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BOREAL SHIELD WATERSHEDS

Lake Trout Ecosystems *in a Changing Environment*

Edited by
**J.M. Gunn, R.J. Steedman,
and R.A. Ryder**



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chapter thirteen

Species introductions and their impacts in North American Shield lakes

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Introduction

The aquatic biota of the world is rapidly being homogenized as a result of the introduction of species beyond their native range (Rahel, 2000; Ricciardi and MacIsaac, 2000). While

the geographic range of species naturally changes in response to climate and other environmental factors, increased trade and human activities combined with current and past fisheries management practices have provided many aquatic species with the opportunity to colonize and survive in far-flung regions of the world that were never before accessible (Moyle, 1986; Claudi and Leach, 1999). For example, 176 exotic fish species (species originating from outside the continent) now occur within the United States (Claudi and Leach, 1999). Another 331 species native to the United States now occur outside their native range (Claudi and Leach, 1999). A variety of other aquatic invaders span a wide range of taxonomic groups, with amphibians, mollusks, plants, and crustaceans the taxa most well represented (for a listing, see Claudi and Leach, 1999). Invasive species are now widely recognized as a major threat to aquatic ecosystems and biodiversity (Sala et al., 2000; Coblentz, 1990; Soule, 1990; Wilcove and Bean, 1994; Naiman et al., 1995), and the rate of new invasions continues to increase (Mills et al., 1994). In addition, exotic species have caused tremendous economic impacts, estimated to exceed \$137 billion annually in the United States alone (Pimentel et al., 2000).

Despite the magnitude of the invasive species problem in freshwaters, perhaps the majority of species introductions have minor or no observable adverse impacts on native species and ecosystems. But for the smaller number of high-impact invaders, ecological effects can be severe and range from the extirpation of entire faunas (e.g., native cichlids by Nile perch *Lates niloticus* in Lake Victoria, native bivalves by zebra mussels *Dreissena polymorpha* in Lake St. Clair) to the complete restructuring of the ecosystem in which changes brought about by the invader cascade through the food web, producing a variety of unpredictable and often undesirable ecological alterations (Zaret and Paine, 1973; Spencer et al., 1991; Lodge, 1993; Strayer et al., 1999; Vander Zanden et al., 1999).

Throughout this chapter, we use terminology consistent with that of Lodge (1993). A "colonist" is a species that has arrived at a site outside its previous range. If a population establishes, it can be referred to as "introduced" or as an "invader." Species native to other continents are called "exotic," while species native to that continent but occurring outside their native range are "nonnative." Whether an invader has a measurable impact on the invaded ecosystem or native community is a separate consideration.

Another important distinction is the means by which a nonnative or exotic species arrives. Intentional introductions most often involve the stocking of game fish into previously unoccupied waters. In addition, nonnative fish and invertebrates have often been stocked to provide forage, usually for other nonnative species. A well-known example is the introduction of the freshwater shrimp *Mysis relicta* into lakes of western North America, Sweden, and Norway, which has dramatically altered the food web of these ecosystems (Richards et al., 1975; Goldman et al., 1979; Spencer et al., 1991). Exotics are also stocked for the purpose of biological control, such as the use of western mosquitofish *Gambusia affinis* to control biting insect populations.

In addition to these intentional introductions, many introductions are unintentional. The dumping of unused live bait has been identified as a particularly important vector of nonnative species dispersal (Litvak and Mandrak, 1993; Ludwig and Leitch, 1996; Litvak and Mandrak, 1999). Ballast water discharge of oceangoing ships has been most responsible for the introduction of exotic species, primarily of Eurasian origin, into the Laurentian Great Lakes (Ricciardi and MacIsaac, 2000). The Great Lakes, in turn, act as a source population from which these exotics disperse into smaller inland lakes.

While lakes of the Precambrian Shield have been invaded by a number of nonnative species, Shield lakes do not provide ideal habitat for many potential invasive species. Water temperatures are too cold for many fish of southerly (primarily U.S.) distribution. Furthermore, the low concentration of dissolved ions (typically $\text{Ca}^{2+} < 5 \text{ mg/l}$) will preclude potential invaders such as zebra mussels, which require dissolved calcium concentrations

in the range of 15 to 30 mg L^{-1} (Mellina and Rasmussen, 1994; Ramcharan et al., 1992). For these reasons, Shield lakes are not likely to rival heavily invaded ecosystems such as the Laurentian Great Lakes, the Chesapeake Bay, and the San Francisco Bay estuary in terms of sheer numbers of invaders (Ricciardi and MacIsaac, 2000; Cohen and Carlton, 1998; Ruiz et al., 1999).

Yet despite the relatively small number of potential invaders, a developing literature indicates that Shield lake ecosystems and their biota can be highly sensitive to species invasions. While quantitative comparisons with other ecosystem types are not possible, dramatic impacts on native species and ecosystems in Shield lakes are well documented, perhaps more so than for many other ecosystem types. Because of the underlying ancient igneous bedrock, thin soils, a relatively recent (10,000 years) origin, and the lack of urban and agricultural development, Shield lakes are unproductive and support relatively few fish and invertebrate species. Barriers to fish and invertebrate dispersal during postglacial times also limited species distribution, further contributing to the low species richness. Compared to terrestrial and riverine ecosystems, lakes tend to be isolated from each other and can be considered islands of water in a sea of land (Magnuson, 1976).

