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Contributed Papers

Threats to Imperiled Freshwater Fauna

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Abstract: *Threats to imperiled freshwater fauna in the U.S. were assessed through an experts survey addressing anthropogenic stressors and their sources. Specifically, causes of historic declines and current limits to recovery were identified for 135 imperiled freshwater species of fishes, crayfishes, dragonflies and damselflies, mussels, and amphibians. The survey was designed to identify threats with sufficient specificity to inform resource managers and regulators faced with translating information about predominant biological threats into specific, responsive actions. The findings point to altered sediment loads and nutrient inputs from agricultural nonpoint pollution; interference from exotic species; and altered hydrologic regimes associated with impoundment operations as the three leading threats nationwide, accompanied by many lesser but still significant threats. Variations in threats among regions and among taxa were also evident. Eastern species are most commonly affected by altered sediment loads from agricultural activities, whereas exotic species, habitat removal/damage, and altered hydrologic regimes predominate in the West. Altered sediment loading from agricultural activities and exotic species are dominant problems for both eastern mussels and fishes. However, eastern fishes also appear to be suffering from municipal nonpoint pollution (nutrients and sediments), whereas eastern mussels appear to be more severely affected by altered nutrient impacts from hydroelectric impoundments and agricultural runoff. Our findings suggest that control of nonpoint source pollution associated with agriculture activities should be a very high priority for agricultural producers and governmental support programs. Additonally, the large number of hydropower dams in the U.S. subject to federal re-licensing in coming years suggests a significant opportunity to restore natural hydrologic regimes in the affected rivers.*

Amenazas a la Fauna Dulceacuícola en Riesgo

Resumen: *Se estimaron amenazas a la fauna dulceacuícola de los Estados Unidos en riesgo mediante un estudio de expertos enfocado en estresores antropogénicos y sus fuentes. Se identificaron específicamente las causas de disminuciones históricas y los límites actuales para la recuperación de 135 especies dulceacuícikolas de peces, langostinos, libélulas, mejillones y anfibios en riesgo. El estudio fué diseñado para identificar amenazas con suficiente especificidad como para informar a los manejadores de recursos y reguladores que encaran la traducción de información sobre amenazas biológicas predominantes en acciones específicas y sensibles. Los resultados apuntan hacia cargas de sedimentos y entrada de nutrientes alterados por fuentes agriculturales sin puntos de contaminación; interferencia de especies exóticas y regímenes hidrológicos alterados asociados a operaciones de retención, como las amenazas más importantes a nivel nacional, acompañadas por muchas otras menores pero aún significativas amenazas. Tambien fueron evidentes variaciones entre regiones y entre taxas. Las especies del este son mas comunmente afectadas por cargas de sedimentos de actividades agriculturales, mientras que las especies exóticas, la remoción/daño del hábitat y alteración de regimen hidrológico predominaron en el oeste. Cargas de sedimentos alteradas por actividades agriculturales*

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Richter, BD et al. (1997)

y especies exóticas son problemas dominantes tanto en mejillones como en peces del este. Sin embargo, los peces del este aparentemente también sufren de descargas municipales sin puntos de contaminación (nutrientes y sedimentos), mientras que los mejillones parecen ser mas severamente afectados por la ateración de nutrientes debido a retenciones hydroeléctricas y descargas agriculturales. Nuestros resultados indican que el control de fuentes de contaminación sin puntos asociadas a actividades agriculturales deben ser de alta prioridad para los productores agrícolas y programas de soporte gubernamental. Adicionalmente, la gran cantidad de represas en los Estados Unidos sujetas a re-expedición de licencias federales en los próximos años, sugiere una oportunidad significativa para restablecer los regímenes hidrológicos en los ríos afectados.

Introduction

A quiet crisis is taking place beneath the surface of the world's rivers and lakes. Conservative estimates suggest that 20% of the world's freshwater fishes are extinct or in serious decline (Moyle & Leidy 1992). Within North America the number of freshwater fishes considered by the American Fisheries Society to be endangered, threatened, or of special concern increased from 251 to 364 in the 1980s, a 31% increase (Williams et al. 1989). Healthy stocks of salmon and steelhead in the Pacific Northwest are outnumbered more than three to one by those that are either extinct or at risk of extinction (Huntington et al. 1996; Nehlsen et al. 1991). Sixty-three percent of California's fish species and subspecies are extinct, endangered, or declining (Moyle & Williams 1990). Eighteen of approximately 300 species of freshwater mussels north of Mexico are presumed extinct, 44 are listed or federally proposed as endangered, and another 69 may be endangered (Bogan 1993).

Aquatic fauna are proportionately more threatened than terrestrial species (Stein & Chipley 1996; Flack & Chipley 1996; Master 1990). Whereas 14% to 18% of terrestrial vertebrates (birds, mammals, and reptiles) and butterflies in the U.S. are classed as vulnerable, imperiled, or extinct, the proportion of aquatic biota similarly classed ranges from 35–37% for amphibians and fishes to 65% for crayfish, and 67% for unionid mussels. By virtually any measure, a large proportion of the world's freshwater fauna appears vulnerable to extinction.

Halting this massive loss of aquatic biodiversity requires scientific information on its causes, identified with sufficient detail and ranked by their magnitudes, to guide conservation efforts. A survey of expert knowledge of threats to imperiled species provides one means to rapidly and reliably assemble such information. We report on the results of an experts survey for imperiled freshwater fauna of the U.S.

Previous studies (Miller et al. 1989; Williams et al. 1989; Noss & Cooperrider 1994; Allan & Flecker 1993; Naiman et al. 1995), although varying in the detail with which they describe threats to aquatic fauna, generally concur that the most important threats fall generally within the categories of habitat destruction and fragmentation, pollution, and exotic species. For example, in an analysis of North American fish extinctions, Miller et al. (1989) concluded that physical habitat alteration was the most common cause (implicated in 73% of extinctions), followed by introduced species (68%), chemical alteration of habitat (38%), hybridization (38%), and overharvesting (15%). Threats seldom act alone, as documented by the Environmental Defense Fund (Wilcove & Bean 1994). The number of threats endangering fish in the U.S. range from 1 to 15, with an average of 4.5. Less than 7% of federally listed fishes have a single overriding threat to their survival, whereas more than 40% had 5 or more major threats.

