Chapter 1

Introduction to mussels and mussel ecology

Freshwater mussels are a conspicuous and important element of aquatic ecosystems in much of North America and throughout the world. Mussels are bivalve mollusks and, generally speaking, are built much like marine bivalves. Most people today associate bivalves exclusively with marine systems and aren't aware that bivalves live in freshwater at all. Part of the reason for this is that mussels have disappeared from many rivers and lakes in the last 100 years. However, mussels remain abundant in many places and can occur at densities greater than 100 animals per square meter. Freshwater mussels also are a surprisingly diverse group of animals. North America has the richest fauna on Earth, with more than 300 species, but Southeast Asia and Central America also have greater than 100 species (Graf and Cummings 2007).

People in the past had a greater awareness of these animals. Prehistoric Americans made great use of mussels. They ate them, used mussel shells and pearls to make jewelry and implements, and tempered pottery with lime slaked from the shells (Chapter 9). Mussels also were well known to people in historical times. Pearl hunting and the mother-of-pearl button industry employed thousands of people during the first half of the twentieth century, and nearly everyone wore clothing with shell buttons. People have adorned their graves with mussel shells, paved roads with them, and fattened hogs on mussel meat. The Cherokees referred to mussels as *dagvna* and to Muscle (Mussel) Shoals on the Tennessee River as *dagvnahi* or *dagunawelahi*, which means "place of mussels" (Bright 2004). Shell Creek, Nebraska, was named from the Pawnee word *skā pĭr 'ĭ ūs kĭts' ū*, meaning "shell water" (from *skā pĭr rūs*, "clamshell"; Grinnell 1913), and the Rio Concho, Texas, named by early Spanish explorers, means "river of shells." Across North America, the abundance of place-names referring to freshwater mussels (Table 1.1) attests to the indelible impact these animals have had on the cultural landscape and shows how plentiful and conspicuous mussels must have been.

The main reason people today know about mussels is because of the recognition that we are rapidly losing this unique part of our natural and cultural heritage. Within

Table 1.1. *Place-names in North America likely referring to freshwater mussels*

Place	U.S. states and Canadian provinces
Clam Brook	NF (2)
Clam Cove	NV
Clam Creek	AK, MB, MT, ON
Clam Falls	WI
Clam Lake	AK (3), BC, CO, MA, MB, MI (2), MN (3), MT, NS (2), ON (4), SK, WI (2)
Clamshell Lake	MN, ON (2), NS
Clamshell Pond	MA, NH, NY
Clam River	MA, MI (2), NF (2), WI
Mussel	AL
Mussel Bar	AR
Mussel Bayou	LA
Mussel Brook	NF
Mussel Creek	AL, BC, MO, SC
Mussel Fork	MO
Mussel Lake	OR, MS
Mussel Run	NC, TX
Mussel (Muscle) Shoals	AL (2), KY (2), MO, OK, TX
Mussel Slough	CA
Mussel Swamp	VA
Mussel Point	AR
Musselshell River	MT
Musselshell Creek	ID, NC, MN
Pearl Bayou	MS
Pearl Branch	AR, KY, MO (2)
Pearl Brook	MA, NJ
Pearl Creek	AB, AK (3), CO (2), ID (5), LA, MN, MT, NE, NV, NY, ON (2), OR, SD (2), SK (2), WA (2), WI
Pearl River	LA/MS, NF, ON
Pearl Island	ID, IL, IN, KY
Pearl Lake	AB, BC, CO, CA (2), GA, ID, IL, MB (2), MI (3), MN (5), MT (2), ND, NF, NH, NY, ON (8), OR, PA, QE (3), SD, SK, TX, UT, WI (2)
Pearl Pond	KY, ME (3)
Shell Branch	OK, TN
Shell Brook	ON, SK
Shell Creek	AL, BC, GA, ID, TN, MB, MN, NE, OK, WY, YT
Shell Lake	AK, BC, CA, GA, IN, MB (3), MI, MN, MS, NE, ND, OK, ON (2), SK, WI, WY
Shell Lake Slough	AR
Shell Pond Brook	NH
Shell Pond	NF
Shell Run	IN, VA, WV
Shell River	MB, MN

