Photo: Luiz Marigo – Mamirauá

8

The dynamic ecology of aquatic animal populations and communities

SUMMARY

A great number of animal species are distributed throughout inland waters. The various phyla or classes make up different proportions of the inland aquatic fauna.

Many species of the freshwater fauna originated from land animals. Over time, passive and active invasions occurred from land and sea systems into inland aquatic systems. The present chapter describes the dynamics and interactions of the aquatic fauna, including the structure and functioning of food chains, seasonal cycles, migration (horizontal, vertical and latitudinal), and distribution. The composition and abundance of the fauna and the use of aquatic animals as indicators of water pollution are also discussed.

Freshwater animals include a varied and rich population of organisms from many phyla and classes. These organisms can be found in all freshwater ecosystems. They come from different origins: some originated from land-dwelling predecessors that migrated to freshwater ecosystems; others migrated from oceans to inland waters.

8.1 ZOOPLANKTON

Chapter 6 describes the zooplankton in freshwater systems, including a wide variety of **micro-zooplankton** (protozoa and rotifers) and **meso-zooplankton** (crustaceans, cladocerans, and cyclopoid and calanoid copepods). *Chaoborus* and Mysidacea larvae sometimes can be found in lakes, reservoirs, and ponds and form part of the **macro-zooplankton**. Most zooplankton organisms measure 0.3 to 0.5 millimetres in length. They represent an important link in the food chain in all freshwater ecosystems, estuaries, oceans, and coastal waters. Most of these organisms feed on phytoplankton or bacterioplankton. Rotifers, cyclopoid copepods and worms may even prey on other types of zooplankton.

The principal metabolic and behavioural features of freshwater zooplankton include seasonal cycles, spatial and temporal succession, vertical migration, reproduction and basic aspects of the life cycle, including development and feeding. The main groups of zooplankton include non-photosynthesizing protozoa, rotifers, many subclasses of crustaceans, and some coelenterates, flatworms, and insect larvae. Very few invertebrate larvae occur in freshwater plankton, as compared with marine plankton. Additional freshwater zooplankton groups include amoebae, ciliates, *Mesostoma* flatworms, and eggs and larvae of several freshwater fish species.

Life cycles and reproduction

The reproductive rates and growth rates of zooplankton depend on environmental factors such as water temperature, food availability, levels of dissolved oxygen, and general conditions of water quality in aquatic ecosystems. Specific reproductive features vary among the different groups of zooplankton. Rotifers are often parthenogenetic, i.e., adults produce eggs with diploid chromosomes and do not require a sexual phase for reproduction. The life cycles of crustacean zooplankton (including both cladocerans and copepods) are more complex.

Cladocerans are usually parthogenetic. In conditions of extreme overcrowding, males develop from diploid eggs; sexual reproduction with eggs and haploid sperm then occurs. Copepods are not parthenogenetic, but they can reproduce rapidly due to the female's sperm reserve, which allows fertilization of multiple clutches from a single copulation (see Figure 8.1).

Cyclomorphosis is an important phenomenon that occurs in zooplankton, particularly in crustaceans. Many zooplankton organisms change their morphology at different phases of the seasonal cycle. In many aquatic ecosystems, summer populations present different characteristics from winter populations. Examples of cyclomorphosis include the formation of spines or "helmets" in some species, as shown in Figure 8.2. Various factors influence and regulate cyclomorphosis, including high temperature, abundance of available food, and turbulence, according to Jacobs (1967). Lampert and Sommer (1997) described how the presence of dissolved chemical substances

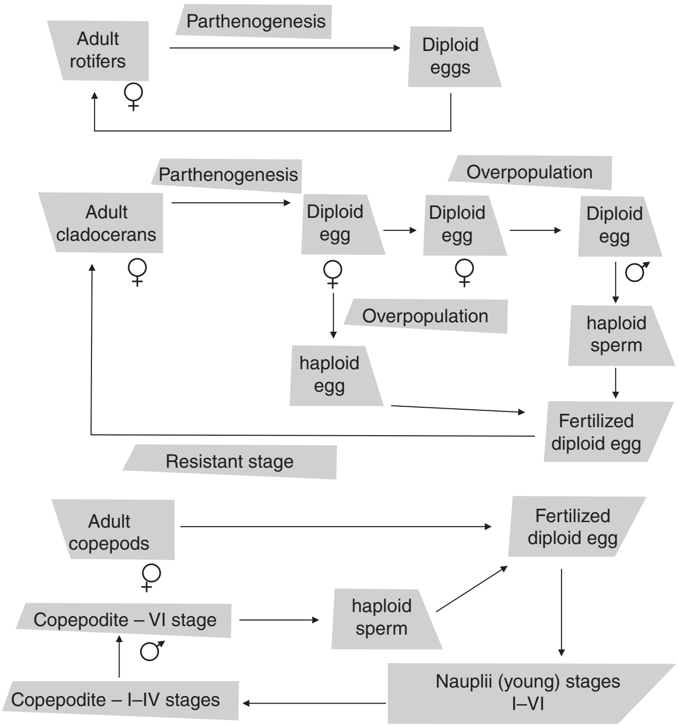
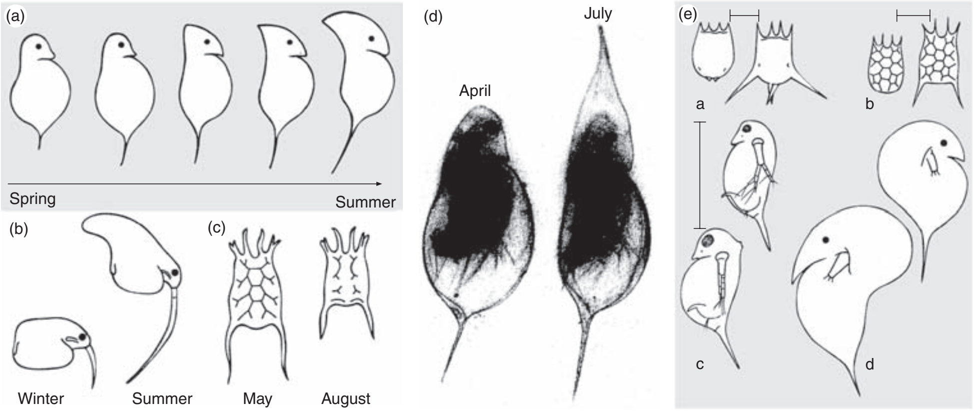


Figure 8.1 Types of reproduction of rotifers, cladocerans and copepods.



a – Induction of temporary spines in the rotifer *Brachionus calyciflorus* rotifer by the rotifer predator *Asplanchna*; scale 100 µm (*Halbach*, 1969).
b – Induction of permanent spines in rotifer *Keratella testudo* by *Asplanchna*; scale of 100 µm (Stemberger, 1988).
c – Induction of a bulge in the upper part of the carapace in *Daphia pulex* by *Chaoborus* larvae; scale of 1 mm (Havel and Dodson, 1984).
d – Induction of a 'hood' or 'helmet' in *Daphia carnicata* by *Anisops*; size of *Daphnia*, approximately 5 mm (Grant and Dayly, 1981).

Figure 8.2 Cyclomorphosis of zooplankton. a) Seasonal alterations in the morphology of *Daphnia retrocurva*, b) winter and summer forms; c) Morphology of the rotifer *Keratella quadrata* in May and August; d) Cyclomorphosis in *Daphnia cuccullata*; round carapace (April) and with helmets (July); e) The morphs produced in the presence or absence of predators are placed next to each other for comparison.
Source: Modified from Lampert and Sommer (1999).

produced by predators can lead to the development of spines and other formations in *Daphnia*, making it more difficult for predators to capture the organism.

Cyclomorphosis occurs in different groups, influenced by abiotic and biotic factors. A morphological change induced by the presence of predators is called **chemomorphosis** (Horne and Goldman, 1994). However, some authors believe that such morphological variations are, in truth, features of different species and not morphological variations within the same species.

Among microplanktonic organisms, some protozoan species in the protozooplanktonic group have been studied extensively over the last 40 years (Labour-Parry, 1992). Studies in marine waters have shown the abundance of ciliates and flagellates; and subsequent studies in lakes, rivers and reservoirs have shown the importance of these organisms as components of freshwater plankton. Protozooplankton contains representatives of all groups of free-living protozoa: ciliates, flagellates and sarcodines. Some groups, such as Foraminifera, are exclusively marine. Ciliated tintinnids can occur in oceans and fresh water, although few species are found in inland ecosystems. Dinoflagellates are an important marine group, and some important freshwater species exist as well. Among freshwater proto-zooplanktonic organisms, varying degrees of symbiosis with algae have been noted, especially with ciliated protozoa of the *Stentor* genus.

Nearly 7,000 species of ciliated protozoa (both free-swimming and parasitic) have been identified. Their main morphological feature consists of a membrane with cilia and membranelles used for feeding and movement. In harsh conditions of desiccation or salinity, some ciliates or other protozooplanktonic components can form cysts. The cysts, which vary in form, can survive through long periods of desiccation or other unfavourable conditions. The capacity of some *Strombidium* ciliates to retain plastids from various prey is important in the flow of carbon and transfer of energy in aquatic systems (Matsuyama and Moon, 1999) (see Figure 8.3).

Many ciliated proto-zooplankton have a combined autotrophic-heterotrophic mode. Retaining plastids from prey species provides the capacity to fix carbon through photosynthesis. Ciliated plankton in the genera *Vorticella* and *Epistylis* are also common in some lakes. They are sessile ciliates, feeding on small particles and bacteria. In some cases, diatoms serve as a substratum for epibiont protozoa.

Regali Seleghim and Godinho (2004) described the colonization of copepods, cladocerans, and rotifers by *Rhadostyla* spp. and *Scyphidia* spp. These epibionts can take advantage of free transportation to areas where food is more abundant, avoid predation by zooplankton (Henebry and Ridgway, 1979) or be transported to areas with better physical and chemical conditions of survival.

Protozooplanktonic flagellates, common in all aquatic systems, are a morphologically and physiologically heterogeneous group. They use their flagella for movement and feeding. These organisms are generally unicellular, but there are instances of phytoflagellate and zooflagellate colonies. Reproduction is asexual in all flagellate groups.

The **heterotrophic flagellate** group includes a variety of physiologically and morphologically diverse species of fungi (*Phytomastigophora* and *Zoomastigophora*). Among phyto-flagellates, the dino-flagellate group is common in marine and coastal waters (e.g., *Noctiluca* spp.). The most common genera of freshwater dino-flagellates

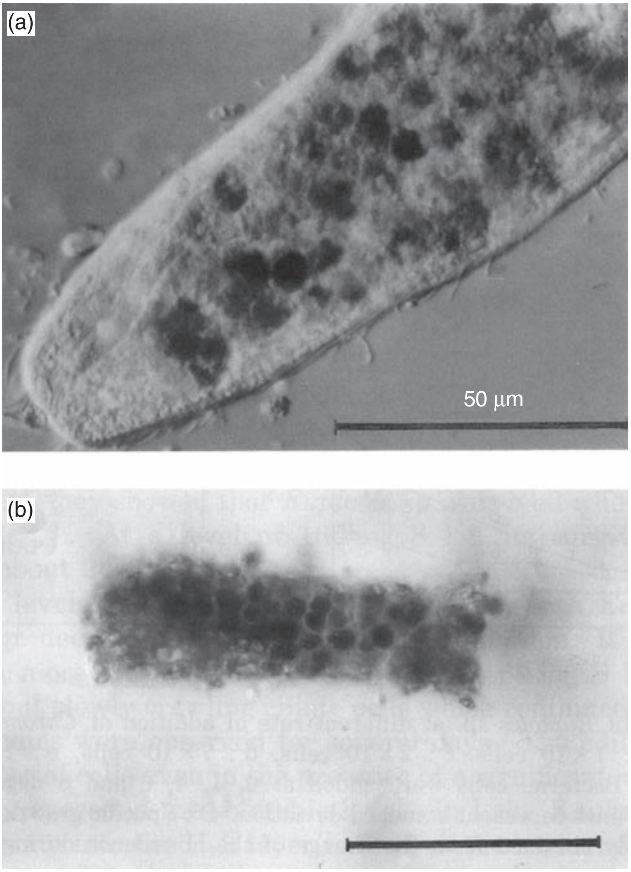


Figure 8.3 Microphotographs of *Tracheloraphis* sp. (a) and *Spirotrichia* (b). The two species include many cells of *Chromatium* sp. and *Macromonas* sp. in their structure (Lake Kaiike).
Source: Matsuyama and Moon (1999).

are *Ceratium*, *Peridinium*, *Gymnodinium* and *Cystodinium*. Choano-flagellates are common in saltwater but not in fresh water.

Phagotrophic phytoflagellates ingest suspended particles, bacteria and dissolved organic matter (Porter, 1988). Mixotrophic phytoflagellates, especially dinoflagellates, are common in some freshwater ecosystems. Foraminifera, Radiolaria and Heliozoa are Sarcodines that are found mainly in marine, oceanic and coastal waters. Thecamoebae occur in freshwater plankton.

8.1.1 Spatial distribution and seasonal cycle

The composition and structure of micro-, meso- and macro-zooplanktonic communities vary greatly through space and time. In general, mesozooplankton (or metazooplankton) includes several dominant species, such as cladocerans and rotifers, which vary spatially and seasonally, depending on factors such as light intensity, dissolved oxygen levels, food availability, competition, predation, parasitism and the hydrodynamics of aquatic systems.

Spatial variation and distribution of zooplankton depend on various physical, chemical and biological factors. It is important to understand the spatial variation in aquatic ecosystems in order to assess and identify the distribution of organisms, prepare sampling programmes, and apply statistical methods (Legendre *et al.* 1989, 1990). According to Armengol *et al.* (1999), **spatial heterogeneity in reservoirs**, for example, is a structural and functional feature of ecosystems and not the result of a random process (Legende, 1993).

The distribution of plankton communities, zooplankton in particular was studied by Patalas & Salki (1992), Betsil & Van den Avely (1994). More recently in Barra Bonita reservoir Matsumura-Tundisi & Tundisi (2005) studied the zooplankton distribution in this artificial ecosystem. A detailed study of spatial distribution in the UHE Carlos Botelho reservoir (Lobo/Broa), by Bini *et al.* (1997), showed a high degree of spatial heterogeneity in the ecosystem. The number of copepods and nauplii of copepods increased in the zone of influence of the Lobo and Itaqueri Rivers, and the number of cladocerans increased toward the reservoir's limnetic zone. Abiotic factors such as levels of nutrients and suspended matter influence and affect spatial distribution.

Marzolf (1990) presented a theoretical model describing the abundance of zooplankton along a reservoir's longitudinal axis, as determined on two main factors: current velocity and the transfer of material (clay, nutrients, dissolved organic matter), in addition to available food (phytoplankton, specifically, nanophytoplankton). If current velocity is a significant factor in zooplankton distribution, there is an increase in the direction toward the dam. If the transfer of material is predominant, zooplankton density is greater in the region of the reservoir under the influence of the rivers. In cases where the two factors are equally important, distribution in the reservoir is similar to a 'frequency distribution' with positive asymmetry. The interacting current velocity and zooplankton distribution, and even transfer of material, appear to be the main factors influencing spatial distribution of zooplankton in UHE Carlos Botelho reservoir (Lobo/Broa).

Patalas and Salki (1992) determined that the morphology of lakes, the geology of the drainage basin, and the location of the main tributaries are key factors in the patterns of zooplankton distribution.

In the case of spatial distribution of zooplankton in the Barra Bonita reservoir, Matsumura Tundisi and Tundisi (2005) concluded that certain key factors – such as **current velocity, suspended organic particulate matter, the presence or absence of pollutants and contaminants** – were responsible for the relative abundance and composition of species in three study sites: the Tiete River, the Piracicaba River, and the confluence of the Tiete and Piracicaba Rivers. The communities of zooplankton and phytoplankton in these three areas present a mosaic of microhabitats, judged according to Margalef (1997) and Reynolds (1997). The study by Matsumura Tundisi and Tundisi (2005) also presents the hypothesis and theory that countless tributaries of the Barra Bonita reservoir contribute to a large amount of spatial heterogeneity, in which the discharge point of each tributary produces a frontier of water mass with varying density and nutrient levels, thus adding to the spatial heterogeneity and expansion capacity of feeding niches and favourable abiotic conditions.

8.1.2 Seasonal cycle

Fluctuations and the seasonal cycle of zooplankton in lakes and inland aquatic ecosystems depend on a range of factors. Burgis (1964), for example, considered variable precipitation (rainfall) to be the predominant factor affecting the biomass and succession of species in Lake George (Africa). Matsumura Tundisi and Tundisi (1976) determined that precipitation is a decisive factor in the seasonal cycle of zooplankton in the UHE Carlos Botelho reservoir (Lobo/Broa).

