Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels

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Abstract

Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels.— Conservation of biodiversity requires reliable evidence of the causes of extirpation. Using freshwater mussels as an example, we performed the first–ever systematic assessment of the evidence for endangerment of any group of organisms. We surveyed articles publishing conclusions about the cause of local extirpation by assessing the quality of evidence on an objective scale. We found that only 48% of studies presented plausible links between extirpation and causes. Analyses lacked resolution since more than 75% of all studies considered (n = 124) suggested multiple causes of extirpation. Studies performed over large areas and those presenting less evidence postulated the most causes. Despite the frequently weak evidence, there was substantial agreement on the identity of causes; the most frequent was habitat destruction or alteration but many others were postulated. Although mussel extirpation is undoubtedly real, the evidence could be stronger. In these animals and others, evidence of the causes of extirpation has often been circumstantial. We present a systematic approach ecologists can use to strengthen the evidence concerning the causes of extirpation. We also reflect on the link between the strength of evidence and research funding priorities.

Key words: Evidence, Extinction, Extirpation, Freshwater, Mussels.

Resumen

Sospechas y evidencia: revisión de las causas de la extinción local y del declive de los mejillones de agua dulce.— La conservación de la biodiversidad requiere pruebas fiables de las causas de extinción local. Utilizando los mejillones de agua dulce como ejemplo, llevamos a cabo esta valoración sistemática, la primera que se ha realizado, de la evidencia de peligro para cualquier grupo de organismos. Revisamos artículos que publicaban conclusiones sobre las causas de las extinciones locales, evaluando la calidad de las pruebas según una escala objetiva. Encontramos que únicamente el 48% de los estudios presentaban relaciones plausibles entre la extinción local y sus causas. Los análisis carecían de resolución, dado que más del 75% de los estudios considerados (n = 124) sugerían múltiples causas de extinción local. Los estudios llevados a cabo en grandes áreas, y los que presentaban menos pruebas, son los que abogaban por un mayor número de causas. A pesar de las evidencias, que frecuentemente eran débiles, existía un acuerdo sustancial sobre la identidad de las causas; la más frecuente era la destrucción o alteración del hábitat, pero se postulaban muchas más. A pesar de que la extinción local de los mejillones de agua dulce es indudablemente una realidad, las pruebas podrían ser más consistentes. En estos animales y en muchos otros, la evidencia de las causas de su extinción local a menudo ha sido circunstancial. Presentamos aquí un estudio sistemático que pueden utilizar los ecólogos, para fortalecer las evidencias concernientes a las causas de las extinciones locales. También hemos reflejado la relación entre la fortaleza de la evidencia y las prioridades económicas de las investigaciones.

Palabras clave: Evidencia, Extinción, Extinción local, Agua dulce, Mejillones.

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Introduction

Declining biodiversity is a consequence of the accumulation of local extinction or extirpation events that can eventually extinguish the last remaining populations of species. The population extinction rate in tropical forest regions is 0.8% per year with 16 million populations lost per year (Hughes et al., 1997). In terrestrial mammals, 50% of historic ranges have been lost where human activity is intense, signaling a substantial threat to global species diversity (Ceballos & Ehrlich, 2002; Doherty et al., 2003). Biodiversity is also declining in aquatic ecosystems (Petts, 2001) due to population and species loss rates that are often higher than those seen in terrestrial ecosystems (Ricciardi & Rasmussen, 1999; Richter et al., 1997; Strayer et al., 2004).

Although widespread extirpation is known to occur, the causes of these events may be difficult to discern. In general terms, the decline and extirpation of populations has been attributed to a variety of broad mechanisms mediated by human population growth and impact (Kremen et al., 2002; Luck et al., 2003). Specifically, local loss of species is seen as a consequence of reduction in habitable area and environmental deterioration (Brinson & Malvarez, 2002), as well as the transformation and fragmentation of natural habitats (Wilcox & Murphy, 1985; Poole & Downing, 2004). Miller & Payne (2007) give an example of a species of mussel for which both the decline and cause of decline have apparently been misjudged.

In spite of the importance of understanding the causes of extirpation, the evidence supporting cause–effect relationships varies greatly in strength. Many judgments of its cause have been based on projections of potential harmful effects (Leuven & Poudevigne, 2002). The IUCN Redlist (www.redlist.org), one of the most valuable sources of data on lost biodiversity and its cause, is based on methods involving estimation, inference and projection, as well as temporal extrapolation of current or potential threats. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulates world trade in endangered organisms. The extensive evidence required by CITES (*e.g.*, Favre, 1989), to document an importer's contention that a species is not in "decline" or "threatened", underscores the difficulty of obtaining consistent evidence of the source of threats to species.

An essential step in slowing the global decline of biodiversity is to identify and discontinue its causes. Our principal goal therefore was to summarize the evidence used to discern the causes of decline and extirpation in a frequently studied group of organisms and the causative factors that this evidence supports. Freshwater mussels are among the most endangered faunal groups on the planet (Strayer et al., 2004); therefore we use them here as a case study of the processes used to analyze the causes of declining biodiversity. They are sensitive and vulnerable to many different sources of perturbation that lead to altered community composition (Strayer et al., 1996, 2004) and offer a rich literature for analysis because they have been declining for decades (Matteson & Dexter, 1966). They are decreasing precipitously in North America (Suloway, 1981) and are among the most seriously impacted aquatic animals worldwide (Williams et al., 1993; Bogan, 1993). The high rate of mussel extinction (1.2% per decade) (Ricciardi & Rasmussen, 1999) makes them an important, yet challenging, group for analyzing the causes of extirpation and decline.

Our objective was to summarize analyses publishing conclusions and interpretations of the causes of decline and extirpation. We aimed to determine the strength of evidence used by studies drawing conclusions about its causes, determine the most frequently hypothesized causes of it, and quantify the spatial and temporal evolution or ecology's view of this important problem. Further objectives were to use these analyses to focus on efficient means of collecting evidence about the causes of extirpation and discuss the accessibility of funding to support improved analyses of them.

Methods

Assessing the strength of the evidence

It is generally agreed that "cause" is difficult to determine in the natural sciences (Fox, 1991; Holland, 1991). The philosophical issues surrounding the determination of cause–effect relationships in the natural sciences is a debate we do not reopen here (*c.f.* Peters, 1991). Instead, what natural and social scientists do is collect evidence that either supports or refutes causal hypotheses. In many fields (*e.g.*, science, law, medicine, epidemiology), it is necessary to assemble imperfect evidence that supports or refutes one or more hypotheses concerning the causation of events (*e.g.*, crimes, diseases, epidemics, extirpation).

One of the earliest approaches to the collection of evidence concerning the association between a negative effect (disease) and a biological cause (vector) is embodied in Koch's Postulates (see Fox, 1991). These postulates formalized the need to show a correlation between a postulated cause and effect, then to follow the correlation analysis with experimentation that verifies the biological plausibility of the correlation.

Criminal and civil law in the United States (*e.g.*, Osterburg & Ward, 2004) and other nations (Delmas–Marty & Spencer, 2002) have used sets of evidentiary criteria. Legal scales of many nations admit the varying strength of admissible evidence by arranging criteria into categories of evidentiary plausibility. Criminal investigators around the world recognize levels of evidence ranging from hunches, guesses and gut feelings to corroborated facts, direct observations, physical evidence, and expert interpretation of evidence (*e.g.*, table 1). Contrary to popular belief, few criminal proceedings require "proof" but require the bulk of evidence to support the causal connection between a suspect and a crime.

Because we wished to evaluate the variable strength of evidence for judgments of causes ("suspects") of decline and extirpation, and because we

Table 1. Determination of levels of certainty and proof in United States criminal and civil law (Osterburg & Ward, 2004).

Tabla 1. Determinación de los niveles de certidumbre y pruebas de las leyes civiles y criminales de Estados Unidos (Osterburg & Ward, 2004).

Level of Proof	Evidence	Quantity	Uncertainty	Investigation	Legal use	Scientific utility
Intuition / speculation	Hunch, guess, gut feeling, impression, surmise	Articulable suspicion about possible facts but insufficient to be convincing	Considerable and apparent	Useful during early stages	None	Discovery and hypothesis formulation
Probable Cause	Facts a reasonable person would accept	*Prima facie*, presumptive but disputable facts	Better than apparently uncertain but possibly uncertain	Basis for arrest or search warrant	Basis for binding over to next stage	Basis for theory development through hypothesis testing
Preponderance of Evidence	Corroborated facts, eyewitness testimony, physical evidence, expert interpretation of evidence	Over 50% of facts in support	Some uncertainty permitted	Shows the investigation is on the right track. May be used to induce confessions or informants	Civil law standard of proof	Basis for theory development through continued testing of hypotheses
Clear and Convincing	Same as preceding ↑	>> 50% and almost as many supporting facts as below ↓	A little uncertainty may remain	Same as above ↑	International law standard of proof	Basis for theory development through continued testing of hypotheses
Beyond Reasonable Doubt	Same as preceding ↑	Sufficient facts to preclude all other competing hypotheses	Almost none	Basis for criminal conviction	Criminal law standard of proof	Theory

sought to decrease subjectivity as much as possible, we defined an evidentiary typology based loosely on the United States' legal model (table 2). Our typology was a clear scoring rubric that we felt would allow us to objectively assign evidentiary quality to individual studies. As in criminal investigations, we defined five levels of evidence. The five types of evidence are distinguished by (1) the degree of documentation of decline or extirpation (*i.e.*, "the crime"), (2) the weight of evidence offered for the presence of one or more potential causative agents before or during the decline (*i.e.*, "opportunity"), and (3) the preponderance of evidence of links between extirpation and causative agents (*i.e.*, "the evidence"; see table 2 for operational classification criteria).

The first two levels of evidence (table 2; levels 1 and 2) included literature reviews of postulated causes, either with or without direct observation of decline or local extinction events. In both of these, there was no documentation of either a causative agent or the link of a cause with extirpation. The third category, corresponding roughly to "circumstantial evidence", included studies that observed disappearances or declines of organisms correlated in time with the occurrence of postulated causes, but that offered little or no independent evidence of a link between them. Studies classified with level 4 evidence documented extirpation events or severe declines, observed potential causative agents, and made strong linkages between disappearances and

Table 2. Evidentiary typology used in the analysis of studies of decline and extirpation in freshwater mussels.

Tabla 2. Tipología de evidencias utilizada en el análisis de los estudios de declive y extinción local de los mejillones de agua dulce.

