Effects of human shoreline development on littoral macroinvertebrates in lowland lakes

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Summary

1. The shores of many lakes have been substantially altered by human developments such as erosion control structures or recreational beaches. Such alterations are likely to increase in the future, yet almost nothing is known about their impacts on the littoral macroinvertebrate community.

2. Macroinvertebrates were studied in seven German lowland lakes exhibiting natural shorelines (reference), retaining walls, ripraps and recreational beaches to examine impacts on the eulittoral (0–0·2 m water depth) and infralittoral (0·2–1·2 m water depth) communities associated with the three types of shoreline development.

3. Among sites, eulittoral species richness and abundance of Coleoptera, Gastropoda, Trichoptera, shredders and xylophagous species were lowest on beaches and retaining walls but ripraps did not differ significantly from natural shorelines. Retaining walls and ripraps had no significant impact on the infralittoral macroinvertebrate community. Conversely, beaches had significantly lower infralittoral species richness and abundance of Ephemeroptera, Trichoptera and shredders than natural shorelines. Furthermore, species richness was correlated positively with habitat heterogeneity expressed as number of habitat types.

4. Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of developed shorelines due to increasing abundances of Chironomidae. The remaining macroinvertebrate major groups decreased with increasing proportion of shoreline development.

5. *Synthesis and applications*. The biological impacts of shoreline development in lowland lakes depend upon the extent to which structural complexity and heterogeneity of littoral habitats are reduced. Hence, we recommend that management programmes focus upon the conservation of littoral habitat complexity and habitat heterogeneity. The biological effects of shoreline development may be assessed efficiently by combining an assessment of the morphological status of lakeshores and information on macroinvertebrate indicator species with a defined response to the loss of their preferred habitats.

Key-words: biodiversity, coarse woody debris, habitat complexity, lake management, macrophytes, recreational beaches, retaining walls, riparian clearcutting, ripraps

Introduction

Lakeshores have always been a preferential place for human settlement and various other human activities (Liddle & Scorgie 1980; Ostendorp, Schmieder & Jöhnk 2004), leading to shoreline development and the discharge of waste water on lakeshores. While the discharge of waste water has been widely reduced, shoreline development represents a current threat to the ecological integrity of lakes world-wide (Stadelmann 1990; Bryan & Scarnecchia 1992; Engel & Pederson 1998; Elias & Meyer 2003; Toft *et al.* 2003; Teiber 2003). Moreover, the intensity of shoreline development is expected to increase in the future (Walz, Brüggemann & Ostendorp 2002; Schmieder 2004).

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Table 1. Area, trophic status, hydraulic residence time (RT), shoreline length (L_{shore}) and the percentages of natural shorelines (Natural), retaining walls and ripraps (Erosion control), and beaches on total shoreline length at the seven studied lakes

Lakes	Area (km^2)	Trophic status	RT (year)	L_{shore} (km)	Shoreline type (%)		
					Natural	Erosion control	Beach
Grienericksee	2·69	Eutrophic	0·40	6·4	76	21	3
Langer See	2·51	Hypertrophic	0·10	18·3	35	61	4
Müggelsee	7·70	Eutrophic	0·16	11·1	63	29	8
Plauer See	6·70	Hypertrophic	0·01	15·7	86	14	–
Ruppiner See	6·33	Eutrophic	11·00	36·8	87	13	–
Unteruckersee	10·40	Mesotrophic	2·00	16·7	91	8	1
Werbellinsee	1·80	Mesotrophic	54·79	24·4	83	11	6

In general, shoreline development is considered to impact the littoral zone through alteration or loss of littoral habitats such as a reduction of macrophyte stands, most prominently the littoral reed belts (Sukopp 1971; Radomski & Goeman 2001; Elias & Meyer 2003) and an alteration of sediment particle size composition (Jennings *et al.* 2003). Also, the amount of coarse woody debris (CWD) in the littoral zone can be reduced substantially in lakes with a high proportion of shoreline development (Christensen *et al.* 1996; Marburg, Turner & Kratz 2006).

