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Borders of Biodiversity: Life at the Edge of the World's Large Lakes

YVONNE VADEBONCOEUR, PETER B. McINTYRE, AND M. JAKE VANDER ZANDEN

The great lakes of the world represent a global heritage of surface freshwater and aquatic biodiversity. Species lists for 14 of the world's largest lakes reveal that 15% of the global diversity (the total number of species) of freshwater fishes, 9% of noninsect freshwater invertebrate diversity, and 2% of aquatic insect diversity live in this handful of lakes. The vast majority (more than 93%) of species inhabit the shallow, nearshore littoral zone, and 72% are completely restricted to the littoral zone, even though littoral habitats are a small fraction of total lake areas. Most fish species exploit benthic resources, which increases food web complexity. Moreover, littoral zones are both more negatively affected by human activity and less intensively studied than offshore waters. Conservation of the remarkable biodiversity and biotic integrity of large lakes will require better integration of littoral zones into our understanding of lake ecosystem functioning and focused efforts to alleviate human impacts along the shoreline.

Keywords: great lakes, littoral zone, fish, invertebrates, species-area curves

Over two-thirds of the liquid surface freshwater on Earth is contained in a handful of large lakes (Herendorf 1990). These lakes are regional centers of commerce and human activity. Their societal and economic importance is linked to international shipping, commercial fisheries, subsistence fisheries, drinking-water supply, waste disposal, and recreation (Beeton 2002). Unfortunately, the ecological function of large lakes has been persistently degraded through shortsighted management in support of regional economies. Although the expansive open-water (pelagic) zone dominates the physical footprint of most large lakes, the lake edge is the nexus of human interactions with lakes and is often highly modified for diverse human uses (Schmieder 2004, Mackey and Goforth 2005, Carpenter et al. 2007, Goforth and Carman 2009). The nearshore environment is also a critical habitat for many organisms within lakes. In the present study, we assess how species of fishes and invertebrates are distributed among major habitat zones in 14 of the world's largest lakes.

There are 253 freshwater lakes in the world with a surface area of more than 500 square kilometers (km²) and over 75 lakes with a maximum depth of more than 100 meters (m) (Herendorf 1990). Some large lakes have persisted for millions of years, acting as living museums of evolutionary processes. Others, like the Laurentian Great Lakes of North America, are relatively young, and their species assemblages are composed of widely distributed postglacial colonists. Regardless of morphometry and age, the world's large lakes are all characterized by spectacular vistas that leave an impression of vast expanses of water. Indeed, the open-water, offshore zones of large lakes represent the largest extent of truly pelagic freshwater in the world and often support large international fisheries.

The importance of the nearshore habitat for many species is well accepted (Kalff 2001), but littoral processes are poorly

integrated into ecologists' understanding of how lake ecosystems function (Schindler and Scheurell 2002, Vadeboncoeur et al. 2002, Schmieder 2004). Nowhere is this more true than in the large lakes of the world, even in cases in which the littoral zone represents a substantial portion of the total lake area (table 1). With a few important exceptions (e.g., the unique species flocks of ancient lakes that are intensively studied; Brooks 1950, Rossiter and Kawanabe 2000), littoral communities in large lakes are poorly described, and ecosystem-scale studies in the nearshore zone are few (Niemi et al. 2007). The lack of research emphasis on littoral zones in large lakes belies their socioeconomic and ecological importance. Humans build structures, recreate, fish, extract water, and dump ballast at lake edges. These activities have diverse and largely uncharacterized impacts on littoral biota. As one step in quantifying the ecological importance of the edges of great lakes, in this article, we describe the spatial distribution of species in 14 of the world's largest lakes and compare patterns of endemism and resource use among habitats. We found that the majority of species are associated with the littoral habitat at the edges of the lakes and that the vast majority of fish species feed on benthic or littoral resources. These results indicate that improved management of littoral zones is essential for the effective preservation of food web integrity and the conservation of freshwater species.

Compilation of species lists

We collected data from the literature on species composition in large freshwater lakes (for which the surface area was greater than 500 km²). With the exception of Lakes Erie and Victoria, we also selected lakes for which the maximum depth exceeded 100 m (table 1). Thus, there was a clear distinction between the littoral and open-water

Table 1. Morphometric characteristics of the study lakes.

Lake	Lake location (countries)	Maximum depth (m)	Mean depth (m)	Depth of 1% light (m)	Lake area (km ²)	Littoral area (km ²)	Littoral zone (percentage of surface area)
Constance	Austria, Germany, Switzerland	252	90	17	518.5	59.0	11.4
Biwa ^a	Japan	103	41	17	682.6	206.5	30.3
Hovsgol ^a	Mongolia	270	138	51	2750	591.8	21.5
Baikal ^a	Russia	1741	740	25	32,822	1106.2	3.4
Titicaca ^a	Bolivia, Peru	304	107	23	8236	3098.0	37.6
Victoria	Kenya, Tanzania, Uganda	84	40	11	66,768	11,035.9	16.5
Tanganyika ^a	Burundi, Democratic Republic of Congo, Tanzania, Zambia,	1470	572	35	32,976	2247.7	6.8
Malawia	Malawi, Mozambique, Tanzania,	706	292	33	29,721	3181.3	10.7
Erie	Canada, United States	64	18	16	25,481	9538.8	37.4
Huron	Canada, United States	229	53	27	59,656	17,456.1	29.3
Michigan	United States	282	84	24	57,800	11,528.2	19.9
Ontario	Canada, United States	245	86	19	18,601	2663.8	14.3
Superior	Canada, United States	407	148	35	81,996	7901.1	9.6
Tahoe	United States	501	313	58	485.5	49.5	10.2

Note: The lakes were included in the database on the basis of lake size and the availability of sufficient data to generate species lists. The lake ages are not universally agreed on because of the dynamic nature of lakes in landscapes.

m, meters; km², square kilometers

^aLakes more than 100,000 years old and referred to as *ancient lakes* in the text

habitats in all of the studied lakes. We used primary research articles, monographs, government agency data, the World Lakes Database (<http://wldb.ilec.or.jp>), and input from experts to generate species lists and compile the morphometric characteristics of the lakes. Only lakes with reasonably complete species data already available were included in this study.

We restricted our analysis to fish, crustaceans, insects, and mollusks, because these taxa account for 89% of the described freshwater animal species (Balian et al. 2008), and the data on other animal taxa are inconsistent or scarce. We gathered data on only species presence because of a lack of available information to address patterns of relative abundance. We generated virtually complete lists of fishes for every lake, including many undescribed species recognized by experts. Lists of invertebrates, especially insects, are often incomplete because of limited sampling of benthic habitats. Where possible, our final lists were reviewed by experts on each lake's fauna. We also characterized the diet of most fish species using FishBase (Froese and Pauly 2009), the primary literature, and input from experts. Our diet categories include benthic resources (attached algae, macrophytes, and benthic invertebrates), planktonic resources (phytoplankton and zooplankton), and fish (which cannot be unambiguously categorized as benthic or pelagic).