Although such analyses help spotlight general categories of human land and water use that affect aquatic biodiversity, they do not necessarily direct attention to specific, responsive actions. Resource managers and regulators cannot address the effects of threats such as habitat fragmentation or even physical habitat alteration until they understand which specific stressors and sources of stress are the leading culprits and which actions might produce the greatest improvements in aquatic biological conditions. A stressor is a specific type of disruption of ecological processes or conditions that adversely affects a species, the elimination of which would promote species recovery. A stressor's source is a specific kind of human activity that triggers or releases that stressor, a reduction of which would reduce the action or impact of the stressor.

For example, the U.S. Environmental Protection Agency's (EPA) most recent analysis of Clean Water Act Section 305(b) 1992 state reports (Environmental Protection Agency 1994) identified siltation as the leading cause of water quality impairment across the U.S., reported for 45% of the river miles assessed by the states, followed by nutrient pollution (37%), pathogen indicators (27%), pesticides (26%), and organic enrichment and resultant low levels of dissolved oxygen (24%). The EPA further found that agricultural practices accounted for the impairment of 72% of the stream miles assessed, followed by municipal point sources (15%), urban runoff and storm sewer discharges (11%), resource extraction (11%), industrial point sources (7%), silviculture (7%), and hydrologic/habitat modification. (A subsequent U.S. Geological Survey study also implicated agricultural practices as the leading causes of nutrient enrichment in U.S. rivers and lakes overall [Puckett 1995], but implicated municipal sources as additionally important in many localities.)

The EPA report presents one of the few examples of a study that discriminates between stressors and sources. However, the report focuses on those conditions responsible for water quality impairment in general rather than for species endangerment in particular. An assessment of water quality across the entire country necessarily covers all water bodies and stream reaches, including many that do not harbor imperiled species. Further, the report does not link particular stressors to particular sources, although the data presumably could be reanalyzed to examine such linkages. As a result, the report does not provide the kind of detailed guidance that biological resource managers most need.

To better address this need for greater specificity in identifying leading threats to freshwater species, we surveyed biologists familiar with threats to individual species. We sought to answer the question, "Among the multitude of threats to aquatic biodiversity in the U.S., are there a few specific threats that prevail so overwhelmingly as to deserve focused attention?"

Survey Methods

Species Selection and Species Experts

Using information in the Natural Heritage Central Databases maintained by The Nature Conservancy, we developed a list of all freshwater fishes, crayfishes, dragonflies and damselflies, mussels, and predominantly aquatic amphibians occurring in the U.S. We then selected those species with a conservation status rank (Master 1991) indicating that the species is globally imperiled. Simple random selection of half the species resulted in a list of 236 species for which to seek expert evaluation. We also sought to explore differences in our results according to geographic region and identified species as "western" or "eastern" based on whether their ranges extended westward or eastward from the continental divide, the most prominent aquatic zoogeographic divide in the U.S.

We sought threat information about the selected species by surveying biologists who were knowledgeable about a particular species, had worked with the species recently, and were aware of its current situation. The central databases maintained by The Nature Conservancy for the Network of Natural Heritage Programs and Conservation Data Centres provided our initial references to leading authorities for many of the species. We also contacted Natural Heritage Program offices directly to obtain further potential leads; many of the biologists contacted referred us to others.

We limited the number of species assigned to any one biologist whenever possible, to reduce the impacts of individual biologists' perspectives on the survey results. In total 89 biologists provided responses for 135 species (Table 1). We received three biologists' responses for 2 species, two biologists' responses for 10 species, and a single biologist's response for each of the remaining 123 species. Our discussions below address only the 135 species for which we received at least one response.

Survey Questionnaire

Our questionnaire surveyed biologists to determine what they thought were the leading stressors and sources of these stressors affecting imperiled species in the United States. The questionnaire included lists of possible stressors and sources (Tables 2 and 3), along with a glossary of terms (available on request) to further clarify the definition of each stressor and source. For each species we provided a separate questionnaire that prompted the respondent to (1) identify all stressors significantly affecting the species, using the list shown in Table 2; (2) identify all "primary" source types significantly associated with each stressor, using the list shown in Table 3; and (3) where appropriate, further identify all "secondary" source types significantly associated with each stressor, again using the list shown in Table 3. The first 10 primary source types are categories of land or water use; secondary source types are categories of human activity that can be associated with any of these first 10 primary source types; and an additional 10 primary types cover other sources not easily classified according to a dominant land or water use.

Additionally, we asked the biologists to consider separately which stressors and sources were responsible for historic declines and which ones currently limit the recovery of the species. Because we included species in our study based on knowledge of their vulnerability alone, we also asked each respondent to check off one of the following choices: "rarity not known to be caused

Table 1. Number of species by taxon for which surveyed biologists provided valid responses.

	Valid responses			
Taxon	*Historic conditions*	*Current conditions*	*Current & historic*	*Total*
Amphibians	0	1	3	4
Crayfish	0	7	14	21
Fish	2	4	54	60
Mussels	2	0	37	39
Odonates	0	2	9	11
Total	4	14	117	135

Table 2. List of stressors affecting imperiled species in the U.S. as listed for survey respondent selection.

Aquatic habitat stressors
1. Channel or shoreline: changes in morphology or bed structure
2. Dissolved oxygen (DO) regime alteration
3. Hydrologic regime alteration (includes flow or depth conditions; timing, duration, frequency etc.)
4. Nutrients, changes in inputs
5. Organic matter, changes in inputs
6. pH regime alteration
7. Salinity regime changes
8. Bed sediment load changes, including siltation
9. Suspended solids and/or turbidity alteration
10. Water temperature regime alteration
11. Other aquatic habitat alteration (respondent was asked to specify)

Toxins
12. Herbicides and fungicides
13. Halogens and halides (e.g., chloride, trihalomethanes)
14. Fish-killing agents (e.g., rotenone)
15. Insecticides
16. Lampricides
17. Metals
18. Moluscicides
19. Organic solvents (e.g., benzene, phenol)
20. Other hydrocarbons (e.g., dioxins, PCBs)
21. Mixed, cumulative effect*
22. Other toxins (respondent was asked to specify)

Other habitat stressors
23. Air temperature changes
24. Fire—manipulation of timing or frequency
25. Fire—suppression
26. Food supply or ecosystem tropic structure—depletion or alteration
27. Habitat destruction
28. Habitat fragmentation (e.g., barriers to movement, exclusion from habitat)
29. Other habitat degradation, including crushing, trampling, earth moving, inundation (respondent was asked to specify)

Other organism stressors
30. Competition
31. Complications due to small populations (e.g., inbreeding, stochastic fluctuation, etc.)
32. Genetic alteration (e.g., hybridization)
33. Overharvesting or legal, intentional collecting or killing
34. Parasitism
35. Predation
36. Poaching, vandalism, harassment, or indiscriminate killing
37. Unintentional capture or killing (e.g., artillery explosions, roadway casualties)
38. Vertebrate animal damage control (includes trapping, shooting, poisoning)
39. Radiation exposure increase (e.g., increased UV radiation)
40. Other stressor (respondent was asked to specify)

**This category refers to a situation where levels of individual toxins may not be remarkable (and may not even exceed allowable levels), but the cumulative effect is one of the top stressors.*

by anthropogenic factors" or "natural rarity is one factor in addition to others indicated below." All 135 of the evaluated species were identified as suffering from at least some historic or current anthropogenic threat.

