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PRIMARY RESEARCH PAPER

How much is enough? Adequate sample size for littoral macroinvertebrates in lowland lakes

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Abstract Littoral macroinvertebrates are increasingly used for assessing the ecological status of lakes according to the EU Water Framework Directive. This requires harmonised sampling methods, but information on the appropriate spatial scale of the sampling as well as on the adequate sample sizes are mostly lacking. In this study, we compared the spatial variability of littoral (<1.2 m water depth) macroinvertebrate community composition within habitats and within sites to test whether habitat-specific sampling can reduce their spatial variability. Furthermore, we determined the sample size necessary to obtain maximum species richness for a given habitat type. Spatial variability of macroinvertebrate community composition was significantly lower within habitats than within sampling sites, except for communities of coarse woody debris. Species–area curves revealed that a sample size of 1 m^2 per habitat was not sufficient to obtain the maximum species richness due to the dominance of rare species, which suggests that compilation of taxon inventories may require more exhaustive sampling with sampling sizes substantially larger than 1 m^2. Separate analysis for species assigned to incidence classes showed that a mean area of 0.63 m^2 per habitat is sufficient to record all species with frequent and medium incidences, and 76% of the rare species. We conclude that habitat-specific sampling is an effective way to reduce the inherent spatial variability of littoral macroinvertebrate communities and that a sample size of 0.63 m^2 per habitat is sufficient to represent their dominant and subdominant elements. The application of this adequate sample size to other lake types than large oligotrophic lakes has to be exercised with caution, in particular if community composition and richness patterns differ. However, our results are based on data from lakes that represent the typical lake type found throughout the Central Baltic ecoregion ensuring its wider applicability in this ecoregion.

Keywords Coarse woody debris · Spatial variability · Species richness · Species–area curves · Water Framework Directive

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Introduction

One of the inherent characteristics of the littoral zone is the high heterogeneity due to strong gradients of abiotic factors that govern environmental conditions within this zone. For example, the exposure of the lake to the main wind direction creates a lateral gradient of hydraulic disturbances caused by wind-induced waves (Hofmann et al., 2008). The impact of wind-induced waves gradually decreases with increasing depth creating a vertical gradient of hydraulic disturbance towards the profundal zone (Rowan et al., 1992). Along with wind exposure, sediment particle size composition and organic matter (OM) content change such that fine sediment particles and OM tend to accumulate either at wind-sheltered shorelines or in deeper littoral areas (Bloesch, 1995; Cyr, 1998). Furthermore, lateral variations of shoreline hydromorphology result in a high spatial heterogeneity that is reflected in the diversity of littoral habitats, such as submerged and emergent macrophytes, stones and sand. At lakes surrounded by forest, riparian trees provide habitats created by coarse woody debris (CWD) and submerged tree roots that further increase habitat heterogeneity and reflect a strong spatial coupling between littoral and riparian zones (Schindler & Scheuerell, 2002). The gradient of increasing spatial heterogeneity from the profundal to the littoral zone is associated with changes in composition and species richness of macroinvertebrate communities. Especially macroinvertebrate richness, abundance and biomass have been found to be higher in the littoral than in the sublittoral or profundal zone (Särkkä, 1983; Czachorowski, 1993; Stendera & Johnson, 2008). With increasing richness and abundance of littoral macroinvertebrate communities there is also an increase in the spatial variability of macroinvertebrate distribution towards the littoral zone (Dall et al., 1990; Death, 1995; Harrison & Hildrew, 2001; Stoffels et al., 2005). This heterogeneous distribution has been one of the frequently cited reasons not to incorporate littoral macroinvertebrates into lake monitoring and assessment approaches (Hellawell, 1986; Downes et al., 1993; James et al., 1998). The few studies available have shown that much of the spatial variability of littoral macroinvertebrates is associated with small-scaled spatial heterogeneity amongst littoral habitats (Tolonen et al., 2001; Weatherhead & James, 2001). This suggests that there is a need for a clear stratification by habitat when sampling for littoral macroinvertebrates. However, attempts to quantify the extent to which the spatial heterogeneity of littoral macroinvertebrate communities can be reduced by habitat-specific sampling are rare.