The biological impacts of human shoreline development have been quantified mainly for littoral fish communities, particularly on spatial aggregation (Scheuerell & Schindler 2004), species richness (Jennings *et al.* 1999) and production (Schindler, Geib & Williams 2000; Radomski & Goeman 2001). Impacts on littoral macroinvertebrates are likely, as macroinvertebrates exhibit a stronger dependence on littoral habitats and are less mobile than fish. However, we are aware of only one study that examined the impacts of shoreline development on littoral macroinvertebrates. Bänziger (1995) compared macroinvertebrate communities of shorelines subjected to three different types of developments with those of five types of natural shorelines in Lake Geneva, a large prealpine Swiss lake. She found species diversity and abundance to be lowest at developed shorelines. However, the validity of these results in other lake types is unknown, and the impact of recreational use on littoral macroinvertebrates has, to our knowledge, never been examined. An understanding of the ecological impacts of shoreline development in various lake types forms a prerequisite for a scientifically based ecological management of lakeshores. In particular, this applies to the assessment of their ecological status as well as the identification and implementation of effective restoration measures to improve heavily degraded shores.

In this study, we aimed to quantify the impact of three types of shoreline development on macroinvertebrate communities of seven German lowland lakes differing in trophic status and hydrological regime. We compared two types of erosion control structures (retaining walls, ripraps) and one type of recreational use (beaches) with natural shorelines to test (1) for alterations of the macroinvertebrate communities associated with the three types of shoreline development and (2) whether alterations of the macroinvertebrate communities are also detectable among the studied lakes.

Methods

STUDY SITES

Seven study lakes were chosen to allow for a sampling design stratified by shoreline type. The lakes are located in North-east Germany (52°24′10″–53°18′40″ N, 12°52′40″–13°52′40″ E) and differ in trophic status and hydrological regime (Table 1). Within the lakes, four different shoreline types, i.e. natural shorelines (reference), beaches (recreational use), retaining walls and ripraps (erosion control structure) were chosen. Local ripraps consisted of layered, rectangular stones and covered the shore from above the water line down to a water depth of about 0·5 m.

As beaches and ripraps were not present in all studied lakes, a total of 20 stations were sampled.

MACROINVERTEBRATE SAMPLING

Macroinvertebrates were sampled in autumn (October 2003) and spring (April 2004) at each of the 20 stations both in 0–0·2 m water depth (referred to hereafter as eulittoral) and in 0·2–1·2 m water depth (referred to hereafter as infralittoral). Not all infralittoral habitat types were present at all shoreline types, which prevented a balanced sample design for reed and stone habitats (Table 2). Moreover, the presence of CWD habitats was restricted to natural shorelines because all developed shorelines were situated in urban areas where riparian trees were absent.

We sampled each habitat type separately using sampling techniques that were best adapted to the different degree of spatial complexity of the habitats. This ensured a maximum sampling efficiency and comparability of the samples. Macroinvertebrates from CWD habitats were brushed from three pieces of CWD with comparable states of decay, and subsamples were sieved trough a mesh (250 μm). Subsequently, length and diameter of

Table 2. Habitat types within the eulittoral and infralittoral zones sampled for macroinvertebrates. The number of replicates per habitat type is given in brackets

| | Reference | Recreational use | Erosion control structure | |
	Natural shoreline	Beach	Riprap	Retaining wall
Eulittoral	Roots (5)	Sand (5)	Stones (5)	Concrete (5)
Infralittoral	Coarse woody debris (5)	–	–	–
	Reed (5)	–	Reed (2)	Reed (2)
	Sand (5)	Sand (5)	Sand (5)	Sand (5)
	Stones (5)	–	Stones (2)	Stones (5)

each piece of CWD was measured, and surface area was calculated assuming a cylindrical shape. Similarly, 10 stones were chosen randomly from each sample point and attached macroinvertebrates were brushed off. From each stone, surface area was calculated based on its length, height and width. We took five 1-m sweeps from reed habitats using a hand net (250-μm mesh, width 24 cm). We estimated the sampled area of reed habitats by multiplying hand net width with length of the sampled area. We took five subsamples from sub-merged roots of riparian trees with a hand net (250-μm mesh, width 24 cm), and estimated the sampled area by multiplying hand net width with the respective sampling depth. Sand habitats were sampled with 10 subsamples using a modified Surber sampler for lentic conditions (area 0·05 m², 250 μm mesh). Retaining walls were sampled with 10 subsamples using a scratch net (250 μm mesh, Hydrobios, Germany). Here, the sampled area was calculated by multiplying net frame width (13 cm) with the respective sampling depth. Sub-sequently, subsamples from each habitat type were pooled to create a composite sample per habitat type. Samples were preserved in the field and macroinvertebrates were identified in the laboratory to the lowest taxonomic level possible. Information on the functional feeding groups was taken from Schmedtje & Colling (1996).

