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## CHAPTER 8 Clams and Mussels (Mollusca: Bivalvia)

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I. Introduction	215
II. Unionacea	217
A. Taxonomy and Systematics	217
B. Life Cycle	218
C. Food and Feeding	221
D. Biotic Associations	222
E. Chemical and Physical Parameters	240
F. Adverse Anthropogenic Effects on Mussels	246
G. Mussels as Indicator Organisms	254
III. Sphaeriidae	254
References	257

### I. Introduction

The North American freshwater bivalved molluscan fauna consists of three elements. The vast majority of native species belongs to the Unionacea (the freshwater mussels or naiades) and Sphaeriacea (the pill and finger nail clams), two superfamilies of worldwide distribution. Also representing the Sphaeriacea, *Corbicula manilensis* (Philipp) is an introduced Asiatic species which poses economic and biotic threats. Third, there is minor

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representation of several groups of essentially marine bivalves. These animals reflect phylogenetically diverse, more or less unsuccessful attempts to colonize continental waters. None of them is a legitimate freshwater species, although several can tolerate extremely low salinities. For instance, I have taken *Polymesoda caroliniana* (Bosc) in the company of freshwater mussels in tidewaters of the St. Johns river system of northeastern Florida. Nevertheless, for the purposes of this volume, these faunal elements are considered extralimital. For the student interested in pursuing the natural histories of these species, some references are included in the bibliography: Hopkins (1970), Hopkins and Andrews (1970), Morrison (1955), Wolfe (1971), and van der Schalie (1933).

Like the essentially marine elements, in contrast to the Unionacea and the other Sphaeriacea, and as an alien, *Corbicula* will receive rather short shrift here. *Corbicula* is itself a pollutant, and its own pollution biology has not been of great interest to students who would prefer to see it eliminated! It is the threat which *Corbicula* poses to the native fauna as a competitor for free-swimming larva, unknown among native bivalves, and its ability to exploit virtually any substrate. Thus the range and population sizes of *Corbicula* have exploded since the first wild populations were discovered on the West Coast about 35 years ago.

Matters of geographic and ecologic distribution, normal ecology and life cycle, and economic and biotic problems may be surveyed through Sinclair's (1971) bibliography, which, though not exhaustive, provides an excellent overview of the *Corbicula* story. Little has been added to it since, but this pest has recently made its way into the Atlantic drainage (Sickel, 1973; Fuller and Powell, 1973), and W. M. Richardson *et al.* (1970) have discovered a natural enemy.

My treatments of the Unionacea and Sphaeriidae, also, display certain limitations in scope. I am especially mindful of the general lack of chemical data. Unfortunately, we do not know the limits of the tolerance by a single species for a single chemical parameter. On the other hand, the two groups share an indifference to natural variations in water chemistry over a range much wider than might a priori be supposed: for example, unionid mussels are not "supposed" to live in soft water or at low pH, but they can and do (Harman, 1969). Under the circumstances, I see no advantage in tabulating chemical data, and not many are discussed. Interested students can find copious information of this sort in papers by Cvancara and Harrison (1965), Dawley (1947), Imlay and Paige (1972), Morrison (1932), Patrick *et al.* (1967), Shoup *et al.* (1941), Wurtz and Roback (1955), and others.

## 8. Clams and Mussels (*Mollusca: Bivalvia*)

### II. Unionacea

#### A. TAXONOMY AND SYSTEMATICS

The vast majority of the North American freshwater bivalve fauna consists of the mussels, Margaritiferidae and Unionidae. The somber beauty of their shells has occasioned enormous interest among naturalists since the first quarter of the last century. The rather large size of many of these animals might lead one to believe that distinguishing among our many score species would be an easy matter. Unfortunately, their variable morphologies and the uncritical gaze of most observers have combined to produce many times more names than are warranted. The resulting taxonomic confusion remains incompletely resolved to this day, and there is no one work which may be used to identify all species reliably. As Ortmann (1924) would have it, "we are able to control the identification" of perhaps a majority, but certainly not all, of our fauna. Correlating modern taxonomy with older nomenclature is an additional difficulty, particularly when early usage was not shared up by reference to published concepts or figures which can be re-evaluated today.

In sharp contrast to the difficulties inherent in species determinations, most of the nearctic naiad genera recognized by Heard and Guckert (1971) and Valentine and Stansbery (1971) are readily identified with one or more of a number of works—Clench (1959), Haas *et al.* (1969), Heard (1968), Ortmann (1912), Pennak (1953), Valentine and Stansbery (1971), or Walker (1918).

The van der Schalties (1950) recognized six major zoogeographic subdivisions of the North American naiades: the Pacific, Ozarkian, Mississippian, Cumberlandian, Apalachicolan, and Atlantic faunas. Somewhere between the rather antipodal viewpoints of Ingram (1948) and Hannibal (1912) lies a true taxonomic appreciation of the Pacific drainage naiades. The Ozarkian fauna has never been monographed; Call's (1895) is a relevant paper, but it is out of date and was published before certain characteristically Ozarkian elements were distinguished (see, for example, Ortmann and Walker, 1912). Much of this fauna is common to the Mississippian and Cumberlandian regions, as well. The papers by Ortmann (1918) and Neel and Allen (1964) form a good introduction to the latter fauna, while a number of papers are very helpful for the Mississippian, which has received most attention of the six: Baker (1928), Call (1900), Heard and Burch (1966), Goodrich and van der Schalie (1944), Murray and Leonard (1962), Parmalee (1967), Simpson (*in Baker*, 1898), Starrett (1971), and Valentine and Stansbery (1971). The works by Starrett and by Murray and Leonard are particularly useful in coordinating early and recent nomenclature.

The fauna of the Canadian interior basin is an outgrowth of the Mississippi and has been wonderfully monographed by Clarke (1973). The taxonomy of Atlantic drainage naiades of Canada and the United States, including peninsular Florida, is in very good condition in view of papers by Athearn and Clarke (1962), Clarke and Berg (1959), Clarke and Rick (1963), Fuller (1971, 1972, 1973), Harman (1970b), Johnson (1970, 1972), and Shelley (1972). The Appalachian fauna, also, is quite well understood taxonomically (Athearn, 1964; Clench and Turner, 1956; Fuller and Bereza, 1973; Johnson, 1967, 1968). Westward from the Appalachian region, however, knowledge of the mussel fauna is very imperfect. Two papers by van der Schalie (1938c, 1939b) amount to the only introduction of any scope to the rich fauna of the Alabama river system. Grantham's (1969) treatment of the naiades of the adjoining state of Mississippi is helpful. A gaggle of papers (Frierson, 1897, 1902, 1911; Vaughan, 1892; Vanatta, 1910; Shira, 1913; Coker, 1915) may aid in understanding the fauna of Louisiana, which has never been considered as a unit. Strecker (1931) provided an excellent overview of Texan mussels. There are few species known from Arizona (Stearns, 1883; Taylor, 1966; Bequaert and Miller, 1973) or New Mexico (Cockerell, 1902; Henderson, 1933). Certain essentially Mexican elements—notably *Popenaias* (also in peninsular Florida) and *Cyrtoneias* (Heard and Guckert, 1971)—occur in the extreme western Gulf drainage of the United States. On the excellent chance that other exotics will be discovered there, I mention the great works on Mexican and Central American naiades by Fischer and Grosse (1894) and von Martens (1900), as well as an informative paper by Pilsbry (1910).

Until the reevaluation by Heard and Guckert (1971), there had been little improvement on the system of naiad classification developed by Ortmann, the main features of which are embodied particularly well in his 1912 and 1919 papers. At this time I prefer a variation on Heard and Guckert which recognizes two families, Margaritiferidae and Unionidae, with four subfamilies in the latter: Ambleminae, Unioninae, Lampsilinae, and Anodontinae.

#### B. LIFE CYCLE

Many of the ecologically significant aspects of mussel biology are revealed by a skeletal account of their normal life cycle. Its great weaknesses lie in the prerequisites and consequences of the period of larval parasitism on a vertebrate host. Stein (1971) has made the point emphatically, and further details may be gained from the better naiad natural histories, including Lefevre and Curtis (1912), Coker *et al.* (1921), Baker (1928), and Pennak (1953).

#### 8. Clams and Mussels (*Mollusca*: *Bivalvia*)

Sperms are shed into the water from the male gonad. So far as is known, sperm are aggregated in volvocoid bodies (Edgar, 1965), which are drawn into the female on her inhalant current. Utterback (1931) observed a female *Lampsilis ovata* (Say 1817) fanning sperm bodies into her mantle cavity with her mantle flaps. Wherever water currents are reduced (see Section II, F, 2), especially in ponds and lakes, fertilization of ova is less likely, mussel populations are often small, and individuals may be scattered too far apart to breed effectively (Wilson and Clark, 1912b). The level of glochidial infection on fishes may be very low in lakes (Evermann and Clark, 1918).

The fertilized ova are incubated for varying periods of time in varying portions (the marsupium) of the gills which are permanently modified to that end. During this time they are liable to attack by bacteria and protozoans (see Sections II, D, 2 and 4). Mature larvae are minute bivalved creatures (glochidia), microspined and/or hooked (Arey, 1924). In spite of great mortality in the marsupium (Ellis, 1929), glochidia are shed in enormous numbers, sometimes reckoned in the millions (Merrick, 1930). In the Margaritiferidae and in all unionid subfamilies but (at least most of) the Lampsilinae, the glochidia are discharged through the excurrent aperture, individually, in small aggregates, or in large masses. Glochidia are often suspended in the water on mucous lacework (Matteson, 1955; Yokley, 1972), the more readily to come into contact with suitable host fishes (see Section II, D, 16), and fish may actually devour masses of glochidia (e.g., Chamberlain, 1934). Certain fish feed upon mussels and are thus infected. Howard (1914c) believed that potential hosts are attracted to mussel beds to feed on them and associated foodstuffs, including fortuitous egg masses.

Among the Lampsilinae the glochidia are discharged through minute pores in the marsupium directly outside into the water near the incurrent aperture (Ortmann, 1910). In advanced genera, such as *Lampsilis* itself, the marsupium occupies the postbasal portion of the outer female demibranch and may be protruded through the valves, where it is apt to be touched, even attacked, by curious or predatory fish which have been attracted by the colors, piscine shapes, and undulatory movements of the mantle flaps. Aspects of this sophisticated device for increasing the chances of glochidial infection have been observed and/or discussed by numerous authors, including Kirtland (1851), Wilson and Clark (1912b), Utterback (1915–1916), Coker *et al.* (1921), Baker (1922), and Howard and Anson (1922). Flaps have been figured by Welsh (1961), Harman (1970), Kraemer (1970), and Fuller (1971).

Since mussels do not have free-swimming larvae, the glochidial hosts serve to disperse them. Glochidia have been detected alive in plankton (Kofoid, 1910; Clark and Stein, 1921), and those of *Margaritifera falcata* (Gould 1850), for example, can remain alive as plankters for as many as

11 days (Murphy, 1942), but it is highly unlikely that planktonic glochidia contribute significantly to mussel dispersal or even to successful host infection. The vast majority of glochidia fail to infect at all, and the vast majority of these fall to the bottom, where they are subject to predation (see Sections II,D,5 and 10) and smothering.

The glochidia of Anodontinae are unusually large, hooked, and equipped with a "thread gland," which is thought to aid in host infection; significantly, these glochidia are usually found in successful infection only on tougher tissues, such as fins, and even under scales. *Megalomias gigantea* (Barnes 1823), the Washboard (Ambleminae), and *Elliptio dilatata* (Rafinesque 1820), the Lady Finger or Spike (Unioninae), possess thread glands, and each of them can infect fins almost as readily as the more delicate tissue of gills (Howard, 1914c).

Tactile stimuli are sufficient to induce glochidial attachment on host tissue (Arey, 1921), but chemical stimuli are required to prolong attachment until host tissue can encyst the glochidia by epithelial proliferation (Howard, 1914c; Arey, 1921; Heard and Hendrix, 1964; Lukacsovics and Labos, 1965). Profound qualitative changes take place during encystment, and some glochidia increase greatly in size (Coker and Surber, 1911; Murphy, 1942). Having reared glochidia through successful metamorphosis in a solution of salts, sugars, and amino acids, Ellis and Ellis (1926) concluded that the parasitic life is not absolutely necessary, but does provide nourishment (see, also, Arey, 1932b; Blystad, 1923; Ellis, 1929; Jones, 1950; and Yokley, 1972), protection against bacterial and protozoan attack, and the opportunity of dispersal. That the Ellises managed this without glochidial mortality reminds one of the enormous loss of larvae in nature, else our waterways would be choked with mussels.

There are a few mussels—*Anodonta imbecilis* Say 1829, a Floater or Paper Shell (Howard, 1914d; Clark and Stein, 1921; E. Allen, 1924); *Strophitus undulatus* (Say 1817), the Squaw Foot (Lefevre and Curtis, 1911, 1912); and *Obliquaria reflexa* Rafinesque 1820, the Three-horned Warty Back (Lefevre and Curtis, 1912; Howard, 1914c; Utterback, 1915–1916)—whose parasitism, allegedly or definitely, is only facultative. Perhaps this harkens back to early times before larval incubation and parasitic dispersal (see Howard, 1953, and Sellmer, 1967). In those trying times the widespread hermaphroditism known among mussels (van der Schalie, 1970; Heard, 1970a) must have been most advantageous (see Tomlinson, 1966).

