vanheurckii* var. *1*

in the eastern region of the loch. *Tabellaria quadriseptata* was widely distributed in the loch but with three small high abundance patches in the southern basin (Fig. 3). *Brachysira brebissonii* and *Aulacoseira perglabra* were concentrated in the loch centre. *Eunotia vanheurckii* var. 1 was mainly found in the northern and middle basin.

Ordination analysis

The gradient length of the first axis explored by DCA is 1.75 SD. This indicates that species turnover was at a range where linear species response models RDA could be suitable.

The environmental variables included dry weight, LOI, PAR, temperature and theoretical bottom shear stress (TBSS). Forward selection identified LOI, PAR and TBSS as significant environmental variables for the later ordination analysis and variation partition methods. Spatial variables PCNM1, PCNM2, PCNM3 and PCNM4 were calculated and all four variables were included in the later analysis. RDA captures the variance in the species-environment and space relationship quite well; 77.3% by the first two axes (Tab. 2). The first ordination axis was negatively related to LOI (r = – 0.772) and PAR (r = –0.437). PAR, TBSS, PCNM1 and PCNM 3 were positively related to axis 2.

Tab. 2. Summary statistics for the first four axes of the redundancy analysis (RDA) of diatom-environment and space with Hellinger transformation of diatom species, z – standardization of environmental variables and down-weighting of rare species. Only environmental variables selected in the forward selection procedure are presented in the ordination. TBSS = theoretical bottom shear stress, LOI = loss of ignition, PAR= photosynthetically active radiation, PCNM = principal coordinates of neighbour matrices.

Axes	1	2	3	4
Eigenvalue:	0.184	0.094	0.036	0.018
Species-environment and space correlations:	0.858	0.75	0.705	0.669
Cumulative percentage variance				
of species data:	18.4	27.8	31.3	33.1
of species-environment and space relation:	51.2	77.3	87.2	92.2
Weighted correlation with species axes				
TBSS	0.005	0.311	0.610	–0.050
PAR	–0.437	0.456	–0.097	0.061
LOI	–0.772	–0.203	–0.105	0.103
PCNM1	0.262	0.314	–0.390	0.406
PCNM2	0.196	0.019	0.312	0.327
PCNM3	–0.157	0.378	–0.181	–0.284
PCNM4	0.139	0.128	–0.188	–0.179

Variation partitioning

The variation in surface sediment diatom assemblages was partitioned into four parts: environmental variation (E), spatial variation (S), spatially structured environmental variation (ES) and unexplained variation (U). Their respective percentages were 27.3%, 8.6%, 4.8% and 59.3%.

Discussion

Spatial distribution of surface sediment diatoms

Georeferencing and organized sampling techniques are of major benefit in assessing the spatial distribution of modern diatoms in a lake (Watts and Halliwell 1996). For the Round Loch of Glenhead these techniques have demonstrated major differences in the distribution of benthic diatoms according to species and to spatial location. *Tabellaria quadriseptata* occurred almost evenly everywhere in the loch. Although it can be transported around the lake basin, its wide spatial distribution indicated that it could be a habitat generalist taxon. On the other hand, there were clearly patchy distributions of *Navicula madumensis*, *Brachysira brebissonii*, *Eunotia vanheurckii* var. *1* and *Aulacoseira perglabra*. The reasons for the different spatial distribution of surface sediment diatom assemblages are discussed below.

In Lake Salkolanjärvi, results indicated that water depth was the main environmental variable controlling the distribution of surface sediment diatoms (KAUPPILA 1998). Arguably, water depth is an integrated variable, correlated directly or indirectly with light, temperature and other environmental variables. In this study, underwater light PAR and water temperature, rather than water depth, were considered. RDA indicated that there was a significantly negative correlation between LOI and RDA axis 1 ($r = -0.77$), suggesting the influence of substrate on the diatom assemblages. *Eunotia vanheurckii* var. 1 is a typical epipsammic diatom in upland lochs (ALLOTT 1991). One of its aggregation areas was a sandy area in the loch (Fig. 3) and this patchy distribution probably supports the influence of substrate on the distribution of this diatom.