STATISTICAL ANALYSIS

Initially, we eliminated species from the data set that were recorded in only one lake. As there were no sig-nificant differences in community composition among seasons using analysis of similarity (ANOSIM, PRIMER, version 5; Primer-E Ltd, Plymouth, UK) for any of the four shoreline types, we pooled the data from both sampling dates for further analyses.

We constructed species–area curves (PCORD, version 4·25; MjM Software, Gleneden Beach) to verify whether species richness was affected by differences in the number of samples of each shoreline type. This analysis revealed that the curve for each shoreline type reached its asymptote, indicating that sampling effort was sufficient at all shoreline types (Fig. 1). We converted species densities into relative abundances and calculated relative abundances of the macroinvertebrate major
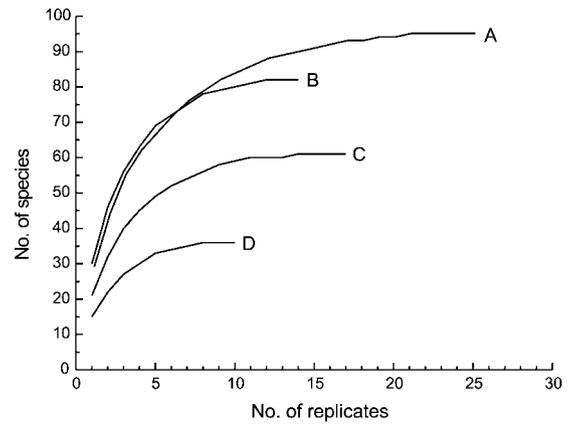

Fig. 1. Species–area curves for (a) natural shoreline, (b) riprap, (c) retaining wall and (d) recreational beach.

groups, relative abundances of the functional feeding groups and species richness to test for differences between natural and developed shorelines by means of nonparametric Mann–Whitney U-tests (SPSS, version 9·0; SPPS Inc., Chicago, IL, USA).

Indicator species analysis (IndVal, Dufrene & Legendre 1997) was used to detect macroinvertebrate species that are characteristic for a habitat or shoreline type, respectively (PCORD, version 4·25; MjM Software). We also tested whether species richness depended on hab-itat heterogeneity expressed as the number of habitat types using Spearman's correlation analysis (SPSS, version 9·0; SPPS Inc.).

For statistical analyses of the effects of shoreline development among lakes, we estimated whole-lake littoral macroinvertebrate density by calculating the weighted average density based on the proportion of shorelines represented by natural shorelines, shorelines with retain-ing walls and shorelines with recreational beaches (Table 1). Similarly, we calculated whole-lake relative abundances of the macroinvertebrate major groups. We restricted this analysis to the five lakes (Grienericksee, Langer See, Müggelsee, Unteruckersee, Werbellinsee) which had natural shorelines, shorelines with retaining walls and shorelines with recreational beaches.