After remaining encysted for varying lengths of time, glochidia help initiate rupture of their cysts (Arey, 1932a) and drop from the host. If they land on suitable substrate, development ensues. A "suitable substrate" is firm (but yielding) and stable (Negus, 1966); shifting sands and fine muds are, as a rule, inimical to mussels, young and old alike. Some juvenile mussels

have a byssus, which provides purchase on solid objects (Kirtland, 1840; Sterki, 1891a,b; Frierson, 1903; Isely, 1911; Coker, 1912; Howard, 1914c). Read and Oliver (1953) observed juveniles only on gravel shoals, clamped to algal filaments or attached to rocks by their byssi. As requirements for successful mussel reproduction, Isely (1911) included sand- and silt-free riffles, abundant food and dissolved oxygen, and holdfasts for the byssi. He added that mussels radiate to other habitats as they grow larger. Possibly the difference between adult and juvenile habitats is a device meant to reduce competition for space (d'Eliseu, 1972). "Competition" among mussels—even for such essentials as food and space—seems a rather passive affair, depending primarily on degrees of success in reproduction. Perhaps it is really superior reproductive ability that accounted for the "competitive" succession of mussel families during geological time that was cited by Bănărescu (1971).

#### C. FOOD AND FEEDING

W. R. Allen (1914) believed that a suspension of any finely divided, decaying tissue will serve as food for mussels. Churchill (1916) showed that mussels can utilize nutrient in solution, including fat (Churchill, 1915; Coker *et al.*, 1921). There seem to be no interspecific differences in feeding among naiades; identifiable stomach contents are almost invariably mud, desmids, diatoms, and other unicellular algae (see Section II,D,3) (Evermann and Clark, 1918; Coker *et al.*, 1921). W. R. Allen (1921) found nannoplankton very important in the mussel diet, and Read and Oliver (1953) felt that mussels prefer zooplankton to phytoplankton. Churchill and Lewis (1924) concluded that microorganisms, especially Protozoa (see Section II,D,4), and detritus form the sole food of mussels and noted that larger populations develop below areas where disintegration of rich vegetation is occurring (see Section II,F,6). Mussel food may include rotifers and flagellates, also (Wilson and Clark, 1912a). Living and active diatoms have been observed at the posterior ends of mussels' alimentary canals (Wilson and Clark, 1912a; Coker *et al.*, 1921). Finally, several unnatural substances have sustained mussel life: strained beef and beef heart (Salbenblatt and Edgar, 1964), "baby food beef" (Edgar, 1965), and trout fry food (Imlay and Paige, 1972).

Thus a heterogeneous collection of observations on mussel food has accumulated over the years, and the mussel diet is reasonably well understood: it consists primarily of detritus and animal plankters. (It might usefully be emphasized that the prevalent notion that mussels feed mainly on diatoms is a myth.)

There are very few observations on mussel feeding activity. W. R. Allen (1921) wrote that sand and mud are usually sorted from foodstuffs, but

Churchill and Lewis (1924) and Coker *et al.* (1921) felt that rejection of a potential food is accomplished, not by ciliary sorting, but by refusal to feed. There is unresolved difference of opinion here.

#### D. BIOTIC ASSOCIATIONS

Reproduction, habitat, and food are commonly discussed aspects of a natural history of any group of organisms, but their relationships with other plants and animals are often treated rather superficially. It happens, however, that mussel symbioses and other biotic relationships are critically important ingredients of their normal and pollution ecologies—and of any attempt to understand the value of mussels as indicator organisms.

##### 1. Viruses (Virulenta)

Pauley (1968a,b) described the "spongy" disease of the foot that has been detected in *Margaritifera falcata*. Watery lesions develop, and the affliction can involve the reduction of epithelium to necrotic, squamous tissue, which may disappear altogether. These remarks are offered here on the chance that they represent a viral infection.

##### 2. Bacteria (Schizomycetes)

Particularly under conditions of siltation (see Section II,F,3), (unspecified) bacteria may attack glochidia while still in the marsupium (Ellis, 1929). Imlay and Paige (1972) found that growth of *Ambleria plicata* (Say 1817), the Three Ridge or Blue Point, can be retarded by sufficient quantities of (unspecified) bacteria. Apparently, bacteria pose a threat to mussels only when their populations expand upon suitable environmental disturbance, doubtless particularly with organic enrichment (see Section II,F,6).

##### 3. Algae (particularly Chlorophyta)

Very little specific information is available on the important relationship between mussels and algae. Vinyard (1955) felt that there are possibly undescribed genera and species of algae growing on "clams and snails," suggested that some of these associations may prove highly specific, and pointed out the previous lack of literature on the subject. Wilson and Clark (1912a) noted abundant multicellular algae, especially the green alga *Cladophora*, on the shells of living mussels, and W. R. Allen (1914), alleging that it may have a nutritional role, remarked the "private garden" of diatoms and other algae which often adorn the posterior ends of shells. Wilson and Clark (1912b) suggested that such algae may help aerate stagnant water near the mussel and provide it with added buoyancy. All these ideas remain untested, and the one indisputably important role that algae play in mussel lives, though commonly overestimated, is as food (see Section II,C).

#### 8. Clams and Mussels (Mollusca: Bivalvia)

##### 4. Protozoans (Protozoa)

Other than as an extremely important food (see Section II,C), protozoans have rather little to do with mussels. Coker *et al.* (1921) observed the familiar genera *Paramecium* and *Vorticella* in the mantle cavity and on the mantle, respectively, and members of a small group of thigmotrichous ciliates are regularly associated with mussels (Kelly, 1902). These include *Heterocinetopsis uniodarum* Jarocki and Raabe, which Antipa and Small (1971) tentatively considered parasitic, and several species of *Conchophthirus*. Combining their data with Kelly's (1902), Antipa and Small found *C. curtus* Engelmann present, as a commensal, in 81.5% of the mussel species examined for it at that time. They felt that mussels whose shells gape in life are especially susceptible to protozoan infestation—one would thus expect less infection among Ambleminae and Unioninae than among Anodontinae and Lampsilinae—and Wilson and Clark (1912a) thought *Conchophthirus* universally distributed among species of their acquaintance. Kidder (1934) considered *C. curtus* and *C. anodontae* (Ehrenberg) both commensals. J. H. Penn (1958) noted heavy infections with *C. curtus* in all individual mussels examined and interpreted the species as a world-wide "parasite." The more recent of these papers include lengthy bibliographies, and information about specific associations between these thigmotrichs and their mussel hosts may be gained from any of the papers cited above. Environmental disturbances could scarcely increase the size, but perhaps the variety, of protozoan infections of mussels.

##### 5. Flatworms (Platyhelminthes: Turbellaria)

Howard and Anson (1922) reported a member of the genus *Stenostomum* (Rhabdocoela) which was preying upon glochidia that had fallen to the stream bed. The occasional occurrence of "planarians" (probably Tricladida) within mussels was thought unimportant by Kelly (1902).

##### 6. Flukes (Platyhelminthes: Trematoda)

Freshwater mussels are afflicted with members of several trematode families, most of which are classified among the digenetic flukes, that is, in the order Digena in Hyman's (1951) arrangement, which first subdivides the Trematoda at ordinal level. Perhaps the most familiar of these is *Allocreadium ictaluri* Pearse (Allocreadiidae), which, argued Hopkins (1934), is the organism whose irritating presence leads to pearl formation in mussels (see Section II,D,15); Seitner (1951) wrote a life history of *A. ictaluri*. This is one of the "distomids," references to which are so common in the naiaid literature. The old family Distomidae has been dismembered and its elements, scattered among modern digenetic families (Hyman, 1951). Gastrostomes of the genus *Bucephalus* (Bucephalidae) affect mussels quite

differently, often damaging or destroying gonad tissue (Kelly, 1902; Wilson and Clark, 1912a,b; Lefevre and Curtis, 1912). It is the rare paper (e.g., Gentner and Hopkins, 1966) which correlates individual mussel species with any variety of "distomids" identified and classified according to recent concepts and nomenclature. Other trematode host-parasite relationships of varying taxonomic reliability can be found in Leidy (1858), Fischthal (1954), and Coil (1954). Allocreadiids and bucephalids can interfere with mussel lives so profoundly under the best of circumstances that it is hard to imagine that they could do a great deal more damage in a disturbed environment.

More common is information about members of the other group of flukes which infect mussels, the family Aspidogastridae in the order Aspidobothrea. In North America these parasites fall into the genera *Cotyllogaster*, *Cotylaspis*, and *Aspidogaster*. Hendrix and Short (1965) showed that all *Cotylaspis* infecting Nearctic naiades are *C. insignis* Leidy. Each of the other two genera includes only one species parasitic upon North American mussels (Stromberg, 1970): *A. conchicola* von Baer and *Cotyllogaster occidentalis* Nickerson. The latter is rarely recorded from Nearctic mussels (Kelly, 1926), but the former is common and may cause disease involving severe modification or destruction of affected host tissue (Pauley and Becker, 1968). The following works list most of the published records associating specific mussels with *C. insignis* and *A. conchicola*: Gentner and Hopkins (1966), Hendrix (1968), Hendrix and Short (1965), Kelly (1902), Kofoid (1899), Leidy (1858, 1859), Monticelli (1892), Najarian (1955, 1961), Pauley and Becker (1968), Stromberg (1970), Stunkard (1917), Osborn (1898a,b), Utterback (1916), van Cleave and Williams (1943), Vidrine (1973), and Wilson and Clark (1912b).

#### 7. Roundworms (Nematoda)

Wilson and Clark (1912a) detected roundworms in the alimentary canals of mussels. Coker *et al.* (1921) confirmed the phenomenon and pronounced the worms parasites. Nothing is known about nematodes' potential for damage to mussels.

#### 8. Rotifers (Rotifera)

Rotifers can play an apparently insignificant role in the diet of mussels (Wilson and Clark, 1912a).

#### 9. Bryozoans (Entoprocta and Ectoprocta)

Wilson and Clark (1912a) noted a member of the ectoproct genus *Plumatella*—probably *P. repens* (Linnaeus) or a close relative—growing on various *Anodonta* and *Amblema plicata*. I have seen the ectoproct *Urnatella gracilis* Leidy on mussels, mostly *Elliptio complanata* (Lightfoot), in the Potomac

#### 8. Clams and Mussels (Mollusca: Bivalvia)

River, Maryland and Virginia, and the ectoproct *Pottsiella erecta* (Potts) on *Unionus tetrasmus* (Say 1831) in numerous waterways of the southeastern states. Are these consistently specific associations? An indeterminate bryozoan was reported by Williams (1969) on "baldies" (i.e., shells which are nearly or quite denuded of periostracum) in Kentucky Lake, an impoundment on the Tennessee River. In view of the common association of divers bryozoans with healthy mussels, no given significance can reasonably be attached to Williams' observations.

#### 10. Aquatic Earthworms (Annelida: Oligochaeta)

*Chaetogaster limnaei* von Baer, a naid worm, was reported within mussels by Kelly (1902), who thought it might be a predator. *Chaetogaster diaphanus* (Gruithuisen) definitely preys upon glochidia which have fallen to the bottom (Howard and Anson, 1922). The latter species, at least, plays a probably minor role in regulation of naiad population sizes. My taxonomic usage here has followed Brinkhurst (*in* Brinkhurst and Jamieson, 1971).

#### 11. Leeches (Annelida: Hirudinea)

Leeches are often found attached to dead or living mussel shells, but perhaps it is nothing more than the solid substrate provided by the shell which attracts the leech. Leeches are commonly "parasitic" in mussels and have been thought to eat their mucous (Wilson and Clark, 1912a; Coker *et al.*, 1921). *Placobdella montifera* Moore has been observed in mussels, but was not noticed to feed upon them (Moore, 1912). Kelly (1902) thought unimportant the occasional occurrence of leeches within mussels. The only leeches which I have found actually inside (i.e., within the mantle cavity) living mussels are *P. parasitica* (Say) and *P. montifera*. The former association is rare; the latter is regularly encountered, but there seems to be no pattern of species which serve as "hosts." The advantages secured by *P. montifera*—other than clandestine shelter—are unclear. In any event, although leech populations can reach epidemic proportions, these animals seem to pose no threat to mussels, even though the relationship is more common in lentic situations. Finally, glochidia have been observed attached to leeches (Seshaiya, 1941), but successful metamorphosis is doubtful. My taxonomic usage here has followed Sawyer (1972).

#### 12. Copepods (Arthropoda: Crustacea: Copepoda)

Wilson (1916) concluded that piscine immunity to glochidia can be induced by copepod infection, but that the opposite is true, as well. However, Cope's (1959) data indicated that this is true neither everywhere nor with all species—which is hardly surprising in view of the fact that glochidial infection can induce immunity to itself (Arey, 1932c).

### 13. Crayfish (Crustacea: Decapoda)

Wilson and Clark (1912a) observed crayfish feeding upon dead mussels and wondered if the crustaceans might not have killed them. I am not aware that the possibility has been verified.

### 14. Insects (Arthropoda: Insecta)

Wilson and Clark (1912a) reported midge larvae (Diptera: Chironomidae) in the mantle cavity of an unspecified mussel. Doubtless this was an accidental intrusion; the record, to my knowledge, has not been duplicated.

### 15. Water Mites (Arthropoda: Acari)

The nonmarine aquatic mites include a family, the Unionicolidae, many of whose members are symbiotic with freshwater mussels. These mites are *Najadicola ingers* (Koenike) and numerous species of *Unionicola*. The symbiosis may be parasitic or commensalistic, depending upon the species of mite and/or the stage in its life cycle. The given mite may exploit numerous mussel species, and the given mussel may harbor more than one species of mite. Some instances of apparently well developed specificity were revealed by Mitchell and Wilson (1965) and Davids (1973), whereas *U. formosa* Dana and Whelpley, for example, parasitizes several different *Anodonta* (Mitchell, 1957). The genus *Anodonta* seems to support a characteristic assemblage of *Unionicola* species (*ibid.*), at least some of which may be present in great numbers, particularly in naturally lentic or even in impounded habitats, where *Anodonta* are peculiarly well suited to survival.

