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Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles of habitat, lake morphology, aquatic chemistry and sediment composition

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Abstract Macroinvertebrates are one of the key components of lake ecosystems and are required to be monitored alongside other biological groups to define ecological status according to European Union legislation. Macroinvertebrate communities are highly variable and complex and respond to a diverse series of environmental conditions. The purpose of this study was to examine the relative importance of environmental variables in explaining macroinvertebrate abundance. A total of 45 sub-alpine lakes were sampled for macroinvertebrates in the shallow sublittoral. Environmental variables were grouped into four types: (1) aquatic physical and chemical parameters, (2) littoral and riparian habitat, (3) lake morphometric parameters and (4) sediment chemical characteristics. Nonparametric multiplicative regression (NPMR) was used to model the abundance of individual macroinvertebrate taxa. Significant models were produced for nine out of the 24 taxa examined. Sediment characteristics were the group most frequently included in models and also the factors to which taxa abundance was the most sensitive. Aquatic physical and chemical variables were the next group most frequently included in models although chlorophyll *a* was not included in any of the models and total phosphorus in only one. This indicates that many taxa may not show a direct easily interpretable response to eutrophication pressure. Lake morphometric factors were included in several of the models although the sensitivity of macroinvertebrate abundance tended to be lower than for sediment and aquatic physical and chemical factors. Habitat factors were only included in three models although riparian vegetation was found to have a significant influence on the abundance of *Ephemera danica* indicating that ecotone integrity is likely to play a role in its ecology. Overall, the models tended

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to be specific for species with limited commonality across taxa. Models produced by NPMR indicate that the response of macroinvertebrates to environmental variables can be successfully described but further research is required focussing in more detail on the response of key taxa to relevant environmental parameters and anthropogenic pressures.

Keywords Lake macroinvertebrates ·
Sub-alpine lakes · Nonparametric multiplicative regression · Water Framework Directive

Introduction

Macroinvertebrate communities in lakes constitute a significant biomass and play an important role in overall production (James et al., 1998). The current legislative structure for managing inland, transitional and coastal waters in Europe is the Water Framework Directive (WFD: Directive, 2000). This requires that lake macroinvertebrates are included in monitoring programmes alongside other biological elements. Three aspects of the macroinvertebrate community are referred to in the WFD: taxonomic composition and abundance, diversity and the ratio of sensitive taxa to insensitive taxa (Annex 5). Monitoring and ecological assessment must be targeted to detect anthropogenic induced changes in these aspects away from minimally disturbed reference conditions. The current approach is to develop assessment systems based on a biological element tailored to detect a response to a specific pressure (Free et al., 2006; Lyche Solheim & Gulati, 2008; Tóth et al., 2008). However, for littoral and sublittoral macroinvertebrates there are currently no established metrics that meet the directives requirements and often variation in macroinvertebrate communities or metrics remains poorly explained (Moss et al., 2003; O'Toole et al., 2008). Several reasons may explain this, such as the high habitat variability and complex communities with variable lifecycles having a heterogeneous distribution within lakes (Jokinen, 1985; Moss et al., 2003; White & Irvine, 2003). In addition, important controlling variables may be frequently overlooked such as the influence of the riparian in allochthonous carbon contribution to the littoral zone (France, 1995). A prerequisite to developing an assessment system must be to develop a greater understanding of what environmental variables macroinvertebrate species respond to. This must include an examination of variables associated with natural variation as well as those likely to be indicative of anthropogenic influence.

Aquatic chemistry variables are frequently used to explain the variation in macroinvertebrate communities in aquatic ecosystems (Heino, 2000). Alkalinity has been shown to be significant in determining the littoral community composition of lakes close to reference condition (Little et al., 2006) and also as a significant covariate affecting the response of many ecological assessment metrics when tested alongside variables indicative of eutrophication such as total phosphorus and chlorophyll *a* (O'Toole et al., 2008). The influence of total phosphorus on eulittoral macroinvertebrate communities has been found to vary depending on habitat sampled: being important on sandy substrates but less important than wind exposure on reed and stone habitats (Brauns et al., 2007a). The responses of macroinvertebrates to trophic state are likely to be indirect and modified by the influence of other factors such as fish, oxygen dynamics and macrophytes (Langdon et al., 2006). Macrophyte diversity tends to show a unimodal response to eutrophication, and this may elicit a similar response for macroinvertebrate communities as macrophytes provide shelter, habitat and refuge from predators, and moreover act as a food source (Weatherhead & James, 2001; Declerck et al., 2005; Rennie & Jackson, 2005; Free et al., 2006; Penning et al., 2008). Macrophytes have been found to be the biological group most useful in explaining taxa richness in lakes and have been associated with macroinvertebrate diversity (Palmer, 1981; Declerck et al., 2005; Free et al., 2009).

The unique habitat represented by the land water interface (ecotone) is a zone of change extending from the near shore littoral to the riparian zone above the bank and typical water level. This zone has been identified as an important hydromorphological component supporting ecological quality and is subject to anthropogenic pressures that can alter the nature and flow of energy and material to lakes (Naiman & Décamps, 1997; Ostendorp, 2004; Ostendorp et al., 2004; Rowan et al., 2006). An increased proportion of shoreline development has been associated with an increase in abundance of Chironomidae in the littoral while other macroinvertebrate groups decline (Brauns et al., 2007b). Macroinvertebrates may therefore prove

to be a useful group to use to assess habitat loss associated with shoreline development. Similarly, artificial water level fluctuations can lead to habitat alteration in the littoral resulting in significant changes in the macroinvertebrate community (Brauns et al., 2008; Mastrantuono et al., 2008). However, few studies to date have addressed the need to develop a greater understanding of the role of shoreline hydromorphological modification on lake biota (Ostendorp, 2004; Rowan et al., 2006).