Results

EFFECTS OF SHORELINE DEVELOPMENT – AMONG SITES

Among sites, eulittoral species richness was signifi-cantly lower on beaches and on retaining walls than on natural shorelines, but did not differ significantly between ripraps and natural shorelines (Fig. 2a). Relative abundances of Coleoptera, Crustacea, Gastropoda and Trichoptera were significantly lower on beaches than on natural shorelines and relative abundances of Gastropoda and Hirudinea were significantly lower on retaining walls than on natural shorelines (Table 3). IndVal analysis revealed *Bithynia tentaculata* (L.) (Gastropoda) (IV = 71·4, *P* = 0·016), *Ischnura elegans*
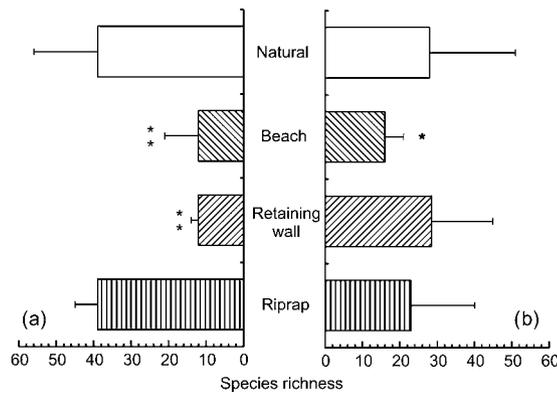
Fig. 2. Median species richness (+ max) of natural and developed shorelines (beach, retaining wall, riprap) within the (a) eulittoral and (b) infralittoral zones. Significant differences (Mann–Whitney *U*-test) between natural and each type of developed shorelines are indicated by asterisks (**$P < 0.01$, *$P < 0.05$).

Vander Linden (Odonata) (IV = 55·9, $P = 0.046$), *Lype phaeopa* McLachlan (Trichoptera) (IV = 75·2, $P = 0.004$) and *Platambus maculatus* (L.) (Coleoptera) (IV = 60·0, $P = 0.038$) as highly characteristic species for natural shorelines. Moreover, the occurrence of *I. elegans*, *L. phaeopa* and *P. maculatus* was restricted to natural shorelines and relative abundance of *B. tentaculata* was significantly higher at natural shorelines than at beaches or retaining walls (Mann–Whitney *U*-test, $P = 0.008$). None of the recorded species was characteristic for beaches or retaining walls, whereas *Dugesia lugubris/polychroa* (Turbellaria) (IV = 80·0, $P = 0.003$), *Cyrnus trimaculatus* (Curtis) (Trichoptera) (IV = 79·4, $P = 0.002$) and *Erpobdella octoculata* (L.,) (Hirudinea) (IV = 72·3, $P = 0.020$) were highly characteristic

species for ripraps. Differences between shoreline types were also discernible in the functional feeding group composition. The abundances of piercer, shredder and xylophagous species were significantly lower at beaches than on natural shorelines (Table 4). Similarly, the abundances of predator, shredder and xylophagous species were significantly lower on retaining walls than on natural shorelines. In contrast, we found no significant differences in the abundances of the functional feeding groups between ripraps and natural shorelines.

In contrast to the eulittoral zone, no significant differences were found in species richness (Fig. 2b) nor major macroinvertebrate or functional feeding groups (Tables 3 and 4) between retaining walls, ripraps and natural shorelines in the infralittoral zone. Conversely, infralittoral species richness, relative abundances of Crustacea, Ephemeroptera and Trichoptera (Table 3) and in relative abundance of shredders (Table 4) were significantly lower on beaches than on natural shorelines. None of the recorded infralittoral species was indicative for natural or developed shorelines.

Spearman's correlation analysis revealed that species richness was significantly positively correlated with the number of habitat types (Spearman's $\rho = 0.77$, $P = 0.000$, $n = 20$) and median species richness decreased from 63 species at natural shorelines with all five habitat types present to 17 species at recreational beaches with only one habitat type present.

EFFECTS OF SHORELINE DEVELOPMENT – AMONG LAKES

Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of developed shorelines and was almost three times higher in

Table 3. Median relative abundance (min–max) of macroinvertebrate major groups on the four shoreline types, given separately for eulittoral and infralittoral zones. Significant differences (Mann–Whitney *U*-test) between natural and each type of developed shorelines are indicated by asterisks (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$)