The proliferation of water mites and the damage they can do can be indirect, adverse effects of man's impact upon formerly lotic waterways. A heavy mite infestation may lead to shredding of portions of the gills, a favorite locus of attack, or even to death (Davids, 1973). Mite eggs can form the nuclei of pearls (Wilson and Clark, 1912a). A sense of aspects of the biology and host relationships of *Najadicola ingers* is sought in papers by Humes and Jamnback (1950), Humes and Russell (1951), and Humes and Harris (1952). Information on host relationships and natural histories of several species of *Unionicola* is given by Dana and Whelpley (1836), Evermann and Clark (1918), Kelly (1902), Leidy (1884), Marshall (1926), Mitchell (1955, 1957, 1965), Mitchell and Wilson (1965), Murray and Leonard (1962), Utterback (1916), Wilson and Clark (1912b), and Wolcott (1898, 1899). Sadly, in view of superior species concepts and nomenclature developed in the later papers many records in the earlier ones must be considered suspect.

### 16. Fishes (Chordata: Vertebrata: Pisces)

A few kinds of fishes prey heavily upon mussels (Baker, 1916), but the practice commonly results in parasitism by glochidia. The relationship

### 8. Clams and Mussels (Mollusca: Bivalvia)

between predator and prey is mutualistic at worst. Catfish often eat benthic mollusks, including mussels (Kendall, 1910), and *Aplodinotus grunniens* Rafinesque, the Freshwater Drum, feeds on little else (Forbes and Richardson, 1908). Drum host glochidia of at least 11 species of mussels (Table I). They are most readily infected when crushing the shells of larvigerous females of fragile species, such as members of the lampsilline genera *Lepidotea*, *Proptera*, *Ellipsaria*, and *Truncilla*.

Other than their difficulties at the hands of man, the most important biotic relationship involving mussels is the almost universal parasitism of their glochidia upon fishes. Especially under the crowded conditions of fish hatcheries (Murphy, 1942) glochidial infestation may produce host mortality (Ellis, 1929), but in nature the glochidium is normally a "good" parasite. Glochidial infection induces in the fish an immunity which strengthens with repeated infections. In certain cases, immunity can provide protection against attack by copepods, as well (see Section II, D, 12).

Disruption of the relationship between mussel and fish usually depends on destruction of the mussel habitat (see, in particular, Sections II, F, 1 and 2) and/or on elimination of the host. The latter difficulty concerns us here. This is the most subtle and poorly known aspect of naiad pollution biology. We are largely or completely ignorant of the identities of the potential fish hosts for most mussels. The information in Table I provides (generally inadequate) knowledge of these relationships for only perhaps one fifth or so of the Nearctic naiad fauna. Here is an area where the most informative and practical kind of observation and research can be accomplished in field and laboratory. Accurate knowledge would allow prediction that a given mussel will be threatened when its glochidial hosts are disturbed by waterway alteration.

Conner (1905) was first to identify partners in a Nearctic mussel-host relationship. At about this time, the United States Bureau of Fisheries Laboratory at Fairport, Iowa, became the center of research on the artificial propagation of freshwater mussels, whose seemingly inexhaustible supplies were dwindling (Kunz, 1898; Simpson, 1899; Smith, 1899; Coker, 1916, 1919). Commencing with the pioneering studies by Lefevre and Curtis (1910a,b, 1911, 1912), the staff and associates of the Laboratory produced a long series of papers on naiad natural history, which included much information on glochidial hosts of commercial species (Table I, in part), as well as some of lesser value. Many unpublished data on noncommercial species were lost when the Laboratory was destroyed by fire in 1917 (Coker *et al.*, 1921). From the mussels' point of view, so to speak, this was a tragedy on the order of the TVA damming of the Tennessee River, the current excesses of our Army Corps of Engineers, and three centuries' agrarian malpractice in the eastern United States. The Fairport Laboratory was rebuilt, but, with depletion of the mussel and stocks the advent of plastic buttons shortly there-

TABLE I

CERTAIN NEARCTIC FRESHWATER MUSSELS (UNIONACEA) AND THEIR KNOWN AND/OR IMPLICATED GLOCHIDIAL HOST FISHES<sup>a</sup>

Mussel	Host fish	References
Margaritiferidae	Salmonidae	
<i>Margaritifera falcata</i> (Gould)	<i>Oncorhynchus tshawytscha</i> (Walbaum), Chinook Salmon	Davis (1946)
	<i>Salmo gairdneri</i> Richardson, Rainbow Trout	Davis (1934), Murphy (1942), K. A. Wilson and Ronald (1967)
	<i>S. trutta</i> Linnaeus, Brown Trout	Murphy (1942)
	<i>Salvelinus fontinalis</i> (Mitchill), Brook Trout	Murphy (1942)
	Cyprinidae	
	<i>Rhinichthys osculus</i> (Girard), Speckled Dace	Murphy (1942)
	<i>Richardsonius egregius</i> (Girard), Lahontan Redside	Murphy (1942)
	Catostomidae	
	<i>Catostomus tahoensis</i> Gill and Jordan, Tahoe Sucker	Murphy (1942)
2. <i>M. margaritifera</i> (Linnaeus)	Salmonidae	
	<i>Salmo trutta</i> (Linnaeus)	Clarke and Berg (1959)
	<i>Salvelinus fontinalis</i> (Mitchill)	Clarke and Berg (1959)
Unionidae:		
Amblyminae:		
<i>Amblyma plicata</i> (Say)	Lepisosteidae	
	<i>Lepisosteus platostomus</i> Rafinesque, Shortnose Gar	Coker <i>et al.</i> (1921), Howard and Anson (1922)
	Esocidae	
	<i>Esox lucius</i> Linnaeus, Northern Pike	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
	Catostomidae	
	<i>Carpionodes velifer</i> (Rafinesque), Highfin Carpsucker	Howard (1914c)
	Ictaluridae	
	<i>Ictalurus punctatus</i> (Rafinesque), Channel Catfish	Howard (1914c)
	<i>Pylodictis olivaris</i> (Rafinesque), Flathead Catfish	Howard (1914c)
	Percichthyidae	
	<i>Morone chrysops</i> (Rafinesque), White Bass	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
	Centrarchidae	
	<i>Ambloplites rupestris</i> (Rafinesque), Rock Bass	Stein (1968)
	<i>Lepomis cyanellus</i> Rafinesque, Green Sunfish	Stein (1968)
	<i>L. gibbosus</i> (Linnaeus), Pumpkinseed	Coker <i>et al.</i> (1921), Stein (1968)

<sup>a</sup>See pp. 238-239 and 273.

TABLE I (continued)

Mussel	Host fish	References
	<i>L. gulosus</i> (Cuvier), War-mouth	Coker <i>et al.</i> (1921), Howard (1914c), Pearse (1924), Stein (1968)
	<i>L. macrochirus</i> Rafinesque, Bluegill	Howard (1914c), Stein (1968)
	<i>Micropterus salmoides</i> (Lacépède), Largemouth Bass	Coker <i>et al.</i> (1921), Howard (1914c), Lefevre and Curtis (1912), Reuling (1919)
	<i>Pomoxis annularis</i> Rafinesque, White Crappie	Coker <i>et al.</i> (1921), Howard (1914c), Surber (1913), C. B. Wilson (1916)
	<i>P. nigromaculatus</i> (Lesueur), Black Crappie	Coker <i>et al.</i> (1921), Howard (1914c)
	Percidae	
	<i>Stizostedion canadense</i> (Smith), Sauger	Coker <i>et al.</i> (1921), Howard (1914c), Surber (1913), C. B. Wilson (1916)
	Clupeidae	
4. <i>Fusconata ebena</i> (Lea)	<i>Alosa chrysochloris</i> (Rafinesque), Skipjack Herring	Coker (1919), Coker <i>et al.</i> (1921), Howard (1914c, 1917), Surber (1913), C. B. Wilson (1916)
	Centrarchidae	
	<i>Lepomis cyanellus</i> Rafinesque	Coker <i>et al.</i> (1921)
	<i>Micropterus salmoides</i> (Lacépède)	Howard (1914c)
	<i>P. nigromaculatus</i> (Lesueur)	Howard (1914c)
	Centrarchidae	
5. <i>F. flava</i> (Rafinesque)	<i>Lepomis macrochirus</i> Rafinesque	Howard (1914c)
	<i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921), Howard (1914c), C. B. Wilson (1916)
	<i>P. nigromaculatus</i> (Lesueur)	Surber (1913), C. B. Wilson (1916)
	Amiidae	
	<i>Amia calva</i> Linnaeus, Bowfin	Howard (1914c)
	Anguillidae	
	<i>Anguilla rostrata</i> (Lesueur), American Eel	Coker <i>et al.</i> (1921), Surber (1915), C. B. Wilson (1916)
	Clupeidae	
	<i>Alosa chrysochloris</i> (Rafinesque)	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
	<i>Dorosoma cepedianum</i> (Lesueur), Gizzard Shad	Coker <i>et al.</i> (1921), Howard (1914c)
	Catostomidae	
	<i>Carpionodes velifer</i> (Rafinesque)	Howard (1914c)
	Ictaluridae	
	<i>Ictalurus melas</i> (Rafinesque), Black Bullhead	Coker <i>et al.</i> (1921), Howard (1914c)

6



TABLE I (continued)

Mussel	Host fish	References
	<i>I. nebulosus</i> (Lesueur), Brown Bullhead	Coker <i>et al.</i> (1921)
	<i>I. punctatus</i> (Rafinesque)	Coker <i>et al.</i> (1921), Howard (1914c)
	<i>Pygodictis olivaris</i> (Rafinesque)	Coker <i>et al.</i> (1921), Howard (1914c)
	Percichthyidae	
	<i>Morone chrysops</i> (Rafinesque)	Coker <i>et al.</i> (1921), Howard (1914c), C. B. Wilson (1916)
	Centrarchidae	
	<i>Lepomis macrochirus</i> Rafinesque	Coker <i>et al.</i> (1921), Howard (1914c)
	<i>Micropterus salmoides</i> (Lacépède)	Howard (1914c)
	<i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921)
	<i>P. nigromaculatus</i> (Lesueur)	Coker <i>et al.</i> (1921), Howard (1914c)
	Percidae	
	<i>Stizostedion canadense</i> (Smith)	Howard (1914c)
	Sciaenidae	
	<i>Aplodinotus grunniens</i> Rafinesque, Freshwater Drum	Coker <i>et al.</i> (1921), Howard (1914c), Surber (1913, 1915), C. B. Wilson (1916)
7	<i>Quadrula metanetra</i> (Rafinesque)	Centrarchidae <i>Lepomis cyanellus</i> Rafinesque <i>L. macrochirus</i> Rafinesque
	Percidae	
	<i>Stizostedion canadense</i> (Smith)	Coker <i>et al.</i> (1921), Howard (1914c)
	Ictaluridae	
	<i>Ictalurus punctatus</i> (Rafinesque)	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
	<i>Pygodictis olivaris</i> (Rafinesque)	Coker <i>et al.</i> (1921)
	Centrarchidae	
	<i>Lepomis macrochirus</i> Rafinesque	Howard (1914c)
	<i>Micropterus salmoides</i> (Lacépède)	Howard (1914c)
	<i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921), Surber (1913), C. B. Wilson (1916)
	<i>P. nigromaculatus</i> (Lesueur)	Howard (1914c)
8	<i>Q. pustulosa</i> (Lea)	Acipenseridae <i>Scaphirhynchus platyrhynchus</i> (Rafinesque), Shovelnose Sturgeon
	Ictaluridae	
	<i>Ictalurus melas</i> (Rafinesque)	Coker <i>et al.</i> (1921), Howard (1913, 1914c)
	<i>I. nebulosus</i> (Lesueur)	Coker <i>et al.</i> (1921), Howard (1914c)
	<i>I. punctatus</i> (Rafinesque)	Coker <i>et al.</i> (1921), Howard (1913, 1914c)

TABLE I (continued)

Mussel	Host fish	References
	<i>Pygodictis olivaris</i> (Rafinesque)	Coker <i>et al.</i> (1921), Howard (1913, 1914c), C. B. Wilson (1916)
	Centrarchidae	
	<i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921), Surber (1913), C. B. Wilson (1916)
10	<i>Q. quadrina</i> (Rafinesque)	Ictaluridae <i>Pygodictis olivaris</i> (Rafinesque)
	Unionidae:	
	Unioninae	
	<i>Elliptio complanata</i> (Lightfoot)	Percidae <i>Perca flavescens</i> (Mitchill), Yellow Perch
11	<i>E. crassidens</i> (Lamarck)	Clupeidae <i>Alosa chrysochloris</i> (Rafinesque)
12	<i>E. dilatata</i> (Rafinesque)	Clupeidae <i>Dorosoma cepedianum</i> (Lesueur)
13		Ictaluridae <i>Pygodictis olivaris</i> (Rafinesque)
	Centrarchidae	
	<i>Pomoxis annularis</i> Rafinesque	Howard (1914c), C. B. Wilson (1916)
	<i>P. nigromaculatus</i> (Lesueur)	Howard (1914c)
	Percidae	
	<i>Perca flavescens</i> (Mitchill)	Howard (1914c)
14	<i>Plethobasus cyprius</i> (Rafinesque)	Percidae <i>Stizostedion canadense</i> (Smith)
15	<i>Pleurobema cordatum</i> (Rafinesque)	Cyprinidae <i>Notropis ardens</i> (Cope), Rosefin Shiner
	Centrarchidae	
	<i>Lepomis macrochirus</i> Rafinesque	Coker <i>et al.</i> (1921), Surber (1913)
	Unionidae:	
	Anodontinae	
	<i>Alasmidonta calceola</i> (Lea)	Percidae <i>Etheostoma nigrum</i> Rafinesque, Johnny Darter
16		Cottidae <i>Cottus bairdi</i> Girard, Mottled Sculpin
	<i>A. marginata</i> (Say)	Catostomidae <i>Catostomus commersoni</i> (Lacépède), White Sucker <i>Hypentelium nigricans</i> (Lesueur), Northern Hog Sucker <i>Moxostoma macrolepidotum</i> (Lesueur), Shorthead Redhorse
17		Morrison (in Clarke and Berg, 1959)
		Morrison (in Clarke and Berg, 1959)
		Howard and Anson (1922)
		Howard and Anson (1922)
		Howard and Anson (1922)