Another reason for the low consideration of littoral macroinvertebrates is the lack of harmonised sampling standards with regard to sampling sizes (Solimini et al., 2006) as attempts to define adequate sample sizes for macroinvertebrates in lakes are rare. Veijola et al. (1996) demonstrated that a sample size of 0.29 m^2 is sufficient for obtaining a representative sample of the profundal macroinvertebrate community associated with organic sediments. Cheruvelil et al. (2000) showed that areas of 0.41–0.63 m^2 are sufficient to representatively sample littoral macroinvertebrates associated with submerged macrophytes. These results may not be directly applicable to the other habitats found in the littoral zone as macroinvertebrate community composition and species richness differs amongst habitats (Brauns et al., 2008; Tolonen & Hämäläinen, 2010). Moreover, macroinvertebrate species richness is dependent on the spatial complexity of the habitat (Brauns et al., 2007b) such that spatially complex habitats within the littoral may have to be sampled with a higher intensity than spatially uniform profundal habitats.

The European Water Framework Directive (WFD) necessitates that the ecological status of lakes is assessed by using biological quality elements such as macroinvertebrates (European Commission, 2000). Recent studies suggest that monitoring and assessment approaches predominantly focus on the littoral zone (Irvine, 2004; Garcia-Criado et al., 2005; Brauns et al., 2007b; Donohue et al., 2009a). Hence, information on spatial variability of the macroinvertebrate community as well as on the adequate sample size required to achieve a representative sample of littoral macroinvertebrates constitutes a prerequisite for the development of WFD compliant monitoring protocols and assessment methods.

In this study, we investigated the macroinvertebrate communities inhabiting common littoral habitats at wind-exposed and wind-sheltered shorelines of two oligotrophic lowland lakes. There were two objectives to the study: First, we tested whether and to which extent habitat-specific sampling can reduce the spatial variability of littoral macroinvertebrate communities by comparing the spatial variability of macroinvertebrate community composition within habitats and within sites. Second, we determined the sample size necessary to obtain maximum species richness for a given habitat type and tested whether the derived adequate sample size differs amongst habitat types, between wind-exposed and wind-sheltered sites and between lakes.

Methods

This study was conducted at two North-German lowland lakes, Lake Stechlin (53°9′6″N, 13°1′34″E) and Lake Wittwesee (53°7′28″N, 12°56′11″E). Both are large oligo- to mesotrophic lakes with a surface area of 4.12 and 1.46 km^2, respectively. Within each lake, we established a 100-m long sampling site at the wind-exposed, northern shore and at the wind-sheltered, southern shore. The sampling sites were chosen to encompass the five major habitat types found in lowland lakes, i.e. CWD, reed (*Phragmites australis*, Cav. Trin. ex Steud.), sand, stones and submerged tree roots. This was possible for all but the wind-sheltered site at Lake Wittwesee, where the root habitat was absent. Submerged macrophytes were absent in the range of depths investigated during the study.

Macroinvertebrate samples were taken from each habitat type present at each site and lake at a water depth <1.2 m in March 2008. Our previous studies have shown that compositional dissimilarities of the littoral macroinvertebrate community between spring and autumn are negligible suggesting that the spring samples taken in this study provide a representative picture of the macroinvertebrate community of the studied lakes (Brauns et al., 2007a; Brauns et al., 2008).

Ten replicates were collected from every habitat type, with the area sampled per replicate fixed to 0.1 m^2, resulting in a total sampling area of 1 m^2 per habitat type. The habitat-specific sampling followed the description given in Brauns et al. (2007a). Briefly, samples from CWD and stones were collected by brushing off attached macroinvertebrates. Reed and root habitats were sampled using a hand net. Sand habitats were sampled using a modified Surber sampler for lentic conditions (area 0.05 m^2; 250-µm mesh). Replicate samples from each habitat, site and lake were stored separately and processed in the laboratory by sorting, counting and indentifying. The determination level was species except for Chironomidae (subfamily), remaining Diptera (family) and Oligochaeta (order). The complete species list is available upon request from the corresponding author.