Results

We did not receive equivalent levels of information for all of the 135 species evaluated. Our respondents provided information on both historic and current threats for 117 species, on historic threats alone for 4 species, and on current threats alone for 14 species. The final database thus contains information on historic threats for 121 species and on current threats for 131 species (Table 1).

The current ranges of the sampled species distributed somewhat unevenly across the country (Figs. 1a and 1b), reflecting the influence of several factors. The biogeography of the species in our sample is a product of their habitat (primarily lotic) requirements and their patterns of evolutionary isolation. Today, of course, their occurrences are further restricted to those waters not so badly impaired as to eliminate them entirely. Figures 1a and 1b show concentrations of imperiled vertebrate spe-

Table 3. List of sources of stressors affecting imperiled species in the U.S. as listed for survey respondent selection.

Primary sources associated with land or waterway use for agricultural, industrial, livestock, municipal, and silvicultural activities
Agricultural (not including silvicultural)
Industrial—power generation (e.g., thermal, hydroelectric)
Industrial—mineral extraction
Industrial—other
Industrial right of way (e.g., power lines, pipeline)
Livestock (grazing, feedlots, etc.)
Municipal (urban, suburban, rural residential)
Roadways—public, nonspecific use
Silvicultural
Waterway navigation
Other primary sources
Atmospheric deposition
Climate alteration or atmospheric change
Economic use of the species
Exotic or introduced species other than livestock
Native species
Recreational use of habitat or species
Scientific use of the species
Species management
Other land management
Other sources of stressors (respondent was asked to specify)
Secondary sources associated with land or waterway use for agricultural, industrial, livestock, municipal, and silvicultural activities
Conversion of land or waterway to new use (including land cover alteration)
Drainage of channel alteration (including flood control)
Ground water depletions or augmentations
Impoundment operations (e.g., dams, reservoirs)
Nonpoint release of sediment or pollutants (e.g., runoff, infiltration, aerosol release)
Point source release of pollution (including spills, facility discharges)
Surface water depletions or augmentations
Other (respondent was asked to specify)

cies in the West and Southeast and a concentration of imperiled invertebrate species in the Southeast.

Summary of Leading Threats

Our data structure allowed us to analyze the leading stressors under historic and current conditions, the leading sources of these stressors, and, most importantly, the leading stressor:source combinations identified by our respondents.

Stressors

Figure 2a shows the pattern of identification of stressors among all 135 evaluated species. The five leading stressors implicated as causing historic declines are hydrologic regime alteration, streambed sediment load changes (including siltation), habitat destruction, channel or shoreline changes in morphology or bed structure, and changes in nutrient loads (refer to Table 3 for definitions of terms). The five leading stressors implicated as *currently limiting the recovery* of the species are similar, but with some important distinctions. Streambed sediment load changes and hydrologic regime alteration again lead the list; interactions with other species emerges as an additional prominently cited threat, followed by altered nutrient inputs and habitat destruction. The reporting of changes in channel or shoreline as a stressor is much greater, whereas the reporting of competition is much less between the reports for historic versus current conditions.

The level of detail encoded in the stressor list affects this pattern of responses. For example, the section of the list covering toxic contamination provides a detailed suite of choices, whereas other single choices such as "hydrologic regime alteration" simultaneously cover a wide range of possible alterations of habitat. By grouping stressor types together into larger categories of similar threats, we overcame this unevenness in the level of detail in the original coding list, even though the list of stressors was not originally designed for this purpose. Specifically, we combined (1) stressor 4, "nutrients, changes in inputs" with stressor 5, "organic matter, changes in inputs" to create a larger category of "altered nutrient inputs;" (2) stressors 8 and 9, both of which involve impacts of "altered sediment loads;" (3) stressors 12 through 22, all of which identify "toxic contaminants;" (4) stressors 1, 27, 28, and 29, "channel or shoreline changes", "habitat destruction," "habitat fragmentation," and "other habitat degradation" to create the larger category of "habitat removal and damage;" and (5) stressors 30, 32, 34, and 35, covering "competition," "genetic al-

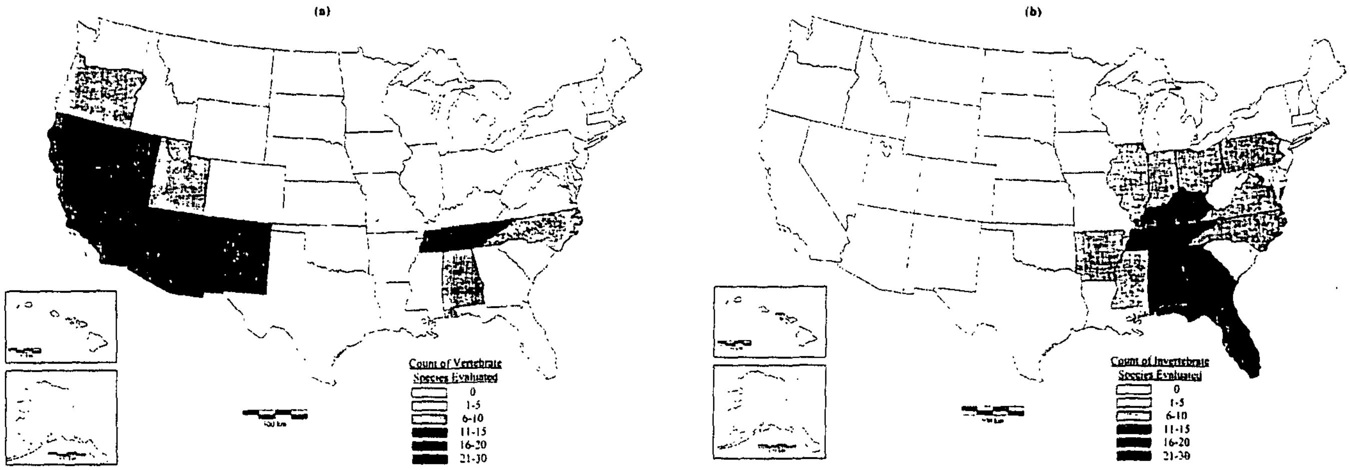

Figure 1. Distribution of species evaluated by state: vertebrates (a) and invertebrates (b).

teration," "parasitism," and "predation" to create the larger category of "intra/inter-species problems."