The overall result is that Shield lakes have relatively simple, species-poor food webs that may be more vulnerable to perturbations than more productive, species-rich systems (McCann et al., 1998). In addition, these lakes are typically home to species such as lake trout *Salvelinus namaycush* and brook trout *Salvelinus fontinalis*, which are highly vulnerable to exploitation, habitat disturbance, and food web perturbations. So while relatively few nonnative species are presently invading Shield lakes, growing evidence indicates that they are having substantial impacts on Shield lake ecosystems (Evans and Loftus, 1987; Yan and Pawson, 1997; Vander Zanden et al., 1999; Yan et al., 2001).

Species invasions and introductions in Shield lakes must also be considered within the context of the predicted climate changes due to anthropogenic greenhouse gas emissions. Global circulation models (GCMs) that simulate a doubling of atmospheric CO_2 concentrations predict substantially warmer mean air temperatures as well as trends toward dryer conditions for much of the Canadian Shield (Magnuson et al., 1997). Climate warming will undoubtedly affect Shield lakes in a multitude of interconnected ways (reviewed in Magnuson et al., 1997), including a predicted increase in epilimnetic and hypolimnetic water temperatures (Destasio et al., 1996). Such warming will certainly have major implications for the thermal habitat of fish in lakes.

In addition, climate warming is predicted to increase the invasion rates of certain species (Jackson and Mandrak, 2002). The northern limit of smallmouth bass *Micropterus dolomieu* is effectively set by the short summer growing season of north-temperate lakes (Mandrak, 1989; Shuter and Post, 1990). Shuter and Post (1990) reported size-dependent over-winter starvation for smallmouth bass and yellow perch *Perca flavescens*. Population viability is thus contingent on their ability to complete a minimal amount of growth during their first summer (Shuter et al., 1980, 1989). Summer growth and over-winter survival of young-of-the-year (YOY) increase with water temperature and decrease as a function of latitude. Based on the Shuter model, the expected increases in water temperature would shift the zoogeographic boundaries for these cold-limited fish species (such as bass) northward by 500 to 600 km (Shuter and Post, 1990; Magnuson et al., 1997), which is likely to have important food web impacts (Vander Zanden et al. 1999).

The fundamental theme in this chapter is predicting, from easily measurable and readily available lake characteristics such as those presented in the appendices of this book, occurrences and impacts of invaders in individual Shield lakes. By focusing on predicting occurrences and impacts in individual lakes, lakes that are most vulnerable to invaders can be identified. This should be useful to lake managers for several reasons. For example, invader prevention efforts and education campaigns can target those lakes

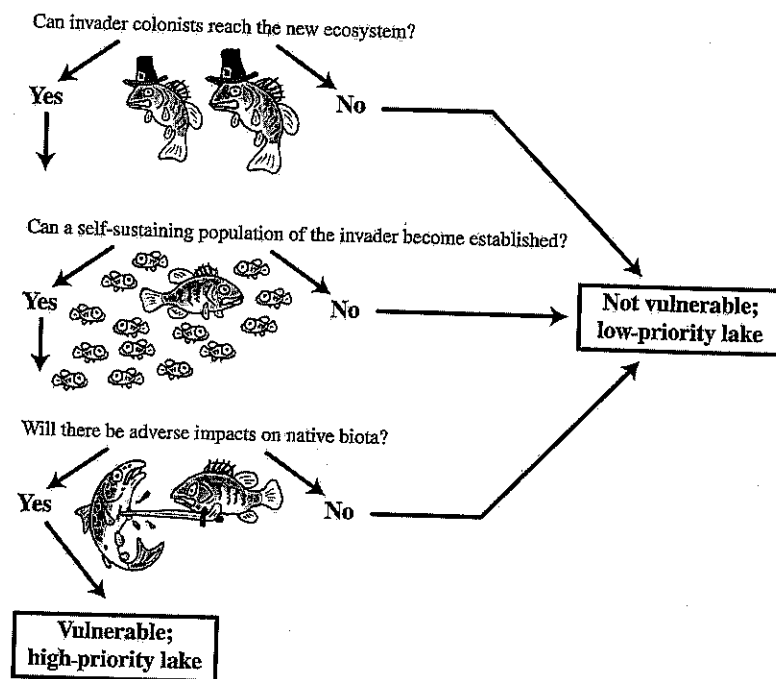


Figure 13.1 Three levels or filters of the invasion process used to examine the vulnerability of Shield lakes to aquatic invaders.

identified as vulnerable, allowing optimal use of limited management resources. Furthermore, efforts to monitor invader distribution and impacts can target systems identified as most vulnerable (likely to be invaded).