Fluctuations in the level of the Amazon River affect the seasonal cycle of zooplankton: high densities of zooplankton are associated with lower water levels in the river. The same occurs in lakes in the Pantanal Mato-grossense. In these cases, an abundance of food occurs during periods of isolation of the lakes due to decomposition of macrophytes and other organisms.

Seasonal variations in zooplankton can therefore be related to climatic factors (mainly precipitation and wind), hydrographic and hydrological factors (periods of flooding and large volumes of rivers and lakes, interspersed with periods of reduced volumes). In a study of Dom Helvécio Lake, Parque Florestal do Rio Doce (MG), Matsumura Tundisi and Okano (1983) found that several species of copepods had different seasonal cycles (see Figure 8.4). According to the authors, factors such as patterns of thermal stratification and circulation, which occur in summer (December-March) and winter (June-September) respectively, can cause seasonal fluctuations in species in addition to predation by *Chaoborus* larvae (mainly in the **limnetic** zone) on the nauplii of cyclopoids (and not on the nauplii of calanoids, which are more abundant near the coastal zone where *Chaoborus* larvae are less abundant). *Thermocyclops minutus* and *Tropocyclops prasinus* peak in abundance during different periods in the lake, mainly because they have different reproductive periods.

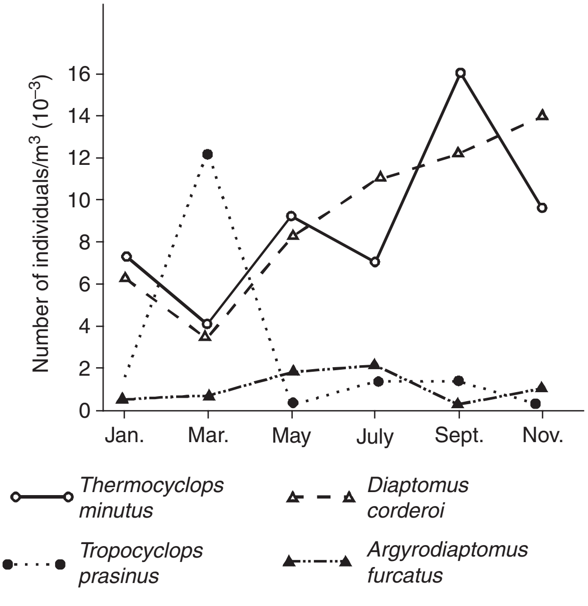


Figure 8.4 Pattern of seasonal fluctuation of copepod species in Lake Dom Helvécio in 1978.

The seasonal cycle of zooplankton, therefore, involves a number of biological factors, including reproductive period, co-existence with other species and impact of predation (intra-zooplanktonic or on other organisms, such as fish), as well as abiotic factors such as precipitation, stratification and vertical circulation. Water temperature clearly plays an important role in the reproduction and physiology of zooplankton organisms, and consequently, in the seasonal cycle. Ritzier (1995) verified that *Thermocyclops decipiens* and *Mesocyclops kieferi* are the dominant species in the Barra Bonita reservoir (SP.), coexisting throughout the year.

During periods of thermal stratification in summer, *M. kieferi* is abundant from 0 to 10 meters deep, and *T. decipiens* occurs from 5 to 10 meters deep; the two species are therefore in part spatially segregated during the season. In winter, during periods of thermal instability, organisms of the two species are more uniformly distributed. *Thermocyclops decipiens* and *Mesocyclops kieferi* are omnivorous organisms with high levels of detritus in their diet. Observations and laboratory studies show that the development phases, mortality rates and reproductive rates of both species are attuned to the environment, giving them competitive advantages and explaining their predominance in the Barra Bonita reservoir (Rietzler, 1995).

According to Espindola (1994), the presence of different *Notodiaptomus* species in the Barra Bonita reservoir throughout the seasonal cycle *(Notodiaptomus iheringi, Notodiaptomus cearensis,* and *Notodiaptomus conifer*) is due to qualitative variation in available food associated with climatic factors (such as precipitation), hydrographic factors (dissolved oxygen and temperature), and hydraulic factors (water flow and retention time). These are the main factors that determine the seasonal cycle of zooplankton and the population dynamics of these calanoid species. The pressure from predation by vertebrates (fishes) and invertebrates *(Mesocyclops* sp. and *Asplanchna* sp.) also contributes to fluctuations in the population density of *Notodiaptomus* spp. (including a new species not yet described found in the reservoir).

N. cearensis and *N. conifer* presented higher levels of production of eggs and greater **longevity** at 23°C (give or take 1°C). The temperature of 18°C (give or take 1°C) limited the development and growth of populations of the species. For these organisms, **diatoms** (*Aulacoseira distans*) and Chlorophyta (*Chlamydomonas* sp. and *Monoraphidium* sp.) were the preferred food. Espindola (1994) determined that the temporal segregation and the effects of temperature on the development of different species, and available food (along with hydrologic and hydrographic conditions), were all factors influencing the spatial and temporal distribution of species in the Barra Bonita reservoir.

Padovesi Fonseca (1996) presented similar conclusions on the population dynamics of zooplankton in a small reservoir (the **Jacaré-Pepira reservoir**, Brotas – SP). The reservoir is shallow, turbulent and subject to the changing influences of precipitation, wind and thermal variations throughout the seasonal cycle.

In conclusion, according to Lampert and Sommer (1997), abiotic factors (including precipitation, wind and **hydrodynamic conditions**) and biotic factors (including available food resources, reproductive rate, changing levels of competition and predation, and shifts in feeding habits from herbivore to detritivore) are key factors in the seasonal cycle of zooplankton and the dynamic alterations and succession.

Reproductive strategies such as rapid growth (maximum growth rate of the population – r_{max} – r strategists) with rapid dispersal and colonization capacity, as compared to slower growth and reproduction (k strategists), are factors that determine the seasonal cycle and appropriate and efficient use of energy for reproduction (r strategists) or defence against predators and minimization of mortality with reduction of the specific metabolic rate and reproductive rate (k strategists). The ability of populations to survive throughout the seasonal cycle thus depends on a balance between reproduction and mortality. **Phenotypic** and **genotypic variations** occur in these populations.

In an in-depth study on a tropical lake (Lake Lanao) in the Philippines, Lewis (1979) examined seasonal variations and abundance of phytoplankton, herbivores and carnivores in weekly samples from August 1970 to October 1971 (see Figure 8.5). The period of vertical circulation in the lake did not favour phytoplankton growth and development because the availability of underwater solar radiation was limited. This is a common process in many tropical lakes: limited underwater solar radiation due to circulation and excess suspended material resulting from precipitation and drainage, drastically reducing light penetration.

Calijuri and Tundisi (1990) recorded reductions up to 80% in underwater light penetration at the Barra Bonita reservoir (SP). In the lake region of Cananéia (SP), Tundisi and Matsumura Tundisi (2001) observed drastic reductions in the euphotic zone with marked reduction in the depth of primary production.

Still, according to the study by Lewis (1979), herbivores probably consume approximately 10% of the primary production annually. In the lake, the carnivores are almost entirely limited to *Chaoborus* larvae, which prey extensively on herbivorous zooplankton. The studies by Lewis show that the development cycles of different stages of copepods are closely interrelated (a calanoid species and a cyclopoid species), which generally does not occur in community structure and dynamics. Seasonal variations in the herbivore communities of Lake Lanao are attributed to variations in quantity and not quality of food (phytoplankton). Variations in the development of herbivores, as a result of the variability and fluctuations in phytoplankton, occurred

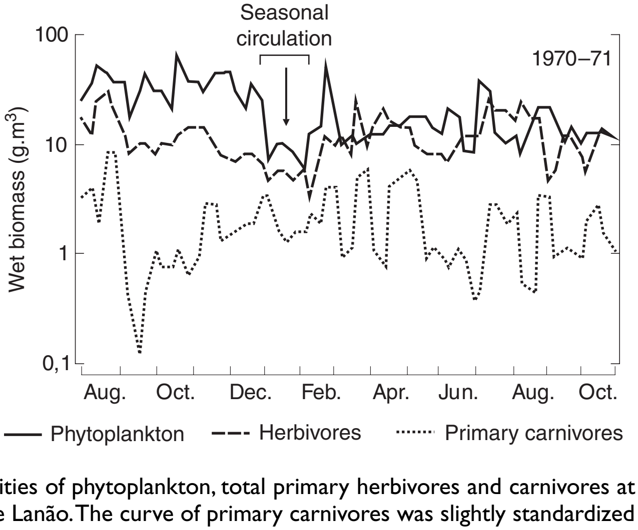


Figure 8.5 Quantities of phytoplankton, total primary herbivores and carnivores at weekly intervals in Lake Lanão. The curve of primary carnivores was slightly standardized (14-day period).
Source: Modified from Lewis (1979).

as a result of the availability of various components, the size of available phytoplankton and their digestibility and capacity to support various herbivore communities.

According to Rocha *et al.* (1995), abundance and seasonal cycles in tropical and subtropical lakes and reservoirs in Brazil are related to fluctuations in hydrometric level, thermal structure, circulation, retention time (in reservoirs) and availability of food (phytoplankton and detritus).

8.1.3 Distribution and vertical migration

Zooplankton in both inland waters and ocean waters present a vertical migration pattern over a 24-hour period that varies from species to species and with the development stages of different species. Zooplankton generally spends the day towards the bottom of lakes and reservoirs, migrating at night toward the surface. Cases of 'reverse' vertical migration exist in which the zooplankton migrates to the bottom of an aquatic ecosystem during the night and remains on the surface during the day. The diurnal movements of freshwater zooplankton were first recorded by Neissman (1877b) in Lake Constance, followed by Pavesi (1882) in Italian lakes, Francé (1894) in Lake Balaton, Stever (1901) in small lakes along the Danube River, and Lorenzon (1902) in Lake Zurich.

Later studies to identify the causes of vertical migration led to experiments examining the role of light intensity in the phenomenon, variations in horizontal and vertical light rays (Bauer, 1909) and the positive phototactic response in relation to gradients of light intensity. Many researchers argue that zooplanktonic organisms tend toward a **negative geotaxis** in darkness and a **positive geotaxis** during periods of light. Tundisi and Matsumura Tundisi (1968) observed positive geotaxis in *Pseudodiaptomus austus* under illumination in experiments conducted in the lake region of Cananéia in the state of Sao Paulo.

Effects of polarized light (Baylor and Smith, 1953), increases in the specific density of organisms due to feeding (and subsequent sinking because of the inability to sustain themselves on the surface), and effects of hydrostatic pressure have been the subjects of much experimental research (Hutchinson, 1967). The diurnal cycle of light and darkness undoubtedly plays an important role in the vertical migration of zooplankton over the course of a 24-hour period.

The typical **migratory** trajectory of zooplankton is a vertical upward movement toward the surface during the night and a vertical downward movement toward the bottom during the day. The process of vertical migration appears to involve a relatively small expenditure of energy (Hutchinson, 1967).

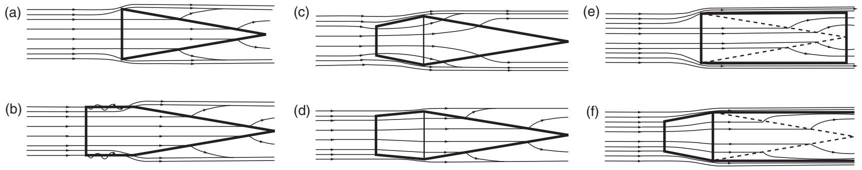
The theory of an **endogenous rhythm** that regulates vertical migration and zooplankton movement was presented by Harris (1963), Hurt and Allanson (1976), and Zaret and Suffern (1967). In a detailed study of the vertical migration of zooplankton in Lake Dom Helvécio (Parque Florestal do Rio Doce – MG), Matsumura Tundisi *et al.* (1997) showed that the calanoids *Argyrodiaptomus furcatus* and *Scolodiaptomus corderoi* presented different vertical migration patterns. *A. furcatus* remained near the metalimnion during the diurnal period and migrated toward the surface during the nocturnal period. While *S. corderoi* remained near the metalimnion during the diurnal period, since part of the population also inhabits the metalimnion. Few individuals migrate at night toward the surface. During periods of vertical homogeneity in the

Collection and measurement of zooplankton

The collection of plankton and, more specifically, zooplankton, began over 150 years ago. Darwin was one of the first to use a plankton net on board the Beagle on his transoceanic voyage. Conical collection nets with mesh openings ranging from a few millimetres to centimetres were used to collect plankton for long-term oceanographic and limnological studies. These nets were used vertically, horizontally and obliquely to sample a taxonomically varied and diverse community, biologically and ecologically important.

The development of more sophisticated collecting methods began with the need to better characterize the plankton community and quantify it in terms of number of individuals, volume, or wet or dry weight. The evolution of collection technology and quantification of zooplankton included: conical-shaped nets adapted to flow meters to measure the volume of water sampled; closing nets to control the volume and the sampled depth for studies on vertical migration; suction pumps for sampling determined volumes with flow meters and hoses at certain depths.

Measures to calculate the biomass of zooplankton include: calculation of dry weight, total volume of sample (in cm^3 or mm^3); wet weight of plankton collected; total carbon sample collected. In all these techniques, microscopic observation of the sample is vital for classification and species composition. Plankton-collecting nets generally have 50-micron mesh for meta-zooplankton, $>100\,\mu m$ for macro-zooplankton, and $<30\,\mu m$ for micro-zooplankton. A variety of filtering systems and nets with different meshes (100, 50, 25, 10, 5 and $2\,\mu m$) are used for classifying the size of organisms and their quantitative importance. Figure 8.6 shows the water-flow patterns in some types of plankton-sampling nets.



a – 'Simple' conical net
b – Conical net with porous collar
c – Conical net with a non-porous collar, reducing the inflow
d – Conical net with a system of reducing the entrance of water
e – Conical net with a non-porous framework
f – Conical net with a non-porous framework and a non-porous system of reducing the entrance of water

Figure 8.6 Patterns of flow associated with some basic types of plankton nets. Each type has a different filtering efficiency.

water column, the population is distributed homogenously, with a small accumulation on the bottom. *A. furcatus* presents a reverse migration toward the bottom of the lake during the period of vertical homogeneity in the water column.

Thermocyclops minutus presents vertical migration to the epilimnion-metalimnion interface during the lake's stratification period, remaining in the deepest part of the metalimnion during the day. *Tropocyclops prasimus cenidionalis* does not migrate vertically during the stratification period, but instead remains in the deepest part of the metalimnion during this period. During periods of vertical homogeneity in the lake, this species migrates to the depth of 5 metres during the day. Such examples of vertical migration in a lake that stratifies in summer and is thermally and chemically homogenous in winter (see Figure 8.7) clearly show that there are several different types of behaviour:

- species that inhabit the epiliminion and migrate vertically in that layer (*S. corderoi* and *A. furcatus*);
- species that inhabit the epilimnion-metalimnion interface with vertical migration in intermediate layers;
- species that remain in the metalimnion while presenting vertical migration, such as *T. prasinus*.

The vertical distribution of zooplankton varies with the intensity of thermal stratification and circulation. Figure 8.8 illustrates the vertical movements of different zooplankton species in Lake Dom Helvécio. While two species of calanoid copepods remain in the epilimnion during the stratification period, a cyclopoid species explores the epilimnion-metalimnion interface and another explores the metalimnion. This is a clear and interesting example of the exploitation of resources by different zooplankton populations through the presence or absence of vertical migration activity.

According to Lampert and Sommer (1997), the stimulus for the beginning and ending of vertical migration is the relative (and not absolute) change in light intensity. Phototaxis and geotaxis are essential in the regulation of vertical migratory behaviour in zooplankton.

Vertical migration of zooplankton must undoubtedly provide some advantages, such as more efficient use of energy during migration and more rapid population growth. The presence of zooplankton on the surface at night would provide the advantage of obtaining richer food, such as phytoplankton, and at the same time, would prevent deleterious effects on the population from mortality due to ultraviolet radiation. Another hypothesis on vertical migration is that it provides an important mechanism to avoid predation, especially visual predation by plankton-eating fishes.

