

Introduction to Mollusca and the Class Gastropoda

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INTRODUCTION TO FRESHWATER MEMBERS OF THE PHYLUM MOLLUSCA

Diversity

Molluscs (also called mollusks) are soft-bodied, unsegmented animals, with a body organized into a muscular foot, a head, a visceral mass containing most of the organ systems, and a fleshy mantle that secretes the calcareous

shell. The phylum Mollusca has about 100,000 described species and potentially 100,000 species yet to be described (Strong et al., 2008). It is divided among seven classes (Ruppert et al., 2004) and is present on nearly every continent. Freshwater molluscs are classified into gastropods (snails and freshwater “limpets”) and several groups of bivalves (mussels and clams) that have repeatedly colonized freshwater. Gastropods have a univalve shell and possess a

file-like radula used in feeding on the periphyton coverings of rocks or plants (Figure 18.1). Mussels and clams have a hinged, bivalved shell and are generally suspension and/or deposit feeders.

Freshwater molluscs are common animals in lakes and streams. The worldwide diversity is estimated at somewhat over 5000 species. Freshwater gastropods comprise ~4000 species (Strong et al., 2008), whereas bivalves number about 1200 species in total (Bogan, 2008) and include ~900 unionid mussels (Graf and Cummings, 2007), ~196 clams in the family Sphaeriidae, and several less speciose orders.

General Systematics and Phylogenetic Relationships of Mollusca

Evolutionary hypotheses for the major groups of molluscs are controversial largely because of the extreme diversity in the phylum. Morphological hypotheses generally placed the Caudofoveata and Solenogastres as plesiomorphic based on their simple worm-like body plan and lack of a shell (Kocot et al., 2011). More recent attempts that combine morphology and molecular systematics did not result in robust relationships (Kocot et al., 2011). Kocot et al. (2011) used sequences from 308 genome and transcriptome genes and considered gastropoda and bivalvia as more recent sister taxa (Figure 18.2). The freshwater gastropods and bivalves are buried within these lineages because of multiple instances of colonizing freshwater. The gastropods and



FIGURE 18.1 A freshwater gastropod. Photograph courtesy of Chris Lukhaup.

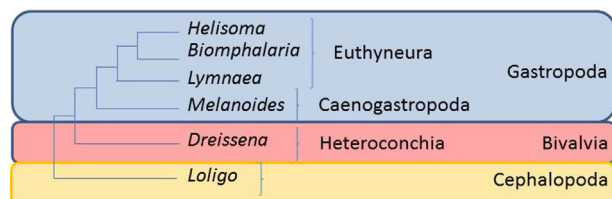


FIGURE 18.2 Composite phylogeny for molluscs. From Kocot et al. (2011).

bivalves share common ancestors that are united by a single pair of foot retractor muscles and neuron cell bodies concentrated in paired ganglia (Ruppert et al., 2004). Gastropods and cephalopods (e.g., squids) are sister taxa with an ancestor possessing a high, conical shell. Gastropods underwent torsion to develop a coiled, asymmetric shell and anterior mantle cavity. Cephalopods diverged into pelagic predators with advanced neuromuscular systems. Gastropods can be further divided between pulmonates, which breathe with a lung and evolved from terrestrial snails, and caenogastropods, which respire with a gill and evolved from marine gastropods. Throughout the chapter we will contrast the anatomy and ecology of these two gastropod groups.

Mollusc Anatomy and Physiology

A generic description of mollusc anatomy reveals a bilaterally symmetric body with a ventral foot. The dorsal portion of the body is covered by a shell that protects internal organs. The shell is lined by an epidermis, the mantle that secretes the shell. Muscles along the shell allow the animal to pull down the shell to the substratum to isolate the animal. This generic mollusc has gills (ctenidia) that are heavily lined with blood vessels, muscles, and nerves. Gills are positioned to allow water movements between their filaments, resulting in diffusion into and out of the blood vessels. The generic mollusc has a mouth containing a radula, a scraping organ that is lined with teeth. The radula can be moved out of the mouth to allow scraping the substrate, to remove material from a substratum and bring it into the mouth. The mouth is connected to a stomach by a tube, the esophagus. Digestive enzymes are secreted into the stomach from adjacent digestive glands. The pH of the stomach is reduced, allowing mucus decreased viscosity for moving food particles. A coiled intestine forms remaining particles into fecal pellets that are released into the posterior portion of the mantle cavity and carried out by an exhalant current.

Shell Morphology

Freshwater molluscs possess a shell that is a single shell in gastropods, or two shells in bivalves. The shell is composed of an outer periostracum of organic (mostly protein) material that may limit shell abrasion or dissolution of shell calcium carbonate by acid waters. Beneath the periostracum is a thick layer of crystalline calcium carbonate with some protein material interlaced. Calcium carbonate is either absorbed directly from water or is sequestered from food.

Bivalve Shells

Bivalve molluscs have two shells connected by ligaments and muscles. External shell characteristics are used in identification of taxa. Although freshwater mussels are predominately elongate-oval, shell variation is immense

within and among species. A mantle that lines the shell is present, and isolates the internal organs from extra-visceral water. The mantle attaches to and produces the shell. See Chapter 19 for details of mussel anatomy and physiology.

Gastropod Shells

All gastropods have a single shell, but the shape varies considerably among major groups. Freshwater “limpets” have a simple conical shell and the planorbid gastropods have a planospiral shell with the whorls all in one plane (Figure 18.3). The whorls are elevated in a spire in the pulmonate families Physidae and Lymnaeidae and in caenogastropod families. Gastropod shell terminology can be illustrated with a spiral shell (Figure 18.3). The pointed end of the shell opposite the aperture is the apex. Shell length in spiral shells is measured from the apex to the lower tip of the aperture, while the greatest diameter is used in planospiral shells. The spire is separated into a number of whorls by sutures. The initial shell of a newly hatched snail is the most apical whorl. The final whorl represents the most recent growth and ends in the aperture from which the foot protrudes. Whorls can be rounded and have deep sutures as in a typical lymnaeid shell (Figure 18.3), or whorls can be flattened with shallow sutures as in the Pleuroceridae (Figure 18.3). If whorls are flat, the shell is termed “cone-shaped.” Moderately inflated whorls produce a sub-globose shell, and shells that are almost circular are globose. There is a continuum between these three shell shapes. Shell thickness

varies from thin and fragile, as in many pulmonates, to thick and resistant-to-crushing, as in the caenogastropods.

Part of the aperture is often reflected over the body whorl (Figure 18.3) to form an inner lip. The presence of a channel between the inner lip and the body whorl results in the terminology of umbilicate or perforate (the opening of the channel is called the umbilicus and leads up and inward to the columella). Shells can have spines, ridges along the margins of the whorls called “carina,” colored bands, or small malleations or hammerings on the surface. Ridges at right angles to the whorls are called “costae,” and smaller ridges running spirally along the whorls are “lirae.” The growth lines of the operculum are used for classification of caenogastropods. Growth lines that are completely within each other produce a concentric operculum. A paucispiral or multispiral operculum has lines that are arranged in a spiral (Figure 18.3).

General Soft Anatomy

Molluscs have soft parts that consist of a head, foot, visceral mass, and mantle (Figure 18.4). The mantle epidermis secretes proteins, calcium salts, and mucus, and contains sensory elements (Ruppert et al., 2004). Aquatic pulmonates and caenogastropods have eyes at the base of their tentacles, unlike terrestrial gastropods whose eyes are at the tips of the tentacles. The muscular foot has cilia and a secretory epithelium to secrete mucus for locomotion. Pedal muscles produce waves of contraction to push the

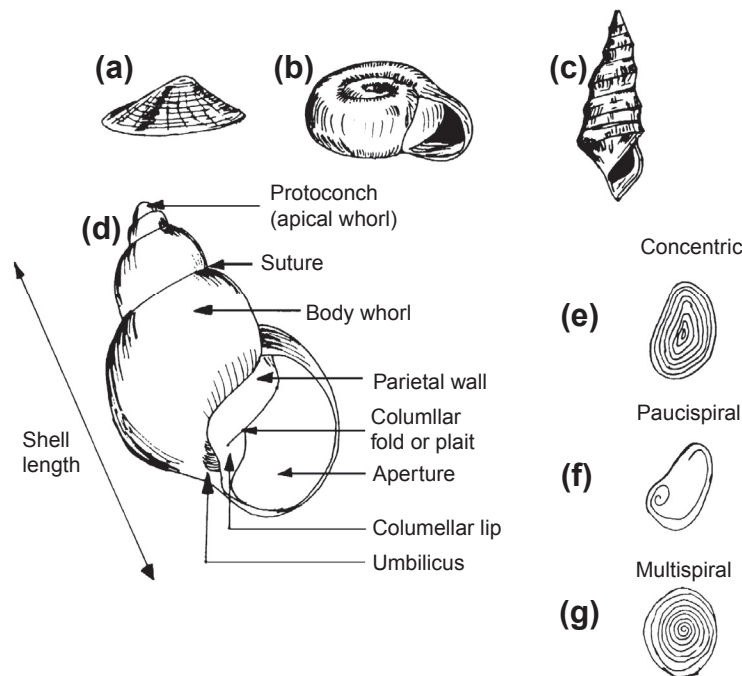


FIGURE 18.3 Basic anatomy of the shell, including shell architecture (conical, a; planospiral, b; spiral c, d); major features of the shell (d); and three types of opercula (e, concentric; f, paucispiral; and g, multispiral).

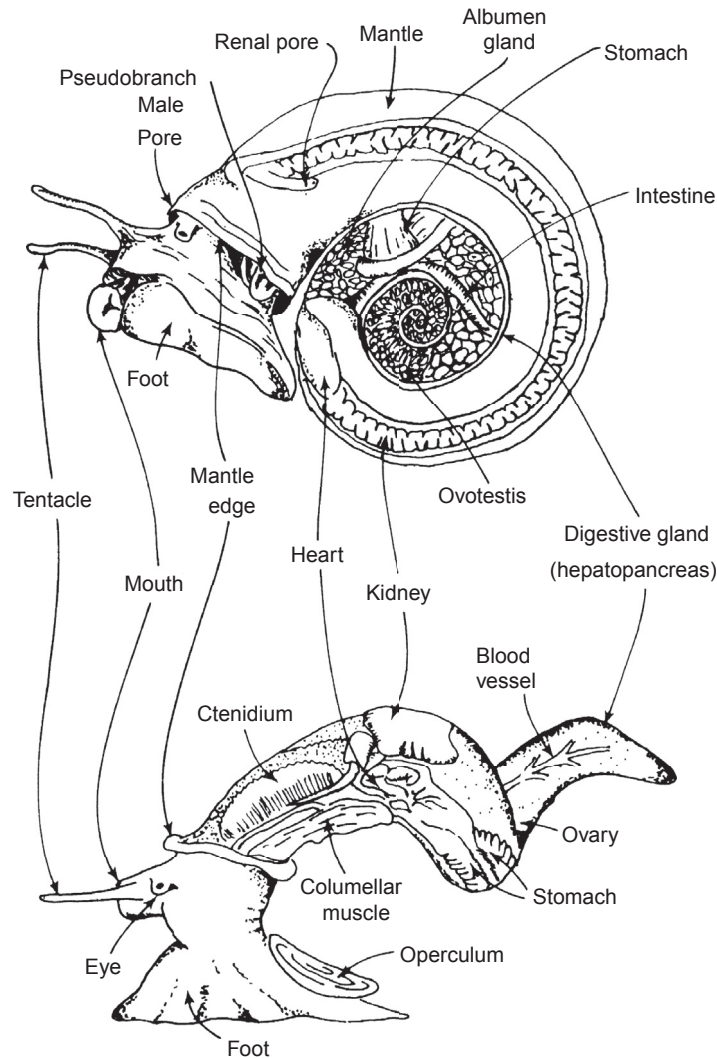


FIGURE 18.4 Basic internal anatomy of a planorbid pulmonate (above, after [Burch \(1989\)](#)), and a Pleurocerid coenogastropod (below, after [Pechenik \(1985\)](#)).

animal forward. The visceral hump includes most organs of digestion and reproduction. The mantle covers the visceral mass, and underlays the shell, which it secretes. The anterior mantle, over the head, possesses a mantle cavity where the gill or ctenidium is located in caenogastropods. Gastropods have ganglia innervating each of these areas. Detailed information on internal anatomy can be found various texts (e.g., [Pechenik, 1985](#); [Barnes, 1987](#)).

Digestive System

In snails, food is brought into the mouth by rasping movements of the radula, a file-like structure ([Figure 18.5](#)) resting on a cartilage (the odontophore) to which muscles that extend and retract the radula are attached. When the radula is extended, it contacts the substrate, and algal particles are scraped off when retractors pull the radula back into the

mouth. The radula may also pulverize food particles by grinding them against the roof of the mouth. A long esophagus leads to the stomach, located in the visceral mass. Some gastropods possess a specialized crop where sand grains further abrade food particles. Digestive enzymes are produced by the digestive gland, the hepatopancreas. Snails are one of the few animal groups to possess cellulases ([Kesler, 1983](#); [Kesler et al., 1986](#)) that degrade algal cell walls.

In bivalves, water containing particles is pulled into the incurrent siphon by water movements created by cilia that cover the ctenidia surfaces ([Pechenik, 1985](#)). Particles are captured by ctenidia and carried to labial palps and into the mouth for further sorting and digestion. Particles are trapped in mucus and carried through the esophagus to a stomach. The stomach contains a rotating crystalline style that begins digestion. The crystalline style is composed of proteins including digestive enzymes, and rubs against a

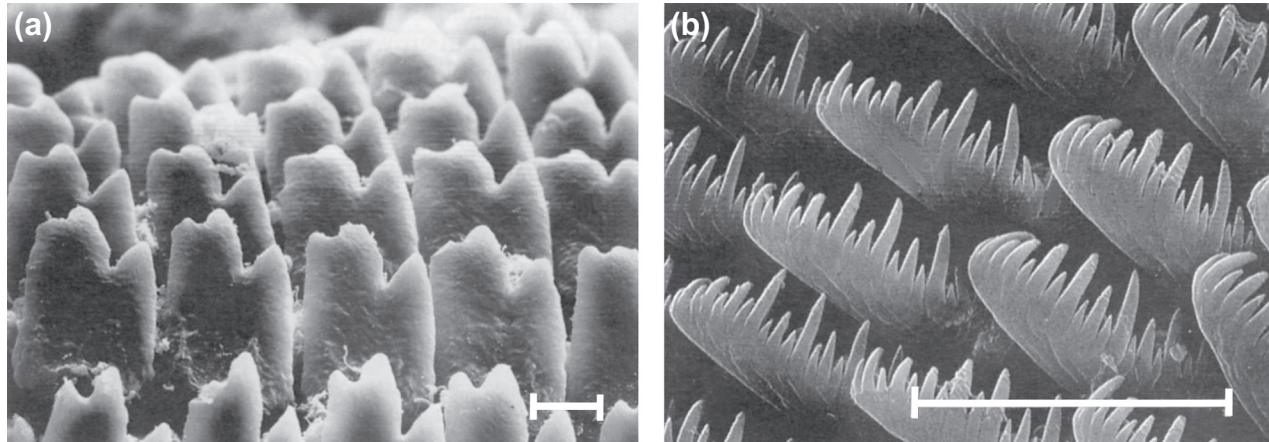


FIGURE 18.5 Scanning electron microscope photographs of radular teeth of (a) *Pseudosuccinea columella* and (b) *Physella vernalis*. From Kesler et al., 1986. Note the lymnaeid has fairly large teeth with few cusps. These teeth, along with large, cropping jaws in the buccal mass, a grinding gizzard equipped with sand, and high cellulose levels allow it to specialize on filamentous green algae (Kesler et al., 1986). *Physella* has many small teeth with long cusps, arrange in chevron-shaped rows, useful for piercing detritus and attached bacteria.

chitinous gastric shield to begin crushing and digesting of food particles. A digestive gland is adjacent and connected to the stomach. The stomach empties into an intestine that winds through the digestive gland and gonad to a rectum. The intestine is lined with cilia and additional digestion may occur here. Waste particles are compacted into fecal pellets. Additional details for bivalves are given in Chapter 19.

Respiratory and Circulatory Systems

Molluscs possess circulatory systems with a heart and blood vessels. The heart pumps blood that is drained from the gills into an aorta that carries blood to smaller branching vessels and eventually to tissue spaces and sinuses surrounding the viscera. Blood is collected by veins and routed to nephridia and then transported back to the gills and the heart.

The respiratory system of gastropods differs radically between caenogastropods and pulmonates. Freshwater caenogastropods have a single ctenidium or gill (Aldridge, 1983). The ctenidium, usually in the mantle cavity, has leaf-like triangular plates richly supplied with blood vessels. Oxygen-poor blood passes across the plates in the direction opposite to oxygen-rich water currents (generated by ctenidial cilia). This countercurrent mechanism assures diffusion of oxygen from water into the blood. Pulmonates lost their gill during their intermediate terrestrial phase and have a vascularized pocket in the mantle used as a lung (hence their name). The opening of the lung is the pneumostome. Pulmonates either rely on surface breathing or have a limited capacity for oxygen transfer across their epithelial tissues (McMahon, 1983). Some physids and lymnaeids fill the mantle pocket with water and use it as a derived gill (Russell-Hunter, 1978). Ancyliids and planorbids have readapted further to aquatic conditions by using a conical extension of epithelium as a gill, and planorbids also have a respiratory pigment, hemoglobin, which increases the efficiency of oxygen transport (McMahon, 1983).

Respiration in bivalves is achieved by gas exchange in the ctenidia (gills) with circulatory fluid. External water is moved across the ctenidia surface by the action of cilia. Freshwater bivalves carry oxygen dissolved in the circulatory fluid, without using respiratory pigments. Additional details for bivalves are given in Chapter 19.

