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ROSEMARY MACKAY FUND ARTICLE

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In this third article of the series, D. L. Strayer outlines the problems facing conservation of freshwater invertebrates and recommends possible strategies for effective conservation of freshwater invertebrate biodiversity. David Strayer is a Senior Scientist at the Institute of Ecosystem Studies in Millbrook, New York. He studies the distributional ecology and roles of freshwater invertebrates.

Challenges for freshwater invertebrate conservation

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Abstract. Freshwater invertebrate conservation faces 5 important challenges. First, ~10,000 species of freshwater invertebrates around the world may already be extinct or imperiled. Second, human pressures on freshwater resources are intense and will increase in the coming decades, putting yet more species at risk. Third, scientific knowledge about freshwater invertebrates, although substantial and useful for many groups, is far less than for the vertebrates for which much of contemporary conservation biology was designed. Even the best-known freshwater invertebrates that have achieved legal protection are perhaps 1% as well studied as the typical vertebrate. Fourth, because freshwater ecosystems are downhill from and embedded in their watersheds, freshwater conservation usually has to manage entire watersheds rather than small local sites where imperiled species occur. Fifth, society spends only modest amounts of money for freshwater invertebrate conservation. The median expenditure in Fiscal Year 2003 for freshwater invertebrate species on the US Endangered Species List was only US$24,000, and only a small minority of imperiled species is listed and receives even this modest attention. Considering these serious challenges, I believe that we need to think deliberately about the best approaches for conserving freshwater invertebrate biodiversity. The best solution may be to move away from a species-based approach that is largely derived from a terrestrial model towards broader, regional approaches that try to satisfy legitimate human needs for fresh water while preserving as much biodiversity as possible.

Key words: endangered species, conservation, extinction, biodiversity, threats, rivers, groundwaters, lakes, endemism.

Freshwater invertebrate conservation faces huge challenges. On one hand, the field is more active and visible than it ever has been. Freshwater invertebrates are routinely accepted as targets of conservation efforts and are legally protected in many countries. Papers on freshwater invertebrate conservation are common subjects at scientific meetings, and invertebrate conservation now even has its own textbook (New 1995). Nevertheless, large declines or extinctions of many freshwater invertebrates have already occurred (Taylor et al. 1996, Master et al. 2000, Lydeard et al. 2004), and the immense pressures that humans are placing on the world's fresh waters are rapidly increasing (Jackson et al. 2001, Malmqvist and Rundle 2002, Postel 2003), suggesting that declines and extinctions will become more severe. Will existing conservation efforts be enough to protect the world's freshwater invertebrate fauna against these rising pressures?

I have serious doubts that current conservation efforts will ultimately be adequate to protect the world's freshwater invertebrate fauna. I believe that conservation of freshwater invertebrates has been hampered by the severity of human impacts to fresh waters and their inhabitants, the very limited resources (money, scientific effort) that have been applied to conservation problems, frequent adherence to a conservation approach that was developed largely for terrestrial birds and mammals, and an overly reactive

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approach, in which conservation activities often have been reactions to acute threats rather than actions designed to enhance long-term population viability. Consequently, conservation activities have been and will continue to be inadequate to protect freshwater invertebrate populations and species. I believe that it is time to rethink our approach to freshwater invertebrate conservation, if we are serious about preventing local and global extinctions of this fauna.

I will review the characteristics of freshwater habitats and invertebrates that affect their conservation, summarize what is known about the conservation status of freshwater invertebrates, lay out leading challenges for freshwater invertebrate conservation, and discuss alternative strategies for conserving freshwater invertebrates. I hope that the information and ideas presented here will spur thought and discussion about the best approaches to freshwater invertebrate conservation.

The Freshwater Realm and its Invertebrate Inhabitants

The nature of freshwater habitats

Problems of freshwater invertebrate conservation arise from 3 characteristics of freshwater habitats themselves. First, fresh waters are scarce compared with other habitats on the Earth. The *total* surface area of fresh waters of all kinds is only 5–10 million km^2 (Shiklomanov 1993, Cole et al. 2006), less than the area of Europe, and vastly smaller than the marine (361 million km^2) or terrestrial (138 million km^2) realms.

Second, all freshwater habitats are islands in a sea of dry land and salt water. The largest of these islands, the Laurentian Great Lakes, is not quite as big as Italy. Like oceanic islands, each freshwater habitat is more-or-less isolated from other freshwater habitats, and the inhabitants of fresh waters have limited opportunities to disperse across the lakes and drainage basins that form the islands of the freshwater world. Even within contiguous drainage networks, the specific habitats that individual species occupy (e.g., large-river riffles, spring-fed headwater streams, profundal lake sediments) often are isolated, accentuating the insular nature of freshwater habitats.

Third, because freshwater habitats are embedded in and downhill of the terrestrial world, they derive much of their character from their drainage basins. In particular, human activities in the drainage basin (land clearing, industry, fertilization, etc.) often have strong effects on freshwater habitats. These effects combine with direct human effects on fresh waters (e.g., dams, water abstraction, industrial and domestic effluents, fishing, introductions of alien species) and the strong geographic focus of human settlements and activities around fresh waters to concentrate human impacts on fresh waters more than on any other part of the landscape.

These 3 factors have several important consequences for conservation. The largest possible geographic range of freshwater invertebrates is much smaller than that of terrestrial and marine invertebrates. Many species of freshwater invertebrates, like other island biota, have small ranges, often a single drainage system. Many freshwater habitats have been badly degraded by human activities in these habitats and in their watersheds. The fragmentation of fresh waters may make it difficult for freshwater invertebrates to disperse across the fragmented landscape to adjust their geographic ranges in response to changing conditions (e.g., climate change). Last, it is difficult to manage the quality of freshwater habits without managing the surrounding landscape.

The world's freshwater invertebrate fauna

The invertebrates are a phylogenetically scattered and biologically diverse group of animals, far more varied than the vertebrates from which they are separated. What unites this disparate group, in a conservation sense, is that they are not vertebrates and, therefore, not usually well studied, and they often receive different or lesser legal protection than vertebrates.

Invertebrates live nearly everywhere in fresh water—perhaps only the most grossly polluted waters and deep ground waters lack invertebrates. Densities of invertebrates are often $10^6/m^2$ in the sediments (e.g., Strayer 1985, Palmer 1990) and 10^5 to $10^6/m^3$ in the open water (Wetzel 2001). Although there have been no complete inventories of the invertebrate fauna of any body of fresh water, it appears that local faunas may contain hundreds to thousands of species (Table 1).

Table 1. Species richness of freshwater invertebrates at 3 relatively well-studied sites (Danube: Humpesch and Fesl 2005; Breitenbach: Zwick [cited in Allan 1995]; Mirror Lake: Walter 1985). None of the lists is complete. nd = not determined.

