

# Putting the Lake Back Together: Reintegrating Benthic Pathways into Lake Food Web Models

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**L**akes are often used as model ecosystems because they have clearly defined boundaries and identifiable connections with adjacent ecosystems. Furthermore, small lakes are tractable units for construction of ecosystem energy budgets and whole-ecosystem experiments. Thus, limnology has contributed substantially to the understanding of basic ecological principles. However, limnologists themselves are inconsistent in their treatment of the very boundaries that make lakes such valuable conceptual models for ecosystem ecology. The body of limnological research in recent decades has had an overwhelmingly pelagic focus, with the benthic habitat often viewed as merely a source or sink of pelagic nutrients or energy. Two seminal papers in ecology, “The Trophic Dynamic Aspect of Ecology” (Lindeman 1942) and “The Lake as a Microcosm” (Forbes [1887] 1925), fully integrated benthic processes into their description of lake dynamics. Even though these works are still frequently cited, benthic and pelagic habitats have often been treated as discrete food webs with parallel but separate compartments of bacteria, primary producers, and consumers. Thus, most limnologists study either the benthic or, more often, the pelagic habitat, although research on the role of macrophytes in shallow lakes is one important exception (Sand-Jensen and Borum 1991, Scheffer et al. 1993, Jeppesen et al. 1998). We examined the role of benthic primary and secondary production in lake food webs to demonstrate that division of lakes into benthic or pelagic habitats, to be studied in isolation by different researchers, skews the perception of lake food webs. This is particularly true for most of the world’s lakes, which are small and have high ratios of littoral surface area to pelagic volume (Wetzel 1990). We chose to use the word *reintegrating* in our title because we are appealing for a return to the roots of limnological research, in which benthic pathways are viewed as fundamental to a thorough understanding of lake ecosystem function.

LAKE ECOLOGISTS TEND TO FOCUS THEIR RESEARCH ON PELAGIC ENERGY PATHWAYS, BUT, FROM ALGAE TO FISH, BENTHIC ORGANISMS FORM AN INTEGRAL PART OF LAKE FOOD WEBS

The relative frequency with which benthic and pelagic habitats are studied should reflect the prevailing perception of their relative importance. In order to compare the relative research effort devoted to the two habitats, we searched the BIOSIS literature database for papers published from 1990 to 1999. We divided the lake food web into three production groups: (1) primary producers (periphyton [benthic algae], macrophytes, phytoplankton), (2) heterotrophic bacteria (epiphytic, planktonic, and sediment-associated bacteria), and (3) invertebrate consumers (zoobenthos, zooplankton). We limited our search to studies that measured primary pro

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ductivity and heterotrophic bacterial productivity rather than biomass because we were interested in energy flow in lake food webs. However, we found measurements of invertebrate consumer productivity to be rare and invariably based on biomass estimates. Therefore, for this group we included studies in which either productivity or biomass were measured. We did not include fish production in our literature search because many fish use both habitats or undergo ontogenetic habitat shifts. We did, however, use fish diets to assess the level of integration between benthic and pelagic food webs. Our purpose was not to find all papers published in the last decade but to get a representative sample of the frequency with which the two habitats were studied.

The literature search confirmed our impression that pelagic processes are the focus of limnology. Limnologists measured phytoplankton productivity about 10 times more often than they measured periphyton productivity. Of 193 studies in which primary productivity in lakes was measured, 91% measured phytoplankton productivity alone, 4.5% only periphyton productivity, and 4.5% primary productivity in both habitats (Figure 1a). Bacterial productivity was measured in 53 papers. Of those, 89% measured bacterioplankton productivity, 7.5% measured only benthic bacterial productivity, and 3.5% measured both benthic and planktonic bacterial productivity (Figure 1b). Of 59 papers quantifying invertebrates in lakes, 73% made measurements for only zooplankton biomass or productivity, 15% only for zoobenthos, and 12% for invertebrates in both habitats (Figure 1c).

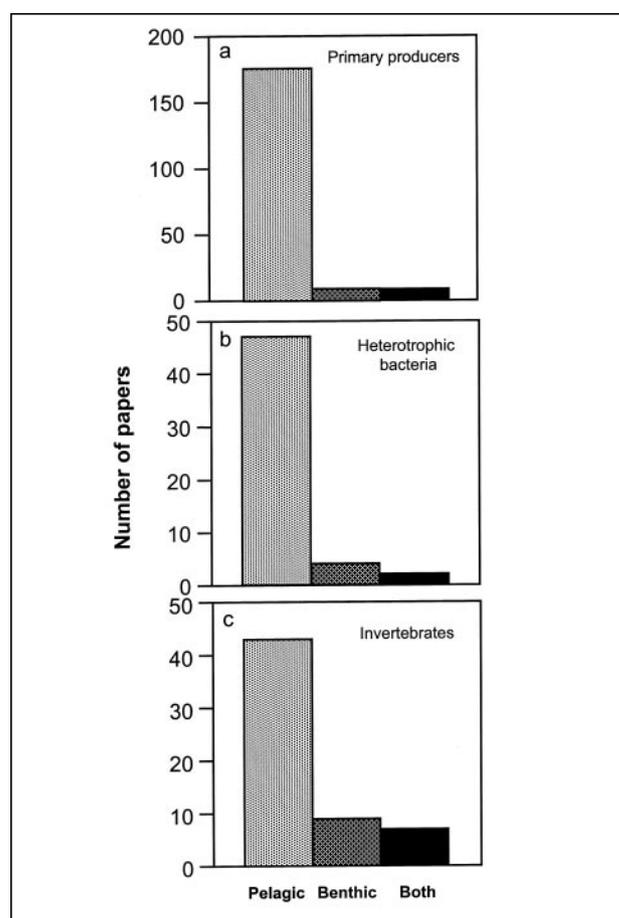
Given the preponderance of research on pelagic habitats and the scarcity of productivity measurements for both habitats, one might question whether the current depiction of lake ecosystem dynamics is complete. Of course, the scope of some ecological questions is never intended to extend beyond specific organisms or interactions, and there is nothing inherently wrong with confining one's research scope to planktonic processes. Increasingly, however, ecologists are assessing human impacts on the structure and functions of lake ecosystems, and scaling up to the whole-ecosystem level has been problematic (Schindler 1998). Furthermore, many human perturbations are likely to alter linkages between benthic and pelagic habitats, linkages that are currently only poorly understood (Lake et al. 2000). Using planktonic processes as an index of whole-lake ecosystem dynamics may then be justified if

- the contribution of benthos to ecosystem function is minor
- benthic and pelagic communities are discrete and function independently with few strong interactions across habitat boundaries
- the relative contribution of benthos to whole-lake productivity does not vary across lake size and nutrient gradients

In the following sections, we use data from the literature to show that benthic organisms can contribute substantially

to whole-lake production, that energetic links across habitat boundaries are common, and that the importance of benthic communities is a function of lake size.

