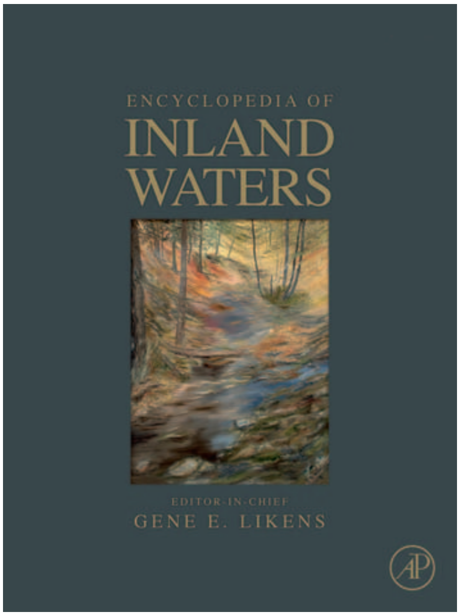

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Benthic Invertebrate Fauna, Lakes and Reservoirs

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Introduction

Benthos includes all animals that live in association with surfaces in lakes and reservoirs. This includes animals that live in and on sediments of all kinds (mud, sand, stones), as well as animals that live in, on, or around aquatic plants or debris. Animals large enough to be retained on a coarse sieve (usually 0.5-mm mesh) are called macrobenthos, those that pass through a coarse sieve but are retained on a fine sieve (usually ~0.05 mm) are called meiobenthos, and those that pass through even fine sieves sometimes have been called microbenthos, although this last term is rarely used. It is customary to ignore the small benthic animals, but studies have shown that animals too small to be caught on a 0.5-mm mesh may constitute >95% of the individuals, ~25% of the biomass, ~50% of the metabolic activity, and >50% of the species in a zoobenthic community.

Composition and Biological Traits of the Lacustrine Zoobenthos

The density of zoobenthos depends strongly on the mesh size of the sieve used for the study (Figure 1). Densities of macrobenthos (i.e., animals large enough to be caught on a 0.5-mm mesh) in lakes typically are 1000–10 000 m^{-2}, while the total density of all benthic metazoans probably usually is ~1 000 000 m^{-2}. There is a great deal of variation in densities within and among lakes, so that densities reported for a given mesh size range over ~100-fold within and among lakes.

Estimates of zoobenthic biomass usually include only the macrobenthos and exclude large bivalves. Because small benthic animals usually constitute a small part of zoobenthic biomass, estimates of the biomass of the macrobenthos probably are nearly equivalent to the entire zoobenthos. However, it appears that the meiobenthos may be especially important in unproductive habitats (Figure 2). Macrobenthic biomass without large bivalves ranges from ~0.2 to 100 g dry mass m^{-2}, and dense populations of large bivalves can increase these values by >10 g DM m^{-2}. Zoobenthic biomass rises up to a point with increasing phytoplankton production, then asymptotes or even declines with further increase in phytoplankton production. Zoobenthic biomass also tends to be highest in shallow lakes, where rooted plants are abundant, where the lake bottom is flat or gently sloping, in warm lakes or in the epilimnion of stratified lakes, and in lakes of low color.

There are relatively few data on the production rates of entire macrobenthic assemblages and almost no estimates that include the small benthic animals. One would expect to see as much variation in rates of production as in biomass, and based on the expected ratio of annual production to biomass of ~5 for animals of macrobenthic size, production of the lacustrine macrobenthos might range from ~1 to 500 g DM m^{-2} $year^{-1}$. Production of smaller benthic animals in lakes might be about the same order of magnitude, based on the sparse data now available. Production of the macrobenthos increases with increasing primary production (Figure 3), with no hint of an asymptote or downturn at very high primary production, as has been seen for macrobenthic biomass.

The lacustrine zoobenthos is enormously diverse; a typical lake contains hundreds of species from 12 to 15 animal phyla (Table 1, Figure 4). The macrobenthos often is numerically dominated by oligochaetes and chironomid and chaoborid midges, although large-bodied mollusks may dominate the biomass of the community. Aquatic insects other than dipterans (such as mayflies) may be abundant, especially in shallow lakes. Nematodes usually are by far the most numerous of the meiobenthos (and of the zoobenthos as a whole), although gastrotrichs, rotifers, and microcrustaceans often are abundant as well. Many important families are ecologically important in lakes around most parts of the world, including the Chironomidae and Chaoboridae in the Diptera; the Ephemeridae in the Ephemeroptera; the Tubificidae (including the 'Naididae') in the Oligochaeta; the Unionidae and Sphaeriidae in the Bivalvia; the Lymnaeidae and Planorbidae in the Gastropoda; the Chydoridae, Canthocamptidae, and Cyclopidae among the microcrustaceans; and the Chaetonotidae in the Gastrotricha. In contrast, several important groups are restricted to particular biogeographic regions (mysid shrimps and gammarid amphipods chiefly in the Northern Hemisphere, hyriid bivalves in the Southern Hemisphere) or habitats (ephydrid flies or brine shrimp in fishless or saline inland waters). Human introductions have vastly increased the ranges

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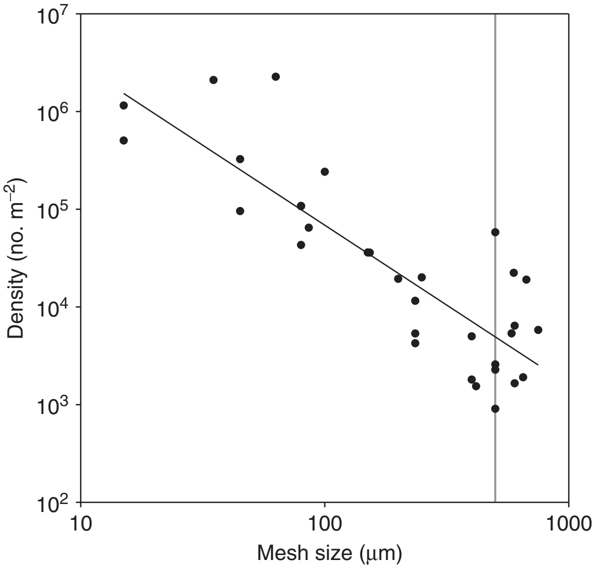

Figure 1 Reported density of zoobenthos as a function of sieve mesh size in a series of lakes from the northern temperate zone ($r^2 = 0.72$, $p < 0.000001$). The vertical gray line marks the 500-μm mesh commonly used for macrobenthos.

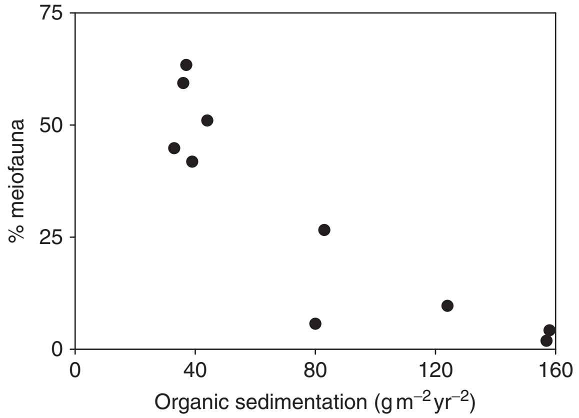

Figure 2 Percentage of zoobenthic biomass belonging to the meiofauna, as a function of organic sedimentation at various sites in the profundal zone of Lake Paijanne, Finland ($r^2 = 0.79$, $p = 0.0006$). Adapted from Hakenkamp *et al.* (2002), after data of Särkkä (1995).

of several ecologically important species of the lacustrine zoobenthos that once had small geographic ranges, most notably *Dreissena* spp. (zebra mussels, Bivalvia), *Mysis* (opossum shrimp, Crustacea), and several crayfish species.

