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Lakeshore modification reduces secondary production of macroinvertebrates in littoral but not deeper zones

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Abstract. Littoral macroinvertebrates are an integral component of lake food webs, but their productivity may be affected by shoreline alteration. We hypothesized that human modification of lake shores simplifies habitat diversity, which, in turn, affects littoral macroinvertebrate production and patterns of depth-production relationships. Furthermore, we expected that lakeshore modification would favor non-native species, potentially compensating for negative effects of lakeshore modification on production of native taxa. To test these ideas, we estimated benthic macroinvertebrate production in the upper littoral, middle littoral, and profundal zones of a large lowland lake (Lake Scharmützelsee) in Northeast Germany. We collected samples between April and November 2011 along depth transects established at both natural and modified shorelines. We found that production in the upper littoral zone was significantly lower at beaches than natural shores or marinas, but no difference existed between natural shorelines and marinas. The substantially lower production at beaches was correlated with lower habitat diversity, resulting from a lack of macrophytes. Additionally, production declined with increasing water depth at natural shores and marinas, but at beaches, production was highest in the middle littoral zone. Production of native taxa was lower at marinas than at natural shorelines, but production of non-native species offset these declines. The increased productivity of non-native species in upper littoral habitats at modified shorelines demonstrates that shoreline development has compromised the function of the littoral zone in Lake Scharmützelsee. Extrapolating depth- and habitat-specific production estimates to the entire lake showed that 33% of whole-lake benthic secondary production occurred in the upper littoral zone, even though this depth zone comprised only 7% of total lake area. Additionally, we estimated that completely replacing natural habitats with beaches would reduce whole lake benthic secondary production by 24%. Our results highlight the crucial role of the littoral zone for whole lake ecosystem functioning and the high susceptibility of littoral benthic secondary production to lakeshore modification by human activities.

Keywords: depth-production relationship, ecosystem functioning, habitat diversity, lake, non-native species, shoreline development

A significant portion of benthic secondary production in lakes occurs in the littoral zone (e.g. Vadeboncoeur et al. 2002, Sierszen et al. 2014). Littoral macroinvertebrates are a major trophic link between primary producers and fish in lake ecosystems (Covich et al. 1999, Schindler & Scheuerell 2002), and macroinvertebrates can contribute >60% of the diet (based on stable isotope estimates) of fish (Vander Zanden et al. 2006). Additionally, benthic filter feeders can alter lake ecosystem structure by regulating phytoplankton biomass, and thus, water transparency (MacIsaac 1996, Genkai-Kato et al. 2012). Secondary production is a direct measure of the role macroinvertebrates play in littoral carbon flux and ecosystem functioning, but it is rarely quantified because measuring macroinvertebrate biomass and growth is time consuming.

In natural temperate and subpolar lakes, macroinvertebrate secondary production is typically highest in the upper littoral zone and declines monotonically with water depth (Lindegaard 1992, Babler et al. 2008, Butkas et al. 2010, Northington et al. 2010). The high productivity in the upper littoral zone is a result of warm temperatures, high oxygen availability, and high food quality (Downing 1984, Jónasson et al. 1990). In addition to having higher production, the littoral zone also has higher macroinvertebrate diversity because it is typically more heterogeneous than deeper zones of lakes that lack sufficient light and structural complexity (e.g. James et al. 1998, Heino 2000, Vadeboncoeur et al. 2011). Human modification of lakeshores and littoral zones reduces the abundance and changes the taxonomic composition of macroinvertebrate assemblages (Brauns et al. 2007, McGoff et al. 2013, Pätzig et al. 2015), but how these changes affect secondary production remains unknown. Shoreline development decreases habitat complexity when natural riparian vegetation is replaced with pavement or highly manicured vegetation, or when stakeholders remove within-lake habitat such as coarse woody debris, reed belts, or aquatic vegetation

(Christensen et al. 1996, Francis & Schindler 2006, Radomski 2006). Alteration or loss of natural physical habitat structure may change the availability of organic matter resources that support secondary production (Rosenberger et al. 2008, Francis et al. 2007, Brauns et al. 2011). In some instances, however, shoreline development can increase habitat complexity by introducing new, sometimes novel, hard structures such as wood pilings or metal sheeting. In a previous study, we showed that these structures, and their indirect effects, can provide sufficient habitat to increase macroinvertebrate diversity (Pätzig et al. 2015), but it is not clear if this increase in diversity translates into higher secondary production