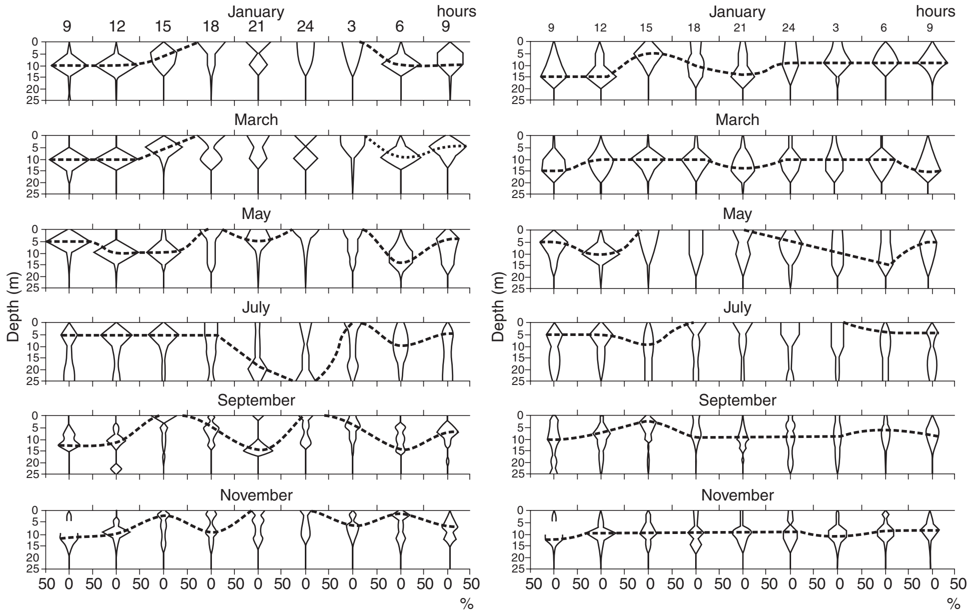
Mechanical stimulation resulting from the presence of predators promoted rapid migration of zooplankton in experimental tanks (Ringelberg, 1991). One theory states that chemical substances released by predators may stimulate zooplankton to migrate (Loose *et al*., 1993). Changes in the reverse migration of copepods also occurred when *Chaoborus* larvae, common in Lake Gwendolyne (British Columbia, Canada), were eliminated with the introduction of trout. During the day, individuals of *Diaptomus* were found on the lake's surface, and at night they migrated to deeper water to avoid predation by *Chaoborus*. With the disappearance of the larvae, the reverse migration stopped. When water containing *Chaoborus* larvae was introduced into experimental tanks, the organisms immediately began to migrate in reverse, indicating chemical stimulation (4-hour response period).

Other hypotheses on vertical migration involve genetic exchange during the migration period and an optimization of the grazing pressure on phytoplankton by zooplankton. During the day, the absence of grazing by zooplankton optimized the growth and reproduction of the phytoplankton biomass (Lampert and Sommer, 1997).

Many zooplanktonic species avoid the littoral zones of lakes and reservoirs, involving **horizontal migrations** that keep them away from the edges. A combination

(a) *Argyrodiaptomus furcatus* (*A. furcatus furcatus* + *A furcatus exilis*): vertical migration in the epilimnion

(b) Migration of *Scolodiaptomus corderoi*



(c) *Themocyclops minutus*: example of vertical migration at the epiliminion/metalimnion interface

(d) *Tropocyclops prasinus* f. *meridionalis*: this species does not migrate, it remains in the metalimnion during the period of stratification.

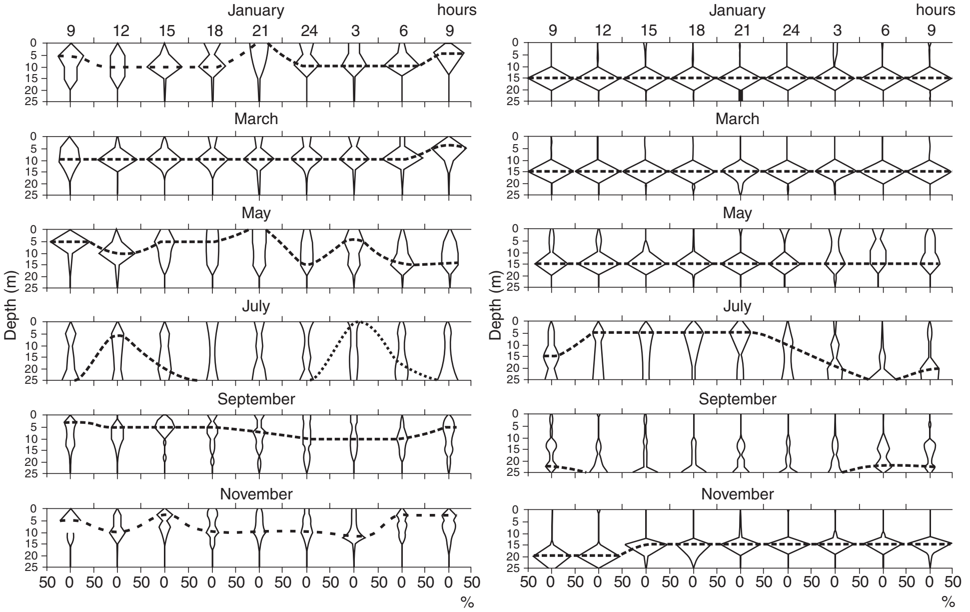


Figure 8.7 Patterns of vertical migration of copepod species in Lake Dom Helvécio during1979.
Source: Matsumura Tundisi *et al.* (1997) in Tundisi and Saijo (1997).

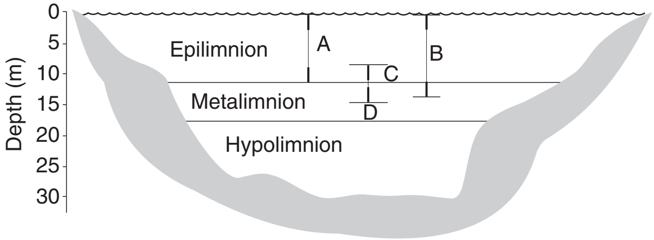


Figure 8.8 Illustration of the vertical movements of copepod populations in the Lake Dom Helvécio. *Source*: Matsumura Tundisi *et al.* (1997) in Tundisi and Saijo (1997).

of predation and competition can control the horizontal structure and distribution, as previously discussed.

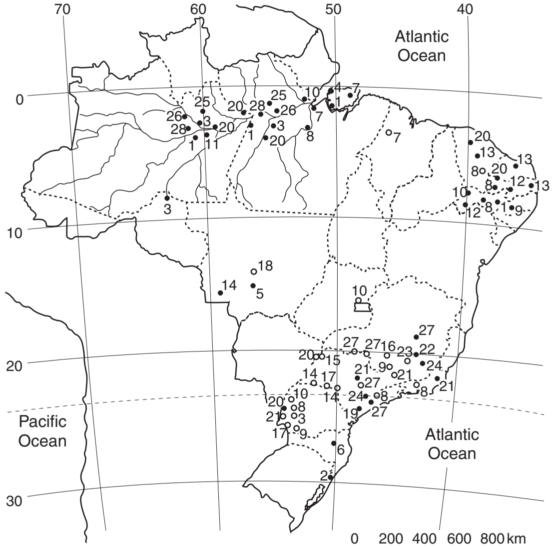
Episodes of vertical migration by zooplankton species and their maintenance strategies in optimal reproductive and developmental regions were described by Tundisi (1970) for *Pseudodiaptomus acutus* in the lagoon region of Cananeia; by Rocha and Matsumura Tundisi (1995) for *Argyrodiaptomus furcatus* in the UHE Carlos Botelho reservoir (Lobo/Broa); and for *Acartia tonsa* by Tundisi (unpublished results) for in an estuary in Southampton, England.

These are examples of different species and latitudes, from tropical estuaries (lagoon regions of Cananeia), to subtropical reservoirs (UHE Carlos Botelho – Lobo/Broa) and temperate zone estuaries (Southampton, England) with similar reproductive behaviour and tolerance for different environmental factors.

8.1.4 Latitudinal distribution

A series of studies describe the distribution of calanoid copepods at different latitudes in the South American continent. According to Matsumura Tundisi (1986), there are no cosmopolitan species of calanoids; a species that occurs in one continent, for example, does not occur in another (Dussart *et al.*, 1984). Brandorf (1976) reviewed the distribution of Diaptominae genera and species in South America. In her study on the latitudinal distribution of calanoids, Matsumura Tundisi (1986) examined 20 species of the Diaptominae family, in the genera *Notodiaptomus*, *Argyrodiaptomus*, *Odontodiaptomus*, *Rhacodiaptomus*, *Aspinus*, and *Trichodiaptomus*. According to this author and Brandorf (1976), among the main genera in South America, *Argyrodiaptomus* species are the most common in the continent. Seven species belonging to this genus (*A. aculeatus*, *A. argentinus*, *A. bergi*, *A. furcatus*, *A. denticulatus*, *A. azevedo*, and *A. granulosus*) can be found between 25° and 40° South latitude. Four species occur between 15° and 25° South latitude: *A. aculeatus*, *A. neglectus*, *A. furcatus*, and *A. azevedoi*. Only one species occurs between 0° and 10° South latitude: *A. azevedoi*. Thus, the genus *Argyrodiaptomus* is characteristic of the continent of South America.

Odontodiaptomus paulistanus is extremely common in reservoirs in the state of São Paulo, between 20°S and 23°S latitude. The genus *Notodiaptomus* (with 22 species) is widely distributed throughout South America. *N. iheringi* is common in reservoirs in the state of São Paulo, especially in eutrophic systems, and *N. cearensis* is common



1 – *Notodiaptomus amazonicus* (PE, AM, PA);
2 – *Notodiaptomus anisiti* (RS);
3 – *Notodiaptomus coniferoide* (RO, AM, PA, PR);
4 – *Notodiaptomus dahli* (PA);
5 – *Notodiaptomus deitersi* (MT);
6 – *Notodiaptomus gibber* (SC);
7 – *Notodiaptomus henseni* (PA, MA);
8 – *Notodiaptomus iheringi* (PB, PE, CE, PA, RJ, SP, PR);
9 – *Notodiaptomus isabelae* (PE, MG, PR);
10 – *Notodiaptomus jatobensis* (PE, P A, GO, PR);
11 – *Notodiaptomus kieferi* (AM);
12 – *Notodiaptomus nordestinus* (PA, PE);
13 – *Notodiaptomus cearensis* (CE, PB, RN);
14 – *Notodiaptomus conifer* (SP, MT);
15 – *Notodiaptomus spinuliferus* (SP);
16 – *Notodiaptomus dubius* (MG);
17 – *Notodiaptomus transitans* (SP, PR);
18 – *Notodiaptomus venezolanus deevoyorum* (MT);
19 – *Argyrodiaptomus aculeatus* (SP);
20 – *Argyrodiaptomus azevedoi* (CE, PR, PB, PA, AM, SP);
21 – *Argyrodillptomus furcatus* (SP, RJ, PR, MG);
22 – *Argyrodiaptomus neglectus* (MG);
23 – *Argyrodillptomus furcatus exilis* (MG);
24 – *Odontodiaptomus paulistanus* (SP, MG);
25 – *Rhacodiaptomus retroflexus* (AM, PA);
26 – *Aspinus acicularis* (AM, PA);
27 – *"Diaptomus" corderoi* (MG, SP);
28 – *Trichodiaptomus coronatus* (SP, AM, PA).

Figure 8.9 Latitudinal distribution of calanoid copepods in Brazil's inland aquatic ecosystems.
Source: Tundisi Matsumura (1990).

in reservoirs in the Northeast. *N. conifer* occurs between 10°N and 36°S latitude, commonly in lakes and reservoirs, especially reservoirs along the Paranapanema River. Figure 8.9 shows the distribution of the most common calanoid species in Brazilian aquatic systems.

What factors determine the latitudinal distribution of these species? Physical and chemical conditions are important, and in particular the relationship with temperature and conductivity.

The association of temperature, salinity, and conductivity most likely determines the osmotic conditions needed for the establishment and development and colonization of calanoid species. According to Hutchinson (1967), the occurrence of endemic species is common among calanoids, given this group's tendency to create well-established latitudinal populations and exploit microhabitats. Calanoid copepods of inland waters present greater regional endemnicity than any other group of planktonic organisms. A small difference in tolerance to temperature, pH, and conductivity is probably enough to isolate these species. Even in lakes located close together, such as those in Parque Florestal do Rio Doce, there is an absence of some species, also observed by Lewis (1979) in Lake Lanao in the Philippines and adjacent systems.

In experiments on tolerance to conductivity/salinity and temperature of calanoid species in the state of São Paulo, Tundisi (unpublished results) obtained the following tolerance gradient for these factors: *Notodiaptomus iheringi* > *Argyrodiaptomus furcatus* > *Argyrodiaptomus azevedoi*, which may explain the dominance and succession of these genera and species in different ecosystems, as verified by Rietzler (1995) in the succession of *Argyrodiaptomus furcatus* and *Notodiaptomus iheringi* in the UHE Carlos Botelho (Lobo/Broa) and Barra Bonita reservoirs.

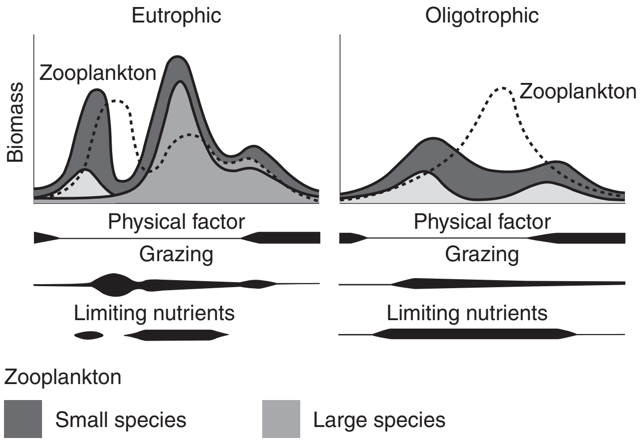


Figure 8.10 Illustration of the PEG model of seasonal zooplankton succession in eutrophic and oligotrophic lakes in temperate regions. The horizontal black symbols indicate the relative importance of the selection factors, i.e., physical factors, predation or availability of food. *Source*: Adapted from Lampert (1997).

8.1.5 Interrelationships phyto-zooplankton

The feeding habits of herbivorous zooplankton involve a selective process with a variety of structures and behaviours. Seasonal succession of phytoplankton and the corresponding succession of herbivorous zooplankton are the subject of many studies on inland and marine ecosystems (Raymont, 1963; Reynolds, 1984, Sommer, 1989; Lewis, 1979; Rocha and Matsumura Tundisi, 1997). Succession in phytoplankton and zooplankton in temperate-region lakes was expressed using the PEG model (*Plankton Ecology Group* – International Association of Limnology). Figure 8.10 shows the succession model for temperate-zone eutrophic and oligotrophic lakes. To a certain extent, however, patterns are much more complex and difficult to predict in tropical lakes and reservoirs, where the physical controls of the process (such as hydrology and hydrodynamics) can be much more effective and the cycles are faster, with interactions and overlapping of herbivores, detritivores and carnivores.

The concepts of **selective feeding** and **competition for resources** – strategies to prevent the overlapping of feeding niches – apply equally to planktonic communities in both temperate and tropical lakes. However, cycles in tropical lakes are faster and the alternatives are much more important. Tropical systems – affected by hydrological cycles, high temperatures and accelerated biogeochemical processes – are much more dynamic and complex than temperate-region systems. Studies on several tropical lakes, summarized by Talling and Lemoalle (1998), corroborate this hypothesis.

The authors outlined the processes and interactions of phyto-zooplankton and predation by *Oreochromis niloticus* (tilapia) and *Haplochromis nigripinnis* in Lake George (Africa) over 24-hour cycles (see Figure 8.11). Alternative predator-prey feeding cycles by zooplankton on phytoplankton and by fishes on zooplankton occur in short periods, and these processes control the metabolism of lakes, since in tropical regions they overlap the seasonal cycles and appear to be more significant (Barbosa and Tundisi, 1980).