Excretory and Neural Systems

The excretory organs of molluscs are metanephridial organs called kidneys. Tubules in the kidneys are where wastes are removed from blood and then are secreted through the tubule wall and into renal pores that drain to the outer mantle cavity.

The nervous system of a generic mollusc is a nerve ring that encircles the esophagus and is connected to two pairs of nerve cords that extend posteriorly. These innervate the foot muscles, the mantle and the visceral organs. Most molluscs other than bivalves have sensory organs including a pair of eyes, and tentacles. Mussels lack these but may have statocysts and sensory osphradia that are chemoreceptors adjacent to gills.

Freshwater molluscs have a permeable epidermis and are subject to osmotic inflow of water from their hypo-osmotic surroundings. Thus, they must pump out excess water in their urine. The gastropod coelom is little more than a small cavity (pericardium) surrounding the heart. The coelomic fluid is largely a filtrate of the blood, containing waste molecules such as ammonia that are filtered across the wall of the heart. Additional wastes are actively secreted into the coelom by the walls of the pericardium. The coelomic fluid then enters a metanephridial tubule (the coelomoduct), where selective resorption of salts and further secretion of wastes occurs. The urine is then discharged into the mantle cavity. Freshwater gastropods excrete nitrogen both as ammonia and as urea. Ammonia is adaptive in aquatic environments because, although it is toxic, it is extremely soluble and readily diffuses away. Pulmonate

gastropods often produce urea, which is better in terrestrial situations or during hibernation or estivation, because it is relatively nontoxic and can be stored in the blood until able to be excreted (McMahon, 1983).

Environmental Physiology

Freshwater molluscs are restricted to waters with sufficient calcium concentrations for shell construction. Although it may not take much energy to absorb calcium from water, assuming adequate water hardness, it may be energetically costly to secrete calcium into the shell against an electrochemical gradient. McMahon (1983) and Lodge et al. (1987) discussed the degree of calcium regulation, and the relationship of external calcium level to shell thickness and growth. Shell accretion may lag behind rapid tissue growth in eutrophic habitats, producing thinner-shelled individuals (McMahon, 1983).

Increased water temperature increases oxygen consumption and impacts metabolic activity of all freshwater molluscs. Freshwater invertebrates are strongly impacted by temperature regimes that provide developmental cues, rates of egg development, and juvenile growth (Olden and Naiman, 2010). Water temperature is a cue for release of glochidia (Watters and O'Dee, 2000), seasonal movements (Amyot and Downing, 2003), and other attributes of glochidia (Golladay et al., 2004) for bivalves.

Pulmonate gastropods usually face wider extremes of temperature variation than do most caenogastropods (McMahon, 1983). Most temperate pulmonates, for example, can withstand temperatures near 0°C for extended periods. This is undoubtedly adaptive because of the seasonal and diurnal variation in temperature in many pond habitats. Pulmonates better regulate changes in metabolic rate with changing temperature than do caenogastropods. For example, Q10 values for 18 pulmonates were less (mean of 2.2) than values in 13 caenogastropods (mean of 2.8) (McMahon, 1983). As mean temperature increases, snails grow faster and reproduce at an earlier age, with more generations per year. Increasing water temperature is also the cue for onset of reproduction in many temperate pulmonates. The ability of pulmonates to reproduce in cold water allows them to breed early in the spring, and juveniles to grow rapidly to adult size before the end of the summer. Pulmonates can secrete a mucus covering, called an epiphragm, to retard moisture loss during dry periods (Boss, 1974; Jokinen, 1978).

In terms of adaptation to hypoxia, pulmonates (1) tolerate greater variation in dissolved oxygen than do caenogastropods (possibly because caenogastropods rarely experience hypoxia in the fast-flowing rivers they inhabit) and (2) also regulate oxygen consumption at varying levels of dissolved oxygen better than caenogastropods, which are oxyconformers (Hershler et al., 2007). Pulmonates

apparently withstand lower oxygen tensions by surface breathing or by reliance on anaerobic metabolism (McMahon, 1983).

Reproductive System and Larval Development

Molluscs have extreme variation in reproductive characteristics. A generic mollusc is dioecious with paired gonads. Eggs or sperm are released into the coelomic cavity and carried outside by ducts. Fertilization is external and the zygote develops into a gastrula and then a free-swimming trochophore larva. Trochophore larvae develop into a veliger in marine taxa. The veliger larvae have a well-developed foot, shell, and other structures. A veliger will settle on the bottom of the water body and metamorphose into the adult form. In freshwater unionid bivalves, larvae develop into glochidia that are brooded and later released to attach to fish hosts used for dispersal; others have direct development into adults (Sphaeriidae or pill clams); while some retain the veliger larval form (e.g., *Dreissena* or zebra mussels). Freshwater gastropods also have great variation in developmental patterns. Gastropods can be oviparous, ovoviviparous, or viviparous. Larval forms are present in some taxa. For example, the neritids are oviparous and deposit eggs on substrates that hatch into a swimming larval form. The larvae undergo metamorphosis into the adult form. Oviparous taxa have direct development, while ovoviviparous species brood their young and release them at a larger size.

FRESHWATER MEMBERS OF THE CLASS GASTROPODA

Snails are among the most common organisms along the margins of lakes and streams. They feed on detritus, graze on the periphyton covering of macrophytes or cobble, or even float upside down at the water surface, supported by the surface tension, and feed on algae trapped in the same fashion (Figure 18.6). In fact, gastropods often control



FIGURE 18.6 *Thiara winteri* gastropods grazing on glass. Photograph courtesy of Chris Lukhaup.

the amount and composition of periphyton in both lotic and lentic environments. They are also the basis of food chains dominated by sport fish. Predators, by controlling snail populations, may indirectly facilitate algal producers. Another intriguing aspect of freshwater snails is their extensive intraspecific variation in life histories, productivity, morphology, and feeding habits that adapt them to live in uncertain freshwater habitats. Unfortunately, several groups of freshwater gastropods in North America and elsewhere have a large number of species at risk of extinction (Figure 18.7(a); *Balanocochlis* from Malaysia).

General Systematics and Phylogenetic Relationships

Gastropod systematics have been revised with modern phylogenetic methods into classifications that differ drastically from a few decades ago. Table 18.1 describes the classification of freshwater gastropods using taxonomy that reflects evolutionary relationships. Freshwater

gastropods are dominated by Caenogastropoda and Heterobranchia (pulmonate heterobranchs). Additional heterobranchs that invaded freshwater include members of Valvatidae, Glacidorbidae, and Acochlididae. Groups of gastropods that are exclusively freshwater are Viviparoidae, Glacidorboidea, and Hygrophila (Strong et al., 2008, Figure 18.7(b) and (c); *Bellamyia angularis* and *Bellamyia purificata*).

The most diverse group of living gastropods is the Caenogastropoda, which includes several groups that have independently colonized freshwater habitats. This group has been a topic of recent systematic revision, as summarized in the following few paragraphs. This group includes about 60% of living gastropod species. Architaenioglossa is a nonmarine grouping that is sister to other living caenogastropods and includes two freshwater families, the Ampullariidae and Viviparidae (Ponder et al., 2008). Sorbeoconcha includes freshwater Thiaridae and related families. The Hypsogastropoda includes freshwater Hydrobiidae and related families.

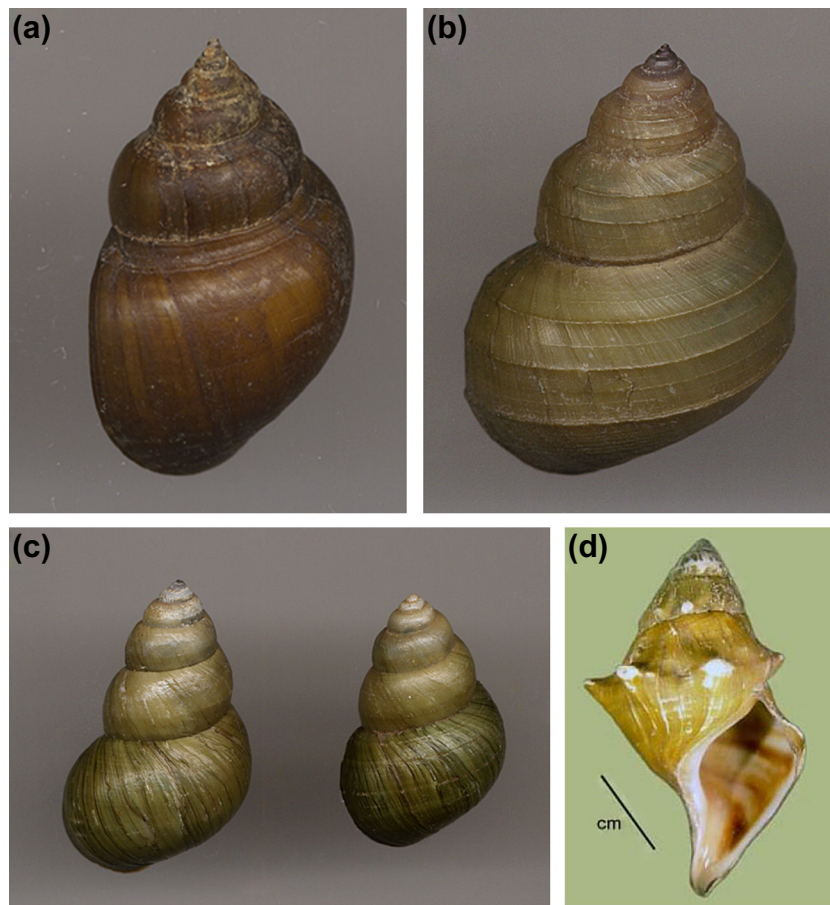


FIGURE 18.7 (a) *Balanocochlis glandiformis* is an example of a freshwater gastropod at risk of extinction. Photograph courtesy of Martin Kohl. (b) *Bellamyia angularis* is a Viviparid example of freshwater gastropods that are exclusively freshwater. Photograph courtesy of Martin Kohl. (c) *Bellamyia purificata* is a Viviparid example of freshwater gastropods that are exclusively freshwater. Photograph courtesy of Martin Kohl. (d) *Io fluvialis* is a Pleurocerid example of freshwater gastropods that evolved to inhabit freshwater independently. Photograph courtesy of Alan Covich.

TABLE 18.1 Classification of North American Gastropods in the Context of Current Evolutionary Relationships Hypothesized for the Gastropoda

Neritimorpha
Superfamily Neritoidea
Family Neritidae
Caenogastropoda
Architaenioglossa
Superfamily Ampullarioidea
Family Ampullariidae
Superfamily Viviparoidae
Family Viviparidae
Sorbeoconcha
Superfamily Cerithioidea
Family Pleuroceridae
Hypsogastropoda
Superfamily Rissooidea
Family Amnicolidae
Family Assimineidae
Family Cochliopidae
Family Hydrobiidae
Family Lithoglyphidae
Family Pomatiopsidae
Heterobranchia
Superfamily Valvatoidea
Family Valvatidae
Pulmonata
Basommatophora
Hygrophila
Superfamily Acroloxoidea
Family Acroloxidae
Superfamily Lymnaeoidea
Family Lymnaeidae
Superfamily Planorboidea
Family Planorbidae ¹
Family Ancyliidae ¹
Family Physidae

¹Current evidence indicates that Ancyliidae should be placed within the family Planorbidae.

Cerithioidea includes about 14 families and more than 200 genera that are mostly marine species (Lydeard et al., 2002). Three groups of Cerithioidea evolved to inhabit freshwater separately (Pleuroceridae (Figure 18.7(d); *Io fluvialis*), Melanopsidae, and Thiaridae). The phylogenetic relationships of these families were polyphyletic in the mitochondrial rDNA sequence analyses of Lydeard et al. (2002). Pleuroceridae occur in the eastern United States, and the subfamily Semisulcospirinae occurs in the western United States with a single genus, *Juga* (Holznagel and Lydeard, 2000; Lydeard et al., 2002; Minton and Lydeard, 2003). *Juga* is more closely related to East Asian taxa than to pleurocerids (Holznagel and Lydeard, 2000; Lydeard et al., 2002; Strong, 2005; Strong and Frest, 2007). Although no comprehensive phylogeny for the Pleuroceridae has been published, several studies provide some information. A composite phylogeny showing the placement of North American Pleuroceridae and Semisulcospirinae is shown in Figure 18.8. Nomenclatural changes and new or re-descriptions are likely for these taxa.

Evolutionary relationships among the higher caenogastropod taxa were examined by Ponder et al. (2008). Although there is little phylogenetic resolution for the Hypsogastropoda, other sister taxa have monophyletic hypotheses based on morphology and molecular evidence (Ponder and DeKeyser, 2008). The Rissooidea (Truncatelloidea) is the most diverse group of Hypsogastropoda and has evolved to occupy niches including freshwater, marine, and terrestrial habitats (Ponder and DeKeyser, 1998). The rissooideans include Hydrobiidae, Pomatiopsidae, and Assimineidae in North America. The Hydrobiidae are the most diverse family with several thousand species and more than 300 genera distributed around the world. Hershler and coauthors have studied the systematics of North American hydrobiids, which includes multiple spring endemics of conservation concern (Hershler et al., 2002b, 2010).

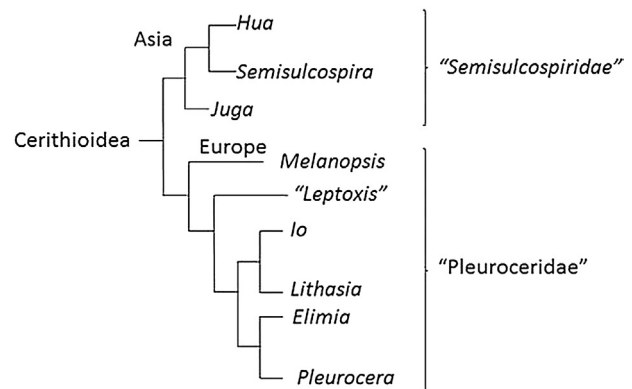


FIGURE 18.8 A composite phylogeny of Pleuroceridae and Semisulcospiridae of North America derived from Holznagel and Lydeard (2000), Lydeard et al. (2002), Minton and Lydeard (2003). Pleuroceridae as depicted includes taxa from Europe formerly from the family Melanopsidae. Quotations refers to polyphyletic taxa.

The Architaenioglossa is sister to all other living caenogastropods and includes two freshwater families, the Ampullariidae and Viviparidae (Ponder et al., 2008). Sorbeoconcha includes caenogastropods excluding architaenioglossans, with freshwater groups of Thiaridae and related families (Lydeard et al., 2002).

Basommatophora (pulmonate gastropods) is monophyletic and includes all pulmonate gastropods in five families: Acroloxidae, Chiliniidae, Lymnaeidae, Physidae, and Planorbidae (including the Ancyliidae) (Correa et al., 2010). The biogeography of this group spans Europe, Australia, Africa, North America, and South America. Correa et al. (2010) concluded that the Basommatophora has three old centers of diversification: North America Eurasia and the Indo-Pacific region. The nomenclature of many of these taxa needs to be updated.

Evolutionary relationships have been studied at local geographic scales for many taxa in lower taxonomic analyses. In North America, phylogenetic hypotheses exist for additional groups of freshwater gastropods. Holznagel et al. (2010) analyzed relationships of pulmonate gastropods using 2S rRNA sequences including several freshwater groups (Figure 18.9). These analyses allowed examination

of evolutionary transitions among freshwater, marine, and terrestrial habitats. Freshwater snails occur in the Hygrophila, Glacidorbidae, and Onchidiidae (Holznagel et al., 2010).

Recent Systematic Studies

Gastropod systematists are currently actively studying many disparate groups of freshwater taxa (Ponder and Lindberg, 2008). However, given the relatively low number of systematists who work with freshwater gastropods, few taxa have been studied in detail. We describe several taxa that have had recent detailed systematic studies.

Lymnaeidae are worldwide in their distribution, with highest diversity in North America (Burch, 1980, 1982, 1988). Phylogenetic hypotheses for pulmonates demonstrated that Radix is a polyphyletic genus (see Correa et al., 2010), Stagnicola caperata (Say 1829) and Fossaria spp. are closely related, but Lymnaea stagnalis Linnaeus likely has European origins (Remigio, 2002).

The Physidae are a globally distributed taxon with considerable morphological diversification, resulting in similarly high ecophenotypic plasticity (DeWitt et al., 2000; Dillon and Wethington, 2006). Experimental evidence demonstrated the ability for interbreeding among individuals in nominal species from widely separated geographic sources (Dillon et al., 2002).

In Africa, Wilson et al. (2004) verified high endemism (25–70 species of paludomid gastropods) in East African Lake Tanganyika (Wilson et al., 2004). The Pachychilidae group of Southeast Asia (Figure 18.10(a) and (b); Faunus ater and Tylomelania sulawesi) were used as models for evolution of viviparity by Köhler et al. (2004). Viviparity evolved multiple times and in freshwater lineages, suggesting a link for life-history traits and reproductive mode (Figure 18.11). Von Rintelen and Glaubrecht (2005) analyzed the evolution of anatomical characters

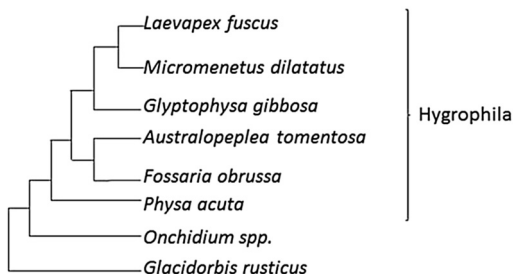


FIGURE 18.9 Composite phylogeny for freshwater pulmonates. From Holznagel et al., (2010).