Shoreline development may also facilitate the establishment of invasive species (Johnson et al. 2008, Brabender et al. 2016), especially in lakes connected to navigable rivers (Bobeldyk et al. 2005, Leuven et al. 2009). The New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) and the Ponto-Caspian zebra mussel *Dreissena polymorpha* (Pallas, 1771) are examples of widespread and successful invaders that can dominate secondary production and material flux in new habitats (Alonso & Castro-Díez 2012, Griffiths et al. 1991, Hall et al. 2006, Van der Velde et al. 2002). Invasions can result in large increases in macroinvertebrate production as observed in Lake Simcoe (Canada) where *D. polymorpha* increased total secondary production 14-fold after establishment (Ozersky et al. 2012). If shoreline modification facilitates the establishment and persistence of non-native invertebrates, total production may not change, or could substantially increase, in spite of reduction in littoral habitat complexity.

We hypothesized that reductions in habitat diversity caused by lakeshore modification would decrease production in the upper littoral zone, thereby altering the expected relationship between production and depth. We also hypothesized that the introduction of novel substrates into the littoral zone, which in our study occurred at marinas, may shift the contribution to production from a dominance of native to a dominance of non-native species. Finally, we expected a decline in macroinvertebrate diversity and biomass caused by habitat simplification would be associated with a reduction in total macroinvertebrate production at the whole-lake scale.

METHODS

Study site and sampling

We measured benthic macroinvertebrate production at three depths in Lake Scharmützelsee, a stratified, mesotrophic lake in the Northeast Germany lowlands (Fig. 1, Grüneberg et al. 2011). The lake has a surface area of 12.1 km², a mean depth of 8.9 m, and a maximum depth of 29.5 m. It is connected to the navigable Dahme waterway system. Fifty seven percent of the lakeshore is undeveloped. Of the remaining lakeshore, 25% has shore reinforcements such as sheet pilings, and 18% is beaches, grasslands or parks (Fernando 2010).

We established 3 sampling transects at natural shorelines, 2 at marinas, and 3 at beaches. We incorporated the natural variation in wind and wave exposure by choosing one transect per shore type at the exposed east shore and one at the wind-sheltered western shore. Each transect was 30 – 50 m wide and comprised one homogenous shore type to avoid edge effects from neighboring habitats. The transects extended from the upper littoral zone (0 – 1.5 m water depth), through the middle littoral zone (1.5 – 4 m), and to the profundal (> 8 m) zone (terminology following Hutchinson 1967) (Fig. 1). At natural transects, trees dominated the riparian vegetation, and the upper littoral zone contained dense reed belts. In contrast, the riparian vegetation of marinas and beaches was replaced by lawns. At marinas, natural habitats in the upper littoral zone, such as reed belts, had been replaced by sheet pilings and piers. In the upper littoral zone of beaches, natural habitats had been simplified to facilitate swimming, and thus consisted predominantly of sandy substrate (Pätzig et al. 2015).

We sampled macroinvertebrates from each transect in the upper littoral, middle littoral, and upper profundal zone. We sampled 2 natural shores, 1 marina, and 1 beach monthly from April 2011 to November 2011 and sampled the remaining 4 transects in April, July, September and November 2011. We sampled half of the transects less frequently because of limited resources for sampling and laboratory work. We did not sample during winter because macroinvertebrate growth is slowed by low water temperatures, which likely resulted in an over estimation of total annual production (Dolbeth et al. 2012).

We sampled benthic macroinvertebrates from all habitats that occurred within each transect, including reed, stones, soft bottom, submerged macrophytes, and two types of artificial substrates (sheet piling and piles) following Pätzig et al. (2015). At each depth, we matched sampling effort with the relative surface area of each habitat type. For soft-bottom sediments and submerged macrophytes, we used a D-frame net with 500 µm mesh size to sample the upper littoral zone and a Van-Veen-grab (30 × 20 cm wide) to sample the deeper zones. Separating submerged macrophytes from the remaining sample was done with a 10-mm box sieve. Reed was sampled by cutting 10 stems between the lake bottom and the water surface. In the laboratory, macroinvertebrates attached to emergent and submerged macrophytes were collected alive from the plants and added to the corresponding macroinvertebrate sample. For sheet pilings and timber sheet piles, we used a scrape net (500 µm mesh). Stones were collected randomly and macroinvertebrates were brushed off carefully. After sampling, we pooled between one and four habitat-specific samples into a single composite sample (total area of 0.18 m^2) for each depth in each transect and stored them for further processing in 70% ethanol. We then subsampled the composite samples following the methods of the AQEM consortium (2002) and identified individuals to species or the lowest taxonomic level possible (for more details see Pätzig et al. 2015). Information about non-native taxa was obtained from the software ASTERICS Version 4.0.4 (Schmidt-Kloiber et al. 2014).

