

Ecological Effects of *Micropterus* Introductions: the Dark Side of Black Bass

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Abstract.—Largemouth bass *Micropterus salmoides* and smallmouth bass *M. dolomieu* are two widely introduced species of fish prized for their angling potential. The introductions of these species, although commonly done by management agencies and the public, typically involve little or no consideration of the impacts these species may have on other species of fish and the aquatic ecosystems. Field studies and review of literature are used to document various direct and indirect effects of bass occurrence in reducing diversity of small-bodied fish species, creating more homogeneous fish communities, increasing competition among small-bodied fish, reducing energy flow to other game fishes, altering planktonic and benthic communities, and potentially changing habitat complexity. Discussed within is also the fact that, although there is public concern regarding introduction of predatory species that may affect terrestrial systems, there appears limited interest regarding the negative impacts that bass may have on aquatic ecosystems.

Introduction

Recreational fishing represents both a major activity and business, particularly in North America. Within warm and cool freshwater environments, angling for bass, in particular largemouth bass *Micropterus salmoides* and smallmouth bass *M. dolomieu*, is a major focus. To facilitate angling, management agencies often use stocking programs to enhance existing populations and stock lakes, reservoirs, and river systems where these two species of bass may not occur naturally. In addition to stocking by official agencies, many authorized (e.g., farm ponds) and unauthorized introductions occur with fish being moved between waterbodies by the public. Distributions of these two species have expanded from approximating the Mississippi River basin, Gulf of Mexico region, and portions of the Great Lakes basins to include virtually all of the United States, southern regions of Canada warm enough to support the species, most of Mexico and central America, large areas of Europe, southern Africa, South America, parts of Asia and many oceanic islands (e.g., Robbins and MacCrimmon 1974; Azuma and Motomura 1999; Gratwicke and Marshall 2001). These species have become some of the most widely distributed aquatic species in the world in order to provide angling opportunities. The management of these species and the enhanced fish-

ing opportunities are generally considered a success, but such evaluations of "success" are limited in the breadth of their considerations. These introductions typically have been made with limited or no consideration about the ecological consequences of such actions. Ironically, this symposium represented the 25th anniversary of the publication the first Black Bass Symposium proceedings, the same year at which John Magnuson's presidential address warned of the consequences due to fish introductions (Magnuson 1976). Although the introduction of exotics from other continents generates considerable concern among most resource managers and the public, there appears to be no comparable response to moving *Micropterus* spp. around in North America or elsewhere despite their strong ecological impacts.

This paper examines several of these ecological consequences through results from two studies, plus published studies are drawn upon extensively in an extended discussion. Despite the species being introduced to systems worldwide, almost all of the studies examining the ecological aspects of these introductions are derived from comparative or experimental studies in North America. This paper focuses on the direct and indirect ecological effects attributable to black bass and similar predators such as Northern pike *Esox lucius*. Fish communities and species richness from two sets of Ontario lakes that contain bass are contrasted to those lakes that do not have bass present. The findings from this bass comparison are contrasted with the results of a trout *Salvelinus* pres-

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ence-absence comparison from the same lakes. The goal of this paper is not to advocate the elimination of stocking programs entirely, but rather to emphasize that we must consider the broader and permanent environmental impacts due to black bass introductions.

Methods

Field Sampling

Drainage-basin survey. Species were sampled from 52 lakes in the Black and Hollow River drainage basins of south-central Ontario, Canada (Figure 1). Selected lakes had surface areas of 5 ha or greater, and a minimum depth of 3 m or more to reduce the probability of complete winterkill. Each lake was sampled using baited minnow traps, plastic traps, fine- and coarse-mesh trapnets, and multi-panel monofilament gillnets having 15 × 8 m panels ranging in size from 3.75 to 7.5 cm stretched mesh. Lakes were sampled between three and seven nights in duration with all gears being used in each suitable habitat. Several lakes were resampled during a different time of the sampling

season to assess the reliability of initial surveys due to seasonal effects. No additional species were detected during the resampling periods (for additional details see Jackson 1988).

Size-restricted survey: To limit effects due to lake size and habitat heterogeneity, a set of lakes from the Black and Hollow River drainage (six lakes) and adjacent Algonquin Provincial Park (eight lakes) were chosen. These two regions are physically adjacent and therefore share similar environmental conditions. These lakes were restricted to those with a maximum of 50 ha in surface area and were classified into those known to contain or lack smallmouth bass (MacRae 1999; MacRae and Jackson 2001). Lakes were chosen such that aside from the presence or absence of smallmouth bass, the environmental conditions of the two sets of lakes were comparable in terms of surface area, depth, and water chemistry. Areas with the most complex habitats (i.e., submerged woody material and aquatic vegetation) and the simplest within each lake were located. Within these two habitat types, fishes were first enumerated using a visual sampling technique in which a snorkeling observer swam transects identifying the species and counting individuals



Figure 1. Map showing the location of the study sites. The “+” indicates the location of the Black and Hollow River lakes (Jackson 1988) and the open circle indicates the Algonquin Park lakes (MacRae 1999; MacRae and Jackson 2001).

(MacRae and Jackson 2001). Following the visual survey, baited minnow traps were placed in each habitat type and retrieved the following day to provide estimates of catch per unit effort. Whole-lake estimates of species presence-absence are used here.

Data Analysis

Fish species composition was reduced to species presence-absence because of sampling bias imposed by each sampling gear and lake characteristics. As a result of the bias, interlake comparisons across gears and species are not based on reliable estimates of relative abundance (Jackson and Harvey 1997). In addition, multi-lake comparisons based on presence-absence data have been found to capture the dominant community patterns (Jackson et al. 1992; Jackson et al. 2001). Total species richness within each lake was compared between lakes containing or lacking bass (both *M. dolomieu* and *M. salmoides*). Because richness is positively correlated to lake surface area, an analysis of covariance (ANCOVA) was used to contrast the richness of lakes with bass, from those lacking bass, while controlling for the area effect. Due to the vulnerability of cyprinids to predation, a parallel ANCOVA was carried out contrasting the cyprinid species richness in the two classes of lakes, relative to surface area. To compare whether similar relationships exist for salmonids as for bass, ANCOVAs examining total species richness and cyprinid species richness were done using the presence or absence of brook trout *Salvelinus fontinalis* and/or lake trout *S. namaycush* in the lakes.