FIGURE 18.10 (a) Faunus ater is from the Indo-West Pacific region. (Photograph courtesy of Martin Kohl.) (b) Tylomelania sulawesi is an example of an endemic from Southeast Asia. (Photograph courtesy of Chris Lukhaup.)

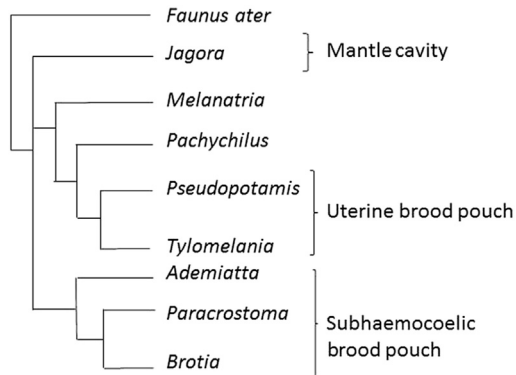


FIGURE 18.11 Phylogenetic hypothesis for Pachychilidae gastropods with origins of different viviparity modes. From Köhler et al. (2004).

for an adaptive radiation of 34 described Pachychilidae taxa from Sulawesi, Indonesia. Glaubrecht and Köhler (2004) examined molecular and morphological diversity for seven endemic viviparous freshwater Cerithoidea species in *Brotia* from rivers of Thailand. The endemic species of *Brotia* were monophyletic; and although the morphotypes were distinctive morphologically, they had low levels of genetic variation, indicating recent reproductive isolation.

The systematics of freshwater gastropods is currently an active field of study that is necessary for recognition of unique lineages as primary conservation units (Perez and Minton, 2008). Pleuroceridae, for example, has 500 nominal species that were erected based on the immense phenotypic variation in shells (Dillon and Davis, 1980). Johnson et al. (2013) recognized 162 species of pleurocerids and suggested that the current classification requires substantial revision to reflect evolutionary history. In contrast, Dillon and colleagues have proposed synonymization of many of these taxa based on both genetic analyses and conclusions that observed shell variations are largely ecophenotypic or plastic (Dillon and Robinson, 2011; Dillon et al., 2013).

Evolutionary Pathways

Marine caenogastropods are ancestral to freshwater caenogastropods, terrestrial pulmonates, and freshwater pulmonates. Freshwater caenogastropods adapted to dilute osmotic conditions of estuaries and then rivers, and most modern families are widespread because their adaptive radiations predated continental breakups and drift. Davis (1979, 1982) and Clarke (1981) described how caenogastropod dispersal is limited to slow movement of adults along streams and rivers. Such populations are likely to become isolated, promoting chances of speciation and adaptive radiation. Examples include adaptive radiations of hydrobiids (Davis, 1982) and pleurocerids in lotic habitats (Burch, 1989; Lydeard et al., 1997).

In contrast, pulmonates have more widespread distributions (including within North America), possibly due to their greater rates of passive dispersal on birds and insects. Pulmonates predominate in shallow, ephemeral habitats (temporary ponds) with durations less than 1000 years. Populations are not likely to persist in such locations for a sufficient time for speciation, and this has probably restrained pulmonate speciation in comparison to freshwater caenogastropods (Clark, 1981; Davis, 1982; Russell-Hunter, 1983).

Pulmonates apparently evolved from intertidal caenogastropods that relied less and less on aquatic respiration. Extant estuarine pulmonates like *Melampus* may resemble these ancestral species. Intermediate terrestrial pulmonates lost the ctenidium and gave rise to modern terrestrial pulmonates (order Stylommatophora) and aquatic pulmonates (order Basommatophora). Caveats for this description of the evolution of freshwater snails include issues with phylogenetic analyses; that is, the paucity of systematic information for many groups, and the poor fossil record (only shells are preserved, which often show convergence). Other explanations are available for current distributions, as in hydrobiids and pomatiopsids (Davis, 1982): (1) phylogenetic events such as centers of origin and adaptive radiation; (2) past history events such as continental drift and geological alteration of stream and river flow; (3) dispersal powers; and (4) ecological factors. Based on these explanations (Davis, 1982), one can rank gastropod groups from those with broad distributions but low diversity to the reverse: monoeccious pulmonates > parthenogenetic caenogastropods > viviparous caenogastropods > oviparous caenogastropods.

Distribution and Diversity

Regional diversity patterns for freshwater gastropods are currently nearly impossible to determine reliably due to a lack of consistent taxonomy, including nominal taxa that inflate species richness (Strong et al., 2008). Strong et al. (2008; their Table 1) summarized currently recognized species of freshwater gastropods by zoogeographical region. They categorized global hotspots of diversity into four habitats: springs and groundwater, large rivers and their tributaries, ancient oligotrophic lakes, and monsoonal wetlands. Global diversity patterns for freshwater gastropods that emerge are depicted in Figure 18.12. Highest species richness is in the Palaearctic, followed by Nearctic, Australasian, Neotropical, Afrotropical, and Pacific Oceanic Islands. An additional complication to understanding regional distribution and diversity patterns is the lack of reviews at the scale of continents (e.g., Africa; Brown, 1980) or ecoregions.

Shell anatomy is used to classify genera, although many species show considerable variation in shell characters. Based on past descriptions of species distributions, however, it is apparent that species of pulmonate gastropods

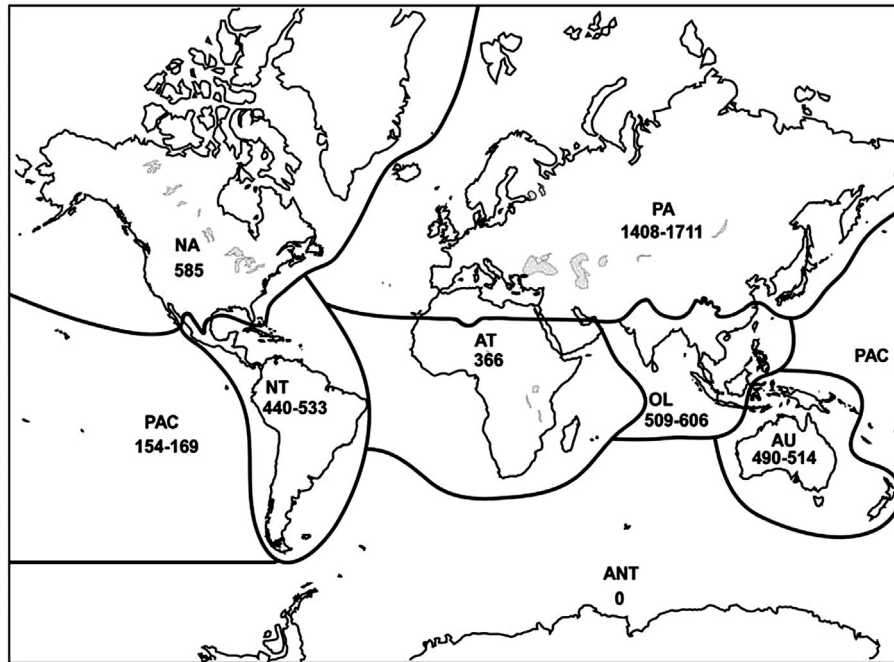


FIGURE 18.12 Hotspots of gastropod diversity. A–H. Springs and groundwater. I–Q. Lakes. R–X. Rivers. Y. Monsoonal wetlands. A. Southwestern USA. B. Cuatro Ciénegas basin, Mexico. C. Florida, USA. D. Mountainous regions in southern France and Spain. E. Southern Alps and Balkans region; Northern Italy, Austria, former Yugoslavia, Bulgaria, Greece. F. Great Artesian basin, Australia. G. Western Tasmania, Australia. H. New Caledonia. I. Titicaca, Peru–Bolivia. J. Ohrid and Ohrid basin, former Yugoslavia. K. Victoria. Kenya, Sudan, Uganda. L. Tanganyika, Burundi, Tanzania, D.R. Congo. M. Malawi; Malawi, Mozambique. N. Baikal, Russia. O. Biwa, Japan. P. Inle. Burma. Q. Sulawesi lakes, Indonesia. R. Tombigbee–Alabama Rivers of the Mobile Bay Basin. S. Lower Uruguay River and Rio de la Plata; Argentina, Uruguay, Brazil. T. Western lowland forest of Guinea and Ivory Coast. U. Lower Zaire Basin. V. Zrmanja. W. Northwestern Ghats, India. X. Lower Mekong River; Thailand, Laos, Cambodia. Y. Northern Australia. *From Strong et al. (2008).*

are more widely distributed than species of caenogastropods, including the pleurocerids. The greater distribution of pulmonates may relate to life-history adaptations, such as shorter life-cycles and greater passive dispersal potential of air-breathing juveniles (Brown and Johnson, 2004). The shells of pleurocerids are generally more solid than in pulmonates, and the aperture may bear a shell canal anteriorly. Pleurocerid females may also be distinguished by their possession of an egg-laying sinus on the right side of the foot (Dazo, 1965; Strong, 2005).

Caenogastropods

The taxonomy and systematics of the family Pleuroceridae are poorly understood and are based on morphological characters that might mask true species delineations (Minton and Lydeard, 2003). Most of the recognized pleurocerid genera appear to be polyphyletic (Holznagel and Lydeard, 2000; Minton and Lydeard, 2003; Minton et al., 2005). Pleurocerids have a distribution centered in the southeastern and central United States, with greatest diversity in the Mobile basin and Ohio basin watersheds. Historically, diversity was highest in Alabama (100 species), followed by Tennessee (36 species), Georgia (20 species), and Kentucky

(15 species) (Burch, 1989). The most species-rich river system was the Coosa River in Alabama (45 species), followed by the Tennessee River (29 species), and the Cahaba and Cumberland Rivers (15 species each). *Elimia* is the most diverse pleurocerid genus and has >100 species. *Gyrotoma*, known for its characteristic slit in the body whorl, had 6 species in Alabama rivers, but all are now extinct (Table 18.2). The taxonomy of pleurocerids is based on shell characters, although many species have plastic morphology. Many of the pleurocerids are polyphyletic. The systematics of this group will likely be modified with molecular and morphological information. Many of the pleurocerids of the southeastern United States are of conservation concern or are extinct (Table 18.3). Two pleurocerid subfamilies occur in Asia: oviparous Pleurocerinae and ovoviparous Lavigiinae that includes *Semisulcospira* (Dudgeon, 1999). *Semisulcospira* occurs in northeast Asia and Japan and south into northern Vietnam and Guangdong Province, China (Liu et al., 1993). Asian Pleuroceridae are not well known (Dudgeon, 1999).

Viviparids are worldwide in distribution, and fairly diverse with 29 species in North America (Burch, 1989; Neves et al., 1998). As the name implies, they are ovoviviparous, holding their developing embryos in a brood pouch.

TABLE 18.2 Number of Extinctions in Pleurocerid and Hydrobiid Genera and their Original Distributions (States)

Family	Genus	Number of Extinctions	Original Distribution
Pleuroceridae	<i>Athearnia</i>	1	Tennessee, Virginia
	<i>Elimia</i>	15	Alabama, Georgia
	<i>Gyrotoma</i>	6	Alabama
	<i>Leptoxis</i>	12	Alabama, Georgia, Kentucky, Ohio, Tennessee
Hydrobiidae	<i>Clappia</i>	1	Alabama
	<i>Fluminicola</i>	1	Georgia
	<i>Marstonia</i>	1	Alabama
	<i>Pyrgulopsis</i>	3	Nevada
	<i>Somatogyrus</i>	2	Arizona

Data were taken from NatureServe (2007), with additions by P. Johnson, Alabama Aquatic Biodiversity Center.

TABLE 18.3 The Diversity of Freshwater Snail Families in North America¹

Higher Taxom ²	Family	Number of Genera	Number of Species	Area of Greatest Diversity ³
Neritomorpha	Neritidae	1	5	SE
	Caenogastropoda			
	Ampullaridae	2	4	SE
	Bithyniidae	1	1	NE
	Hydrobiidae	28	306	U
	Micromelaniidae	1	1	ES
	Pleuroceridae	7	170	U
	Pomatiopsidae	1	6	ES, W
	Thiaridae	2	3	SW, SE
	Viviparidae	5	29	SE, C
Heterobranchia	Acroloxiidae	1	1	NE
	Ancylidae	4	13	U
	Lymnaeidae	9	58	N
	Physidae	4	43	U
	Planorbidae	11	47	U
	Valvatidae	1	11	U

¹Data compiled from Burch (1989) and Neves et al. (1998).

²See Table 18.1.

³N = North; E = East; W = West; S = South; U = Ubiquitous.

Sexes are dimorphic, with females living longer and reaching larger sizes. Populations in northern states are biennial or perennial and iteroparous, while populations in southern states have shorter life-cycles. Males are recognized by an enlarged right tentacle used in copulation. *Campeloma*, *Lio-plax*, and *Tulotoma* are endemic to North America. Although the first two genera are widespread, *Tulotoma* was once considered extinct and has only recently been rediscovered in Alabama rivers. *Viviparus* is quite common in rivers and lakes throughout eastern North America. Snails in the genus *Bellamyia* occur in Africa, India, and Southeast Asia (Figure 18.7(b); *B. angularis*).

The Bithyniidae are the smallest of the Viviparaceae, usually less than 20 mm in shell height (Dudgeon, 1999). The habitat is usually standing water or slow-flowing streams. Eggs are laid by females in masses with each egg enclosed by a capsule. Genera in tropical Asia include *Bithynia*, *Digonostoma*, *Mysorella*, *Parabithynia*, *Emmericiopsis*, *Hydrobioides*, *Mysorella*, *Parabithynia*, *Parafossarulus*, *Pseudovivipara*, *Sataria*, and *Wattebladia* (Dudgeon, 1999). A key for Bithyniidae of Thailand was developed by Chitramvong (1992).

Ampullarids (or apple snails) are a tropical, mostly amphibious family with a mantle cavity provided with both a gill and a lung. The Pilidae or “apple snails,” including snails in the genus *Pila*, are the most common and widely distributed genus in tropical Asia (Dudgeon, 1999). An exotic from South America, *Pomacea canaliculata* Lamarck, occurs in polluted streams in Hong Kong and southern China (Dudgeon, 1999). The two genera present in Florida, *Pomacea* and *Marisa*, are quite large snails (50–60 mm). The planospiral-shelled *Marisa* has also been introduced to rivers in central Texas. Apple snails (*Pomacea*) lay calcareous eggs on emergent vegetation, evidently to escape aquatic egg predators. Adults can also use a siphon to route air to their lung while submerged to escape predation by avian predators. *Marisa*, in contrast, lays strings of gelatinous egg masses underwater. Apple snails are common in the aquarium trade, and escape into subtropical areas in the southern states has occurred, with invasive populations in many of the states bordering the Gulf of Mexico.

The Neritidae are primarily a marine, tropical group (Figure 18.13), but a few species have invaded estuarine and freshwater habitats—for example, *Neritina reclivata* (Say 1822) in some southern US states (Florida, Georgia, Alabama, and Mississippi). Their paucispiral, calcareous operculum has a pair of projections that lock the operculum against the teeth on the aperture, providing a stronger defense. Freshwater neritid gastropods occur in coastal streams of tropics and subtropics throughout the world.

The 11 North American valvatids are Holarctic in distribution (Table 18.3) and occur mostly in lakes in northern states. Valvatids are egg-laying hermaphrodites, with a single, feather-like gill carried on the left side and a pallial



FIGURE 18.13 *Clithon* is a Neritid. Neritidae are a marine, tropical group that moved into estuarine and freshwater habitats. Photograph courtesy of Chris Lukhaup.

tentacle carried on the right side of the shell as the animal crawls. Valvatids have small (~5 mm diameter) dextral shells, with a corneous, slightly concave and thin, multispiral operculum. The spire is only slightly elevated, and the shells are sometimes carinated.

A single genus of Littorinidae occurs in tropical Asian streams, but higher diversity is in mangroves and brackish water (Dudgeon, 1999).

Davis et al. (1986) and Wilke et al. (2001) defined the Pomatiopsidae as distinct from Hydrobiidae. Additional information for a smaller group of Mediterranean Hydrobiinae was found by Wilke (2003), including a new genus, *Salenthydrobia*. Other molecular studies on hydrobiids include use of refugia by *Bythinella* spp. during the recent glaciation. European *Bythinella* species that inhabit springs survived the Pleistocene glaciation in small northern refugia (Benke et al., 2009). Tropical Asia genera include *Clenchella*, *Rehderiella*, *Gluviopupa*, and *Tatea* (Dudgeon, 1999).

Hydrobiids are extremely diverse and widespread in freshwater, with brackish water and marine representatives as well. Their small size but thick shell protects them from fish predation, and they dominate the gastropod assemblage of many northern lakes (Brown, 1998). There are 103 genera worldwide (Burch, 1989), and they are diverse in North America (Table 18.3). The small, dextral shells have generally a paucispiral operculum. Because of the similarity of their shells, the structure of the verge (penis) is used in classification. The family Hydrobiidae is, in fact, the largest family of North American freshwater molluscs (Burch,

1989; Kabat and Hershler, 1993). *Ammicola* (8 species) is widespread and abundant in lakes and rivers and occurs in >40 US states and across the southern provinces of Canada (Burch, 1989). Other abundant genera include *Somatogyrus* (38 species), *Marstonia* (15 species), and *Fontigens* (11 species). *Pyrgulopsis* (Hershler and Sada, 2002) and *Tryonia* (Hershler, 2001; Hershler et al., 2005) have diversified extensively in the western United States and northern Mexico (Hershler, 1984; Hershler and Thompson, 1992; Liu and Hershler, 2005). Most western North America hydrobiids are endemic to isolated groundwater seeps, single springs, or spring complexes (Hershler, 2001; Hershler and Liu, 2004; Hershler et al., 2002a,b), in part because springs provide thermal stability and uniform flows.