Environmental variables

We collected environmental variables that were potentially associated with biological differences among shore types and depth zones. We calculated wind exposure (Brodersen 1995) to account for the effects of wind and waves at each location (Table 1). Wind data were obtained from a nearby weather station (Lindenberg 52° 13' N, 14° 07' E; source: National Meteorological Service) between 2009 and 2011. We used ArcGis 10 (Esri, Redlands, CA USA) and maps with water depth contours (MLUL 2002) to determine bed slope (°) of each depth zone (Table 1).

At each depth zone in each transect, we measured total macrophyte biomass as the sum of the dry weight of submerged macrophytes and reeds. Our estimates of submerged macrophytes and reed biomass were based on samples taken during peak biomass in September 2011. We used a D-net (500 µm mesh, area 0.16-0.18 m^2) to sample submerged macrophytes together with macroinvertebrates in the upper littoral and a Van-Veen-grab (area 0.18 m^2) in deeper depth zones at each location. We quantified reed biomass in the upper littoral zone by determining stem density from an area of 0.16 m^2 (dense stands) and 1 m^2 (sparse stands) replicated 3 times per transect. From each transect, we cut 10 stems between the water surface and the lake bottom, dried them at 60 °C for 24 h, and weighed them to the nearest 0.01 g (Table 1).

We also obtained measurements of the organic matter content in bottom sediments at each sampling location in each transect. In the upper and middle littoral zone, we took five 6-cm diameter sediment cores. We then extracted the uppermost 2 cm of each core, dried it at 60°C for at least 12 hours, and determined ash free dry mass by combusting samples for 3 h at 500°C. We averaged unpublished ash free dry mass data previously (April 2007) obtained by staff at Brandenberg University of Technology Cottbus-Senftenberg from three locations in the profundal zone near our transects. These data were treated with a similar procedure as describe above.

We calculated mean annual temperature in each transect for the upper and middle littoral zones and for the profundal zone at east and west sides of the lake. We recorded water temperature with 16 temperature loggers in total (VEMCO Minilog, VEMCO Division, AMIRIX Systems Inc., Bedford, Canada) placed at each transect at upper (0.5-0.8 m depth) and middle littoral (2 m depth) zones at 20-minute intervals from May 2011 through September 2011. We also used a multiparameter probe (Hydrolab DS5, OTT Hydromet, Kempten, Germany) to measure temperature twice each month in different depths of the pelagic zone at various sites of Lake Scharmützelsee. We used these monthly temperature data to complete the logger data of the upper and middle littoral zones to calculate mean annual temperature during 2011 (Table 1). For all profundal sites, we used only the bi-monthly roughly 30-centimeter interval measurements from the multiparameter probe at depths between 8 to 15 m (Table 1).

We characterized habitat diversity in each depth zone of each transect by counting the number of habitat types and visually estimating their percentage contribution to total area (Table 1). We used the Hill number, $N1 = Exp(H')$, to quantify habitat diversity, because its properties allow direct comparison (Jost 2006). $N1$ is the exponential version of the Shannon index, $H' = -\sum_i^S p_i \ln p_i$, where p_i is the proportion of the area belonging to the i^{th} habitat, and S is the total number of all habitats (Jost et al. 2006).

Macroinvertebrate diversity, biomass, and secondary production between shore types and depth zones

We also used the Hill number to quantify macroinvertebrate diversity, but in this case p_i is the proportion of the individuals belonging to the i^{th} species, and *S* is the total number of all species (Jost et al. 2006).