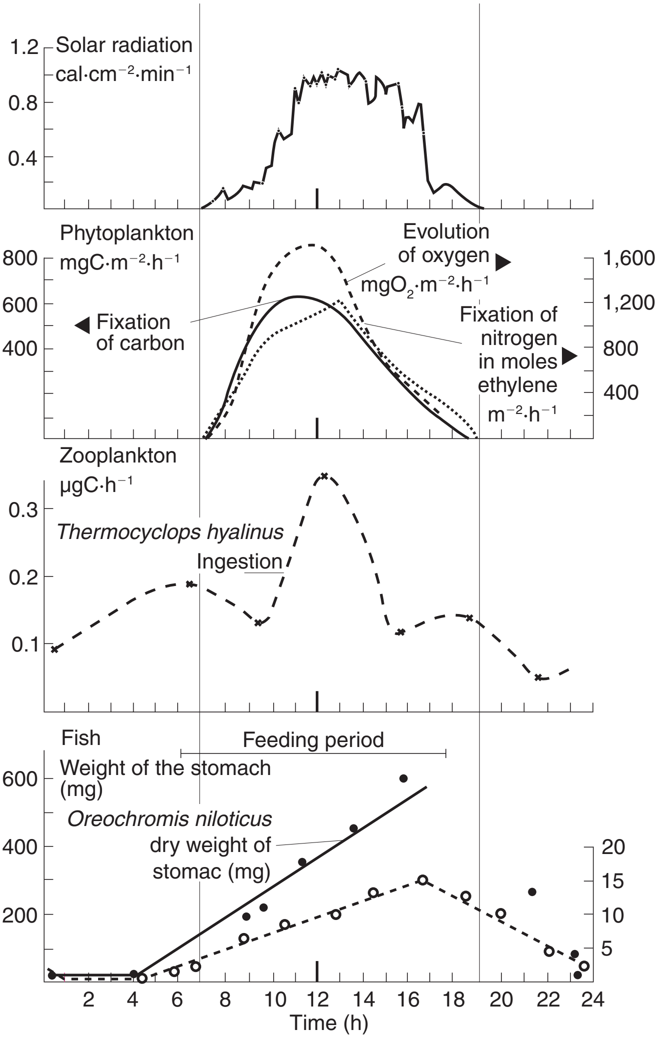


Figure 8.11 Diurnal cycles of solar radiation, fixation of carbon and nitrogen and food intake by zooplankton in Lake George.
Source: Modified from Talling and Lemoalle (1998).

8.1.6 Diapause

Resistant eggs and succession in zooplankton

Many freshwater calanoid species produce resistant eggs, especially in temporary lakes or waters. In South America, resistant eggs found in dry lake sediment that subsequently hatched to become *Argyrodiaptomus funcentus* adults were identified by Sars (1901), who also cultivated *Tropodiaptomus australis* in Australia with the same method, i.e., using dry sediment. The colonization of temporary waters is an adaptive strategy for a large number of calanoid species.

Laps and Hlekseev (2004) and Alekseev and Lampert (2004) described the production of resistant eggs in *Daphnia*, which reproduces parthenogenetically, but occasionally produces eggs through sexual reproduction, resulting in resistant eggs, carried by the female. Environmental stimuli such as photoperiod or availability of food are essential for production of resistant eggs, which develop in favourable conditions. Calanoid eggs can survive for 300 years before they hatch (Harrison *et al.*, 1995).

In many ecosystems the presence of a reserve of resistant eggs plays a key role in the succession and colonization of zooplanktonic species. Most likely chemical factors stimulate the development of these eggs, such as favourable pH conditions or salinity/conductivity. Resistant eggs can also play a role in detecting contamination and pollutants in lakes and reservoirs. Favourable chemical factors may promote the development of resistant eggs through biochemical stimulation; or physical factors may be associated with chemical factors. Physical factors include water temperature and sediment temperature, and length of photoperiod.

8.2 BENTHIC MACROINVERTEBRATES

As discussed in Chapter 6, the range of benthic fauna species is wide and varied, and includes herbivores, detritivores and predators. These organisms process the energy from internal and external sources in rivers, which is a product of the activities of periphyton, leaves, plant residues or organic matter produced by humans or animals.

In lakes, reservoirs or coastal and oceanic areas, these organisms largely depend on the production of organic matter that settles to the bottom of the ecosystem. A benthic invertebrate community is also important in the processing of organic material in rivers (and in the recuperation of rivers).

Aquatic insects are common in benthic macroinvertebrate communities in inland waters, with great diversity in rivers and streams. Species in the orders Ephemeroptera, Plecoptera, Trichoptera, Diptera and Odonata account for a majority of the biomass. Other important macroinvertebrate groups include molluscs, annelids and crustaceans. There are no macroinvertebrate benthic insects in marine environments.

In lakes, benthic organisms are classified as deep benthos and **littoral benthos**. Temperature, light intensity, currents, and dissolved oxygen levels all vary more widely in a 24-hour period in the littoral zone. The deeper zones in lakes are chemically and physically more uniform, except in eutrophic lakes during the stratification period, when anoxia and non-hypolimnic deoxygenation occur. Amphipods, larvae of chironomids and oligochaetes, molluscs and *Chaoborus* larvae are the most common organisms in the benthic animal community.

In the littoral zone, the presence of macrophytes provides rich and varied spatial heterogeneity, with niches that depend on the type of substratum and available food. Organic detritus is an important food source. Jónasson (1978) showed high species diversity in the littoral zone of Lake Esrom, Denmark, as compared with the benthic fauna in the lake's deep regions.

The structures of macro-vertebrate benthic communities can be altered by the production of fish, which greatly affects the community's biomass and species diversity. *Chaoborus* larvae are sensitive to chemical substances released by fish and may flee from predation, hiding in the sediment.

Table 8.1 Density (in individuals · m^{-2}) and biomass (g · dry weight · m^{-2}) of zoobenthos and chaoborids and chironomids in D. Lake Helvécio (Parque Florestal do Rio Doce – MG).

	Station							
Animals	*I*	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*
Mollusca*		#			#	15		15
Hyridae				(61.93)		(130.81)		
Corbiculidae					(0.04)			
Planorbidae						15		
Oligochaeta						(0.09)		
Tubificidae					370	415		15
Odonata					(0.21)	(0.20)		(+)
Libellulidae						30		
						(7.34)		
Trichoptera					89	44	60	
					(0.07)	(0.03)	(0.04)	
Diptera								
Chaoboridae	44	30	44	15	74	15	60	44
	(0.03)	(+)	(0.01)	(0.01)	(0.11)	(+)	(0.04)	(+)
Chironomidae								
Tanypodinae		30	15	44	637	696	60	44
		(0.14)	(0.10)	(0.02)	(0.17)	(0.23)	(+)	(0.02)
Chironominae					578	830	119	119
					(0.43)	(0.28)	(0.09)	(0.07)
Total	44	60	59	59	1,748	2,075	299	237
	(0.03)	(0.14)	(0.11)	(0.03)	0.99	70.14	0.14	130.9
Planktonic Chaoboridae	1,380	354	113	0	n	n	n	n

+ <0.01 gm^2, * with shell; # only the shell, n – not sampled
Source: Fukuhara *et al.* (1997).

The life cycles of benthic macroinvertebrates include three or four stages in the case of insects: egg, nymph and adult, or egg, larva, pupa and adult. Most benthic organisms reproduce once a year, but in temperate climates some species require more than one year to complete the life cycle (Usinger, 1956).

Substratum type, current velocity and transportation of sediment are all factors that affect the composition, structure and functioning of benthic macroinvertebrate communities. In the different regions of rivers, current velocity and substratum type affect the composition, diversity and succession of different species of benthic macroinvertebrates (Welch, 1980), whose life cycle depends on and is controlled by the availability of food (Horne and Goldman, 1994).

Table 8.1 shows the density (in individuals · m^{-2}) and biomass (grams of wet-weight · m^{-2}) of zoobenthos and chaoborids and chironomids in Lake Dom Helvecio (Parque Florestal do Rio Doce – MG). The deep benthic fauna of this lake specifically include chaoborids and chironomids. *Chaoborus* occurs especially in deep regions with low (even near-zero) levels of dissolved oxygen. Near the littoral zone of this lake and in another lake (Lake Jacare), Planorbidae, Tubificidae, Trichoptera and Hirudinea are common.

Table 8.2 Density of *Chaoborus* and *Chironomus* larvae in several lakes in the tropical region.

Tropical lakes	*Chaoborids (ind · m²)*	*Chironomids (ind · m²)*	*Notes*
L. D. Helvécio	27–996	36–249	Jun, 1.3–33.0 m, Fukuhara *et al.*, 1997
L. Jacaré	9–320	36–720	Jun, 1.5–8.5 m, Fukuhara *et al.*, 1997
L. D. Helvécio	178–1,288	44–733	Aug, 10–23 m, Fukuhara *et al.*, unpublished
L. Carioca	155–400	22–89	Aug, 3.5–8.0 m, Fukuhara *et al.*, unpublished
L. Tupé (Rio Negro)	0–400	0	Aug–Apr, deep waters, Reiss, 1977b
L. Tupé (Rio Negro)	−2,180	15–570	Dec–Mar, littoral, Reiss, 1911b
Magalhas Lagoon	0–45	178–2,581	Dec, 0.2–3.5 m, Reiss, 1973
Ubaraha Lagoon	0	179–223	Dec, 0.2–1.5 m, Reiss, 1973
Cueiras River	0–44	0–2,729	Oct, 1.5–4.5 m, Reiss, 1977b
UHE Carlos Botelho (Lobo/Broa) Reservoir	1,909, 1,747	1,215, 1,014	1971 and 1979, Strixino and Strixino, 1980
UHE Carlos Botelho (Lobo/Broa) Reservoir	1,742	1,253	Jun, 10.4 m, Fukuhara *et al.*, unpublished
L. Victoria (Ekumu Bay)	2,000–2,500	1,000	MacDonald, 1956

Table 8.2 shows the density of *Chaoborus* and *Chironomus* larvae in some tropical lakes. Fukuhara *et al.* (1997) showed the emergence *en masse* of *Chaoborus* (*Edwardsops*) *magnificus* in Lake Dom Helvécio, influenced by the lunar cycle. Hare and Carter (1986) also showed the lunar effects on the emerging adults of tropical insect species.

The physical, chemical and biological factors that control and regulate benthic macroinvertebrates and their physiology and distribution, in addition to those already mentioned (substratum type, current speed and predation), include water temperature and dissolved oxygen levels. These two key factors help determine the survival rate and optimum reproductive conditions of benthic species.

The respiration rates of these organisms depend on water temperature and availability of dissolved oxygen. The number of species that tolerate varying ranges of water temperature is a key feature of the aquatic environment.

Because of these characteristics – response to environmental factors and location on or in a substratum – benthic macroinvertebrates are excellent indicators of environmental conditions and contamination or pollution in rivers, streams, lakes and reservoirs.

Roldán (2006) described the processes of determining the 'ecological status' implemented by the European Union's Com-97 directive, which proposes that the water basin be the unit of study and that the ecological status of each water basin be determined and compared with reference data (Pratt and Rume, 1999).

The European standard cites the **communities of organisms** as indicators of the ecological status in different aquatic ecosystems. According to Roldán (2006), an organism is a good indicator of water quality when it is found in an ecosystem with defined characteristics and the population of the species is greater than or similar to the populations of other species that share this ecosystem or habitat. For example, in mountain rivers with clear oligotrophic water with an average temperature <15°C and 90–100% saturation of dissolved oxygen, the most common benthic invertebrates are likely to be Ephemeroptera, Trichoptera, and Plecoptera, with considerable

Chart 8.1 Indices of species diversity.

Shannon-Weaver (1949):

$$H' = -\sum_{i=1}^{S} (n_i / n) \ln (n_i / n)$$

H' – diversity index
n_i – number of individuals per species
n – total number of individuals
ln – natural logarithm

Simpson (1949):

$$I = -\sum \frac{n_i(n_i - 1)}{N(N - 1)}$$

where:
n_i – number of individuals per species
N – number of individuals

Margalef (1951):

$$I = (S - 1) / \log_n N$$

S – number of species
N – number of individuals
log n – natural logarithm

Source: Roldan (2006).

numbers of crustaceans, Hemiptera, Diptera and Hymenoptera. In highly turbid eutrophic rivers with high levels of organic material and low levels of dissolved oxygen, dominant populations of oligochaetes, chironomids and certain species of molluscs occur, which are found in smaller proportions in uncontaminated water.

The type of benthic macroinvertebrates present can therefore be a measure of pollution levels, and Gletti and Bonazzi (1981) consider them to be the best indicators of water quality. A community's response to pollution or optimal water quality can be determined by the index of diversity, as seen in indices by Shannon-Weaver (1949), Simpson (1949) and Margalef (1951) (see Chart 8.1). Roldán (2006) applied the Biological Monitoring Working Party (BMWP, established in England in 1970) to rivers in Colombia to utilize benthic macro-invertebrates and other **aquatic invertebrates** to determine water quality. Table 8.3 shows the orders, families, genera and species used as indicators of water quality.

In one study, Marchese M. and Ezcurra de Drago (2006) used benthic macroinvertebrates as indicators of water quality, especially **macroinvertebrates** present in a eutrophication in the middle of the Paraná River. According to the study, the composition and structure of the macroinvertebrates indicate changes in water quality and the introduction of energy in the aquatic systems. The authors applied the Shannon-Weaver index to each aquatic ecosystem, comparing total and relative density of benthic organisms in each aquatic environment, as well as the degree of eutrophication and contamination. For example, the oligochaete *Tubiflex tubiflex* (*blanchardi* variety) is

Table 8.3 Classes of water quality, BMWP/Col values, meaning and colours for cartographic representations.

Class	*Quality*	*Bmwp/Col*	*Meaning*	*Color*
I	Good	>150 101–120	Very clean to clean water	Blue
II	Acceptable	61–100	Slightly polluted water	Green
III	Uncertain	36–21	Moderately polluted water	Yellow
IV	Critical	16–35	Very polluted water	Orange
V	Very critical	<15	Highly polluted water	Red

BMWP/Col – Biological Monitoring Working Party/Colombia index.
Source: Roldan (2006).

associated with highly conductive waters (Marchese, 1988). Chart 8.2, from Marchese and Ezcurra de Drago (2006), presents the gradient of indicator species typical in a specific trophic environment, from oligotrophic environments to eutrophic environments in aquatic ecosystems in the middle of the Paraná River.

8.3 COMPOSITION AND RICHNESS OF PLANKTON SPECIES AND ABUNDANCE OF ORGANISMS IN PELAGIC AND LITTORAL REGIONS OF LAKES AND RESERVOIRS

As already discussed, the origin of a lake, its trophic state, colonization process and the presence or absence of toxic substances and pollutants are all interdependent factors that control and limit planktonic composition and the abundance and diversity of species. Lakes and reservoirs can have fundamental differences, for example, from retention time, vertical circulation periods and contributions from tributaries. Patalas (1975) noted significant differences between the abundance of plankton species in small ($<24\,km^2$) and big ($>50\,km^2$) lakes. Plankton in the limnetic or pelagic region differs significantly from plankton in the coastal region. To a certain extent, the diversity of plankton species may also be the result of only collecting samples in certain regions. In reservoirs with marked spatial heterogeneities (Straškrába *et al.*, 1993; Armengol *et al.*, 1999), large sampling errors can occur because of the differences and the accumulation of plankton in the areas of tributary estuaries, for example.

A comparison between the Barra Bonita reservoir (SP.) and Lake Dom Helvécio (Parque Florestal do Rio Doce – MG) (Tundisi and Matsumura Tundisi, 1994) showed 37 species of zooplankton in the limnetic regions of the reservoir (20 rotifers, 8 cladocerans and 9 copepods), and only 16 species in the lake (6 rotifers, 5 cladocerans and 5 copepods). This difference is probably the result of the reservoir's large spatial heterogeneity, the multiple mixing with many annual circulations and the effect of 114 tributaries, each discharging from 2 to $15\,m^3 \cdot s^{-1}$, thus contributing to increased diversity. Temporal changes (due to eutrophication) are also observed in zooplankton succession in Barra Bonita reservoir (Matsumura Tundisi and Tundisi, 2003).

The **pelagic environment**, according to Margalef (1962) and Reynolds (1997), is made up of a mosaic of microhabitats with overlapping and constantly changing components, responding to forcing functions such as wind and retention time (in the case of reservoirs) (Matsumura Tundisi and Tundisi, 2003).

Chart 8.2 List of association of indicator species of a trophic gradient of environments of the middle Paraná River.

Oligotrophic Environments
↓

- Oligochaetes
  - *Narapa bonettoi*
  - *Haplolaxis aedeochaeta*
- Turbellarians
  - *Myoratronectes paranaensis*
- Nematodes
  - *Tobrilus* sp.
- Diptera chironomids
  - *Tanytarsus sp.*
  - *Parachironomus* sp.
  - *Glyptotendipes* sp.
- Ephemeroptera
  - *Campsurus* cf. *notatus*
- Oligochaetes
  - *Paranadriluys descolei*
  - *Bothrioneurum americanun*
  - *Aulodrilus pigueti*
  - *Pristina americana*
  - *Paranais frici*
- Diptera chironomids
  - *Polypedilum* spp.
  - *Cryptochironomus* sp.
  - *Coelotanypus* sp.
  - *Ablabesmyia* sp.
- Lamellibranch molluscs
  - *Pisidium* sp.
  - *Corbicula fluminea*
- Oligochaetes
  - *Branchiura sowerbyi*
  - *Limnodrilus udekermianus*
  - *Nais variabilis*
  - *Nais communis*
  - *Dero multibranchiata*
  - *Dero sawayai*
- Diptera chironomids
  - *Axarus* sp.
  - *Goeldochironomus* sp.
- Gastropod molluscs
  - *Heleobia parchappei*
- Diptera chironomids
  - *Chironomus xanthus*
  - *Chironomus gr. decorus*
  - *Chironomus gr. riparius*
- Oligochaetes
  - *Tubifex tubifex* (blanchardi form)
  - *Limnodrilus hoffmeisteri*

↓
Eutrophic environments

Source: Marchese and Ezcurra de Drago (2006).