Davis et al. (1986) described nine Pomatiopsids from Yunnan, China in the family Triculinae. Morphological shell variation is high. This family includes multiple species that transmit Asian *Schistosoma* parasites of humans. This is the largest coenogastropod family in tropical Asia, with extensive speciation in south and east Asia (Dudgeon, 1999). Endemics include the genera *Delavaya*, *Fenouilia*, *Gamatricula*, *Guoia*, *Halewisia*, *Hydrorissioia*, *Jinhongia*, *Jullienia*, *Lithoglyphopsis*, *Lacunopsis*, *Neotricula*, *Pachydrobia*, *Paraprososthenia*, *Robertsia*, and *Wuconchona* (Dudgeon, 1999). The six North American pomatiopsids are similar in general anatomy to the hydrobiids. Pomatiopsids are, however, amphibious, inhabiting stream banks, while hydrobiids are truly aquatic (Burch, 1989). Systematics of worldwide pomatiopsids are discussed by Davis (1979), who suggested that Pomatiopsidae origins were Gondwanaland, with subsequent transfer to Asia with collision of plates that formed the Himalayas. The resulting stream captures produced the large rivers of Southeast Asia. Wilke et al. (2001) described systematics of several Pomatiopsidae taxa in their molecular treatment of Hydrobiids.

The Stenothyridae occur on wood or sandy or muddy substrates and feed on decomposing organic matter (Dudgeon, 1999). These are primarily brackish, but *Gangetica* and *Stenothyra* are freshwater genera (Dudgeon, 1999). They have separate sexes and are oviparous. Freshwater *Stenothyra* occur only in lotic habitats.

The Thiariidae family is taxonomically unstable, partly due to high intraspecific variation in shell morphology among some taxa (*Melanoides* and *Thiara*; Dudgeon, 1999). Widely distributed Asian genera include *Adamieta*, *Antimelania*, *Brotia*, *Neoradina*, *Paracrostoma*, *Sermyla*, *Stenomelania*, and *Sulcospira* (Dudgeon, 1999). An example of an endemic is *Tylomelania*, which occurs only in Sulawesi (Figure 18.10(b)). Thiariid females are parthenogenetic, brooding eggs in a pouch in the neck region, which opens on the right side. This primarily tropical genus has had some species invade North America. In contrast, the similar-shelled pleurocerids, discussed above, are dioecious and oviparous.

Pulmonates

Ancylids, or freshwater limpets, have a worldwide distribution, and all possess a simple cone-shaped shell. In North America, they have reached moderate diversity (Table 18.3). Ancylids have sinistral shells, with the apex inclined slightly to the right and the gill (pseudobranch) and many of the internal organs opening on the left side of the body. Their streamlined shape allows them to colonize fast-flowing streams, where they are often common on rocks or macrophytes. *Ancylus* is distributed from northern Africa to the Caspian Sea and the Transcaucasian region, with isolated occurrences in Egypt, southern Arabia, and Turkestan (Soldatenko and Starobogatov, 2004). Albrecht et al. (2006) detected eight species of *Ancylus* they described as a species flock from Lake Ohrid, on the border of Albania and Macedonia. There are four families of freshwater pulmonates in Asian streams: Lymnaeidae, Physidae, Planorbidae, and Ancylidae (Dudgeon, 1999). Pulmonates are not as widespread and abundant as coenogastropods in Asia.

The family Acroloxidae occurs mainly in Eurasian lakes and ponds. Only one species of *Acroloxus* occurs in the United States (Colorado) and southeastern Canada. Since the apex in *Acroloxus* is tipped to the left, the aperture is considered to be dextral, unlike the ancylid limpets.

Lymnaeids are worldwide in distribution, and are the most diverse pulmonate group in the northern United States and Canada (Table 18.3). Lymnaeids have broad triangular tentacles and lay long, sausage-shaped egg masses. Lymnaeids have fairly uncomplicated, large teeth on their radula, which are useful for cropping long strands of filamentous algae. One group of lymnaeids, found along the Pacific coast of North America, has limpet-shaped shells, but they are larger than ancylids. Building on the earlier work of Baker (1911), Burch (1989) recognized 55 species of lymnaeids in seven genera: *Acella*, *Bulimnea*, *Fossaria*, *Lymnaea*, *Pseudosuccinea*, *Radix*, and *Stagnicola*. *Acella haldemani* (Binney) can be recognized by its extremely elongated shell and *Bulimnea megasoma* (Say) by its large size and extremely wide body whorl. *L. stagnalis* (adults ~5 cm in length) is a fairly common circumboreal species found in permanent ponds. *Pseudosuccinea columella* (Say 1817) is a common amphibious species with a large aperture and clear shell that is found just above the water's surface, while *Galba* (= *Fossaria*) are the smallest lymnaeids, with shell lengths <10 mm, and often occur in temporary habitats. Hubendick (1951) was more of a systematic "lumper" and only recognized 13 species of lymnaeids in North America and placed them in only one genus, *Lymnaea*.

Members of the widespread pulmonate genus *Physa* also have a worldwide distribution and are ubiquitous in North America (Table 18.3). Indeed, few aquatic environments lack natural or introduced populations of physids. Their shells are small, sinistral, with raised spires.

Their tentacles and foot are slender; they sometimes have finger-like mantle masses extending over the shell. Their radular teeth are smaller and more complicated in shape than those of the lymnaeids, and they are better at harvesting more tightly attached periphyton species like diatoms or in feeding on detritus. Their rate of crawling is much more rapid than most gastropods, and this along with their early age at maturity and high fecundity explains why they are so widespread (Brown et al., 1998). Recent research suggests that the species diversity of physids has, however, been exaggerated because of the eco-phenotypic plasticity in shell morphology that occurs in the group. For example, Britton and McMahon (2004) found considerable shell-shape variation in a single population of *Physa virgata* Gould (= *acuta*), where shell shape varied from fat (e.g., relatively large body whorl) to thin (acute spire angle and elongated shell) and had both a genetic and environmental basis. Thin shell shape probably has an adaptive basis for shell-invading predators like crayfish to consume, while fat shells are more difficult for molluscivorous fish to consume by crushing the shell. Physids may face a tradeoff, as evolving a rotund shell may increase susceptibility to crayfish, and an elongate shell to fish (DeWitt et al., 2000).

Recent systematic work based on molecular methods (Wethington and Lydeard, 2007) indicated, in fact, that many physid "species" are potentially ecophenotypic variants of two major species complexes. *Physa gyrina* (Say 1821) is fairly common and is the only physid where (1) adult shell length is >10 mm, (2) the shell spire is not elevated significantly above the body whorl, and (3) egg masses contain more than 20 eggs. The other major species complex belongs to *Physa acuta* Draparnaud, which subsumes several junior synonyms: *P. virgata* (Gould 1855), an ecomorph common in southern states; *Physa heterostropha* Say, in midwestern states; and *Physa integra* Haldeman, in northern states. This molecular data supports experimental work indicating reproductive isolation only between *P. gyrina* and *P. acuta* (Dillon et al., 2002, 2005).

Planorbids (ramshorn snails) are also widespread and fairly diverse snails (Table 18.3), and their planospiral shells range in size from minute (1 mm) to large (30 mm) in North America. They possess hemoglobin as a respiratory pigment, sometimes giving the tissue a red hue. Their egg cases are flat and circular, with harder membranes than those of the lymnaeids or physids. Their systematics were first treated by Baker (1945) and revised by Hubendick (1955), who also proposed linking planorbids to the ancylids (Hubendick, 1978). This latter proposal has recently received renewed support from studies of their molecular genetics. Burch (1989), however, revised their taxonomy, removing all but one species (*Helisoma anceps* Menke) from the genus *Helisoma*.

Reproduction and Life History

Freshwater snails are extremely interesting because of the variety of observed life-history patterns (Dillon, 2000). For example, freshwater pulmonates are oviparous (egg-laying) hermaphrodites, and are usually annual and semelparous (e.g., they reproduce once and die). On the other hand, almost all caenogastropods are dioecious, and are often iteroparous, with perennial life-cycles. Caenogastropods can be oviparous or ovoviviparous (Russell Hunter, 1978; Calow, 1978, 1983; Brown, 1983). Annual species have essentially a one-year life-cycle, whereas perennials often live and reproduce for 4–5 years.

Russell-Hunter (1978) and Calow (1978) classified life histories for freshwater gastropods (Figure 18.14). At one end are annual adults that reproduce in the spring and die (i.e., there is complete replacement of generations). Most pulmonates belong to this group, including species of *Lymnaea*, *Physa*, and *Aplexa* (the original studies are listed in Calow, 1978). In the second category (Figure 18.14), reproduction occurs in both spring and late summer, with both cohorts surviving the winter, or (Figure 18.14) where there again is complete replacement of generations. Figure 18.14 shows three reproductive intervals, with varying degrees of replacement of generations. These would predominantly be populations in subtropical or tropical environments. Finally,

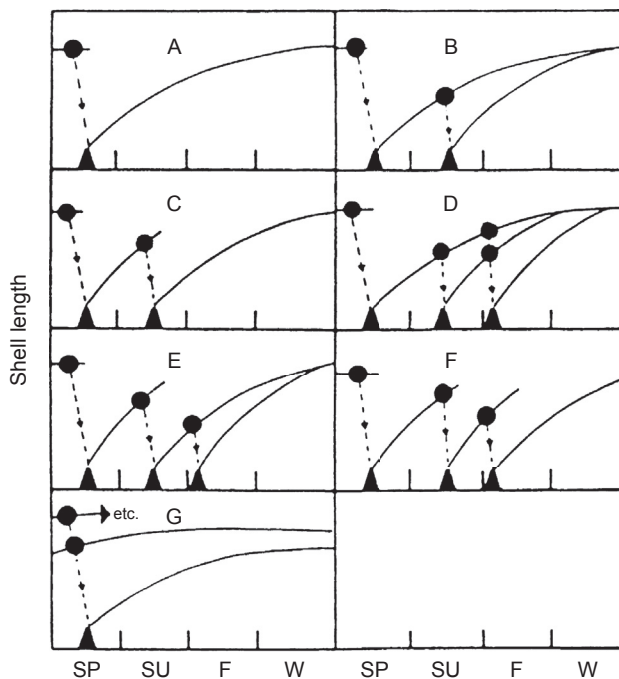


FIGURE 18.14 The variety of life-cycles in freshwater snails. Curves represent the growth of individual cohorts (in mm shell length), circles represent size at maturity, and triangles represent appearance of egg cases in samples. Panel A represents annual semelparity and B through F represent increasing numbers of cohorts per year, while panel G represents perennial iteroparity. See discussion in text. From Calow, 1978.

there are populations that can truly be considered perennial and iteroparous (Figure 18.14), with most being caenogastropods. For example, the pleurocerid genus *Elimia* has life-cycles lasting from 6 to 11 years in Alabama streams, with several cohorts overlapping at any one time (Richardson et al., 1988; Huryn et al., 1994). Adults reproduce in the spring and summer and are more common in areas of low current velocity, while juveniles are common in the fall in high-flow areas (Huryn et al., 1994; Johnson and Brown, 1997).

Marine snails have enormous fecundity, but individual eggs are extremely small. Most marine snails are caenogastropods, and freshwater caenogastropods (their descendants) probably have retained small eggs as a result. In fact, viviparids and thiarids may have evolved ovoviviparity (and in some cases the production of larger embryos) to cope with the much more unpredictable conditions in freshwaters (Calow, 1978, 1983). Similarly, the loss of the planktonic veliger and shortening of the developmental period in oviparous freshwater snails have been attributed to the more variable physicochemical conditions (Calow, 1978).

Reproductive effort (percent of energy devoted to reproduction) is lower in iteroparous freshwater snails than in semelparous ones (Browne and Russell-Hunter, 1978). For example, pulmonate families are semelparous with relatively high reproductive output (Brown, 1983). Pulmonates also reproduce at smaller sizes and earlier ages, produce more eggs, and have larger clutch sizes, greater shell growth rates, shorter life-cycles, and smaller final shell sizes than viviparid caenogastropods.

The reduced fecundity but increased parental care found in viviparids (versus semelparous pulmonates) increases offspring survival. Life tables for *Viviparus georgianus* Lea (Jokinen et al., 1982) and for the pulmonate *Lymnaea elodes* Say (Brown et al., 1988) indicate that survival to maturity is indeed much less than 1% in all of the pulmonate populations, but over 40% in the ovoviviparous viviparid. Caenogastropods are also sexually dimorphic in life-history patterns. Female viviparids live longer (males usually survive for only one reproductive season) and reach larger sizes (Browne, 1978; Jokinen et al., 1982; Pace and Szuch, 1985; Brown et al., 1989).

Numerous studies have implicated periphyton productivity (Eisenberg, 1966, 1970; Burky, 1971; Hunter, 1975; Browne, 1978; Brown, 1985) in determining voltinism patterns, growth rates, fecundity, and gastropod secondary production (see review in Russell Hunter, 1983). Other important factors include water hardness and temperature. For example, populations of *Elimia* in limestone-substrate streams in Alabama have greater annual production than populations in relatively impermeable slate or sandstone-substrate streams (Huryn et al., 1995), both because of the higher alkalinity, and greater buffering of low

temperatures in the winter by groundwater. Similarly, populations of *L. stagnalis* in Canada often take several seasons to complete their life-cycle (while populations are annual in the warmer waters of Iowa (Brown, 1979). As the photoperiod lengthens, the snails switch from storing energy to reproducing and using up energy stores (Ter Matt et al., 2007).

Lymnaea peregra Müller in wave-swept habitats in English lakes have r-selected life-history traits (e.g., early reproduction and high reproductive output) in comparison to populations in less-harsh habitats (Calow, 1981). However, other studies of life-history variation in molluscs do not agree as well with the predictions of r and K theory (see discussion in Burky, 1983). Transplant studies, where individuals from separate populations are reared in a common environment, have usually indicated that environmental effects on life histories are much more important than genetic differences between populations. For example, populations of *L. elodes* reared in more productive ponds lay nine times as many eggs, have an annual versus a biennial reproductive cycle, and reach larger individual sizes (Brown, 1985).

Although genetic polymorphism has been studied using gel electrophoresis in terrestrial pulmonates and freshwater caenogastropods more than in aquatic pulmonates, freshwater snails still appear to have levels of genetic polymorphism intermediate to terrestrial and marine species (Brown and Richardson, 1988). Terrestrial snails inhabit patchily distributed microclimates, which increases chances for low population densities and self-fertilization, resulting in little genetic polymorphism within populations. Freshwater snails decline to low densities because of seasonal bottlenecks and thus may also self-fertilize. Marine environments are less seasonal, and many marine snails have planktonic larvae, facilitating gene flow and increasing polymorphism.

Caenogastropoda

Caenogastropods are usually dioecious, and males either use the enlarged right tentacle as a copulatory organ (in the viviparids), possess a specialized penis or verge (in the hydrobiids, pomatiopsids, and valvatids), or have no copulatory organ (thiarids and pleurocerids). Many pleurocerids lay clutches of a few eggs, whereas viviparids lay eggs that hatch and develop in a fold of the anterior mantle (the pallial oviduct), and are born free living. Some viviparids in the genus *Campeloma* are parthenogenetic (Johnson, 1992). One group of native freshwater snails, family Valvatidae, is hermaphroditic. The invading hydrobiid, the New Zealand mud snail *Potamopyrgus antipodarum* Gray is parthenogenetic, with males rare or non-existent in populations. Thiarids are frequently parthenogenetic, but nominally parthenogenetic populations have males that may be sterile. Thiarid populations that are invasive are composed of parthenogenetic individuals (Dudgeon, 1999). Most thiarids are ovoviviparous with a cephalic brood pouch to incubate hatchlings. An exception is *Stenomelania*, with planktonic veliger larvae. *F. ater* (Figure 18.10(a)) is an oviparous Thiarid that is widely distributed and occurs in lower reaches of streams and rivers in fresh or brackish locations. Males produce spermatophores and females lay large eggs from a grooved “ovipositor” on the foot (Starmühlner, 1974).

