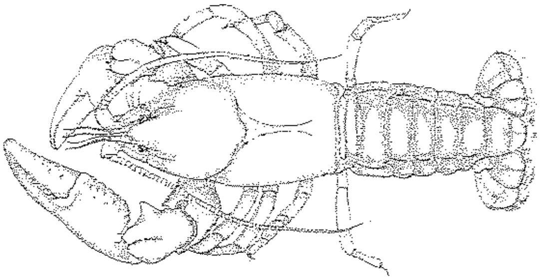


Ecology and Classification of North American Freshwater Invertebrates

Edited by

James H. Thorp
Water Resources Laboratory
and Biology Department
University of Louisville
Louisville, Kentucky

and

Alan P. Covich
Department of Zoology
University of Oklahoma
Norman, Oklahoma

Academic Press, Inc.
Harcourt Brace Jovanovich, Publishers
San Diego New York Boston
London Sydney Tokyo Toronto

Front cover photograph:
Scanning electron micrograph of a heterotardigrade, *Echiniscus spiniger*.
See Figure 15.1 for details. Courtesy of Diane R. Nelson.

This book is printed on acid-free paper. ∞

Academic Press, Inc.
San Diego, California 92101

United Kingdom Edition published by
Academic Press Limited
24–28 Oval Road, London NW1 7DX

Library of Congress Cataloging-in-Publication Data

Ecology and classification of North American Freshwater invertebrates
/ edited by James H. Thorp, Alan P. Covich.
p. cm.
ISBN 0-12-690645-9
1. Freshwater invertebrates--North America--Ecology.
2. Freshwater invertebrates--North America--Classification.
I. Thorp, James H. II. Covich, Alan P.
QL151.E36 1191
592.092'97--dc20 90-46694
CIP

Printed in the United States of America
91 92 93 94 9 8 7 6 5 4 3 2 1

Mollusca: Bivalvia

11

Robert F. McMahon
Department of Biology
The University of Texas at Arlington
Arlington, Texas 76019

Chapter Outline

I. INTRODUCTION

Freshwater bivalve molluscs (class Bivalvia) fall within the subclass Lamellibranchia and are characterized by greatly enlarged gills with elongated, ciliated filaments for filter feeding. As the name implies, the mantle tissue underlying the shell is separated into left and right shell-secreting centers or lobes. However, the bivalved shell is a single structural entity. In early development, the bivalve mantle (tissue outgrowth from the dorsal side of the visceral mass enfolding the body and secreting the shell) is dorsally divided by anterior and posterior bifurcations into right and left portions, which always remain connected by a mid-dorsal isthmus (Allen 1985). Bivalves, as do all molluscs, secrete a shell made up of proteinaceous and crystalline calcium carbonate elements (Wilbur and Saleuddin 1983). The right and left mantle halves secrete shell material with a high proportion of crystalline calcium carbonate to form the left and right valves. The adjoining isthmus primarily secretes proteinaceous material to form an elastic hinge ligament dorsally connecting the two valves (Fig. 11.1). The hinge ligament is external in all freshwater bivalves. Its elastic properties force the valves apart when shell adductor muscles are relaxed. Anterior and posterior shell adductor muscles (Fig. 11.2) run between the valves and function in opposition to the hinge ligament to close the valves on contraction.

Ecology and Classification of North American Freshwater Invertebrates

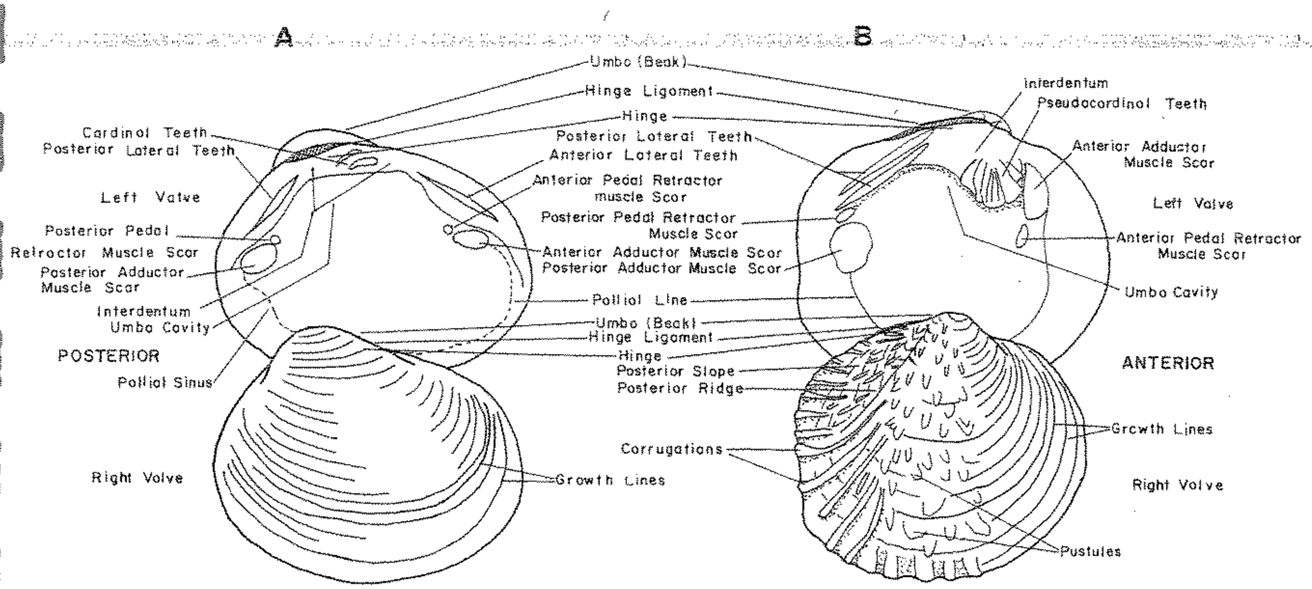


Figure 11.1 General morphologic features of the shells of (A) corbiculacean and (B) unionacean freshwater bivalves.

The left and right mantle lobes and overlying shell valves extend anteriorly, posteriorly, and ventrally to enclose the entire body of the bivalve. Surrounded by the valves, cephalic sensory structures have become vestigial or lost and external sensory functions relegated to the mantle edge, which is exposed directly to the external environment. Bivalves, compared to other molluscs, are laterally compressed and expanded dorso-ventrally. Being entirely enclosed within the shell valves and mantle protects soft tissues from sediment abrasion and prevents invasion of the mantle cavity by fine sediment, which could interfere with ciliated gill-filtering mechanisms. This adaptation, in conjunction with both lateral body compression and evolution of a highly extendable, spadelike foot adapted for burrowing, has allowed bivalves to become perhaps the most successful infaunal filter feeders of marine and freshwater habitats.

The bivalve fauna of North American freshwaters is the most diverse in the world, consisting of 260 native and 6 introduced species (Burch 1975a,b). This diversity is greatest among unionacean mussels (superfamily Unionacea, 227 native species in 44 genera), many species of which have unique morphological adaptations and highly endemic, often endangered populations. In contrast, the sphaeriids (family Sphaeriidae, 33 native and 4 introduced species in four genera) have far fewer species and genera but are more widely distributed and cosmopolitan than most unionaceans (several sphaeriid genera and species have pandemic distributions). North American freshwaters have also been invaded by an exotic southeast Asian species, *Corbicula fluminea* (family Corbiculidae), which has spread throughout the freshwater drainage systems of the coastal and southern United States and Mexico, becoming the dominant benthic species in many habitats (Counts 1986, McMahon 1983a). Another exotic species, *Dreissena polymorpha*, the zebra mussel, was discovered in Lake St. Clair and Lake Erie in 1988. Based on the size–age structure of present populations, it appears to have been introduced to the Great Lakes from Europe/Asia in 1985 or 1986 (Hebert *et al.* 1989, Mackie *et al.* 1989).

II. ANATOMY AND PHYSIOLOGY

The majority of North American freshwater bivalve species fall into two superfamilies: the Corbiculacea and the Unionacea. The general external and internal features of these two groups are relatively similar (Fig. 11.2). Indeed, the anatomical features of lamellibranch bivalves are highly sterotypic and, therefore, will be discussed in general terms here.

A. External Morphology

1. Shell

The bivalve shell is composed of nonliving calcium carbonate ($CaCO_3$) crystals embedded in a proteinaceous matrix, both secreted by the underlying living mantle. The shell of most bivalves consists of three distinct portions: an outer proteinaceous periostracum secreted from the periostracal groove in the mantle edge, an underlying prismatic layer, and

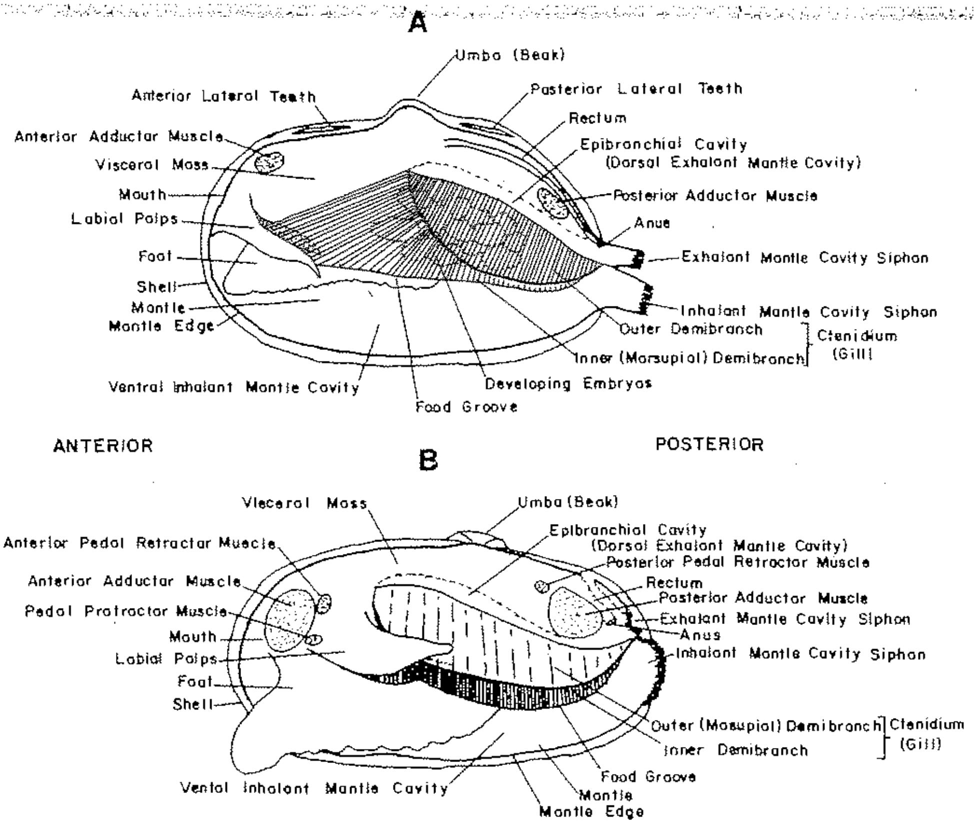


Figure 11.2 General external anatomy of the soft tissues of (A) corbiculacean and (B) unionacean freshwater bivalves.

inner layer of nacre. The last two layers are formed from $CaCO_3$ crystals in an organic matrix. Sphaeriids uniquely lack the nacreous layer. The periostracum is initially secreted free from other shell material, but soon fuses with the underlying, primarily calcareous prismatic layer secreted by a portion of the mantle edge just external to the periostracal groove (Fig. 11.3). The prismatic shell layer is a single layer of elongated calcium carbonate crystals oriented at 90° to the horizontal plane of the shell (Fig. 11.3). The free edge of the periostracum seals the extrapallial space between the mantle and shell from contact with the external medium, allowing $CaCO_3$ concentrations in extrapallial fluid to reach the saturation level required for crystal deposition (Saleuddin and Petit 1983). In unionaceans, the tripartite periostracum is secreted as an outer layer forming the external proteinaceous surface of the shell, and middle layer apparently involved with formation and organization of the prismatic layer, and an inner layer association with the initial formation of the nacreous layer at the growing shell edge (Saleuddin and Petit 1983). The periostracum is relatively impermeable to water, preventing dissolution of $CaCO_3$ from the shell surface. The nacreous (pearly) shell layer is continuously secreted by the underlying mantle epithelium and consists of consecutive layers of small $CaCO_3$ crystals parallel to the plane of the shell (Fig. 11.3). Accumulation of nacreous layers through time thickens the shell, accounting for its strength and rigidity.

Calcium (Ca^{2+}) and bicarbonate (HCO_3^-) ions necessary for deposition of shell $CaCO_3$ crystals are transported from the external medium across the external epithelium into the hemolymph (blood). Bicarbonate ions are also generated from metabolically released CO_2 ($CO_2 + H_2O \leftrightarrow H^+ + HCO_3^-$). The mantle transports these ions from the hemolymph into the extrapallial fluid where they are deposited as shell crystals (Wilbur and Saleuddin 1983).

Formation of $CaCO_3$ crystals requires release of protons (H^+) ($Ca^{2+} + HCO_3^- \leftrightarrow CaCO_3 + H^+$), which must be removed from the extrapallial fluid to maintain the high pH required for $CaCO_3$ deposition (pH range 7.4–8.3). A proposed mechanism involves the combination of H^+ with HCO_3^- to form H_2CO_3, then its dissociation into CO_2 and H_2O, which diffuse into the hemolymph. The presence in mantle tissue of the enzyme carbonic anhydrase, which catalyzes this latter reaction, is evidence for this mechanism (Wilbur and Saleuddin 1983). Extra-

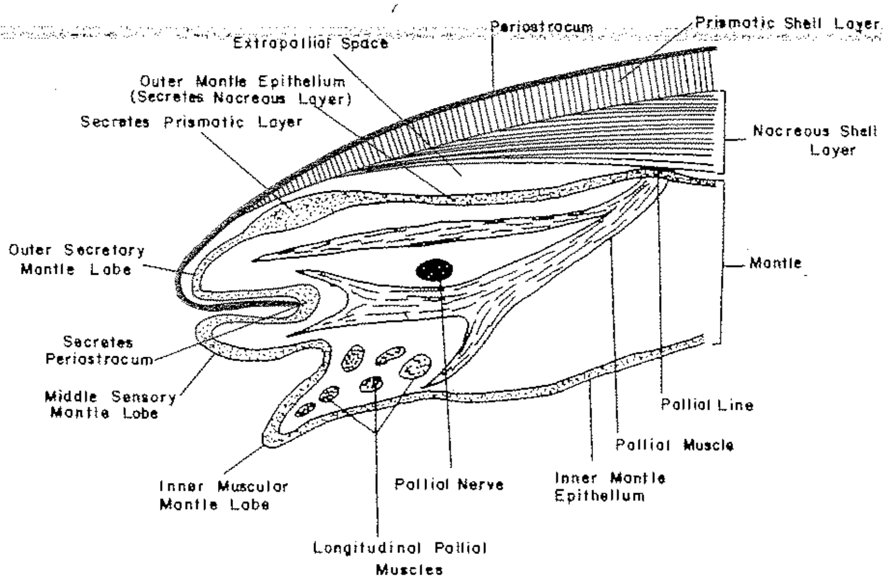


Figure 11.3 A cross-section through the mantle and shell edges of a typical freshwater unionacean bivalve displaying the anatomic features of the shell, mantle, and mantle edge. Sphaeriids have a complexed cross-lamellar shell structure and lack nacre but their mantle edge has a similar structure.

pallial fluid pH is higher is freshwater bivalves than marine bivalves, favoring $CaCO_3$ deposition at the lower Ca^{2+} concentrations characteristic of the dilute hemolymph concentration of freshwater species (Wilbur and Saleuddin 1983).

Shell $CaCO_3$ and organic matrix material precipate from the extrapallial fluid. In freshwater bivalves, Ca^{2+} and HCO_3^- are actively concentrated in the extrapallial fluid, favoring deposition as $CaCO_3$ crystal (Wilbur and Saleuddin 1983). The organic shell matrix, which separates individual crystals and binds them and crystal layers into a unified structure, is also involved with crystal formation. It has crystal-nucleating sites (possibly calcium-binding polypeptides) on which $CaCO_3$ crystals initially develop, eventually growing to form a new, nacreous shell layer (Wilbur and Saleuddin 1983).

It has been proposed that a minimum of one ATP molecule is required for every two Ca^{2+} ions deposited, with additional ATP required for active HCO_3^- transport (Wilbur and Saleuddin 1983). Thus, fast-growing species or those with massive shells must devote a relatively high proportion of maintenance energy to shell mineral deposition. Deposition of the proteinaceous shell matrix (including the periostracum) also demands energy, requiring four ATP for each peptide bond formed. Although rarely more than 10% of shell dry mass, the highly condensed shell matrix can account for one-third to one-half of the total body dry organic matter (shell + tissue organic matter) or up to one-third of the total energy devoted to growth (Wilbur and Saleuddin 1983). Thus, fast-growing, thin-shelled species devote proportionately far less energy to shell production than do slower-growing, thick-shelled species, allowing allocation of a greater amount of energy to growth and reproduction (thereby increasing fitness). However, a thinner, more fragile shell increases the probability of predation or lethal desiccation during emergence, reducing fitness. Therefore, the balance struck between energy allocation to shell formation and tissue growth in a species represents an adaptive strategy, evolved under species-specific niche selection pressures (see Section III.B).

The shell surface may be marked with concentric or radial corrugations, ridges, or pigmented rays or blotches in the periostracum. These, along with the shape of the posterior ridge and outline shape of the shell are diagnostic taxonomic characters. Another major external feature is the umbos or beaks, anteriorly curving, dorsally expanded structures, representing the oldest portions of the shell valves (Fig. 11.1).

Internally, major shell features include the hinge and projecting hinge teeth, which interlock to hold the valves in exact juxtaposition and form the fulcrum on which they open and close, and various muscle insertion scars. These are also major diagnostic characters (see Section V). In corbiculaceans, massive conical cardinal teeth form just below the umbos (one in the right valve and two in the left). Anterior and posterior to these lie the lateral teeth, usually elongated lamellae (Fig. 11.1A). Unionaceans have no true cardinal teeth. Instead, massive, raised, pseudocardinal teeth develop from anterior lateral teeth just anterior to the umbos and serve a similar function. Elongated, lamellar, posterior lateral teeth extend posterior to the umbos (Fig. 11.1B). In the Anodontinae, hinge teeth are vestigial or lost. The internal nacreaus layer may have species-specific colors. Muscle scars mark the insertion points of the anterior and posterior shell adductor muscles, the anterior and posterior pedal retractor muscles, and anterior pedal protractor muscles, and the pallial line muscles, which attach the margin of the mantle to the shell (Figs. 11.2 and 11.3). Posteriorly, the pallial line may be indented, marking the pallial sinus into which the siphons are withdrawn (Fig. 11.1A).

2. *Locomotory Structures*

With the exception of the epibenthic *Dreissena polymorpha*, the vast majority of North American freshwater bivalves are burrowers in benthic sediments. Some species can be found above the substratum on exposed rocky bottoms, but they still use the foot to wedge into crevices or under rocks. In all cases, locomotion is achieved with a highly muscular, flexible, protrusible anterioventrally directed foot (Figs. 11.1 and 11.2).

Bivalve burrowing mechanics have been described in detail by Trueman (1983). The burrowing cycle is initiated with relaxation of the adductor muscles, allowing shell valves to be forcibly opened against the surrounding substratum by expansion of the hinge ligment, anchoring the bivalve in place. Contraction of the transverse and circular muscles around the foot hemolymph sinuses, acting as hydraulic skeletons, then causes the foot to decrease in diameter and to elongate, forcing it forward into the substratum as the open valves are wedged in place against the burrow walls. Once extended into the substratum, the distal end of the foot is expanded by a flow of blood into its hemocoels, anchoring it in its new position in the substratum. Adductor muscle contraction then rapidly closes the valves, releasing their hold on the burrow walls and forcibly expelling water from the pedal gape downward into the sediments. This blast of water loosens compacted sediments at the anterior edge of the shell. Thereafter, anterior and posterior pedal retractor muscle contractions pull the shell forward into the loosened sediments against the anchored foot tip. Once a new position is achieved, the adductor muscles again relax to reanchor the shell valves against the substratum and the burrowing cycle is repeated. As North American bivalves have relatively short siphons (highly reduced or absent in some *Pisidium*), they generally burrow to depths where the posterior shell margin is either buried just beneath the sediment surface or extended slightly above it.

Many juvenile freshwater bivalves can crawl over the substratum surface for considerable distances before settlement. Indeed, juveniles of some species can traverse even relatively smooth vertical surfaces. Crawling is achieved by extension of the foot, anchoring its tip with mucus and/or a muscular attachment sucker, followed by contraction of pedal muscles to pull the body forward. The capacity for surface locomotion is greatly reduced in most adult unionaceans, but retained to varying degrees in adult sphaeriids and *Corbicula fluminea*. The zebra mussel, *Dreissena polymorpha*, though normally attached to hard substrata by proteinaceous threads (the byssus), is capable of extensive surface locomotion. Such locomotion is particularly common in juvenile and immature specimens. After shedding its byssus, this mussel employs pedal locomotion to move to a new location where the byssal attachment is reformed (Mackie *et al.* 1989).

B. *Organ System Function*

1. *Circulation*

Circulation in bivalves has been reviewed by Jones (1983). Bivalves have an open circulatory system, in which the circulatory fluid is not continually enclosed in vessels (i.e., a closed circulatory system), but rather passes through open, spongy hemocoels (blood sinuses) in which the hemolymph bathes the tissues directly before returning to the heart. The open circulatory system of bivalves is associated with large hemolymph volumes, which account for 49–55% of total corporal water (Burton 1983, Jones 1983). The ventricle of the heart uniquely surrounds the rectum and pumps oxygenated hemolymph from the gills and mantle via the kidney through anterior and posterior blood vessels (Fig. 11.4), which subdivide into many smaller vessels including pallial arteries to the mantle and visceral arteries to the body organs and foot. The arteries further subdivide into many tiny vessels that eventually open into the hemocoels where cellular exchange of nutrients, gases, and wastes occurs. Blood returns via hemocoels to the gills and mantle and thence to the heart. Evolution of an open circulatory system in molluscs has been associated with reduction of the coelom. The ventricle is surrounded by one of the few coelomic remnants, the pericardial cavity, surrounded by the pericardial epithelium (pericardium). The only other coelomic remnants are spaces comprising the kidneys and gonads.

The hemolymph of freshwater bivalves, as in most lamellibranch species, has no specialized re-

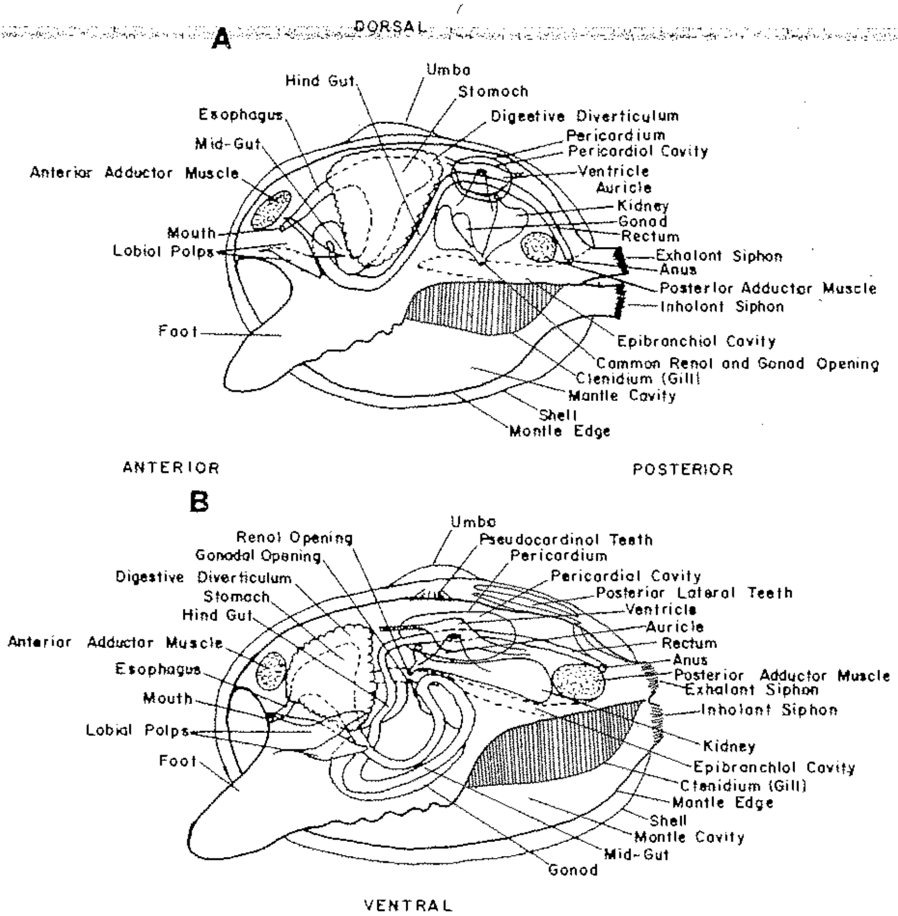


Figure 11.4 General internal anatomy, organs, and organ systems of the soft tissues of (A) corbiculacean and (B) unionacean freshwater bivalves.

ratory pigments for O_2 transport (Bonaventura Bonaventura 1983). Instead, oxygen is dis- ved directly in hemolymph fluid, making its O_2 rrying capacity essentially that of water. How- , the very low metabolic rates, reduced oxygen ands, and extensive gas-exchange surfaces of valves allow maintenance of a primarily aerobic abolism, in spite of reduced hemolymph O_2 car- g capacity.

ills and Gas Exchange

lamellibranch bivalves, including all North nerican species, the gills (Fig. 11.2) are greatly anded beyond requirements for respiratory gas hange, as they are also utilized for filter feeding e., suspension feeding), the main method of food uisiton for the majority of species (see Section C.2). The gill axes extend anteriolaterally along er side of the dorsal portion of the visceral mass. any long, thin, inner and outer gill filaments ex- d from either side of the gill axes. The gill fila- nts are fused together (an evolutionarily advanced condition) but penetrated by a series of pores or ostia (i.e., the eulamellibranchiate condition). From the axis, the filaments first extend ventrally (descending filament limbs) and then reflect dorsally (ascending filament limbs), attaching distally to either the dorsal mantle wall (outer gill filaments) or the dorsal side of the visceral mass (inner gill filaments) to form two v-shaped curtains known as the inner and outer demibranchs. The demibranchs completely separate the mantle cavity into ventral inhalent and dorsal exhalant portions (Fig. 11.5). The descending and ascending portions of the filaments are periodically cross-connected by tissue bridges called interlamellar junctions. The area between descending and ascending filaments is called a water tube or interlamellar space (Fig. 11.5). Gill feeding and respiratory currents are maintained by lateral cilia on the sides of the external surfaces of the filaments (Fig. 11.5A), which force water through the ostia into the water tubes. Inhalent water passes through the gill ostia to the water tubes to be carried to the dorsal exhalant mantle cavity or epibranchial cavity (formed by connection of the

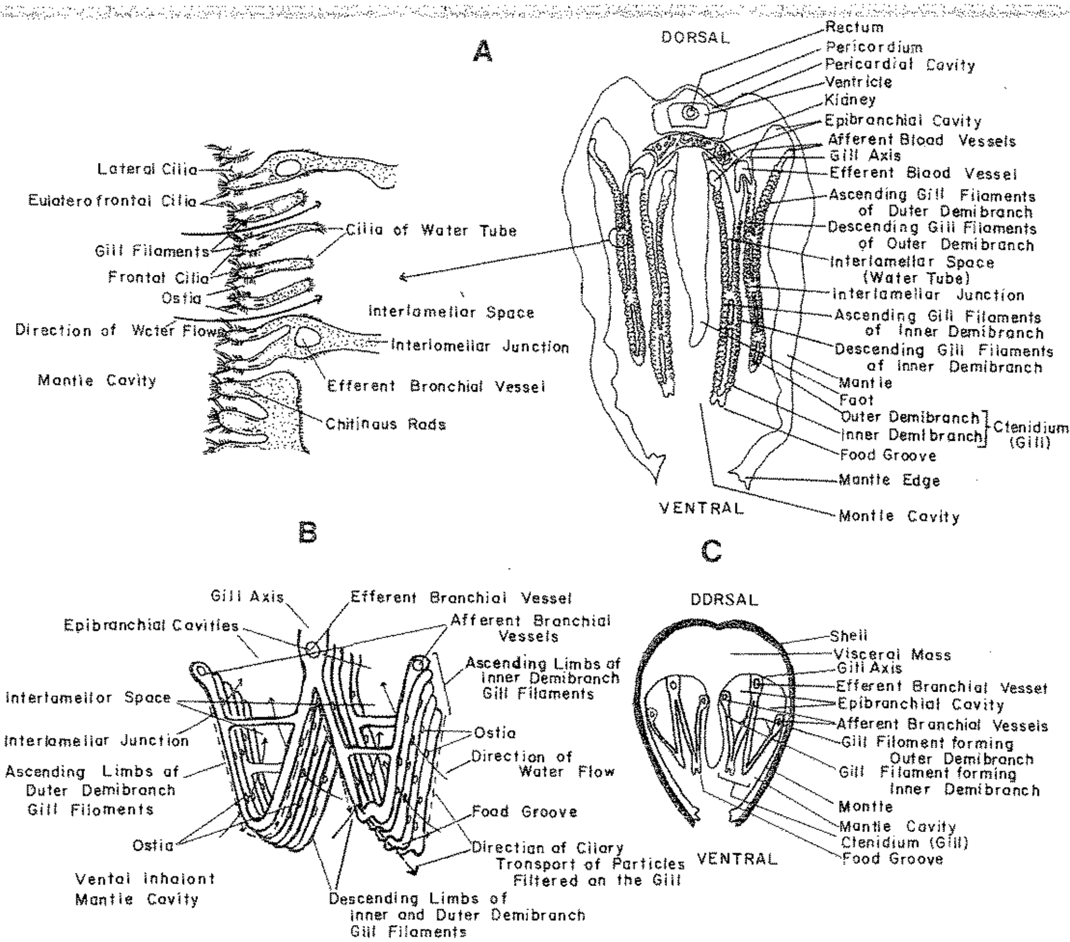


Figure 11.5 The structural features of the gills (ctenidia) of freshwater bivalves. (A) Cross-section through the central visceral mass, ctenidia, and mantle of a typical freshwater unionid, with high-magnification view showing details of filaments, ostia, and ciliation. (B) Diagrammatic representation of the respiratory and feeding water currents across the ctenidium. (C) Diagrammatic cross-sectional representation of lamellibranch bivalve ctenidia.

distal ends of the inner and outer demibranchs to the mantle wall or visceral mass, respectively) where it flows posteriorly to exit via the exhalant siphon (Figs. 11.2 and 11.5).

3. *Excretion and Osmoregulation*

Freshwater bivalves, as all freshwater animals, have hemolymph and tissue osmotic concentrations greater than their freshwater medium, resulting in a constant ion loss and water gain. This osmotic problem is compounded in bivalves by extensive mantle and gill surface areas over which such water and ion flux can occur (Burton 1983, Dietz 1985). To reduce ion and water fluxes, freshwater bivalves have the lowest hemolymph and cell osmotic concentrations of any metazoan, being 25–50% of that found in most other freshwater species (Burton 1983, Dietz 1985). In spite of these characteristics, the extensive epithelial surface areas of bivalves cause water and ion fluxes to be greater than in other freshwater species (urine clearance is 20–50 ml/kg/hr) (Dietz 1985).

In unionaceans, sodium is taken up in exchange for outward transport of hemolymph cations such as H^+ or NH_4^+ and, perhaps, Ca^{2+}. Chloride ion uptake is in exchange for HCO_3^- or OH^-. Active Ca^{2+} uptake has also been reported (Burton 1983). In freshwater snails, the major source of calcium ions is ingested food (McMahon 1983b); however, the relative roles of food and external medium as sources for shell Ca^{2+} are unknown in freshwater bivalves. Sodium uptake does not require the presence of Cl^-, indicating that the transport systems of these two ions operate independently (Burton 1983). Active transport appears to be the major route by which unionaceans gain ions from the medium, but in *Corbicula fluminea* exchange diffusion (transport of an ion in one direction in hange for diffusion of a second ion species down concentration gradient in the opposite direction) ccounts for 67% of Na^+ uptake. *Corbicula flu*- *ea* has much higher ion transport rates and he- ymph ionic concentrations than do unionaceans, ecting its geologically recent penetration of eshwaters (Dietz 1985). Interestingly, exchange usion may account for up to 90% of Cl^- turnover nionaceans in pond water, but when individuals e salt-depleted, active transport dominates Cl^- ake (Dietz 1985). Na^+ and Cl^- uptake can occur r the general epithelial surface of unionaceans, t the majority occurs over the gills (Dietz 1985).

Excess water is eliminated through the renal or- s or kidneys. The walls of the auricles initially afilter the blood. Under the hydrostatic pressure nerated by auricular contraction, blood fluid con- ng ions and small organic molecules passes as a essentially isosmotic and isoionic to the hemo- mph through the auricle walls into the pericardial ty. Filtration appears to occur through podocyte of the pericardial gland lining the inner auricular surface and perhaps through the efferent branchial vein, carrying hemolymph from the longitudinal vein of the kidney to the auricles (Martin 1983) (Fig. 11.6). Only larger blood proteins, lipids, and carbohydrate molecules cannot pass the pericardial gland filter. The filtrate passes from the pericardial cavity through left and right renopericardial openings in the pericardial wall into the renopericardial canals and thence into the left and right renal organs or kidneys. Larger organic waste molecules enter the filtrate by active transport across the kidney walls. The excretory fluid is released through nephropores (Fig. 11.6) opening into the epibranchial cavities to be carried out the exhalant siphon (Figs. 11.2 and 11.4A) (Martin 1983).

While not studied in freshwater bivalves, it is presumed that the bivalve kidney is the site of major active ion resorption from the filtrate back into the hemolymph as in freshwater snails (Little 1985). As kidney walls appear relatively impermeable to water, active ion resorption from the filtrate allows formation of a dilute excretory fluid (filtrate osmo-

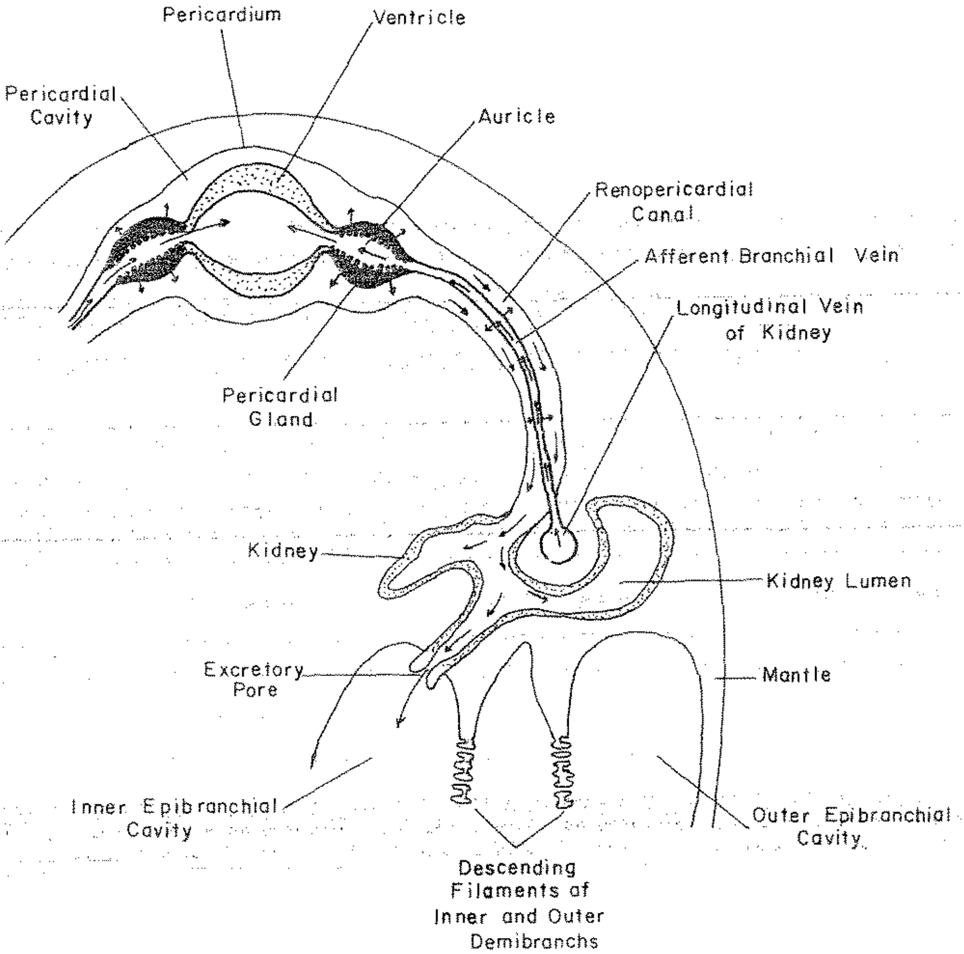


Figure 11.6 Cross-sectional representation of the anatomic features of the excretory system of a typical reshwater bivalve. Arrows indicate pathways for the excretion of excess water in the hemolymph through the xcretory system to be eliminated at the excretory pore. (Redrawn from Martin 1983.)

larity is 50% that of the hemolymph in the unionid *Anodonta cygnea*, Martin 1983) facilitating removal of excess water. Filtrate ion resorption is energetically less expensive than recovery from freshwater because concentration gradients between the kidney filtrate and hemolymph are reduced relative to those between hemolymph and freshwater. Excretory fluid production is high, approximately 0.03 ml/g wet tissue/day in *A. cygnea*. In spite of renal absorption of major ions, the excreted filtrate has a higher ionic concentration than freshwater, thus ions are lost with urine excretion. These ions and those lost by diffusion over body and gill surfaces must be recovered by active transport from the medium across epithelial surfaces (particularly those of the gills) to the hemolymph (for details see Section II.C.6).

4. *Digestion and Assimilation*

As lamellibranchs, the vast majority of freshwater bivalves are suspension feeders, filtering unicellular algae, bacteria, and suspended detrital particles from the pallial water flow across the gill. Material filtered on the gill is passed to the labial palps for cilia-mediated sorting of food from nonfood before being carried on ciliary tracts to the mouth. Some species also have mechanisms for gathering organic detrital particles from the substratum. Filter and detritus feeding are described in Section III.C.2. The present discussion is devoted to the processes of digestion and assimilation.

The bivalve mouth is a simple opening flanked laterally by left and right pairs of labial palps, whose ciliary tracts deliver food to the mouth as a constant stream of fine particles. Food entering the mouth passes a short ciliated esophagus where it is bound into a mucus rope before entering the stomach. The stomach, which lies in the anterior-dorsal portion of the visceral mass (Fig. 11.4), is a complex structure, containing ciliated sorting surfaces and openings to a number of digestive structures and organs. On its ventral floor, posterior to the midgut opening, is an elongated evagination of the stomach wall called the style sac. Cells at the base of the style sac secrete the crystalline style, a long mucopolysaccharide rod projecting dorsally from the style sac into the stomach. The cells lining the style sac secrete digestive enzymes into the style matrix. Their cilia function to rotate the crystalline style slowly. The stomach and style have pH levels ranging from 6.0–6.9, style acidity varying with phase of digestion (Morton, 1983).

The free end of the style projects against the roof of the stomach where it rotates against a chitinous plate, the gastric shield. The gastric shield is penetrated by microvilli from epithelial cells underlying it. These cells are considered to secrete digestive enzymes through these microvilli onto the shield surface (Morton 1983). Rotation of the style mixes stomach contents and winds the esophageal mucus thread containing freshly ingested food onto the free end of the style where slow release of its embedded enzymes begins the process of extracellular digestion. Wear from abrasion of the style tip against the gastric shield causes attached food particles to be carried dorsally to the gastric shield. Here, style tip rotation causes food to be triturated in direct contact with digestive enzymes concentrated by release from the eroding style matrix and epithelia underlying the gastric shield.

After this initial trituration, food particles released into the stomach may have several fates. Particles entering the midgut may either be passed to the hindgut and thence to the rectum to be egested, or returned back to the stomach from the midgut for further extracellular breakdown. This size-based particle sorting is effected by a ciliated ridge, the typhlosole, running the length of the midgut. Sufficiently small particles are eventually carried on ciliary tracts in the stomach to the digestive diverticulum for the final intracellular phase of digestion (Fig. 11.4); these diverticula have the lowest fluid pH of any portion of the gut (Morton 1983). Larger particles are recycled to the stomach for further trituration and enzymatic digestion. Thus, particles may pass over gut ciliated sorting surfaces and be exposed to digestive processing several times before acceptance for assimilation or rejection as feces.

Digestive cells lining the lumina of terminal tubules in the digestive diverticulum take up fine food particles by endocytosis into food vacuoles, where the final stages of digestion and absorption take place. After completion of this intracellular phase of digestion, the apical portions of digestive cells, which contain vacuoles with undigested wastes, are shed into the tubule lumina to be carried as fragmentation spherules into the stomach by ciliated rejection pathways. The breakdown of these spherules in the stomach is hypothesized to be a major source of stomach acidity and extracellular digestive enzymes (Morton 1983).

Undigestible matter passes through the relatively short hindgut into the rectum and out the anus, which opens into the epibranchial cavity on the posterior face of the posterior adductor muscle near the exhalant siphon. Feces are expelled on exhalant pallial currents (Fig. 11.4). Mucous secreted by hindgut and rectal cells binds undigested particles into discrete feces before egestion, preventing recirculation of fecal material with inhalant currents.

The cerebropleural and visceral ganglia of freshwater bivalves release neurohormones influencing glycogenesis (Joose and Geraerts 1983). The vertebrate glycogenetic hormones, insulin and adrenalin, have effects similar to those in vertebrates when administered to unionaceans. Injection of vertebrate insulin into *Lamellidens corrianus* caused decreased blood glucose levels and an increase in foot and digestive diverticulum glycogen stores, while injection of adrenaline induced breakdown of glycogen stores and increased blood sugar levels (Jadhav and Lomte 1982b). Gut epithelial cells produce an insulin-like substance (ILS) in *Unio pictorum* and *Anodonta cygnea*, the release of which is stimulated by elevated hemolymph glucose levels. ILS, in turn, stimulates activity of glycogen synthetase, an enzyme involved in the uptake of glucose into cellular glycogen stores, leading to return of hemolymph glucose to normal levels (Joose and Geraerts 1983). Cerebropleural ganglionic neurosecretory hormones regulate accumulation and release of proteinaceous and nonproteinaceous energy stores from the digestive diverticulum and foot of *Lamellidens corrianus* (Jadhav and Lmote 1983).

Reproductive Structures

The gonads of freshwater bivalves, as in almost all bivalves, are paired and lie close to the digestive diverticulum. In unionaceans, they lie so closely together that the paired condition is often hard to discern. Unionacean gonads envelop the lower portions of the intestinal tract and sometimes extend into proximal portions of the foot (Fig. 11.4B), while in sphaeriids and *Corbicula fluminea*, gonads lie more dorsally in the visceral mass, extending along the stomach, intestine, and digestive diverticulum (Fig. 11.4A) (Mackie 1984). The gonoducts from each gonad are short, and open into paired gonopores in the epibranchial mantle cavity allowing released gametes to be discharged from the exhalant siphon (Fig. 11.4). In freshwater unionaceans, which are generally gonochoristic (except for a few hermaphorditic species of *Anodonta*), the tracts and openings of the renal and reproductive systems are entirely separate. This is considered to be an evolutionarily advanced condition (Fig. 11.7C). In sphaeriids and *C. fluminea*, which are hermaphroditic, the gonads are comprised of distinct regions or zones in which either male or female acini produce eggs or sperm. In these groups, ducts carrying eggs or sperm unite into a single gonoduct from each gonad. These open either into the distal end of the kidney—allowing discharge of gametes through the renal canal and nephridiopore (Fig. 11.7A)—or into the gonoduct and nephridial canal, which discharge through a common pore on a papilla extending into the epibranchial cavity (Fig. 11.7B) (Kraemer *et al.* 1986, Mackie 1984). The zebra mussel, *Dreissena polymorpha*, is gonochoristic.