	Danube River, Austria	Breitenbach, Germany	Mirror Lake, New Hampshire
Insecta	881	642	91
Rotifera	nd	106	75
Nematoda	nd	125	20
Annelida	89	56	25
Mollusca	68	12	6
Crustacea	23	24	52
Turbellaria	25	50	23
Others	36	29	50
Total	**1122**	**1044**	**342**

TABLE 2. Summary of the known freshwater invertebrate fauna of the world, excluding wholly parasitic forms. Compiled from Parker (1982) and many other sources. Number of species on the IUCN Red List (IUCN 2005) include all categories except "Least Concern."

Phylum	Number of described families	Approximate number of described species	Number of species on IUCN Red List (% of described species)
Porifera (sponges)	3	150	0
Cnidaria (hydras, jellyfish)	5–6	30	0
Platyhelminthes (flatworms)	~30	1000	1 (0.1%)
Nemertea	5	12	0
Gastrotricha	7	200	0
Micrognathozoa	1	1	0
Rotifera	23	2000	0
Nematoda (roundworms)	~30	1500	0
Nematomorpha (horsehair worms)	6	300	0
Annelida (oligochaetes, leeches, polychaetes)	36	1100	1 (0.1%)
Mollusca (snails, mussels, clams)	58	7000	716 (10.2%)
Bryozoa (moss animalcules)	~6	50	0
Entoprocta	1	2	0
Crustacea	~135	8000	480 (6.0%)
Chelicerata (mites)	50	5000	0
Tardigrada (water bears)	3	120	0
Uniramia (insects)	~175	64,000	171 (0.4%)

These dense assemblages of invertebrates play important roles in the functioning of freshwater ecosystems and directly affect human welfare. Invertebrates regulate rates of primary production, decomposition, water clarity, thermal stratification, and nutrient cycling in lakes, streams, and rivers (e.g., Mazumder et al. 1990, Feminella and Hawkins 1995, Wallace and Webster 1996, Graça 2001, Vaughn and Hakenkamp 2001, Vanni 2002). Invertebrates are the primary food of many freshwater fish (Gerking 1994), as well as many other vertebrates that live in or around the water (e.g., Gray 1993, Krusic et al. 1996), and so are key links in food webs. Some species of freshwater invertebrates (mussels, decapods) are harvested from the wild or farmed and support regionally important fisheries (e.g., Claassen 1994). Last, freshwater invertebrates are vectors or intermediate hosts for some of the most devastating and difficult-to-control human diseases (e.g., malaria, schistosomiasis, river blindness; e.g., Brown 1994, Kettle 1995).

Freshwater invertebrates are diverse. About 90,000 species representing 17 phyla and ~570 families have been formally described (Table 2). In terms of described species, the richest groups of freshwater invertebrates are the insects (especially the dipterans), crustaceans, mollusks, and mites (Fig. 1). However, new species are described each year, even in well-known groups in well-explored regions (e.g., mollusks in North America, for which Hershler [1998, 1999] described 2 new genera and 63 new species). Perhaps something like 20,000 to 200,000 species of freshwater invertebrates remain to be discovered. Even higher taxonomic groups are still discovered regularly—in 2000, a new phylum or class of invertebrate, the Micrognathozoa, was described from fresh waters in Greenland (Kristensen and Funch 2000).

Two further aspects of freshwater invertebrate biology are of special interest to conservation: the status of knowledge about these animals and patterns of endemism and diversity.

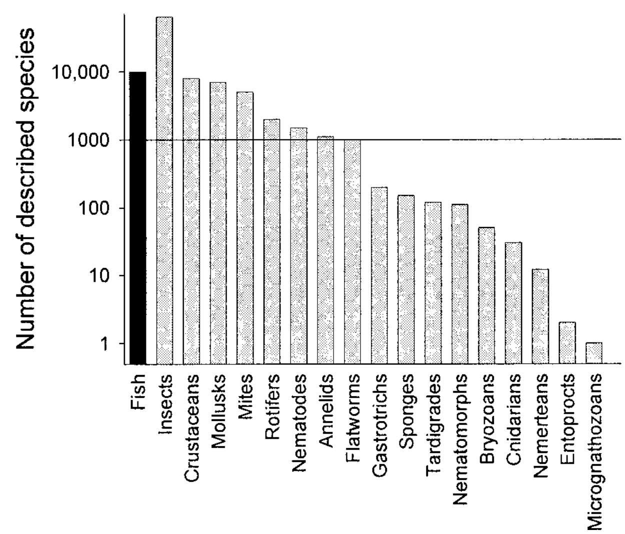

FIG. 1. Numbers of described species of freshwater invertebrates. The black bar shows the number of described species of freshwater fishes for comparison. Compiled from Parker (1982) and many other sources.

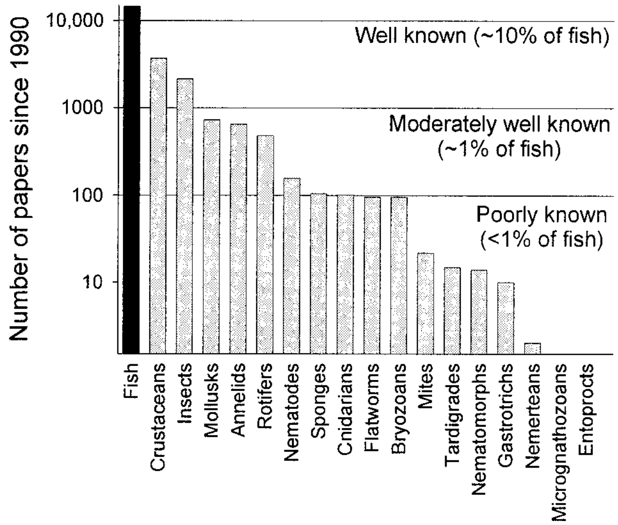

FIG. 2. Numbers of recent (1990–2004) scientific papers on freshwater invertebrates. The black bar shows the number of recent scientific papers on freshwater fishes for comparison. Based on searches of the Web of Science in March 2004 using the key words *freshwater* plus the name of each higher taxon (e.g., Nematod*).

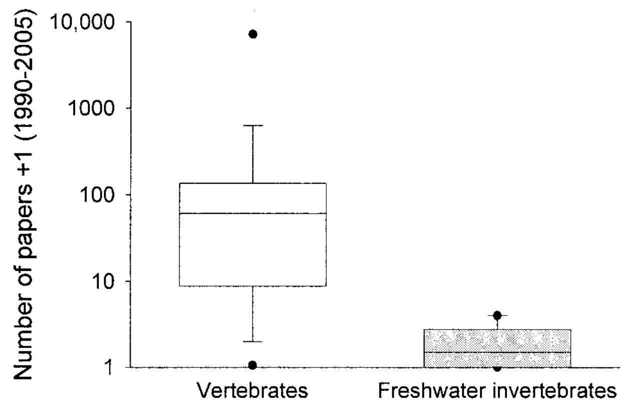

FIG. 3. Scientific attention paid to legally listed vertebrates and freshwater invertebrates. Figures are the numbers of scientific publications (plus 1, to allow for display on a logarithmic y-axis) from 1990 to 20 July 2005 listed by the Web of Science for 20 species of vertebrates and freshwater invertebrates randomly chosen from the US Endangered Species List. Only full species living in the US were included. Horizontal line shows the median, box shows the 25th and 75th percentiles, whiskers show the 5th and 95th percentiles, and circles are outliers.

