Human lakeshore development alters the structure and trophic basis of littoral food webs

Mario Brauns[1]*†, Björn Gücker[2], Carola Wagner[1]‡, Xavier-F. Garcia[1], Norbert Walz[1] and Martin T. Pusch[1]

[1]*Department of Shallow Lakes and Lowland Rivers, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 301, D-12587 Berlin, Germany; and* [2]*Department of Biosystems Engineering, Federal University of São João del-Rei, Av. Visconde do Rio Preto, Colônia do Bengo, 36301-360, São João del-Rei, MG, Brazil*

Summary

1. Shoreline development and the associated loss of littoral habitats represent a pervasive alteration of the ecological integrity of lakes and have been identified as major drivers for the loss of littoral biodiversity world-wide. Little is known about the effects of shoreline development on the structure of, and energy transfer in, littoral food webs, even though this information is urgently needed for management and mitigation measures.

2. We measured macroinvertebrate biomass and analysed potential food resources using stable isotopes (δ^{13}C, δ^{15}N) and mixing models to compare the complexity and the trophic base of littoral food webs between undeveloped and developed shorelines in three North German lowland lakes.

3. The lower diversity of littoral habitats found at developed shorelines was associated with lower diversity of food resources and consumers. Consequently, the number of trophic links in food webs at developed shorelines was up to one order of magnitude lower as compared with undeveloped shorelines.

4. Mixing model analysis showed that consumer biomass at undeveloped shorelines was mainly derived from fine particulate organic matter (FPOM) and coarse particulate organic matter of terrestrial origin (CPOM). The contribution of CPOM to consumer biomass was twofold lower at developed shorelines, and consumer biomass was mainly derived from FPOM and suspended particulate organic matter.

5. *Synthesis and application.* Shoreline development impacts the flow of organic matter within littoral food webs primarily through the reduction in littoral habitat diversity. These effects are exacerbated by clearcutting of the riparian vegetation, which disrupts cross-boundary couplings between the riparian and the littoral zone. Lakeshore conservation should focus on preserving the structural integrity of the littoral zone, while restoration of coarse woody debris, reed and root habitats can be a cost-efficient measure to improve degraded lakeshores. The local effects of shoreline development demonstrated in this study might lead to whole-lake effects, but future studies are needed to derive thresholds at which shoreline development has consequences for the structure and functioning of the entire ecosystem.

Key-words: aquatic-terrestrial coupling, coarse woody debris, habitat loss, macroinvertebrates, retaining walls, riparian clearcutting, SIAR

*Correspondence author. Department River Ecology, Helmholtz Centre for Environmental Research GmbH - UFZ, Brückstr. 3a, D-39114 Magdeburg, Germany. E-mail: mario.brauns@ufz.de

Present addresses:
†Department River Ecology, Helmholtz Centre for Environmental Research GmbH – UFZ, Brückstr. 3a, D-39114 Magdeburg, Germany.
‡Department of Biological Oceanography, Leibniz-Institute for Baltic Sea Research Warnemünde, Seestrasse 15, D-18119 Rostock, Germany.

Introduction

Human modifications of lakeshores and changes in riparian land use constitute an increasing threat to the ecological integrity of lakes world-wide (Schnaiberg *et al.* 2002; Carpenter *et al.* 2007). For example, housing density around lakes in Wisconsin (USA) has increased more than fivefold over the last 60 years (Gonzales-Abraham *et al.* 2007). Similar trends are apparent in Central Europe, where housing density at Lake Constance (Germany) has more than doubled since 1960

(Schmieder 2004). It is expected that human use of lakes and lakeshores will continue and will extend into areas that are currently unimpaired (Peterson *et al.* 2003).

Aside from inputs of nutrients, shoreline development affects the littoral zone mainly through the alteration and loss of littoral habitats. The organic matter content of littoral habitats can be substantially lower at developed than at undeveloped shorelines, and macrophytes are often absent at developed shorelines (Elias & Meyer 2003; Francis *et al.* 2007). Such effects on littoral habitat diversity are intensified by clear-cutting of the riparian vegetation, resulting in a reduction in habitat provided by coarse woody debris (CWD) (Christensen *et al.* 1996) and submerged tree roots (Brauns *et al.* 2007). Thereby, human impacts on the structure of the littoral zone can have considerable consequences for littoral biotic communities such as strong reductions in species richness and production of littoral fish communities (Jennings *et al.* 1999; Schindler, Geib & Williams 2000). Similarly, macroinvertebrate species richness decreases with increasing intensity of shoreline development, and macroinvertebrate community composition is altered at highly developed shorelines (Brauns *et al.* 2007; Rosenberger *et al.* 2008). Human disturbances that affect species diversity may have consequences that go beyond impacts on community structure because littoral species constitute a functionally important part of the lake food web. Hence, alterations of littoral biodiversity following habitat loss might disrupt species interactions, thereby altering food web structure.

The decline of habitat heterogeneity following shoreline development may also have impacts on the diversity and quantity of food resources for littoral food webs. For example, the loss of CWD and macrophytes may be associated with a reduction in surface areas for the growth of periphyton that contributes substantially to whole-lake primary production and constitutes an important food resource for littoral consumers (Vadeboncoeur, Vander Zanden & Lodge 2002). Moreover, the littoral is not only spatially but also energetically coupled to the riparian zone via terrestrial inputs of dissolved and particulate organic matter. As a consequence, terrestrial subsidies can contribute up to 70% to the biomass of littoral consumers (Cole *et al.* 2006; Solomon *et al.* 2008). However, the terrestrial–aquatic coupling depends on the integrity of the riparian vegetation and may be strongly disrupted by removal of the riparian vegetation, as is often found along developed shorelines (France, Culbert & Peters 1996). Overall, human shoreline development may have the potential to drastically alter the structure and trophic basis of littoral food webs but empirical evidence as to what extent shoreline development can have such functional consequences is largely lacking.

In this study, we used the stable isotope composition of consumers and potential food resources, mixing model analysis and estimates of macroinvertebrate biomass to quantify the effects of shoreline development on the structure and trophic basis of littoral food webs of three North German lowland lakes. Specifically, we tested the hypothesis that lower habitat diversity at developed shorelines is associated with lower species richness and thus food web complexity. Furthermore, we hypothesised that shoreline development alters the trophic basis of macroinvertebrate food webs by reducing the diversity of food resources.