When we rearranged the list of stressors in this manner and reevaluated the responses, a new pattern emerged (Fig. 2b). Stressor 3, altered hydrologic regime, was the only frequently reported stressor not included in one of the rearranged stressor groups. Direct removal or damage to habitat was implicated as a threat for nearly 60% of species under historic and nearly 50% under current conditions; threats arising from intra- and inter-species interactions were implicated for 21% of species under historic and 37% under current conditions; altered sediment loads were implicated for approximately 35% of species under both historic and current conditions; altered hydrologic regimes remained a frequently implicated threat, at 34% under historic conditions and 28% under current conditions; altered nutrient inputs were implicated for 30% of all species under historic and 25% under current conditions; and toxic contaminants as a group were implicated for 16% of species under historic and 23% under current conditions. Two noticeable shifts were evident among these results: intra- and inter-species interactions

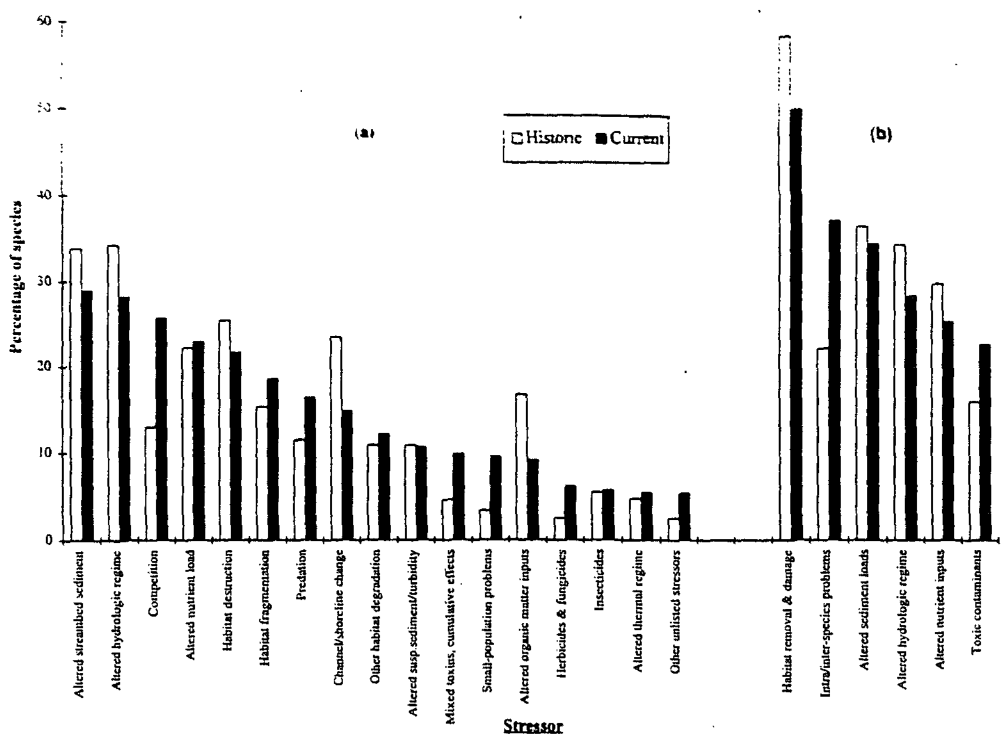

Figure 2. Stressors implicated for historic versus current conditions for all species evaluated: individual stressors (a) and grouped stressors (b). Only those stressors implicated for more than 5% of species under either historic or current conditions are shown.

were implicated as threats 75% more often and toxic contaminants 40% more often under current than under historic conditions.

The results for the grouped stressors were not simply the sums of the percentages for the individual stressors making up the groups. The questionnaire allowed each respondent to report more than one stressor as a threat for any single species. When tabulating the results for the grouped stressors, however, we recorded a grouped stressor as implicated for a species whenever *any one* member of that group was implicated for that species by a respondent, regardless of how many additional members of that group the respondent had listed. Grouping stressor types of course sacrifices some information and may not precisely match the intent of the respondents who listed the individual stressors.

Sources of Stressors

Figures 3a and 3b show the patterns of identification of primary and secondary sources, both individually and in combination among the 135 evaluated species, for historic and current conditions respectively. The four leading primary sources of stressors implicated as causing historic declines were agricultural land use, municipal land use, the power generation industry, and exotic species. The leading primary sources implicated as currently limiting species recovery were the same, but exotic species and the power generation industry switch rank orders. The change in reporting of exotic species as a threat under current versus historic conditions constituted a 73% increase. The leading secondary sources of stressors implicated for both historic and current conditions were nonpoint source pollution, impoundment operations, and land and waterway conversion; many of the primary source categories, however, had no applicable secondary sources.

The patterns of combination of primary and secondary source information (Figs. 3a & 3b) indicate that agricultural nonpoint pollution, hydroelectric impoundment operations, and exotic species (with no secondary sources applicable) were reported as the leading sources of stressors under both historic and current conditions. Several combinations of secondary sources associated with agriculture and municipal land use also were implicated prominently, including agricultural impoundment operations, land and waterway conversion, drainage and channel alteration, surface water depletion and augmentation, and municipal nonpoint pollution and land and waterway conversion.