We used GIS (geographic information system) data to analyze the bathymetry of each lake and light profiles from the literature to determine the depth at which only 1% of the incoming

surface light remains (i.e., *compensation depth*; figure 1). It is generally assumed that 1% light represents a threshold for photosynthetic growth, but benthic photosynthetic organisms can occur at far greater depths in large lakes. For example, the compensation depth in Lake Baikal is 25 m (Straškrábová et al. 2005, Katano et al. 2008), but benthic algae grow to depths of between 70 and 200 m (Brooks 1950, Kiyashko et al. 1998). Similarly, in Lake Tahoe, viable aquatic mosses were collected from 140 m at a time when the 1% light threshold was 90 m (Sudeep Chandra, Department of Natural Resources and Environmental Science, University of Nevada, Reno, personal communication, 30 January 2010). Therefore, the 1% light level is a very conservative estimate of the depth to which benthic photosynthesis may occur, but we used the compensation depth to operationally divide the lake into three ecological zones. The *littoral zone* is the nearshore habitat where light intensity is sufficient for algae and plants to grow on the bottom. The unlit area of the lake that is deeper than the compensation depth is the *profundal zone*. Negligible photosynthesis occurs in the profundal zone. Finally, the pelagic water overlying the profundal zone is the *open-water zone*. The open-water zone is not contiguous with the lake bottom.

Organisms in aquatic ecosystems are classified on the basis of whether they live on the lake bottom (benthic) or in the water column (planktonic invertebrates and nektonic fish). Most invertebrate species are adapted to live either in the water column or on the bottom, but some species use both habitats. For this article, we did not try to categorize fish species by their use

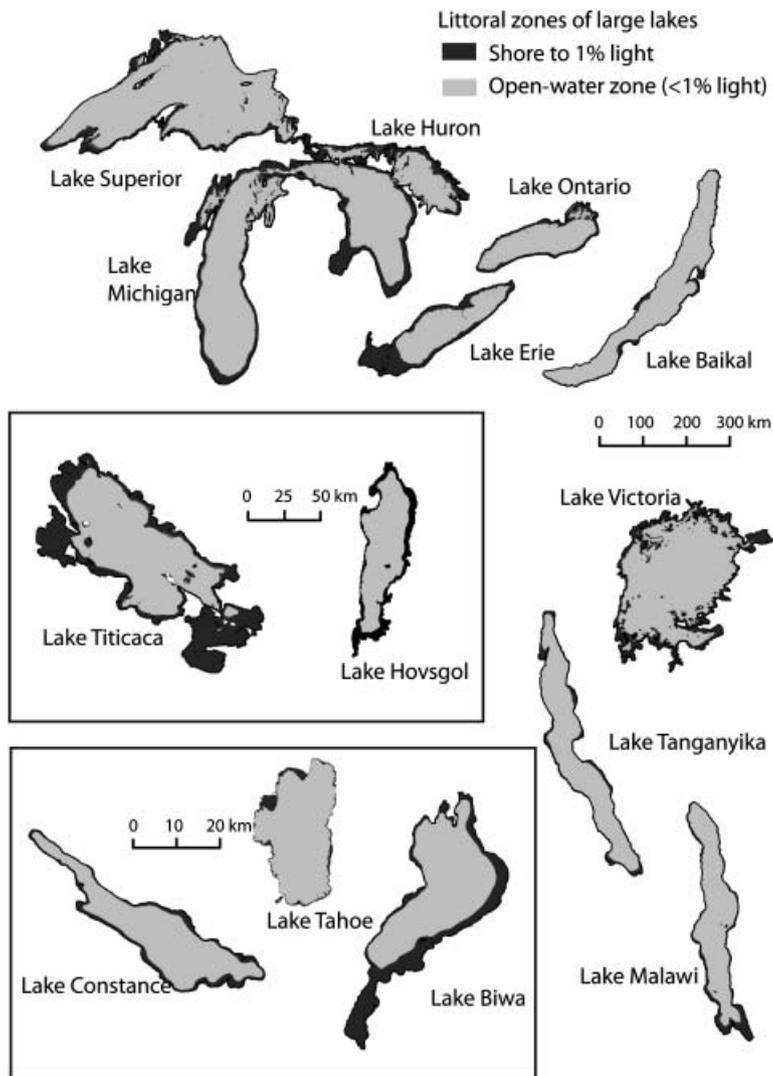


Figure 1. Scale maps of the 14 large lakes. We conservatively define the littoral zone as the area from the shoreline to the depth at which the only 1% of incoming light reaches the lake bottom (compensation depth). Beyond the littoral zone, the lakes are divided into the well-lit open-water zone (surface to compensation depth) and the profundal zone (compensation depth to the lake bottom).

of benthic or water-column habitat. A species' association with the benthos or the water column is distinct from its association with the zones of a lake. However, benthic animals can live only in the littoral and profundal zones, and a single benthic species can have a depth distribution that spans the littoral–profundal boundary. Swimming organisms such as zooplankton and fish can live in the littoral, profundal, or open-water zones, and may traverse the boundaries of these zones in order to exploit resources from multiple parts of the lake.

We used natural history observations from the literature to categorize each invertebrate species as benthic, planktonic, or both. This trait is based on the biology of the invertebrate and is not specific to the lake in which the species occurred. We used recorded depth distributions, light data,

and expert judgment to assign fish and invertebrates to the littoral, open-water, and profundal zones. Increased algal growth due to nutrient loading has reduced light penetration in some of these lakes, compressing the littoral zone. Therefore, we attempted to compare a species' depth distribution with the light climate at the time of collection, not with the lake's current light penetration, when assigning species to habitats. We also categorized each species as *native* (the lake is within the larger geographic range of the species), *endemic* (the worldwide distribution of the species is restricted to the lake), or *introduced* (the species has not occurred in the lake historically). We assumed that a species was native if we found no information to the contrary.

Using the compiled data, we were able to estimate the percentage of all freshwater species (total global diversity) that occur in the studied lakes. We were also able to describe the distribution of species richness (total number of species in an area) among the littoral, profundal, and open-water zones of each lake.

Large-lake contributions to global freshwater biodiversity

The 14 lakes together contain at least 1989 individual species of fish and 2614 species of mollusks, crustaceans, and insects (figure 2). Our database contains 787 species of fish (primarily in Lake Malawi and Lake Victoria) and 23 species of Lake Tanganyika gastropods that have been identified by experts but have not yet been formally described. We added these species to Balian and colleagues' (2008) totals to calculate their contributions to global biodiversity. The 14 lakes contain roughly 5% of the global species diversity of the groups that we cataloged (Balian et al. 2008), but this figure is skewed by the low percentage of global freshwater insect diversity (2%) found in the lakes. The focal lakes contain about 12% of the global freshwater species diversity of noninsect invertebrates and fishes combined. If taxonomists and evolutionary biologists have expended greater effort in describing species in large, ancient lakes than they have in the surrounding river habitats, then our estimates of the contributions of these lakes to global freshwater fish diversity may be inflated. Nevertheless, these few lakes clearly support a disproportionate fraction of global freshwater species.

About 15% of the global freshwater fish diversity (Lévêque et al. 2008), including at least 50% of cichlid diversity, occurs in these large lakes. Despite their potential mobility, the overwhelming majority of the fish species (94%) in our survey occur in only one of the studied lakes, and most of the fish species in our database (84%) are endemic (figure 2).