Tundisi, Jose Galizia, and Takako Matsumura Tundisi. Limnology, Taylor & Francis Group, 2011. ProQuest Ebook Central, http://ebookcentral.proquest.com/lib/hec-ebooks/detail.action?docID=870725.

According to Margalef (1991), the permanent re-organization of a system, as the result of **external energy**, interrupts the irregularities in the system and breaks down the horizontal axis in heterogeneous units in the space where phytoplankton and zooplankton communities gather. Horizontal mixture and vertical instability are factors that can contribute to increased planktonic diversity. In systems with continual instability, the **intermediate disturbance** hypothesis (IDH) (Padisák *et al.,* 1999) can be applied. The function of tributaries and their discharging waters is to add horizontal discontinuities in the aquatic system and thus lead to new groupings of communities along the horizontal axis, in short periods of time and in **mesoscale** structures (1 to 20 km).

In the case of zooplankton, the presence of **resistant eggs** of many species can affect species diversity in a certain time frame. Resistant eggs develop during favourable periods when water quality is good. They can influence succession and the abundance of zooplankton species. Likewise, resistant forms of phytoplankton (such as colonies or quiescent cells of *Aulacoseira* spp. in the sediment) can lead to a rapid increase of species in the water column, promoted by the action of forcing functions such as the wind. The interrelationships between phytoplankton and zooplankton are equally important in determining changes in the succession process of pelagic communities. Food availability, size, shape and nutritional status alter the succession of zooplankton species, in cases where predation (grazing) can significantly modify the composition of species and phytoplankton succession (Raymont, 1963; Reynolds, 1984, 1997).

In the shallowest littoral regions, the seasonal cycle and succession of phytoplankton and zooplankton are altered by the presence of species that periodically resuspend from the sediment, such as several *Aulacoseira* spp. – or the emergence of resistant copepod eggs, as demonstrated by Rietzler *et al.* (2004) and Matsumura Tundisi and Tundisi (2003).

The planktonic species inhabiting the pelagic and littoral regions in lakes and reservoirs have different physiological features, different morphological adaptations and different reproductive and growth requirements. An assemblage of species thus responds in different ways to environmental variability and the frequency of disturbances. Each planktonic community is the result of a combination of biological, chemical, and physical factors producing different associations that change through time and space.

Research studies are needed to identify the frequency, magnitude and direction of those changes. Knowledge of the biology and its responses with the limitations of different species is therefore essential for predicting the response.

8.4 FISH

Chapter 6 presented data on the composition of fish communities in inland waters. Fish play a significant role in the functioning of the ecological dynamics of aquatic communities, since their function is important, both quantitatively and qualitatively, in the food web and in planktonic, benthic and nectonic communities. Spatial movements of fish and migration complicate the quantitative calculation of their impact on food networks and structures of aquatic communities. Fish excrete detritus and ammonia and remove sediments, and therefore play an important role in the biogeochemical cycles of lakes, reservoirs, rivers and associated areas. Migratory fish such as salmon (**anadromous fish**), which live in oceans and reproduce in rivers, or

catadromous fish, which live in inland waters and migrate to the ocean to reproduce, play an extremely important role in many aquatic ecosystems. For example, large balizador catfish (Barthem and Goulding, 1997) in Amazonian rivers (as described in the previous chapter), play an important role in the food chain and the structure of aquatic communities there.

Fish comprise nearly 40% of the vertebrate species on the planet. Communities of tropical and subtropical fish in the South American region have been studied extensively, especially in the Amazonian region (Goulding, 1979, 1981; Goulding *et al.*, 1988) and the São Francisco River (Sato and Godinho, 1999; Godinho and Godinho, 2003). Similarly, a series of extensive scientific works were conducted on water basins in the upper Paraná (Augustine and Ferreira, 1999, Agostinho *et al.*, 1987, 1991, 1993, 1994, 1999; Bonetto, 1986a; Menezes and Gery, 1983; Vazzoler and Menezes, 1992). Chart 8.3 outlines the main ecological features of tropical fish communities.

The seasonality of habitats, according to Lowe-McConnell (1999), affects fish behaviour and physiology in tropical aquatic systems, ranging from specific spatial dynamics (for example, flooding and drought) that create different habitats each year to the more stable conditions of some natural lakes and equatorial reefs. Seasonality and environmental variations affect fish and their feeding habits, life cycles, reproduction, and migrations. Migrations result from seasonal hydrological cycles and are used for reproduction, feeding and escape from predators.

Chart 8.3 Ecological attributes of communities of tropical fish.

Seasonality of the environment	*Very seasonal* ⟶	*Not seasonal*
Examples:	Floodplain Pelagic zone	Lacustrine littoral Coral reefs
Response of fish population:	Fluctuates greatly due to: (1) migration (high mobility), (2) rapid multiplication	Remains constant through the year and year to year
Life cycle:	Short, precocious maturation, low longevity	Long: Retarded maturation (frequent change of sex); high longevity
Growth rates:	Rapid	Generally slower?
Egg laying:	Seasonal, rapid response to supply of nutrient	Multiple through the year
Feeding:	Facultative, or specialized, adapted to low trophic levels	
Production/biomass ratio:	High	Very high
Behaviour:	Simple; uniform; formation of shoals	Complex, with learning, territoriality; symbiosis
Predominant selection:	Type-*r*, biotic and abiotic agents	Type-*K*; mainly biotic agents
Diversity:	Not very diverse, dominant species	Highly diverse, lacking dominants
Community:	Rejuvenated	Very mature
Implications:	Resilient?	Fragile?

Source: Lowe-McConnell (1999).

The migration and population dynamics of some fish species (including reproduction, mortality, and fluctuations in population levels) are related to the patterns of hydrological fluctuation in rivers, lakes and natural flood channels; productivity; and biogeochemical cycles in the flooded areas. Longer or shorter life cycles, more efficient use of **food resources**, early maturation and high fecundity are features of those species living in areas with widely oscillating hydrological variations on the **flood plains** (Agostinho *et al.*, 1999). Modes of reproduction in tropical freshwater fish vary from a single "big bang" spawn (as in the case of *Anguilla* species) to total and partial spawns (Chart 8.4).

The numbers of mature oocytes in ovaries of tropical freshwater fish are presented in Table 8.4.

Certain features of tropical fish, such as growth and maturation, depend directly on temperature: tropical species have faster growth rates, earlier maturation, and shorter lifespans than temperate-region fish. Some cichlid species in Lake Tanganyika, for example, have a life cycle of 1.5 to 2 years. Many species of small characins in Lake Chad in Africa do not live more than two years. Growth rates obviously vary according to feeding habits, environmental conditions, food availability, water temperature and population density (Lowe-McConnell, 1999). Growth rates of tilapia have been studied extensively because of the species' commercial importance (Pullin and Lowe-McConnell, 1982). The growth and maturation rates of these species (*Oreochromis niloticus* and *O. mossambicus*) vary widely in response to environmental conditions.

In addition to the studies by Barthes and Goulding (1997) on fish in the Amazon region, further studies were done on the tambaqui (Araujo-Lima and Goulding, 1997). Two volumes (published by Val, Almeida Val and Randall, 1996; and Val and Almeida Val, 1999) presented an overview of the physiology and biochemistry of tropical fish, particularly Amazonian species. The authors described the complex interactions and physiological role of **Amazon fish** species in widely varying environmental conditions, including **hydrological fluctuations**, food availability, and different bio-geochemical cycles and oscillating patterns in two physiologically important factors: dissolved oxygen and water temperature.

Amazonian fish fauna (in which there are nearly 2,000 species), according to Val *et al.* (1999), evolved in a highly varying ecosystem and, therefore, populations may periodically adjust their biochemical and physiological patterns to the widely varying conditions. These physiological adjustments make it possible for Amazonian fish to survive conditions of anoxia, high sulphurous gas levels and low ionic levels. According to Walker and Henderson (1999), the physiology of Amazonian fish can be viewed as an intermediary process between fish ecology and evolution, including reproductive rate, life cycle, general metabolism and behaviour.

The ability to survive at low levels of dissolved oxygen is an extremely important physiological feature of Amazonian fishes: respiration of air, metabolic depression, morphological specializations, and adjustments in oxygen transportation are some of the most common physiological adaptive features of Amazonian fish species (Val, 1999). Variations in dissolved oxygen levels depend on processes such as photosynthesis by aquatic plants; the morphometry of canals, rivers and lakes; decomposition of organic material; respiration by organisms; and hydraulic and hydrodynamic movements and shifts. During periods of flooding, anoxia or hypoxia can occur in

Chart 8.4 Types of reproduction in representation of fresh water tropical fish.

Type of fecundity	*Seasonality in reproduction*	*Examples*	*Movements and parental care*
"Big bang" ++++	Once in a life-time	*Anguilla*	Very long migrations, catadromes without parental care
Total egg-layers +++	Very seasonal with floods; annual or biannual	Many charcoides Prochilodus Salminus Hydrocynus Many cyprinids Some siluroids *Lates* (Lake Chad)	Fish 'spawning', very long migrations No parental care Local movements: pelagic eggs
Partial egg-laying ++	Prolonged season During high-water season(s)	Some cyprinids Some caracoids: *Serrasalmus* *Hoplias* Some siluroids: *Mystus*	Principal local movement Put eggs in plants (m, m + f) Puts eggs on the bottom (m) Guard eggs and young (m)
Classified as: egg-layers, small clutches +	High-water season, may begin at the end of the dry season or be non-seasonal	*Arapaima*	Guard eggs and young; nests on bottom (m + f)
		Some anabantoids	Guarding eggs, bubble nest superficial (m)
	End of rains	*Hoplosternum*	Guard eggs in nests surface (m)
		Hypostolllus	Guard eggs; marginal burrows (gender?)
		Loricaria parva	Guards eggs under rocks (m)
		[a]*Loricaria* spp.	Carries eggs on the lower lip (m)
		Aspredo sp.	Carries eggs in the womb (f)
		Osteoglossum Cichlids:	Offspring to Mouth (m)
		[a] Most South American species	Guarding eggs and young (m + f)
		[ab] Most African species	Brood eggs and young in the mouth (f)
		[b]*Sarotherodon galilaeus*	Brood eggs and young in the mouth (m + f)
		S. melanotheron	Brood eggs and young in the mouth (m + f)
		sting rays	Viviparous
		[b] Pecilids	Viviparous
		Anableps	Viviparous
		Annual cyprinodont species	Leave eggs in the mud during the dry season

m – male; f – female; [a] – end of the dry season; [b] – not seasonal

Source: Lowe-McConnell (1999).

some lakes, subjecting fish to increased stress. Chart 8.5 describes Amazonian fish species that electively or mandatorily breathe air.

Understanding these Amazonian fishes' tolerance to hypoxia is one of the great challenges in tropical fish physiology, and studies continue to show there are big opportunities for greater understanding of the physiological and adaptive processes involved in these conditions (Almeida Val, Val and Hochahka, 1993).

Table 8.4 Number of mature oocytes in the ovaries (fecundity) from representative examples of tropical freshwater fish.

Protopterus aethiopicus	1,700–2,300
Arapaima gigas	47,000
Osteoglossum bicirrhosum	180
Mormyrus kannume	1,393–17,369
Marcusenius victoriae	846–16,748
Gnathonemus longibarbis	502–14,642
Hippopotamyrus grahami	248–5,229
Pollimyrus nigricans	206–739
Petrocephalus catostoma	116–1,015
Alestes leuciscus	1,000–4,000
Alestes nurse	17,000
Alestes dentex	24,800–27,800
Alestes macrophthalmus	10,000
Hoplias malabaricus	2,500–3,000
Salminus maxillosus	1,152,900–2,619,000
Prochilodus scrofa	1,300,000
Prochilodus argenteus	657,385
Labeo victorianus	40,133
Catla catla	230,830–4,202,250
Lates niloticus	1,140,700–11,790,000
[a]*Mystus aor*	45,410–122,477
Hypostomus plecostomus	115–118
Arius sp.	118
Loricaria sp.	c.100
Oreochromis leucostictus	56–498
Oreochromis esculentus	324–1,672
Pseudotropheus zebra	17–<30
Cichla ocellaris	10,203–12,559
Astronotus ocellatus	961–3,452
Anableps anableps	6–13 embryos

[a] Can spawn 5 times in a season, the majority of species above this in the table (except *Arapaima* and *Osteoglossum*) are total number of eggs; those below are in multiple spawnings.
Source: Lowe-McConnell (1975).

8.4.1 Fish production and limnology

Potential fish production is dependent on the trophic state of the waters supporting the fish community. Other factors such as growth and reproductive rates and environmental features also will affect the yield. Use of indices such as the MEI (Morphoedaphic Index) can help assess the potential biomass of fish in lakes and reservoirs (MEI = STS/z, with STS = suspended total solids and z = average depth of lake or reservoir) (Oglesby, 1982). Such a measure is useful for predicting the total production of fish in an aquatic ecosystem.

In inland ecosystems, the fish production depends to a certain extent on the **ecological functioning** and primary productivity of each ecosystem. In some tropical regions, including large inland deltas and flood valleys of the Amazon and Parana rivers, fish production plays a significant role in the regional economy (Petrere, 1992; Goulding, 1999; Roosevelt, 1999; and Barthem, 1999).

Chart 8.5 Amazonian fish that are facultatively or obligatorily air-breathing. The structures associated with oxygen uptake are indicated. Families are arranged according to trend from generalized structures to specialized structures.

			Structures			
Families and species	*Optional*	*Obligatory*	*BL*	*SK*	*SI*	*FBB*
Lepidosirenidae						
Lepidosiren paradoxa		X	X			
Arapaimidae						
Arapaima gigas		X	X			
Erythrinidae						
Erythrinus erythrinus	X		X			
Hoplerythrinus unitaeniatus	X		X	X	X	
Doradidae						
Doras	X				X	
Callichthyidae						
Callichthys	X				X	
Hoplosternum	X				X	
Loricariidae						
Plecostomus	X				X	
Ancistrus	X				X	
Rhamphichthyidae						
Hypopopus	X					X
Electrophoridae						
Electrophorus		X				X
Synbranchidae						
Synbranchus marmoratus	X					X

BL – Swimming bladder and lung; SK – skin; SI – Stomach and intestine;
FBB – Pharyngeal and branchial diverticula, and in the mouth.
Source: Val *et al.* (1999).

The **construction of reservoirs** affects fishing and fish production in inland waters (Agostinho *et al.*, 1994, 1999; Tundisi *et al.*, 2006). Reservoirs can also provide interesting possibilities for raising species under controlled conditions. The introduction of exotic species into reservoirs to increase fish production can be an interesting solution, but also risks potential problems, especially in the case of pelagic predators (Leal de Castro, 1994).

Raising some fish species in aquaculture (ponds or networks of ponds) can be an appropriate solution to increase fish stocks and fishery production, but of course this technology can affect the ecosystem's water (reservoir or lake) due to rapid eutrophication.

The factors affecting fishery production or characteristics of inland ecosystems are related to those that impact the environment or the biology of the commercial fish species or their physiology, reproduction and survival. These factors include:

- introduction of exotic species, which alter food web (Figure 8.12);
- eutrophication;

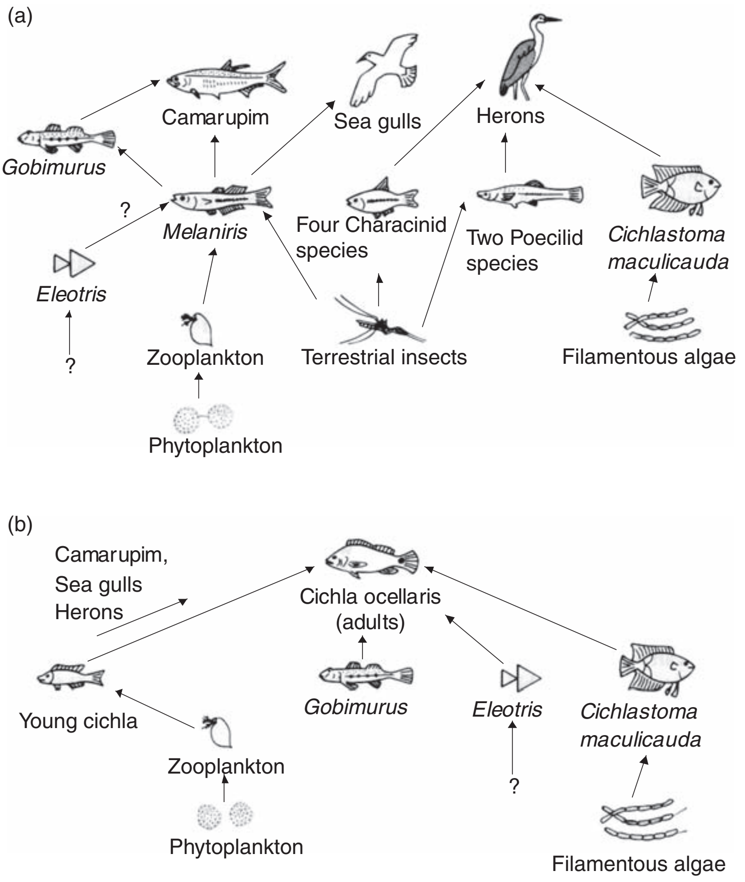


Figure 8.12 Impact of the introduction of exotic species in Lake Gatun and their effects of the food web.
Source: Horne and Goldman (1994).

