Zooplankton and other invertebrates

(Primary reference: Ecology and Classification of North American Invertebrates, J.H. Thorp and A. P. Covich, Eds. QL 151 E36 1991)

Porifera (Sponges)

Diversity: There are about 300 species of freshwater sponges world-wide, and about 30 in the U.S. and Canada. In most lakes and streams, populations of freshwater sponges are unlikely to play a major role in ecosystem function [but there are some exceptions where sponges are important]. A few species are very widespread and others [for lack of data?] seem to be more narrow in their habitat requirements.


Porifera
Spongillidae
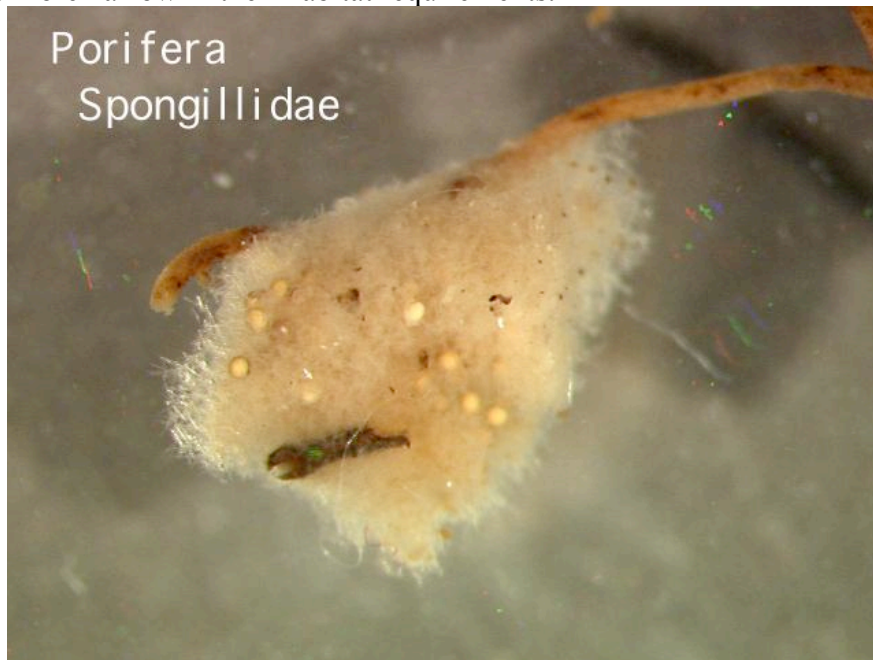
Morphology and feeding: A sponge can be considered a series of progressively finer filters with a mechanism that circulates water through them. Sponges are capable of removing particles ranging from large algae to bacterial cells less than 1 micron in diameter and possibly colloidal organic matter. Choanocyte chambers are the keystones of the sponge feeding system. Choanocytes serve as the final filters in the feeding system. Flagella beating within these chambers is primarily responsible for setting up the flow of water through the sponge. A second feature of sponge feeding involves the capacity of the cells within the canal network to engulf particles through phagocytosis. Sponges are selective feeders, not in the initial uptake of particles as selective feeding is typically defined but in their ultimate use of these resources."
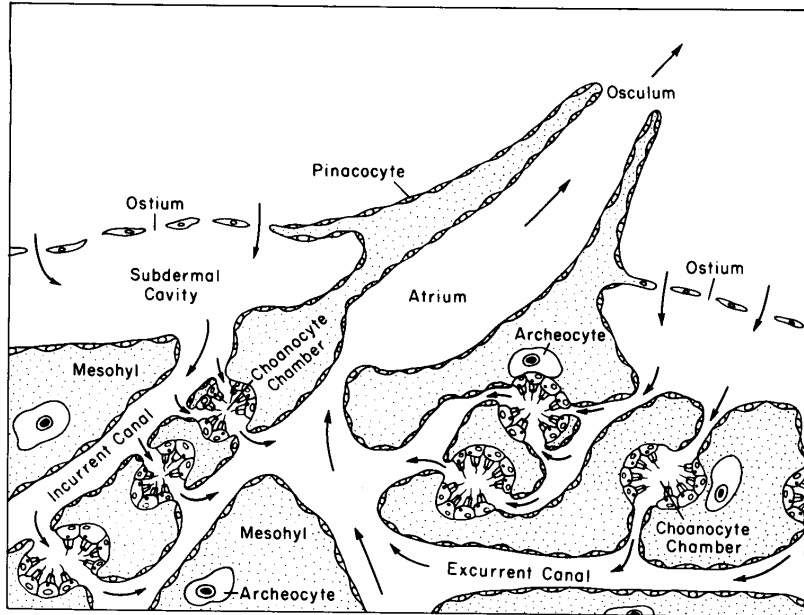
Figure 4.4 A schematic diagram indicating the primary components of the sponge feeding canal system. The diagram is not drawn to scale but Fig. 4.5 provides an indication of the size and arrangement of the feeding system in an actual sponge. Water flow patterns are indicated by arrows.

A sponge **skeleton** consists siliceous **spicules** and an organic skeleton of collagen.
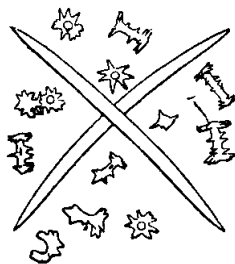
Fig. 11.14. Spicules of *Meyenia robusta*. Three types of spicules figured: smooth skeleton spicules; coarsely-spined gemmule birotulates; single rotules; exceedingly misshapen forms. × 100. (After Potts.)

Life history. Both sexual and asexual reproduction occur. There are both active growth stages and dormant stages. The dormant stage, or **gemmule**, appears typically during winter, or other period of stress. Gemmules exhibit a form of diapause or dormancy. Gemmules are also likely the principle means of dispersal.
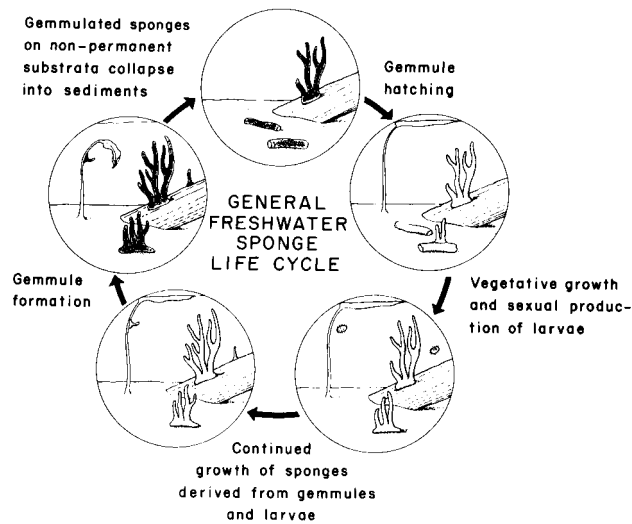
Figure 4.8 General features of the annual life history of freshwater sponges (see text for detailed explanations).

Habitat and ecology. Sponges need a hard substrate to attach. Populations are commonly sparse as a result. Symbiosis with algae is very common.