In our examination of species invasions and impacts in Shield lakes, we deconstruct the invasion process into three sequential components or filters; each should be considered in an effort for ultimate prediction of the dynamics and impacts of a known invader for individual lakes (Figure 13.1). The three components can be assessed using semiquantitative criteria (for example, the presence or absence of public road access). Alternatively, quantitative techniques such as logistic regression, discriminant function analysis, or artificial neural networks (ANNs) can be used to predict species presence or absence (Ramcharan et al., 1992; MacIsaac et al., 2000; Olden and Jackson, 2001). In either case, assessment of the three filters requires some knowledge of the biology of the invader and its interactions with natural ecosystems. The information required to address these questions will often be available in public databases. It must be recognized that determining the vulnerability of an individual lake to a given invader is a probabilistic exercise, and that this approach represents a caricature of the highly complex and unpredictable dynamics of species invasions on the landscape. Still, the value of this approach is that it provides predictions of the specific location of species invasions before they occur (Vander Zanden et al., in press).

The first filter is whether colonists can reach an uninvaded ecosystem (Figure 13.1). This depends on the dispersal mechanisms and potential of the invader as well as interactions with both human and nonhuman dispersal vectors. Factors such as road access, the presence of boat launches, and urban and residential development may be important determinants, although natural dispersal through interconnected waterways must also be considered.

The second filter is whether the invader is capable of surviving, reproducing, and establishing a self-sustaining population in the novel ecosystem. In many cases invader colonists may reach a given ecosystem, but environmental or biotic conditions are not appropriate and a population cannot establish. It should be noted here that the failure of an invader to establish a population following introduction does not mean that conditions are not appropriate for establishment because stochastic factors play an important role in determining invader establishment (Pimm, 1991).

The third filter is whether an established invader has adverse impacts on the native ecosystem or biota. This will depend on the population size or density of the invader, the strength and nature of biotic interactions (predation and competition) between the invader and native species, whether the invader occupies an "empty niche," and whether the invader has ecosystem-altering potential in its new ecosystem. This third filter will most likely be the most difficult to address. An invader can only establish if the first two filters are satisfied (colonists reach the novel system, and the conditions are appropriate for the invader to establish). An invasion is of particular ecological concern if all three questions are answered affirmatively (Figure 13.1).

This chapter focuses on several animal invaders that may have already invaded Shield lakes, are likely to continue to spread, and have the potential for dramatic impacts on Shield lake ecosystems. For each invader we separately consider the filters of the invasion process. The invaders examined in this chapter are (1) smallmouth bass and rock bass *Ambloplites rupestris*, (2) rainbow smelt *Osmerus mordax*, (3) the spiny water flea *Bythotrephes*, (4) zebra mussel and quagga mussel *Dreissena bugensis*, (5) rusty crayfish *Orconectes rusticus*, and (6) *Daphnia lumholtzi*. In the final section, we briefly mention other potential invaders of Shield lakes. Recent efforts have been made to predict the identity of future invaders (Ricciardi and Rasmussen, 1998; Kolar and Lodge, 2001). It is hoped that efforts to predict the identity, occurrences, and impacts of future invaders will contribute to the development of management strategies that can limit the further spread of species with the greatest potential impacts on Shield lake ecosystems.

Invaders in Shield lakes

Smallmouth bass and rock bass in Ontario

Smallmouth bass and rock bass were historically confined to Mississippi and Great Lakes drainage systems (Scott and Crossman, 1973; Lee et al., 1980). During the past century, these and other species of the family Centrarchidae have been widely introduced beyond their native range and now occur in much of western North America, many East Coast drainage systems, and northward into Shield lakes in regions of Ontario, Quebec, New Brunswick, Nova Scotia, and western Canada (MacCrimmon and Robbins, 1975; Lee et al., 1980; McNeill, 1995; Rahel, 2000). The northward range expansion of smallmouth bass and rock bass (hereafter referred to together as bass) into lakes of the Canadian Shield presently continues at a rapid pace. While resource management agencies no longer stock bass into new water bodies, bass continue to expand their range as a result of unauthorized introduction by anglers, accidental bait bucket transfers, and natural dispersal through drainage networks. Also, smallmouth bass and largemouth bass *Micropterus salmoides* have been introduced into dozens of countries on nearly every continent, although the ecological impacts of their introduction outside North America are virtually unknown (McDowall, 1968; Robbins and MacCrimmon, 1974; Welcomme, 1988).

Adult rock bass and smallmouth bass have broad, generalist diets and feed on a mix of prey fish, crayfish, and other zoobenthos with zooplankton, amphibians, songbirds, and small mammals in the diet on occasion (Hodgson and Kitchell, 1987; Hodgson et al.,

Table 13.1 Comparison of Central Ontario Lakes with and without Smallmouth Bass and Rock Bass

Type	Number of lakes	Prey fish species richness	Minnow catch rate ^a	Lake trout trophic position	Lake trout $\delta^{13}\text{C}$
Bass	5	2.4	6.6	3.28	-29.20
No bass	5	8.2 ^b	35.8 ^c	3.90 ^c	-27.48

Note: Values are means across five lakes.

