

The Ecology of Freshwater Molluscs

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1 · Introduction

The invasion launched by elements of the molluscan army upon fresh water has aptly been characterized as ‘desultory’ (Deaton and Greenberg 1991). Dozens of offensives seem to have taken place, sporadically timed over hundreds of millions of years, some ultimately carrying the works, others now witnessed only in the fossil record. The diversity of freshwater molluscs is vast. Yet it is my thesis here that in their interactions with the environment and with each other, freshwater molluscs share enough similarities that some intellectual profit may be gained by examining their ecology together.

We might begin with a brief overview of the forces (Tables 1.1 and 1.2). The larger freshwater bivalves belong to the order Unionoidea, an ancient group of six families whose fossil record extends to the Devonian period. They are distinguished by a parasitic larval stage that is unique among the Bivalvia. The best-known families are the Margaritiferidae and the highly diverse Unionidae, both worldwide. The hyriids of Neotropical and Australian regions are less studied, while the Neotropical mycetopodids, and the Ethiopian mutelids and etheriids, remain rather obscure.

The smaller infaunal freshwater bivalves belong to the superfamily Corbiculoidea. This is a somewhat younger group, generally hermaphroditic, with a fossil record beginning in the Jurassic and Cretaceous periods. The two corbiculoid families may represent separate invasions of fresh water (Park and O’Foighil 1998). Bivalves of the worldwide family Pisidiidae hold developing embryos for extended periods, ultimately releasing juveniles quite large in relation to their own bodies. The family Corbiculidae (restricted to old world tropics and subtropics until recently) release juveniles as smaller ‘pediveligers’. The Dreissenoidea is much less diverse than the Unionoidea or Corbiculoidea, the freshwater *Dreissena* being restricted to the Ponto-Caspian basins until recently.

Table 1.1. *A classification of some of the genera of freshwater bivalves more commonly mentioned in this work*

Class Bivalvia	
Subclass Paleoheterodonta	Subclass Heterodonta
Order Unionoidea	Order Veneroidea
Superfamily Unionacea	Superfamily Corbiculoidea
Family Margaritiferidae	Family Corbiculidae
<i>Margaritifera</i>	<i>Corbicula</i>
<i>Cumberlandia</i>	Family Pisidiidae
Family Unionidae	<i>Pisidium</i>
Subfamily Anodontinae	<i>Eupera</i>
<i>Anodonta</i>	<i>Sphaerium</i>
<i>Anodontoidea</i>	<i>Musculium</i>
<i>Cristaria</i>	Superfamily Dreissenoida
Subfamily Ambleminae	Family Dreissenidae
<i>Amblema</i>	<i>Dreissena</i>
<i>Actinonaias</i>	<i>Mytilopsis</i>
<i>Elliptio</i>	
<i>Fusconaia</i>	
<i>Lampsilis</i>	
<i>Unio</i>	
<i>Villosa</i>	
Family Hyriidae	
<i>Diplodon</i>	
<i>Hyridella</i>	
Superfamily Etheriacea	
Family Etheriidae	
Family Mutelidae	
Family Mycetopodidae	

Source: modified from Vaught (1989).

They doubtless represent yet another separate invasion from the sea (their oldest fossils are Eocene), retaining the overall aspect of edible marine mussels. By virtue of their ability to spin strong byssal attachment threads, they have occupied the epifaunal habitat not exploited by unionoids or corbiculoids. They have also retained a planktonic larval stage in their development.

Among the bivalves, adaptation to fresh waters does not seem to have been rare nor restricted to the unionoids, corbiculoids, and dreissenoids. Freshwater or brackish/freshwater species are to be found among the Arcidae, Mytilidae, Trapeziidae, Donacidae and Cardiidae, to name but a few families. Although quite interesting from many points of view, the

Table 1.2. *A classification of some of the gastropod genera more commonly mentioned in the present work*

Class Gastropoda	
Subclass Pulmonata	Subclass Prosobranchia
Order Basommatophora	Order Archaeogastropoda
Family Acroloxidae	Superfamily Neritoidea
<i>Acroloxus</i>	Family Neritidae
	<i>Neritina</i>
	<i>Theodoxus</i>
Family Lymnaeidae	Order Mesogastropoda
<i>Lymnaea</i>	Superfamily Viviparoidae
<i>Pseudosuccinea</i>	Family Viviparidae
<i>Galba</i>	<i>Bellamyia</i>
<i>Myxas</i>	<i>Cipangopaludina</i>
<i>Radix</i>	<i>Viviparus</i>
<i>Stagnicola</i>	<i>Campeloma</i>
	<i>Tilotoma</i>
Family Physidae	Family Ampullariidae
<i>Physa</i>	<i>Marisa</i>
<i>Aplexa</i>	<i>Pila</i>
Family Planorbidae	<i>Pomacea</i>
<i>Planorbis</i>	Superfamily Valvatoidea
<i>Anisus</i>	Family Valvatidae
<i>Gyraulus</i>	<i>Valvata</i>
<i>Armiger</i>	Superfamily Rissoidea
<i>Segmentina</i>	Family Hydrobiidae
<i>Biomphalaria</i>	<i>Amnicola</i>
<i>Helisoma</i>	<i>Hydrobia</i>
<i>Menetus</i>	<i>Potamopyrgus</i>
<i>Planorbula</i>	Family Bithyniidae
<i>Promenetus</i>	<i>Bithynia</i>
<i>Bulinus</i>	<i>Hydrobioides</i>
	Family Micromelaniidae
	<i>Pyrgula</i>
	Family Pomatiopsidae
	<i>Oncomelania</i>
	<i>Pomatiopsis</i>
	<i>Tricula</i>
Family Ancyliidae	Superfamily Cerithioidea
<i>Ancylus</i>	Family Thiaridae
<i>Rhodacmaea</i>	<i>Melanoides</i>
<i>Ferrissia</i>	<i>Thiara</i>
<i>Hebetancylus</i>	<i>Pachymelania</i>
<i>Laevapex</i>	Family Melanopsidae
	<i>Melanopsis</i>