Almost all North American freshwater bivalve species are ovoviviparous, brooding embryos through early development stages in the gill. The single exception is *D. polymorpha*, which releases both sperm and eggs externally, leading to external fertilization and development of a free-swimming veliger larval stage (Mackie *et al.* 1989). In brooding species, the interlamellar spaces of the demibranchs are modified to form marsupia (brood chambers). Fully formed juveniles are released from the exhalant siphon in sphaeriids and *C. fluminea*. In unionaceans, bivalved glochidium larvae are released from the exhalant siphon, from specialized gill pores, or by rupture of the ventral portion of the gill. Glochidia parasitize a fish host before metamorphosing into a juvenile. The outer demibranchs form the marsupium in most unionacean species except for members of the subfamily Ambleminae, in which marsupia are formed in both the inner and outer demibranches (Burch 1975b). The inner demibranchs serve this purpose in sphaeriids and *C. fluminea*. Members of the unionid genus *Lampsilis* develop marsupia only in the posterior portion of the outer demibranchs and release glochidia from small pores in the marsupial demibranch directly into the inhalant mantle cavity. In *C. fluminea*, developing embryonic stages are brooded directly within inter-

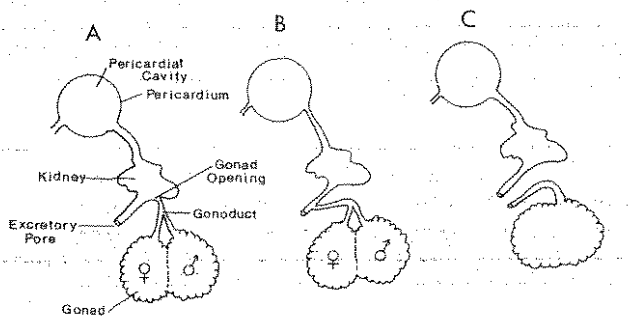


Figure 11.7 Schematic representations of typical reproductive systems of bivalves. (A) The primitive condition in some marine bivalve species: male or female gametes are released from the gonoduct opening into the kidney and passed externally through the excretory pore (shown here is a primitive marine hermaphroditic bivalve; the anatomy is essentially similar in gonochoristic species). (B) Hermaphroditic freshwater corbiculacean bivalves (*Corbicula fluminea* and sphaeriids): male and female gametes are passed through the gonoduct into the kidney duct close to the excretory pore from which gametes are shed. (C) Gonochoristic freshwater unionids: gametes pass to the outside through a gonoduct and gonopore totally separate from the kidney duct and excretory pore. (After Mackie 1984).

lamellar spaces without other specialized brooding structures. In sphaeriids, fertilized eggs are enclosed in specialized brood chambers formed from evaginations of the gill filaments into the interlamellar space. In anodontid unionaceans, the interlamellar space of the marsupial demibranchs is divided by septa into a separate interlammelar cavity associated with each filament. Each interlamellar cavity is further divided into inner and outer water tubes carrying water to the epibranchial cavity and a central marsupium containing developing glochidia, an advanced tripartite structure that does not occur in other unionaceans. In the primitive Margartiferidae and the Ambleminae, the entire outer demibranch forms the marsupium, while in the Pleurobemini and Lampsilini, marsupia are limited to just a portion of outer demibranch (Burch 1975b, Mackie 1984).

Some unionaceans display sexual dimorphism, a characteristic generally rare in other freshwater bivalves. In such species, incubation of glochidia results in massive distension of the outer demibranch marsupium (Mackie 1984). In female lampsilids and dysonomids, the posterior portions of the valves are greatly inflated (relative to the condition in males) to afford space for the expanded posterior marsupia of the outer demibranchs (Fig. 11.28A,H). Similar general inflation of female shells, but much less obvious, occurs in some anodontids (Burch 1975b, Mackie 1984).

Hermaphroditic unionaceans and all sphaeriids are generally simultaneous hermaphrodites, producing mature eggs and sperm concurrently in the gonads. *C. fluminea* has an unusual pattern of producing only eggs at earliest maturity (shell length ≈ 6 mm) followed somewhat later by sperm production. It then remains simultaneously hemaphroditic throughout the rest of life (Kraemer and Galloway, 1986).

As bivalves are relatively sessile and individuals can be widely separated from each other, copulatory organs would be useless and are therefore lacking. In freshwater species other than *D. polymorpha*, in which eggs are fertilized externally (Mackie *et al.* 1989), sperm is released to surrounding water to be taken up on the inhalant currents of other individuals and carried to unfertilized eggs retained in the gill marsupia. Self-fertilization appears to be relatively common in sphaeriids, occurring near the conjunction of male and female gonoducts (Mackie 1984). In *C. fluminea,* developing embryos occur in the lumina of gametogenic follicles and gonoducts, suggesting that self-fertilization can take place within the gonad itself (Kraemer *et al.* 1986). The ability to self-fertilize makes hermaphroditic species highly invasive, as described in Section III.B.

The main stimulus for reproduction appears to be temperature. Gametogenesis and fertilization begin when ambient temperature rises above a critical level or falls within critical limits. Other environmental factors that may affect reproduction but require further study are neurosecretory controls, density-dependent factors, diurnal rhythms, and parasites. While clear evidence for neurosecretory and density controls of reproductive cycles has been demonstrated in sphaeriids (Mackie 1984), such observations have not been made for other freshwater bivalves. Certainly, evidence of increasing activity and metabolic rate during dark hours in unionaceans (McCorkle *et al.* 1979) and *C. fluminea* (McCorkle-Shirley 1982) suggests that spawning activity and glochidial or juvenile release rates may also display diurnal rhythmicity.

The sperm of freshwater bivalves may have ellipsoid or conical nuclei and an acrosome of variable complexity depending on species (Mackie 1984). The sperm of corbiculacean species have elongate heads and that of *C. fluminea* is unusually biflagellate (Kraemer *et al.* 1986). Sperm with elongate heads appear adapted for swimming in gonadal and oviductal fluids more viscous than water and are associated with internal fertilization in gonadal ducts rather than externally in marsupia (Mackie 1984).

The eggs of freshwater bivalves are round and generally larger with greater yolk stores than marine species with planktonic larval stages. Again, the exception is *D. polymorpha* with relatively small eggs (40–70 μm diameter) associated with retention of a free-swimming veliger, which feeds and grows considerably in the water column before settlement and juvenile metamorphosis (Mackie *et al.* 1989). The larger, yolky eggs of all other species contain nourishment required for development to the juvenile or glochidium stage. The Sphaeriacea produce the largest eggs and have, correspondingly, the smallest brood sizes ranging from 6–24/adult in *Sphaerium,* 1–135/adult for *Musculium* and 3.3–6.7/adult for *Pisidium* (Burkey 1983). Adult *Musculium partumeium*, which are only 4 mm in length release juveniles 1.4 mm long (Hornbach *et al.* 1980, Way *et al.* 1980). In contrast, unionaceans and *C. fluminea* have smaller eggs and release smaller glochidia or juveniles than sphaeriids (generally < 0.2 mm diameter) and have much larger brood sizes (10^3–10^6/adult) (Burky 1983, McMahon 1983a). The evolutionary implications of these major differences in fecundities of freshwater bivalves are discussed in Section III.B.

The egg is surrounded by a vitelline membrane that is relatively thin in sphaeriids and thicker in unionaceans and *C. fluminea* (Mackie 1984). In the latter two groups, it remains intact throughout most of development, but disintegrates during early development in sphaeriids (Heard 1977, Mackie 1984), an adaptation that may allow developing embryos to absorb maternally supplied nutrients from brood sacs without embryos and/or from nutrient cells lining the interlamellar space (Mackie 1978).

6. Nervous System and Sense Organs

In bivalves, the head is entirely enclosed within the valves and is, therefore, no longer in direct contact with the external environment. This condition has led to loss of cephalic structure, the head consisting of only the mouth opening and attachment points of the labial palps (Fig. 11.2). The cephalic sense organs found in other molluscan classes have been lost in bivalves, along with the associated cephalic concentration of central nervous system ganglia. Thus, the bivalve nervous system is far less centralized than in the majority of molluscs. A pair of cerebropleural ganglia lie on each side of the esophagus near the mouth, interconnected by commissures dorsal to the esophagus (Fig. 11.8). From these extend two pairs of nerve chords. A pair of dorsal nerve chords extend posteriorly through the visceral mass to a pair of visceral ganglia on the anterior-ventral surface of the posterior adductor muscle (Barnes 1986). The second pair of nerve chords extend ventrally to innervate a pair of pedal ganglia in the foot.

The pedal and cerebropleural ganglia exert motor control over the pedal and anterior adductor muscles, while control of the posterior adductor muscles and siphons is mediated by the visceral ganglia. Coordination of foot and valve movements, as occurs in burrowing behavior (see Section II.A.2), resides in the cerebrospinal ganglia.

Associated with enclosure and reduction of head sense organs is the development of sense organs in those tissues most directly exposed to the external environment, the mantle edge and siphons. On the mantle edge, sense organs reach their highest concentrations in the middle sensory mantle lobe (Fig. 11.3). Photoreceptor cells (but not distinct eyes as in some marine genera) detect changes in light intensity associated with shadow reflexes, phototaxis, and diurnal rhythms; while tentacles and stiffened immobile cilia associated with tactile mechanoreceptor sense organs perceive direct contact displacement (touch) or vibrations passing through the water. On the siphon margins, such tactile receptors prevent drawing of large particles on inhalant currents into the mantle cavity. When large particles contact these tentacles, the siphons are closed by sphincter muscles and then retract. Stronger stimuli cause the valves to close rapidly forcing water under high pressure from the siphons, thereby ejecting any impinging material. Under intense stimulation of the mantle or siphons, the siphons are withdrawn and valves closed tightly, a common predator defense in all freshwater bivalve species.

A pair of statocysts lying near or within the pedal ganglion of the foot are innervated by commissures from the cerebropleural ganglion (Fig. 11.8). Such statocysts are greatly reduced in sessile marine species (e.g., oysters), suggesting their importance to locomotion and burrowing in free-living freshwater species. Statocysts in freshwater bivalves have been described by Kraemer (1978). They are lined with ciliary mechanoreceptors responding to pressure exerted by a calcareous statolith or series of smaller

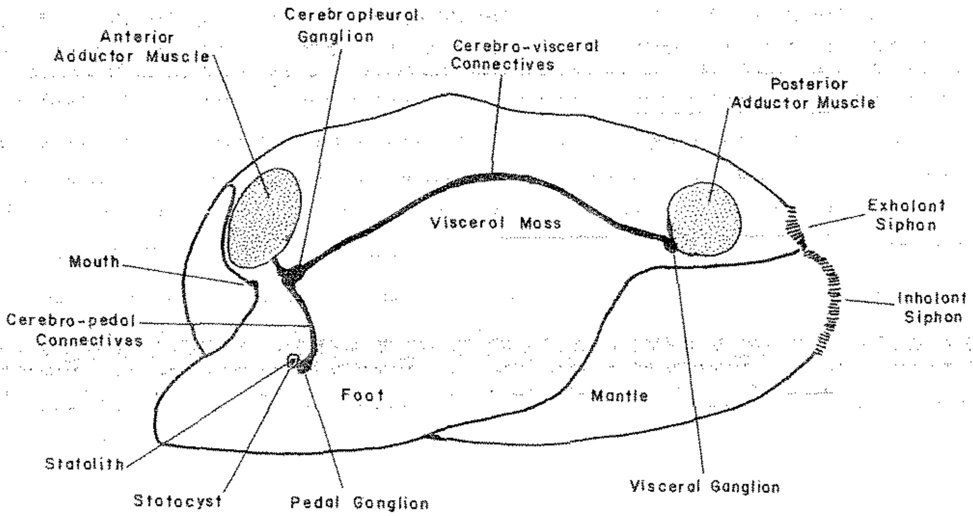


Figure 11.8 The anatomic features of the central nervous system of a typical unionid freshwater bivalve (central nervous system anatomy is essentially similar in freshwater corbiculacean bivalves).

granular statoconia within the statocyst vesicle. As gravity sensing organs, statocysts detect body orientation and thus function in bivalve geotactic and positioning responses particularly during burrowing and pedal locomotion.

C. Environmental Physiology

1. Seasonal Cycles

Freshwater bivalves display seasonal variation in physiological response associated with both temperature and reproductive cycles. While such cycles have been studied more thoroughly in marine species (Gabbott 1983), limited research on freshwater taxa has revealed interesting observations. Metabolic rates show major seasonal variation in freshwater bivalves (for reviews see Burky 1983, Hornbach 1985). As in almost all temperate zone animals, the metabolic rate in freshwater bivalves is generally greatest in summer and least in winter due to temperature effects (Burky 1983, Hornbach 1985). Annual variation in metabolic rate can be extensive (Table 11.1). Maximal summer oxygen consumption rates, or $\dot{V}_{O_2}$ may be 20–33 times the minimal winter rates over a seasonal range of 2–22°C in *Sphaerium striatinum* (Hornbach *et al.* 1983) or as little as 2.3 times the minimal winter rates in *Pisidium walkeri* (Burky and Burky 1976) (Table 11.1).

An immediate temperature increase causes a corresponding increase in the metabolic rate of ectothermic animals such as bivalves. Acute, temperature-induced changes in the metabolic rate or $\dot{V}_{O_2}$ (or in any rate function) are described by Q_{10} values (i.e., the factor by which a rate function changes with a 10°C increase in temperature) as follows:

$$Q_{10} = \frac{\text{RATE}_2^{(10/\text{Temp}_2 - \text{Temp}_1)}}{\text{RATE}_1}$$

where Rate_1 is the rate at the higher temperature, Rate_2, the rate at the lower temperature, Temp_2, the higher temperature and Temp_1, the lower temperature (°C). The Q_{10} for metabolic rate in the majority of ectothermic animals is 2–2.5, essentially that for chemical reaction rates. Thus, Q_{10} values outside this range indicate active metabolic regulation, values less than 1.5 suggest metabolic suppression with increasing temperature, and above 3.0, metabolic stimulation. Freshwater bivalve Q_{10} values are

Table 11.1 Seasonal Variation in the Oxygen Consumption Rates ($\dot{V}_{O_2}$) of Selected Species of Freshwater Bivalves

Species and Source	mg Dry Tissue Weight	Max. $\dot{V}_{O_2}$ µl O_2/hr	Min. $\dot{V}_{O_2}$ µl O_2/hr	Ratio Min : Max $\dot{V}_{O_2}$	$Q_{10(Acc.)}$[a]	Seasonal Temperature Range (°C)
Sphaerium striatinum	25 mg	31.5	1.40	22.5 : 1	4.7	2–22
Hornbach *et al.*	7 mg	15.8	0.78	20.3 : 1	4.5	2–22
(1983)	2 mg	8.7	0.24	33.6 : 1	5.8	2–22
Pisidium compressum	3 mg	0.71	0.04	17.5 : 1	—	—
Way and Wissing	0.9 mg	0.27	0.03	9.0 : 1	—	—
(1984)	0.05 mg	0.13	0.02	6.5 : 1	—	—
Pisidum variabile	3 mg	1.13	0.22	5.14 : 1	—	—
Way and Wissing	0.9 mg	0.42	0.10	4.20 : 1	—	—
(1984)	0.05mg	0.02	0.15	7.50 : 1	—	—
Pisidium walkeri	1.3 mg	0.85	1.11	2.3 : 1	1.4	1–26
Burky and Burky (1976)	0.02 mg	0.017	0.0074	2.3 : 1	1.4	1–26
Corbicula fluminea	348 mg	430.6	34.4	12.5 : 1	3.2	7–29
Williams (1985)	204 mg	308.2	31.5	9.8 : 1	2.8	7–29
	60 mg	143.3	25.8	5.6 : 1	2.2	7–29
Anodonta grandis	10 g	4690.0	400.0	11.7 : 1	2.7	6–31
Huebner (1982)	5 g	2690.0	250.0	10.8 : 1	2.6	6–31
Lampsilis radiata	5 g	2090.0	170.0	12.3 : 1	2.8	6–31
Huebner (1982)	2 g	810.0	80.0	10.1 : 1	2.6	6–31

[a] $Q_{10(Acc.)}$ is the respiratory Q_{10} value computed from a change in the $\dot{V}_{O_2}$ value recorded for acclimated individuals at respective acclimation temperatures.

highly variable between and within species, ranging from 0.2–14.8 for 20 species of sphaeriid (Hornbach 1985). Far less information is available for unionaceans. In *Lampsilis radiata*, Q_{10} values range from 1.88–4.98 and for *Anadonta grandis*, from 1.27–10.35 (Huebner 1982). Temperature range of determination, body mass, and season may affect Q_{10} values in some species but not in others such that no general patterns emerge. Rather, metabolic response to temperature appears to have evolved under species-specific microhabitat selection pressures in freshwater bivalves (Hornbach 1985).

Without a capacity for regulation of metabolic rate, massive seasonal metabolic fluctuations could cause energetic inefficiency; rates being suboptimal during colder months and supraoptimal during warmer months. Thus, many ectothermic species display a capacity for metabolic temperature acclimation or compensation involving adjustment of the metabolic rate over a period of a few days to several weeks in a new temperature regime. Typically, metabolic rates are adjusted upward upon acclimation to colder temperatures and downward upon acclimation to warmer temperatures, which dampens metabolic fluctuation with seasonal temperature change, allowing maintenance of a more optimal metabolic rate throughout the year.

For most species, such typical seasonal acclimation is only partial, with metabolic rates not returning to absolutely optimal levels. Such partial metabolic temperature compensation can be detected by comparing Q_{10} values of $\dot{V}_{O_2}$ in instantaneous response to acute temperature change with those measured at the temperature of acclimation over a wide range of ambient temperatures (Acclimation Q_{10} or $Q_{10(Acc.)}$. If the $Q_{10(Acc.)}$ approximates 1.0, metabolic temperature compensation is nearly perfect with $\dot{V}_{O_2}$ regulated near the optimal level throughout the year. If $Q_{10(Acc.)}$ is less than 2.0 or considerably less than acute Q_{10}, acclimation is partial, with the metabolic rate approaching, but not reaching, the optimal level. If $Q_{10(Acc.)}$ is approximately equal to 2.0–2.5 or the acute Q_{10}, the species is incapable of temperature acclimation. If the $Q_{10(Acc.)}$ is greater than 3.0 or acute Q_{10}, inverse or reverse acclimation is displayed, in which acclimation to colder temperatures further depresses metabolic rate and acclimation to warmer temperatures further stimulates metabolic rate.

Three general patterns of metabolic temperature acclimation occur in freshwater bivalves; (1) no capacity for acclimation ($Q_1{}^0{}_{(Acc.)}$ equivalent to acute Q_{10}) displayed by the unionids *A. grandis* and *L. radiata* (Huebner 1982), (2) partial acclimation by Pisidium walkeri ($Q_{10(Acc.)}$ is considerably less than maximal acute Q_{10}) (Burky and Burky 1976), and (3) reverse acclimation ($Q_{10(Acc.)}$ greater than acute Q_{10}) by *Sphaerium striatinum* (Hornbach *et al.* 1983) and *C. fluminea* (Williams 1985) (Table 11.1). The adaptive significance of reverse acclimation in bivalves is unclear (for hypotheses regarding its selective advantage, see McMahon 1983b), but for freshwater bivalves, that of reduction of energy store catabolism while inactive over winter appears most parsimonious (Burky 1983).

The $\dot{V}_{O_2}$ is also related to individual size or biomass in all animals as follows:

$$\dot{V}_{O_2} = aM^b$$

were $\dot{V}_{O_2}$ is oxygen consumption rate or metabolic rate, M, individual biomass, and a and b are constants. The equation may be rewritten as a linear regression with $\dot{V}_{O_2}$ and M transformed into logarithmic values:

$$\mathrm{Log}_{10}\,\dot{V}_{O_2} = a + b\,(\mathrm{Log}_{10}\,M)$$

in which a and b are the Y-intercept ($\dot{V}_{O_2}$ at $\mathrm{Log}_{10}\,M = 0$ or $M = 1$) and the slope (increase in $\mathrm{Log}_{10}\,\dot{V}_{O_2}$ for each unit increase in $\mathrm{Log}_{10}\,M$), respectively. Thus, a is a measure of the relative magnitude of $\dot{V}_{O_2}$ and b, the rate of increase with increasing biomass. If $b = 1$, $\dot{V}_{O_2}$ increases in direct proportion with M. If $b > 1$, $\dot{V}_{O_2}$ increases at a proportionately greater rate than M and if $b < 1$, $\dot{V}_{O_2}$ increases at a proportionately lesser rate than M. Thus, b values of less than one indicate that weight-specific $\dot{V}_{O_2}$ (O_2 uptake per unit body mass) decreases with increasing size and values of greater than one indicate that it increases with increasing size. Conventional wisdom states that animal b values range between 0.5–0.8. While generally true for vertebrates, it is less characteristic of invertebrates, including freshwater bivalves. Among 14 species of sphaeriids, b values ranged from 0.12–1.45 (Hornbach 1985). Limited data suggest that unionaceans have more typical b values of 0.90 for *L. radiata* and 0.77 for *Anodonta grandis* (Huebner 1982). The b value can also change with season in some species (Hornbach *et al.* 1983, Way and Wissing 1984), but remains constant in others (Burky and Burky 1976, Huebner 1982). It can vary with reproductive condition, increasing when adults brood juveniles in *P. compressum* (Way and Wissing 1982) and *Musculium lacustre* (Alexander 1982), but is not correlated with reproductive cycles in other species (Burky 1983, Hornbach 1985). The metabolic rate may also vary with physiologic state, declining in *Musculium partumeium* during midsummer when the habitats are dry and clams estivate (Burky 1983, Burky *et al.* 1985b, Way *et al.* 1981).

Comparison of a values in sphaeriids indicates that the metabolic rate of species of *Pisidium* (mean $a = 0.399$) is about 1/3 that of species of *Musculium* (means $a = 1.605$) or *Sphaerium* (mean $a = 1.439$) (Hornbach 1985). Reduced metabolic rate in *Pisidium* species may be related to their reduced gill surface area (Hornbach 1985), hypoxic mud burrowing, and interstitial suspension-feeding habits (Lopez and Holopainen 1987). The reduced metabolic demand of profundal pisidiids could account for their generally high tolerance of hypoxia (Burky 1983, Holopainen 1987, Holopainen and Jonasson 1983, Jonasson 1984a, 1984b).

Annually, values of a in *C. fluminea* varied from -0.12–1.43 (mean = 0.72) (Williams 1985). The annual range in values of a for *A. grandis* was (-0.13)–(-1.098) (mean $a = -0.563$) and for *L. radiata*, (-0.403)–(-1.331) (mean $a = -0.800$) (Huebner 1982). The high a values of *C. fluminea* relative to unionids and sphaeriids (range = 0.399–1.605) indicate that it has a higher $\dot{V}_{O_2}$ relative to other species, while the low values for unionaceans indicate a relatively reduced $\dot{V}_{O_2}$. Shell and tissue growth account for a major portion of metabolic energy utilization, being over 20% of total metabolic rate in young *Mytilus edulis* (Hawkins *et al.* 1989). Thus, in slow-growing unionacean species (see Section III.B.2), metabolic costs are depressed relative to the rapidly growing *C. fluminea*.

In some sphaeriid species, $\dot{V}_{O_2}$ is influenced by growth and reproductive cycles (Burky 1983, Hornbach 1985); maximal metabolic rates occur during periods of peak adult and brooded juvenile growth (Burky and Burky 1976, Hornbach *et al.* 1983, Way *et al.* 1981, Way and Wissing 1984). Peaking of metabolic rates during maximal growth and development of brooded juveniles may result from the elevated metabolic demands associated with accelerated tissue growth (Hawkins *et al.* 1989), the higher respiratory rates of brooded juveniles, and the energetic costs of providing maternal metabolites to brooded juveniles (Burky 1983, Mackie 1984). In contrast, metabolic rates in *C. fluminea* (Williams 1985) and unionids (Huebner 1982) are unaffected by embryo brooding. These species do not provide embryos with maternal nourishment (Mackie 1984), suggesting that it must have a high metabolic cost in sphaeriids.

Rates of filtration also vary seasonally in sphaeriids. In both *S. striatinum* (Hornbach *et al.* 1984b) and *M. partumeium* (Burky *et al.* 1985a), filtration rates decreased with increased particle concentration and decreased temperature. Elevated ambient temperatures induce maximal filtration during summer months, but there was also a tendency for filtration to peak during periods of peak reproduction. In *M. partumeium*, the filtration rate declined in midsummer coincidently with the metabolic rate (Way *et al.* 1981) as individuals estivated during habitat drying (Burky 1983).

Freshwater bivalves also display distinct seasonal cycles in tissue biochemical composition. While data are sparse, variation in biochemical composition appears to be related primarily to the reproductive cycle, as occurs in marine bivalves (Gabbot 1983). In the freshwater unionid *Lamellidens corrianus*, whole body protein, glycogen, and lipid contents reach maximal levels during gametogenesis and gonad development and minimum levels during glochidial release (Fig. 11.9A); a pattern repeated particularly for protein and lipids in the majority of individual tissues (Fig. 11.9B–D) (Jadhav and Lomte 1982a). Similarly, overwintering, nonreproductive individuals of *C. fluminea* have twice the biomass and higher levels of nonproteinaceous energy stores than reproductive individuals in summer (Williams 1985, Williams and McMahon 1989). Thus, reproductive effort appears to require massive mobilization of organic energy stores from somatic as well as gonadal tissues to support gamete production in this species.

In the sphaeriids *Sphaerium corneum* and *Psidium amnicum*, tissue glycogen content increases after reproduction in the fall and was associated with a 2–3 fold increase in survival of winter-conditioned individuals under anoxic conditions. As glycogen is a major substrate for anaerobic metabolism (de Zwaan 1983), glycogen-poor, summer-conditioned individuals were relatively intolerant of anoxia (Holopainen 1987). Thus, fall accumulation of glycogen stores not only supports gametogenesis the following spring but also provides the anaerobic substrate for survival of prolonged anoxia when ice cover prevents surface gas exchange (Holopainen 1987).

2. *Diurnal Cycles*

Freshwater bivalves also display diurnal cycles of metabolic activity. Active uptake of Na^+ is greatest during dark hours in both *C. fluminea* (McCorkle-Shirley 1982) and the unionid, *Carunculina parva texasensis* (Graves and Dietz 1980). Diurnal Na^+ transport rhythm was lost in constant light, suggesting that rhythmicity of ion uptake is driven exogenously by changes in light intensity. Such diurnal ion transport rhythms appear to be closely linked to activity rhythms. In the unionid *Ligumia subrostrata*, valve gaping activity peaked 1–2 hr after onset of darkness and remained elevated during dark pe-

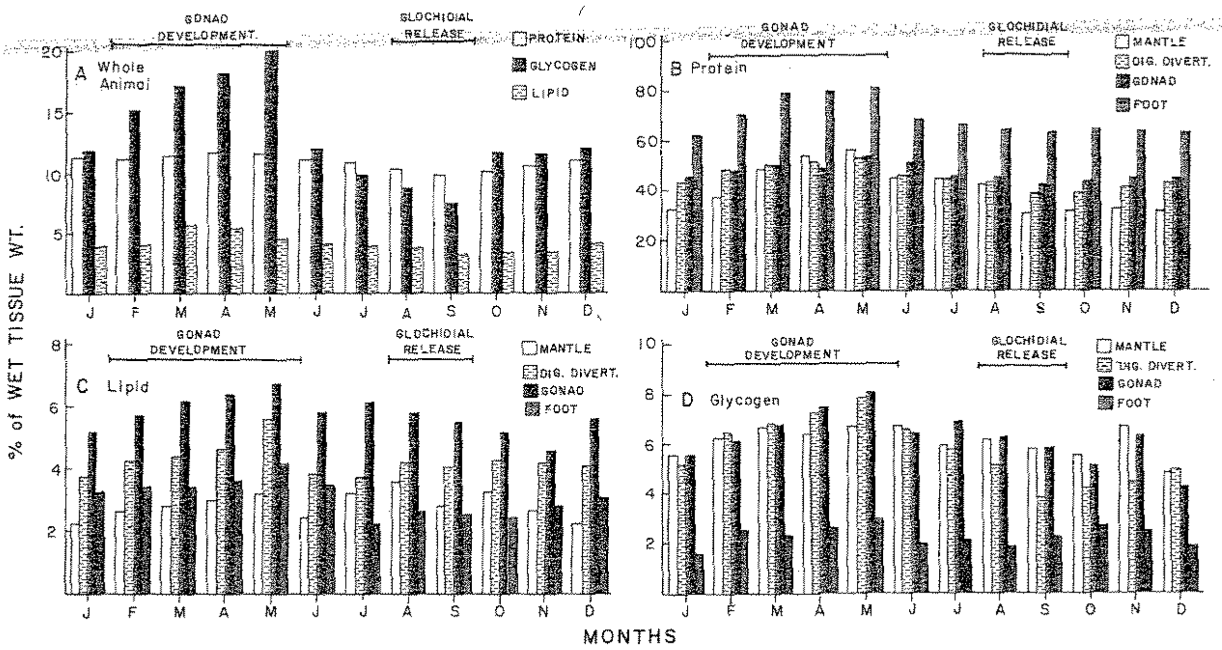


Figure 11.9 Seasonal variation in the protein, lipid, and glycogen contents of the whole body and various tissues of the freshwater unionid mussel, *Lamellidens corrianus*, relative to the reproductive cycle. All organic contents are expressed as percentage of wet tissue weight. (A) Annual variation in whole body contents of protein (open histograms), glycogen (solid histograms), and lipid (cross-hatched histograms). Remaining figures represent levels of protein (B), lipid (C), or glycogen (D) in the mantle (open histograms), digestive diverticulum (cross-hatched histograms), gonad (solid histograms), and foot (stippled histograms). Horizontal bars at the top of each figure represent reproductive cycles, indicating periods during which either gonads develop or glochidia are released. Gonad development is associated with increases in organic content, and glochidial release, with decreases in organic content of the whole body and various tissues. (From data of Jadhav and Lomte 1982a.)

s. Rhythmic valve gaping behavior was lost in stant light, again suggesting primary respon- eness to exogenous changes in light intensity Corkle *et al.* 1979). Rhythmic patterns of oxygen umption in *L. subrostrata* appeared driven by anges in light intensity, declining immediately an increase in intensity and increasing after a ease in intensity. Rhythmic respiratory behav- , however, had an endogenous component as it rsisted in constant light for 14 days (McCorkle *et* 979). This evidence suggests that at least some water bivalves may be more active during dark urs. Such activity rhythms may be correlated with al feeding and vertical migration cycles, indi- als coming to the surface to feed at night and reating below it during the day, thus avoiding al predators; however this hypothesis requires e research.

Other Factors Affecting Metabolic Rate

r than seasonal and temperature effects (de- ibed earlier), $\dot{V}_{O_2}$ can be suppressed by chemical tants such as heavy metals, ammonia, and cyanide, which degrade metabolic processes (Lomte and Jadhav 1982a). Increased levels of suspended solids impaired $\dot{V}_{O_2}$ and induced apparent starvation in three unionid species, indicating that suspended solids interfered with maintenance of gill respiratory and filter-feeding currents (Aldridge *et al.* 1987). Individual metabolic rates may also be dependent on population density. The metabolic rates of specimens of *Elliptio complanata* declined with density, the $\dot{V}_{O_2}$ of a single individual being three times that of individuals held in groups of seven or more. This species may release a pheromone that induces the reduction of the metabolic rate in nearby individuals (Paterson 1983).

A number of unionaceans and sphaeriids display varying degrees of respiratory oxygen dependency such that, when subjected to declining oxygen concentrations, $\dot{V}_{O_2}$ declines proportionately with a decline in ambient partial pressure of oxygen (P_{O_2}) (Burky 1983). Such species are generally intolerant of prolonged hypoxia and, thus, are restricted to well-oxygenated habitats. In contrast, some species are oxygen independent and regulate $\dot{V}_{O_2}$ at relatively constant levels with declining oxygen tension until a critical P_{O_2} is reached, below which $\dot{V}_{O_2}$ declines proportionately with further decline in O_2 concentration. Such species survive in aquatic habitats periodically subjected to prolonged hypoxia. The profundal sphaeriids *Sphraeium simile* and *Pisidium casertanum* are periodically exposed to hypoxia and are relatively oxygen independent (Burky 1983). Two unionids, *Elliptio companata* and *Anodonta grandis*, inhabiting mud and sand in a small eutrophic Canadian lake, were extreme oxygen regulators maintaining a nearly constant $\dot{V}_{O_2}$ down to 1 mg O_2/liter ($P_{O_2} \approx$ 18 torr) (Fig. 11.10) (Lewis 1984). In these northern temperate species, the ability to regulate $\dot{V}_{O_2}$ is highly adaptive, as ice cover causes lentic habitats to become severely hypoxic during winter months and individuals overwinter burrowed deeply into hypoxic sediments (Lewis 1984). In contrast, more tropical species not experiencing winter hypoxia are more oxygen dependent (Das and Venkatachari 1984, McMahon 1979a). The $\dot{V}_{O_2}$ of the subtropical species, *C. fluminea*, approaches near zero levels after a decline in O_2 tension of just 30% of full air saturation, indicative of extreme oxygen dependence (McMahon 1979a). This response may account for the restriction of *C. fluminea* to well-oxygenated habitats and its intolerance of hypoxic waters receiving organic wastes (McMahon 1983a).

Many species of freshwater bivalves are very tolerant of acute hypoxia or even anoxia. Such tolerance is highly adaptive, as hypoxic conditions may occur below the thermocline of stratified lakes or above reducing substrata with heavy organic loads and/or dense animal populations (Butts and Sparks 1982). Profundal sphaeriids tolerate acute hypoxia throughout summer months after thermocline formation (Holopainen and Jonasson 1983, Jonasson 1984a, 1984b), surviving 4.5 to greater than 200 days of complete anoxia, depending on season and temperature (Holopainen 1987). The unionid, *Anodonta cygnea* can survive 22 days of anoxia (Zs.-Nagy *et al.* 1982).

When anoxic, bivalves rely on anaerobic metabolic pathways. These pathways are not those of glycolysis; instead, they involve alternative pathways, simultaneously degrading glycogen and

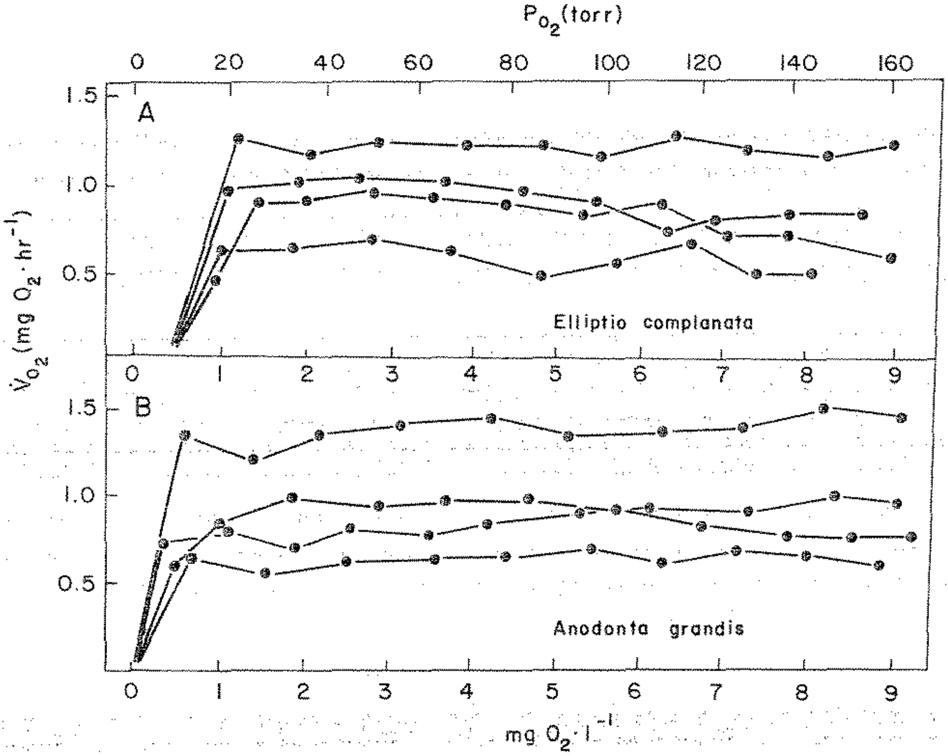


Figure 11.10 Respiratory responses of the freshwater unionid mussels, *Elliptio complanata* and *Anodonta grandis* to declining ambient oxygen tensions from near full air saturation (8–9 mg O_2/liter, lower horizontal axis, Po_2 = 140–160 torr or mg Hg, upper horizontal axis) to the concentration at which O_2 uptake ceases. Respiratory responses of four individuals of *E. complanta* (A) and four individuals of *A. grandis* (B). Both species maintained normal oxygen uptake rates at a Po_2 as low as 15–20 torr (9–13% of full air saturation) suggesting high capacity for oxygen regulation. (Redrawn from Lewis 1984.)

aspartate or other amino acids to yield the endproducts alanine and succinate. During prolonged anaerobiosis, succinate can be further degraded into volatile fatty acids such as propionate or acetate (van den Thillart and de Vries 1985, de Zwaan 1983, Zs.-Nagy *et al.* 1982). Anoxic for 6 days, *Anodonta cygnea* maintained 52–94% of aerobic ATP levels, higher than could occur by typical glycolytic pathways, and associated with its ability to anaerobically oxidize succinate while producing ATP molecules (Zs.-Nagy *et al.* 1982). These alternative pathways are more efficient than glycolysis (which yields only 2 moles of ATP per mole of glucose catabolized), producing 4.71–6.43 moles of ATP per mole of glucose (de Zwaan 1983). Thus, they allow tolerance of more extended anaerobiosis than does the less efficient glycolysis and the higher energy yields of these alternate pathways allow excretion of anaerobic endproducts, preventing retention of lactate to lethal levels as occurs in glycolytic species during anaerobiosis (de Zwaan 1983).

During anaerobiosis, the buildup of acidic, anaerobic endproducts in the tissues and hemolymph can cause considerable acidosis (decline in pH). As freshwater bivalves have no respiratory pigments, their blood has little inherent buffering capacity (Byrne 1988, Heming *et al.* 1988). Instead, bivalves mobilize calcium carbonate from the shell to buffer respiratory acidosis. Thus, when anaerobic, the pH of the pallial fluid of *Margaritifera margaritifera* remains highly constant, but its Ca^{2+} concentration increases (Heming *et al.* 1988). Similarly, blood Ca^{2+} levels rise eight-fold in *Ligumia subrostata* exposed to an atmosphere of nitrogen (Dietz 1974). Emersed in nitrogen for 72 hr, the blood Ca^{2+} concentrations of *C. fluminea* rose nearly five-fold, partially buffering accumulated respiratory acidosis (Byrne 1988).

The gills of unionaceans (Silverman *et al.* 1983; Steffens *et al.* 1985) harbor extensive extracellular calcium phosphate concretions that could also buffer hemolymph pH. However, rather than releasing calcium, the mass of these concretions increases during prolonged anoxia. Indeed, their mass is related inversely to blood pH and directly to blood calcium concentration. This suggests that calcium released from the shell during anoxia is sequestered in the gill concretions, preventing loss of diffusion to the external medium. This response is adaptive as it reduces the necessity for Ca^{2+} uptake to replace lost shell calcium on return to aerobic conditions (Silverman *et al.* 1983).

4. Desiccation Resistance

Freshwater bivalves may be exposed to air for weeks or months during seasonal dry periods or unpredictable periods of extreme drought (McMahon 1979b, 1983a, McMahon and Williams 1984). Lack of mobility leaves some species stranded in air as water levels recede, while other species occur in habitats that dry completely. Unlike other freshwater species, bivalves have no obvious adaptations or structures for maintenance of aerial gas exchange when out of water.

Many species of sphaeriids inhabit temporary ponds and survive periods of several months in air during drying (for a review see Burky 1983). In some cases, both adults and juveniles survive emersion (Collins 1967, McKee and Mackie 1980; in others, only recently hatched juveniles survive (McKee and Mackie 1980, Way *et al.* 1981). Sphaeriids burrow into sediments prior to air exposure. Oxygen consumption and filtration rates decline in *M. partumeium* prior to pond drying as individuals begin to estivate prior to prolonged emersion (Way *et al.* 1981, Burky *et al.* 1985a,b). Reduction in metabolic demand while emerged allows long-term maintenance in air on limited energy reserves.

Sphraeium occidentale (Collins 1967) is exposed in air for several months in its ephemeral pond habitats. In air, the $\dot{V}_{O_2}$ of *S. occidentale* is 20% of aquatic rates, gas exchange apparently taking place across specialized pyramidal cells extending through punctae in the shell. Gas exchange through shell punctae allows continual valve closure, minimizing water loss. In *C. fluminea*, aerial $\dot{V}_{O_2}$ is 21% of the aquatic rate (McMahon and Williams 1984). In air, *C. fluminea* periodically gapes the valves and exposes mantle edge tissues fused together with mucous (McMahon 1979b, Byrne 1988, Byrne *et al.* 1988). Mantle edge exposure is associated with high rates of aerial O_2 uptake while no O_2 consumption occurs during valve closure (Byrne 1988, McMahon and Williams 1984). During mantle edge exposure, bursts of metabolic heat production occur, suggesting that mantle edge exposure allows periodic aerobic recharging of spent ATP and phosphagen stores depleted during longer periods of valve closure (Byrne 1988). Periodic exposure of mucus-sealed mantle edges greatly reduces the tissue surface area exposed to the atmosphere and the duration of such exposure. In contrast, intertidal species gape more continually in air exposing moist mantle tissues directly to the atmosphere through parted mantle edges or open inhalant siphons. Consequently, they generally have higher levels of evaporative water loss than freshwater species when emersed (McMahon 1988). The degree of mantle edge exposure activity in *C. fluminea* is reduced with increased temperature, decreased relative humidity, and increasing duration of emersion. This suggests that individuals respond to increasing dessication pressure by greater reliance on anaerobic metabolism, reducing the degree of mantle edge exposure and associated evaporative water loss (Byrne 1988, Byrne *et al.* 1988, McMahon 1979b). Emersed unionaceans also display periodic mantle edge exposure (Heming *et al.* 1988), including *Ligumia subrostrata* whose aerial oxygen consumption is 21–23% of aquatic rates (Dietz 1974). In air, unionaceans and *C. fluminea* utilize shell Ca^{2+} to buffer accumulating HCO_3^- (Byrne, 1988, Dietz 1974, Heming *et al.* 1988). Both Ca^{2+} and HCO_3^- accumulate in the mantle cavity fluids of emersed pearl mussels, *Margaritifera margaritifera* (Heming *et al.* 1988). Mantle edge exposure is also associated with release of CO_2 generated by metabolic and shell-buffering processes (Byrne 1988, Heming *et al.* 1988).

Oxygen uptake rates are elevated on resubmersion after prolonged emersion in both *C. fluminea* (Byrne 1988) and the unionid *Lamellidens corrianus* (Lomte and Jadhav 1982b). In marine intertidal bivalves, elevated $\dot{V}_{O_2}$ 1–2 hr after reimmersion has been considered payment of an oxygen debt resulting from oxidation of anaerobic endproducts accumulated during air exposure (de Zwann, 1983). However, in *C. fluminea*, $\dot{V}_{O_2}$ remained elevated for at least 12 hr after reimmersion, suggesting that it was the result of a process other than typical oxygen debt payment, such as the increased metabolic demands associated with tissue damage repair or excretion of accumulated metabolic wastes. Lack of typical oxygen debt payment suggests that *C. fluminea* remains primarily aerobic when in air (Byrne 1988).

Among freshwater species, some unionaceans appear most tolerant of emersion and can survive for months or even years in air (Dance 1958, Dietz 1974, Hiscock 1953, White 1979). Certainly, the ability of some species of unionaceans to tolerate extraordinary periods of emersion and/or to migrate up and down the shore with changing water levels (White 1979) may partially account for the dominance of unionaceans in larger North American river drainages characterized by major seasonal water level fluctuations. Patterns of bivalve growth, reproduction and other important life-history phenomena may be driven in part by seasonal water level variation. Thus, human regulation of river flow and level may have contributed to the extirpation of many unionacean species from North American drainage systems.