Cnidaria (or Coelenterates)

Diversity: Although this taxon is extremely diverse in the sea, there are just a few freshwater species. Most abundant is the genus **Hydra**. There are a few other freshwater species, including:

(1)   the freshwater jellyfish Craspedacusta and Limnocodium
(2)   Calposoma, a polyp
(3)   Polypodium, a sturgeon parasite
(4)   Various estuarine species, e.g. Cordylophora

Craspedacusta sowberii, an introduced cnidarian, has been reported from lakes in Oregon, Washington, and Idaho.
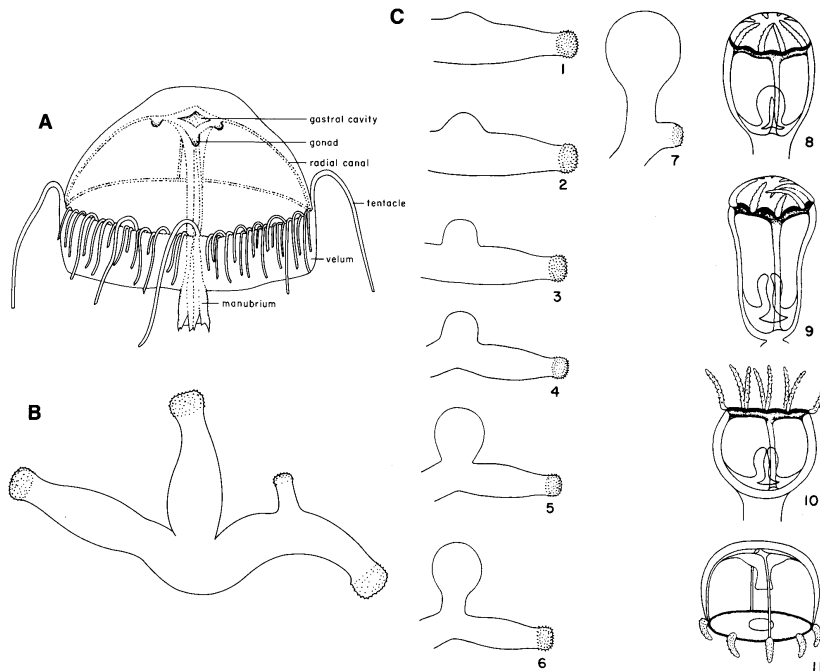
Figure 5.9 (A) *Craspedacusta sowberii,* also named *Limnocodium victoria* (see text); (B) larval stage of A, also named *Microhydra ryderi* (see text); (C) stages in development of *Craspedacusta.* (Redrawn from Payne
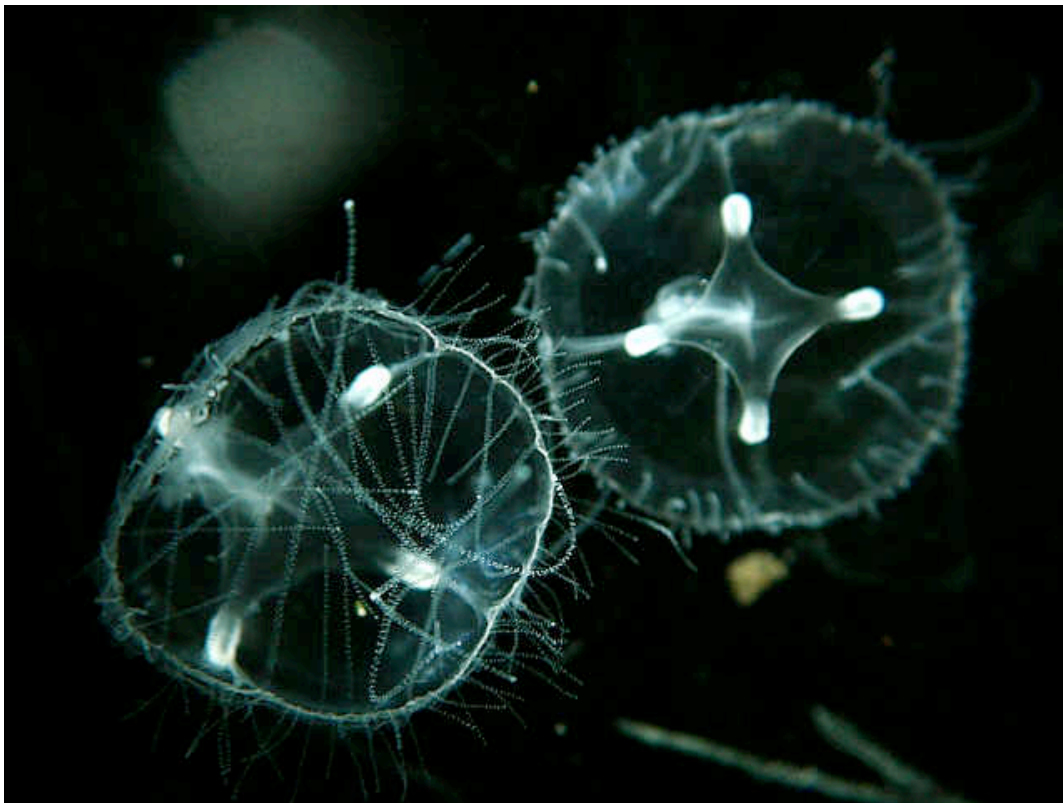
Morphology and feeding: Coelenterates have a distinctive body plan based on radial symmetry. There is a characteristic central body cavity surrounded by 2 distinct layers, ectoderm and endoderm. Between the two layers is the noncellular mesoglea. All

species have unique endocellular capsules called **nematocysts**, or stinging cells. After prey has been stung by the nematocysts, tentacles move it into the digestive cavity (or coelenteron) where it is digested in a matter of hours.

Life history: The basic cnidarian life cycle involves and alteration of generations between **polyp and medusa phases**. In **Hydra**, reproduction is largely by asexual budding but when conditions are unfavorable, sexual reproduction may occur.
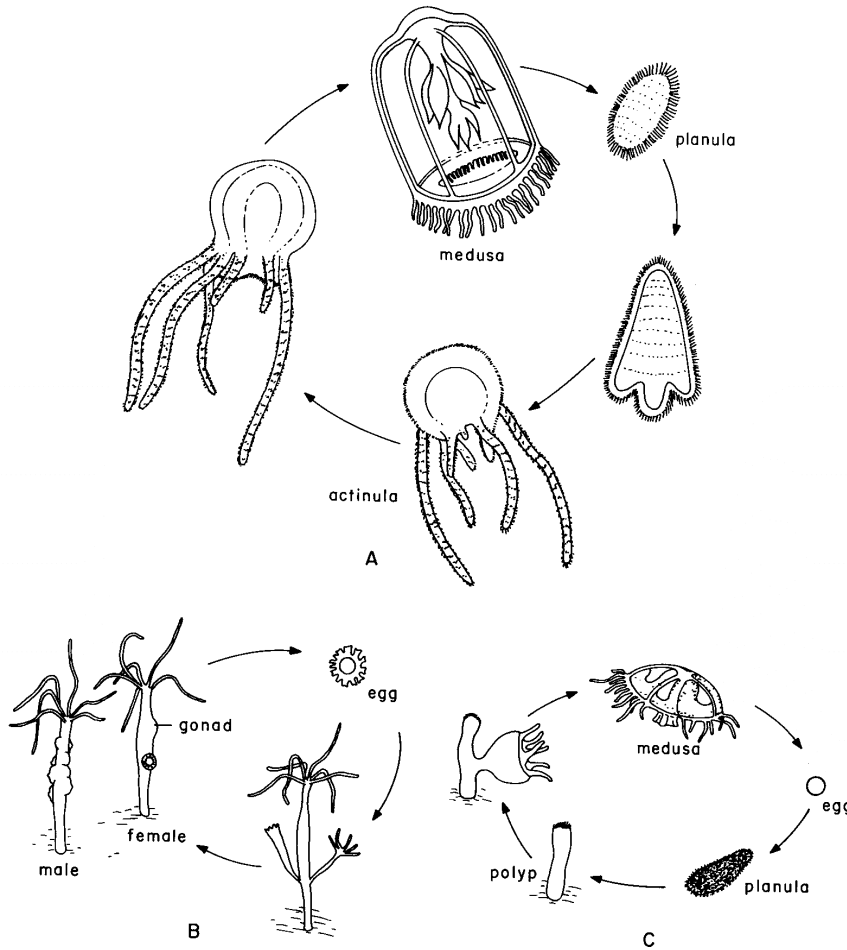
Figure 5.5 (A) Sexual medusa produces larva; larva forms new medusa; (B) Sexual polyp generates new polyp; (C) polyp produces medusa which becomes sexual and forms new polyp. (Redrawn from Barnes 1966).