Table 1.2 (*cont.*)

Family Pleuroceridae <i>Amphimelania</i> <i>Goniobasis</i> <i>Pachychilus</i> <i>Paludomus</i> <i>Brotia</i> <i>Juga</i> <i>Pleurocera</i> <i>Semisulcospira</i>
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Source: modified from Vaught (1989).

freshwater members of such primarily marine groups are at present too poorly known to have much impact upon our discussions here.

Most species of gastropods belong to what has for many years been called the subclass Prosobranchia, a universally distrusted collection of taxa not fitting into other groups (Ponder 1988b). They share a few (probably ancestral) characters: they breathe through gills, carry an operculum, and are usually gonochoristic and occasionally parthenogenetic, but only rarely hermaphroditic. Prosobranchs have invaded fresh waters on at least as many occasions as the number of their superfamilies listed in Table 1.2, plus twice again for minor groups (buccinids and marginellids) not treated in this volume. Most of the families are effectively worldwide in distribution: the neritids, viviparids, hydrobiids, pomatiopsids, and pleurocerids. The valvatids are restricted to the northern hemisphere, while the melanopsids and bithyniids were both restricted to the eastern hemisphere until recently. The thiarids and ampullariids are circumtropical, with distributions reaching to the subtropics.

As their name implies, snails of the subclass Pulmonata have lost their gills and now respire over the inner surface of their mantle, effectively a lung. The four major (and several minor) freshwater pulmonate families belong to the order Basommatophora, so named because their eyes are at the base of their tentacles. (The primarily terrestrial Stylommatophora have eyes at their tentacle tips.) They seem to have derived from a single ancient invasion of fresh water, dating at latest to the Jurassic period (Starobogatov 1970). Minor families (including the limpet-shaped Acroloxidae and two others not treated here) are held to be the most ancestral of the freshwater pulmonates, by virtue of anatomical detail (Hubendick 1978). The worldwide Lymnaeidae, with their rather ordinary looking, dextral shells of medium to high spire, are believed the next

most ancestral. Members of the primarily holarctic Physidae are distinguished by their inflated shells coiled in a left-handed ('sinistral') fashion, quite unusual in the class Gastropoda. Members of the worldwide Planorbidae are also sinistral, but often planispiral. The members of the worldwide Ancyliidae are limpet-shaped.

Most freshwater pulmonates carry an air bubble in their mantle cavity, which they replenish periodically at the surface, and which they use to regulate their buoyancy. This allows many species to exploit warm, eutrophic habitats where dissolved oxygen may be quite low. Some (especially smaller, cold-water) species do not seem to surface-breathe, however, and their mantle cavities are found to be filled with water. Pulmonates typically have much lighter shells than prosobranchs, and lack an operculum. Other major, although less immediately apparent, pulmonate distinctions include radulae with many small, simple teeth per row and reproductive hermaphroditism.

Authors have sometimes held that the freshwater environment is more harsh than the marine environment (Macan 1974). Temperature fluctuation is typically more extreme in fresh waters, and freezing more likely. Water levels and current speeds are more unpredictable in fresh waters than in the ocean, as is the chemical composition of the medium. Given that all classes of molluscs evolved in the sea, and all share the same broad body plan, it is not surprising that their freshwater representatives, although quite diverse, display some broad points of resemblance.

Osmoregulatory adaptation is one area of striking similarity. Marine molluscs generally conform to sea water, osmotically equivalent to a 0.56 M solution of NaCl. Freshwater molluscs have evolved much lower body fluid concentrations, the equivalent of about a 0.040–0.070 M NaCl solution for gastropods, and 0.020–0.040 M for bivalves. The osmolalities of freshwater bivalves are among the lowest recorded for any animal (Pynnönen 1991, Dietz *et al.* 1996). By way of comparison, freshwater crustaceans, insects, and fish all generally show osmolalities in excess of 0.100 M as NaCl.