	Eulittoral zone				Infralittoral zone			
	Natural	Beach	Retaining wall	Riprap	Natural	Beach	Retaining wall	Riprap
Bivalvia	3·8	0·0	0·1	0·2	0·5	0·0*	0·2	0·5
	(0·0–9·1)	(0·0–0·2)	(0·0–1·8)	(0·0–27·1)	(0·0–5·3)	(0·0–0·1)	(0·0–5·6)	(0·0–20·3)
Chironomidae	74·4	91·7	87·1	85·7	87·6	96·0*	82·3	86·0
	(11·9–91·5)	(32·4–98·7)	(66·7–96·2)	(40·9–95·5)	(27·8–98·7)	(91·2–98·8)	(44·8–99·3)	(34·1–96·4)
Coleoptera	0·2	0·0*	0·0	0·0	0·0	0·0	0·2	0·0
	(0·0–2·2)	(0·0–0·0)	(0·0–0·1)	(0·0–0·2)	(0·0–2·1)	(0·0–0·0)	(0·0–0·2)	(0·0–0·1)
Crustacea	12·4	0·0*	0·4	0·8	1·1	0·0*	0·5	0·6
	(0·4–69·7)	(0·0–6·1)	(0·1–7·0)	(0·1–30·7)	(0·0–38·4)	(0·0–0·4)	(0·0–46·3)	(0·0–28·9)
Ephemeroptera	1·3	0·0	0·0	1·3	0·2	0·0*	0·1	0·4
	(0·0–3·5)	(0·0–0·2)	(0·0–1·7)	(0·0–2·7)	(0·0–5·8)	(0·0–0·1)	(0·0–15·6)	(0·0–2·3)
Gastropoda	0·7	0·1*	0·0**	0·2	1·2	0·1	0·4	0·6
	(0·2–6·7)	(0·0–0·4)	(0·0–0·0)	(0·1–0·5)	(0·0–12·5)	(0·0–0·5)	(0·0–1·3)	(0·1–6·5)
Hirudinea	0·0	0·0	0·0*	0·0	0·0	0·0	0·0	0·0
	(0·0–0·1)	(0·0–0·0)	(0·0–0·0)	(0·0–0·3)	(0·0–0·3)	(0·0–0·0)	(0·0–0·4)	(0·0–0·1)
Oligochaeta	1·2	6·6	10·9	1·6	2·6	3·1	9·8	4·0
	(0·5–7·1)	(1·0–60·7)	(1·0–30·0)	(0·4–12·3)	(0·0–63·8)	(1·0–8·5)	(0·0–29·5)	(0·0–54·0)
Trichoptera	0·5	0·0**	0·6	1·1	0·3	0·0***	0·6	0·1
	(0·4–0·8)	(0·0–0·1)	(0·1–2·7)	(0·1–5·4)	(0·0–1·2)	(0·0–0·0)	(0·0–3·8)	(0·0–1·4)

Table 4. Median relative abundance (min–max) of the macroinvertebrate functional feeding groups on the four shoreline types, given separately for eulittoral and infralittoral zones. Significant differences (Mann–Whitney *U*-test) between natural and each type of developed shoreline are indicated by asterisks (***P < 0·001, **P < 0·01, *P < 0·05)

	Eulittoral zone				Infralittoral zone			
	Natural	Beach	Retaining wall	Riprap	Natural	Beach	Retaining wall	Riprap
Collector/gatherer	10	13	9	9	17	13	14	16
	(7–17)	(11–16)	(7–11)	(11–16)	(4–38)	(13–16)	(5–41)	(7–29)
Filterer	15	17	20	16	16	17	16	17
	(12–37)	(16–17)	(15–35)	(16–17)	(7–37)	(16–17)	(11–67)	(16–75)
Parasite	21	28	30	21	14	27***	15	17
	(6–35)	(26–35)	(25–36)	(6–28)	(2–23)	(22–28)	(3–23)	(2–23)
Piercer	33	28*	26	33	21	30	28	25
	(5–45)	(5–45)	(20–38)	(5–45)	(5–42)	(29–30)	(6–45)	(3–33)
Predator	4	4	3*	3	5	4	5	4
	(3–13)	(3–4)	(3–4)	(2–5)	(1–8)	(4–5)	(3–23)	(3–9)
Scraper	6	8*	6	8	11	8	10	10
	(4–8)	(6–8)	(5–14)	(2–12)	(4–17)	(8–10)	(6–19)	(3–14)
Shredder	2	0**	0*	1	2	0*	1	1
	(1–16)	(0–1)	(0–1)	(0–2)	(0–11)	(0–1)	(0–3)	(0–8)
Xylophagous	4	0*	0*	0	0	0	0	0
	(0–18)	(0–0)	(0–0)	(0–1)	(0–67)	(0–0)	(0–0)	(0–0)