Statistical analyses

Spatial variability

We analysed whether the spatial variability of littoral macroinvertebrates was lower within habitats than within sites, i.e. to which extent habitat-specific sampling can reduce the spatial variability of littoral macroinvertebrates. Spatial variability of littoral macroinvertebrate communities was expressed as the compositional dissimilarity of each replicate to its group centroid, whereas the centroid depicts the average community composition of either habitat or site. For analysis of the within-habitat variability, we used the 10 replicate samples from each habitat as statistical replicates and calculated abundance as the number of individuals/m^2 for each replicate sample. For analyses of the within-site variability, we pooled the habitat-specific replicate samples into one sample for each habitat such that habitats were replicates for the sites.

We tested whether spatial variability was larger within habitats than within sites using permutational analysis of multivariate dispersions (PERMDISP, PRIMER, Version 6, PRIMER-E Ltd., Plymouth, U.K.). PERMDISP compares the average dissimilarity of replicates to their centroid based on an F statistic and calculates significance levels by permuting the least-squares residuals (999 permutations) (Anderson, 2006). All analyses were conducted on Bray–Curtis dissimilarity matrices (Bray & Curtis, 1957) calculated from untransformed abundance data to conserve the full variability in the data.

Adequate sample size

We used a three-step procedure to determine the sample size necessary to obtain the maximum species richness for a given habitat. First, we established species–area curves for each habitat at each shoreline type and lake ($N = 19$). This analysis was supplemented by calculation of a nonparametric estimator of species richness (Chao2) as well as an estimate for the average sampling effort necessary to reach the estimated species richness (G) (Chao et al., 2009). Second, we defined that the adequate sample size should encompass a sampling area at which all frequently occurring species, all intermediately occurring species and as many rare species as possible can be obtained. Hence, we classified macroinvertebrate species into incidence classes based on their frequency of occurrence within the 10 replicate samples from each habitat, i.e. frequent species (occurred in 8–10 replicates), intermediate species (5–7 replicates) and rare species (1–4 replicates). We then constructed species–area curves for each of the three incidence classes to determine the sample size necessary to capture all species of a given incidence class. In the third step, we averaged the resulting sample size for each incidence class to derive an overall adequate sample size per habitat. We subsequently determined the proportion of total observed species richness that would have been obtained with this sampling size.

All species–area curves were established using the species-accumulation routine of PRIMER (Version 6) with 999 permutations of the initial sample order. Subsequently, we tested whether the adequate sample size and the corresponding obtained proportion of total species richness differed amongst habitat types, wind-exposed and wind-sheltered sites and lakes using Kruskal–Wallis tests followed by Dunn's multiple comparisons for habitat comparison and Mann–Whitney test for shoreline type and lake comparisons (GraphPad Prism, Version 4, GraphPad Software, Inc., La Jolla, CA, U.S.A.).

Results

Spatial variability

The analysis of the spatial variability of littoral macroinvertebrates revealed that the overall mean (±95% CI) spatial variability within sites amounted to 54.69 (±2.96) and was significantly higher (PERMDISP, $F = 6.46$, $P = 0.001$, $N = 209$) than spatial variability within habitats that amounted to 50.65 (±1.33). The reed community mainly contributed to the overall lower within-habitat variability as its spatial variability was always significantly lower within habitats than within sites (Fig. 1). Furthermore, communities from root and stone habitats had a significantly lower within-habitat than within-site variability in three out of four sites (Fig. 1). Conversely, spatial variability of littoral macroinvertebrates within CWD did not significantly differ from within-site variability at neither of the studied sites (Fig. 1).