At a smaller scale, the habitat provided by the substrate plays an important role in determining species composition. The evaluation of sediment chemical characteristics such as nutrients and metal concentration can provide highly informative time-integrated data on pressures affecting lakes and their catchments (Premazzi et al., 1986). However, the effects of sediment contamination on macroinvertebrates can be difficult to determine; bioassays have indicated that while a negative growth response can be observed for some species, often the higher trophic state accompanying sediment contamination can stimulate growth in other species (De Lange et al., 2005). At a larger scale, lake morphology can influence macroinvertebrates with both exposure and habitat richness increasing with lake area, while the relative importance of the catchment and riparian zone decreases (Spence, 1982; Vestergaard & Sand-Jensen, 2000; Trigal et al., 2007). Depth is one of the strongest gradients structuring macroinvertebrates in lakes and is often closely related to oxygen concentration (Jónasson, 1978; Rossaro et al., 2007).

The relative sensitivity of macroinvertebrates to different pressures in different zones (littoral, sublittoral and profundal) remains unquantified (Solimini et al., 2006), but the sublittoral has typically received less attention than other zones (Bazzanti et al., 1994). This may not be justified as the sublittoral has been shown to be generally the best in detecting anthropogenic impact, at least for acidification pressure. This was largely owing to low among-year variation in metric values (Johnson, 1998). Similarly, Hämäläinen et al. (2003) found that sublittoral communities had lower variation in density and species number than deeper communities among years in a pristine lake. Such low variation in reference conditions is desirable as it makes the detection of anthropogenic impact easier and a "sufficient level of confidence about the values for the reference conditions" is required by the WFD (Annex II, 1.3). Here, data are used from the sublittoral of 45 sub-alpine lakes to examine the relative role of habitat, lake morphology, aquatic chemistry and sediment composition in determining the abundance of macroinvertebrate species using nonparametric multiplicative regression (NPMR). This will provide an indication of which environmental variables and anthropogenic pressures macroinvertebrates in the sublittoral are most responsive to.

Methods

Field and laboratory analysis

A total of 45 sub-alpine lakes were sampled in Austria, Germany and Italy. Biological samples were taken from soft sediment in the shallow sublittoral (typically at 4.5 m depth) using an Ekman grab (225 cm^2). The substrate sampled was typically composed of clay, silt or sand fractions. Sampling was carried out from late March to mid June 2006. Three sites around each lake were sampled with two replicates per site (6 samples per lake in total). Samples were sieved in the field using a mesh size of 250 μm. Samples were preserved in either 70% ethanol or 5% formalin. Specimens were sorted and identified to the lowest taxonomic level possible by the same group of taxonomists in the Università degli Studi di Milano minimising problems associated with varying degrees of taxonomic expertise.

Water samples were taken from a mid-lake station at three depth intervals: sub-surface, 2.5 and 5 m. Sub-surface samples for determination of total phosphorus were also taken at sublittoral sites. On site measurements were made of temperature, oxygen, pH, conductivity and Secchi depth from mid-lake samples. Alkalinity was measured by titration with H_2SO_4 according to Mackereth et al. (1989) or HACH (1997). Chlorophyll a was measured spectrophotometrically following hot methanol extraction (Standing Committee of Analysts, 1980). Total phosphorus was measured according to Eisenreich et al. (1975). Sediment samples (100 g) were also taken from each of the sublittoral stations and dried at 40°C. The sample was then sieved through a 2-mm mesh and ball-milled. Loss on ignition was measured at 550°C according to Heiri et al. (2001). Sub-samples were processed for determination of major and minor elements using

wavelength-dispersive X-ray fluorescence according to Vaccaro et al. (2007). All the laboratory analyses were carried out at the Joint Research Centre.

A habitat survey focussing on a section of littoral, shore and riparian zone adjacent to each of the three sites was carried out for each lake according to the lake habitat survey (LHS) (Rowan et al., 2004, 2006). The occurrence of 18 potential pressures within a 50 m radius of each site was recorded and summed (see Pilotto et al., 2008 for more details). The naturalness of the riparian zone was assessed using three components: (1) vegetation complexity (count of presence of up to 8 natural structural vegetation types), (2) vegetation longevity (presence of >10% cover of canopy trees >0.3 m in diameter) and (3) naturalness of land cover (cover was assessed as being subject to intensive anthropogenic management or as near-natural). Each component was equally weighted and the sum was expressed on a scale from 0 to 1 (Pilotto et al., 2008). The occurrence of up to ten macrophyte groups was recorded using a 5-point scale of cover on the LHS field survey forms. From this, an indicator of overall macrophyte abundance was estimated by cubing each cover category followed by addition. This was done to obtain closer approximate cover values from the five categories. The lake habitat survey involved recording details on a large number (76) of categories from the sites. In addition to the three summary parameters mentioned above, additional variables recorded by the lake habitat survey were selected for inclusion in statistical analysis by screening using NPMR. Variables that were identified as having the best fit of measured variables for any of the macroinvertebrate species recorded were selected for inclusion. The morphometric parameters: lake altitude, area and maximum depth were obtained from national authorities. The index of lake basin shape (ILBS) was calculated as maximum depth (m) divided by the square root of lake area (km^2) according to Nürnberg (1995). Slope was approximated from estimates of sublittoral site depth and distance from the shore measured during the lake habitat survey.