Scientific knowledge about freshwater invertebrates

Scientific knowledge of freshwater invertebrates varies enormously from group to group. The best-studied groups (insects, crustaceans, and mollusks) have very roughly the same number of described species as freshwater fish, but have received only ~1/10th of the attention from scientists (Fig. 2). Nevertheless, we know the distributions, life histories, and basic ecology of many species of many members of these groups, as well as some of the planktonic rotifers and larger annelids, at least in North America, Europe, Australia, New Zealand, and a few other regions. We have been able to define the conservation status and threats for some species, and remedial action has even begun in some cases. These are the freshwater invertebrates that have made it onto the conservation agenda and that appear on various endangered species lists. Even for these "well-studied" groups, though, there are huge information gaps, especially for smaller animals and those living in developing countries or underground habitats.

If we look in a little more detail at these well-known invertebrates, we see that even they are much less well known than the vertebrates that are the more conspicuous targets of conservation efforts. For species on the US Endangered Species List, these best known of the freshwater invertebrates are about as well studied as the least studied of the listed vertebrates (Fig. 3). The typical freshwater invertebrate on the US Endangered Species List has received ~1% of the scientific attention of the typical vertebrate on the list. Such basic information as population size, life-table parameters (fecundity, annual recruitment, and survivorship), and temporal trends in population or range size is rarely available. Remember, these are the well-known invertebrates.

At the other end of the spectrum are the freshwater animals that have been living on the dark side of the scientific moon, and which have received little serious attention from scientists and conservationists (Fig. 2). Certainly, some of these groups contain just a few, rarely encountered species, but others are widespread and abundant. For instance, gastrotrichs probably occur in most freshwater habitats around the world, often at densities of 10,000 to 1,000,000/m^2 (Strayer and Hummon 2001, Balsamo and Todaro 2002). Nevertheless, we have only recently uncovered the most basic aspects of their life history (Weiss and Levy 1979, Hummon 1984a, b, c, 1986, Weiss 2001), which we still do not understand fully, and we cannot describe the global distribution or conservation status of even one freshwater gastrotrich species.

The relative scientific neglect of freshwater invertebrates has 2 interesting consequences for conservation. First, it can seriously slow conservation efforts. As currently practiced in many countries, species-based conservation is an information-hungry enterprise. Listing a species for legal protection requires information on the taxonomic limits of the species, its past and present geographic range and abundance, and current trends in range, population size, or viability. Designing recovery plans requires information on distribution and viability of remaining populations, threats to those populations, and activities that are likely to improve the long-term prospects for the species. Last, assessing and modifying the conservation activities in a recovery plan require solid experimental, monitoring, or modeling information. This information typically has to be extensive and of good quality because it may have to withstand legal challenges. We have none of this information for most freshwater invertebrates, and reasonably complete information for just a few species. As a consequence, most freshwater invertebrate species are invisible to conventional species-based conservation.

Second, enormous opportunities exist for research on the distribution and basic biology of freshwater invertebrates. Much of this work does not require expensive research equipment or highly specialized skills and could be done by any careful, dedicated person with modest training and equipment. In particular, this research is suitable for many people who do not usually participate in scientific research, including high school and college teachers, anglers, recreational boaters, outdoor enthusiasts, and other amateurs. Such *pararesearchers* have made important contributions to freshwater invertebrate research in the past (e.g., Bryant Walker, a lawyer from Detroit who published extensively on freshwater mollusks, and wrote the mollusk chapter in the 1st edition of Ward and Whipple [Goodrich 1936, 1939]; Leslie Hubricht, a tabulating machine mechanic, who wrote >100 scientific papers on freshwater invertebrates and land snails [Solem 1986]). Pararesearchers are very effectively engaged in other areas of natural-history research, including surveys of birds, amphibians, butterflies, and the like, where information they gather is routinely used for conservation and scientific research. There is potential for the freshwater invertebrate research community to inspire, organize, and support research activities by a large latent community of pararesearchers who have interests in freshwater ecology, conservation, or general natural history. This research could augment the ability of an overextended community of professional researchers to fill important gaps in knowledge about the basic biology, distribution, and conservation status of freshwater invertebrates. Effectively expanding the role of pararesearchers in freshwater invertebrate conservation will require a concerted effort by the research community to find and engage pararesearchers, provide them with technical information and inspiration, validate and organize the data they collect, and make their findings available to the broader research and conservation community. The North American Benthological Society (NABS) may be able to play a leading role in engaging the pararesearch community because some of the information needed by pararesearchers is already available on the NABS web site (www.benthos.org) and in NABS publications.

Patterns of endemism and diversity

Many freshwater invertebrates have small ranges (Fig. 4), probably as a result of the insular nature of freshwater habitats, the limited ability of many species to disperse across the intervening terrestrial and marine landscapes, range fragmentation by vicariant events, and the narrow habitat requirements of many species. The degree of endemism depends on at least 4 factors.

First, groups that are unable to disperse readily across drainage divides exhibit high endemism. Thus, we expect higher endemism in groups that cannot tolerate desiccation and have no aerial or resting stages than among groups that can fly (many insects) or have resting stages (cladoceran ephippia, ectoproct statoblasts) that can be passively transported across the landscape. For instance, unionoid mussels have a higher degree of endemism than dragonflies (Fig. 5).

Second, there can be large differences in endemism across the species of a single taxonomic group living in different habitats. The structure of the habitat can slow dispersal by selecting for traits that discourage dispersal or by making dispersal difficult, or the distribution of the habitat may be especially insular and thereby encourage endemism. Thus, groundwater species exhibit much higher endemism than their relatives that live in surface waters (Fig. 6). Groundwater animals often are poor swimmers, reluctant to detach from sediment particles, fragile, negatively phototactic, slow-growing, and have low fecundity and no pigments to protect themselves from ultraviolet light. Groundwater habitats are fragmented and often are connected to one another (if at all) by tortuous paths with slow water movement. Probably all of these factors lead to low dispersal rates and high endemism in groundwater species.

Third, there are large regional differences in endemism among regions of different ages. Young regions (e.g., recently glaciated areas) are not old enough to have evolved their own species and are populated by wide-ranging species that could disperse fast enough to reach these regions since the ice left. Ancient sites that were not recently glaciated, submerged by the sea, or desiccated support higher endemism than recently disturbed regions (Fig. 7).