- acute chronic water toxicity;
- effects of morphological changes on aquatic ecosystems (rivers, canals, reservoirs);
- heat pollution;
- invasive and haphazard use of water basins, affecting habitats and **riparian vegetation**.
- reforestation of riparian forests;
- changes in the fish species' reproductive areas.

8.5 FOOD CHAINS AND FOOD WEBS

In aquatic ecosystems, energy flows through a series of trophic levels. Primary photosynthetic production provides the quantity and quality of food available for herbivores and carnivores. Many aquatic organisms are omnivorous and vary their diet according to the time of year and availability of food. According to Horne and Goldman (1994), the concept of trophic levels is idealized and schematic. In greater complexity beyond the so-called **trophic chain** (food chain) is the **trophic food web**, which is **dynamic**. The most accurate terminology is **dynamic trophic food web** because it changes through time and space.

Food chain dynamics are complex, and determining structure and efficiency calls for special techniques and methods. The contents of zooplankton and fish digestive systems must be determined, as well as energy efficiency levels at each stage in the trophic food web.

Different aquatic organisms ingest different types of food, and their alimentary organ structures are morphologically varied, presenting different efficiencies. The different types of feeding groups of aquatic organisms include:

- **Herbivores**: feed on aquatic plants, phytoplankton, periphyton or macrophytes.
- **Carnivores:** feed on herbivorous aquatic organisms or other aquatic animals.
- **Detritivores:** feed on vegetal remains, sediment or animal remains.
- **Omnivores**: varied feeding habits, including eating plants, animals or detritus suspended in water or in sediment.

Aquatic organisms can capture or filter foods and be classified by feeding-system type:

- **Filter feeders** (or **suspension feeders**)**:** the classic case of straining suspended particles (phytoplankton, bacteria or organic material) is planktonic copepods, especially calanoids (see Figure 8.13).

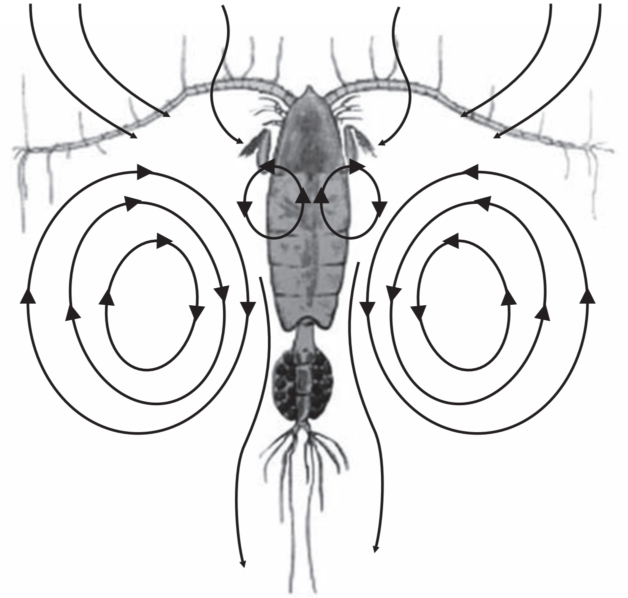


Figure 8.13 Filtering mechanisms of herbivorous copepods, represented by an original scheme for *Calanus finmarchicus* (Marshall, 1972) but valid for herbivorous copepods of inland waters in general (see also color plate section, plate 16).
Source: Modified from Marshall and Orr (1972).

- **Collectors:** organisms that **collect** different-sized suspended particles in water or on river and lake bottoms.
- **Scrapers**: organisms that **scrape** the surface and feed on microphytobenthos, bacteria, or aggregated organic matter or particles.
- **Sediment collectors:** organisms that collect, aggregate and consolidate sediment particles rich in organic material.

The feeding rates of these organisms and the energy content of each component are measured with a **calorimeter** pump. It is also important to identify the composition of each component of the trophic web: organisms are generally categorized by functional groups (such as herbivores, omnivores or carnivores).

Biological pyramids with the nutritional value of each trophic level can be identified, from phytoplankton and periphyton (at the base of the food network) to carnivorous predators (large fish or other vertebrates) at the top. Figure 8.14 illustrates a classic food network in a lake with a multiple-component trophic network.

The importance of vertebrate predators in the trophic network dynamics and the theory of trophic cascade (Carpenter *et al.*, 1985) have been described by many authors (including Kerfoot and Sih, 1987). The theory emphasizes the role of predatory fishes in trophic network structures, particularly in the composition and dynamics of the zooplankton community, whose primary prey is the photosynthetic phytoplankton.

Further evidence (presented by Dumont, Tundisi and Roche, 1990) shows that predation on zooplankton plays a significant role in the structure and dynamics of zooplanktonic communities. According to Lair (1990), predation by other invertebrates on zooplankters effectively controls micro-planktonic rotifers and small crustaceans in particular. According to Lair, in lakes where intra-zooplanktonic predation is intense, it can directly affect phytoplanktonic productivity and succession.

Blaustein and Dumont (1990) in Dumont *et al.* (1990) described predation by *Mesostoma* spp. (Platyhelminthes) on *Chydorus sphaericus* and *Moina micrura* (see Figure 8.15).

Planktonic *Mesostoma* spp. occur in many tropical lakes, including African lakes (Dumont *et al.,* 1973) and several lakes in Parque Florestal do Rio Doce – MG (Rocha *et al.,* 1990). These organisms establish themselves at various different depths in the water column and prey on zooplankton and mosquito larvae (*Aedes* spp.) (McDaniel, 1977).

In **rice cultivation fields** in California, the presence of *Mesostoma lingra* controlled mosquito larvae (*Culex tarsalis*) (Case and Washimo, 1979).

Dumont and Schoreels (1990) described the predation of *Mesostoma lingra* on *Daphnia magna*. Rocha *et al.* (1990) showed the impact of *Mesostoma* preying on zooplankton in lakes in Parque Florestal do Rio Doce, and in particular, the species' vertical migration in Lake Dom Helvécio in a 24-hour period. The nightly migration to the surface probably coincides with predation on zooplankton. In turn, *Mesostoma* is preyed on by *Chaoborus* and *Mesocyclops* spp.

Mesostoma spp. inject their prey with a paralyzing neotoxin and apprehend the prey with mucous. Predation on ostracods, according to Rocha *et al.* (1990), consists of introducing the pharynx between the two valves and a sucking motion of the entire contents of the organism. Matsumura Tundisi *et al.* (1990) compared the predation

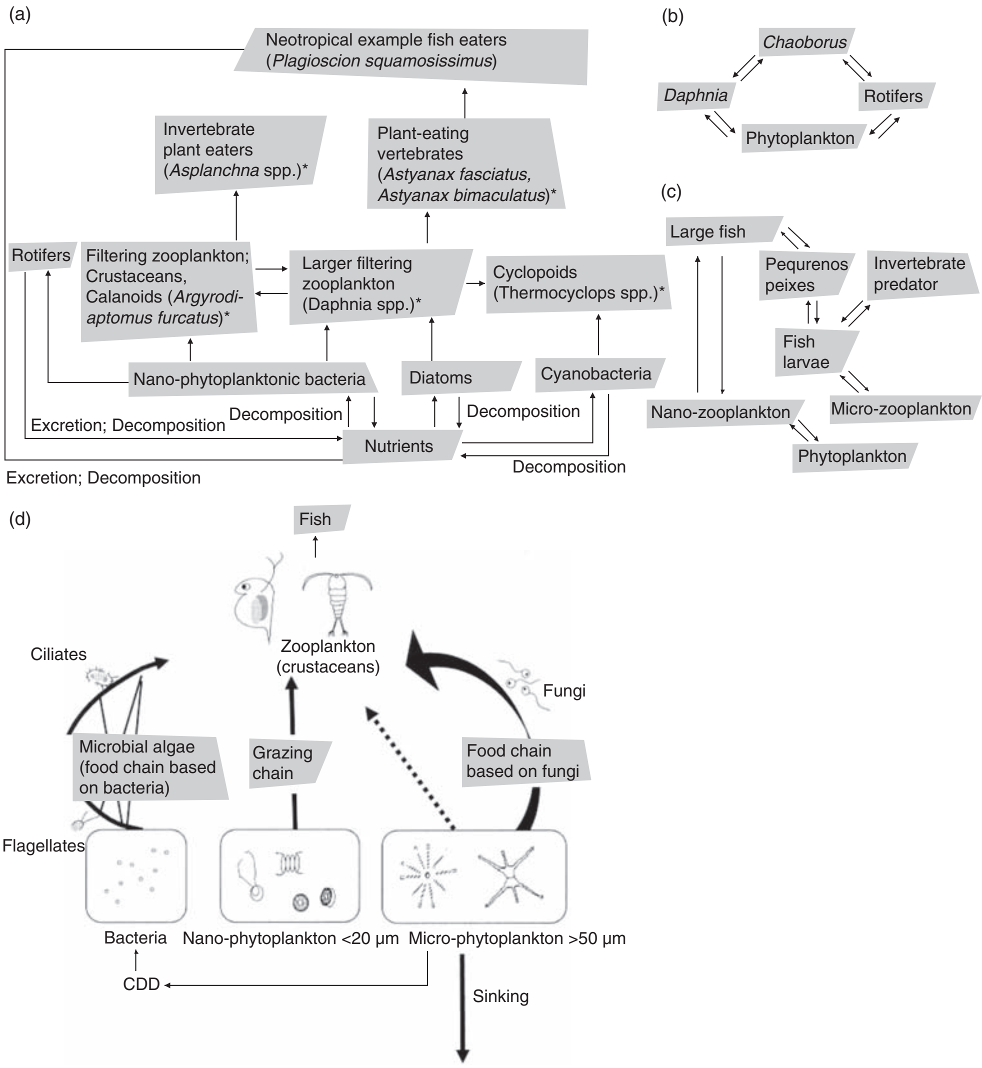
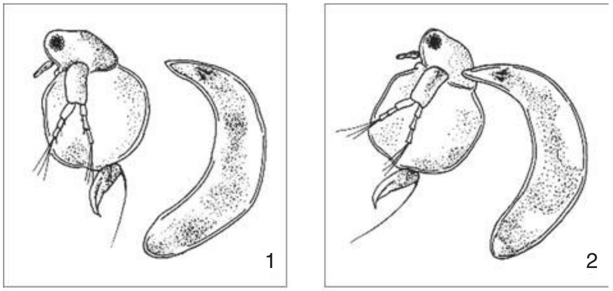


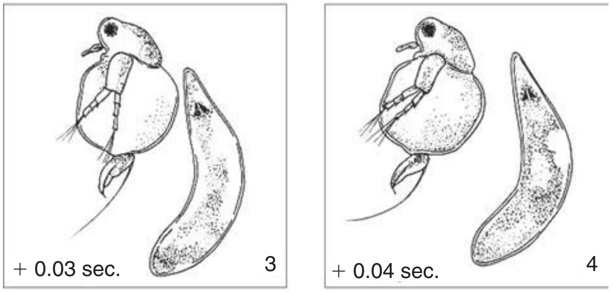
Figure 8.14 Classic food web in lentic aquatic ecosystems. (a) Interactions of components, with neo-tropical examples; (b) *Chaoborus* predating on *Daphnia*. The direction of the arrow indicates control of predators over prey; (c) Invertebrate predator and different stages of fish development; (d) Fungi-based food chain.

by *Mesocyclops* spp. on *Ceriodaphnia cornuta* and *Brachionus calyciflorus* in the Barra Bonita reservoir (see Figure 8.16).

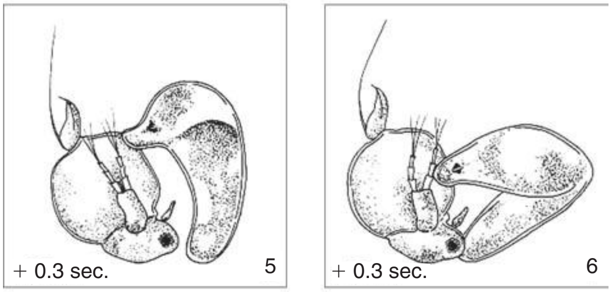
The results clearly indicate intra-zooplankton predation is a **regulating factor** in food chains and food webs in lakes and reservoirs. The argument by Fernando *et al.* (1990) that the diversity of invertebrate predators is reduced in tropical lakes is no longer well accepted because of the wealth of information that now exists on intra-zooplanktonic predation.



Attack Contact



Breaking contact Antenna of paralyzed prey



Second contact Prey covered by mucous layer

Total time from first contact ~0.4 sec. Total time from first contact ~0.7 sec.

Figure 8.15 *Mesostoma* spp. attacking *Moina micrura*.
Source: Modified from Dumont, Tundisi and Roche (1990).

In addition to intra-zooplanktonic predation, zooplanktonic predation by invertebrates is probably a significant factor regulating zooplanktonic biomass, as shown by Perticarrari *et al.* (2004) in Lake Monte Alegre in Ribeirao Preto.

Arcifa *et al.* (1998) described the composition, fluctuations and interactions of a planktonic community in a shallow tropical reservoir (Lake Monte Alegre) that has been extensively studied over time. Through multivariate analysis, four periods over the course of a year were identified. Phytoplanktonic biomass was greater in periods III and IV (September and March) and zooplanktonic biomass was more abundant

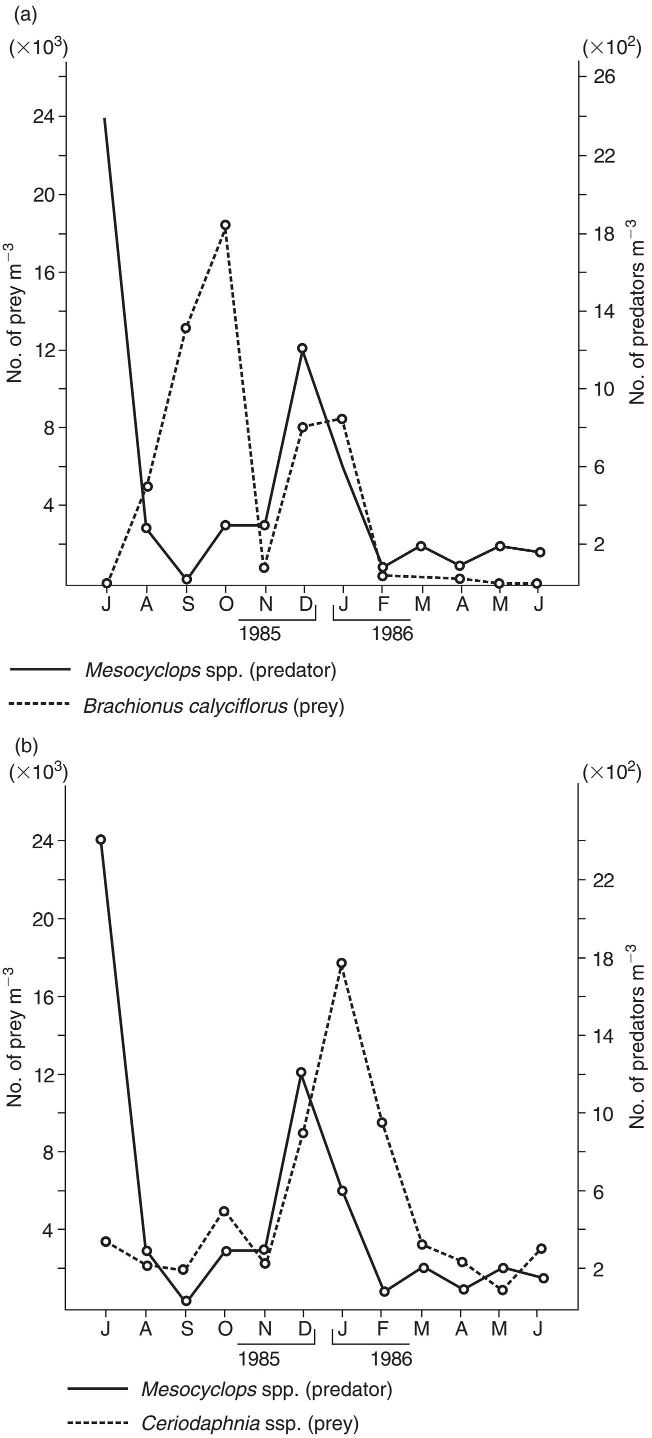


Figure 8.16 Seasonal fluctuation of predators *Mesocyclops longisetus* + *Mesocyclops kieferi* in the Barra Bonita reservoir (SP); (a) seasonal fluctuation of the prey *Brachionus calyciflorus*, and (b) of the prey *Ceridaphnia cornuta*.