Statistical analyses

Nonparametric multiplicative regression was used to model species responses to environmental variables. NPMR has the capacity to deal with quantitative and categorical variables and can define complex response surfaces using predictors in a multiplicative rather than in an additive way (McCune, 2006a). The technique has recently been applied to model the response of lichens to climate change (Ellis et al., 2007) and the distribution of tree species (Yost, 2008). NPMR was applied to 29 macroinvertebrate taxa from 134 sites using the software HyperNiche version 1.12 (McCune & Mefford, 2004). Infrequently occurring taxa, found in less than 10 samples, were excluded from analysis. The response of each taxa was estimated using a local mean multiplicative smoothing function with Gaussian weighting. Models of taxa abundance were produced by adding predictors stepwise with fit expressed as a cross-validated R^2 ($\times R^2$). In order to ensure parsimonious models, additional variables were added only if a 5% improvement in $\times R^2$ was achieved. Models were evaluated using a computationally intensive Monte Carlo procedure where abundance was randomised, the procedure rerun, and the proportion of models (with the same number of predictors) with an $\times R^2$ greater than or equal to the original model evaluated. The sensitivity, a measure of influence of each parameter included in the model, was estimated by altering the range of predictors by ± 0.05 (i.e. 5%) with resulting deviations scaled as a proportion of the observed range of the response variable. This means that a value of 1 would correspond to change of equal magnitude in response and predictor variables. A principal components analysis (PCA) was performed on log $(x + 1)$ transformed data (with the exception of pH) to show relationships among environmental variables using PC-ORD Version 5 (McCune & Mefford, 2006). The 34 environmental variables selected for model development were grouped into four types: (1) aquatic physical and chemical variables, (2) habitat (littoral and riparian characteristics derived from a lake habitat survey), (3) lake morphometric parameters and (4) sediment characteristics (Table 1).

Results

A total of 270 biological samples were analysed from the 45 lakes where 10,996 individuals were counted and identified to species or a higher taxonomic level. Ninety-seven taxa were found, the group containing

Table 1 Summary statistics for environmental variables included in model development

Variable	Abbreviation	Type	Min.	Median	Mean	Max.
Temperature (°C)	Temp.	Aquat.	8.7	13.3	14.1	22.6
O_2 saturation (%)	Oxy.%	Aquat.	36	105	105	136
Total phosphorus at site (μg l^{-1})	TP_site	Aquat.	2	11	16	111
pH	pH	Aquat.	7.5	8.3	8.3	8.8
Conductivity (μS cm^{-1})	Cond.	Aquat.	133	348	340	563
Alkalinity (meq l^{-1})	Alk.	Aquat.	1.1	3.5	3.4	5.3
Secchi depth (m)	Secchi	Aquat.	1.3	3.5	4.2	11.0
Chlorophyll a (μg l^{-1})	Chl_a	Aquat.	0.2	2.7	4.3	36.4
Woody shrubs & seedlings <0.5 m in height (cover)	Shrub <.5	Habitat	0	0	0.2	3
Artificial land type (cover)	Artificial	Habitat	0	0	0.2	4
Emergent reeds/sedges/rushes (abundance)	Reeds	Habitat	0	2	1.7	4
Macrophyte abundance	Mac.abun	Habitat	0	8	16.8	72
Anthropogenic pressures in riparian (sum of count)	Pressures	Habitat	0	1	1.5	6.5
Naturalness of site's riparian	Naturaln	Habitat	0	0.5	0.4	1
Site depth (m)	Site_Z	Morpho.	3.3	4.5	4.5	6
Altitude (m)	Altitude	Morpho.	74	503	462	893
Area (km^2)	Area	Morpho.	0.2	1.4	2.6	10.8
Depth at mid lake (m)	Depth_ML	Morpho.	6	23	26	62
Slope (%)	Slope	Morpho.	0	30	30	90
Mean depth/square root of lake area	ILBS	Morpho.	5.2	17.2	21.7	84
Loss on ignition at 550°C (%)	LOI550	Sed.	1.4	8.8	11.9	64
Ca (wt%)	Ca	Sed.	1.1	24.8	21.6	34.3
K (wt%)	K	Sed.	0.01	0.45	0.59	2.26
Mg (wt%)	Mg	Sed.	0.3	1	1.3	8.7
S (wt%)	S	Sed.	0.05	0.24	0.3	1.18
P (wt%)	P	Sed.	0.01	0.07	0.07	0.23
Pb (mg/kg)	Pb	Sed.	25	39	48	137
Zn (mg/kg)	Zn	Sed.	5	43	75	439
Cu (mg/kg)	Cu	Sed.	<2	13	22	237
Ni (mg/kg)	Ni	Sed.	<2	11	25	153
Cr (mg/kg)	Cr	Sed.	<2	1	30	230
Al (wt%)	Al	Sed.	<0.002	0.9	1.6	8
Co (mg/kg)	Co	Sed.	<1.0	3	5	26
As (mg/kg)	As	Sed.	<7	<7	18	85

Variables are grouped into four types: Aquat. = aquatic physical and chemical parameters, Habitat = littoral and riparian characteristics derived from a lake habitat survey, Morpho. = Lake morphometric parameters, Sed. = sediment chemical characteristics

the most taxa were the Chironominae with a total of 32 taxa identified. The Tubificidae were the most abundant group accounting for 45% of the individuals found. On average, 16 taxa were found per lake with species richness ranging from 7 to 38 taxa. Fifty-four percent of the taxa found occurred rarely, being found in three or less of the 45 lakes.