Stressor and Source Interactions

The preceding summaries highlight leading stressors and leading sources, but these results beg the question, "What are the dominant sources of each of the leading stresses?" For this analysis, we again used the aggregated categories of stressors (Fig. 2b), but limited this combined analysis to current threats. The predominant primary-secondary source combinations for four of the six leading stressor groups were habitat removal and damage; intra/inter-species problems (not illustrated); altered sedi-

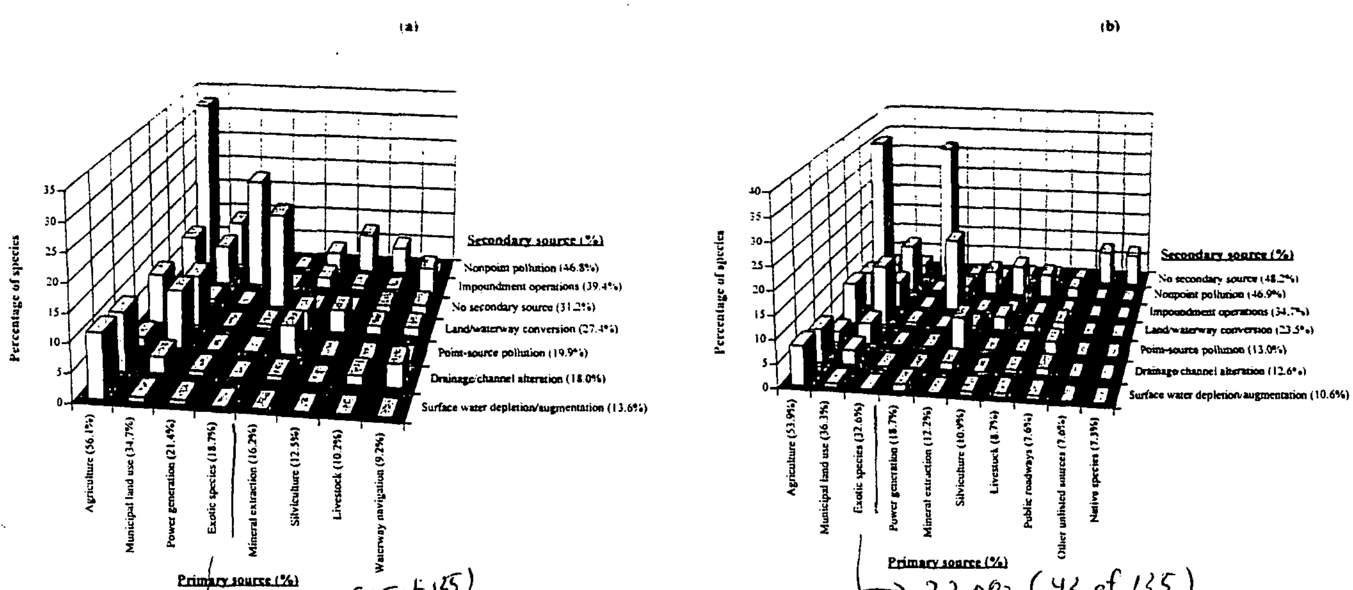

Figure 3. Primary and secondary sources implicated for all species evaluated: for historic conditions (a) and for current conditions (b). Only those sources implicated for more than 5% of species under either historic or current conditions are shown. The labels along the two source axes indicate the percentage of species for which each individual primary and secondary source was implicated.

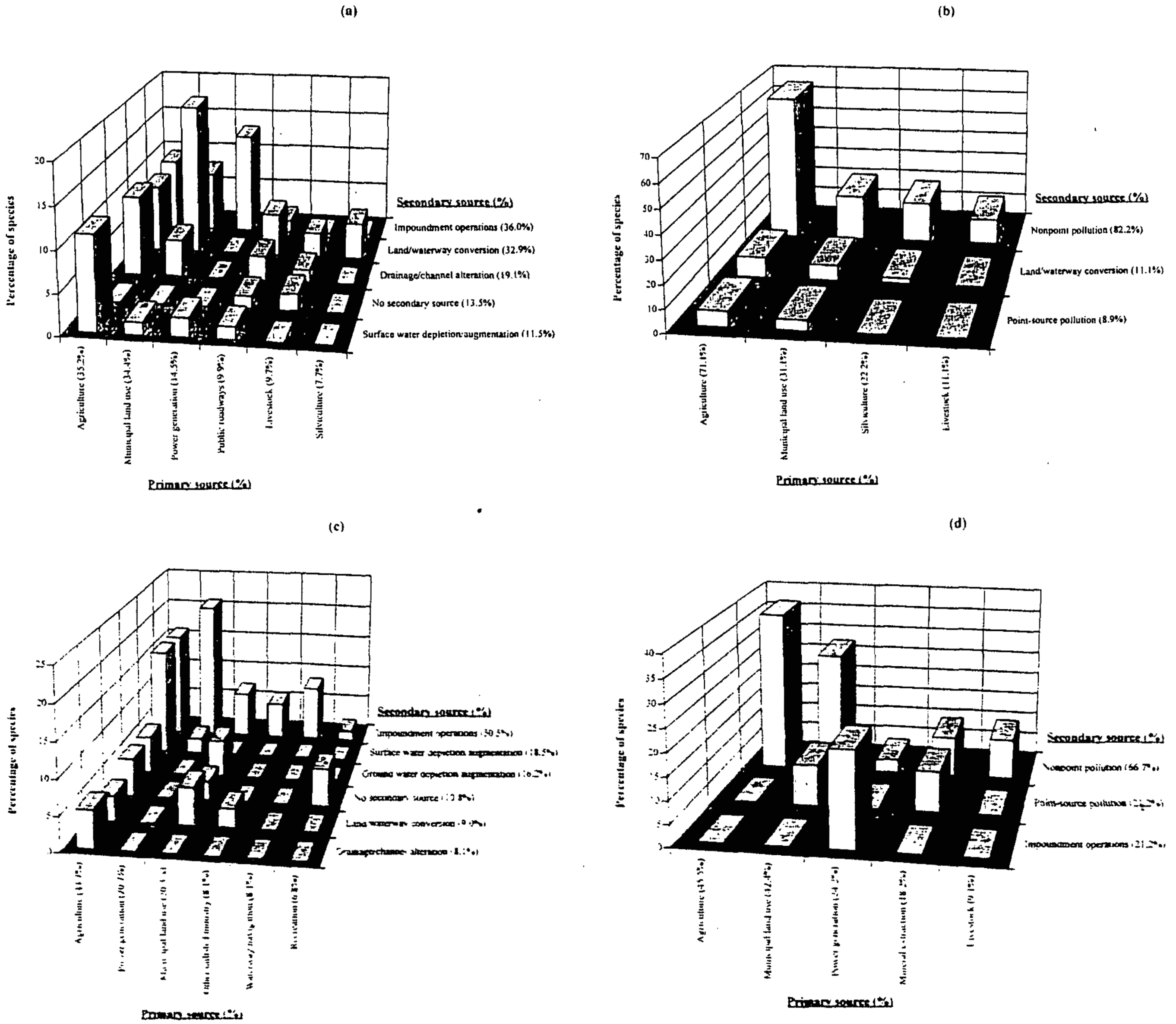

Figure 4. Primary and secondary sources implicated for current conditions for those 65.333 species for which habitat removal & damage *was reported as a significant stressor (a); those 45 species for which* altered sediment loads *was reported as a significant stressor (b); those 37 species for which* altered hydrologic regime *was reported as a significant stressor (c); those 33 species for which* altered nutrient inputs *was reported as a significant stressor (d). Only those sources implicated for more than 5% of species are shown. The labels along the two source axes indicate the percentage of the species for which each individual primary and secondary source was implicated.*

ment loads; altered hydrologic regimes; altered nutrient inputs; and toxic contaminants (not illustrated) (Fig. 4a-4d). (The fractional counts of species shown in Fig. 4's caption indicate that, although one or more species were addressed by multiple experts, only some of the respondents implicated this particular stressor.)