TABLE I (continued)

Mussel	Host fish	References
	<i>Pomoxis annularis</i> Rafinesque	Lefevre and Curtis (1910b), Morrison ( <i>in</i> Clarke and Berg, 1959), C. B. Wilson (1916)
	<i>P. nigromaculatus</i> (Lesueur)	C. B. Wilson (1916)
	Percidae	
	<i>Etheostoma exile</i> (Girard), Iowa Darter	Morrison ( <i>in</i> Clarke and Berg, 1959)
	<i>E. nigrum</i> Rafinesque	Hankinson (1908), Morrison ( <i>in</i> Clarke and Berg, 1959)
	<i>Perca flavescens</i> (Mitchill)	Lefevre and Curtis (1910b)
	Sciaenidae	
	<i>Aplodinotus grunniens</i>	C. B. Wilson (1916)
	Rafinesque	
22	<i>A. imbecilis</i> Say	Clarke and Berg (1959)
	Cyprinidae	
	<i>Semotilus atromaculatus</i> (Mitchill), Creek Chub	Tucker (1927)
	Centrarchidae	
	<i>Lepomis cyanellus</i> Rafinesque	Davenport and Warmuth (1965), Johnson (1946)
23	<i>A. implicata</i> Say	Davenport and Warmuth (1965)
	Clupeidae	
	<i>Alosa pseudoharengus</i> (Wilson), Alewife	
	Catostomidae	
	<i>Catostomus commersoni</i> (Lacépède)	Davenport and Warmuth (1965)
	Percichthyidae	
	<i>Morone americana</i> (Gmelin), White Perch	Davenport and Warmuth (1965)
	Centrarchidae	
	<i>Lepomis gibbosus</i> (Linnaeus)	Davenport and Warmuth (1965)
	Petromyzontidae	
	<i>Petromyzon marinus</i> Linnaeus, Sea Lamprey	K. A. Wilson and Ronald (1967)
24	<i>Anodontoidea ferrussacianus</i> (Lea)	
	Cottidae	
	<i>Cottus bairdi</i> Girard	Morrison ( <i>in</i> Clarke and Berg, 1959)
	Anguillidae	
	<i>Anguilla rostrata</i> (Lesueur)	C. B. Wilson (1916)
25	<i>Arcidens confragosa</i> (Say)	
	Clupeidae	
	<i>Dorosoma cepedianum</i> (Lesueur)	Surber (1913), C. B. Wilson (1916)
	Centrarchidae	
	<i>Ambloplites rupestris</i> (Rafinesque)	Surber (1913)
	<i>Pomoxis annularis</i> Rafinesque	Surber (1913), C. B. Wilson (1916)
	Sciaenidae	
	<i>Aplodinotus grunniens</i> Rafinesque	C. B. Wilson (1916)

TABLE I (continued)

Mussel	Host fish	References
	Centrarchidae	
	<i>Ambloplites rupestris</i> (Rafinesque)	Howard and Anson (1922)
	<i>Lepomis gibbosus</i> (Cuvier)	Howard and Anson (1922)
18	Salmonidae	
	<i>Oncorhynchus nerka</i> (Walbaum), Sockeye Salmon	Cope (1959)
	<i>O. tshawytscha</i> (Walbaum)	Cope (1959)
	Gasterosteidae	
	<i>Gasterosteus aculeatus</i> Linnaeus, Threespine Stickleback	Cope (1959)
19	<i>A. californiensis</i> Lea	d'Eliscu (1972)
	Poeciliidae	
	<i>Gambusia affinis</i> (Baird and Girard), Mosquitofish	Lefevre and Curtis (1910b)
20	<i>A. cataraeta</i> Say	
	Cyprinidae	
	<i>Cyprinus carpio</i> Linnaeus, Carp	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
21	<i>A. grandis</i> Say	
	Lepisosteidae	
	<i>Lepisosteus spatula</i> Lacépède, Alligator Gar	Surber (1913), C. B. Wilson (1916)
	Clupeidae	
	<i>Alosa chrysochloris</i> (Rafinesque)	C. B. Wilson (1916)
	<i>Dorosoma cepedianum</i> (Lesueur)	
	Cyprinidae	
	<i>Cyprinus carpio</i> Linnaeus	Lefevre and Curtis (1910b), Morrison ( <i>in</i> Clarke and Berg, 1959)
	<i>Notemigonus chrysoleucas</i> (Mitchill), Golden Shiner	Lefevre and Curtis (1910b), Read and Oliver (1953)
	Ictaluridae	
	<i>Ictalurus natalis</i> (Lesueur), Yellow Bullhead	C. B. Wilson (1916)
	Gasterosteidae	
	<i>Culaea inconstans</i> (Kirtland), Brook Stickleback	Morrison ( <i>in</i> Clarke and Berg, 1959)
	Percichthyidae	
	<i>Morone chrysops</i> (Rafinesque)	C. B. Wilson (1916)
	Centrarchidae	
	<i>Ambloplites rupestris</i> (Rafinesque)	Lefevre and Curtis (1910b), Tucker (1928), C. B. Wilson (1916)
	<i>Lepomis cyanellus</i> Rafinesque	Tucker (1928)
	<i>L. macrochirus</i> Rafinesque	Lefevre and Curtis (1910b), Morrison ( <i>in</i> Clarke and Berg, 1959), Penn (1939), C. B. Wilson (1916)
	<i>L. megalotis</i> (Rafinesque), Longear Sunfish	Penn (1939)
	<i>Micropterus salmoides</i> (Lacépède)	Morrison ( <i>in</i> Clarke and Berg, 1959), Penn (1939), C. B. Wilson (1916)

TABLE I (continued)

Mussel	Host fish	References
26	<i>Lasimona complanata</i> (Barnes)	Lefevre and Curtis (1910b)
	Cyprinidae <i>Cyprinus carpio</i> Linnaeus	Lefevre and Curtis (1912)
	Centrarchidae <i>Lepomis cyanellus</i> Rafinesque	Lefevre and Curtis (1910b)
	<i>Micropterus salmoides</i> (Lacépède)	Lefevre and Curtis (1912)
	<i>Pomoxis annularis</i> Rafinesque	Lefevre and Curtis (1910b)
27	<i>L. costata</i> (Rafinesque)	Ellis and Keim (1918)
	Cyprinidae <i>Cyprinus carpio</i> Linnaeus	Howard (R. L. Barney in Baker, 1928)
28	<i>Strophitus undulatus</i> (Say)	Ellis and Keim (1918)
	<i>Fundulus zebrius</i> Jordan and Gilbert, Rio Grande Killifish	Howard (R. L. Barney in Baker, 1928)
	<i>Semotilus atromaculatus</i> (Mitchill)	Howard (R. L. Barney in Baker, 1928)
	Centrarchidae <i>Lepomis cyanellus</i> Rafinesque	Howard (R. L. Barney in Baker, 1928)
	<i>Micropterus salmoides</i> (Lacépède)	Howard (R. L. Barney in Baker, 1928)
Unionidae:		
Lampsilinae		
29	<i>Actinonaias carinata</i> (Barnes)	Coker <i>et al.</i> (1921)
	Anguillidae <i>Anguilla rostrata</i> (Lesueur)	Coker <i>et al.</i> (1921)
	Ictaluridae <i>Noturus gyrinus</i> (Mitchill), Tadpole Madtom	Coker <i>et al.</i> (1921)
	Percichthyidae <i>Morone chrysops</i> (Rafinesque)	Coker <i>et al.</i> (1921), Surber (1913), C. B. Wilson (1916)
	Centrarchidae <i>Ambloplites rupestris</i> (Rafinesque)	Lefevre and Curtis (1910b)
	<i>Lepomis cyanellus</i> Rafinesque	Coker <i>et al.</i> (1921), Lefevre and Curtis (1912), C. B. Wilson (1916)
	<i>L. macrochirus</i> Rafinesque	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
	<i>Micropterus dolomieu</i> Lacépède, Smallmouth Bass	Coker <i>et al.</i> (1921), Howard and Anson (1922)
	<i>M. salmoides</i> (Lacépède)	Coker <i>et al.</i> (1921), Lefevre and Curtis (1910b, 1912), Reuling (1919), C. B. Wilson (1916)
	<i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921), Lefevre and Curtis (1912), C. B. Wilson (1916)
	<i>P. nigromaculatus</i> (Lesueur)	Coker <i>et al.</i> (1921)
	Percidae <i>Perca flavescens</i> (Mitchill)	Coker <i>et al.</i> (1921), Lefevre and Curtis (1910b)

## 8. Clams and Mussels (Mollusca: Bivalvia)

TABLE I (continued)

Mussel	Host fish	References
30	<i>Carunculina parva</i> (Barnes)	<i>Stizostedion canadense</i> (Smith)
		Centrarchidae
	<i>Lepomis cyanellus</i> Rafinesque	Coker <i>et al.</i> (1921), Pearse (1924)
	<i>L. gulosus</i> (Cuvier)	Mermilliod (1973)
	<i>L. humilis</i> (Girard), Orangespotted Sunfish	C. B. Wilson (1916)
	<i>L. macrochirus</i> Rafinesque	Mermilliod (1973)
	<i>Pomoxis annularis</i> Rafinesque	Mermilliod (1973)
	Cyprinidae <i>Cyprinus auratus</i> (Linnaeus)	Chamberlain (1934)
31	<i>Lampylis orbiculata</i> (Hildreth)	Percidae <i>Stizostedion canadense</i> (Smith)
32		Coker <i>et al.</i> (1921), Surber (1913), C. B. Wilson (1916)
	Sciaenidae <i>Aplodinotus grunniens</i>	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
	Rafinesque	
	Centrarchidae <i>Lepomis macrochirus</i> Rafinesque	Coker <i>et al.</i> (1921)
33	<i>L. ovata</i> (Say) (including <i>L. ventricosa</i> ) (Barnes)	Coker <i>et al.</i> (1921)
34		Coker <i>et al.</i> (1921), Lefevre and Curtis (1912), Reuling (1919)
	<i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
	Percidae <i>Perca flavescens</i> (Mitchill)	Coker <i>et al.</i> (1921)
	<i>Stizostedion canadense</i> (Smith)	Coker <i>et al.</i> (1921), C. B. Wilson (1916)
35	<i>L. radiata lateola</i> (Lamarck)	Ictaluridae <i>Noturus gyrinus</i> (Mitchill)
	Percichthyidae <i>Morone chrysops</i> (Rafinesque)	Coker <i>et al.</i> (1921)
	Centrarchidae <i>Ambloplites rupestris</i> (Rafinesque)	Coker <i>et al.</i> (1921), Corwin (1920)
	<i>Lepomis macrochirus</i> Rafinesque	Evermann and Clark (1918, 1920)
	<i>Lepomis macrochirus</i> Rafinesque	Coker <i>et al.</i> (1921), Everman and Clark (1918, 1920), Howard (1922)
	<i>Micropterus dolomieu</i> Lacépède	Coker <i>et al.</i> (1921), Corwin (1920)
	<i>M. salmoides</i> (Lacépède)	Coker <i>et al.</i> (1921), Arey (1923), Howard (1914b, 1922), Reuling (1919)
	<i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921), Howard (1922)
	<i>P. nigromaculatus</i> (Lesueur)	Coker <i>et al.</i> (1921), Howard (1922)
	Percidae <i>Perca flavescens</i> (Mitchill)	Coker <i>et al.</i> (1921), Corwin (1920), Pearse (1924)
	<i>Stizostedion canadense</i> (Smith)	Coker <i>et al.</i> (1921), Corwin (1920)
	<i>S. vitreum</i> (Mitchill), Walleye	Coker <i>et al.</i> (1921), Corwin (1920, 1921).