Patterns of species composition were summarized using multivariate ordination methods. Species occurring in less than five percent of the lakes were deleted as they contribute little to general community patterns and often lead to an "outlier" condition. The similarity of species from the 52 lakes in the Black and Hollow Rivers system were quantified using the Phi similarity coefficient (denoted as S; Jackson et al. 1989). These species have been shown to exhibit nonrandom patterns in community composition based on this measure (Jackson et al. 1992) and the measure is not influenced by species richness or by species frequency of co-occurrence (Jackson et al. 1989) unlike more commonly applied measures, such as Jaccard's coefficient. The similarity measure was converted into a distance measure by taking the square root of its complement (i.e., the multivariate distance between two lakes). A principal coordinates analysis (PCoA) was then applied to this matrix of be-

tween-species distances to graphically summarize the similarities of the species. A similar Phi-based distance matrix and PCoA was applied to summarize relationships among the lakes. The species presence-absence data from the restricted lake size survey was summarized using a correspondence analysis (Jackson and Harvey 1997; Legendre and Legendre 1998). This technique has an advantage in that positions of species and lakes can be interpreted jointly to relate species composition directly to the similarity of lakes.

Results

Drainage-basin study

Lake surface area was a significant factor associated with total species richness per lake ($P < 0.0001$). The increase in the number of species relative to lake area (i.e., the regression slope) was not significantly different in lakes with bass from lakes without bass ($P = 0.323$). The lakes containing either bass species had an average of 1.4 fewer species (including bass) than lakes without bass, but were not significantly different ($P = 0.101$) after controlling for lake area (Figure 2a). There was no difference ($P = 0.361$) in the slopes of regression lines comparing cyprinid richness relative to lake area for lakes with bass relative to lakes without bass. Cyprinid richness was associated strongly with lake area ($P = 0.011$), and lakes with bass averaged 2.9 fewer species of cyprinids than lakes without bass ($P < 0.0001$) after controlling for lake area (Figure 2c). Tests comparing the presence or absence of trout within these lakes showed total species richness to be strongly related to lake area ($P < 0.0001$) but again had similar regression slopes ($P = 0.361$). Lakes containing trout differed significantly in the number of species present ($P = 0.0001$), but lakes with trout averaged 3.2 more species (including trout) than lakes without trout (Figure 2b). There was no difference in the slopes ($P = 0.541$) of cyprinid richness relative to lake area for lakes with trout versus lakes without trout. Cyprinid richness was related to lake surface area ($P = 0.02$) and lakes containing trout averaged 2.3 more species of cyprinid ($P = 0.001$) than lakes without trout after controlling for lake area (Figure 2d).

The principal coordinates results of the fish species (Figure 3) shows most of the cyprinid species are positioned towards the left-end of Axis 1 with species such fathead minnow, northern redbelly dace, and pearl dace being the most extreme in their location. Species located at the opposite end

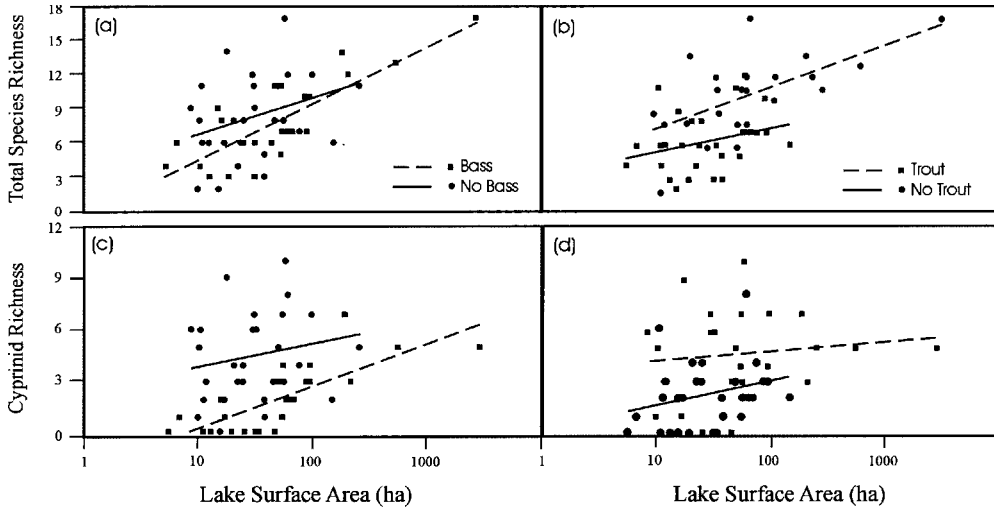


Figure 2. (a) Scatterplot of total species richness per lake, versus lake area for lakes with bass and lakes without bass. (b) Scatterplot of total species richness per lake, versus lake area for lakes with trout and lakes without trout. (c) Scatterplot of cyprinid richness per lake, versus lake area for lakes with bass and lakes without bass. (d) Scatterplot of cyprinid richness per lake, versus lake area for lakes with bass and lakes without trout. Lines represent the least-squares regression lines of richness, versus lake area for each group of lakes