Because the lacustrine zoobenthos is so diverse, it is difficult to generalize about the biological traits of its members. The largest animals in the community (bivalves and decapods, $>10^1$ g dry mass) are more

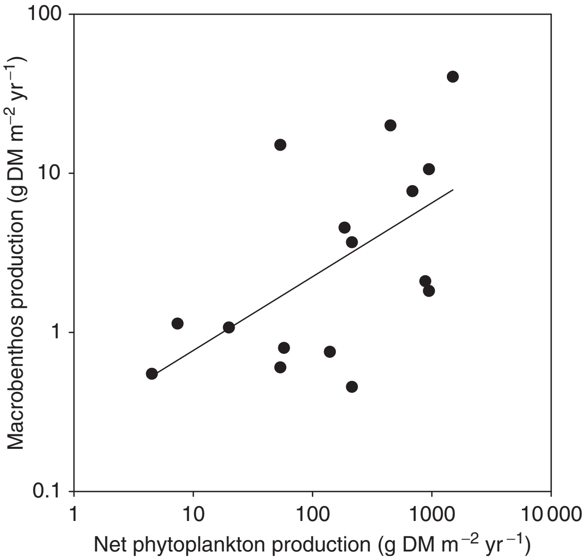

Figure 3 Relationship between production of macrobenthos and production of phytoplankton in a series of lakes ($r^2 = 0.34$, $p = 0.02$). Adapted from data of Kajak *et al.* (1980).

Table 1 Estimates of species richness of the zoobenthos (excluding parasitic forms) in Mirror Lake, a small, unproductive lake in New Hampshire (USA), and typical densities of major phyla in lakes

Phylum	*Estimated number of species in Mirror Lake*	*Typical density in lakes (no. m^{-2})*
Porifera (sponges)	4	NA
Cnidaria (hydras and jellyfish)	2	100–1000
Platyhelminthes (flatworms)	40	1000–50 000
Nemertea (ribbon worms)	1	<100
Gastrotricha	30	100 000–1 000 000
Rotifera	210	10 000–250 000
Nematoda (roundworms)	35	100 000–1 000 000
Annelida (earthworms, leeches)	30	5000–50 000
Mollusca (snails, clams)	6	100–1000
Ectoprocta (moss animicules)	2	<100
Crustacea (water-fleas, seed shrimp, copepods, and relatives)	70	20 000–200 000
Chelicerata (mites)	50	1000–10 000
Tardigrada (water-bears)	5	1000–50 000
Uniramia (insects)	120	1000–50 000

Many lakes around the world contain the same phyla and a comparable numbers of species as Mirror Lake, but have not been so well studied.

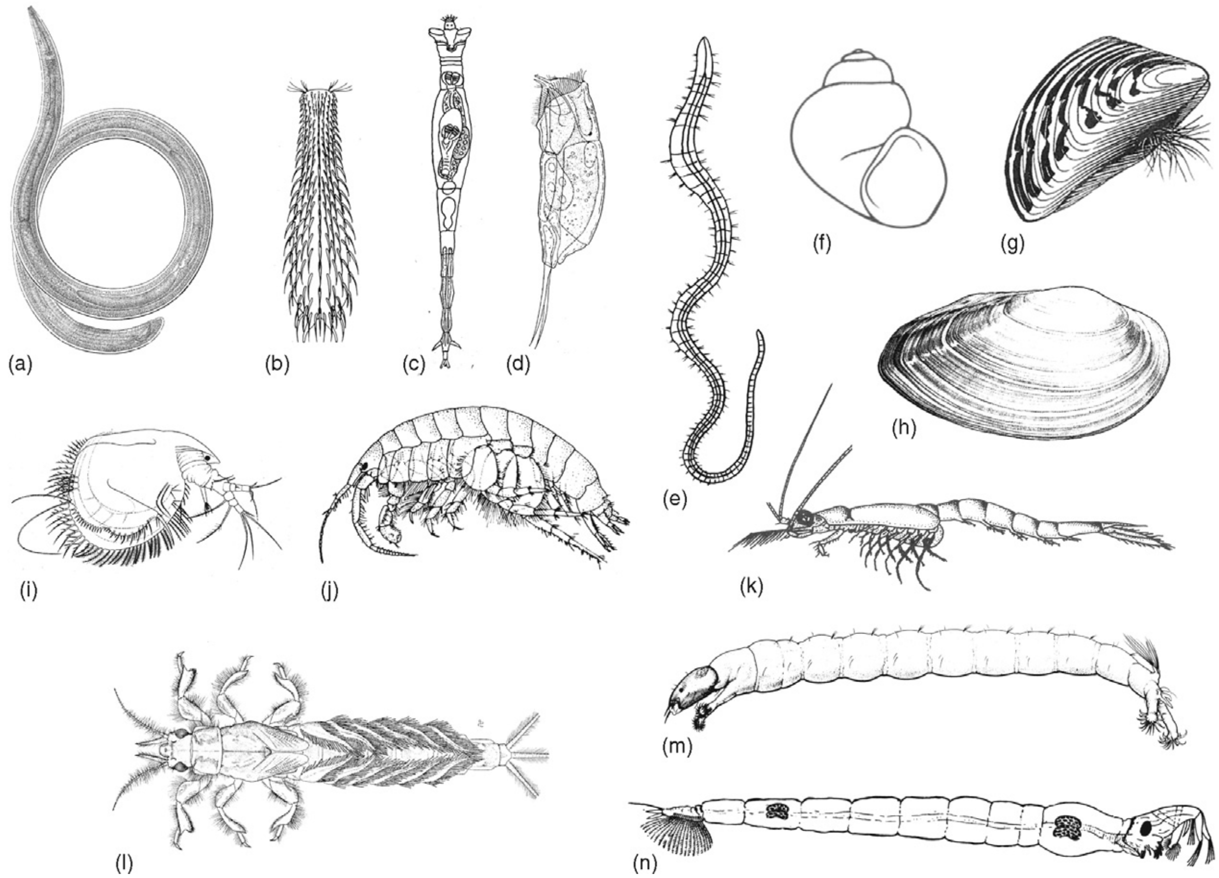

Figure 4 Some important members of the lacustrine zoobenthos. Typical adult body lengths are given in parentheses. (a) a nematode (2 mm); (b) a gastrotrich (0.2 mm); (c) a bdelloid rotifer (0.5 mm); (d) a ploimate rotifer (0.1 mm); (e) a tubificid oligochaete (50 mm); (f) a hydrobiid snail (3 mm); (g) the bivalve *Dreissena* (20 mm); (h) a unionid bivalve (75 mm); (i) a cladoceran (1 mm); (j) an amphipod (10 mm); (k) a mysid shrimp (20 mm); (l) an ephemerid mayfly (20 mm); (m) a chironomid (10 mm); (n) the phantom midge *Chaoborus* (10 mm).

than 10 billion times larger than the smallest (rotifers and gastrotrichs, $\sim 10^{-9}$ g DM), so this community spans an enormous range of body sizes. Life spans of zoobenthic animals range from less than a week (rotifers, gastrotrichs) to decades (bivalves). Some species have tough long-lived resting stages (sponge gemmules, ectoproct statoblasts, cladoceran ephippia) that allow populations to reestablish themselves after long unfavorable periods, and assist in passive dispersal between lakes. Various species burrow into the sediments (bivalves, tubificid oligochaetes, *Chaoborus*), glide at the sediment–water interface (gastrotrichs, ploimate rotifers, flatworms), attach (sessile rotifers) or mine (some chironomids in the genus *Cricotopus*) in aquatic plants, or crawl on or attach to solid object such as stones (*Dreissena*, many gastropods).

The zoobenthos includes species that suspension-feed on phytoplankton (many bivalves and some chironomids) or interstitial bacteria (*Pisidium*), graze on benthic algae (gastropods and many rotifers), deposit-feed on sedimented detritus and bacteria (tubificid oligochaetes), are predators on other benthic animals (odonates, tanypodine chironomids, dicranophorid rotifers) or zooplankton (*Chaoborus*), feed on either the leaves (crayfish, chrysomelid beetles) or roots (dorylaimid nematodes, larvae of the beetle *Donacia*) of rooted plants, or shred leaves of terrestrial plants that fall into the water (isopods, caddisflies). Not surprisingly, passive suspension- feeders such as hydropsychid caddisflies and black flies are much rarer in lakes than in flowing waters, presumably because currents in lakes are too slow or undependable to provide them with food.