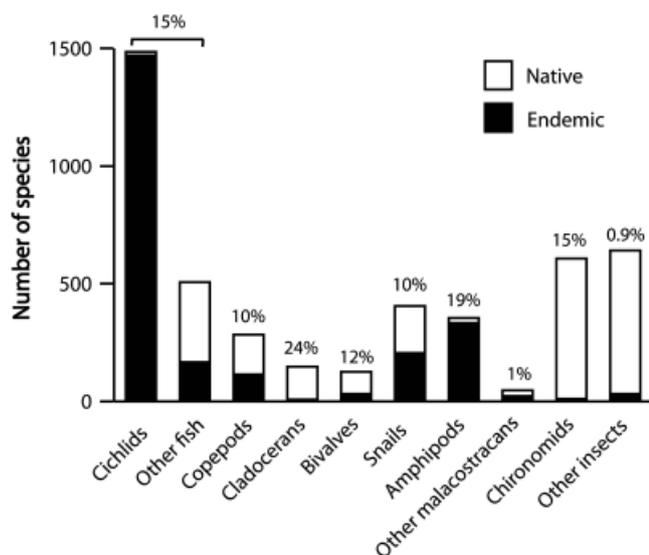


Figure 2. Rates of endemism within broad taxonomic groups. The numbers above the bars denote the estimated percentage of global diversity occurring in the 14 lakes for each taxonomic group. Fishes are divided into Cichlidae and all other families. Amphipods are graphed separately from other malacostracans (isopods, decapods, and mysids). Mollusks are divided into bivalves and snails (gastropods). Aquatic insects are divided into the Chironomidae and all other families.

This pattern is driven by the high diversity and endemism of fishes in the African rift valley lakes (figure 3; Snoeks 2000). None of the Laurentian Great Lakes contains its own extant endemic fish, although the interconnected system as a whole does contain several endemic species.

The lakes contain between 10% and 25% of the global freshwater diversity for noninsect invertebrates (figure 2). About one-quarter of the global amphipod and cladoceran diversity and about 10% of the freshwater diversity of bivalves, snails, copepods, and chironomids reside in these 14 lakes. Endemic species make up 15% to 71% of the molluscan fauna in the ancient lakes (those more than 100,000 years old), whereas the Laurentian Great Lakes, Lake Constance, and Lake Tahoe lack endemic mollusks. A high percentage (66% to 99%) of amphipods occurring in ancient lakes are endemic. In contrast to other groups, the insects found in these 14 lakes represent less than 2% of the global aquatic insect species diversity, and endemism among the insects is low (figure 2). There is considerable uncertainty in the conservative estimates of the global diversity of freshwater animals (Balian et al. 2008), and the numbers of invertebrate species in some of our study lakes are certainly underestimates, but these large lakes clearly support a substantial proportion and unique assemblage of global freshwater biodiversity.

It is striking that so much global freshwater diversity is contained in such a small number of water bodies. This concentration of biodiversity, combined with high rates of endemism (figure 2), forms a compelling argument for a strong conser-

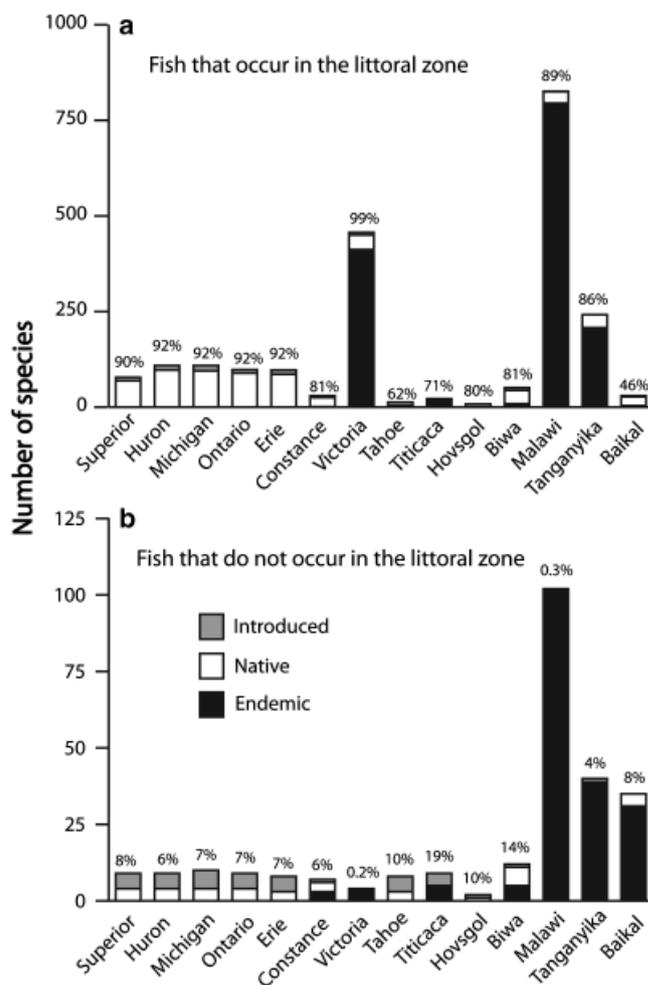


Figure 3. Distribution of fish species within each of the 14 study lakes. The lakes are organized in order of increasing age. (a) Species whose distribution includes the littoral zone. The number above each bar indicates the percentage of species that occurs in the littoral zone, either exclusively or in addition to another habitat. (b) Species whose distribution does not include the littoral zone. The percentage of species occurring only in the open-water zone appears above each bar.

vation focus on the fauna of large lakes. However, it is equally remarkable that these lakes contain more than two-thirds of the liquid freshwater on Earth but support only 2% to 25% of the global freshwater diversity in each taxonomic group. To explore this seeming paradox, we evaluated the extent to which these species use the vast open-water habitat.

Distribution of animals within large lakes

In all of the lakes except Baikal and Tahoe, more than 80% of the fish species use the littoral zone (figure 3a). Only in Lakes Biwa and Tahoe do more than 10% of the species use only the open-water zone (figure 3b). Salmonids are the sole family of fishes for which the majority of species are associated with the open-water zone, rather than the littoral or profundal

zones (figure 4a). Cyprinids also include numerous species that specialize in open-water habitats (figure 4a). Several fish families are largely littoral but have a few open-water representatives. For instance, the species flock of cyprinodontids in Lake Titicaca includes several open-water species (Dejoux and Iltis 1992). Clupeidae, a pelagic marine family, has endemic members in Lake Tanganyika (Sarvala et al. 1999),