PAR correlated to RDA axis 1 and 2. PAR is a major regulator of photosynthesis and consequently plays an important role in driving algal productivity and determining species composition in lakes (HILL 1996). TBSS correlated to axis 2, indicating the influence of wind stress on the spatial distribution of diatoms in the loch. Although the GAM that fitted the distribution of *Tabellaria quadriseptata* did not include TBSS, wind and wave action may be responsible for the relatively even distribution of this species. *Aulacoseira perglabra*, a planktonic diatom species, is not found living in the loch today (e.g. JONES 1987, ALLOTT 1991, YANG 2009), but was abundant in the early Holocene (JONES 1987). The current occurrence of these diatoms in the deeper water surface sediments are probably the result of sediment resuspension processes from the exposure of old sediment surfaces in this region of the loch. The GAM models that fitted *Aulacoseira perglabra* included TBSS, supporting this interpretation. Comparisons between the distribution of macrophytes and surface sediment diatoms show no clear relationship, probably because the epiphytic diatoms were removed and re-distributed effectively by water turbulence.

The influence of spatial variables

Although the role of spatial variables is increasingly recognised in the ordination analysis of organism composition (e.g. WAGNER 2003, BORCARD et al. 2004, BEISNER et al. 2006), spatial variables have seldom been considered in the analysis of diatom distributions. Spatial structures observed in floristic composition can arise from: (1) autogenous structure (S), independent of any environmental variation; and (2) exogenous structure (ES), which results when species respond to environmental variables that are themselves spatially structured (FORTIN and DALE 2005, JONES et al. 2008). Before the introduction of the variation partition technique (BORCARD et al. 1992), S and ES were not distinguished and both considered together as spatial variables in most studies. In the present study, we can extract the variation explained commonly by environmental and spatial variables (ES) by partial ordination analysis. The result indicates that 36% (=4.8/(4.8+8.6)) of the variation in the spatial sub-models was due to environmental interaction. The contribution of unique spatial variables to the total variability of the surface sediment diatom assemblage was only 8.6%. However, although this is a relatively small figure the result highlights the importance of considering spatial variables separately from environmental variables in accounting for variability in surface sediment diatom composition. The small value of total diatom variation explained by spatial structure alone (8.6%) suggests that no significant unique spatial-structuring of diatom variation was missed in the Round Loch of Glenhead. The positive relationship between both PCNM1 and PCNM3 and RDA species axis 2 (Tab. 2) confirmed the influence of spatial variables on surface sediment diatom composition. The unique spatial pattern (S) is more important to species that are habitat generalists or that aggregate in habitat patches (CRIST et al. 2006).

Further research

In this study, the combined contribution of environmental and spatial variables to the variation in diatom composition was only 40.7%. The high unexplained contribution may result from both insufficient measurement of variables and the limitations of using a single time period for sampling in a system that is quite dynamic (BEISNER et al. 2006). In addition the factors that control the distribution of dead cells from living ones will differ. In the case of dead cells it is important to understand the taphonomic processes that control the transport, deposition and resuspension of cells across the lake basin, and in the case of living cells diatom distributions may be controlled as much by seasonal variability in hydrochemistry and by grazer suppression as by water depth and habitat (KOETSIER 2005). Identifying the factors that control diatom distributions across lake basins with respect to both living and dead cells remains an important area for research (YANG et al, in preparation). This is relevant to attempts to improve the design of field sampling programmes, especially those that aim to characterise the floras of a whole lake rather than of a localised sampling site within a lake.

Conclusions

Study of the spatial distribution of surface sediment diatoms in the Round Loch of Glenhead has indicated that many taxa (*Navicula madumensis*, *Brachysira brebissonii*, *Aulacoseira perglabra* and *Eunotia vanheurckii* var. 1, in particular) were unevenly distributed in the loch. The results of ordination analysis showed that LOI and PAR were negatively correlated to RDA diatom variation axis 1, while PAR, TBSS and the spatial variables (PCNM 1 and PCNM3) were positively correlated with axis 2. These observations suggest that substrate, wind-induced water turbulence and the spatial configuration of the loch basin significantly influence benthic diatom distributions in the loch. We conclude that the distribution of diatom taxa is related to the habitats in the lake as well as to transport processes and sediment resuspension. In the case of *Aulacoseira perglabra*, resuspension of diatom valves from exposed old sediment surfaces is suspected.

Unique spatial variables, not considered in former studies on diatom distribution, explained 8.6% of the total variability of the surface sediment diatom composition. Although this value is not very high, the result confirmed the importance of spatial variables independent of environmental variables in explaining the variability in surface sediment diatom composition.

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