Benthic animals have several adaptations for dealing with low oxygen concentrations that occur in many benthic environments. Some burrowing animals (chironomids and mayflies) produce currents to bring oxygenated water into the otherwise anoxic sediments in which they burrow. Species in several taxonomic groups (e.g., cladocerans, chironomids, gastropods) produce hemoglobin, which improves oxygen transport under hypoxic conditions. A few species of nematodes, bdelloid rotifers, gastrotrichs, tubificid oligochaetes, copepods, ostracods, and chironomid and chaoborid midges are commonly found in the anoxic profundal sediments of productive lakes. These animals apparently survive extended anoxia either by using anaerobic metabolism of substances like glycogen or by going into extended diapause. Finally, many of the benthic animals (e.g., many insects and pulmonate snails) avoid the problem of low dissolved oxygen altogether by obtaining their oxygen from the air.

Methods of Study

A few members of the lacustrine zoobenthos are large enough to be directly observed in situ (e.g., by SCUBA or mask-and-snorkel), but most species must be collected and brought into the laboratory for study. Scientists have invented a wide range of gear to collect benthic animals (Figure 5). Most often, scientists use grabs, corers, sweep nets, closing bags or boxes, or traps to collect animals or sediments. Often, animals need to be separated from the sediments or plants in which they live. This is usually accomplished by washing the sample through a sieve, most often of 0.1–1-mm mesh, sometimes followed by staining the sample with a dye such as Rose Bengal or examining the sample under a low-power microscope to aid in finding the animals. More or less experimental methods such as density-gradient centrifugation using silica sols (e.g., Ludox®) or application of ice or gentle heat are sometimes used as well.

Variation in the Lacustrine Zoobenthos

One of the chief characteristics of the zoobenthos is its extreme patchiness. The abundance and species composition of the zoobenthos varies within lakes, at scales ranging from centimeters (replicate samples at a single site) to kilometers, as well as among lakes. A number of factors are known to affect the abundance and species composition of the zoobenthos.

Variation within Lakes

The composition of the zoobenthos almost always varies greatly with water depth within a lake. The abundance of nearly every species in the zoobenthos varies with water depth (Figure 6), and species richness often is much lower in the deep waters of a lake than near the shore (Figure 7). Many studies have also reported variation in the total numbers or biomass of benthic animals with water depth in individual lakes. No single pattern of variation of abundance or biomass with water depth applies to all lakes, because the many mechanisms that link water depth to the zoobenthic community vary in strength across lakes and produce a wide range of patterns in different lakes.

The most important factors that cause zoobenthic composition and abundance to vary with water depth include dissolved oxygen, quantity and quality of organic matter inputs, temperature, sediment grain size and compaction, disturbance, and depth-dependent biotic interactions. The relative contributions of each of these factors and their interactions in driving zoobenthic community structure have not yet been disentangled. In stratified lakes, concentrations of hypolimnetic dissolved oxygen fall through the stratified period, and often reach zero at the sediment surface by the end of the summer. Only a few species of animals can tolerate hypoxic ($<2\,\mathrm{mg\,l^{-1}}$) or anoxic conditions for any period of time. The hydrogen sulfide that often accompanies anoxia also is toxic to most animals. Thus, inadequate dissolved oxygen at the sediment surface probably is a major cause of the vertical zonation of the zoobenthos and low species richness in profundal sediments. Nevertheless, declines in richness often occur well above the depth of oxygen depletion (Figure 7), so factors other than oxygen must be important as well. Although few zoobenthic species can tolerate anoxia, these species may be abundant, so low dissolved oxygen does not necessarily reduce zoobenthic density or biomass. Even in unstratified lakes, periods of warm, windless weather may reduce mixing enough to cause short-term depletion of oxygen at the sediment surface and catastrophic losses of benthic animals. Such ephemeral stratification and oxygen depletion killed nearly the entire population of ~2500 metric tons (dry mass) of the mayfly *Hexagenia* in the shallow western basin of Lake Erie in late summer 1953.

Temperatures in the hypolimnion of a stratified lake are much lower and steadier than in the epilimnion. These low temperatures slow metabolic rates of benthic animals, may not meet thresholds for growth and reproduction of many species, and presumably exclude many species from profundal sediments.

The food base for the zoobenthos changes from the shoreline to the profundal zone. Aquatic plants and attached algae grow only in relatively shallow or clear water. In deep water, freshly settled phytoplankton supplements older detritus washed in from the watershed and littoral zone, and the amount and quality of organic matter reaching the profundal sediments of deep lakes probably declines with increasing water depth. The deposition of this sinking organic matter on the lake bed is highly uneven,

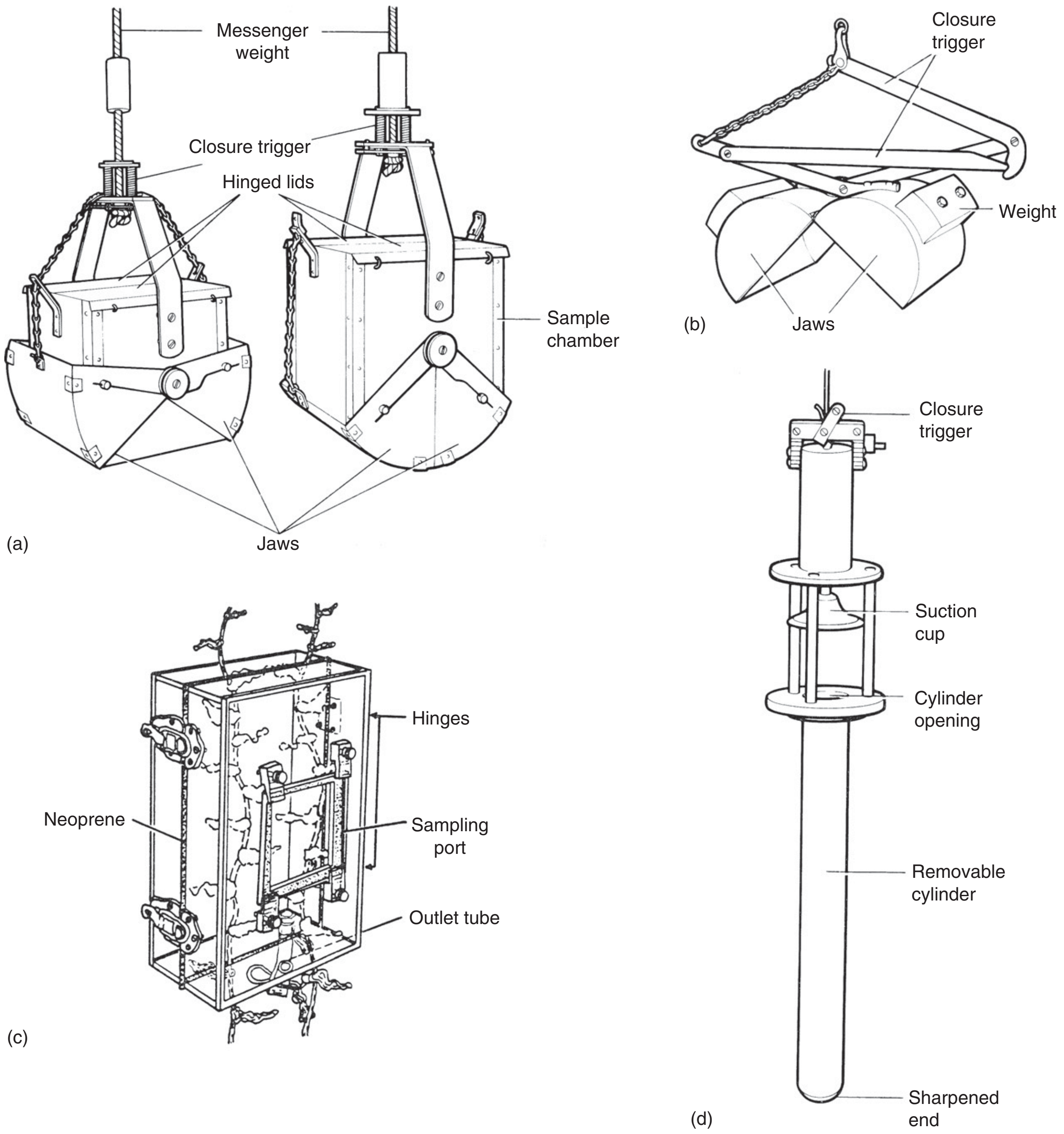

Figure 5 Four samplers commonly used for quantitative studies of the lacustrine zoobenthos. (a) Ekman grab; (b) PONAR grab; (c) Downing box sampler for vegetation-dwelling invertebrates; (d) Kajak-Brinkhurst corer. Adapted from Downing (1984, 1986).