Materials and methods

SAMPLING AND SAMPLE PREPARATION

The study was conducted at three North German lowland lakes that differ in trophic status and have widely differing proportions of developed shorelines (Table 1). Within each lake, we established a 100m long sampling site at an undeveloped shoreline, a retaining wall and a recreational beach, respectively. Sampling sites within each lake were located at a distance of *c.* 500 m from each other to ensure that effects of natural environmental variables (e.g. wind exposure) are comparable. Shoreline development at the studied lakes was associated with the absence of riparian vegetation at the retaining walls of Lake Grienericksee and Lake Unteruckersee. The remaining developed shorelines exhibited riparian vegetation less dense as compared with undeveloped shorelines.

In October 2005, macroinvertebrates were sampled from each habitat present at each shoreline type (water depth < 1·2 m). At undeveloped shorelines, macroinvertebrates were sampled from CWD, reed, sand, stones and submerged tree roots, except for the undeveloped shoreline at Lake Langer See, which lacks a stone habitat. At retaining walls, macroinvertebrate were sampled from concrete walls, sand and stones. At beaches, macroinvertebrates were sampled from sand only, as no other habitats were present. The habitat-specific sampling is described elsewhere (Brauns *et al.* 2007). Briefly, we collected samples from CWD and stones by brushing off macroinvertebrates. Reed and roots were sampled with a hand net. Sand was sampled using a Surber sampler modified for lentic conditions (area 0·05 m^2, 250-µm mesh). Concrete walls were sampled by scraping a defined area using a special scrape net (250-µm mesh; Hydrobios, Kiel, Germany). The sampled area of each habitat was restricted to 0·2 m^2. The areal coverage of the sampled habitats was estimated using a tape measure.

In the laboratory, habitat-specific samples were processed by sorting, counting and identifying macroinvertebrates to the lowest

Table 1. Geographical location, surface area, total phosphorus concentration (TP, mean annual concentration in 2005), shoreline length (L_{shore}) and the percentage of undeveloped shorelines, retaining walls and recreational beaches on total shoreline length at the studied lakes

| | Geographical location | | Area (km^2) | TP (µg L^{-1}) | L_{shore} (km) | Shoreline type (%) | | |
	Latitude	Longitude				Undeveloped	Retaining wall	Beach
Grienericksee	53°06′22″	12°53′12″	2·7	115	6·4	76	21	3
Langer See	52°24′32″	13°36′50″	2·5	161	18·3	35	61	4
Unteruckersee	53°16′41″	13°51′51″	10·4	30	16·7	91	8	1

feasible taxonomic level (see Table S1 in Supporting Information). Macroinvertebrates were then kept individually for 24 h in filtered lake water to allow for gut clearance. Molluscs were removed from their shells, and macroinvertebrates were dried at 60 °C until constant weight. Dry weight of each species was determined by weighing 5–100 individuals per habitat-specific sample to the nearest 0·01 mg. Individual weights were used to calculate species-specific biomass.

For stable isotope analysis, we sampled all potential food resources present at each shoreline type. Coarse particulate organic matter of terrestrial origin (CPOM), i.e. decaying leaves from riparian trees and herbaceous riparian vegetation, was collected by hand. Fine particulate organic matter (FPOM) from reed stands and sand was sampled using a sediment corer (Uwitec, Mondsee, Austria). The upper 1 cm of each core was extracted and stored separately in acid-washed boxes. CPOM and FPOM samples were examined under a microscope, and invertebrates were removed. Suspended particulate organic matter (SPOM) was sampled by filtering lake water through precombusted Whatman GF/F filters. Periphyton was brushed from CWD, concrete, reed, submerged roots and stones into lake water filtered through Whatman GF/F filters. In the laboratory, periphyton samples were processed by removing detritus and invertebrates under 20× magnification using forceps. We were unable to obtain sufficient amounts of periphyton from submerged roots; we therefore used stable isotope values of periphyton from CWD from the same sampling site assuming that signatures are comparable. After processing, resource samples were dried at 60 °C until constant weight was reached.

STABLE ISOTOPE ANALYSIS

To prepare samples for stable isotope analysis, macroinvertebrates and food resources were ground with mortar and pestle, and Crustacea were acid treated to remove inorganic carbon (Yamamuro & Kayanne 1995). Each macroinvertebrate sample for stable isotope analysis consisted of several individuals from the same habitat to obtain sufficient material for analysis. Samples from unionids corresponded to single individuals.

Two subsamples of each species (∼500 μg) and food resource (2–21 mg) from each habitat were loaded into tin capsules. Carbon (C) and nitrogen (N) content and stable isotopes of C and N were analysed on a Carlo Erba NC2500 elemental analyser connected to a Finnigan MAT Delta Plus mass spectrometer at Cornell University's Stable Isotope Facility. Stable isotope data are expressed as the relative difference between ratios of samples and standards (PeeDee Belemnite for δ^{13}C, atmospheric N for δ^{15}N):

$$\delta R(\text{‰}) = [(R_{\text{SAMPLE}}/R_{\text{STANDARD}}) - 1] \times 10^3 \qquad \text{eqn 1}$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

Analytical precision (SD from in-house standards) from multiple runs was 0·08‰ for δ^{13}C and 0·14‰ for δ^{15}N.

MIXING MODELS AND FOOD WEBS

The contribution of food resources to consumer diet was estimated using their δ^{13}C and δ^{15}N values and mixing model analysis. We analysed stable isotope data separately for each habitat, which allowed us to constrain the number of potential food resources to those that were accessible to a given species in its habitat (Table S1). The habitat-specific analysis did not allow the determination of the degree of distinctness of resource isotopic signatures within a habitat. However, we tested whether isotopic signatures of resources significantly differed

across sites using *t*-tests and ANOVA followed by Scheffè's *post hoc* test (PASW version 17; SPSS Inc., Chicago, IL, USA). We assumed that if food resources were distinct at the site scale, they should be distinct at the habitat scale too. This assumption is corroborated by previous studies demonstrating that the spatial variability of isotopic signatures is smaller within than among sampling sites (Jennings *et al.* 1997; Syväranta, Hämäläinen & Jones 2006).

The contribution of food resources to consumer diet was determined using the SIAR software (Version 4.0.2). SIAR is based on a Bayesian approach that estimates probability distributions of resource contributions to a consumer diet by accounting for all uncertainties of the input data (Parnell *et al.* 2010). Because consumer data were unreplicated at the habitat scale, we used the SIAR function 'siarsolomcmcv4' that does not include a residual error term (Parnell *et al.* 2010) and is analogous to the mixing model proposed by Moore & Semmens (2008). We accounted for trophic fractionation using fractionation factors and uncertainties published in Post (2002), i.e. 0·4 ± 1·3‰ for δ^{13}C and 3·4 ± 1·0‰ for δ^{15}N. For running the mixing models, the appropriate number of iterations (up to 1×10^7) was chosen according to SIAR's convergence diagnostic. From the resulting up to 33 200 dietary proportions, we calculated the mean and variance.