in periods I, II and IV (April–August and January–March). In period III (September–December), zooplanktonic levels dropped as a result of factors such as predation by fish, excess suspended solids and predation by *Chaoborus*. Another possible cause for the drop was the abundance of *Aulacoseira granulata,* little used as food by zooplankton (see Figure 8.17). The authors also attributed the initial decline of zooplankton

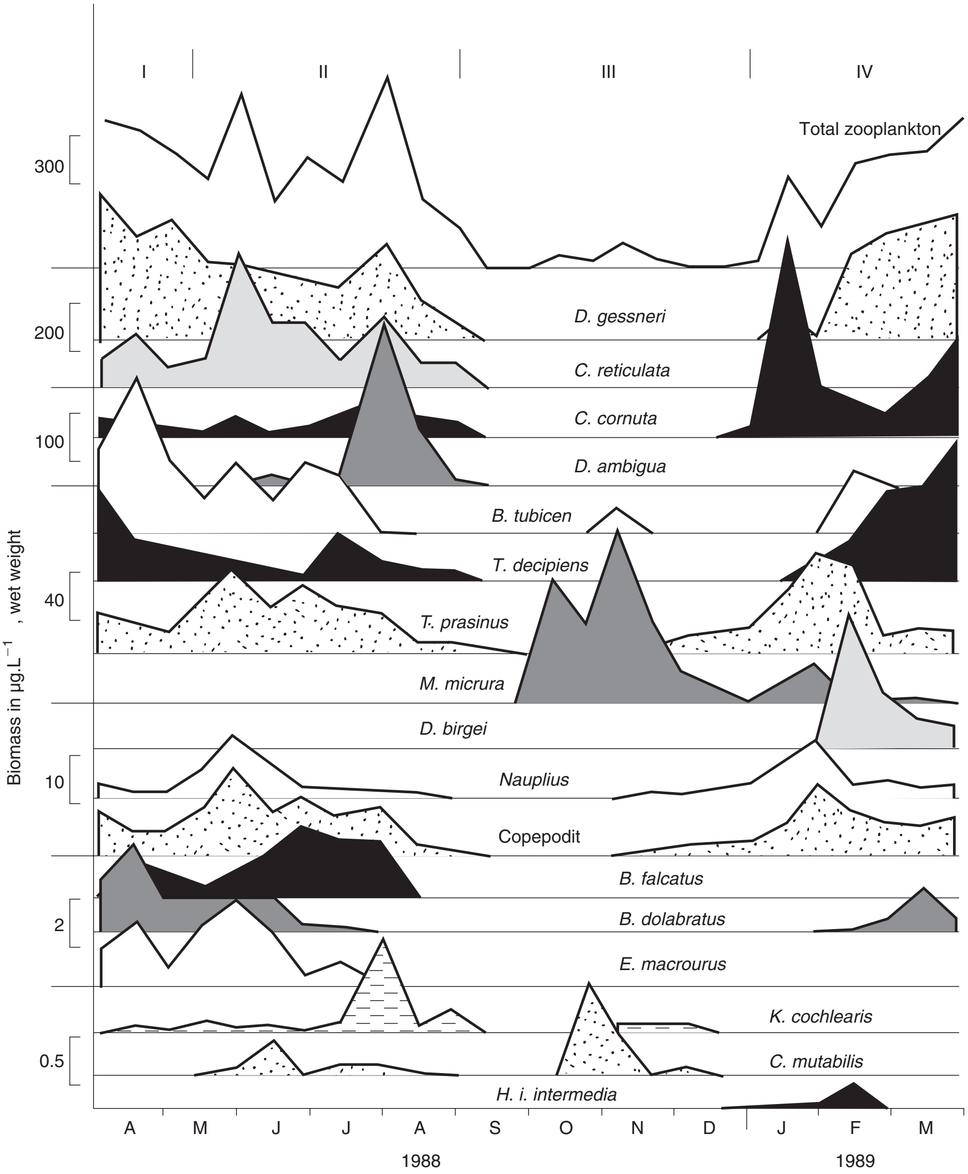


Figure 8.17 Fluctuations of biomass in $\mu g \cdot L^{-1}$ (wet weight) of species of zooplankton (total in periods from I to IV).
Source: Arcifa *et al*. (1998).

during the period of depression to the effect of cold fronts and the cooling of the water column.

According to Arcifa (2000), who studied the eating habits of *Chaoborus* spp. in Lake Monte Alegre, the principal components of their diet in periods I and II were *Aeridium* and zoo-flagellates, while microcrustaceans of the *Bosmina* genus were the principal components in periods III and IV. Predation by chaoborids, according to Arcifa, could be an important quantitative factor in the control of the *Bosmina tubicen* population in the lake (Arcifa *et al.*, 1992). On the other hand, the reverse migration of zooplankton could be a possible attempt to escape *Chaoborus* larvae.

The quantitative determination of intra-zooplanktonic pressure still presents a basic methodological challenge. Mesocosm experiments that allow the manipulation of environmental factors, as demonstrated by Lazzaro *et al.* (unpublished), can help resolve and quantify this problem.

Hrbáček *et al.* (1961), Hrbáček (1962), Brooks and Dodson (1965), and Straškrába (1965) studied the predation of planktivorous fish on zooplankton and the impact on food webs. These pioneer works showed that with planktivorous fish, zooplankton communities were composed of small organisms in comparison with those in lakes with no planktivorous fish.

Lazzaro (1987) studied plankton-eating fish and their features, evolution, and feeding and selection mechanisms. These fish can be optionally or exclusively planktivorous. Fish that feed on particulate matter can feed by random selection of prey or by filter feeding. Fish can also use vision to select prey, or chemical-reception. In experiments Werner (1977) showed feeding by selection. **Filter feeders** pump water and filter material during swimming motion. In conclusion, fish have a range of behavioural mechanisms for feeding and predation.

An important problem to consider in **feeding chains** and webs is the concept of control of the chain or the trophic cascade from the top of the food chain, as theorized by Carpenter *et al.* (1985). The concepts of control or flow of energy from the top of the food web and control of this flow from the base of the food web (*top-down and bottom-up*, respectively) have long been a topic of discussion. The traditional concept of control from the base of the food web, which holds that each prey "can feed several predators", relies on the view that all trophic levels are positively correlated and control is exercised by nutrients (limiting factor).

Higher levels of nutrients result in greater primary productivity and in effect, a chain: greater biomass of phytoplankton, greater biomass of zooplankton, greater biomass of planktivorous fish and greater biomass of piscivores. At the same time, the concept of control of the food web from the top holds that a greater number of piscivorous fish leads to less planktivorous fish and, as result of a chain reaction, greater biomass of zooplankton, reduced biomass of phytoplankton and higher levels of available nutrients. Mesocosm experiments sought to prove the two hypotheses. In one, planktivorous fish were added, which led to reduced zooplanktonic biomass and increased phytoplanktonic biomass. When mesocosms were fertilized (Tundisi and Saijo, 1997), higher levels of phytoplankton were obtained, producing a controlling effect from the base of the food chain (Lampert and Sommer, 1997). The population dynamics of phytoplankton, zooplankton and fish therefore influence these two types of food web organization (Vanni *et al.,* 1997). The structure of the ecosystem is organized based on nutrient levels (involving external or internal load), and the predators present at the top of the food web. This hypothesis of control of the food web structure based on predators at the top is used in **biomanipulation** of lakes and reservoirs to control eutrophication.

Biomanipulation in management of lakes and reservoirs has been the subject of many studies over the last 20 years (De Bernardi and Giussiani, 2001). In Brazil, an important study was conducted on Lake Paranoá in Brasilia (Starling and Lazzaro, 2007), where an **eco-technology** was developed based on biomanipulation and the introduction of sterile silver carp for the biological control of cyanobacteria, converting a significant portion of the primary productivity into commercially valuable fish biomass. The authors found it problematical that in this conversion, **cyanotoxins** were incorporated into commercial fish and that the process was unsustainable over long periods of time. Other effects of the fish-zooplankton interactions on water quality were shown by Arcifa *et al.* (1986) and Attayde (2000), who conducted studies to demonstrate the direct and indirect effects of fish predation and excretion on food webs.

The two controls are interdependent and not exclusive, and both hypotheses, as well as more recent findings, point to a preponderance of one or another control during certain periods (Horne and Goldman, 1994; Lampert and Sommer, 1997). Bechara *et al.* (1992) showed the important effects of control from the top of the food web in streams, but the mechanisms of control from the base of the food webs are equally efficient in these ecosystems (see Figure 8.18).

Fish play an important role in trophic webs, as has been shown. In lakes and rivers in the Amazon region, two basic types of trophic networks can be found. Walker (1995) showed that protozoa such as amoebas, ciliates and fungi play an important role in preserving streams that receive litter from the forest. Goulding (1980) and Araujo-Lima and Goulding (1997) showed the importance of herbivorous fish that feed on fruits and seeds in Amazonia. According to the authors, species of fish such as tambaqui (*Colossoma macroponum)* and other herbivores play a key role in dispersing fruit and seeds in the region.

An important role played by bacteria in food webs is the so-called **microbial loop** initially described by Azam for marine ecosystems, and which is also applied to lakes, reservoirs, rivers, streams and associated areas of temperate and tropical regions. According to this theory and as confirmed in application of **experimental methods**, bacteria play a fundamental role in processing dissolved organic matter (DOM), as well as detritus from excretion and decomposition of planktonic organisms, fishes and benthic macroinvertebrates and microinvertebrates. The processing of all this material, part of which is excreted by photosynthetic phytoplankton (Tundisi, 1965; Vieira *et al.,* 1998), occurs through the action of bacteria that quickly recycle dissolved organic and particulate matter. Figure 8.19 shows the food web with the microbial loop included. Figure 8.20 illustrates a food web based on the **micro-lithosphere** and the relevant role of photosynthetic pico-phytoplankton in the flow of energy.

Various authors describe the predation by carnivorous aquatic plants on protozoa, rotifers and culicine (mosquito) larvae (Brumpt, 1925; Hegener, 1926). Such predation may have a significant quantitative effect of predation on zooplankton as shown by Rocha and Matsumura Tundisi (unpublished) for masses of *Utricularia* sp. feeding on zooplankton in Lake Verde (Parque Florestal do Rio Doce). Somenson and Jackson (1968) demonstrated significant quantitative effects of predation by *Utricularia gibba* on *Parenecia multimicronucleatun.* Predation by aquatic plants on

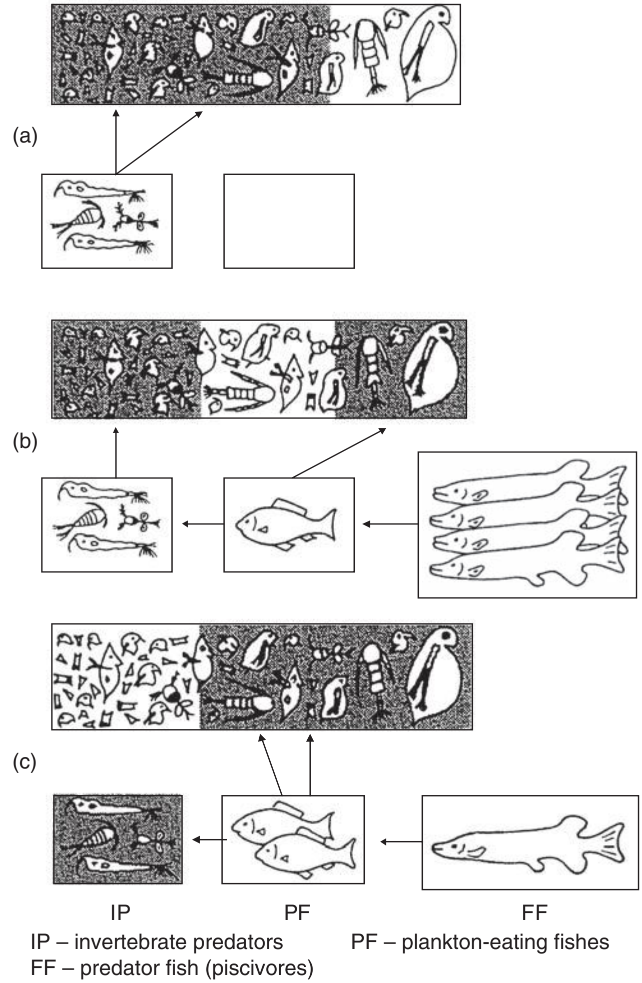


Figure 8.18 Effects of different vertebrate, invertebrate and zooplankton predators on the composition of zooplankton a) Without plankton-eating fish → larger zooplankton; b) Large populations of predatory fish, few planktophages → medium-sized zooplankton; c) Few predator fish, many planktophages → microzooplankton.
Source: Straškrába and Tundisi (2000).

zooplankton is considered a nutritional alternative for sources of nitrogen in environments with low inorganic nitrogen levels.

Detritivores play an important role in inland aquatic ecosystems. In small rivers in tropical forests, detritivores assume quantitatively important dimensions. Walker (1985), studying small streams in the Amazon, observed that the detritus includes remains of vegetation, organisms, fish and fruit. Such detritus is immediately attacked by decomposing fungi, which constitute the first food item. The detritus and litter along with the decomposers, bacteria and fungi, together with algae (desmids and

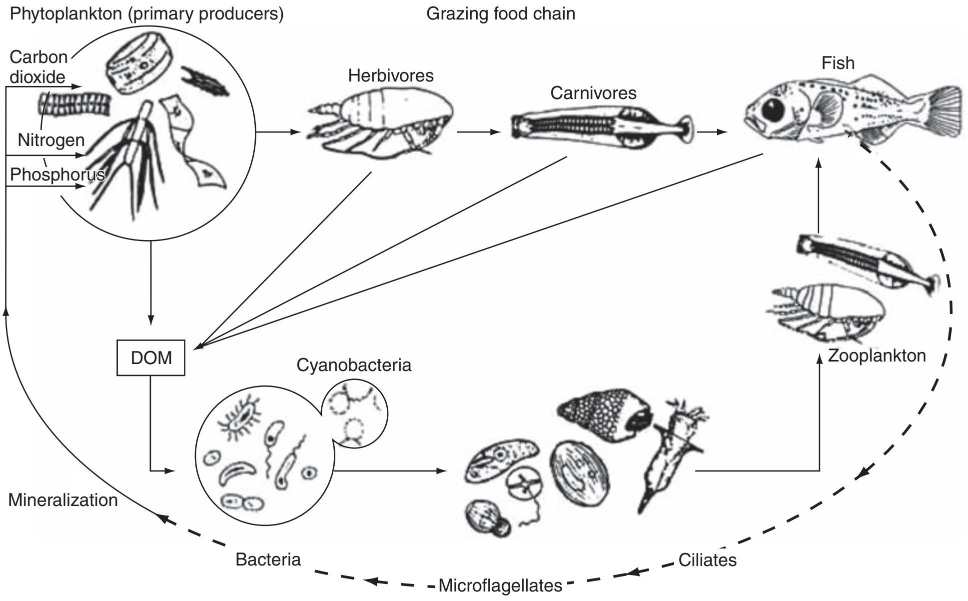


Figure 8.19 The "microbial loop". Classic figure produced initially to emphasize the role of bacteria in the mineralization of organic material. The reserve of dissolved organic material is used almost exclusively by heterotrophic bacteria and supports significant secondary production by bacteria. This figure shows see that the microbial loop is related to the grazing-feeding chain.
Source: Azam *et al.* (1983).

diatoms) are used as food by primary consumers such as flagellates, rotifers, cyclopoid copepods and ostracods.

The system of streams in the Amazonian forest receives an enormous quantity of vegetation remains (6–10 ton · ha^{-1} · $year^{-1}$; Klinge, 1977), which maintains a significant food chain with many alternatives. In these ecosystems, the diversity of food resources constitutes the base of stability, preventing a super- specialization of consumers. In addition to exploitation of the various alternatives, there are also various feeding techniques that allow improved and optimal exploration. In systems where the food chain essentially begins with detritus and decomposing fungi, algae and bacteria, the food of higher invertebrates and fish depend primarily on this source. The biomass thus produced in small streams feeds the great rivers of the system.