depending on wave energy and the slope of the bottom. It seems reasonable to suppose that the quantity and quality of food is usually highest in the littoral zone and in depositional areas, and leads to variation in zoobenthic biomass (Figure 8).

Sediment grain size and heterogeneity also vary with water depth, typically changing from a highly patchy mosaic of coarse sediments in shallow water to a monotonous plain of fine-grained sediments in the profundal zone. Because of the many mechanisms that link benthic animals to their sediments, this variation in sediments must have a large effect on the kinds of benthic animals that can live at different depths in a lake. High heterogeneity in shallow-water sediments probably is a major cause for the high species richness in the littoral zoobenthos.

Disturbance from wave-wash, ice-push, or fluctuating water levels often causes a zone of markedly

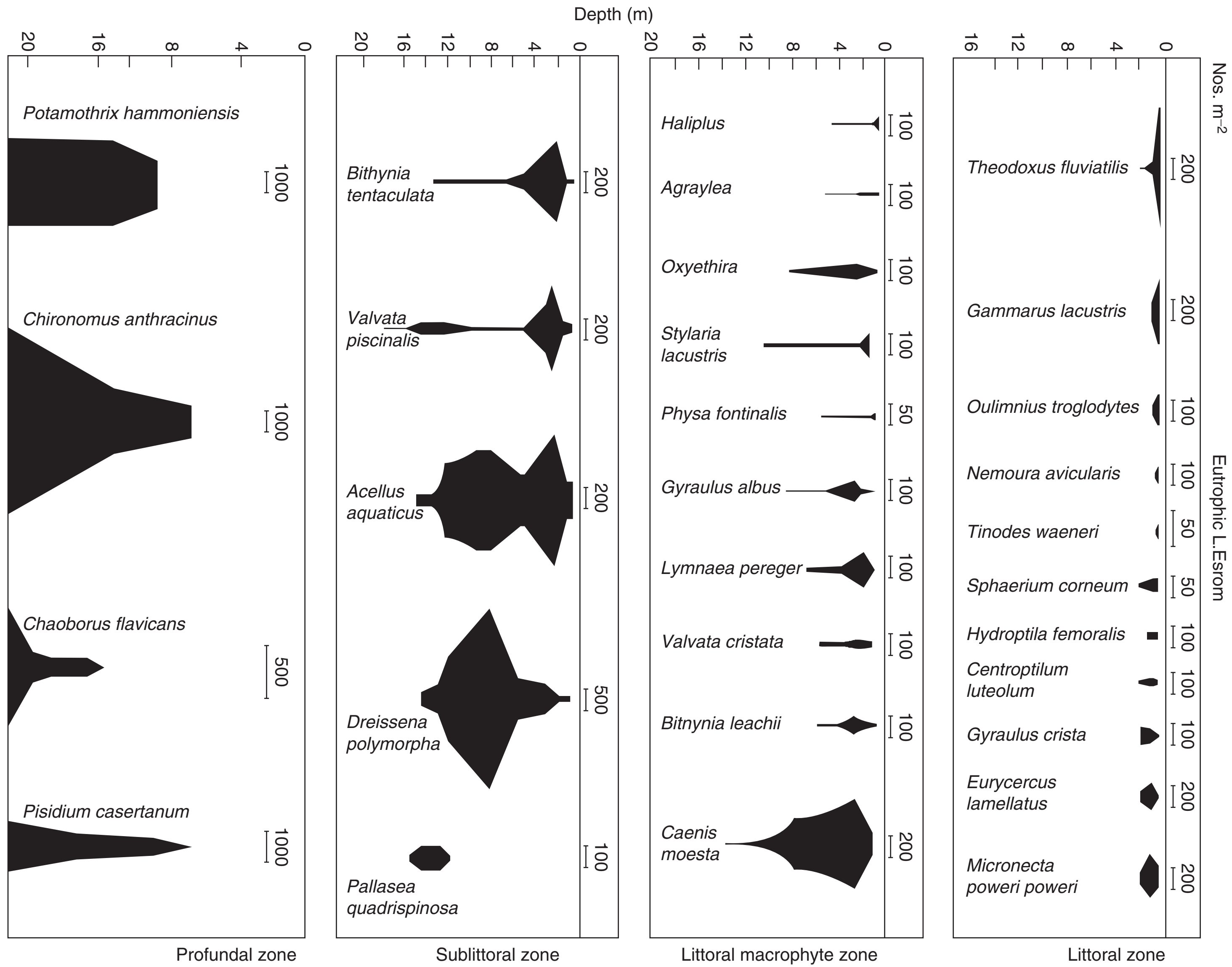

Figure 6 Distribution of benthic animals with water depth in eutrophic Lake Esrom, Denmark. Adapted from Jonasson (2004).

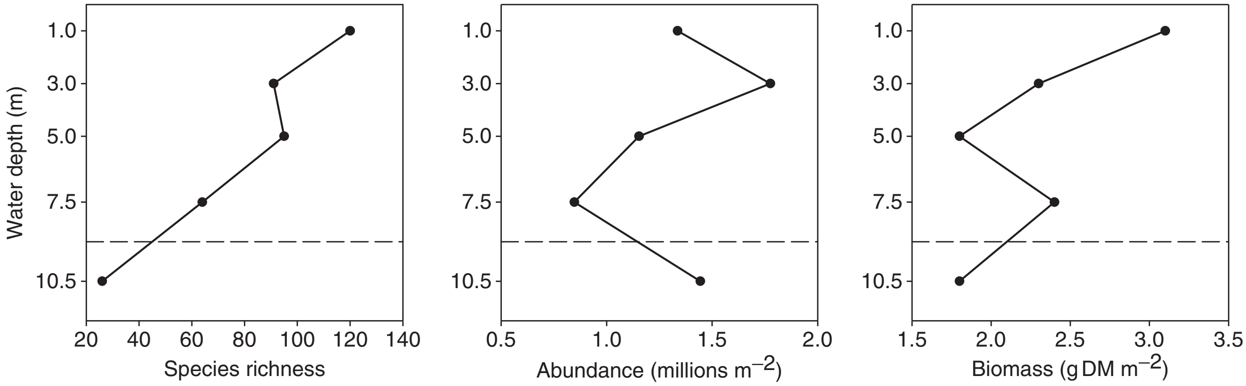

Figure 7 Species richness, abundance, and biomass of benthic animals (including all metazoans) as a function of water depth in Mirror Lake, a small unproductive lake in New Hampshire. The dashed horizontal line shows the depth at which oxygen at the sediment surface falls below 1 mg l^{-1} by late summer. Adapted from Strayer (1985).