Hydra: Hydra is the most common and wide-spread cnidarian in fresh water. The genus is often sessile but may appear in the plankton. Hydra is widespread, from the tropics to polar lakes. Some are green because of symbiotic Chlorella (likely a facultative association).

5

Flatworms

Diversity: About 400 species have been described, mostly in Europe (reflecting scholarship on the group and not any pattern of species diversity). Flatworms are common and numerous in freshwater habitats. Most are small and become unrecognizable in preservation; study of live specimens is the best method.

Morphology and feeding: Flatworms are the simplest bilaterally symmetrical metazoans. They have a ciliated epidermis, an intestine with an anus, a ventral mouth and a complex reproductive system. A distinctive structure are the rhabdoids, rod-like light refracting structures, possible associated with mucus production. Flatworms consume algae, bacteria, protozoa and other small invertebrates. They are both predators and scavengers.
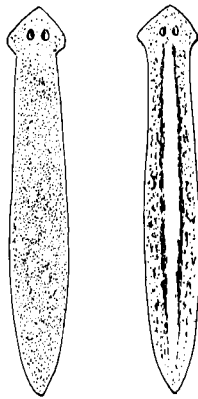
Moderate size, 15–18 mm long, often smaller, color very variable, most commonly spotted brown and white or brown with a wide white mid-dorsal streak; most common N. A. triclad. Everywhere in ponds, lakes, rivers, on vegetation, under stones. Breeds spring and early summer; capsules stalked, under stones. Old name, *Planaria maculata*. See Kenk (1944).

◄ **Fig. 13.4.** Two main color patterns of *Dugesia tigrina*.

Life history: For the most part, miniatures of the adults hatch from eggs, and initially lack only a mature reproductive system. As a rule, they are hermaphroditic. Vegetative reproduction, via longitudinal division may occur in some taxa.

Habitat and ecology: Most are free-living although a few may be ectoparasites on crustacea. They are widespread, from the poles to the tropics, although diversity may be less in high latitudes. Some species are global, others more restricted. Diversity may be high: e.g. 23 species reported from Mirror Lake, New Hampshire. A notorious feature: flatworms are capable of learning, especially things relevant to their habitat.

Gastrotrichs

Diversity: Gastrotrichs are among the most abundant and poorly know of the freshwater invertebrates. They are ubiquitous in the benthos and periphyton and may reach abundances of 10^4 to 10^5 m^{-2}! Although none are truly planktonic, some appear in the water column, especially in shallower lakes. Thorp and Covich (reference above) list about a dozen genera.

Morphology and feeding: Gastrotrichs are very small (50-80 μm long) bilaterally symmetrical animals. They feed on bacteria, algae, protozoans and detritus.
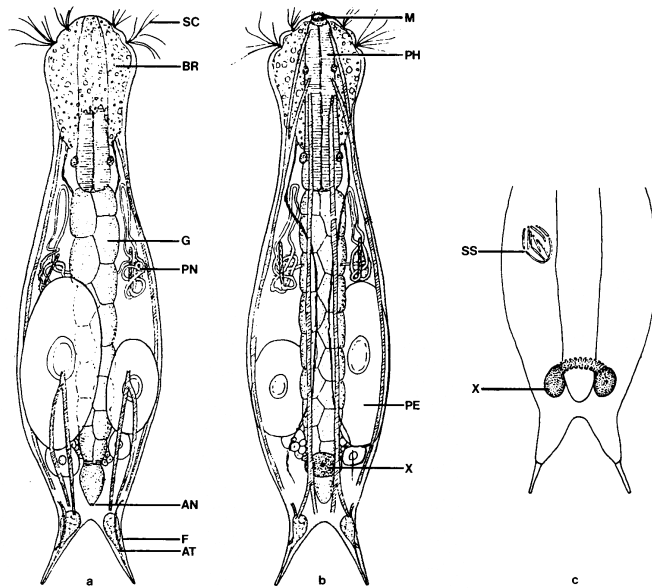
Figure 7.2 Schematic illustration of a typical chaetonotid gastrotrich showing (a) dorsal view, (b) ventral view, and (c) posterior end of a hermaphrodite, showing sexual organs, AT, adhesive tubes; AN, anus; BR, brain; F, furca; G, gut; M, mouth; PH, pharynx; PE, parthenogenetic egg; PH, protonephridium; SC, sensory cilia; SS, sperm sac; X, X-organ. [Modified from Voigt (1958) and Kisielewska (1981).]

Life history: Until recently, populations of freshwater gastrotrichs were thought to consist entirely of parthenogenetic females. However, more detailed recent studies have dispelled this notion, and have revealed a **remarkable life cycle** among the freshwater gastrotrichs that includes parthenogenetic and hermaphroditic sexual aspects to the life cycle. The life cycle is unique among invertebrates.