Even a cursory examination of all benthic–pelagic links that affect lake function would be a daunting task, one we do not attempt to undertake here. Rather, we limit our scope primarily to energy pathways. We do not, for example, evaluate the role of organisms in transport of nutrients or contaminants between habitats. Nor do we dwell on complex interactions or trophic cascades. Instead, for simplicity, we focus on interactions among organisms at the same trophic level or at adjacent trophic levels. Even such direct interactions across habitats are poorly understood, but are likely to be substantially altered by human perturbation such as eutrophication and global climate change (Lake et al. 2000). The available evidence makes it clear that our understanding of lake food webs



**Figure 1.** Frequency of publication on benthic versus pelagic habitats for (a) primary producers, (b) heterotrophic bacteria, and (c) invertebrates. The search was conducted on the BIOSIS database for papers published from 1990 to 1999. We restricted our search to papers that measured whole-community productivity (rather than productivity for species subsets). Laboratory experiments, literature surveys, methodological studies, and paleolimnological estimates were excluded from the counts.

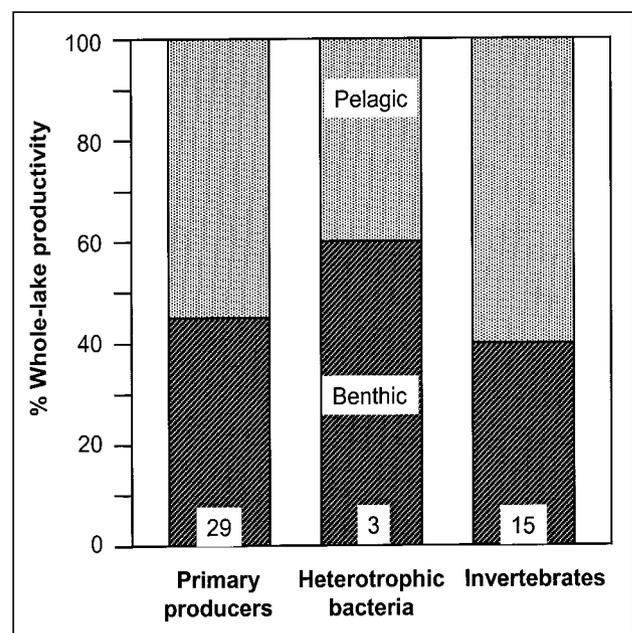
would improve substantially if we viewed benthic and pelagic habitats as functionally integrated pathways for resource and energy flux in lake ecosystems.

### **Benthic contributions to whole-lake primary, bacterial, and invertebrate productivity**

The role of benthic primary production in lakes is largely unstudied (Lowe 1996). We found published concurrent measurements of productivity of phytoplankton, submerged macrophytes, and periphyton on natural substrata for only 29 lakes worldwide (Jónasson et al. 1990, Ramlal et al. 1994, Lodge et al. 1998, Vadeboncoeur et al. 2001). These lakes range from 0.2 to 34 meters mean depth and 1.7 to 99,000 hectares surface area. The studies—many of which date back to the 1970s and the International Biological Program—used widely different methods, so the results are only generally comparable. Nevertheless, when annual primary productivity per square meter of lake area was estimated, benthic productivity was, on average,  $58 \text{ g} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$  compared with  $69 \text{ g} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$  for phytoplankton. Periphyton and submerged macrophytes constituted more than 50% of productivity in half of the lakes for which data were available and, on average, made up 46% of whole-lake primary productivity (Figure 2). Therefore, benthic primary productivity in lakes is often similar to or greater than that of phytoplankton. If one accepts that whole-ecosystem productivity (i.e., of higher trophic levels) is to some extent constrained by the amount of carbon fixed within the ecosystem, then benthic primary production constitutes a largely overlooked energy input to lake food webs.

We found three whole-lake scale comparisons of benthic and pelagic bacterial productivity but no data compilations for bacteria. Whole-lake benthic bacterial productivity was two to five times greater than bacterioplankton productivity in Mirror Lake, New Hampshire (Likens 1985). Similarly, bacterial productivity on macrophytes alone (i.e., not including sediment-associated bacteria) in two Danish lakes was one to seven times that of bacterioplankton on a whole-lake scale (Theil-Nielsen and Søndergaard 1999). Whole-lake sediment bacterial production was estimated to be one to three orders of magnitude higher than whole-lake measurements of bacterioplankton production in Quebec lakes (Jacob Kalff [McGill University, Montreal, Canada], personal communication). Very real methodological hurdles prevent precise estimates of benthic bacterial productivity (Kemp 1990), but the few whole-lake estimates we found strongly suggest that benthic bacterial productivity is at least of similar magnitude to that of bacterioplankton and dominates microbial productivity in some lakes (Figure 2). The high rates of bacterial production on sediments and macrophytes have potentially profound implications for the flux of dissolved organic carbon (DOC) between benthic and pelagic zones and for the use of benthic bacterial production by consumers (Johnson et al. 1989, Kemp 1990, Wetzel 1990).