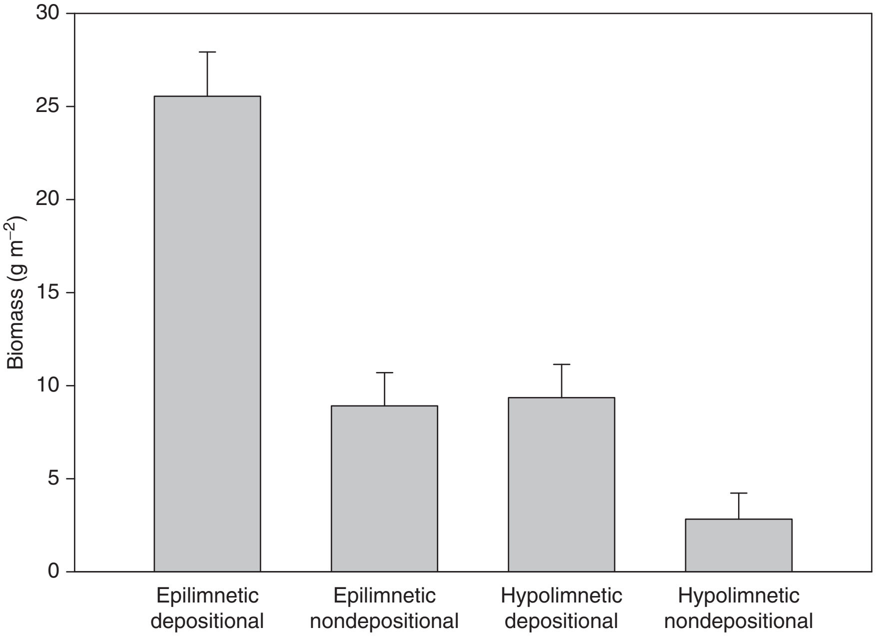

Figure 8 Mean (±1SE) biomass (wet mass) of macrobenthic animals at various sites in Lake Memphremagog, Quebec, as a function of thermal and depositional regime. Adapted from Rasmussen and Rowan (1997).

reduced zoobenthic density and diversity near the water's edge, particularly in large lakes and reservoirs.

Finally, many of the biotic interactions that affect the zoobenthos are depth-dependent. Fish predation can have very large effects on the number, size, and species composition of benthic animals (Figure 9). The numbers and kinds of fish change from the littoral to the profundal zone; indeed, anoxic profundal sediments may be free from fish predation. Likewise, the density and kind of macrophytes, which are important in providing surfaces for attachment, shelter from predation, and food for benthic animals, change markedly with water depth, and can drive major changes in the zoobenthos. Thus, biotic interactions underlie much of the within-lake variation in the zoobenthos.

Most benthic animals are found near the sediment surface (Figure 10), presumably because food (benthic algae and sinking phytoplankton) and oxygen are most available there. Nevertheless, animals can be found deeper in lake sediments, sometimes reaching depths of more than 50 cm. Tubificid oligochaetes feed head down in the sediments, so it is easy to understand why they reach deep below the sediment–water interface, but the activities of other benthic animals that live deep within-lake sediments (e.g., some candonid ostracods, midges and bdelloid rotifers) are less well understood.

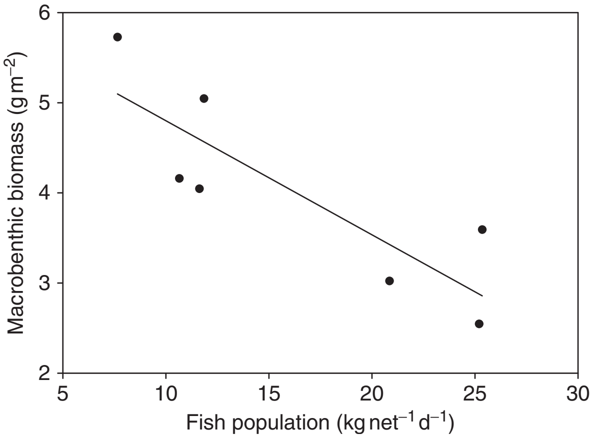

Figure 9 Dependence of macrobenthic biomass (wet mass) on fish predation in the Finnish Lake Pohjalampi. Each point is one year during a long-term experimental manipulation of fish populations. Adapted from Leppä *et al.* (2003).

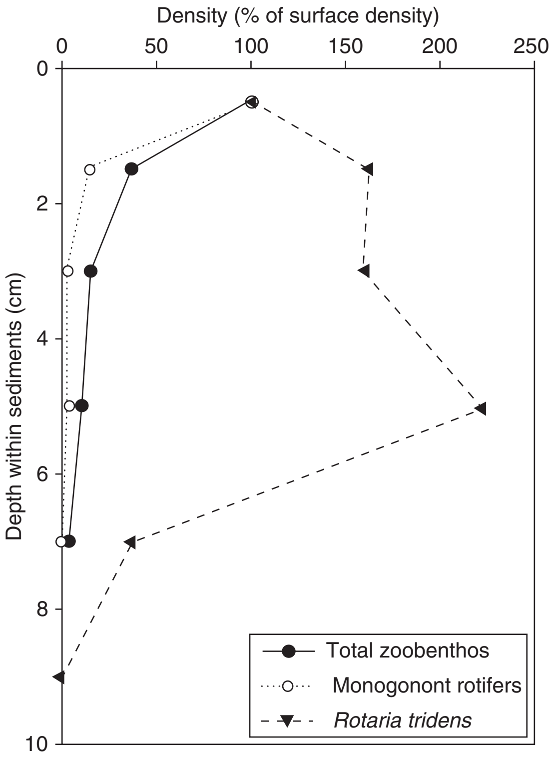

Figure 10 Vertical distribution of benthic animals within the sediments of Mirror Lake, New Hampshire. The three lines show the distributions of all benthic animals, a surface-dwelling taxon (monogonont rotifers), and a taxon that lives deeper in the sediments (the bdelloid rotifer *Rotaria tridens*). Modified from Strayer (1985).

Variation across Lakes

Organic matter inputs, especially phytoplankton production, affect the numbers and kinds of benthic animals in lakes (Figure 11). Typically, lakes with higher organic matter inputs support more benthic animals (Figures 3 and 11), although there is some evidence that very high inputs of organic matter may actually reduce numbers of benthic animals, possibly by increasing the area of anoxic sediments. The kinds of benthic animals change with lake productivity as well. Indeed, one of the earliest systems for classifying the productivity of lakes was based on the composition of the profundal zoobenthos.

Lake morphometry has a strong influence on zoobenthic communities. Small, shallow lakes tend to support higher densities of benthic animals than do

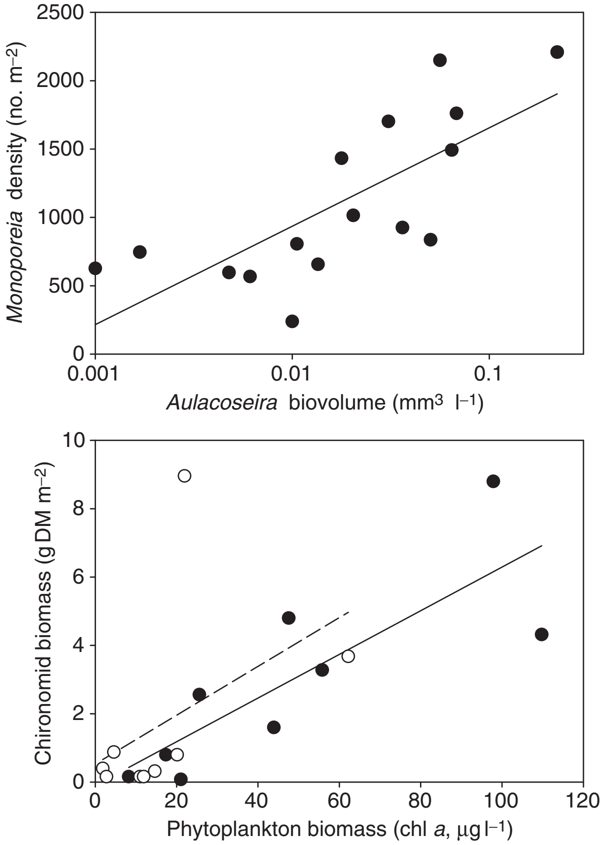

Figure 11 Examples showing the dependence of the zoobenthos on phytoplankton. The upper panel shows the numbers of the amphipod *Monoporeia affinis* in Lake Erken, Sweden, as a function of the amount of the important planktonic diatom *Aulacoseira* in the previous year ($r^2 = 0.54$, $p = 0.0008$). The lower panel shows the biomass of chironomids in April–May at two sites in Lake Balaton, Hungary, as a function of phytoplankton biomass in the previous summer (for black circles, $r^2 = 0.66$, $p = 0.008$; for white circles, $r^2 = 0.20$, $p = 0.23$). Adapted from Johnson and Wiederholm (1992) and Specziár and Vörös (2001).

large, deep lakes. This pattern probably has at least three causes: (1) macrophytes, which support dense and diverse zoobenthic communities, are most abundant in small, shallow lakes; (2) shallow lakes are less likely to stratify than deep lakes, resulting in higher concentrations of dissolved oxygen at the sediment surface; (3) sinking phytoplankton (and other food particles) are less likely to be degraded before reaching the sediment surface in shallow lakes than in deep lakes.