Note: Names from coastal areas are not included because they likely refer to marine bivalves (e.g., Mussel Point, Clam Rock). Numbers in parentheses indicate multiple place-names in a state or province. Data from Geographic Names Information System, U.S. Geological Survey (http://geonames.usgs.gov/), and Geographical Names of Canada, Natural Resources Canada (http://geonames.nrcan.gc.ca/).

the last 100 years, we've already lost forever 30–40 species, and many more are highly vulnerable to extinction in the near future (Chapter 10). Understanding the ecology of freshwater mussels is central in our efforts to save what's left. Highlighting the fascinating ways mussels go about their lives and the vital ecological role they play also will help increase awareness and concern for these animals.

1.1. Terminology

A few notes on terminology are necessary at the outset. When I say *mussels*, I am referring to freshwater bivalves of the order Unionoida, and I will mostly be discussing the North American fauna (north of Mexico), which includes the families Unionidae and Margaritiferidae. The order Unionoida contains about 85 percent of all freshwater bivalve species worldwide, and nearly 70 percent are members of the family Unionidae (Section 1.2).

The name "mussels" is somewhat confusing. When I tell people I study mussels, or when someone asks why I'm lying in a stream with my face in the water, almost invariably, the first question they ask is, "Can you eat 'em?" The answer is, "Yes . . . well, maybe," but we'll talk about that in Chapter 9. If there is a second question, often it is, "What's the difference between a clam and a mussel?" In marine waters, these terms are somewhat distinct and therefore useful: *clam* usually refers to an infaunal bivalve that burrows into the bottom (e.g., hard clam, *Mercenaria mercenaria*), and *mussel* refers to an epibenthic bivalve that attaches itself to hard substrates (e.g., blue mussel, *Mytilus edulis*). This convention is followed for some freshwater bivalves, including fingernail clams (Sphaeriidae) and Asian clams (*Corbicula*), which burrow, and zebra mussels (*Dreissena*), which attach onto hard objects. Unfortunately, and for reasons unknown to me, the Unionoida are usually referred to as mussels even though they burrow into the substrate like marine clams, but the terms *mussel* and *clam* are often used interchangeably. Prior to the 1970s, scientists referred to freshwater mussels as *naiads* or *najades*. In Greek mythology, Naiads were nymphs who inhabited and gave life to fresh waters. A Naiad was intimately connected to a specific body of water, and her existence depended on it; if a stream dried up, its Naiad expired. Clearly "naiad" is a fitting name for freshwater mussels. Unfortunately, naiad is already applied to the larvae of several aquatic insects as well as to aquatic plants of the genus *Najas*.

So what should we call them? The logical thing would be to start calling them *freshwater clams* owing to their burrowing habits, but this would just confuse everyone. In this book, I will follow common and long-standing usage and refer to our subjects as *freshwater mussels* or, simply, *mussels*, even though this terminology is arbitrary. I once asked my grandfather whether the familiar roadside animal should be called a groundhog or a woodchuck. He replied, "It should be called a groundhog because that's what it is." You can't argue with that, so call them what you like.

Table 1.2. *Freshwater representatives in the class Bivalvia worldwide*

Major groups	Families	Number of genera	Number of species	Native distribution
Subclass Protobranchia[1]	–	0	0	–
Subclass Pteriomorpha				
Order Arcoida	Arcidae	1	4	OL
Order Mytiloida	Mytilidae	3	5	AT, OL
Subclass Paleoheterodonta				
Order Unionoida	Etheriidae	4	4	AT[2]
	Hyriidae	17	71	NT, AU
	Iridinidae	6	43	AT
	Margaritiferidae	3	12	PA, NA, OL
	Mycetopodidae	12	36	NT
	Unionidae	142	674	PA, NA, AT, NT, OL, AU
Subclass Heterodonta				
Order Veneroida	Cardiidae	2	5	PA
	Corbiculidae	3	6	PA, AT, OL, AU
	Sphaeriidae	5	196	PA, NA, AT, NT, OL, AU
	Dreissenidae	3	5	PA, AT
	Solenidae	1	1	OL
	Donacidae	2	2	AT
	Navaculidae	1	2	OL
Order Myoida				
	Corbulidae	1	1	PA
	Erodonidae	2	2	AT, NT
	Teridinidae	1	1	NT
Order Anomalodesmata				
	Lyonsiidae	1	1	NT