Summary statistics for environmental variables included in model development are listed in Table 1. Typically (in ≥90% of cases) the sub-alpine lakes

sampled were of medium size (0.4–11 km^2), high alkalinity (>1.9 meq l^{-1}), mid altitude (214–725 m) and medium depth (mid-lake depth typically 8–52 m). A PCA was preformed to show relationships among environmental variables (Fig. 1). The majority of the sediment chemistry variables were positioned along axis 1 of the PCA. This axis also represented a gradient of decreasing organic matter content (LOI550: loss on ignition at 550°C) and increasing Ca concentration from left to right in the ordination. Axis 2 was most strongly ($r \geq 0.55$) correlated with the morphometric parameters ILBS and lake depth in addition to the aquatic physical and chemical parameters Secchi depth, TP and chlorophyll *a*. The third axis (not presented) was most highly correlated to lake area and loss on ignition at 550°C.

The NPMR models were run for the 29 taxa that occurred most frequently (occurring in ≥10 samples, Table 2). A total of nine models had a $P < 0.05$, while two had a $P = 0.10$. The environmental variables included in models were not consistent across macroinvertebrate taxa indicating that they were responsive to a diverse series of factors. *Pisidium casertanum* (Poli) had a $\times R^2$ of 0.62 with five variables being included in the model but having the highest sensitivity value for K (0.19) which was highly negatively correlated to Ca ($r = -0.83$, Fig. 1). The amount of artificial land cover in the riparian was also significant for *P. casertanum* as it was for *Polypedilum nubeculosum* (Meigen) but both taxa had a very low sensitivity to this factor (<0.01). The only other habitat factor that was included in any of the other significant models was the riparian cover

Fig. 1 Axis 1 and 2 of PCA of log transformed environmental variables. Axis 1 and 2 represented 26.9 and 11.5% of variation, respectively. Abbreviations are listed in Table 1. The numbers in parentheses indicate the frequency with which each variable was included in significant NPMR models
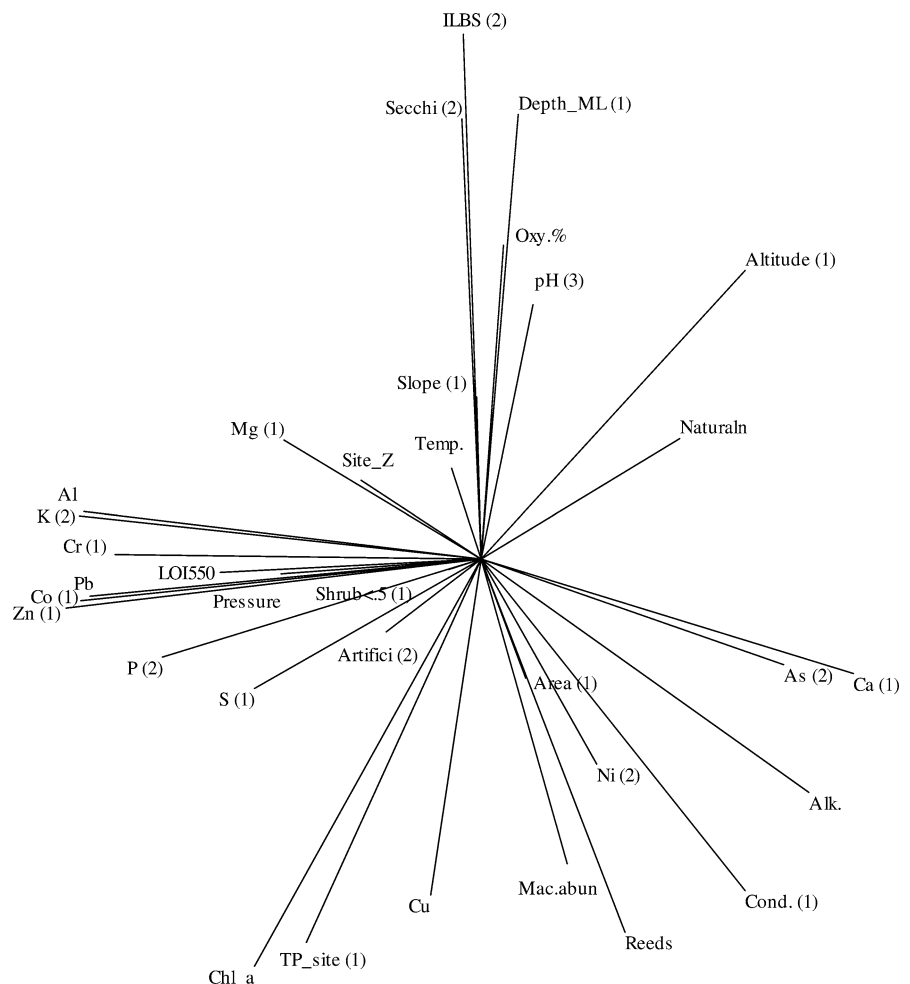
Table 2 Results of NPMR models for macroinvertebrate taxa