Fourth, some evolutionary lines seem intrinsically prone to speciate and may exhibit extraordinarily high

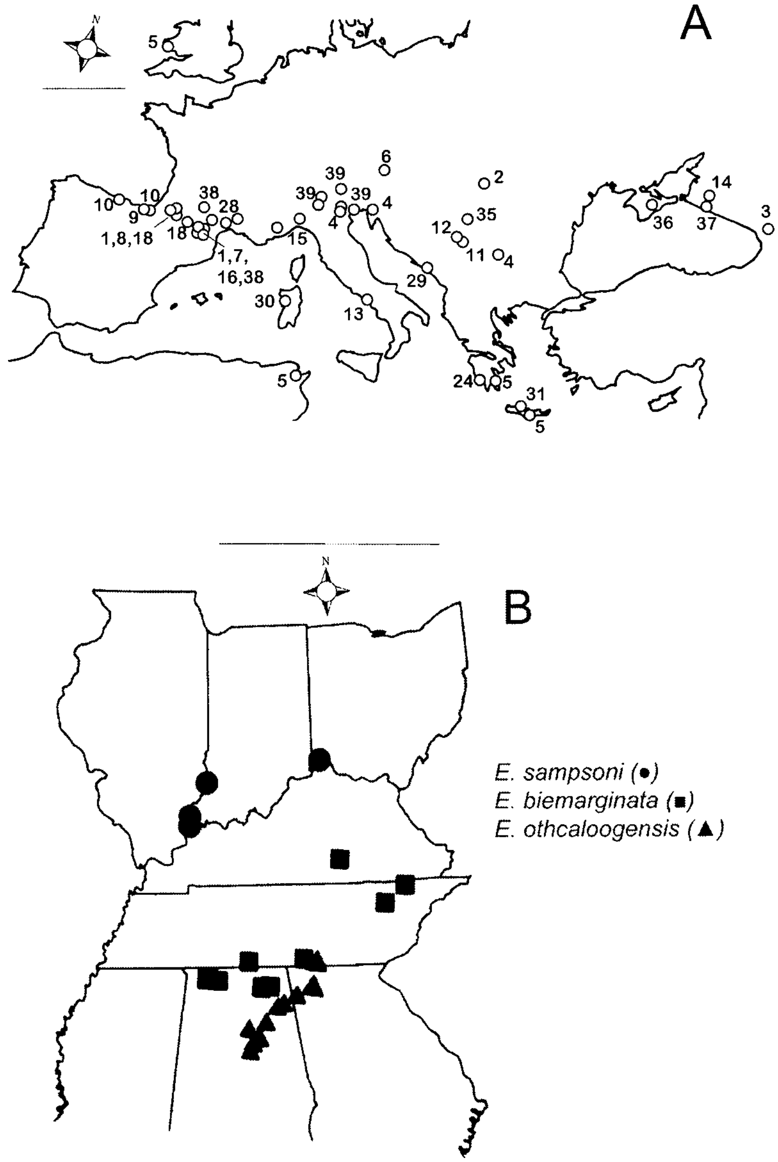

FIG. 4. Examples of freshwater invertebrate species with small geographic ranges. A.—Ranges of species of the groundwater cyclopoid copepod *Speocyclops* in Europe. Each number represents a different species or subspecies. Modified from Lescher-Moutoué (1973). B.—Ranges of 3 species (all now extinct) of the unionid bivalve *Epioblasma* in southeastern North America. From Johnson (1978) and Parmalee and Bogan (1998). Scale bars show 500 km.

endemism. Examples include the gammarid amphipods of Lake Baikal, which radiated into a flock of >250 species (Kozhova and Izmest'eva 1998), and hydrobiid snails, which often produce diverse local faunas (e.g., Bole and Velkovrh 1986, Ponder et al. 1989, Hershler 1998, 1999). It is not yet clear what contributes to the development of such diverse flocks of endemic species, but traits such as a requirement for outcrossing (as opposed to selfing, hermaphroditism, or parthenogenesis), production of large young, livebearing (as opposed to egg-laying), and narrow habitat requirements have been suggested as traits that lead to rapid local speciation (Michel 1994, Martens 1997, Schon and Martens 2004).

Contrary to the idea that freshwater invertebrates are highly endemic, many common freshwater invertebrate species are said to have large ranges, in some cases covering >1 continent. However, recent critical taxonomic studies based on morphological or molecular characters have shown that such familiar wide-ranging "species" as the gastropod *Ancylus fluviatilis*, the oligochaete *Tubifex tubifex*, the cladocerans *Chydorus sphaericus* and *Sida crystallina*, the mysid *Mysis relicta*, and the amphipod *Hyalella azteca* actually

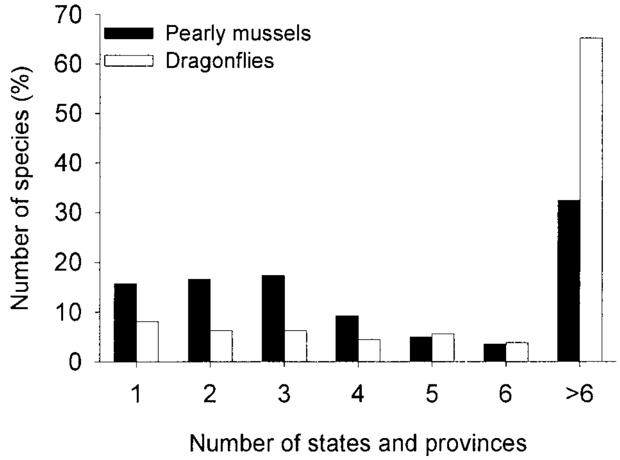

FIG. 5. Number of states or provinces occupied by species of North American dragonflies (Anisoptera) and pearly mussels (Unionoida). From Strayer (2001), after Williams et al. (1993) and Bick (1999).

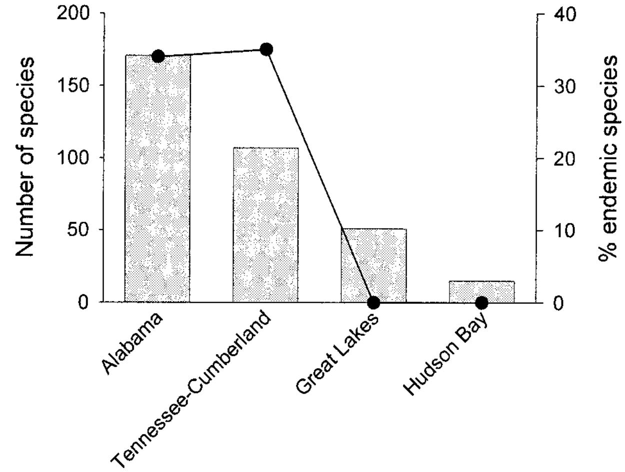

FIG. 7. Species richness and endemism of unionoid mussels in 2 unglaciated basins (Alabama and Tennessee–Cumberland) and 2 glaciated basins (Great Lakes and Hudson Bay) in eastern North America. From Clarke (1973), Burch (1975), Lydeard and Mayden (1995), Strayer and Jirka (1997), and Parmalee and Bogan (1998).

consist of several species, each with its own, smaller range (e.g., Frey 1987, Vainola et al. 1994, Witt and Hebert 2000, Beauchamp et al. 2001, Cox and Hebert 2001, Pfenninger et al. 2003). Even single species may show considerable geographic variation in genetic structure that is consistent with past isolation and drainage history (King et al. 1999, Nagel 2000, Hebert et al. 2003). Thus, claims about broad geographic ranges in freshwater invertebrates (for species other than widely introduced aliens) should be treated cautiously until critical studies have been made to verify the conspecificity of populations.