Pulmonata

Adult pulmonates are generally simultaneous hermaphrodites, with the ability to self-fertilize with a fitness loss (Dillon, 2000). The diverse reproductive strategies include sperm storage, multiple insemination, sperm sharing, mixed mating, and aphyally (Dillon, 2000). The basic components of the pulmonate reproductive system are shown in Figure 18.15. Sperm and eggs are produced in the ovotestis and exit via a common hermaphroditic duct in all pulmonates except

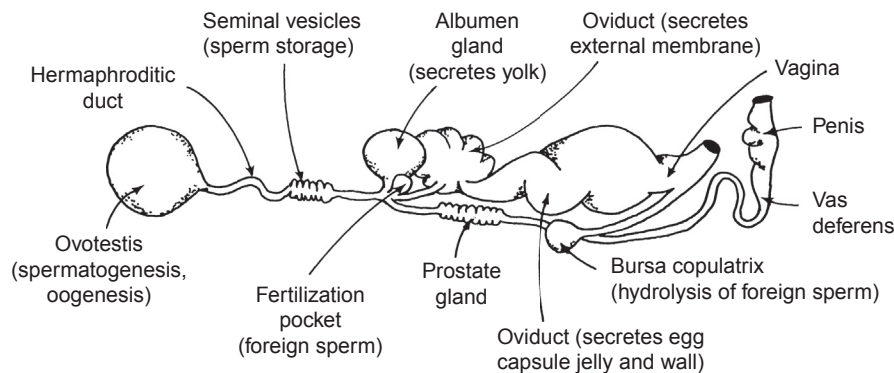


FIGURE 18.15 Anatomy of the reproductive system of the monoecious pulmonate *Physa* (after Duncan, 1975). Sperm are produced in the ovotestis, stored in the seminal vesicle, exit via vas deferens, and are inserted into the vagina of a second individual via the introvertible penis, or may fertilize the same individual's eggs in the hermaphroditic duct. Most foreign sperm are hydrolyzed in *Physa* in the bursa copulatrix, but some do fertilize eggs in the fertilization pocket. The albumen gland secretes yolk around the egg, and the oviduct wall secretes both the egg membrane and the jelly and external wall of the egg case.

ancylids, which have two openings and thus obligate cross-fertilization. The albumen gland adds protein and nutrients to the eggs. Eggs are fertilized in the hermaphroditic duct near the junction of the hermaphroditic duct and the oviduct by either the same individual's sperm or by sperm from another individual. The external egg membranes are then secreted in the oviduct. Eggs are laid in gelatinous egg cases and attached to plants or rocks. Males have an introvertible penis and fertilization is internal. [Duncan \(1975\)](#) described details of egg and sperm formation, copulation and fertilization, and egg capsule deposition. Although pulmonates are simultaneous hermaphrodites, most species outcross when possible. Pulmonates that self-fertilize usually mature at later ages and have lower fecundity. For example, *Physella heterostropha* suffers a reduction of 65% in fecundity when not allowed to outcross ([Wethington and Dillon, 1993](#)). Snails act as males or females based on the amount of stored sperm that they possess ([Wethington and Dillon, 1996](#)). Similarly, the African snail *Bulinus globosus* (Morelet 1866) suffers a 50% reduction in fecundity and an 18% reduction in hatching rate under obligate self-fertilization, indicating a significant "genetic load" of recessive lethal genes ([Jarne et al., 1991](#)).

Why then does hermaphroditism occur at all in freshwater snails? Pulmonates are slow-moving and go through seasonal "bottlenecks" (precipitous declines in density). The chances of finding a mate in such situations are small, providing a selective advantage for monoecy. Pulmonates are dispersed passively as spat trapped in mud on birds' feet ([Boag, 1986](#) and references therein), and solitary, monoecious immigrants have an obvious advantage. The cost of inbreeding depression is evidently less than not being able to reproduce at all. Parthenogenesis (being able to reproduce without males) may have a similar adaptive value for caenogastropod snails that are isolated in small headwater streams ([Vail, 1978](#)).

GENERAL ECOLOGY AND BEHAVIOR

Habitat and Food Selection and Effects on Producers

Habitat Choice

Habitat selection in gastropods seems based on shell shape, life history, and physiology, as illustrated by the ecology of pulmonates and caenogastropods (formerly Prosobranchia) ([Brown et al., 1998](#)). Pulmonates can use aerial respiration and have shells with higher drag coefficients. They have life-history characteristics such as higher reproductive rates, shorter life-cycles, and stronger dispersal abilities. Caenogastropods, in contrast, have gills and are limited to aquatic habitats. Their shells tend to be streamlined, and these snails have life-history characteristics that are the opposite of pulmonates. Habitats with increased disturbance, decreased

predation pressure, and more abundant food resources are often characterized by dense populations of pulmonates.

Habitat selection varies among major groups and individual taxa. Slow-moving, silty habitats are occupied by pulmonates or detritivorous caenogastropods such as viviparids, whereas fast current areas are dominated by limpets or caenogastropod grazers like pleurocerids ([Harman, 1972](#); [Dudgeon, 1999](#)). [Greenwood and Thorp \(2001\)](#) studied two caenogastropods in the Ohio River, a large river. They found substantial variation in distributions, diets, and substrate use of the two primary species. *Campeloma decisum* (Say 1817) is positively rheotactic (moves upstream) and aggregates at any barrier (e.g., logs, riffle zones, etc.; [Bovbjerg, 1952](#)). *P. integra* and *Lymnaea emarginata* Say prefer cobble substrata with attached periphyton, while *H. anceps* and *Campeloma rufum* prefer sand ([Clampitt, 1973](#); [Brown and Lodge, 1993](#)). Most gastropods in northern Wisconsin lakes, however, prefer periphyton-covered cobble over sand or macrophytes ([Brown and Lodge, 1993](#)). Cobble, since it offers greater surface area and is present year-round, develops a richer periphyton coating. Substrate selection may even occur on a finer level; for instance, gastropods from an English pond prefer periphyton from the macrophytes on which the snails normally reside ([Lodge, 1986](#)). Snails often move among habitats as well. Migrations occur to deeper lake waters in the fall and back to the littoral zone in the spring ([Boag, 1981](#)). Pond pulmonates, on the other hand, burrow into the substrate with declining temperatures ([Boerger, 1975](#)).

Snail Diets

Freshwater gastropods are herbivores or detritivores, but occasionally ingest carrion ([Bovbjerg, 1968](#)) or small invertebrates associated with periphyton ([Cuker, 1983](#)). Periphyton is easier to scrape, and contains higher concentrations of nitrogen and other limiting nutrients than macrophyte tissue ([Russell-Hunter, 1978](#); [Aldridge, 1983](#)). For example, periphyton carbon-to-nitrogen (e.g., carbohydrate-to-protein) ratios are below 10.1:1, while macrophytes have ratios of 24.1:1 ([McMahon et al., 1974](#)). Algal and diatom remains, therefore, are dominant in the guts of snails ([Calow and Calow, 1975](#); [Kesler et al., 1986](#)). However, gastropods at high densities can exhaust periphyton and then consume macrophytes, suppressing macrophyte species richness ([Sheldon, 1987](#)). An additional feeding mechanism in Bithyniidae and Viviparidae is to trap food particles from their respiratory current in mucus, and then ingest the mucus ([Dudgeon, 1999](#)). [Dudgeon and Yipp \(1985\)](#) found diet overlap among caenogastropods and pulmonates in Hong Kong streams. However, the diet specialists tend to use directed foraging behavior (not random) compared to generalist feeders.

Dillon (2000) summarized the diets and habitats for 13 freshwater gastropod families, including physids, planorbids, *Biomphalaria*, *Bulinus*, lymnaeids, and limpets. Dillon (2000) also summarized diets of caenogastropods including a neritid *Theodoxus*, multiple pleurocerids (*Elimia*, *Juga*, and *Leptoxis*), hydrobiids, (*Potamopyrgus*, *Ammicola*), ampullariids (*Pomacea*), viviparids (*Campeloma*, *Viviparus*), bithyniids, (*Bithynia*), and valvatids (*Valvata*).

Feeding preferences for the freshwater gastropod families are summarized in Table 18.4. Lymnaeids are classified as “micro-herbivores,” scraping algae and diatoms from rocks or macrophytes. For example, although the lymnaeid *P. columella* is an omnivore, it still consumes more algae than the sympatric *Physa vernalis* Taylor & Jokinen (Kesler et al., 1986). The lymnaeid also possesses higher levels of cellulases, as well as a radula and jaws well adapted for cropping algae (Figure 18.5), and a gizzard filled with sand that can macerate food. The physid, a detritivore, lacks these adaptations.

Both the limpet family Ancyliidae and the caenogastropod family Pleuroceridae also graze on periphyton (Table 18.4). *Ancylus fluviatilis* Müller selectively grazes diatoms, but this limpet has little effect on periphyton communities, due either to adaptations of algal and diatom species to grazing, or to relatively low limpet abundances (Calow, 1973a,b). Aldridge (1983) concluded that pleurocerid

grazers feed on periphyton rather than macrophyte tissue, again because of higher levels of nitrogen.

The caenogastropod *Bithynia tentaculata* Linnaeus both grazes on periphyton and uses its ctenidium to capture phytoplankton. The latter is consolidated into a mucus string that loops from the mantle cavity to the mouth (Brendelberger and Jurgens, 1993). Indeed, filter feeding may be more efficient than scraping as increasing levels of phytoplankton shade out periphyton; this may explain why this genus has become so abundant in nutrient-rich, eutrophic lakes in the state of New York (Tashiro, 1982; Tashiro and Colman, 1982).

Viviparus georgianus is a micro-algivore (Duch, 1976; Jokinen et al., 1982) or a detritivore (Pace and Szuch, 1985). Most viviparids, however, are probably detritivores or utilize bacteria associated with detritus (Table 18.4). As macrophytes decompose, nitrogen levels increase, again increasing their value as food resources. For example, *Viviparus* reaches extremely high densities (from 151 to 608/m²) in wooded streams in Michigan (Pace and Szuch, 1985) and in detritus-rich bayous in Louisiana (up to 1700/m²; Brown et al., 1989). Viviparidae (Viviparidae, Ampullaridae, and Bithyniidae) supplement radula feeding by trapping and ingesting suspended particles by ciliary tract feeding (Dudgeon, 1999). Ampullaridae snails tend to be large (>10 cm in height or diameter) and occur in slow-flowing streams and ponds. *Pila* leaves streams to forage for plants, using a “lung” for respiration.

Both physids (Kesler et al., 1986) and planorbids (Calow, 1973b, 1974a) prefer detritus (Table 18.4). For example, although widely-spread species like *P. gyrina* and *Planorbella* (formerly *Helisoma*) *trivolvus* Say did not prefer detritus over periphyton in laboratory experiments, another physid, *Aplexa hypnorum* Linnaeus, much more common in wooded ponds with a rich detritus food base, did (Brown, 1982).

Originally, snail algivores were considered indiscriminate grazers, taking all components of the periphyton (Hunter, 1980; Russell-Hunter, 1983). However, limpets and planorbids are selective (Calow, 1973a,b), and *L. peregra* grazes selectively on filamentous green algae (Lodge, 1985). *Planorbis vortex* L. ingests diatoms in greater quantities than found in the periphyton, but is still predominantly a detritivore.

Gastropods locate macrophytes through distant chemoreception (Croll, 1983). For example, *L. peregra* is positively attracted to *Ceratophyllum demersum* L., because of dissolved organic materials excreted by the macrophyte (Brönmark, 1985). Similarly, *Potamopyrgus jenkinsi* (Gray 1843) orients toward both plant and animal extracts (Haynes and Taylor, 1984), while *Biomphalaria glabrata* Say either orients toward or away from specific macrophytes (Bousefield, 1979).

TABLE 18.4 Feeding Preferences of Freshwater Snails

Feeding Type	Family	Reference
Algivores (scrapers)	Ancyliidae	Calow (1973a,b), 1975
	Lymnaeidae	Bovbjerg (1968), Brown (1982), Calow 1970, Coker (1983), Hunter (1980), Kairesalo and Koskimies (1987), Kesler et al. (1986), Lodge (1986)
	Neritidae	Jacoby (1985)
	Pleuroceridae	Aldridge (1982, 1983); Dazo (1965), Goodrich (1945)
	Viviparidae	Duch (1986), Jokinen et al. (1982)
Detritivores or bacterial feeders	Physidae	Brown (1982), Kesler et al. (1986), Townsend (1975)
	Planorbidae	Calow (1973b, 1974a,b)
	Viviparidae	Chamberlain (1958), Pace and Szuch (1985), Reavell (1980)
Filter feeders	Bithyniidae	Tashiro (1982), Tashiro and Colman (1982), Brendelberger and Jurgens (1993)
	Viviparidae	Brown et al. (1989)

Effects of Snail Feeding

Freshwater snails are grazing omnivores that consume primarily periphyton or macrophytes. Exceptions include members of the predominantly marine Buccinidae, Marginellidae, and Acochliiida and freshwater Glacidorbidae, which are predators (Strong et al., 2008). The Viviparidae and Bithyniidae are in part ctenidial suspension feeders, and the Ampullariidae feed on bryozoans and planorbid eggs (Strong et al., 2008). Although diet studies exist for several species, there is little thorough coverage of taxa. Rollo and Hawryluk (1988) showed that *L. elodes* Say and *P. gyrina* modified their feeding rate when supplied reduced-quality diets, to maintain growth and reproduction. Dillon (2000) reviewed diet studies for freshwater snails.

Almost all experimental manipulations have indicated snail grazers can decrease periphyton standing crops (Table 10.3; see review in Brönmark, 1989b). For example, *Physa* at high densities reduces algal biomass by 97%, and richness by 66% (Lowe and Hunter, 1988). In some cases snails also increase algal production, perhaps by decreasing total biomass and lowering algal competition for light or nutrients, removing senescent cells, or increasing rates of nutrient cycling. Pulmonate gastropods can also alter the quality (e.g., nitrogen to carbon ratios and chlorophyll-*a* levels) of periphyton (Hunter, 1980), as can caenogastropods in streams (Steinman et al., 1987). Although low levels

of grazing may stimulate production, higher snail densities decrease both biomass and production (McCormick and Stevenson, 1989; Swamikannu and Hoagland, 1989). Grazing may not, however, have as much of an impact on shaded streams, where light may be the primary limiting factor (Hill and Harvey, 1990). Even in unshaded streams, there may be little overall effect of grazers, because the loss of the algal over story to grazing is compensated for by the competitive release and increased growth of adnate forms (Hill and Harvey, 1990).

Snail grazers selectively remove larger filamentous green algae, and leave smaller, adnate species behind (Table 18.5). Under slight gastropod grazing pressure, periphyton assemblages are dominated by filamentous green algae, but more intensely grazed assemblages are dominated by more tightly adhering species or by toxic species such as cyanobacteria. Snail grazers may, in fact, indirectly facilitate macrophytes by eating the periphyton that limits macrophyte growth. For example, the growth of *C. demersum* increased when gastropod grazers were present (Brönmark, 1989a), although increased growth also occurred when plants were exposed only to snail-conditioned water, indicating increased nutrient recycling was the cause (Underwood, 1991). Similarly, when sunfish depress snail abundances and increase periphyton abundance in fish enclosures (Table 18.5), they may indirectly depress macrophytes (Martin et al., 1992). The molluscivorous tench can have similar cascading effects on European gastropods, periphyton, and macrophytes

TABLE 18.5 The Effects of Experimental Manipulations of Gastropods on Periphyton Biomass, Production, and Assemblage Structure

Group	Decreased Algal Species Biomass	Increased Algal Production?	Favored Adnate Species?	Studies
Caenogastropods				
<i>Elimia</i> or <i>Juga</i> (N=11)	73%	17%	100%	Mulholland et al. (1983), Steinman et al. (1987), Lamberti et al. (1987), Marks and Lowe (1989), McCormick and Stevenson (1989), Hill and Harvey (1990), Mulholland et al. (1991), Tuchman and Stevenson (1991), Hill et al. (1991), Rosemond et al. (1993)
<i>Theodoxus</i> (N=1)	Y	N	Y	Jacoby (1985)
<i>Ammicola</i> (N=1)	Y	N.M.	Y	Kesler (1981)
Pulmonates				
<i>Physella</i> (N=3)	100%	N.M.	100%	Doremus and Harman (1977), Lowe and Hunter (1988), Swamikannu and Hoagland (1989)
<i>Promenetus</i> (N=1)	N	N	N	Doremus and Harman (1977)
<i>Lymnaea</i> , <i>Physella</i> , and <i>Helisoma</i>	Y	Y	Y	Hunter (1980)

Percentages refer to the number of studies noting an effect. For Single studies, Y=effect, N=no effect, N.M.=not measured.

(Figure 18.16). Thus, interactions between gastropod predators, snails, periphyton, and macrophytes may be very complex in natural systems.

Dispersal

A tropical family of gastropods, the Neritidae, includes several freshwater genera that occur in coastal streams (Figure 18.13; Pace, 1973; Ford and Kinzie, 1982; Schneider and Frost, 1986; Pyron and Covich, 2003; Blanco and Scatena, 2005). Growth rates and fecundity were studied by Shigemiya and Kato (2001) in Japan. The life histories of these snails includes reproduction in freshwater with eggs masses deposited on

stone surfaces. Following hatching, veliger larvae are washed downstream to estuarine reaches where pediveligers settle (Shigemiya and Kato, 2001). Small adults remain in the estuary or marine environment or migrate upstream to freshwater flowing environments (Shigemiya and Kato, 2001). Migration patterns vary among taxa and location with seasonal migrations and migrations that coincide with increased discharge events (Blanco and Scatena, 2005). Neritid snails have been studied in streams of Central America (Schneider and Frost, 1986), the Caribbean (Pyron and Covich, 2003; Blanco and Scatena, 2005, 2006; Ferney and Blanco, 2012), and Pacific islands of Hawaii (Way et al., 1993), Japan (Nishiwaki et al., 1991), and French Polynesia (Resh et al., 1990). Genetic studies of neritids demonstrated considerable marine dispersal of larvae among rivers on the same island, indicating constant recolonization of streams (Cook et al., 2009).