Taxa	$\times R^2$	P	Var. 1	Tol.	Sen.	Var. 2	Tol.	Sen.	Var. 3	Tol.
Ablabesmyia spp.	0.12	0.19	Altitude	41.0	1.70	Chl_a	1.8	1.25		
Cladotanytarsus spp.	0.12	0.48	Reeds	0.6	0.25	Secchi	2.9	0.11	Pb	5.6
Psectrocladius spp.	0.02	0.76	Depth_ML	5.6	0.77	S	0.1	1.36		
Sialis spp.	0.04	0.43	LOI550	3.1	0.93	ILBS	15.8	0.47		
Tub.ha + t	0.05	0.33	Temp.	2.8	0.29	Alk.	0.2	0.98		
Chironomus anthracinus	0.03	0.24	Temp.	2.1	0.24	Pressure	0.3	0.51		
Asellus aquaticus	0.69	0.10	Temp.	1.4	0.09	Chl_a	5.4	0.02	Depth_ML	13.9
Pisidium casertanum	0.62	**<0.05**	Artificial	0.2	0.00	K	0.1	0.19	Mg	3.4
Procladius choreus	0.08	0.43	LOI550	6.3	0.91	Slope	0.1	0.68		
Ephemera danica	0.34	**<0.05**	Shrub <.5	0.9	0.04	Area	2.1	0.18	Cond.	42.9
Cryptochironomus defectus	0.13	0.48	Mg	0.4	1.25	P	0.0	0.73	Ni	15.2
Einfeldia dissidens	0.26	0.43	Shrub <.5	0.6	0.03	Secchi	1.9	0.09	Ca	11.6
Chaoborus flavicans	0.67	**<0.05**	TP_site	10.9	0.09	Secchi	0.5	0.13	Co	3.8
Tanytarsus gregarius	0.32	0.24	LOI550	3.1	0.26	Temp.	2.78	0.04	Shrub <.5	1.8
Limnodrilus hoffmeisteri	0.88	0.14	Area	1.6	0.01	K	0.2	0.05	Co	1.3
Dicrotendipes nervosus	0.32	0.19	Temp.	1.4	0.13	Depth_ML	11.1	0.06	Mg	4.2
Paralauterborniella nigrohalteralis	0.03	0.52	Pb	5.6	2.66	Slope	0.1	0.65		
Polypedilum nubeculosum	0.52	**<0.05**	Artificial	0.2	0.00	pH	0.8	0.01	Depth_ML	5.6
Erpobdella octoculata	0.00	**<0.05**	K	0.9	0.10	P	0.0	0.39		
Glyptotendipes pallens	0.78	**<0.05**	Secchi	0.5	0.08	Ca	18.2	0.00	S	0.1
Conchapelopia pallidula	0.36	0.24	LOI550	6.3	0.18	Reeds	0.2	0.00	Depth_ML	36.1
Microtendipes pedellus	0.75	0.10	Area	1.1	0.09	S	0.1	0.22	P	0.0
Chironomus plumosus	0.19	0.19	P	0.0	0.13	Zn	195.3	0.02	Cu	11.8
Dreissena polymorpha	0.06	0.62	As	4.1	0.64	Slope	0.1	0.33		
Pseudochironomus prasinatus	0.29	0.29	Secchi	1.0	0.26	Pb	33.6	0.03	Naturaln	0.1
Branchiura sowerbyi	0.26	**<0.05**	P	0.0	0.12	Zn	86.8	0.10		
Bithynia tentaculata	0.05	0.19	Shrub <.5	0.5	0.01	Co	2.6	0.03		
Ceratopogonidae	0.56	**<0.05**	Altitude	81.9	0.19	pH	0.1	0.44	Ni	30.4
Cladopelma viridula	0.03	**<0.05**	pH	0.1	0.09	Slope	0.1	0.05		

Table 2 continued

Taxa	Sen.	Var. 4	Tol.	Sen.	Var. 5	Tol.	Sen.	Var. 6	Tol.	Sen.
Ablabesmyia spp.										
Cladotanytarsus spp.	1.20									
Psectrocladius spp.										
Sialis spp.										
Tub.ha + t										
Chironomus anthracinus										
Asellus aquaticus	0.03	Mg	1.3	0.06	S	0.3	0.01	Natural n	0.2	0.03
Pisidium casertanum	0.01	Ni	98.8	0.01	ILBS	23.6	0.01			
Procladius choreus										
Ephemera danica	0.33	As	8.2	0.46						
Cryptochironomus defectus	0.56									
Einfeldia dissidens	0.04	Pressure	0.3	0.19						
Chaoborus flavicans	0.09									
Tanytarsus gregarius	0.00	Altitude	204.8	0.07	Cond.	64.4	0.09			
Limnodrilus hoffmeisteri	0.19									
Dicrotendipes nervosus	0.01	Al	0.8	0.14						
Paralauterborniella nigrohalteralis										
Polypedilum nubeculosum	0.16	As	8.2	0.10	ILBS	11.8	0.08			
Erpobdella octoculata	0.13									
Glyptotendipes pallens	0.01	S	0.3	0.06	Pressure	1.3	0.04			
Conchapelopia pallidula	0.04	As	40.8	0.01						
Microtendipes pedellus	0.35	Pressure	2.3	0.02						
Chironomus plumosus										
Dreissena polymorpha										
Pseudochironomus prasinatus	0.33									
Branchiura sowerbyi										
Bithynia tentaculata										
Ceratopogonidae	0.08	Cr	45.8	0.05						
Cladopelma viridula										