SIAR was also used to estimate the contribution of resources to the biomass of secondary consumers. For that, we estimated consumer trophic position by relating their δ^{13}C and δ^{15}N values to a site-specific trophic baseline derived from stable isotope values of all non-predatory macroinvertebrates (Vander Zanden & Rasmussen 1999). We then used SIAR to estimate the contribution of potential macroinvertebrate prey to the biomass of secondary consumers. Based on estimated contributions of food resources to prey biomass, we used ratio calculation to estimate the resource contribution to secondary consumer biomass.

To compare resource contributions among shoreline types and lakes, we first calculated macroinvertebrate biomass of each site by weighting individual biomasses with the proportional coverage of each habitat. We then calculated the sum of the contributions of the individual resource items to weighted consumer biomass for the resource categories: CPOM, FPOM, periphyton, and SPOM. This calculation is subjected to error propagation as each dietary estimate has an individual uncertainty. Hence, we calculated a global standard deviation for each resource category contribution by summing the variances of the estimates for each resource item.

An initial inspection of the data revealed that contributions of SPOM to consumer biomass were more than threefold higher at Lake Langer See and more than twofold higher at Lake Unteruckersee than at Lake Grienericksee (data not shown). This was mainly because of the invasive mussel *Dreissena polymorpha* (Pallas) that contributed on average 42% to total biomass at the undeveloped shoreline of Lake Langer See and 8% at Lake Unteruckersee but was absent from Lake Grienericksee. Hence, we removed *D. polymorpha* from the food web analyses to allow for a better comparison among lakes.

Macroinvertebrate food webs were constructed for each shoreline type and lake based on information on the trophic position of consumers and the resource contribution to their biomass.

STATISTICAL ANALYSIS

Habitat diversity was calculated using the areal proportions of the habitats at each site and the Shannon–Weaver index. We used correlation analysis (Spearman's ρ, PASW version 17; SPSS Inc.) to test for relationships between habitat diversity and consumer biomass,

number of trophic links, number of available food resources and number of consumers in the food webs.

We conducted an exploratory analysis on the effects of shoreline development on the whole-littoral scale. Therefore, we estimated whole-littoral macroinvertebrate biomass by calculating the weighted average biomass based on the proportion of undeveloped and developed shorelines (Table 1). We then calculated the difference of relative whole-littoral biomass to a whole-littoral biomass with no shoreline development to compare effects among lakes.

Results

ISOTOPE SIGNATURES

Stable isotope biplots revealed sufficient separation between most food resources to be included into mixing model analysis. CPOM resources were significantly different in $\delta^{13}C$ from FPOM (ANOVA, Scheffè's *post hoc* test, $P = 0.030, n = 20$) and from periphyton (Scheffè's *post hoc* test, $P = 0.029, n = 21$) but not from SPOM (Scheffè's *post hoc* test, $P = 0.810$,

$n = 11$). The $\delta^{15}N$ values of CPOM resources differed significantly from all other resources (ANOVA, Scheffè's *post hoc* test, $P = 0.003$ at the lowest). FPOM from reed stands differed significantly in $\delta^{13}C$ from FPOM from sand (*t*-test, $t = 2.52$, $P = 0.046, n = 12$) but not in $\delta^{15}N$ (*t*-test, $t = 0.02$, $P = 0.988, n = 12$). FPOM signatures from reed and sand overlapped at the beach at Lake Unteruckersee (Fig. 1) and were pooled for mixing model analysis.

Carbon isotope values of periphyton from CWD and reed differed significantly from that of concrete and stones (*t*-test, $t = 2.35, P = 0.034, n = 11$) (Fig. 1). Stable isotope values of periphyton from CWD overlapped with those from reed at the undeveloped shoreline of Lake Grienericksee. However, our habitat-specific approach enabled a separate analysis for both resources because it is unlikely that consumers from CWD have fed on periphyton from reed.

FOOD WEB STRUCTURE

Weighted consumer biomass did not significantly decrease with decreasing habitat diversity (Fig. 2a). There was a signifi-
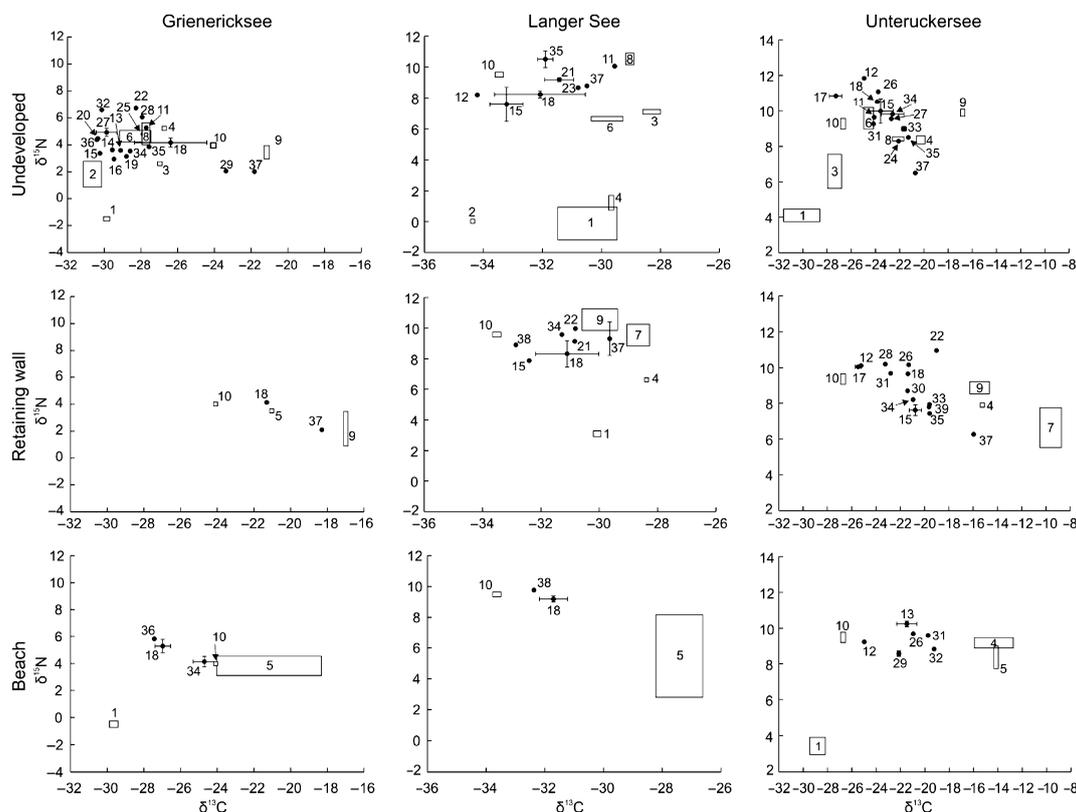