Adequate sample size

Species–area curves did not reach their asymptotes before the sample size of 1 m^2 was reached suggesting that this area was not sufficient to capture all species potentially present in a given habitat (Fig. 2A; Table 1). Hence, percentage differences between observed and estimated species richness ranged from 40 to 93%. Calculation of the estimator for the sampling effort necessary to reach the estimated species revealed that a mean (±95% CI) additional area of 6.4 m^2 (±2.4) was necessary to capture the estimated species richness (Table 1).

Species–area curves constructed for each of the three incidence classes revealed that for the frequently occurring species, the species–area curves reached their asymptotes at a mean (±95% CI) sampled area of 0.30 ± 0.01 m^2 (Fig. 2B; Table 2). For the intermediately occurring species, a mean sampled area of 0.58 ± 0.02 m^2 was sufficient to capture all species present within this incidence class. Species–area curves for rare species showed that a mean sampled area of 1 m^2 was necessary to capture all rare species present (Fig. 2B, Table 2).

Based on the individual sample sizes for each incidence class, the overall mean (±95% CI) adequate sample size for littoral macroinvertebrates amounted to 0.63 ± 0.08 m^2 (Table 2). The corresponding proportion of total observed species richness that would have been obtained with this sample size ranged from 79 to 92%.

There were no significant differences in adequate sample sizes neither amongst habitat types (Kruskal–Wallis test, $P = 0.619$), nor types of wind exposure (Mann–Whitney test, $P = 1.000$) or between lakes (Mann–Whitney test, $P = 0.156$).

Discussion

Spatial variability

Spatial variability was always lower within a single habitat when compared to variability within a sampling site. This suggests that macroinvertebrate communities from a given habitat are rather homogenous with most habitat types supporting a distinct community. Whilst macroinvertebrate communities from reed, root and stones were homogenous,