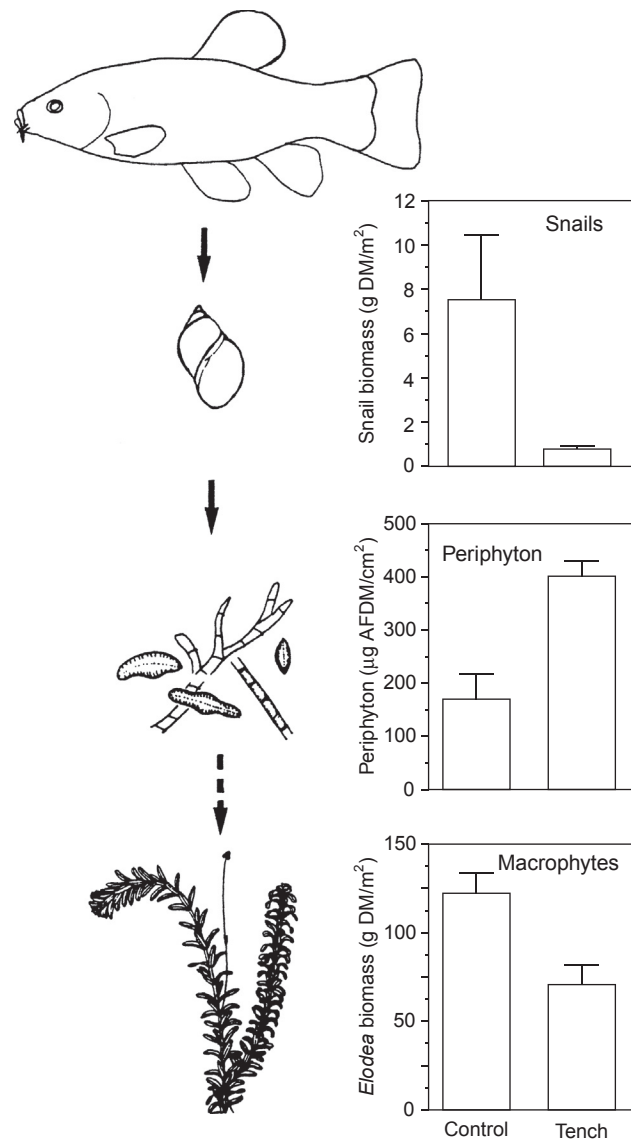


FIGURE 18.16 Cascading effects of a molluscivorous fish (the tench) on gastropods, periphyton, and macrophytes, based on a field manipulation (from Brönmark and Vermaat, 1998). Note how snails are depressed, periphyton increases, and macrophytes are shaded and decrease.

Population Regulation

Food Quality

One of the first demonstrations of population regulation under field conditions was with *L. elodes* (Eisenberg, 1966, 1970). When the density of adult snails in pens in a small pond was increased, adult fecundity declined, as did juvenile survival. With addition of a high-quality resource, spinach, an increase in the number of eggs per mass occurred. Evidently, the availability of micronutrients in periphyton was the crucial variable (Eisenberg, 1970). Brown (1985) provided additional evidence by transferring juvenile *L. elodes* among a series of ponds differing in periphyton productivity. There was an exponential increase in growth with increasing pond productivity, and snails in the most productive pond laid nine times as many eggs as snails in the two less productive ponds. A number of field studies also provide indirect evidence for the importance of resource abundance. For example, populations in more eutrophic habitats have more generations a year, more rapid shell growth, and lay more eggs (Burky, 1971; Hunter, 1975; McMahon, 1975; Eversole, 1978). Highly eutrophic sites may however be detrimental to gastropods, as gastropod diversity declined over a 50-year period as Lake Oneida, New York, became highly productive (Harman and Forney, 1970). In lotic systems, manipulation of periphyton resources and the abundances of caenogastropod grazers have indicated both that food resources can control snail density and size distributions, and that the snails can in turn control their food resources (Hill et al., 1991; Rosemond et al., 1993).

Parasitism

Although less studied than the role of periphyton, the parasitic larvae of trematode worms may also impact snail population dynamics and evolution (Holmes, 1983; Dillon, 2000). The adult worm produces eggs that are expelled in the feces of

the final host and hatch into an infectious larval stage called a miracidium. Once inside the snail host, miracidia asexually produce several stages (redia and sporocysts), which eventually produce thousands of cercaria that infect the final host or another intermediate host. Infections either accelerate or decelerate snail growth (Brown, 1978; Anderson and May, 1979; Holmes, 1983, see discussion in Minchella et al., 1985). Immediately after infection or exposure, snail egg production rates increase dramatically (Minchella and Loverde, 1981), evidently to lessen the eventual costs to fitness. As parasites consume the ovitestic and hepatopancreas, however, both growth and egg production of “patent” snails (those infections in the final stage where cercaria are emerging from snails) drop below that of uninfected snails (Minchella et al., 1985). Infected snails are castrated, and frequently have increased mortality (Davies et al., 2002) and reduced growth (Hay et al., 2005). Snail invaders may also have dramatic impacts on final host populations. *V. georgianus* and *Bythinia tentaculata* have invaded upper midwestern lakes in the United States in recent years, and digenetic trematodes they harbor have subsequently caused massive die-offs in final waterfowl hosts (Hoeve and Scott, 1988).

The role of trematodes in controlling snail populations is unclear, as prevalence (percent of population infected) varies considerably (Brown, 1978; Holmes, 1983). For example, prevalence in *L. elodes* in Indiana ponds varied from as low as 4% to as high as 49% (Brown et al., 1988). Prevalence was higher in less productive ponds, evidently because food limitation caused longer snail life-cycles that increased chances for snails to be located by miracidia. Life-table models predicted that the number of offspring produced per adult in the next generation declined by 14% to 21% in parasitized populations of *L. elodes*. In the case of *Physa acuta*, trematode infections cause increases in grazing rates, and the trematodes, therefore, indirectly affect periphyton biomass and composition (Bernot and Lamberti, 2008).

Trematode parasites and their snail hosts are also extremely interesting from a coevolutionary viewpoint (Holmes, 1983; Minchella et al., 1985). Because invertebrates cannot easily acquire resistance to parasites, frequency-dependent selection may operate to ensure the fitness of any genotype less vulnerable to a particular

trematode (Holmes, 1983). Parasites may also cause a shift in investment of resources from costly reproduction to growth and maintenance, and thus even increase survivorship of infected snails (see also Baudoin, 1975; Minchella et al., 1985; Sandland and Minchella, 2004). One evolutionary model, called the “red queen” hypothesis, suggests that gastropods are constantly evolving new phenotypes merely to stay ahead of their trematode parasites. For example, the New Zealand mud snail *Potamopyrgus* has both sexual morphs (able to produce genetically more variable offspring through recombination) and parthenogenetic morphs. The frequency of sexual reproduction is positively correlated with trematode prevalence, as one would expect if sexual morphs have an advantage (Lively, 1987). Sexual morphs are also more common in shallow water, where waterfowl (the final hosts) occur (Lively and Jokela, 1995). Infected snails are also more likely to forage during the day than uninfected snails or gravid females, suggesting parasites may modify snail behavior so they are more likely to be consumed by waterfowl, to complete the life-cycle (Levri and Lively, 1996). Experimental studies have suggested trematode populations are locally adapted to better infect their own host populations than snails from different lakes (Lively, 1989). Gene flow has not swamped such local adaptation, even though rates of gene flow are greater among parasite populations than among their snail hosts (Dybdahl and Lively, 1996). However, sexual reproduction may not be favored in all snail-trematode systems. In *Campeloma*, trematode metacercaria actually feed on sperm, and parthenogenetic morphs thus have an advantage (Johnson, 1992).

Caenogastropod taxa (e.g., *Melanoides*, *Oncomelania*, *Semisulcospira*, *Tricula*) tend to be intermediate hosts for trematode parasites that infect birds and mammals (Dudgeon, 1999). The systematics and ecology of these taxa are well-studied largely because of directed research toward parasitology.

Production Ecology

Average standing crop biomass, productivity, and turnover times differ between caenogastropods and pulmonates (Table 18.6). Standing crops are greater on the average for

TABLE 18.6 Comparison of Average Standing Stocks, Productivity, and Turnover times for Populations of Pulmonate and Prosobranch Snails

Taxon	Mean Biomass \pm SE (gCm ⁻² , N) ¹	Mean Production \pm SE (mgCm ⁻² day ⁻¹)	Mean Turnover time (days) \pm SE (N) ¹
Pulmonata	0.98 \pm 0.50 (6)	5.71 \pm 2.44 (10)	98.0 \pm 9.46 (10)
Caenogastropoda	4.64 \pm 1.80 (4)	3.56 \pm 0.51 (5)	385.3 \pm 33.5 (4)

¹N = Number of species averaged. Reported in Russell-Hunter and Buckley (1983).

caenogastropods than for pulmonates, although caenogastropod populations studied to date have not included genera with smaller individuals such as *Ammicola* and *Valvata*.

Even if pulmonates have lower standing stocks, their rapid growth and short life-cycles still result in higher average production rates and shorter turnover times (Table 18.6). For example, two pleurocerid grazers in an Alabama stream, *Elimia cahawbensis* (Lea 1861) and *Elimia clara* (Anthony 1845), have considerable biomasses of 2–5 g ash-free dry mass (=AFDM) per m², but slow growth rates and long life-cycles result in relatively low rates of secondary production (0.5–1.5 g AFDM m²). The combination of high biomass and low production results in a low production to biomass ratio of 0.3 (Richardson et al., 1988). Caenogastropod detritivores may, however, have higher production rates. *Viviparus subpurpureus* (Say 1829) and *C. decisum*, with high densities and short life-cycles in Louisiana bayous, have high standing crop biomasses (10–20 g AFDM/m²) and production rates (20–40 g AFDM/m²/yr), among the highest known for freshwater molluscs (Richardson and Brown, 1989).

Ecological Determinants of Distribution and Assemblage Structure

Snails in freshwater ecosystems are nonrandom species assemblages (Pyron et al., 2009; Hoverman et al., 2011) that are strongly influenced by predators and competitors (Turner et al., 2007). Lodge et al. (1987) concluded that at large, biogeographic scales, the variables that controlled assemblage structure were colonization ability and water chemistry; while disturbance regime, competition, and predation were stronger explanatory variables at local scales. Although water chemistry variables contribute to freshwater snail distribution and abundance patterns, a minimal level of water hardness (calcium concentration) is required to support snail physiology. Briers (2003) showed that calcium requirement of British freshwater gastropods was a strong predictor of range size. Species that were classified as calciphiles that require high levels of environmental calcium had smaller range sizes than species able to use a wider range of environmental calcium. Dussart (1979) studied snail assemblages (*B. tentaculata*, *Gyraulus albus* Müller, *Planorbis planorbis* Linnaeus, and *L. peregra*) in northwest England and found that substrate composition was more important than water chemistry in determining abundance patterns. Local environmental variables (substrate composition, water conductivity) were predictors of local assemblage composition for assemblages in Indiana in the United States (Pyron et al., 2009). Smaller drainage water bodies had higher abundances of pulmonates than caenogastropods (Brown et al., 1998; Pyron et al., 2009). Brown et al. (1998) predicted that abundance differences are due to physiological adaptations of pulmonates. Caenogastropods occur in

larger rivers because of their ability to withstand competition, and inability to withstand harsh physicochemical variation in smaller streams.

Watershed Connections and Chemical Composition

Although relatively few studies have examined the structure of freshwater snail communities (Hoverman et al., 2011), some have predicted species richness using environmental and biotic variables (Lodge et al., 1987). The number of lake connections (inlets and outlets that act as dispersal corridors) was correlated with species richness in northern highland lakes of Wisconsin and Michigan in the United States (Lewis and Magnuson, 2000). Species richness of pulmonates in individual watersheds increased with watershed size (Dillon and Benfield, 1982). Species turnover among lakes was important in the structure of snail assemblages of lakes in a Michigan preserve (Hoverman et al., 2011).

Water hardness and pH are often considered major factors determining the distributions of freshwater snails (Russell Hunter, 1978; Okland, 1983; Pip, 1986). However, in lake districts with adequate calcium (above about 5 mg/l CaCO₃), or in the normal (nonacidified) range of pH, relationships between physicochemical parameters and gastropod diversity are less clear (Lodge et al., 1987). For example, species in New York lakes overlap broadly in the ranges of physicochemical variable they occur in (Harman and Berg, 1971). Physicochemical parameters therefore set the limits for gastropod distributions, but are not as important in explaining the relative abundance patterns and densities of gastropods in most hardwater, circum-neutral lakes.

Biogeographic Factors

On a biogeographic scale, a factor determining gastropod distributions is dispersal ability. For example, relatively isolated lakes in upper watersheds in Wisconsin have fewer species than lowland lakes that are well connected by river corridors to other lakes (Lewis and Magnuson, 2000). Studies have also indicated diversity increases with the area of lakes and ponds (Lassen, 1975; Browne, 1981; Brönmark, 1989a; Dillon, 2000). Since immigration rates generally increase and extinction rates decrease with habitat size, larger habitats, all else being equal, usually support more species (MacArthur and Wilson, 1967). After dispersal, successful colonization depends on the presence of suitable substrates. For example, a significant relationship exists between the number of gastropod species and the number of substrates in lakes and streams in New York in the United States (Harman, 1972). In fact, substrate preferences determined in the laboratory are good predictors of the types of ponds in which snails are common, such as algivores in open ponds and detritivores in wooded ponds (Brown, 1982). Gastropod diversity is also

positively related to macrophyte biomass, probably because macrophytes increase surface area for periphyton colonization (Brown and Lodge, 1993).

Regional patterns for species richness at broad continental scales are shown in Figure 18.12. In tropical freshwaters, caenogastropods have higher species richness than pulmonates (Dudgeon, 1999). For example, 89% of freshwater gastropods in Java are caenogastropods and 11% are pulmonates (van Benthem Jutting, 1956). Canadian gastropods have the opposite pattern, with 16% caenogastropods and 84% pulmonates (Dudgeon, 1999).

Flow and Hydroperiod

Disturbance may also determine the assemblage of snails. In temporary ponds, diversity is lowered by frequent drying; and in habitats that go hypoxic, diebacks of macrophyte and gastropod populations will also occur (Lodge and Kelly, 1985; Lodge et al., 1987). Disturbance may also limit some species from disturbance-prone areas (wave-swept shores, littoral zones of reservoirs, etc.). In streams, current velocity may affect distribution and growth. For instance, adult *Elimia* avoid high-flow areas, perhaps because increased flow makes movement more difficult and lowers grazing rates or increases metabolic rates—both factors lowering adult size (Johnson and Brown, 1997). Juveniles are more common in fast-flowing areas because they are smaller and can exploit the boundary layer.

Predation

Predation is predicted to have a strong effect on local assemblages, and competition is predicted to be a strong influence in temporary ponds (Brown, 1982). The strength of competition in local assemblages appears to be slight compared to effects of disturbance regime and predation (Lodge et al., 1987). Brown et al. (1998) predicted that pulmonate taxa have increased competitive ability and caenogastropod taxa have decreased competitive ability at sites where food is a limiting factor.

Snail assemblage composition is not random as well across gradients of aquatic habitat permanence and predation risk. In northwestern Pennsylvania, vernal ponds have short hydroperiods but few predators; these systems are dominated by *P. vernalis*. Permanent ponds have the highest biomass of invertebrate predators, and are dominated by *Physa ancillaria* (Say 1825). Lakes have the highest biomass of fish predators, and are also dominated by *P. ancillaria*. *Physa acuta* is the only species that is a habitat generalist, evidently because of its high degree of phenotypic plasticity (Turner and Montgomery, 2009).

Competition

In large lakes, biotic interactions such as interspecific competition or predation are important in determining gastropod

diversity and abundance (Lodge et al., 1987). In regards to competition, some evidence suggests it is rare in freshwater snails. For example, pulmonate pond snails in the midwestern United States overlap little on food and habitat dimensions of the niche, although some species do compete (Brown, 1982). Other studies also indicate differences in resource utilization. For example, the ancyloid, *A. fluviatilis* prefers diatoms and is found on the top of cobble where periphyton is abundant, whereas the co-occurring planorbid, *Planorbis contortus* L. is a detritivore, and occurs more often under stones where detritus accumulates (Calow, 1973a,b; 1974a,b). Similarly, *P. columella* (Say 1817) and *P. vernalis* possess differences in their gut and radulae allowing coexistence in New England ponds (Kesler et al., 1986). Furthermore, niche partitioning may also be facilitated by differences among snails in enzymatic activity (Calow and Calow, 1975; Brendelberger, 1997) or radular morphology.

There is indirect evidence for competition. For instance, there are often fewer coexisting congeners in field samples than would be expected, based on mathematical simulations (Dillon, 1981, 1987). Second, competition has been inferred from changes in relative abundance of gastropod species through time, that is, by apparent competitive exclusion (Harman, 1968). Third, niche overlap can in fact be higher in more diverse snail assemblages found in large lakes. For example, the abundances of gastropod species in lakes are often positively associated in macrophyte beds, and experiments show most species have similar preferences for macrophytes (Brown, 1997). Finally, pulmonates are common in ponds or in vegetated areas of lakes, while caenogastropods are rare in ponds and common in lakes and rivers. One explanation could be competitive exclusion of pulmonates from lakes by caenogastropods, or exclusion of caenogastropods from ponds by the same mechanism. However, additional explanations include greater vulnerability of caenogastropods to hypoxic conditions in ponds, poorer dispersal abilities of caenogastropods, or the fact that thin-shelled pulmonates are more vulnerable to shell crushing fish common in lakes or rivers (Brown et al., 1998).

Snail Response to Predators

Adaptations to predation by aquatic organisms include morphological and chemical defenses, modified behavior, and life-history modifications (Kerfoot and Sih, 1987). The study of predation using freshwater snails as a model has been instructive due to multiple predators that specialize on freshwater snails and influence populations, and the large variation in body size and degree of shell development (Rundle and Brönmark, 2001). Predators include fishes, decapod crustaceans, and leeches (Brönmark and Malmqvist, 1986; Brown and Strouse, 1988; Covich et al., 1994). Predators that crush shells have preferences for thin-shelled snails (Stein et al., 1984; Sloatweg, 1987; Osenberg and Mittelbach, 1989; Alexander and Covich, 1991a; Nyström et al., 1999).

Behavioral responses to predators include reduced activity, remaining under cover, and crawling out of the water (Alexander and Covich, 1991b; Turner, 1997).