Land and waterway conversion for municipal land use and hydroelectric impoundment operations dominate among the sources of habitat removal and damage (Fig. 4a). Agriculture is also implicated as responsible for significant habitat removal and damage as consequences of associated impoundment operations, land and waterway conversion, drainage and channel alteration, and surface water depletion and augmentation. Interference from exotic species dominates as the reported source of intra- and inter-species problems, implicated for nearly 80% of all species for which this stressor was reported, with interference from native species also significant (20% of affected species). Agricultural nonpoint pollution is reported overwhelmingly as the dominant source of altered sediment loads (Fig. 4b), with municipal land use, silviculture, and livestock also reportedly contributing strongly to the nonpoint sediment pollution.

Agricultural and hydroelectric impoundments and agricultural surface water depletions and augmentations together dominate in the reporting of sources for altered hydrologic regimes (Fig. 4c). Agricultural and municipal nonpoint pollution dominate among the reported sources of altered nutrient inputs (Fig. 4d), with the effects of hydroelectric impoundments prominently implicated as well—the latter presumably reflecting the altered chemistry of discharges from the hypolimnion of impounded reservoirs. Finally, agricultural nonpoint pollution overwhelmingly dominates among the listed sources of toxic contaminants (reported for 57% of the species for which this stressor was reported). Point-source pollution, reported for 24% of these species, was a distant second among secondary sources, and mineral extraction (reported for 14% of these species) a distant second among primary sources.

Analysis of Threats by Region and Taxon

An analysis of similarities and differences in the threats reported for species with ranges restricted to "western" versus "eastern" states (among the lower 48 states) provides further useful information on the roles of different threats in different regions of the country. Figure 5 shows the pattern of co-reporting of stressor groups with primary and, where applicable, secondary sources. for the East (n = 83 and 91.5 species) and West (n = 31.1667 and 34 species) under historic and current conditions. Altered sediment loads due to agricultural nonpoint pollution is the leading stressor-source combination reported for eastern species under both historic and current conditions. Interference from exotic species, toxic contaminants, and altered nutrient inputs due to agricultural nonpoint pollution, habitat removal, and damage due to municipal land or waterway conversion are all implicated for the East with moderate frequency, reported to be limiting the recovery of more than 10% of eastern species.

In contrast, interactions with exotic species is the leading threat reported for western species under both historic and current conditions. Further, none of the other leading eastern threats qualifies as a leading historic or current threat in the West. Instead, habitat removal and damage and altered hydrologic regimes due to agricultural surface water depletions and augmentations are the next most frequently implicated threats among western species. Additional important western threats include habitat removal and damage and altered hydrology due to agricultural and hydroelectric impoundments.

The results obtained in the comparison of reported threats to eastern versus western species suggest there are significant differences in stressors and sources of those stressors between the two regions. Some of the differences between East and West, however, may stem from differences in ecological sensitivities among eastern versus western species rather than from differences

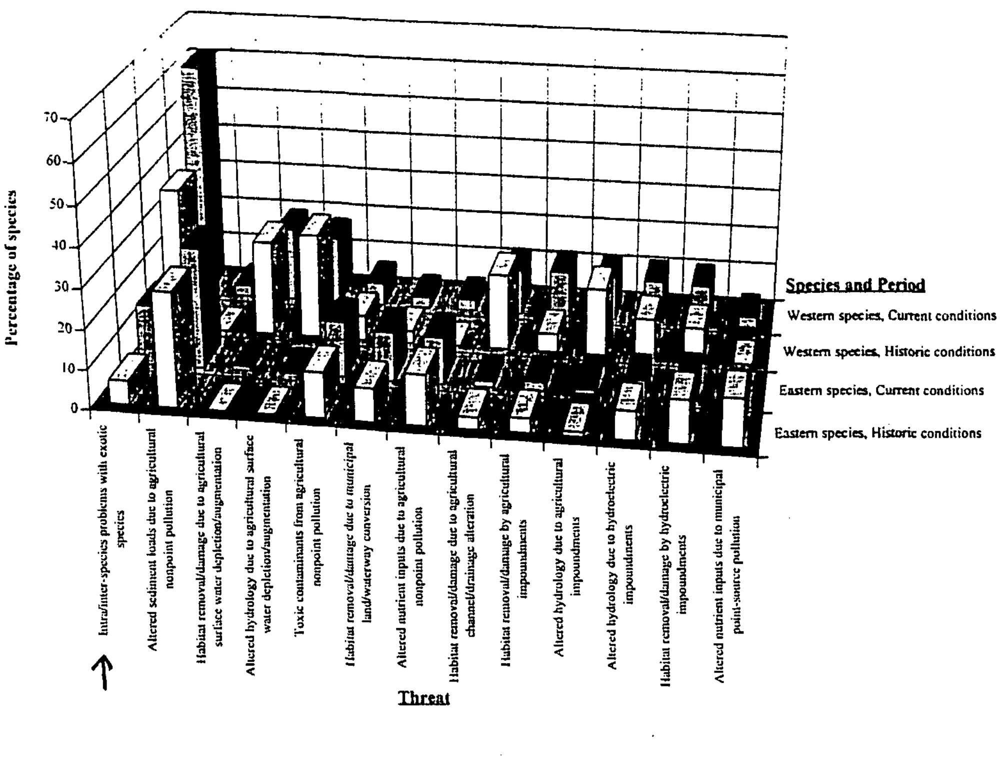

Figure 5. Leading threats (stressor group + primary/secondary source) implicated for historic versus current conditions for eastern versus western species. Only those implicated for more than 10% of eastern or western species under either historic or current conditions are shown.

