AMER. ZOOL., 33:599–609 (1993)

Freshwater Bivalve Extinctions (Mollusca: Unionoida): A Search for Causes[1]

ARTHUR E. BOGAN[2]

Research Associate

Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213–4080

SYNOPSIS. The freshwater bivalves (Mollusca: Order Unionoida) are classified in six families and about 165 genera worldwide. Worldwide rate of extinction of freshwater bivalves is poorly understood at this time. The North American freshwater fauna north of Mexico is represented by 297 taxa in two families. There are 19 taxa presumed extinct, 44 species listed or proposed as federally endangered, and there are another 69 species that may be endangered. A number of these endangered species are functionally extinct (individuals of a species surviving but not reproducing). Extinction of North American unionoid bivalves can be traced to impoundment and inundation of riffle habitat in major rivers such as the Ohio, Tennessee and Cumberland and Mobile Bay Basin. Damming resulted in the local loss of the bivalves' host fish. This loss of the obligate host fish, coupled with increased siltation, and various types of industrial and domestic pollution have resulted in the rapid decline in the unionoid bivalve fauna in North America. Freshwater communities in Europe have experienced numerous problems, some local unionoid populations have been extirpated, but no unionoid species are extinct. Three taxa from Israel are now reported as extinct. Other nations such as China that have problems with soil erosion and industrial pollution or have numerous dams on some of the rivers (*e.g.*, South America: Rio Parana) are probably experiencing problems of local extirpation if not the extinction of their endemic freshwater bivalve fauna.

INTRODUCTION

"To keep every cog and wheel is the first precaution of intelligent tinkering."

Aldo Leopold

Freshwater environments are some of the most fragile in the world, but yet we are constantly manipulating them to fit our needs with little thought as to long term effects (Kaufman, 1992). Since the development of irrigation, mankind has been altering the flow of freshwater for agricultural purposes. Now we are faced with the cumulative effects of this tinkering (*e.g.*, Reynolds, 1988; Benke, 1990; Allan and Flecker, 1993). Freshwater ecosystems in North America north of Mexico are home to about 12,580 described species of invertebrates, of which 820 are mollusks (Williams and Neves, 1992).

The phylum Mollusca has been very successful in invading the freshwater habitats. Eighteen families of bivalves have invaded freshwater, but only about nine have radiated there (Table 1). I will restrict my discussions to one order of bivalves, the Unionoida, divided into 2 superfamilies and constituent families (Table 1). This group has been the most successful in radiating in freshwater if number of recognized genera (165) is an indicator of success. Unionoida have a unique life history trait: they have an obligate parasitic stage on fish. Larval Unionoidea, termed glochidia are released by the female, and to be successful must attach to the gills of a particular host fish. There it resides for a short period, metamorphoses and drops from the gill of the

[1] From the Symposium *The Crisis in Invertebrate Conservation* presented at the Annual Meeting of the American Society of Zoologists and the Canadian Society of Zoologists, 27–30 December 1992, at Vancouver, British Columbia.

[2] Mailing address: 36 Venus Way, Sewell, NJ 08080-1970.

TABLE 1. *Bivalve families with at least one representative species found in freshwater*[a]

Taxon	Larval type
Subclass Pteriomorphia	
Order Arcoida	
Arcidae	veliger[b]
Order Mytiloida	
Mytilidae	veliger
Subclass Paleoheterodonta	
Order Unionoida	
Unionoidea	
Unionidae	glochidia[c]
Margaritiferidae	glochidia
Hyriidae	glochidia
Etherioidea	
Mutelidae	haustoria[d]
Mycetopodidae	lasidia[e]
Etheriidae	?
Subclass Heterodonta	
Order Veneroida	
Corbiculidae	direct development[f]
Sphaeriidae	direct development
Dreissenidae	veliger
Solenidae	veliger
Donacidae	veliger
Solecurtidae	veliger
Order Myoida	
Corbulidae	veliger
Erodonidae	veliger
Teredinidae	veliger
Subclass Anomalodesmata	
Lyonsiidae	veliger

[a] The information presented iin this table was compiled from Turner (1966), Morton (1968), Davis (1982), Taylor (1988), Deaton and Greenberg (1991).

[b] Veliger—the free swimming larval stage characterized by ciliated velar lobes used in swimming and feeding.

[c] Glochidia—the bivalved larvae of Unionoidea which are generally parasitic on the gills of fish.

[d] Haustoria—the larval stage of the Mutelidae, composed of a soft body, bilobed anteriorad, with 3–7 small hooks on the posterior end and a very long filamentous tentacle. The larval stage develops distally on a tube on the side of the fish. After metamorphosis, the juvenile bivalve is cut free along an abscision zone to begin life as a free living bivalve (see Parodiz and Bonetto, 1963).

[e] Lasidia—the larval stage of the Mycetopodidae is similar to the haustoria of the Mutelidae except that the filamentous appendages are quite different. Larval development here is not by attachment to the body of the fish with tubular appendages but by a cyst-like structure (see Parodiz and Bonetto, 1963).