Note: opsi=fast hatching eggs

tachy= eggs that have a resting or dormant stage that is resistant to dessication and other environmental hazards
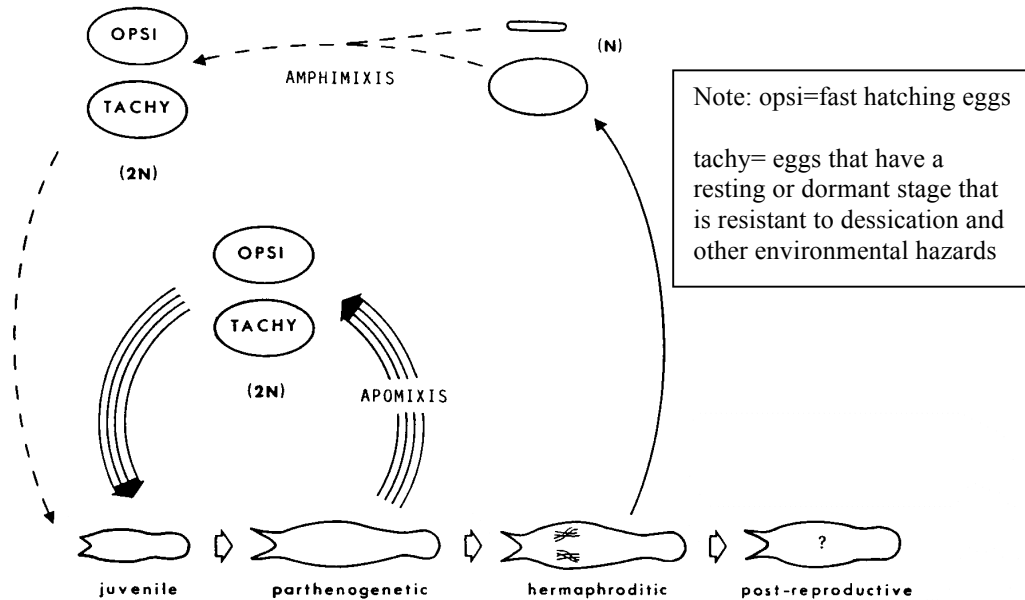
Figure 7.3 Schematic diagram of the proposed generalized life cycle for freshwater chaetonotid gastrotrichs, based predominantly on the study of *Lepidodermella squamata*. Dashed lines show hypothetical events that have not yet been demonstrated. OPSI, opsiblastic egg; TACHY, tachyblastic egg. [From Levy (1984), after ideas presented by Levy and Weiss (1980), with permission of the authors.]

Habitat and ecology: Although it has been demonstrated that gastrotrichs are often extremely abundant, it has not been demonstrated how important they are in natural food chains. The single study cited, from Mirror lake, suggests that gastrotrichs represent less than 1% of the benthic community production. Gastrotrichs are among the few animals commonly found in anaerobic environments, remaining abundant even after extended anoxia.   The physiological basis of this has not been studied (PhD material here!).

Nematodes (roundworms)

Diversity: Nematodes have a very diverse ecology. There are predaceous and parasitic species (endo and ecto) in marine, freshwater and soil habitats. Most are small, 1 cm or less. Thorp and Covich give a key that cites 66 genera of obligately freshwater species.

Morphology and feeding. Nematodes have a non-cellular layered cuticle. They lack circular muscles (longitudinal muscles only), which explains their characteristic movement. They have a complete digestive system: stoma, pharynx, intestine, anus. Free-living species eat bacteria or algae, but many species are parasitic, at least during part of their life cycle.

Life history: Nematode eggs have chitin in their shell. Post-embryonic development is similar to the gradual metamorphosis in insects. The juveniles closely resemble the adults and are accordingly called juveniles, not larvae. All nematodes undergo 4 molts and have 6 stages during their development (egg, first through 4th stage juvenile, adult).

Habitat and ecology: Nematodes are probably the most abundant animals in freshwater. In Mirror lake, they made up 60% of all the benthic metazoans but only 1% of the biomass. Their ecological significance in freshwater has not been assessed.

Mollusks (gastropods and bivalves)

Gastropods

Diversity: Thorp and Covich list several hundred species for North America. Snails are among the most ubiquitous organisms in the shallow zones of lakes and streams. Gastropods are overall the most diverse of the mollusks, making up 3/4 of all mollusk species.

Morphology and feeding: The most striking aspect of gastropod anatomy is the shell. Shells are conical (e.g. limpets), spiral but in one plane (e.g. Planorbidae) or the spiral may be elevated into a spire (many examples). The shell is composed of $CaCO_3$ and a protein cover. Soft parts are separated into 4 basic areas: head, foot, viscera, and mantle. The foot has cilia and a secretory epithelium. They move by mucus secretion and waves of muscle contraction. A distinctive feature of the digestion system is the **radula**, which can scrape off periphyton or pulverize the substrate. Snails are unusual among animals in that they possess cellulases.

Life history: Life history patterns are diverse: from oviparous (egg layers), hermaphroditic (both sexes in one individual), semelparous (dies after 1 reproductive event) to dioecious (male and female individuals), iteroparous (more than one reproductive event in lifespan) and ovoviviparous (develop in eggs retained in mother's body).

Habitat and ecology: Substrate selection is well documented: e.g. stream snails may prefer periphyton covered cobbles over sand or macrophytes. Most snails are either herbivorous or detritivorous. Some consume macrophytes, and may control macrophyte abundance.

The New Zealand mudsnail (Potamopyrgus antipodarum) is a relatively recent invader in Oregon freshwater.

Bivalves

Native clams and mussels have very broad distributions across North America, although **native species seem to be on the decline, perhaps due to degradation of water quality**. Some introduced species also have very broad distributions, e.g. *Corbicula fluminea*. Zebra mussel (*Dreissena polymorpha*), a Caspian species has entered North American waters and is spreading rapidly. The first introduction, via ballast water, was in Lake St. Clair in 1985-86. It spreads by attaching to boat hulls and trailers or by the juveniles drifting with the currents. Populations can be extremely high: 7000 to 114,000 individuals per square meter with biomass up to 15 kg/m^2!

Corbicula

Bryozoans

Bryozoans are among the most commonly encountered animals that attach to submerged surfaces in freshwater. They vary from wisps of stringy material to massive growths weighing several kilograms (e.g. locally, *Pectinella magnifica*). In some respects, bryozoans are a biological oddity, and **not much is known about many aspects of their biology and ecology**. They are composed of colonial zooids fused into a single structure. Feeding mechanisms are complex, but depend on cilia bringing food to the mouth. Reproduction may involve encapsulated dormant buds, or sessoblasts, floatoblasts, piptoblasts. The colonies may be sexually active for a brief season, and budding occurs in all species.

Bryozoans live in warm water (15-28 degrees) and need a surface to attach. Colonies are in turn colonized by a general **aufwuchs** community (the community of plants and animals that are attached to or move about on the surfaces of submerged stems, leaves, rocks, sticks, or debris). Chironomids may burrow in to the colony (and be picked out by fish).

Pectinella magnifica is a common bryozoan in Oregon lakes

Major taxa (major in the sense that they are quantitatively significant in <u>pelagic food chains</u>.)

Protozoa

Taxa

Phylogenetically, the protista represent a grade, not a clade, and the kingdom Protista is not a natural taxonomic unit. That is, the protista do not represent a single evolutionary lineage, but rather organisms of a similar level of morphological structure and complexity that have different, but convergent, evolutionary history.

The protista can be grouped together because of their similar *ecological* function. The free-living protists include cilieates, most of the flagellates, and the sarcodines [amoebas]. These protists are eukaryotes, usually unicellular. They possess a

nuclear envelope, eukaryotic ribosomes, mitochondria, flagella, etc. i.e., they represent a grade of morphological complexity. They commonly "eat" by phagocytosis.

Flagellates: Flagellates are the most abundant of the protozoa. Note that many are also photosynthetic, as well as consuming bacteria and other particles, and can best be described as mixotrophic. Some examples:
➢   Dinoflagellates   Ceratium, Peridinium
➢   Chrysomonads   Dinobryon, Synura
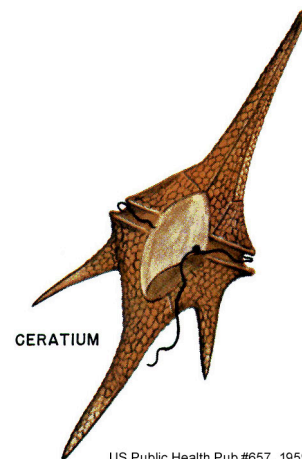
➢　　　　　Euglenids　　　　Euglena
➢　　　　　Volvocales　　　　Volvox, Eudorina

A chrysomonad
(note 2 flagella)

Ciliates: Most feed on bacteria, algae, detritus, and other protists.
Example: Paramecium

Sarcodines
Sarcodines are not often abundant.