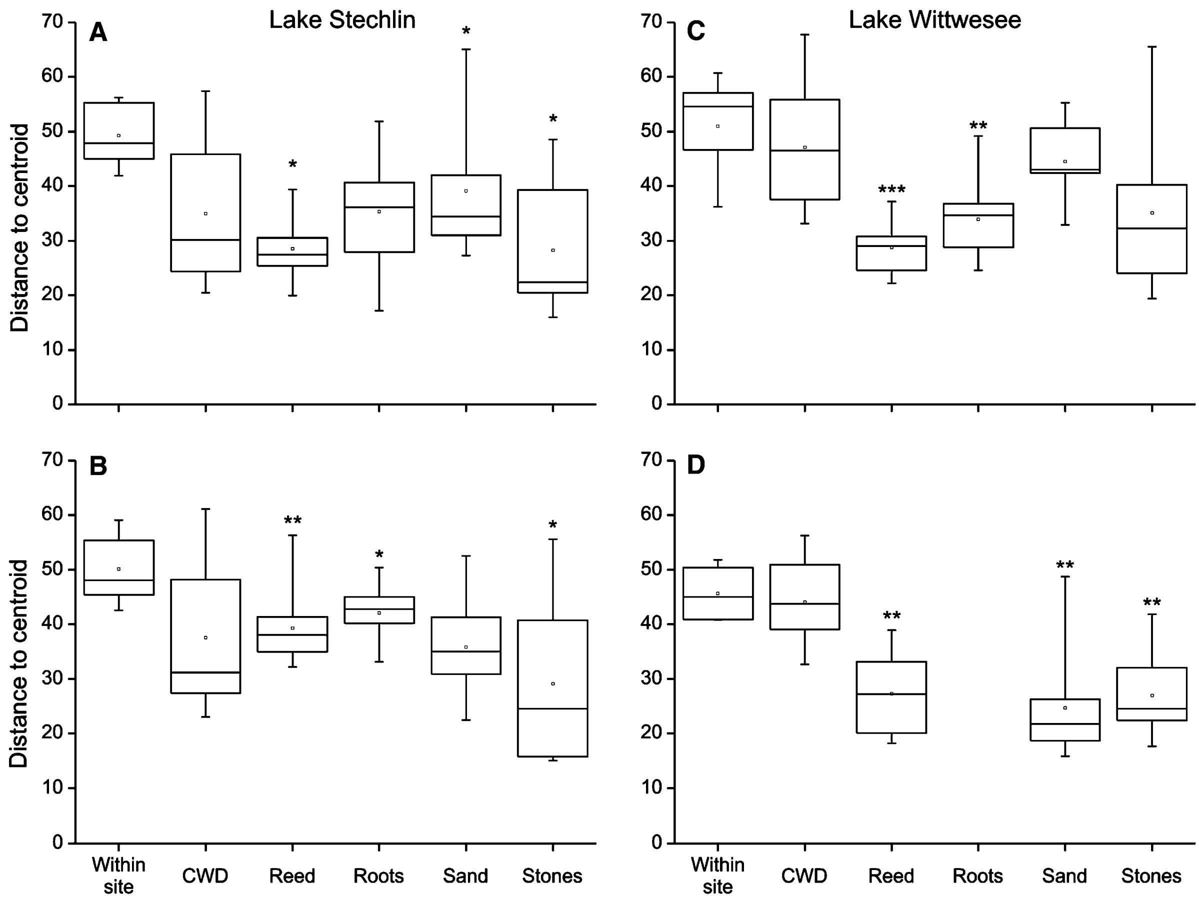

Fig. 1 Spatial variability of littoral macroinvertebrate community composition within habitats and within sites expressed as distance (Bray–Curtis dissimilarity) to group centroid at the wind-exposed (**A**, **C**) and wind-sheltered (**B**, **D**) shoreline of Lake Stechlin and Lake Wittwesee. The root habitat was absent at the wind-sheltered shoreline of Lake Wittwesee. Significant differences of within-habitat and within-site spatial variability (Permutational analysis of multivariate dispersions) are indicated by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) (*CWD* coarse woody debris)

communities of CWD appeared to be spatially more variable with no significant differences in spatial variability between habitat and sites. Thus, it seems that there is no specific macroinvertebrate community associated with CWD such that community composition may be more dependent on the location and distance of this habitat to the next habitat than to the physical properties of CWD. Nevertheless, our data show that habitat-specific sampling is an effective way to reduce the spatial variability of littoral macroinvertebrate communities which lends empirical support to previous studies that called for a sampling strategy stratified by habitat type (Tolonen et al., 2001; Weatherhead & James, 2001; Tolonen & Hämäläinen, 2010).

Adequate sample size

Species–area curves conducted for the habitat types suggested that a sample size of 1 m^2 was not enough to capture all species possibly present at a given habitat. This concurs with findings in streams demonstrating that sample sizes of more than 1 m^2 are necessary to capture all species (Vlek et al., 2006; Raunio & Anttila-Huhtinen, 2008). Our results showed that a mean total area of 6.4 m^2 would have been necessary to capture all rare species potentially present at a given habitat (Table 1). This rather large sampling size resulted mainly from the occurrence of rare species being found in one or two replicate samples per habitat only (Table 1). This finding is in