Note: List includes all subclasses of bivalves but shows only orders and families with freshwater representatives. Abbreviations for distribution refer to major biogeographical regions: PA, Palearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian (classification adapted from Giribet 2008; data from Bogan 2008 and Graf and Cummings 2007).

[1] Includes Nuculanoidea

[2] Putative Etheriids also occur in the Neotropical and Oriental regions, but the taxonomic placement of these species is uncertain (Graf and Cummings 2007).

1.2. Freshwater mussels in the context of global bivalve diversity

The class Bivalvia contains approximately 20,000 living species worldwide, the vast majority of which are marine; only about 1,000 species live strictly in fresh waters (Haszprunar et al. 2008). However, freshwater representatives occur in most major bivalve groups and in 19 families (Table 1.2), indicating that there have been multiple, independent bivalve invasions of fresh waters around the world. Most bivalve groups contain few freshwater members; 13 of the 19 families with freshwater representatives

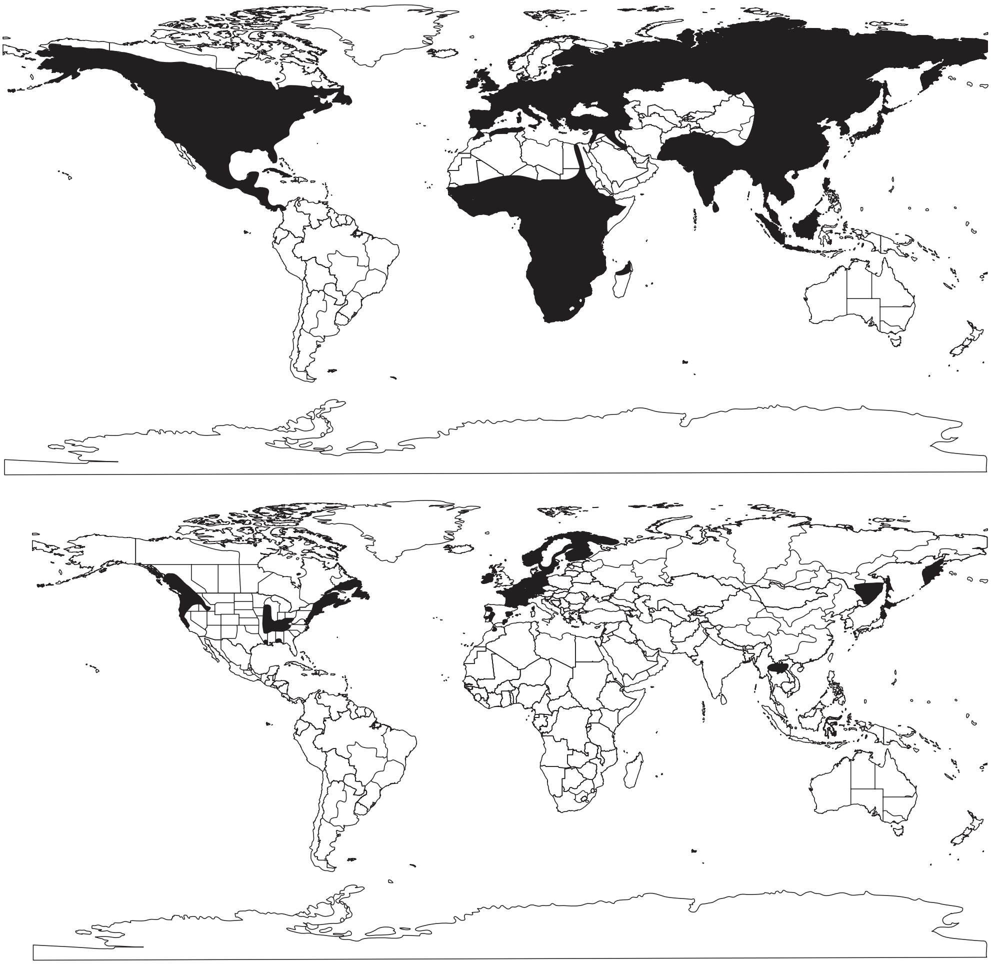

Figure 1.1. Global distribution of the families (top) Unionidae and (bottom) Margaritiferidae (from Bogan 2008).