Quality level	Level of evidence	Documentation of extirpation or decline	Documentation of potential causative agent	Evidence of link between extirpation and causative agent
1	Speculation	No; cited or extrapolated from other studies	No; implied by literature review	No; implied from other studies
2	Observed effect but not cause	Yes	No; implied by literature review	No; implied from other studies
3	Concurrent cause/effect	Yes	Yes; observed at least one causal factor implicated by other studies	No; lacking direct linkage between extirpation event and postulated cause(s)
4	Preponderance of evidence	Yes	Yes	Yes; study gives strong evidence of links to some but not all potential causes; or weak links to some postulated causes
5	Clear and convincing	Yes	Yes	Yes; study gives strong evidence of links to all postulated causes

some, but not all, potential causes. The highest level of evidence (level 5) made plausible links between all postulated causes and extirpation events or severe declines. Some subjectivity is inevitable in the evaluation of the strength of evidence so we looked at each study carefully, used a reproducible checklist or scoring rubric of criteria (table 2), scored the articles independently among us (JAD, PVM, DAW), and document our judgments in appendix 1. Although we read the articles critically, we strove to be as fair as possible in our triple–blind assessments.

Information and data sources

We sought to capture information on the types of causes that have been most frequently cited in published research, the strength of evidence for the causes of extirpation, how the suggested causes of extirpation have changed over the last several decades, and the sources of funding used to support the collection of evidence. Therefore, we examined published papers drawing conclusions about the cause of mussel extinction or extirpation to establish current and past consensus. Generally, these publications included those that are currently used as evidence for the existence or causes of mussel extirpation (*e.g.*, Rypel et al., 2009; Jones & Byrne, 2009; Doyle & Yates, 2009; Schofield et al., 2004) and those that are currently cited in reviews of the topic (*e.g.*, McGoldrick et al., 2009; Hanlon et al., 2009; Vaughn et al., 2008; Hoftyzer et al., 2008; Bogan, 2008). Our search was not exhaustive but it was systematic. We searched electronic indexes of journal articles (*e.g.*, *Biosis Previews*) available in the Parks Library of Iowa State University (www.lib.iastate.edu/collections/db/indexabst_name.html) in 2004. Example search terms were "freshwater", "mussel", "decline", "extirpation", "reasons for decline", "unionidae", "causes of decline", "loss", and "biodiversity". Then, in order to fairly represent review articles as well as the primary studies from which they were created, we followed the trail of literature citations from the bibliographies of articles found in searches of electronic indexes to assemble a reference list that was as complete as practically possible. We included all publications that reported conclusions about one or more species of freshwater mussels. The publications we included thus likely contain both those cited as support for determining conservation status of species as well as those building general consensus about declines occurring in mussels, in general. Information about the number and types of postulated causes was taken from authors' narratives and all causes were

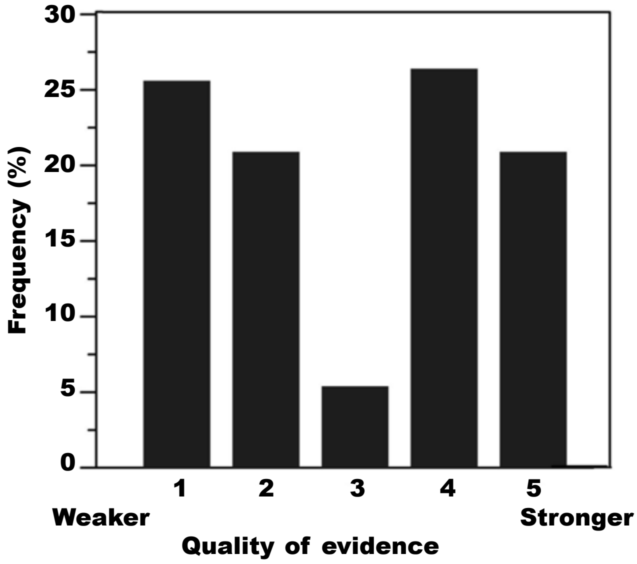

Fig. 1. Frequency histogram showing the strength of evidence presented by the recent scientific literature regarding the decline and extirpation of freshwater mussels. Quality categories of evidence are defined in table 2 and are based on a modification of the model used in United States criminal law.

Fig. 1. Histograma de frecuencias que muestra la fortaleza de las pruebas presentadas en la literatura científica reciente, en relación al declive y la extinción local de los mejillones de agua dulce. Las categorías de la calidad de las pruebas se definen en la tabla 2, y se basan en una modificación del modelo utilizado en la legislación criminal en Estados Unidos.

catalogued. Some of these causes overlap and many are not mutually exclusive but we had no choice but to accept the assessments provided by the authors of each of the studies. The quality of the evidence presented for connections between extirpation and potential causal factors was evaluated by multiple investigators following the scale presented in table 2. Since authors evaluated extirpation on many spatial scales, we quantified the approximate geographical scale by reference to the land area of political units indicated by the authors. Temporal trends in evidence were evaluated by correlation with publication dates of articles since actual years of extirpation were rarely clearly stated. Information on funding support for these studies was extracted from Acknowledgments sections of the articles. We summarized the sources of funding acknowledged by all 124 studies, counting each funding source with equal weighting.

We extracted information on the probable causes of mussel extirpation from 124 published articles (see the appendix). These articles reviewed extirpation for geographic areas ranging from single river drainages to water bodies throughout the world. Most of the studies concerned North America and Europe but some studies examined extirpation in South America. The earliest article reviewed was published in 1910 (Isely, 1910) and the median year of publication was 1995. A full list of the references and data is contained in the appendix.

Results

The strength of evidence

The published evidence diagnosing the causes of decline and extirpation varied from weak and speculative to strong and convincing. Many studies presented plausible evidence of links to all identified potential causes. Less than 50% of the studies presented any evidence of linkages between postulated causes and mussel disappearance events (fig. 1). The distribution of the quality data appear somewhat bimodal.

The evidentiary record appeared equally strong across the years of publication (fig. 2). There was no discernible correlation between our assessments of the quality of evidence and the publication year of articles on mussel extinction ($p > 0.05$).

Possible causes of extirpation in mussels

The articles we reviewed considered seventeen different factors postulated as causes of extirpation in freshwater mussels, and figure 3 offers a qualitative view of these changes. Some of these causes are not fully independent but we were bound to report the factors indicated by the authors of articles. The earliest studies cited physical and biotic changes in the environment. Water pollution, hydrologic change, and the destruction of habitat they caused were suspected in the early

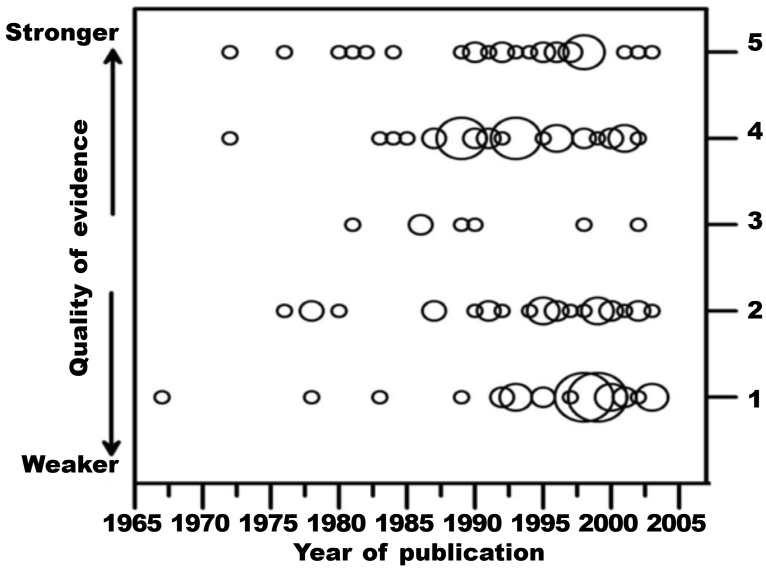

Fig. 2. Temporal progression of the strength of evidence presented by the ecological literature regarding the causes of decline and extirpation of freshwater mussels. Not shown are data from Isley (1910) that were judged to be of quality level 3. Quality categories of evidence are defined in table 2. The sizes of the "bubbles" are proportional to the number of studies that fall on the same point. The largest corresponds to n = 5.

Fig. 2. Progresión temporal de la fortaleza de las purebas presentadas en la literatura ecológica, concerniente a las causas del declive y la extinción local de los mejillones de agua dulce. No se muestran los datos de Isley (1910), que se juzgó eran de un nivel de calidad de 3. Las categorías de la calidad de la evidencia se definen en la tabla 2. El tamaño de las "burbujas" es proporcional al número de estudios que caen en el mismo punto. El de mayor tamaño corresponde a n = 5.

1900s and were frequently cited during the 1960s and 1970s. Water pollution and water quality degradation included eutrophication, silt transport, acidification, organic and metallic pollution, and feminization by estrogenic pollutants. Hydrologic changes influencing mussel extirpation included alterations of flow regimes, diversion to irrigation, increased flashiness and low water from drainage projects, channelization, greater extremes in velocity, alterations of depth profiles, and water level fluctuation in lacustrine environments. Habitat destruction and alteration occurred through siltation, dredging, destruction of specific habitat types (*e.g.*, riffles destroyed through impoundment), and reduction in oxygenated habitat. Also among the earliest cited causes of extirpation were increased predation by fish and mammals and alterations to benthic communities through habitat degradation.

By the 1990s, other population and community influences (*e.g.*, recruitment failure due to rare host fish, competition from exotics), large–scale environmental changes (*e.g.*, climate change, dams, impoundments, riparian destruction, agriculturalization of watersheds), and direct exploitation by humans were frequently cited causes of extirpation. This accumulation of ideas, causes, and technologies, over time, has complicated potential interpretations. Following advances in conservation biology and genetic methodologies, the causes suggested most recently implicate the small population phenomenon, restricted range limitations and genetic changes (fig. 3).

Quality evidence helps to focus on specific causes. When considering the strongest evidence, habitat alterations are among the most highly cited causes of mussel decline (fig. 4). Mussels are nearly sessile organisms that require good water quality and stable substrata. This is why water pollution, water quality degradation, and habitat destruction were each implicated by > 20% of the studies employing the strongest evidence. This same sensitivity to habitat is indicated by the relative importance of dams and impoundments and associated hydrologic change as causes of local extinction. Native freshwater mussels use a specific intermediate host fish to carry their larvae so many of the studies indicated that failed recruitment and lack of appropriate host fish caused decline. Causes that require a high degree of technical analysis to discern were among the least frequently cited. This may be simply because these methods are less easily employed rather than the relative importance of the causes these methods can discern.