Fig. 1. Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of macroinvertebrates and resources found at the studied shoreline types. Stable isotope values of potential resources (mean) are shown as boxes delineated by ± 1 SD, and values of macroinvertebrates are given as mean (± 1 SD) if species occurred on more than one habitat. Resources (circles) are the following: Terrestrial coarse particulate organic matter from (1) alder leaves and (2) herbaceous riparian vegetation; fine particulate organic matter (3) in reed stands, (4) on sand, and (5) from submerged macrophytes; Periphyton on (6) coarse woody debris, (7) concrete, (8) reed and (9) stones; and (10) suspended particulate organic matter. Species are as follows: (11) *Acroloxus lacustris*, (12) *Anodonta cygnea*, (13) *Asellus aquaticus*, (14) *Bithynia leachi*, (15) *B. tentaculata*, (16) *Caenis* sp., (17) *Chelicorophium curvispinum*, (18) Chironominae, (19) *Cloeon dipterum*, (20) *Dikerogammarus haemobaphes*, (21) *D. villosus*, (22) *Erpobdella octoculata*, (23) *Gyraulus albus*, (24) *Haliplus* sp., (25) *Lype phaeopa*, (26) *Molanna angustata*, (27) *Mystacides niger/longicornis*, (28) Oligochaeta, (29) *Oulimnius* sp., (30) *Physa fontinalis*, (31) *Pisidium* sp., (32) *Platambus maculatus*, (33) *Pontogammarus robustoides*, (34) *Potamopyrgus antipodarum*, (35) *Radix balthica*, (36) *Sphaerium corneum*, (37) *Tinodes waeneri*, (38) *Unio tumidus* and (39) *Valvata piscinalis*.
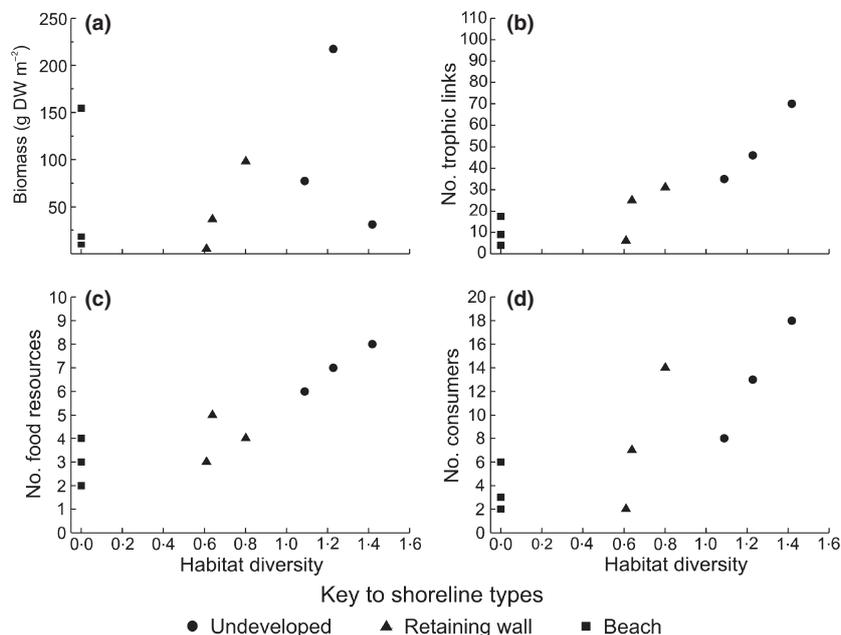
Fig. 2. Relationship between habitat diversity and (a) weighted macroinvertebrate consumer biomass (g DW m^{-2}), (b) number of trophic links, (c) number of available food resources and (d) number of consumers.

cant decrease in number of trophic links (Spearman's $\rho = 0.92$, $P = 0.001$, $n = 9$, Fig. 2b), number of available food resources (Spearman's $\rho = 0.89$, $P = 0.001$, $n = 9$, Fig. 2c) and macroinvertebrate consumer richness (Spearman's $\rho = 0.85$, $P = 0.004$, $n = 9$, Fig. 2d) with decreasing habitat diversity. Accordingly, the number of trophic links was highest at undeveloped shorelines (Fig. 2b) and on average twofold lower at retaining walls and fivefold lower at beaches. The substantial reduction in trophic complexity was particularly apparent at Lake Grienericksee, where the food web at the undeveloped shoreline had 70 trophic links and three trophic levels, while the food web at the retaining wall and beach had only six and nine trophic links, respectively (Fig. 3). These differences between developed and undeveloped shorelines were mostly the result of the absence of CWD, reed and roots from developed shorelines. At undeveloped shorelines, CWD, reed and roots together contributed on average 56% to total weighted biomass, 58% to macroinvertebrate consumer richness and 60% to total number of trophic links (Table 2).

The number of secondary consumers was highest at retaining walls, followed by undeveloped shorelines, whereas secondary consumers were absent at beaches (Fig. 3). Secondary consumers were represented by the leech *Erpobdella octoculata* (Linnaeus) that occurred at undeveloped shorelines and at retaining walls, and by the diving beetle *Platambus maculatus* (Linnaeus) that was restricted to the root habitat at the undeveloped shoreline of Lake Grienericksee (Fig. 3).

At the lake scale, shoreline development resulted in a clear decrease in whole-littoral macroinvertebrate biomass compared with a hypothetical whole-littoral biomass with no shoreline development. At Lakes Unteruckersee, Grienericksee and Langer See, where 9%, 24% and 65% of the shoreline

have been developed, respectively, whole-littoral macroinvertebrate biomass was estimated to reach 95%, 80% and 64%, respectively, of the theoretical whole-lake biomass that would be expected without any shoreline development.

TROPHIC BASIS OF FOOD WEBS

Food webs at undeveloped shorelines were mainly based on FPOM and terrestrial CPOM, together contributing 74% to total weighted macroinvertebrate biomass (Fig. 4). Major differences in the trophic basis of food webs between developed and undeveloped shorelines were found in the contribution of CPOM, which was twofold lower at retaining walls and beaches than at undeveloped shorelines. At developed shorelines, food webs were mainly based on FPOM and SPOM that together contributed 80% to total weighted macroinvertebrate biomass (Fig. 4). Differences between retaining walls and beaches were marginal except for periphyton that did not contribute to biomass at beaches probably because of the lack of solid habitats suitable for periphyton growth (Fig. 4).