^a Grams of fish/trap/day.

^b $p < .001$ between lakes with and without bass (one-tailed t test).

^c $p < .05$ between lakes with and without bass (one-tailed t test).

Source: Data from Vander Zanden et al. (1999).

1991; D.E. Schindler et al., 1997; Vander Zanden and Vadeboncoeur, 2002). Bass are efficient piscivores that can have substantial impacts on littoral prey fish diversity, abundance, and community structure in north-temperate lakes (Mittelbach et al., 1995; Chapleau et al., 1997; Vander Zanden et al., 1999; Whittier and Kincaid, 1999; Findlay et al., 2000). Considering the important top-down role of bass in structuring pelagic food webs and their range expansion during the last century, it is critical to examine the broader impacts of bass introductions on native species. Of particular concern is that reductions in forage fish following bass introductions into lakes could have adverse impacts on native top predators such as lake trout and brook trout, which rely on littoral prey fish (Olver et al., 1991; Vander Zanden et al., 1999).

Lakes of central and northern Ontario are rapidly being invaded by bass. We previously examined a series of nine Ontario lakes, five of which had been recently invaded, along with four uninvaded reference lakes (Vander Zanden et al., 1999). All of these lakes supported native, self-sustaining lake trout fisheries. Like most small headwater lakes in the region, these lakes lacked pelagic prey fish such as rainbow smelt, cisco, and lake whitefish, which are the preferred prey of lake trout. In the absence of these preferred prey fish, lake trout consume a mix of zooplankton, zoobenthos, and littoral prey fish such as minnows (family Cyprinidae) (Martin, 1970; Martin and Fry, 1972; Vander Zanden and Rasmussen, 1996). Among the nine lakes, littoral prey fish catch rates and species richness were significantly lower in lakes with bass relative to lakes without bass (Table 13.1). More compelling evidence comes from long-term (1981 to 1999) quantitative electrofishing monitoring of fish population abundance in seven lakes in the Haliburton Forest Preserve, Ontario. Abundance of cyprinids (expressed as number per square meter) is negatively correlated with centrarchid abundance (smallmouth bass and rock bass; Figure 13.2): $\log(\text{cyprinid abundance}) = -0.65 \log(\text{centrarchid abundance}) + 0.70$, $r^2 = .43$.

To address the broader food web consequences of bass introductions in central Ontario lakes, carbon and nitrogen stable isotopes were used to quantify differences in food web structure related to bass invasion (Vander Zanden et al., 1999). Corresponding with reduced littoral prey fish in invaded lakes, lake trout trophic position (based on $\delta^{15}\text{N}$ values) was reduced, indicating a diet consisting of invertebrates rather than fish. The $\delta^{13}\text{C}$ values indicated that lake trout relied primarily on littoral prey fish in lakes without bass and depended on zooplankton where they are sympatric with bass (Table 13.1, Figure 13.3).

In addition to this comparative analysis, long-term studies of two recently invaded lakes, MacDonald Lake and Clean Lake, revealed the food web consequences of bass impacts. In MacDonald Lake, littoral prey fish populations declined dramatically following bass establishment. Stable isotope analysis of freezer-archived muscle tissue samples collected throughout this period revealed a concurrent decline in lake trout trophic position (Figure 13.4). The invasion and establishment of bass into Clean Lake followed that

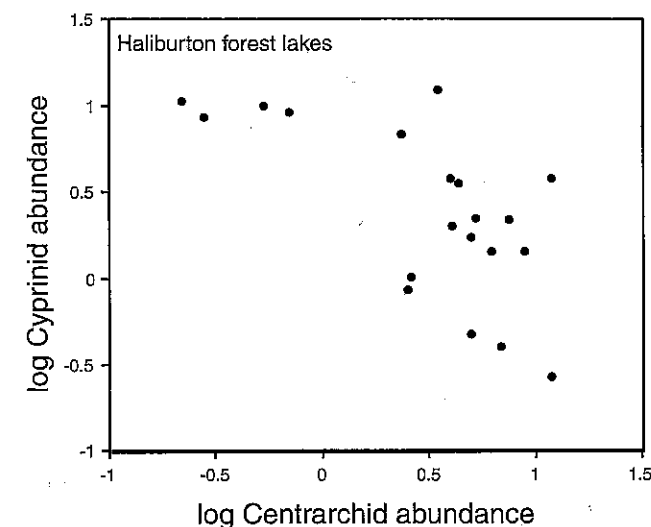


Figure 13.2 The relationship between centrarchid and cyprinid abundance (number of individuals) based on long-term (1981 to 1999) monitoring in seven lakes located in the Haliburton Forest Preserve, ON.