We estimated taxon-specific mean annual macroinvertebrate biomass by averaging taxon-specific mass across sampling dates after summing individual mass-estimates obtained from taxon-specific length-mass relationships. We measured the body length from each individual to the nearest 0.01 mm with a digital microscope (Nikon SMZ 1500, Düsseldorf, Germany). For 7 of 91 taxa we did not have enough measurements from our own data to accurately estimate length-mass relationship, so we therefore used literature-based length-mass regressions (Online supplement 1). For the majority of observed taxa (83 of 91), we calculated individual dry mass (ash free dry mass for Gastropoda and Sphaeriidae) based on allometric regression equations developed from our own data (Online supplement 1, Mährlein et al. 2016). Back transformation of these log-log-regressions to the usually applied power function for the non-linear length-mass relationship introduces a systematic underestimation into estimates. This underestimation arises because logged data predict geometric rather than the arithmetic mean mass. We therefore corrected our dry weight estimates with Duan's smearing factor, SF $= \frac{1}{n}\sum_{i=1}^{n} e^{\varepsilon_i}$, where ε_i are the residuals from the fitted log-linear model and *n* the number of observations (Duan 1983, Mährlein et al. 2016). We also applied conversion factors to correct for preservation effects for all dry mass estimates, because we used preserved specimens (Online supplement 1, Mährlein et al. 2016). The final equation was $M_{SE} = e^{\ln a + b \cdot \ln L} \cdot SF \cdot CF$, where M_{SE} represents the mass with standard error, ln *a* and *b* are the intercept and slope of the linear regression function, L is the length of body dimension, SF is Duan's smearing factor, and CF is the conversion factor from preserved to unpreserved mass (Mährlein et al. 2016). Additionally, estimating the dry mass of large individuals outside of the length range can lead to serious errors, because mass increases more rapidly for older, larger individuals than it does for younger, shorter ones (Johnston and Cunjak 1999). To avoid these errors, we assigned length measures of large individuals outside the specific length range of a taxon's regression to the maximum length value used in each regression. We only had to make this adjustment for 0.2% of almost 48,500 individuals across taxa. Dry mass of Oligochaeta (1 of 91 taxa) was determined directly by weighing fragmented individuals present in our samples to the nearest 0.01 mg.

We used the empirical, multi-parameter artificial neural network (ANN) model developed by Brey et al. (Brey et al. 1996, Brey 2012) to estimate secondary production. Cohort based production methods are prohibitively expensive because of the high number of samples needed to adequately characterize growth and biomass over time and space. ANNs are powerful machine learning techniques that represent a multilayer architecture of nodes (artificial neurons) that are highly interconnected. Based on self-learning, ANNs are able to generalize, and therefore predict, complex patterns when they are calibrated with training data (Dayhoff and DeLeo 2001). The Brey ANN model (Brey et al. 1996, Brey 2012) is based on the experiences gained from multiple linear regression models that describe relationships between production to biomass ratios (P/B) and various biotic and abiotic predictors (e.g. Banse and Mosher 1980, Plante and Downing 1989). It includes 20 input variables that account for the effects of organism traits (e.g. alimentation, feeding, and mobility type) and environmental conditions (e.g. type of water body, water temperature, and water depth) to estimate the P/B ratio (Online supplement 2). Of the 20 input variables, the average individual body mass for each taxon influences production estimates the most (Brey 2012). We used the geometric mean mass to calculate the average individual body mass for each taxon in the ANN model, because organism growth is an exponential function of time (Benke and Huryn 2007). After estimating the P/B ratio for each taxon and sampling site with the ANN model, we estimated taxon-specific production by multiplying the P/B ratio by taxon-specific mean annual biomass. Rare taxa, including Coleoptera, Heteroptera, Lepidoptera, other Diptera, Turbellaria, and Unionidae, with abundances < 1% of total annual abundance were excluded from the statistical analysis as their occurrences are subject to large uncertainties. By excluding Unionidae, we underestimated total biomass to some extent, but we do not expect that this error substantially affected production estimates because Unionidae grow slowly (Negus 1966).

Finally, we tested if differences in sampling frequency (4 transects in 8 m, 4 transects in 4 m) affected estimates of secondary production by comparing the production values based on the total dataset (including half of transects sampled at 8 and the other half at 4 dates) with a subset (4 dates) of the total dataset. We fit a major-axis regression (R 3.4.1, function ‘ma’ from the package ‘smart’ (Han and Liu 2015) based on log-transformed data to examine correlations between the two different data sets. Production estimates based on four sampling dates were highly correlated with those from eight dates ($R^2 = 0.97$), indicating that the bias due to different sampling frequency was negligible. We therefore used all transects in further analyses without correcting for differences in sampling frequency.