We cannot yet produce global maps showing patterns of species richness and endemism among freshwater invertebrates, but several hot spots of high richness and endemism are well known. Highly diverse and endemic assemblages of freshwater invertebrates occur in ancient river systems like the Tennessee and Mobile basins in the southeastern United States (Benz and Collins 1997) and the Mekong and other rivers in southeastern Asia (Dudgeon 2000a) and in ancient lakes such as Baikal, Tanganyika, and Malawi (Martens et al. 1994, Rossiter and Kawanabe 2000). Many groundwater and spring systems in ancient terrain (e.g., Cuatro Cienegas: Hershler 1985; the Australian mound springs: Ponder et al. 1989, Knott and Jasinska 1998; the Edwards Aquifer in Texas: Holsinger and Longley 1980, Hershler and Longley 1986; Balkan karst: Sket et al. 2004) contain a very high proportion of endemics, although overall species richness may not be as high as in surface waters. Of particular interest, the few studies that have been done suggest that the tropics do not support especially diverse communities of freshwater invertebrates (e.g., Lévêque 2001, Vinson and Hawkins 2003), although this question is far from settled.

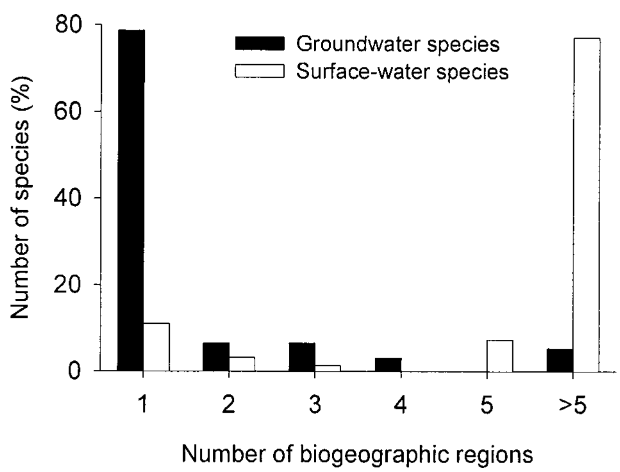

FIG. 6. Number of biogeographic regions occupied by groundwater and surface-water cyclopoid copepod species in Europe. From Strayer (1994), after Kiefer (1978) and Lescher-Moutoué (1986).

Threats to Freshwater Invertebrates

Human activities always have been centered on fresh waters. Of course, humans need fresh water to drink, but we also use fresh water for irrigation, waste disposal, navigation, hydroelectric power generation, fishing, recreation, and many other activities. The choicest lands for agriculture often are on floodplains and lake plains, and most of the world's great cities were built on rivers or lakes. Thus, the fullest impacts of the Earth's large human population have always been focused on freshwater habitats.

Humans use a large fraction of available fresh water globally. One analysis estimates that humans now appropriate >½ of the world's accessible freshwater runoff (Jackson et al. 2001). Although there are promising signs that per capita water use has been leveling off or even falling in recent years (Gleick 2001), overall water use by humans is projected to rise as the human population rises through the 21st century (Gleick 2003). Thus, there is every reason to think that human impacts on freshwater ecosystems will intensify through the 21st century, unless we radically change our patterns of water use.

The following discussion of threats to freshwater invertebrates is brief because there are several excellent recent reviews of threats to freshwater ecosystems (Jackson et al. 2001, Beeton 2002, Brinson and Malvárez 2002, Brönmark and Hansson 2002, Malmqvist and Rundle 2002, Danielopol et al. 2003). These threats fall into 5 classes: habitat destruction and degradation, pollution, introductions of alien species, direct harvest, and global climate change.

Habitat destruction and degradation

It is difficult to overstate the extent to which humans have changed freshwater habitats, which probably has been the most important human cause of endangerment and extinction of freshwater invertebrates (Richter et al. 1997, Dudgeon 2000a, b). Dams have been a primary cause of habitat loss and fragmentation. There are >45,000 large dams (either >15 m high or 5–15 m high and with a volume >3,000,000 m^3) today (Malmqvist and Rundle 2002), and perhaps a million smaller, but ecologically significant, dams (Oud and Muir 1997, cited in Jackson et al. 2001). River systems that are moderately or strongly affected by dams now cover >½ of the world; only tundra regions are drained predominantly by undammed rivers (Nilsson et al. 2005).

Dams create problems for freshwater invertebrates in several ways. The pond above the dam is not suitable habitat for most running-water species, and the reach below the dam may have such unnatural regimes of flow, temperature, and sediment supply that few native species can live there. The dam and reservoir are barriers to the dispersal of many running-water species, so that populations above and below the dam become effectively isolated. Dams and other barriers such as levees and culverts can reduce the viability of regional invertebrate metapopulations and reduce the ability for invertebrate species to migrate across the landscape in response to factors such as climate change. Last, dams and reservoirs allow humans to capture river flow more effectively for irrigation and other uses, so dams often are associated with water abstraction. Humans have been so good at capturing river flows that some of the world's major rivers such as the Ganges, the Colorado, and the Yellow no longer run to the sea during dry periods (Postel 2003). Thus, strong, pervasive effects of a dam may be felt over hundreds of kilometers of river (Rosenberg et al. 1997).

Although rates of dam-building have slowed (Malmqvist and Rundle 2002), and some dams are being removed (Hart and Poff 2002, Heinz Center 2002), dozens of new large dams are still being built or planned around the world, and dam building is extending into the few remaining free-flowing rivers (Dudgeon 2000b, Nilsson et al. 2005). The number of dams and their cumulative ecological impacts are likely to continue to rise for some time. Over the long term, we can expect a new class of effects to appear as reservoirs fill with sediment and dam function changes.

Habitat alterations other than impoundment also have been of primary importance in endangering freshwater habitats and species. Channelization and levee construction, destruction of wetlands and other shallow-water habitats by dredging, draining, or filling (Brinson and Málvarez 2002), lowering of regional water tables (Danielopol et al. 2003, Hancock et al. 2005), destruction of riparian vegetation (Naiman and Décamps 1997), hardening of shorelines, removal of wood (Maser and Sedell 1994, Christensen et al. 1996), and instream gravel mining (Hartfield 1993) all have been practiced around the world and have severe effects on freshwater invertebrates.