have six or fewer freshwater species. By far the greatest freshwater radiation has occurred in the order Unionoida, which contains nearly 850 species and encompasses all diverse freshwater bivalve families with the single exception of the Sphaeriidae (order Veneroida). The Unionoida is the only bivalve order that has no marine representatives, although at least one North American species can tolerate brackish water (Section 4.1.B). All other bivalve orders with freshwater representatives have much higher diversity in marine waters, suggesting that their few freshwater species are relatively recent, adventitious colonizers of fresh waters.

The Unionoida is distributed worldwide, with the exception of Antarctica and the Pacific Oceanic Islands (Bogan 2008). The Unionidae is the most cosmopolitan family in the order, occurring widely in North America, Central America, Africa, Europe, and Asia (Figure 1.1). The Margaritiferidae also is wide ranging, but its current distribution is localized and apparently a relic of a previously wider range (Smith 2001; Figure 1.1). The remaining families of Unionoida are restricted to only one or two biogeographical regions, and none of these families occur in North America (Table 1.2).

In addition to being the most widely distributed family, the Unionidae contains about 80 percent of the species in the order (Table 1.2). Diversity of Unionidae is concentrated in eastern North America (about 300 species), southeastern China and Indochina (150 species), and Mesoamerica (90 species); most other regions within the family's range have fewer than 20 species (Graf and Cummings 2007). Although species richness is greatest in North America, higher-level freshwater bivalve diversity is the lowest of any biogeographical region. The Neotropical, Afrotropical, Palearctic, and Oriental regions each have freshwater members of seven to nine families in three to four orders, and the Australasian region has freshwater representatives in four families (Table 1.2). In contrast, North America has freshwater representatives of only three families in two orders: Sphaeriidae (fingernail clams, order Veneroida), Margaritiferidae, and Unionidae (both Unionoida). Representatives of two additional families, Corbiculidae and Dreissenidae (both Veneroida), have been introduced into North America by humans (Chapter 10).

Most North American species are members of the family Unionidae, and five species are in the family Margaritiferidae. Evolutionary relationships within the Unionidae are becoming better known through molecular genetics techniques. Current classifications recognize five tribes (plus an Old World lineage including *Gonidea*), representing distinct evolutionary (monophyletic) lineages, within the family (Graf 2002; Campbell et al. 2005; Figure 1.2), and I use this classification throughout this book. Assignment of genera to these tribes is well supported in most cases, but concepts of the genera themselves are in flux. Many long-used genera, such as *Anodonta, Fusconaia, Lampsilis, Quadrula*, and *Villosa*, are unnatural groupings each containing multiple independent lineages (e.g., Serb et al. 2003; Campbell et al. 2005; Zanatta et al. 2007a). A sixth unionid tribe may be necessary to contain the genus *Reginaia* (including "*Fusconaia*" *ebena* and "*F*". *rotulata*), which is not clearly associated with any currently recognized tribe (Campbell and Lydeard 2012a). These studies show the inadequacy of current classifications, but new generic classifications are only now being formally proposed (e.g., Roe and Hartfield 2005; Campbell and Lydeard 2012a). Numerous genera will need to be resurrected from synonymy or newly named to portray higher-level diversity in the Unionidae, underscoring the remarkable divergence within this family.