Strayer and Likens (1986) compiled data on whole-lake zooplankton and benthic invertebrate productivity from 14 lakes. To this, we added data from three more lakes (Jónasson et al. 1990, Lindegaard 1994, James et al. 1998). We found that, on average, zoobenthos productivity makes up 42% of whole-lake secondary (benthic invertebrate plus zooplankton) productivity (Figure 2). This is a conservative estimate because the actual contribution of benthic invertebrates is consistently underestimated because samples are passed through relatively coarse sieves ( $500 \mu\text{m}$ ) before processing. This eliminates meiobenthic organisms, which can constitute 50% of total benthic invertebrate assimilation (production plus respiration) (Strayer and Likens 1986). The finding of substantial benthic invertebrate contribution to whole-lake secondary production is consistent with the dominance of



**Figure 2.** Average percentage contribution of benthic and pelagic producers to whole-lake primary, bacterial, and invertebrate productivity. The numbers within bars are the number of whole-lake estimates found for each group. Estimates for benthic contribution are conservative; we excluded emergent macrophytes from total macrophyte productivity; for heterotrophic bacterial productivity, a range of values of the benthic contribution was given for all three lakes, and we chose the lowest value. Also, for two of the lakes, bacteria productivity on sediments was not measured. Benthic secondary productivity in most of the studies included organisms retained in a  $500\text{-}\mu\text{m}$  sieve, a process that underestimates secondary productivity by up to 50%. Primary producer data sources are Jónasson et al. 1990, Ramlal et al. 1994, Lodge et al. 1998, Vadeboncoeur et al. 2001; for heterotrophic bacteria, Likens 1985, Theil-Nielsen and Søndergaard 1999; for invertebrates, Strayer and Likens 1986, Jónasson et al. 1990, Lindegaard 1994, James et al. 1998.

benthic invertebrates in many fish diets (Schindler et al. 1996, Vander Zanden et al. 1997).

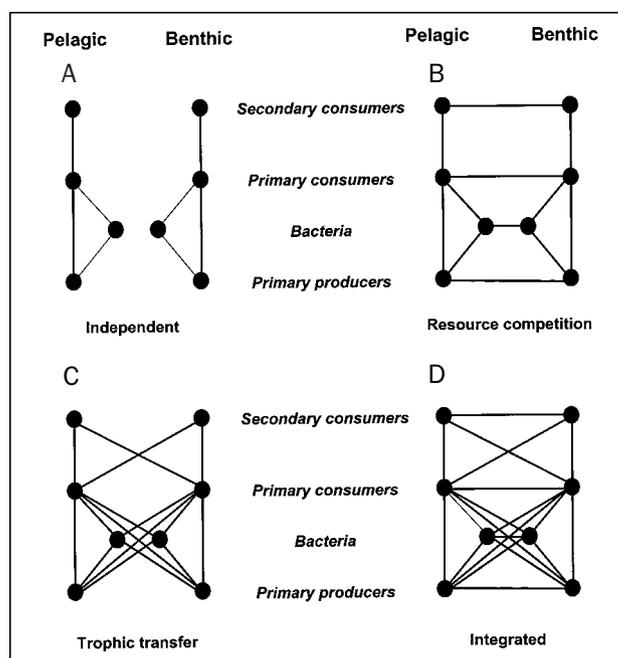
The contrast between Figure 1 and Figure 2 is striking. Although benthic organisms contribute substantially to whole-lake primary, secondary, and bacterial production, limnologists rarely quantify benthic contributions. If benthic and pelagic food web dynamics are strongly linked (Forbes [1887] 1925, Lindeman 1942), then it is important to note that limnologists rarely measure productivity in both habitats. This suggests that our understanding of dynamic feedbacks between trophic groups at the whole-lake scale lags far behind our understanding of pelagic trophic dynamics.

### ***Benthic–pelagic links: Resource and energy flux across habitat boundaries***

We present four heuristic models to conceptualize links between benthic and pelagic food webs. In model A, benthic and pelagic food webs have parallel but unlinked communities of primary producers, heterotrophic bacteria, invertebrate consumers, and fish (Figure 3a). If benthic and pelagic food webs are discrete and noninteractive, then disregarding benthic production will not distort understanding of the dynamics of pelagic food webs. In model B, benthic and pelagic organisms within a trophic category have access to the same resource pools at the whole-lake scale (Figure 3b). In this model, exploitation of a resource in one habitat reduces its availability to trophic counterparts in the other habitat—for example, increased carbon mineralization by bacterioplankton might reduce substrate availability for profundal benthic bacteria. Model C postulates that trophic transfers occur across habitat boundaries (Figure 3c) and that organisms in one habitat consume food produced in the other habitat; for example, benthic chironomids consume settled phytoplankton. In model D, the food webs in the two habitats are fully integrated (Figure 3d). Competitive interactions for resources occur within trophic categories in the two habitats, and energy flows across habitat boundaries through consumption. If strong interactions characteristic of either model B or model C are evident, then model A does not adequately describe lake food webs. Conversely, if there is evidence that both competitive interactions and trophic transfers are important, then model D represents the most comprehensive portrayal of lake food webs. Following are some examples from the literature of both lateral (within trophic categories) and vertical (between trophic categories) interactions between benthic and pelagic food webs that together suggest that model D most accurately represents the way lakes function. We suggest that the strength of the interactions between benthic and pelagic communities is strongly affected by lake size. Similarly, the direction of resource or energy flow between the two habitats is strongly influenced by water-column nutrient gradients.

***Allocation of resources between benthic and pelagic habitats.*** When the lake is viewed as an integrated whole, the possibility arises that use of a resource in the pelagic

habitat will reduce availability of that resource in the benthic habitat, and vice versa (Figure 3b). A precondition for these lateral interactions is that organisms in the two habitats rely on the same resources. Both benthic and pelagic primary producers depend on light and inorganic nutrients. Because benthic primary producers are more effective than phytoplankton at sequestering phosphorus from sediment interstitial water, they regulate the availability of sediment nutrients to phytoplankton in oligotrophic lakes (Hansson 1988, 1990). Conversely, high levels of phytoplankton production reduce light penetration to the sediments in eutrophic lakes, and thus limit periphyton and macrophyte productivity (Sand-Jensen and Borum 1991, Hansson 1992, Scheffer et al. 1993, Havens et al. 2001). When oligotrophic soft-water lakes in northern Michigan were fertilized, phytoplankton biomass and productivity increased, which reduced light penetration and hence reduced periphyton productivity on sediments and substantially damped the whole-lake increase in primary productivity (Vadeboncoeur et al. 2001).