Statistical analyses

Comparison among shore types and depth zones – The small sample sizes (*N*=3 for both beaches and natural sites and *N*=2 for marinas) precluded us from using inferential statistics to test for differences among shore types and depth zones. Instead, we interpreted 95% confidence intervals (CI) of habitat, species diversity, biomass, and secondary production estimates by considering means with non-overlapping CIs as implying real differences between shore types and depth zones (Babler et al. 2008, Cross et al. 2011). Similarly, 95% confidence intervals (CI) and the proportions of native and non-native production were calculated to account for shifts in dominance relations between shore types and depth zones.

Correlating habitat diversity with production – To determine if secondary production was associated with habitat diversity across shore types and depth (*N*=24), we conducted a linear regression analysis with R's standard function 'lm' (R Core Team 2017). Residuals of the fitted model were checked for normal distribution and homoscedasticity.

Estimating whole-lake secondary production

To estimate how changes in depth-specific production scale up to the whole-lake, we first estimated mean production for each shore type in the upper littoral. We then multiplied these values by the proportion of upper littoral area represented by the different shore types to estimate total production at this depth zone. For the middle littoral and profundal zone, we calculated mean production across all shoreline types, and multiplied these values with the area of each depth zone. We added the values of all zones together to estimate whole-lake benthic secondary production.

To determine how lakeshore development influenced secondary production at the lake-scale, we examined 7 scenarios that described how varying the amount of shoreline development changed whole-lake secondary production. The proportional amount of the three shore types on total shoreline length were set to range between 30 and 100 %. At the extremes of these scenarios, we calculated whole-lake littoral production assuming the entire upper littoral zone consisted of natural sites and compared this value with values based on scenarios where the entire upper littoral zone consisted of marinas or beaches, respectively. We propagated the individual errors of shoreline-specific production through each calculation and obtained a 95% CI for the estimated whole-lake secondary production for each scenario. Scenarios were considered significantly different when 95% CI's did not overlap.

RESULTS

Effects of lakeshore modification on habitat diversity

Habitat diversity appeared to differ between some shore types and depth zones, but not all (Fig. 2). In the upper littoral zone, beaches tended to have lower habitat diversity (1.5 ± 0.7) than natural sites (2.1 ± 0.3) or marinas (2.4 ± 0.6). No differences in habitat diversity were apparent between shore types based on data from middle littoral and profundal zones. Habitat diversity generally decreased with increasing depth irrespective of shore type. Mean habitat diversity across all shore types (±95CI) in the upper littoral zone (2 ± 0.4) was not clearly different from that in the middle littoral (1.5 ± 0.2), but mean habitat diversity in both littoral zones was higher than that in the profundal zone (1.0 ± 0) (Fig. 2).

Effect of lakeshore modification on macroinvertebrate diversity, biomass, and production

Macroinvertebrate diversity, biomass, and production did not always exhibit expected patterns (Fig. 3, Table 2). Diversity appeared to be clearly lowest in the profundal zone, but differences were less apparent between the two littoral zones (Fig. 3A). Mean annual biomass and annual secondary production in the upper littoral was significantly higher at natural sites than at beaches (Fig. 3B, C). There were no differences in biomass and secondary production among shore types in the middle littoral and profundal zone (Fig. 3B, C). Biomass and secondary production at natural sites and marinas were highest in the upper littoral and declined with increasing water depth. At beaches, biomass and secondary production was highest in the middle littoral and significantly lower in the upper littoral and profundal zones (Fig. 3B & C). However, production of just native species in the upper littoral zone at marinas was about 40% lower than that observed at natural shorelines. In the upper littoral zone of both modified shore types, non-native taxa such as *Potamopyrgus antipodarum* and Pontogammaridae accounted for roughly half of the secondary production, whereas non-native species contributed only 15% to secondary production in the upper littoral zone at natural transects (Fig. 3D). In the middle littoral zone, the contribution of native and non-native taxa to total secondary production did not differ among the shore types (Fig. 3D). Non-native taxa were absent from the profundal zone.

Habitat diversity predicts secondary production

We examined the potential of habitat diversity to predict benthic secondary production across shore types and depth zone. The model showed that habitat diversity was significantly positively related to secondary production (adjusted $R^2 = 0.68$, $F_{1,22} = 49.2$) (Fig. 4).