[f] Direct development—release of juveniles directly from the female without an external veliger or parasitic life stage.

fish to begin life as a juvenile clam if it lands in suitable habitat (Table 1 for definitions). The developmental pattern is similar in the Etheroidea but the larval stages, lasidia and haustoria, are morphologically distinct and the process of metamorphosis are different from those of the Unionoidea. It is because of this unique dependency upon a particular host fish that unionoids are so sensitive to disturbances of the freshwater ecosystem. They are threatened not only by actions which directly impact them, but also any actions which might affect their host fish populations. Without the host fish the unionoid species is unable to complete its reproductive cycle and faces extinction. Destruction of the freshwater fauna has been reported by Ortmann (1909) and van der Schalie (1938) and van der Schalie and van der Schalie (1950). Extinction of freshwater bivalves has been happening since at least 1900, but has only recently begun to be recognized (Stansbery, 1970, 1971). We are now however poised on the brink of a major and widespread extinction event (Stansbery, 1970, 1971; Palmer, 1986). Unionoid bivalves are very long lived (30–130 years according to Bauer (1992)), so impacts on a population may not be immediately detectable. Decline, local extirpation and the final extinction of freshwater bivalve species is directly tied to the degradation and loss of essential habitat.

Extirpation is the loss of a local population of a species while the species continues to exist in other parts of its range. Extinction is the complete loss of all individuals and populations of a species.

NOMENCLATURE

The higher bivalve classification used here follows Vaught (1989). The taxonomy of the North American freshwater bivalves is that presented in Turgeon *et al.* (1988). Table 1 provides the higher freshwater bivalve classification used in this paper to the family level. The taxonomy of the freshwater bivalves of the world exclusive of North America is based on the works of Haas (1969) and Starobogatov (1970, 1992). A revised classification of freshwater bivalves is currently in preparation (see Bogan and Woodward, 1992).

UNIONOID BIVALVE FAUNAS BY GEOGRAPHIC REGION

The unionoid bivalve faunas are treated by major geographic area, citing major works summarizing the unionoid fauna. I discuss documented extinctions and identify some of the environmental changes which contribute to the destruction of the unionoid fauna.

Australia

Smith (1992) summarized the known nonmarine molluscan fauna of Australia and listed 17 species (Hyriidae: 17 species). Ponder *et al.* (1989) discussed the destruction of the artesian spring heads and the endemic gastropod fauna in Australia. Their comments can be generalized for the rest of the freshwater fauna and problems with pollution and river modification are assumed but the extent is unknown. However, no freshwater species are listed as extinct in Australia at this time (Ponder, personal communication, October, 1992).

Indian subcontinent

Subba-Rao (1989) provided the most recent summary of the freshwater mollusks of India, Pakistan, Bangladesh, Burma and Sri Lanka (Unionidae: 52 species; Margaritiferidae: 1 species; Etheriidae: 1 species). Very little information is known about this fauna beyond sketchy notes on their distribution. Pollution appears to be the major impact but nothing is known regarding mollusk extinctions in these countries.

China and Southeast Asia

The fauna of this huge region is diverse and must be examined by area or country. Freshwater bivalves have been described from Asia for many years but the fauna is still very poorly understood. Suzuki and Horikosi (1944) provided an early list of the unionoid fauna of China. Liu (1979) produced the only recent handbook on the freshwater mollusks of China (Margaritiferidae: 1 species; Unionidae: 37 species). Niu (1990) and He (1991) summarized some of the problems of deforestation, poor farming practices, and subsequent erosion in China, impacts exacerbated by rapidly increasing domestic and industrial pollution. Jin *et al.* (1990) documented the loss of certain lakes, including decrease in overall size of others with their increasing eutrophication. Decrease in lake size is linked to siltation and to land reclamation. These two papers point to the very large problems of erosion and pollution in China. These factors combined with some of the recent damming projects, are resulting in big lake and big river species being locally extirpated, but at present there is no evidence of complete extinction of any freshwater bivalve. Habe (1990) reported the freshwater molluscan fauna of Japan. Kim (1985), Kwon and Habe (1979), and Yoo (1969) documented the freshwater bivalve diversity in Korea (Unionidae: 10 species) and pointed out, at least for the Han River, problems with pollution and declines in populations. Brandt (1974) monographed the non-marine aquatic mollusks of Thailand (Margaritiferidae: 1 species; Unionidae: 32 species). There is a recent monograph of the freshwater mollusks of Vietnam by Dang, but I have not been able to examine a copy of this work (Unionidae: 39 species; E. Petro, personal communication, September, 1992).*

Europe and the former Soviet Union

Zhadin (1952) and Haas (1969) provided summaries of the freshwater bivalve fauna of these regions (Margaritiferidae: 2 species, Unionidae: 8 species). Altaba (1990) reported that *Margaritifera auricularia* (Spengler, 1793) was facing extinction by reduction to a single population in the lower Ebro River, Spain. He attributed this decline to problems with pollution and over-harvesting for shells and pearls, and further noted that the suggested host fish is also endangered in Europe. Young and Williams (1983) and Bauer (1988) blamed the decline in *Margaritifera margaritifera* (Linne, 1758) on pollution and over-harvesting. Although local populations of European unionoids are locally endangered no species is known to be extinct (Wells and Chatfield, 1992) (Bauer, Dyduch-Falniowska, Finet, Gittenberger, van Goethem, Grossu, Jungbluth, Kilias, Kiss, Knudsen, Naggs, Petro, Ross,