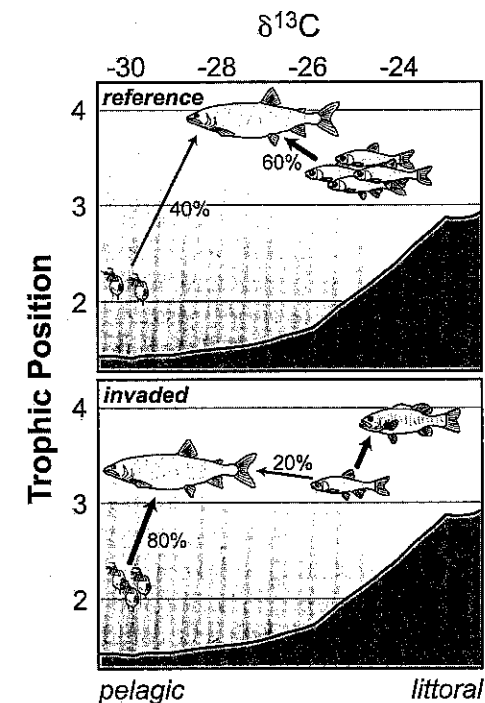


Figure 13.3 Food web structure based on carbon and nitrogen stable isotope studies of Shield lakes with and without smallmouth and rock bass. (Adapted from Vander Zanden et al., 1999.)

of MacDonald Lake, but some 6 years later, and the trophic position of Clean Lake lake trout did not show a marked change (Figure 13.4). The full impact of the bass invasions was not realized at that time, but has been subsequently. Ongoing monitoring of Clean Lake has chronicled a decline in prey fish, and Clean Lake has followed the same trajectory as MacDonald Lake (J.M. Casselman and D.M. Brown, unpublished data).

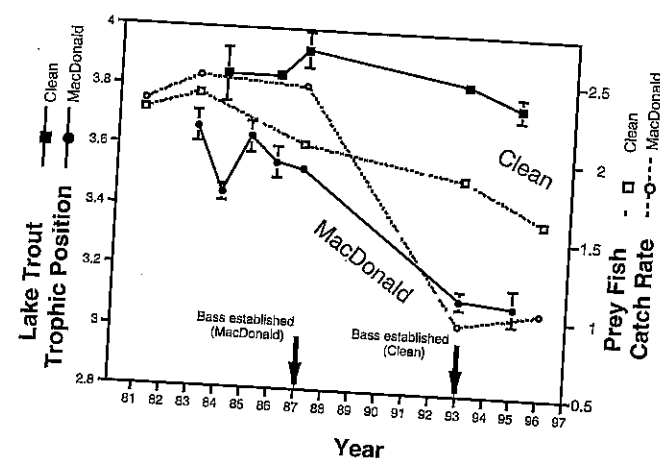


Figure 13.4 Long-term changes in minnow abundance as estimated by quantitative electrofishing and the corresponding shifts in lake trout trophic position. The arrows indicate the year both smallmouth bass and rock bass had become fully established. (Adapted from Vander Zanden et al., 1999.)

Invasion has affected angling success for lake trout. Although anglers initially saw increased catches, these catches quickly declined in response to change in the food web and lake trout predation activities and feeding. The more experienced anglers modified their fishing methods to simulate plankton and attract plankton-feeding lake trout. Subsequently, anglers have lost interest in this one-time spectacular recreational fishery. The loss of this resource has been far-reaching and insidious and has caused anglers to advocate stocking.

Competition between bass and lake trout has not been generally recognized, and it has been erroneously assumed that bass introductions have no effect on lake trout populations (Martin and Fry, 1972; Scott and Crossman, 1973; Olver et al., 1991). This interaction has been overlooked because bass inhabit inshore, littoral areas while lake trout inhabit offshore, pelagic areas. Despite these differences, bass and lake trout often share a common resource, and the introduction of bass has translated into the interruption of the trophic linkage of prey fish and lake trout. This change has directly affected lake trout growth rates, biomass, and productivity. Somatic growth and growth potential of lake trout were reduced 25 to 30% in MacDonald Lake following bass establishment. Even greater losses in reproductive growth were realized. This loss in lake trout growth and productivity, which was chronicled over time in MacDonald and Clean Lakes, has also been observed from point-in-time surveys in other lakes throughout the Haliburton Highlands of Ontario.

These invasions have been devastating to lake trout productivity. Invariably, anglers lose interest in these once-good lake trout fisheries and advocate the need for stocking, although such actions provide minimal benefit and could decrease the growth of existing lake trout because fish prey production has been diminished. The only advantage in stocking would be to provide potential prey for lake trout; this is an inefficient and unproductive way to try to bolster lake trout productivity and angling success.

Studies are under way to partition the relative importance of the different bass species in these invasions. This is not easy to separate given that smallmouth bass and rock bass often are coinvasers, and where one establishes it is not long until the other appears. There is, however, evidence that rock bass has the more important and devastating effect (J.M. Casselman and D.M. Brown, unpublished data).

Considering the tremendous number of Shield lakes (Olver et al., 1991), designing and implementing a management plan to minimize the adverse impacts of bass introductions is a daunting task. Using the framework of Figure 13.1, individual lakes in central Ontario that are vulnerable to bass invasion have been identified (Vander Zanden et al., in press). The analysis was performed using Geographic Information System (GIS) and included the central Ontario's more than 700 lakes containing a resident lake trout population. The study addressed the following questions:

1. Which lakes are likely to receive bass colonists?
2. Which lakes are likely to be able to support a bass population?
3. Which lakes are likely to be adversely impacted if bass establish a population?