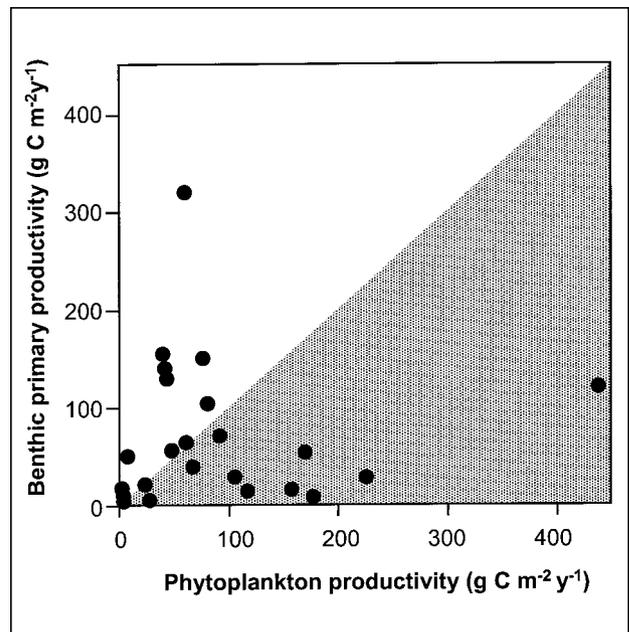
**Figure 3.** Conceptual models illustrating possible levels of benthic–pelagic coupling of lake food webs. Model A represents independent benthic and pelagic linear food chains, including primary producers (phytoplankton, periphyton, and macrophytes), a microbial loop through bacteria, primary consumers (zooplankton, benthic grazers), and secondary consumers (predatory invertebrates, carnivorous fish). The lines represent trophic interactions. Model B shows interhabitat resource competition between organisms within the same trophic category. Model C represents vertical trophic transfers across habitat boundaries. Model D represents a fully integrated lake food web that includes both resource competition and trophic interaction between benthic and pelagic habitats.

Paleolimnological evidence also supports this inverse relationship between benthic and pelagic primary producers. Benthic diatoms dominated species assemblages in a Swedish lake before AD 1300, when the catchment was forested, but planktonic forms increased markedly when agriculture began in the area (Anderson et al. 1995). Similarly, estuaries switch from predominantly benthic to predominantly pelagic primary productivity in response to anthropogenic increases in nitrogen (Borum and Sand-Jensen 1996, Havens et al. 2001). Inverse relationships between benthic algae and phytoplankton indicate that limnologists might usefully view lake eutrophication from a different perspective: Lakes with high water quality are characterized not just by low phytoplankton levels; they also appear to be systems in which benthic organisms dominate whole-lake primary productivity.

Such patterns have led to the hypothesis that there is a unimodal pattern of periphyton primary productivity along a total phosphorus (TP) gradient (Sand-Jensen and Borum 1991, Hansson 1992, Havens et al. 2001). Phytoplankton and periphyton productivity are expected to be positively related to the availability of water-column nutrients in oligotrophic lakes. However, at a certain point periphyton productivity is expected to decline because phytoplankton blooms reduce light penetration to benthic surfaces. We used the literature data compiled for Figure 2 to test for this pattern. Unfortunately, TP data were not available for many of the lakes; we therefore used phytoplankton productivity as an index of TP. The whole-lake estimates of primary productivity support the hypothesized unimodal pattern (Figure 4). Initially, the relationship between periphyton and phytoplankton productivity is positive. However, as lakes become more eutrophic, periphyton productivity declines and most likely becomes less important to energy flow in lake ecosystems.

Although there is a general transition from benthic to pelagic domination of primary productivity along a eutrophication gradient, alternate stable states can occur in shallow lakes at intermediate nutrient concentrations (Scheffer et al. 1993). At a given TP concentration, shallow lakes with large littoral zones can alternate between clear-water states with high densities of macrophytes and periphyton and low phytoplankton concentration, and turbid states with low macrophyte density and high levels of phytoplankton (Scheffer et al. 1993). In shallow lakes, macrophytes stabilize the sediments, reducing wind-generated turbidity and phosphorus suspension. Macrophytes also facilitate top-down control of phytoplankton by providing zooplankton a refuge from predatory fishes and consequently enhancing water clarity (Jeppesen et al. 1997). Again, the desirable clear-water state in these shallow lakes is associated with high benthic primary productivity of macrophytes and their associated epiphytes.

The limited available evidence suggests that the contribution of benthic bacteria to whole-lake heterotrophic bacterial production is substantial (Figure 2). Do bacteria in the two habitats rely on the same pools of DOC and nutrients? High macrophyte and periphyton production in the littoral zone represents a potentially large source of DOC for both groups



**Figure 4.** Whole-lake benthic primary productivity (periphyton plus macrophytes) as a function of phytoplankton productivity. In the shaded region, phytoplankton productivity is greater than or equal to benthic primary productivity. The plot includes only lakes in which periphyton was measured on all dominant benthic substrata. Data sources: Jónasson et al. 1990, Ramlal et al. 1994, Lodge et al. 1998, Vadeboncoeur et al. 2001.

of bacteria (Reitner et al. 1999, Theil-Nielsen and Søndergaard 1999). Epiphytic bacterial productivity per mm<sup>3</sup> macrophyte volume has been found to be 1000 times greater than bacterioplankton productivity per mm<sup>3</sup> water volume, an indication that macrophytes and littoral zones are areas of highly concentrated, labile DOC (Theil-Nielsen and Søndergaard 1999). Any uptake of exuded DOC by bacteria attached to macrophytes and sediments must mediate or delay the flux of benthic DOC to bacterioplankton in the open water. Conversely, mineralization of planktonic detritus by pelagic bacteria is expected to reduce substrate availability to profundal benthic bacteria. Our survey of the literature revealed that benthic bacterial productivity is rarely measured, and we found no direct assessments of the influence of DOC uptake by benthos on pelagic bacteria, or vice versa. The possibility that the two habitats exhibit inverse patterns of bacterial production similar to patterns seen in primary producers merits exploration.