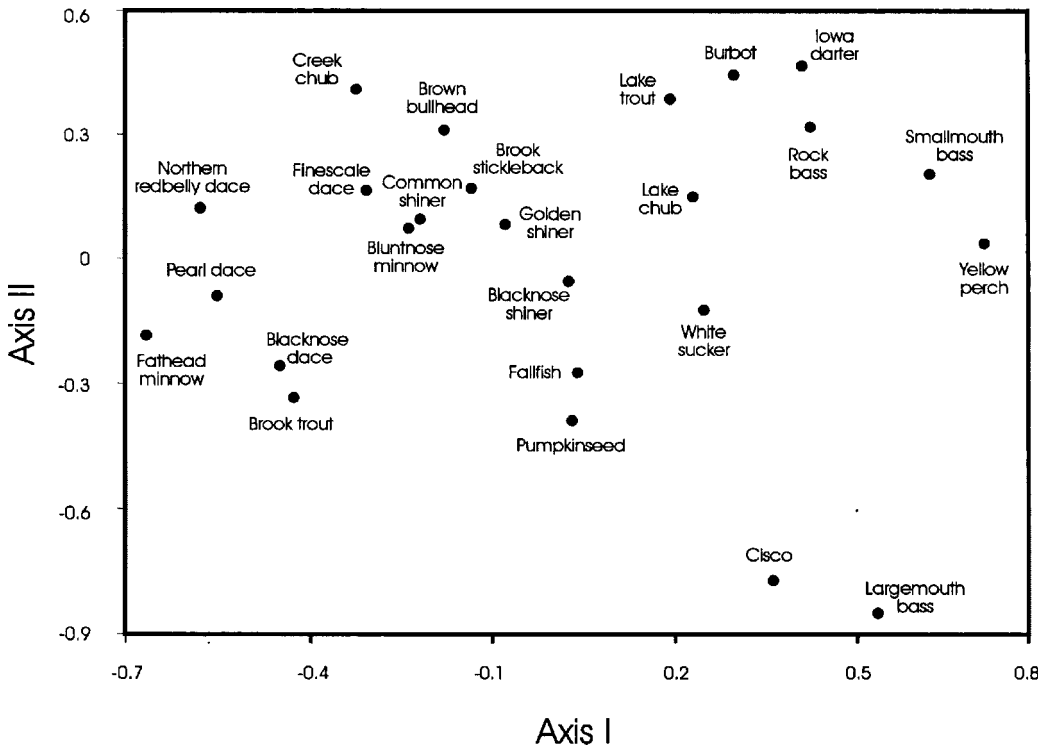


Figure 3. First two axes from a principal coordinates analysis of a Phi distance matrix based on fish species presence-absence data from the Black and Hollow Rivers basin. Proximity of species to one another provides a measure of their probability of jointly occurring in lakes within the watershed. For example, fathead minnow and pearl dace occur together frequently whereas fathead minnow and largemouth bass do not.

of Axis 1 include both bass species and yellow perch. Most species to the right of the center are large-bodied and/or cold-water species, whereas almost all species to the left are small-bodied species. A notable exception to this trend is brook trout that is positioned close to blacknose dace, pearl dace, and fathead minnow. In general, the pattern along Axis 1 is one progressing from small-bodied species at the left end towards species of increasing body size and piscivorous diets at the right end.

The PCoA of the lakes (Figure 4) shows a strong contrast between lakes containing bass and those that do not. Lakes in which bass were present (coded as "bass") are positioned on the right end of Axis 1, whereas lakes lacking bass are positioned towards the left end. Given the results found in the fish ordination and in results published previously (Harvey

1981; Jackson et al. 1992), a set of species has been coded as being highly vulnerable to predation. This set of species includes fathead minnow, pearl dace, northern redbelly dace, and finescale dace. Lakes containing two or more of these species are designated as having the vulnerable "minnow" assemblage, whereas lakes having one or fewer of these species and lacking bass are coded as "other." The "other" lakes show an intermediate position between those lakes containing the "minnow" assemblage and the "bass" lakes. Four lakes contained both the "bass" and "minnow" assemblages and three of these are among the four largest lakes.

Size-restricted survey

The correspondence analysis shows smallmouth bass, largemouth bass, and rock bass all positioned