Each of these three filters was modeled separately, and the subset of lakes classified as positive for all three criteria is considered vulnerable. These individual lakes should be the focus of management efforts aimed at slowing or halting further bass impacts.

Which lakes are accessible to bass colonists? To be accessible, a lake either must have road access or must occur in a drainage system already invaded by bass. This is a reasonable set of assumptions because bass are rapidly expanding their range due to unauthorized introduction by anglers, accidental bait bucket transfers, and natural dispersal through drainage networks (M.J. Vander Zanden, personal observation). Because the vast majority of lakes in central Ontario have public road access, only a relatively small number of lakes located in provincial parks (notably Algonquin Provincial Park) are protected from bass colonists due to their remote location and roadless status.

Which lakes are capable of supporting bass populations? Models that predict bass presence or absence in Ontario lakes based on glacial history, local and regional environmental variables, and biotic variables have been developed (Vander Zanden et al., in press). Using ANN models, lakes were classified according to bass presence or absence with 77 to 90% accuracy. When the predictions of the neural network model were examined for the 771 central Ontario lakes containing lake trout, bass were predicted but not observed (i.e., false presence) in 59 of these lakes. Thus while bass do not presently occur in these 59 lakes, the model indicates that these lakes have the appropriate conditions for supporting self-sustaining bass populations. These lakes are likely to be capable of supporting bass populations (note that this observation is independent of whether colonists are able or likely to colonize these lakes).

In which lakes will bass have adverse impacts on the native biota? Food web studies using diet data and stable isotopes indicated that lake trout are linked to the pelagic food web in lakes containing pelagic prey fish such as rainbow smelt, lake herring *Coregonus artedii*, and lake whitefish *Coregonus clupeaformis* (Vander Zanden and Rasmussen, 1996; Vander Zanden and Rasmussen, 2002; Vander Zanden et al., in press). In lakes lacking pelagic prey fish, lake trout tend to be linked to the littoral food web through consumption of littoral prey fish (Vander Zanden and Rasmussen, 1996; Vander Zanden et al., 1999). Because the availability of littoral prey fish is a function of bass presence, competitive bass-trout interactions are predicted to occur only in lakes lacking pelagic forage fish. Thus, the presence of pelagic prey fish mediates the strength of bass-lake trout interactions. If pelagic prey fish are present, lake trout are buffered from impacts of bass on littoral prey fish populations (Figure 13.5) (Vander Zanden and Rasmussen, 2002; Vander Zanden et al., in press). With bass-lake trout interactions predictable from species composition, we can identify lake trout populations likely to be impacted by bass introductions. Of the 59 lake trout lakes classified as capable of supporting bass (Filter 2), 38 did not contain pelagic prey fish and are thus vulnerable to bass impacts based on food web considerations.

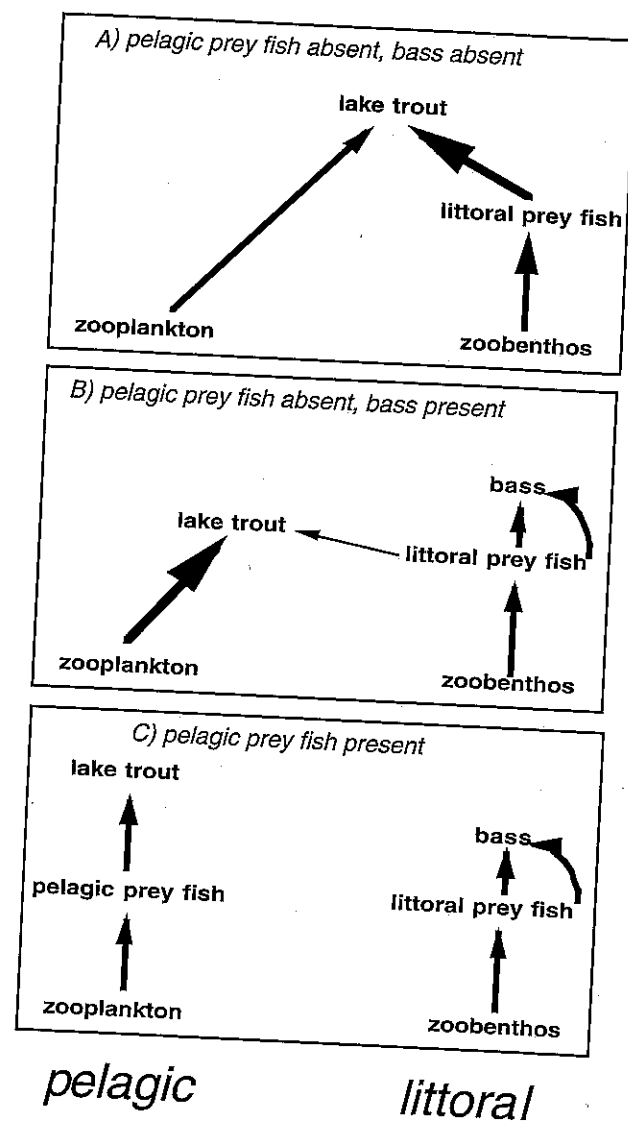


Figure 13.5 A summary of food web structure for three general food web types based on stable carbon and nitrogen isotopes: A) bass absent, pelagic prey fish absent; B) bass present, pelagic prey fish absent; C) pelagic prey fish present. (Based on Vander Zanden et al., 1999, in press; Vander Zanden and Rasmussen, 2002.)