Compensatory changes in secondary production in one habitat as a result of food depletion in the complementary habitat are difficult to isolate. The productivity of profundal benthic filter feeders and deposit feeders depends on settling phytoplankton (Jónasson 1972). The degree to which zooplankton reduce phytoplankton biomass, and potentially food availability to the zoobenthos, varies with the lake trophic status and pelagic food web structure. Lellák (1966) found an inverse relationship between zooplankton and

zoobenthic productivity in five backwaters of the Elbe River that were subjected to a series of fish removals. He attributed this change to increased availability of food to zoobenthos when zooplankton grazing on phytoplankton was alleviated. Evidence that zoobenthos can affect phytoplankton availability to zooplankton is equivocal. Exotic mussels (*Dreissena* spp.) in North American lakes have the capacity to filter the equivalent of entire lake water columns in a matter of days (Strayer et al. 1999), drastically reducing phytoplankton concentrations. Small zooplankton in Lake Erie and the Hudson River have declined since the mussel invasion (MacIsaac 1996, Strayer et al. 1999), but in the Hudson River, this decline has been attributed to direct predation by zebra mussels, not competition for food. It is unclear whether declines in larger taxa, which are relatively invulnerable to zebra mussel predation, reflect only normal temporal variability (Strayer et al. 1999). In Lake Erie, the benthic–pelagic link between zebra mussels and plankton has led to marked improvements in water clarity, and the majority of whole-lake invertebrate production now occurs in the benthos (Johannsson et al. 2000). Similarly, the zebra mussel invasion has transformed the structure and function of the Hudson River ecosystem to a greater extent than almost any other human perturbation (Strayer et al. 1999).

**Trophic transfers between habitats.** When viewed from a different perspective, some of the lateral interactions across habitat boundaries discussed above can represent vertical trophic transfers of energy (Figure 3d). For example, phytoplankton-derived production moves up the food chain and traverses habitat boundaries when it is consumed by benthic deposit-feeders.

Benthic primary production is a potential source of autochthonous production available to consumers and heterotrophic bacteria. In the current debate over whether planktonic systems are heterotrophic or autotrophic, littoral sources of DOC are sometimes invoked to account for the missing carbon, but are often lumped with terrestrial detritus as “allochthonous carbon.” We found no estimates of the rate of flow of littoral DOC to the pelagic zone, but there is substantial experimental evidence that both benthic algae and macrophytes are sources of labile DOC that enhance bacterioplankton productivity. Bacterioplankton exposed to macrophyte-derived DOC increased productivity by a factor of four, but did not increase productivity in response to amendments of DOC derived from terrestrial detritus (Wehr et al. 1999).

Bacterioplankton from estuaries showed a similar fourfold increase in productivity when exposed to macrophyte leachate (Hopkinson et al. 1998). In a large lake with an extensive reed bed, bacterioplankton productivities appeared closely coupled with macrophyte DOC rather than phytoplankton DOC (Reitner et al. 1999). Benthic algae and littoral sediments also constitute a largely neglected pool of DOC in lakes. Algae on sediments (epipelon) release significant amounts of DOC to the overlying water during photosynthesis (Hellman

1997). Hopkinson and colleagues (1998) filter-sterilized water collected from directly over estuarine sediments and from the water column and inoculated the samples with bacterioplankton. Bacterioplankton productivity in water originating above the sediments was over three times greater than in water column controls. Hopkinson and colleagues attributed this increase to DOC released from sediment detritus and epipellic algae. Given the shift in distribution of primary production from the benthic to the pelagic habitat along a eutrophication gradient that we have described, there should be an inverse relationship between the amounts of autochthonous DOC produced by the two habitats. Thus, it is likely that the degree to which the littoral zone functions as a source of labile DOC diminishes with increasing nutrient enrichment, while the importance of the benthos as a sink for POC (particulate organic carbon, composed of settled phytoplankton) increases. This hypothesis is consistent with the finding that bacterial respiration exceeds phytoplankton productivity in oligotrophic lakes, with that effect diminishing with increasing eutrophication (del Giorgio et al. 1997).

Benthic and pelagic primary production is incorporated into organisms in the complementary habitat through food web linkages, either directly by primary consumers or indirectly through predation on consumers. The phytoplankton subsidy to the profundal zoobenthos is one of the most widely recognized benthic–pelagic links (Jónasson 1972). Zoobenthic biomass and productivity increase in response to subsidies of high-quality detritus or phytoplankton (Rasmussen 1985, Johnson et al. 1989). Comparative studies show that population dynamics of profundal amphipods are correlated with interannual variation in planktonic diatom abundance (Johnson and Wiederholm 1992). However, the importance of settling phytoplankton is not limited to organisms in the profundal zone. Densities and emergence of littoral chironomids increased when *in situ* mesocosms were experimentally fertilized (Blumenshine et al. 1997). Similarly, stable isotope data suggest that settling phytoplankton is increasingly incorporated into littoral food webs along a gradient of oligotrophic to eutrophic lakes in Denmark.

Compared with the role of phytoplankton in lake food webs, that of benthic primary production is largely understudied. Zooplankton can graze on periphyton. Periphyton is a main food item for many cyprinids (Schindler et al. 1996) and many cichlids in the Rift Valley lakes of Africa (Hecky and Hesslein 1995). We know that zoobenthic invertebrate grazers can exert a strong top-down influence on benthic algae (Steinman 1996). However, there are few quantitative estimates of the extent to which zoobenthos use benthic algae as an energy resource in lakes (Lowe 1996), though Strayer and Likens (1986) estimated that periphyton made up 50% of the diet of zoobenthos in Mirror Lake, New Hampshire. Benthic secondary production and biomass are generally much higher in the littoral zone than in the phytoplankton-fueled profundal zone (Jónasson 1972, Rasmussen and Rowan 1997). This is partly because of high temperature and oxygen levels in the epilimnion, but it is also likely that high levels of

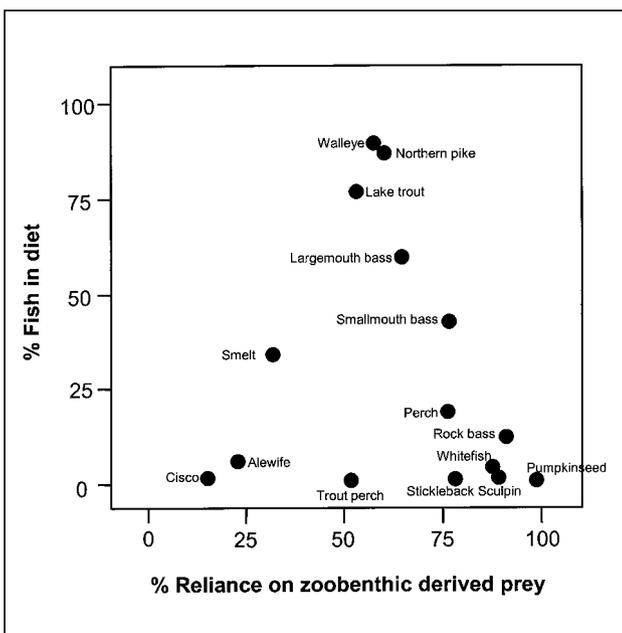
periphyton production leads to high levels of benthic macroinvertebrate production. Carbon stable isotope analysis is the most promising tool for establishing the importance of carbon fixed by periphyton in benthic and pelagic food webs. Currently the best evidence for the importance of periphyton in lake food webs is indirect and comes from fish diet data combined with stable isotope analyses of fish.