Table 5. Whole-lake littoral macroinvertebrate density and whole-lake littoral relative abundances of the macroinvertebrate major groups

	Grienericksee	Langer See	Müggelsee	Unteruckersee	Werbellinsee
Whole-lake density	2250	8562	9148	3300	2184
Bivalvia	0·1	0·7	0·6	1·2	0·9
Chironomidae	86·5	96·4	84·6	72·5	76·9
Coleoptera	0·1	0·0	0·0	0·1	1·6
Crustacea	0·1	0·6	4·4	3·4	5·1
Ephemeroptera	1·7	0·1	0·7	0·2	3·5
Gastropoda	0·9	0·1	1·1	2·1	1·3
Hirudinea	0·1	0·0	0·0	0·0	0·0
Oligochaeta	9·0	0·6	6·8	18·5	8·0
Trichoptera	0·3	0·3	0·2	0·3	0·5

lakes with high proportions of shoreline development than in lakes with low proportions of shoreline development (Table 5). Similarly, the relative abundance of Chironomidae increased from 72·5% in Lake Unteruckersee with lowest proportions of shoreline development to 96·4% in Lake Langer See with the highest proportion of shoreline development. The remaining macroinvertebrate major groups, particularly Coleoptera, Gastropoda and Oligochaeta, decreased in abundance with increasing proportions of retaining walls or recreational beaches (Tables 1 and 5).

Discussion

Earlier studies on the impacts of human shoreline development on lakes focused mainly on littoral habitats and littoral fish communities (Christensen *et al*. 1996; Jennings *et al*. 1999; Radomski & Goeman 2001; Elias & Meyer 2003; Jennings *et al*. 2003; Scheuerell & Schindler 2004). Our study demonstrates that, independently of the lake type, shoreline development through erosion control structures and creation of recreational beaches had significant impacts on both eulittoral and

infralittoral macroinvertebrate communities. However, the degree and spatial extent of the impacts differed between the types of shoreline development.

Within the eulittoral zone, the impacts of development on macroinvertebrate species richness and the abundance of several major taxonomic and functional feeding groups (Tables 3 and 4) can be attributed to the reduction of habitat complexity, as roots with their complex three-dimensional structure at natural shorelines were replaced by habitats with lower complexity at developed shorelines (concrete, sand, cf. Table 2). Habitat complexity is one of the key environmental factors influencing macroinvertebrate communities because complex habitats provide more ecological niches (O'Connor 1991), decrease the predation risk by limiting the foraging success of predators (Thompson 1987; Warfe & Barmuta 2004) and may also provide refuge against wind-induced wave disturbance. Consequently, natural shorelines harboured characteristic species such as *B. tentaculata*, *I. elegans* and *P. maculatus* with a strong preference for root habitats. This dependence upon the presence of a certain habitat type makes these species highly vulnerable to the loss of their preferred

habitat. Consequently, habitat specialists are those components of the community that are affected most severely by human shoreline development.

In addition to structural properties, complex habitats exhibit a higher available surface for the growth of periphyton (Bowen, Kaushik & Gordon 1998) and the sedimentation of particulate organic matter (Taniguchi & Tokeshi 2004). Hence, functional feeding groups such as piercer, shredder and xylophagous species may have benefited from these food resources at natural shorelines.

Due to their low structural complexity, retaining walls and beaches did not have characteristic species in the eulittoral zone, indicating that there is no distinct community associated with these types of shorelines. Interestingly, ripraps had no significant impact on eulittoral macroinvertebrates in the studied lakes, even if ripraps had a distinct community that comprised mainly lithobiontic species. Presumably, the arrangement of stones at ripraps created a structural complexity of large and small crevices that resembled that created by root habitats at natural shorelines. This view is supported by experiments showing that colonization baskets filled with cement balls to mimic ripraps exhibited higher species richness and macroinvertebrate abundance than baskets with cement blocks that mimic retaining walls (Schmude *et al.* 1998).