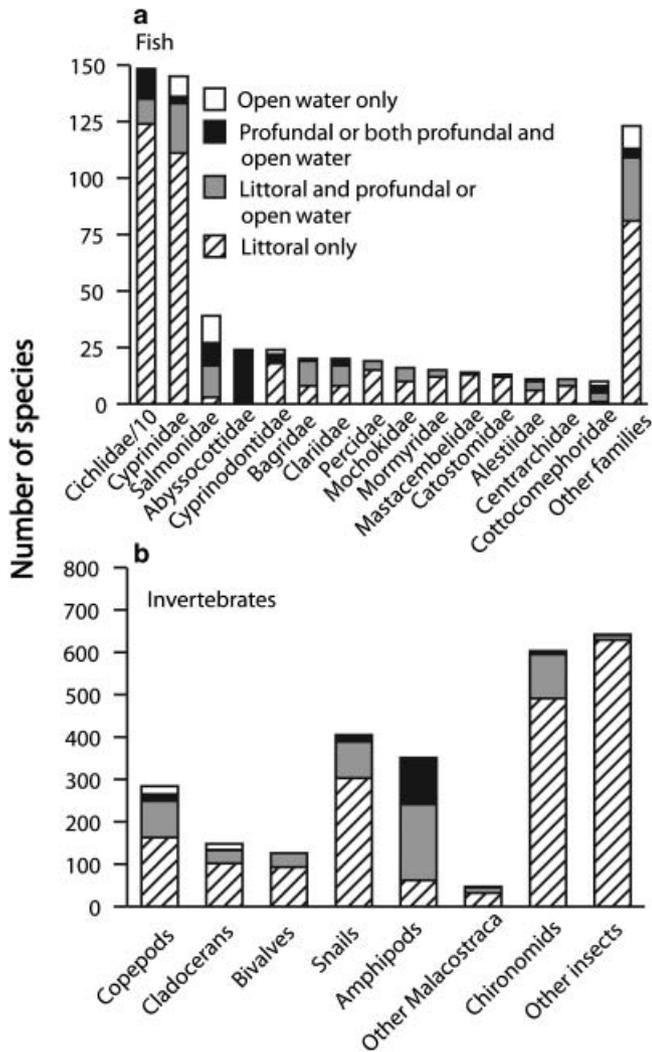


Figure 4. The number of animal species that occur exclusively in the littoral zone; in the littoral zone and the profundal or the open-water zone; exclusively in the profundal zone or in the profundal and the open-water zone; and exclusively in the open-water zone. (a) Fish families: The values for the family Cichlidae are divided by 10 to fit the graph. The actual cichlid numbers are 10 times greater than those shown. Forty-six families with fewer than 10 species occurring in the lakes are aggregated into “other families.” (b) Major taxonomic groups of macroinvertebrates: The amphipods are separated from other Malacostraca (isopods, decapods, and mysids); insects are separated into the dipteran family Chironomidae and all other aquatic insect families.

and marine clupeids have successfully invaded the Laurentian Great Lakes from the Atlantic Ocean, severely disrupting open-water food webs (Madenjian et al. 2002). The endemic family Abyssocottidae specializes in exploiting the profundal zone of Lake Baikal (Koshova and Izmet'syeva 1998). Despite these special cases, successful expansion into offshore habitats is a rare occurrence in most fish families (figures 3a and 4a). Rather, the majority of fishes in these large lakes are littoral. Indeed, habitat partitioning within the littoral zone is a key factor in fostering diversification into species flocks within ancient lakes (Sideleva 2000, Sturmbauer 2008).

The overwhelming majority of invertebrates in all of the taxonomic groups and in all of the lakes are benthic and use the littoral zone either exclusively or in conjunction with the profundal zone (figure 5a; also see table S1 in the supplementary online materials at www.jstor.org/stable/10.1525/bio.2011.61.7.7). This is strikingly evident in lakes for which there are complete species lists in published compilations (Lakes Baikal, Biwa, Hovsgol, Tahoe, Titicaca, and Tanganyika). Across the lakes, an average of 80% (range of 47%–92%) of the invertebrate species occur exclusively in the littoral zone, and 82% to 99% of the invertebrate species have a lakewide distribution that includes the littoral zone (figures 4b and 5, table S1). Lake Baikal has the lowest percentage of species that use the littoral zone (82%), but this difference is eliminated if the littoral zone is defined on the basis of the maximum depth at which littoral primary producers occur, rather than by the depth of 1% light. The vast majority of invertebrates that do not occur in the littoral zone of Lake Baikal are profundal amphipods, and less than 1% of invertebrate species occur exclusively in the open-water zone. A lack of sampling effort in Lake Victoria and the lack of chironomid data for Lake Malawi lead us to suspect that we are underestimating the number of littoral invertebrates in these tropical lakes.

More than 60% of the species in almost all of the invertebrate groups in the studied lakes occur only in the littoral zone (figure 4b). Copepods and cladocerans are two groups of crustaceans that are typically associated with open-water zooplankton communities but are actually overwhelmingly dominated by littoral species (figures 4b and 5). The higher species richness of copepod and cladocerans in the littoral than in the open-water zone is also a characteristic of smaller lakes and challenges the perception of these two groups as primarily “planktonic” (Walseng et al. 2006). Despite this skew in invertebrate habitat use, a comprehensive list of open-water zooplankton species is available for all 14 of our study lakes, whereas data are scarce and inconsistent for littoral copepods and cladocerans. The majority of truly open-water invertebrates are copepods and cladocerans, and these are the only groups in which individual species are widespread, occurring in more than 6 of the 14 lakes. Of 312 copepod and cladoceran species whose distribution is restricted to littoral zones, widespread species include *Sida crystallina* (nine lakes) and *Eurycercus lamellatus* and *Simocephalus vetulus* (eight lakes). The majority of the widespread taxa are open-water species: *Bosmina longirostris* is present in 12 lakes; *Leptodora kindtii* and *Macrocyclus albidus* each occur

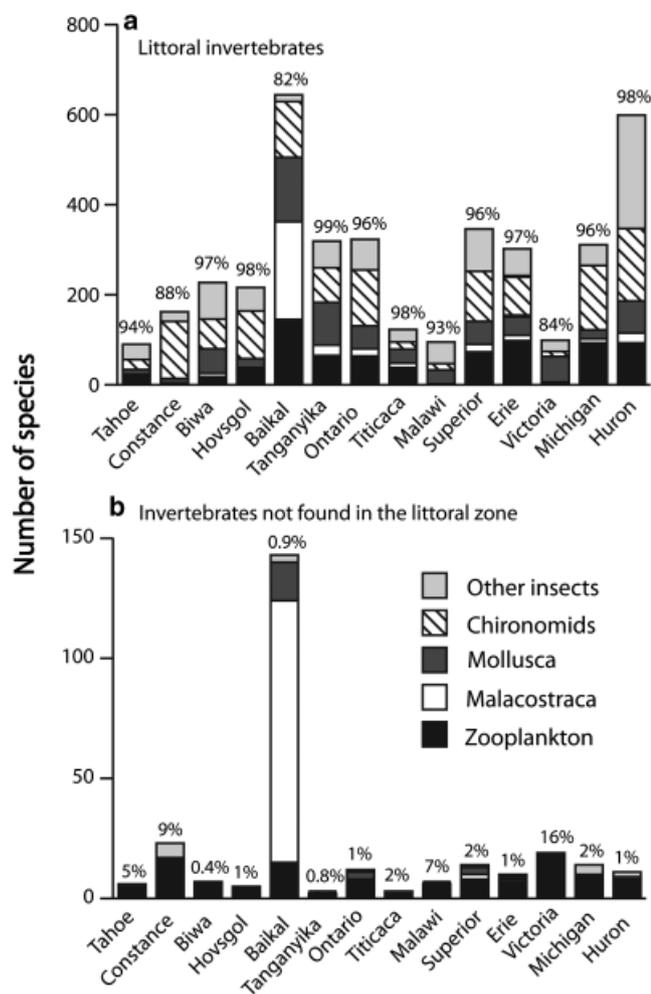


Figure 5. Distribution of the invertebrate species within each of the 14 study lakes. The lakes are organized in order of increasing littoral area. (a) Species whose distribution includes the littoral zone. The number above each bar indicates the percentage of species that occur in the littoral zone either, exclusively or in conjunction with another habitat. (b) Species whose distribution does not include the littoral zone. The percentage of species occurring only in the open-water zone appears above each bar. Zooplankton includes copepods and cladocerans; Malacostraca includes amphipods, isopods, decapods, and mysids; Mollusca includes bivalves and snails (gastropods). See table S1 in the supplementary online materials at [dx.doi.org/10.1525/bio.2011.61.7.7](https://doi.org/10.1525/bio.2011.61.7.7) for species totals in each habitat and group.