TABLE I (continued)

Mussel	Host fish	References
<i>L. teres</i> (Rafinesque)	Acipenseridae <i>Scaphirhynchus platyrhynchus</i> (Rafinesque)	Coker <i>et al.</i> (1921), Surber (1913), C. B. Wilson (1916)
	Lepisosteidae <i>Lepisosteus osseus</i> (Linnaeus), Longnose Gar <i>L. platostomus</i> Rafinesque	Coker <i>et al.</i> (1921), Jones (1950), Reuling (1919), C. B. Wilson (1916) Coker <i>et al.</i> (1921), Howard (1914a), Howard and Anson (1922), Jones (1950), Reuling (1919), C. B. Wilson (1916)
	Centrarchidae <i>Lepomis cyanellus</i> Rafinesque <i>L. gulosus</i> (Cuvier) <i>L. humilis</i> (Girard) <i>Micropterus salmoides</i> (Lacépède) <i>Pomoxis annularis</i> Rafinesque	Coker <i>et al.</i> (1921), Surber (1913) C. B. Wilson (1916) Coker <i>et al.</i> (1921), Surber (1913) Coker (1919), Coker <i>et al.</i> (1921), C. B. Wilson (1916) Coker <i>et al.</i> (1921), Surber (1913), C. B. Wilson (1916) Coker <i>et al.</i> (1921), Surber (1913)
<i>Leptodea</i> <i>fragilis</i> (Rafinesque)	Sciaenidae <i>Aplodinotus grunniens</i>	Howard (1913), C. B. Wilson (1916)
<i>Ligumia recta</i> (Lamarck)	Anguillidae <i>Anguilla rostrata</i> (Lesueur)	Coker <i>et al.</i> (1921)
	Centrarchidae <i>Lepomis macrochirus</i> Rafinesque	Clarke and Berg (1959), Coker <i>et al.</i> (1921), Lefevre and Curtis (1912), C. B. Wilson (1916) Lefevre and Curtis (1912)
	<i>Micropterus salmoides</i> (Lacépède) <i>Pomoxis annularis</i> Rafinesque	Clarke and Berg (1959), Coker <i>et al.</i> (1921), Lefevre and Curtis (1912), C. B. Wilson (1916)
	Percidae <i>Stizostedion canadense</i> (Smith)	Pearse (1924)
<i>L. subrostrata</i> (Say)	Centrarchidae <i>Lepomis cyanellus</i> Rafinesque <i>L. macrochirus</i> Rafinesque <i>Micropterus salmoides</i> (Lacépède)	Lefevre and Curtis (1912) Lefevre and Curtis (1912) Lefevre and Curtis (1912)
<i>Obovata</i> <i>olivaria</i> (Rafinesque)	Acipenseridae <i>Scaphirhynchus platyrhynchus</i> (Rafinesque)	Coker <i>et al.</i> (1921), Howard (1914a)
<i>Ellipsaria</i> <i>lineolata</i> (Rafinesque)	Centrarchidae <i>Lepomis cyanellus</i> Rafinesque	Surber (1913), C. B. Wilson (1916)

## 8. Clams and Mussels (Mollusca: Bivalvia)

TABLE I (continued)

Mussel	Host fish	References
	Percidae <i>Stizostedion canadense</i> (Smith)	Surber (1913)
	Sciaenidae <i>Aplodinotus grunniens</i> Rafinesque	Coker (1919), Coker <i>et al.</i> (1921), Howard (1914a), Howard and Anson (1922), C. B. Wilson (1916)
42	<i>Proptera alata</i> (Say)	Howard (1913), C. B. Wilson (1916)
43	<i>Proptera</i> <i>laevissima</i> (Lea)	Surber (1913), C. B. Wilson (1916)
44	<i>P. purpurata</i> (Lamarck)	Coker and Surber (1911), Howard and Anson (1922), Surber (1912, 1913), C. B. Wilson (1916)
45	<i>Truncilla dona-</i> <i>ciformis</i> (Lea)	Surber (1913, 1915), C. B. Wilson (1916)
	Percidae <i>Stizostedion canadense</i> (Smith)	Surber (1913), C. B. Wilson (1916)
	Sciaenidae <i>Aplodinotus grunniens</i> Rafinesque	Howard (1913, 1914a), Howard and Anson (1922), Surber (1912, 1913), C. B. Wilson (1916)
46	<i>T. truncata</i> Rafinesque	C. B. Wilson (1916)
	Sciaenidae <i>Aplodinotus grunniens</i> Rafinesque	C. B. Wilson (1916)

after, the mussel fishery declined, the Bureau lost interest, and most additional information about mussel hosts has trickled down the decades in scattered, shorter papers.

As an aid to the interested researcher and fisheries biologist alike, and because of my belief in the importance to mussels of such information in the days to come, I have assembled in Table I all information on glochidial hosts that is known to me. Insofar as possible, the tabulated data have been brought taxonomically up to date. For the fishes, Trautman (1957) and Jordan *et al.* (1930) have been invaluable, and the vernacular and scientific nomenclature in Bailey *et al.* (1970) has been followed precisely. Simpson (1900), Frierson (1927), Murray and Leonard (1962), Johnson (1970), and Starrett (1971) have been used in the updating of naiaid nomenclature.

The information in Table I reveals some points of interest and significance. The Centrarchidae (sunfishes, basses) are identified or implicated as hosts for more than half the mussel species listed. The 11 centrarchids involved come to over one third of the species given by Bailey *et al.* (1970) for the United States and Canada, and they are a higher representation than exists for any other family. About one-fifth of all known mussel hosts are centrarchids, and about two-fifths of known records involve this family. The White Crappie, *Pomoxis annularis* Rafinesque, a centrarchid, hosts more kinds of glochidia (16 species) than any other fish will tolerate. Clearly, the Centrarchidae are the most important host family. Fortunately, the family contains many durable and widespread species and theoretically provides a host fish reservoir of some permanence. Of course, we cannot assume that the mussel fauna will survive simply because the centrarchids do, and, of course, only a limited variety of mussel glochidia is recorded from centrarchids. Incidentally, the importance of the Drum (Sciaenidae) and of *Stizostedion canadense* (Smith), the Sauger (Percidae), is scarcely less.

Not mentioned in Table I are several less specific records. Morrison (*in* Clarke and Berg, 1959) and Read and Oliver (1953) listed indeterminate species of *Notropis* (Cyprinidae) as hosts for a Floater, *Anodonta grandis* Say 1829. Young (1911) gave the Banded Killifish, *Fundulus diaphanus* (Lesueur) (Cyprinodontidae), as host for at least one unspecified mussel. Williams (1969) did likewise for the Spotted Sucker, *Minytrema melanops* (Rafinesque) (Catostomidae), in Kentucky Lake. According to C. L. Hubbs (*in* Jordan *et al.*, 1930), *Lepomis euryorus* McKay is a hybrid between the centrarchids *L. cyanellus* Rafinesque, the Green Sunfish, and *L. gibbosus* (Linnaeus), the Pumpkinseed; Coker *et al.* (1921) gave *euryorus* as a glochidial host for *Amblyma plicata*. On the Blackstripe Topminnow, *Fundulus notatus* (Rafinesque) (Cyprinodontidae), Shira (1913) found a glochidium smaller than, but very similar to, that of a Pocketbook, *Proptera capax* (Green 1832).

Fishes have enormous influence on mussel distribution. For example, Wilson and Dangle (1914) noted that above the Falls of St. Anthony at Minneapolis, Minnesota, on the Mississippi River there were Mucklets (representing the lampsiline genera *Lampsilis* and *Actinonaias*), but none of the "Quadrula-group" (primarily the amblemine genera *Amblyma*, *Quadrula*, and *Megaloniaias*). They felt that no host fishes for the latter group had been able to surmount the Falls. Similarly, Wilson and Dangle believed that the St. Louis River gorge at Carlton, Minnesota, had blocked all glochidial hosts because no mussels whatsoever were found in the river above it. A third example of this sort concerns Cumberland Falls on the Cumberland River in Kentucky; only a few members of the rich naiad fauna in this river occur above the Falls (Wilson and Clark, 1914; Neel and Allen, 1964).

## 8. Clams and Mussels (Mollusca: Bivalvia)

239

Anthropogenic changes in the fish fauna are a real and present danger to mussels. Athearn (1967) emphasized the adverse effects of wholesale destruction of "trash" fish, many of which are mussel hosts (Table I); Heard (1970) told how *Anodonta imbecilis* and another Floater, *A. peggyae* Johnson (1965, are being destroyed in Lake Talquin, an impoundment on the Ochlocknee River, Florida, by rotenone treatments intended to eliminate a "pest" fish, *Dorosoma cepedianum* (Lesueur), the Gizzard Shad. After each intensive application, the shore would be littered with dead and dying bivalves of these and other species. Ironically, it is *A. imbecilis*—otherwise an enormously tolerant species—that is being eliminated. It is an additional irony that this Shad is a glochidial host for at least four species of mussels (Table I), including representatives of *Anodonta* and of *Megaloniaias*, another genus known from the Ochlocknee system. Although this is the least important point, it must finally be added that Lake Talquin happens to be the type locality of *A. peggyae*. An "improvement" in the fish fauna from the angler's point of view is not necessarily in the best interests of all organisms concerned.

One last point about mussels and fishes: the really successful mussels— notably *Amblyma plicata*, *Anodonta grandis*, and the Washboard, *Megaloniaias gigantea* (Barnes 1823)—parasitize large number of host fishes (15, 19, and 16 species, respectively).

## 17. Amphibians (Vertebrata: Amphibia)

There is a record (van der Schalie, 1937) of a small mussel in the stomach of a frog, and Howard (1951) suggested that the mudpuppy, *Necturus maculosus* Rafinesque, may devour *Simpsoniconcha ambigua* (Say 1825). Perhaps it is in this way that the latter's glochidia get on *Necturus*, its only recorded host (Howard, 1914c, 1915, 1951). In addition, Seshaiya (1941) described successful glochidial metamorphoses on tadpoles. The limited information indicates that mussels derive little harm and much good from their associations with Amphibia.

## 18. Reptiles (Vertebrata: Reptilia)

Turtles will occasionally (and insignificantly) feed on mussels (Coker *et al.*, 1921).

## 19. Birds (Vertebrata: Aves)

As predators on young fishes, waterfowl interfere with naiad reproduction (Baker, 1922), and some birds prey directly upon adult mussels. Simpson (1899) recounted how crows would drop mussels through distances sufficient to break their shells. Coker *et al.* (1921) confirmed Simpson's observation and added that shorebirds will feed upon mussels stranded in

shallow waters. Snyder and Snyder (1969) gave detailed accounts of the ways Limpkins, Everglade Kites, and Boat-tailed Grackles employ to open mussel shells. These records are few and bird predation upon mussels, light.

#### 20. *Mammals* (Vertebrata: Mammalia)

A few aquatic mammals feed more or less heavily on mussels: otter, mink, and muskrat (Coker, 1912; Evermann and Clark, 1918; Simpson, 1899; Parmalee, 1967; van der Schalie, 1938b; Williams, 1969; Wilson and Clark, 1912a,b). There is a small number of more detailed observations on the habits of muskrat. Wilson and Clark (1914) noted their preference for Pigtoes (*Fusconaia* or *Pleurobema*) in the Cumberland River. Muskrats have severely restricted the ranges of several species in shallow waters: *Anodonta* spp. (Headlee, 1906), *Lasmigona costata* (Rafinesque 1820) (Zetek, 1918), and *L. costata* and *Strophitus undulatus* (van Cleave, 1940). Raccoon are occasional mussel predators (Simpson, 1899), and hogs can root mussel beds to pieces (Kirtland, 1851; Meek and Clark, 1912).

Aboriginal man consumed mussels in great numbers (Matteson, 1953; J. L. Murphy, 1971; Ortman, 1909a; Roscoe, 1967; Stansbery, 1966b; van der Schalie and Parmalee, 1960; Wilson and Clark, 1912a). Documentations are few, but modern man will occasionally feed on mussels (e.g., Wilson and Clark, 1912b).

Sadly, modern man's associations with freshwater mussels have not all been of the culinary variety. The ways in which his activities and his wastes have affected mussels are, against a backdrop of "normal" chemical and physical needs, the main theme of the next pages of this chapter.

### E. CHEMICAL AND PHYSICAL PARAMETERS

#### 1. *Temperature*

A modest fund of not usually very specific information is available on the effects of temperature upon freshwater mussels. The blood of the Eurasian *Anodonta cygnea* (Linnaeus 1758) freezes at  $-0.078^{\circ}\text{C}$  (Potts, 1954); the slight difference between that figure and the freezing point of water cannot be of great comfort to the mussel. Salbenblatt and Edgar (1964) contributed the useful information that temperature tolerances do indeed vary among species: specifically,  $29^{\circ}\text{C}$  was lethal for most *Anodontoides ferussacianus* (Lea 1834) tested, whereas most *Anodonta grandis* and Mucklets, *Lampsilis radiata luteola* (Lamarck 1819), survived.

Edgar (1965) observed sperm release by *Anodontoides ferussacianus* stimulated by a drop from  $27^{\circ}$  to  $22^{\circ}\text{C}$ . Having disproved the significance in this matter of dissolved oxygen, pH, and carbon dioxide, Chamberlain (1934)

#### 8. *Clams and Mussels* (*Mollusca: Bivalvia*)

confirmed only temperature as the determining factor in the discharge of egg masses by the Arkansas Fan Shell, *Cyprogenia aberii* (Conrad 1850). Sudden drops in temperature promote egg mass abortion (Matteson, 1948). Low temperature dulls glochidial response (see Section II, B) to opportunities for infection (Arey, 1921). Warmer water often shortens the period of glochidial encystment (Young, 1911). Whereas the glochidia of northern populations of *Anodonta grandis* would ordinarily overwinter in the marsupia before host infection in the spring, G. H. Penn (1939) described autumnal release of *grandis* glochidia in New Orleans.

Low temperature represses development of the mussel's digestive style (W. R. Allen, 1921). Oxygen consumption rises with temperature (Lukacsos-vics and Salánki, 1964). Hobden (1970b) showed that semipurified digestive gland catalase exhibits optimal activity at  $10^{\circ}\text{C}$  in *Elliptio complanata*. Mantle flap movement in *Lampsilis radiata luteola* varies directly with change in temperature (Griet, 1926).

There is disagreement about what inspires mussels, ordinarily very sedentary, to move about. Movement was ascribed to changes in water depth by Wilson and Clark (1912a), van der Schalie (1938b), and Grantham (1969). Evermann and Clark (1918) stated that in winter mussels *sometimes* move farther offshore and burrow more deeply into the substrate, and van Cleave (1940) noted some White Heel Splitters, *Lasmigona complanata* (Barnes 1823), which moved to deeper waters with a  $10^{\circ}\text{F}$  drop in temperature. Bovjerg (1957), however, was convinced that only starvation regularly stimulates mussel activity.