We found considerable variation in resource contributions with shoreline type and lake. At the undeveloped shoreline of Lake Grienericksee, the biomass of trophic level 2 and 3 was mainly derived from CPOM and FPOM (Table 3). At the retaining wall, trophic level 2 biomass was mainly derived from SPOM, to a lesser extent from FPOM, and CPOM was absent (Table 3).

At the undeveloped shoreline of Langer See, the food web was mainly based on terrestrial CPOM and to a lesser extent on SPOM and periphyton (Table 3). At the retaining wall, contributions of CPOM and SPOM were comparable to those at the undeveloped shoreline. At the beach food web, the
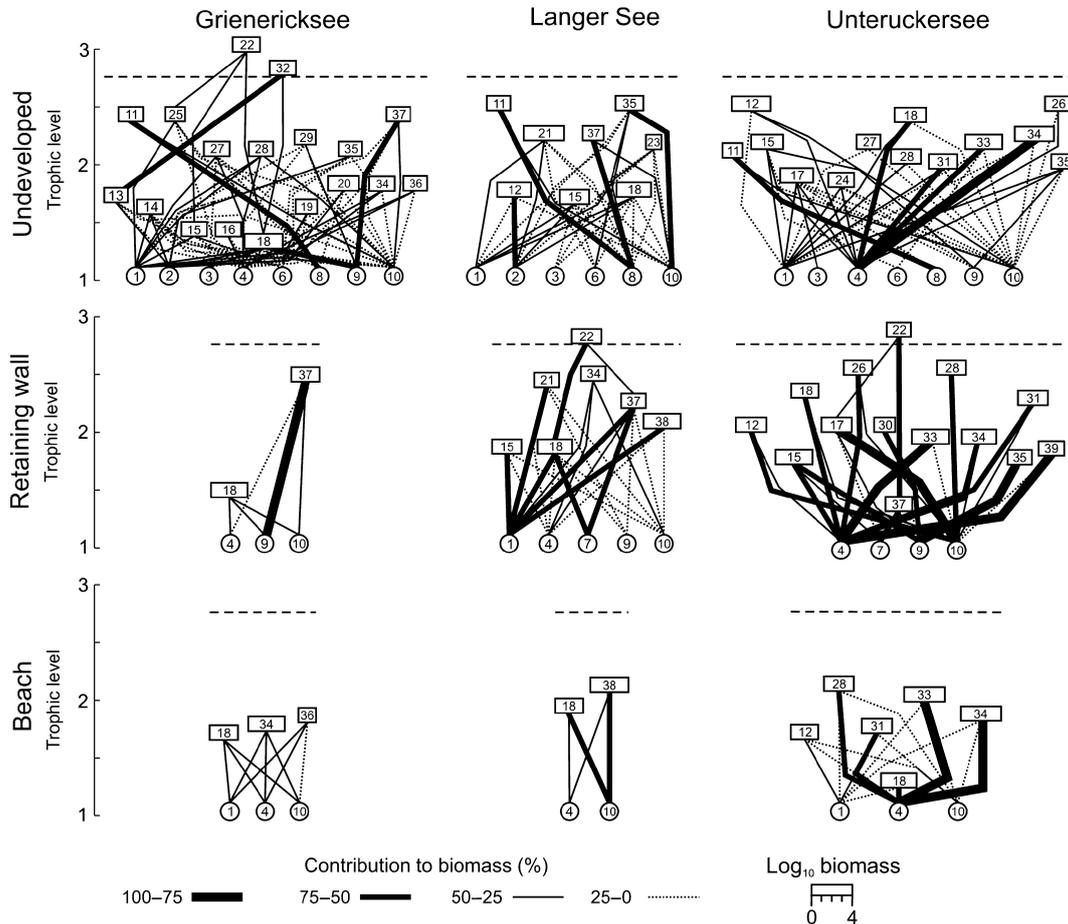
Fig. 3. Macroinvertebrate food webs of undeveloped and developed shorelines at the studied lakes. The width of consumer boxes is proportional to their weighted $\log_{10}$ biomass (mg DW m^{-2}). Trophic links are depicted by lines, whose thickness corresponds to the percentage contribution of resources to consumer biomass. If a species was recorded on more than one habitat, means for biomass and biomass contribution are given. The vertical position of food resources and macroinvertebrates represents their trophic level. Food resources were assigned to trophic level one, and the trophic level of macroinvertebrate consumers was calculated after Vander Zanden & Rasmussen (1999). The dashed line depicts the distinction between primary and secondary consumers. See Fig. 1 for codes to resources and species.

Table 2. Percentage contribution of individual habitats to total weighted biomass, total consumer richness and total number of trophic links at undeveloped shorelines

	Grienericksee			Langer See			Unteruckersee		
	Biomass	Consumer richness	Trophic links	Biomass	Consumer richness	Trophic links	Biomass	Consumer richness	Trophic links
Coarse woody debris	19	17	24	17	20	20	1	9	7
Reed	45	17	14	14	40	43	0	14	11
Roots	6	25	28	57	25	27	8	9	7
Sand	26	25	18	11	15	10	79	45	47
Stones	4	17	16	–	–	–	12	23	28

majority of macroinvertebrate biomass was derived from SPOM because CPOM and periphyton were absent.

At undeveloped shoreline of Lake Unteruckersee, consumer biomass was mainly derived from FPOM (Table 3). Marginal differences in resource contributions were found between the retaining wall and the undeveloped shoreline except for CPOM that was absent at the retaining wall.