Within the infralittoral zone, erosion control structures had no significant impact on the macroinvertebrate community. Similarly, infralittoral fish species richness and abundance did not differ significantly between natural and developed shorelines in US lakes (Bryan & Scarnecchia 1992). Our findings may be attributable to the limited spatial extent of retaining walls and ripraps, where impacts hardly extend to the infralittoral zone. However, reed habitats were present at only two of the five sampling stations for ripraps and retaining walls (Table 2). Hence, we cannot exclude completely the possibility that erosion control structures may impact infralittoral macroinvertebrate communities due to habitat loss even if we did not find significant impacts in the course of this study.

In contrast, recreational beaches affected the macroinvertebrate community of the infralittoral zone, which is likely to be attributed to the loss of all but the sand habitats. Similarly, intensive recreational use was demonstrated to cause a loss of reed stands at German lakeshores by more than 1 km of shoreline per year (Sukopp 1971).

As a common effect of all types of shoreline development, CWD was absent due to either removal from the littoral zone or to the lack of riparian trees that prevented CWD supply. Consequently, xylophagous species, particularly *L. phaeopa*, were nearly absent from developed shorelines. However, non-xylophagous species such as *Dreissena polymorpha* (Pallas) (Bivalvia), *Radix balthica* (L.) (Gastropoda) and *Tinodes waeneri* (L.) (Trichoptera) occurred on stone habitats at shorelines with erosion control structures in similar abundances to CWD habitats at natural shorelines. Hence, for these species CWD may be substituted by other habitat

types exhibiting similar physical characteristics, such as stones. Similarly, France (1997) concluded that most species found on CWD habitats in boreal lakes used CWD as a habitat supplying biofilm or refuge against predation rather than as a direct food resource.

Species richness decreased with decreasing number of littoral habitats present at each shoreline type. The reduction of littoral habitat heterogeneity was especially apparent at beaches where all but the sand habitats were absent. Consequently, macroinvertebrate species richness was lowest here and we conclude that the impact of shoreline development on macroinvertebrates depends on the extent to which the heterogeneity of littoral habitats is reduced.

Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of shoreline development, most probably a result of the increasing abundances of Chironomidae in line with increases in their preferred sand habitats at recreational beaches and concrete habitats at retaining walls (Table 3). The remaining macroinvertebrate major groups decreased with increasing proportion of shoreline development, indicating that shoreline development may cause a homogenization of the macroinvertebrate community. This substantial reduction of whole-lake littoral biodiversity is most probably occurring in those lakes where shorelines have been modified to a large extent.

IMPLICATIONS FOR SHORELINE MANAGEMENT

In the littoral zone of lakes, the mosaic of habitat types creates a high spatial heterogeneity which is associated with a high diversity in food resources. Therefore, littoral macroinvertebrates species richness, abundance and biomass are higher than in the sublittoral or profundal zones (Särkkä 1983; Czachorowski 1993). Hence, human disturbances to the littoral zone affect a crucial biotic component of lake ecosystems whose diversity or biomass may not be substituted by communities from other lake zones. Thus, the strength of the impacts of shoreline development depended upon the extent to which habitat complexity and habitat heterogeneity are altered. Our results across lakes of different trophic state or hydrological regime indicate that the impact of shoreline development may also be applicable to other lake types. We recommend that management efforts to protect the integrity of lake ecosystems should place more emphasis on the morphological status of the littoral zone and that conservation of habitat complexity and habitat heterogeneity within the littoral zone should be a primary aim. In cases where shoreline development is inevitable, our results can be applied to weigh different types of shoreline modification or erosion protection against their biological impacts. Furthermore, our results may serve as the basis for a prediction system using indicator species with a defined response to the loss of their preferred habitat. By linking this approach with methods that focus on the

assessment of the morphological status of lakeshores (e.g. Rowan *et al.* 2006), lake managers would be enabled to assess rapidly the biological effects of shoreline development. The dependence of macroinvertebrate communities on the presence of certain habitat types may also be used to develop and implement site-adapted simple and cost-effective restoration measures. Specifically, artificial enhancement of habitat complexity may offer a promising strategy in urban lakes that are subjected to several types of human shoreline development.

Acknowledgements

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