TABLE 2. *List of extinct freshwater bivalve taxa by geographic area.*

North America [19]
Alasmidonta mccordi Athearn, 1964
Alasmidonta robusta Clarke, 1981
Alasmidonta wrightiana Walker, 1901
Epioblasma arcaeformis (Lea, 1831)
Epioblasma biemarginata (Lea, 1857)
Epioblasma flexuosa (Rafinesque, 1820)
Epioblasma florentina florentina (Lea, 1857)
Epioblasma haysiana (Lea, 1834)
Epioblasma lenior (Lea, 1842)
Epioblasma lewisii (Walker, 1910)
Epioblasma obliquata perobliqua (Conrad, 1836)
Epioblasma personata (Say, 1829)
Epioblasma propinqua (Lea, 1857)
Epioblasma sampsonii (Lea, 1861)
Epioblasma stewardsonii (Lea, 1852)
Epioblasma torulosa gubernaculum (Reeve, 1865)
Epioblasma torulosa torulosa (Rafinesque, 1820)
Epioblasma turgidula (Lea, 1858)
Medionidus mcglameriae van der Schalie, 1939
Israel [3]
Leguminaia saulcyi (Bourguignat, 1852)
Potomida littoralis delesserti (Bourguignat, 1852)
Unio elongatus eucirrus (Bourguignat, 1857)

Salvini-Plawen, Sattmann, Turner, Woodward, personal communication, 1992).

Africa

The African freshwater bivalve fauna is comprised of four families (Etheriidae: 1 species; Mutelidae: 28 species; Margaritiferidae: 1 species; Unionidae: 26 species). Mandahl-Barth (1988) summarized the freshwater bivalve fauna but overlooked the recent works of Brown (1967), Appleton (1979), and van Damme (1984). Nagel (1991) listed freshwater mollusks including bivalves collected in Sierra Leone. Altaba (1990) noted that *Margaritifera auricularia* (Spengler, 1793) is extinct in Morocco. Appleton (personal communication, September 1992) reported the disappearance of *Cafferia caffer* (Krauss, 1848) [Unionidae] from part of its former range, possibly due to agricultural development or loss of fish hosts. Nothing else is currently known concerning the status of other species, but impoundments and pollution are probably adversely impacting these bivalves.

Middle East

There are no recent comprehensive studies of freshwater bivalves of the Middle East; only limited data on species distributions are provided by Haas (1969). Heller (personal communication, October 1992) stated that three species have become extinct in Israel due to the rivers drying up (Table 2).

South America

There is no recent paper since the seminal work of Ortmann (1921) followed by Haas (1931) that surveyed the freshwater bivalve fauna of South America. The taxonomy used here for South American unionoids follows Parodiz and Bonetto (1963) (Hyriidae: 7 genera; Mycetopodidae: 9 genera). Rivers of South America are poorly known biologically and the impact of deforestation can only be guessed. The Rio Parana is being adversely impacted by the construction of a series of dams. Di Persia and Olazarri (1986) presented a list of the zoobenthos of the Uruguay River basin (Hyriidae: 8 species; Mycetopodidae: 13 species) and reported the fauna was extirpated for approximately 120 km behind the Salto Grande Dam. Quintana (1982) summarized the molluscan fauna of Paraguay (Hyriidae: 11 species; Mycetopodidae: 18 species). Due to poor and generally historic information, evidence of extinction is lacking.

Central America

This geographic division encompassed the area from Mexico to Panama. The basic information on the unionoid fauna of this area is severely limited (*e.g.*, Olivera and Polaco, 1991) to the early works of von Martens (1890–1901) and Fischer and Crosse (1894). The taxonomy of the Unionidae and Mycetopodidae occurring in this region is currently confusing and poorly understood. Haas (1929) listed the freshwater bivalve fauna as he understood it at that time (Unionidae: 67 species; Mycetopodidae: 3 species). The number of taxa are probably excessive for the unionids, but may be quite conservative for the mycetopodids. The most recent work is that of Goodrich and van der Schalie (1937) and van der Schalie (1940) on the mollusks of the Peten and Alta Vera Paz. Fred Thompson (personal communication, July 1992) noted that many rivers of Central America are suffering from municipal pollution and the freshwater molluscan fauna is declining in diversity. Alcocer-Durand and Escobar-Briones (1992) documented the destruction of the aquatic biota of the Mexico Basin that includes one species of unionid, *Anodonta impura* Say, 1829, locally extirpated due to draining of the lakes and swamps. We can only assume that, with increased population growth and municipal and industrial pollution, the fauna is being adversely impacted, but the impact is unknown.

North America

The freshwater bivalve fauna of North America north of, but including the Rio Grande, historically supported the most species rich freshwater bivalve fauna in the world (Margaritiferidae: 5 species; Unionidae: 292 species). Turgeon *et al.* (1988) listed 13 freshwater bivalves as presumed extinct. Neves (n.d.) recorded 297 species and subspecies of unionoid bivalves as living in North America, and that 19 taxa were presumed extinct (Table 2); 44 taxa are currently listed as federally endangered or threatened, and 69 taxa are listed as candidates for federal protection. The unionoid fauna of the eastern United States has been intensely studied for over 150 years. The fauna is summarized by Burch (1975) and Clarke (1981) and listed by Turgeon *et al.* (1988). The greatest decline is among the endemic species of the southeastern United States particularly in the Mobile Bay, Tennessee and Cumberland River drainage basins. Ortmann, as early as 1909 (Ortmann, 1909, 1918), documented the effects of pollution on the destruction of the freshwater molluscan fauna. Impoundment was implicated in the destruction of the unionid fauna by van der Schalie (1938) and van der Schalie and van der Schalie (1950). Extinction of unionid species was reported by Stansbery (1970 [7 species extinct]; 1971 [11 species extinct]). Sadly almost half of the freshwater bivalve taxa listed for North America are either extinct or in serious jeopardy of extinction. Hartfield (personal communication, November, 1992) has suggested that possibly ten species of *Pleurobema* in the Mobile Bay Basin are now presumed extinct since they have not been collected alive in a number of years. Dramatic declines in diversity and population sizes have been recently documented (Dennis, 1987; Anderson *et al.*, 1991; Nalepa *et al.*, 1991; Williams *et al.*, 1992). Several of the federally listed endangered taxa are functionally extinct, that is, the taxon is represented in the wild by senescent adults which have ceased reproducing.