#### 2. *Light*

W. R. Allen (1923) offered the following observations and speculations on the relationship between mussels and light. Sudden reductions in light, as a shadow passing over a mussel, cause it to contract its mantle "siphons," possibly because shadows are so often cast by predators. Perhaps the dappling among weeds induces the same response, which would explain why only a few species of mussels are commonly found in weed beds. On the other hand, bright light stimulates movement, probably to start the mussel on his quest for deeper water (i.e., less light) away from the shallows with their hazards, dessication, predation, and the like. Although this pattern of motion would be appropriate to most mussels, the Lilliput Shell, *Carunculina parva* (Barnes 1823), for example, may be extremely abundant in a few inches depth, following the water's rise and fall, seeking its margin (Clench and Turner, 1956; Grantham, 1969; Isely, 1925; Murray and Leonard, 1962; Utterback, 1915-1916). One wonders in what way turbidity (see Section II, F, 3) and great depth (see Section II, F, 2) disturb naiad phototaxes.

### 3. Hardness

In central New York state, Clarke and Berg (1959) found no unionid mussels in waters of less than 47 ppm hardness (as  $\text{CaCO}_3$ ), but Harman (1969) found several species at levels as low as 21 ppm. Although hardness (especially the availability of calcium) is essential to the welfare of mussels, there seems to be no published information about exact levels at which hardness determines the presence or absence of a given mussel species. Soft, poorly buffered waters may experience rapid changes in pH, which can, in turn, do harm to mussels (*ibid.*). At least some American species can combat this by drawing upon shell materials for buffers (Ellis *et al.*, 1931), and the Eurasian *Anodonta cygnea* (Linnaeus 1758) can take calcium from its valves when the diet is poor in this element (de Waele, 1930).

Calcium is antagonistic to metals, and alkaline waters (Section II, E, 4) precipitate them as insoluble, harmless hydrates (Wurtz, 1962).

### 4. Alkalinity

New York state's Tioga River was "practically devoid of molluscan life" wherever Harman (1970) found about 15 ppm or less of total alkalinity. Similarly, Pennak (1953) stated that Anodontinae rarely live at levels of "bound  $\text{CO}_2$ " less than 15 mg/liter, yet Morrison (1932) found an anodontine species, *Anodonta c. cataracta* (Say 1817), a Floater or Paper Shell, in water with only 2.6 ppm of "fixed  $\text{CO}_2$ ."

### 5. pH

In a study of the Big Muddy River, a naturally acidic stream in Illinois, Jewell (1922) reported nine mussel species and concluded that their distributions had to do with substrate type, not water quality. Harman (1969) implied that pH has less to do with mussels than is commonly supposed. Morrison reported mussels living throughout a broad range (5.6 to 8.3) of pH. Ellis *et al.* (1931) showed that mussel blood pH varies widely in the subneutral range. Nevertheless, the blood is readily modified by the surrounding waters (*ibid.*). Thus, when Matteson (1955) introduced mussels into lake waters of pH 4.4 to 6.1, the intolerable acidity induced a response akin to aestivation: the valves clamped shut, and the mussels gradually lost weight. Matteson suggested that declining pH of water in the mantle cavity can have a lethal effect. In fact, low pH reflects a chemical regime featuring so much dissolved carbon dioxide that mussels' gas exchange is probably impeded. Despite the prevailing subneutral pH of mussel blood, some physiological functions proceed best in the basic pH range; for example, Hobden (1970b) showed that semipurified digestive gland catalase of *Elliptio complanata* has optimal activity at pH 7.8.

### 8. Clams and Mussels (Mollusca: Bivalvia)

Ellis' (1936) data suggest that low pH allows suspended materials to remain in suspension, thereby doubtless interfering with some aspects of mussels' biological activities (see, for example, Section II, F, 3). Wurtz (1962) pointed out that acidic waters bring metals (including toxins) into solution.

#### 6. Arsenic

Ellis (1937) reported that 16 ppm of sodium arsenite in "hard water" are fatal to *Amblema plicata* in 3-16 days.

#### 7. Cadmium

Solutions of  $\text{CdCl}_2$  above 0.001M significantly inhibit respiration of *Anodonta cygnea* (Lukacsovics and Salánki, 1964).

#### 8. Chlorine

Reporting on the mussels of Turtle River, North Dakota, Cvancara and Harrison (1965) recorded none where the river flows through a belt of naturally saline soils and chloride concentration rises to 87 ppm and above. Ironically, the heightened chloride level was accompanied by unusually high dissolved oxygen and low turbidity (as ppm of  $\text{SiO}_2$ ).

Destruction of mussels by chloride-laden oil field brine was first reported by Shira (1913). Williams (1969) reviewed the tale of oil brine damage in the Green River of Kentucky. In 1958 the chloride concentration shot from fewer than 10 to more than 1000 ppm. Mussel bed recruitment became possible in the afflicted area only where high flow and dissolved oxygen levels obtained just below dams. *Amblema plicata* and *Megalomias gigantea*, two very valuable commercial species, withstood brines best among mussels. Much of the magnificent mussel fauna (Ortmann, 1926) was badly damaged or destroyed, but remnants remain, as at Munfordville, where Stansbery (1965b) secured over 60 species some years ago.

#### 9. Copper

Imlay (1971) reported that several months' exposure to 25 ppb of copper was lethal to certain unspecified mussels. Wurtz (1962) considered copper second only to zinc (Section II, E, 16) in toxicity among metals.

#### 10. Iron

Hobden (1970a) presented a detailed account of iron concentration by *Elliptio complanata*. There was little metabolic turnover or excretion of the iron. Hobden wondered if excretion was naturally inadequate or uptake, hyperactive. He thought that the high concentrations might be an emergency store, but noted that no known enzyme system needs so much of this trace element.

that gravity hinders respiration, by rendering portions of the gills unsuitable for gas exchange (Howard, 1914c; W. R. Allen, 1921; Matteson, 1955).

In Imlay's (1971) experiment, *Amblema plicata* doubtless survived total lack of oxygen because, as a powerful species whose valves fit closely, it is able to clamp shut very tightly. Shells of members of the genus *Anodonta* usually gape even when closed, so the animals cannot rely upon a supply of water hermetically sealed within the mantle cavity, plus the lowered metabolic rate of dormancy, to see them safely through periods of marginal oxygen. Anodontae must survive these conditions on physiological aptitude alone. This is one of the reasons, of course, why they can so successfully exploit impoundments (see Section II, F, 2).

Lukacovics (1966) found that *Anodonta cygnea* experienced 95% mortality within three days under hypoxic conditions, but American species—with the possible exception of West Coast forms (see Hannibal, 1912)—appear more durable. *Anodonta imbecilis* Say 1829, for example, evolves enough metabolic oxygen to ensure survival when the dissolved oxygen of the surrounding water is exhausted (Eddy and Cunningham, 1934). Similarly, Hiestand (1938) demonstrated that *A. imbecilis* can respire normally at down to about 0.73 ml/liter of oxygen and concluded that this species either uses very little or can very delicately adjust metabolic rate. Larger mollusks have the lower metabolic rates (*ibid.*); perhaps this is one reason—in addition to increased buoyancy—why many anodontae are so corpulent. These remarkable faculties are not limited to *Anodonta* among anodontine genera. Cole (1926) found *Anodontoides ferrussacianus* active as far as one foot below the surface of organic silt where the dissolved oxygen was only 6% of that in the stream flowing above.

W. R. Allen (1923) made the disconcerting point that at lower levels of oxygen, before the mussel is stimulated to close its valves tightly, it tends to gape in an effort to maximize the passage of water to the gills. At this time, of course, the animal is extremely vulnerable.

Grantham (1969) found no mussels alive where dissolved oxygen occasionally dropped as low as 3 mg/liter. Ellis (1931a) felt that mussels would not survive at oxygen levels below 5 mg/liter.

Badman and Chin (1973) studied the metabolic responses of a Pigtoe, *Pleurobema*, to anaerobic conditions.

#### 14. Phosphorus

Starrett (1971) felt that in the Illinois River there was in 1966 no apparent correlation between mussel abundance and the total phosphate load, including industrial wastes and agricultural run-off. Thus it seems that the phosphorus threat to mussels lies in the contribution which phosphates make to organic enrichment (Section II, F, 6).

#### 11. Mercury

Yokley (1973) noted that certain mussels—*Elliptio crassidens* (Lamarck 1819), the Elephant Ear, and *Cyclonaias tuberculata* (Rafinesque 1820), the Purple Warty Back—can accumulate in the soft tissues not quite 3 µg of mercury, apparently without ill effect. Evidently there is no published information on lethal and sublethal effects upon mussels by this much publicized element. Wurtz (1962) considered mercury's (and silver's) toxicity to be exceeded only by zinc's (Section II, E, 16) and copper's (Section II, E, 9).

#### 12. Nitrogen

Starrett (1971) furnished an account of the possible effects of nitrogen on mussels in the Illinois River. Nitrogen (as ammonia) exceeded 6.0 ppm throughout the upper river, where (in 1966) no mussels had occurred. Mussels reappeared where ammonia nitrogen was at or below 6.0 ppm. Noting the deleterious effect of this substance upon fish, Starrett assumed that the adverse effect on mussels had been nothing more than interference with their glochidial hosts. Emphasizing that they are not hosts, he listed these four as the only common fishes in the upper Illinois: *Notropis atherinoides* Rafinesque, the Emerald Shiner; *Ictalurus melas* (Rafinesque), the Black Bullhead; *Carassius auratus* (Linnaeus), the Goldfish; and *Cyprinus carpio* Linnaeus, the Carp. Starrett was unaware that at least the latter three are glochidial hosts (Table I). Moreover, the glochidia in question represent several species designated by Starrett as still alive in the lower river. Perhaps ammonia nitrogen has a direct effect upon mussels, after all.

Of course, nitrogen (chiefly as nitrate) plays an important role in the eutrophication of waterways (see Section II, F, 6).

#### 13. Oxygen

In Imlay's (1971) experiments, adults and juveniles of several unspecified "riffle species" of mussels required 2.5 ppm of dissolved oxygen for survival at laboratory temperatures corresponding to those of the summer, when oxygen levels are usually least. *Amblema plicata* survived for 10 weeks at 0 ppm of oxygen; this is a "pool" species which is tolerant of other adversities, as well, including muddy bottoms and other conditions associated with impoundment (see Section II, F, 2) (Baker, 1922; Imlay, 1972a; Isely, 1925; Howard, 1914c; Murray and Leonard, 1962; Parmalee, 1967; Starrett, 1971; Williams, 1969; Wilson and Clark, 1914; Wilson and Dangiade, 1914). However, all species examined by Imlay required 6 ppm of dissolved oxygen for normal growth. Ellis (1931b) found that mussels become inactive when oxygen tension is no greater than one-fifth of saturation. It is a curious irony



### 15. Potassium

Lukašovics and Salánki (1968) found *Anodonta cygnea* more sensitive to  $K^+$  than to any other cation, and Imlay (1971) added several observations on the relation of potassium to mussels. The natural absence of mussels from certain areas (for example, in the western Mississippi basin) is probably due to the presence of potassium in toxic quantities (see Section II.E.8). The lowest lethal level is between 4 and 7 ppm. Potassium is a common pollutant from industry, particularly paper mills (see Section II.F.5); irrigation return water; and petroleum brine. Further details concerning the important role of potassium in the life of mussels were summarized by Imlay (1973).

### 16. Zinc

Wurtz (1962) considered zinc the most toxic of heavy metals, followed by copper (Section II.E.9), mercury (Section II.E.11), and silver. Mulligan *et al.* (1960) implied that levels of zinc averaging 65 ppm had at least aided in the extermination of mussels in afflicted portions of the Nolichucky River in Tennessee.

## F. ADVERSE ANTHROPOGENIC EFFECTS ON MUSSELS

There is no question that the mussel fauna has suffered severely from anthropogenic substances and activities (see Section II.D.20). In a comparison of the evidence from Indian shell middens and from modern collections, Stansbery (1965a) concluded that seven Unioninae had disappeared from the Scioto River of Ohio during historic times. Stansbery (1970b) listed 41 of 103 Ohio River drainage naiades as rare and endangered, including eight species—all in the riffle-adapted lampsiline genus *Dysnomia* (see Stansbery, 1971)—which he thought probably extinct. Dimeen (1971) found in the St. Joseph River, Indiana, only about one half of the species recorded by Wenninger (1921) and van der Schalie (1936). Parmalee (1967) felt that at least 12 species of the original mussel fauna were missing in Illinois, but, after a more detailed study of the Illinois River in 1966, Starrett (1971) concluded that more than 25 species had disappeared since 1900, with five more excessively rare and none living in the upper river (see Section II.E.12). Other equally distressing illustrations of degradation appear in the pages to come. The story is an old one (see Ortman, 1909b, and Kirtland, 1851), recently reviewed by Stansbery (1970b).

### 1. Channelization

Wilson and Clark (1912a) pointed out that canals need not be inferior mussel habitats if their walls and floors are stable. Kirtland (1851) thought them superior places, in fact, but deplored how they tended to accumulate

## 8. Clams and Mussels (Mollusca: Bivalvia)

"filth." Channelization, of course, straightens and deepens winding waterways until they are virtual canals. Wilson and Clark (1912b) remarked the total loss of mussel fauna in those portions of the Yellow and Kankakee Rivers of Indiana which had been straightened and dredged. In perhaps the earliest indictment of channelization, they told how these practices changed the rivers into motionless pools (see "Dams," below) alternating with unbroken stretches where silt and sand constantly scud along the bottom. No mussels live in rolling sand and on shifting bars (Williams, 1969). Williams noted, also, the utter destruction of mussels and their habitats by gravel dredging in the Ohio River, and Baker (1922) made the same point about the fauna in the Big Vermilion River of Illinois.