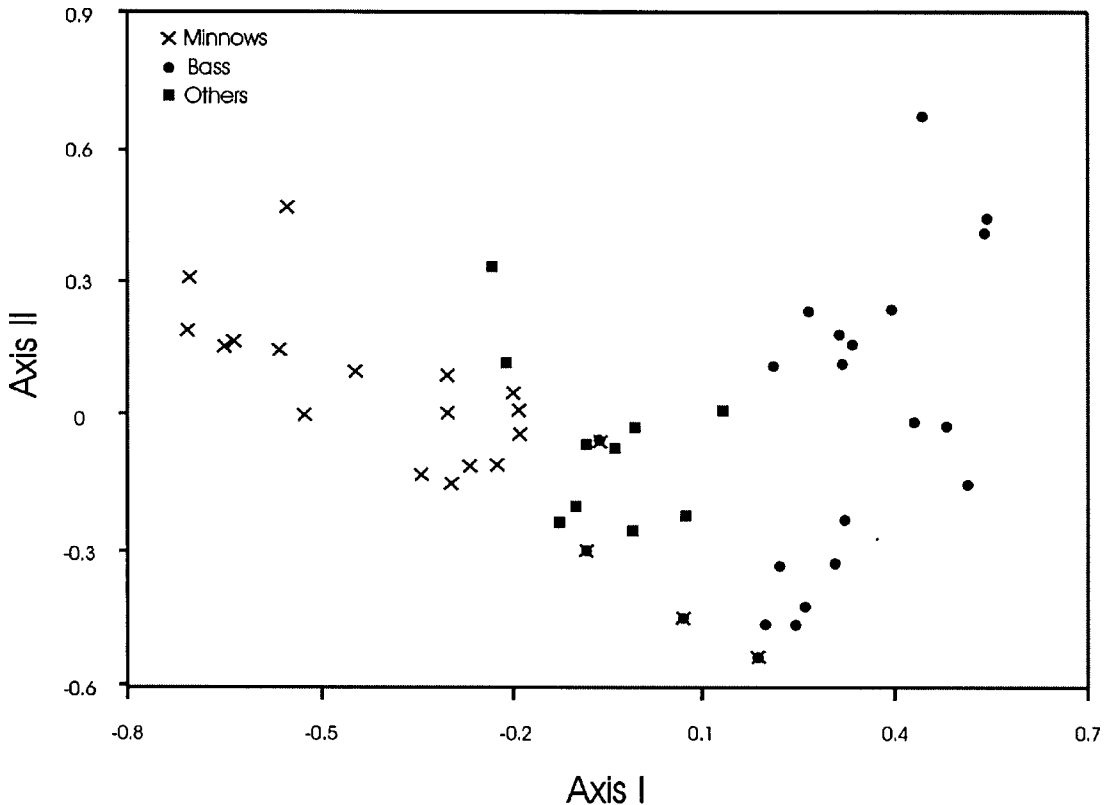


Figure 4. First two axes from a principal coordinates analysis of a Phi distance matrix based on fish species presence-absence data from the Black and Hollow Rivers basin. Each point represents a lake based on its species composition and points positioned closer to one another have more similar species composition. "Minnow" lakes are those containing two or more species of fathead minnow, pearl dace, finescale dace, and northern redbelly dace, and do not contain bass; "Bass" lakes contain either smallmouth or largemouth bass; and "Others" do not contain bass or two or more species of this cyprinid assemblage. Note: Four lakes contain both the bass and minnow assemblages.

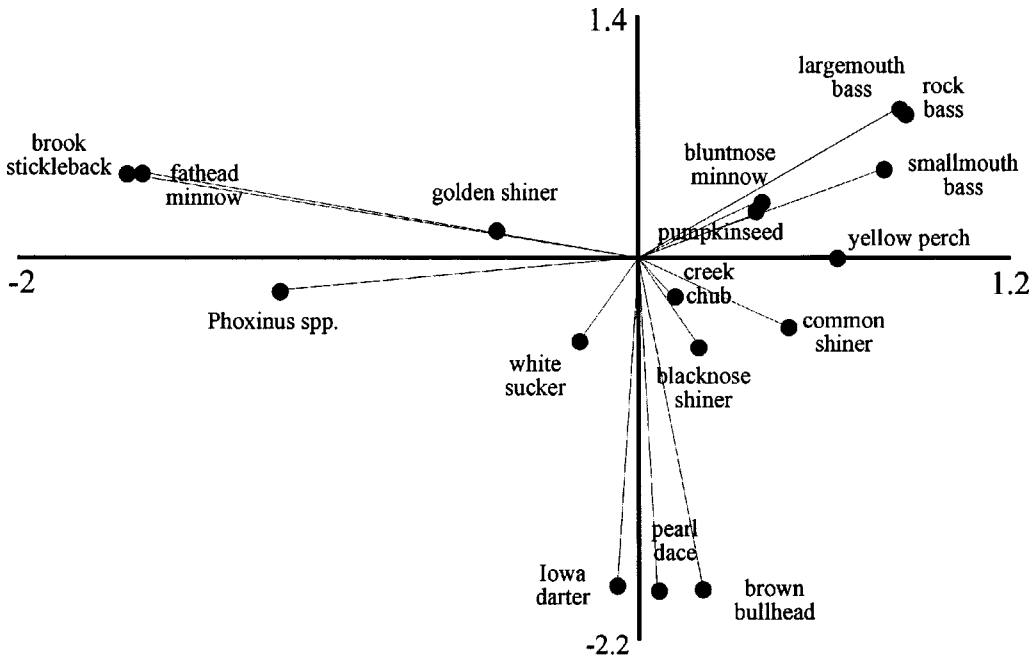


Figure 5. First two axes from a correspondence analysis of fish species presence-absence data. Species having positive associations are those that would have a small angle between vectors drawn from the origin to the species positions (i.e., brook stickleback and fathead minnow). Species having negative associations are those with angles approaching 180 degrees (i.e., fathead minnow and smallmouth bass). Redrawn with permission from MacRae and Jackson (2001).

at the far right-end of Axis 1 (Figure 5). The establishment of largemouth bass in one of these lakes is a recent event and was not found in these lakes during previous surveys (Jackson 1988). Because they were only found in lakes classified as “bass” in the design, this did not compromise the “bass” versus “no bass” contrast. This positioning of these species contrasts with the positions of species such as fathead minnow, brook stickleback, and *Phoxinus* (both *Phoxinus* species, northern redbelly dace, *P. eos*, and finescale dace, *P. neogaeus*, were pooled because distinguishing between these species was impossible during underwater surveys). The angle between vectors joining species provides a measure of their association. Angles close to zero indicate a positive association between the species in the ordination space. These species tend to co-occur and represent assemblages found across lakes. In contrast, angles approaching 180 degrees indicate species having negative associations and more mutually exclusive distributions. Iowa darter, pearl dace and brown bullhead also show negative associations with respect to bass occurrence, but are largely uncorrelated with the distribution of *Phoxinus*, fathead minnow and brook stickleback as shown by the vector angles approximating 90 degrees.

The ordination plot showing the lakes (Figure 6) clearly indicates the difference between the “bass” and “no bass” lakes. As with the drainage basin survey, there is a separation between lakes containing bass and those where bass were absent, but the separation in the size-restricted survey is more distinct. Positions of lakes without bass range from the extreme left-end of Axis 1 to the middle of Axis 1, and lower end of Axis 2. In contrast the lakes containing bass show a compact grouping positioned towards the right end of Axis 1. The group of lakes containing bass shows much less variability in their ordination position than lakes without bass.