Discussion

Previous research has shown that human development of lakeshores and the associated reduction in littoral habitat diversity has profound effects on the composition and biodiversity of littoral communities (Schindler, Geib & Williams 2000; Brauns *et al.* 2007). In this study, we demonstrated that shoreline
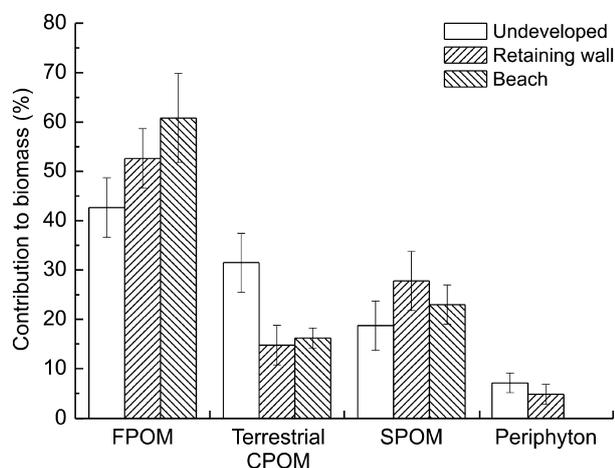
Fig. 4. Percentage contribution of food resources to total macroinvertebrate biomass at undeveloped shorelines, retaining walls and beaches across the three studied lakes. For each proportional contribution, the overall uncertainty (± 1 SD) is given as the sum of uncertainties of each individual mixing model run. Contributions to biomass were calculated excluding the invasive *Dreissena polymorpha* (Bivalvia) to allow for comparisons among lakes.

development not only affects the structure of littoral communities but also their functioning, which was evident in substantial differences in the structure and the transfer of organic matter through macroinvertebrate food webs of undeveloped and developed shorelines.

In accordance with our first hypothesis, food web structure in terms of trophic links declined with decreasing habitat diversity, reflecting significant relationships between shoreline morphology and both species richness and number of available food resources. The lower trophic complexity of food webs at developed shorelines was mainly because of the absence of CWD, reed and submerged tree roots. These habitats contributed substantially to food web complexity as well as to consumer richness at undeveloped shorelines. The remaining habitats at developed shorelines could not compensate for the absence of CWD, reed and submerged tree roots. An exception was the sand habitat at the undeveloped shoreline at Lake Unteruckersee that alone contributed 79% to total weighted biomass (Table 2). However, modifications of the sand habitat of the recreational beach at Lake Unteruckersee, in particular the physical impairment via human trampling, were associated with a decline of total weighted biomass and food web complexity compared with the undeveloped shoreline (Fig. 3).

The simplification of food webs at trophic level 3 was particularly apparent at beaches, because macroinvertebrate predators were absent from the studied beach food webs. Retaining walls harboured predator populations even though food web complexity was lower compared with undeveloped shorelines. In our study, predatory *E. octoculata* and *P. maculatus* were only found at undeveloped shorelines and retaining walls. *Platambus maculatus* commonly inhabits spatially complex habitats, such as tree roots (Hendrich 2003), and is indeed among the first species to become extinct if such habitats are lost from the littoral zone. In contrast, *E. octoculata* is a habitat

Table 3. Percentage contribution of food resources to total weighted macroinvertebrate biomass at undeveloped shorelines, retaining walls and beaches. The trophic level (TL) of macroinvertebrates was calculated following Vander Zanden & Rasmussen (1999) and rounded to integers. For each contribution, the uncertainty (± 1 SD) is given as the sum of uncertainties of individual mixing model runs. Contributions were calculated excluding invasive *Dreissena polymorpha* (Bivalvia) to allow for comparisons among lakes (– = food resource not present)

| | Grienericksee | | | | Langer See | | | | Unteruckersee | | | |
| | Undeveloped | | Retaining wall | Beach | Undeveloped | Retaining wall | | Beach | Undeveloped | Retaining wall | | Beach |
	TL 2	TL 3	TL 2	TL 2	TL 2	TL 2	TL 3	TL 2	TL 2	TL 2	TL 3	TL 2
Fine particulate organic matter	25 ± 6	24 ± 5	33 ± 7	30 ± 7	2 ± 1	17 ± 6	23 ± 2	32 ± 7	64 ± 10	69 ± 7	0	78 ± 10
Periphyton	14 ± 4	18 ± 5	22 ± 4	–	19 ± 6	2 ± 1	8 ± 1	–	1 ± 0	2 ± 1	55 ± 7	–
Suspended particulate organic matter	25 ± 5	20 ± 7	45 ± 6	31 ± 6	20 ± 4	14 ± 5	5 ± 8	68 ± 7	17 ± 5	29 ± 7	45 ± 0	3 ± 2
Terrestrial coarse particulate organic matter	36 ± 4	38 ± 0	–	39 ± 4	60 ± 7	66 ± 6	64 ± 0	–	18 ± 5	–	–	19 ± 2

generalist (Mann 1953) that may persist as long as solid habitats remain. This observation does not entirely follow the prediction that species at higher trophic levels are among the first to disappear as a result of habitat loss (Ryall & Fahrig 2006). Instead, our results indicate that there is no overall response of littoral macroinvertebrate predators to habitat loss, but that their extinction threshold is determined by the degree of species-specific habitat specialisation.

According to hypothesis 2, we found differences in the trophic basis of littoral food webs not only between lakes but also between shoreline types. Major differences were observed for contributions of terrestrial CPOM, as CPOM contributed half as much to weighted consumer biomass at developed than at undeveloped shorelines. The lower significance of terrestrial CPOM was probably the result of the removal or thinning of the riparian vegetation at developed shorelines. Consequently, CPOM was absent at three of six developed shorelines and scarce at the remaining sites (Table 3). These results support earlier findings that terrestrially derived organic matter is an important subsidy for littoral communities at undeveloped shorelines (Solomon *et al.* 2008; Weidel *et al.* 2008). However, our results demonstrate that human shoreline development adversely affects this energetic coupling between the littoral and the riparian zone by disrupting flows of organic matter across the aquatic–terrestrial boundary.

The alteration of the trophic basis of macroinvertebrate food webs was also reflected in differing contributions of periphyton to consumer biomass. Periphyton contributions did not differ between retaining walls and undeveloped shorelines but periphyton did not contribute to macroinvertebrate biomass at beaches. The absence of periphyton at beaches may be the result of the loss of solid habitats enabling periphyton growth, because CWD, reed and stones were lacking at beaches. This result may partially be biased because of our inability to discriminate benthic FPOM into epipsammic algae and detritus. However, we think that epipsammic algae marginally contributed to consumer biomass as we did not observe conspicuous algal mats or a distinct epipsammic periphyton during sampling. Periphyton growth may have been restricted by sediment instability caused by wind-induced waves that are characteristic for the investigated lakes with their large surface area. This assumption is corroborated by a study in a lake of similar morphology (Lake Erken, Sweden), where epipsammic algae contributed only 0·1–1·5% to total FPOM standing stocks (Hillebrand & Kahlert 2002). Moreover, the physical disturbance by human trampling at recreational beaches may have prevented a notable growth of epipsammic periphyton in the studied lakes.