The mode of nitrogen excretion or detoxification during emersion is an unresolved question in freshwater bivalves. Ammonium ion (NH_4^+) is the major nitrogenous excretory product of aquatic molluscs (Bishop *et al.* 1983). Due to its toxic effects on oxidative phosphorylation even at low concentrations, ammonium ion is generally not accumulated in emersed molluscs and its high solubility in water precludes its release to the atmosphere as ammonia gas. Instead, when emersed, many aquatic species detoxify ammonium ion by conversion to less toxic compounds such as urea or uric acid, which are accumulated in the hemolymph and kidneys to be excreted on resubmersion. However, freshwater bivalves do not appear to have the capacity to produce urea or uric acid (Bishop *et al.* 1983, Vitale and Friedl 1984).

Without the capacity to detoxify accumulating ammonia, how do freshwater bivalves tolerate prolonged emersion? Recent studies of ammonia excretion in emersed *C. fluminea* indicate that, unlike intertidal bivalves (Bishop *et al.* 1983), this species does not catabolize amino acids during emersion, preventing ammonium ion accumulation (Byrne 1988). Further evidence for protein catabolism suppression in emersed freshwater bivalves is the near total dependence of the unionids *Lamellidens corrianus* and *L. marginalis* on "carbohydrate catabolism while emersed (Lomte and Jahav 1982c, Sahib *et al.* 1983).

Of interest is the report that individuals of *Sphraeium occidentale* and *Musculium securis* were more tolerant of emersion when drawn from populations estivating in a dry pond than when drawn from a submerged population in a permanent pond (McKee and Mackie 1980). Thus, tolerance of prolonged air exposure may depend on physiological and biochemical alterations in estivating individuals including, perhaps, increased dependence on carbohydrate catabolism previously described for *C. fluminea* and unionaceans. Entrance into estivation in response to emersion may be controlled by neurosecretory hormones (Lomte and Jadhav 1981a).

5. Gill Calcium Phosphate Concretions in Unionaceans

Dense calcium phosphate concretions occur in the tissues of unionid bivalves. Intracellular calcium phosphate concretions in unionacean mantle tissue may be a source of calcium for shell deposition (Davis *et al.* 1982, Jones and Davis 1982). Dense deposits of extracellular calcium phosphate concretions (1–3 μm in diameter) occur in the gills of unionaceans (Silverman *et al.* 1983, 1988, Steffens *et al.* 1985). Gill calcium phosphate concretions account for up to 60% of gill dry weight in some species (Silverman *et al.* 1985, Steffens *et al.* 1985). They are most dense along a series of parallel nerve tracts running 90° to the long axis of the gill filaments, density declining in the ventral portions of the demibranchs (Silverman *et al.* 1983, 1985, Steffens *et al.* 1985).

Besides storing shell Ca^{2+} that is released to bufer respiratory acidosis during hypoxia (see Section I.C.3), gill concretions provide a ready source of maternal calcium available for rapid shell developnent in brooded glochidia (Silverman *et al.* 1985, 987). Thus, during glochidial incubation, the mass and density of gill concretions decline, particularly in the outer marsupial gill. The gill concretion nasses of individuals of *L. subrostrata* and *A. grandis grandis* brooding glochidia were only 47% and 70% of that during nonreproductive periods, espectively (Silverman *et al.* 1985). Indeed, ^{45}Ca racer studies indicated that 90% of glochidial shell calcium was of maternal origin in *A. grandis grandis*, the most likely source being gill mineral oncretions, with nonmateral calcium accounting for only 8% of glochidial shell calcium in *L. subrostrata* (Silverman *et al.* 1987).

D. *Water and Salt Balance*

Living in an extremely dilute medium, freshwater valves constantly gain water and lose ions. Excess water is eliminated as a fluid hypo-osmotic to the tissues via the kidneys and lost ions are recovered a active transport over the gills and other external pithelial surfaces as described in Section II.B.3. *C. fluminea* is relatively tolerant of salinity compared to other freshwater species, surviving longrm exposures to 10–14 ppt sodium (McMahon 1983a, Morton and Tong 1985). Above this salinity, it is incapable of maintaining hemolymph ion or osotic concentrations and becomes isosmotic with the medium (Gainey and Greenberg 1977). Freshwater unionids, with much lower hemolymph osotic concentrations, generally lose osmoregulary capacity and cannot regulate volume above 3 ppt sodium (Hiscock 1953). In contrast, hyperosotically stressed specimens of *C. fluminea* inease the blood osmotic concentration by actively increasing the free amino acid pools in the blood. This phenomenon also occurs in a number of estuane species (Gainey 1978a, 1978b, Gainey and reenberg 1977, Matsushima *et al.* 1982), preventng water loss by remaining isosmotic with the meum. This capacity is unexpected in freshwater species, which are never exposed to hyperosmotic medium and probably reflects the recent penetration f freshwater by *C. fluminea* from an estuarine anstor.

Both unionaceans and *C. fluminea* respond to emolymph ion depletion (via maintenance in an tremely dilute medium) by increasing the rate of tive Na^+ uptake, allowing maintenance of hemolymph ion concentration (Dietz 1985). The activity of ($Na^+ + K^+$)-activated ATPase, an enzyme associated with active sodium transport, increased in the mantle and kidney tissues of salt-depleted individuals of *C. fluminea*, suggesting activation of sodium transport. This response did not occur in the unionid *Lampsilis claibornesis*, indicating that regulation of active ion uptake has been lost in unionids with a much longer evolutionary history in freshwaters (Deaton 1982). In *Anodonta woodiana*, mantle cavity water had an osmotic concentration of 34 mosmol/liter, 76% that of hemolymph (45 mosmol/liter with pallial concentrations of Na^+, K^+, and Cl^- maintained at 71%, 76%, and 72% of blood levels, respectively, even in an extremely dilute medium (less than 1 mosmol/liter). Maintenance of elevated mantle water ion concentrations suggests that it acts as a buffer, reducing the gradient for and thus the rate of diffusive ion loss from tissues to the dilute freshwater medium (Matsushima and Kado 1982).

In both unionaceans and *C. fluminea*, the enzyme carbonic anhydrase (CA), which catalyzes formation of carbonic acid (H_2CO_3) from water and carbon dioxide, occurs in gill and mantle tissues. H_2CO_3 degrades into H^+ and HCO_3^- (bicarbonate ion), which appear to function as counter ions exchanged for Na^+ and Cl^- actively taken up from the medium. Bivalves in an extremely dilute medium increase CA activity specifically in the gill and mantle. Inhibition of CA activity by acetazolamide causes reduction in both hemolymph Na^+ and Cl^- concentrations and net Na^+ and Cl^- uptake rates, which is strong evidence for its ion regulatory role (Henery and Saintsing 1983).

The osmotic concentration of freshwater bivalves, particularly unionaceans, is the lowest recorded for multicellular freshwater invertebrates, that for *Anodonta cygnea* being 40–50 mosmol/liter or 4–5% of seawater, while that for other freshwater species is 100–400 mosmole/liter or 10–40% of seawater (Burky 1983). The apparent adaptive advantage of such low hemolymph osmotic concentrations is a reduction of the gradient for water gain from, and ion loss to, the dilute freshwater medium. This reduces transepithelial osmosis and ion diffusion rates across extensive mantle and gill surfaces to those which can be balanced by water excretion and active ion recovery mechanisms at energetically feasible levels (Burton 1983). Studies have shown that the hydrostatic pressure generated by the ventricle and auricles in *A. cygnea* is great enough to allow sufficient filtration of hemolymph plasma into the pericardial space to account for urine formation. As ventricular hydrostatic pressures in *A. cygnea* are approximately twice those of the marine clam *Mya arenaria*, capacity for excretion of excess water is greater in freshwater species compensating for the increased water gain associated with hyperosmotic regulation (Jones and Peggs 1983). Exposure of *Anodonta* sp. to a very dilute medium caused the appearance of extensive extracellular membrane spaces in the deep infoldings of kidney epithelial cells, perhaps allowing active ion uptake from the excretory fluid, producing a dilute urine or increased transport of excess water into the kidney (Khan *et al.* 1986).

The hormonal control of osmoregulation in freshwater bivalves has been reviewed by Dietz (1985). Cyclic AMP (cAMP) stimulates active uptake of Na^+ by unionaceans, while prostaglandin inhibits it and prostaglandin inhibitors stimulate it (Dietz *et al.* 1982, Graves and Dietz 1982, Saintsing and Dietz 1983). Serotonin stimulates tissue accumulation of cAMP, inducing increased Na^+ uptake (Saintsing and Dietz 1983). Thus, an antagonistic relationship exists between serotonin and prostaglandins in modulating adenylate cyclase-catalyzed cAMP stimulation of Na^+ active uptake. Not surprisingly, high concentrations of serotonin are found in the gill nerve tracts of unionaceans (Dietz 1985). The circadian rhythms of Na^+ uptake in freshwater clams (Graves and Dietz 1980, McCorkle-Shirley 1982) may be mediated by this antagonistic hormonal system (Dietz 1985).

When either their cerebropleural or visceral ganglia were ablated, individuals of the unionid *Lamellidens corrianus* rapidly gained water, indicating loss of osmoregulatory ability. Injection of ganglionic extracts restored normal osmoregulatory capacity, suggesting that ganglionic neurosecretory hormones are involved in regulation of water balance (Lmote and Jadhav 1981b). The pedal ganglion of *A. cygnea* has a higher affinity for serotonin and other monoamines controlling ion and water balance at low temperatures, indicating a seasonal component to hormonal control of osmoregulation (Hiripi *et al.* 1982).

III. ECOLOGY AND EVOLUTION

A. Diversity and Distribution

The distributions of freshwater bivalves, particularly unionaceans, in North America have been well described. Species distribution maps for unionaceans and sphaeriids have been published for Canada (Clarke 1973) and the United States (LaRocque 1967a). North American distribution records for the vast majority of species are provided in Burch (1975a, 1975b). LaRocque (1967b) also describes living and Pleistocene fossil assemblages at specific North American localities. In addition, there is a massive literature, too numerous to cite here, describing species occurrences at specific sites or species assemblages in various drainage systems in North America.

Distribution data for North American sphaeriids indicate that all native (non-introduced) species have broad distributions, often extending from the Atlantic Coast to the Pacific coast. Introduced to North America from southeast Asia in early 1900s (McMahon 1982), *Corbicula fluminea* (i.e., the light-colored shell morph of *Corbicula*) has a similarity widespread North American distribution. It extends into the drainages of the west coast of the United States and the southern tier of states, and throughout drainages east of the Mississippi River, with the exception of the most northernly states (Counts 1986, McMahon 1982), and into northern Mexico (Hillis and Mayden 1985) (Fig. 11.11). A second, unidentified species of *Corbicula* (i.e., the dark-colored shell morph) is restricted to isolated, spring-fed drainages in southcentral Texas and southern California and Arizona (Fig. 11.11). (Hillis and Patton 1982, Britton and Morton 1986, McLeod 1986). In contrast, North American unionacean species generally have more restricted distributions. Few species range on both sides of the continental divide and a surprisingly large number are limited to single drainage systems (Burch 1975b, LaRocque 1967a).

The widespread distributions of sphaeriids and *Corbicula* relative to unionaceans in North America may reflect fundamental differences in their capacities for dispersal. Unionaceans depend primarily on host fish transport of the glochidium for dispersal (Kat 1984), thus their ranges reflect those of their specific glochidial host fish species. While host fish transport of glochidia increases the probability of their dispersal into favorable habitats, as host fish and adult unionacean habitat preferences generally closely coincide (Kat 1984), it greatly limits the extent to which such dispersal can occur, leading to development of highly endemic species. For example, electrophoretic studies of peripheral populations of Nova Scotian unionid species suggest that invasion of new habitats is primarily by host fish dispersal (Kat and Davis 1984); therefore, barriers to fish dispersal are also barriers to unionid dispersal. Thus, the distribution of modern and fossil North American interior basin unionacean assemblages are limited to areas below major waterfalls in the drainage systems of Lake Champlain (New York, Vermont, Quebec), because these falls act as upstream migration barriers to host fish dispersal (Smith 1985a). Further, the recent re-establishment of *Anodonta impicata* populations in the upper portions of the Connecticut River Drainage closely fol-

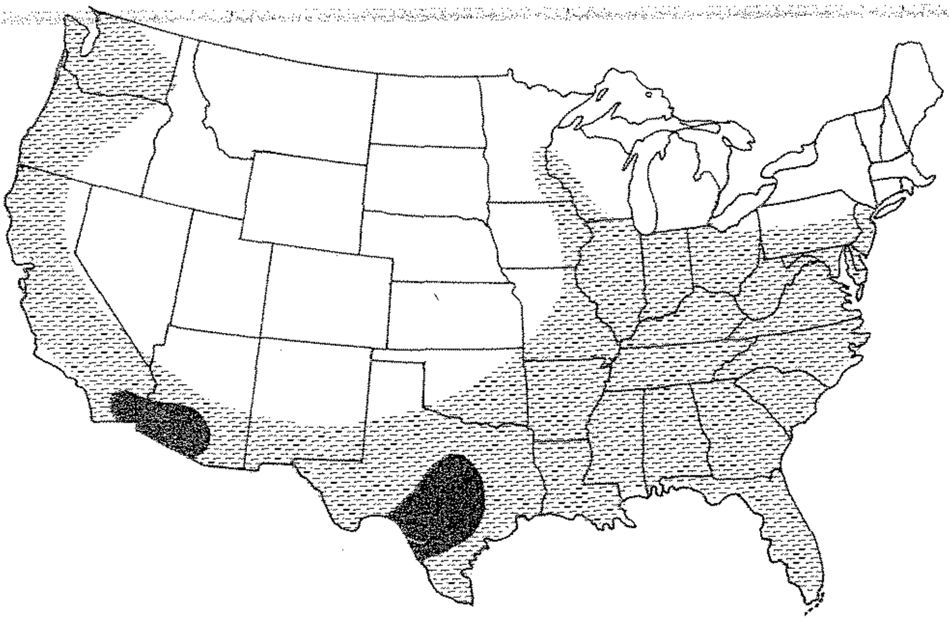


Figure 11.11 Distribution of *Corbicula* in the United States. Hatched area is the distribution of the light-colored shell morph of *Corbicula*, *Corbicula fluminea*. The darkly stippled areas are distribution of the dark-colored shell morph of *Corbicula*, yet to be assigned a species designation.

lowed the restoration of its anadromous glochidial clupeid fish host populations, by the building of fishways past numerous manmade impoundments that previously prevented upstream fish host dispersal (Smith 1985b).

Sphaeriids and *C. fluminea* have evolved mechanisms allowing dispersal between drainage systems, making them more invasive than unionaceans and accounting for their more cosmopolitan distributions. Juvenile sphaeriids disperse between drainage systems by clamping their shell valves onto limbs of aquatic insects, the feathers of water fowl (Burky 1983), or even the limbs of salamanders (Davis and Gihen 1982). Some sphaeriid species survive ingestion and regurgitation by ducks, which commonly feed on them, allowing long-distance dispersal (Burky 1983). The rapid spread of *C. fluminea* through North American drainage systems (McMahon 1982), while in part mediated by human vectors, also has resulted from the natural dispersal capacities of this species. The long mucilaginous byssal thread produced by juveniles or the filamentous algae on which they can settle becomes entangled in the feet or feathers of shore birds or water fowl, making them juvenile transport vectors between drainages (McMahon 1982, 1983a). Its natural capacity for dispersal is highlighted by its spread into northern Mexico drainage systems where human-mediated transport is highly unlikely (Hillis and Mayden 1985), and into southern Britain during interglacial periods (McMahon 1982). Adult zebra mussels, *Dreissena polymorpha*, attach to floating wood or boat hulls with byssal threads, facilitating transport over long distances (Mackie *et al.* 1989), and can also be transported between drainage systems attached to macrophytic vegetation utilized by nesting shore birds and water fowl.

Juveniles of *C. fluminea* can be transported long distances downstream passively suspended in water currents (McMahon and Williams 1986b, Williams and McMahon 1986). Water currents also disperse the actively swimming veliger stage of *D. polymorpha* (Mackie *et al.* 1989). Adult *C. fluminea* can also leave sediments to be carried downstream over the substratum by water currents (Williams and McMahon 1986). This process is assisted by production of a mucus dragline from the exhalant siphon, which increases the drag exerted on individuals by water currents (Prezant and Chalermwat 1984). Such passive dispersal of juvenile and adult *C. fluminea* on water currents not only accounts for the extraordinary ability of this species to invade the downstream portions of drainage systems after introduction (McMahon 1982), but also is the basis for its impingement and fouling of small-diameter piping and other components of industrial, agricultural, and municipal raw-water systems (McMahon 1983a). Similarly, current-mediated transport of free-swimming veligers and adults of *D. polymorpha* (adults attached to floating substrata or carried over the bottom as bysally attached clumps of individuals) on water currents accounts for its rapid dispersal through European drainage systems after it escaped from the Caspian Sea in the late eighteenth century (Morton 1969). This species has rapidly spread downstream throughout Lake Erie from its original upstream introduction in Lake St. Clair in 1985–1986 (where it was apparently transported from Europe in ship ballast water) (Mackie *et al.* 1989) (Fig. 11.12). Zebra mussels had invaded Lake Ontario, the St. Lawrence River, portions of lakes Superior, Huron, and Michigan and the western portion of the Erie–Borge Canal by the fall of 1990 when the final revision of this chapter was completed. Capacity for downstream transport and byssal attachment to hard surfaces make *D. polymorpha* destined to be a major North American biofouling pest species, recapitulating its recent history in Europe. Major incidents of zebra mussel fouling are already being reported in raw-water facilities on Lakes St. Clair, Erie, and Ontario (Mackie *et al.* 1989). Passive, current-mediated downstream transport is also reported for juvenile sphaeriids (*Pisidium punctiferum*) (McKillop and Harrison 1982) and may be an important but uninvestigated means of dispersal for many species in this family. In contrast, passive downstream transport is extremely rare in unionaceans (Imlay 1982), making them reproductively isolated.

As both sphaeriids and *C. fluminea* are self-fertilizing hermaphrodites (see Section II.B.5, introduction of only a single individual can found a new population. In contrast, *D. polymorpha* and the majority of unionids are gonachoristic, requiring simultaneous introduction of males and females to found a new population, thus reducing the probability of successful invasion of isolated drainage systems.

There have been major declines of unionacean populations and species diversity in North America over the last century. Over 25 unionacean species are on the Federal Register's Endangered Species list, with additional species on state lists and new species being added yearly (Laycock 1983, Taylor and Horn 1983, White 1982). Massive historical losses of unionacean species from river drainage systems are revealed by comparison of present day species assemblages with those of earlier surveys of living species or with recent fossil assemblages (Ahlstedt 1983, Hartfield and Rummel 1985, Havlik 1983, Hoeh and Trdan 1984, Miller *et al.* 1984, Neves and Zale 1982, Parmalee and Klippel 1982, 1984, Starnes and Bogan 1988, Stern 1983, Taylor 1985). Extirpations of sphaeriid faunae are far less common, but have occurred (Mills *et al.* 1966, Paloumpis and Starrett 1960). Unionacean assemblages in Indian middens near the upper Ohio River yielded at least 32 species, while a 1921 survey of its bivalve fauna yielded only 25 midden species and a 1979 survey, only 13 midden species in the same area—indicating massive species extirpation (Taylor and Spurlock 1982). Similar historical loss of Indian midden species has occurred in the Tennes-

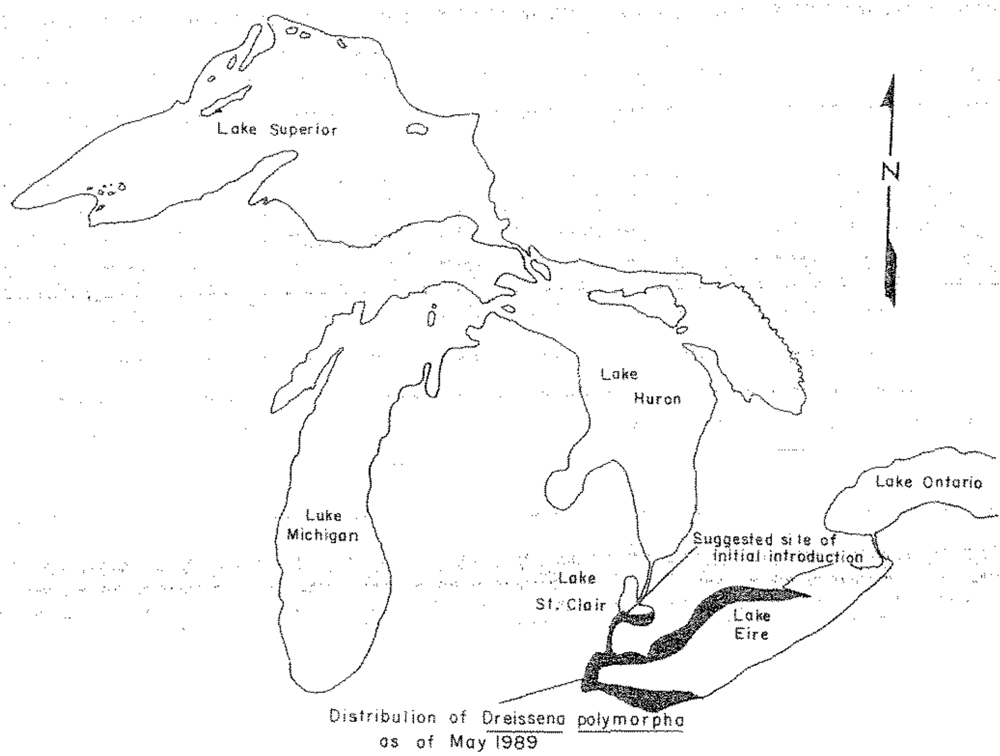


Figure 11.12 Distribution of the zebra mussel, *Dreissena polymorpha* in the Great Lakes of North America as of May 1989.

es River Drainage (Parmalee 1988, Parmalee *et al.* 982). Further evidence of the changing environmental conditions in the upper Ohio River is demon- rated by the establishment of 15 unionid species eviously unreported from Indian middens or earlier surveys (Taylor and Spurlock 1982).

Postulated causes for the massive decline in orth American unionacean populations are numer- s. The freshwater pearling industry can extirpate entire populations (Laycock 1983), overfishing for arls being a major factor in the recent decline of e pearl mussel, *Margaritifera magaritifera* in Great Britain (Young and Williams 1983a). Extensive artificial impoundments of drainage systems w flow velocity and subsequent accumulation of t causes reductions in mussel faunae (Duncan and Thiel 1983, Parmalee and Klippel 1984, Starnes and gan 1988, Stern 1983). Impoundments may also minate fish glochidial hosts (Mathiak 1979) or revent dispersal of glochidia by fish hosts (see ear- r discussion). They may also damage downstream ionacean populations by releasing cold hypolim- ic water (Ahlstedt 1983, Clarke 1983) or by induc- ng major short-term oscillations in flow rate, either uring the bottom of suitable substrata for mussels ing periods of high flow or causing prolonged erial exposure of mussels during periods of low w (Miller *et al.* 1984). Channelization of drainage tems for navigation or flood control is detrimen- al to unionaceans. Increased flow velocity and ropeller wash elevate suspended solids, which in- fere with mussel filter feeding and oxygen con- mption (Aldridge *et al.* 1987, Payne and Miller 987). It also reduces availability of stabilized sedi- nts, sand bars, and low flow areas, all preferred onacean habitats (Hartfield and Ebert 1986, ayne and Miller 1989, Stern 1983, Way *et al.* 0a).

Pollution adversely affects bivalves. Mussel una receiving industrial pollution (Zeto *et al.* 87), urban waste water effluents (sewage, silt, pes- des) (Gunning and Suttkus 1985, St. John 1982, es and Zale 1982), or silt and acid discharges om mines (Taylor 1985, Warren *et al.* 1984) be- e severely depauperate or totally extirpated. advent of modern sewage treatment on the Pearl ver, Louisiana, allowed re-establishment of five ionid species previously absent for at least 20 s (Gunning and Suttkus 1985).

hysical factors also influence bivalve distribu- ns. While environmental requirements are spe- specific, a number of generalities appear war- d. Sediment type clearly affects distribution tterns. Unionaceans are generally most success- n stable, coarse sand or sand–gravel mixtures are generally absent from substrata with heavy silt loads (Cooper 1984, Salmon and Green 1983, Stern 1983, Way *et al.* 1990a). In the Wisconsin and St. Croix Rivers only 7 of 28 unionid species occurred in sand–mud sediments, the majority preferring sand–gravel mixtures. Only three species, *Anodonta grandis*, *Lampsilis anodontes*, and *L. radiata*, typically inhabited sand–mud substrata (Stern 1983). In contrast, *C. fluminea* has much broader sediment preferences, successfully colonizing habitats ranging from bare rock through gravel and sand to sediments with relatively high silt loads (McMahon 1983a). Broad sediment preference has allowed this species to invade a wide variety of North American drainage systems; however, its optimal habitat is well-oxygenated fine sands or gravel–sand mixtures (Belanger *et al.* 1985).

In contrast to unionaceans, species diversity in the genus *Pisidium* increases with decreasing particle size (Fig. 11.13A), becoming maximal at a mean particle diameter of 0.18 mm (Kilgour and Mackie 1988). In southeastern Lake Michigan, *Pisidium* density and diversity were maximal in very fine sand–clay and silt–clay sediments, while peak *Sphaerium* diversity occurred at somewhat larger particle sizes (Zdeba and White 1985). These observations suggest differences in substratum preference among sphaeriid genera, perhaps associated with sediment oranic detritus feeding mechanisms in *Pisidium* (see Section III.C.2).

Apparent differences in substratum preferences may be associated with species-specific differences in optimal water velocities. Unionaceans are most successful where water velocities are low enough to allow sediment stability, but high enough to prevent excessive siltation (Salmon and Green 1983, Stern 1983, Way *et al.* 1990a), making well-oxygenated, coarse sand and sand–gravel beds optimal habitats for riverine species. Low or variable velocities allow silt accumulations that either make sediments too soft for maintenance of proper position (Lewis and Riebel 1984, Salmon and Green 1983) or interfere with filter feeding and gas exchange in unionaceans (Aldridge *et al.* 1987). In contrast, periodic scouring of substrata exposed to high flow velocities can both remove substrate and mussels and prevent their successful resettlement (Young and Williams 1983b). Sediment type did not affect the burrowing ability of three lotic unionid species (*A. grandis*, *Elliptio complanata*, and *Lampsilis radiata*) (Lewis and Riebel 1984), suggesting that it is not involved in substratum preferences. *C. fluminea*, with its relatively heavy, ridged shell and rapid burrowing ability, is better adapted for life in high current velocities and unstable substrata than are most unionaceans (McMahon 1983a). Indeed, in the Tangipahoa River, Mississippi, it successfully colonizes

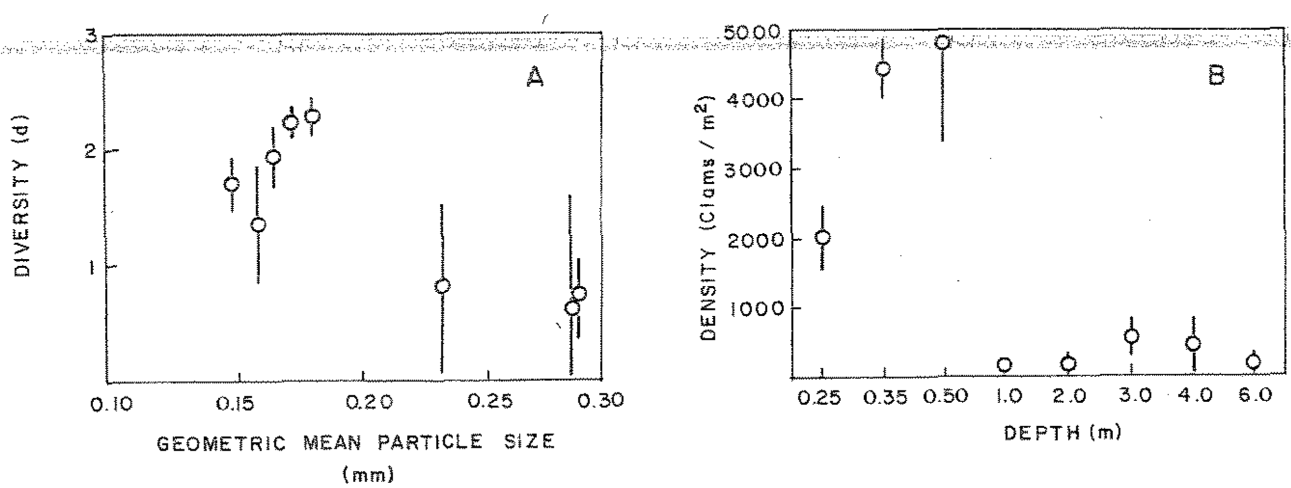


Figure 11.13 Sediment relationships in sphaeriid clam communities from sites along a depth transect in Britannia Bay, Ottawa River, Canada. (A) Mean sphaeriid diversity (Shannon-Weaver d) values for various sphaeriid communities in relation to mean sediment geometric particle size. (B) Mean sphaeriid density values at various depths. Vertical bars about points are 95% confidence limits. Note increase in diversity with decrease in mean particle size of sediments and maximization of density at depths of less than one meter. (Redrawn from data of Kilgour and Mackie 1988.)

unstable substrata from which unionaceans are excluded (Miller *et al.* 1986). In contrast to the majority of unionaceans and *C. fluminea,* many sphaeriid species occur in small ponds and the deeper portions of large lakes, where water flow is negligible and the substratum has both a high silt content and a heavy organic load. The preference of a number of sphaeriids for low flow habitats and silty sediments may be associated with their interstitial sediment feeding mechanisms, particularly in the genus *Pisidium* (Lopez and Holopainen 1987) (see Section III.C.2). Adult byssal thread attachment to hard substrata not only allows *D. polymorpha* to inhabit relatively high flow areas compared to other bivalves (the postveligor successfully settles at flow rates up to 1.5m/sec.), but also makes it a highly successful epibenthic species in lentic habitats characterized by a preponderance of hard substrata from which native North American species are generally eliminated (Mackie *et al.* 1989).

Water depth also affects freshwater bivalve distributions. Most species of unionaceans prefer shallow water habitats generally less than 4–10 m in depth (Machena and Kautsky 1988, Salmon and Green 1983, Stone *et al.* 1982, Way *et al.* 1990a), although some species can be found in the deeper regions of lotic habitats if they are well oxygenated. *C. fluminea* is also restricted to shallow, near-shore habitats in lentic waters (although they can be found in deeper waters if they are well oxygenated) (McMahon 1983a), as are the majority of *Sphaerium* and *Musculium* species (Fig. 11.13B) (Kilgour and Mackie 1988, Zdeba and White 1985). In contrast, some species of *Pisidium* inhabit the profundal regions of lakes (Holopainen and Jonasson 1983, Kilgour and Mackie 1988, Zdeba and White 1985; for a review see Burky 1983). The depth distributions of *D. polymorpha* vary between habitats; however, adults are rarely found in great numbers above 2 m and dense populations can extend to depths of 4–60 m, but always occur in well-oxygenated waters above the epilimnion. Younger, recently settled individuals tend to migrate toward deeper water after settlement (Mackie *et al.* 1989).

The limitation of most bivalves to shallow habitats when they occur in lentic waters may be associated with their relatively poor tolerance of hypoxia. In lentic habitats, waters below the epilimnion are often depleted of dissolved oxygen. As with the vast majority of unionaceans *Sphaerium* and *Musculium* species (Burky 1983) and *C. fluminea* (McMahon 1983a) cannot maintain normal rates of O_2 uptake under severely hypoxic conditions. Thus, they are mostly restricted to shallow, well-oxygenated habitats. In contrast, many species of *Pisidium* are extreme regulators of $\dot{V}_{O_2}$ when hypoxic (see Burky 1983 and references therein), allowing them to inhabit the deeper hypolimnetic regions of lakes where summer ambient O_2 tensions fall to near zero levels (Holopainen 1987, Holopainen and Jonasson 1983, Jonasson 1984a, 1984b). However, during summer hypoxic periods, growth and reproduction are retarded in profundal *Pisidium* populations, indicating that low oxygen tensions can have deleterious effects on even hypoxia-tolerant species (Halopainen and Jonasson 1983). Hypoxia-intolerant *C. fluminea* invaded the profundal regions of a small lake only after artificial aeration eliminated hypoxic hypolimetic waters (McMahon 1983a). Sewage-induced hyoxia in the Pearl River, Louisiana, eliminated its unionid fauna (Gunning and Suttkus 1985). Even ighly hypoxia-tolerant profundal *Pisidiid* commuties have been exterminated by extreme hypoxia induced by sewage effluents (Jonasson 1984a). The low tolerance of most unionaceans to even moderate ypoxia (Burky 1983) renders them highly sucepble to wastewater release, a factor implicated in the decline of North American faunae.

Ambient pH does not greatly limit the distribution f freshwater bivalves. The majority of species prefer alkaline waters with the pH above 7.0; species diversity declines in more acidic habitats (Oknd and Kuiper 1982). However, unionaceans can grow and reproduce over a pH range of 5.6–8.3, a pH of less than 4.7–5.0 being the absolute lower mit (Fuller 1974, Hornbach and Childers 1987, Kat 82, Okland and Kuiper 1982). Some sphaeriid species are relatively insensitive to pH or alkalinity. No differences in species richness or growth and production occurred in sphaeriid fauna from six lakes of extremely low alkalinity relative to those with higher alkalinity levels (Rooke and ackie 1984a, 1984b, Servos *et al.* 1985). Maximal boratory growth and reproduction in *Musculium partumeium* occurred at pH 5.0, suggesting adaptaon of this species to moderately acidic habitats ornbach and Childers 1987).

Habitats of low pH generally also have low calcium concentrations. Low pH leads to shell dissoluon and eventual mortality in older individuals if ell penetration occurs (Kat 1982). Sphaeriids have been reported from waters with calcium concentraons as low as 2 mg Ca/liter, while the unionid *liptio companata* occurs in lakes with 2.5 mg Ca/liter (Rooke and Mackie 1984a). Freshwater bilves can actively take up Ca^{2+} from the meum at concentrations as low as 0.5 mM Ca/liter (0.02 mg Ca/liter, see Section II.A.1), a level far below the minimal tolerated ambient Ca^{2+} concenations of 2–2.5 mg/liter. Thus, minimal environental calcium limits are much greater than those allowing active Ca^{2+} uptake. As such, the minimum bient calcium concentration tolerated by freshater bivalves appears to be the concentration at which the rates of calcium uptake and deposition to the shell exceed the calcium loss rate from shell ssolution and diffusion, allowing maintenance of ell integrity and growth. As many factors affect shell deposition and dissolution rates (e.g., temperare, pH, and calcium concentration), the minimal lcium concentration and/or pH tolerated by a species may vary greatly between habitats dependent interacting biotic and abiotic parameters and are ten species specific. Waters with low calcium concentrations usually have low concentrations of other biologically important ions, making them inhospitable to bivalves even if calcium concentrations are suitable for maintaining shell growth.

Temperature influences bivalve species distributions; species have specific upper and lower limits for survival and reproduction (Burky 1983). For example, intolerance of temperatures below 2°C prevents *C fluminea* from expanding into drainages in the north central United States, which reach 0°C in winter (Fig. 11.11) (Counts 1986, McMahon 1983a). This results in massive low temperature winter kills in populations on the northern edge of its range (Cherry *et al.* 1980, Sickel 1986). Thus, *C. fluminea* populations north of the 2°C winter water temperature isotherm are restricted to areas receiving heated effluents (Counts 1986, McMahon 1982, 1983a). In contrast, the maximal temperature for the development of *D. polymorpha* eggs is 24°C and for larval development, 25°–27°C (Mackie *et al.* 1989). Such temperature maxima make this species unlikely to colonize drainage systems in the extreme southern and southwestern United States where ambient summer water temperatures routinely reach 30°–32°C.

Water level variation can affect bivalve distributions. Declining water levels during droughts or dry periods expose relatively immotile bivalves for weeks or months to air. Some species are adapted to withstand prolonged emersion, while others are emersion-intolerant (McMahon 1983a) (see Section II.C.4). The tendency for restriction of many bivalve populations to shallow near-shore waters makes them highly susceptible to emersion when water levels decline. Many sphaeriid species and a few unionacean taxa are highly tolerant of air exposure and thus able to survive prolonged seasonal emersion in ephemeral or variable level habitats (Burky 1983, White 1979). These species display unique adaptations to emergence described in Section II.C.4.

Freshwater bivalve distribution is also related to stream size or order. The number of unionacean species in drainage systems in southeastern Michigan increased proportionately with the size of the drainage area; this was mainly in response to species additions (Strayer 1983) (Fig. 11.14). However, variation in species richness could not be completely accounted for by drainage area size (note the high degree of variation in species richness values at specific drainage area values in Fig. 11.14). This suggests that other environmental variables may affect mussel distribution patterns. Among these are surface geology and soil porosity. Porous soils retain water, buffering runoff so streams draining them have relatively constant flow and are rarely dry. Therefore, they support greater numbers of mussel

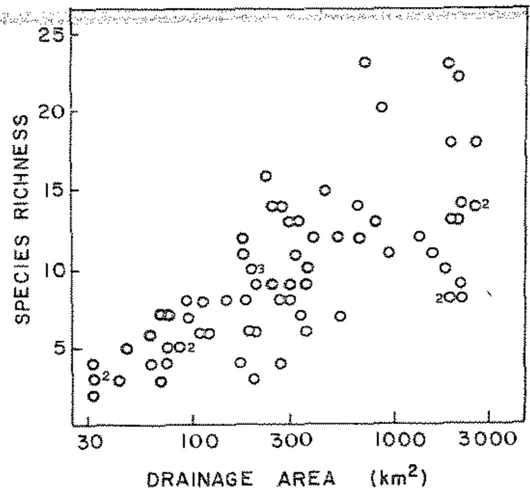


Figure 11.14 Unionid mussel species richness (total number of species present at a particular site) as a function of stream size measured by its total drainage area in km^2 in southeastern Michigan, United States. Numbers next to points indicate the number of observations falling on that point. The relationship between drainage area and mussel species richness was statistically significant ($r = 0.68, P < 0.001$). (Redrawn from Strayer 1983.)

species than streams draining soils of poor water infiltration capacity, whose drainages are prone to flooding–drying cycles. In such streams, exposure of mussels to air or low oxygen in stagnant pools during dry periods, and bottom scouring and high silt loads during floods all induce mortality, reducing species richness (Strayer 1983). Indeed, the stability of water flow, high O_2 concentrations, reduced risk of flooding, and reduction of silt loading associated with larger stream size appear to account for the increased bivalve species richness associated with them (Fig. 11.14) (Strayer 1983). However, some unionacean species, such as *Amblema plicata,* are adaptated to small, variable flow streams and, in southeastern Michigan, occur almost exclusively in such habitats from which other unionaceans are virtually excluded (Strayer 1983).

B. Reproduction and Life History

North American freshwater bivalves display extraordinary variation in life history and reproductive adaptations. Life-history traits (e.g., those affecting reproduction and survival, including growth, fecundity, life span, age to maturity, and population energetics) have been reviewed for freshwater molluscs (Calow 1983, Russell-Hunter and Buckley 1983) and specifically for freshwater bivalves (Burkey 1983, Mackie 1984, Mackie *et al.* 1989, McMahon 1983a). Most research on life-history traits involves the Sphaeriidae, with a paucity of information for unionaceans. Sphaeriids are good subjects for studies of life histories because of their greater abundances, ease of collection and laboratory maintenance, relatively simple hermaphroditic life cycles, ovoviviparity, semelparity, release of completely formed immature adults, and relatively short life spans. In contrast, unionaceans are more difficult subjects for life-history studies because they are gonochoristic, long-lived, interoparous, often rare and difficult to collect, and have life cycles complicated by the parasitic glochidial stage. The life-history traits of *C. fluminea* and *D. polymorpha* have been intensely studied due to their invasive nature and economic importance as fouling organisms (Mackie *et al.* 1989, McMahon 1983a).

1. Unionacea

The life-history characteristics of freshwater unionaceans are clearly different from those of the sphaeriids, *C. fluminea* or *D. polymorpha* (Table 11.2). The majority of unionid species live in large, stable aquatic habitats where they are generally buffered from periodic catastrophic population reductions that are typical of smaller, unstable aquatic environments (see Section III.A). In such stable habitats, long-lived adults accumulate in large numbers (Payne and Miller 1989), which can lead to competition for space and food. A few species preferentially inhabit ponds (Burch 1975b), but their life history traits have not been studied.

An important aspect of the unionacean life-history traits is their unique parasitic larval stage, the glochidium (Fig. 11.15B). With the single exception of *Simpsonichoncha ambigua,* whose glochidial host is the aquatic salamander, *Necturus maculosus,* all other North American unionaceans have glochidia that parasitize fish. The significance of the glochidial stage to unionacean reproduction has been reviewed by Kat (1984). Details of glochidial incubation and development in outer demibranch marsupial brood pouches were described previously in Section II.B.5. The glochidium has a bivalved shell adducted by a single muscle. Its mantle contains sensory hairs. In the genera *Unio, Anodonta, Megalonaias,* and *Quadrula,* a long threadlike structure projects from the center of the mantle tissue beyond the ventral edge of the valves. Its function is unknown, but it may be involved with the detection of, and/or attachment to, fish hosts.

There are three general forms of glochidia. In the subfamily Anodontina, "hooked glochidia" occur, with triangular valves from whose ventral edges project an inward curving hinged hook covered with smaller spines (Fig. 11.15B). On valve closure, the hooks penetrate the skin, scales, or fins of fish hosts

Table 11.2 Summary of the Life History Characteristics of North American Freshwater Bivalves, Unionacea, Sphaeriidae, *Corbicula fluminea*, and *Dreissena polymorpha*

Life History Trait[a]	**Unionacea**	**Sphaeriidae**	***Corbicula fluminea***	***Dreissena polymorpha***
Life span	< 6–> 100 yr (species dependent)	< 1–> 5 yr (species dependent)	1–5 yr	4–7 yr
Age at Maturity (yr)	6–12 yr	> 0.17–< 1.0 yr (1 yr in some species)	0.25–0.75 yr	1–2 yr
Reproductive Mode	Gonochoristic (a few hermaphroditic species)	Hermaphroditic	Hermaphroditic	Gonochoristic
Growth Rate	Rapid prior to maturity, slower thereafter	Slow relative to Unionids or *C. fluminea*	Rapid throughout life	Rapid throughout life
Fecundity (young/average adult/breeding season)	200,000–17,000,000	3–24 (*Sphaerium*) 2–136 (*Musculium*) 3–7 (*Pisidium*)	35,000	30,000–40,000/female
Juvenile size at Release	Very small 50–400μm	Large 600–4150 μm	Very small 250 μm	Extremely small 40–70 μm
Relative Juvenile Survivorship	Extremely low	High	Extremely low	Extremely low
Relative Adult Survivorship	High	Intermediate	Low 2–41%/yr	Intermediate 26–88%/yr
Semelparous/Iteroparous	Iteroparous	Semelparous or iteroparous	Generally iteroparous	Iteroparus
No. of Reproductive Efforts/Year	1	1–3 (continuous in some species)	2	1 (2–8 months long)
Assimilated Energy Respired (%)	–	21–91% (avg. = 45%)	11–42%	–
Nonrespired Energy in Growth (%)	85.2–97.5	65–96% (avg. = 81%)	58–71%	96.1%
Nonrespired Energy in Reproduction (%)	2.8–14.8	4–35% (avg. = 19%)	15%	4.9%
Turnover Time in Days (Mean standing crop biomass : biomass production/day ratio	1790–2849	27–1972 (generally < 80)	73–91	53–869 (dependent on habitat)

[a] See text for literature citations for data on which this table was based.

allowing glochidial attachment and encystment on host external surfaces. The majority of North American unionaceans produce "hookless glochidia," characterized by more rounded valves bearing reinforcing structures and/or a series of small spines or stylets on their ventral margins. These generally attach and encyst on the gills of fish hosts. "Axe-head glochidia" of the genus *Proptera* have a distinctly flared ventral valve margin, and near-rectangular valves which may have hooklike structures on each corner. Their host attachment sites are unknown (Kat 1984).