Pollution

Pollution also has been widespread and has had strong, pervasive effects on freshwater invertebrates. Point-source pollution by toxins, nutrients, and organic matter (which can supply N and P and deplete dissolved O_2) has been severe nearly everywhere in industrialized societies. Substantially under control in many parts of Europe and North America (although problems with some substances such as endocrine disrupters remain; Gagné et al. 2001, Brönmark and Hansson 2002), point-source pollution still is severe in many less-developed countries (Brönmark and Hansson 2002). In China, for example, ~5% of the length of rivers is too polluted to support any fish life (Dudgeon 2000a). Even in cases in which point-source pollution has been controlled, its effects may linger for many decades, either because the pollutants are persistent (e.g., metals, organochlorines), or because dispersal by the species extirpated during past episodes of pollution is slow enough to cause long time-lags between recovery of the chemical environment and the biota (Malmqvist and Rundle 2002). Nonpoint-source pollution from the watershed, typically sediments and nutrients from agricultural and suburban areas, is widespread around the world. Nonpoint-source pollution can have strong, persistent effects on freshwater invertebrates (e.g., Waters 1995, Richter et al. 1997, Harding et al. 1998), and has proven more difficult to control than point-source pollution. Even more diffuse are pollutants delivered from the airshed; acidity, N, Hg, and other contaminants from industrial activities cross national boundaries to reach fresh waters around the world, where they may affect invertebrates (Brönmark and Hansson 2002, Malmqvist and Rundle 2002). Thus, pollution is a threat to diversity of invertebrates in many of the world's fresh waters. Perhaps the nature of this pollution has been shifting from local point-source problems towards regional to global problems of more diffuse origin as locally severe problems are dealt with and the global human population and its activities grow.

Alien species

Introductions of alien species are now widespread around the world (Cox 1999) and have begun to homogenize the freshwater fauna (Rahel 2002). Some of these introductions are deliberate (e.g., the widespread stocking of salmonids and other sport fish), but most are unintentional (e.g., the release of species in ballast water or from unwanted pets or bait). Alien species often have strong, long-lasting ecological effects. For instance, the arrival of zebra mussels in eastern North America radically changed the physical, chemical, and biological characteristics of many lakes and rivers (e.g., Strayer et al. 1999). Competition with zebra mussels led to the extirpation of many populations of native unionid mussels (Ricciardi et al. 1998, Strayer 1999). Ricciardi et al. (1998) predicted that the zebra mussel invasion will be the final blow that will drive ~60 species of North American unionids into global extinction. Other alien species (especially sport fish) may be important predators of freshwater invertebrates. Brown trout introduced to Tasmania probably preyed on and reduced the range of the endemic anaspidacean crustacean *Anaspides tasmaniae*, which had not been previously exposed to predatory fish (Fletcher 1986). Many other alien plants, microbes, invertebrates, fishes and other vertebrates, and diseases have been moved around the world and have had strong ecological effects (e.g., Cox 1999, Mack et al. 2000). Because the number of new alien invasions is rising in many parts of the world and the effects of established aliens tend to be cumulative and difficult to reverse, the introduction of alien species is a difficult and growing problem in freshwater invertebrate conservation.

Direct harvest

Direct harvest has contributed to the endangerment of a few freshwater invertebrates. Humans have collected freshwater mussels for their shells, pearls, and meat since prehistoric times. Especially in the last 200 y, harvests have depleted many populations in Europe and the Americas (Claassen 1994, Ziuganov et al. 1994, Beasley 2001). Some harvests seem almost incredible. In 1913 alone, >13 million kg of shells were taken from living mussels in Illinois waters (Claassen 1994), and musselers removed 100 million mussels from a single 73-ha bed on the Mississippi River (Carlander 1954). These fisheries were targeted chiefly at abundant species, but the bycatch of rare species may have been substantial. Other freshwater invertebrate species also are taken in large numbers. Harvests of Australian crayfish from the wild are hundreds of tons/y, and have contributed to the endangerment of some species (Geddes and Jones 1997). Large numbers of the medicinal leech, *Hirudo medicinalis*, were taken in the 18th and 19th centuries when blood-letting was common; imports into France were 19 to 57 million animals/y in 1827 to 1843 (Elliott and Tullett 1984). It is unclear, however, the extent to which overcollecting contributed to the current vulnerable status of this species (Elliott and Tullett 1984, IUCN 2005). Collection of invertebrates for bait or the pet trade also could contribute to local depletion of populations. Invertebrates sometimes are protected by harvest regulations (e.g., closed seasons, size regulations, bag limits), but such regulations may be inadequately conceived and poorly enforced.

Freshwater invertebrates such as prawns and mussels are now being farmed in aquaculture operations. Aquaculture may pose threats to wild populations of invertebrates by spreading disease or foreign genetic material, as has been discussed for fish aquaculture (Goldberg et al. 2001). Last, harvest of fish, other vertebrates, or plants may have strong cascading effects on freshwater invertebrates, as has been described for marine fisheries (Scheffer et al. 2005).

Global climate change

Human activities are expected to cause large changes in global climate in the 21st century. It is difficult to make precise predictions about how these changes will affect specific bodies of fresh water, but it is expected that the effects of climate changes may be widespread, large, and varied. Environmental factors such as temperature, hydrology, water level, sea level, lake stratification, the nature and severity of disturbances, increases in damaging ultraviolet light, water chemistry, riparian vegetation, and food quality all may be affected (Brönmark and Hansson 2002, Malmqvist and Rundle 2002). Thomas et al. (2004) concluded that climate change could extinguish 9 to 52% of terrestrial species, with species having poor dispersal abilities falling near the upper end of the range. Aquatic species will have to disperse to bodies of water with suitable ecological conditions (if such locations exist) to survive climate change.

Freshwater invertebrates exhibit a wide range of dispersal abilities. Actual measurements of long-term dispersal rates of freshwater invertebrates are difficult to make (Bohanak and Jenkins 2003, Havel and Shurin 2004), but at least some zooplankton and aquatic insects have dispersal rates that may be sufficient to keep up with climate change (cf. Bohanak and Jenkins 2003, Havel and Shurin 2004, Macneale et al. 2005). However, the dispersal rates of many other freshwater invertebrates across drainages appear to be very slow (van der Schalie 1945, Strayer 1994)—almost surely too slow to keep up with the pace of climate change that current models predict. Further, human modifications to waterways (e.g., impoundments) probably will make long-distance dispersal more difficult in the future than it was in the past. Thus, we can expect climate change to endanger or extinguish many species of freshwater invertebrates in the coming century, especially those that disperse slowly and are not dispersed by humans. Furthermore, because the dispersal rates of different species are likely to be so different, climate change will not cause literal displacement of familiar communities, but rather recombination of fast and slow dispersers into novel communities for which properties and biotic interactions will not always be predictable. Such a phenomenon occurred as terrestrial vegetation moved north following the retreat of Pleistocene glaciers (e.g., Davis 1981), but has not been well studied for freshwater communities.