The detritus-based food chain is also important in flooded areas and floodplain lakes, where extensive growth and decomposition of aquatic **macrophytes** occur. In Amazonian reservoirs, where forest areas are flooded, the flooded areas present considerable accumulation of vegetation detritus (vegetation and decomposition), and, therefore, a detritus-based food chain quickly develops, resulting in rapid growth of a shrimp (*Macrobrachium* sp.).

Commercially important **detritivorous fish** are very common in South American rivers. Catella and Petrere (1996) discussed the importance of detritus in the diet of fish species in floodplain lakes. Through this **detritus chain**, the food web can contract,

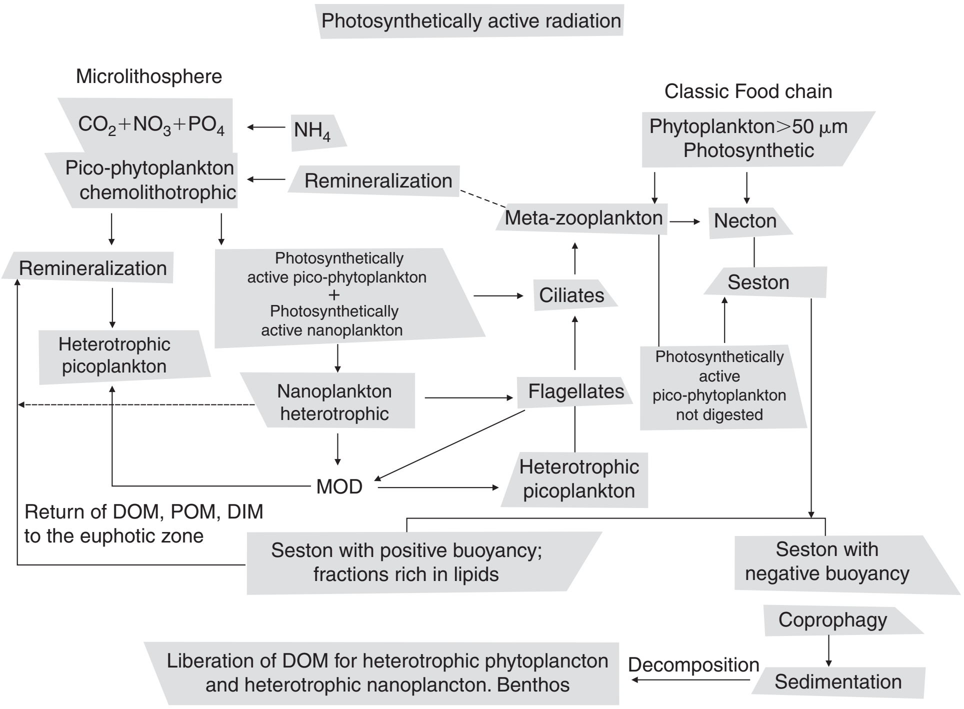


Figure 8.20 Major routes of transfer of organic matter under chemolithotrophic and photosynthetic conditions and *Chemolithotrophy* by different size fractions of phytoplankton: fractions >50 µm, nano-phytoplankton (<20 µm), pico-phytoplankton (0.2–3.0 µm). There is a difference between photosynthetically active pico-phytoplankton, chemolithotrophic pico-phytoplankton, **photosynthetically active nano-phytoplankton** and heterotrophic nano-phytoplankton. DOM – dissolved organic matter; POM – particulate organic matter; DIM – dissolved inorganic matter.
Source: Modified from Stockner and Antia (1986).

increasing the efficiency of communities in Neotropical floodplain lakes and rivers. The stomach contents of detritivorous fish present a large variety of different components, such as algae, bacteria, fungi, vegetative remains and unidentified portions of food items. Araújo-Lima *et al.* (1986) conducted studies that identified the sources of energy for detritivorous fish, and Forsberg *et al.* (1993) presented information on **autotrophic sources** of carbon for fish in the Central Amazon. Through the use of techniques to analyze the stomach contents of fish and ^{13}C carbon isotopes, Vaz *et al.* (1999) identified organic particulate matter as the main carbon source for characiform fish and catfish in the Jacaré-Pepira River and the Ibitinga Reservoir (state of São Paulo). In regions with fast-flowing rivers, the main source is allochthonous material, and in Ibitinga Reservoir, the main source is phytoplankton. In regions of the river with marginal lagoons, the principal food source is **particulate detritus material,** where bacteria can also be a significant source of carbon.

Araújo-Lima *et al.* (1995) conducted a broad review of the trophic relationships in fish communities in neotropical rivers and reservoirs. The authors concluded that omnivorous fish are abundant in streams, floodplain communities are dominated by detritivores, and piscivores are common in reservoirs and river channels.

Impact of the introduction of invasive exotic species in fresh water

The intentional or accidental introduction of aquatic species (fish, molluscs or crustaceans) can have a significant impact on food webs. In a recent publication, Rocha *et al.* (2005) described the impact of the introduction of *Cichla* cf. *ocellaris* on the food web in the UHE Carlos Botelho (Lobo/Broa) Reservoir, as well as the impact of the introduction of molluscs and exotic filter feeders into the food web in reservoirs in the Medio Tiete. The introduction of *Plagioscion squamosissimus* into the reservoirs caused substantial changes in the reservoirs' trophic webs, especially in the pelagic region where this species, a piscivorous fish, is an efficient predator (Leal de Castro, 1994; Stefani *et al.* 2005). Similarly, the introduction of golden mussels (*Limnoperna fortune*) in rivers, lakes and reservoirs of the **La Plata Water basin** has produced countless changes in the food web (see also Chapter 18).

8.6 BIOINDICATORS: ORGANISMS AS INDICATORS OF POLLUTION IN NATURAL WATERS

The structure and function of many freshwater and marine ecosystems have been and are being extensively altered due to the growing pressures of human populations and economic development in many regions, which can lead to significant changes in soil use and air pollution, with impacts on surface and ground water resources (see Chapter 18). These impacts are global, regional and local and range from climatic changes to deforestation of riparian forests, changes in the flow of rivers, and the introduction of exotic species. The spatial and temporal changes in these processes affect the structure and function of aquatic ecosystems and make it difficult to assess and predict the consequences under the effects of multiple **stress factors**. Researchers, decision-makers, planners and environmental managers now recognize the need to use scientifically based ecological approaches to monitor and predict the effects of these changes on the structure and function of ecosystems.

The sensitivity of an aquatic community (or populations of different species) can be a key indicator of environmental conditions (Loeb, 1994). Organisms and communities may respond to different changes in resources or alterations in environmental variables such as salinity/conductivity, water temperature, or organic and inorganic pollutants.

Hutchinson (1958) defined **hyper-volume** as the set of responses of an organism to all the factors affecting its ability to survive and reproduce. When changes occur in these factors, there is a corresponding shift in hyper-volume to a new spatial and temporal organization of favourable factors and the very survival of the organism. Stress factors affecting an organism or community can be physical, chemical or biological.

In order to define a set of stress factors in an environment, it is necessary to consider their attributes, that is, their variables and the hierarchy of factors affecting organisms, populations and communities.

Biological monitoring, and the evaluation of stress factors affecting organisms, populations and communities, are essential components for evaluating and predicting the responses of these organisms to physical, chemical and biological changes. The concepts of a niche and hyper-volume for each organism (based on environmental and biological variables) provide a theoretical basis for biological monitoring and the use of organisms, populations and communities as indicators to evaluate impacts. To a certain degree, biological monitoring enables the prediction of impacts and the evaluation of ecological risk and consequences of impacts. Any kind of stress occurring in an aquatic ecosystem directly affects organisms, populations and communities, which are the ecosystem's fundamental components.

The first researchers to study bacteria in an aquatic ecosystem to assess their response to organic pollution were Kolkwitz and Marsson (1909). Kolkwitz later expanded this concept – the *Saprobien system* – in 1950 (Hynes, 1994), followed by many studies that attempted to encode biological systems responding to the impact of mining and heavy metals, for example, or the effects of organic pollution.

Regional and local studies have produced many advances, and a mere list of species is not satisfactory, as Patrick (1951) already affirmed in a study on diatomaceous **organisms** as indicators. Macrophytes, benthic macroinvertebrates, planktonic organisms, crustaceans, and periphyton were all used to categorize local and regional indices, such as those proposed by Cairns *et al.* (1968) for North America and by Roldán (2006) for Colombia. Currently indices have been determined for the acidification of water, various **industrial effluents** and other stress factors.

What, then, are the basic methodological principles for efficient use of bioindicators? First, it is important to understand basic ecosystems, community structure and their interrelationships. Diversity indices applied to planktonic or nektonic communities are fundamental. It is also important to permanently maintain a local reference site that remains unaffected, to enable ongoing comparisons with the impacted ecosystem. Another essential aspect that should be considered is the **continuity** of evaluation of the impacted system, to enable ongoing comparisons.

The presence of certain pollution-indicating species is another fundamental requirement. These species often function as an early warning. Their disappearance may indicate alterations underway or significant stress factors at work in communities or populations (Matsumura Tundisi *et al.,* 2006) (see Figure 8.21).

Rocha *et al.* (2006) studied the biodiversity of reservoirs on the Tiete River under the effects of eutrophication and concluded that different **biological indicators** illustrated the eutrophic conditions in these reservoirs: greater abundance of oligochaetes, fish-eating birds and emergent macrophytes. A drop in the biomass of submerged macrophytes – as the amount of eutrophication increases and transparency of the reservoirs decreases – is another indicator.

Parasites on fish can also be indicators of eutrophication and environmental stress (Silva-Sousa *et al.*, 2006). The absence of ecto-parasites on fish is another indicator of stress factors related to increased **pesticides** in water.

The requirements for effective biomonitoring are therefore multiple, and are related to collecting and determining the biodiversity of organisms and species. In some cases, however, collection systems – for periphyton and macroinvertebrates, for example – can be used to monitor the growth, structure and impact of stress factors. Artificial substrata have been extremely useful in studies on the response of periphyton communities, auto-ecology of diatomaceous species (Patrick, 1990) or benthic macroinvertebrates (Pareschi, 2006).

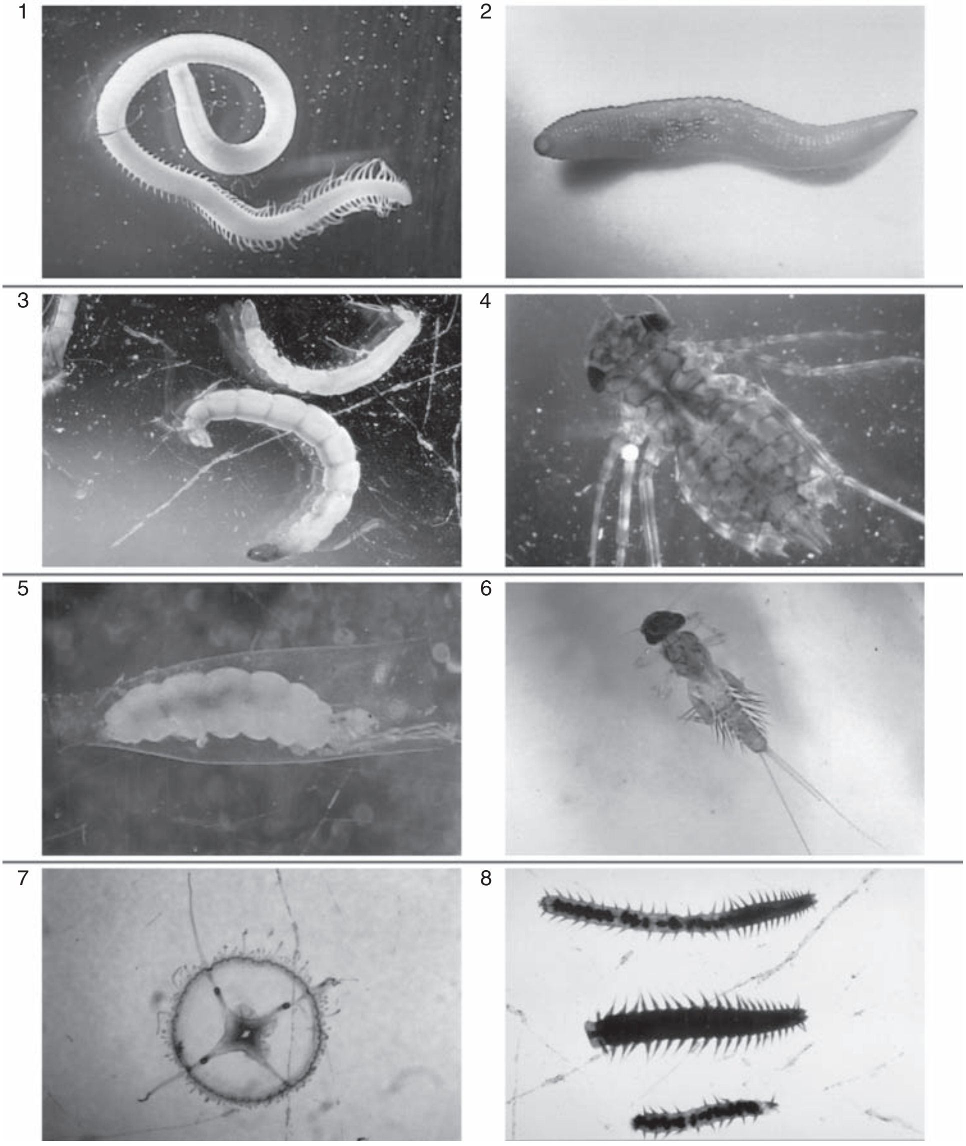


Figure 8.21 Organisms resistant to pollution: (1) *Branchiura sowerbyi* (Oligochaeta, Tubificidae, collected in the Ibitinga reservoir, middle Tietê, SP), (2) Hirudinea, Glossiphonidae (collected in the Xingu River, AM), (3) *Coelotanypus* sp (Chironomidae larvae, Tanypodinae); organisms tolerant to average pollution – (4) Libellulidae (Odonata larva, collected in the Ibitinga reservoir, middle Tietê, SP); organisms sensitive to pollution – (5) Trichoptera (larva inside the house, collected in the Xingu River, AM), (6) Ephemeroptera, Leptophlebiidae (larva, collected on the Xingu River, AM), (7) *Craspedacusta sowerbyi* (Cnidaria, rare, collected in the Tocantins river, TO), (8) Freshwater Polychaeta (often collected in the Xingu River, MA) (see also color plate section, plate 17).

Photos: Daniela Pareschi Cambeses.

Ghetti and Ravere (1990) used the following categories to describe biological monitoring of inland waters in Europe:

- analysis of natural communities (especially in rivers);
- toxicity tests to assess impact of discharges;
- bioassay for rapid assessment of effluent control;
- **bioaccumulation** tests;
- use of biological indicators in environmental impact studies.

Organisms used from both the structural/functional and taxonomic points of view are in the categories **plankton**, periphyton, microbenthos, macrobenthos and nekton. De Pauw *et al.* (1991) outlined seven saprophytic indices, 45 biotic indices, 24 diversity indices and 19 comparative indices.

Periodic toxicity tests using organisms include tests with *Daphnia, Phosphoreum* (photobacteria – inhibition of the bioluminescence of bacteria); tests with various fish species and toxicity tests with algae.

According to Cairns and Smith (1994), the main objectives of biological monitoring include:

- early assessment of the deterioration in the quality of the ecosystem in order to avoid deleterious effects;
- determining the impact of episodic events, such as accident spills of toxic substances, or the illegal dumping of residues and effluents;
- detecting tendencies or cycles;
- determining environmental effects from the introduction of genetically modified organisms.

More recently, systems such as microcosms and mesocosms have been introduced to evaluate impacts, along with the use of some species as early **information systems** to detect possible alterations (Cairns and Smith, 1994).

Fish as bioindicators

Fish can be effectively used as bioindicators. Because they are sensitive to many variables in water quality, they are used in bioassays to determine the toxicity of industrial chemicals or municipal effluents or other products resulting from human activity, such as mining. Initially these tests involved only acute toxicity and the immediate effect of pollutants. Currently, several species are used to determine chronic toxicity and near-lethal effects that include changes in behaviour and metabolism. The integrated approach is now better understood, including water chemistry, toxicology and its impacts on fish physiology, through the use of on-site tests with organisms submitted to various toxicological conditions and measuring the effects on behaviour, metabolism (renal excretion, for example, or accumulation of toxins in gills) and enzymatic response, such as determining the levels of the P450 enzyme in the cytochrome of the liver of fish.

This page intentionally left blank