Glochidia initially attach to fish hosts by clamping (or snapping) the valves onto fins, scales, and/or gill filaments. Glochidia do not appear to be host-specific in attachment; rather, they attach to any fish they contact (Kat 1984). Released glochidia display snapping behavior (i.e., host attachment behavior), whereby valves are periodically rapidly and repeatedly opened and shut. Valve snapping by *M. margaritifera* glochidia is greatly stimulated by the presence of mucus, blood, gill tissue, or fins of their brown trout host, but not by water currents or direct tactile stimulation (the latter causes prolonged valve closure) (Young and Williams 1984a). This suggests that glochidia use chemical cues to detect and attach

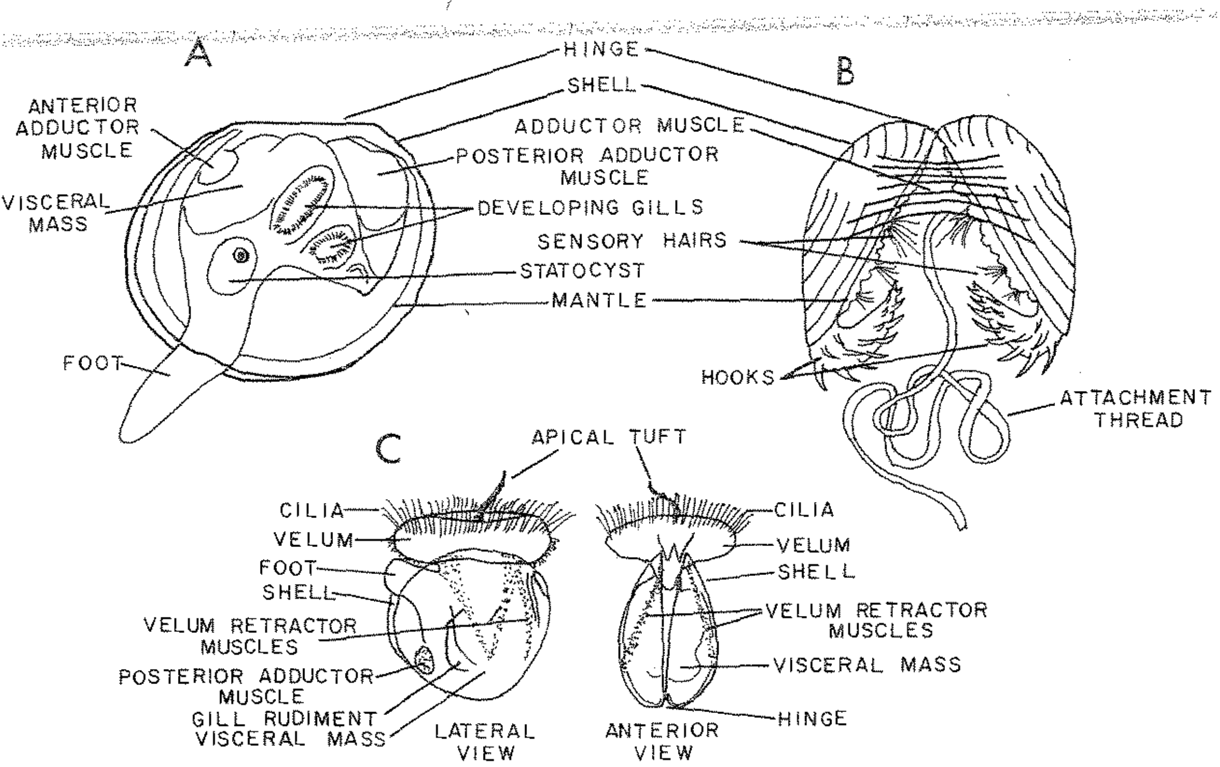


Figure 11.15 Anatomic features of freshwater bivalve larval stages. (A) The D-shaped juvenile of *Corbicula fluminea*, the freshwater Asian clam (shell length = 0.2 mm). (B) The glochidium larva of unionids, which is parasitic on fish. Depicted is a glochidium of *Anodonta* characterized by the presence of paired spined hooks projecting medially from the ventral edges of the shell; not all unionid species have glochidia with such hooks (50–400 μm in diameter depending on species. (C) Lateral and anterior views of the free-swimming, planktonic, veliger larva of *Dreissena polymorpha*, the zebra mussel; the veliger is 40–290 μm in diameter and uses the ciliated velum to swim and feed on phytoplankton. The juveniles of freshwater sphaeriid species are large and highly developed, having essentially adult features at birth (Figs. 11.2A and 11.4A).

to host fish. Fuller (1974) provided an extensive list of suitable fish hosts for the glochidia of many unionacean species.

Glochidia encyst in host tissues within 2–36 hr of attachment and may or may not grow during encystment, depending on the species. The time to juvenile metamorphosis and excystment is also species-dependent, ranging from 6–160 days; however, it is reduced at higher temperatures (Kat 1984, Zale and Neves 1982). Unsuitable host fish reject glochidia, sloughing them off after encystment (Kat 1984), with the fish blood serum components apparently dictating host suitability (Neves *et al.* 1985). As glochidia attach readily to unsuitable hosts (Kat 1984, Neves *et al.* 1985, Trdan and Hoeh 1982), host suitability appears to be more dependent on fish immunity mechanisms than on glochidial host recognition. Indeed, even suitable host fish can reject glochidia. Prior to metamorphosis, the number of glochidia of *M. margaritifera* encysted on a natural population of brown trout declined, suggestive of host rejection (Young and Williams 1984b). In the laboratory, only 5–12% of *M. margaritifera* glochidia that successfully encysted in appropriate host fish actually completed development to the point of excystment as free-living juveniles, indicating host rejection of most encysted individuals (Young and Williams 1984a).

Unionaceans display a number of adaptations that increase the likelihood that glochidia will come into contact with fish hosts (Kat 1984). Glochidial release occurs once per year, but the duration of release is species dependent. Cycles of gametogenesis and glochidial release may be controlled by neurosecretory hormones (Nagabhushanam and Lomte 1981). Tachytictic mussels are short-term breeders, whose glochidial development and release take place between April and August; in many of these species, shedding of glochidia corresponds with either migratory periods of anadromous fish hosts, or the reproductive and nesting periods of host fish species. The fish hosts of these species often construct nests in areas where unionacean populations are the most dense. Residence of adult unionaceans on host nesting sites, host nest construction by fanning away of substrata, and the fanning of developing embryos in nests all provide optimal conditions for glochidial–host contact and encystment. Thus, a high proportion of nest-building fish species, such as centrarchids, are common hosts for North American unionaceans (Fuller 1974, Kat 1984). In contrast, bradytictic unionacean species retain developing glochidia in gill marsupia throughout the year, releasing them in summer (Kat 1984).

When shed from adult mussels, glochidia are generally bound together by mucous into discrete packets, which either dissolve (releasing glochidia) or are maintained intact as discrete glochidial "conglutinates" of various species-specific forms and colors. Glochidia with attachment threads (Fig. 11.15B) are released in tangled mucus threads, forming loosely organized webs that dissolve relatively rapidly. Many of these glochidia possess hooks and attach to the external surfaces of fish hosts. In some unionaceans, such mucilaginous networks of glochidia persist, suspending glochidia above the substratum, thus enhancing the possibility of host contact.

Unionids with hookless glochidia that attach to fish gills may release conglutinates that mimic the vermiform food items of their fish hosts, and thus resemble brightly colored oligochaetes, flatworms, or leeches. Some species hold their vibrant, wormlike conglutinates partially extruded from the exhalant siphon, making them more obvious to fish hosts. Consumption of such conglutinates releases glochidia within the buccal cavity of the fish, where they can be carried directly onto gill filament attachment sites by respiratory currents.

The most unusual form of unionid host food mimicry involves use of pigmented muscular extensions of the mantle edges in female lampsilids. These mantle flaps (Fig. 11.16) resemble the small fish prey of their piscivorous fish hosts. Gravid females extend the posterior shell margins well above the substratum and periodically pulsate the mantle flaps to mimic a small, actively swimming fish. When a fish attacks these mantle flap lures, glochidia are forcibly released through pores in the posterior portion of the marsupial gill (often projected between the mantle flaps, Fig. 11.16) assuring glochidial contact with the fish host (Kat 1984).

As the glochidia of some species do not grow while encysted, the degree to which they are parasitic on fish hosts has been questioned. However, recent *in vitro* glochidial culture experiments suggest that glochidia both absorb organic molecules from fish tissues and require fish plasma for development and metamorphosis (Isom and Hudson 1982) in a true host–parasite relationship.

As in other parasitic species, glochidia are shed in huge numbers to ensure the maximum potential for host contact and attachment. Fecundity in unionaceans is reported to range from 200,000–17,000,000 glochidia/female/breeding season (Parker *et al.* 1984, Paterson 1985, Paterson and Cameron 1985, Young and Williams 1984b). Nonetheless, chances for glochidial survival to metamorphosis are extremely small. In a natural population of *M. margaritifera* that does not produce glochidial conglutinates, only 0.0004% of released glochidia successfully encysted in fish hosts. Of these, only 5% were not rejected before full development and excystment; and, of those successfully metamorphosing, only 5% successfully became established as juveniles in the substratum (Young and Williams 1984b). Thus, overall, only 1 in every 100,000,000 shed glochidia became settled juveniles. High glochidial mortality makes the effective fecundity of unionaceans extremely low, which is not unusual for a species in a stable habitat. Based on these data and the fecundity ranges listed in Table 11.2, only 0.002–0.17 juveniles from each female unionacean's annual reproductive effort would successfully settle in the sediment. Therefore, the main advantages of the parasitic glochidial stage appear to be directed dispersal by fish hosts into favorable habitats (Kat 1984) and utilization of fish host energy resources by glochidia to complete development to a juvenile size that is large enough to complete effectively for limited resources after settlement in adult habitats. Utilization of fish host energy stores by glochidia prevents their direct competition with adults for limited food and space resources during early development, as occurs in juvenile corbiculaceans and *D. polymorpha*. Glochidial parasitism of fish hosts also allows female unionaceans to devote relatively small amounts of nonrespired, assimilated energy to reproduction (2.8–14.5% of total nonrespired, assimilated energy), leaving the majority for somatic tissue growth (Table 11.2) (James 1985, Negus 1966, Paterson 1985). This allocation of a high proportion of energy to tissue growth is characteristic of species adapted to stable habitats. As unionaceans are long-lived and highly iteroparous, with greater than 6–10 reproductive periods throughout life, allocation of the majority of nonrespired energy to growth increases the probability of adult survival to the next reproductive period. Increased growth rate and reduction of reproductive effort increases the ability to compete and reduces the probability of predation and/or mortality that is associated with reproductive effort or removal from the substratum during periods of high water flow. All of these characteristics increase fitness in stable habitats (Sibly and Calow 1986).

In the majority of unionaceans, the greatest shell growth occurs in immature individuals in the first

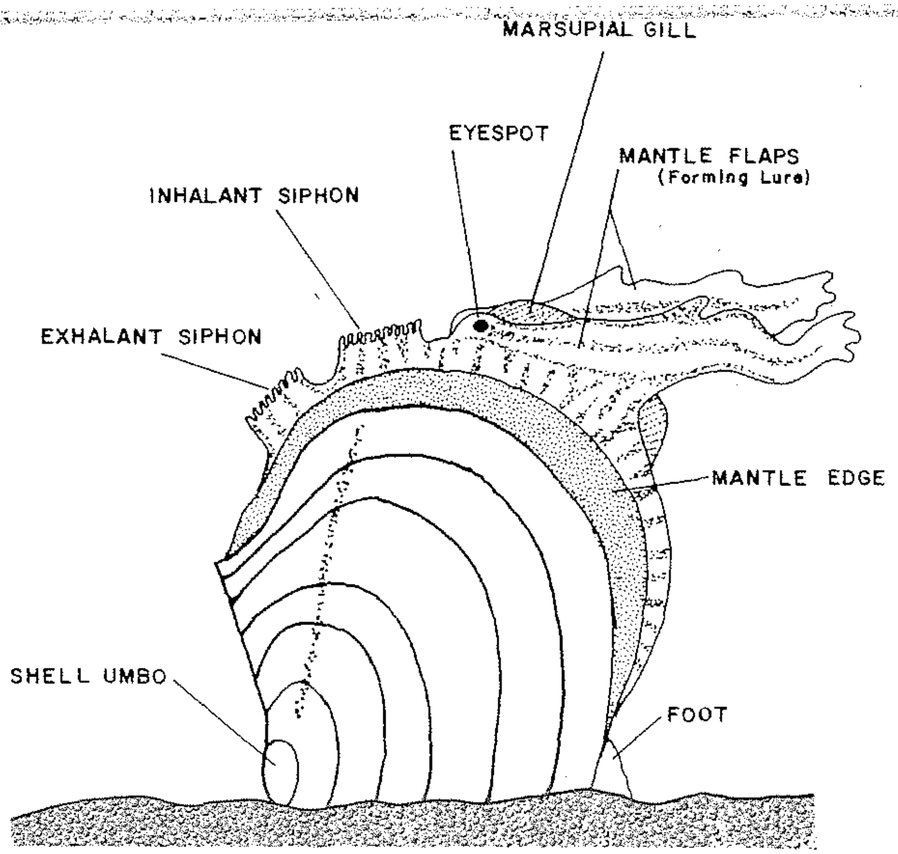


Figure 11.16 The modified mantle flaps of a female specimen of *Lampsilis ventricosa*, which mimic the small fish prey (note eye spot and lateral line-like pigmentation) of the predatory fish species that are hosts to the glochidia of this species. The posterior portions of the marsupial outer demibranchs are projected from the mantle cavity to lie between the mantle flap lures. When the mantle flap lures are disturbed by an attacking fish, glochidia are released through pores in the marsupial gill ensuring maximal contact with the fish host. Mantle flap lures are characteristic of the unionid genus *Lampsilis*.

four years of life (Fig. 11.17A). Indeed, relative shell growth rate in young unionids is greater than in sphaeriids or even the fast-growing species, *C. fluminea* and *D. polymorpha* (Table 11.2). In unionaceans, the shell growth rate declines exponentially with age, but the rate of tissue biomass accumulation remains constant or actually increases with age (Figs. 11.17A, B; see also Houkioja and Hakala 1978). Thus, early in life, increases in shell size and biomass occur preferentially over tissue accumulation; whereas after maturity (> 6 yr), shell growth slows and tissue is accumulated at a proportionately higher rate. The delayed maturity of unionids (6–12 yr, Table 11.2) allows all available nonrespired assimilation to be devoted to growth early in life.

Once mature, large adult unionaceans display high age-specific survivorship between annual reproductive efforts, being 81–86% in 5–7 year old *Anodonta anatina* (Negus 1966) and generally greater than 80% in mature *M. margaritifera* (12–90 yr) (Bauer 1983). High adult survivorship, long life spans, and low juvenile survivorship of unionaceans accounts for the preponderance of large adult individuals in natural populations (Bauer 1983, James 1985, Negus 1966, Paterson 1985, Paterson and Cameron 1985, Tevesz *et al.* 1985). Populations dominated by adults are characteristic of stable, highly competitive habitats (Sibly and Calow 1986).

The preponderance of large, long-lived adults in unionacean populations causes them to be characterized by high proportions of standing crop biomass relative to biomass production rates. This relationship between standing crop biomass and biomass production rate can be expressed as turnover times, the time in days required for the population production of biomass to be equivalent to the average population standing crop biomass. Such turnover times can be computed in days as the average standing crop of a population divided by its mean daily productivity rate (Russell-Hunter and Buckley 1983). Turnover times have been based on dry weight, organic carbon, or nitrogen biomass units or energetic units in studies of freshwater molluscs (Russell-Hunter and Buckley 1983). Long-lived unionids,

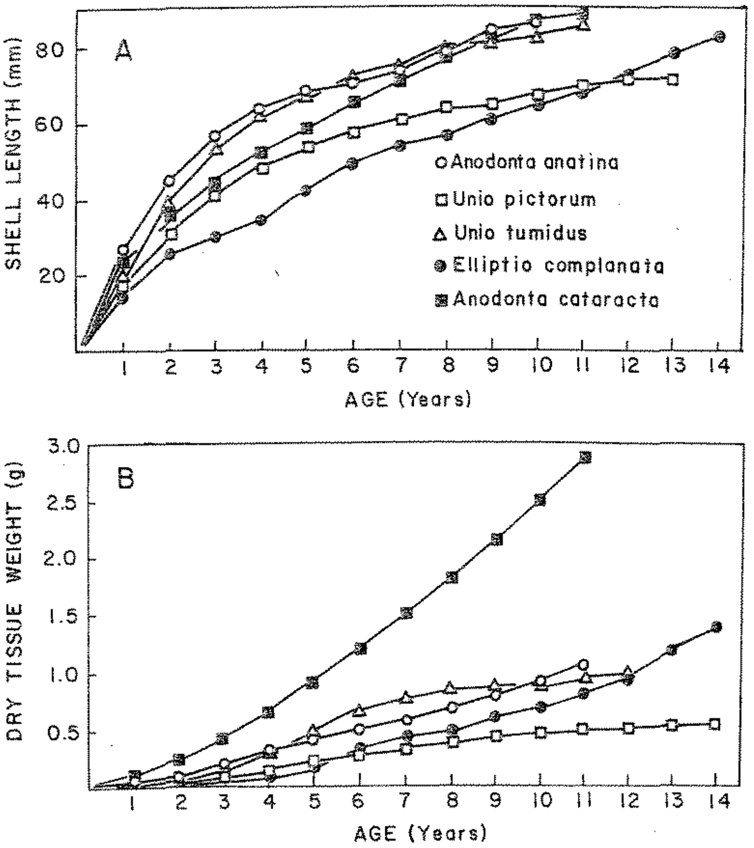


Figure 11.17 The shell and tissue growth of selected species of unionids (*Anodonta anatina*, open circles, *Unio pictorum*, open squares; *Unio tumidus*, open triangles; *Elliptio complanata*, solid circles; and *Anodonta cataracta*, solid squares). (A) Mean shell length increase with increasing age over the entire life span of each species. (B) Mean dry tissue weight increase with increasing age over the entire life span of each species. Note that increase in shell length declines with age in most species, while dry tissue weight increases either linearly or exponentially with age. [From data of Negus (1966), Paterson (1985), and Paterson and Cameron (1985)].

with populations dominated by large adults, have extremely long turnover times ranging from 1790–2849 days (computed from data in James 1985, Negus 1966, Paterson 1985) compared with sphaeriids (27–1972 days), *C. fluminea* (73–91 days), or *D. polymorpha* (53–869 days) (Table 11.2). Such extended turnover times are characteristic of long-lived, iteroparous species from stable habitats (Burky 1983, Russell-Hunter and Buckley 1983).

In only one aspect do unionaceans deviate from the life-history traits expected of species inhabiting stable habitats and experiencing extensive competition. That is in the production of very large numbers of very small young (glochidia). However, as described earlier, this is essentially an adaptation that ensures a sufficiently high probability of glochidial contact with appropriate fish hosts to maintain adequate juvenile recruitment rates. Accordingly, those species producing conglutinates that resemble fish host prey items have a higher probability of glochidial–host contact and, thus, produce fewer and larger glochidia. *M. margaritifera* releases very small, free-living glochidia and has extraordinarily high fecundities (up to 17,000,000 glochidia/female) (Young and Williams 1984b), while species with conglutinates mimicking host prey items have much lower fecundities (200,000–400,000 glochidia/female) and larger glochidia (Kat 1984).

Extended life spans, delayed maturity, low effective fecundities, reduced powers of dispersal, high habitat selectivity, poor juvenile survival and extraordinarily long turnover times make unionaceans highly susceptible to human perturbations. Because of these life-history traits (particularly long life spans and low effective fecundities), unionacean populations do not recover rapidly once decimated by pollution or other human-mediated habitat disturbances (see Section III.A). Successful settlement of juveniles appears to be particularly affected by such disturbance, with population age–size structures marked by periods when entire annual generations are not recruited (Bauer 1983, Negus 1966, Payne and Miller 1989). Disturbance-induced lack of juvenile recruitment raises the specter of many North

American unionacean populations being composed of slowly dwindling numbers of long-lived adults destined for extirpation as pollution or other disturbance prevents juvenile recruitment to aging populations.

2. *Sphaeriidae*

The Sphaeriidae display great intra- and interspecific variation in life-history characteristics (for reviews see Burky 1983, Holopainen and Hanski 1986, Mackie 1984, Way 1988). Like unionaceans, their life-history traits do not fall neatly into suits associated with life in either stable or unstable habitats. Instead, they are a mixed bag, including the short life spans, early maturity, small adult size, and increased energetic input to reproduction associated with adaptation to unstable habitats, and the slow growth, low fecundity, and release of extremely large, fully developed young associated with adaptation to highly stable habitats (Sibly and Calow 1986) (Table 11.2). Sphaeriids are very euryoecic, with some members inhabiting stressful habitats such as periodically drying ephemeral ponds, and small streams prone to flash flooding and drying while others live in highly stable, profundal lake habitats (Burky 1983). [Here I attempt to generalize the life-history traits of sphaeriids within adaptive and evolutionary frameworks. However, the degree of inter- and intraspecific life-history variation within this group is such that for every generality drawn, specific exceptions can be cited.]

Of prime importance in understanding sphaeriid life-history traits is their ovoviviparous mode of reproduction. All species brood developing embryos in specialized brood chambers formed from evaginations of the exhalant side of the inner demibranch gill filaments. Maternal nutrient material is supplied to embryos developing in marsupia allowing considerable growth during development and release as fully formed miniature adults (see Section II.B.5). Thus, even though the sphaeriids have the smallest adult sizes of all North American freshwater bivalves, they release, by far, the largest young (Mackie 1984, Burky 1983). Based on data for 13 species, average birth shell length in sphaeriids ranges from 0.6–4.15 mm (Burky 1983, Holopainen and Hanski 1986, Hornbach and Childers 1986, Hornbach *et al.* 1982, Mackie and Flippance 1983a) making them much larger than unionacean glochidia (0.05–0.4 mm), juveniles of *C. fluminea* (0.25 mm), or veliger larvae of *D. polymorpha* (0.04–0.07 mm) (Table 11.2). Based on these shell length values, newborn sphaeriids have 3.4 to $2.1(10^5)$ times greater biomass than recently hatched individuals of other groups. Ratios of maximum adult shell length : birth shell length (adult SL : birth SL) in sphaeriids range from 2.8 : 1 to 5.4 : 1, suggesting that newly released juveniles have biomasses that are 0.6–4.6% of the maximum adult biomass. There is a significant direct relationship between these two parameters, shown in Fig. 11.18.

The extremely large size of their offspring greatly reduces the fecundity of sphaeriids. Published values for average clutch sizes range from 3–24 young/adult for *Sphaerium*, 2–136 young/adult for *Musculium*, and 1.3–16 young/adult for *Pisidium* (Burky 1983, Holopainen and Hanski 1986). Even with reduced fecundity, the biomass of the large juveniles produced requires allocation of relatively larger amounts of nonrespired energy for reproduction ($\bar{x} = 19\%$, for a review see Burky 1983) compared to either unionaceans (< 14.8%), *C. fluminea* (15%), or *D. polymorpha* (4.9%) (Table 11.2). As developing juveniles have relatively high metabolic rates (Burky 1983, Hornbach 1985, Hornbach *et al.* 1982) and are supported by energetic transfer from adults (Mackie 1984), estimates of reproductive costs based solely on biomass of released juveniles

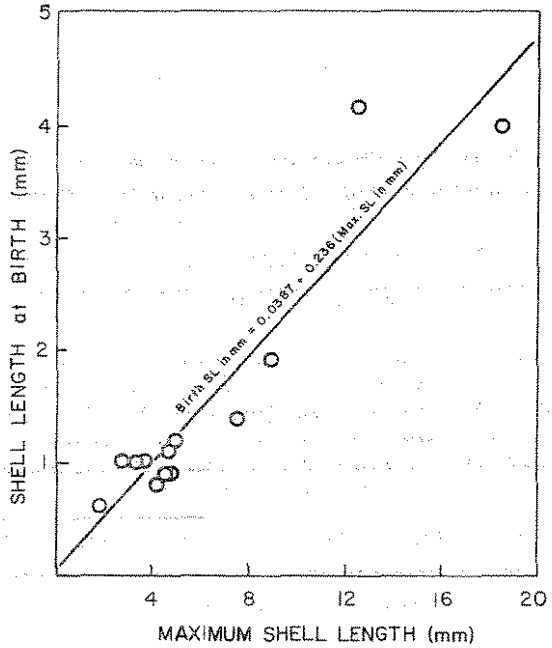


Figure 11.18 The relationship between shell length (SL) of juveniles at birth and maximal SL of adults for 13 species of sphaeriid freshwater clams. Note that juvenile birth length increases linearly with maximal adult size, suggesting that adult size may limit juvenile birth size in sphaeriids. The solid line represents the best fit of a linear regression relating birth size to maximal adult size as follows: Birth SL in mm = 0.0387 + 0.236 (maximal adult SL in mm) ($n = 13$, $r = 0.935$, $F = 76.3$, $P < 0.0001$). [Data from Holopainen and Hanski (1986), Hornbach and Childers (1986), Hornbach *et al.* (1982), and Mackie and Flippance (1983a).]

may be gross underestimates of actual costs in this group.

Life history hypotheses would predict the low fecundity and large birth size characteristic of sphaeriids to be adaptations maximizing fitness in stable habitats. However, the majority of sphaeriid species inhabit highly variable small ponds and streams or the profundal portions of large lakes subject to summer episodes of prolonged hypoxia (Burky 1983, Holopainen and Hanski 1986). Burky (1983) and Way (1988) have argued that while such habitats appear unstable, the harsh conditions associated with them are seasonally predictable, making them, in reality, stable. Thus, sphaeriid species inhabiting them have evolved adaptations preventing catastrophic population reductions during seasonally predictable epidoses of environmental stress (see Section II.C). This allows populations to reach carrying capacity and has lead to selection of life-history adaptations generally associated with the intense intraspecific competition that is characteristic of life in stable habitats.

Seasonal episodes of water level fluctuation and hypoxia can more severely impact smaller individuals. Thus, production of large, well-developed juveniles by sphaeriids may increase their probability of surviving predictable epidsodes of environmental stress. As such stresses can cause high adult mortality (Burky *et al.* 1985b, Holopainen and Jonasson 1983, Hornbach *et al.* 1982, Jonasson 1984b), fitness would also be increased by devoting greater proportions of nonrespired assimilation to production of greater numbers of young in any one reproductive effort, as chances of adult survival to the next reproduction are low. Thus, sphaeriids as a group devote relatively higher proportions of energy to reproduction than do other freshwater bivalves (Burky 1983) (Table 11.2). This combination of *r*-selected and K-selected traits, allowing optimization of fitness in habitats subject to periodic, predictable stress as displayed by sphaeriids, is a life-history strategy referred to as bet hedging (Stearns 1977, 1980).

The early maturation that is characteristic of many sphaeriid species (Burky 1983, Holopainen and Hanski 1986) (Table 11.2) is also adaptive, as it allows reproduction to occur before onset of seasonal episodes of environmental stress. This trait is displayed by sphaeriid species inhabiting ephemeral ponds and streams. These species are characterized by rapid growth, early maturity, and reduced numbers of reproductive efforts. Thus, *Musculium lacustre, Pisidium clarkeanum,* and *P. annandalie* from temporary drainage furrows in Hong Kong live less than one year and have only one or two reproductive efforts (Morton 1985, 1986). An ephemeral pond population of *Musculium partumeium* had a life span of one year, was semelparous, reproduced just prior to pond-drying, and devoted a relatively large proportion of nonrespired assimilation (18%) to reproduction (Burky *et al.* 1985b). Ephemeral pond populations of *M. lacustre* are similarly univoltine and semelparous, devoting 19% of nonrespired energy to reproduction (Burky 1983). *Sphaerium striatinum,* in a population subject to periodic stream flooding, had life spans of one year or less and reproduced biannually (Hornbach *et al.* 1982), devoting 16.1% of nonrespired assimilation to reproduction (Hornbach *et al.* 1984a). In contrast, when populations of these species occur in more permanent habitats, they become bivoltine, reproducing in both spring and fall. Spring generations are iteroparous and reproduce in the fall and following spring; whereas fall generations are semelparous and reproduce only in the spring (Burky 1983, Burky *et al.* 1985b).

Some species of *Pisidium* live in the deeper, profundal portions of larger, more permanent lentic habitats where they are subjected to hypoxia after formation of a hypolimnion. A number of *Pisidium* species tolerate these hypoxic periods (see Section II.C.3, Burky 1983, Holopainen 1987, Holopainen and Hanski 1986, Holopainen and Jonasson 1983). As profundal species are tolerant of prolonged hypoxia, such environments are more stable than small ponds and streams, although they are far less productive, reducing food availability (Holopainen and Hanski 1986). Thus, sphaeriid populations in profundal habitats display much different life-history strategies than those in small ponds and streams (Burky 1983, Holopainen and Hanski 1986). Profundal populations display reduced growth rates, longer life spans of 4–5 yr, delayed maturation often exceeding one year, high levels of interoparity, and univoltine reproductive patterns (Holopainen and Hanski 1986), all life-history traits characteristic of more stable habitats (Sibly and Calow 1986). However, shallow-water and profundal populations of the same species of *Pisidium* may display quite different life-history tactics. Compared to profundal populations, shallow-water populations of the same species grow more rapidly, mature earlier, have shorter life spans, and tend toward semelparity (Holopainen and Hanski 1986), all life-history traits associated with unstable habitats (Sibly and Calow 1986). As pisidiids have well-developed dispersal capacities, it is unlikely that the broad variation in the life-history tactics of populations of the same species occupying different habitats primarily results from genetic adaptation to specific microhabitats. Rather, the majority of such variation is likely to represent environmentally induced, nongenetic, ecophenotypic plasticity. This wide inter- and intrapopulation plasticity in life-history traits is reflected in the highly variable turnover times reported for sphaeriids (27–1972 days, Table 11.2).

The growth rates of freshwater bivalves are highly dependent on ecosystem productivity. Populations from productive habitats have greater levels of assimilation and thus allocate greater absolute amounts of nonassimilated energy to growth (Burky 1983). Shallow, freshwater habitats are usually highly productive, warm, and rarely oxygen-limited; therefore, they support higher growth rates. Conversely, profundal environments are less productive, cooler, and often oxygen-limited, leading to lower bivalve growth rates. Since sphaeriids mature to a species-specific size irrespective of growth rate (Burky 1983, Holopainen and Hanski 1986), rapid growth leads to early maturity in shallow-water habitats and slow growth to delayed maturity in profundal habitats. Sphaeriids also have species-specific terminal sizes at which individuals die whether that size is attained rapidly or slowly. As growth rate determines the time required to reach terminal size, fast-growing individuals from shallow water habitats reach terminal sizes more rapidly (often within less than one year) allowing participation in only one or two reproductive efforts, while slow-growing individuals from profundal habitats (Holopainen and Hanski 1986) reach terminal size more slowly, allowing participation in a greater number of reproductive efforts.

This fundamentally ecophenotypic nature of intraspecific life-history variation in sphaeriids has been demonstrated for *Pisidium casertanum*. When individuals of this species were reciprocally transferred between two populations with different life-history traits or co-reared under similar laboratory conditions, the majority of life-history trait differences proved to be environmentally induced. However, electrophoresis indicated genetic differences between the populations and transfer and laboratory co-rearing experiments indicated that a small portion of the observed life-history variation could be genetically based (Hornbach and Cox 1987).

Such extensive capacity for ecophenotypic plasticity may account for the euryoecic nature and cosmopolitan distributions of sphaeriids (see Section III.A). Certainly, the capacity to adjust growth rates, maturity, reproductive cycles, life cycles, and energetic allocation patterns to compensate for broad habitat variation in biotic and abiotic factors allows species in this group to have relatively wide niches and thus broad distributions.

3. *Corbicula fluminea*

The introduced Asian freshwater clam, *Corbicula fluminea*, unlike unionaceans and sphaeriids, displays life-history traits clearly adapted for life in unstable, unpredictable habitats (McMahon 1983a). As such, it has been the most invasive of all North American freshwater bivalve species. *C. fluminea* grows very rapidly, in part because it has higher filtration and assimilation rates than other bivalve species (Foe and Knight 1986a, Lauritsen 1986a, Mattice 1979). In a natural population, only a relatively small proportion of assimilation (29%) was devoted to respiration (Table 11.2), the majority (71%) being allocated to growth and reproduction (Aldridge and McMahon 1978). These data were confirmed by laboratory studies showing that 59–78% (Lauritsen 1986a) or 58–89% of assimilation (Foe and Knight 1986a) went to tissue production. Thus, *C. fluminea* has the highest net production efficiencies recorded for any freshwater bivalve species, which is reflected by its very low turnover times, ranging from 73–91 days (Table 11.2).

The very high proportion of nonrespired assimilation (85–95%) devoted to growth in *C. fluminea* (Aldridge and McMahon 1978, Long 1989), sustains high rates of growth (shell length = 15–30 mm in the first year of life, 35–50 mm in the terminal third to fourth year) (McMahon 1983a). High growth rates decrease the probability of predation, as many fish and bird predators feed only on small individuals (McMahon 1983a; see also Section III.C.3) and, thus, increase the probability of survival to the next reproduction in this iteroparous species. Indeed, the increase in shell size occurs at the expense of tissue production during summer maximal growth periods (Long 1989), suggesting that larger shells optimize fitness. The high growth rates of *C. fluminea* allow it to sustain the highest population production rates (10.4–14.6 g organic carbon/m^2 yr, Aldridge and McMahon 1978) reported for any species of freshwater bivalve (Burky 1983).

Newly released juveniles are small (shell length = 250 μm) but completely formed, having a well-developed and characteristically D-shaped bivalved shell, adductor muscles, foot, statocysts, gills, and digestive system (Kraemer and Galloway 1986) (Fig. 11.15A). As juveniles are denser than water, they settle and anchor to sediments or hard surfaces with a mucilaginous byssal thread. However, they are small enough (0.25 mm) to be suspended on turbulent water currents and dispersed great distances downstream (McMahon 1983a). A relatively low amount of nonrespired assimilation is allocated to reproduction (5–15%, Aldridge and McMahon 1978, Long 1989), equivalent to that expended by unionids but less than the average expended by sphaeriids (19%, Table 11.2). However, the elevated assimilation rates of this species allow allocation of higher actual values of energy to reproduction than occur in other freshwater bivalves.

Because the juvenile of *C. fluminea* is small (organic carbon biomass = 0.136 μg, Long 1989), fecundity is large, ranging from 97–570 juveniles/adult/day during reproductive seasons, for an average annual fecundity estimate of 68,678 juveniles/adult/yr (McMahon 1983a). Juvenile surivorship to successful settlement is extremely low and mortality rates remain high throughout adult life (74–98% in the first year, 59–69% in the second year, and 93–97% in the third year of life, computed from the data of McMahon and Williams 1986a, Williams and McMahon 1986), making the vast majority of individuals in populations juveniles and immatures. High adult mortality and population dominance by immature individuals is characteristic of species adapted to unstable habitats (Charlesworth 1980, Sibly and Calow 1986, Stearns 1980).

The majority of North American *C. fluminea* populations display two annual reproductive periods, one in spring and early summer and the second in late summer (McMahon 1983a). *C. fluminea* is hermaphroditic and capable of self-fertilization (Kraemer and Galloway 1986, Kraemer *et al.* 1986) such that single individuals can found a new population. Spermiogenesis occurs only during reproductive periods, but gonads contain mature eggs throughout the year (Kraemer and Galloway 1986, Long and McMahon 1987).

C. fluminea matures within 3–6 months at a small shell length of 6–10 mm (Kraemer and Galloway 1986). Thus, juveniles born in the spring may grow to maturity and participate in the reproductive effort the following fall (Aldridge and McMahon 1978, McMahon 1983a) (Table 11.2). The maximum life span is highly variable between populations and temporally within populations, ranging from 1–4 yr (McMahon 1983a, McMahon and Williams 1986a). Early maturity allows individuals of this iteroparous species to participate in 2–7 reproductive efforts, depending on life span.

The relatively short life span, early maturity, high fecundity, bivoltine juvenile release patterns, high growth rates, small juvenile size, and capacity for downstream dispersal of *C. fluminea* makes it both highly invasive and well adapted for life in truly unstable, disturbed lotic habitats that are subject to unpredictable catastrophic faunal reductions. Its extremely high reproductive potential and growth rates allow it to reach or re-establish high densities after invading a new habitat or after catastrophic population declines. Thus, it is highly successful in North American drainage systems that are subjected to periodic human interference such as channelization, navigational dredging, pearling, sand and gravel dredging, commercial and/or recreational boating, and organic and/or chemical pollution, compared to far less resilient unionaceans or sphaeriids (McMahon 1983a).

Surprisingly, *C. fluminea* is more susceptible to environmental stresses such as temperature extremes, hypoxia, drying, and low pH than are most sphaeriids and unionaceans (Byrne 1988, Byrne *et al.* 1988, Kat 1982, McMahon 1983a), making its populations more susceptible to declines from human disturbance. With only a limited capacity to tolerate unpredictable environmental stress, why is *C. fluminea* so successful in disturbed habitats? The answer lies in its ability to recover from disturbance-induced catastrophic population crashes much more rapidly than either sphaeriids or unionids. *C. fluminea* rapidly re-establishes populations even if disturbance has reduced them to a few widely separated individuals, as all individuals are hermaphrodites capable of self-fertilization and have high fecundities. Downstream dispersal of juveniles from viable upstream populations also allows rapid reinvasion of decimated populations. After juvenile reinvasion of depauperated populations, the accelerated growth, high fecundity, and relatively short life spans of this species allows rapid population re-establishment, including normal age–size distributions and densities within 2–4 years (for examples see McMahon 1983a). Biannual reproduction in *C. fluminea* also increases the probability of surviving catastrophic density reductions, as it prevents loss of an entire generation to a chance environmental disturbance (bet hedging, Stearns 1980). The capacity for rapid recolonization of habitats from which populations have been extirpated allows *C. fluminea* to sustain populations in substrata that are subject to periodic scouring during floods; the slower growing and maturing unionids are eliminated from such habitats (Way *et al.* 1990a).

Like sphaeriids, North American *C. fluminea* populations display an extraordinary degree of interpopulation variation in life-history traits. As there is little or no genetic variation among North American populations (McLeod 1986), this interpopulation life-history variation must be ecophenotypic. Growth rates increase and time to maturity and life spans decrease in populations from more productive habitats (McMahon 1983a). On the northern edge of its North American range, low temperatures reduce growth and reproductive periods, making populations univoltine rather than bivoltine in reproduction. I have observed univoltine reproduction and semelparity in a slow-growing population of *C. fluminea* within an oligotrophic Texas lake. Even within populations, life-history tactics vary greatly, dependent on year-to-year variations in temperature and primary productivity (McMahon and Williams 1986a, Williams and McMahon 1986). As in sphaeriids, the capacity for substantial ecophenotypic life-history trait variation is highly adaptive in *C. fluminea*, as it allows colonization of a broad range of habitats. Being at once highly euryoecic and highly invasive has made it the single most successful and economically costly aquatic animal species introduced to North America (Isom 1986).

4. *Dreissena polymorpha*

The zebra mussel, *Dreissena polymorpha*, is the most recently introduced bivalve species to North American freshwaters (Hebert *et al.* 1989). Like *C. fluminea*, many of its life-history characteristics (reviewed in Mackie *et al.* 1989) make it highly invasive. Unlike all other North American bivalve species, it releases sperm and eggs to the surrounding medium such that fertilization is completely external. A free-swimming planktonic veliger larva (Fig. 11.15C) hatches from the egg and remains suspended in the water column where it feeds and grows for 8–10 days before settling to the substratum. This behavior enhances the dispersal ability of the zebra mussel. Adults attached to floating objects by the byssus can also be transported long distances downstream. Adults become sexually mature in the second year of life (first year in some North American populations) and typically have life spans ranging from 5–6 yr and, like *C. fluminea*, sustain high growth rates throughout life (Fig. 11.19). *Dreissena polymorpha* is iteroparous and univoltine; an individual participates in 3–4 annual reproductive periods over the course of its life. The egg and freshly hatched veliger are small (diameter = 40–70 μm), but the post-veliger grows to 180–290 μm just prior to settlement and juvenile metamorphosis (Mackie *et al.* 1989), indicative of a 100–400 fold increase in biomass during planktonic growth.

Maximal *D. polymorpha* adult size ranges from 3.5–5 cm depending on growth rate, which, like terminal size, is dependent on the primary productivity and temperature of the habitat. Like *C. fluminea*, *D. polymorpha* allocates an extremely high percentage (96.1%) of nonrespired assimilation to somatic growth, leaving only 3.9% for reproduction (Mackie *et al.* 1989) (Table 11.2). Allocation of a large proportion of nonrespired assimilation to growth allows individuals to rapidly increase in size, making them more competitive and less subject to predation (Sibly and Calow 1986). Zebra mussel veligers settle on the shells of established individuals, forming thick mats or clusters of individuals many shells deep (Mackie *et al.* 1989). In such mats, competition for space and food are very intense. Thus, rapid growth of an individual to a large size is highly adaptive as it increases the probability of development of a stable byssal holdfast to the substratum and the positioning of siphons at the mat surface, where food and oxygenated water are most available. In spite of the low levels of energy devoted to reproductive effort by *D. polymorpha*, its very small eggs make individual fecundity large, ranging from 30,000–40,000 eggs/female.

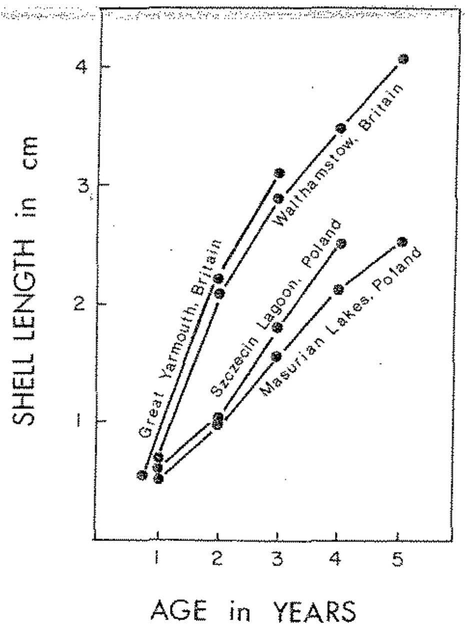


Figure 11.19 Shell growth rates in European populations of the zebra mussel, *Dreissena polymorpha*. (Redrawn from Morton 1969.) Growth rates in North American populations in Lake Erie are similar to or faster than those depicted here for fast-growing British populations.