CONTRIBUTING CAUSES OF EXTINCTION

Factors affecting a species that result in its extinction are varied and usually intricately interrelated. Freshwater bivalves are long-lived organisms, thus the cause or causes of species extinction may not be immediately apparent. The most tenuous part of the life cycle of a unionoid bivalve is the requirement of an obligate fish host. If a fish host is absent, the species (*e.g.*, *Obovaria retusa* (Lamarck, 1819); *Plethobasus cooperianus* (Lea, 1834); *Pleurobema taitianum* (Lea, 1834)) has become functionally extinct and will become totally extinct at the time when the last surviving individual of the species dies. None of these factors alone would contribute to the extinction of a species, but there is some evidence that, since unionoid bivalves are so long-lived (up to 130 years [Bauer, 1992]), individually, impacts are minor but become cumulative and thus lethal with the passage of time.

Habitat destruction

Freshwater bivalves are filter feeders and cannot withstand heavy loads of silt. Most species are not adapted to life in a soft silty substrate. When covered with a layer of silt, these species simply suffocate because they are not able to escape. Sources of increased siltation are headcutting, gravel washing operations, coal washing, poor agricultural practices (runoff), cutting of riparian forests, and clear cutting of major portions of the watershed (Starrett, 1971; Fuller, 1974; Newbold *et al.*, 1980; Dennis, 1985; Hartfield, 1993).

Pollution from papermills, tanneries, chemical factories, steel mills, etc. were implicated early this century in the destruction of the freshwater bivalve fauna (*e.g.*, Ortmann, 1909, 1918). Untreated effluents from municipal sources as well as non-point source domestic pollution enrich the local waters in which they are discharged (Starrett, 1971).

Ortmann (1909) clearly documented the role of acid mine runoff in the destruction of the freshwater fauna of western Pennsylvania. Many of the streams he listed as devoid of freshwater bivalves are still lacking a mussel fauna. He also implicated brine coming from oil wells and the dumping of chemicals from oil refining as being detrimental to the freshwater fauna. Fuller (1974) pointed out the destructive role of chlorine laden oil field brine on freshwater bivalves. Anderson *et al.* (1991) pointed to recent strip mining in the watershed for the decline in the unionid fauna of the Little South Fork of the Cumberland River in southern Kentucky.

Modification of the channel of a river or stream for navigation, flood control, or improved drainage has strong impacts on the benthic fauna. In-stream gravel mining operations remove the substrate in which unionoids live and increases downstream siltation. A result of channel modification, dredging, or channelization is headcutting. Portions of a stream above the immediate impact can be altered by the resulting channel adjustments (Hartfield, 1993). Headcutting is a major problem in some of the rivers in Southeastern North America on the coastal plain and has resulted in at least the local destruction of the freshwater bivalve fauna in several rivers (Hartfield, 1993). Damming dramatically alters the environment of what was formerly a free-flowing river by altering the fish fauna, substrate composition, benthic community, water chemistry, amount of dissolved oxygen, and water temperature. The extirpation of parts of the freshwater bivalve fauna as the direct result of damming is well documented (Lewis, 1868; Ortmann, 1909, 1924; Scruggs, 1960; Isom, 1969; Fuller, 1974; Williams *et al.*, 1992).

The effects of pesticides and heavy metals have recently been reviewed by Fuller (1974) and Havlik and Marking (1987). Heavy metals such as cadmium can be toxic to freshwater bivalves. Unionoids take up and concentrate heavy metals, contaminants, and pesticides from the water column thus making them good indicator organisms for environmental pollution and stress. A lampricide was recently proven to be lethal to the pink heelsplitter (*Potamilus alatus* (Say, 1817)) (Bills *et al.*, 1992). These substances in the water column may not be toxic to the animal at a given time but their effects may be cumulative. The presence of these pollutants in the environment adds to the stress on the animals.

Host fish

I noted earlier the critical importance of obligate fish hosts for the development and metamorphosis of the larval stages of unionoids. It is for this reason that freshwater mussel assemblages in rivers that have been dammed have either become totally depleted or severely reduced in numbers since the altered environment is usually unsuitable for survival of the host fish. Fuller (1974) and Hoggarth (1992) have provided a summary of information on the known probable host fish for glochidia. These data cover only about one fourth of the species of North American freshwater bivalves. The information on host fishes for freshwater bivalves in the rest of the world is substantially less. Understanding this relationship and knowing which fish species are utilized by which unionoid species is essential before any attempts are made to preserve an endangered freshwater bivalve species. Without the host fish necessary for the continued reproduction of a given species, all conservation efforts will be in vain.

Commercial exploitation

Freshwater bivalves formed the basis for the pearl button industry in the first third of the twentieth century in North America, and today they are extensively harvested for the Japanese cultured pearl industry. The collecting of specimens of *Margaritifera margaritifera* to extract pearls has had a major impact on populations in Europe (Young and Williams, 1983). These activities annually destroy large numbers of adult clams and in some places severely impact entire populations. When species are limited in range or to isolated populations, harvesting of this type can prove to be the final impact resulting in extinction. Hartfield (personal communication, October, 1992) commented that he felt commercial exploitation had not contributed to the extinction of any unionoid species in North America.