in 9 lakes; and *Holopedium gibberum*, *Acanthocyclops vernalis*, and *Daphnia galeata* each occur in 8 lakes. It is possible that some of these widespread open-water taxa may in fact be different species on different continents or may even represent cryptic species introductions.

Amphipoda is the most diverse group of crustaceans in these lakes and is the only taxonomic group in which the majority of species are not completely restricted to the littoral zone (figure 4b, table S1). About 70% of the

amphipod species in our survey occur only in the littoral zone or have a distribution that spans the littoral–profundal boundary. In addition to being diverse, amphipods dominate the benthic biomass in the deep waters of many of the cold lakes, including Lakes Baikal, Tahoe, and Titicaca and the Laurentian Great Lakes (Dejoux and Iltis 1992, Frantz and Cordone 1996, Koshova and Izmet'yeva 1998, Sierszen et al. 2006). In Lakes Baikal and Titicaca, amphipod diversity has arisen through adaptive radiations, and many of the endemic species of Lake Baikal are restricted to the profundal zone. Amphipods are notably absent from the African rift valley lakes, reflecting the generally low amphipod diversity in the African tropics (Vainölä et al. 2008). Instead, these tropical lakes have fascinating assemblages of crabs and shrimp, many of which are endemic.

There were comprehensive lists for the mollusks in most lakes, and the adults of all of the mollusks in these lakes are benthic. Virtually all mollusks in the lakes occur only in the littoral zones, although most of the lakes have a few species whose distribution extends into the profundal zone. Only 4% of the mollusk species occur exclusively in the profundal zone (table S1).

We initially chose to include insects because insects dominate benthic macroinvertebrate community richness in most freshwater lakes. However, insects proved to be the most difficult group for which to compile taxonomic information. Nearshore sampling intensity was low and spatially restricted in most of the lakes. The inventories of insects in Lakes Victoria and Malawi are partial at best. Nonetheless, insects make up the majority of the invertebrate diversity in 10 of our 14 lakes (figure 5).

Flies in the family Chironomidae usually dominate insect species richness (figure 5, table S1). In contrast to other insect taxa, chironomids in the focal lakes represent a percentage of global species diversity (15%) comparable to the noninsect taxonomic groups (figure 2). Chironomids thrive in the soft sediments that cover much of the bottom of large lakes and are easily sampled from a boat. In the lakes with comprehensive lists, over 90% of the chironomid species occur only in the littoral zone, but a few species are exclusively profundal (figure 4b). The chironomid species lists were incomplete for the African rift valley lakes. A death assemblage study in Lake Tanganyika (Eggermont and Verschuren 2003) yielded a chironomid species richness (77 species) comparable to that of the chironomids in the large temperate lakes (figure 5, table S1). A spatially restricted analysis of Lake Victoria sediments yielded 23 chironomid species in the littoral zone (Eggermont and Verschuren 2004), and no comprehensive data were available for Lake Malawi. We speculate that more sampling would reveal that the chironomid species richness values in Lakes Malawi and Victoria are comparable to that in Lake Tanganyika.

In most of the lakes, the littoral and benthic invertebrates were sampled predominantly from soft sediments. Spatially extensive sampling of the shallow (less than 5-m-deep water) rocky shores of Lakes Erie, Huron, Ontario, Superior,

and Malawi reveals that the majority of nonchironomid insect diversity occurs in these nearshore rocky habitats (Barton and Hynes 1978, Abdallah and Barton 2003). The rocky shores of Lake Michigan were not included in the Canadian study (Barton and Hynes 1978), and we found only a minimal amount of spatially explicit information on the zoobenthos of Lake Michigan (Winnell and White 1985). The lack of attention to Lake Michigan's littoral habitats is sufficiently egregious to inspire the aptly titled book chapter "Submerged terra incognita: Lake Michigan's abundant but unknown rocky zones" (Janssen et al. 2005). Rocky shores are hot spots of ecological activity for Lake Michigan's fish community, but they are virtually unknown ecologically. Lake Michigan's rocky shores have been so dramatically altered by the invasion of dreissenid mussels that their historical species assemblages will probably remain unknown (Janssen et al. 2005). The lack of accessible compilations on zoobenthic diversity in Lake Michigan and in the other Laurentian Great Lakes has been lamented for decades (Robertson 1984). The situation stands in stark contrast to the relatively comprehensive information available in published monographs for Lakes Baikal, Biwa, and Tanganyika, and even Lakes Titicaca and Hovsgol (Horie 1984, Coulter 1991, Dejoux and Iltis 1992, Koshova and Izmet'syeva 1998, Gouldin et al. 2006). This disparity is especially shocking, given the resources available for research on the Laurentian Great Lakes. This lack of knowledge constrains our ability to respond effectively to the diverse anthropogenic threats to the Laurentian Great Lake communities.

Diversity, habitat structure, and productivity

Ecosystem age, isolation, productivity, size, and latitude may all influence species richness patterns (Barbour and Brown 1974, Rosenzweig 1992, Brown 1999, Dodson et al. 2000). Fourteen lakes is simply too small a sample size to statistically untangle the effects of these diverse correlates with species richness. The effect of latitude is particularly difficult to quantify, given the spatial clumping of the Laurentian Great Lakes and of the African great lakes. Assessing relationships between species richness and ecosystem age is also problematic, because there is more uncertainty associated with estimates of each lake's age than with its species richness. There is no correlation between our best estimates of ecosystem age and total species richness (Spearman rank correlation, $r = -.086$, $p = .77$ for fish; $r = -.068$, $p = .82$ for invertebrates). Ancient tectonic lakes have a higher proportion and total number of endemic species than do more recently formed lakes, but Lake Victoria is an exception to this trend. Lake Victoria has dried out in the last 15,000 years but has a substantial number of endemic mollusks and fishes. The lack of a correlation between estimated lake age and species richness allows us to explore the effects of ecosystem size on the diversity patterns of the lakes.