Dreissena polymorpha population densities range from 7000–114,000/m^2 and standing crop biomasses from 0.05–15 kg/m^2 (Mackie *et al.* 1989). The high population densities and biomass result from the tendency of juveniles to settle on substrata already inhabited by adults. Also, adults attach to the shells of other adults by the byssus to form dense mats or clumps that are many layers of individuals thick. High individual growth rates and population densities lead to very high population productivities, estimated to be 0.05–14.7 g C/m^2/yr (computed from dry tissue values in Mackie *et al.* 1989), values comparable to those of highly productive *C. fluminea* populations. However, as population growth and

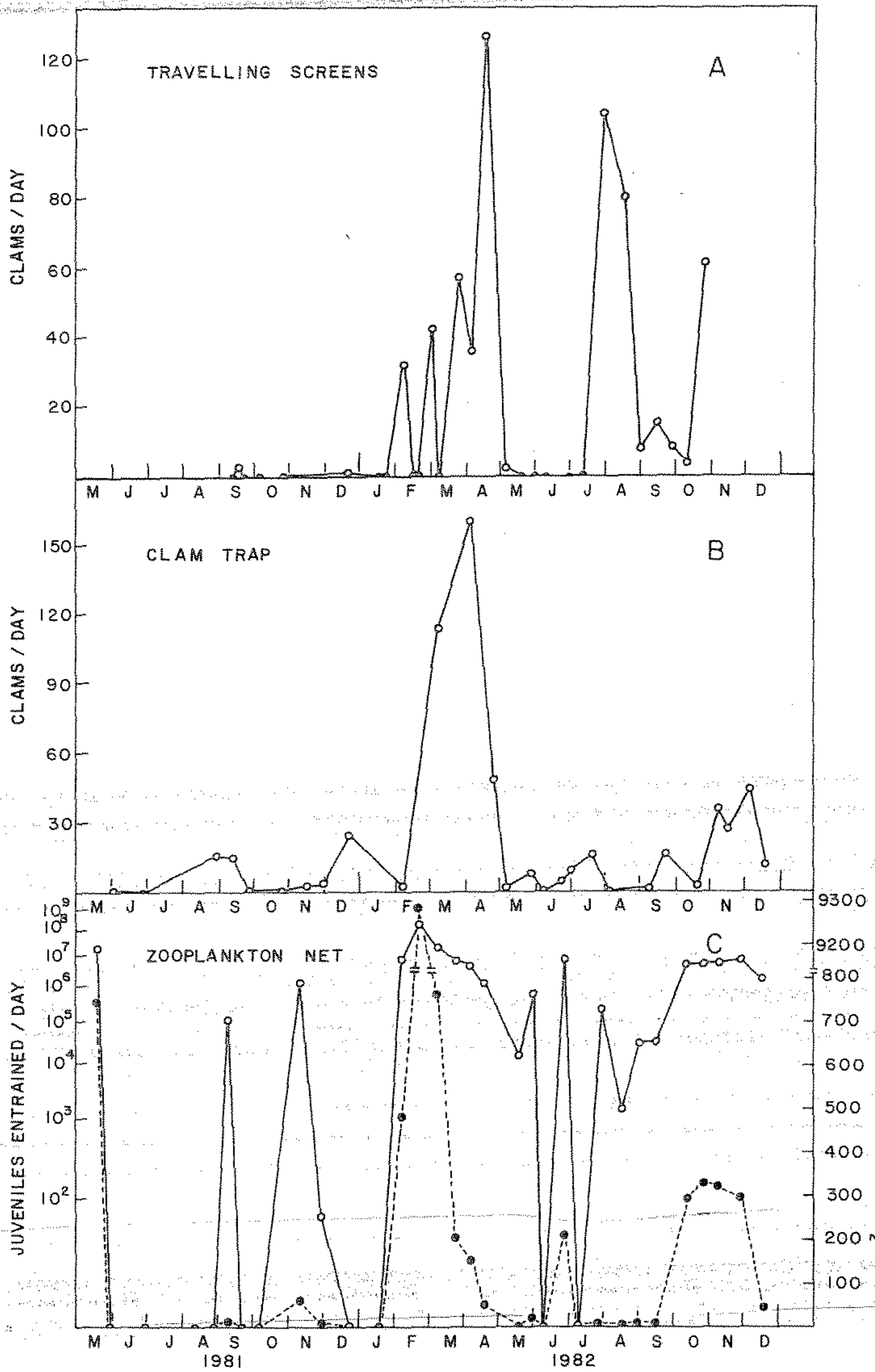


Figure 11.20 Seasonal variation in downstream dispersal behavior by juvenile, subadult, and adult *Corbicula fluminea* in the intake canal of a power station. (A) Rate of impingement of adults dispersing downstream onto traveling screens in front of water intake embayments (shell length > 10 mm). (B) Rate of retention of subadults (shell length = 1–7 mm) in a clam trap held on the substratum surface of the intake canal. (C) Juveniles suspended in the water column (shell length < 2 mm). Right ventrical axis is density of juveniles in the intake

productivity are highly habitat-dependent in this species, turnover times are variable, ranging from extremely low values of 53 days to relatively high values of 869 days (Table 11.2).

The life-history traits of a high growth rate throughout life, high fecundity, short life spans, and the capacity for both adult and larval stage downstream dispersal make *Dreissena* (like *Corbicula*) a highly invasive species. However, unlike *C. fluminea*, *D. polymorpha* populations tend to be restricted to much more stable habitats such as larger, permanent lakes and rivers. Its apparent preference for more stable habitats is reflected by its original distribution in the Caspian Sea and Ural River (large stable habitats), avoidance of shallow, near-shore habitats, relatively long age to maturity (generally in the second year of life), iteroparity, gonochorism, and relatively high adult survivorship (26–88% per year) (Mackie *et al.* 1989).

Restriction of its original range to the Caspian Sea and Ural River also suggests a limited natural capacity for dispersal between isolated drainage systems. Dispersal of the species through Europe occurred only in the nineteenth century (and continues in western Asia today). This recent dispersal was accomplished primarily by human vectors, including transport of adults attached to boat hulls, ballast water dumping, and transport of veligers through canal systems interconnecting catchments. Adults have a relatively low tolerance to prolonged air exposure (Mackie *et al.* 1989), precluding extensive natural overland dispersal unless it is human-mediated. Thus, the future dispersal of this species between catchments in North America will be primarily by human vectors, with larger, permanent bodies of water most susceptible. Without natural dispersal vectors, dispersal of *D. polymorpha* through North American drainages may proceed at a somewhat slower pace than that recorded for *C. fluminea*, but human activities will ensure that this species will eventually be widely distributed in North American freshwaters.

C. Ecological Interactions

1. Behavioral Ecology

Other than detailed studies of burrowing (see Section II.A.2), information on bivalve behavior is sparse. Indeed, a recent major review of molluscan neurobiology and behavior (Willows 1985, 1986) was entirely devoid of bivalve references. Lack of information about bivalves reflects the difficulties associated with making behavioral observations on predominantly sessile, infaunal species completely surrounded by a shell, rather than a lack of complex and intriguing behaviors.

A number of interesting behaviors are associated with reproduction in freshwater bivalves, including those involved with ensuring glochidial contact with fish hosts in unionaceans (see Section II.B). Adult *C. fluminea* display unique downstream dispersal behavior associated with reproductive periods. While juvenile clams (SL < 2 mm) are found suspended in the water column throughout the year, immatures (SL $= 2$–7 mm) and adults (SL > 7 mm) leave the substratum to be carried passively downstream over the sediment surface ("rolling") on water currents only prior to reproductive periods (Fig. 11.20). Dispersing adults have lower dry tissue weights, lower tissue organic carbon to nitrogen ratios (Williams and McMahon 1989), higher levels of ammonia excretion, and reduced molar oxygen consumption to nitrogen excretion ratios than those remaining in the substratum (Williams 1985, Williams and McMahon 1985), which are indicative of poor nutritional condition. Thus, downstream dispersal allows starving individuals to move away from areas of low food availability and high intraspecific competition into areas more nutritionally favorable for reproductive efforts (Williams 1985, Williams and McMahon 1986, 1989).

Some adult unionacean bivalves and *C. fluminea* display surface locomotory behavior. Surface locomotion involves the same movements of the foot and valves described in Section II.B.2 for burrowing but is horizontal rather than vertical. Indeed, surface locomotion by unionaceans is fairly common (Imlay 1982). Tracts left in sediments by surface locomoting uninaceans are 3–10 m long (Golightly 1982), indicative of major short-term horizontal displacement. The adaptive significance of surface locomoation through sediments in freshwater bivalves is not well understood. Such behavior could attract potential predators. However, it may be involved with pedal feeding on organic sediment deposits (for details see Section III.C.2).

canal water column (solid circles connected by dashed lines). Left vertical axis is number of juveniles entrained daily with intake water (open circles connected by solid lines). Note that adult and subadult clams display significant downstream dispersal behavior during only two periods, March–May and July–August just prior to the spring and fall reproductive periods of the population (April–July and September–November). Juveniles occurred in the water column throughout the year; peak juvenile water column densities occurred during reproductive periods and midwinter periods of low ambient water temperature. (From Williams and McMahon 1986.)

Some species, such as *Anodonta grandis*, migrate vertically on the shore with seasonal changes in water level (White 1979), thereby avoiding prolonged emersion. Other species such as *Uniomerus tetralasmus*, *C. fluminea*, and some sphaeriids remain in position and suffer prolonged emersion during periods of receding water (see Section II.C.4). In Texas, I have observed fire ants, *Solenopsis invincta*, killing bivalves exposed to air by receding water levels. [Hence, this introduced insect species may represent a new threat to unionaceans and sphaeriids throughout its expanding range in the southeastern United States.]

Some sphaeriids, *C. fluminea*, and *D. polymorpha* are also capable of crawling over hard substrata or macrophytes. *Sphaerium corneum* holds the shell valves erect and moves over hard substrata or macrophytes by extending the foot tip, anchoring it with mucus, and then contracting pedal muscles to draw the body forward (Wu and Trueman 1984). Juvenile and young specimens of *C. fluminea* move over hard substrata in the same manner, while adults similarly crawl over hard surfaces lying on one of the valves (Cleland 1988). Small specimens of *D. polymorpha* are highly active crawlers and can climb smooth vertical surfaces. Young individuals of this species routinely discard their byssus and migrate to new positions where they resecrete attachment threads. As an example, juveniles settling in shallow water during the summer may migrate to deeper waters in the winter (Mackie *et al.* 1989).

Freshwater bivalves also detect and respond to a number of external environmental cues. Chief among these responses is valve closure in response to irritating external stimuli. Stimuli for valve closure are likely detected by sense organs concentrated on the mantle edge and the siphons (see Section II.B.6). Valve closure effectively seals internal tissues from the damaging effects of external irritants. Almost all freshwater bivalves tolerate some degree of facultative anaerobiosis (see Section II.C.3). Thus, individuals exposed to irritants can remain anaerobic with the valves clamped shut for relatively long periods until external conditions become more favorable. Freshwater bivalves close the valves on exposure to heavy metals (Doherty *et al.* 1987), chlorine, and other biocides (Mattice 1979, Mattice *et al.* 1982, McMahon and Lutey 1988), and high levels of suspended solids (Aldridge *et al.* 1987). This ability allows *C. fluminea* to avoid intermittent exposure to chlorination or other biocides, making chemical macrofouling control of this species extremely difficult (Goss *et al.* 1979, Mattice *et al.* 1982). Valve closure in immediate response to tactile stimulation of the mantle edge or siphons is also a predator defense mechanism common to all freshwater species.

Also of interest are the reactions of freshwater bivalves to prolonged emersion. The physiological adaptations to emersion are discussed in Section II.C.4). Here, behavioral responses are described in greater detail. *C. fluminea*, when exposed in air, displays four major responses: (1) escape behavior involving extending the foot in an attempt to burrow; (2) valves gaped widely with mantle edges parted, opening the mantle cavity directly to the atmosphere; (3) valves narrowly gaped with mantle edges exposed, but cemented together with mucus; and (4) valves clamped shut. Behaviors (1) and (2) are never displayed more than 6% of the time in air. Exposure of sealed mantle edges is associated with aerial gas exchange (Byrne 1988, McMahon and Williams 1984), but results in evaporative water loss. When valves are closed, water loss is minimized; but oxygen uptake ceases (Byrne *et al.* 1988, McMahon and Williams 1984). As temperature increases (Table 11.3) or relative humidity decreases, duration of mantle edge exposure decreases relative to that with the valves clamped shut (Byrne 1988, Byrne *et al.* 1988, McMahon, 1979b). Hence, behaviors associated with water loss are reduced in response to increased desiccation pressure. Indeed, relative humidities near zero or temperatures above 30°–35°C cause the valves to remain continually closed (Byrne 1988, Byrne *et al.* 1988, McMahon 1979b) (Table 11.3), preventing excessive water loss but making individuals continually anaerobic. I have observed similar behaviors in emerged unionaceans. Some species plug the siphons with mucus to further reduce water loss and spend less time with the mantle edges exposed than does *C. fluminea*. Ability of emersed individuals to adjust behaviors associated with aerobic gas exchange to external dessication

Table 11.3 The Effects of Temperature on the Percentage of Time Spent in Various Valve Movement Behaviors in Emerged Specimens of *Corbicula fluminea*[a]

Temperature (°C)	Time with Valves Closed (%)	Time with Mantle Edge Exposed (%)	Time with Mantle Edge Parted or Attempting to Burrow (%)
15	29.5	65.8	4.7
25	51.2	43.5	5.3
35	90.5	9.1	0.4

[a] From Byrne (1988).

pressures is a complex behavior, requiring the capacity to sense, integrate, and respond to external temperature and relative humidity levels and internal osmotic concentration. Certainly, the capacity for such behaviors is worthy of further experimental investigation.

Freshwater bivalves may also have as yet undiscovered circadian patterns of behavior. Both ion uptake and oxygen consumption rates are greater during dark than light hours in unionaceans and *C. fluminea* (Graves and Dietz 1980, McCorkle *et al.* 1979, McCorkle-Shirley 1982; see also Section II.C.2), strongly suggesting the presence of circadian-activity patterns in feeding, reproduction, and burrowing. I have recorded increases in the density of juvenile *C. fluminea* in the water column during dark hours, suggesting that adults preferentially release juveniles at night. Freshwater bivalves may have circadian burrowing cycles, retreating more deeply into sediments during light hours to avoid visually oriented predators like fish and birds. These speculations require further investigation.

2. *Feeding*

Most freshwater bivalves primarily feed by filtering suspended material from water as it passes over the gills. The anatomy of bivalve gills is described in Section II.B.2. Water flow across the gills is maintained by the beating of powerful lateral cilia located along each side of the filaments. Projecting laterally from each side of the leading edge of the filament are tufts or cirri of partially fused eulaterofrontal cilia at intervals of 2–3.5 μm (Fig. 11.5A and 11.21). The primary filtering mechanism is composed of eulaterofrontal cirri on adjacent filaments, which project toward each other forming a stiffened grid. Water is driven through this grid by the lateral cilia, and suspended seston (phytoplankton, bacteria, and fine detritus) is retained on the eulaterofrontal cilia. The filtering mechanism probably functions both by forming a filtering mesh and creating eddies in which seston particles settle. The mesh size of the eulaterofrontal cirri (2–3.5 μm) is highly correlated with the size of particles filtered. Particles removed range in size from 1.5–10 μm, with *D. polymorpha* and *C. fluminea* both able to efficiently filter much smaller particles ($\leq 1.0\ \mu$m) than the majority of freshwater species (Fig. 11.22) (Jorgensen *et al.* 1984, Paterson 1984, Way 1989, Way *et al.* 1989).

Some investigators claim that the gill is covered with a fine mucus net acting as the primary filter (for a review see Morton 1983). While the degree to which mucus is involved in the filtering mechanism continues to be debated, there is little doubt that the dense meshwork formed by the eulaterofrontal cilia could act as an effective filter (Morton 1983, Way 1989).

The basal portions of the eulaterofrontal cilia contain stiffening elements, but the free distal ends beat at right angles to the filament axis, apparently driving particles trapped by the eulaterofrontal cirri onto the leading edge of the gill filament. There, particles are carried along bands of frontal cilia running the length of the filament (Figs. 11.5A and 21), either dorsally or ventrally. Particles are deposited in specialized food grooves on the ventral edge of the demibranchs and/or at the base of the gill axis (depending on the species) (Figs. 11.2 and 11.5A–C). In sphaeriids, *C. fluminea*, and presumably unionaceans, the cilia of food grooves are differentiated from other forms of gill ciliation (Way *et al.* 1989). Unique, long frontal cirri of fused cilia beating at a right angle to the long axis of the filaments are also associated with the frontal cilia of sphaeriid and corbiculacean bivalves (Fig. 11.21A,B). Their function has yet to be elucidated (Way *et al.* 1989).

Cilia in the food groove carry filtered particles anteriorly to the labial palps, which are paired triangular flaps located on each side of the mouth (Figs. 11.2 and 11.4). The outer labial palp lies against the outer ventral side of the outer demibranch, and the inner palp, against the inner ventral side of the inner demibranch (Fig. 11.2). The epithelial surfaces of the palps facing away from the demibranchs are smooth. In contrast, the palp surfaces adjacent to the demibranchs are highly corrugated into a series of parallel ridges and channels lying obliquely to the ciliated oral groove that leads to the mouth. The oral groove is formed between the fused dorsal junction of the inner and outer labial palps (Morton 1983). The corrugated palp surface sorts filtered particles into those accepted for ingestion and those rejected. Generally, smaller particles are carried over the upper edges of palp corrugations by cilia beating at right angles to the long axis of the corrugations. Particles carried over palp corrugations are deposited in the oral groove ciliary tract, which carries them to the mouth for ingestion. Denser, larger particles fall between the corrugations where cilia carry them to the ventral edge of the palp. Here, they are bound in mucus and carried by a ciliated ventral groove to the tip of the palp for release onto the mantle as pseudofeces (Morton 1983). Pseudofeces are carried by mantle cilia to accumulate at the base of the inhalant siphon (Fig. 11.2), where they are periodically expelled with water forced violently from the inhalant siphon by rapid valve adduction (i.e., valve clapping) (Morton 1983).

The palps also sort medium-sized particles.

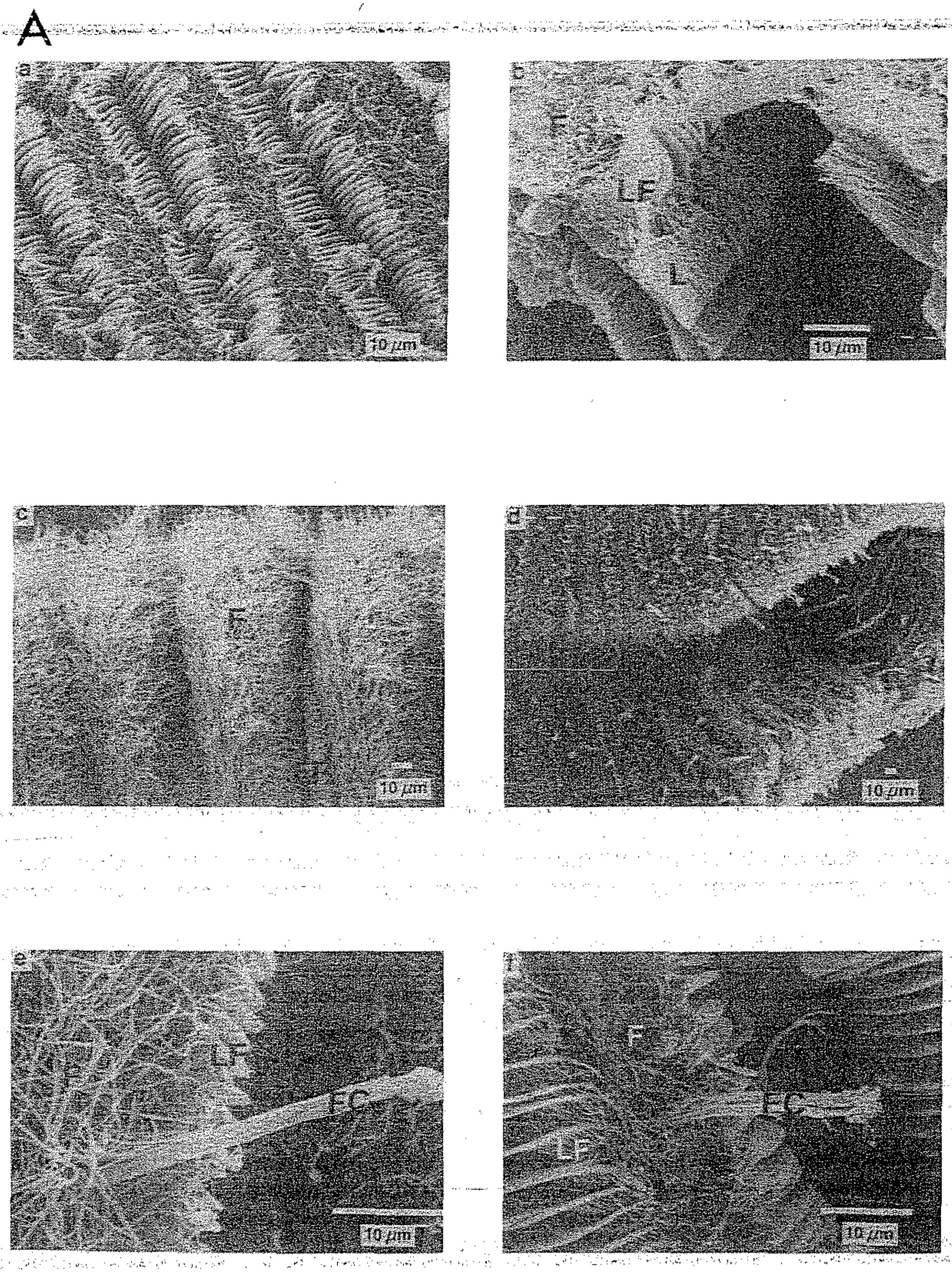
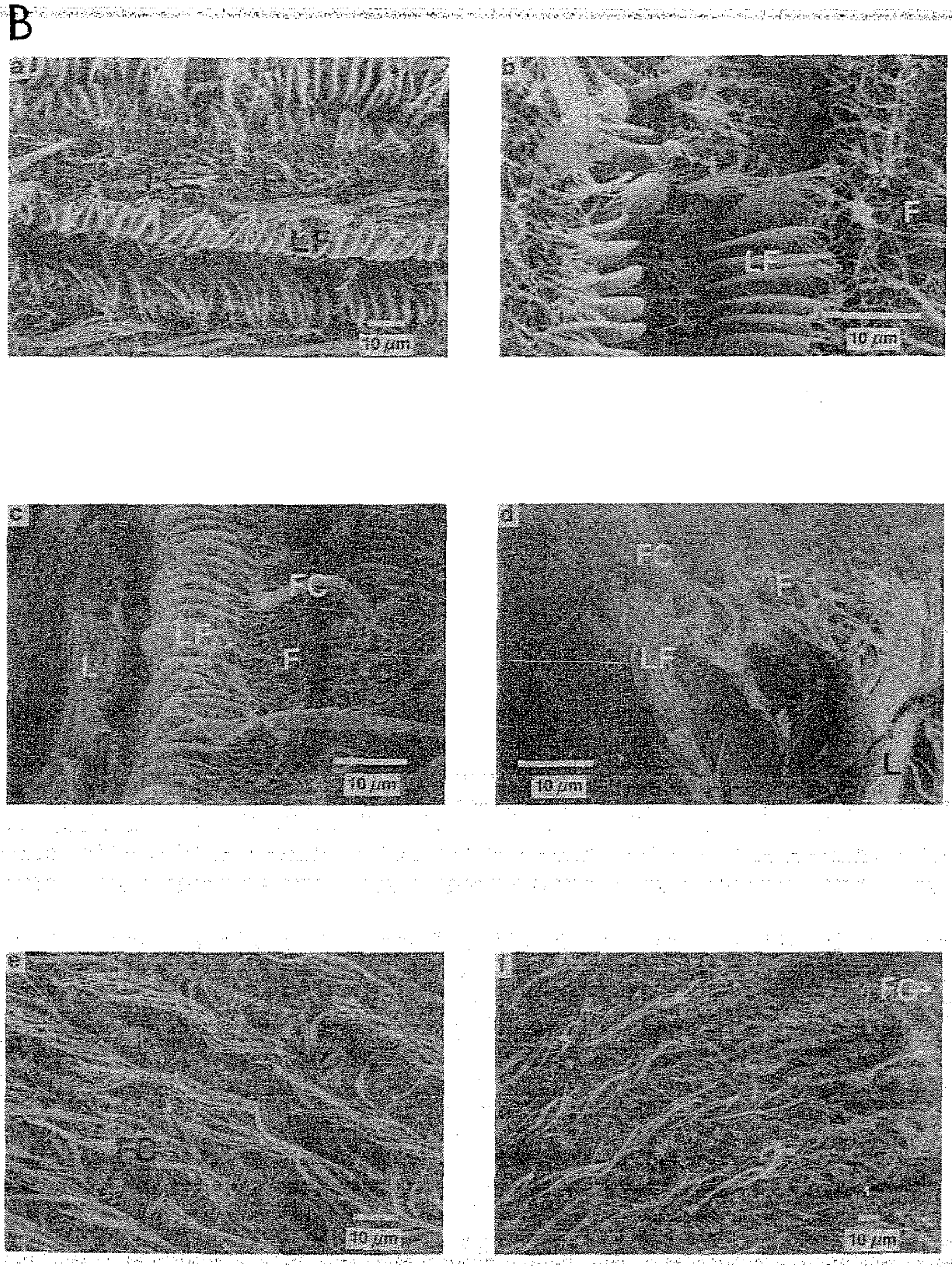


Figure 11.21 Scanning electron micrographs of the gill ciliation of representative freshwater bivalves. (A) *Musculium transversum* (Sphaeriidae): (a) arrangement of frontal and eulaterofrontal ciliation on the leading edges of the filaments in the mid-gill region; (b) oblique view of a cross-sectional fracture of the gill showing frontal and eulaterofrontal cilia on the leading edge of the filament and lateral cilia on the side of the filament; (c) ciliation of the food groove on the ventral edge of the gill; (d) posterior portion of the outer (foreground) and inner (background) demibranchs of the gill, (e) a frontal cirrus formed from fused cilia emerging between the eulaterofrontal and frontal cilia on the leading edge of a filament; (f) a frontal cirrus emerging from a band of



frontal cilia. (B) *corbicula fluminea* (Corbiculidae): (a) leading edge of a gill filament showing frontal, eulaterofrontal, and lateral cilia and frontal cirri; (b) high-magnification view of frontal and eulaterofrontal cilia; (c) oblique view of a longitudinal fracture through the mid-gill region showing all four types of ciliation, including lateral cilia lining the sides of the gill filament; (d) cross-section of the mid-gill region showing the origin of the frontal cirrus; (e) lower region of the gill showing the presence of less well organized frontal cilia; (f) food

(*Figure continues*)

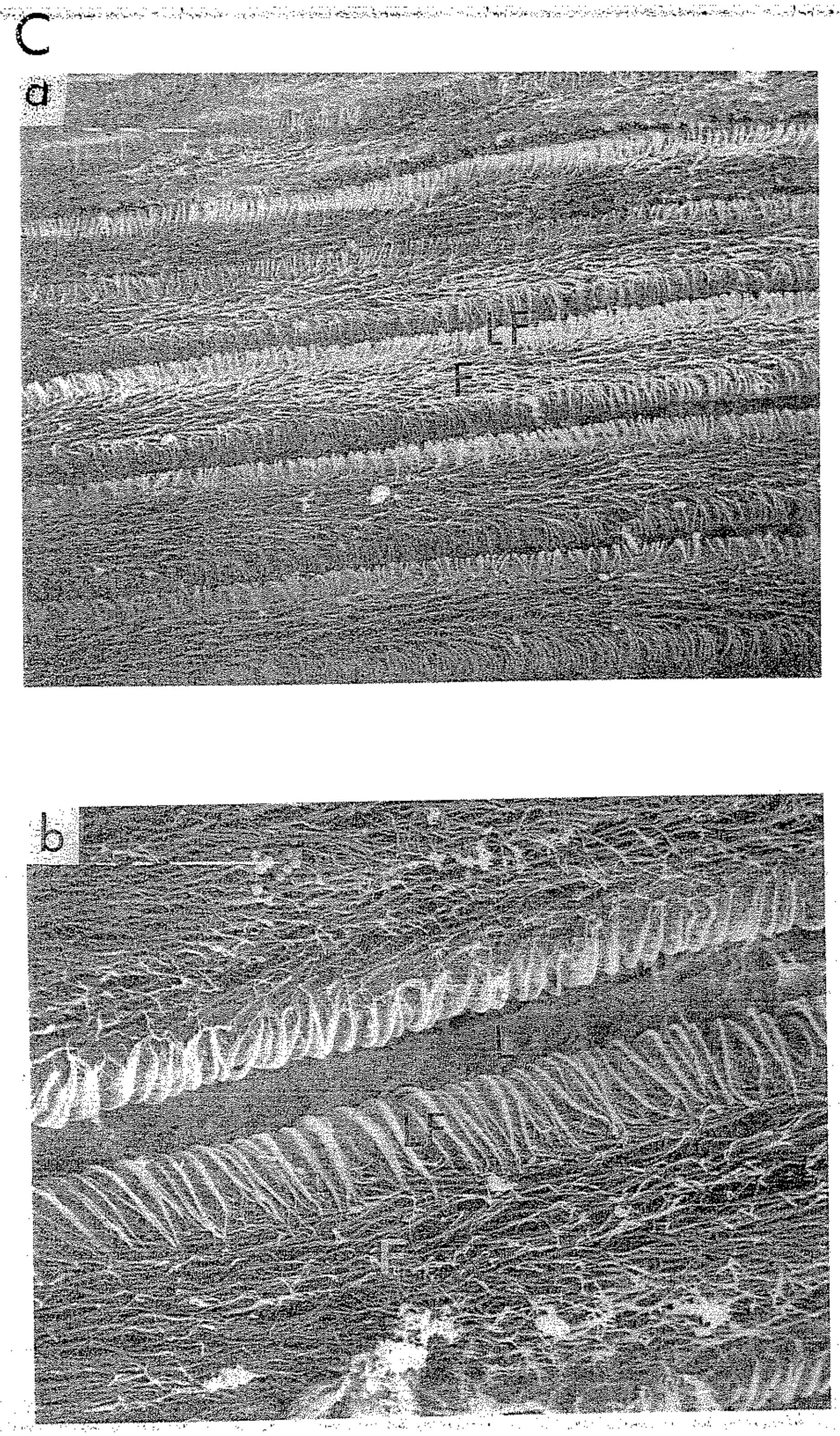


Figure 11.21 (Continued)

groove region at the ventral edge of the inner demibranch; note loss of ciliary organization in food groove, including lack of frontal cirri. (C) *Oliquaria reflexa* (Unionidae): (a) frontal and eulaterofrontal ciliation on the leading edges of several gill filaments (500X); (b) high-power view showing lateral cilia on sides of the gill filaments between tracts of frontal and eulaterofrontal cilia on adjacent filaments. Note lack of frontal cirri characteristic of the gill ciliation of Sphaeriidae (A) and *Corbicula* (B). Label key for all parts is: F, frontal cilia; FC, frontal cirrus; L, lateral cilia; LF, eulaterofrontal cilia; and FG, food groove. (Photomicrographs supplied by Tony Deneka and Daniel J. Hornbach (Macalester College) and Carl M. Way (U.S. Army Corps of Engineers, Waterways Experiment Station).

Smaller medium-sized particles tend to remain longer on the corrugation crests than in the intervening grooves, and eventually reach the oral groove for ingestion. Larger medium-sized particles tend to remain longer in the grooves between corrugations and are eventually rejected as pseudofeces. Thus, particle sorting on the labial palps appears to be strictly a function of particle size and, perhaps, density.

The width of palp corrugations and gill filaments can be adjusted by both muscular activity and degree of hemolymph distension of gill and palp blood sinuses, thus allowing active size selection of particles filtered and accepted for ingestion (Morton 1983). When individuals of the mussel *Elliptio companata* were fed on natural seston, the percentage of particles that were retained declined linearly over a particle size range of 5 μm (nearly 100% retention) to > 10 μm (less than 10% retention), suggesting size selection (Paterson 1984). Similar selection for particles most common in the ambient water column has been reported for *Musculium transversum* (Way 1989) and *C. fluminea* (Way *et al.* 1990b). In addition, different mussel species are reported to select quite different algal types. In the same river pool, a population of *Amblema plicata* ingested a greater proportion of green algae, a lower diversity of algal species, and different algal species compared to a sympatric population of *Ligumia recta* (Bisbee 1984). Such interspecific differences in particle selection may allow sympatric species to avoid intense competition for food resources.

The filtering rate of bivalves can be computed as follows:

$$C = M/t(1\text{n } C_o/C_t)$$

where M = volume of the suspension filtered, t = time of filtration, and C_o and C_t = concentrations of filtered particles at times O and t, respectively (Jorgensen *et al.* 1984). Filtration rates appear to be relatively elevated in *C. fluminea* compared to other freshwater bivalves. For a 25 mm SL specimen, the rate ranged from 300–2500 liter/hr depending on temperature and seston concentration (Foe and Knight 1986b, Lauritsen 1986b, Long 1989, Way *et al.* 1990b). Increased filtration rate may be associated with specialized frontal cirri on the gill filaments of this species (Fig. 11.21B) (Way *et al.* 1989). The filtering rate of specimens of *C. fluminea* fed on nautral seston concentrations was not significantly correlated with field ambient water temperature (Long 1989) and was independent of temperature between 20° and 30°C in the laboratory (Lauritsen 1986b), suggesting an unusual capacity for temperature compensation of gill ciliary filtering activity. The filtration rate is also somewhat independent of temperature in *Sphaerium striatinum* and *Musculium partumeium*, reaching maximal values during spring and fall reproductive periods when ambient water temperatures were well below midsummer highs (Burky *et al.* 1981, 1985a, Way *et al.* 1981).

Above an upper critical limit, high concentrations of suspended particles reduce filtering rates (Burky 1983, Burky *et al.* 1985a, Morton 1983, Way 1989, Way *et al.* 1990b). Increased particle concentration depressed the filtering rate of *S. striatinum* (Hornbach *et al.* 1984b) and *M. partumeium* (Burky *et al.* 1985a) at concentrations well below those of natural seston. In both species, however, rate of particle ingestion becomes nearly constant above the critical particle concentration, suggesting that the observed reduction in filtering rate is associated with control of the ingestion rate. Particle concentrations within ambient seston concentrations do not affect the filtering rate in *C. fluminea* (Mattice 1979, Long 1989); ingestion rates increase directly with concentration (Long 1989). However, the filtration rate in *C. fluminea* declined 3-fold with increasing particle concentration between 0.33 and 2.67 μl algal volume/liter suggesting inhibition at very high concentrations. Increasing algal concentration over this range still resulted in a 3.5-fold rise in ingestion rate (Lauritsen 1986b). Similar reduction in filtration rate at particle concentrations above natural levels has been reported for both *C. fluminea* (Way *et al.* 1990b) and *M. transversum* (Way 1989). In contrast to *C. fluminea*, the filtration rate of the mussel *E. complanta* was depressed by increasing natural seston concentrations (Paterson 1984). The filtration rate varied between different populations of *C. fluminea*, but the amount ingested was highly similar, suggesting regulation of the filtration rate to control ingestion rates (Way *et al.* 1990b). Such data indicate both that the seasonal and environmental responses in filter feeding of freshwater bivalves are species-specific and laboratory measurements of filtration and consumption rates are likely to be invalid unless carried out at natural seston concentrations and sizes.

Suspended silt in the water column can inhibit filtering and consumption rates in freshwater bivalves, perhaps by overwhelming ciliary filtering and sorting mechanisms. Very high levels of suspended silt caused significant reduction in the filtering and metabolic rates of three species of unionaceans whether exposure was infrequent (once every 3 hr or frequent (once every 0.5 hr), suggesting interference with ciliary maintenance of water flow over the gills. Furthermore, those individuals experiencing frequent exposure greatly increased reliance on carbohydrate catabolism (Aldridge *et al.* 1987), a phenomenon symptomatic of short-term starvation (Cleland 1988). For these reasons, unionaceans can be eliminated from habitats with high silt loads (Adam 1986). In contrast, suspended sediments within a naturally occurring concentration range did not affect shell or tissue growth in *C. fluminea* (Foe and Knight 1985). This may account in part for its ability to colonize lotic environments with greater flow rates and levels of suspended solids than are tolerated by most unionacean species (Payne and Miller 1987; see also Section III.A). Surprisingly, growth in juvenile unionaceans was stimulated rather than inhibited in the laboratory by small amounts of suspended silt in their algal food (Hudson and Isom 1984).

In smaller streams, where phytoplankton productivity may be extremely low, most suspended organic matter available to filter feeders is either particulate organic detritus or heterotrophic bacteria and fungi (Nelson and Scott 1962). While experiments are few, at least some freshwater bivalves can efficiently filter suspended bacteria. Certainly, *D. polymorpha* appears capable of efficiently extracting particles of bacterial size (< 1.0 μm in diameter) (Fig. 11.22) as can *C. fluminea* (Way *et al.* 1990b). In contrast, *M. transversum* (Way 1989) and unionaceans (Fig. 11.22) cannot efficiently filter bacterial-sized particles. As bacteria and detrital particles may comprise the vast majority of organic matter in some aquatic habitats, this mode of feeding is deserving of greater experimental attention.

At least some freshwater bivalve species may also supplement filter feeding by consuming organic detritus or interstitial bacteria from sediments. The infaunal habit of many members of *Pisidium* suggests dependence on food sources other than plytoplankton. Many species of *Pisidium* can efficiently filter small interstitial bacteria. They burrow continually through sediments with the shell hinge downward. In this position, dense bacterial populations are drawn with interstitial water through the parted ventral mantle edges into the mantle cavity and filtered on the gills, thus making up the majority of ingested organic matter (Lopez and Halopainen 1987). Both *Pisidium casertanum* and *P. conventus* feed in this manner and can filter, ingest, and assimilate interstitial bacteria of much smaller diameter (< 1 μm) than considered filterable by most bivalves (Lopez and Holopainen 1987) (Fig. 11.22). The capacity to filter rich interstitial bacterial flora may be associated with the characteristically reduced ctenidial surface areas as well as low filtration and metabolic rates of *Pisidium* species compared to those of *Sphaerium* or *Musculium* (Hornbach 1985, Lopez and Holopainen 1987). In another mode of deposit feeding, *M. transversum* reportedly uses its long inhalant siphon to vacuum detrital particles from the sediment surface on inhalant currents for filtration (Way 1989).

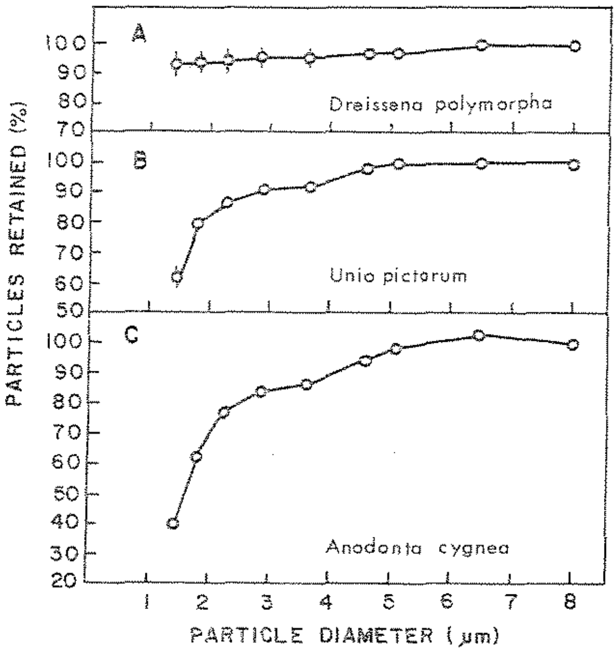


Figure 11.22 Relationship between the percentage of suspended particles regained by the gill filtering mechanism of freshwater bivalves and particle size, as particle diameter in micrometers. Horizontal axis for all figures is the percentage of total particles retained from suspensions passing over clam gill filtering systems in *Dreissena polymorpha* (A), and the unionid mussels, *Unio pictorum* (B), and *Anodonta cygnea* (C). Vertical lines about points are standard deviations. Note that all three species efficiently retained particles of 2.5–8 μm, equivalent to most unicellular algae, but only *D. polymorpha* efficiently retained particles of 1 μm equivalent to bacteria. (Redrawn from Jorgensen *et al.* 1984.)

Pedal feeding on sediment organic detritus may be another important feeding mechanism in some freshwater species. Such pedal feeding is known to occur in a few marine and estuarine bivalves (Morton 1983), but has been little studied in freshwater species. *Corbicula fluminea* draws sediment detrital particles dorsally over the ciliated foot epithelium into the mantle cavity, where they accumulate in the food groove on the ventral edge of the inner demibranch. Eventually, they are carried with particles filtered on the gill to the palps for sorting and ingestion (Cleland 1988, Way *et al.* 1990b). Cellulose particles (40–120 μm in diameter) soaked in various amino acid solutions and mixed with sediments will accumulate in the stomachs of individuals of *C. fluminea* exhibiting pedal-feeding behavior (R. F. McMahon personal observation). Similar pedal feeding has been reported in *M. transversum*

(Way 1989). Such observations suggest that pedal deposit feeding is an important auxiliary feeding mode, at least in corbiculacean species.

Pedal feeding may be much more common in freshwater species than previously suspected. In a stream *S. striatinum* population, only 35% of the total organic carbon assimilated could be accounted for by filter feeding, leaving the remaining 65% to come from sediment detrital sources (Hornbach *et al.* 1984a), presumably from pedal feeding. Other sphaeriid species reach highest densities in silt-laden sediments of high organic content (Zdeba and White 1985) or in habitats receiving organic sewage effluents, both strongly suggestive of dependence on pedal deposit-feeding mechanisms (Burky 1983). Pedal deposit-feeding mechanisms may explain the extensive horizontal locomotion through sediments observed in a number of freshwater bivalves (Imlay 1982, Way 1989; see also Section II.D), as it would allow sediments laden with organic detritus to be renewed continually at the foot surface. Certainly, this unique feeding mode deserves further investigation.

3. Population Regulation

There has been little detailed research regarding regulation of freshwater bivalve populations. Most of the information is anecdotal. Fuller (1974) reviews the known abiotic and biotic factors affecting population density and reproductive success of freshwater bivalves. Catastrophic abiotic factors recognized as causing periodic reductions in bivalve populations are reviewed in Section III.B. Among these are accumulations of silt in the sediments of impounded rivers and silt suspended in the water column during periods of flooding. Silt interferes with gill filter feeding and gas exchange mechanisms (Aldridge *et al.* 1987, Payne and Miller 1987) and can cause massive mortality in unionacean populations (Adam 1986). In contrast, many sphaeriids thrive in sediments with high silt loads (Burky 1983, Kilgour and Mackie 1988), associated with their partial or complete dependence on detrital food sources (see Section III.C.2). Even the shell growth of *C. fluminea*, a species tolerant of high turbulence and suspended silt, can be temporarily inhibited by periods of high flow and turbidity (Fritz and Lutz 1986).

Temperature extremes also affect freshwater bivalve populations. The tolerated temperature range of *C. fluminea* is 2°C (Mattice 1979) to 36°C (McMahon and Williams 1986b). Both cold-induced winter kills (Blye *et al.* 1985, Sickel 1986) and heat-induced summer kills (McMahon and Williams 1986b) are reported for this species. Temperature limitations for other North American species are not as well studied; but on average they appear to have broader upper and lower temperature limits than *C. fluminea* (Burky 1983). Even within the tolerated range, temperature may have detrimental effects on reproductive success. Sudden temperature decreases cause abortive release of developing glochidia in unionaceans (Fuller 1974), and temperatures above 30–33°C inhibit reproduction in *C. fluminea* (Long and McMahon 1987). Sphaeriid densities were reduced in midsummer in an area receiving heated effluents from an electric generating station (Winnell and Jude 1982). Elevated temperatures in areas receiving heated effluents may also stimulate bivalve growth, inducing early maturity and increasing reproductive effort. They may provide heated refugia in which populations may overwinter as occurs in the northernmost populations in *C. fluminea* in North America (Counts 1986, Cairns and Cherry 1983, McMahon 1982, 1983a).

Low ambient pH can also depauperate or completely extirpate bivalve populations. Bivalve populations have been eliminated from habitats receiving acid mine drainage (Taylor 1985, Warren *et al.* 1984). Highly acidic waters cause shell erosion and eventual death (Kat 1982). Perhaps of more importance than pH in regulating freshwater bivalve populations are water hardness and alkalinity. Unionaceans do not occur in New York drainage systems with calcium concentrations of less than 8.4 mg Ca/liter (Fuller 1974). In waters of extremely low alkalinity, calcium concentrations may be too low for shell calcium deposition; the lower limit for most bivalves is 2–2.5 mg Ca/liter (Okland and Kuiper 1982, Rooke and Mackie 1984a). Growth and fecundity rates were suppressed in a *Pisidium casertanum* population in a pond with a low calcium concentration relative to a population in a pond with a higher calcium concentration (Hornbach and Cox 1987). Waters of low alkalinity have little pH-buffering capacity and are, therefore, subject to major seasonal pH variation. This makes them particularly sensitive to acid rain, which detrimentally affects bivalve faunae (Rooke and Mackie 1984a). Shell calcium content can be related to water calcium concentration. Of ten species of Canadian freshwater bivalves, two sphaeriid and one unionacean species displayed no relationship between shell calcium content and water calcium concentration. In contrast, shell calcium content decreased with increased water calcium concentration in two sphaeriid species and increased with water calcium concentration in four sphaeriid and two unionacean species (Mackie and Flippance 1983b).