We used published fish diet data to evaluate the role of zoobenthos in the diets of a wide variety of fish of the North Temperate Zone (Vander Zanden and Rasmussen 1996, Vander Zanden et al. 1997). Comparing the diets of 15 species of North American fish, we found that on average 50% of the diet by volume consisted of zoobenthos. Nonpiscivorous fish showed the greatest specialization, with individual species feeding predominantly on either benthic or pelagic prey (Figure 5). Piscivores tended to be generalists; their diets contained about 40% zoobenthos on average. However, this is a conservative estimate of top predators' ultimate reliance on benthic resources, because many of their prey (forage fish) consumed large amounts of zoobenthos. We quantified predators' "indirect" reliance on zoobenthos by accounting for the amount of zoobenthos consumed by forage fish (Vander Zanden and Vadeboncoeur forthcoming). Thus, if a piscivore consumed an entirely zooplanktivorous fish, the indirect contribution of zoobenthos for that forage fish would be zero. Conversely, if a piscivore consumed a fish that ate nothing but zoobenthos, the proportion of the piscivore diet represented by that fish would be added to the direct consump-

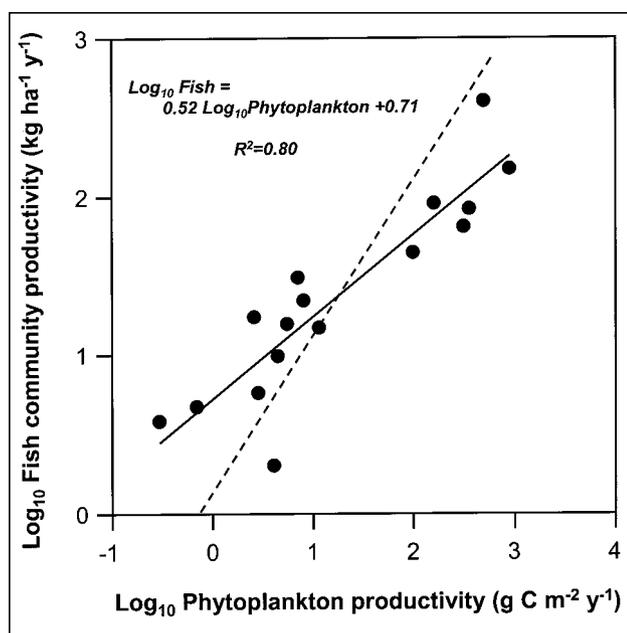
tion of zoobenthos with a weighting factor of one. We found that for the 15 species of fish we examined, the average species got 65% of its diet, either directly or indirectly, from zoobenthos. Thus, fish function as a strong link between benthic and pelagic food webs by depending heavily on zoobenthos. This energetic link may be crucial to the persistence of pelagic trophic cascades because it provides top predators with an alternative energy source (Polis and Hurd 1996, Schindler et al. 1996, Post et al. 2000).

Two lines of evidence suggest that fish reliance on zoobenthos reflects a dominant energetic pathway from periphyton to zoobenthos to fish in lake food webs. Stable isotope analysis indicates that up to 50% of the carbon assimilated by a broad range of fish species worldwide was originally fixed by periphyton, not phytoplankton (Hecky and Hesslein 1995). Furthermore, when Downing et al. (1990) compared fish productivity as reported in a variety of published studies, they found that phytoplankton productivity was one of the best predictors of fish productivity. However, the apparent efficiency of transfer of phytoplankton production to fish declined as whole-lake phytoplankton productivity increased. Increases in phytoplankton productivity should result in a constant proportional increase in fish productivity if the efficiency of trophic transfer does not vary along a eutrophication gradient. On a log-log plot, the slope of this relationship would equal 1. In fact, the slope of this relationship is significantly less than 1 (slope = 0.52, standard error = 0.069,  $p < 0.001$ ; Figure 6). Why might oligotrophic lakes have greater fish productivity per unit of phytoplankton productivity than eutrophic lakes? Declining transfer efficiency of phytoplankton production may reflect a suite of phenomena associated with eutrophication. For instance, toxic or inedible taxa can dominate phytoplankton in eutrophic lakes and may not be transferred to higher trophic levels. Also, visual predators may have reduced capture success in turbid, eutrophic lakes. Benthic-pelagic coupling may also contribute to the pattern. Oligotrophic lakes are dominated by periphyton rather than phytoplankton (Figure 4). The higher rate of transfer efficiency of pelagic primary production in oligotrophic lakes compared with the rate in eutrophic lakes may partly reflect a cryptic energy subsidy to fish through the generally unmeasured periphyton production pathway. Thus, the hypothesis that benthic algae are a major energy source for fish is supported by a variety of data, including stable isotopes (Hecky and Hesslein 1995, Vander Zanden and Vadeboncoeur forthcoming), the reliance of fish on zoobenthos (Figure 5), and declining fish-to-phytoplankton productivity as eutrophication increases (Figure 6).

Based on our analysis of research patterns in the literature, it is clear that limnologists perceive within-habitat interactions to be the most important in lake food webs. Of the 305 papers we examined, fewer than 6% quantified productivity in both habitats (Figure 1). Admittedly, our survey methods did not target research in which productivity of different trophic levels in different habitats was measured in single studies (e.g., primary productivity of phytoplankton and



**Figure 5.** Use of zoobenthos by North Temperate Zone fish. We determined the indirect use of benthos by piscivorous fish by calculating the relative contribution of zoobenthos to the diets of prey fish and weighting the "fish" fraction of the piscivore diet by this value. Data are compiled from Vander Zanden et al. 1997.