Temperature affects both the number and kinds of benthic animals in lakes. Tropical lakes support different species than do temperate lakes (or arctic lakes), although groups such as chironomids, *Chaoborus*, and oligochaetes are abundant over wide latitudinal ranges. Warm lakes tend to support higher zoobenthic densities than do cold lakes.

Several aspects of water chemistry have strong effects on the zoobenthos. Saline lakes contain distinctive communities of benthic animals. Very salty lakes may contain just a few species of benthic animals, even though overall abundance or biomass of the zoobenthos may not be reduced. Soft water lakes of low pH and low calcium typically contain different species than do hard water lakes, and often are poor in shell-bearing animals (mollusks, ostracods) that need calcium to build their shells. Consequently, the recent acidification from atmospheric deposition has had important effects on the zoobenthos. High concentration of dissolved organic matter in lake water may reduce abundance of benthic animals.

Finally, differences across lakes in biotic interactions can have strong effects on the number and kinds of benthic animals. Only a few examples are well known. Fishless lakes usually contain large, active invertebrates (e.g., swimming or crawling insects) that are quickly eliminated if fish are introduced. Crayfish and large bivalves can have strong effects on other benthic animals, as has been shown when invasions of lakes by alien crayfish and *Dreissena* have caused very large changes in benthic animal communities. It seems likely that other unstudied biotic interactions are responsible for variation in the zoobenthos across lakes.

Roles of the Lacustrine Zoobenthos

Secondary production by the zoobenthos in most lakes is modest (Table 2), and energy flow through the zoobenthos certainly is much smaller than that passing through microbial communities. Nevertheless, benthic animals play important roles in lake ecosystems, and even in human affairs. Broadly speaking, the ecological roles of the zoobenthos can be defined as food web or nontrophic roles.

As participants in lacustrine food webs, benthic animals consume phytoplankton, aquatic plants, animals, bacteria, and detritus. Consumption rates can be high enough to control the amount and composition of these food resources. The best-known examples involve the consumption of plankton by benthic animals. Suspension-feeders such as *Dreissena*, sponges, and cladocerans may be abundant enough to reduce phytoplankton biomass, or change its composition (Figure 12). Likewise, benthic animals that eat zooplankton (*Chaoborus*, mysids) can exert strong control on zooplankton communities,

Table 2 Secondary production by the macrozoobenthos and zooplankton in several lakes, expressed as a percentage of net organic inputs to the lake

Lake	*Mean depth (m)*	*Net organic inputs ($g\ C\ m^{-2}\ yr^{-1}$)*	*Production of zoobenthos (%)*	*Production of zooplankton (%)*
Tundra pond, AK	<1	26	7	0.8
Marion, BC	2	110	3	0.9
Myvatn, Iceland	2	330	6	1.3
Wingra, WI	3	610	0.4	4
Kiev Reservoir, Ukraine	4	280	6	7
Rybinsk Reservoir, Russia	6	93	0.3	2
Mirror, NH	6	49	12	5
Red, Russia	7	140	1	7
Findley, WA	8	12	6	2
Naroch, Belarus	9	160	0.8	5
Mikołajskie, Poland	11	260	2	21
Esrom, Denmark	12	160	6	7
Pääjärvi, Finland	14	60	3	12
Dalnee, Russia	32	260	1	22

Most benthic data exclude the meiofauna, and are therefore underestimates. Because of methodological differences among studies, data are only approximately comparable. Compiled from many sources.

with effects that ramify through the ecosystem (Figure 16). Although relatively few benthic animals (crayfish, plant–parasitic nematodes, and some aquatic insects) eat or destroy aquatic plants, they can strongly affect macrophyte biomass and species composition; indeed, benthic animals have been used for biological control of nuisance weeds such as milfoil. Much less is known about the influence of the zoobenthos on attached algae, bacteria, and detritus, although these are the primary foods of most benthic animals. Further, some benthic animals have highly specialized diets and might therefore have selective effects on food resources. Benthic animals probably often control the amount and kind of attached algae in lakes, and it seems likely that most particles of detritus pass through at least one benthic animal before being buried in the lake bottom. Thus, there is ample evidence that benthic animals can control the amount and character of food resources in lakes, although we do not yet know how often and under what conditions such strong control occurs.

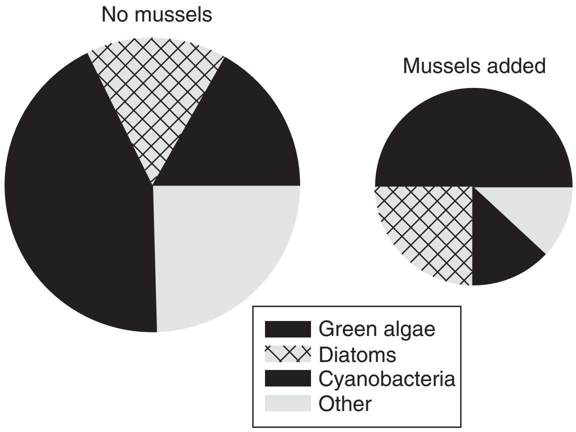

Figure 12 Changes in the amount and composition of phytoplankton in two small Dutch lakes following the experimental addition of *Dreissena polymorpha* to one of the lakes. The area of each circle is proportional to the biovolume of the phytoplankton in each lake. Adapted from data of Reeder *et al.* (1993).

Benthic animals release nutrients such as inorganic nitrogen and phosphorus when they consume food. Such nutrient regeneration may be important to phytoplankton and attached periphyton in nutrient-limited lakes.

The predominant fate of zoobenthic production is to be eaten, whether by other members of the zoobenthos, fish, or terrestrial predators (Table 3). Consequently, the zoobenthos serves as an important link to higher trophic levels. Almost all lake-dwelling fish depend to some extent on zoobenthos, and benthic animals are the primary food of many fish species (Figure 13). Large populations of birds, bats, spiders, and other predators may be drawn to lakes or lakeshores to feed on benthic animals, including emerging insects.

Although it has been customary to treat the plankton and the benthos as belonging to separate food webs, many species of the zoobenthos depend either directly or indirectly on the plankton for food, and there are strong reciprocal links between the plankton and the zoobenthos. The pelagic and benthic zones of lake are linked by many strong connections (Figure 14), and function as an integrated system.