 Reproduction

Most reproduce by binary fission, although sexual reproduction occurs in a few. Many produce resistant cysts when conditions become adverse (p396).

Identification is by the locomotive shape (the shape they take when moving), characteristics of the cell coat, and the shape of the nucleus.

Rotifers

Most rotifers are sessile, but there are about 100 species of completely planktonic species.

Morphology is variable; some have a rigid **lorica** (cuticle).

The **Corona** is the anterior ciliated feeding structure that gives the group its name. The cilia provide both locomotion and feeding. The digestive system contains a complex muscular pharynx, termed the mastax, and a set of jaws or trophi unique to rotifers that function to seize and disrupt food particles. Most are omniverous but a few are predatory (e.g. Asplanchna, figure 16-9)
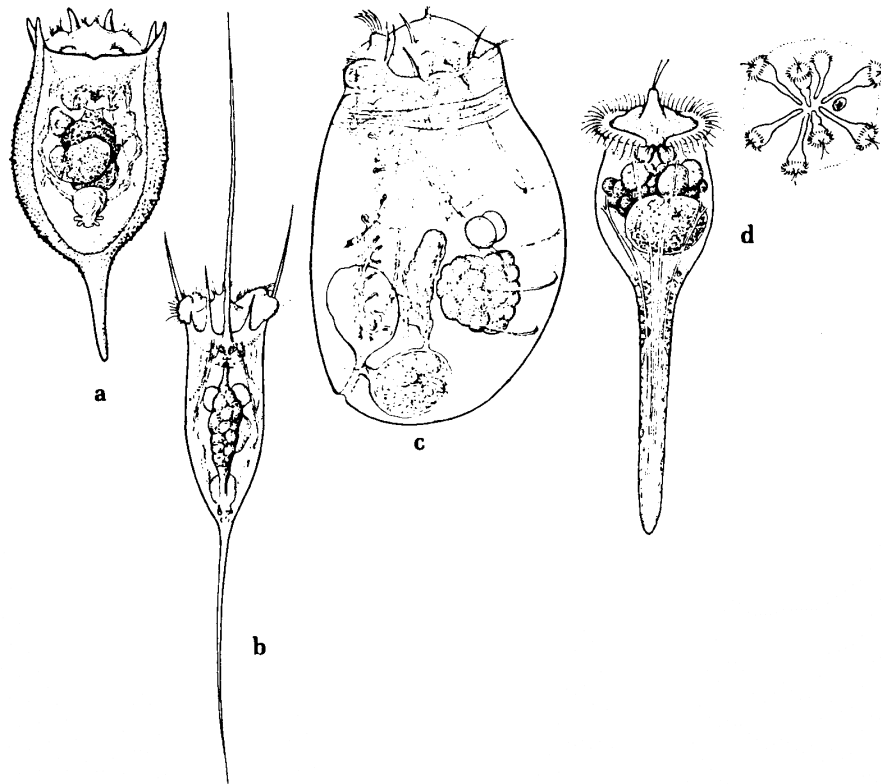
FIGURE 16-9 Exemplary planktonic rotifers: (a) *Keratella cochlearis*; (b) *Kellicottia longispina*; (c) *Asplanchna girodi*; (d) *Conochilus unicornis* singly and in a colony. (From Ruttner-Kolisko, A.: III. Rotatoria. Das Zooplankton der Binnengewässer. I. Teil. *Die Binnengewässer* 26:99–234, 1972, from various sources.)

Classification
There are 3 groups of rotifers, variously defined as classes or other taxa.

Class Seisonidea. There is only one genus, Seison, with 2 species of parasitic marine rotifers.

Class Bdelloidea. This taxon is recognized by the structure of the ovaries, pedal glands, and trophic structures. There are 18 genera and over 360 species. The individuals are exclusively female. Most are attached.

Class Monogonata. There are at leas 95 genera and approximately 1600 species, with benthic, free-swimming, and sessile species. All are assumed dioecious but for many species, males have never been observed. When they do occur, males are structurally reduced with only a vestigial gut. Some are raptorial, a few parasitic, but most feed by "sedimentation".

13

Reproduction and life cycle

Most of the population most of the time consists of amictic (no sexual recombination) parthenogenetic females (2N) that lay amictic eggs that again produce amictic females. Over the summer, many generations may occur.

Sometimes (mechanisms not clear) amictic (2N) eggs hatch to make mictic females (2N). Mictic females produce haploid mictic eggs. If not fertilized, these eggs hatch to form small, short-lived males. The males copulate, within hours of hatching, with mictic females.

The 2N fertilized eggs produced by mictic females are thick-walled resistant "resting eggs", which hatch weeks or months later after a prolonged diapause. These eggs hatch to form (exclusively) parthenogenetic amictic females.
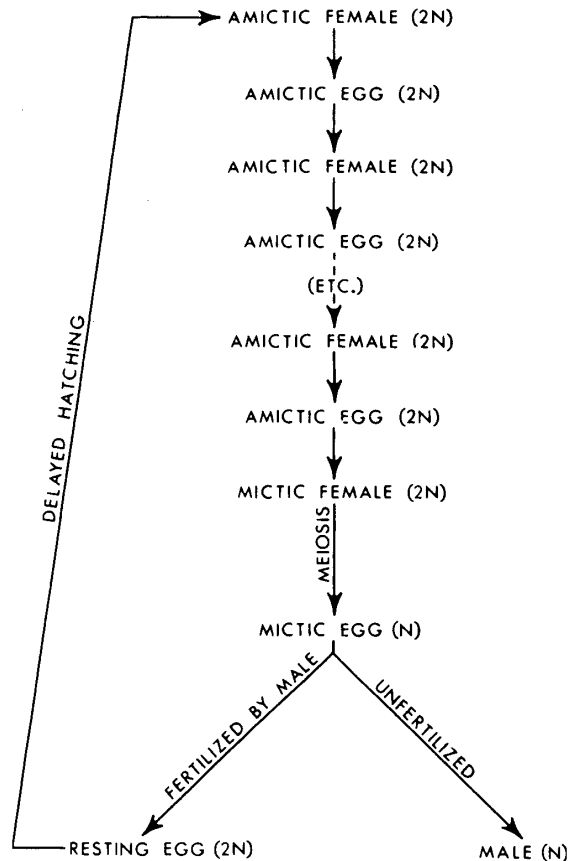
AMICTIC FEMALE (2N)

AMICTIC EGG (2N)

AMICTIC FEMALE (2N)

AMICTIC EGG (2N)

(ETC.)

AMICTIC FEMALE (2N)

AMICTIC EGG (2N)

MICTIC FEMALE (2N)

MEIOSIS

MICTIC EGG (N)

DELAYED HATCHING

FERTILIZED BY MALE   UNFERTILIZED

RESTING EGG (2N)   MALE (N)

FIGURE 16-17 Diagrammatic sequence of the reproductive life history characteristic of most planktonic and many benthic rotifers. (Redrawn from Pennak, 1953.)