The many thousands of Shield lakes that dot the north-temperate landscape provide a distinct management problem of how to apply limited resources to combat the spread of nonnative species and minimize potential adverse impacts. By separately considering the elements of the invasion process (Figure 13.1), lakes that are vulnerable to a particular invader were identified. In our study, roughly 5% of the lake trout lakes were classified as vulnerable to bass invasions, and these lakes should be the focus of efforts to prevent future invasion. While prevention of future introductions is the backbone of a successful invader management strategy, mitigating impacts where invaders have already established will require the development of techniques to reduce impacts. If historic levels of lake trout production are to be realized through natural reproduction and self-sustaining lake trout populations, then these bass invaders must be eliminated or at least substantially

reduced. Yet to date, there are few examples of successful eradication of aquatic invaders: The extirpation of nutria from England during the 1980s and trout from small Sierra Nevada (California) lakes are among the few success stories. The limited potential for eradication of invaders underscores the central role of prevention as the most effective strategy for minimizing invader impacts.

Rainbow smelt

Rainbow smelt are an anadromous species native to coastal waters of Canada and the United States; they have a historical range that extends from coastal Labrador to New Jersey. In addition, there are a number of native landlocked freshwater populations of rainbow smelt along the Atlantic coast. Smelt were originally introduced into the Great Lakes drainage in 1912 into Crystal Lake, Michigan. Smelt spread to nearby Lake Michigan by 1923 and subsequently spread to the rest of the Great Lakes during the following decade (Dymond, 1944; Christie, 1974; Bergstedt, 1983).

Smelt have since dispersed beyond the Great Lakes into inland lake and river systems. Smelt were stocked into Lake Sakakawea, North Dakota, a reservoir on the Missouri River in 1971, and subsequently spread through much of the Missouri and Mississippi drainage systems (Mayden et al., 1987). Smelt have been stocked into other reservoirs of the western United States and have similarly expanded their range (Jones et al., 1994; Johnson and Goettl, 1999). This species now occurs in the Hudson Bay drainage waters of northwestern Ontario, Manitoba, and Minnesota (Franzin et al., 1994) and has recently reached Hudson Bay via the Nelson River (Remnant et al., 1997). Smelt continue to colonize Shield and non-Shield lakes within the Great Lakes drainage basin (Evans and Loftus, 1987; Hrabik and Magnuson, 1999). In the most comprehensive synthesis of smelt biology in inland lakes, Evans and Loftus (1987) reported the presence of smelt in 194 inland Ontario lakes, of which only 4 are thought to be native, relict populations. There are undoubtedly many more introduced smelt populations in lakes of the Canadian Shield, although little effort has been made to document their ever-expanding distribution.

In this section we examine the three filters of the invasion process (Figure 13.1) for rainbow smelt. Efforts to identify lakes that are likely to receive smelt colonists require an understanding of the mechanisms of smelt dispersal. Smelt can spread rapidly across the landscape once they have been introduced, as evidenced by their rapid downstream colonization of the Missouri/Mississippi and Hudson Bay drainages (Franzin et al., 1994; Remnant et al., 1997). Yet anthropogenic introductions, either intentional or accidental, are thought to be the primary vector of smelt introduction into new lakes.

This conclusion has been reached by numerous authors based on the close association of smelt with urban and cottage development and lake appearances that cannot be explained by dispersal from nearby lakes (Evans and Loftus, 1987; Hrabik and Magnuson, 1999). In northern Wisconsin, smelt have been deliberately introduced into lakes by anglers with the intention of increasing opportunities for netting smelt during their spring spawning runs (called *smelting*; T. Hrabik, July, 2002, personal communication). Another likely vector is the unintentional introduction of fertilized eggs into lakes while cleaning and processing smelt collected from other lakes. While perhaps discouraging, this also suggests that the spread of smelt is partially preventable and that educational efforts could reduce their spread into new waters. The available evidence indicates that lakes occurring in the same drainage as other smelt lakes as well as lakes with road access and cottage development should be considered open to rainbow smelt colonists. In addition, lakes with a large number of nearby smelt populations are far more likely to receive smelt colonists than lakes in regions lacking smelt populations.