The lakes in this study are analogous to oceanic islands, in that they are isolated ecosystems embedded in an opposing (terrestrial versus aquatic) landscape. Species-area curves summarize the positive nonlinear relationship between bio-

diversity and habitat availability. This relationship emerges from limits on dispersal, population persistence, and speciation that collectively permit more species to persist in large habitat patches than in small ones (Rosenzweig 1992). We used analyses of covariance to characterize the relationship between species richness and habitat area for each of the three major habitat types (littoral, profundal, and open water) in our analysis. When an individual species was found in more than one habitat zone, it was included in all of the applicable habitat totals. Both species richness and habitat surface area were \log_{10} transformed. An initial test for the homogeneity of slopes showed no significant interaction between habitat type and habitat surface area for the invertebrates or fishes. Therefore, the final analysis included only habitat surface area and a categorical variable for habitat type. The degrees of freedom in each analysis were set as the number of lakes considered, because the habitats within lakes are not independent. Lake Victoria and Lake Malawi were omitted from the invertebrate analysis because of insufficient sampling of benthic invertebrates.

Species richness was positively related to habitat surface area for both fish ($F(1,10) = 21.11$, $p < .001$, slope = 0.37) and invertebrates ($F(1,8) = 14.91$, $p < .005$, slope = 0.20; figure 6). The effect of habitat type on species richness is significant and had very low p -values (fish, $F(2,10) = 27.41$, $p < .001$; invertebrates, $F(2,8) = 81.05$, $p < .001$). Interestingly, the expected positive relationship between habitat area and species richness is evident within habitats among lakes but not across habitats within lakes (figure 6). The littoral zones, which are the smallest habitats in these lakes, have both a much higher total number of species (species richness) and a much higher number of species per unit area (species density) than either the open-water or the profundal zones (figure 6). Average species densities in the littoral zone are about 10 times higher for fish and about 50 times higher for invertebrates than species densities in the open-water zones (figure 6). The profundal species richness values are intermediate between those of the open-water and littoral communities but are closer to the open-water values. The slope of the species-area curve for fish (0.37) and that for invertebrates (0.20) are at opposite ends of the range of values reported in the literature for a broad array of plants and animals (Barbour and Brown 1974, Rosenzweig 1992, Kreft et al. 2008).

The higher species richness in the littoral and profundal zones compared with that of the open-water zone (figure 6) probably reflects variation along two key environmental axes: physical complexity and light. Only the littoral and profundal zones include benthic surfaces, whereas only the littoral and open-water zones receive sufficient light for autotrophic production to accumulate. A positive correlation between structural heterogeneity and community complexity is recognized across ecosystems (Rosenzweig 1992, Brown 1999, Killimanis et al. 2008). Physical structure enhances the number of niche axes, enabling species coexistence and potential diversification. Interestingly, the physical heterogeneity of the littoral

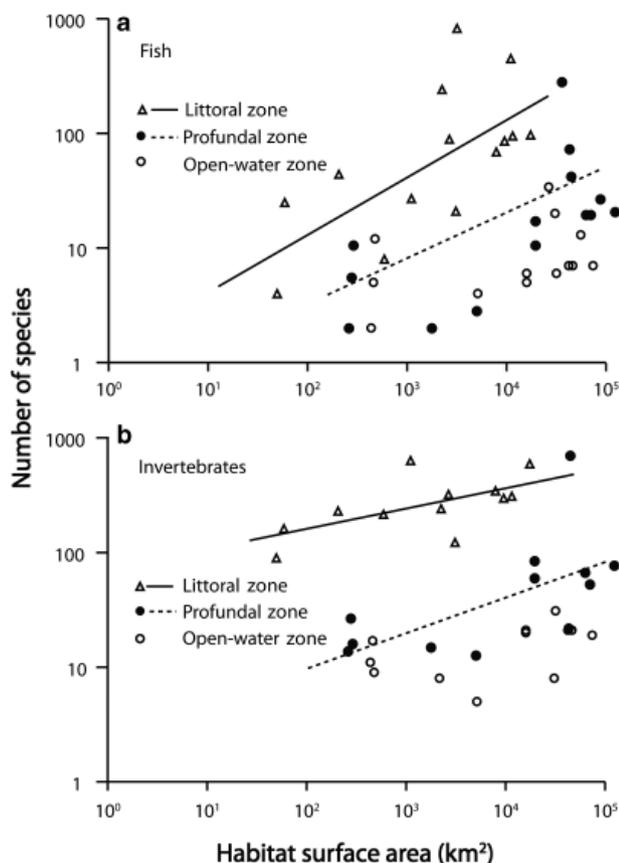


Figure 6. Species-area relationships for faunal assemblages in the littoral, profundal, and open-water zones. Each point represents the total number of species that use each zone in a single lake. A single species is included in more than one regression if it occurs in multiple zones within the lake. An analysis of covariance (see the text) demonstrated significant effects of both habitat area and habitat type (littoral, profundal, open water) for both fish and invertebrates. Here, we present individual regression statistics for taxa within the habitats. (a) Habitat surface area relationships for fish ($N = 14$ lakes). Littoral zone: $\log_{10}(\text{species richness}) = 0.18 + 0.49(\log_{10}(\text{littoral surface area}))$ ($r^2 = .42$, $p < .01$). Profundal zone: $\log_{10}(\text{species richness}) = -0.42 + 0.41(\log_{10}(\text{profundal surface area}))$ ($r^2 = .45$, $p < .009$). The regression for the open-water zone was not significant ($r^2 = .17$, $p > .16$). (b) Species richness–habitat surface area relationships for invertebrates ($N = 12$ lakes). Lakes Malawi and Victoria were omitted from the analysis because of a lack of sampling effort for the benthic communities. Littoral zone: $\log_{10}(\text{species richness}) = 1.84 + 0.18(\log_{10}(\text{littoral surface area}))$ ($r^2 = .39$, $p < .03$). Profundal zone: $\log_{10}(\text{species richness}) = 0.38 + 0.30(\log_{10}(\text{profundal surface area}))$ ($r^2 = .39$, $p < .03$). The regression for the open-water zone was not significant ($r^2 = .22$, $p > .13$).

and profundal zones in these lakes is largely abiotic, which contrasts with terrestrial and many benthic marine habitats, such as coral reefs and kelp forests, where the organisms themselves create three-dimensional structures. Although some of

the lakes have some submerged plants, habitat heterogeneity is largely confined to variation in mineral texture (e.g., sand, mud, cobble, bedrock).

An analysis of the habitat use of invertebrates in the 14 lakes shows that more than 95% of the species have benthic rather than planktonic habits, despite the modest physical complexity of the lake-bottom habitat. This estimate is conservative. In addition to excluding some groups that include planktonic species (e.g., rotifers), we also excluded annelids, ostracods, nematodes, bryozoans, and other minor phyla that are overwhelmingly benthic. Planktonic species are a small component of the invertebrate diversity in our study lakes. However, as many as 50% of the planktonic species occur in the open-water habitat. This result suggests that a primary barrier to invertebrates' exploiting the open water is the adoption of a planktonic life style.

The positive association between physically complex habitats (i.e., littoral and profundal) and species diversity underscores the enormous potential for partitioning on benthic surfaces relative to that in an open volume of water. Species inhabiting the open water are often distributed throughout the lake and tend to have large populations. The focus of limnologists and fisheries biologists on the open-water zones of large lakes in part reflects the fact that the open water, because of its large size, almost certainly supports the majority of lakewide zooplankton and fish production. A few species of fish support vast inland fisheries, and a relatively small number of zooplankton species support those fish. Within-lake turnover of open-water taxa is low across spatial gradients because the water column is a fluid, miscible habitat with few persistent dispersal barriers.