Fresh waters are extremely variable in their ionic concentration, but typically range about the order of 0.005 M NaCl, very much lower than any of the figures cited above. So since molluscan tissues are highly permeable to water, freshwater molluscs nevertheless have substantial osmoregulatory chores to perform. Their overall strategy involves active transport of ions from the medium and production of copious urine hypo-osmotic to their hemolymph. Reviews of water balance and excretion in the freshwater molluscs have been offered by Machin (1975), Burton (1983), Little (1981, 1985), Dietz (1985), and Deaton and Greenberg (1991).

Active transport of Na^+ , Ca^{+2} , and Cl^- , even against sharp concentration gradients, has been documented in all groups of freshwater molluscs. It is not certain whether the process may be localized (the gills are often mentioned) or whether all body surfaces are involved. Ions may also be exported as required to maintain electrical balance, as for example H^+ or NH_3^+ , may be exchanged to balance Na^+ uptake, and HCO_3^- exchanged for Cl^- (Byrne and Dietz 1997). Voluminous urine is produced by ultrafiltration of haemolymph across the heart wall of freshwater molluscs into the pericardial cavity, where it is conducted to the kidney. The lining of the kidney resorbs Na^+ and Cl^- , and perhaps Ca^{+2} and K^+ as well.

Osmotic regulation in the reverse direction, balancing salt concentrations higher in the environment than in the organism, is unknown in the Mollusca. Thus the process of adaptation to fresh waters seems to be irreversible. Although some freshwater mollusc populations can be found tolerating low salinities, none has apparently recolonized the sea.

I am not aware of any direct estimates of the energetic cost of osmoregulation in freshwater molluscs. But a wealth of indirect evidence (reviewed in Chapter 8) suggests that in many waters of the earth, the price of osmoregulation may be so high as to limit the success of molluscan colonists. It also seems possible that adaptation to fresh water is at least partly responsible for the suppression of the larval dispersal stages so common in marine molluscs. With their high surface-to-volume ratios and reduced shells, planktonic larvae may simply be unable to gather enough fuel to fire the machinery necessary for osmotic balance. With few exceptions, all freshwater molluscs pass their larval stages in the egg, or enfolded within their parents.

This brings to the fore a second point of general similarity over all groups of freshwater molluscs. They are poor dispersers in an environment notably difficult to colonize. The directionality of freshwater flow is in some places powerful, and in other spots negligible. But without exception, all successful molluscan colonists of fresh waters have adapted to directional flow at some point in their evolutionary history. Osmoregulatory barriers are certainly not the only conceivable explanation for the general absence of a conventional larval stage from the life history of freshwater molluscs. Their turbulent medium interferes with the external union of egg and sperm. Planktonic larvae are swept away.

The general suppression of the larval stage in the freshwater Mollusca has yielded a large group of obligately aquatic organisms that do not swim. Some groups (e.g. the unionoids) have evolved unique solutions

to this problem. But on a fine spatial scale, freshwater molluscs appear generally immobile, helpless to avoid predators, parasites, or the ecologist's sampling device. On a coarse geographic scale, one must figure high the likelihood that freshwater mollusc distributions derive from vagaries of chance colonization.

Fretter and Graham (1964) pointed out that hermaphroditism seems to be more common in freshwater molluscs than in those that inhabit the sea. This third point of general similarity may be a consequence of the second, that their dispersal capabilities are so poor. 'Reproductive assurance,' the certainty that all simultaneous hermaphrodites can find at least one partner (themselves), has for years been a leading hypothesis for the origin of hermaphroditism (Heath 1977). I would strengthen Fretter and Graham's generalization a bit by adding that it seems to me that asexual reproduction is more common in freshwater than in marine molluscs. Not only can hermaphroditic pulmonate snails and corbiculoid bivalves self-fertilize, they often do. Parthenogenesis has evolved three times in freshwater prosobranchs, but not in their marine ancestors.

The success that freshwater molluscs have enjoyed, together with their relative immobility, constitute for me the most persuasive arguments for a unified treatment of their ecology. Bivalves and gastropods, pulmonates and prosobranchs, are easier to sample than just about any other animal. A biologist need only walk to the creek bank, or row to mid lake, and drop his or her sampling gear, and the molluscs below are as helpless as ferns. But in contrast to the situation in plants, a biologist can fairly assume that the molluscs inhabiting any patch of sampled habitat are not entirely a function of a passive process, for molluscs are not rooted. They could leave if they wished. Study of population biology or community ecology is thus greatly facilitated.

In the two chapters that follow, emphasis will often come to rest upon the undeniable biological diversity of freshwater molluscs. Touching on the broad themes of habitat, diet, and reproduction in filter-feeding and grazing organisms, the reviews of Chapters 2 and 3 will traverse most of the territory of benthic ecology. But the common elements of the biology of freshwater molluscs will be featured in the six chapters that form the body of this book. A general life history model is developed in Chapter 4, the consequences of competition, predation, and parasitism explored in Chapters 5–7, and all this material is placed into a general community-ecological context in Chapters 8 and 9.