According to current concepts, North American species are distributed among approximately 50 genera (Figure 1.2). Estimates of species diversity are about 300, but totals vary slightly among recent accounts (Williams et al. 1993; Turgeon et al. 1998; Graf and Cummings 2007) and will likely increase with additional research (Chapter 3). The vast majority of these species are endemic to North America. Only two are shared with the Palearctic region (eastern pearlshell, *Margaritifera*

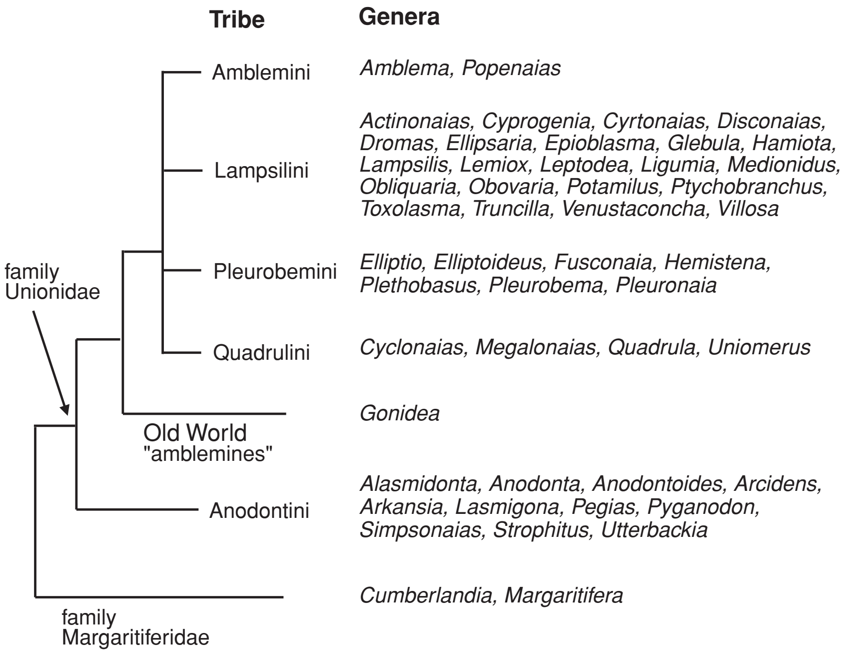

Figure 1.2. Diversity and phylogenetic relationships of North American freshwater mussels; two genera of uncertain phylogenetic affinity (*Plectomerus* and *Reginaia*) are omitted (adapted from Campbell et al. 2005; Graf and Cummings 2007).

margaritifera, and Yukon floater, *Anodonta beringiana*), and at least two are shared with Mexico (Tampico pearlymussel, *Cyrtonaias tampicoensis*, and Texas hornshell, *Popenaias popeii*). Similarly, most genera are unique to North America. In addition to the four genera listed previously, only *Potamilus* and *Megalonaias* potentially have representatives in other regions (Mesoamerica; Graf and Cummings 2007).

The great diversity of the Unionoida, its worldwide distribution, and its lack of marine members suggest that these animals have inhabited fresh waters for a very long time. Indeed, the group's fossil record extends to the Upper Devonian (416–365 million years ago (mya); Giribet 2008). North American unionoids first appeared in the Triassic (250–200 mya), and by the Cretaceous (145–65 mya), the group attained morphological and taxonomic diversity comparable to the Recent fauna (Watters 2001). The antiquity of the Unionoida is further supported by its phylogenetic position within the class Bivalvia. The Unionoida is related most closely to the marine order Trigonioida (Graf and Cummings 2006; Giribet 2008). The Trigonioida is an ancient lineage that was diverse and widespread in the Mesozoic (250–65 mya) but is represented today by only six or seven surviving species restricted to marine waters off Tasmania and Australia (Giribet 2008). Clearly the Unionoida, particularly the Unionidae, is a unique and characteristic component of freshwater ecosystems around the world.