In addition to differences between shoreline types, there was considerable natural variation in consumer resource use at undeveloped shorelines of the studied lakes (Table 2). This may be because of differences in macroinvertebrate community composition between lakes and an associated differing consumer feeding ecology. For example, the macroinvertebrate community of Lake Grienericksee was dominated by indigenous species, whereas Lake Langer See and Unteruckersee exhibited communities dominated by the nonindigenous

amphipods *Dikerogammarus villosus* (Sowinsky) and *Pontogammarus robustoides* Sars and the snail *Potamopyrgus antipodarum* (Grey) (Table S1). Previous studies have shown that nonindigenous species can have different feeding strategies than their native counterparts (Statzner, Bonada & Doledec 2008). This may explain the high contribution of FPOM to consumer biomass at the undeveloped shoreline of Lake Unteruckersee. Alternatively, indigenous consumers encountered at the undeveloped shorelines that were studied may have more flexible feeding strategies than commonly assumed. For example, terrestrial CPOM had the highest contribution to the biomass of the snail *Bithynia tentaculata* (Linnaeus) at Lake Grienericksee (46%), whereas FPOM had the highest contribution to the biomass of this species at Lake Unteruckersee (63%). Similarly, SPOM contributed most to the biomass of the snail *Radix balthica* (Linnaeus) at Lake Langer See (60%), whereas terrestrial CPOM had the highest contribution to the biomass of this species at Lake Unteruckersee (44%). These differences in feeding ecology may be because of differences in the quantitative availability of food resources at undeveloped shorelines and may have forced omnivorous consumers to adjust their diet to the local resource availabilities. Despite the natural variation in consumer resource use among lakes, human shoreline development had evident effects on the trophic base of the studied food webs suggesting that the results of the present study are robust and may be applicable to a wider variety of lake types.

The adverse effects on macroinvertebrate biomass that were demonstrated at the site scale may also lead to impacts at the whole-littoral scale. An exploratory analysis indicated that whole-littoral macroinvertebrate biomass may substantially decrease with increasing percentage of shoreline development. At Langer See, the lake exhibiting the highest percentage of shoreline development, estimated whole-littoral macroinvertebrate biomass was 36% lower than expected without shoreline development. It is unclear to what extent potential whole-littoral impacts on macroinvertebrate biomass may affect fish because mass-balanced food web studies for lakes subjected to shoreline development are largely lacking. In a whole-lake CWD manipulation experiment, Sass *et al.* (2006) removed 75% of the CWD from Little Rock Lake (WI, USA) to simulate the loss of CWD associated with residential shoreline development. While there were no changes in macroinvertebrate community composition and density (Helmus & Sass 2008), largemouth bass *Micropterus salmoides* (Lacépède) had lower growth rates and yellow perch *Perca flavescens* (Mitchill) declined in population density (Sass *et al.* 2006). This suggests that the removal of CWD following moderate shoreline development may not exert effects on fish because of reductions in benthic prey but rather by the reduction in the physical shelter provided by littoral CWD. In our lakes however, reductions in littoral habitat diversity were considerably higher in comparison with the study cited above because in addition to the absence of CWD, reed and submerged tree roots were also absent at developed shorelines. These habitats contributed on average 56% to total weighted biomass at undeveloped shorelines and their absence at developed shorelines may be the

cause for the lower whole-littoral biomass at the highly developed Lake Langer See. Such substantial reductions of prey biomass as well as littoral structure may be severe enough to directly affect fish biomass because retaining walls and beaches represent the dominant shoreline types in highly developed lakes (Sly 1991; Schindler, Geib & Williams 2000).

IMPLICATIONS FOR SHORELINE MANAGEMENT

We have demonstrated that shoreline development adversely affects the structure of the littoral zone and is associated with a lower diversity of food resources and lower consumer species diversity. Hence, food webs at developed shorelines had an up to one order of magnitude lower complexity because of the substantially lower number of trophic links between macroinvertebrate consumers and food resources. Moreover, clear-cutting or thinning of the riparian vegetation at developed shorelines diminished the supply of terrestrial organic matter to littoral food webs suggesting that human shoreline development decouples the littoral from the riparian zone. These results reveal that ecological effects of human activities in the littoral zone may go beyond simple alterations of littoral communities and have the potential to drastically alter the structure of, and the energy transfer in, littoral food webs.

Our limited understanding of food web effects and whole-lake impacts of human activities in the littoral zone currently hampers the identification of effective measures for the restoration of lakes subjected to intensive shoreline development. Hence, we advocate integrative approaches to the assessment of shoreline development by quantifying fish and benthic secondary production, as well as matter fluxes between trophic compartments under different development scenarios. Such comprehensive ecosystem function analysis would allow for the determination of thresholds at which shoreline development severely affects biomass production and the organic matter transfer within food webs.

Our habitat-specific results provide a first approach to cost-efficient restoration measures. Shorelines affected by erosion control structures such as retaining walls could be restored by replacing these structures with more appropriate stake palisades in front of lake shores. Such measures have been successfully implemented at Lake Constance (Germany), where a double palisade of stakes was installed in front of the shoreline to protect the reed belt against erosion (Ostendorp *et al.* 1995). Furthermore, littoral habitat diversity behind the stake palisade could be increased by restoring reed stands and planting of native riparian trees to allow for the supply of CWD and submerged root habitats. In cases of retaining walls that cannot be replaced, the establishment of reed stands should be fostered by protecting the upper littoral zone from lake-side disturbances, such as boating. The energetic coupling of littoral food webs to the riparian zone evidenced in our study suggests that the riparian vegetation should be conserved or restored at shorelines developed by retaining walls. Here, our data show that impacts of retaining walls on the trophic base of littoral food webs may be less severe as long as the riparian vegetation is not impacted.

An ecologically meaningful restoration of recreational beaches is unlikely because of their persistent use, but it is highly recommended to restrict their spatial extent to keep whole-lake impacts as low as possible. However, we strongly advocate that lakeshore conservation and impact mitigation strategies should primarily focus on conserving the structural integrity of the littoral zone.

Acknowledgements

References

Brauns, M., Garcia, X.-F., Walz, N. & Pusch, M.T. (2007) Effects of human shoreline development on littoral macroinvertebrates in lowland lakes. *Journal of Applied Ecology*, **44**, 1138–1144.

Carpenter, S.R., Benson, B.J., Biggs, R., Chipman, J.W., Foley, J.A., Golding, S.A., Hammer, R.B., Hanson, P.C., Johnhos, P.T.J., Kamarainen, A.M., Kratz, T.K., Lathrop, R.C., McMahon, K.D., Provencher, B., Rusak, J.A., Solomon, C.T., Stanlay, E.H., Turner, M.A., Vander Zanden, M.J., Wu, C.H. & Yuan, H.L. (2007) Understanding regional change: a comparison of two lake districts. *BioScience*, **57**, 232–335.