The dominance of habitat loss in the decline of mussel populations is clear (see also, Strayer et

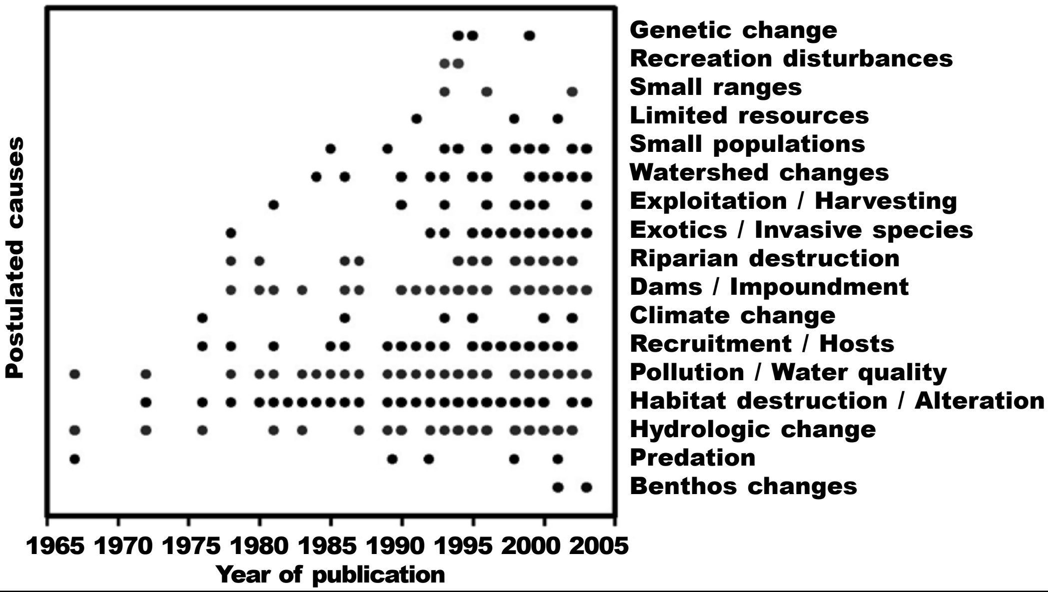

Fig. 3. Temporal progression of detailed causes postulated for the local disappearance or decline of mussel populations. Not shown are the data of Isley (1910) who indicated that mussel disappearances were due to changes in the benthic community, predation, changes in stream hydrology, habitat destruction, and water pollution.

Fig. 3. Progresión temporal de las causas detalladas que se han postulado para la desaparición local o el declive de las poblaciones de mejillones. No se muestran los datos de Isley (1910), que indicaba que las desapariciones de los mejillones se debían a cambios en la comunidad bentónica, a la depredación, a los cambios hidrológicos del caudal, a la destrucción del hábitat y a la contaminación del agua.

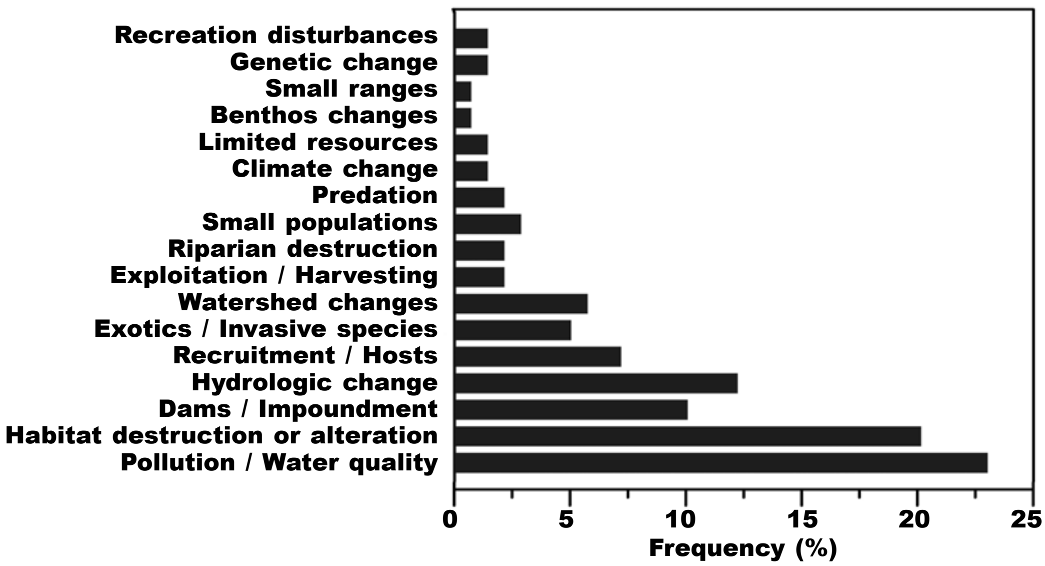

Fig. 4. Frequency histograms grouping the seventeen major causes of the decline and extirpation of mussels, showing only the results of studies for the two highest categories of evidence (see table 2).

Fig. 4. Histogramas de frecuencia agrupando las diecisiete causas principales de declive y extinción local de los mejillones, mostrando sólo los resultados de los estudios de las dos categorías de evidencia más altas (véase tabla 2).

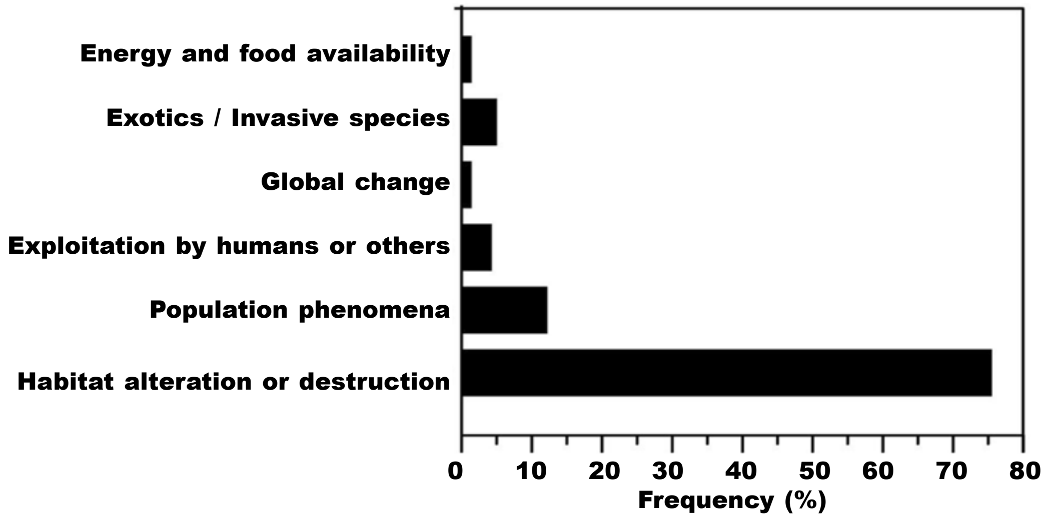

Fig. 5. Frequency of broad categories of postulated causes indicated by studies offering the two strongest categories of evidence. Broad categories group individual factors shown in figures 3 and 4. "Habitat alteration and destruction" here includes all forms of habitat change (*e.g.*, pollution, damming, hydrologic change, watershed change, riparian destruction, recreational disturbance). Population phenomena include recruitment, host availability, small population effects, genetic change, and small ranges; exploitation here includes human and other sources of predation; energy and food availability includes resource limitation and benthos changes.

*Fig. 5. Frecuencia de las grandes categorías de causas postuladas, indicadas por los estudios que ofrecen las dos categorías de mayor robustez de la evidencia. Las grandes categorías agrupan los factores individuales que se muestran en las figuras 3 y 4. Aquí, el término "alteración y destrucción del hábitat" incluye todas las formas de cambio del hábitat (*p.ej. *contaminación, construcción de presas, cambios hidrológicos, cambios en la cuenca, destrucción de las riberas, perturbaciones debidas a actividades recreativas). Los fenómenos poblacionales incluyen: reclutamiento, capacidad de los huéspedes, efectos de las poblaciones pequeñas, cambio genético y extensiones pequeñas. La explotación incluye la depredación humana o de otro tipo, y la disponibilidad de alimentos y energía incluye la limitación de los recursos y los cambios bentónicos.*

al., 2004). Considering only the studies offering the two strongest categories of evidence, > 75% of the analyses implicated habitat alteration or destruction in the loss of mussels (fig. 5). No other broad category of cause is so obvious to ecologists and no other was suggested by > 15% of studies. There is some danger of tautology in these conclusions, however, because the loss of organisms implies that there is no longer a suitable place for them to live.

One cause or many?

More than 75% of the analyses of extirpation cited more than one likely cause. There were three main reasons for this: (1) studies presenting weaker evidence had resolving power low enough that they could not distinguish among putative causal agents; (2) single extirpation events resulted from multiple causal factors working in concert; and (3) extirpation events across a large or heterogeneous geographical area may sometimes be postulated to be caused by a list of single causal factors.

The increased resolving power of stronger evidence is illustrated by figure 6. Studies involving the two lowest quality categories of evidence suggested an average of more than three causes per study. Studies drawing connections between most or all potential causal agents and observed extinction events (table 2; quality levels 4 and 5) suggested an average 2.7 and 1.7 causes, respectively. Our analysis suggests that the use of refined methods can cut the number of postulated causes of extirpation by nearly half, suggesting that rigorous methodologies could bring more clarity to the search for causes of declining biodiversity. A cluster analysis on the co–occurrence of postulated causes (not presented here) suggested that some causes showed a greater than random likelihood of co–occurrence while others were less strongly associated.

More recent analyses seem to advance an increasing number of potential causes (fig. 7). Studies in the 1960s and 1970s indicated between 1 and 3 potential causes for extirpation events. Studies published in the 1990s and 2000s advanced between 1 and 9 causes for local mussel extinction. This temporal prolifera-

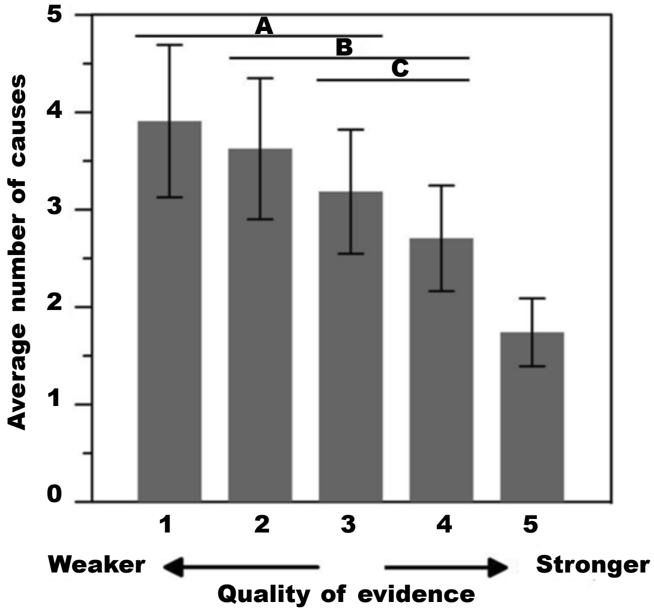

Fig. 6. Average number of causes indicated by studies of decline and extirpation of freshwater mussels calculated for categories of the strength of evidence. Error bars indicate ± 1 standard deviation. Quality categories of evidence are defined in table 2. Differences between the categories of evidence–strength were determined using single factor analysis of variance (Zar, 1996). Significant differences were found between the following groups: 1,5 and 2,5 ($p < 0.0001$); 1,4 ($p = 0.009$); 3,5 ($p = 0.002$); 4,5 ($p = 0.014$). Treatments with similar results are shown by bars bridging across categories.