Introduced species

Clarke (1988) suggested that in North America the introduced asian clam (*Corbicula fluminea* (Müller, 1774), competes with native unionoids and causes a decline and/or possible local extinctions of native freshwater bivalves. Recently a more destructive introduced bivalve pest, the zebra mussel (*Dreissena polymorpha* (Pallas, 1771)), has been introduced into North America and is a major threat to native unionoids in large lakes, impounded large rivers and potentially smaller rivers and streams. The larval zebra mussel settles on any hard substrate in large numbers, especially unionoid bivalve shells, potentially killing or at least weakening the freshwater bivalves to which they attach (Mackie, 1991; Schloesser and Kovalak, 1991; Hunter and Bailey, 1992).

DISCUSSION

Unionoid bivalves have radiated in freshwater lakes and rivers since at least the Triassic, and have developed a unique life history that is very intimately tied to their obligate fish hosts. Unionoid bivalves have evolved where they exploit habitats in riffle and shoal areas of large rivers (*e.g.*, the Mississippi River, Mekong River, Yangtze River, Rio Parana basins), the same habitats which are actively being affected by impoundments for navigation, flood control and hydro-electric production. Major problems facing freshwater bivalve survival are: 1) The current understanding of the systematics, ecology and host fish/bivalve relationships in the Order is very poor outside of Europe and North America, 2) The long term perspective of species distribution and abundance is lacking, 3) The rate of deforestation, water quality degradation, and stream channel alteration is continuing to increase. The unique life history of unionoids is also actually contributing to their decline and extinction, because the weak link in a freshwater bivalve's reproduction is the dependence on an obligate host fish. When the host fish disappears the species becomes functionally extinct.

Extinction of the 18 taxa in North America is not clearly due to a single cause but is the long term combination of a suite of detrimental factors. The cumulative effects of impoundment, of dumping of municipal and industrial pollutants into the rivers, deforestation, channel modification, and over-harvesting have contributed to the extinction of at least 18 species adapted to the riffle and shoal habitats of big rivers in North America. The species of *Epioblasma* listed as extinct were found in the Tennessee, Cumberland and Ohio River basins. The status of freshwater bivalve faunas outside of Europe and North America is unknown. There are some suggestions that single episodes of pollution or impact upon a species are not the cause of unionoid population declines but the long term cumulative effects of multiple impacts (Nalepa *et al.*, 1991). A major shortcoming in our understanding of the cause or causes of extinction in unionoid bivalves, is our tremendous lack of knowledge on the life history, fish hosts, ecology, distribution both modern and historic, and the confused state of unionoid systematics.

Carpenter *et al.* (1992) projected changes in freshwater ecosystems and suggested that the reflected changes in elevated water temperatures will affect fish distributions. If changes such as those projected occur, they will have an effect on freshwater bivalves with potential host fish loss and local extirpation of existing host specific taxa. I have suggested that freshwater bivalves in eastern North America may have remained in place south of the glacial maximum during the Pleistocene and did not move south in response to colder temperatures as did the mammals and birds (Bogan and Grady, 1991). Freshwater bivalves that have invaded Canada (Clarke, 1981) will continue to expand their ranges north.

The positive side to the freshwater bivalves imperilment is that people are beginning to understand that the aquatic ecosystem is very complex and fragile. Preservation of individual species is not the answer, but rather a focus on the preservation of the diversity of aquatic communities found in natural ecosystems and watersheds will conserve the endangered species and its habitat. We are aware of the various symptoms of what is causing extinctions and must become more proactive in planning and management of aquatic resources. The fact that we are unable to put a monetary value on a species does not mean that that species is not a critical part of the aquatic ecosystem (Williams and Neves, 1992).

Acknowledgments

This paper would not have been possible without the generous assistance, reprints and letters from the following individuals, all of whom are gratefully acknowledged: Dr. C. C. Appleton, University of Natal, Pietermaritzburg, South Africa; Dr. Richard N. Kilburn, Natal Museum, Pietermaritzburg, South Africa; Helmut Sattmann, Natural History Museum, Vienna, Austria; Dr. Luitfried Salvini-Plawen, Institute for Zoology, University of Vienna, Vienna, Austria; Dr. Helena Ross, Ulster Museum, Belfast, U.K.; Dr. P. Graham Oliver, National Museum of Wales, Cardiff, U.K.; Dr. Jürgen H. Jungbluth, Neckarsteinach, Germany; Dr. Rudolf Kilias, Museum für Naturkunde, Humboldt University, Berlin, Germany; Dr. Joseph Heller, Dept. of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, Israel; Dr. Jorgen Knudsen, Zoological Museum, Copenhagen, Denmark; Dr. Winston Ponder, Australian Museum, Sydney, Australia; Dr. Hans Turner, Natural History Museum, Basel, Switzerland; Dr. Gerhard Bauer, Lehrstuhl für Tierökologie, University of Bayreuth, Germany; Dr. Alexandru V. Grossu, Bucharest, Romania; Dr. Peiyi Pae, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, People's Republic of China; Dr. Yves Finet, Museum of Natural History, Geneva, Switzerland; Fred Naggs, The Natural History Museum, London, United Kingdom, Dr. Edmund Gittenberger, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands, Dr. Jackie Van Goethem, Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium. Dr. James D. Williams, U.S. Fish and Wildlife Service, Gainesville, Florida; Robert S. Butler (USFWS), Jacksonville, Florida; Paul Hartfield (USFWS), Jackson, Mississippi; Clif Coney, Los Angeles County Museum of Natural History, Los Angeles, California; Dr. Paul W. Parmalee, McClung Museum, University of Tennessee, Knoxville, Tennessee; Dr. W. R. Hoeh, CTAG, Cook College, Rutgers University, New Brunswick, New Jersey; and Dr. Richard Neves, Virginia Polytechnic Institute, Blacksburg, Virginia, all kindly provided their own unique perspectives on the problems of unionoid extinctions in North America. Richard Neves and Paul Hartfield kindly made available copies of their manuscripts in press for my use. Dr. Paul W. Parmalee, Robert Butler and Paul Hartfield critically reviewed a draft of the manuscript and provided numerous helpful suggestions. Three anonymous reviewers are thanked for their detailed remarks. Mrs. Cynthia M. Bogan provided technical and critical assistance. Dr. Michael Hadfield is thanked for organizing this symposium and providing travel funds to attend the symposium.