The major nontrophic role of the zoobenthos is sediment mixing (bioturbation). Three activities are important: (1) feeding, especially by conveyor-belt feeders such as tubificid oligochaetes, which feed in deep layers of the sediments and leave fecal pellets at the sediment surface; (2) burrow construction and ventilation, which are done by ephemerid mayflies and some chironomids; (3) ordinary locomotion by large, active animals such as *Chaoborus* and unionid bivalves. Bioturbation mixes sediments and increases

Table 3 Estimated fate of zoobenthic production in several lakes

Lake	*Production (gDM m^{-2} yr^{-1})*	*Fate (% of production)*			
		Invertebrate predation	*Fish predation*	*Bird predation*	*Emergence*
Myvatn, Iceland	42	5–52[a]	43	9	48
Mirror, NH	14	80	15	nd	25
Paajarvi, Finland	3.8	50	40	nd	6
Batorin, Belarus	2.6[b]	46	194	nd	nd
Naroch, Belarus	2.6[b]	22	42	nd	nd
Ovre Heimdalsvatn, Norway	2.4[c]	25–28[a]	70	2	3
Myastro, Belarus	0.8[b]	72	272	nd	nd

Data are approximate, so percentages do not sum to 100%; nd = not determined. Data are from after various sources.
[a] Estimated by difference.
[b] Growing season only; macrobenthos.
[c] Macrobenthos.

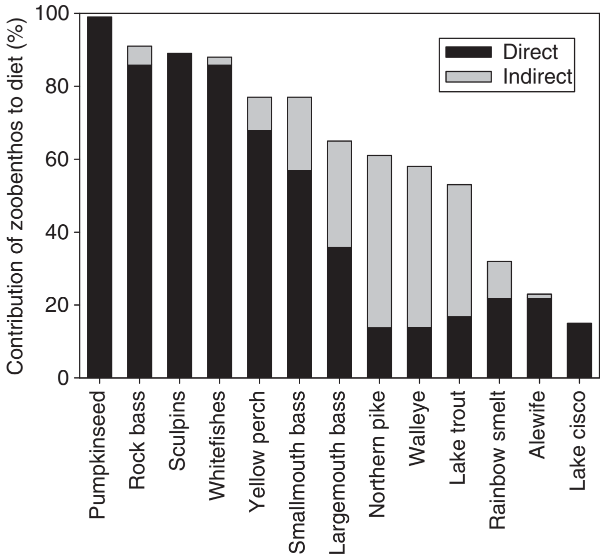

Figure 13 Contribution of zoobenthos to the diets of common species of fish in northeastern North American lakes. 'Indirect' consumption of zoobenthos is consumption of fish that were supported by zoobenthos. Adapted from data compiled by Vadeboncoeur *et al.* (2002).

exchange of dissolved substances (e.g., oxygen, ammonium) between the overlying water and the sediment pore-water. These activities can have large effects on nutrient regeneration and cycling and burial of toxins. In addition, shell-building benthic animals (chiefly large bivalves) can alter the character of benthic habitats through accumulations of their living and dead shells. Such shell accumulations, which can probably reach masses >1 kg m^{-2}, serve as habitat or spawning sites for other animals, as well as altering biogeochemical transformations at the sediment–water interface.

Applied Issues

Some of the most important diseases of humans and wildlife are carried by benthic animals. Chief among these are diseases caused by trematodes (or flukes), in which freshwater snails, and occasionally decapods, serve as intermediate hosts. In a typical life cycle (Figure 15), eggs shed from the definitive host hatch into swimming larvae (miracidia) that seek out and penetrate an aquatic snail. Many species of freshwater snails serve as hosts for the various trematodes that affect humans, livestock, and wildlife. After undergoing development in the snail, a second free-swimming larval stage (the cercaria) may either enter the definitive host directly when the host is in the water, enter a second intermediate host (a fish or decapod), or encyst on an aquatic plant. The trematode passes from the second intermediate host or aquatic plant into the definitive host when uncooked fish, decapods, or aquatic plants are eaten. Adult trematodes may live in the intestines, liver, blood vessels, or lungs of humans or other vertebrates, and often cause chronic, debilitating diseases. The most important of the snail-borne diseases is schistosomiasis, a debilitating disease caused by the genus *Schistosoma*, which affects ~200 million humans throughout the tropical world. Other significant snail-borne diseases include liver flukes (especially *Fasciola hepatica* and *Opisthorchis sinensis*), which cause large damage to sheep and cattle, as well as affecting millions of people, and various intestinal or lung flukes, which affect many people around the world. Trematodes using freshwater snails as intermediate hosts also affect many vertebrate species other than humans. In fact, cercaria of trematode species that use birds as definitive hosts sometimes burrow into humans. Although such cercariae do not develop normally in humans, they can cause a skin irritation known as 'swimmer's itch' and thereby limit recreational use of lakes. The acanthocephalans are another important group of parasites carried by freshwater benthic animals. Adult acanthocephalans are intestinal parasites of many fishes and other aquatic vertebrates, and benthic crustaceans usually serve as their intermediate hosts.

Human-caused changes to natural habitats sometimes increase disease problems (e.g., impoundments have increased prevalence of schistosomiasis), and ecological interventions (e.g., habitat management, introductions of predators or other biological controls) may be implemented as part of integrated programs of disease control.

Other benthic species are pests. Fouling species such as *Dreissena*, *Corbicula*, and occasionally sponges and ectoprocts block water intakes and may force plant operators to use mechanical cleaning, biocidal chemicals, or pipe coatings to keep water flowing. It appears that large emergences of chironomid midges may be a major cause of 'hay fever' and asthma in some parts of the world. Mass emergences of lake-dwelling insects (chiefly ephemerid mayflies or chironomid and chaoborid midges) may be so large that they cause traffic hazards, produce windrows of dead insects that need to be cleaned up with heavy equipment, and even short-circuit power plants.

Although there has been some interest in biomanipulation to increase the positive impacts of benthic animals, or reduce their negative impacts, such efforts have not proceeded as far as in the pelagic zone, where biomanipulation is now widely practiced. At least three types of biomanipulation have been considered involving benthic animals. Because benthic

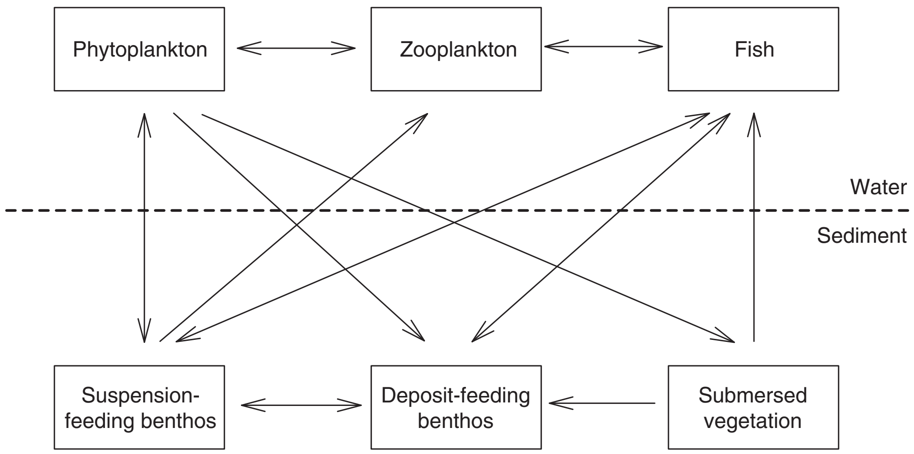

Figure 14 Major interactions between lacustrine communities (Strayer, 2006). Arrows show the hypothesized direction of control; note that many interaction arrows cross between the sediments and the pelagic zone.