Abbreviations of environmental variables are listed in Table 1. Tub.ha + t = sum of *Ilyodrilus templetoni* + *Potamothrix hammoniensis*. Significant models are highlighted in bold

$\times R^2$ cross-validated R^2, *Var.* variable, *Tol.* tolerance, *Sen.* sensitivity

of woody shrubs & seedlings (<0.5 m in height) which was significant but with a low sensitivity (0.04) for the mayfly *Ephemera danica* Müller (Table 2). *E. danica* was found to have higher sensitivity values for As, conductivity and lake area, in descending order. The influence of As appeared counterintuitive when response curves (not presented) were examined, in which high As values corresponded to high nymph abundance.

Chaoborus flavicans (Meigen) differed from the other taxa in being more sensitive to aquatic physical and chemical parameters used to indicate eutrophication: total phosphorus (TP) concentration and Secchi depth in addition to Co (Table 2). *Glyptotendipes pallens* Meigen was also modelled by Secchi depth along with Ca and S. Models for two taxa, *Cladopelma viridula* (L.) and *Erpobdella octoculata* (L.), had a very poor $\times R^2$ of 0.03 and <0.01, respectively. *Branchiura sowerbyi* Beddard was modelled by two sediment chemical characteristics P and Zn. Despite altitude often being a surrogate of anthropogenic pressure and other environmental parameters such as temperature it was only included once in a model for Ceratopogonidae which largely occurred in lakes below 500 m in altitude. Models developed for two taxa, *Asellus aquaticus* (L.) and *Microtendipes pedellus* (De Geer) had a *P* of 0.10 but nonetheless when plots of observed versus estimated abundance are examined the predictions are of similar quality to models with $P < 0.05$ (Fig. 2).

Out of the nine significant models the frequency of inclusion of environmental variables for the four groups was habitat: 3, lake morphology: 6, aquatic physical and chemical parameters: 7 and sediment chemical composition: 14 (Table 2). The numbers in parentheses in the PCA diagram (Fig. 1) indicate the frequency with which each variable was included in models. Most of the sediment chemistry variables that were included in models occurred along axis 1 of the PCA. Whereas the majority of lake morphology and aquatic chemistry variables included were most highly correlated to axis 2.

An examination of the relative importance of environmental variables across a series of taxa can be achieved by summation of the sensitivity of variables included in significant models (Ellis et al., 2007). Figure 3 shows the sum of sensitivity for the four groups of variables included in model development. Overall macroinvertebrates appeared to be most

sensitive to sediment chemistry. Some physical and chemical variables such as pH and conductivity had relatively high levels of sensitivity while others indicative of eutrophication such as TP and chlorophyll *a* recorded low values. Overall habitat variables, including macrophyte abundance, were rarely included in models and had low sensitivity. In contrast, all of the morphometric parameters were included in at least one model although sensitivity tended to be lower compared with some of the aquatic and sediment chemical parameters.

Discussion

The 45 lakes examined represented a limited environmental gradient in having similar typological parameters of high alkalinity, medium size, medium depth and occurring at a sub-alpine altitude range. They were however, subject to a range of pressures having total phosphorus concentrations up to 111 μg l^{-1}, and many had significantly altered riparian zones. While the limited typology is likely to limit the widespread use of models and limit the applicability of conclusions it would be expected that this would make the effect of pressure across lakes of a similar typology more apparent. However, despite eutrophication being one of the principal pressures affecting sub-alpine lakes (Salmaso et al., 2007), little direct evidence was found to indicate that many macroinvertebrate species in the sublittoral showed a clear response to this pressure. Chlorophyll *a* was not included in any of the significant models and TP in only one (Table 2). However, some species may respond more clearly than others to eutrophication. The model for *Chaoborus flavicans* included TP and Secchi depth. This species may be more sensitive to pelagic indicators of production owing to its coupling to the pelagic zone and has also been shown in community analysis to be one of the species most closely associated with indicators of eutrophication, being associated with high concentrations of TP and NH$_4$–N (Riccardi et al., 2002; Rossaro et al., 2007). Late summer chlorophyll *a* concentrations have been previously shown to have a strong positive relationship with the following year's chironomid biomass in the sublittoral of lake Balaton (Specziár & Vörös, 2001). This study was of a synoptic nature with data for TP and chlorophyll *a* being collected from one date only whereas ideally annual