References

Alcocer-Durand, J. and E. G. Escobar-Briones. 1992. The aquatic biota of the now extinct lacustrine complex of the Mexico Basin. Freshwater Forum 2(3):171–183.

Allan, J. D. and A. S. Flecker. 1993. Biodiversity conservation in running waters. Identifying the major factors that threaten destruction of riverine species and ecosystems. Bioscience 43(1):32–43.

Altaba, C. R. 1990. The last known population of the freshwater mussel *Margaritifera auricularia* (Bivalvia, Unionoida): a conservation priority. Biol. Conser. 52:271–286.

Anderson, R. M., J. B. Layzer, and M. E. Gordon. 1991. Recent catastrophic decline of mussels (Bivalvia, Unionidae) in the Little South Fork Cumberland River, Kentucky. Brimleyana (17): 1–8.

Appleton, C. C. 1979. The Unionacea (Mollusca, Lamellibranchiata) of South-Central Africa. Ann. south African Mus. 77(9):151–174.

Bauer, G. 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in Central Europe. Biol. Cons. 45:239–253.

Bauer, G. 1992. Variation in the life span and size of the freshwater pearl mussel. J. Anim. Ecol. 61: 425–436.

Benke, A. C. 1990. A perspective on America's vanishing streams. J. N. Am. Benthol. Soc. 9(1):77–88.

Bills, T. D., J. J. Rach, L. L. Marking, and G. E. Howe.