Christensen, D.L., Herwig, B.R., Schindler, D.E. & Carpenter, S.R. (1996) Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications*, **6**, 1143–1149.

Cole, J.J., Carpenter, S.R., Pace, M.L., Van de Bogert, M.C., Kitchell, J.L. & Hodgson, J.R. (2006) Differential support of lake food webs by three types of terrestrial organic carbon. *Ecology Letters*, **9**, 558–568.

Elias, J.E. & Meyer, M.W. (2003) Comparisons of undeveloped and developed shorelands, northern Wisconsin, and recommendations for restoration. *Wetlands*, **23**, 800–816.

France, R.L., Culbert, H. & Peters, R. (1996) Decreased carbon and nutrient input to boreal lakes from particulate organic matter following riparian clear-cutting. *Environmental Management*, **20**, 579–583.

Francis, T.B., Schindler, D.E., Fox, J.M. & Seminet-Reneau, E. (2007) Effects of urbanization on the dynamics of organic sediments in temperate lakes. *Ecosystems*, **10**, 1057–1068.

Gonzales-Abraham, C.E., Radeloff, V.C., Hawbaker, T.J., Hammer, R.B., Stewart, S.I. & Clayton, M.K. (2007) Patterns of houses and habitat loss from 1937 to 1999 in northern Wisconsin. *Ecological Applications*, **17**, 2011–2023.

Helmus, M.R. & Sass, G.G. (2008) The rapid effects of a whole-lake reduction of coarse woody debris on fish and benthic macroinvertebrates. *Freshwater Biology*, **53**, 1423–1433.

Hendrich, L. (2003) Die Wasserkäfer von Berlin – Struktur der aquatischen Käferfauna in anthropogen beeinflussten Gewässern von Berlin. PhD thesis, Technical University of Berlin, Berlin.

Hillebrand, H. & Kahlert, M. (2002) Effects of grazing and water column nutrient supply on biomass and nutrient content of sediment microalgae. *Aquatic Botany*, **72**, 143–159.

Jennings, S., Renones, O., MoralesNin, B., Polunin, N.V.C., Moranta, J. & Coll, J. (1997) Spatial variation in the N-15 and C-13 stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: implications for the study of trophic pathways. *Marine Ecology-Progress Series*, **146**, 109–116.

Jennings, M.J., Bozek, M.A., Hatzenbeler, G.R., Emmons, E.E. & Staggs, M.D. (1999) Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. *North American Journal of Fisheries Management*, **19**, 18–27.

Mann, K.H. (1953) The life history of *Erpobdella octoculata* (Linnaeus, 1758). *Journal of Animal Ecology*, **22**, 199–207.

Moore, J.W. & Semmens, B.X. (2008) Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters*, **11**, 470–480.

Ostendorp, W., Iseli, C., Krauss, M., Krumscheid-Plankert, P., Moret, J.L., Rollier, M. & Schanz, F. (1995) Lake shore deterioration, reed management and bank restoration in some Central-European lakes. *Ecological Engineering*, **5**, 51–75.

Parnell, A.C., Inger, R., Bearhop, S. & Jackson, A.L. (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE*, **5**, e9675, doi:10.1371/journal.phone.0009672.

Peterson, G.D., Beard. Jr, T.D., Beisner, B.E., Bennet, E.M., Carpenter, S.R., Cumming, G.S., Dent, C.L. & Havlicek, T.D. (2003) Assessing future ecosystems services: a case study of the Northern Highlands Lake District, Wisconsin. *Conservation Ecology*, **7**, 1–24.

Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**, 703–718.

Rosenberger, E.E., Hampton, S.E., Fradkin, S.C. & Kennedy, B.P. (2008) Effects of shoreline development on the nearshore environment in large deep oligotrophic lakes. *Freshwater Biology*, **53**, 1673–1691.

Ryall, K.L. & Fahrig, L. (2006) Response of predators to loss and fragmentation of prey habitat: a review of theory. *Ecology*, **87**, 1086–1093.

Sass, G.G., Kitchell, J.F., Carpenter, S.R., Hrabik, T.R. & Marburg, A.E. (2006) Fish community and food web responses to a whole-lake removal of coarse woody habitat. *Fisheries*, **31**, 321–330.

Schindler, D.E., Geib, S.I. & Williams, M.R. (2000) Patterns of fish growth along a residential development gradient in north temperate lakes. *Ecosystems*, **3**, 229–237.

Schmieder, K. (2004) European lake shores in danger – concepts for a sustainable development. *Limnologica*, **34**, 3–14.

Schnaiberg, J., Riera, J., Turner, M.G. & Voss, P.R. (2002) Explaining human settlement patterns in a recreational lake district: Vilas County, Wisconsin, USA. *Environmental Management*, **30**, 24–34.

Sly, P.G. (1991) The effects of land-use and cultural development on the Lake Ontario ecosystem since 1750. *Hydrobiologia*, **213**, 1–75.

Solomon, C.T., Carpenter, S.R., Cole, J.J. & Pace, M.L. (2008) Support of benthic invertebrates by detrital resources and current autochthonous primary production: results from a whole-lake C-13 addition. *Freshwater Biology*, **53**, 42–54.

Statzner, B., Bonada, N. & Doledec, S. (2008) Biological attributes discriminating invasive from native European stream macroinvertebrates. *Biological Invasions*, **10**, 517–530.

Syväranta, J., Hämäläinen, H. & Jones, R.I. (2006) Within-lake variability in carbon and nitrogen stable isotope signatures. *Freshwater Biology*, **51**, 1090–1102.

Vadeboncoeur, Y., Vander Zanden, M.J. & Lodge, D.M. (2002) Putting the lake back together: reintegrating benthic pathways into lake food web models. *BioScience*, **52**, 44–54.

Vander Zanden, M.J. & Rasmussen, J.B. (1999) Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. *Ecology*, **80**, 1395–1404.

Weidel, B., Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L. & Solomon, C.T. (2008) Carbon sources supporting fish growth in a north temperate lake. *Aquatic Sciences*, **70**, 446–458.

Yamamuro, M. & Kayanne, H. (1995) Rapid direct determination of organic carbon and nitrogen in carbonate-bearing sediments with a Yanaco MT-5 CHN analyzer. *Limnology and Oceanography*, **40**, 1001–1005.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Mean proportional contribution of food resources to the diet of macroinvertebrate consumers found at each habitat.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.