Fig. 6. Número promedio de las causas, indicado por los estudios del declive y la extinción local de los mejillones de agua dulce, calculado para las categorías de la fortaleza de la evidencia. Las barras de error indican una desviación estándar de ± 1. Las categorías de la calidad de la evidencia se han definido en la tabla 2. Las diferencias entre las categorías de fortaleza de la evidencia se determinaron mediante un análisis factorial simple de la varianza (Zar, 1996). Se hallaron diferencias significativas entre los siguientes grupos: 1.5 y 2.5 (p < 0,0001); 1.4 (p = 0,009); 3.5 (p = 0,002); 4.5 (p = 0,014). Los tratamientos con resultados similares se indican mediante barras que forman puentes entre las categorías.

tion of suggested causes is due both to increased awareness of potential causes within the scientific community and increased technical knowledge and techniques for determining causal connections. Examples of the former concept might be repeated citation of seminal publications and analyses or the fact that earlier studies did not have access to as many datasets and analyses as the latter ones. Examples of the latter phenomenon might be improved inferential abilities resulting from increased access to molecular methods, genetic analyses, GIS methods and data, and accumulating survey data. The data suggest, however, that recent publications do not always pin–point specific causes of mussel decline.

The spatial scale of analysis also influences the number of potential causes of extirpation (fig. 8). Inferences drawn for areas of < 40,000 km^2 (*i.e.*, a moderately sized US state, small Canadian province, or EU nation) usually advanced only one or two causes, while reviews for very large areas (*e.g.*, large countries, or continents) indicated many causal factors. Therefore, when spatial and technical resolution is high, the number of potential causes was determined with greater precision and may be reduced to one or two suspects.

Strong consensus

Despite the range of strength of evidence employed, ecologists have come to a striking consensus about the causes of decline and extirpation in freshwater mussels. More than 75% of the articles presenting strong evidence indicated that some form of habitat alteration or destruction has led to the local extinction of populations (fig. 5). Specific impacts have derived from pollution and water quality degradation, perturbation of specific habitat types, impoundment and damming, hydrological alteration of flow regime, watershed and riparian perturbation, and disturbance by human recreation. Although such factors as exotic and invasive species, direct exploitation, and global change have captured the public interest, habitat de-

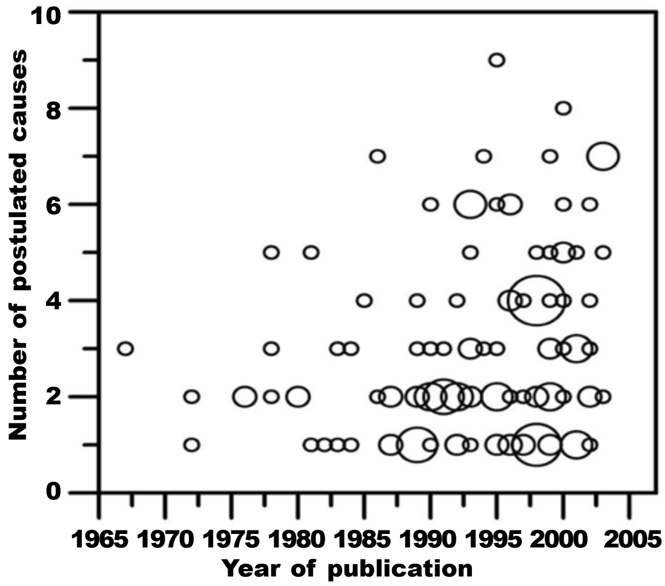

Fig. 7. Relationship between the number of causes implicated by studies of decline and extirpation of mussels and the publication year of manuscripts. The sizes of the "bubbles" are proportional to the number of studies that fall on the same point. The largest corresponds to n = 6. The data show a positive relationship between publication year and number of causes indicated by authors (r = 0.22, n = 124, p = 0.01).

*Fig. 7. Relación entre el número de causas implicadas en los estudios del declive y la extinción local de los mejillones, con el año de publicación de los artículos originales. Los tamaños de las "burbujas" son proporcionales al número de estudios correspondientes a cada punto. La mayor corresponde a n = 6. Los datos demuestran una relación positiva entre el año de publicación y el número de causas indicadas por los autores (*r *= 0,22,* n *= 124,* p *= 0,01).*

struction is overwhelmingly implicated by the scientific literature. This consensus represents the published conclusions of 124 publications and the opinions of more than 200 aquatic scientists. The overall prescription from this analysis is that watershed and habitat restoration is a prerequisite to restoring populations.

Variable funding sources

More than 43% of these studies acknowledged no funding source for their research. The two most common funding sources were federal and state/provincial agencies (fig. 9). The third most frequently acknowledged source was the home institution of the investigators, including universities, departments, programs, research centers, museums, and state–federal fish and wildlife research organizations. Major funding panels were a distant fourth place in supporting extirpation research.

Discussion

A stronger record of evidence is needed

In the mussel literature, < 50% of the published articles met the two strongest scientific standards of evidentiary inference. All but the two best categories in table 2 lacked the fundamental characteristic that the majority of supporting facts (*i.e.*, evidence of a plausible link between disappearance and causative agent; table 2) agree with the hypothesized cause of extinction. This may be partially because many of the articles publishing interpretations of the causes of mussel extirpation and decline were performed for other purposes and partially because conclusions were drawn without presenting conclusive evidence. Only 48% of the articles publishing interpretations and conclusions about the subject, however, shed new light on the problem. The bimodal distribution of quality data (fig. 1) may derive from the criterion in quality level 3 of concurrent observation of cause and effect –this is difficult for long–lived organisms such as freshwater mussels.

Further, because local species extirpations may be increasingly scrutinized by scientists and legal entities, it is desirable that analyses come as close as possible to both scientific and legal plausibility. Our evidentiary typology parallels levels of certainty and proof sought by legal courts (*c.f.*, tables 1 and 2) (Delmas–Marty & Spencer, 2002; Osterburg & Ward, 2004). According to Osterburg & Ward (2004), only the two strongest categories

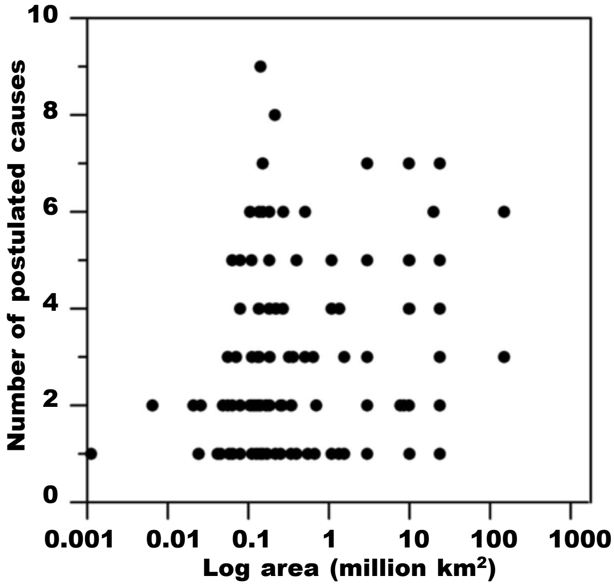

Fig. 8. Relationship between the number of causes implicated by studies of decline and extirpation of freshwater mussels and the geographical area for which inferences were made. Geographical areas were derived from standard sources of data on world political units.

Fig. 8. Relación entre el número de causas implicadas en los estudios del declive y extinción local de los mejillones de agua dulce y área geográfica para la cual se hicieron las deducciones. Las áreas geográficas se tomaron de las bases de datos estándar de las unidades políticas mundiales.

in figure 1 would have evidentiary characteristics similar to legally persuasive evidence. Less than half of the published articles drawing conclusions about the causes of local extinction would, in themselves, contribute strong linkages of cause and effect. The overall conclusion about the role of habitat destruction in extirpation is likely to be robust, but the conclusions and interpretations deriving from individual publications may be controversial without presentation of stronger evidence.

The frequent weakness of evidence of the causes of extirpation is a problem that is not unique to freshwater mussels but extends to many other groups of organisms. For example, studies stemming from the concern that amphibian populations are declining globally has been termed "anecdotal" (Houlahan et al., 2000), permitting little consensus about the causes of postulated extirpations (Blaustein et al., 1994). Declining biodiversity in the marine benthos is projected to have large impacts on the function of marine ecosystems but evidence concerning causative agents is poorly developed (Solan et al., 2004). Evidence about the factors causing the decline and extirpation of bat species has been called "speculative and unsubstantiated" (O'Donnell, 2000). Determining the cause of extinction in some organisms has been so elusive that some have expressed surprise at the disappearance of endangered organisms from pristine environments (Shuey, 1997) and others have suggested the impossibility of ascribing the cause of extirpation in small populations (Ginsberg et al., 1995).

The problem and challenge of multiple concurrent causes

Multiple concurrent causes of extirpation may complicate determination of the ultimate reason for decline. We found the three most frequently co–occurring causes of extirpation to be water quality degradation, habitat destruction and hydrologic change. These are linked because hydrologic change can degrade both water quality and habitat, and poor water quality can arise from landscape changes that alter hydrology and destroy specific habitats. Other suggested causes co–occurred. These were: (1) damming and hydrologic change; (2) increased pollution through watershed alteration; (3) habitat destruction mediated by watershed development; (4) decreased host fish for larvae through stream impoundment; (5) hydrologic alteration and riparian zone reduction due to watershed change; (6) hydrologic alteration, pollution, damming and habitat alteration; and (7) the loss of host fish through multiple impacts of watershed alteration.