Conversely, the littoral communities of ancient lakes have fascinated evolutionary biologists because species finely partition benthic habitats, and species turnover is high across small spatial scales (Rossiter and Kawanabe 2000). Even in younger lakes, individual benthic taxa have restricted depth distributions and affinities for particular types of sediment (Reiss 1968, Frantz and Cordone 1996). In the African lakes, rocky outcrops alternate with expanses of sand or mud that act as dispersal barriers for both fish and gastropods. Limited gene flow across nonpreferred habitats appears to enable evolutionary divergence, even along short stretches of coastline (Sturm-bauer 2008). Therefore, large-lake communities exemplify the importance of habitat structure as a driver of species richness. The high species richness of littoral and even profundal zones relative to that of physically less structured open waters has clearly arisen repeatedly around the world under a variety of climates and time spans of lake history. Across all of these lakes, the differences in slope between the species-area curves for fishes and invertebrates suggests that fishes are more responsive to structural heterogeneity, although this interpretation could be biased by differential taxonomic resolution.

A second major axis of variation among the three zones is that of light and heat, which drive spatial variation in productivity and temperature. By definition, the littoral and open-water zones are photic zones in which primary

production occurs. In contrast, the profundal zone is aphotic and is also colder than the surface water for most or all of the year. In many tropical lakes, the warm surface-water mass is less dense than the profundal zone year-round. This prevents the water column from completely mixing, creating persistent low oxygen in the deeper waters of the African great lakes. The impact of light and heat on oxygen concentrations may affect species richness more strongly than temperature per se. Among-lake differences in mean annual surface temperature are comparable to many within-lake depth gradients (Barbour and Brown 1974). Although tropical lakes have the highest fish diversity, one of the coldest lakes, Baikal, has both the highest profundal and the highest total invertebrate species richness of all the lakes in the study. In contrast to temperature, hypoxic or anoxic conditions constrain the habitability of the profundal zone, reducing its effective size. Profundal hypoxia occurs in the African lakes and large lakes affected by eutrophication, but profundal species richness is lower than that in the littoral zones in all of the lakes, not just those with profundal hypoxia (figure 6, table S1). Therefore, temperature and low oxygen alone appear insufficient to explain the consistently lower species richness in the profundal zones than in the littoral zones.

In addition to affecting temperature, light penetration affects the relative availability of resources among zones in a lake. Photosynthetic organisms are the energy foundation of virtually all ecosystems, and species richness is often positively related to regional primary productivity (Rosenzweig 1992). Open-water primary production is limited to phytoplankton, whereas both phytoplankton and attached algae contribute to littoral zone primary production. Profundal organisms are dependent on organic detritus input raining down from the open-water zone. This detritus is often of low quality. Although ecosystem production has not been calculated for many of these lakes, primary production is efficiently converted into zooplankton and fish within the photic zone (Sarvala et al. 1999). Therefore, only a small fraction of whole-lake carbon fixation is available for transport to the profundal zone as detritus. In addition to decreased species richness, invertebrates are less abundant in the profundal zone (Reiss 1968, Frantz and Cordone 1996, Sierszen et al. 2006). We posit that low area-specific resource availability contributes to the lower species richness and lower invertebrate abundance in the profundal zone relative to the littoral zone, although this has not been tested.

Resource availability as a driver of species richness is more complex when the littoral and open-water zones are compared. High overall littoral productivity cannot explain the differences in species richness between the littoral and open-water zones because, at the whole-lake scale, open-water phytoplankton is responsible for more than 95% of the total primary production in large lakes (Loeb et al. 1983, O'Reilly 2006, Vadeboncoeur et al. 2008). Productivity per unit area is a more relevant index of the number of species that a given area can support. Littoral primary productivity has been measured in only a few of the 14 lakes. The available

evidence indicates that that the sum of periphyton and phytoplankton production per square meter of littoral zone is of similar magnitude to, and not markedly higher than, the phytoplankton primary production per square meter of the open-water zone (O'Reilly 2006). Therefore, the higher diversity in the littoral zones of these lakes does not appear to be a function of unusually high area-specific productivity in the littoral zone. Rather, the littoral zone supports many more species per unit of primary production than does the open-water zone.

The idea that habitat productivity has a strong influence on species richness is deeply rooted in the ecological understanding of species diversity patterns (Rosenzweig 1992, Dodson et al. 2000). The comparison of littoral and open-water species assemblages demonstrates that adjacent habitats with similar area-specific primary productivity, climates, and ecosystem ages support vastly different numbers of species. Stable isotope data from a few of our focal lakes show that the high diversity in the littoral zone is energetically dependent on periphyton production (Hecky and Hesslein 1995, Yoshii 1999, Kidd et al. 2001, Vander Zanden et al. 2003). This scenario raises an intriguing question: How can roughly equivalent amounts of area-specific primary production support orders of magnitude more species per unit area in the littoral zone than in the open-water zone?

One possibility is that greater efficiency of energy transfer in littoral food webs has the potential to increase the number of species supported by primary producers (Hecky and Hesslein 1995). In aggregate, littoral-zone communities might have lower biomass-specific metabolic rates, higher assimilation efficiencies, or higher consumption efficiencies than open-water communities. There is evidence that fish have higher ecological efficiencies when feeding on zoobenthos than when feeding on zooplankton (Vander Zanden et al. 2006). Higher ecological efficiencies may be a fundamental property of littoral zones because of the larger body size of the primary consumers in periphyton-based versus phytoplankton-based food chains (Vander Zanden et al. 2006). However, it is not clear that higher ecological efficiencies will necessarily correlate with higher species richness in the littoral zone, because there is an inverse relationship between body size and species richness (Brown et al. 2004). Furthermore, vastly higher ecological efficiencies would be required in order to generate the order-of-magnitude-higher species densities that characterize the littoral zone (figure 6).

Although the ecological efficiency argument is intriguing, the higher diversity per unit of primary production in the littoral zone is more likely to reflect an underlying relationship between species abundance and habitat heterogeneity. In any ecosystem, a few species are common (i.e., they have high population sizes) and the vast majority of species are rare (Brown 1999). Habitat homogeneity and low species richness in the open water translates to widespread and abundant populations of a few common open-water species. In contrast, littoral species finely partition a modest area of

habitat; they are rare and persist at low total population sizes relative to open-water species. In finely partitioning physical habitat, species also finely partition primary production. The fascinating littoral species flocks that have informed our understanding of evolutionary processes are composed of relatively uncommon species with spatially restricted distributions (Rossiter and Kawanabe 2000, Sturmbauer 2008). This makes the endemic assemblages in ancient lakes particularly vulnerable to exploitation (e.g., fisheries) and habitat modification (e.g., lakeshore development).

Biological links between littoral and open-water habitats

The species richness patterns summarized above demonstrate that littoral and benthic habitats support a large majority of species, even in the world's largest lakes. In Baikal, Titicaca, and the African rift valley lakes, much of this biodiversity is endemic and should be a high priority for conservation. However, endemism is not the only determinant of the value of littoral biotic complexity. We believe that littoral biodiversity has a functional importance that is independent of the uniqueness of its component species. Food web structure is a determinant of ecosystem function, and most analyses of lake food webs have been focused on pelagic organisms (Carpenter and Kitchell 1993). However, if foraging fish link littoral and open-water habitats in large lakes, then the exclusion of the littoral zone from ecosystem research limits understanding of the ways in which large lakes function.