1992. Effects of the lampricide 3-Trifluoromethyl-4-Nitrophenol on the Pink Heelsplitter. U.S. Fish and Wildl. Serv. Res. Publ. 183. 7 pp.
Bogan, A. E. and F. V. Grady. 1991. Two Pleistocene molluscan faunas from Eastern West Virginia. *In* J. R. Purdue, W. E. Klippel, and B. W. Styles (eds.), *Beamers, bobwhites and blue-points: Tributes to the career of Paul W. Parmalee,* pp. 189–213. Illinois State Museum Scientific Papers, Vol. 23, Springfield and The University of Tennessee, Department of Anthropology Report of Investigations No. 52, Knoxville.
Bogan, A. E. and F. R. Woodward. 1992. A review of the higher classification of Unionoida (Mollusca: Bivalvia). Unitas Malacologica Abstracts of the Eleventh International Malacological Congress, Siena, Italy, pp. 17–18.
Brandt, R. A. M. 1974. The non-marine aquatic Mollusca of Thailand. Arch. Molluskenk. 105(1-4):i–iv, 1–423.
Brown, D. S. 1967. A review of the freshwater Mollusca of Natal and their distribution. Ann. Natal Mus. 18(3):477–494.
Burch, J. B. 1975. *Freshwater Unionacean Clams (Mollusca: Pelecypoda) of North America,* Rev. ed. Malacological Publications, Hamburg, Michigan.
Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global change and freshwater ecosystems. Ann. Rev. Ecol. Syst. 23:119–139.
Clarke, A. H. 1981. *The Freshwater Mollusks of Canada.* National Mus. Nat. Sci. National Mus. of Canada. Ottawa, Canada.
Clarke, A. H. 1988. Aspects of Corbiculid-unionid sympatry in the United States. Malacology Data Net. 2(3/4):57–99.
Davis, G. M. 1982. Historical and ecological factors in the evolution, adaptive radiation, and biogeography of freshwater mollusks. Amer. Zool. 22: 375–395.
Deaton L. E. and M. J. Greenberg. 1991. The adaptation of bivalve molluscs to oligohaline and freshwaters: Phylogenetic and physiological aspects. Malacol. Rev. 24(1-2):1–18.
Dennis, S. 1985. Distributional analysis of the freshwater mussel fauna of the Tennessee River System, with special reference to possible limiting effects of siltation. Tenn. Wild. Res. Agency. Nashville, Tennessee. No. 85-2.
Dennis, S. 1987. An unexpected decline in populations of the freshwater mussel *Dysnomia (=Epioblasma) capsaeformis,* in the Clinch River of Virginia and Tennessee. Virginia J. Sci. 38:281–288.
Di Persia, D. H. and J. Olazarii. 1986. Zoobenthos of the Uruguay System. *In* B. R. Davies and K. F. Walker (eds.), *The ecology of river systems,* pp. 623–629. Dr. W. Junk Publishers, Dordrecht, The Netherlands.
Fischer, P and H. Crosse. 1894. Etudes sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. Miss. Sci. au Mexique et dans l'Amerique Centrale, 2, pt. 7, sigs. 73–82.
Fuller, S. L. H. 1974. Clams and mussels. *In* C. W. Hart, Jr. and S. L. H. Fuller (eds.), *Pollution ecology of freshwater invertebrates,* pp. 215–273. Academic Press, New York.
Goodrich, C. and H. van der Schalie. 1937. Mollusca of Petén and North Alta Vera Paz, Guatemala. Univ. Mich. Mus. Zool., Misc. Publications No. 34:1–50, pl. 1, 1 map.
Haas, F. 1929. Bemerkungen über mittelamerikanische Najaden. Senckenbergiana 11(5/6):310–344.
Haas, F. 1931. Versuch einer kritischen Sichtung der südamerickanischen Najaden, hauptsächlish and Hand der Sammlung des Senckenberg-Museums III. Senckenbergiana 13(2):87–110, fig. 33–37.
Haas, F. 1969. Superfamilia Unionacea. Das Tierreich (Berlin). Lieferung 88. x + 663 pp.
Habe, T. 1990. A list of the non-marine aquatic Mollusca of Japan. Hitachiobi 54: 3–6; 55: 3–9; 56: 3–7. [in Japanese]
Hartfield, P. 1993. Headcuts and their effect on freshwater mussels. *In* K. Cummings (ed.), *The conservation and management of freshwater mussels.* (In press)
Havlik, M. and L. L. Marking. 1987. Effects of contaminants on naiad mollusks (Unionidae): A review. U.S. Fish and Wildlife Series, Research Publication. 164:1–20.
He, B. 1991. *China on the edge: The crisis of ecology and development.* China books and periodicals, Inc. San Francisco, California.
Hoggarth, M. A. 1992. An examination of the glochidia-host relationships reported in the literature for North American species of Unionacea (Mollusca: Bivalvia). Malacology Data Net 3(1-4):1–30.
Hunter, R. D. and J. F. Bailey. 1992. *Dreissena polymorpha* (zebra mussel): Colonization of soft substrate and some effects on unionid bivalves. The Nautilus 106:60–67.
Isom, B. G. 1969. The mussel resource of the Tennessee River. Malacologia 7(2-3):397–425.
Jin, X., H. Liu, Q. Tu, Z. Zhang, and X. Zhu. 1990. *Eutrophication of lakes in China.* The Fourth International Conference on the Conservation and Management of Lakes "Hangzhou '90." Beijing, China.
Kaufman, L. 1992. Catastrophic change in species-rich freshwater ecosystems. Biosci. 42(11):846–858.
Kim, D. K. 1985. A review on the study of molluscan fauna in the Han River. Korean J. Malacology 1(1):51–63.
Kwon, O. K. and T. Habe. 1979. A list of non-marine Molluscan fauna of Korea. The Korean J. Limnology 12(1-2):25–33.
Lewis, J. 1868. Remarks on the mollusks of the valley of the Mohawk. Am. J. Conch. 4:241–245.
Liu, Y.-y. 1979. *Freshwater mollusks.* Economic Fauna of China. Science Press. Beijing, People's Republic of China. [In Chinese]
Mackie, G. L. 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha,* in relation to native bivalves and its potential impact in Lake St. Clair, Hydrobiologia. 219:251–268.
Mandahl-Barth, G. 1988. *Studies on African freshwater bivalves.* Danish Bilharziasis Laboratory, Charlottenlund, Denmark.
Morton, J. E. 1968. *Molluscs.* Hutchinson University Library, London.
Nagel, K.-O. 1991. On some freshwater Molluscs