Conservation Status of Freshwater Invertebrates

There are no good estimates of how many species of freshwater invertebrates are extinct or endangered. The most comprehensive list of endangered animals available is the World Conservation Union (IUCN) Red List, which lists 1369 species of freshwater invertebrates as vulnerable, endangered, or extinct (Table 2). Nevertheless, the IUCN list is clearly incomplete. A few groups of large, conspicuous, and attractive animals dominate the Red List (mollusks, decapods, and odonates make up 77% of listed species of freshwater invertebrates). Smaller and less conspicuous animals may be equally imperiled, but there is insufficient information on the status and trends of their populations to assess their conservation status. The Red List of freshwater invertebrates also is geographically nonrepresentative, with 73% of species from North America, Europe, Australia, or New Zealand. This geographic bias may reflect the geographical distribution of invertebrate conservation biologists as much as the actual distribution of endangered freshwater invertebrates.

The Red List and comparable estimates of the number of imperiled species include only species for which there is firm, positive evidence that populations or ranges have shrunk to the threshold of viability. We could, instead, classify species as demonstrably imperiled, demonstrably safe, or lacking information for a firm classification of status. Only the mollusks, decapods, and odonates appear to be well assessed by IUCN, so the last category (unclassifiable species) contains >90% of freshwater invertebrates, including tens of thousands of species that have not yet been described by scientists (including species that went extinct before they were seen by scientists), as well as tens of thousands of described species that lack sufficient information for a formal conservation assessment. Thus, the true number of imperiled and extinct species lies somewhere in the very broad limits between the number of demonstrably imperiled species and the number of demonstrably imperiled plus insufficiently known species.

As an alternative to the Red List figures, we might accept the IUCN figures as reasonably accurate for mollusks, decapods, and odonates; ~8% of described species in these groups are listed. If the IUCN percentage (8%) applies to all freshwater invertebrates, of which there are perhaps 150,000 species in total (see above), then ~12,000 species of freshwater invertebrates are now imperiled or have been extinguished by human activities. This number is large, but it could easily be too low. For example, Wilcove and Master (2005) estimated that 32% of freshwater invertebrate species in the US for which conservation status has been assessed are imperiled or extinct.

An alternative approach for assessing the global endangerment of the freshwater invertebrate fauna is to identify regions and habitats in which damaging human activities coincide with areas of high endemism. I suggest that freshwater invertebrate species in 4 areas are especially at risk.

Old river systems often support endemic species. Many river systems have suffered badly from impoundment and other physical modifications, water withdrawals, and pollution. Thus, most old river systems probably contain imperiled or extinct endemic invertebrates. For example, the rivers of the American Southeast contain a highly endemic fauna of freshwater invertebrates and have been deeply modified by dams, landuse practices, pollution, and other human impacts (Benz and Collins 1997). As a consequence, among the mollusks (which have received the most study), 4 genera and ~60 species are now extinct, and hundreds of additional mollusk species, representing >½ of the native fauna, are threatened or endangered. Hundreds of southeastern crayfish and aquatic insects are likewise rare or endangered, and additional species of small, poorly known animals like copepods, isopods, amphipods, and oligochaetes are doubtlessly extinct or at risk of extinction. The species most likely to survive massive transformation of river systems are good dispersers that live in many drainage basins and habitat generalists that can tolerate nonriverine environments. Very few river systems have escaped human impacts (Nilsson et al. 2005), and even these systems are facing impoundment and other large modifications in the coming decades (e.g., Dudgeon 2000a, b).

A 2nd habitat from which many freshwater invertebrate species probably have been lost is groundwater systems in arid and semiarid regions (e.g., northern Africa, the American Great Plains and Southwest, northern Chinese plains, Australia). Groundwaters and springs typically support highly endemic invertebrate faunas that probably disperse slowly and are sensitive to human impacts. Humans in arid regions around the world are pumping water out of aquifers for agriculture and domestic use faster than it can be replenished. In many areas, water tables have already fallen by tens of meters, and continue to decline >1 m/y (Danielopol et al. 2003). We do not know if the groundwater biota can keep up with such rapid declines. Groundwater withdrawals already have dried up many springs. Further withdrawals will dry up many more springs, aquifers, and small streams, resulting in species extinctions (e.g., Ponder 1986). It is possible that groundwater systems in arid lands around the world are experiencing large but unseen losses in biodiversity.

Third, the impacts of global climate change on freshwater invertebrate species are likely to vary regionally. Climate change is projected to be most severe in mid to high latitudes (Intergovernmental Panel on Climate Change 2001). Many high-latitude areas were glaciated and have low endemism, so impacts of climate change on freshwater biodiversity may be most severe at mid latitudes. These impacts may be especially severe in regions where fresh waters already have been damaged by human activities and for poorly dispersing species.

Last, we can predict that freshwater invertebrates will become endangered in the future in regions where the human population is growing rapidly (e.g., much of Africa) or where economies are developing rapidly (e.g., China and Southeast Asia). Threats will be especially severe in regions where population and economic growth occur in ancient river basins or semiarid regions.

Conservation Solutions

Let me close by describing 5 major challenges for the conservation of freshwater invertebrates and laying out some alternative approaches for confronting those challenges. First, human pressure on fresh waters is enormous and will increase over the coming century. Humans need fresh water for many purposes, and these needs are growing. Despite signs that per capita water use is declining in some countries (Gleick 2001), human population growth and economic development almost surely will drive up overall use of fresh water. Thus, most of the threats associated with human activity will intensify through the 21st century. Second, we are in a conservation situation where many species and populations already are extinct or endangered and many more are trending downward. We do not have the luxury of time to plan for a future conservation crisis; we are in the midst of one. Third, most species of invertebrates are far too poorly known at present to qualify for a species-based vertebrate paradigm to conservation. We just do not have the necessary information to list and protect freshwater invertebrate species one by one. Fourth, in fresh waters, conservation typically has to protect landscapes, not just local sites where species occur. We need to plan and manage at least over whole drainage basins, and sometimes larger areas than that (Wishart and Davies 2003). Fifth, so far, we have been spending only a modest amount of money on invertebrate conservation. In Fiscal Year 2003, the median amount spent by federal and state agencies on conservation-related activities for freshwater invertebrate species on the US Endangered Species List was $24,000 (Fig. 8). Of course, the many imperiled species in the US that are not formally listed (Wilcove and Master 2005) and imperiled species living in less prosperous or less conservation-minded countries than the US received essentially no money.