The influence of some causes of extirpation may be amplified in the presence of others. For example, cluster analyses of co–occurrence of causes in the articles we canvassed (not presented here) indicated

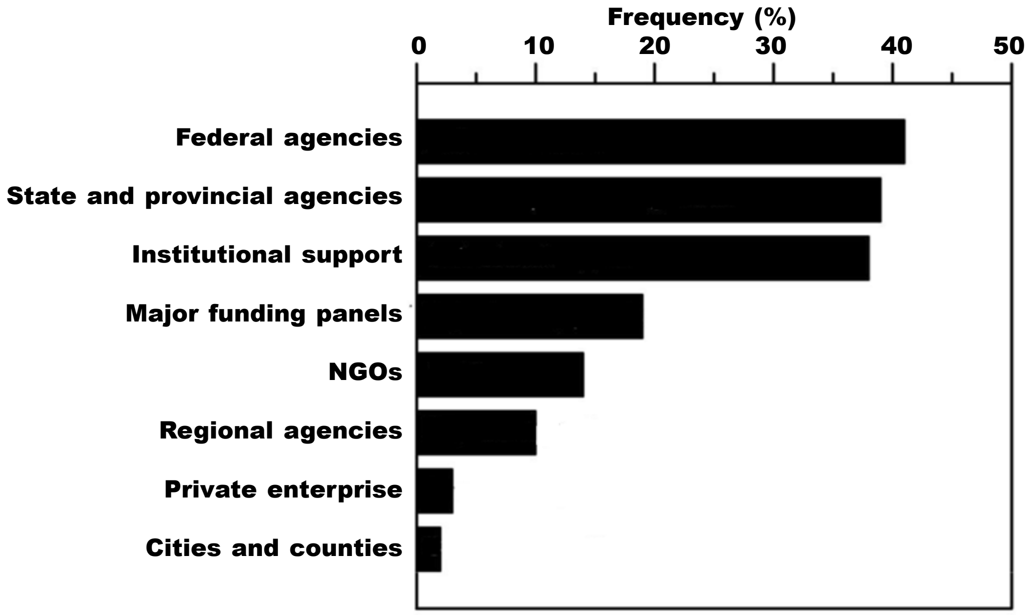

Fig. 9. Frequencies of funding sources acknowledged by the authors of the 124 published articles reviewed in this manuscript. Fifty–six of these publications listed no funding sources. For those acknowledging funding, we counted every one, attributing each to the categories shown in the figure. Federal agencies include offices of the federal government whose principal role is not funding research but managing resources. State and provincial agencies are the equivalent organizations representing state or provincial political units. Institutional support indicates that funding was received from the institution employing the authors, unless this is an agency listed under one of the other categories. Major funding panels are those federal agencies whose principal role is to dispense research funding (*e.g.*, US National Science Foundation, Natural Sciences and Engineering Research Council of Canada). NGOs signifies non–governmental organizations.

*Fig. 9. Frecuencias de las financiaciones agradecidas por los autores, en los 124 artículos revisados en este estudio. Cincuenta y seis de dichos artículos no incluían el origen de sus recursos monetarios. En los casos en que se agradecían las aportaciones de fondos, contamos cada una de ellas, atribuyendo cada artículo a las categorías que se presentan en esta figura. Las agencias federales incluyen oficinas del gobierno federal, cuya función principal no es financiar la investigación, sino la gestión de los recursos. Las agencias estatales y provinciales son las organizaciones equivalentes, que representan a los estados o las unidades políticas provinciales. Financiación institucional indica que los fondos se recibieron de instituciones que empleaban a los autores, a menos que se tratara de una agencia que entrase en una de las demás categorías. Los mayores financiadores eran aquellas agencias federales, cuyo papel principal es dispensar fondos para la investigación (*p.ej. *National Science Foundation de Estados Unidos, y Natural Sciences and Engineering Research Council de Canadá). NGOs significa organizaciones no gubernamentales (ONGs).*

that water pollution may be most frequently indicated in analyses of mussel communities that may have been weakened through impoundment or hydrologic variation. Likewise, exploitation was indicated as frequently problematic in studies of communities that were weakened by damming, water quality degradation, or hydrologic change.

Concurrent, multiple causes of extirpation are common in many environments and organisms. Extirpation and decline have been postulated to result from multiple causes in organisms as diverse as birds (Doherty et al., 2003; Jarvi et al., 2004; Goerck, 1997; Van–Noorden, 1997; Legendre et al., 1999), mammals (Lunney et al., 2002), fish (Marschall & Crowder, 1996; Yoshiyama et al., 1998), terrestrial snails (Forys et al., 2001), marine foraminifera (Keller, 1986, 1988), amphibians (Carey, 1993), and human populations (Chakrabarty & Rao, 1988). Multiple causes of extirpation have been so pervasive that paleobiologists suggest their complexities may have been mistaken for chance extinctions (Eble, 1999).

Implications for mussel conservation and restoration biology

It is vital to provide quality evidence linking specific causes with extirpation events. In the case of freshwater mussels, many species have been extirpated without high quality evidence documenting their decline (*e.g.*, *Epioblasma* spp.). Specific linkages need to be defined in order to better understand the process of extinction. Collecting quantitative data on potential parameters causing decline while documenting patterns of community distributions will go far in the defense of the persistence of freshwater mussels. Conservation ecologists are now forecasting major declines in biodiversity far into the future and most projections derive from mechanistic models of the process of the extinction and evolution of species. These projections will be inaccurate if salient mechanisms leading to extirpation have been misjudged or unmeasured.

Further, conservation and restoration require knowledge of pathways through which extirpation has occurred. If mechanisms could be better understood, management could target remediation of causative factors to prevent further extinctions, augment populations, and restore extant species that are currently on an extinction trajectory. Finally, science must offer organized, systematic, convincing arguments of scientific, social, and legal value. For example, new regulations are most readily enacted on the basis of compelling evidence (*e.g.*, Environment Canada, 2009). Science can promote conservation by defining consistent standards and approaches allowing the reliable interpretation of data. Both the scientific understanding of mussel extirpation and social mechanisms for slowing it require high quality evidence.

Systematizing the collection of causal evidence

The ideal field process for determining the association between an effect (disease) and a cause (vector or agent) has been summarized for epidemiology in Bradford–Hill's (Bradford–Hill, 1965) criteria. These criteria (Holland, 1991) need to be modified (Strayer et al., 2004) to address the association between species or population declines and causal agents. Satisfaction of the following criteria could be adopted in extirpation studies.

Demonstrate that an extirpation or decline even has occurred

This can be difficult because populations can become functionally extinct long before they disappear. For example, populations that fall below the minimum viable population (MVP) size (Reed et al., 2003) or density (Silva & Downing, 1994) may constitute effective extirpation. On the other hand, even the apparent absence of a species in a given locality is dependent upon sampling effort (Strayer, 1999).

Identify putative causes that are plausible, coherent, and have analogues

Once extirpation has been documented, an essential step is to assemble a list of potential causes. Such a list is required by CITES listing and the endangered species recovery plans of several nations (*e.g.*, Environment Canada, 2009, CITES, 2007, United States Fish and Wildlife Service, 1973). The biology of the organism or the causes advanced through analogy with similar extirpation events (*e.g.*, figs. 3, 4) and known or well–studied cases of extirpation can suggest suspects. These criteria ensure that hypothesized causes agree with *a priori* ecological or biological knowledge. Coherence with an organism's biology and past experience in other systems will provide a logical and biologically consistent explanation.

Establish the temporality of cause and effect

The list of plausible suspected causes can be narrowed by finding those that preceded the observed decline. In practice, establishing temporality can be difficult since little historical data may be available on changes in environments or species populations, biological causes such as lack of host fish may be difficult to discern (*e.g.*, Payne & Miller, 1989), diverse life–stages may react differently to environmental alterations (Cope et al., 2009), and different agencies may be locally responsible for monitoring environment and biology. Extirpation may also be difficult to correlate with environmental change since extinction debts (Tilman et al., 1994) and very long life–spans (Anthony et al., 2001) can cause extirpation to lag decades after environmental change (Poole & Downing, 2004).

Demonstrate the strength, consistency, and specificity of associations

The list of plausible, coherent and temporally consistent causes can be narrowed by finding those with the strongest (*e.g.*, most significant) association with extirpation. It should be borne in mind that this association may be linear or non–linear. Consistency concerns the generality of the association between cause and effect across distinct populations. Specificity of association requires that a given cause yields a specific effect. Specificity and consistency may be most useful in diagnosing declining populations since characteristics of the decline (*e.g.*, population structure, altered growth, impediments to reproduction) may point to specific causes.

Identify gradients of causes and effects

Gradients of causative agents associated with rates of decline (*e.g.*, dose–response analyses) can provide evidence of causal links. If rates of decline of populations or regional frequencies of extirpation are correlated with the intensity of exposure to environmental change, this can provide strong evidence of causal associations when viewed within the context of strength of association and biological plausibility.

Use experiment to demonstrate linkage of causes with effects

Natural or experimental manipulation of exposure to potential causative agents can be useful when seeking the cause of extirpation in wild populations. "Natural experiments", where manipulation has been done by accident or unwittingly, can be analyzed (*e.g.*, Smith et al., 1993) to provide tests of plausibility. Another approach is to use preventive actions to see whether removal of plausible causal factors leads to reversal or stabilization of declines.

This systematic approach to studying the link between postulated cause and effect has been successful in epidemiology for decades. It is our opinion that applying elements of this approach would strengthen knowledge of the causes of extirpation.

Funding: one possible reason that strong evidence for cause–extirpation linkage is rare

Systematic analysis of species declines and extirpation is costly and requires long–term funding commitments; this need is exacerbated by mussels' long life–spans, their parasitic reproductive habit, and their frequent low abundance. Our survey suggests that the paucity of targeted funding may contribute to weak inference. Although all of the studies we analyzed drew conclusions and made interpretations about the causes of extirpation, investigation of the cause of extirpation was not the only question under study in many of the cases we reviewed. From the breadth of topics analyzed in these publications, it appeared to us that the collection of evidence on the causes of extirpation was frequently a by–product of a study that may have been funded for other purposes. We feel that reliable analyses of the causes of extirpation are too fundamental to rely upon chance or serendipitous investigations to reveal interpretable evidence. Therefore, we cataloged funding sources to understand how analyses of the causes of extirpation are supported.

We summarized the sources of funding acknowledged by all 124 studies, counting each funding source mentioned with equal weighting. More than 43% of these studies acknowledged no funding source for their research. The apparent lack of research support for so many studies is of concern to the conservation of these imperiled organisms. In fact, Strayer (2006) has noted that funding of such initiatives has been so scarce that median expenditure in 2003–2004 in the United States for endangered freshwater invertebrates was only $24,000 (US), and few invertebrates receive even this modest attention. The two most common funding sources acknowledged by the studies we reviewed were federal and state/provincial/regional agencies (fig. 9). Most of these were governmental organizations charged with the management or protection of resources (*e.g.*, Environment Canada, US Environmental Protection Agency, US Fish and Wildlife Service, US Geological Survey). Major funding panels were a distant fourth place in supporting extinction research. The two most frequently cited such funding agencies, the Natural Sciences and Engineering Research Council of Canada and the United States National Science Foundation, funded about the same number of studies. The quality assessment of evidence presented in studies funded by major funding agencies averaged 2.47, ranging from 1–5. This is slightly better than the average of all studies (see fig. 1). NGOs (*e.g.*, Nature Conservancy, National Geographic Society, World Wildlife Fund, and various shell clubs) were nearly as frequently acknowledged as major funding agencies. Apparently, the testing of hypotheses about the sources of extirpation are infrequently funded by major agencies, while much of this research has been supported by funding sources oriented toward the management of natural resources.