Lowering of habitat water levels during extreme droughts or dry periods can produce massive mortalities by exposing bivalves to air. Lowering of lake levels caused near 100% mortality in emerged *C. fluminea* populations (White 1979), a result that probably reflects its poor dessication tolerance (Byrne *et al.* 1988). Many unionacean species are relatively tolerant of prolonged emersion. When sympatric populations of nine unionacean species, the sphaeriid *Musculium transversum*, and *C. fluminea* were exposed on land for several months, both the *M. transversum* and *C. fluminea* populations suffered 100% mortality. The unionaceans, however, suffered only 50% mortality because they either migrated downshore or resisted dessication (White 1979).

Low environmental O_2 concentrations can be detrimental to freshwater bivalves. Continual eutrophication of Lake Estrom, Denmark, so reduced ambient profundal O_2 concentrations (0–0.2 mg O_2/liter for three months) that massive reductions of sphaeriid populations ensued (Holopainen and Jonasson 1983, Jonasson 1984a, 1984b), even in species generally highly tolerant of hypoxia such as *Pisidium casertanum* and *P. subtruncatum*. The lower critical O_2 limit for maintenance of aerobic respiration in both species was 1.7 mg O_2/liter (Jonasson 1984b).

Various forms of pollution are also highly detrimental to freshwater bivalves (for a review see Fuller 1974) including chemical wastes (Zeto *et al.* 1987), asbestos (Belanger *et al.* 1986a), organic sewage effluents (Gunning and Sutkkus 1985, Neves and Zale 1982, St. John 1982), heavy metals (Belanger *et al.* 1986b, Fuller 1974, Lomte and Jadhav 1982a), chlorine and paper mill effluents (Fuller 1974), and acid mine drainage (Taylor 1985, Warren *et al.* 1984). Potassium ion, even in low concentration ($>$ 4–7 mg K^+/liter), can be lethal to freshwater bivalves. Populations can be seriously affected or even extirpated in watersheds where potassium is naturally abundant (as occurs in the western Mississippi basin) (Fuller 1974).

Little hard experimental information is available on the biotic factors controlling freshwater bivalve populations. In some *C. fluminea* populations, massive die-offs (particularly of older individuals) have been observed after reproductive efforts (Aldridge and McMahon 1978, McMahon and Williams 1986a, Williams and McMahon 1986), probably as a result of major reductions in the tissue energy reserves of postreproductive individuals (Williams and McMahon 1989). Such postreproductive mortality in adult individuals also occurs in sphaeriids (Burky 1983).

Freshwater bivalves are hosts for a number of parasites. They are intermediate hosts for digenetic trematodes (Fuller 1974). While such infections cause sterility in gastropods, their effects on freshwater bivalves are unknown. Parasitic nematode worms inhabit the guts of unionaceans (Fuller 1974). The external oligochaete parasite *Chaetogaster limnaei* resides in the mantle cavities of unionaceans (Fuller 1974) and *C. fluminea* (Sickel 1986). All of these parasites probably contribute to the regulation of freshwater bivalve population densities, but the degree to which they do has received little experimental attention.

Water mites of the family Unionicolidae, including the genera *Unionicola* and *Najadicola*, are important external parasites of unionaceans. Both mature and pre-adult mites are parasitic, attaching to gills, mantle, palps, and the visceral epithelium (depending on species) (for life histories of the Unionicolidae see Mitchell 1955; see also Chapter 16). Heavy mite infestations of unionacean gills can cause portions of the gills to be shed, abortion of developing glochidia, or even death of infected hosts (Fuller 1974), perhaps making unionicolid mites a major regulator of unionacean populations.

Disease has been little studied. Available evidence indicates little viral or bacterial involvement in massive die-offs of *C. fluminea* (Sickel 1986) or unionacean (Fuller 1974) populations.

Predation may be the most important regulator of fresh water bivalve populations. Shore birds and ducks are major feeders on sphaeriids and small specimens of *C. fluminea* (Dreier 1977, Fuller 1974, Paloumpis and Starrett 1960, Smith *et al.* 1986, Thompson and Sparks 1977, 1978). Indeed, *C. fluminea* densities were 3–5 times greater in enclosures excluding diving ducks (Smith *et al.* 1986). Water fowl feeding also significantly reduces *D. polymorpha* populations (Mackie *et al.* 1989). Crayfish also feed on small bivalves including *C. fluminea* (Covich *et al.* 1981) and *D. polymorpha* (Mackie *et al.* 1989), and in some habitats may have significant influence on bivalve population densities. Fire ants (*Solenopis invincta*) prey heavily on clams periodically emersed by receding water levels. In addition, turtles, frogs, and the mudpuppy salamander *Necturus maculosus* have all been reported to feed to a limited extent on small or juvenile bivalves (Fuller 1974). Free-living oligochaetes prey on freshly released glochidia (Fuller 1974).

Perhaps the major predators involved in regulation of freshwater bivalve populations are fish. A number of North American fish species have been identified as molluscivores (Table 11.4). While the majority of molluscivorous fish feed on small bivalve species or immature specimens (SL $<$ 7 mm) of larger bivalve species, several routinely take larger

Table 11.4 List of Major Fish Predators of Freshwater Bivalves[a]

Family	Genus and Species	Common Name
Clupeidae	*Alosa sapidissima*	American Shad
Cyprinidae	*Cyrinus carpio*	Common Carp
Catostomidae	*Ictiobus bubalus*	Smallmouth Buffalo
	Ictiobus niger	Black Buffalo
	Minytrema melanopus	Spotted Sucker
	Moxostoma carinatum	River Redhorse
Percichthyidae	*Roccus saxatilis*	Striped Bass
Ictaluridae	*Ictalurus furcatus*	Blue Catfish
	Ictalurus punctatus	Channel Catfish
Centrarchidae	*Lepomis gulosus*	Warmouth
	Lepomis macrochirus	Bluegill
	Lepomis microlophus	Red-ear Sunfish
Sciaenidae	*Aplodinotus grunniens*	Freshwater Drum
Acipenseridae	*Acipenser fulvesens*	Lake Sturgeon

[a] Data from Fuller (1974), McMahon (1983a), Robinson and Wellborn (1988), and Sickel (1986).

adult bivalves, including carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*) and freshwater drum (*Aplodinotus grunniens*). This latter species crushes large bivalve shells with three massive, highly muscularized pharyngeal plates, as do carp to a lesser extent. In contrast, channel catfish swallow bivalves intact (J. C. Britton, personal communication). The majority of molluscivorous fish limit predation to smaller bivalves because the shells of larger individuals are too strong to crack or crush. The shell strength of *C. fluminea* increases exponentially with size [$\log_{10}$ force in newtons to crack the shell $= -0.76 + 2.31$ ($\log_{10}$ SL in mm)]; it is 6.5 times stronger than that of the very thick-shelled estuarine bivalve *Rangia cuneata* (Fig. 11.23) (Kennedy and Blundon 1983).

In some instances, fish predation significantly depletes freshwater bivalve populations. The diversity and density of sphaeriids increased in habitats from which molluscivorous fish were excluded (Dyduch-Falniowska 1982). Robinson and Wellborn (1988) reported that 11 months after settlement, the densities of a spring cohort of *C. fluminea* were 29 times greater in enclosures excluding fish.

As fish are intermediate hosts for the glochidia of unionaceans, the size of fish host populations can significantly influence mussel reproductive success. The absence of appropriate fish hosts has caused the extirpation of unionaceans in a number of North American habitats (Fuller 1974, Kat and Davis 1984, Smith 1985a, 1985b; see also Section III.A). Indeed, restoration of fish host populations has produced remarkable recoveries in some endangered unionacean populations (Smith 1985b). Thus, human activities reducing population densities of fish glochidial hosts can result in the destruction of unionacean populations. Therefore, relationships between unionaceans and their glochidial host fish should be

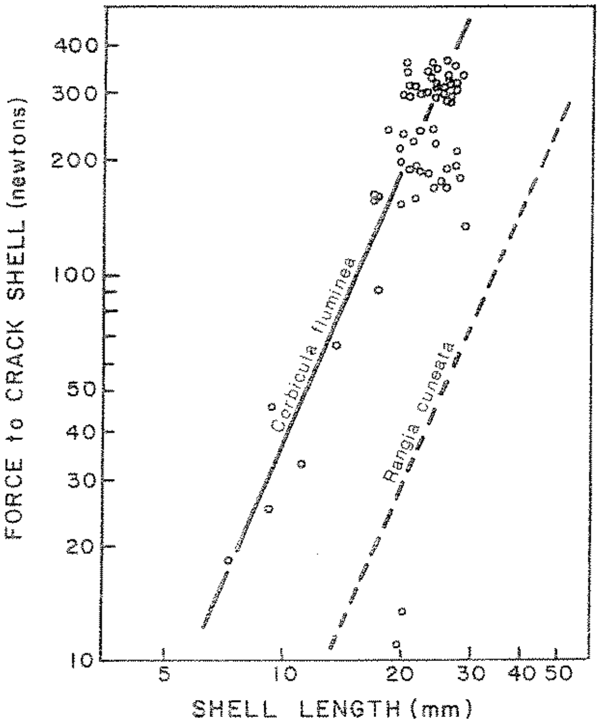


Figure 11.23 Shell strength of *Corbicula fluminea*. Solid line is the best fit of a geometric mean estimate of a least squares log–log linear regression, relating shell length (SL) to force required to crack the shell (open circles) as follows: Log_{10} force to crack the shell in newtons $= -0.76 + 2.31$ ($\log_{10}$ mm SL). Dashed line is the best fit of a similar log–log linear regression for the estuarine wedge clam, *Rangia cuneata*, as follows: $\log_{10}$ force to crack the shell in newtons $= -1.73 + 2.42$ ($\log_{10}$ SL in mm). *R. cuneata*, with the strongest shell of eight tested estuarine bivalve species, has a thicker shell than does *C. fluminea*. However, as the regression slope values for the two species are nearly equal, the elevated y-intercept for *C. fluinea* (-0.76 compared to -1.73 for *R. cuneata*) indicates that its shell is approximately an order of magnitude stronger. (Redrawn from Kennedy and Blundon 1983.)

an important consideration in the future management of drainage systems and their fisheries to ensure continued health of remaining unionacean faunae.

Mammals also prey on freshwater bivalves. Otters, minks, muskrats, and raccoons all routinely include bivalves in their diets and may limit population growth in some species (Fuller 1974). Raccoons and muskrats feed extensively on *C. fluminea* and may account for the large reductions of adult clam densities in the shallow, near-shore waters of some Texan rivers, where favored feeding sites are marked by accumulations of thousands of open shells (personal observation). Even wild hogs have been reported to root in and destroy shallow water beds of unionacean mussels (Fuller 1974). Muskrats annually ate 3% of individuals in a population of *Anodonta grandis simpsoniana* in a small Canadian lake or 31% of its annual tissue production. The muskrats preferentially consumed larger mussels (shell length > 55 mm), strongly affecting the size–age structure of the population; this resulted in a decline in the biomass of large individuals in the mussel population and a significant reduction in the reproductive effort of the mussel population (Hanson *et al.* 1989).

There have been no experimental evaluations of interspecific or intraspecific competition among freshwater bivalves; only highly anecdotal observations have been made. Unionacean or sphaeriid population declines coincident with the establishment of *C. fluminea* populations have occurred in a number of North American habitats (McMahon 1983a, Sickel 1986). However, invasion by *C. fluminea* does not appear to be a primary cause of reductions in native bivalve populations. Rather, habitats are first made inhospitable to indigenous species by channelization, dredging, pollution, over-fishing or other water management practices. *C. fluminea,* which is highly invasive and more tolerant of the higher current velocities, increased levels of suspended solids, and silting caused by such practices, rapidly colonize such disturbed habitats from which other species have been extirpated (McMahon 1983a). In contrast, establishment of *C. fluminea* populations in drainage systems not subject to human interference has had little effect on native bivalve populations (McMahon 1983a, Sickel 1986). This may suggest an inability by *Corbicula* to outcompete native species in most natural North American habitats.

Published experimental investigations of intraspecific, density-dependent, population regulation mechanisms in freshwater bivalves are also lacking. However, some evidence is available from descriptive field studies. In *C. fluminea,* extremely successful recruitment of newly settled juveniles is known to occur after adult populations have been decimated (Cherry *et al.* 1980, McMahon and Williams 1986a, 1986b); whereas, juvenile settlement is generally far less successful in habitats harboring dense adult populations. High adult density may prevent successful recruitment of juveniles, thus preventing extensive juvenile–adult competition for limited food and space resources. This hypothesis was tested by placing sand-filled trays with different densities of adult *C. fluminea* in a lake harboring a relatively dense *Corbicula* population. The results indicated that while adult density had no effects on either adult or juvenile growth rates, it clearly affected success of juvenile settlement. Settlement in the tray without adults was 8702 juveniles/m^2. Maximal settlement (26,996 juveniles/m^2) occurred in the tray with 329 adults/m^2; while juvenile settlement was least at the highest adult densities of 659 and 1976 clams/m^2 being only 8642 and 3827 juveniles/m^2, respectively (R. F. McMahon unpublished). This clearly indicated a significant inhibitory effect of adult density on successful juvenile settlement. The mechanism of density-dependent juvenile settlement has not yet been clarified for this species. Mackie *et al.* (1978) found that high adult densities in *Musculium securis* caused significant reductions in the number of juveniles incubated, implying that intraspecific adult competition can regulate reproductive effort. In addition, interspecific competition between *M. securis* and *M. transversum* caused reduction in reproductive capacity in the subdominant species, with species dominance dependent on habitat. Such experiments clearly show that intraspecific density effects and interspecific competition both contribute to regulation of freshwater bivalve populations and, therefore, are deserving of greater experimental attention.

4. *Functional Role in the Ecosystem*

Bivalves have a number of important roles in freshwater ecosystems. Because they can achieve very high densities and are filter feeders, they are important second trophic level consumers of phytoplanktonic primary productivity. Unionaceans, with filtering rates on the order of 300 ml/g dry tissue/hr (Paterson 1984), can account for a large proportion of total animal consumption of phytoplankton productivity. As unionacean densities are reported to range from 15 individuals/m^2 (Paterson 1985) to 28 individuals/m^2 (Negus 1966) and dry tissue standing crop biomasses from 2.14 g/m^2 (Paterson 1985) to 17.07 g/m^2 (Negus 1966), filtering by unionacean communities could be as high as 15–122.9 liter/m^2/day. Thus, on an annual basis, a unionacean community in a eutrophic European lake was estimated to filter 79% of total lake volume, removing 92–100% of all suspended seston from the filtered water. However, even with such high cropping rates, the high reproductive rates of phytoplankton resulted in unionaceans reducing seston concentrations by only 0.44% (Kasprzak 1986). While the unionacean community accounted for only 0.46% of seston removed by all phytoplanktivorous animals in the lake, they accounted for 85% of the standing crop biomass of the phytoplanktivorous community. They also contained in their biomass a high proportion of the total phosphorus load of the lake, greatly limiting the phosphorus available for phytoplankton production. Similarly, populations of *D. polymorpha* in five European lakes had an average dry weight biomass 38 times that of submerged macrophytes and average standing crop phosphorus and nitrogen contents 2.94 (range = 0.39–7) and 4.21 (range = 0.59–9.4) times that of submerged macrophytes, respectively, greatly reducing availability of these growth-limiting inorganic nutrients to the aquatic plant community (Stanczykowska 1984).

Sphaeriids also have important impacts on phytoplankton communities in lentic habitats. The sphaeriid community of an oligotrophic lake comprised only 0.12% of the total biomass of the phytoplanktivores and 0.2% of the bivalve biomass, but accounted for 51% of total seston consumption (Kasprzak 1986). This probably resulted from their relatively high rates of filtration and population productivity (Burky *et al.* 1985a, Hornbach *et al.* 1984a,b). In smaller lotic and lentic habitats, sphaeriids can consume a major portion of primary productivity. In a canal community dominated by sphaeriids (98% of the biomass of phytoplanktivores), they accounted for 96% of total seston consumption (Krasprzak 1984). A stream population of *S. straitinum* was estimated to filter 3.67 g organic carbon/m^2/yr or 0.0004% of organic carbon in the seston flowing over them (Hornbach *et al.* 1984a). In contrast, filtration by a pond population of *M. partumeium* removed 13.8 g C/m^2/yr as seston (Burky *et al.* 1985a). Using the data of Burky *et al.* (1985b), standing crop seston levels for the entire pond were estimated to range annually between 46 and 550 g carbon. Average annual consumption of seston organic carbon by the *M. partumeium* community was estimated to be roughly 3.9 g C/day, yielding a population feeding rate of 0.7–8.5% of total standing crop seston carbon per day. These data indicate that sphaeriid communities crop a significant portion of the primary productivity of their small lentic habitats on a daily basis.

With its extremely high filtering rates and capacity to develop very dense populations (McMahon 1983a), *C. fluminea* is potentially a major consumer of phytoplankton productivity. In the Potomac River, phytoplankton densities and chlorophyll *a* concentrations declined in the water column as it passed over dense beds of *C. fluminea*, both measures falling to levels 20–75% lower than upstream values; current phytoplankton levels in this river section are considerably lower than those recorded prior to *C. fluminea* invasion. Based on filtering rates, population size distributions, and adult densities, it was estimated that the *C. fluminea* population filtered the entire water column in the 3–4 day time period required for it to pass over the river reach where it was most dense (Cohen *et al.* 1984).

The great reduction in phytoplankton density and chlorophyll *a* concentration must have been due to clam filter feeding, particularly as discharge volume variation, zooplankton feeding, toxic substances, and nutrient limitations were not different from other river sections (Cohen *et al.* 1984). Similarly, Lauritsen (1986b) estimated that a *C. fluminea* population of 350 clams/m^2 in the Chowan River, North Carolina, at an average summer depth of 5.25 m and clam filtering rate of 564–1010 ml/hr filtered the equivalent of the entire overlying water column every 1–1.6 days. At an average depth of 0.25 m, an average current flow of 18.5 m/min, and an average clam filtering rate of 750 ml/hr (Lauritsen 1986b), the equivalent of the entire water column of the Clear Fork of the Trinity River flowing over a *C. fluminea* population with an average adult density of 3750 clams/m^2 would be filtered every 304 m of river reach or every 16 min (R. F. McMahon personal observation). Such massive turnover of the water column by dense bivalve populations could keep seston concentrations at minimal levels and greatly limit the energy available to other seston-feeding species. Consumption of the majority of primary productivity by dense bivalve populations and the accumulation of that production in large, relatively long-lived, predator-resistant adult clams may not only limit the inorganic nutrients available for primary productivity and the energy available to other primary consumers but may also divert energy flow away from higher trophic levels. Such diversion of energy flow by massive freshwater bivalve populations away from higher trophic levels could lead to reductions in predatory game fish stocks in habitats with dense bivalve populations. This hypothesis has interesting implications for management of game fish stocks, but it is one that awaits field and experimental confirmation. In this regard, the long-term ecological impacts of the apparent reduction of phytoplankton biomass in Lake Erie by zebra mussels should prove most interesting.

Bivalves, by filtering suspended seston, act as water clarifiers and organic nutrient sinks. When co-cultured with channel catfish, *C. fluminea* significantly increased ambient water O_2 concentrations by reducing seston and turbidity levels (Buttner 1986). Dense bivalve populations, by removing phytoplankton and other suspended material from natural water columns, significantly increase clarity; and, by binding suspended sediments into pseudofeces, they accelerate sediment deposition rates (Prokoprovich 1969). Dense populations of *D. polymorpha* clarify water and increase sedimentation rates in European canals (see Mackie *et al.* 1989 and references therein) and may similarly improve the water quality in Lake Erie as populations eventually reach maximal densities. By increasing water clarity and therefore depth of light penetration, bivalves may stimulate the growth of rooted aquatic macrophytes.

Because freshwater clams filter suspended organic detritus and bacteria and consume interstitial bacteria and organic detritus in the sediments (see Section III.D.2), they may also be significant members of the aquatic decomposer assemblage. Lopez and Holopainen (1987) presented evidence that *Pisidium casertanum* and *P. corneum* feed primarily by filtering interstitial bacteria from the sediments. Hornbach *et al.* (1982, 1984a) estimated that only 24–35% of the total energy needs of the population of *Sphaerium striatinum* are met by filter feeding, the remaining coming from assimilation of sediment organic detritus. *C. fluminea* pedally feeds on sediment detritus and can reduce sediment organic contents by 50% within 25 days (Cleland 1988), thus clearly exerting a major impact on the decomposer community. *Musculium transversum* utilizes its long inhalant siphon to vacuum organic detritus from the sediment surface (Way 1989). The detritivorous habit of many freshwater bivalve species may divert primary productivity ordinarily lost to respiration of the detritivorous community back into bivalve tissue where it can become reavailable to higher trophic levels.

The activity of freshwater bivalves may also directly affect the physical characteristics of their habitats. Deposition of calcium in the shells of growing clams may reduce ambient water calcium concentrations. In a population of *C. fluminea* with an average density of 32 clams/m^2, annual fixation of shell $CaCO_3$ was 0.32 kg $CaCO_3$/m^2/yr (Aldridge and McMahon 1978). At this rate, annual shell $CaCO_3$ fixation in populations of 100,000 clams/m^2 (Eng 1979) could be as great as 50–60 kg $CaCO_3$/m^2/yr. Such rapid removal of calcium to shells accumulating in the sediments could lead to a considerable reduction in water hardness, particularly in lentic habitats. Seasonal cycles of shell growth could induce seasonal cycles in ambient water calcium concentration, with calcium concentrations being greatest in winter when shell growth is minimal and least in summer when shell growth is maximal (Rooke and Mackie 1984c). Bivalve activity can also affect the flux rates of solutes between sediments and the overlying water column. Unionacean mussels enhanced the release of nitrate and chloride and inhibited $CaCO_3$ release from surrounding sediments (Matisoff *et al.* 1985). Dense populations of sphaeriids can be the principal effectors of sediment dissolved oxygen demand, in some habitats reported to reach levels characteristic of semipolluted and polluted streams (Butts and Sparks 1982).

Small bivalves (sphaeriids, juvenile unionaceans, *D. polymorpha,* and *C. fluminea*) can be a major food source for a number of second trophic level carnivores, including fish and crayfish (see Section III.C.3). Bivalve flesh has a relatively low caloric content, 3.53–5.76 kcal/g ash-free dry weight (Wissing *et al.* 1982), reflecting low lipid and high protein content. *C. fluminea* has tissue organic C : N ratios ranging from 4.9–6.1 : 1, indicative of flesh protein contents of 51–63% of dry weight (Williams and McMahon 1989). High protein content makes bivalve flesh an excellent food source to sustain predator tissue growth.

Many freshwater bivalve populations are highly productive (particularly sphaeriids, *C. fluminea,* and *D. polymorpha*), thus they rapidly convert primary productivity into tissue energy available to third trophic level predators. Productivity values range from a low of 0.019 g C/m^2/yr for *Pisidium crassum* population to a high of 10.3 g C/m^2/yr for a *C. fluminea* population; the average for 11 sphaeriid species and 2 species of *Corbicula* was 2.5 g C/m^2/yr (Burky 1983). Other more recent values include 12.8–14.6 g C/m^2/yr for an Arizona canal population of *C. fluminea* (computed from the data of Marsh 1985) and 1.07 g C/m^2/yr for a New Brunswick lake population of the unionacean *Elliptio complanata* (computed from the data of Paterson 1985).

Furthermore, bivalves are generally more highly efficient at converting consumed and assimilated food energy into new tissue than most second trophic level aquatic animals because their sessile, filter-feeding habits minimize energy expended in food acquisition, allowing more efficient transfer of energy from primary production to bivalve predators. Thus, bivalves can act as important conduits of energy fixed by photosynthesis in phytoplankton to higher trophic levels in the ecosystem. However, such trophic energy transfer is mainly through smaller species and juvenile specimens, as large adult bivalves are relatively immune to predation.

The measure of efficiency of conversion of assimilated energy (energy absorbed across the gut wall) into energy fixed in new tissue growth is net growth efficiency:

$$\% \text{ Net Growth Efficiency} = P/A(100)$$

where P = productivity rate or rate of energy or organic carbon fixation into new tissue growth by an individual or population and A = assimilation rate or rate of energy or organic carbon assimilated by an individual or population. The greater the net growth efficiency of a second trophic level species, the more efficient is its conversion of assimilated energy into flesh, and, therefore, the greater the potential for energy flow through it to third trophic level predators (for detailed discussions of bivalve energetics see Burky 1983, Holopainen and Hanski 1986, Hornbach 1985, Russell-Hunter and Buckley 1983). Net growth efficiencies, computed as 100% − the percentage of assimilated energy respired values (Table 11.2), are 9–79% in sphaeriids (average = 55%) and 58–89% in *C. fluminea*, indicating relatively efficient conversion of assimilated energy into flesh compared to other aquatic second trophic level animals.

5. *Bivalves as Biomonitors*

Freshwater bivalves, particularly larger unionaceans and *C. fluminea*, may also be excellent biomonitors of water pollution and other environmental perturbations. Characteristics making them excellent biomonitors (for a review see Imlay 1982) include long life span, and growth and reproductive rates sensitive to environmental perturbation (Burky 1983). They are readily held in field enclosures without excessive maintenance. Shell growth is sensitive to environmental variation and/or disturbance (Belanger *et al.* 1986a, 1986b, Burky 1983, Fritz and Lutz 1986, Way and Wissing 1982, Way 1988), and the valves remain as evidence of death, allowing mortality rates to be estimated. Shells are easily marked by tags (Young and Williams 1983c), paint, or shell-etching (McMahon and Williams 1986a).

Bivalves are collectible throughout the year and are easily shipped alive long distances from field sites to the laboratory. Because adults of large species tend to remain in place (exception is *C. fluminea*), they are subjected to conditions representative of the monitored environment throughout life (Imlay 1982). Shell growth in annual increments allows determination of annual variation in heavy metal pollutant levels over long periods by analysis of metal levels in successively secreted shell layers (Imlay 1982). Large size allows analysis of pollutant levels in single individuals, and the wide geographical ranges of some species (Imlay 1982) allow direct comparisons across drainage systems. Table 11.5 indicates the types of pollutants and environmental perturbations for which freshwater bivalves have been used as biomonitors.

D. Evolutionary Relationships

Sphaeriids, dreissenids, corbiculids, and unionaceans represent separate evolutionary invasions of freshwaters. Sphaeriids, dreissenids, and corbiculids, all in the order Veneroida, are quite distinct from unionaceans in the order Unionoida (Allen 1985). The Veneroida became successful infaunal filter feeders through evolution of inhalant and exhalant siphons, allowing sediment burrowing while maintaining respiratory and feeding currents from the overlying water column. Their eulamellibranch gills with fused filaments (Fig. 11.5) were a clear advancement over the primitive (i.e., filibranch) condition with separate gill filaments attached only by interlocking cilia (Allen 1985).

The family Sphaeriidae in the superfamily Corbiculacea has a long fossil history in freshwater extending from the Cretaceous (Keen and Dance 1969) and has evolved along two major lines. The first, represented by *Pisidium*, involves adaptation to life in organically rich sediments with the capacity to filter interstitial bacteria (Lopez and Holopainen 1987); this makes them dominant in the profundal regions of lakes. The second, represented by *Sphaerium* and *Musculium*, involves adaptation to life in small, shallow lentic or lotic habitats subject to predictable seasonal perturbation such as habitat-drying. Their adaptations include estivation during prolonged emergence (see Section III.A). Like many of the Veneroida, the byssus is absent in the adults of most species. They have also evolved an unusual shell made fragile by lack of a nacreous layer.

The superfamily Unionacea, like the Sphaeriidae, has a long fossil history in freshwater, extending at least from the Triassic (Hass 1969). A long fossil history and tendency for reproductive isolation due to gonochorism and the parasitic glochidial stage (see Section III.A) has led to extensive radiation in the Unionacea, represented worldwide by 150 genera and a great number of species (Allen 1985). Their origin remains unclear. Similarity of shell structure suggests a possible relationship to shallow-burrowing marine fossil species in the order Trigonida (Allen 1985). Like the majority of sphaeriid species, adults lack a byssus, which would be of no use in their soft sediment, infaunal habitats. They are the dominant bivalve fauna in shallow regions of

Table 11.5 List of Recent Investigations Involving Utilization of Bivalves to Monitor Effects or Levels of Pollutants in Freshwater Habitats

Pollutant Monitored	Species Utilized	Literature Citation
Arsenic	*Corbicula fluminea*	Elder and Mattraw (1984), Price and Knight (1978), Tatem (1986)
	8 Unionid species	Price and Knight (1978)
Cadmium	*Anodonta anatina*	Hemelraad *et al.* (1985)
	Anodonta cygnea	Hemelraad *et al.* (1985).
	Corbicula fluminea	Elder and Mattraw (1984), Graney *et al.* (1984), Price and Knight (1978), Tatem (1986)
	8 Unionid species	Price and Knight (1978)
Chromium	*Corbicula fluminea*	Elder and Mattraw (1984), Tatem (1986)
Copper	*Corbicula fluminea*	Annis and Belanger (1986), Elder and Mattraw (1984), Foe and Knight (1986c), Tatem (1986)
Iron	*Corbicula fluminea*	Tatem (1986)
Lead	*Corbicula fluminea*	Annis and Belanger (1986), Elder and Mattraw (1984), Price and Knight (1978), Tatem (1986)
	8 Unionid species	Price and Knight (1978)
Manganese	*Corbicula fluminea*	Elder and Mattraw (1984), Tatem (1986)
Mercury	*Corbicula fluminea*	Elder and Mattraw (1984), Price and Knight (1978)
	8 Uniondid species	Price and Knight (1978)
Tin	*Anodonta* sp.	Herwig *et al.* (1985)
Zinc	*Corbicula fluminea*	Belanger *et al.* (1986b), Elder and Mattraw (1984), Foe and Knight (1986c)
Asbestos	*Corbicula fluminea*	Belanger *et al.* (1986a, 1987)
Octachlorostyrene	*Lampsilis radiata siliquiodea*	Pugsley *et al.* (1985)
Polychlorinated Biphenols (PCBs)	*Corbicula fluminea*	Elder and Mattraw (1984), Tatem (1986)
	Lampsilis radiata siliquiodea	Pugsley *et al.* (1985)
Pesticides	*Corbicula fluminea*	Elder and Mattraw (1984), Hartley and Johnston (1983), Tatem (1986)
Sewage Effluents	*Corbicula fluminea*	Foe and Knight (1986c), Horne and MacIntosh (1979), Weber (1973)
Power Station Thermal Effluents	*Corbicula fluminea*	Dreier and Tranquilli (1981), Farris *et al.* (1988), Foe and Knight (1987), McMahon and Williams (1986b)

larger, relatively stable lentic and lotic habitats, particularly in sand–gravel substrata not subject to disturbance by currents (see Section III.A).

The Sphaeriidae and Unionacea, with long fossil histories in freshwater, have evolved quite distinct niches. While both occur in relatively stable habitats, the majority of sphaeriids live in smaller ponds and streams (including those with predictable seasonal perturbation) or in the profundal regions of large lakes; whereas, the majority of unionaceans colonize stable sediments of shallow portions of larger rivers and lakes (see Sections III.A and III.B for descriptions of the adaptations of two of these groups to their respective habitats).

C. fluminea has entered freshwater only in recent (Pleistocene) times (Keen and Casey 1969) and, therefore, is unlikely to complete effectively with sphaeriids or unionaceans, as the long fossil histories of these latter groups have made them highly adapted to their preferred stable freshwater habitats. Indeed, *C. fluminea* does not appear to have a serious impact on native North American bivalve fauna in undisturbed freshwaters (see McMahon 1983a and references therein). Rather, this species is adapted for life in highly unstable habitats that are subject to periodic catastrophic perturbation, particularly flood-induced sediment disturbance; such environments are generally unsuitable for sphaeriids or unionaceans (see Section III.A). Among its adaptations to high-flow lotic habitats with unstable substrata are: (1) capacity for rapid burrowing; (2) a strong, heavy, concentrically sculptured, inflated shell; and (3) juvenile retention of a byssal thread—all of which allow maintenance of position in sediments (Vermeij and Dudley 1985). Additionally, its high fecundity, elevated growth rate, early maturity, and extensive capacity for dispersal (see Section III.B) allow it to both invade habitats from which other bivalves have been extirpated and rapidly recover from catastrophic population reductions. Thus, *C. fluminea* is a successful recent invader of freshwaters because it has evolved a niche in unstable, disturbed habitats not greatly utilized by either sphaeriids or unionaceans. Freshwater *Corbicula* are considered to have evolved from an estuarine *Corbicula* ancestor inhabiting the upper, near freshwater portions of estuaries (Morton 1982).

The superfamily Dreissenacea containing *D. polymorpha*, while superficially resembling mytilacean mussels (superorder Pterioida), is placed in the Veneroida because of its advanced eulamellibranch ctenidium. Adult dreissenaceans retain an attachment byssus, considered a primitive condition. In contrast, the mytiliform shell with its reduction of the anterior ends of the valves and the anterior adductor muscle, is considered to be a derived characteristic, resulting from adaptation to an epibenthic niche characterized by byssal attachment to hard surfaces (Allen 1985, Mackie *et al.* 1989). *D. polymorpha* probably evolved from an estuarine dreissenacean ancestor of the genus *Mytilopsis*. As with *C. fluminea*, its fossil record indicates a recent Pleistocene introduction to freshwaters (Mackie *et al.* 1989). Also like *C. fluminea*, *D. polymorpha* appears to have successfully colonized freshwaters because its niche (an epibenthic species attached to hard substrata) is not occupied by the infaunal, burrowing sphaeriids and unionaceans, minimizing competition with these more advanced groups. However, *D. polymorpha* may have an indirect detrimental competitive impact on native North American unionacean faunae, because of its tendency to settle and grow on portions of unionid shells exposed above the substratum. Dense mats of *D. polymorpha* byssally attached to the exposed siphonal area of unionacean shells could interfere with their respiratory and feeding currents, leading to eventual death. This aspect of the interaction of *D. polymorpha* with unionaceans merits further study.

Freshwater bivalves display a number of characteristics that are uncommon in comparable marine species. Most shallow-burrowing marine species are gonochoristic with external fertilization and free-swimming planktonic veligers. A planktonic veliger is nonadaptive in lotic freshwater habitats, as it would be carried downstream before settlement, eventually leading to elimination of upstream adult populations. Thus, the veliger stage has been completely suppressed in sphaeriids, which brood developing embryos in gill marsupia and release large, fully formed juveniles immediately ready to take up life in the sediment. In unionids, eggs are retained in gill marsupia and hatch into the glochicia, whose parasitism of fish hosts both allows upstream as well as downstream dispersal and permits release of well-developed juveniles into favorable habitats (see Section III.B). Even the recently evolved *C. fluminea* has suppressed the veliger stage of its estuarine ancestors (Morton 1982), producing a small, but fully formed juvenile whose byssal thread allows immediate settlement and attachment to the substratum. Retention of external fertilization and a free-swimming veliger in *D. polymorpha* are primitive characteristics reflecting its relatively recent evolution from an estuarine ancestor.

Downstream veliger dispersal would appear to preclude zebra mussels from high-flow lotic habitats, unless upstream impoundments provide a source of replacement stock. In fact, in Europe and Asia, this species is most successful in large lentic or low-flow lotic habitats such as canals or large rivers (Mackie *et al.* 1989). Serial impoundment of rivers will provide lentic refugia for this species in otherwise lotic drainages, facilitating its invasion of North American waters.

Another common adaptation in freshwater species is evolution of hermapharoditism with a capacity for self-fertilization. Hermaphroditism makes all individuals in a population reproductive, allowing rapid population expansion during favorable conditions. Hermaphroditism allows sphaeriids to re-establish populations after predictable seasonal perturbation and in *C. fluminea*, along with high fecundity, allows rapid re-establishment of populations after catastrophic habitat disturbance. It makes both sphaeriids and *C. fluminea* invasive, as the introduction of a single individual can lead to the founding of a new population. In contrast, the gonochorism of the majority of unionaceans and *D. polymorpha* limits their invasive capacity, reflected by their tendency to inhabit stable, relatively undisturbed waters.

Finally, unionaceans and sphaeriids have different shell morphologies relative to comparable shallow-burrowing marine bivalves. Freshwater species generally do not have denticulated or crenulated inner valve margins, extensive radial or concentric shell ridges, tightly sealing valve margins, well-developed hinge teeth, overlapping shell margins, or uniformally thick, inflated, strong shells to the degree displayed by shallow-burrowing marine species (Vermeij and Dudley 1985). These shell characteristics allow shallow-burrowing marine species to maintain position in unstable substrata and/or resist to shell cracking or boring by large predators common in marine habitats. Lack of such structures in unionaceans and sphaeriids reflects their preference for stable sediments and the general absence of effective predators on adult bivalves; certainly, there are no shell-boring predators of North American freshwater species. Indeed, the shells of freshwater unionaceans display considerably less nonlethal, predator-induced damage than shallow-burrowing marine species (Vermeij and Dudley 1985). While retention by *C. fluminea* of a thick, extremely strong shell (Kennedy and Blundon 1983) lacking pedal and siphonal gapes, well-developed hinge teeth, shell inflation, and concentric ornamentation may represent a primitive condition, it appears to allow this species to be successful in sediments too unstable to support unionacean or sphaeriid faunae. Such primitive characteristics may reflect similar adaptations in the immediate estuarine ancestor of this recently evolved freshwater species.

IV. COLLECTING, PREPARATION FOR IDENTIFICATION, AND REARING

A. Collecting

Small sphaeriid clams are best collected by removing sediments containing clams with a: (1) trowel or shovel (shallow water); (2) long handled dip net or shell scoop with a mesh of less than 0.35 mm (moderate depths) or by Ekman, Ponar, or Peterson dredges (deeper water), the heavier Ponar and Peterson dredges being better in lotic habitats. Drag dredges may also be used but must have sediment catch bags of small mesh (1 mm or less). Williams (1985) described an easily and inexpensively made drag dredge for use from a small boat. Use of scuba is also an effective way of collecting sphaeriids. Larger sphaeriid species can be separated from fine sediments with a 1 mm mesh sieve, but a 0.35 mesh is required for smaller specimens. Fragile sphaeriids should be separated from sediments by gentle vertical agitation of the sieve at the surface of the water to prevent shell damage. All coarse material should be removed from the sample prior to sieving to avoid shell breakage. Exceptionally small, fragile species can be collected by washing small quantities of sediment into settlement pans, specimens being revealed after sediments settle and the water clears.

Ekman, Ponar, or Peterson dredges are best for quantitative samples of sphaeriids because they remove a specific area of surface sediments. Quadrat frames can also be used (Miller and Payne 1988). These are driven into or placed on the substratum and all surface sediments within the frame collected for sorting. Such frames can be utilized in shallow or deeper waters (the latter in conjunction with scuba equipment). Drag dredging at specified speeds for known intervals allows partial sample quantification. Core sampling devices consisting of tubes driven into the substratum to remove sediment segments of specific depth can yield both accurate estimates of density and sediment depth distributions of sphaeriid populations. Core samplers are limited by sampling a small surface area and are, therefore, best utilized with dense populations and/or repetitive sampling.

The low densities of some unionacean populations can make their collection difficult. Where populations are dense, shoveling sediments through a sieve allows collection of a broad range of sizes and age classes (Miller and Payne 1988). As unionaceans are larger than sphaeriids, sieve mesh sizes of 0.5–1 cm may be appropriate unless recently settled juveniles must be collected. In less dense, shallow water populations, hand-picking using a glass-bottomed bucket to locate specimens can often suffice. In turbid waters and/or soft sediments (sand or mud), shell rakes may be utilized. Hand-picking and shell rakes select for larger, older individuals. In shallow, turbid water, raking of hands and fingers systematically through soft sediment while feeling for burrowed mussels can be effective, but also selects for larger individuals and can lead to cut fingers. On rocky or boulder bottoms, unionaceans generally accumulate in crevices or near downstream bases of large rocks. Here, only hand-picking (in conjunction with scuba techniques in deeper water) is effective. Unionaceans may also be efficiently collected by various forms of drag or brail dredges. Mussel brails (often used by commercial shellers) consist of a bar with attached lines terminating in blunt-tipped gang hooks. When dragged over unionid beds, mussels clamp the valves onto the hooks allowing them to be brought to the surface.

Quantitative sampling of unionaceans can be accomplished with quadrats, along with scuba in deeper waters (Miller and Payne 1988). Only heavy Ponar and Peterson dredges bite deeply enough into the substratum to take large unionacean species.

In sparse populations, errors in density estimates can result from the small surface areas that these dredges sample, requiring repetitive samples to improve accuracy. Drag dredges sample larger areas and may be partially quantitative, but generally do not provide accurate density estimates. Unionaceans may also be collected during natural or planned water level draw-downs (White 1979) by collecting either emerged individuals or those migrating downshore and accumulating at the edge of the water. As a great many North American unionacean species are presently endangered, one should ascertain the endangered status of any species before permanently removing specimens from their natural habitats. Take only a few living specimens for identification, making the remaining collection from dead shells.

C. fluminea is easily collected because it occurs in high densities, prefers shallow waters, and is easily recognized in the field. Individuals are readily separated from sediments with a 1 mm mesh sieve. Qualitative samples are best obtained by shovel or drag dredge (Williams 1985, Williams and McMahon 1986) and quantitative samples by quadrat frame (Miller and Payne 1988) or Peterson (Aldridge and McMahon 1978), Ponar, or Ekman dredges (Williams and McMahon 1986). In rock or gravel substrata, *C. fluminea* are best taken by hand, hand trowel, or shovel; collected sediments should be passed through a coarse mesh sieve to separate specimens from sediments. In fast-flowing streams, specimens of *C. fluminea* accumulate in crevices or behind the downstream sides of large rocks.

Because if its byssal attachment to rocks and other hard surfaces and its preference for deeper waters (< 1–2 m), *D. polymorpha* is best collected by scuba with manual removal, using quadrats for quantification. Ripping of individuals from the byssus attachment damages tissue, thus the byssus should be cut with a knife or sharp trowel before removal. Juveniles can be collected after they have settled on bare settlement blocks or submerged buoys set out during the reproductive season. Ekman, Ponar, Peterson, and drag dredges are generally not suitable for collection of attached epibenthic species such as *D. polymorpha*.

Juveniles of sphaeriids and *C. fluminea* can either be surgically removed from adult brood sacs or collected from sediments just after release with a fine mesh sieve (mesh size < 0.35 mm). Juvenile *C. fluminea* can also be obtained by release from freshly collected, gravid adults left in water for 12–24 hr (Aldridge and McMahon 1978). *C. fluminea* juveniles and *D. polymorpha* veligers may be collected from the water column with a zooplankton net towed behind a boat or held in a current. Their density in the water column may be quantitatively sampled by passing known volumes of water through a zooplankton net. Recently settled juveniles of unionaceans may be sieved from sediments. Glochidia can be surgically removed from demibranchs of gravid females or encysted glochicia from the fins, pharyngeal cavity, or gills of their fish hosts (for a list of unionacean fish hosts see Fuller 1974).