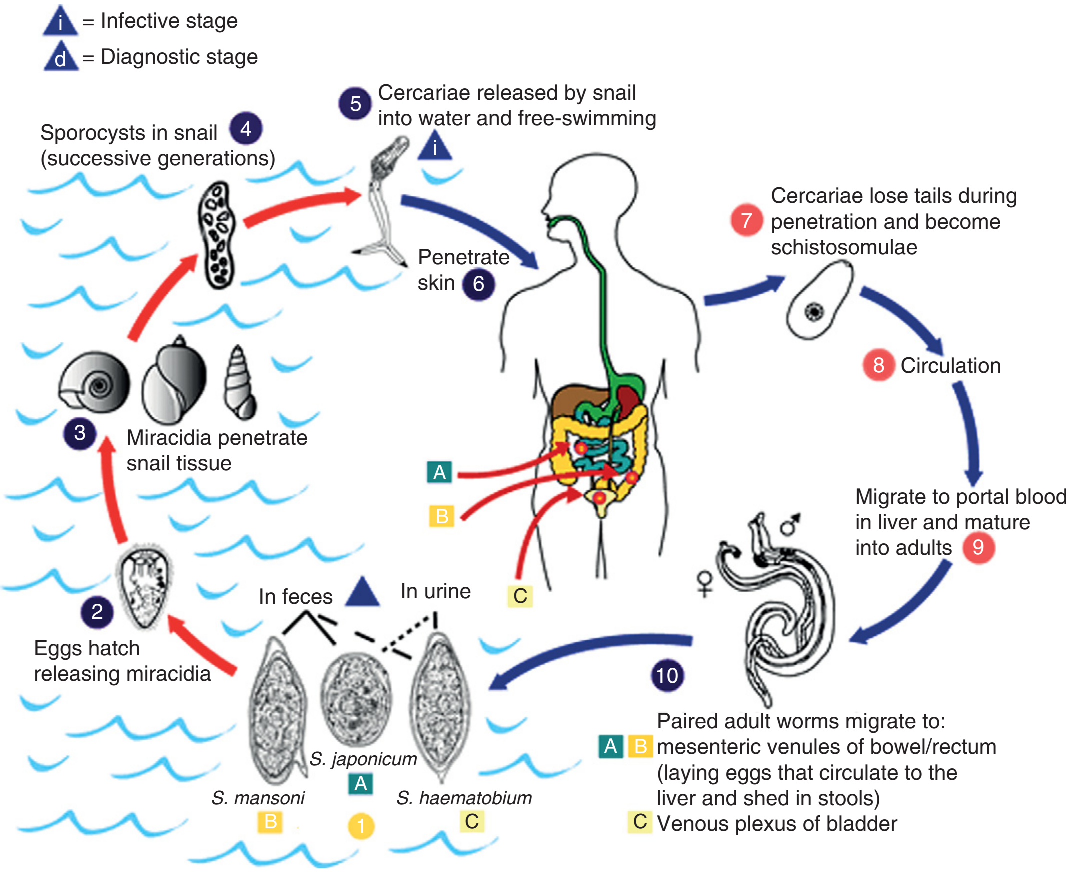

Figure 15 Life cycles of three species of the blood fluke *Schistosoma*. From the Centers for Disease Control.

suspension-feeders may control phytoplankton biomass and composition, some studies have sought to manage nuisance phytoplankton by increasing populations of benthic suspension-feeders (Figure 12). Benthic animals are valuable food for fish, so fisheries managers often have introduced large benthic animals (crayfish and the opossum shrimp *Mysis*) to lakes to increase growth rates or biomass of fish populations. Such introductions rarely have been supported by a careful analysis of likely impacts, and introductions of forage invertebrates sometimes have led to undesirable and unforeseen impacts (Figure 16). Finally,

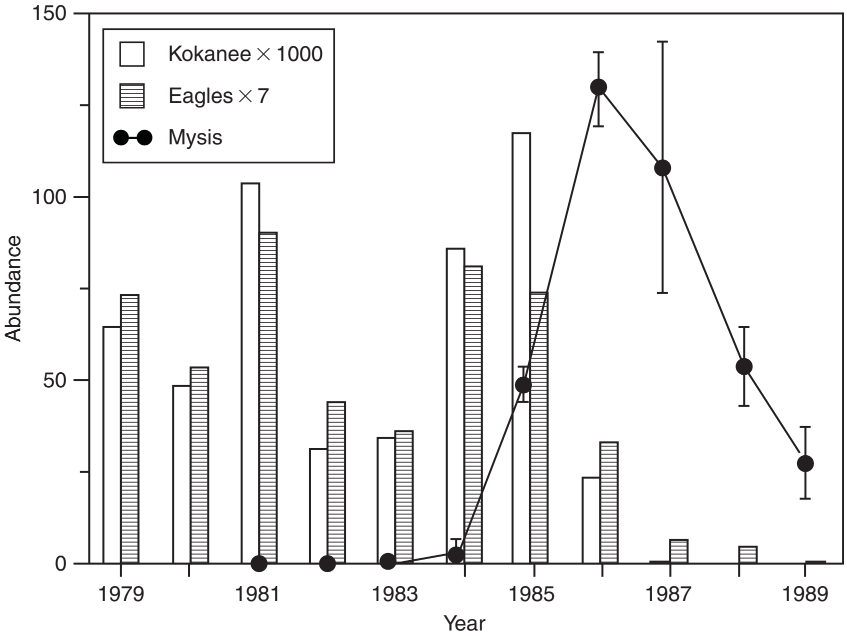

Figure 16 Undesirable effects following the introduction of the opossum shrimp *Mysis* to Flathead Lake, Montana. Data on kokanee salmon and eagles are peak counts from a tributary stream used by the salmon for spawning. Adapted from Spencer *et al.* (1991).

there have been a few attempts to increase populations of benthic animals to control populations of animals that carry diseases. Probably, the most prominent examples have been the additions of predators or competitors of the snails that carry schistosomiasis. Clearly, biomanipulation of lakes using benthic animals is still in its infancy.

Like other freshwater plants and animals, human activities have harmed some species of the lacustrine zoobenthos, which are now extinct or imperiled. Several activities have been especially harmful. Large water diversions have caused some lakes to become excessively salty or even dry up altogether, endangering or eliminating the benthic animals that formerly lived there. Many lakes have been badly polluted by toxins from industry and other sources or sediment from poor land-use practices. Nutrient loading from fertilizers or domestic wastes has increased the productivity of many lakes, leading to anoxic sediments, with obvious consequences for benthic animals. Many of the alien species (sport fish, aquatic plants, and invertebrates) that have been introduced into lakes around the world have had strong effects on benthic animals. An accounting of the summed effects of these harmful activities on benthic animals does not exist, but surely many populations in individual lakes have been imperiled or eliminated. In the case of ancient lakes that support endemic species of benthic animals, local extirpations would translate into global extinctions for the species. Extinctions among the endemic fish species of ancient lakes are well known, and presumably, such extinctions have occurred among the zoobenthos as well.

A few species of benthic animals are harvested from lakes or reservoirs for human use. Important fisheries for wild or cultured populations of various freshwater decapods (crayfishes, prawns, crabs) are scattered in lakes, ponds, and wetlands around the world. Several of the large bivalves have been harvested for millennia for food, pearls, and mother-of-pearl, although the largest fisheries for these animals are in rivers rather than in lakes. Particularly in the nineteenth century, large numbers (>10 million animals/year) of the medicinal leech (*Hirudo medicinalis*) were taken from the wild. Other members of the lacustrine zoobenthos (adult chaoborid midges, eggs and adults of corixid bugs, snails) are harvested in large numbers for human food locally.

Glossary

Benthos – The community of organisms living around surfaces (e.g., sediments, plants) in aquatic ecosystems.

Bioturbation – Sediment mixing caused by the activities of organisms.

Macrobenthos – Benthic animals large enough to be retained on a coarse (usually ~0.5-mm mesh) sieve.

Meiobenthos – Benthic animals too small to be retained on a coarse (usually ~0.5-mm mesh) sieve, but large enough to be retained on a fine (usually ~0.05-mm mesh) sieve.

Zoobenthos – The community of animals living around surfaces (e.g., sediments, plants) in aquatic ecosystems.

See also: Amphipoda; Annelida, Hirudinea (Leeches); Aquatic Ecosystems and Human Health; Aquatic Insects – Ecology, Feeding, and Life History; Aquatic Insects, Classification; Biodiversity of Aquatic Ecosystems; Biomanipulation of Aquatic Ecosystems; Cladocera; Copepoda; Decapoda; Diptera (Non-Biting Flies); Ephemeroptera (Mayflies); Gastrotricha; Invasive Species; Littoral Zone; Mollusca; Nematoda; Regulators of Biotic Processes in Stream and River Ecosystems; Rotifera; Trophic Dynamics in Aquatic Ecosystems.

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