The adaptive significance this common pattern of rotifer life cycle is complex. [Read: be careful about assuming that the adaptive significance is fully understood. Evolutionary theory about the benefits and adaptive significance of sex is surprisingly elusive!] However, it is clear that the combination of parthenogenesis for most of the time with sexual reproduction "on demand" combines the best of rapid population increase while preserving the recombination benefits of sexual reproduction.

Cladocera

Taxonomy

Cladocerans are members of the subphylum crustacea with small, flattened, leaf-like legs (Branciopods). There are 8 orders of Branchiopods, 4 of which (Anomopoda, Ctenopoda, Onychopoda, and Haplopoda) are referred to as cladocerans. The organisms now commonly called cladocera (this term now has no taxonomic significance) are grouped today into 4 orders, 11 families, about 80 genera, and roughly 400 species.

Cladocerans, or water fleas, have a single central compound eye and possess a carapace that is used as brood chamber. In most species, the carapace wraps around the entire body except for the head. Adults are 0.2 to 18.0 millimeters long. They have 4 to 6 pairs of thoracic legs and paired appendages (2nd antennae) used for swimming. The number of molts is variable, but 4 pre-adult instars are common (within the range of 2 to 8). Longevity and development time vary strongly with temperature. The number of adult molts is highly variable, up to 20. An important detail: partially developed young are released at the next molt.
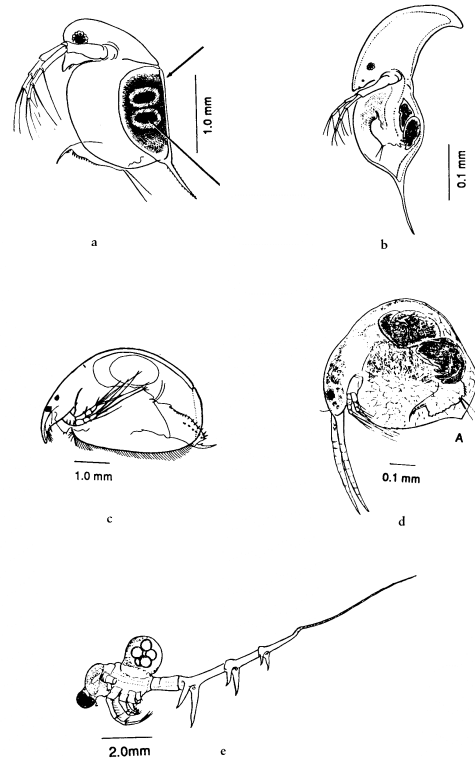
Eggs are retained in the brood pouch where they gradually assume the general appearance of the adult. After release from the brood chamber, the animals can grow only by molting, when enough energy has been stored.

FIGURE 16-11 Examples of common planktonic cladocerans. (a) *Daphnia pulicaria* carrying resting eggs within a protective ephippium case; (b) *Daphnia retrocurva* with an elongated helmet of the carapace; (c) a common littoral species, *Alona bicolor*; (d) *Bosmina (Eubosmina) coregoni*; and (e) a common predaceous cladoceran *Bytholtrephes cederstroemii*. (From Dodson and Frey, 1991, with permission.)

A few representative genera:

Family Daphniidae: Daphnia, Simocephalus, Ceriodaphnia

Family Bosminidae: Bosmina, Bosminopsis

Life cycle is parallel to rotifers described above.

Most individuals are parthenogenetic females. Eggs are produced parthenogenetically within the brood pouch where they develop into "small adults". No free-living larvae! Young are released when the mother next molts.

Aside: note that this mode of reproduction introduces a time lag into population density. It has been demonstrated that egg production is lower at higher population density. This, together with the intrinsic time lag in the release of the young, can introduce population oscillations.

This parthenogenetic cycle of reproduction can continue for many generations with the possible rapid population increase.

With the onset of adverse conditions, some eggs may develop into males (presumably 1N). Males are smaller than the females. Males copulate with females, fertilizing haploid (1N) eggs. "Adverse conditions" can include shorter days, lack of food, etc.

Fertilized egg develops as distinctive, resistant, ephippial egg (or **ephippium**). There is usually just one ephippium per female. Ephippial egg hatches, after diapause, to form parthenogenetic female.

Ephippia can accumulate on windrows on the shore, where they may easily be dispersed by contact with birds, etc.
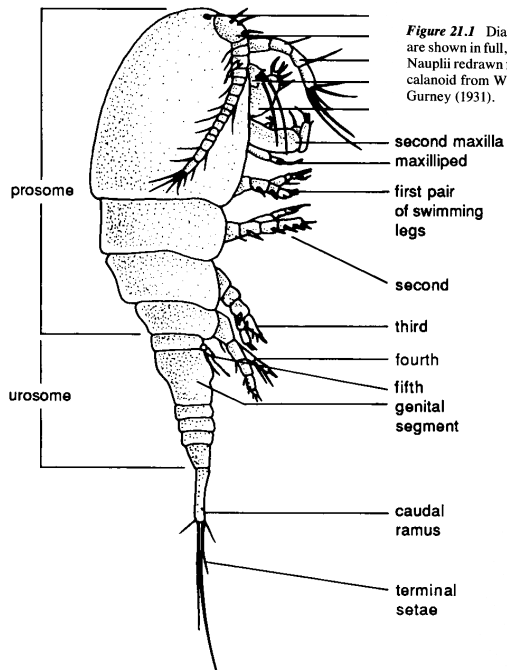
Copepods

Taxonomy

There are 3 major types of copepods: calanoid, cyclopoid, and harpacticoid.

Calanoids are predominantly "filter feeders". Many cyclopoids are carnivorous, although some are herbivorous. Many are raptorial. Harpacticoids are benthic sediment feeders or scrapers.
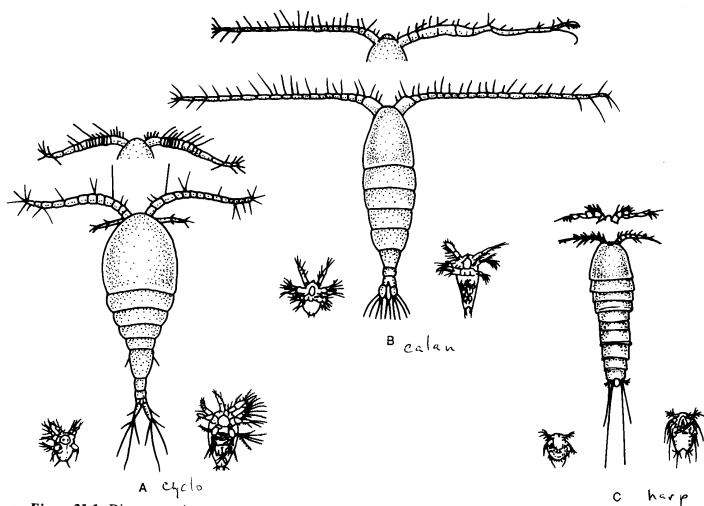
Figure 21.1 Diagrammatic representations of the three major orders of free-living copepods. Adult females are shown in full, while the adult male first antennae and early- and late-stage nauplii are shown for each group. Nauplii redrawn from Gurney (1932), male cyclopoid antennae from Wilson (1932), adult female cyclopoid and calanoid from Williamson (1980, 1987), adult harpacticoids from Coker (1934), calanoid male antennae from Gurney (1931).