### 2. Dams

Riffle conditions are usually best for juvenile mussels, but adults, especially of the heavy-shelled commercial species, often do better in quieter waters (Wilson and Clark, 1912c; Dangle, 1914). In theory, then, one might expect that impounded waters behind dams would provide an especially good mussel habitat. For a variety of reasons, this is not the case, even though certain mussels (especially *Anodonta*, other advanced Anodontinae, and lightly built lampsiline species) are peculiarly suited to impoundment conditions.

Probably the most critical adverse effect of impoundment upon mussels is disruption of their reproductive processes. The deeper, cooler waters of western Lake Erie delay maturation of certain Lampsilinae (Stansbery, 1967). Discussing the commercial species of Kentucky Lake, Williams (1969) noted that many individual fishes bore glochidial infections, but the level of infection on each was very low (see Scruggs, 1960). Williams found no mussels less than four years old, few less than 13, and no recruitment in the preimpoundment beds, by then under 55 feet of water. On the other hand, he discovered that many females were gravid. Therefore, the minimal reproduction was not due to problems with adult fertility or glochidial host availability, but, perhaps, to host sickness, loss of glochidia in the substrate (see Section II.F.3), or attacks upon larvae by microorganisms (see Ellis, 1929; "Bacteria," Section II.D.2; and "Protozoans," Section II.D.4).

Impoundment can profoundly disturb the fish fauna, driving out glochidial hosts in the process. Ellis (1931a) reported breeding grounds for fish and plankton were disappearing around Lake Keokuk, a Mississippi River impoundment, due to weed clearing for pleasure boating, as well as construction of roads and riprap along the margins. Isom and Yokley (1968a) noted that the mussel fauna of Bear Creek, a Tennessee River tributary, now differs from Ortman's (1925) records; since the Creek was then still pristine, they attributed the faunal changes to failure of glochidial hosts to traverse

the lower portion of the Creek, impounded by back-up of the Tennessee. These authors (1968b) interpreted a decline in the mussel fauna of the Duck River—again judged against Ortmann's (1924) records—in the same way. A specific example is Yokley's (1972) forecasting the doom of *Fusconaita ebena* (Lea 1831), the Ebony Shell, in Kentucky Lake because its host, *Notropis ardens* (Cope), the Rosefin Shiner, no longer tolerates this impoundment. Similarly, Coker (1929) reported that *Lampsilis teres* (Rafinesque 1820), aptly y-clept the Yellow Sand Shell, had been found in 1926 abundant on sand bars thrown up between wing dams in Lake Keokuk. Five years later Ellis (1931b) found that these bars had muddied and become largely devoid of *teres*, in spite of an increase in gars (*Lepisosteus*), this species' best hosts (Table I). *Lampsilis teres* was the species most readily killed by silt during Ellis' (1936) experiments.

Thus adult and juvenile mussels, also, can be hurt by impoundment. Baker (1922) noted that parasitism upon *Lampsilis radiata luteola* was heavier above than below the dam across the Big Vermilion River at Homer Park, Illinois, even though this was then a very low dam. Again in contrast to Ortmann's (1918) previous records, Isom (1971) determined a net loss of 60 species from the Tennessee River in the Fort Loudon Reservoir area; he attributed this disaster to periodic oxygen sag (Section II,E,13). Perhaps because of low oxygen and temperatures, but also because mussel species seek their individual optimal water depths (W. R. Allen, 1923), mussels are rarely found at great depths—notwithstanding Reigle's (1967) record of *Anodonta grandis* alive, but stunted, at 102 feet in Lake Michigan. Parasitism, low temperature, oxygen sag, and the water pressure at great depths are undoubtedly inimical to mussels and their glochidial hosts, but siltation (Section II,F,3) is the most important of the many adverse effects associated with damming. Saving this one rather graphic illustration, siltation problems are discussed below: Scruggs (1960) found that *Pleurobema cordatum* (Rafinesque 1820), a Pigtoe, was able to reproduce in Wheeler Reservoir on the Tennessee River and that adults were surviving impoundment. Populations were in decline, however, not because of commercial fishery pressure, but because most juvenile mussels did not survive the silt accumulating on the bed of the old river channel. Wilson and Danglede (1914) recounted allegations that mussels were buried one and three feet deep in the floors of the Shell River and Lake Bemidji, Minnesota, respectively. These reports have been neither confirmed nor complemented since.

Spillways below dams holding back shallow impoundments often support rich naiad populations. Baker (1922) reported 28 species below Homer Park dam, but 10 fewer just above. Doubtless the difference has much to do with the adverse impoundment effects behind the dam, but Baker emphasized the salubrious features below: the Big Vermilion's original stable

bottom, with the advantages of highly oxygenated water laden with nutrients from the impoundment. However, the promise of the spillway is usually ultimately unfulfilled. The one below Magnolia Springs in Jenkins County, Georgia, supports large populations of numerous naiad species, including the rare Atlantic Pigtoe, *Fusconaita masoni* (Conrad 1834). The Springs are used as a fish hatchery, and, judged by the quantity of vegetation in the spillway, the water falling over its dam is nutrient-rich. Here is induction of impoundment conditions in one part of a waterway by the nice union of eutrophication and actual ponding in another. The spillway has changed little enough since W. J. Clench, K. J. Boss, and I visited in 1961, but the day will come when it is choked with weeds, and only *Anodonta* and the abundant *Unio merus terralasmus* will survive. Another instance of snatching a little bit of victory from the jaws of overwhelming defeat is Williams' (1969) ironic account of how, in the wake of petroleum brine pollution (see Section II,E,8), mussel beds recruited successfully only in the fast waters below dams in the Green River.

Dams oppress mussels in additional ways; some are rather subtle, but as effectively lethal as the foregoing examples. Wing dams, for instance, create novel water currents, which move sands over mussel beds and sweep juveniles onto these shifting bars (see Williams, 1969), where they, too, are smothered (Grier, 1922).

Clench, Boss, Fuller, and H. D. Athearn once searched for mussels on a shoal below a rather high dam spanning the Ogeechee River of Georgia. Only the painfully cold water released at the foot of the dam was flowing through the shallows below. Some effects of low temperatures upon mussels have already been discussed (Section II,E,1). The incomparable Athearn found several living mussels; the rest of us found none.

Long ago Simpson (1899) warned that waterways will occasionally dry out below dams. Grier (1922) noted that the high sand bars thrown up by wing dams can become an excellent habitat for many valuable species, but these will be left to desiccate when the water falls. Most mussels experience difficulty in escaping the consequences of falling waters (Grier, 1922; Parmalee, 1955). Coker (1915) made the point that flooding—which, of course, is not always checked by dams—and other fluctuations in water level can interrupt naiad growth; this is particularly disadvantageous to the mussel industry (Section II,F,4). Dessiccation is the most important consequence of reduced water level; most mussels weather it poorly. For all their resistance to environmental turmoil, the advanced Anodontinae, with their thin and poorly fitted valves, are among these. In general, the Lamprosilinae are sensitive and mobile; they move to deeper waters rather readily. *Carricillina parva* (see Section II,E,2) and *Proptera laevisima* (Lea 1830) (Isely, 1925; Riggs and Webb, 1956) are able examples. Like most Ambleminae, *Amblema*

*plicata* is resistant to dessication (Wilson and Clark, 1914; Howard, 1914c), probably because of its thick and closely fitting valves. This is the more remarkable because Prosser and Weinstein (1950) demonstrated that blood amounts to less than 10% of the volume of *A. plicata*. A unionine species, *Unionites tetralasmus*, is that mussel most notoriously resistant to dessication, as reported by many authors, signally Simpson (1892), Strecker (1908), and Isely (1914). This species, incidentally, manages to survive in probably more types of demanding habitat than any other Nearctic mussel. Perhaps this has to do with the fact that it possesses the highest blood cell count, including phagocytes, among species studied by Dundee (1953).

Mussels' true mettle has been severely tested by impoundment. For example, Bates (1962) noticed that only eight species had invaded the post-impoundment Kentucky Lake shallows, and only two of them had been listed by Ortman (1925) or van der Schalie (1939a) as members of the pre-impoundment mussel fauna of the lower Tennessee River: *Quadrula quadrula* (Rafinesque 1820), the Maple Leaf, and *Truncilla donaciformis* (Lea 1928), the Fawn's Foot. The six pioneers were three species of *Anodonta*, *Proptera laevis*, *Leptodea fragilis* (Rafinesque 1820), and *Carunculina parva*.

### 3. Silt

Anything which obstructs current—dams, weed beds, and so forth—slows them and creates eddies, which allows settling of suspended silt (Ellis, 1931a). Wing dams (Section II,F,2) are particularly reprehensible because they set up powerful currents which shift bars, erode stream banks, and increase silt (Ellis, 1931b). These phenomena disturb the existing stream bed and render it unstable. Silt limits light penetration (Ellis, 1936), dulling the sensitivity of mussels' phototactic responses and reducing the production of mussel foodstuffs. Suspended silt causes mussels to remain closed almost half again as much as otherwise (*ibid.*); Stansbery (1970a) showed that siltation can retard growth of *Amblyema plicata*. On the other hand, mussels can feed in water so choked by silt that they are invisible in this suspension (Churchill and Lewis, 1924). Williams (1969) observed coal dust in mussels' digestive tracts, but observed no ill effects. Nevertheless, Headlee (1906) showed that choking the gills with sediment has a terminal effect, and Ellis (1936) saw dying mussels with quantities of silt in their mantle cavities and gills. In spite of their ability to secrete copious mucous in order to remove silt, most of the mussels in Ellis' (1936) experiments died in one quarter to one inch of silt, and all were doomed when fully covered. Silt carries organic materials from suspension into the stream bed, causing them to remain longer and in higher concentrations (*ibid.*). Thus the adverse effects of enrichment (Section II,F,6) are increased and localized. Lefevre and Curtis

### 8. Clams and Mussels (Mollusca: Bivalvia)

(1912) reviewed divers aspects of the negative effects of silt upon mussels. As a classic example, we have Stansbery's (1964) report that since the impoundment of much of the Mussel Shoals in the Tennessee River there has been a net loss of 30 species from the fauna outlined by Ortman (1925). Much recent work concerning the effect of silt upon aquatic invertebrate organisms is reviewed by Chutter (1969).

#### 4. The Mussel Industry

Those readers who never saw Burt Lancaster brail for mussels in "The Kentuckian" or never read Mannix' (1965) article in *True* ("The Man's Magazine"), those unfortunates, I say, are probably unaware of the commercial interest taken in mussels during the last century. Contemporary accounts of the early pearl and mussel shell fisheries are available (Kunz, 1894, 1898a,b; Carlander, 1954; Temté, 1968; Coker, 1919; Smith, 1899; Vertrees, 1913), as well as papers which consider ways to conserve the mussel resource for, and in spite of, the industry (Simpson, 1899; Coker, 1914; Smith, 1919; van der Schalie, 1938a; Krumholz *et al.*, 1970; Jorgensen and Sharp, 1971). Aside from the outright destruction of animals killed for their shells and pearls, harvesting has these deleterious effects: reduction in breeding stock to the point where reproduction does not offset mortality; destruction and disruption of the stream bed; abortion of gravid females when disturbed (J. F. Boepple *in* Simpson, 1899); waste deaths of juveniles below useful and legal limits; and deaths of adults which cannot rebury themselves after being needlessly uprooted (see Imlay, 1972b). Fishing pressure and the use of plastic in button manufacture nearly terminated the shell industry after World War I, but the use of spheres of American mussel nautilus as cultured pearl nuclei by the Japanese revitalized the harvest during the 1960's. The use of scuba and other diving gear enables shellers to collect entire beds. However localized and imperfectly lethal, this may be the greatest threat to commercially valuable mussels today.

#### 5. Wood Products Wastes

Simpson (1899) mentioned the adverse effect upon mussels of sawdust as a false streambed. Similarly, Wilson and Dangle (1914) noted bark dislodged from logs driven downstream coating the bottom of the Prairie River of Minnesota. Ortman (1918) cited the damage done mussels by wastes from wood pulp and paper mills (see Section II,E,15) in the upper Tennessee River drainage. Mackie and Qadri (1973) found mollusks, including unionid mussels, limited by wastes from the same sorts of mills in Ottawa River, Canada. Finally, all flora and fauna have been completely destroyed for 15 miles downstream to the Gulf from a paper mill on the Fenholloway River of Florida (Heard, 1970b).

### 6. Organic Enrichment

A certain amount of eutrophication may be of service to mussels (van der Schalie, 1938b), presumably by increasing the amount of available food (Section II, C). Churchill and Lewis (1924) recorded an instance of unusual concentration of mussels below an area where rich vegetated disintegrated, and Coker *et al.* (1921) found healthy, even exaggerated, growth of mussels in water that was influenced by sewage. Nevertheless, too great organic enrichment, from whatever source(s), induces conditions akin to those of ponding and impoundment (see Section II, F, 2). There is proliferation of submerged vegetation, which contributes to a softer bottom with the products of its own decay mixed with silt which it strains from the water; the current slackens; and (Grantham, 1969) there develop increased bacterial oxygen demand, increased carbon dioxide, and lowered pH. These conditions are inimical to the great majority of mussels. In addition to phosphates, nitrates, and other ordinary ingredients of eutrophication, many sources of organic pollution include toxic substances, as well. Thus, for example, Mackie and Qadri (1973) found that mussels (and other mollusks) were severely limited by slaughter house wastes in the Ottawa River, Canada. Similarly, sewage has been responsible for total destruction of mussels in portions of the Kankakee River of Indiana (Wilson and Clark, 1912b) and the Salt Fork of the Vermilion River of Illinois (Baker, 1922).