Fig. 2 Plot of observed and estimated abundance (ind. m^2) for six species of macroinvertebrates. Abundance estimates were made using NPMR models listed in Table 2
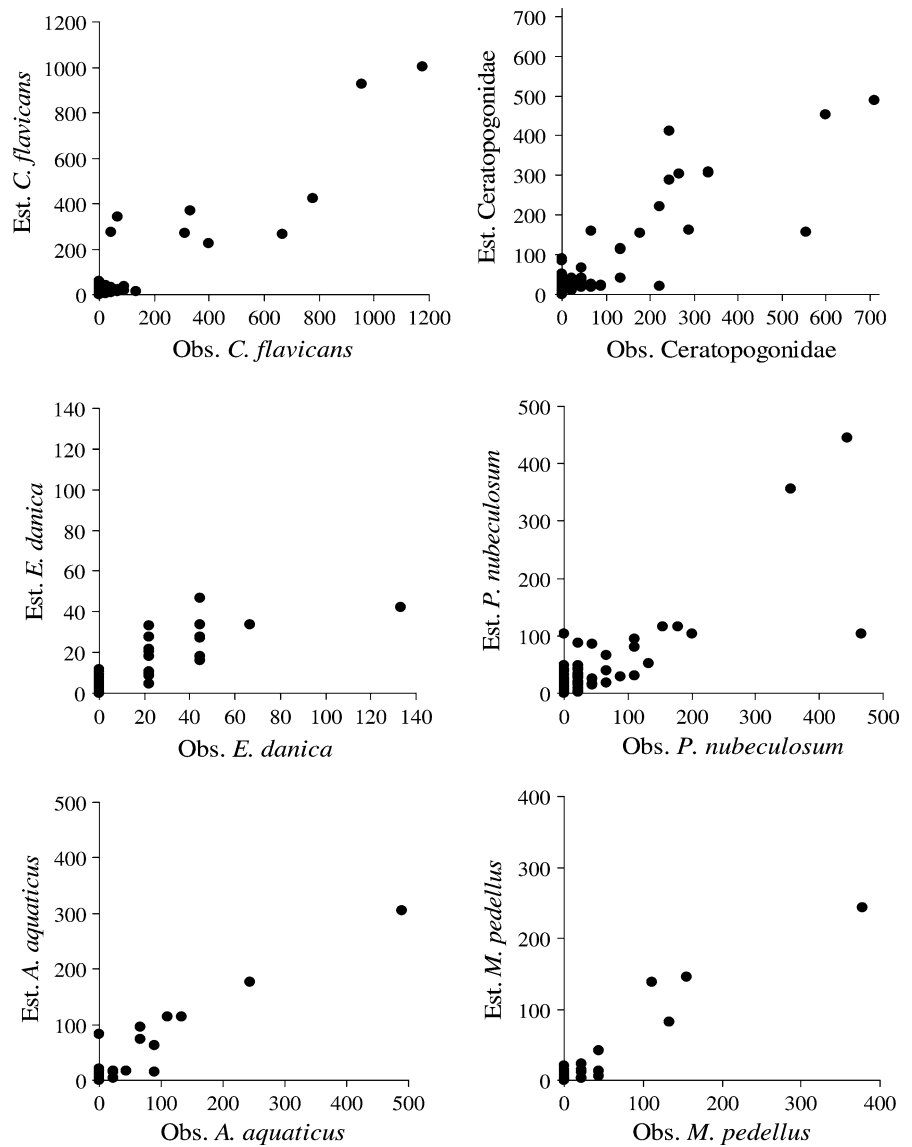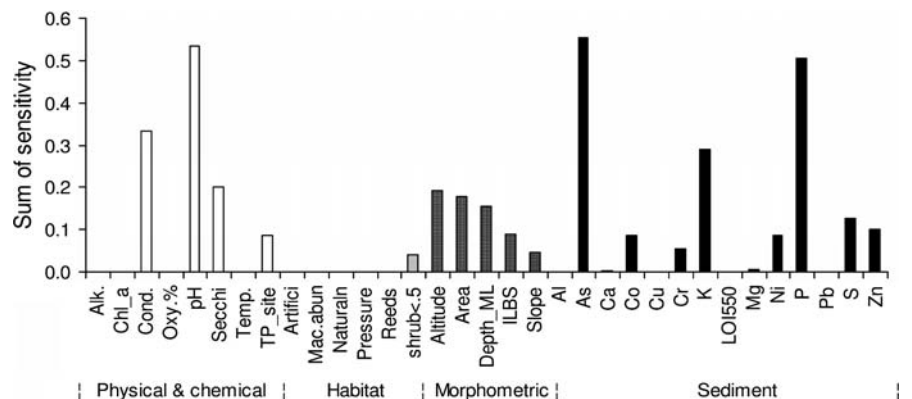

Fig. 3 Sum of sensitivity values from macroinvertebrate models for aquatic physical and chemical variables (*white*), habitat variables derived from the lake habitat survey (*grey*), lake morphometric parameters (*hatched*) and sediment chemical composition (*black*). Abbreviations of environmental variables are listed in Table 1

averages or summer averages in the case of chlorophyll *a* may have proved more suitable for modelling. Often, a clearer influence of eutrophication is found when time-series of macroinvertebrates are examined (Lods-Crozet & Lachavanne, 1994; Specziár & Vörös, 2001). The limited influence among lakes found in this study perhaps reflects the varied indirect and complex responses that occur in different lake environments.