Snails with pseudo-lungs (the pulmonates), such as *Physa*, can partially avoid predation by leaving the water (Crowl and Covich, 1990; Mower and Turner, 2004). Gastropods that possess escape behaviors to avoid predators may experience reduced selection for morphological variation, compared to taxa that cannot escape by leaving the water (Ross et al., 2014). Exceptions to this pattern are species like *Campeloma*, a caenogastropod with reduced availability of shape variation. Species like *Campeloma* likely avoid predation by large body size, thick shell, presence of an operculum to cover the shell opening when the foot is withdrawn, and burrowing in sediments. Gastropods with taller shell spires are more susceptible to predation than gastropods with disc-like shells (Cotton et al., 2004). Thin-shelled species that are more vulnerable to predation thus use behavioral avoidance mechanisms, and thicker-shell species (e.g., *Campeloma*) tend to move under cover or have a mixed response (Rundle and Brönmark, 2001; Brönmark et al., 2011).

Physid gastropods have been excellent models for investigating predator–prey interactions. *P. gyrina* respond in different ways to crayfish and fish predators, using covered habitats in the presence of fish, or crawling above the water line when crayfish predators are active (Turner et al., 1999). The increased use of covered habitats, or habitats near the water surface, can also decrease periphyton biomass in those habitats (Turner et al., 2000). Smaller physids also tend to use behavioral avoidance like crawling out more than larger conspecifics that have thicker shells (DeWitt et al., 1999). Exposure to chemical cues from predators can also alter physid shell morphology. Elongate shells with narrow apertures decrease risk of crayfish predators, whereas a more rotund shell spreads crushing forces over a greater area and reduces risk from fish predators (DeWitt, 1998). These anti-predator responses in physids also have a spatial and temporal component, decaying over time or space. Snails do not respond to fish predators at greater than 1 m distance, nor to chemical cues older than about 40 h (Turner and Montgomery, 2003). Physids are also much more likely to respond to predation on conspecifics or congeners than more distantly related prey (Turner, 2008). Nor are these responses confined to physids alone. Hydrobiids of the genus *Ammicola* use periphyton-rich sand substrates in the spring, but switch to less-periphyton rich macrophytes in the summer, when crayfish predators are more abundant, resulting in a depression of snail growth rates (Lewis, 2001). The lymnaeid *Radix* also responds morphologically to predator cues, with a rotund shell again more resistant to fish predation (Lakowitz et al., 2008). Small lymnaeids or thin-shelled snails are also more vulnerable to crayfish predation (Brown, 1998; Nystrom and Perez, 1998). *Physa acuta* in

particular has been used as a model for predator effects (Crowl and Covich, 1990; DeWitt et al., 1999; Turner et al., 1999). *Physa* and many other gastropods detect predators by chemicals in the water (Covich et al., 1994). In the presence of crayfish—a size-selective shell-entry predator—*Physa* had fast growth and narrow apertures (Auld and Relyea, 2008). Auld and Relyea (2008) found increased shell thickness and delayed reproduction as a response to predator cues. However, increased shell thickness only occurred in *Physa* that had available mates. Auld and Relyea (2011) demonstrated that increases in shell thickness, mass, and shell dimension of snails induced by predator cues resulted in lower predation rates. Hoverman et al. (2005) also found delayed reproduction and fecundity in *Planorbella trivolvis* that were exposed to crayfish predators.

Indeed, Lodge et al. (1987) argued that predators determine the composition of gastropod assemblages in lakes. Indirect evidence includes the fact that gastropods have a number of anti-predator adaptations. These include thick shells to protect against shell-crushing predators (Vermeij and Covich, 1978; Stein et al., 1984; Brown and DeVries, 1985; Brown, 1998; DeWitt, 1998; Krist, 2002), as well as escape behaviors such as shaking the shell, crawling above the water to protect against shell-invading invertebrate predators (Townsend and McCarthy, 1980; Brönmark and Malmqvist, 1986; Brown and Strouse, 1988; Alexander and Covich, 1991a,b; Covich et al., 1994), or seeking underwater refugia (Turner, 1997). Molluscivores are common in lakes and rivers. For example, the pumpkinseed sunfish, *Lepomis gibbosus* L., and the redear or shell-cracker sunfish, *L. microlophus* (Guenther 1859), specialize on gastropod prey, and have pharyngeal teeth adapted to crush shells. Crayfish will select snails instead of grazing on macrophytes if given a choice (Covich, 1977), using their mandibles to chip shells back from the aperture, and selecting species with thinner shells (Brown, 1998).

Although Osenberg (1989) argued that lentic snail assemblages are limited by food resources, most experimental evidence supports a strong role for predators in determining snail diversity and abundance (Table 18.7). For example, the central mud minnow can significantly lower the density of relatively thin-shelled snails in permanent ponds. When fish densities were manipulated in pens, the number of eggs and juveniles of *L. elodes* was significantly less in the presence of fish. The small, gape-limited fish feed on eggs and juveniles and may restrict *L. elodes* from permanent habitats such as large marshes or lakes. Pumpkinseed sunfish also strongly prefer large, weak-shelled gastropod species in laboratory experiments, and thin-shelled species also decline dramatically in pumpkinseed enclosures in lakes (see references in Table 18.7). Thus, most thin-shelled pulmonates should occur in lakes only in macrophyte beds, where they have a refuge from visual predators. Moreover, sandy areas should be dominated by

TABLE 18.7 Summary of Experimental Field Manipulations Testing the Role of Snail Predators in Controlling Their Prey

Study	Prey	Predator	Conclusions
Brown and Devries (1985)	<i>Lymnaea elodes</i>	Mud minnows	Decreased abundance of eggs and juveniles of thin shelled <i>L. elodes</i> .
Sheldon (1987)	Assemblage	Sunfish	Removal of fish increased snails which decreased macrophytes through herbivory.
Kesler and Munns (1988)	Assemblage	Belostomatid bugs	Decreased snail abundances in New England pond.
Osenberg (1989)	Assemblage	Littoral sunfish	Fish controlled only rare, large snail species, competition considered more important.
Hershey (1990), Merrick et al. (1991)	Assemblage	Lake trout	Trout removed better competitor (<i>L.elodes</i>), favored poorer competitor, <i>Valvata</i> .
Martin et al. (1992)	Assemblage	Smallmouth bass Largemouth bass	Fish decreased snails 10-fold, increased periphyton biomass 2-fold, decreased algal cell size, decreased macrophytes.
Brönmark et al. (1992)	Assemblage	Pumpkinseed sunfish	Fish decreased snails, increased periphyton, favored adnate algae.
Bronmark (1994)	Assemblage	Tench	Fish decreased snails, increased periphpton, decreased macrophytes.
Lodge et al. (1994)	Assemblage	<i>Orconectes rusticus</i>	Crayfish decreased snails and macrophytes, had no effect on periphyton.
Daldorph and Thomas (1995)	Assemblage	Sticklebacks	Fish decreased thin-shelled snail species, increased periphyton.
Brönmark and Weisner (1996)	Assemblage	Piscivores and mol-luscivores	Molluscivores did decrease snails, but piscivores did not control increase in snails indirectly.

"Assemblage" refers to a natural community of gastropods.

thicker-shelled pulmonates like *Planorbella*, or by caenogastropods. Indeed, gastropod distributions among habitats within Indiana and Wisconsin lakes follow these patterns (Lodge et al., 1987; Brown and Lodge, 1993; Lodge et al., 1998). In fact, fish predators may indirectly benefit poorer gastropod competitors by preferentially removing dominant species. Lake trout, for example, preferentially consume larger lymnaeids, releasing valvatids from competition in Arctic lakes (Hershey, 1990; Merrick et al., 1991). However, experimental manipulations suggest such indirect effects do not extend through four trophic levels. Piscivores in Swedish lakes cannot depress predators to the extent that interactions cascade down the food web to facilitate snails and negatively impact periphyton (Brönmark and Weisner, 1996).

Invertebrate, shell-invading predators may also limit snail populations, or cause shifts in gastropod relative abundances. Although some leeches, such as *Nepheleopsis obscura* Verrill, have fairly low feeding rates (Brown and Strouse, 1988), crayfish can eat over a 100 snails per night. The crayfish *Orconectes rusticus* (Girard 1852) significantly reduced snail abundances in enclosure experiments in Wisconsin lakes (Table 18.7), and an inter-lake survey

indicated that snail abundances were negatively correlated with crayfish catches. Crayfish also affect gastropod habitat selection. For instance, even though cobble habitat is preferred by many snails (see earlier discussion), it also provides refugia for crayfish from fish predators. Crayfish predation overrides the effects of rich food resources (Weber and Lodge, 1990). Crayfish predators also shift size distributions of *P. virgata* upwards in Oklahoma streams, due possibly both to size selective predation and to the snail's diversion of energy from reproduction to growth to reach a size-based refuge from predation (Crowl, 1990; Crowl and Covich, 1990). Interestingly, only snails in vulnerable size classes respond by crawling out of the water after predation by crayfish occurred (Alexander and Covich, 1991b). Other invertebrate predators may also be important. For example, belostomatid bugs can eat as many as five snails per bug per day in the laboratory (Kesler and Munns, 1989).

Fish predators may alter snail foraging behavior as well. In experiments, *Physa* selects refugia in the presence of sunfish predators, only leaving them when sufficiently starved (Turner, 1997). This behavioral interaction may provide an additional explanation for why periphyton biomass increases when fish predators are present. For example, use

of open habitats by snails decreases with increasing predation risk to sunfish with the result that periphyton biomass also increases (Turner, 1997). Interestingly, such indirect facilitation of periphyton does not occur upon experimental addition of crayfish, probably because crayfish are also omnivorous and graze on periphyton (Lodge et al., 1994). In fact, behavioral avoidance of predators may be a more successful strategy than thicker shells. Thus, *P. acuta*, although it is smaller and has a thinner shell than *L. elodes*, suffers less from fish predation because it resorts to habitat refugia in the presence of molluscivorous fish while the lymnaeids does not (Mower and Turner, 2004).

Anti-predator adaptations can include multiple predator responses in a species. Trait compensation and co-specialization were demonstrated in *Physa* spp. where more vulnerable, smaller snails used stronger anti-predator behavior than large snails (DeWitt et al., 1999). Larger snails with reduced aperture size (a response to predation) exhibited less anti-predator behavior.

The cues that snails release as a response to predation can affect species interactions in local communities. Turner et al. (2000), for example, found that nonlethal effects of predators on snail behavior resulted in reductions in snail grazing on periphyton. Parasites can also have indirect effects on communities. Bernot and Lamberti (2008) tested this hypothesis in an experiment by infecting *P. acuta* with a trematode and quantifying that snail grazing on algae increased compared with uninfected snails. The algal assemblage changed from diatoms and cyanobacteria to one dominated by *Cladophora*. These changes in the algal assemblage were predicted to have effects on ecosystem function.

Flexibility in Shell Architecture

Evolutionary responses of shell architecture thus occur due to selective pressures of predation (DeWitt et al., 2000; Covich, 2010) and local and regional environmental variables. DeWitt et al. (2000) identified morphological responses in *Physa* that differ with local fish and crayfish predation. Increased shell thickness in pleurocerid taxa that are susceptible to predation by large-bodied fishes (freshwater drum, suckers) is presumably an additional response to ecological selective pressures. Whether similar morphological responses to predators occur in other taxa is unknown, but likely. Fish, crayfish, and other invertebrates are potential predators of freshwater gastropods and likely influence shell evolution (Vermeij and Covich, 1978; DeWitt et al., 2000; Turner and Montgomery, 2009). Local environmental variables, including flow (Holomuzki and Biggs, 2006; Minton et al., 2008), resource availability (Hoverman et al., 2005), and substrate composition (Dunithan et al., 2012), also influence morphological variation in freshwater gastropods. Morphological variation in a mollusc resulting from flow variation was first described by Ortmann (1920) for

unionid mussels, called Ortmann's law (Goodrich, 1937; Minton et al., 2010; Dillon, 2011; Dillon et al., 2013). Similar morphological patterns were identified at a smaller scale of hundreds of meters for the pleurocerid *Elimia potosiensis* Pilsbry (Minton et al., 2010).

Brönmark et al. (2011) demonstrated that shell shape in *Radix balthica* Linnaeus was also flexible. Snails from populations without fish had narrow shells with well-developed spires. Snails from populations exposed to fish had more rotund shells with a low spire, characteristics that increase survival rate from predators that crush shells. Brönmark et al. (2011) used common garden experiments where snails were exposed to fish cues, resulting in a rounder body shape compared to control snails. The round body shape characteristic was thus phenotypically plastic and responded to predator cues, reinforcing the evolutionary importance of phenotypic plasticity.

Parasite infection can also influence body size or shell morphology. Although many additional studies exist (Żbikowska and Żbikowska, 2005), we present only a few examples here. Krist (2000) experimentally induced shell size variation with infections from the digenean *Proterometra macrostoma* Horsfall in *Elimia livescens* Menke. The shell morphology of the mud snail *Zeacumantus subcarinatus* (Sowerby 1855) was altered by infection of trematode parasites (Hay et al., 2005). These and others suggest that morphological modifications of shell shape with parasite infection are a selective host response rather than a parasite modification (Levri et al., 2005; Lagrue et al., 2007).

This phenotypic plasticity in shell morphology in response to biotic and abiotic environmental factors has also become highly controversial because it calls into question the identification of some taxa, including federally listed species (<http://fwgna.blogspot.com>, accessed 2/20/2013). This contentious issue will likely demand resolution soon.

Conservation Ecology

The need for conservation of freshwater snails worldwide is as urgent as for North American taxa (Lydeard et al., 2004; Brown et al., 2008). Similar to declines seen in unionid mussels, freshwater snail diversity has also declined in the United States in the last 100 years (Neves et al., 1998; Stewart, 2006). The quite diverse gastropod assemblages in rivers in the southeastern United States have been seriously affected by habitat alteration. Pleurocerids are quite common in shallow riffles, where water is warm and well-oxygenated, and rough substrates provide refugia from flow and sedimentation. Impoundments often change these habitats to hypoxic, cold water habitats with little periphyton food. Some gastropod species are threatened because they are also limited to geographically isolated springs, whose existence is increasingly threatened by rising demands for groundwater.

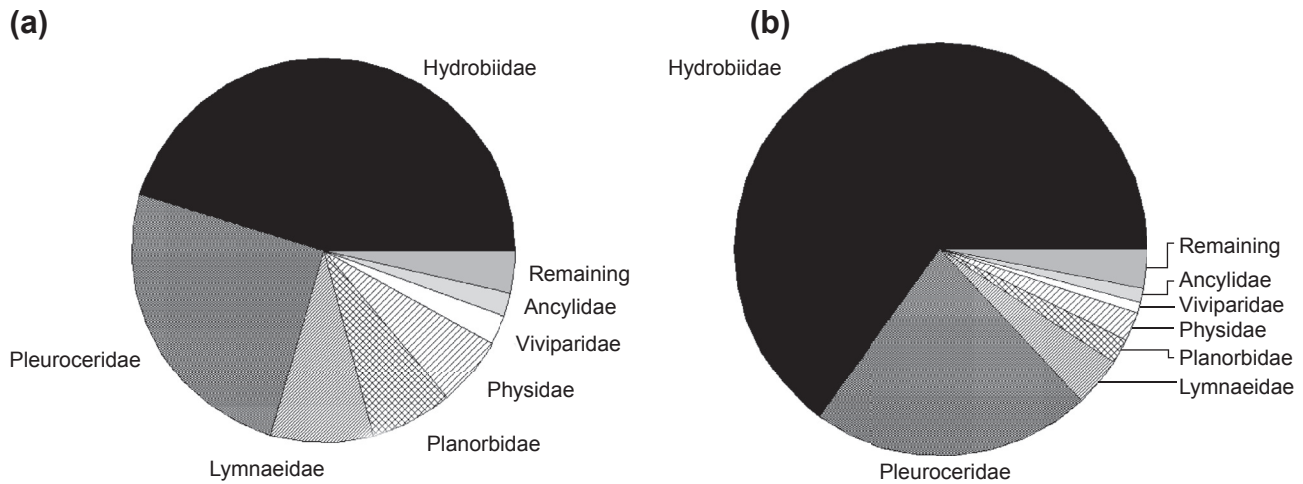


FIGURE 18.17 (a) Relative diversity of families of freshwater snails. (b) Fraction of snail species at risk of extinction that belong to each family. Remaining refers to remaining families (*Valvatidae*, Potamiopsidae, Neritinae, Ampullaridae, and *Acroloxidae*) that are not as diverse. At-risk is defined as having a global ranking of G2 or less, indicating only a few populations remain. Note that the two most diverse families, Pleuroceridae and Hydrobiidae, also have the most at-risk species, because their populations are often fragmented between different rivers or springs.

North American pleurocerid and hydrobiid gastropods are highly endangered (Lydeard and Mayden, 1995; Neves et al., 1998; Brown et al., 2008; Perez and Minton, 2008). In the United States, ~74% of the species of Hydrobiidae and ~45% of the Pleuroceridae (the two largest snail families in North America; Figure 18.17) are considered at risk, with a Nature Conservancy rank of $\leq G2$, indicating these species have few remaining populations and therefore face imminent risk of extinction (Figure 18.17). The pleurocerid *Elimia* has experienced the greatest number of extinctions, all in river systems in Alabama and Georgia (Table 18.2), followed in order by the pleurocerid genera *Leptoxis*, *Gyrotoma*, and *Athearnia*. A smaller number of hydrobiids have become extinct, but the fact that many species in the western and southeastern United States are found at only a few isolated springs puts them at considerable risk. At the current time, 21 species of gastropods are listed as endangered or threatened (Table 18.8). Nine of the species are hydrobiids from western states or Alabama. Five of the species are pleurocerids found in the Mobile River watershed in the Southeast. Three species are viviparids from Alabama watersheds. However, the only listed physid has been recently recognized to be a junior synonym of *P. acuta* (Rogers and Wethington, 2007), and two more of the species are currently under study to be de-listed, based on the discovery of additional populations (see footnotes in Table 18.8). Because the families Pleuroceridae and Hydrobiidae have the most at-risk species in North America, we will briefly discuss their ecology.