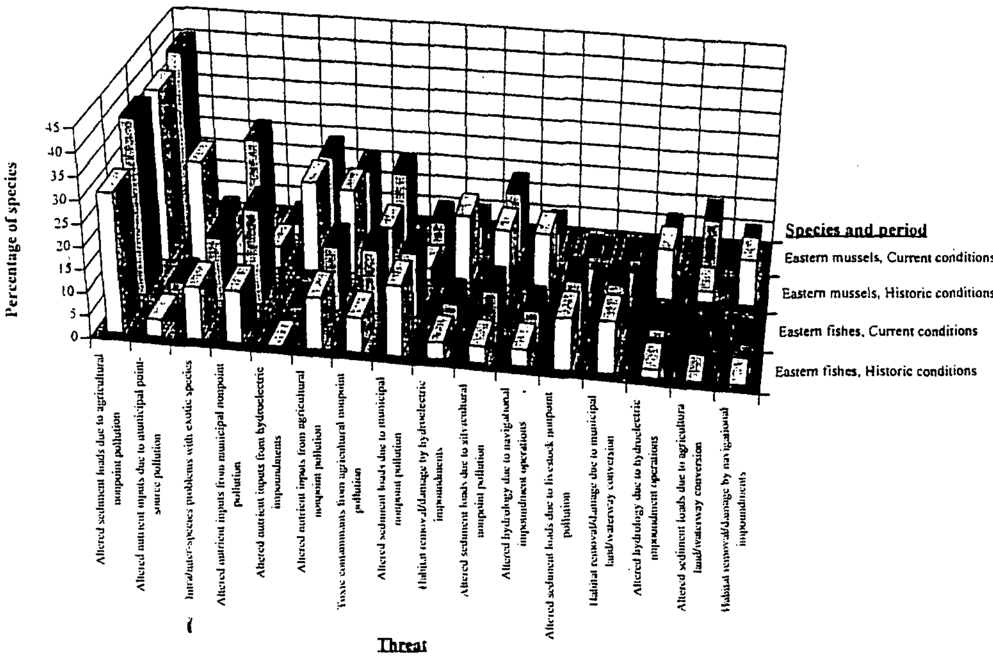

Figure 6. Leading threats (stressor group + primary/secondary source) implicated for historic versus current conditions for eastern fish versus eastern mussel species. Only those threats implicated for more than 10% of fish or mussel species under either historic or current conditions are shown.

in the history of land use alone. The invertebrate (predominantly mussel) species evaluated are distributed unevenly between eastern and western states, whereas vertebrates (almost entirely fishes) are distributed more evenly (Figs. 1a & 1b). For this reason, we also carried out the "East versus West" comparison using fishes alone. The results for eastern versus western fishes were similar to those obtained for all species (and hence are not illustrated). Altered sediment loads due to agricultural nonpoint pollution and exotic species lead the list of eastern stressor-source combinations for the fishes, and problems with exotic species and habitat removal and damage due to agricultural surface water depletions or augmentations lead the list of western stressor-source combinations.

We also compared the threats reported for fishes versus mussels in the East alone, in order to more thoroughly examine the extent to which our results capture differences in ecological sensitivities among species. While a comparison among all taxa would be desirable, only the fishes and mussels are represented by sufficient numbers among the evaluated eastern species (fishes = 26 and 28 species, mussels = 39 and 37 species for historic and current conditions, respectively) to allow a robust comparison. Figure 6 shows the co-reporting of stressor groups with primary and, where applicable, secondary sources, for eastern fishes versus eastern mussels.

Altered sediment loads from agricultural nonpoint sources leads the list of stressor—source combinations implicated as historically and currently affecting both eastern fishes and eastern mussels. However, compared to mussels, fishes are reported as being historically and currently more often affected by altered sediment loads and nutrient inputs due to municipal nonpoint pollution and much less affected by altered nutrient inputs due to hydroelectric impoundments. Eastern fishes are also reported as historically much less affected than mussels by municipal point source pollution or by habitat removal/damage and altered hydrology due to hydroelectric and navigation impoundments. Eastern fishes are reported as historically more affected than mussels by exotic species but somewhat less affected than mussels currently. Exotic species are also implicated as a factor limiting the recovery of mussels ten times more often currently than historically. On the other hand, the threat of altered nutrient inputs due to municipal point-source pollution is reported only one-tenth as often for current conditions as it is for historic conditions.

Discussion and Conclusions

Our results highlight three threats to freshwater aquatic ecosystems as the most significant overall, with some variation across regions and among taxa: agricultural nonpoint pollution leading to streambed sedimentation and suspended sediment loading as well as nutrient loading; interactions with exotic species; and impoundment operations resulting in altered hydrology and in habitat destruction and fragmentation. The implicated impoundment operations were attributed primarily to hydroelectric and agricultural purposes.

Our results indicate that significant agricultural impacts include not only increased sedimentation, but also habitat destruction and fragmentation, toxic chemical contamination, hydrologic regime alteration, altered nutrient inputs, changes in channel and shoreline morphology, and turbidity. Other sources of nonpoint-source pollution such as municipal land use were much less common than agriculture, but were implicated as significant historic and current threats across all species.

The combined effects of competition, predation, and hybridization by non-native species appear to be widespread and increasing among the species sampled. The patterns of reporting indicate that fish species have been subject to these impacts for some time, with exotic species reported as historical causes of declines for more than 25% of the fish species but for less than 3% of the mussel species sampled. For both fish and mussel species, however, exotic species are reported as currently limiting population recoveries for much larger percentages of the species sampled: 37% among fishes (14% for eastern and 60% for western fishes) and 22% among mussels. The reported increase in the effects of exotic species on mussels largely may be due to the recent introduction and rapid spread of the zebra mussel, (*Dreissena polymorpha*). These results also correlate with the fact that, as a result of long-term stocking efforts by state and federal agencies, exotic (mostly translocated North American and introduced European) fishes now comprise more than 25% of the freshwater recreational fishery in the U.S. (Moyle 1976). Introduced species thus appear to be increasing threats for imperiled species whose ranges and population sizes may have declined historically for a suite of other reasons. Introduced species may compete directly with native species for food or physical habitat, may interfere with the reproduction or maintenance of native species, or may prey upon or hybridize with native species (Stein & Flack 1996).