Figure 21.2 Generalized body parts of a copepod. (Redrawn from Smith and Fernando 1978.)

Life cycle

Both males and females are present. Eggs hatch as small free-living larvae known as **nauplii** (singular, nauplius). Copepod nauplii are similar to other crustacean nauplius larvae (barnacles, crabs, shrimp, etc.). Nauplii go through 6 instars, followed by 6 sub-adult and adult copepodite instars. Copepodite #6 is the adult.

Cladocerans and copepods lend themselves to population dynamic analysis. Population growth rates can be estimated from observations of the egg ratio (#eggs/female) and knowledge of the developmental time of the eggs and young.

In addition, given the distinct naupliar and copepodite stages, cohort analysis can be applied to copepods.

Such analysis can provide estimates of population dynamics: that is, birth rates and death rates in addition to observations of changes in population size.

Filter feeding

Mechanisms

- Rotifers feed by "sedimenting" mostly small particles. Feeding is selective. Some rotifers are raptorial.
- Cladocera pump water through their valves with 5 pairs of setose legs. The setae catch the particles. Cladocera are also selective. A particular species is capable of filtering a particular size range of particles.
- Copepods: harpacticoids scrape. Cyclopoids are raptorial and bring particles to their mouth. Many are carnivorous. Calanoids don't "strain" particles, but in effect are filter feeders. They bring food in by creating "microcurrents" by rapid vibration of the second antennae, mandibular palps, first maxillae, and maxillipeds. Small particles are captured passively. Larger food particles are captured actively with an outward fling of the second maxillae followed by an inward sqeeze to remove excess water.

Quantitative considerations

Zooplankton can have appreciable effects on the phytoplankton populations and can affect seasonal succession. The effect of feeding by zooplankton ranges from insignificant to overwhelming.

Filtration rate: volume of water that contains the food particles filtered by an animal in a given time.

Feeding rate: quantity of food ingested by an animal in a given time.

Protozoa and the microbial loop.

- The size cutoff for particles that can be captured by the zooplankton is approximately 5 μm. The picoplankton are phytoplankters 2 μm and less, and in oligotrophic lakes in particular, picoplankton can represent a significant fraction (up to 1/2 or more) of the primary productivity. These small particles and their productivity can enter the "microbial loop".
- Wetzel reports that bacteria metabolize a very significant fraction of the total primary productivity. Usually, most of this metabolism takes place in the littoral or in the sediment (benthic). The bacteria metabolize up to 50% of the particulate organic matter and the dissolved organic matter.
- "The *microbial loop* is simply a model of the pathways for carbon and nutrient cycling through microbial components of pelagic aquatic communities. As implied by the term "loop", much of the energy and nutrients are confined to the microbial community. However, as indicated by the arrows to the metazoa, a *portion* is transferred to the zooplankton.

CARBON FIXATION PATHWAY
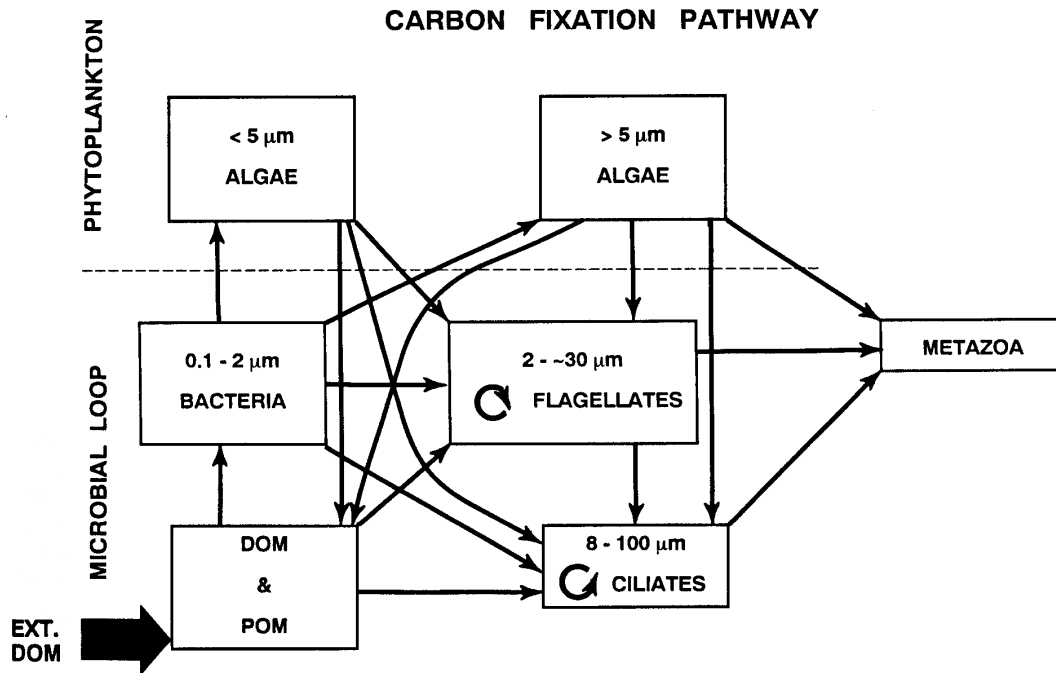
FIXED CARBON TRANSFORMATION & RECOVERY PATHWAYS

FIGURE 16-7 Trophic interactions within the microbial food web, which is separated here into phytoplankton and "microbial loop" (bacterial and protistan) components. Note the many direct links among heterotrophic and autotrophic microbes, as well as ingestion of phytoplankton by flagellates and ciliates and ingestion of bacteria by mixotrophic algae. The curved arrows in the flagellate and ciliate compartments indicate further predator–prey interactions within these broad classes of organisms. In this model, production of the <5-μm algae is accessible to metazoa only after being transformed into larger protozoan cells. A large portion of the dissolved organic matter (DOM) enters the pelagic from littoral and allochthonous sources in most lakes and rivers. (Modified from Sherr and Sherr, 1988.)

Summary: bacteria and protozoa represent a significant fraction of the total metabolism of the pelagic. This significance is a relatively recent discovery and is not yet fully understood.

Vertical migration

One of the most marked behaviors of the zooplankton is the common pattern of vertical migration of the crustacea, especially cladocera, and insect larvae. Vertical migration is very widespread, more the rule than the exception.

Proximal cue:

The common pattern of behavior is ascent to the near surface at dusk and descent to deeper water at sunrise. The **proximal cause is almost certainly light intensity (avoidance of bright light)**, resulting in a circadian rhythm of vertical migration. However, it is probably not an endogenous rhythm, but one that relies on light as a proximal cue, although light intensity, light color, light polarization, and other factors have been shown to have an effect.

Variation:

The pattern varies by species, gender, age, time of year, water transparency, presence of other species, etc. *Twilight migration* (some passive sinking in the middle of the night) is not uncommon. *Reverse migration* (up in the morning, down in the evening) occurs but only rarely.