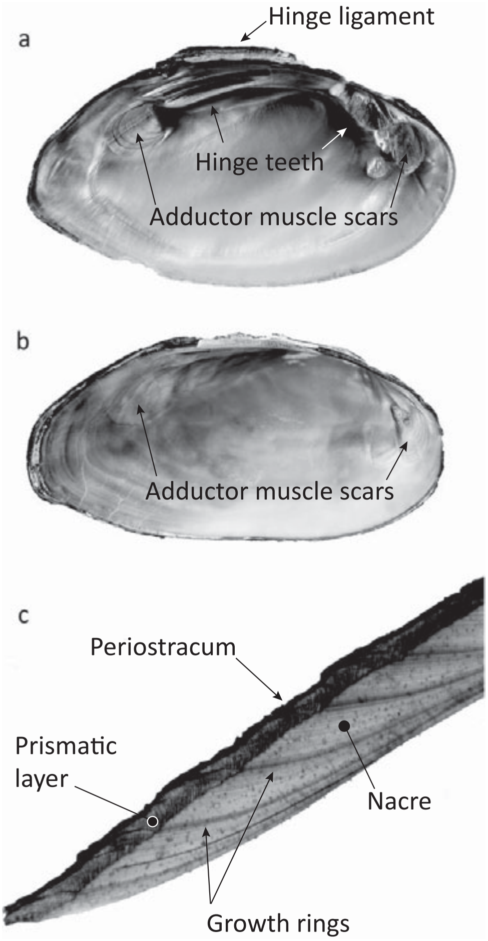

Figure 1.3. Structure of freshwater mussel shells. (a) Interior of the left valve of the Alabama spike, *Elliptio arca*, showing hinge ligament, hinge teeth, and attachment site for adductor muscles (muscle scars). (b) Interior of the alewife floater, *Anodonta implicata*, showing lack of hinge teeth (Richard T. Bryant, photos). (c) Cross section of mussel shell (W. R. Haag, photo).

1.3. Shells

The most conspicuous feature of a mussel is the shell. The shell is the animal's main defense against the world and gives support to the otherwise amorphous body mass. Shell morphology is highly variable and is interesting ecologically because shell features greatly influence how the animals interact with their environment. Furthermore, shells provide a record of growth and other events in the life of an individual. They are also simply gorgeous (see Plates).

The shell consists of two valves, which are held together by a springlike hinge ligament along the dorsal margin and by a pair of adductor muscles within the shell (Figure 1.3). Because muscle tissue can exert force only by contracting, the shell is

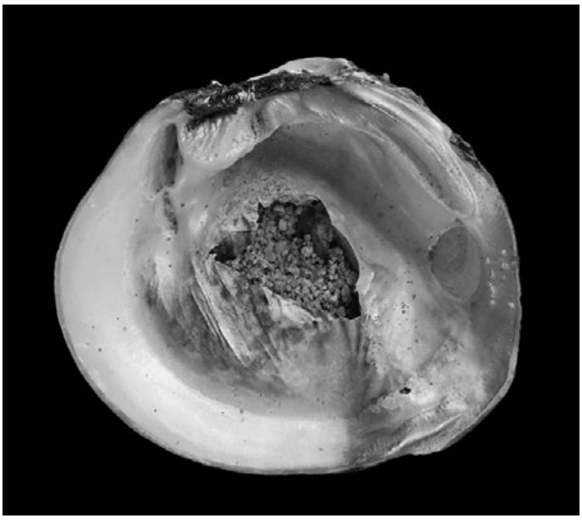

Figure 1.4. Shell of the Alabama orb, *Quadrula asperata*, showing sand grains covered by nacre; nacre has been punctured to show sand (Richard T. Bryant, photo).

opened by relaxing the adductor muscles, allowing the hinge ligament to pull the valves apart slightly; the shell is closed by contracting the adductor muscles. Shells of most species have hinge teeth, which interlock to hold the valves in juxtaposition, but teeth are reduced or absent in the Anodontini (Figure 1.3).