**Figure 6.** Annual fish community production as a function of phytoplankton production (Downing et al. 1990). The dashed line has a slope of 1 and is the expected relationship if the ratio of fish production to phytoplankton production is constant. The actual relationship has a slope significantly less than 1, suggesting that the efficiency of energy transfer from phytoplankton to fish declines as eutrophication increases. One possible explanation for this decline is that benthic algae provide a substantial energetic subsidy to fish in oligotrophic lakes, inflating the apparent ratio of fish production to phytoplankton production.

secondary productivity of benthic invertebrates). However, it seems that limnologists operate under the implicit assumption that pelagic and benthic food webs are parallel and independent. This conceptual model (Figure 3a) artificially constrains understanding of food web dynamics. For instance, there is compelling evidence that at the base of the food web, benthic and pelagic primary productivity are inversely correlated at broad scales because of common resource needs (Figure 3b; Sand-Jensen and Borum 1991, Hansson 1992, Vadeboncoeur et al. 2001). There is some evidence of similar compensatory interactions between benthic and pelagic invertebrates (Lellák 1966, Jeppesen et al. 1997, Strayer et al. 1999). Many trophic transfers across habitat boundaries are well documented (Figure 3c): Benthic invertebrates consume phytoplankton, fish consume periphyton, and fish forage broadly across both benthic and pelagic food chains. Despite gaps in knowledge, especially concerning benthic bacteria and DOC of benthic origin, these strong benthic–pelagic links indicate that a fully integrated model of lake food webs (Figure 3d) would lead to better predictions of material and energy flow in lakes.

### **Benthic–pelagic links: A question of scale**

What does it mean to the perception of energy flow in lake ecosystems that researchers usually underestimate autochthonous primary productivity and the energetic importance of benthic carbon to pelagic organisms such as fish? In the absence of large allochthonous inputs, primary production determines the availability of energy to higher trophic levels in ecosystems and provides a template of overall ecosystem productivity. When benthic and pelagic food webs are tightly linked, underestimates of total primary production will lead to overestimates of efficiency of energy transfer between primary producers and primary consumers. This will make secondary producers appear more efficient in oligotrophic lakes (Figure 6).

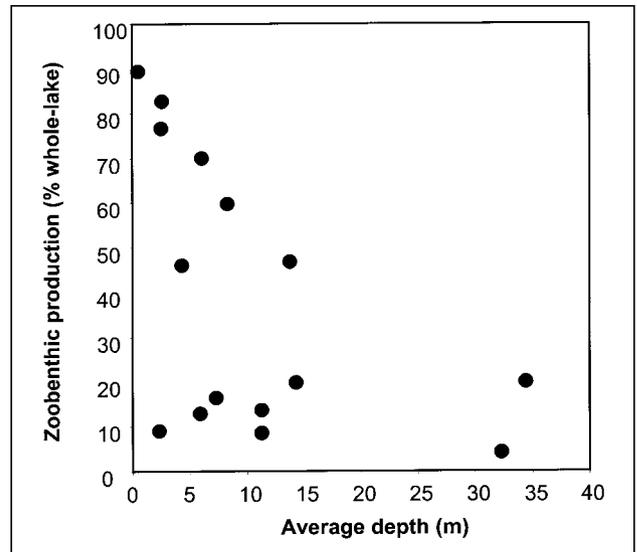
However, the implications of linked benthic and pelagic food webs extend beyond a broader conceptual understanding of lake ecosystem function. Increasingly limnologists are studying lakes in the context of human perturbations. Global climate change, acid deposition, ozone depletion, invading species, and eutrophication are ecosystem-level stressors, and benthic and pelagic organisms can have contrasting responses to these stressors (Schindler 1998, Vinebrooke and Leavitt 1998, Strayer et al. 1999, Vadeboncoeur et al. 2001). The strength and nature of benthic–pelagic links will partly determine how a given perturbation affects the whole ecosystem, yet poor understanding of these linkages severely constrains the ability to predict the effects of anthropogenic stresses (Lake et al. 2000, Palmer et al. 2000). Can one assess, a priori, lakes for which benthic pathways are likely to be important components of the food web? Although the distribution of production between benthic and pelagic habitats within any producer group may vary along water-column nutrient gradients, it will also depend on the relative size of each habitat. Thus, we expect lake size and morphometric characteristics to have a large influence on the strength of benthic–pelagic links and the overall importance of benthic processes in lakes (Fee and Hecky 1992, Schindler 1998).

Lodge et al. (1998) found that mean depth explained some of the variation in the proportion of benthic primary producers' contribution to whole-lake primary productivity. Small, shallow lakes—which comprise the majority of the world's lakes (Wetzel 1990)—have higher ratios of littoral surface area to epilimnion volume than large, deep lakes, and mean depth approximates this ratio. Benthic primary productivity may dominate in shallow lakes, based simply on habitat availability. However, correlations between lake size and eutrophication complicate this generalization. Small lakes may be dominated by periphyton because of a high percentage of littoral area, but they are also highly susceptible to eutrophication and phytoplankton dominance. In shallow, eutrophic Danish lakes, periphyton contributed less than 1% to whole-lake primary productivity, but in shallow, oligotrophic Greenland lakes, periphyton accounted for more than 95% of primary productivity. Large, deep lakes have low ratios of littoral surface area to volume—a situation that favors phy-

toplankton dominance—but they also tend to be oligotrophic and clear, which allows for significant periphyton growth in the littoral zone. Thus, benthic primary productivity is substantial in deep lakes such as Char Lake in the Canadian Arctic (mean depth 10 m), where benthic primary productivity constitutes 88% of whole-lake primary productivity, and Thingvallavatn in Iceland (mean depth = 34 m) where benthos make up 37% of whole-lake primary productivity. Both these lakes are oligotrophic and transparent. Expressing benthic and pelagic productivity per square meter of lake surface area incorporates the combined effects of depth and trophic status (Figure 4). The rate of areal phytoplankton productivity can be high in shallow eutrophic lakes with high phytoplankton productivity per cubic meter of water. It can also be high in large lakes with relatively low volumetric rates of phytoplankton production, but deep photic zones over which those rates are summed.