Nearly 30% of the evaluated species were reported as currently affected by hydrologic regime alteration, and approximately half of these species were reported as currently affected by regime alterations associated with impoundment operations in particular. Impoundment operations also were reported to contribute significantly to habitat destruction and fragmentation and to altered nutrient inputs. Our respondents reported threatening impoundment operations to be associated primarily with power generation and secondarily with agricultural and municipal land use.

The findings concerning impoundment operations are not surprising, with 75,000 large dams (higher than 8 m) and 2.5 million small dams now operating in the U.S. (National Research Council 1992). Dams are probably exacting a similar toll on aquatic biodiversity outside the U.S. Dynesius and Nilsson (1994) estimated that 77% of the total discharge of the 139 largest river systems in North America north of Mexico, in Europe, and in the republics of the former Soviet Union is affected by dams.

A comparison of the findings of previous studies, summarized in our introduction, indicates some differences between these previous studies' findings and ours. We expect these differences arise largely because of differences in the research questions asked and hence in the data developed. In particular, studies that focused on issues of water quality impairment in general rather than on aquatic species imperilment in particular might be expected to produce different results. Also, many of the species we evaluated possess unique or highly specialized feeding, reproductive, or other ecological characteristics, which both limit where they occur naturally and affect their vulnerability to human alterations of the aquatic environment. These species may not naturally occur in "average" waters and so may not be affected to the same degree by those stressors to aquatic biota typical of the nation overall. The geographic coverage of our sample is uneven across the country (Fig. 1), although this distribution reflects the underlying distribution of species known to be imperiled in the taxa we sampled. Further, our sample does not include any extinct species. To the extent that the approximately 40 known recent extinctions in these groups in the U.S. may have occurred more often in the most heavily impaired waters, our sample does not provide information on ecological threats in these most impaired waters. Additionally, the distinction between stressor types and source categories, and the detailed breakdown of stressor types and source categories in our survey, allow us to discriminate more finely among the causes of species decline and poor species recovery than was possible in most previous studies.

Our results must be interpreted in light of their resting on expert opinions rather than on published reports. Expert opinions are colored by the experts' personal concerns and experience. We sought to overcome this difficulty by providing respondents with a checklist of stressors and sources from which to select their responses (Table 2), so that more locally specific threats would have to be considered as examples of more widely applicable categories of threats. We also sought to overcome this difficulty by focusing our respondents' attention separately on the two questions of which threats caused historic declines versus which are currently limiting recovery. We asked our respondents to provide citations for publications supporting their responses as a further check on the extent of their scientific support; 57 (64%) provided citation information for 83 species (61%). Finally, we solicited multiple biologists for their views on some individual species in order to examine the responses for consistency; unfortunately, the number of replicated responses was too small for useful analysis.

Turning finally to the management implications of our study, we must emphasize that our purpose is not to point fingers at specific industries or economic activities, but rather to direct attention toward opportunities for restoring populations of aquatic fauna. Federal and state environmental protection agencies have put considerable effort into reducing point-source discharges of pollution, and our results suggest that these efforts have significantly benefited aquatic biota. However, the apparent seriousness of the threat posed historically by point-source pollution, especially to taxa such as freshwater mussels, reminds us that any relaxation of point-source controls could cause significant biological harm. Chemical pollution remains a serious problem for more than 20% of the species examined.

The EPA and many state agencies also have expended considerable effort combating agricultural nonpoint discharges, with some notable successes such as the Chesapeake Bay (Pendleton 1995). "Best management practices" for controlling runoff from agricultural fields and timber harvest areas have been developed and implemented in many states and are increasingly being used in urban areas as well. Although these efforts largely arise out of concerns about water quality conditions in general, many imperiled aquatic species clearly benefit as well.

On the other hand, efforts to control exotic species generally have been limited to those species interfering with commercial fisheries and industrial activities, such as the sea lamprey (*Petromyzon marinus*) and zebra mussel. Unfortunately for native biota, non-native fishes are still widely introduced for sport fishing throughout the country, and the zebra mussel is but one among many introduced aquatic invertebrates (Coblentz 1990; U.S. Congress, Office of Technology Assessment 1993).

Efforts to restore hydrologic regimes affected by dams generally have been limited in scope to the provision of adequate flows for a single, or at most a few, fish species (Richter et al. 1996; Richter et al. 1997). In the U.S. the Federal Energy Regulatory Commission (FERC) has primary responsibility for determining appropriate instream flow regimes to be released from privately-owned hydropower facilities, which account for 2000 dams in the U.S. (Palmer 1994). With 366 dams coming up for FERC re-licensing by the year 2000 (Palmer 1994), an enormous opportunity exists to improve the flow conditions affecting aquatic biota. Impoundments are often constructed and operated for multiple purposes, including power generation, agricultural and municipal water supply, flood control, navigation control, and recreation. As a result, managing dam placement and operations to protect or restore freshwater biological diversity can address threats arising from several primary sources of harm at once.

Finally, differences in the threats reported for western versus eastern species indicate that no single ranking of threats can be used to guide conservation efforts in all localities. Eastern species are experiencing particular harm from altered sediment loads associated with agricultural nonpoint pollution, with exotic species, toxins, habitat alteration, and nutrient inputs also impacting many species. In the West exotic species are the dominant problem limiting the recovery of imperiled species. However, habitat degradation and altered hydrology due to agricultural surface water depletions and augmentations, and habitat destruction, degradation, and fragmentation and altered hydrology due to agricultural and hydropower impoundments are also limiting the recovery of many western species. Such findings emphasize that resource managers must always pay attention to the local histories and intensities of anthropogenic insults and to the ecology of locally imperiled species, as well as to the relationships of individual stressors with individual source types, in order to develop effective conservation strategies.

Overall, our results serve as a warning that conserving freshwater biological diversity requires actions both more widespread and more focused than previously have been attempted. Reducing point-source releases of toxic substances, organic matter, and nutrients, the core of our nation's water quality agenda for the past several decades, clearly has helped improve average surface water conditions. While reducing use of surface waters as intentional waste disposal sites, however, we have not adequately addressed impacts resulting from our use of these waters as resources for power generation, fisheries recreation, transportation, and supplying the consumptive needs of municipalities and irrigated crops, we have not addressed the effects of land use activities on watershed hydrology, sedimentation, and water chemistry. As the continuing declines in freshwater species indicate, and as the evidence from studies such as ours further highlights, we must work to clearly understand the impacts of our uses of both the land and freshwater resources in order to arrest the loss of our planet's freshwater aquatic heritage.

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