The group of factors most frequently included in models were sediment chemical characteristics (Table 2). Most of the incorporated variables tended to be associated with axis 1 of the PCA (Fig. 1). Their inclusion likely reflects the importance of a principal gradient in sediment chemical and physical composition. Axis 1 indicated a decrease in organic matter (LOI550) content and increasing Ca concentration from left to right in the ordination. Sediment particle size, while not measured directly in this study, appeared from qualitative observations to be associated with this axis with finer sediments having a higher LOI. That many of the sediment chemical variables acted as a surrogate for a principal gradient in sediment physical and chemical composition is a more likely explanation than a direct influence of the many different elements included in models. For example, the positive relationship between *E. danica* and As concentration, while being the best parameter selected stepwise, was more likely a reflection of the associated increase in either Ca concentration or possibly sediment particle size (Fig. 1). This species has previously been associated with high alkalinity lakes (Free et al., 2006). The organic matter content of sediments was not included in any of the models, despite its potential to provide an integrative view of eutrophication and associated increased rates of sedimentation. The importance of sediment chemical composition in modelling macroinvertebrate abundance was clearly apparent, although few previous studies have typically included this information, and wavelength-dispersive X-ray fluorescence spectrometry may prove a useful tool in this regard (Vaccaro et al., 2007).

Lake morphometric factors were included in several of the models although the sensitivity of macroinvertebrate abundance tended to be lower than for sediment and aquatic physical and chemical factors. The ILBS (mean depth/square root of lake area) was significant in two models and has previously been found to be a useful indicator of anoxia

and of a lakes tendency to stratify (Nürnberg, 1995; Irvine et al., 2001). Similarly, mid-lake depth may also have been included as a surrogate for anoxia and stratification tendency, although oxygen saturation itself was not included in any models. One of the perceived benefits of sampling in the shallow sublittoral was that it would be less influenced by anoxia the relative causes of which, such as eutrophication and natural tendency to stratify, can be hard to partition. However, despite the shallow sublittoral being above the typical level of thermocline development, the role of stratification is still likely to be important as it controls the relative supply of resources from the epi- and hypolimnion to the littoral (Brodersen et al., 1998). The interpretation of the sensitivity values for the morphometric factors and other factors is also likely to be influenced by the limited typology sampled (sub-alpine lakes), and they could play a more important role when examined across diverse lake types.

Habitat variables were only included in three models and generally had low sensitivity values. The riparian cover of woody shrubs & seedlings was a significant factor influencing the mayfly *Ephemera danica*. Riparian vegetation cover might be important in providing shelter from wind for adults, although Wright et al. (1981) did not find higher nymph density on a river site with trees compared to one with open grassland. However, further examination of the distribution of mayflies may reveal closer associations with riparian habitat quality/ecotone integrity as this is likely to be a key requirement for adult life stages. Other factors derived from the lake habitat survey such as the index of naturalness, which combined several aspects of riparian habitat quality, were not significant in models. One reason for this may be that macroinvertebrates in the sublittoral may be less affected than those in the shallower littoral where the input of allochthonous carbon from the riparian has been found to be significant (France, 1995). The abundance of macrophytes or reeds was also not included in any significant models. This is likely to be a result of the spring sampling strategy employed when macrophyte growth and abundance is typically much lower than in the summer months. Usually, strong associations are found between macroinvertebrates and macrophytes (e.g. France & Stokes, 1988; Weatherhead & James, 2001; Free et al., 2009).

One of the difficulties of modelling macroinvertebrates is that environmental factors may act at varying spatial scales and in ways not adequately expressed by additive models (Stoffels et al., 2005). One of the benefits of using NPMR to model species response is that the predictors are combined in a multiplicative way better allowing for interactions among predictive variables (McCune, 2006b). NPMR was used to produce significant models for nine of the 29 taxa examined. This indicates that despite the complexity of sublittoral macroinvertebrate communities, it is possible to successfully model many species and that they can be used as environmental indicators. The response to environmental variables appeared quite specific to individual species. This might allow government agencies to focus on specific groups of taxa as indicators of environmental quality, for example, using mayflies to indicate ecotone integrity or others (e.g. *Chaoborus flavicans*) as indicators of eutrophication. However, such an approach would require more comprehensive research into validating relationships. While empirical models were produced using NPMR, ultimately further research should focus on understanding functional relationships (Solimini et al., 2006).

Further study could examine the inclusion of lakes from a broader typology as well as gathering biological and environmental data more intensively over several time periods. This study, for logistic reasons, collected data from three countries from late March to mid June 2006, whereas it is desirable to have biological sampling take place over a more limited period to minimise seasonal differences. A larger data set, including lakes representative of reference conditions, could also be collected to further develop and test model predictions. As sediment composition was frequently incorporated into models, macroinvertebrates may prove useful in detecting changes in the quality and structure of lake sediment resulting from hydromorphological alterations or eutrophication. In addition, biotic interactions among the macroinvertebrate community may explain a large portion of variation and should be considered in models (Tolonen et al., 2001). Predation by fish and also by alien species of crayfish, widespread in the study area, can also exert substantial pressure on macroinvertebrates (Lewin et al., 2004; Souty-Grosset et al., 2006; Gherardi & Acquistapace, 2007; Pilotto et al., 2008). Other zones

also retain attractive features for both monitoring and model development in comparison to the sublittoral, having either higher diversity such as the littoral (Jónasson, 1978) or being useful in detecting the early signs of eutrophication such as the profundal (Bazzanti et al., 1994).

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