We used a fish diet analysis as an index of food web complexity and the importance of benthic and planktonic productivity for supporting biodiversity in the 14 lakes. Stable isotope analyses have demonstrated the importance of littoral production to components of the fish community in many of the focal lakes (Hecky and Hesslein 1995, Bootsma et al. 1996, Yoshii 1999, Vander Zanden et al. 2003, Sierszen et al. 2006). A diet analysis of all of the fish in our database offers a more comprehensive picture of the food webs of the focal lakes. However, we can distinguish only between benthic and pelagic diet items; we are unable to unequivocally determine whether the diet items are derived from littoral or pelagic primary production. However, macroinvertebrate density tends to peak in the midlittoral zone and then decline sharply with depth (Frantz and Cordone 1996, Sierszen et al. 2006), indicating that most of the benthic resources used by fishes are likely to be produced in the littoral rather than in the profundal zone.

Regardless of the habitat that they occupy, the vast majority of fish species use benthic food resources either exclusively or in conjunction with planktonic food items (figure 7). There is a large guild of periphyton grazers in tropical lakes that is largely absent in temperate lakes. For both tropical and temperate lakes, more fish species feed on benthic resources (periphyton and benthic invertebrates) than on items from any other single diet category. The only habitat for which benthos is not the dominant diet category is the open-water zone. Many fish consume

benthic invertebrates and either fish or zooplankton. This indicates strong resource coupling between the benthic and planktonic resource bases within the littoral zone and, potentially, coupling between the littoral and open-water zones. In all, less than 10% of the studied species rely solely on water-column food items (zooplankton, phytoplankton, fish; figure 7). If our spatial and dietary analyses are merged, it is clear that most fish species in large lakes are restricted to the littoral zone and use benthic resources (figures 4a and 7). This finding supports other studies that show strong energetic dependence of fish and invertebrates on littoral primary production pathways (Hecky and Hesslein 1995, Yoshii 1999, Vander Zanden et al. 2003, Hecky et al. 2004, Sierszen et al. 2006).

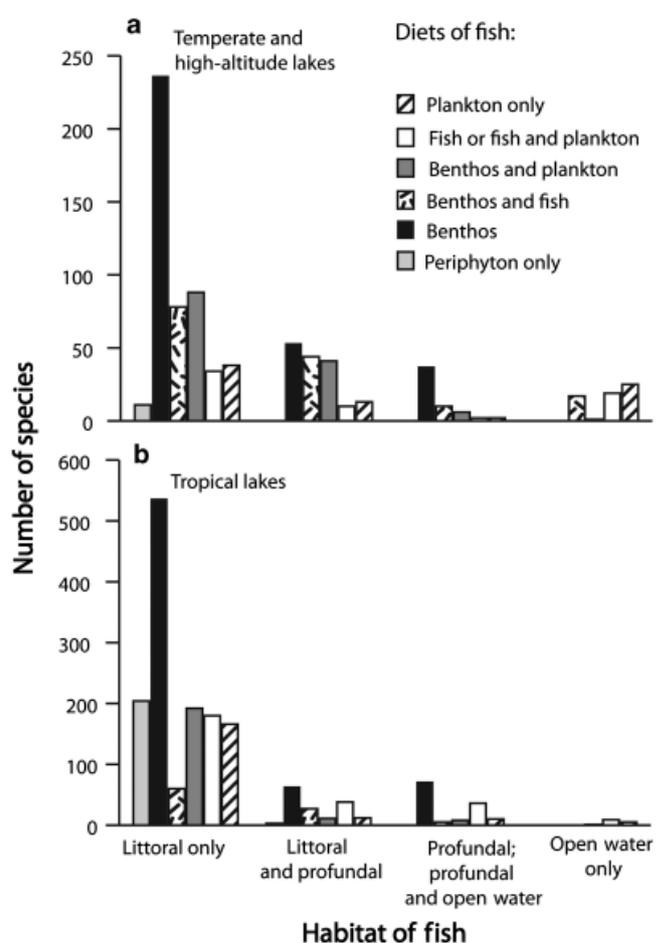


Figure 7. Diets of fish species that occupy different zones of the study lakes. Periphyton only refers to fish species whose diet is exclusively attached algae. Benthos refers to a diet of only benthic macroinvertebrates or of both periphyton and benthic macroinvertebrates. A plankton diet includes zooplankton or phytoplankton. Fish that include other fish in their diets (fish or fish and plankton, benthos and fish) may forage on fish that are littoral or open water, and there was no way to distinguish between those in our analysis. (a) Temperate lakes and Lake Titicaca. (b) Tropical lakes (African rift valley lakes).

The importance of littoral primary production and benthic resources to littoral fishes does not provide a direct index of littoral–open-water coupling, but given the opportunistic nature of fish, foraging across the littoral–open-water interface is highly likely and deserves more research attention. The traditional emphasis on open-water trophic pathways without integrating littoral organisms inhibits our ability to describe and understand the ecosystem dynamics that support the majority of species in all large lakes. Reconfiguration of littoral–pelagic food web links has already had catastrophic consequences in large lakes, regardless of the level of endemism within the lakes (Ojaveer et al. 2002, Balirwa et al. 2003, Vander Zanden et al. 2003, Hecky et al. 2004). The ecological complexity conferred by linking species-rich littoral food webs with less complex open-water food webs is poorly understood, but the diet data indicate that it is a characteristic of all of these large lakes.

Conclusions

The vast majority of fish and invertebrate species live in the shallow edge habitat, which makes up an average of 18% of the surface area of these large lakes (table 1). Together, these 14 lakes support about 15% of the global fish diversity and 3% of insect, mollusk, and crustacean diversity. Most fish species occur in only a single lake, and many are endemic. The heavy concentration of biodiversity in nearshore habitats indicates that littoral ecosystem dynamics must not be overlooked, even in large lakes with vast open waters. The ability of the littoral zone to support so many species per unit area and per unit of primary production provides rich fodder for analyzing basic relationships between species richness and ecological efficiency, habitat structure, and ecosystem productivity. The concentration of species richness in the littoral zone provides a compelling argument for directing research effort toward littoral ecosystem dynamics.

Littoral production is clearly critical for supporting fishes in all habitats, and the dynamic implications of cross-habitat energy and nutrient exchanges merit further research. Both the potential strength and the ultimate vulnerability of these linkages have been painfully demonstrated by the catastrophic effects of species introductions on production dynamics, food webs, and diversity in large lakes (Ojaveer et al. 2002, Balirwa et al. 2003, Hecky et al. 2004).

The concentration of species at lake edges is matched by the focus of human activities on the lakeshore. This focus leaves littoral communities extremely vulnerable to the interacting stresses of habitat modification, eutrophication, invasive species, climate change, and pollutants (Beeton 2002). The lack of ecological research effort on littoral communities and littoral ecosystem dynamics prevents effective and informed responses to the myriad anthropogenic pressures on these communities. The great lakes of the world are not merely vast repositories of freshwater. They are critical habitat for unique and threatened biotic communities about which we still know remarkably little.

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