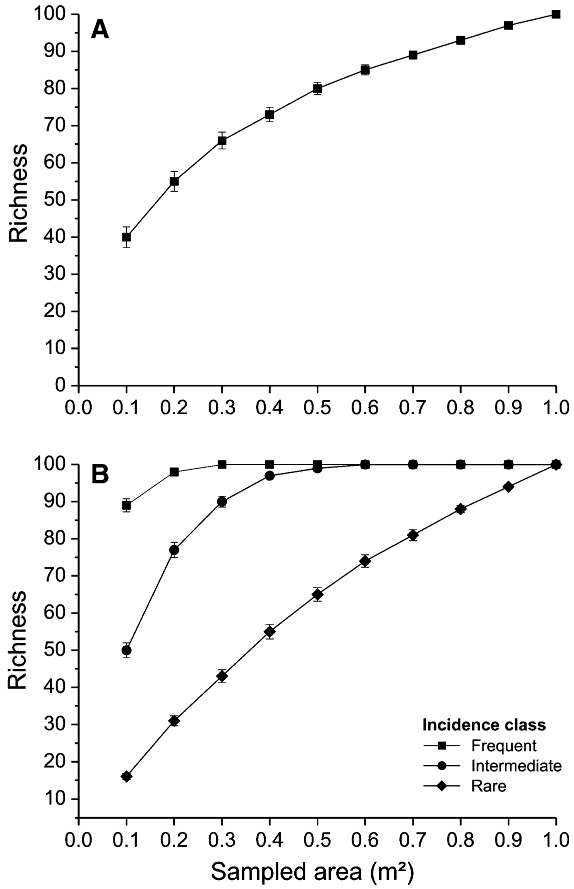

Fig. 2 Species–area curves depicting the relationship between mean cumulative percentage species richness (±95% CI, $N = 19$) and sampled area across all habitats (**A**) and for macroinvertebrate communities classified into incidence classes (**B**). Incidence classes were defined based on the frequency of occurrence of a given species within the 10 replicate samples of a habitat type

line with the general perception that freshwater macroinvertebrate communities tend to be dominated by rare species (Nijboerg & Verdonschot, 2004; Cucherousset et al., 2008). Hence, sample sizes of larger than 1 m^2 are necessary for conservational purposes when it is the aim to give thorough and complete species inventories. However, it is questionable if the sampling of larger areas is feasible for investigations other than species inventories even if rare species may play a role in the assessment of aquatic ecosystems (Cao et al., 1998, 2001).

Assessment and monitoring methods under the WFD require sampling protocols to be conducted in a cost and time efficient manner. Based on species–area curves, we suggest that an area of 0.63 m^2 per habitat is sufficient to capture all species with frequent and medium occurrences and most (76 ± 2%) of the rare species. This adequate sample size was consistent across habitats and was comparable with that for littoral macroinvertebrate communities associated with submerged macrophytes (Cheruvelil et al., 2000). Our adequate sample size for littoral macroinvertebrates was two times higher than that of macroinvertebrates on profundal habitats (Veijola et al., 1996) suggesting that the sample size depends on habitat complexity as well as the depth zone of a

Table 1 Summary statistics on sampling effort for the habitat types at Lake Stechlin and Lake Wittwesee (*CWD* coarse woody debris)

	N	S_{obs}	S_{est}	Singletons	Doubletons	G
Lake Stechlin						
Wind-exposed shore						
CWD	1,246	25	29	7	5	3
Reed	836	37	47	8	3	6
Root	615	36	41	9	7	3
Sand	971	24	38	8	2	10
Stones	3,210	23	27	7	6	2
Wind-sheltered shore						
CWD	5,023	34	40	10	7	3
Reed	1,274	37	48	11	5	5
Root	893	44	57	15	8	5
Sand	675	22	45	10	2	13
Stones	8,154	38	60	12	3	11
Lake Wittwesee						
Wind-exposed shore						
CWD	1,065	30	68	16	3	16
Reed	747	43	47	10	11	2
Root	760	36	44	10	6	4
Sand	362	12	16	4	2	4
Stones	1,110	15	19	5	3	3
Wind-sheltered shore						
CWD	373	22	26	7	5	3
Reed	876	34	45	11	5	5
Sand	1,904	19	48	8	1	22
Stones	3,105	25	27	4	4	2

N total number of individuals (no. m^{-2}); S_{obs} observed species richness, S_{est} estimated species richness based on the Chao2 estimator, *Singletons* number of species present in only one of the 10 replicate samples, *Doubletons* number of species present in only two of the 10 replicate samples, G additional area (m^2) to be sampled to reach 100% of the estimated species richness

Table 2 Sample size (m^2) at which all species from a given incidence class are obtained as derived from species–area curves