Adaptive significance:

Whereas light intensity changes provide the cue, or proximal cause, *predator avoidance* seems to be the principal adaptive significance (or "ultimate" cause). Some evidence:

> The presence (or the smell) of fish induces non-migrators to migrate. They may continue to migrate for some time after the smell disappears. Vertical migration may occur only if there is more than a threshold concentration of a kairomone by fish or other predator (a kairomone benefits the receiver and is detrimental to the producer). The specific chemicals involved are incompletely known. The chemicals may actually be produced by the bacteria associated with the fish rather than the fish themselves.

Other possible benefits to vertical migration include:

- Food quality differences. Algae may be more nutritious to the zooplankton at night because of a better mix of protein and carbohydrate.
- Various metabolic arguments. It has been suggested that zooplankton can more efficiently feed at warmer temperatures (faster filtering) while digesting

at lower temperatures (more efficient investment in growth and reproduction with lower loss due to basic metabolic rate).

Cyclomorphosis

Definition (after Black and Slobodkin, 1987):

Cyclomorphosis is the …"temporal (seasonal or aseasonal) cyclic morphological changes that occur within a planktonic population." Such changes in body shape, spine number and length, eye-spot size, etc. occur in many different groups of zooplankton, but are especially noticeable in the cladocera. Examples from Wetzel, p457:

> Rotifers: *Asplanchna* that are 5 times as long as wide during midsummer, but nearly spherical in late spring; Enlargement of body-wall outgrowths or humps; Reduction in size, e.g. *Keratella* spp.; Production of lateral spines, e.g. *Brachionus*.

> Cladocera: Gradual extension of the anterior part of the head to form a crest or helmet; increase in the tail spine; Reduction in the number of parthenogenetic eggs; Reduction in the size of the eyespot.
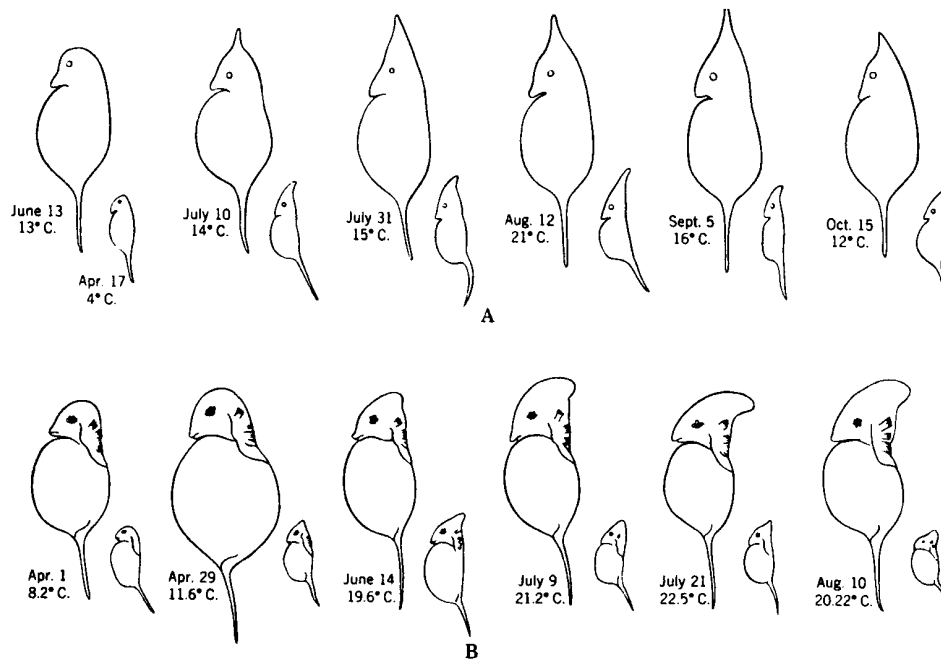

FIGURE 16-38 Cyclomorphosis in (a) *Daphnia cucullata* of Esrom Sø, Denmark and (b) *Daphnia retrocurva* of Bantam Lake, Connecticut. The small individuals at the right are first instar juveniles drawn to the same scale as the adults. (a) From Hutchinson, G. E.: *A Treatise on Limnology*, Vol. 2, New York, John Wiley & Sons, Inc., 1967; (b) From Brooks, John Langdon: Cyclomorphosis in *Daphnia: Ecological Monographs* 16:1946. Copyright 1946 by Duke University Press.)

At least some of the changes are the result of changes within a population: i.e. *not* the result of a succession of genetically different populations. For example, animals generally

lose elongation of body parts when cultured in the laboratory for one or two molts. Adults with extreme morphology, when taken from a natural population to the lab, produce offspring lacking the elongated parts.

Proximal causes: (i.e. cues)

Changes can be induced by physical factors (temperature, turbulence) or by chemical signals released by specific predator species. For example, *Daphnia galeata mendotae* and *D. retrocurva* both produce higher helmets in warm, turbulent laboratory environments. They also develop higher helmets in the presence of two invertebrate predators, *Chaoborus* and *Notonecta*.

Temperature: "It is clear that temperature is a primary stimulus affecting the height of the head helmet in Daphnia and that it is effective during the middle of embryogenesis."

Food supply: "Food supply also affects the specific growth rate and has a relatively greater effect on growth of the head (but helmet length is more strongly correlated with temperature than with food abundance…"

Water turbulence has also been shown to be a significant factor in cladoceran cyclomorphosis. Helmet length is longer in turbulent conditions. Helmet development is distinctly more conspicuous in species typically inhabiting epilimnetic turbulent strata.

"**Organic substances** released by invertebrate (especially Chaoborus) and fish predators can induce cyclomorphotic growth in Daphnia more effectively than can changes in temperature, turbulence and oxygen…"

Adaptive significance: (i.e. "ultimate cause")

"The adaptive significance of cyclomorphic growth appears to center on minimizing two aspects of predatory avoidance.
(1) Predation of cladocerans and other large zooplankton by non-filter-feeding fish, which is a visual process. Cyclomorphic growth keeps small the central portion of the body (thorax, abdomen, and basal portion of the head) that is visible to predators. Thus, when size-dependent planktivory is most intense in summer, the central visible portion of the daphniid body is smallest and the organism is less susceptible to being eaten by fish.

(2) Reduction of capture success by invertebrate and young fish predators. Invertebrate predation by copepods and phantom midge larvae (Chaoborus) is more effective on smaller zooplankton. The large caudal appendage of cladocerans increases handling time and decreases predation.

Top down vs bottom up control of lake trophic state

Bottom up control refers to the dominant role of nutrients in regulating phytoplankton abundance and hence lake trophic state.

Top down control refers to the role of grazing by zooplankton on phytoplankton abundance and trophic state.

Top down control can be important under some conditions, but food webs are complex and top down control can fail due to:

- Ontogeny -- often piscivorous fish are planktivorous when young, and will eat large zooplankton, thus decreasing the amount of zooplankton grazing and decreasing water clarity
- Predator-Prey cycles -- due to natural predator/prey cycles there are periodic releases from top-down predation and decreases in the amount of top-down control
- Replacement of species -- (rearrangement of trophic structure)
  - smaller zooplankton may become abundant, and they don't generally reduce phytoplankton standing stock
  - during eutrophication there are frequently shifts to inedible algae (such as blue-green algae), and these resist top-down control
- Variability in predator diet; plasticity in feeding