Ecology of Pleuroceridae

Pleurocerids are perennial, with life-cycles ranging from 2–10 years (Richardson et al., 1988; Huryn et al., 1994; Dillon, 2000; Brown and Johnson, 2004). Life-history

variation in the pleurocerid *Elimia* is affected by both local and landscape-level factors (Huryn et al., 1995).

Food availability limits individual growth rates in *Elimia* although considerable urban development and nutrient enrichment might be occurring now in streams in the southeastern United States. High current velocity also alters pleurocerid abundances, feeding, and growth. For example, flow refugia are important during spates (Stewart and Garcia, 2002), and *Elimia* orients upstream to minimize drag on the shell (Huryn and Denny, 1997). Johnson and Brown (1997) found that adult *Elimia* density and size decreased in higher flow. Considerable variation in shell anatomy occurs in pleurocerids, and the role of shell shape in the ability to withstand high flows is in need of further study.

Pleurocerids are major players in stream ecology within the southeastern United States. Periphyton abundance is regulated by nutrients (bottom-up) and snail grazing (top-down) in these streams (Rosemond et al., 1993; see earlier discussion). Snails reduced periphyton production by half under ambient nutrient conditions and by two-thirds when nutrients were added. The role of competitive interactions within the fairly diverse pleurocerid assemblages in southeastern rivers has received less study, although Brown et al. (1998) studied competition between the pulmonate *P. trivolvis* and the pleurocerid *Lithasia obovata* Say and found the pleurocerid was a better competitor. Similarly, two co-occurring species of *Elimia* in Alabama streams were both affected by competition, but neither was competitively dominant, allowing co-existence (Cross and Benke, 2002). Lotic gastropods also might be important competitors with insects (Hawkins and Furnish, 1987; Harvey and Hill, 1991). If competition is important, the distribution of pleurocerids in rivers could be due to niche partitioning. For example, pulmonates are common in headwaters or littoral

TABLE 18.8 Federally Listed Species of Gastropods in the United States as of Early 2008, Along with the States in which they are Found

Family	Species	States
Assiminidae	<i>Assimineia pecos</i> (E)	Texas, New Mexico
Hydrobiidae	<i>Jutumia kosteri</i> (E), <i>Pyrgulopsis bruneauensis</i> (E), <i>Pyrgulopsis neomexicana</i> (E), <i>Pyrgulopsis ogmoraphe</i> (E), <i>Pyrgulopsis pachyta</i> (E), <i>Pyrgulopsis roswellensis</i> (E), <i>Taylorconcha serpenticola</i> (T), <i>Tyronia alamosae</i> (E)	New Mexico, Idaho, Tennessee, Alabama
Lymnaeidae	<i>Lanx</i> sp. (E)	Idaho
Pleuroceridae	<i>Athernia anthoni</i> (E), <i>Elimia crenatella</i> (T), <i>Leptoxis taeniata</i> (T), <i>Leptoxis plicata</i> (E), <i>Leptoxis ampla</i> (T)	Tennessee, Alabama, Georgia
Physidae	<i>Physa natricina</i> (E)	Idaho
Valvatidae	<i>Valvata utahensis</i> (E)	Idaho
Viviparidae	<i>Campeloma decampi</i> (E), <i>Lioplax cyclostomatiformis</i> (E), <i>Tulotoma magnifica</i> (E)	Alabama

"E" refers to species listed as endangered and "T" to species listed as threatened.

zones of the Salt River in Kentucky, but are replaced by pleurocerids in higher-order reaches (Brown et al., 1998). Similarly, in the Ohio River, *L. obovata* is common in shallow littoral areas because its relatively large foot adapts it to wave action, while the thick shell of *Pleurocera canaliculum* Say protects it from most fish, and this snail occurs at all depths (Greenwood and Thorp, 2001).

The heavily armored shells of most pleurocerids reduce mortality from predators (Vermeij and Covich, 1978; Stein et al., 1984; Hawkins and Furnish, 1987), although darters feed on juvenile *Elimia* when they are abundant in spring and summer (Haag and Warren, 2006). Crayfish also may affect pleurocerids, as *E. livescens* reared in effluent from crayfish-fed conspecific snails alters shell anatomy to deter crayfish from chipping the shell at the aperture (Krist, 2002).

Ecology of Hydrobiidae

The ecology of hydrobiids has received less study than pleurocerids, but factors that influence the abundance of hydrobiids include substrate size, stream shading, water velocity, and flood frequency (Richards, 2004). Martinez and Rogowski (2011) found that density of a springsnail in Arizona springs varied with water depth, distance from a springhead, and pH. Hydrobiids are relatively resistant to flow in large rivers because they burrow into sediments (Holomuzki and Biggs, 1999; Holomuzki and Biggs, 2000). Hydrobiids are annual and recruitment is continuous in warm springs or seasonal in cold systems (Hershler, 1984). Native North American hydrobiids are sexual, sexual dimorphism is pronounced (females larger than males), and sex ratios commonly are skewed toward females (Hershler, 1984).

Hydrobiids can occur at high densities, and community-level interactions seem possible but remain virtually unexplored. In the western United States, the high diversity of hydrobiids may be due the absence of other gill-breathing snails (i.e., viviparids, pleurocerids). Sympatry of congeneric hydrobiids in most springs is rare, but habitat segregation facilitates coexistence in large springs with greater habitat heterogeneity (Hershler, 1984). The role of predators in controlling hydrobiid populations is also relatively unknown, although *Cyprinodon pecosensis*, *Gambusia affinis*, and cichlids are known predators (Hershler, 1984).

Conservation and Propagation

Successful conservation of extant populations, propagation of at-risk species, and re-introduction of locally extirpated species to stream and spring systems will require more basic research on the life histories and ecology of pleurocerids and hydrobiids (Johnson and Brown, 1997; Brown et al., 2008). For pleurocerids, little is known of reproductive patterns and longevities for *Lithasia*, *Leptoxis*, *Pleurocera*, and *Io* in rivers in Tennessee and Alabama where they are common. Studies that assess the relative roles of periphyton and spates in determining snail population dynamics are needed, as well as more studies of the role of competition and predators. More information is also needed on successful propagation and re-introduction techniques. Captive rearing of pleurocerids is less complicated than for unionid mussels because of the simpler life-cycle, and snails can be induced to reproduce relatively easily in the laboratory (Figure 18.18). Hydrobiids are difficult to identify, and future studies should use molecular and protein markers, shell morphology, and soft anatomy. Biogeographic studies should address how drainage patterns influence spring

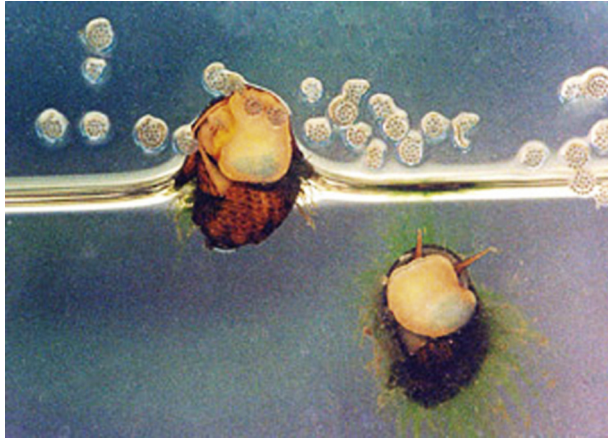


FIGURE 18.18 Close-up of two *Leptoxis foremani* ovipositing on the walls of a glass aquarium in the laboratory. The egg masses are the brown circles just above the water. Aquatic gastropods are easier to propagate in the laboratory because they do not have a larval stage dependent on fish for dispersal, like endangered unionid mussels. Photograph courtesy of Paul Johnson.

habitats, as well as basic information on life history, feeding ecology, population dynamics, and habitat requirements of hydrobiids. Finally, further collaboration is needed among geneticists, taxonomists, and agency staff to develop guidelines for use of genetic data when deciding whether at-risk species, subspecies, and unique population units of pleurocerids and hydrobiids merit protection under state and federal laws (Perez and Minton, 2008).

Successful conservation of extant populations, propagation of at-risk species, and re-introduction of locally extirpated species to stream and spring systems will require more basic research on the life histories and ecology of pleurocerids and hydrobiids (Brown and Johnson, 1997; Brown et al., 2008). For pleurocerids, little is known of reproductive patterns and longevities for *Lithasia*, *Leptoxis*, *Pleurocera*, and *Io* in rivers in Tennessee and Alabama where they are common. Studies that assess the relative roles of periphyton and spates in determining snail population dynamics are needed, as well as more studies of the role of competition and predators. More information is also needed on successful propagation and re-introduction techniques. Captive rearing of pleurocerids is less complicated than for unionid mussels because of the simpler life-cycle, and snails can be induced to reproduce relatively easily in the laboratory (Figure 18.18). Hydrobiids are difficult to identify, and future studies should use molecular and protein markers, shell morphology, and soft anatomy. Biogeographic studies should address how drainage patterns influence spring habitats, as well as basic information on life history, feeding ecology, population dynamics, and habitat requirements of hydrobiids. Finally, further collaboration is needed among geneticists, taxonomists, and agency staff to develop guidelines for use of genetic data when deciding whether at-risk

species, subspecies, and unique population units of pleurocerids and hydrobiids merit government protection (Perez and Minton, 2008).

Invasive Species

Conservation of native snails also requires understanding threats from invasive snail species. Invasive snails affect native snails directly through competition for food (Carlsson et al., 2004) or indirectly through changes in ecosystem function or parasite populations. Thirty-seven nonnative freshwater gastropod species representing nine families are found in North America (NatureServe.org, accessed 2007). Approximately three dozen examples of invasion and transport snails among states are recognized in the United States (Brown et al., 2008). These species have frequently reduced the abundance of native snails and altered ecosystem function, as can be illustrated by two well-known invasive snails: apple snails and the New Zealand mud snail.

Apple snails (family Ampullaridae), especially *P. canaliculata*, originated in temperate Argentina, and have been introduced to various Asian countries (Dudgeon, 1999) and to US states along the Gulf of Mexico as well. Although they take two years to mature in their native habitat, they take only 10 months in Hawai'i and as little as 2 months in Asia, where they lay their characteristic, calcareous egg masses above the water line to avoid predation (Lach et al., 2000). Apple snails are voracious herbivores that can shift wetland food webs away from a macrophyte base to turbid, phytoplankton-based systems (Carlsson et al., 2004).

Pomacea canaliculata has also damaged endangered species and ecosystems (Hall et al., 2003; Carlsson et al., 2004). The channeled apple snail lays bright pink egg masses just above the water's surface (Figure 18.19). The channeled apple snail aggressively feeds on macrophytes and can convert rapidly to bare substrates (Carlsson et al., 2004). In comparison, the invasive ampullarid *Bellamya (Cingopaludina) japonica* von Martens has invaded eastern states but does not have as much impact as the invasive apple snails because it filter-feeds and increases water clarity rather than feeding on macrophytes. Ladd and Rogowski (2012) showed that the prosobranch *Melanoides tuberculata* Müller impacts native snail communities in desert spring systems by direct displacement and introducing foreign trematodes. More work is needed on how invaders interact with native gastropod communities and on mechanisms to control the spread of invasive snails.

However, the most prolific invader is the New Zealand mud snail, *P. antipodarum* (family Hydrobiidae). This species was evidently held in check in its native range by trematode infections. Trematode larvae in New Zealand are locally adapted to parasitize host mud snail populations (see discussion above), and may again explain why sexually reproducing individuals are maintained in populations,



FIGURE 18.19 The channeled apple snail (*P. canaliculata*) is an ampullarid native to South America that has invaded Florida in recent years. The pink egg cases have a calcareous shell to limit desiccation. Photograph courtesy of *Katasha Cornwell*.

due to their genetically variable offspring, or why parthenogenetic morphs cycle in abundance as trematodes adapt to parasitize them (Jokela et al., 2009). In the 1980s, *P. antipodarum* from New Zealand colonized the Snake River in Idaho, in the United States, where it now reaches densities up to 800,000/m² (Figure 18.20), with the highest secondary production values ever recorded for an aquatic invertebrate (Hall et al., 2006). Brenneis et al. (2011) found that invasive New Zealand mud snails altered food webs. New Zealand mud snails consume up to 93% of primary production and alter energy flow (Hall et al., 2006). Their invasive success stems from their rapid growth, early maturity, high reproductive rate, resistance to stresses like desiccation during inadvertent transport between sites, and lack of biological enemies in their invasive range (Alonso and Castro-Diez, 2008). Resource consumption rates are no higher than native species, but enclosure experiments suggest asymmetric competitive effects, with resident species at a disadvantage (Riley et al., 2000). Richards (2004) found that the endangered hydrobiid *Taylorconcha serpenticola* was negatively affected by *P. antipodarum*. This invasive snail also depressed the abundance of other macroinvertebrates in western US rivers (Kerans et al., 2005). The New Zealand mud snail continues to expand its distribution, with additional populations reported recently in estuarine bays in Oregon and in Lake Ontario. Similarly, *P. canaliculata* has recently invaded Florida and several other southeastern states, is larger than the native *P. paludosa*, and may be replacing some populations of the native ampullarid snail.

Other taxa that are extremely vulnerable include the springsnails of Australia and western United States and



FIGURE 18.20 The invading New Zealand mud snail (*Potamopyrgus antipodarum*) reaches high densities in the Snake River in the Western United States, and has impacted other populations of native hydrobiids. Photograph courtesy of *D.L. Gustafson*.

Mexico (Lydeard et al., 2004). Many of the possibly susceptible hydrobiid taxa are, unfortunately, not yet described. They are vulnerable because of invasive species and habitat destruction, including by cattle grazing and numerous human impacts on small spring ecosystems. Habitat modification likely results in population declines, changes in habitat use, and extirpations of freshwater gastropods. Similarly, Van Bocxlaer et al. (2012) found that gastropods in Lakes Malawi and Tanganyika shifted habitat use to shallower water or have been extirpated, probably as a result of increased surface runoff, eutrophication, and surface-water warming.

COLLECTING, CULTURING, AND SPECIMEN PREPARATION

Collecting

A number of sampling techniques exist (reviewed in Russell-Hunter and Buckley, 1983; Dillon, 2000), although some are not quantitative. The least quantitative technique, but one that often gives large numbers of individuals and a good idea of species composition, is sweep netting with a net of 1 mm mesh (Brown, 1979, 1997). In soft sediments or sand, quantitative samples can be collected with Ekman grabs or corers. When sampling macrophytes, the sampler must collect both plants with attached snails, and the substrate with any bottom-dwelling species. Examples of such samplers are described in Gerking (1957), Savino and Stein (1982), and Lodge et al. (1994). In coarse sand, Ponar dredges are the best alternative. In cobble, little recourse to direct counts of given areas by visual search is available. You can estimate densities by covering the rocks with aluminum foil and then estimating the area from weight to area regressions for the foil.

The best sorting technique for gastropods is hand sorting. Large adults can be removed visually and samples washed through a graded series of sieves (≥ 0.5 mm mesh) to remove mud but retain smaller snails. Place those samples in shallow water on flat white trays, tease the vegetation apart, and then examine the whole tray in a systematic fashion to remove small gastropods and egg cases.

Culturing

Temperate gastropods will grow well at 15–20°C, while subtropical species grow better at 20–25°C. Any hard substrate with a dense periphyton covering can be added for food, although artificial foods such as lettuce, cereal, or spinach are sometimes used. Provide food as needed to avoid fouling containers. Detritivores should be fed leaf litter colonized with bacteria and fungi (i.e., held for at least two weeks in a pond or stream). Avoid crowding of snails, as growth and reproduction are sensitive to density. An approximate rule is one snail per liter. Water should be recirculated through a gravel or charcoal filter, or at least be changed weekly. Caenogastropod and pulmonate snails should be paired with conspecifics so that mating can occur. Culturing of “weedy” species like physids is best done at low temperatures to retard egg production, and constant removal of egg cases is necessary to prevent population explosions. Adequate lighting (with a 12L:12D cycle) is necessary to promote periphyton growth in aquaria (“gro lites” work well).

Specimen Preparation and Identification

Identification of freshwater gastropods requires patience and some familiarity with general differences among gastropod groups. For example, individuals should be collected alive if possible so that the presence of an operculum can correctly indicate the specimen is a caenogastropod. In general, gross shell characteristics can initially be used before determining whether an operculum is present. However, some confusion between pulmonate and pleurocerid snails, for example, is a common mistake if novice students use preserved specimens and do not correctly note the presence or absence of an operculum. While there is undoubtedly much eco-phenotypic variation in shell morphology, understanding the basic shell shapes and morphology is still very important in using a dichotomous key, at least at higher levels. If at all possible, a range of shell sizes should be collected, as size is used as a classification trait in several instances. In the case of hydrobiids, little recourse exists to dissecting the snail and observing penial morphology under a dissecting microscope. We hope progress will be made in the future in using molecular characteristics in identification

of gastropods, to help solve the problem with phenotypic plasticity or convergence of shell shapes. However, at the current time, no sophisticated (e.g., using both molecular and morphological traits) overall study of species determination has been done for caenogastropods. Although pulmonate species are somewhat easier to discern, there is still controversy about higher taxonomic levels (genus and above).

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