Conclusion

The global decline in biodiversity is an important threat to ecosystem function and ecosystem services. Global extinction and lost biodiversity occur through the accumulation of local extirpation events, so the collection of evidence about the causes of extirpation is an important goal. Freshwater mussels have been declining for decades, are among the most endangered animal groups on the planet, and have been frequently studied, yet our understanding of the causes of extirpation is varied in resolution. Extirpation results from a diversity of multiple, interacting factors that are difficult to analyze and require substantial analytical power to resolve. Other fields have developed systematic methods for the accumulation of credible evidence of relationships between environmental causes and effects, but literature on this group of organisms suggests that we sometimes rely upon serendipitous studies with low evidentiary power. This problem appears compounded by a funding environment where such studies are done without focused programs contributing substantial, long–term support. We feel that the need for strong evidence about the causes of extirpation is so great, and the field of suspects so large, that a positive step would be to realign funding priorities to encourage the collection of more systematic, conclusive evidence about the suspected causes of decline and extirpation of species.

Finding the means of achieving this is an essential yet controversial topic worthy of more discussion than we could present here. A few reviewers have been concerned, for example, that this critical review will do "…more harm than good…." because it may draw attention to the frailties of some studies. They consider it could therefore be interpreted by governments and anti–conservation groups as falsifying the imperiled status of mussels, in specific, or biodiversity, in general. This would be an inaccurate interpretation of our findings. The evidence of endangerment and extirpation of mussels and other organisms is undeniable and strong in many cases. Our intention has been to examine the quality of evidence cited to support this knowledge to seek more systematic means of marshalling the evidence behind suspected and known cases of extirpation. Further, a few reviewers have been concerned that our judgment of the quality of studies may be subjective and based only on the published evidence. We believe that no one can make a fully objective judgment of all evidence but this is why we created an objective scoring rubric (table 2) to systematize our examination of published accounts, and why we performed the analyses in a triple–blind fashion. Our careful reading may have missed some salient points, but these errors are unlikely to reverse our overall conclusion that improvements can be made. The need for improvement is underscored by the continued reliance of new publications on some of the articles we found to present weak evidence (*e.g.*, Rypel et al., 2009; Jones & Byrne, 2009; Doyle & Yates, 2009; Schofield et al., 2004). It might also be suggested that we should expect low quality evidence of the causes of extirpation when articles draw conclusions about the causes but had diverse research objectives. The paucity of studies having a principal objective of determining the causes of extirpation is underscored by the number of recent publications citing the publications we reviewed here as demonstrations of the causes of extirpation (*e.g.*, Bogan, 2008; Hanlon et al., 2009; Hoftyzer et al., 2008; McGoldrick et al., 2009; Vaughn et al., 2008). The intention of this analysis was to seek means to increase scientific rigor, not to refute the known imperiled situation of mussels, or the utility of the science or publications attempting to determine and document its causes.

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Appendix. Table of evidence used in this manuscript: Q. Quality of evidence; N. Number of causes; * References indicated in these notes refer to citations in original "Reference" indicated inmediately preceding the Q and N data for each assessment.

*Apéndice. Índice de pruebas utilizado en este artículo: Q. Calidad de la evidencia; N. Número de causas; * Las referencias indicadas en este apartado de notas se refieren a las citas que se incluyen inmediatamente antes de Q y N para cada evaluación.*