### 7. Acid Mine Waste

Primarily in the form of mine drainage, acidic waters can have a direct, extraordinarily adverse effect upon mussels. A 1% acetate solution causes the mantle margin to contract, and the effect may be visible after several hours (W. R. Allen, 1923). Only the intensity of the response declines with lower concentrations (*ibid.*). Williams (1969) found only "baldies" (mussels with little or no periostracum) in Kentucky Lake, and Simpson (1899) stated that acid can eat holes through the shell to the animal. Yokley (1973) noted widespread mussel mortality due to acid in Kentucky Lake. I have seen streams where practically all macroinvertebrate life had been exterminated by acid mine wastes in the Slippy Rock Creek drainage of Western Pennsylvania, and as many as 60 years ago such effects were being recorded for portions of the Cumberland River in Kentucky (Wilson and Clark, 1914; Staubsby, 1969). Some mussels remain comparatively free of damage by acids at low concentrations; for example, Wilson and Clark (1914) noticed that *Trichema plicata* was free of corrosion in the Cumberland.

### 8. Pesticides

I am unaware of studies on mortality caused by pesticides in mussels. Bedford *et al.* (1971) found that *Lampsilis radiata luteola* and *Anodonta*

### 8. Clams and Mussels (Mollusca: Bivalvia)

*grandis* are excellent monitors of chlorinated hydrocarbons, including DDT, aldrin, and methoxychlor; they implied that at least one of these substances had been responsible for observed deaths. Miller *et al.* (1966) showed that *Elliptio complanata* concentrated diazinon and parathion at levels greatly in excess of their concentrations in the surrounding water and metabolized them very slowly. Fikes and Tubb (1971) found that *Amblyema plicata* concentrated 20 ppt ("t" for "trillion"! ) dieldrin at measurable levels about 2500 times background levels. Starrett (1971) discovered unexpectedly small concentrations of organochlorine pesticides (DDT, DDE, heptachlor epoxide, and dieldrin), probably because of their adsorption in stream-bed mud (see Ellis, 1936) and/or because of a shift in agricultural usage toward organophosphate varieties. Uptake of dieldrin and DDT by *E. dilatata* and *Anodonta grandis* under experimental conditions was studied by Zabik and Bedford (1972).

### 9. Radionuclides

As in the case of pesticides (Section II, F, 8), I am unaware of studies about the mortality and sublethal effects of radioactive materials upon mussels, but their ability to indicate the presence of substances occurring in extremely low concentrations in nature by accumulating them in readily detectable quantities has received a great deal of inquiry. Lee and Wilson (1969) found that the contrast between Sr/Ca ratios in ancient and modern mussel shells is indicative of different paleohydrologic conditions. On the other hand, Garder and Skulberg (1965) found that uptake in the Eurasian *Anodonta piscinalis* Nilsson 1822 varies with physiological and seasonal conditions. These authors and Nelson (1962, 1964) showed that isotopes of phosphorus, strontium, and cesium have especially great affinity for mussel bodies and/or shells. Nelson (*ibid.*) found that Tennessee River drainage mussels can concentrate Sr<sup>90</sup> at levels from 2500 to 9000 times normal. Brungs (1967) and Harvey (1969) found that mussels concentrated Zn<sup>65</sup> (Section II, E, 16) more heavily than any other isotopes studied by them. Finally, Nelson (1967) studied mussel concentration of nonradioactive isotopes of several elements. These are only a few examples of the rich and useful literature that is abuilding in this area, including studies by Harrison (1969) and Short *et al.* (1969).

### 10. Miscellaneous Pollutants

Gas works wastes, especially tar and oily scum, were reported by Wilson and Clark (1912b) and by Baker (1928) as very damaging to mussels. Wilson and Clark (1912a) cited dye from knitting mills as toxic to mussels. Williams (1969) could find no living mussels for six miles below an industrial area bordering the lower Tennessee River in Kentucky, but he did not dis-

criminate among the pollutants. Coker *et al.* (1921) reviewed the adverse effects of deforestation, including irregular stream flow, high water temperatures, and lowered dissolved oxygen; Grier (1922) recommended reforestation to strengthen stream banks against sand flow and silt runoff. The activities of private conchologists, research malacologists, commercial collectors for biological supply houses, and ecologists conducting biotic surveys all pose threats similar to those inherent in the pearl and shell industry (Section II, F.4). Stansbery (1970b) and van der Schalie (1938a) have reviewed numerous polluting agents, including some rather minor ones.

### G. MUSSELS AS INDICATOR ORGANISMS

The presence of unusually large populations of mussels can be indicative of pollution only in the case of minor degrees of organic enrichment (Section II, F.6). The absence of mussels can logically be an indication of environmental disruption only when and where their former presence can be demonstrated. It is very rare that we can quantitatively and/or qualitatively correlate the composition and size of the mussel fauna with a specific disruption, be it chemical or physical (see Ingram, 1956). Indubitably, we have much to learn. On the other hand, there can be no doubt that mussels have extraordinary value as qualitative indicators of pesticides, radionuclides, and, presumably, other trace substances in nature. Finally, organisms with ecologically narrow habitats are particularly sensitive to change. For example, several Nearctic Margaritiferidae prefer softer, cleaner waters and peculiar substrates (Bjork, 1962; Hendelberg, 1960; McMillan, 1966; Roscoe and Redelings, 1964; Stansbery, 1966a; Stober, 1972). These characteristics may be correlated with glochidial host predilections (Table I). As indicators, the Margaritiferidae must be thought both less useful and more sensitive than the Unionidae.

### III. Sphaeriidae

Until about two decades ago the great majority of literature on Nearctic Sphaeriidae was taxonomic, and most biological data involved such mainstays of "good, old-fashioned natural history" as notes on ranges and habitats. While these observations were often extremely informative, it was only recently that the reasons behind them were sought with any frequency. There is still an insufficiency of this more sophisticated information (but see Ingram, 1956), which accounts for the brevity and other shortcomings of this section almost as much as do the predilections and other weaknesses of the writer!

Thanks to the monographic treatments by Herrington (1962) and Burch (1972), sphaeriid taxonomy is not perfect, perhaps, but quite stable, partic-

### 8. Clams and Mussels (Mollusca: Bivalvia)

ularly when compared to that of most Unionacea. Older nomenclature has been brought up to the present in the light of these works.

Most of the biological literature prior to Herrington's revision is found in his bibliography and is not repeated in mine unless cited in the paragraphs below. Also, some relevant papers (Crowther, 1894; Monk, 1928; Ingram, 1941; Ingram *et al.*, 1953) were not mentioned by Herrington. Some recent European literature (Dance, 1970; Meier-Brook, 1970; Wolff, 1970; Kuiper and Wolff, 1970) contains information on sphaeriids which are Nearctic, as well as Eurasian.

Heard (1962, 1964, 1965b) has provided a great deal of information on aspects of "normal" reproduction and life cycles of many Nearctic sphaeriids, and Herrington (1962), as already noted, has assembled a host of data on "normal" habitats. By and large, the Sphaeriidae are a eurytopic lot, but some have exploited unusual habitats and may be more or less restricted to them. For example, Thomas (1959, 1963, 1965) has found that *Sphaerium partumeium* (Say 1822) exhibits some unusual adaptations (e.g., precocious production of young) to the evaporation of ephemeral pools, which are its usual habitat. Neither the habitat nor, to the best of my knowledge, the adaptation is encountered widely in this genus.

The case of *Sphaerium partumeium* is illustrative of the great success achieved by the family. Like many Unionacea (Section II, B), sphaeriids are hermaphroditic, even self-fertile (Thomas, 1959), and only a single individual may be required to extend a species' ecologic and geographic ranges. Differing from the Unionacea (see van der Schalie, 1945), Sphaeriidae are subject to mechanical distribution as a key element in their vagility. Resistance to desiccation (see Ingram, 1941) and hermaphroditism are thus especially advantageous.

There are some other odd sphaeriid life styles. *Pisidium conventus* Clessin 1877 is most abundant in deep, cool, highly oxygenated lake waters (Rawson, 1953; Heard, 1963; Hamilton, 1971). This habitat is so narrow that disappearance of *P. conventus*—as of certain Margaritiferidae (Section II, G)—would surely indicate an important change in water quality. *P. idahoense* Roper 1890, on the other hand, shows the same predilection for great depths, but it is able to survive lengthy periods with little or no oxygen (Juday, 1908; Cole, 1921). Certainly this species has the lesser value as an indicator organism. *Pisidium ultramontanum* Prime 1865, also, is an indicator, but of another sort: the pattern of its geographical distribution casts light on ancient drainage patterns (Taylor, 1960).

The Sphaeriidae include at least one clear example of the sort of indicator that responds positively to a measure of pollution. *Sphaerium transversum* (Say 1829) was believed by earlier authorities (e.g., R. E. Richardson, 1928) to increase in numbers under the influence of sewage and not to react adversely until such time as the macroinvertebrate fauna had been greatly

simplified. My experience of this creature in numerous eutrophic waters corroborates this point of view precisely. *Sphaerium transversum* belongs to the group *Musculium*, variously regarded as congeneric or subgeneric to *Sphaerium*. *Musculium* has had a reputation as a tolerator of impoundment (Ellis, 1931a). Zetek (1918) reported an oxbow "alive" with *transversum*, and I have found them by the tens of thousands in luxuriant weed beds. In the only paper on the reaction of a single Nearctic sphaeriid to so much as a single form of pollution, Ingram *et al.* (1953) noted a similar, though not so well developed, tolerance of enrichment conditions by *S. striatum* (Lamarck 1818). Silt was the substrate of the only *striatum* I have ever collected. Certainly such sphaeria as these are the sphaeriid analog of the unioniid genus *Anodonta*.

Grantham (1969) listed a number of authorities who have thought of the Sphaeriidae as tolerant of polluted, nearly septic conditions. There is no doubt that certain Sphaeriidae have real value as indicators of environmental disturbance, especially conditions of impoundment and eutrophication. Our knowledge is insufficiently detailed to define sphaeriid "pollution indication" in chemical terms, so, as with the Unionacea, I have refrained from tabulating probably meaningless and possibly misleading water chemistry data. Some can be found in papers on American sphaeriids by Filice (1958, 1959), Gillespie (1969), Thut (1969), Tuthill and Johnson (1969), Tuthill and Laird (1963-1964), and Zumoff (1973). In evaluating the relative worth of sphaeriid groups as indicators in terms of their responses to ecological pressure, it may be instructive to recall that Morrison (1932) stated that the lowest pH levels tolerated by *Sphaerium*, "*Musculium*," and *Pisidium* in northeastern Wisconsin lakes were 6.8, 5.9, and 5.1, respectively. As illustrated above, the group *Pisidium* shows perhaps the greatest tolerance among sphaeriids in other ways, as well. I would add that in my experience *P. compressum* Prime 1851 and *P. casertanum* (Poli 1791) respond almost as favorably to organic enrichment as does *Sphaerium transversum*. Significantly, Herrington (1962) regarded these two as the most common pisidia in North America.

As with unionaceans, once again, the parasites of sphaeriids have been generally ignored by malacologists. Once again, it is tempting to suppose that a correlation can eventually be demonstrated between degree of parasitism and amount of environmental stress. Wolcott (1899) recorded *Unionicola crassipes* (Muller), perhaps a questionable determination (see Section II, D, 15), as a symbiont of *Sphaerium simile* (Say 1816). Several authors have recorded parasitism of sphaeriids by "distomids" (see Section II, D, 6) and other digenetic trematodes (Goodchild, 1939a, b; Gentner and Hopkins, 1966; Groves, 1945; H. E. Henderson, 1938; Parker, 1932; Steelman, 1939; Vickers, 1940).

## 8. Clams and Mussels (Mollusca: Bivalvia)

*Eupera cubensis* (Prime 1865) is my final sphaeriid topic. Heard (1965a) has an elegant taxonomy and partial natural history of this species, which occurs primarily in lower portions of river systems of the Atlantic drainage of the Carolinas to the Caribbean drainage of South America. It is especially likely to be encountered in submerged rootstocks and other tangles, which offer refuge and an avenue to the surface: *Eupera* is often found out of water crawling on roots (Walker, 1915; Althearn in Clench and Turner, 1956; Hubricht, 1966). Heard records it attached, often with a byssus, to the "rims of rusty (but not fresh) beer cans." This species is regularly associated with *Sphaerium transversum*, *Pisidium casertanum*, and *P. compressum* in the Savannah River of Georgia and South Carolina. In enriched areas *E. cubensis* is the one of the four which is lacking if any are lacking at all.

## Acknowledgments

One does not put together an eclectic piece like this without a little help! My thanks go to Ruth Brown, Librarian at the Academy of Natural Sciences of Philadelphia; to two of her associates, Martha Pilling and Tamsen, my sister; to Arlene Mogilefsky, Librarian at the Academy's Department of Limnology; and to my colleague Daniel Bereza. Not has the forbearance of Micki, my wife, gone unnoticed of late months.

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## Addenda

- Burch's (1973) manual provides an excellent overview of the Nearctic unionacean fauna (see Section II, A).
- Conner (1905) identified *Lepomis gibbosus* (Linnaeus) (Centrarchidae) as a glochidial host of *Anodonta cataracta* Say (see Table I).

Stewart-Elder 1978 4 spp.