Effect of lakeshore modification on whole-lake secondary production

Benthic secondary production weighted by area of shore type differed by almost 30-fold across depth zones (Table 2). Mean production was 36 g DW m^{-2} y^{-1} in the upper littoral zone, 17 g DW m^{-2} y^{-1} in the middle littoral zone , and 1.3 g DW m^{-2} y^{-1} in the profundal zone (Table 2). At the whole-lake scale, 33% of the benthic secondary production occurred in the upper littoral zone, although the surface area of this depth zone comprised only 7% of total lake area. The middle littoral zone contributed more than half of the estimated whole-lake benthic production, although it represented only 25% of the total lake area. Production in the profundal zone accounted for only 12% of whole lake benthic production, even though the profundal zone covered almost 70% of the lake area.

Our scenario analysis showed that whole-lake macroinvertebrate production could range from 5.8 ± 2.1 g DW m^{-2} y^{-1} (scenario with 100% beach), to 7.6 ± 2.6 (100% marina), and to 7.7 ± 2.0 (100% natural shores) g DW m^{-2} y^{-1}. Thus, if the entire upper littoral zone consisted of beaches, production would be 24% lower than if the entire upper littoral zone consisted of natural shores or marinas.

DISCUSSION

Human shoreline development is a widespread practice that reduces littoral habitat complexity and degrades the ecological integrity of lakes (Christensen et al. 1996, Francis & Schindler 2006, Brauns et al. 2011). We assessed whether a decrease in zoobenthic production accompanies the previously described reduction in benthic macroinvertebrate diversity associated with shoreline development (Brauns et al. 2007, Pätzig et al. 2015). In Lake Scharmützelsee, shoreline development lowered zoobenthic production in the upper littoral zone, altering the inverse relationship between production and water depth that is typical of natural shorelines. However, this alteration was only evident at beaches where modifications to promote the enjoyment of swimmers reduced littoral habitat heterogeneity. In contrast, areas of the lake modified for boating (marinas) contained novel substrates that supported high biomass of non-native species. Zoobenthic production at marinas was comparable to that at natural shorelines, but non-native species were a larger proportion of production at marinas.

Humans intentionally modify habitat complexity in littoral zones to promote specific uses. Beaches had the lowest habitat diversity of the 3 types of shoreline habitat in Lake Scharmützelsee because the structural complexity provided by macrophytes and reed beds is unsuitable for swimming areas (Table 1). In contrast, to support use by boats, marinas incorporated novel substrates such as sheet metal barriers and wood jetty pilings (Table 1). Macrophyte biomass at marinas was lower than in natural habitats, but they were not altogether absent. The natural shores of Lake Scharmützelsee lack much of the structural complexity provided by tree roots and coarse woody debris that is present in the littoral zones of many lowland lakes (Brauns et al. 2007, 2011). Thus, littoral habitat diversity in constructed marinas was comparable to that of natural areas, but the types of habitats that contributed to this diversity differed between the two shoreline types.

The low variation in habitat diversity among shoreline types was associated with low variation in macroinvertebrate diversity and a dominance in habitat generalists, such as Oligochaeta and Chironomidae. Beaches appeared to have slightly lower macroinvertebrate diversity than marinas or natural areas, but we had limited ability to detect differences in diversity among habitats because we excluded rare species (abundances lower 1%) from our analysis to improve secondary production estimates. In a previous publication on the same lake, we showed that rare species contributed to shoreline-specific responses of macroinvertebrate diversity to lakeshore modification (Pätzig et al. 2015).

There is abundant evidence from rivers and oceans that sand and mud support lower secondary production than more complex-structured habitats that include submerged wood or macrophytes (Benke et al. 1984, Grubaugh et al. 1997, Dolbeth et al. 2003, Wong et al. 2011). In lakes, littoral habitats with dense macrophyte beds typically support high macroinvertebrate diversity (e.g. James et al. 1998, Gabel et al. 2008, Thomaz & Chuna 2010), and the limited data available suggests that secondary production in littoral zones is directly related to habitat structural complexity (Jónasson 1979, Gong et al. 2000). In Lake Scharmützelsee, marinas and natural shorelines had more types of habitats and higher macroinvertebrate biomass and secondary production than beaches, even when a component of that complexity was associated with human created structures. Habitat diversity may generate higher secondary production because littoral zones consisting only of sand and mud have less total surface area for macroinvertebrates to colonize than littoral areas containing vertical surfaces that extend into the water column. Our data suggest that human modifications that add structure to the littoral zones (e.g., marinas) have a less obvious effect on total macroinvertebrate production than modifications (e.g., beach development) that simplify littoral areas.