Reference			Location
Q	N	Notes*	
Aldridge, 1987			Mississippi, USA
4	1	A link was established between the physiological energetics of freshwater mussels and frequent exposure to turbidity and high levels of suspended solids.	
Altaba, 1990			Spain
4	6	Extirpation of *Margaritifera auricularia* was observed and the cause linked was dredging. Several other causes were discussed but no clear links with these were established.	
Anderson et al., 1991			Kentucky, USA
2	2	A decline of freshwater mussels was observed, but no linkages were established with causes. Circumstantial information implies that strip mining might be associated with the decline. Other cited but unestabllished causes include the introduced *Corbicula* (Clarke, 1988), heavy siltation (Ahlstedt, pers. comm.; Schuster, pers. comm.), toxic metals (Dick et al., 1986), and physical disturbances.	
Arter, 1989			Switzerland
4	1	"In the highly eutrophic lake, the mussels grew more quickly and died earlier than in the mesotrophic lake." (p. 97, paragraph 3). Linkage was correlative.	
Bailey & Green, 1989			Northwest territories, Canada
3	4	Low densities of adults co-occurred with lack of juvenile, mussels. Anthropogenic impact is indicated as a cause (Green, 1980) but limitations to the hypothesis are discussed.	
Balfour & Smock, 1995			Virginia, USA
2	2	"…no physical, chemical, or hydrologic factors examined were significantly correlated with mussel abundance" (p. 255, abstract; p. 365, paragraph 1). The short life span is also thought to be caused shell erosion (p. 264, paragraph 2) but no evidence off this is offered.	
Bauer et al., 1991			Germany
4	3	The causes linked to mussel distribution and densities include food availability and hydrochemical factors. Not all suggested causes were linked with solid evidence.	
Beasley & Roberts, 1999			Ireland
1	3	Historical records and data collected were used in this study. No specific links were established. Linkages are cited from other published articles.	
Belanger, 1991			Louisiana, USA
5	2	Decline (p.118, paragraph 4) and mortality (p. 119, paragraph 2) of freshwater mussels was observed. Dissolved oxygen levels were linked as the cause (p. 122, paragraph 2) (p. 123, paragraph 2) and toxicity from STP effluents (p. 123, paragraph 3), total NH_3–N and chronic toxicity (p. 124, paragraph 1) (p. 124-125, paragraph 5).	
Bergman et al., 2000			Kansas, USA
2	8	Archeological records, historical reports, and information from recent surveys (collected in this study) were used. No link to a cause or causes is established. Causes cited from other articles are discussed.	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Blalock & Sickel, 1996			Kentucky, USA
2	6	A decline was observed (abstract) and authors discuss impoundment as a possible cause (citing several other published articles).	
Blalock et al., 2002			Alabama, USA
1	6	Other literature was reviewed and causes cited from other articles were discussed. No direct evidence for causes of decline was presented.	
Bogan, 1993			Worldwide
1	6	A review of mussel abundance and causes for decline and/or literature review extirpation is presented. No direct evidence for causes of decline was provided.	
Bogan, 1998			North America
1	5	No extinction or decline event was observed. Causes for decline were cited from other articles and discussed.	
Bowen et al., 1994			Alabama, USA
2	3	Harvesting was used to survey mussels but no linkage to cited causes from other articles was made.	
Box & Mossa, 1999			North America
1	4	A review of current information on the effects of sediments on unionid mussels, past sampling methods, and research needs is presented.	
Butler, 2003b			Mississippi River, USA
1	7	Status assessment of spectaclecase. Threats include habitat alteration, degradation or loss through impoundments, channelization, chemicals, sedimentation, mining activities. Although many potential causes are cited, no explicit linkage to specific causes was made.	
Butler, 2003c			Mississippi River, USA
1	7	Status assessment of the rayed bean mussel. Threats include habitat alteration, degradation or loss through impoundments, channelization, chemicals, sedimentation, mining activities. Although many potential causes are cited, no explicit linkage to specific causes was made.	
Butler, 2003a			Mississippi River, USA
1	7	Status assessment of the sheepnose mussel. Threats include habitat alteration, degradation or loss through impoundments, channelization, chemicals, sedimentation, mining activities. Although many potential causes are cited, no explicit linkage to specific causes was made.	
Byrne, 1998			Australia
4	2	The reproduction of *Hyridella depressais* studied. Gametogenic or embryonic failure was not linked specifically to decline, but was attributed to functionally extinct mussels, impoundments, fish host availability, exotic species and recruitment.	
Clarke, 1986			New Hampshire and Vermont, USA
3	2	Present distribution and abundance of *Alasmidonta heterodon* in New Hampshire and Vermont was evaluated. Human acitivities, dams, pollution from the pulp and paper industry are indicated as the causes, although no linkages were established or discussed.	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Cooper & Johnson, 1980			Mississippi, USA
5	2	A loss of mussels was observed. "Habitat changes, especially impoundment and channelization of the Yalobusha River, have had a detrimental effect on the previously existing population of bivalve mollusks." (p. 24, paragraph 4).	
Cope et al., 2003			Wisconsin and Minnesota, USA
2	5	An evaluation of recovery and survival after relocation of mussels. Causes are cited from other articles, but there was some indication that, in this study, size fractions of substratum may play a major role (p. 31, paragraph 1).	
Cosgrove & Hastie, 2001			Scotland
1	5	A review of literature indicating river engineering or development projects may be responsible for mussel decline. Additional causes are cited from other articles as well, but no linkages are made.	
Cvancara, 1976			North Dakota, USA
2	2	Specimen of mollusks from the past and present are analyzed to determine local extinction or loss. Possible factors (cited from other articles) are discussed but no linkages of cause and effect were made.	
Cvancara & Freeman, 1978			North Dakota, USA
2	3	Mussels were surveyed in Lake Ashtabula. Fewer species were found in this area than other areas of Sheyenne River. No linkage was found between the number of species and the possible causes reviewed (*e.g.*, reproductive alteration, low levels of oxygen fish host availability, siltation and organic enrichment (p. 7 paragraphs 2-3), decreased biological activity, chemical factors (p. 8 paragraphs 3-4).	
Day et al., 1990			Québec, Canada
5	3	An experiment introduced mussels into pristine and polluted environments. Evidence indicates exposure to stressful environments (toxic chemicals) affects mussels (p. 826, paragraph 1).	
Diamond & Serveiss, 2001			Virginia, USA
4	3	Results indicated multiple land uses and stressors are responsible for the decline of mussels. Some suggested factors were poorer in-stream cover and higher substrate embeddedness, episodic spills of toxic materials, mining and industrial activities, sedimentation, urban areas, habitat fragmentation and recruitment. Some of the potential causes were linked whereas some were cited from other published articles.	
Diamond et al., 2002			Virginia, USA
4	3	"The number of native mussel species present was related to several land uses including (in order of significance) percent urban area, proximity to mining, and percent cropland". Some factors were discussed but not linked.	
Di Maio & Corkum, 1995			Ontario, Canada and Michigan, USA
5	1	An extinction event of juvenile mussels was directly linked to anoxic conditions (hypoxia, thermal stress and acidic conditions) (p.187, paragraph 1-3; pp. 189-190).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Dimock & Wright, 1993			North Carolina, USA
5	1	"The hydrological stability of a drainage basin appeared to influence the species of unionids found in it" (p. 668, paragraph 3) "...the hydrological variability of a drainage basin, as used in this study, can provide a meaningful measure of mussel habitat and used to effectively characterize mussel communities (p. 670, paragraph 4). A loss was not observed although decline was implied.	
Downing et al., 1993			Québec, Canada
4	3	Population size distribution, overall density, and degree of aggregation achieved during spawning (p. 154, paragraph 2) influence successful reproduction in *Elliptio complanata*. Evidence of the linkage was correlative.	
Duncan & Thiel, 1983			Mississippi River, USA
4	3	A survey of mussels was done. Causes cited for decline were impoundment and water quality (Fuller, 1978). Links were established between impoundments, shifting substrates, and dredging. Not all postulated causes are linked explicitly.	
Fleming et al., 1995			North Carolina, USA
4	1	A die-off event occurred (p. 877) and was linked to anticholinesterase poisoning. Other postulated causal factors were observed but were not linked to the mortality of mussels.	
Fuller, 1978			Mississippi River, USA
1	2	An evaluation of impact of dredging and associated activities by United States Army Corps of Engineers. It was found that these had only minor impacts. Only circumstantial evidence was presented and potential impacts of causal factors were implied by reference to other studies (p. 98).	
Gagne et al., 2001			Québec, Canada
4	1	The decline of freshwater mussels was observed and postulated to be multifactorial, including such habitat components as habitat destruction, dredging, channeling, and pollution. Cited factors for which there was no direct evidence included sewage and effluents from paper mills, tanneries, chemical plants, and steel mills; acid mine runoff, heavy metals, and pesticides (Bogan, 1993). "Thus the feminization of mussel populations by environmental estrogens is likely to contribute to this decline." (pp. 267-268, paragraph 2).	
Green, 1972			Canada
4	1	*Lampsilis radiata* and *Pyganodon grandis* differed in distributions due to pH, alkalinity and sodium chloride concentration. (p. 1566, paragraph 3).	
Haag & Warren, 1998			Alabama, USA
3	4	Statements were made indicating fish host densities were too low, impeding freshwater mussel composition, however, a linkage between the factors and the decline does not seem to be made.	
Hallam, 1967			California, USA and Scotland
1	3	An investigation of the validity of ideas published by another author. Mussel decline inferred from a literature review.	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Hanson et al., 1989			Alberta, Canada
5	1	Observed predation on mollusks by muskrats.	
Harman, 1972			New York, USA
5	2	Links were made between mollusk decline and habitat types, indicating substrate types and patterns, as well as chemical stresses and biotic interactions are linked to declines.	
Hartfield & Hartfield, 1996			Alabama, USA
3	4	The mussels were observed in high quality clear streams of Bankhead National Forest, however they were not found in similar streams flowing through private lands, which are more impacted by sedimentation, eutrophication, chicken and cattle feedlot runoff, cultivation, surface mine runoff (p. 372, paragraph 3). No definitive link was made.	
Hastie et al., 2000b			Scotland
1	4	Mussels were surveyed and reasons for decline or lack of decline were reviewed or cited from other studies.	
Hastie et al., 2001			Scotland
5	1	A die-off event occurred (p. 110, paragraphs 2-3) after a 100 year flood event occurred. Strong, plausible link made.	
Hastie et al., 2000a			Scotland
4	2	Lack of suitable river bed substratum characteristics are implicated in the decline of *Margaritafera margaritifera*. Other causes were suggested but not definitively linked.	
Hemelraad et al., 1990			Netherlands
5	1	"After 8 weeks of exposure to cadmium, the clams entered into the lethal phase. Between 8 and 12 weeks of exposure, 90% of the total mortality occurred." (p. 690, paragraph 3).	
Henley & Neves, 1999			Virginia, USA
2	2	A loss of mussels was observed (p. 69, paragraph 3). Possible causes were discussed, but no definitive link was made.	
Hoggarth, 1990			Ohio, USA
3	2	No plausible cause was established observed for change in density/distribution of mussels.	
Holland-Bartels, 1990			Mississippi River, USA
2	2	No event occurred in this study and causes were cited from other articles, no links were independently established.	
Hubbs et al., 2003			Tennessee River, USA
5	2	Low frequency of mussels was observed at the dredged sites and this indicates that bottom substrates were altered by dredging and resource extraction. These operations do not allow mussel populations to become established.	
Hughes & Parmalee, 1999			Tennessee, Alabama, Kentucky, USA
1	2	Consists of a review of other articles looking at pre- and post-impoundment mussel fauna. "Cause and effect in the study of biodiversity versus human activities is certainly speculative…" (p. 26, paragraph 2).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Isely, 1910			Oklahoma, USA
3	5	Juvenile specimens could not be located (p. 77) and this was suggested to cause a decline and disappearance of the mussels. No direct link to a cause is established, however.	
James, 1985			New Zealand
4	4	"The density of mussels in Tapuacharuru Bay appears to be influenced by a number of physical and biological factors (p. 307, paragraph 1), with coarse sand and slope being most important." (p. 311, paragraph 4).	
Jansen et al., 2001			World
1	3	No loss was observed and causes were cited from other sources: muskrat predation, host-fish, and glochidia mortality.	
Jantz & Neumann, 1992			River Rhine
1	4	A review of possible causes of zebra mussel mortality indicating exposure from water level fluctuations, predatory fish, toxicity from pollution, competition from *Corophiun curvispinum* (p. 59, paragraphs 1-5). No original evidence provided.	
Jirka & Neves, 1990			West Virginia, USA
4	2	Survival of mussels in the New River Gorge National River precluded by scarcity of suitable habitat and possibly by lack of suitable fish hosts (p. 138, paragraph 3). No factors were definitively substantiated (p. 139, paragraph 2). Study makes good link to habitat as the cause for decline.	
Johnson & Brown, 1998			Louisiana, USA
4	4	According to this study: "it appears that host fish distribution could play a role in regulating *Margaritifera hembeli* abundance and distribution" (p. 326, paragraph 2). Some other causes were cited from other articles (p. 327, paragraph 2).	
Johnson & Brown, 2000			Louisiana, USA
4	3	The results of this study suggest that residual populations of Louisiana pearl shells are more likely to be found in small headwater streams with harder water and circumneutral pH values (p. 274, paragraph 4). *Margaritiafera hembeli* was found to be positively associated with several microhabitat variables (p. 274, paragraph 5), however juvenile survival is thought to be influenced by other factors than those influencing adults (p. 275, paragraph 4).	
Keller & Zam, 1991			Canada and USA
4	2	*Anodonta imbecilis* was found to be as sensitive to dissolved metal pollution as zooplankton but may be more sensitive than some insects (table 6) (p. 543, paragraph 9). Water hardness was shown to have an effect on metal toxicity to mussels (p. 544, paragraph 2). Furthermore it was postulated that metals can be more toxic to mussels at lower concentrations in combination than they are singly (p. 545, paragraph 2).	
Kelner & Sietman, 2000			Illinois, USA
1	6	Records from recent studies were reviewed and population declines may have been observed. Factors are unclear (p. 373, paragraph 2).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Killeen et al., 1998			Wales
1	2	A die off event occurred (p. 247, paragraph 6) but no link was established to the habitat and stream level as the cause (p. 247, paragraph 2). Effects inferred from literature sources.	
King et al., 1999			Eastern USA
4	5	Populations are observed to be reproductively isolated. Some of the causes are cited from other articles (p. 574).	
Layzer & Madison, 1995			Kentucky, USA
2	2	Mussel distribution is based on simple and complex hydraulic variables, host fish, habitat availability of host fish (pp. 340-343). Direct linkages not substantiated.	
Layzer et al., 1993			Tennessee, USA
4	5	An observed loss of species occurred mainly as a result of construction and operation of Center Hill Dam (p. 68). Some causes inferred from published sources.	
Layzer et al., 1993			Kentucky, USA
4	6	Evidence linked mussel extinction to construction and operation of a dam in the Caney Fork River (p. 69, paragraph 5). Some causes inferred from published sources.	
Lee & DeAngelis, 1997			USA
1	2	A model was used to study the effects of fecundity rate, availability of fish hosts and suitability of the habitat. No event observed and no direct evidence of causes offered.	
Liu et al., 1996			Colorado, USA
4	6	"Although pollution, fluctuation in water levels, and periodic decimation of fish stocks can all contribute to the decline of mussels, it is not known which factor is the most important." (p. 122, paragraph1). Some causes inferred from indirect evidence.	
Makela & Oikari, 1992			Finland
5	1	This study observed the effects of pH on ionic balance in *Anodonta anatina* L.. Deaths were observed at pH 2.6 and below (p. 172, paragraph 3). "This was probably due to the loss of ions" (p. 173, paragraph 3).	
Martel et al., 2001			Ontario, Canada
4	1	A decline was observed (p. 2185) following invasion of *Dreissena polymorpha* (p. 2189). A link was established to this invasion but not to any of the other cited causes listed on p. 2182, paragraph 2.	
Mehlhop & Vaughn, 1994			North America
5	7	Declines have been observed in North America. Threats identified were: water quantity and quality due to habitat destruction, pollution, recreational activities, fish hosts, fragmentation of river drainages through impoundments, channelization and other activities such as timber-harvesting, which alters flow and sedimentation patterns, flow alteration. Linkages judged to be plausible.	
Metcalfe et al., 1998			Canada
1	4	15 of 40 species were identified as extirpated from the Lower Great Lakes drainage (p. 439, paragraph 3). Causes were cited from other articles (p. 425, paragraph 1).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Metcalfe et al., 1998			Canada
2	4	Records showing mussel numbers from 1860 and 1996 were compiled and reviewed and showed evidence of a steady decline (p. 850, paragraph 1) (p. 852, paragraph 3). Cited causes discussed : fish hosts and habitats, water chemistry, agricultural activity, agriculture runoff, roadway crossings, cattle crossings, industrial discharges and storm sewer discharges, dam construction, Metal toxicity. Connections based on inference from the literature.	
Metcalfe et al., 2000			Ontario, Canada
2	5	Causes for mussel decline/extirpation were discussed on p. 446, paragraph 1 but no direct evidence for causes of decline were illuminated.	
Miller & Kott, 1989			Lake Michigan
4	1	Faunal shifts were observed with oscillations in lake level.	
Miller & Payne, 1998			Central USA
1	4	Data from ten years of sampling were reviewed. Causes were discussed (p. 188, paragraph 1) but no direct linkages were made between declines and causes.	
Miller et al., 1986			Illinois, USA
3	7	Cited causes for loss include: sedimentation, navigation activities, pollution, reservoir construction (many with deoxygenated, low pH, and cold water releases), and loss of fish hosts (Fuller, 1974), recruitment, habitat alterations and range. (p. 17). Evidence for cause inferred from principally from literature review.	
Miller et al., 1999			Wisconsin , USA
2	1	The effects of water velocity changes were observed but the authors found that they did not significantly affect the mussels. Other factors were cited from the published literature (p. 241, paragraph 2).	
Morris & Corkum, 1996			Ontario Canada
2	4	A survey of mussels in southwestern Ontario is presented. Many causes are cited from other articles: ammonia and host fish, nitrate, nitrite and phosphate, agricultural activity, stream size and gradient, hydrologic variability and physiography. No direct evidence of causes for decline illuminated.	
Morris & Taylor, 1978			West Virginia, USA
2	5	Mussels were absent from stations 2-6 of Kanawha River. Possible explanations discussed are industrial and organic pollution, habitat destruction from impoundment, and introduced species, but no direct evidence is offered.	
Moulton et al., 1996			USA
4	4	Effects of pesticides on mussels were observed. Mussel deaths were observed (p. 132, paragraph 10). Increased metabolic rate with low dissolved oxygen levels may also be a concern (p. 135, paragraph 3).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Mouthon, 1992			France
5	1	"A deficit in dissolved oxygen in the hypolimnion level and an excess of organic matter in deep sediments, defined in relation to the mineralization potential of each system, are two factors which limit the bathymetric distribution of molluscs in lakes. Low calcium levels can also limit the vertical distribution of gastropods." (p. 155, paragraph 3).	
Naimo, 1995			North America
1	2	A literature review on bioaccumulation, tissue distribution, uptake, elimination, detoxification and ecotoxicological effects of metals on freshwater mussels is presented.	
Naimo et al., 1998			Mississippi River, USA
5	1	A decline of *Amblema plicata plicata* was observed and a link was established experimentally to nutritional resources (p. 127, paragraph 2).	
Nalepa et al., 1991			Lake Erie
2	2	A decline was apparent (table 2, p. 216, paragraph 2). The specific reason for the decrease in unionid populations is likely related to water quality decline. Other cited causes are low oxygen, shifts in fish composition, and zebra mussels. No direct linkages illuminated.	
Nalepa et al., 1996			Canada
5	1	Decline of unionids (p. 362, paragraph 1) was attributed to an increase in zebra mussels (pp. 357-360), (p. 361, paragraph 1).	
National Native Mussel Conservation Committee, 1998			USA
1	4	Freshwater mussel declines are discussed and reviewed in this paper. Causes listed are impoundments, sedimentation, channelization, and dredging, water pollution, and the zebra mussel, habitat degradation, water quality degradation. (p. 1419, paragraph 3).	
Neves, 1999			USA
1	7	A review of conservation of freshwater mussels is offered with no direct analyses of linkages between disappearance and causal factors.	
Neves & Odom, 1989			Virginia, USA
4	1	This study assesses the impact of muskrat predation on endangered mussels (pp. 937-938). Other potential causes were cited from published sources.	
Obermeyer et al., 1997			Kansas and Missouri, USA
5	1	"Sites that were unstable (*i.e.*, loose, shifting substrata) were especially low in unionid numbers" (p. 49, paragraph 2). Inference judged to be strong.	
Parker et al., 1998			West Virginia, USA
5	1	Zebra mussels were linked to the decline of freshwater mussels (pp. 177-178).	
Payne & Miller, 1987			Illinois, USA
2	1	No link was established of the cited effect: water velocity.	
Pynnonen, 1990			Finland
4	2	It was found that adult mussels can withstand severe acidification. Furthermore results "…indicate that the reason for their disappearance from the acidified waters might be due to reproductive failure." (p. 477, paragraph 2).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Rooke & Mackie, 1984			Ontario, Canada
5	1	"Significant differences between mollusk densities in two intermediate-alkalinity lakes indicate that factors other than alkalinity may have affected mollusk distributions (abstract). Inference judged to be strong.	
Schloesser et al., 1997			Lake Erie
5	1	Zebra mussel infestation was found to cause unionid mortality (p. 70, paragraph 2).	
Schneider et al., 1998			Lake Michigan and Ilinois lakes, USA
1	1	A model of the risk of infestation by zebra mussels is reviewed and found to be useful when assessing risk when data on vector movement are not available.	
Strayer, 1980			Michigan, USA
2	2	A survey of mussels was compared to an older survey and decline was observed. Possible cited causes are domestic and industrial pollution low dissolved oxygen, high ammonia, and heavy metals. (p. 148, paragraph 3).	
Straye, 1983			Michigan, USA
1	1	Records and a survey were compiled and causes for the loss of species reviewed. Mussel distributions are controlled by ecological factors associated with stream size and surface geology (p. 261, paragraph 2). "This study clearly shows that the catchment of a stream is partially responsible for the biota of that stream" (p. 263, paragraph 2), although factors are not linked directly with decline.	
Strayer, 1993			Delaware, USA
4	2	Published records were used. Variables looked at were stream size, stream gradient, hydrologic variability, calcium concentration, physiographic province, and the presence or absence of tidal influences. All were found to be useful predictors of mussel distribution with stream size and tide being the most useful (p. 241, paragraphs 3-4). Eutrophication is also thought to play a role in mussel disappearance (p. 242).	
Strayer, 1999a			North America
1	1	A review of impact of alien species on mollusk fauna. Articles citing zebra mussels and the Asian clam, habitat degradation/quality are discussed. No explicit links were established.	
Strayer, 1999b			New York, USA
1	2	A review of other studies shows that flow refuges are not the only means of survival (p. 474, paragraph 2) also environmental factors: dissolved oxygen, sediment size, and frequency of desiccation may also be involved. Inference by literature citation.	
Strayer & Jirka, 1997			New York, USA
1	9	A review of pearly mussel distributions and causes of loss were discussed. No links were established between causal factors and decline.	
Strayer & Ralley, 1993			New York, USA
4	2	Water depth and current speed were predictors of distribution and abundance of unionaceans (p. 254, paragraph 4). The presence or absence of macrophytes, distance from shore, and certain aspects of sediment granulometry had some significance as predictors of survival (p. 255, paragraph 1). Other factors were discussed (pp. 255-256).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Strayer & Smith, 1996			Hudson River, USA
5	1	A decline in unionids was observed following arrival of the zebra mussel. Heavy infestation was not observed therefore the authors concluded the cause to be competition for food (p. 107, paragraph 2).	
Strayer et al., 1996			New Hampshire to North Carolina, USA
4	2	"All populations in our study appear to be vulnerable to loss because of low densities, small ranges, linear ranges, or some combinations of these factors." (p. 315, paragraph 1). Inference strong relative to other studies.	
Strayer et al., 1981			New Hampshire, USA
3	1	The population density, biomass, and annual production of unionids in Mirror Lake were lower than in other ecosystems. Cited factors were substrate and water quality (p. 438, paragraphs 4-5).	
Sylvester et al., 1984			Mississippi River, USA
4	3	Siltation and lack of fish hosts due to pollution and stream alterations proposed as reasons for decline in *Lampsilis higginsi*. Experiments on burrowing rates into various substrates and duration of glochidial infection of host fish used as evidence for postulated causes.	
Taylor, 1989			Ohio, USA
1	2	A species list was generated from other literature to assess changes in freshwater mussel populations. Reviewed causes for decline in mussels: habitat and environmental degradation and modification, depth, and decreased water discharge. Inference by review of literature.	
Tevesz & Redmond, 2002			Ohio, USA
2	2	Loss of species occurred in the lower portion of Cuyahoga River, but little change occurred in the upper reaches that are "less industrially impacted" (p. 16, paragraph 2). No causes are linked directly to this decline although pollution is mentioned because it coincides in time.	
Theler, 1987a			Wisconsin, USA
4	2	The most probable causes for mussel mortality at this site are overharvest, siltation, host fish, dam construction, water depth, habitat modification. Work was performed through archaeological excavation of mussel middens. Links are quite plausible and founded in observation.	
Theler, 1987b			Wisconsin, USA
2	2	Archaeological digs showed mussels present in a region where they are now absent. Reference to times of disappearance and environmental changes rely on literature evidence. Causes for mortality may have been flood erosion or siltation, sedimentation (p. 170, paragraph 6), poor habitat conditions (abstract).	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Thiel, 1981			Mississippi River, USA
5	5	A survey was performed of unionid mussels and when compared to earlier studies "showed a continuing trend of diminishing mussel species diversity". Causes discussed for the continuing trend of diminishing mussel species diversity are harvesting, and impoundments, substrate dredging, sediment and silt, species adaptability. (pp. 20-21). A shift in species dominance has occurred since impoundments (p. 18, paragraph 5).	
Tyrrell & Hornbach, 1998			St. Croix and Mississippi Rivers, USA
5	1	Evidence collected by comparing midden piles with live river collections of mussels. Muskrat predation was found to affect species composition and size structure of mussel communities. Muskrats can shift their preferences among species (p. 309, paragraph 2).	
Vannote & Minshall, 1982			Idaho, USA
5	1	Study suggests that local lithology and fluvial geomorphic processes interact to regulate population size structure and relative abundance (p. 4103, paragraph 1).	
Vaughn, 1993			North America
1	3	Models were developed to examine mussel meta-populations as a means of understanding extinction. Species losses inferred from published data.	
Vaughn, 1997			Oklahoma, USA
2	4	Losses of mussels were observed and causes for decline were cited from other articles. No strong links were established.	
Vaughn & Pyron, 1995			Oklahoma, USA
2	6	*Arkansia wheeleri* was extirpated from below impounded tributary and other cited causes were discussed. No substantial links were made.	
Vaughn & Taylor, 1999			Oklahoma and Arkansas, USA
2	3	This case study examined a mussel extinction gradient downstream from an impoundment. A mussel extinction gradient was observed downstream from impoundment (abstract). Three causes deriving from impoundments are discussed by reference to other published studies (p. 916).	
Waller et al., 1998			Mississippi River
5	1	Toxicity of the fish toxin 3-trifluoromethyl-4-nitrophenol (TFM) is proposed based on laboratory experiments. "TFM caused narcotization of the mussels, as evidence by valve gaping, extension of the foot and lack of movement, even at sublethal concentrations. Once elicited, the mussels remained narcotized for the duration of the exposure period." (p. 116, paragraph 2).	
Watters, 1992			North America
1	2	Literature sources reviewed are listed in table 1.	