B. Preparation for Identification

To preserve bivalves, larger individuals should first be narcotized or relaxed, allowing tissues to be preserved in a life-like state and preservatives to penetrate tissues through gaped shell valves. Live bivalves placed directly in fixatives clamp the valves, which prevents preservative penetration, causing incomplete tissue fixation. There are a number of bivalve relaxing agents (Lincoln and Sheals 1979, Russel 1963), including alcoholized water (either 3% ethyl alcohol by volume with water or 70% ethyl alcohol added slowly drop by drop to the medium until bivalves gape), chloroform added slowly to the medium, methol crystals (one level teaspoon per liter, scattered on the water surface), propylene phenoxetol and phenoxetol BPC (5 ml of product emulsed with 15–20 ml of water added to water containing bivalves or introduction of a droplet equal to 1% of holding water volume), phenobarbitol added in small amounts to the holding medium, magnesium sulfate (introduced into holding medium over a period of several hours to form a 20–30% solution by weight), magnesium chloride (7.5% solution by weight), and urethane.

None of these relaxing agents works equally well with all species. My laboratory tests of narcotizing agents against *C. fluminea* revealed propylene phenoxetol to be the only agent capable of relaxing this species for experimental surgery, and allowing recovery on return to fresh medium. Heating bivalves to 50°C for 30–60 min causes most species to relax and gape widely, but is usually lethal. In larger specimens, wooden pegs or portions of matchsticks forced between the valves prior to fixation allows good preservative penetration of tissues.

The best long-term preservative for freshwater bivalves is 70% ethyl alcohol (by volume with water). Specimens may be initially fixed in 5–10% formaldehyde solutions (by volume with 40% formaldehyde solutions) for 3–7 days. But formaldehyde is acidic and will dissolve calcareous portions of shells unless pH-neutralized by addition of either powdered calcium carbonate ($CaCO_3$) to make a saturated solution, 5 g powdered sodium bicarbonate

($NaHCO_3$) per liter, or 1.65 g potassium dihydrogen orthophosphate and 7.75 g disodium hydrogen orthophosphate per liter (Smith and Kershaw 1979). After 3–7 days in formaldehyde, specimens should be transferred to 70% ethyl alcohol for permanent preservation. Addition of 1–3% glycerin (by volume) to alcohol preservatives keeps tissues soft and pliable (Smith and Kershaw 1979). Smaller bivalve species (shell length < 15 mm) generally do not require relaxation before fixation. Tissues to be utilized in microscopy should be preserved in gluteraldehyde or Bouin's solution.

Dead shells or those from which tissues have been removed can be cleaned with a mild soap solution and soft brush. Organic material can be digested from shell surfaces by immersion in a dilute (3% by weight with water) solution of sodium or potassium hydroxide at a temperature of 70°–80°C, thereafter any remaining organic matter is readily removed with a soft brush. For dry-keeping, the shell periostracal surface should be varnished or covered with petroleum jelly to prevent drying, cracking, and peeling. Numbers identifying collection and specimen can be marked on the inner shell surface with India ink.

To remove soft parts from living bivalves, immerse them in boiling water and remove tissues after valves fully gape. Separated flesh can be fixed in 70% alcohol. For fragile sphaeriids, flesh is best removed with the tip of a fine needle, manipulating specimens with a fine brush. Shells should be dried in air at room temperature, not in an oven; heat causes the shell to crack and the periostracum to crack and peel.

Both soft tissue and shell characteristics are utilized in the identification of freshwater bivalves (see Section V), so both must be preserved for species identification. For unionaceans, *C. fluminea,* and *D. polymorpha,* most diagnostic taxonomic characteristics can be seen by eye or with a 10X hand lens. For sphaeriids, a dissecting microscope with at least 10–30X power or a compound microscope is required (Ellis 1978). Anatomical details are most clearly observed when shells are dry and when soft tissues are held under water.

Identification of recently released juvenile specimens of freshwater bivalves is difficult and may require preparation of stained slide whole mounts. Glochidia are best identified by removal from gravid adults as are juvenile sphaeriids. The D-shaped juvenile of *C. fluminea* (Fig. 11.15A) is highly recognizable and the only juvenile freshwater bivalve to occur in large numbers in the plankton (McMahon 1983a). The planktonic veliger of *D. polymorpha* is clearly distinguishable by its ciliated velum (Fig. 11.15C). The glochidia of many unionacean species have specific fish host species (Fuller 1974), whose identification will assist glochidial identification.

C. Rearing Freshwater Bivalves

For artificial rearing of freshwater bivalves, water in holding tanks should be temperature regulated. Adequate aeration, filtration, and ammonia removal systems are required, as some species have low tolerances of hypoxia and ammonia (Byrne 1988).

As unionaceans and *C. fluminea* are filter feeders of phytoplankton, they require a constant supply of filterable food to remain healthy and growing for long periods. The best food under artificial conditions appears to be algal cultures. When fed monoalgal cultures of the green algae, *Ankistrodesmus* and *Chlorella vulgaris* or the cyanobacterium, *Anabaena oscillarioides,* assimilation efficiences in *C. fluminea* were 47.4–57.7% and net growth efficiencies, 59.4–78.2%, making them excellent food sources (Lauritsen 1986a).

Artificial diets do not appear to be as successful as algal cultures in maintaining clam growth. When fed either ground nine-grain cereal, rice flour, rye bran, brewers' yeast, or artificial trout food, small *C. fluminea* (5–8 mm SL) lost tissue mass on all but nine-grain cereal, the latter supporting little tissue growth. Supplementing these grain diets with live green algae (*Ankistrodesmus* sp.) greatly enhanced tissue growth, but greatest growth occurred in individuals fed pure *Ankistrodesmus* cultures (Foe and Knight 1986b). *C. fluminea* that were fed mixed cultures of the green algae *Pedinomonas* sp., *Ankistrodesmus* sp., *Chlamydomonas* sp., *Chlorella* sp., *Scenedesmus* sp., and *Selenastrum* sp. had maximal growth when the mixtures did not include *Selenastrum,* which proved toxic to this species. Tissue growth rates were greatest in clams fed mixed cultures containing all five of the remaining species and generally declined with the number of algal species in feeding cultures; feeding with cultures of only two algal species generally resulted in starvation (Foe and Knight 1986b). Thus, artificial bivalve cultures appear to be best supported on mixed algal diets, but certain toxic algal species must be avoided.

Temperature also affects growth rate. When 5–8 mm SL specimens of *C. fluminea* were fed mixed algal cultures of *Chlamydomonas, Chlorella,* and *Ankistrodesmus* at 10^5 cells/ml, assimilation efficiencies were greatest at 16 and 20°C (48–51%), declining above and below this range. Tissue growth was maximal at 18–20°C and became negative (tissue loss) at 30°C and above (Foe and Knight 1986a), suggesting 18°–20°C to be the ideal culture temperature for this species and, perhaps, most other North American bivalves. However, tissue growth in natural populations of *C. fluminea* increases with rising temperatures, up to 30°C (McMahon and Williams 1986a), indicating that artificial culture systems are not equivalent to field conditions in supporting bivalve growth. In this regard, excellent tissue growth in *C. fluminea* was supported by algal cultures produced by exposure to sunlight of water taken from the natural habitat of the clam for several days to increase its algal concentration (Foe and Knight 1985). Thus, ideal culture conditions for unionaceans and *C. fluminea* would appear to be a 20°C holding temperature and a feeding medium of natural algal assemblages whose growth has been promoted with inorganic nutrients and exposure to sunlight.

Specimens of both *C. fluminea* and unionaceans may be held for long periods in the laboratory without feeding. *C. fluminea* (light and dark morphs) survived 154 days of starvation at room temperature (22°–24°C) while sustaining tissue weight losses ranging from 41–71% (Cleland *et al.* 1986). Similarly, I have held unionaceans in the laboratory for many months without feeding them. Maintenance at low temperatures (<10°C) greatly prolongs the time bivalves may be held in the laboratory without feeding.

C. fluminea has never been reared successfully to maturity or carried through a reproductive cycle in artificial culture, although field-collected, nongravid adults released juveniles after four months in laboratory culture (King *et al.* 1986). The glochidium stage makes unionaceans difficult to rear in the laboratory as it requires encystment in an appropriate fish host for successful juvenile metamorphosis, but it can be accomplished (Young and Williams 1984a). Glochidia of several unionacean species have been transformed into juveniles *in vitro* in a culture medium containing physiologic salts, amino acids, glucose, vitamins, antibiotics, and host fish plasma (Isom and Hudson 1982). Juvenile *Anodonta imbecilis* and *Dysnomia triquetra* have been successfully cultured in a medium of river water exposed to sunlight for 1–4 days to enhance algal concentration. Addition of silt to this medium enhanced juvenile growth rates in both species, while feeding artificial, mixed cultures of three algal species resulted in starvation (Hudson and Isom 1984).

Many sphaeriid species can be easily maintained in simple artificial culture systems. Ease of artificial culture in this group may relate to their sediment organic detritus (Burkey *et al.* 1985b, Hornbach *et al.* 1984a, 1984b) and sediment interstitial bacteria feeding mechanisms (Lopez and Holopainen 1987), making maintenance of algal cultures as food sources unnecessary. Hornbach and Childers (1987) maintained *Musculium partumeium* through successful reproduction in beakers with 325 ml of filtered river water, without sediments, on a diet of 0.1 mg of finely ground Tetra Min fish food/clam/day. The first generation in this simple culture system survived 380–500 days, a life span essentially equivalent to that in natural populations (Hornbach *et al.* 1980). Similarly, Rooke and Mackie (1984c) maintained 20 adult *Pisidium casertanum* in a 6 liter aquaria with sediments for 35 weeks without feeding, suggesting that individuals fed on sediment bacteria or organic deposits. Live molluscs rapidly remove dissolved calcium from culture media (Rooke and Mackie 1984c), thus calcium levels in holding media should be augmented by addition of a source of $CaCO_3$. The ease with which sphaeriids can be artificially cultured through many generations makes them ideal for laboratory microcosm experiments. Ideal culture conditions appear to include provision of natural sediments, a source of calcium (i.e., ground $CaCO_3$), and finely ground food of reasonable protein content, such as ground aquarium fish food or brewers' yeast, which may be directly assimilated by clams or support the growth of the interstitial bacteria upon which they feed (Lopez and Holopainen 1987).

V. IDENTIFICATION OF THE FRESHWATER BIVALVES OF NORTH AMERICA

A. Taxonomic Key to Superfamilies of Freshwater Bivalvia

There are five bivalve superfamilies with freshwater representatives in North America. Of these, the Unionacea, Corbiculacea, and Dreissenacea contain the true freshwater species and comprise the vast majority of freshwater bivalve fauna. The remaining two superfamilies, Cyrenoidacea and Mactracea contain but one brackish water species, however, each can extend into coastal freshwater drainages and so are included here. In North America, the Dreissenacea is represented by a recently introduced freshwater species and an estuarine species; the Corbiculacea includes 33 native and 5 introduced species in 6 genera; the Unionacea are composed of approximately 227 native species in 44 genera (Burch 1975a, 1975b). Separate taxonomic keys to the genera are provided here for the latter two superfamilies.

1a. Shell hinge ligament is external 2

1b. Shell hinge ligament is internal 4

2a(1a). Shell with lateral teeth extending anterior and posterior of true cardinal teeth (Fig. 11.1), shells of adults generally small (<25 mm in shell length, shell thin and fragile; exceptions are the genera *Polymesoda* and *Corbicula*) .... superfamily Corbiculacea [See Section V.B.]

2b. Shell without lateral teeth extending anterior and posterior of cardinal teeth 3

3a(2b). Shell hinge with two cardinal teeth and without lateral teeth; shell thin and fragile, 12–15 mm long with small umbos; *Cyrenoida floridana* (Dall) (extends from brackish into coastal freshwater drainages in Florida .... superfamily Cyrenoidacea

3b. Shell without true cardinal teeth; when present, lateral teeth only occur posterior to usually well-developed pseudocardinal teeth (Fig. 11.1), pseudocardial teeth absent or vestigial in some species; Shells of adults are generally large (> 25 mm in shell length) .... superfamily Unionacea [See Section V.C.]

4a(1b). Hinge with anterior and posterior teeth on either side of cardinals; Shell massive, adults 25–60 mm shell length, obliquely ovate; *Rangia cuneata* (Gray) (extends from brackish into coastal freshwater drainages from Delaware to Florida to Veracruz, Mexico) .... superfamily Mactracea

4b. Hinge without teeth; shell mytiloid in shape, anterior end reduced and pointed, hinge at anterior end, posterior portion of shell expanded, anterior adductor muscle attached to internal apical shell septum, attached to hard substrata by byssal threads .... superfamily Dreissenacea 5

5a(4b). Periostracum bluish brown to tan without a series of dorsoventrally oriented black zigzag markings, anterior end hooked sharply ventrally, ventral shell margins not distinctly flattened over entire ventral side of valves; restricted to brackish water habitats. *Mytilopsis leucophaeata* (Conrad) (extends into coastal freshwater drainages from New York to Florida to Texas and Mexico) .... *Mytilopsis*

5b. Periostracum light tan and marked with a distinct series of black vertical zigzag markings; anterior portion of shell not ventrally hooked, ventral shell margins extremely flattened, restricted to freshwaters, *Dreissena polymorpha* (Pallas) (Fig. 11.24); (a European species introduced into the Great Lakes in Lake St. Clair and present by August 1990 throughout Lake Erie, extending into western Lake Ontario and the St. Lawrence river. Isolated populations also occur in lakes Huron, Superior, and Michigan; it is likely to spread rapidly through North American freshwaters) .... *Dreissena*

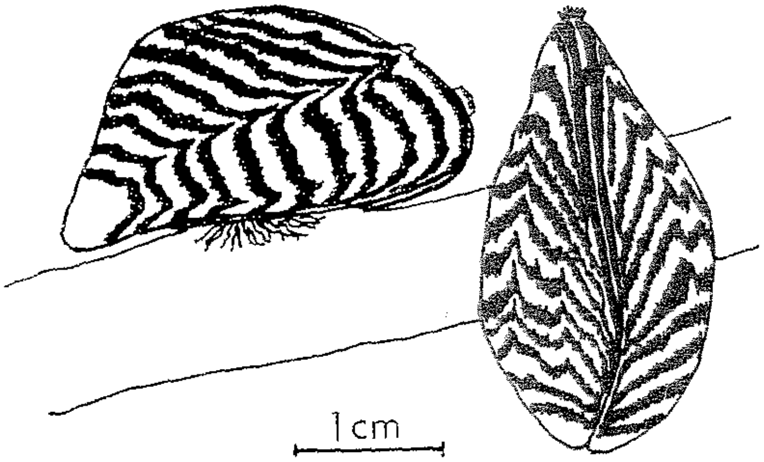


Figure 11.24 The external morphology of the shell of the zebra mussel, *Dreissena polymorpha*.

B. Taxonomic Key to Genera of Freshwater Corbiculacea

This key is based on the excellent species key for North American freshwater Corbiculacea by Burch (1975a) with additional material from Clarke (1973) for the Canadian Interior Basin, and Mackie *et al.* (1980) for the Great Lakes. The Corbiculacea have ovate, subovate, or trigonal shells with lateral hinge teeth anterior and posterior to the cardinal teeth. All North American species except *Corbicula fluminea* are in the family Sphaeriidae. The family designation Pisidiidae has also been commonly applied to this group, but the International Commission of Zoological Nomenclature (ICZN) placed the Sphaeriidae (Name number 573) on the Official List of Family Names (Opinion 1331) in 1985; hence, Sphaeriidae is used as the family designation in this key and the rest of the chapter. In North America, the Sphaeriidae comprise the dominant bivalve fauna in small, often ephemeral ponds, lakes, and streams, the profundal portions of lakes and in silty substrata. Identification is generally based upon shell morphology but requires, in some cases, soft tissue morphology.

1a.	Shells large (maximum adult shell length > 25 mm), thick and massive	family Corbiculidae	2
1b.	Shells generally small (maximum adult shell length < 25 mm), thin and generally fragile	family Sphaeriidae	4
2a(1a).	Maximum adult shell length generally < 50 mm, shell ornamented by distinct, concentric sulcations, anterior and posterior lateral teeth with many fine serrations, simultaneous hermaphrodites, massive numbers of small (length < 0.3 mm) developmental stages (> 1000) incubated directly in inner demibranchs, released juveniles (< 5 mm SL) anchor to substratum with a single mucilaginous byssal thread (Fig. 11.25)	*Corbicula*	3
2b.	Maximum adult shell length generally > 50 mm, shell ornamentation of many fine, closely spaced concentric striations, embryos not incubated in demibranchs, dioecious, periostracum deep brown in color, three cardinal teeth, estuarine, restricted to brackish waters in the tidal portions of rivers. *Polymesoda caroliniana* (Bosc) (Virginia to northern Florida to Texas)	*Polymesoda*	
3a(2a).	Shell nacre white with light blue, rose, or purple highlights, particularly at shell margin, muscle scars of same color intensity as rest of nacre, periostracum yellow to yellow-green or brown with outer margins always yellow or yellow-green in healthy, growing specimens, shell trigonal to ovate, umbos inflated and distinctly raised above dorsal shell margin, shell length : shell height ratio ≈ 1.06, shell length : shell width ratio ≈ 1.47, shell height : shell width ratio ≈ 1.38, concentric shell sulcations widely spaced, 1.5 sulcations/mm shell height (Hillis and Patton, 1982); introduced in the early 1900's, it has spread throughout drainage systems of the United States and coastal northern Mexico (Fig. 11.11), the "light colored shell morph" of *Corbicula* or Asian clam (Fig. 11.25B,C)	*Corbicula fluminea* (Müller)	
3b.	Shell nacre uniformly royal blue to deep purple over entire internal surface, muscle scars more darkly pigmented than rest of nacre, periostracum dark olive green to black, edges of valves in healthy, growing specimens not yellow or yellow-green, shell more ovate and laterally compressed with umbos less inflated and less distinctly raised above the dorsal shell margin than in *C. fluminea*, shell length : height ratio ≈ 1.15, shell length to width ratio ≈ 1.65, shell height : width ratio ≈ 1.43, concentric shell sulcations narrowly spaced, particularly at umbos, 2.1 sulcations/mm shell height (Hillis and Patton 1982); introduced, distribution limited to highly oligotrophic, permanent, spring-fed, calcium carbonate-rich streams in the southwestern United States (Britton and Morton 1986); (Fig. 11.11). Called the dark-colored shell morph of *Corbicula*, its taxonomic status is uncertain, electrophoretic (Hillis and Patton 1982, McLeod 1986) and physiological evidence (Cleland *et al.* 1986) suggest it to be distinct from *C. fluminea* (Fig. 11.25A,D)	*Corbicula* sp.	

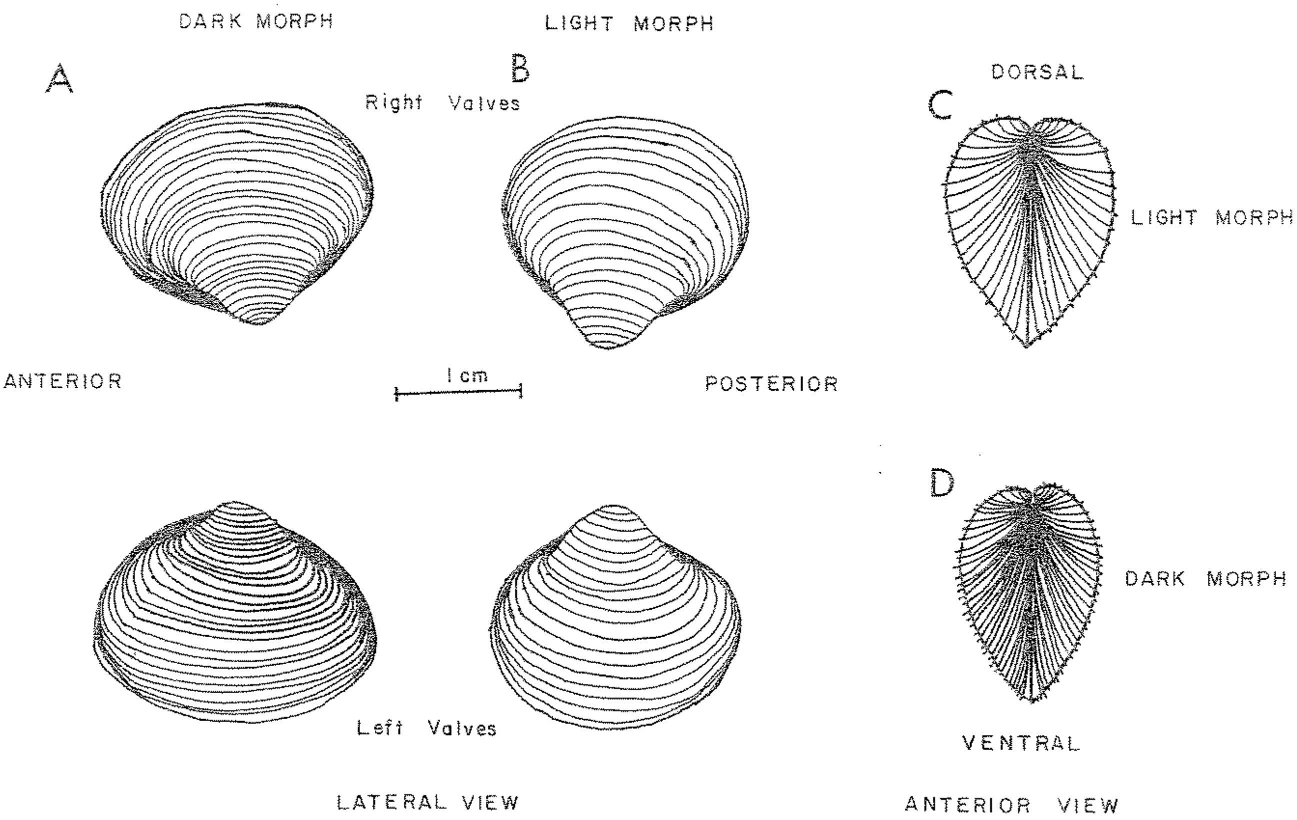


Figure 11.25 External morphology of the shell valves of the light-colored shell morph (*Corbicula fluminea*) and dark-colored shell morph (*Corbicula* sp.) of the North American *Corbicula* species complex. (A) Right and left valves of *Corbicula* sp. (dark-colored morph). (B) Right and left valves of *C. fluminea* (light-colored morph) (C) Anterior view of the shell valves of *C. fluminea* (light-colored morph). (D) Anterior view of the shell valves of *Corbicula* sp. (dark-colored morph). Note the distinguishing shell characteristics of these two species. *C. fluminea,* the white morph, which is widely distributed in North America (Fig. 11.11), has a more nearly trigonal shell, taller umbos, a greater relative shell width and more widely spaced concentric sulcations than does *Corbicula* sp., the dark morph that is limited to spring-fed, alkaline, lotic habitats in the southwestern United States (Fig. 11.11). The dark-colored shell morph also has a dark olive green to black periostracum and deep royal blue nacre, while the light-colored shell morph has a yellow-green to light brown periostracum and white to light blue or light purple nacre.

4a(1b). Both inhalant and exhalant mantle cavity siphons present and well developed, umbos lie anterior of center 5

4b. Only exhalant mantle cavity siphon present, inhalant siphon either absent or formed as a slit in the posterior-ventral mantle edges, umbos posterior of center, generally small, shell length 0.5–12 mm, embryos in inner demibranch held in thick-walled sacs, each with individual chambers for embryos, no byssal gland, 24 species widely distributed in North America; for species identifications and distributions see Burch (1975a) (Fig. 11.26A) .... subfamily Pisidiinae *Pisidium*

5a(4a). Inhalant and exhalant mantle cavity siphons partially fused, embryos incubated in inner demibranchs in thin-walled longitudinal pouches, no byssal gland, shell with two cardinal teeth in each valve, without external mottling .... subfamily Sphaeriinae 6

5b. Inhalant and exhalant siphons not fused, embryos develop in individual chambers formed between inner and outer lamellae of inner demibranchs, functional byssal gland present, only one cardinal tooth in each shell valve, with external, mottled pigmentation, *Eupera cubensis* (Prime) (Atlantic coastal plain drainages from southern Texas to North Carolina, Caribbean Islands) (Fig. 11.26B) .... subfamily Euperinae *Eupera*

6a(5a). Shell sculptured with relatively coarse or widely spaced striae (≤ 8 striae/mm in middle of shell), shell relatively massive and strong, *Sphaerium simile* (Say) (Southern Canada from New Brunswick to British Columbia, south from Virginia to Wyoming, *S. striatinum* (Lamarck) (Canada from New Brunswick to the upper Yukon River, throughout the United States, Mexico, and Central America), *S. fabale* (Prime) (Southern Ontario to Georgia and Alabama) (Fig. 11.26C) .... *Sphaerium*

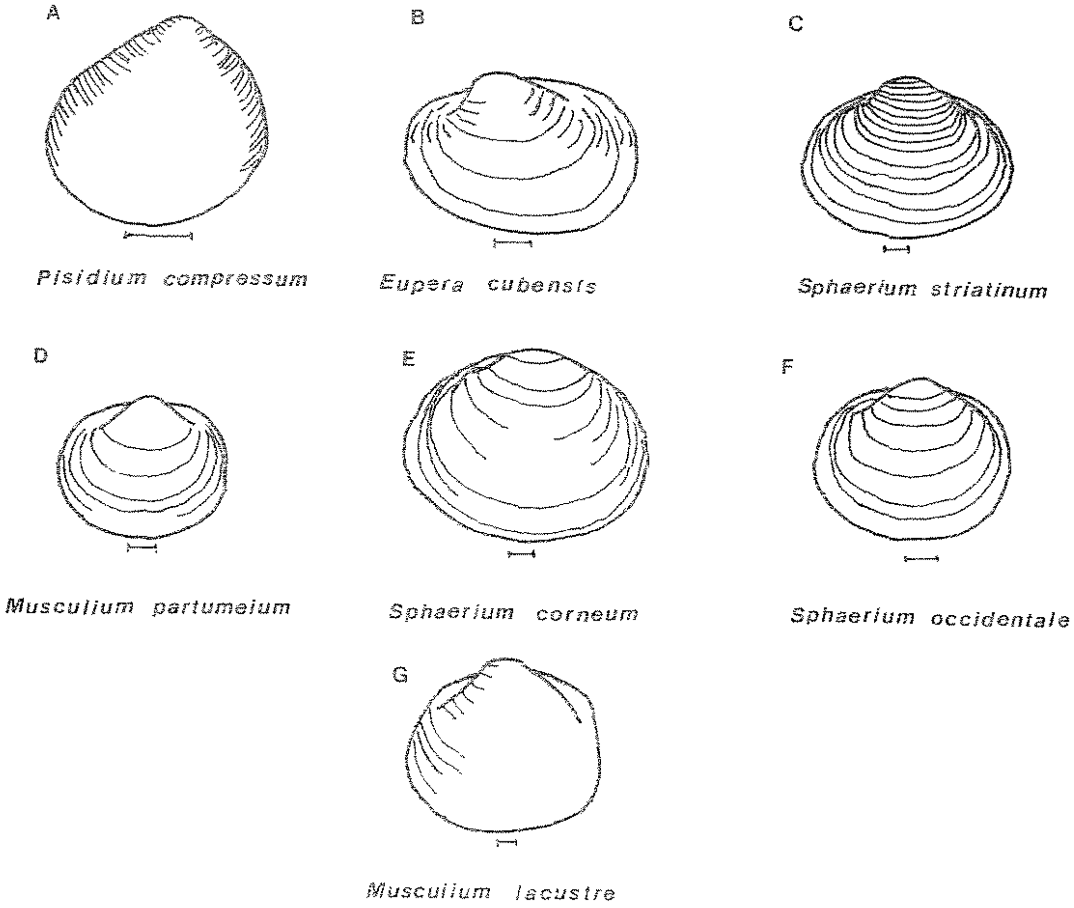
6b. Shell relatively thin, often fragile, with many fine, narrowly spaced striae (≥ 12 striae/mm in middle of shell) 7

7a(6b). Shell of adults < 8 mm in length 8

7b. Shell of adults > 8 mm in length 9

8a(7a). Posterior valve margin at near right angle to dorsal margin, shells roughly rhomboidal, umbos large and distinctly elevated above dorsal shell margin, *Musculium partumeium* (Say) (United States and southern Canada), *M. transversum* (Say) (Canada and the United States east of the continental divide, extending into Mexico), *M. securis* (Prime) (Nova Scotia to British Columbia southwestern Northwest Territories in Canada, United States except for southwest) (Fig. 11.26D) .... *Musculium*

8b. Posterior and dorsal margins rounded or forming an obtuse angle, shells ovate, *Sphaerium corneum* (Linnaeus) (introduced from Europe, localities in southern Ontario and Lakes Champlain and Erie), *S. nitidum* Westerlund (distribution is holarctic, northern Canada to northern United States), *S. occidentale* (Prime) (Canada from New Brunswick to southeastern Manitoba, northern United States south to Florida, west to Utah and Colorado) (Fig. 11.26E, F) .... *Sphaerium*



Pisidium compressum

Eupera cubensis

Sphaerium striatinum

Musculium partumeium

Sphaerium corneum

Sphaerium occidentale

Musculium lacustre

Figure 11.26 Diagrams of the external morphology of the left shell valve of species representative of the North American genera of the freshwater bivalve family, Sphaeriidae. Size scaling bar is 1 mm long.

9a(7b). Umbos large, distinctly elevated above the dorsal shell margin 10

9b. Umbos small, indistinctly elevated above the dorsal shell margin, *Sphaerium corneum* (Linnaeus), (introduced, localities in Ontario, Lakes Champlain and Erie) (Fig. 11.26E) . . . . *Sphaerium*

10a(9a). Shell rounded, umbos not prominent, *Sphaerium occidentale* (Prime) (New Brunswick to southeastern Manitoba, northern United States south to Florida in the east and Utah and Colorado in the west) (Fig. 11.26F) . . . . *Sphaerium*

10b. Posterior end of shell truncate, shell rhomboidal, umbos prominent, *Musculium lacustre* (Müller) (From treeline in Canada south throughout all but southwestern United States into central America) (Fig. 11.26G) . . . . *Musculium*

C. Taxonomic Key to Genera of Freshwater Unionacea

This key is based primarily on the excellent key to the species of North American Unionacea by Burch (1975b) with additional material from Clarke (1973) and Mackie *et al.* (1980). North America has the richest and most diverse unionacean fauna in the world including, conservatively, 227 species in 46 genera. Unionacean taxonomy remains very uncertain because intraspecific, interpopulation ecophenotypic variability often makes identification and systematics difficult. Unionacean shells lack true cardinal teeth and, when present, lateral teeth occur only posterior to pseudocardinal teeth. The Unionacea make up the large bivalve fauna (shell length > 25 mm) of permanent freshwater lakes, rivers, and ponds. Figure 11.27 displays shell-shape outlines and external shell ornamentations referred to in these taxonomic keys.

1a. Posterior mantle margins not fused to form separate anal opening, posterior mantle margins display no thickenings or other structures associated with development of inhalant or exhalant siphons, shell laterally compressed and elongated anterio-posteriorly, adults 80–175 mm in shell length . . . . family Margaritiferidae 2

1b. Posterior mantle margins forming separate anal opening, posterior mantle margins display thickenings and other structures associated with development of distinct inhalent and exhalant siphons . . . . family Unionidae 3

2a(1a). Gill interlamellar junctions scattered and in interrupted rows, but developed as continuous septa, which run obliquely forward (Burch 1975b); shell thin, fragile and highly elongated, pseudocardinal teeth reduced, umbos not distinctly elevated above dorsal shell margin, shell surface usually with heavy growth lines, *Cumberlandia monodonta* (Say) (Ohio, Tennessee and Mississippi River drainages, central United States); (Fig. 11.28A) . . . . subfamily Cumberlandiidae *Cumberlandia*

2b. Gill interlamellar junctions discontinuous, irregularly scattered or falling into oblique rows (Burch 1975b), shell generally more massive, and relatively deeper dorsoventrally than that of *Cumberlandia*, well-developed pseudocardinal teeth. External posterior surface of valves corrugated, *Margaritifera hembeli* (Conrad) (Alabama and Louisiana), external posterior surface of valves smooth, *M. margaritifera* (Linnaeus) (northern United States, east of continental divide, *M. falcata* (Gould) (drainages west of continental divide, southern Arkansas to southern California); (Fig. 11.28B) . . subfamily Margaritiferinae *Margaritifera*

3a(1b). Embryos incubated in all four demibranchs so all four demibranchs are swollen in gravid females . . . . subfamily Ambleminae 4

3b. Embryos incubated only in marsupia formed in the outer demibranchs, so these are swollen in gravid females . . . . subfamily Unioninae 16

4a(3a). Hinge teeth well developed 5

4b. Hinge teeth rudimentary or absent, *Gonidea angulata* (Lea) (west coast drainages from British Columbia to central California, east to Nevada and Idaho); (Fig. 11.28C) . . . . tribe Gonideini *Gonidea*

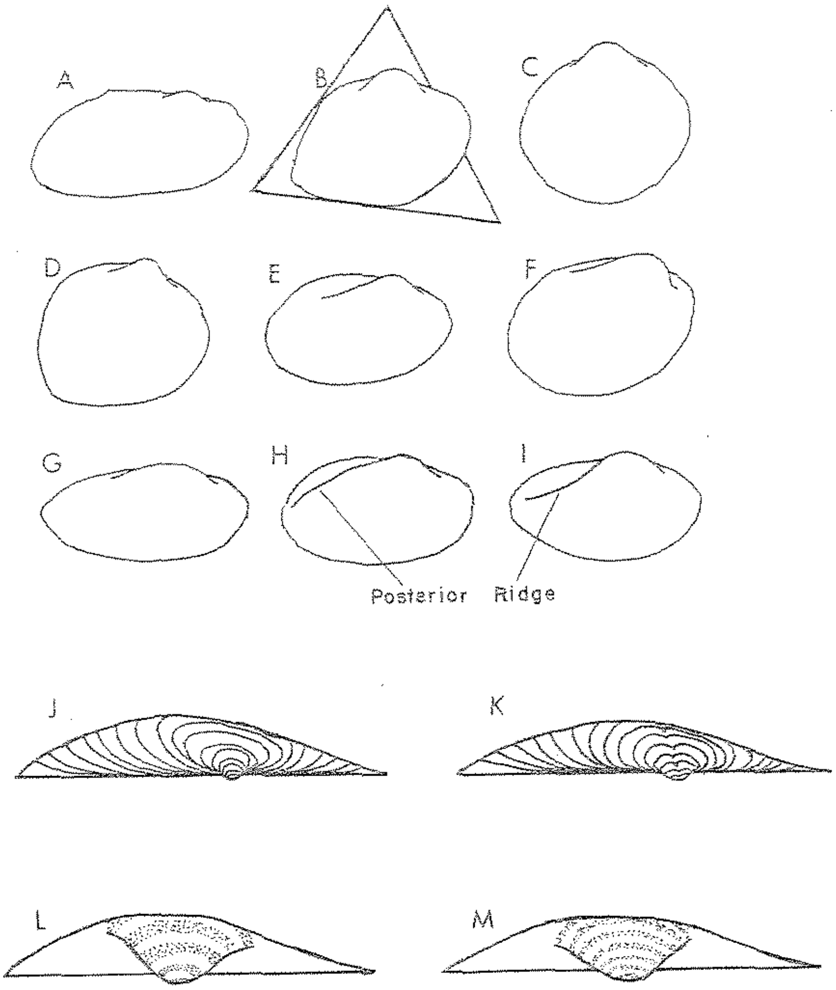


Figure 11.27 Illustrations of the diagnostic shell features or characters used for taxonomic identification in Section V.C. Shell shape descriptions: rhomboidal (A); triangular or trigonal (B); round (C); quadrate (D); oval or ovoid (E and F); and elliptical (G). Posterior shell ridge morphology: posterior ridge convex (H); and posterior ridge concave (I). Concentric ridge structures of umbos: single-looped concentric ridges (J); double-looped concentric ridges (K); coarse concentric ridges (L); and fine concentric ridges (M). (Redrawn from Burch 1975b.)

5a(4a).	Posterior shell slope with distinct pustules or corrugations		6
5b.	Posterior shell slope without distinct pustules or corrugations		14
6a(5a).	Posterior slope of shell abbreviated and steep, shell height nearly equal to shell length, *Quadrula stapes* (Alabama and Tombigbee Rivers)	tribe Amblemini	*Quadrula*
6b.	Posterior slope of shell not steep, shell generally longer than high (if not, posterior slope is not steep)		7
7a(6b).	Posterior external shell surface with distinct pustules		8
7b.	Posterior external shell surface without distinct pustules		10
8a(7a).	Shell roundly oval (shell length : height ratio slightly > 1), angular at intersection of posterior and ventral margins, *Quadrula intermedia* (Tennessee River Drainage)	tribe Amblemini	*Quadrula*
8b.	Shell length distinctly greater than height, rhomboidally shaped		9
9a(8b).	Shell with well-developed posterior ridge, small pustules covering middle and anterior portions of shell, purple to purple-pink nacre, *Tritogonia verrucosa* (Rafinesque) (drainages of the Mississippi River and coastal Gulf of Mexico slope from the Alabama River west to Texas); (Fig. 11.28D)	tribe Amblemini	*Tritogonia*

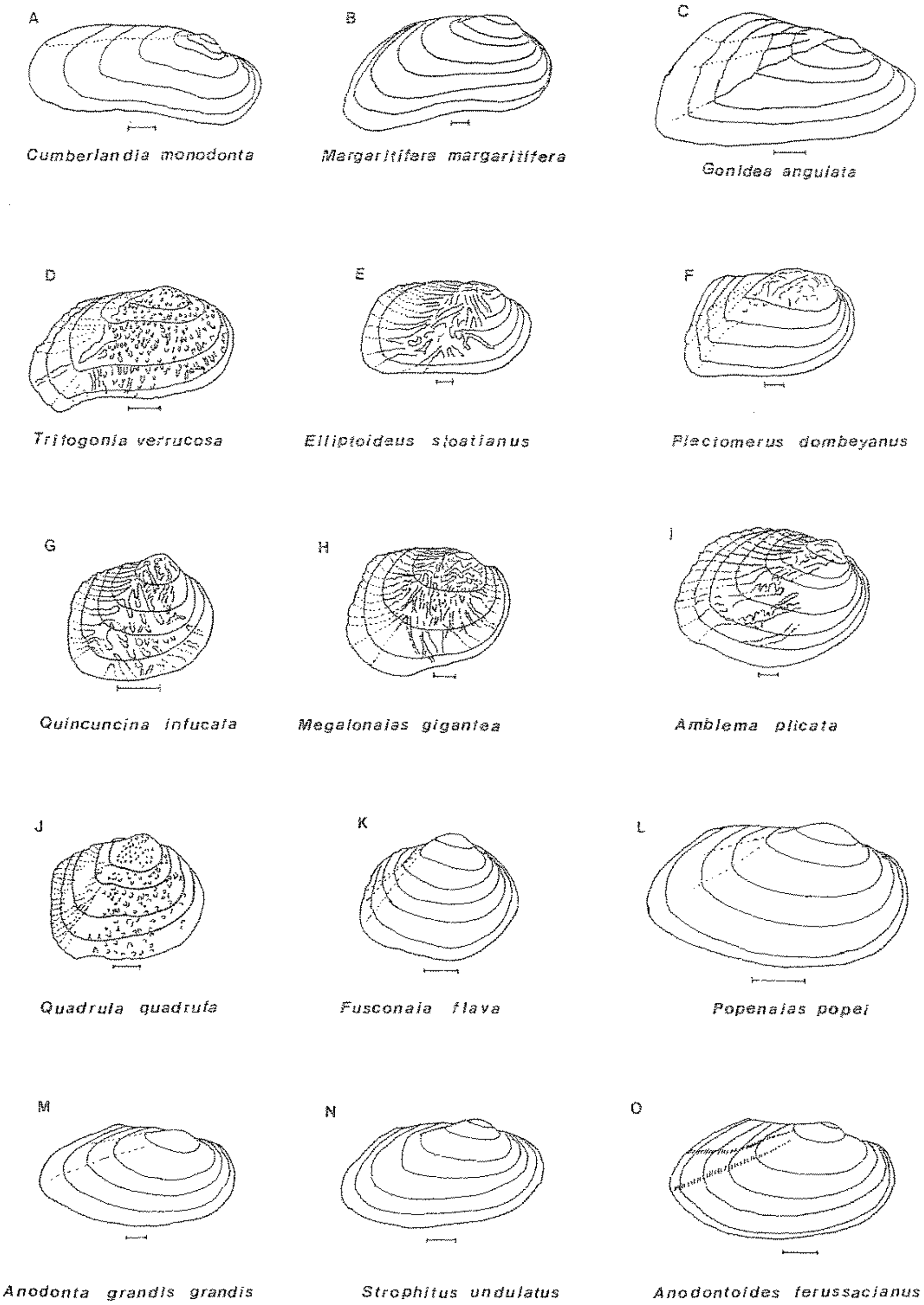
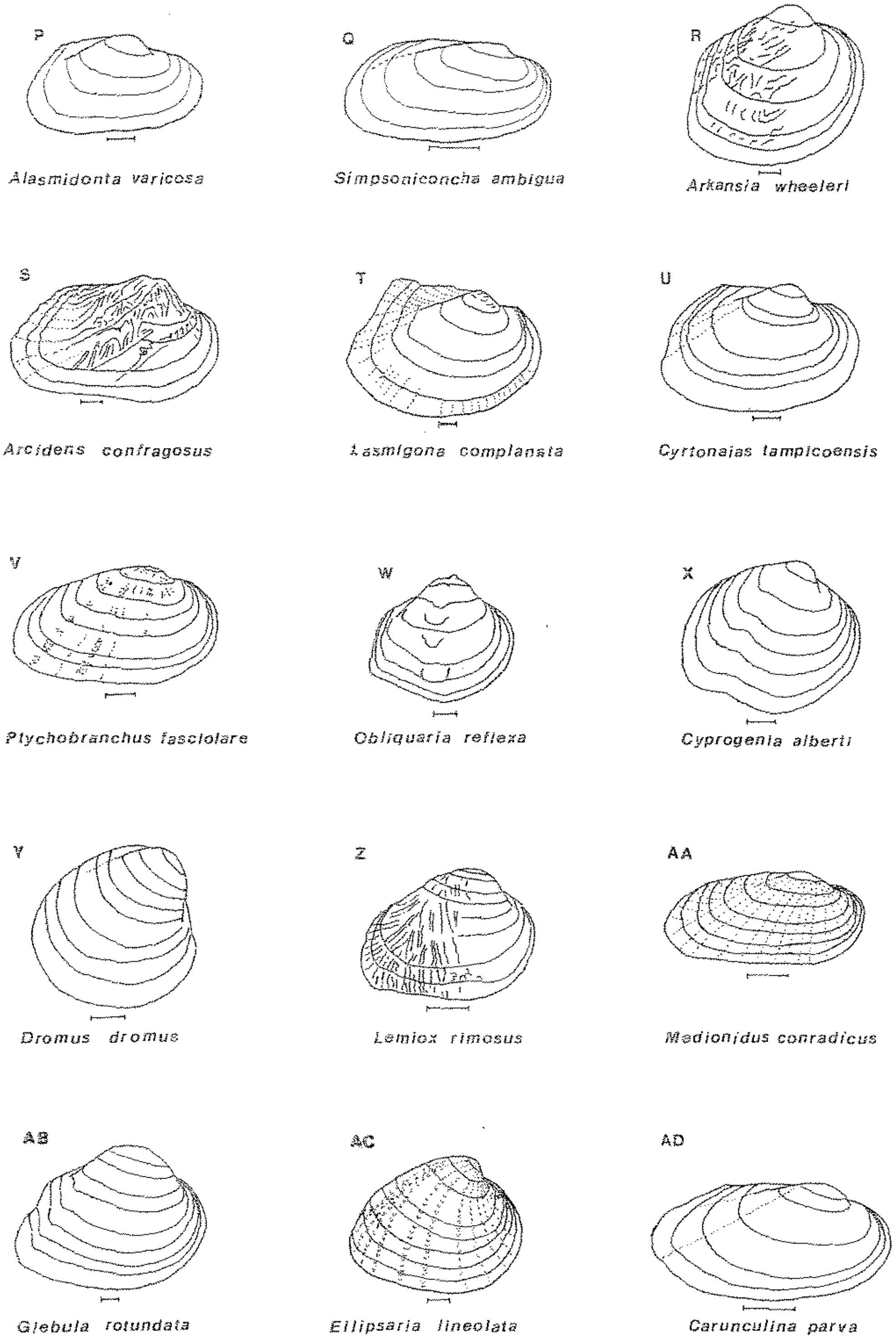


Figure 11.28 Diagrams of the external morphology of the right shell valve of species representative of the North American genera of the freshwater divalve superfamily Unionacea (Fig. 11.28A–AS). Size scaling bar is 1 cm long.