Total macroinvertebrate production in marinas was similar to natural shorelines, because non-native species, especially *P. antipodarum*, contributed greatly to secondary production at marinas with high habitat diversity and novel substrates. In contrast, although the proportion of non-native species production to total production at beaches was similar to marinas, non-native species did not compensate for the loss of native species productivity at beaches, because of overall low habitat diversity. Similarly, Brabender et al. (2016) found that non-native species contributed substantially to total secondary production in a large lowland river with abundant novel habitats (boulders). Modified shorelines of navigable rivers or lakes connected to them, such as Lake Scharmützelsee, are vulnerable to invasion by non-native species, but the ability of non-native species to compensate for native secondary production depends on the local habitat diversity and the level of physical disturbance (e.g., wave exposure, human trampling) (Table 1).

In lake littoral zones, habitat diversity and complexity often decreases with depth as light availability, wave action, and sediment particle size decrease (e.g. Rowan et al. 1992, Cyr 1998, Vadeboncoeur et al. 2011). Habitat diversity, macroinvertebrate biomass, and productivity declined with depth at marinas and natural shorelines, whereas macroinvertebrate productivity exhibited a unimodal relationship with depth at beaches. We suspect that macroinvertebrates in the upper littoral zone of beaches respond negatively to shoreline modifications that reduce habitat complexity, but that the mid-littoral zone was less affected by human activities. For instance, macrophytes were almost absent from the upper littoral zone at beaches, but macrophyte abundance in the mid-littoral did not differ among lakeshore types. Secondary production was similar in this zone across all three shore types. Macroinvertebrates, such as *Gyraulus crista* L. (1758), that are typically associated with macrophytes were absent from the upper littoral zone of beaches, but contributed to secondary production of the middle littoral zone. To assess if the observed unimodal depth-productivity relationship is a general phenomenon at beaches requires further studies in other lake types.

The low habitat diversity in the upper littoral zone of beaches relative to marinas and natural shorelines may indicate lower food availability for macroinvertebrates at beaches (Brauns et al. 2011). Reeds, stones, and novel substrates were not present at beaches. These surfaces support the growth of attached algae and bacteria (periphyton), and this major food resource for macroinvertebrates (Vadeboncoeur and Power, 2017) may have been less abundant at beaches. The availability of another food resource, benthic organic matter, was lower at developed shores compared with unmodified shores in lakes in the USA (Francis et al. 2007). However, in this study we found no significant differences among shore types in organic matter in sediments, an important resource for collector-gatherer species (Table 1). We did not measure all possible food types, and cannot critically evaluate the role resource availability or quality had in controlling secondary production.

Lakeshore modification also may alter secondary production by changing fish predation pressure. Decreases in resources and habitat availability at developed shores can reduce the densities of littoral fish (Scheuerell and Schindler 2004, Gaeta et al. 2011, Lewin et al. 2014). Low fish densities, in turn, may have released macroinvertebrates from predation at the marinas in our study, leading to the observed higher production. We could not test this hypothesis, though, because we did not estimate fish abundance in our study.

Our results support the generalization that macroinvertebrate production is highest in the littoral zone at natural shorelines (e.g. Kajak 1978, Dermott 1988, Lindegaard 1992, Babler et al. 2008, Butkas et al. 2010, Northington et al. 2010). However, we found that at beaches, habitat complexity, biomass, and productivity were all reduced relative to natural shorelines. When we simulated converting all of Lake Scharmützelsee’s shoreline to beaches, whole-lake secondary production was reduced by 24%. The effects of human lakeshore modification on whole lake benthic secondary production make therefore be less strong in lakes with naturally simple littoral zones or lakes with small littoral zones and steep slopes. It may therefore be important for managers to consider ways to mitigate negative impacts on littoral macroinvertebrates, which are key links between primary producers and fish, as well as between benthic and pelagic lake compartments (Vander Zanden et al. 2006).

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FIGURE LEGENDS

Fig. 1: Lake Scharmützelsee and the positions of the eight sampling transects.