Appendix. (Cont.)

Reference			Location
Q	N	Notes*	
Way et al., 1989			Tennessee River, USA
4	3	Mussel samples were taken along a gradient of postulated local extinction causes. Density differed between inshore and off shore sites as did sediment deposition (p. 97, paragraphs 2-3) and water velocity (p. 98, paragraph 1).	
Weinstein, 2002			Texas, USA
5	2	Toxicity analyses of polycyclic aromatic hydrocarbons. "Environmentally relevant concentrations of fluoranthene do pose a significant hazard to the glochidia of at least one species of freshwater mussel" (p. 160, paragraph 1). Cumulative damage was observed during light periods and no repair during dark periods.	
Williams et al., 1993			Canada and USA
1	6	A review of the current status of mussels. Threats are discussed (p. 7, paragraph 1, abstract).	
Williams et al., 1992			Alabama and Mississippi, USA
4	2	"The reduced number of species and individuals in the impounded segment of the Tombigbee River appears to be habitat related." (p. 7, paragraph 1). Impacts of impoundment related causes are reviewed but some connections made directly.	
Yokley, 1976			Tennessee, USA
5	2	A disappearance of mussels was observed. Habitat alteration by dredging was the linked cause through manipulation experiments.	
Zanatta et al., 2002			Lake St. Clair, Canada
2	1	95 sites around Lake St. Clair were surveyed. No live unionids were found at 42 of sites surveyed. 2,356 were found at 33 sites. Zebra mussels are discussed as the cause because mussel species that dominate the fauna are those that other studies have suggested to be resistant to infestation by zebra mussels (p. 482, paragraph 3).	

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