I see 4 broad alternatives to deal with these challenges. First, we could concede that the challenges facing freshwater invertebrate conservation are overwhelming in view of the resources that we can bring to bear on the problem and simply abandon all attempts to conserve freshwater invertebrates. The modest resources now devoted to freshwater invertebrate

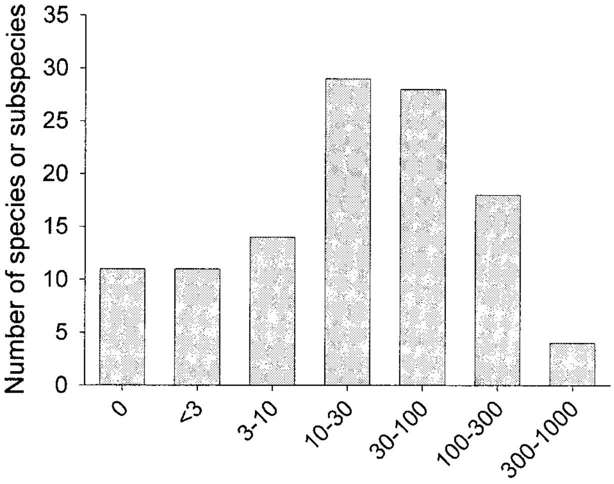

FIG. 8. Total state and federal expenditures in Fiscal Year 2003 for species of freshwater invertebrates listed on the US Endangered Species List. Figures include only activity-related expenditures that could be assigned to an individual species (i.e., not land acquisition or general administrative expenses). From USFWS (2005).

conservation could be diverted to other purposes. Many invertebrate populations and species would persist by chance or as an incidental effect of other conservation and management activities. This alternative obviously has an attractive price, but will fail to protect many populations and species of freshwater invertebrates and does not capitalize on existing and future knowledge about conservation and invertebrate ecology. Following this course also involves some risk to human welfare because freshwater invertebrates are involved in so many ecological functions and services.

Second, we could follow the current path of devoting modest resources to some invertebrates in some parts of the world. Such a course has a modest cost and takes advantage of the excellent work on freshwater invertebrate conservation that is already underway in parts of the world. Nevertheless, we should be honest and recognize that following such a course will fail to protect species and populations of invertebrates in the many regions of the world where efforts toward freshwater invertebrate conservation are negligible. Even in regions where freshwater invertebrate conservation is active, this course will not protect nontarget species, which make up most of freshwater invertebrate species, except as an incidental result of conservation activities for the few targeted species. Further, existing conservation efforts may not be adequate to protect even the best-protected species in the best-protected regions. For example, many species of freshwater mussels appear to be continuing to decline even after being listed on the US Endangered Species List (Biber 2002). An important constraint on many species-based conservation efforts is a legal framework that is narrowly focused on protecting existing individuals and populations of listed species. As a consequence, many conservation activities are reactions to acute threats to remaining populations of a species rather than actions designed to enhance the long-term viability of the species. Last, the public sometimes resents conservation efforts targeted at invertebrates of little apparent practical value, resulting in a significant public backlash. Ultimately, we will achieve only modest success by applying modest resources with the present species-focused approach—we will protect some of the species in some of the places and lose many species and populations whose conservation problems we are unable to document or solve.

Third, we could vastly increase resources devoted to freshwater invertebrate conservation so that it reaches a level comparable to terrestrial vertebrate conservation. Aside from the problems that others have raised about even well-funded species-focused conservation (e.g., Simberloff 1998, Moss 2000), following this course would probably require a 100- to 1000-fold increase in the amount of resources devoted to freshwater invertebrate conservation (Figs 2, 3). It seems unlikely that society will be willing to invest this much in freshwater invertebrate conservation, at least in the short term.

Fourth, we could try to incorporate freshwater invertebrate conservation into broad, regional programs of freshwater supply and protection. This approach is based on identifying regions in which many species of freshwater invertebrates are endangered and providing the maximum feasible levels of habitat protection and enhancement. Many such regions will be so large that humans and their activities cannot be excluded, so this approach must recognize that humans have legitimate needs for fresh water that will have to be satisfied (and, indeed, will increase in many regions) as an integral part of any program of invertebrate conservation. Our knowledge is incomplete, but we already can identify many regions of high diversity or imperilment. We usually can identify the chief problems that generally threaten freshwater resources in these regions (dams, destruction of riparian and nearshore habitats, inefficient water use, pollution, alien species, climate change) without detailed knowledge of specific species biology, and we often can identify potential solutions to these problems. This approach has several possible strengths. It could protect tens to hundreds of species at a time, even if they are not well known (or even discovered). Moving the conservation emphasis away from local protection (e.g., small refuges for endangered populations) to regional water management matches the spatial scale naturally suited to freshwater ecosystems (especially rivers and groundwater flow systems). A regional approach that combines water supply with protection of freshwater ecosystems and communities may be more appealing than species-based programs to a public that is often skeptical of endangered species protection of invertebrates. It also could enlist political allies rather than enemies for the cause of invertebrate conservation. People concerned with clean water for recreation, aesthetics, vertebrate populations, or public health all share the invertebrate conservationist's interest in protecting and enhancing the quality of freshwater habitats. Posing the invertebrate conservation problem in this way shows that economic progress may even be allied with invertebrate conservation. For example, both can benefit from increased water quality and water-use efficiency; indeed, advances in areas such as water-use efficiency in agriculture might be able to save as many invertebrate species as programs narrowly targeted to save one species at a time and save money. Thus, posing the invertebrate conservation challenge as part of a broader endeavor to preserve and enhance freshwater resources reaches beyond the small community of people directly concerned with invertebrates. Of course, some conservation programs already use this approach and even include invertebrate conservation as one of their objectives. The Conasauga River Alliance is one example of such a broad, multi-objective program (http://www.conasaugariver.net/index.html).

Obviously, these 4 courses are not mutually exclusive but can be combined with one another in various ways. My goal in setting them out is not to insist that we literally choose one or another of these alternatives. Rather, it is to encourage conservationists and scientists to think explicitly and realistically about what might be achieved using various approaches to freshwater invertebrate conservation and to make deliberate choices about what courses to follow, rather than reflexively following courses that others set for other species in other habitats.

Last, whatever approaches are pursued, education and monitoring can play important roles. Education can support conservation programs and probably should be matched to specific conservation programs. If conservation programs are targeted broadly at providing water for human needs while causing as little environmental damage as possible, then educational programs might best address the connections between human actions and water quality and quantity, the distinctive nature of regional biotas, and major threats to the biota, not merely the characteristics and needs of individual species. Educational programs can reach several audiences, e.g., the people who will pay for or benefit from any conservation projects or those involved in the political process leading to conservation action.

The only way that we can assess the success of any conservation program and accordingly adjust, expand, or abandon the program is by monitoring its results. At present, we have little information on how freshwater invertebrate populations and communities actually respond to conservation efforts. Without such information, it will be difficult to assess the effectiveness of various conservation strategies and adjust our actions accordingly. This problem will lead to a situation like that described for river restoration by Bernhardt et al. (2005), in which inadequate data on the success of river restoration projects have severely limited opportunities to learn from and improve these expensive projects.

In Conclusion

What are the ultimate prospects for preserving freshwater invertebrate species? It seems clear that we already are in a difficult situation in which many populations and species are in serious trouble, and our difficulties are likely to become more challenging in the near future. I doubt that current approaches to freshwater invertebrate conservation will be adequate to meet these challenges. We may have better success if we view invertebrate conservation as part of a larger problem with the dual goals of preserving freshwater ecosystems and ensuring adequate supplies of fresh water to people, instead of setting apart invertebrate conservation as its own problem. If we so choose, NABS and other scientific societies can play an important role in defining the agenda and developing solutions for freshwater invertebrate conservation.

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