Discussion

Both of the case studies presented here show strong negative associations between small-bodied fishes, primarily cyprinids, and smallmouth bass and largemouth bass. Lakes containing either of the bass species have significantly fewer species of cyprinids than lakes lacking bass. Although bass and other predatory species may not have viable populations in very small north-temperate lakes due to winterkill (Harvey 1981; Tonn and Magnuson 1983;

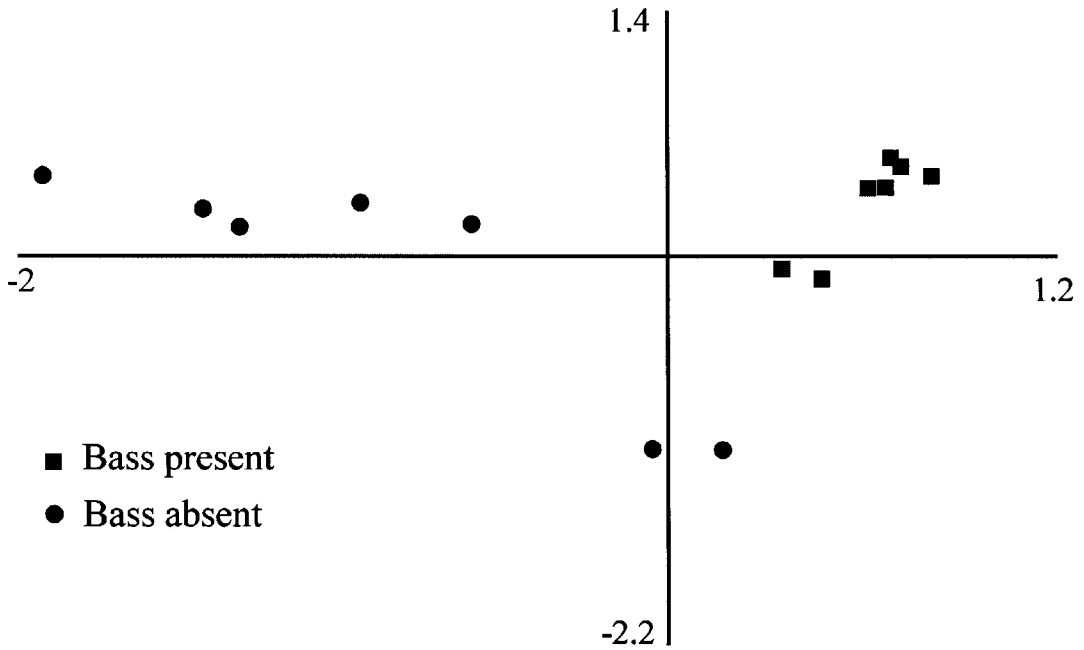


Figure 6. First two axes from a correspondence analysis of fish species presence-absence data showing relative similarity of lakes based on their species composition. Note lakes containing bass are tightly clustered whereas lakes lacking bass show greater variability in their positions. Redrawn with permission from MacRae and Jackson 2001.

Jackson and Harvey 1989), this pattern of reduced species richness holds consistently across the size range of lakes considered. Therefore, simple variation attributable to habitat differences as a function of lake size cannot explain the differences in cyprinid richness. The contrast related to salmonid presence, the other large predators in the lakes, does not show comparable effects. In fact, lakes with trout contain significantly more species of cyprinids, whereas lakes with bass show fewer species, relative to the lakes lacking either set of predators. During summer, bass and trout occupy different regions of these lakes due to their thermal preferences and lake stratification. Bass occupy littoral areas as do most of the cyprinids, whereas trout and cyprinids have limited overlap in their summer habitats. However, small littoral fishes may represent significant components of the annual lake trout diet in some lakes (Vander Zanden et al. 1999a). Differences in habitat use and predator thermal ecology partially explain the differences in why trout do not show as strong a negative effect with cyprinids as do the bass. Differences in foraging efficiency (i.e., gape size) between these groups of predators likely are major contributing factors also.

However, the fact that the lakes with trout have greater cyprinid richness than lakes without trout raises additional questions. A possible explanation for the enhanced richness in lakes containing salmonids relates to fishing practices of anglers. Live baitfish, typically cyprinids, are used by anglers fishing for both trout and bass. It is not uncommon for anglers to release live baitfish at the end of their fishing, and many of these species may not be indigenous to the lakes. These individuals may establish breeding populations in these lakes, thereby increasing the species richness (Litvak and Mandrak 1993). Because both trout and bass lakes would undergo this effect (Chapleau et al. 1997), the resulting differences in richness require that the introduced species establish and become viable in the trout lakes, whereas they do not in the bass lakes, or at least not to a similar extent. Again this emphasizes the potential differences in predatory impact.

Differences in the patterns of trout and bass occurrence with cyprinid species are also evident in the species composition of lakes. There is a strong negative association between smallmouth bass and largemouth bass with the dace species and fathead minnow, whereas brook trout shows a strong positive association with these cyprinids. Lakes con-

taining either or both bass species tend to have very different species composition than lakes lacking the bass. Direct predatory effects due to bass have been identified for lakes (Tonn and Magnuson 1983; Jackson et al. 1992, 2001) and streams (Power et al. 1985; Harvey et al. 1988). It has been found in stream systems that the effects due to largemouth bass are greater than those from smallmouth bass (Harvey et al. 1988), but no discernible difference was found here. The result of bass presence, via introduction or colonization, is a change in the species composition, often with a reduction in the diversity of species within the lakes (i.e., alpha diversity) (Chapleau et al. 1997; Whittier et al. 1997). Lakes where bass have been stocked or colonized from stocked populations also show less variation in their community composition than lakes without bass (Figure 6). This indicates that lakes containing bass have more homogeneous communities than lakes where bass have not established. Radomski and Goeman (1995) showed a reduction in among-lake diversity (beta diversity) or increased homogenization of fish communities as a result of the stocking of walleye, and Rahel (2000) found a general homogenization of fish faunas across the United States, largely as a result of fish introductions.