(Gastropoda and Bivalvia) from Sierra Leone. J. Conch. 34:31–36.
Nalepa, T. F., B. A. Manny, J. C. Roth, S. C. Mozley, and D. W. Schloesser. 1991. Long-term decline in freshwater mussels (Bivalvia: Unionidae) of the western basin of Lake Erie. J. Great Lakes Res. 17(2):214–219.
Neves, R. J. 1993. A state-of-the-unionids address. *In* K. Cummings (ed.), *The conservation and management of freshwater mussels.* (In press)
Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Can. J. Fish Aquat. Sci. 37:1076–1085.
Niu, W.-y. 1990. Analysis and assessment of the eco-environmental situation in China. *In* H. Kawanabe, T. Ohgushi and M. Higashi (eds.), *Ecology for tomorrow.* Physiol. and Ecol. Japan. 27(Special Number):147–150.
Olivera, M. T. and O. J. Polaco. 1991. Breve resena hitorica y bibliografia basica de las investigaciones sobre los moluscos continentales mexicanos. Anales de la Escuela Nacional de Ciencias Biologicas. 34(1-4):109–121.
Ortmann, A. E. 1909. The destruction of the freshwater fauna in western Pennsylvania. Proc. Amer. Philosophical Soc. 48:90–110, pl. 6.
Ortmann, A. E. 1918. The najades (freshwater mussels) of the upper Tennessee drainage. With notes on synonymy and distribution. Proc. Amer. Philosophical Soc. 57:521–626. 1 Map.
Ortmann, A. E. 1921. South American naiades; a contribution to the knowledge of the freshwater mussels of South America. Mem. Carneg. Mus., 8(3):451–670, 34–48 pls.
Ortmann, A. E. 1924. Mussel shoals. Science. 60(1564):565–566.
Palmer, S. 1986. Some extinct Mollusca of the U.S.A. Atala. 13(1):1–7.
Parodiz, J. J. and A. A. Bonetto. 1963. Taxonomy and zoogeographic relationship of the South American naiades. Malacologia, 1(2):179–213, 17 figs.
Ponder, W. F., R. Hershler, and B. J. Jenkins. 1989. An endemic radiation of Hydrobiid snails from artesian springs in Northern South Australia: Their taxonomy, physiology, distribution and anatomy. Malacologia 31(1):1–140.
Quintana, M. G. 1982. Catálogo preliminar del la malacofauna del Paraguay. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," 11(3):61–158.
Reynolds, J. D. 1988. Crayfish extinctions and crayfish plague in Central Ireland. Biol. Conserv. 45(4): 279–285.
Schloesser, D. W. and W. P. Kovalak. 1991. Infestation of unionids by *Dreissena polymorpha* in a power plant canal in Lake Erie. J. of Shellfish Res. 10(2):355–359.
Scruggs, G. D. 1960. Status of fresh-water mussels stocks in the Tennessee River. U.S. Fish and Wildlife Service Special Science Report. No. 370:1–41.
Smith, B. J. 1992. *Zoological Catalogue of Australia,* Vol. 8, *Non-marine Mollusca.* Canberra.
Stansbery, D. H. 1970. 2. Eastern freshwater mollusks. (I). The Mississippi and St. Lawrence River systems. *In* A. H. Clarke (ed.), Papers on the rare and endangered mollusks of North America. Malacologia 10:9–22.
Stansbery, D. H. 1971. Rare and endangered freshwater mollusks in eastern United States. *In* S. E. Jorgensen and R. W. Sharp, (eds.), *Rare and endangered mollusks (Naiads) of the U.S.*, U.S. Department of the Interior, Fish and Wildlife Service, Region 3. pp. 5–18f, 50 figures.
Starbogatov, Ya. I. 1970. Fauna mollyuskov i zoogeographicheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara. Akad. Nauk SSSR, Zool. Inst. Leningrad. [In Russian]
Starobogatov, Ya. I. 1992. Morphological basis for phylogeny and classification of Bivalvia. Ruthenica 2(1):1–25.
Starrett, W. C. 1971. A survey of the mussels (Unionacea) of the Illinois River: A polluted stream. Ill. Nat. Hist. Surv. Bull. 30(5):267–403.
Subba-Rao, N. V. 1989. *Handbook Freshwater Mollusks of India.* Zoological Survey of India, Calcutta. pp. i–xxiii, 1–289.
Suzuki, K. and M. Horikosi. 1944. Unionidae of central China 1. Anodontinae, 2. Unioninae. J. Shanghai Sci. Inst. 14(5):367–398.
Taylor, D. W. 1988. Aspects of freshwater mollusc ecological biogeography. Palaeogeography, Palaeoclimatology, Palaeoecology. 62(1-4):511–576.
Turgeon, D. D., A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, C. F. E. Roper, A. Scheltema, F. G. Thompson, and J. D. Williams. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. American Fisheries Society Special Publication 16:vii, 1–277, 12 color plates.
Turner, R. D. 1966. *A survey and illustrated catalogue of the Teredinidae (Mollusca: Bivalvia).* Mus. of Comparative Zool., Harvard University, Cambridge, Massachusetts.
van Damme, D. 1984. *The freshwater Mollusca of Northern Africa. Distribution, Biogeography and Paleoecology.* Developments in Hydrobiology 25. Dr. W. Junk Publishers, Dordrecht, The Netherlands.
van der Schalie, H. 1938. Contributing factors in the depletion of naiades in Eastern United States. Basteria 3(4):51–57, 1 map.
van der Schalie, H. 1940. Notes on Mollusca from Alta Vera Paz, Guatemala. Occ. Papers Mus. Zool. U. Mich. No. 413:1–11.
van der Schalie, H. and A. van der Schalie. 1950. The mussels of the Mississippi River. Am. Midl. Nat. 44(2):448–466.
Vaught, K. C. 1989. *A classification of the living Mollusca.* American Malacologists, Inc. Melbourne, Florida.
von Martens, E. 1890-1901. Land and freshwater mollusca. Biologia Centrali-Americana. Zoologia, 9:i–xxviii, 1–706, pls. 1–44.
Wells, S. M. and J. E. Chatfield. 1992. *Threatened non-marine molluscs of Europe.* Nature and Environment, No. 64. Council of Europe Press, Strasbourg, France.

Williams, J. D., S. L. H. Fuller, and R. Grace. 1992. Effects of impoundment on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee rivers in western Alabama. Bull. Alabama Mus. Nat. Hist. 13:1–10.

Williams, J. E. and R. J. Neves. 1992. Introducing the elements of biological diversity in the aquatic environment. *In* J. E. Williams and R. J. Neves (eds.), *Biological diversity in aquatic management*. Trans. 57th N. Am. Wild. and Nat. Res. Conf. (1992):345–354

Yoo, J.-S. 1969. Distribution and standing crops of the fresh-water Mollusca in the Han River, Korea. Ann. Res. Bull. (The Attached High School, College of Education, Seoul National University), 12: 79–97.

Young, M. and J. Williams. 1983. The status and conservation of the freshwater pearl mussel *Margaritifera margaritifera* Linn. in Great Britain. Biol. Conser. 25:35–52.

Zhadin, V. I. 1952. Mollusks of fresh and brackish waters of the U.S.S.R. Acad. Sci. Union of Soviet Socialist Republics. Keys to the Fauna of the U.S.S.R. No. 46.

*Note added in Proof

Đặng, N. T. 1980. Định Loại Động Vật Không Xu o ng Sống Nư ớ c Ngọt Bắc Viêt Nam. Nhà Xuất Bản Khoa Học Và Kỹ Thuật, Hanoi. 573 pp.