	Incidence class			Adequate sample size	% S_{obs}
	Frequent	Intermediate	Rare		
Lake Stechlin					
Wind-exposed shore					
CWD	0.3	0.6	1.0	0.63	87
Reed	0.3	0.6	1.0	0.63	91
Root	0.3	0.6	1.0	0.63	88
Sand	0.4	0.6	1.0	0.67	88
Stones	0.3	0.6	1.0	0.63	86
Wind-sheltered shore					
CWD	0.3	0.6	1.0	0.63	87
Reed	0.3	0.6	1.0	0.63	87
Root	0.3	0.6	1.0	0.63	86
Sand	0.3	0.6	1.0	0.63	83
Stones	0.3	0.5	1.0	0.60	86
Lake Wittwesee					
Wind-exposed shore					
CWD	0.3	0.6	1.0	0.63	79
Reed	0.3	0.5	1.0	0.60	87
Root	0.3	0.6	1.0	0.63	88
Sand	0.3	0.5	1.0	0.60	84
Stones	0.2	0.6	1.0	0.60	83
Wind-sheltered shore					
CWD	0.3	0.6	1.0	0.63	86
Reed	0.3	0.6	1.0	0.63	86
Sand	0.3	0.5	1.0	0.60	83
Stones	0.3	0.6	1.0	0.63	92
Mean	0.30	0.58	1.0	0.63	86
95% CI	0.01	0.02	–	0.01	1

Macroinvertebrate incidence classes were defined based on the frequency of occurrence of a species within the 10 replicate samples of a given habitat type. The adequate sample size (m^2) is the mean of the area for each individual incidence class. The proportion on total observed species richness (% S_{obs}) refers to the proportion of species richness that would have been obtained with the adequate sample size

lake. Furthermore, sample size may differ amongst lake types, in particular if macroinvertebrate community composition as well as richness patterns differ. In such cases, application of the adequate sample size derived in this study to other lake types than large oligotrophic lakes has to be exercised with caution. However, our results are based on data from lakes that represent the typical lake type found throughout the Central Baltic ecoregion ensuring its wider applicability in this ecoregion.

Conclusions

The implementation of the WFD in Europe has revived the scientific interest on littoral macroinvertebrate communities, as these are used as biological indicators for the ecological status of lakes. The usability of littoral macroinvertebrates for lake assessment is hampered by lacking information on its spatial variability as well as by harmonised sampling protocols (Solimini et al., 2006; Solheim et al., 2008). The results of this study show that the spatial variability of macroinvertebrate communities inhabiting the upper littoral zone (<1.2 m water depth) is significantly lower within habitats than within sites consisting of several habitats. This suggests that future sampling protocols should adopt a habitat-specific approach because habitat-specific sampling can be an efficient way to overcome the inherent spatial variability of littoral macroinvertebrates. Our results on the adequate sampling size suggest that conservation evaluation and compilation of taxon inventories require exhaustive sampling within and across habitats with sampling sizes substantially larger than 1 m^2. If macroinvertebrate sampling is conducted for purposes other than taxon inventories, our results show that a representative sample of the littoral macroinvertebrate community of a given habitat type can be obtained with a total sample size of 0.63 m^2. We recommend that individual habitats are sampled with a sufficient degree of replication ($n \geq 3$) to account for the small-scale patchiness of littoral macroinvertebrates.

Our results were elaborated using data from lakes that represent the typical lake type found throughout the Central Baltic ecoregion. The applicability to other lake types than large oligotrophic lakes has to be exercised with caution because richness patterns may not be comparable amongst ecoregions and lake types. Different patterns may particularly be expected for lakes subjected to eutrophication. Here, macroinvertebrate community composition has been shown to be less heterogeneous, probably as the result of the incremental loss of rare species that are susceptible to eutrophication (Donohue et al., 2009b). In such lakes, sampling effort in terms of the sample size may be smaller compared with the studied oligotrophic lakes.

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