9b. Posterior ridge low, parallel row of large pustules just anterior and ventral to it, pustules less developed on anterior end, white nacre, *Quadrula cylindrica* (Say) (Ohio, Cumberland, and Tennessee River systems, south to Arkansas and Oklahoma, west to Nevada . . . tribe Amblemini *Quadrula*

10a(7b). Shell rhomboidally shaped, posterior margin relatively straight, pale violet to bronze nacre 11

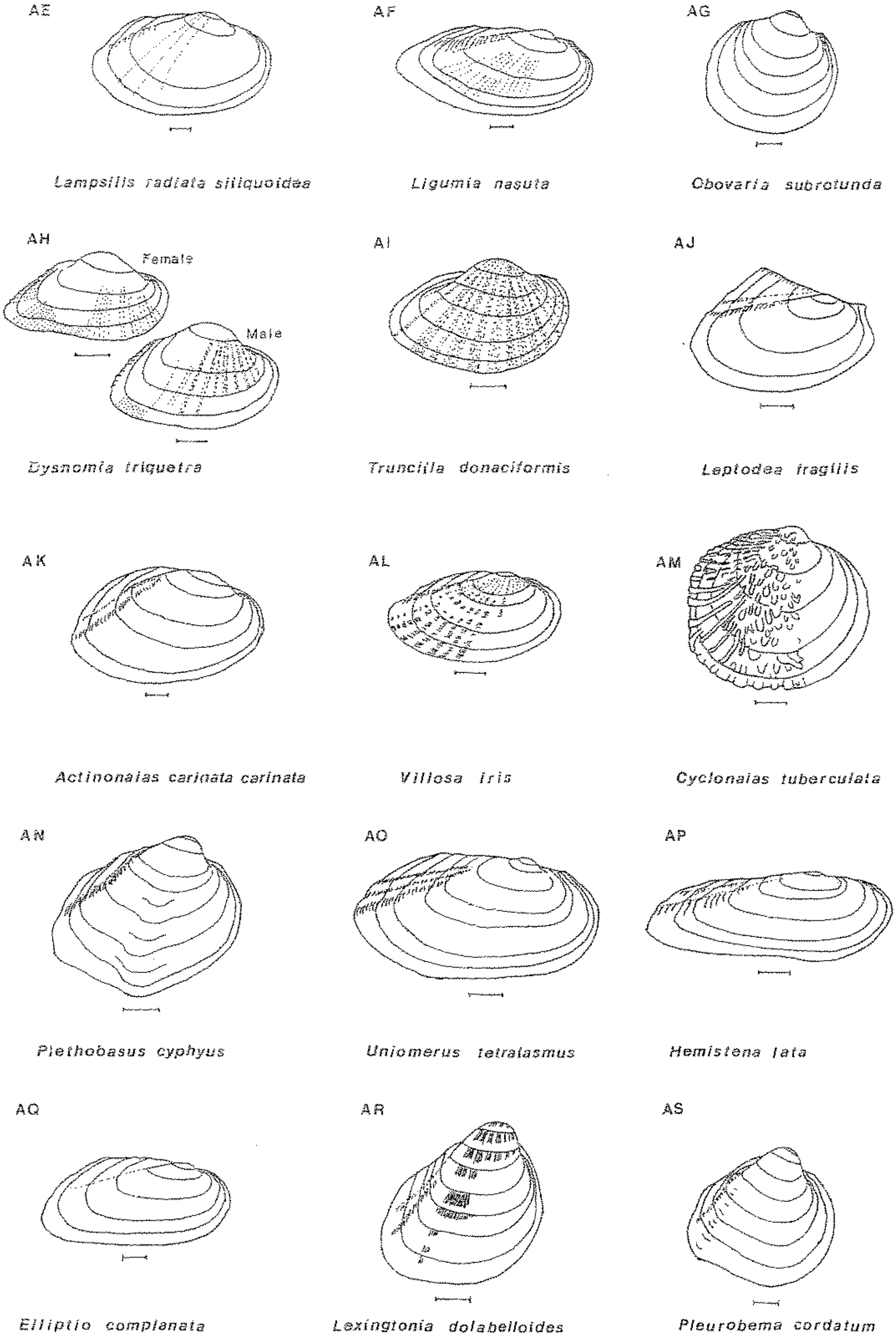


Alasmidonta varicosa
Simpsoniconcha ambigua
Arkansia wheeleri
Arcidens confragosus
Lasmigona complanata
Cyrtonaias tampicoensis
Ptychobranchus fasciolare
Obliquaria reflexa
Cyprogenia alberti
Dromus dromus
Lemiox rimosus
Medionidus conradicus
Glebula rotundata
Ellipsaria lineolata
Carunculina parva

Figure 11.28 (Continued)

10b. Shell elongate oval or round, posterior margin rounded, white nacre 12

11a(10a or 14a). Umbos indistinctly demarked from shell, anterior adductor muscle scar smooth surfaced, *Elliptoideus sloatianus* (Lea) (Apalachicola and Ochlockonee River drainages of Georgia and Florida); (Fig. 11.28E) . . . . tribe Amblemini *Elliptoideus*



Lampsilis radiata siliquoidea *Ligumia nasuta* *Obovaria subrotunda*

Dysnomia triquetra *Truncilla donaciformis* *Leptodea fragilis*

Actinonaias carinata carinata *Villosa iris* *Cyclonaias tuberculata*

Plethobasus cyphyus *Uniomerus tetralasmus* *Hemistena lata*

Elliptio complanata *Lexingtonia dolabelloides* *Pleurobema cordatum*

Figure 11.28 (Continued)

11b. Umbos distinctly demarked from shell, anterior adductor muscle scar rough surfaced, *Plectomerus dombeyanus* (Valenciennes) (coastal Gulf of Mexico slope drainages from Alabama River to eastern Texas, Mississippi drainage north to Tennessee); (Fig. 11.28F) ..... tribe Amblemini *Plectomerus*

12a(10b). Shell small (< 6 cm shell length) with either relatively indistinct or no corrugations, *Quincuncina burkei* (Walker) (Choctawhatcee River drainage, Florida), *Q. infucata* (Conrad) (Suwannee River, west to Apalachicola River, Florida), *Q. guadalupensis* Wurtz (Guadalupe and Leon Rivers, Texas); (Fig. 11.28G) .... tribe Amblemini *Quincuncina*

12b. Shell very large and massive, 13–18 cm in length with deep corrugations 13

13a(12b). Corrugations extend from umbos towards anterior margin, umbos low with large ridges extending to posterior shell margin, white to pink nacre, *Megalonaias gigantea* (Barnes), (throughout Mississippi River drainage, coastal Gulf of Mexico slope drainages from Tombigbee River, Alabama to Nuevo Leon, Mexico, and Ochlockonee River west to Escambia River in Florida Panhandle if *M. boykiniana* (Lea) is a synonym of *M. gigantea*); (Fig. 11.28H) .... tribe Megalonaiadini *Megalonaias*

13b. Corrugations not extending anterior of umbos, shell sculpture consisting of large ridges running from below prominent umbos towards the posterior shell margin, periostracum usually dark brown or black, but may be lighter in color, *Amblema neisleri* Lea (Apalachicola, Chipola, and Flint Rivers, Florida and Georgia), *A. plicata* Say (Mississippi drainage, western New York to Minnesota and eastern Kansas, Gulf of Mexico slope drainages from Texas to western Florida Panhandle, Saint Lawrence River and Great Lakes drainages with exception of those of Lake Superior, Red River of the North, and some other tributaries of Lake Winnipeg, central Canada; (Fig. 11.28I) .... tribe Amblemini *Amblema*

14a(5b). Shell rhomboidal, posterior margin relatively straight 11

14b. Shell round, oval or trigonal, posterior margin curved 15

15a(14b). Shell surface pustulose, often with corrugations, umbos well developed, posterior ridge usually well developed, nine species, occurring in the St. Lawrence and Mississippi Rivers and Gulf of Mexico slope drainages of the United States; a single species, *Quadrula quadrula* (Rafinesque) extends into Canada in the Red River of the North drainage (Clarke 1973); (Fig. 11.28J) .... tribe Amblemini *Quadrula*

15b. Shell surface smooth without pustules, with moderate posterior ridge, umbos well developed, curving anteriorly and medially with few coarse concentric ridges, nacre white, salmon, or pink, 13 species restricted to Mississippi and Gulf of Mexico slope drainages (exception is *Fusconaia flava* (Rafinesque) in the St. Lawrence River drainage, and Red River of the North and Nelson River drainages of central Canada); (Fig. 11.28K) .... tribe Amblemini *Fusconaia*

16a(3b). Exhalant water channels of demibranchs in gravid females undivided by secondary septa, glochidia without hooks (exception is genus *Proptera*, with axehead-shaped glochidia) 17

16b. Exhalant water channels of demibranchs of gravid females divided by secondary cross septa between adjacent primary septa into three channels, glochidia brooded only in middle channels (exception is genus *Strophitus*), glochidia with hooks .... tribe Anodontini 19

17a(16a). Glochidia brooded throughout smoothly swollen outer demibranchs, shells of males and females morphologically similar 18

17b. Glochidia brooded only in specific portions of outer demibranch, usually ventral portions or alternating gill lamellae, gill marsupia not smoothly swollen, instead marked by external annuli, shells of males and females usually morphologically dissimilar .... tribe Lampsilini 36

18a(17a). Bradytictic breeders retaining developing glochidia in gill marsupia throughout the year except during summer, *Popenaias buckleyi* (Lea) (Florida peninsula), *P. popei* (Lea) (southern Texas and northeast Mexico); (Fig. 11.28L) .... tribe Popenaiadini *Popenaias*

18b. Tachytictic breeders retaining glochidia in gill marsupia only during the spring and summer .... tribe Pleurobemini 58

19a(16b).	Hinge teeth absent or, if present, very reduced with only rudimentary pseudocardinal teeth, shell thin and fragile	20
19b.	Hinge teeth distinct although poorly developed in some species, shell thin to moderately thick but not fragile	33
20a(19a).	Pseudocardinal teeth absent	21
20b.	Rudimentary pseudocardinal teeth present	29
21a(20a).	Found in drainages east of the continental divide	22
21b.	Found in drainages west of the continental divide, eight species, for identifications and distributions see Burch 1975b)	*Anodonta*
22a(21a).	Umbos distinctly elevated above dorsal margin	23
22b.	Umbos not distinctly elevated above dorsal margin, four species, *Anodonta suborbiculata* Say (Mississippi and Escambia River drainages), *A. imbecilus* Say (United States east of continental divide), *A. peggyae* Johnson (eastern Alabama to Florida), *A. couperiana* Lea (Florida to North Carolina)	*Anodonta*
23a(22a).	Shell evenly inflated, not noticeably inflated posteriorly	24
23b.	Shell highly inflated posteriorly down to ventral shell margin, *Anodonta gibbosa* Say (Altamaha River drainage, Georgia)	*Anodonta*
24a(23a).	Umbo sculptured with concentric ridges, each of uniform height along its length	25
24b.	Umbo sculptured with concentric ridges with distinct nodules (nodules formed because ridge height not uniform along ridges), *Anodonta grandis grandis* Say (Canadian Interior Basin, St. Lawrence River drainage, and Gulf of Mexico drainages in Louisiana and Texas); (Fig. 11.28M)	*Anodonta*
25a(24a).	Umbos with 3–6 concentric ridges	26
25b.	Umbos with 7–10 concentric ridges, *Anodonta kennerlyi* Lea (found east of the continental divide only in western Alberta	*Anodonta*
26a(25a).	Umbos with single-looped or faintly double-looped concentric ridges; (Fig. 11.27)	27
26b.	Umbos with distinctly double-looped concentric ridges (Fig. 11.27), *Anodonta implicata* Say (coastal drainages from New Brunswick and Nova Scotia to Maryland), *Anodonta cataracta* Say (Gulf of Mexico drainages of Alabama and western Florida, Georgia to lower St. Lawrence River drainage, west to Michigan	*Anodonta*
27a(26a).	Concentric ridges of umbos relatively fine	28
27b.	Concentric ridges of umbos relatively coarse, *Strophitus undulatus* (Say) (Interior Basin from Texas to western Ontario to Saskatchewan, Atlantic coast from Nova Scotia to South Carolina); (Fig. 11.28N)	*Strophitus*
28a(27a).	Concentric ridges on umbos are parallel to growth lines, *Anodonta grandis simpsoniana* Lea (Hudson Bay and arctic Canada)	*Anodonta*
28b.	Concentric ridges on umbos cross growth lines obliquely, *Anodontoides ferussacianus* (Lea) (widely distributed in the North American Interior Basin); (Fig. 11.28O)	*Anodontoides*
29a(20b).	Pseudocardinal teeth very thin, bladelike	30
29b.	Pseudocardinal teeth more massive, tubercular	31
30a(29a).	Shell rhomboidal with distinct posterior ridge, fine, concentric corrugations on posterior slope, *Alasmidonta varicosa* (Lamarck) (lower St. Lawrence River drainage to South Carolina; (Fig. 11.28P)	*Alasmidonta*
30b.	Shell smooth, distinctly ovate without posterior ridge, *Anodontoides radiatus* (Conrad) (Gulf of Mexico drainages of Alabama, Georgia and Florida)	*Anodontoides*
31a(29b).	Posterior external slope of shell without corrugations	32

31b. Posterior external slope of shell with distinct concentric corrugations, *Alasmidonta marginata* Say (upper Mississippi drainage in Ohio, Cumberland and Tennessee Rivers, St. Lawrence drainage from Lake Huron to the Ottawa River), *A. raveneliana* (Lea) (Tennessee and Cumberland River drainages), *A. varicosa* (Lamarck) (lower St. Lawrence River drainage south to upper Savannah River drainage of South Carolina .... *Alasmidonta*

32a(31a). Shell elongately ovate, shell length : height ratio > 2, posterior ridge reduced, *Simpsoniconcha ambigua* (Say) (Ohio River drainage); (Fig. 11.28Q) .... *Simpsoniconcha*

32b. Shell roundly ovate, shell length : height ratio < 1.6 with distinct posterior ridge, *Strophitus subvexus* (Conrad) (Mississippi, Georgia and western Florida) .... *Strophitus*

33a(19b). Shell with large corrugations on disc or posterior slope 34

33b. Shell without corrugations on disc or posterior slope 35

34a(33a). Tubercules occur on first 3–4 mm of umbos, pseudocardinal teeth massive and triangular, *Arkansia wheeleri* Ortmann and Walker (Ouachita Mountains, Kiamichi and Old Rivers, Arkansas and Oklahoma); (Fig. 11.28R) .... *Arkansia*

34b. Tubercules on beak extend down onto shell, pseudocardinal teeth compressed and closely adjacent, *Arcidens confragosus* (Say) (Mississippi drainage southward from Wisconsin and Ohio, Colorado River, Texas and Bayou Teche, Louisiana; (Fig. 11.29S) .... *Arcidens*

35a(33b). Ridges of umbos smoothly concentric without a dorsally directed indentation (single-looped, Fig. 11.27), 11 species, identifications and distributions in Burch (1975b) .... *Alasmidonta*

35b. Concentric ridges of umbos not smoothly concentric but interrupted by a dorsally directed identation (double-looped, Fig. 11.27), five species, identifications and distributions in Burch (1975b); (Fig. 11.28T) .... *Lasmigona*

36a(17b). Glochidia incubated only in ventral portion of outer demibranchs 37

36b. Glochidia incubated only in central or posterior portion of outer demibranchs 38

37a(36a). Ventral, outer marsupial demibranch edge smooth, without folds, shell ovate, inflated, *Cyrtonaias tampicoensis* (Lea) (southeastern Texas to northeastern Mexico and Honduras); (Fig. 11.28U) .... subtribe Longenae *Crytonaias*

37b. Ventral edge of outer marsupial demibranch with 6–20 distinct folds, shell laterally compressed, elongated, subelliptical or rhomboidal, five species, identifications and distributions in Burch (1975a); (Fig. 11.28V) .... subtribe Ptychogenae, *Ptychobranchus*

38a(36b). Marsupium restricted to central portion of outer demibranch ...... subtribe Mesogenae 39

38b. Marsupium restricted to posterior portion of outer demibranch .... subtribe Heterogenae 40

39a(38a). Shell with 3–5 very large tubercules in single medial row extending dorsoventrally, shell roundly ovate, massive hinge teeth, *Obliquaria reflexa* Rafinesque (Mississippi River drainage); (Fig. 11.28W) .... *Obliquaria*

39b. Shell with numerous, various-sized tubercules, pustules or corrugations, without single medial row of large tubercules, *Cyprogenia aberti* (Conrad) (Kansas, Missouri, Oklahoma and Arkansas), *C. irrorata* (Lea) (Ohio, Cumberland, and Tennessee River drainages); (Fig. 11.28X) .... *Cyprogenia*

40a(38b). Marsupium occupies entire posterior portion of the outer demibranch .... subtribe Heterogenae 41

40b.	Marsupium restricted to ventral posterior portion of outer demibranch, *Dromus dromus* (Lea) (Tennessee and Cumberland River drainages); (Fig. 11.28Y) .... subtribe Eschatigenae	*Dromus*
41a(40a).	Posterior slope of shell transversely corrugated	42
41b.	Posterior slope of shell either smooth or radially corrugated	43
42a(41a).	Shell roundly ovate, corrugations cover posterior half of shell extending to ventral margin, *Lemiox rimosus* Rafinesque (Tennessee River drainage); (Fig. 11.28Z)	*Lemiox*
42b.	Shell elongately ovate without radiating corrugations extending to ventral margin, five species (identifications and distributions in Burth 1975b); (Fig. 11.28AA)	*Medionidus*
43a(41b).	Posterior pseudocardinal teeth are deeply divided into parallel, vertical, plicate lamellae (Fig. 11.29), umbos large, inflated, *Glebula rotundata* (Lamarck) (Gulf of Mexico drainages from eastern Texas to Florida panhandle); (Fig. 11.28AB)	*Glebula*
43b.	Posterior pseudocardinal teeth not deeply divided into parallel, vertical lamellae, umbos relatively small	44
44a(43b).	Shell trigonal, dorsal margin arched, laterally compressed, posterior transverse slope reduced and at 90° angle to disc, no wing (Fig. 11.30) extending from dorsal shell margin posterior to hinge, hinge teeth large and massive, *Ellipsaria lineolata* (Rafinesque) (Mississippi, Tombigbee, and Alabama River drainages): (Fig. 11.28AC)	*Ellipsaria*

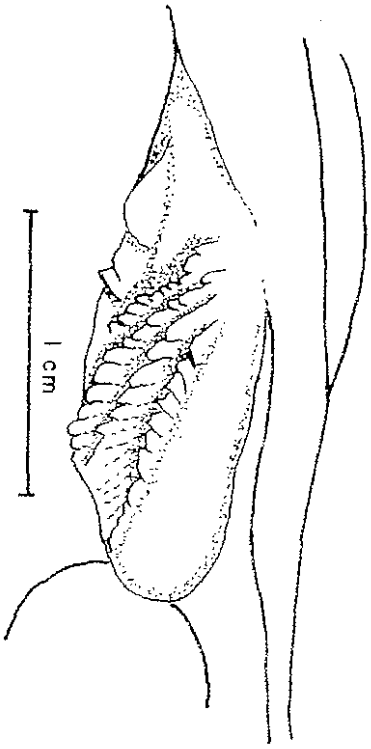


Figure 11.29 Structure of the posterior pseudocardinal teeth of the right valve of *Glebula rotundata*. Note that the posterior pseudocardinal teeth are deeply divided into parallel, vertical, plicate lamellae, a tooth arrangement uniquely characteristic of this species. (Redrawn from Burch 1975b.)

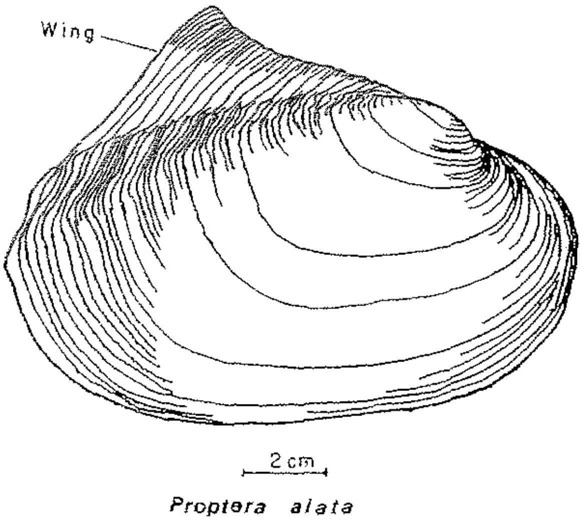


Figure 11.30 Right shell valve of the unionid, *Proptera alata*, showing the thin, extensive dorsal projection of the shell posterior to the umbos forming a "wing" whose presence or absence is a diagnostic characteristic valuable for identification of a number of unionid species. (Redrawn from Burch 1975b.)

44b.	Shell does not display above suite of characteristics, if high, dorsal margin is not generally greatly arched; if arched, shell is inflated, not laterally compressed with a more obtuse posterior slope	45
45a(44b).	In females, inner mantle edges have a well-developed caruncle (Fig. 11.31A) formed from a group of short, crowded papillae just ventral and anterior to the inhalant siphon, adults are small, usually < 4 cm in length, *Carunculina parva* (Barnes) (Mississippi drainage and Florida), *C. pulla* (Conrad) (Georgia to North Carolina); (Fig. 11.28AD)	*Carunculina*
45b.	Females without caruncles on inner mantle edges just ventral and anterior to inhalant siphon, adult shell length generally > 4 cm	46
46a(45b).	Shell elongately ovate, shell length : height ratio > 2	47
46b.	Shell roundly ovate, shell length : height ratio < 2	48
47a(46a, 51b, or 57b).	In females, there is a flap of tissue projecting from the inner mantle edge just ventral and posterior to the inhalant mantle cavity siphon; on medial side, flaps are often colored, and have a black streak and a darkly pigmented spot (Figs. 11.16 and 11.31B); in males, the flaps are rudimentary in structure, 22 species distributed throughout North America, east of the continental divide, species identifications and distributions in Burch (1975b); (Figs. 11.16 and 11.28AE)	*Lampsilis*
47b.	In females, there are a distinct series of papillae projecting from the inner mantle edges just ventral and anterior to the inhalant mantle cavity siphon (Fig. 11.31C); papillae are rudimentary in males, *Ligumia nasuta* (Say) (eastern United States north to the St. Lawrence River drainage of Canada, if *L. Subrostrata* (Say) is a synonym of *L. nasuta*), *L. recta* (Lamarck) (Mississippi, Alabama, and St. Lawrence River drainages, Winnipeg and Red River of the North drainages of Canadian Interior Basin); (Fig. 11.28AF)	*Ligumia*
48a(46b).	Shell round or high oval dorsoventrally (exception is *Obovaria jacksoniana* Frierson, which has a somewhat elongated posterior slope), pseudocardinal teeth massive, five species, identifications and distributions in Burch (1975b); (Fig. 11.28AG)	*Obovaria*

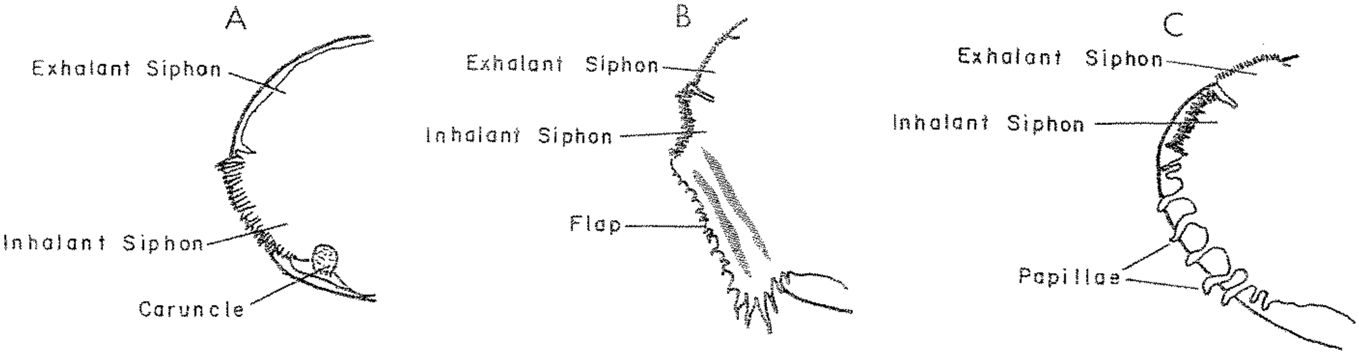


Figure 11.31 Accessory reproductive structures formed from extensions of the posterior mantle edge of female unionids: (A) a caruncle characteristic of the genus *Carunculina;* (B) a mantle flap characteristic of the genus *Lampsilis;* (C) fine papillae or projections characteristic of the genus *Villosa*. In some species, these projections mimic prey of the glochidial fish hosts of a particular unionid species, luring them close to the point of glochidial release. (Redrawn from Burch 1975b.)

48b.	Shell elongate, subelliptical, subrhomboidal, trigonal or oval, pseudocardinal teeth may or may not be massive	49
49a(48b).	Adult shell small, usually < 6 cm in length and massive, sexual dimorphism, females with shell inflated over marsupial portion of outer demibranchs, in some species radiating ridges on posterior slope, 19 species, (southern Canada and eastern United States, Mississippi drainages and Gulf of Mexico slope drainages east of Mississippi River), identifications and distributions in Burch (1975b); (Fig. 11.28AH)	*Dysnomia*
49b.	Shell without above described suite of characteristics	50
50a(49b).	Posterior ridge well developed and angular	51
50b.	Posterior ridge rounded or absent	52
51a(50a).	Shell laterally compressed, umbo cavities shallow, with radiating color bands with or without v-shaped markings, *Truncilla donaciformis* (Lea) (Mississippi, Lake Erie, and Lake St. Clair drainages), *T. macrodon* (Lea) (Texas and Oklahoma), *T. truncilla* Rafinesque (Mississippi, Lake Erie, and Lake St. Clair drainages); (Fig. 11.28AI)	*Truncilla*
51b.	Shell inflated with deep umbo cavities, some species with radiating color bands (without v-shaped markings), others without color bands	47
52a(50b).	Pseudocardinal teeth well developed	53
52b.	Pseudocardinal teeth small or vestigial, four species (St. Lawrence drainage of Canada and United States east of the continental divide), for species identifications and distributions see Burch (1975b); (Fig. 11.28AJ)	*Leptodea*
53a(52a).	Shell with an extensive wing (dorsal extension of the shell posterior to umbos, Fig. 11.30), *Proptera alata* (Say) (Mississippi drainages, St. Lawrence drainage from Lake Huron to Lake Champlain, Red River of the North and Winnipeg River drainages of Canadian Interior Basin); (Fig. 11.30)	*Proptera*
53b.	Shell wing absent or poorly developed	54
54a(53b).	Shell extremely inflated with fine sculpture on umbos, *Proptera capax* (Green) (lower Ohio River drainage)	*Proptera*
54b.	Shell not extremely inflated, or if inflated, has coarse sculpture on umbos	55
55a(54b).	Adult shell large (up to 11.5 cm), nacre purple, *Proptera purpurata* (Lamarck) (eastern Texas, north to Kansas and southern Missouri, western Tennessee to Alabama River drainage)	*Proptera*
55b.	Shell nacre usually white but not purple, may be pinkish-purple in smaller specimens (< 6 cm in SL)	56
56a(55b).	May have crenulations on inner mantle edge just ventral and anterior to inhalant mantle cavity siphon, but without projecting papillae or flaps in this area (see Figs. 11.31B and C for descriptions of mantle papillae or flaps), four species, identifications in Burch (1975b) (Mississippi, Ohio, Tennessee, Cumberland, and St. Lawrence River drainages); (Fig. 11.28AK)	*Actinonaias*
56b.	Distinct papillae or flaps project from inner mantle margin just ventral and anterior to the inhalant mantle cavity siphon (Fig. 11.31B, C)	57
57a(56b).	Long papillae project from posterior inner mantle margins (Fig. 11.31C), 16 species, identifications and distributions in Burch (1975b); (Fig. 11.28AL)	*Villosa*

57b.	Distinct flaps formed on inner mantle edges (Fig. 11.25B)	47
58a(18b).	Pustules on shell surface	59
58b.	Shell surface without pustules	60
59a(58a).	Shell rounded with purple nacre, *Cyclonaias tuberculata* (Rafinesque) (Mississippi drainage, Lake St. Clair drainage, Detroit River and Lake Erie; (Fig. 11.28AM)	*Cyclonaias*
59b.	Shell more ovate, junction of posterior and ventral margins more angular, pustules either cover posterior slope in *Plethobasus cooperianus* (Lea) (Cumberland and Tennessee River drainages) or are limited to a central medial row in *P. cyphyus* (Rafinesque) (Ohio, Cumberland, and Tennessee River drainages, Mississippi drainage north to Missouri and Minnesota; (Fig. 11.28AN)	*Plethobasus*
60a(58b).	Pseudocardinal teeth reduced in size, poorly developed or vestigial	61
60b.	Pseudocardinal teeth robust and well developed	62
61(60a).	Pseudocardinal teeth present, although reduced in size, *Uniomerus tetralasmus* (Say) (Mississippi drainage north to Ohio River, and west to Colorado, Rio Grande drainage, Gulf of Mexico drainages from Texas east to Florida, north to North Carolina; (Fig. 11.28AO)	*Uniomerus*
61b.	Pseudocardinal teeth poorly developed or vestigial, *Hemistena lata* (Rafinesque) (Ohio, Cumberland, and Tennessee River drainages); (Fig. 11.28AP)	*Hemistena*
62a(60b).	Shells generally elevated dorsoventrally, dorsoventrally ovate or roundly oval with some species elliptical, umbos prominent and curving anteriorly well above dorsal margin, white to occasionally pinkish nacre	63
62b.	Shells elongately ovate or rhomboidal (if low triangular, are broadly elliptical or oval with purple nacre), umbos not distinctly elevated above dorsal margin or curving anteriorly, nacre usually purple but may be pink or irridescent, 19 species broadly distributed in North America east of the Continental Divide from Hudson Bay drainages on the north, south to drainages on the Gulf of Mexico coastal slope of The United States, identifications and distributions in Burch (1975b); (Fig. 11.28AQ)	*Elliptio*
63a(62a).	Outer (marsupial) demibranchs of females are deep orange or red when incubating developmental stages and glochidia, *Lexingtonia dolabelloides* (Lea) (Tennessee River drainage), *L. subplana* (Conrad) (North River, Virginia); (Fig. 11.28AR)	*Lexingtonia*
63b.	Outer (marsupial) demibranchs of females are white, grayish, yellowish or, rarely, pale orange, not deep orange or red when incubating developmental stages and glochidia; the systematic status of this genus has not been thoroughly addressed, making species identification difficult, Burch (1975b) lists 32 species, widely distributed in the eastern United States, species distributions in Burch (1975b); (Fig. 11.28AS)	*Pleuroblema*

ACKNOWLEDGMENTS

This chapter is dedicated to David W. Aldridge, Roger A. Byrne, John D. Cleland, David F. Holland, Diana M. Kropf, David P. Long, and Carol J. Williams, all graduate student associates involved with my studies of freshwater bivalves. Brad Shipman and Joseph C. Britton, Gerald Elick, Thomas H. Dietz, Barry S. Payne, and Neal J. Smatresk continue to collaborate in these studies. W. D. Russell-Hunter first introduced me to the study of freshwater molluscs and has been an unfailing colleague through the years. Carl M. Way and Daniel J. Hornbach kindly provided the scanning electron micrographs of freshwater bivalve gill ciliation presented in this chapter. Sussana Lamers assisted with the literature search and organization of library resources. Paula Smallwood provided secretarial assistance and technical support. Joseph C. Britton (Texas Christian University) Gerry L. Mackie (University of Guelph) and Carl M. Way (U.S. Army Corps of Engineers, Waterways Experiment Station, Environmental Laboratory), critically reviewed and made important contributions to an initial draft of the manuscript. An invaluable critical review of the penultimate draft of the manuscript was provided by James H. Thorp, University of Louisville. David F. Holland, Michael L. Moeller, and Randal T. Melton assisted with editing and preparation of the final draft of the manuscript.

LITERATURE CITED

Adam, M. E. 1986. The Nile bivalves: How do they avoid silting during the flood? Journal of Molluscan Studies 52:248–252.

Ahlstedt, S. A. 1983. The Mollusca of the Elk River in Tennessee and Alabama. American Malacological Bulletin 1:43–50.

Aldridge, D. W., and R. F. McMahon. 1978. Growth, fecundity, and bioenergetics in a natural population of the Asiatic freshwater clam, *Corbicula manilensis* Philippi, from north central Texas. Journal of Molluscan Studies 44:49–70.

Aldridge, D. W., B. S. Payne, and A. C. Miller. 1987. The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. Environmental Pollution 45:17–28.

Alexander, J. P. 1982. Energetics of a lake population of the freshwater clam, *Musculium lacustre* Müller (Bivalvia: Pisidiidae), with special reference to seasonal patterns of growth, reproduction and metabolism. Master's Thesis, University of Dayton, Dayton, Ohio.

Allen, A. J. 1985. Recent Bivalva: their form and evolution. Pages 337–403 *in:* E. R. Trueman and M. R. Clarke, editors. The Mollusca. Vol. 10: Evolution. Academic Press, New York.

Annis, C. G., and T. V. Belanger. 1986. *Corbicula manilensis*, potential bio-indicator of lead and copper pollution. Florida Scientist 49:30.

Barnes, R. D. 1986. Invertebrate zoology. 5th Edition. Saunders, Philadelphia, Pennsylvania.

Bauer, G. 1983. Age structure, age specific mortality rates and population trend of the freshwater pearl mussel (*Margaritifera margaritifera*) in north Bavaria. Archiv fuer Hydrobiologie 98:523–532.

Belanger, S. E., J. L. Farris, D. S. Cherry, and J. Cairns, Jr. 1985. Sediment preference of the freshwater Asiatic clam, *Corbicula fluminea*. Nautilus 99:66–73.

Belanger, S. E., D. S. Cherry, and J. Cairns, Jr. 1986a. Uptake of chrysotile asbestos fibers alters growth and reproduction of Asiatic clams. Canadian Journal of Fisheries and Aquatic Sciences 43:43–52.

Belanger, S. E., J. L. Farris, D. S. Cherry, and J. Cairns, Jr. 1986b. Growth of Asiatic clams (*Corbicula* sp.) during and after long-term zinc exposure in field-located and laboratory artificial streams. Archives of Environmental Contamination and Toxicology 15:427–434.

Balanger, S. E., D. S. Cherry, J. Cairns, Jr., and M. J. McGuire. 1987. Using Asiatic clams as a biomonitor for chrysotile asbestos in public water supplies. Journal of the American Water Works Association 79:69–74.

Bisbee, G. D. 1984. Ingestion of phytoplankton by two species of freshwater mussels, the black sandshell, *Ligumia recta*, and the three ridger, *Amblema plicata*, from the Wisconsin River in Oneida County, Wisconsin. Bios 58:219–225.

Bishop, S. H., L. L. Ellis, and J. M. Burcham. 1983. Amino acid metabolism in molluscs. Pages 243–327 *in:* P. W. Hochachka, editor. The Mollusca. Vol. 1: Metabolic biochemistry and molecular biomechanics. Academic Press, New York.

Blye, R. W., W. S. Ettinger, and W. N. Nebane. 1985. Status of Asiatic clam (*Corbicula fluminea*) in south eastern Pennsylvania—1984. Proceedings of the Pennsylvania Academy of Science 59:74.

Bonaventura, C., and J. Bonaventura. 1983. Respiratory pigments: Structure and function. Pages 1–50 *in:* P. W. Hochachka, editor. The Mollusca. Vol. 2: Environmental chemistry and physiology. Academic Press, New York.

Britton, J. C., and B. Morton. 1986. Polymorphism in *Corbicula fluminea* (Bivalvia: Corbiculidae) from North America. Malacological Review 19:1–43.

Burch, J. B. 1975a. Freshwater sphaeriacean clams (Mollusca: Pelecypoda) of North America. Malacological Publications, Hamburg, Michigan.

Burch, J. B. 1975b. Freshwater unionacean clams (Mollusca: Pelecypoda) of North America. Malacological Publications, Hamburg, Michigan.

Burky, A. J. 1983. Physiological ecology of freshwater bivalves. Pages 281–327 *in:* W. D. Russell-Hunter, editor. The Mollusca. Vol. 6: Ecology. Academic Press, New York.

Burky, A. J., and K. A. Burky. 1976. Seasonal respiratory variation and acclimation in the pea clam, *Pisidium walkeri* Sterki. Comparative Biochemistry and Physiology. 55A:109–114.

Burky, A. J., D. J. Hornbach, and C. M. Way. 1981. Growth of *Pisidium casertanum* (Poli) in west central Ohio. Ohio Journal of Science 81:41–44.

Burky, A. J., R. B. Benjamin, D. G. Conover, and J. R. Detrick. 1985a. Seasonal responses of filtration rates to temperature, oxygen availability, and particle concentration of the freshwater clam *Musculium partumeium* (Say). American Malacological Bulletin 3:201–212.

Burky, A. J., D. J. Hornbach, and C. M. Way. 1985b. Comparative bioenergetics of permanent and temporary pond populations of the freshwater clam, *Musculium partumeium* (Say). Hydrobiologia 126:35–48.

Burton, R. F. 1983. Ionic regulation and water balance. Pages 292–352 *in:* A. S. M. Saleuddin and K. M. Wilbur, editors. The Mollusca. Vol. 5: Physiology, Part 2. Academic Press, Orlando, Florida.

Buttner, J. K. 1986. *Corbicula* as a biological filter and polyculture organism in catfish rearing ponds. Progressive Fish-Culturist 48:136–139.

Butts, T. A., and R. E. Sparks. 1982. Sediment oxygen demand—fingernail clam relationship in the Mississippi River Keokuk Pool. Transactions of the Illinois Academy of Sciences 75:29–39.

Byrne, R. A. 1988. Physiological and behavioral responses to aerial exposure in the Asian clam, *Corbicula fluminea* (Müller). Ph.D. Thesis, Louisiana State University, Baton Rouge.

Byrne, R. A., R. F. McMahon, and T. H. Dietz. 1988. Temperature and relative humidity effects on aerial exposure tolerance in the freshwater bivalve *Corbicula fluminea*. Biological Bulletin (Woods Hole, Mass.) 175:253–260.

Cairns, J., Jr., and D. S. Cherry. 1983. A site-specific field and laboratory evaluation of fish and Asiatic clam population responses to coal fired power plant discharges. Water Science and Technology 15:31–58.

Calow, P. 1983. Life-cycle patterns and evolution. Pages 649–678 *in:* W. D. Russell-Hunter, editor. The Mollusca. Vol. 6: Ecology. Academic Press, New York.

Charlesworth, B. 1980. Evolution in age structured-populations. Cambridge University Press, London.

Cherry, D. S., J. H. Rodgers, Jr., R. L. Graney, and J. Cairns, Jr. 1980. Dynamics and control of the Asiatic clam in the New River, Virginia. Bulletin of the Virginia Water Resources Center 123:1–72.

Clarke, A. H. 1973. The freshwater molluscs of the Canadian interior basin. Malacologia 13:1–509.

Clarke, A. H. 1983. The distribution and relative abundance of *Lithasia pinguis* (Lea), *Pleurobema plenum* (Lea), *Villosa trabalis* (Conrad), and *Epioblasma sampsoi* (Lea). American Malacological Bulletin 1: 27–30.

Cleland, J. D. 1988. Ecological and physiological considerations of deposit-feeding in a freshwater bivalve, *Corbicula fluminea*. Master's Thesis, The University of Texas at Arlington.

Cleland, J. D., R. F. McMahon, and G. Elick. 1986. Physiological differences between two morphotypes of the Asian clam, *Corbicula*. American Zoologist 26: 103A.

Cohen, R. R. H., P. V. Dresler, E. P. J. Phillips, and R. L. Cory. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. Limnology and Oceanography 29:170–180.

Collins, T. W. 1967. Oxygen-uptake, shell morphology and dessication of the fingernail clam, *Sphaerium occidentale* Prime. Ph.D. Thesis, University of Minnesota, Minneapolis.

Cooper, C. M. 1984. The freshwater bivalves of Lake Chicot, an oxbow of the Mississippi in Arkansas. Nautilus 98:142–145.

Counts, C. L., III. 1986. The zoogeography and history of the invasion of the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). American Malacological Bulletin, Special Edition No. 2:7–39.

Covich, A. P., L. L. Dye, and J. S. Mattice. 1981. Crayfish predation on *Corbicula* under laboratory conditions. American Midland Naturalist 105:181–188.

Dance, S. P. 1958. Drought resistance in an African freshwater bivalve. Journal of Conchology 24:281–282.

Das, V. M. M., and S. A. T. Venkatachari. 1984. Influence of varying oxygen tension on the oxygen consumption of the freshwater mussel *Lamellidens marginalis* (Lamarck) and its relation to body size. Veliger 26:305–310.

Davis, D. S., and J. Gilhen. 1982. An observation of the transportation of pea clams, *Pisidium adamsi*, by blue-spotted salamanders, *Ambystoma laterale*. The Canadian Naturalist 96:213–215.

Davis, W. L., R. G. Jones, J. P. Knight, and H. K. Hagler. 1982. An electron microscopic histochemical and x-ray microprobe study of spherites in a mussel. Tissue and Cell 14:61–67.

Deaton, L. E. 1982. Tissue (NA + K)-activated adenosinetriphosphatase activities in freshwater and brackish water bivalve molluscs. Marine Biology Letters 3:107–112.

de Zwaan, A. 1983. Carbohydrate catabolism in bivalves. Pages 137–175 *in:* P. W. Hochachka, editor. The Mollusca. Vol. 1: Metabolic biochemistry and molecular biomechanics. Academic Press, New York.

Dietz, T. H. 1974. Body fluid composition and aerial oxygen consumption in the freshwater mussel, *Ligumia subrostrata* (Say): effects of dehydration and anoxic stress. Biological Bulletin (Woods Hole, Mass.) 147:560–572.

Dietz, T. H. 1985. Ionic regulation in freshwater mussels: a brief review. American Malacological Bulletin 3:233–242.

Dietz, T. H., J. I. Scheide, and D. G. Saintsing. 1982. Monoamine transmitters and cAMP stimulation of Na transport in freshwater mussels. Canadian Journal of Zoology 60:1408–1411.

Doherty, F. G., D. S. Cherry, and J. Cairns, Jr. 1987. Valve closure responses of the Asiatic clam *Corbicula fluminea* exposed to cadmium and zinc. Hydrobiologia 153:159–167.

Dreier, H. 1977. Study of *Corbicula* in Lake Sangchris. Pages 7.1–7.52 *in:* The annual report for fiscal year 1976, Lake Sangchris project, Section 7. Illinois Natural History Survey, Urbana.

Dreier, H., and J. A. Tranquilli. 1981. Reproduction, growth, distribution, and abundance of *Corbicula* in an Illinois cooling lake. Illinois Natural History Survey Bulletin 32:378–393.

Duncan, R. E., and P. A. Thiel. 1983. A survey of the mussel densities in Pool 10 of the upper Mississippi River. Technical Bulletin No. 139. Wisconsin Department of Natural Resources, Madison. 14 pp.

Dyduch-Falniowska, A. 1982. Oscillations in density and diversity of *Pisidium* communities in two biotopes in southern Poland. Hydrobiological Bulletin 16:123–132.

Elder, J. F., and H. C. Mattraw, Jr. 1984. Accumulation of trace elements, pesticides, and polychlorinated biphenyls in sediments and the clam *Corbicula manilensis* of the Apalachicola River, Florida. Archives of Environmental Contamination and Toxicology 13:453–469.