Although the direct effects of bass are most readily detected, there are many indirect effects that impact on other fish species and additional components of aquatic ecosystems. Most of these indirect effects are detected through experimental comparisons as they are not as readily detected in large-scale comparative approaches. The risk associated with predation and foraging requirements are conflicting demands on small fish (Fraser and Cerri 1982; He and Kitchell 1990). In lakes with large littoral predators, small-bodied fishes are often found to alter their choice of habitat and foraging behavior. Prey fish remain in more complex habitat because it provides greater protection from predation by bass (MacRae and Jackson 2001). Fish restricted to areas with greater amounts of macrophyte or woody material reduces the range of resources available for foraging, thereby increasing intra- and interspecific competition between small-bodied fishes (Savino and Stein 1989; He and Kitchell 1990; He and Wright 1992; MacRae and Jackson 2001). Nocturnal foraging in other habitats may offset this negative effect somewhat, but will not eliminate it. In turn, this habitat restriction contributes to reduced growth and fecundity of these species, and potentially reduced population size (MacRae 1999). Reductions in population size of small-bodied species can arise to direct pre-

ation effects and due to reduced foraging success. The importance of these complex habitats for smaller species increases when bass are present (Weaver et al. 1997), however, the lakes that are popular for recreational fishing are also the same ones that tend to have residential developments. People tend to remove many of these complex-habitat areas to enhance their use of the shoreline (Christensen et al. 1996). Therefore, while the importance of these habitats increases with bass presence, these habitats are frequently reduced in number and size. This reduction of habitat complexity, or habitat homogenization, enhances the effects due to bass predation. Fewer patches, with increased distances among patches, reduces the probability of individuals dispersing successfully between patches. In larger lakes these patch habitats may function in a metapopulation context, but the combination of increased predation and habitat modification reduces the probability of small fish metapopulations (and meta-assemblages) being maintained (Jackson et al. 2001). Increased emigration of small-bodied species has been shown to occur when pike (He and Kitchell 1990) or largemouth bass (Power et al. 1985) are introduced. Prey species may move from lakes into adjoining streams or nearby lakes if predators are absent from these systems. In general, it can be expected that a reduction in the numbers of small-bodied species, reductions in the numbers of individuals, reductions in growth and production due to predation and restriction to limited habitats will occur.

Indirect effects extend to large-bodied species whose adults are not susceptible to predation by bass. The reduction in the abundance and production of small-bodied fishes, and their restriction to complex habitats may alter the availability of these fishes as food for other predatory species. During spring and fall, lake trout and cyprinids often overlap in their habitat providing the potential for trout to feed on these species. The presence of bass has been found to alter the diet of lake trout (Vander Zanden et al. 1999a; 1999b). Because bass may eliminate some cyprinid species or reduce their abundance via various direct and indirect effects, there may be reduced availability of small fish as food for trout. Lake trout either experience reduced resource availability or must switch to feeding on less optimal prey (Figure 7). Depending on the availability of pelagic forage fishes, such as cisco, lake trout may use zooplankton as their primary source of food. This switch to energetically less profitable resources has major implications for their growth and reproduction. Such effects by bass on

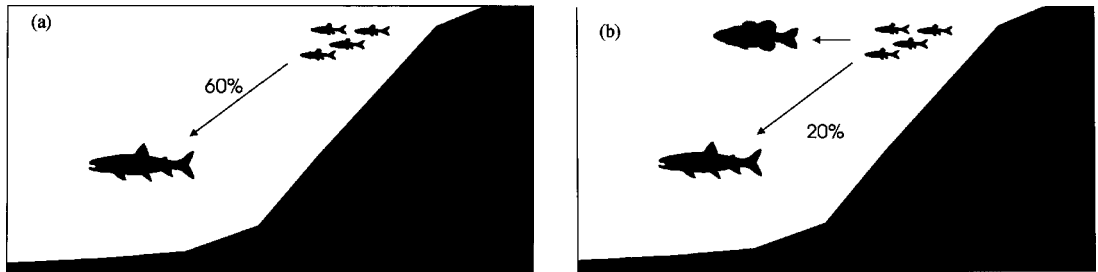


Figure 7 Indirect effects of bass introductions on pelagic lake trout due to changes in the energy pathways of lakes. (a) Lake trout obtained approximately 60 percent of their energy via littoral fishes in lakes without smallmouth bass and pelagic forage fish. (b) In lakes where bass have been introduced, the proportion of energy for lake trout obtained from littoral fishes is reduced to 20 percent. Additional components of lake trout diet in both scenarios are based on pelagic fishes (i.e., cisco) or lower trophic species (i.e., zooplankton). Redrawn with permission from Vander Zanden et al. (1999).

littoral cyprinid assemblages, as well as direct predation due to smaller body size, may explain the negative association between bass and brook trout occurrence because of increased biotic interactions (Brown et al. 2000). Brook trout have been shown to be less successful when present with various littoral species with whom they must compete for food (Bourke et al. 1999).

Indirect effects also occur in other ecosystem components, particularly on lower trophic levels involving pelagic and benthic invertebrate communities (see Matthews 1998 pages 604–611 for a review of associated trophic changes). The trophic cascade is perhaps the best-known phenomenon of top-down impacts stemming from introductions of top predators (Power et al. 1985; Carpenter et al. 1987; Findlay et al. 1994; Mittlebach et al. 1985; Schindler et al. 1997). The changes in abundance of small fishes and changes in their foraging behavior can contribute to differences in zooplankton structure. Fish typically select large-bodied zooplankton such as *Daphnia*. When planktivorous fish are abundant, large-bodied zooplankton are eaten preferentially and, therefore, are rare in abundance relative to small-bodied zooplankton. Larger cladocerans are generally considered to be more effective grazers on phytoplankton, so changes in the zooplankton size-structure result in changes in the phytoplankton communities. Such changes in trophic structure can lead to increased water clarity as a result of predators such as bass being introduced. This increased clarity could provide a positive feedback for the bass and enhance their ability to locate prey, thereby providing further pressure on the small-bodied fishes.