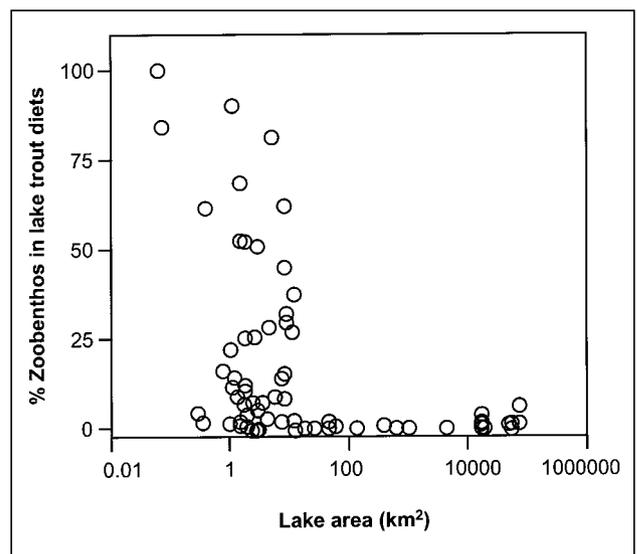
An inverse relationship between depth and the contribution of benthos is seen in consumers as well. Jeppesen et al. (1997) compiled published regressions to postulate that areal densities of profundal zoobenthos are inversely related to mean depth and that the ratio of zooplankton to profundal zoobenthos increases with mean depth. We used the whole-lake data from Figure 2 to show that the relative contribution of zoobenthos to secondary production declines as mean depth increases (Figure 7). Differences in methods introduce some error in any comparisons of whole-lake estimates of productivity, but much of the noise in the relationship may reflect real differences in ecosystem structure and function that override effects of habitat availability. For example, since the invasion of zebra mussels, the production of benthic invertebrates far exceeds that of zooplankton in Lake Erie (Johannsson et al. 2000). The importance of relative habitat availability is reflected in the plastic diets of higher trophic levels as well. Lake trout occur in lakes as small as a few hectares to ones as large as Lake Superior. Although lake trout are piscivores, they often rely heavily on zoobenthos in small lakes (Figure 8), presumably because the littoral habitat dominates secondary production pathways. Zoobenthos disappears from their diets in larger lakes.

These benthic–pelagic links and scaling issues have implications for the ways in which limnologists study and manage lakes. A primary goal of many field experiments that use microcosms or mesocosms is to reproduce natural assemblages of organisms, apply a perturbation, and then extrapolate the results to the whole ecosystem (Pace 2001). In such experiments, the inclusion or exclusion of benthic organisms presents a host of problems. Small-bottle experiments are of such short duration (Lodge et al. 1998) that development of benthic microbiota either does not occur or is viewed as “fouling” if it does. Longer-term mesocosm or bag experiments that are open to the sediment more closely resemble lake ecosystems. However, mesocosm walls accumulate periphyton, which can become the dominant primary producer in experiments designed to test the response of phytoplankton to resource manipulation (Lodge et al. 1998, Schindler 1998). On



**Figure 7.** Relative contribution of zoobenthos to whole-lake secondary productivity (zoobenthos plus zooplankton) related to mean depth. Data sources: Strayer and Likens 1986, Jónasson et al. 1990, Lindegaard 1994, James et al. 1998.

the one hand, the impact of benthic primary producers and microbial biofilms is overestimated in mesocosm experiments. On the other hand, such experiments often completely exclude large mobile organisms, such as fish, that prey heavily on benthic organisms. Experiments at the whole-lake scale are much more realistic in that they account for littoral zone dynamics, but they are often, by necessity, conducted in relatively small lakes in which benthic influences on nutrient dynamics, energy flow, and trophic structure are expected to be substantial (Schindler 1998). Extrapolations of experi-



**Figure 8.** The direct contribution of zoobenthos to lake trout diets across a gradient of lake areas. Data are compiled from Vander Zanden and Rasmussen 1996.

mental responses to larger lakes that are less influenced by benthic energy pathways should be approached carefully. As Fee and Hecky (1992) pointed out, extrapolating from Lake 227 in Canada's Experimental Lakes Area to Lake Superior requires a change of scale equivalent to extrapolating from a 300-mL incubation bottle to Lake 227. Extrapolations should be undertaken only with the understanding that the influence of benthic processes will probably diminish as lake size increases.

## Conclusions

Pelagic organisms have been the focus of lake ecosystem and food web studies in recent decades. Few studies look at benthic productivity in lakes and only 3%–12% of studies examine productivity of primary producers, heterotrophic bacteria, or invertebrates in both benthic and pelagic habitats. However, the productivity of benthic organisms of all these trophic groups can approach or exceed that of organisms in the pelagic zone. There is strong evidence that distribution of primary production between the two habitats varies with lake size and trophic status, and that this variability arises from the different capacities of benthic and pelagic primary producers to sequester light and nutrients. Similarly, the contribution of zoobenthos to invertebrate production is negatively related to lake depth (Figure 7) and correlative evidence suggests that there are inverse relationships in invertebrate biomass in benthic and pelagic habitats (Jeppesen et al. 1997). Exploring similar relationships for heterotrophic bacteria is not feasible with current data sets, though comparable resource needs make such relationships plausible. There are many trophic interactions in which energy crosses the traditional habitat boundaries. This integration of littoral and pelagic production is compellingly demonstrated by the many species of fish that rely on a mix of benthic and pelagic prey.

Variability between benthic and pelagic habitats in resource allocation is expected to lead to high variability among lakes in the relative importance of the two habitats in energy flow through food webs. It is increasingly recognized that external energy subsidies to linear food chains can affect the persistence of trophic cascades or top-down control of resources (Polis and Hurd 1996). Thus, the degree to which fish are subsidized by benthic resources may profoundly affect pelagic community dynamics. Variability in energy flux through benthic and pelagic pathways is particularly critical, given the potential for organisms in the two habitats to respond differently to anthropogenic impacts. Studies of anthropogenic perturbations may reach misleading conclusions regarding ecosystem response to impacts if only the pelagic or the benthic habitat is studied. Incorporating benthic–pelagic trophic coupling into conceptual models of lake ecosystems will contribute to a more comprehensive understanding of trophic dynamics. Forbes ([1887] 1925) provided the conceptual framework for such integration more than a century ago, as did Lindeman (1942) six decades ago. We encourage limnologists to reclaim this influential heritage.

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