Fig. 2: Habitat diversity quantified as Hills number for beaches (triangle), marinas (squares) and natural shorelines (circle) versus depth in Lake Scharmützelsee. Data are means and 95% confidence intervals.

Fig. 3: Macroinvertebrate diversity (A), biomass (B), total production (C), and production by native macroinvertebrates (D) for beaches (triangle), marinas (squares), and natural shorelines (circle) versus depth in Lake Scharmützelsee. Data are means and 95% confidence intervals.

Fig. 4: Associations between macroinvertebrate secondary production and habitat diversity (Hill number N1) across shore types (beaches = triangle, marinas = squares, and natural shorelines = circles) and depth zones (upper littoral = black, middle littoral = dark grey, and profundal = grey).

Table 1: Mean values (± 95% CI) of environmental variables per shore type and depth zone. Habitat diversity was quantified as Hills number, relative wind exposure was calculated as $\boldsymbol{log_{10}(1 + fwhd^{-2})}$, where *f* is the mean weighted wind fetch (km), *w* is the fraction of year with wind directed toward the station, *h* is the mean wind velocity (m/s), and *d* is the sampling depth (m) (Brodersen 1995). DM is dry mass.

	Upper littoral			Middle littoral			Profundal		
Variable	Natural	Marina	Beach	Natural	Marina	Beach	Natural	Marina	Beach
Habitat diversity	2.1 ± 0.2	2.4 ± 0.6	1.5 ± 0.7	1.5 ± 0.4	1.7 ± 0.6	1.2 ± 0.3	1 ± 0	1 ± 0	1 ± 0
Relative wind exposure	0.3 ± 0.2	0.4 ± 0.0	0.7 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Shore slope [°]	1.7 ± 0.5	2.1 ± 0.3	1.6 ± 0.1	3.0 ± 4.9	6.8 ± 6.7	1.9 ± 1.3	7.0 ± 10.0	3.3 ± 5.0	2.5 ± 1.8
Sediment organic matter [% DM]	2.3 ± 1.5	1.4 ± 1.0	1.1 ± 0.5	3.5 ± 4.6	3 ± 4.5	2.8 ± 1.3	20.7 ± 0.0	20.7 ± 0.0	20.7 ± 0.0
Reed and macrophyte biomass [DM g/m²]	304 ± 62	35 ± 33	8 ± 14	26 ± 22	53 ± 63	72 ± 109	0 ± 0	0 ± 0	0 ± 0
Annual water temperature [°C]	11.9 ± 0.1	12.2 ± 0.3	12.4 ± 0.2	12.1 ± 0.2	12.0 ± 0.2	12.1 ± 0.2	9.0 ± 0.6	9.2 ± 1.0	9.0 ± 0.6

Table 2: Benthic macroinvertebrate secondary production (P ± 95% CI) at different shore types and depth zones in Lake Scharmützelsee. In the middle littoral and profundal zones, secondary production of all shore types were averaged. For the calculation of whole lake benthic secondary production the shore type area-weighted estimates for the upper littoral zone were used.

Depth zone	Shore type	Area (m²)	P_{total} (g m^{-2} y^{-1})	$P_{non\text{-}native}$ (g m^{-2} y^{-1})	Area-weighted P g m^{-2} y^{-1}	Total P t y^{-1}	% P of whole lake	% area of whole lake
Upper littoral	Natural	515,004	36.7 ± 1.6	5.5 ± 1.7		18.91	20.70	4.3
	Marina	324,298	35.9 ± 17.3	14.4 ± 2.6		11.65	12.75	2.7
	Beach	6,618	10.3 ± 4.0	5.1 ± 2.7		0.07	0.08	0.1
	Mean				36.2			
	Sum	845,920				30.63	33.52	7.1
Middle littoral	Natural		16.5 ± 6.7	6.8 ± 4.4				
	Marina		17.1 ± 0.6	8.2 ± 2.3				
	Beach		17.2 ±4.7	7.5 ± 3.6				
	Mean				16.91			
	Sum	2,960,168				50.06	54.80	24.5
Profundal	Natural		1.4 ± 1.0					
	Marina		1.1 ± 0.4					
	Beach		1.3 ± 0.2					
	Mean				1.29			
	Sum	8,263,911				10.67	11.68	68.5
Whole lake	Mean	12,069,999			7.57			
	Sum					91.45	100	100