1.3.A. Shell production and growth

The shell is secreted by the mantle, a thin extension of the body wall – unique to mollusks – that underlies the shell. The shell consists of three layers: the periostracum, the prismatic layer, and the nacre (Figure 1.3). Most of the shell is composed of nacre, the lustrous, mother-of-pearl layer visible on the shell interior. The nacre is overlaid by the thin prismatic layer. The nacre and prismatic layer are composed of thin sheets of $CaCO_3$ crystals in an organic matrix including the protein conchiolin. The crystals are oriented parallel to the shell surface in the nacre and perpendicular in the prismatic layer (McMahon and Bogan 2001). Pearls are formed when foreign objects are trapped between the mantle and the shell and encapsulated by nacre; foreign material also is covered by nacre and incorporated into the shell (Rosenberg and Henschen 1986; Neves and Moyer 1988; Figure 1.4). Pearls may be formed particularly around encysted larval trematode parasites, which are common in mussels (Hopkins 1934). The periostracum is a thin, proteinaceous layer that covers the outer shell surface. The periostracum and prismatic layer are secreted only at the mantle edge and are associated with the growing shell margin, but nacre is secreted continuously along the entire inner surface of the shell, thickening and strengthening the shell with age (McMahon and Bogan 2001; Smith 2001). In temperate latitudes, shell secretion

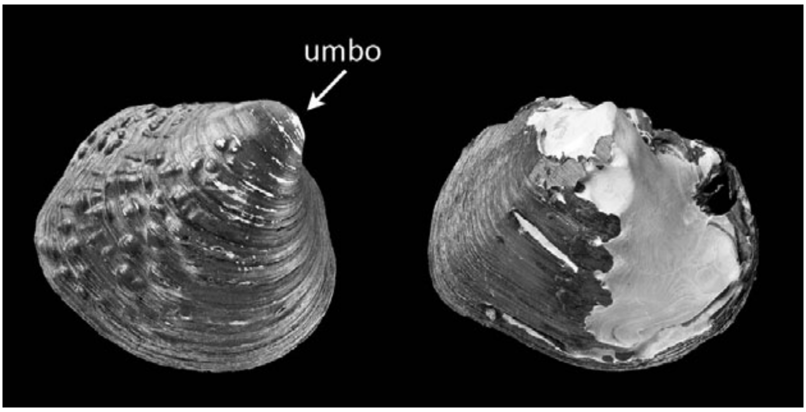

Figure 1.5. (left) Pimpleback, *Quadrula pustulosa*, from a well-buffered stream, showing minimal shell dissolution (Licking River, Kentucky). (right) *Q. pustulosa*, from a poorly buffered stream, showing extensive dissolution (Little Tallahatchie River, Mississippi) (Richard T. Bryant, photos).

occurs primarily in the warm months, beginning in spring at about 12°–15°C and ceasing in fall at about 6°–12°C (Howard 1922; Negus 1966; Dettman et al. 1999).

Because most fresh waters are mildly acidic, shell dissolution represents a major challenge for mussels. The periostracum is relatively impermeable to water, and its proteinaceous structure is resistant to dissolution; therefore this layer is important in protecting the underlying calcareous layers (McMahon and Bogan 2001). Accordingly, the periostracum is generally thicker in freshwater mollusks than in marine species that inhabit well-buffered waters (Watabe 1988). The organic matrix of the nacre also retards shell dissolution (Stanley 1988; Vermeij 1993), and freshwater species that inhabit soft waters have a greater percentage of shell organic material than species inhabiting hard waters (Bauer 2001). Because the periostracum and prismatic layers are secreted only at the shell margin, damage to these structures is not repaired and accumulates over time (Figure 1.5). Adventitious conchiolin layers associated with nacre production are deposited locally by the mantle in response to shell damage (Tevesz and Carter 1980; Day 1984). Nevertheless, mussels often experience shell dissolution at the umbo (the oldest part of the shell; Figure 1.5) or other places where the periostracum has been abraded or damaged. In some cases, dissolution can be extensive, eventually resulting in perforation of the shell and death of the animal (Kat 1982a).

In all bivalves, seasonal variation in shell deposition produces rings, providing a detailed growth record similar to those found in trees; fish spines, otoliths and scales; and permanent, hard structures of many other organisms. Shell deposited during the growing season has a high proportion of $CaCO_3$ relative to the organic matrix. In temperate latitudes, cessation or reduction of growth in winter results in a higher concentration of organic material relative to $CaCO_3$, producing distinct