Differences in fish communities associated with bass and other littoral piscivores may contrib-

ute to differences in benthic invertebrate communities also (Jackson and Harvey 1993). Various studies have suggested changes in the zoobenthic communities ranging from changes in chironomid abundance to large-bodied invertebrates such as odonates (Morin 1984a, 1984b). Crayfish abundance, or their trapability, is reduced when bass are present (Stein and Magnuson 1976; Mather and Stein 1993; Somers and Green 1993). Changes in crayfish abundance or foraging behavior can be important given they are major invertivores and grazers of periphyton and macrophytes (Hill and Lodge 1995; Nystrom et al. 1996; Dorn and Mittlebach 1999). Modifications of this grazing behavior may contribute to differences in macrophyte abundance and density and therefore, changes in habitat complexity. Effects on invertebrate communities can be quite complicated as reduced abundances and modified behavior of predatory invertebrates due to bass presence can also reduce invertebrate predation on smaller invertebrate species (Jackson and Harvey 1993). Therefore, positive impacts on some groups of invertebrates may arise indirectly. Similar negative interactions between bass and small fish species (e.g., *Camptostoma*) lead to changes in the grazing behavior with the result being increased accumulation of large algae, thereby providing more complex habitat for many small species (Power et al. 1985; Gelwick and Matthews 1992). Effects are not limited to purely aquatic groups either, because predators can affect the success of amphibian species (Semlitsch 2000 and references therein).

Are aquatic systems different from terrestrial ones –or simply considered differently? The extent to which largemouth and smallmouth bass are introduced to aquatic systems in North American

and elsewhere is considerable and matched only by their apparent impact on these systems. Their impact ranges from loss of biodiversity to alterations of energy flow to changes in habitat structure. A species having a comparable impact in the terrestrial system would be the wild boar *Sus scrofa*, given that it is a species of interest due to the associated recreational hunting possibilities. Boar alter the habitat in which they live, cause local extinctions, and change trophic dynamics and energy flow of the ecosystem. However, there are many efforts to eliminate introduced populations of this species because of the recognized adverse impact on the environment. Certainly there is not support for widespread introduction of the species throughout North America as its adverse impacts are clear and the "costs" associated with the introduction of this species outweigh the benefits, both at the ecosystem level and the societal level (see Sweitzer et al. 2000 and references therein). The negative ecological effects on the terrestrial system are clearly visible and recognized. In contrast, the effects of black bass introductions may be comparable within aquatic systems, but they continue to be widely stocked and introduced, both legally and illegally. Part of this difference may be due to the misconception that fish do not move between lakes (see He and Kitchell 1990; Jackson et al. 2001 for discussions) or the fact that the impacts by black bass are less visible to the public. There is clear recognition that introducing nonindigenous predators into aquatic systems may have major ecological consequences (Moyle 1986; Crossman 1991; Stiassny 1996), but there appears to be little public awareness about the ecological impact that these commonly stocked species are having. Effects below the water's surface are less noticeable to the public and actions occur within aquatic systems that would not be tolerated in terrestrial systems (e.g., trawlers impacts on the ocean floor habitat and biota). This case of "out of sight –out of mind" may explain the dichotomy in how terrestrial and aquatic systems are considered with respect to introducing major predators.

Conclusions

The presence of bass has been shown to have adverse impacts for many natural components of aquatic ecosystems. These effects have been noted through various comparative studies examining fish communities (or other aquatic groups) in lakes with or without bass, as well as through experimental manipulations. Although many bass intro-

ductions have been made by management agencies, currently the rapid expansion in many areas is due to unauthorized introductions. The loss of biodiversity and homogenization of our ecosystems can be linked to these introductions. As well as these impacts on small-bodied species, there is evidence indicating major effects on other sport fishes, e.g., lake trout, brook trout, walleye. These species tend to be more common at the northern range of the bass distributions. However, given the current northerly expansion of bass and their potential for much wider distribution under climate change scenarios, there may be considerable risk to northern ecosystems. In order to limit the expansion of bass populations into new systems, it is critical that more stringent management be applied. In particular, we need to increase the awareness of anglers and the general public regarding the adverse effects of bass introductions (including ecological and recreational), rather than simply relying on the perceived benefits from angling.

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References

- Azuma, M., and Y. Motomura. 1999. Feeding habits of largemouth bass in a non-native environment: the case of a small lake with bluegill in Japan. *Environmental Biology of Fishes* 52:379–389.
- Bourke, P., P. Magnan, and M. A. Rodriguez. 1999. Phenotypic responses to lacustrine brook charr in relation to the intensity of interspecific competition. *Evolutionary Ecology* 13:19–31.
- Brown, P. J., D. C. Josephson, and C. C. Krueger. 2000. Summer habitat use by introduced smallmouth bass in an oligotrophic Adirondack lake. *Journal of Freshwater Ecology* 15:135–144.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876.
- Chapleau, F., S. C. Findlay, and E. Szenasy. 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Quebec. *Ecoscience* 4:259–268.

- Christensen, D. L., B. R. Herwig, D. E. Schindler, and S. R. Carpenter. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications* 6:1143–1149.
- Crossman, E. J. 1991. Introduced freshwater fishes: a review of the North American perspective with emphasis on Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 48 (Supplement 1):46–57.
- Dorn, N. J., and G. G. Mittlebach. 1999. More than predator and prey: a review of interactions between fish and crayfish. *Vie et Milieu* 49:229–237.
- Findlay, D. L., S. E. M. Kasian, L. L. Hendzel, G. W. Regehr, E. U. Schindler, and J. A. Shearer. 1994. Biomanipulation of lake 22a in the experimental lakes area (ELA): effects on phytoplankton and nutrients. *Canadian Journal of Fisheries and Aquatic Sciences*. 51:2794–807.
- Fraser, D. F., and R. D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. *Ecology* 63:307–313.
- Gelwick, F. P., and W. J. Matthews. 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. *Ecology* 73:1630–1645.
- Gratwicke, B., and B. E. Marshall. 2001. The relationship between the exotic predators *Micropterus salmoides*, and *Serranochromis robustus*, and native stream fishes in Zimbabwe. *Journal of Fish Biology* 58:68–75.
- Harvey, H. H. 1981. Fish communities of the lakes of the Bruce Peninsula. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* 21:1222–1230.
- Harvey, B. C., R. C. Cashner, and W. J. Matthews. 1988. Differential effects of largemouth and smallmouth bass on habitat use by stoneroller minnows in stream pools. *Journal of Fish Biology* 33:481–487.
- He, X., and J. F. Kitchell. 1990. Direct and indirect effects of predation on a fish community: a whole-lake experiment. *Transactions of the American Fisheries Society* 119:825–835.
- He, X., and R. A. Wright. 1992. An experimental study of piscivore-planktivore interactions: population and community responses to predation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1176–1183.
- Hill, A. M., and D. M. Lodge. 1995. Multi-trophic-level impact of sublethal interactions between bass and omnivorous crayfish. *Journal of the North American Benthological Society* 14:306–314.
- Jackson, D. A. 1988. Fish communities in lakes of the Black and Hollow River watersheds, Ontario. M.Sc. thesis, University of Toronto, Toronto, Ontario, Canada.
- Jackson, D. A., and H. H. Harvey. 1989. Biogeographic associations in fish assemblages: local *versus* regional processes. *Ecology* 70:1472–1484.
- Jackson, D. A., and H. H. Harvey. 1993. Fish and benthic invertebrates: community concordance and community-environment relationships. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2641–2651.
- Jackson, D. A., and H. H. Harvey. 1997. Qualitative and quantitative sampling of lake fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2807–2813.
- Jackson, D. A., K. M. Somers, and H. H. Harvey. 1989. Similarity coefficients: measures of co-occurrence and association or simply measures of occurrence? *American Naturalist* 133:436–453.
- Jackson, D. A., K. M. Somers, and H. H. Harvey. 1992. Null models and fish communities: evidence of nonrandom patterns. *American Naturalist* 139:930–951.
- Jackson, D. A., Peres-Neto, P. R., and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors? *Canadian Journal of Fisheries and Aquatic Sciences* 58:157–170.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*, Second English Edition. Elsevier, Amsterdam.
- Litvak, M.K. and N. E. Mandrak. 1993. Ecology of fresh-water baitfish use in Canada and the United States. *Fisheries* 18:6–13.
- MacRae, P. S. D. 1999. A comparative approach to quantify the influence of smallmouth bass predation and habitat complexity on the structure of littoral fish assemblages. M.Sc. Thesis, University of Toronto, Toronto, Ontario, Canada.
- MacRae, P. S. D., and D. A. Jackson. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation, and habitat complexity on the structure of littoral-zone fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 58:342–351.
- Magnuson, J. J. 1976. Managing with exotics – a game of chance. *Transactions of the American Fisheries Society* 105:1–9.
- Mather, M. E., and R. A. Stein. 1993. Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1279–1288.
- Matthews, W. J. 1998. *Patterns in Freshwater Fish Ecology*. Chapman and Hall.
- Mittlebach, G. G., A. M. Turner, D. J. Hall, and J. E. Rettig. 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347–2360.
- Morin, P. J. 1984a. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short-term experiments in a North Carolina farm pond. *Ecology* 65:53–60.
- Morin, P. J. 1984b. Odonate guild composition: experiments with colonization history and fish predation. *Ecology* 65:1866–1873.

- Moyle, P. B. 1986. Fish introductions into North America: patterns and ecological impact, p. 27–43 In H. Mooney and J. Drake editors Ecology of biological invasions in North America and Hawaii. Springer-Verlag, New York, New York.
- Nystrom, P., C. Bronmark, and W. Graneli. 1996. Patterns in benthic food webs: a role for omnivorous crayfish? *Freshwater Biology* 36:631–646.
- Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnow, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* 66:1488–1456.
- Radomski, P. J., and T. J. Goeman. 1995. The homogenizing of Minnesota lake fish assemblages. *Fisheries* 20:20–23.
- Rahel, F. J. 2000. Homogenization of fish faunas across the United States. *Science* 288:854–856.
- Robbins, W. H., and H. R. MacCrimmon. 1974. The black bass in America and overseas. Bio-management and Research Enterprises, Sault Saint Marie, Ontario, Canada.
- Savino, J. F., and R. A. Stein. 1989. Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* 37:311–321.
- Schindler, D. E., S. R. Carpenter, J. J. Cole, J. F. Kitchell, and M. L. Pace. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* 277:248–251.
- Semlitsch, R. D. 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64:615–631.
- Somers, K. M., and R. H. Green. 1993. Seasonal patterns in trap catches of the crayfish *Cambarus bartoni* and *Orconectes virilis* in 6 south-central Ontario lakes. *Canadian Journal of Zoology* 71:1136–1145.
- Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. *Ecology* 58:571–581.
- Stiassny, M. L. J. 1996. An overview of freshwater biodiversity: With some lessons from African fishes. *Fisheries* 21:7–13.
- Sweitzer, R. A., D. Van Vuren, W. M. Boyce, and J. D. Waithman. 2000. Estimating sizes of wild pig populations in the north, and central coast regions of California. *Journal of Wildlife Management* 64:531–543.
- Tonn, W. M., and J. J. Magnuson. 1983. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166.
- Weaver, M. J., J. J. Magnuson, and M. K. Clayton. 1997. Distribution of littoral fishes in structurally complex macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2277–2289.
- Whittier, T. R., D. B. Halliwell, and S. G. Paulsen. 1997. Cyprinid distributions in Northeast U.S.A. lakes: evidence of regional-scale minnow biodiversity losses. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1593–1607.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999a. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature (London)* 401:464–467.
- Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rasmussen. 1999b. Patterns in food chain length in lakes: a stable isotope study. *American Naturalist* 154:406–416.