Table 13.2 Characteristics of Ontario Lakes Containing Rainbow Smelt

	Mean	Minimum	Maximum
Lake area (km ²)	52.3	0.1	4480
Mean depth (m)	11.6	2.0	38.7
Maximum depth (m)	35.7	4.0	213.5
TDS (mg/l)	49.5	5.5	231.4
Surface water pH	7.2	6.0	9.3
Secchi depth (m)	4.9	0.5	10.5
Fish species richness	11.3	3	63

Source: Data from Evans and Loftus (1987).

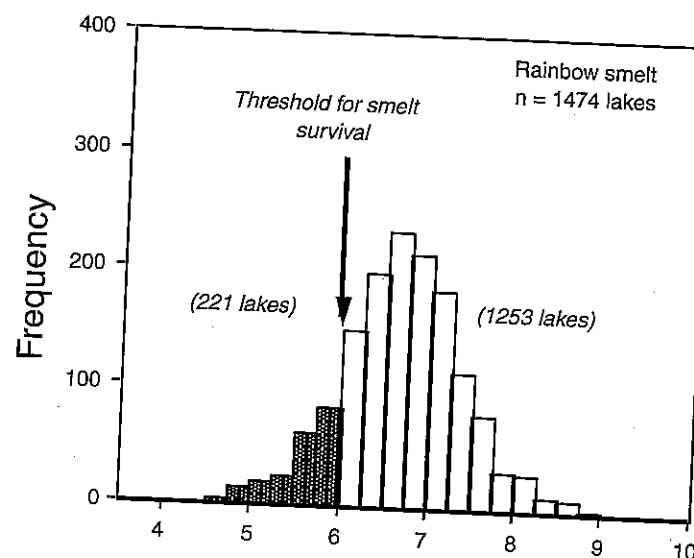


Figure 13.6 Frequency distribution of pH values for North American lake trout lakes (data from Appendix 2). The arrow indicates the threshold pH value of 6.0 for rainbow smelt *Osmerus mordax* occurrence as reported by Evans and Loftus (1987). Low pH is predicted to limit smelt occurrence in 221 of the 1253 Shield lakes for which data are available (<18% of lakes).

To identify lakes capable of supporting rainbow smelt populations Evans and Loftus (1987) summarized the morphometric and limnological parameters for Ontario lakes that contained smelt as of 1987 (reproduced in Table 13.2). While smelt typically inhabit lakes that are relatively deep, low in productivity, and with intermediate transparency, they occur in lakes that span a wide range of conditions, including lakes as small as a few hectares in size and as shallow as 4 m maximum depth (Evans and Loftus, 1987). One significant finding of Evans and Loftus (1987) was that smelt do not occur in lakes with pH less than 6.0, indicating a threshold pH value that may limit smelt occurrences. A frequency distribution of pH values for the available lake trout lakes in North America ($n = 1474$ lakes; data from Appendix 2) was plotted (Figure 13.6). The arrow indicates the pH 6.0 threshold for rainbow smelt; lakes with a pH to the left of the threshold (<18% of the Shield lakes; 221 of the 1474 lakes) are predicted not to support a smelt population. Interestingly, the pH of Shield lakes has been rising during the past two decades due to decreased SO_2 emissions (Stoddard et al., 1999). This result suggests that pH restriction of further smelt invasion might weaken as lakes recover from acidification.

Aside from effects of pH, rainbow smelt distribution does not appear to be severely limited by morphometric and limnological parameters, and rainbow smelt persist in a variety of lakes, reservoirs, and flowage ecosystems if minimal habitat and environmental conditions are met. Development of more sophisticated quantitative models that identify specific lakes likely to support rainbow smelt (Ramcharan et al., 1992; MacIsaac et al., 2000) will be a critical step toward characterizing lake vulnerability.

There has been little progress in understanding why smelt sometimes (but not always) have adverse impacts on native biota. A review of 35 individual cases of rainbow smelt introduction in inland lakes provided substantial evidence for adverse impacts of smelt on native biota, with the most frequent impact declines in lake whitefish and lake herring populations (Evans and Waring, 1987). Adverse impacts on lake trout, walleye *Stizostedion vitreum*, and burbot *Lota lota* populations were also noted. Lake whitefish recruitment failure in Twelve Mile Lake, ON, was attributed to intense rainbow smelt predation on YOY (Loftus and Hulsman, 1986). In Lake Simcoe, ON, declines in lake whitefish were also attributed to smelt introduction, although a positive correlation between yellow perch and smelt abundance was observed (Evans and Waring, 1987). Hrabik et al. (1998) reported different impacts of smelt introduction in two northern Wisconsin lakes. Smelt were a strong competitor of yellow perch in Crystal Lake, WI, but were a major predator of lake herring (cisco) in nearby Sparkling Lake, ultimately causing the extirpation of the lake herring population (Hrabik et al., 1998).

Explicitly viewing smelt from a predator-prey perspective serves as a basis for understanding their impacts as a predator and competitor of the native biota (Hrabik et al., 1998). The available case studies indicate that smelt are often a major player in aquatic food webs, acting as an important prey, predator, and competitor. Smelt often become the dominant fish species in the pelagic zone of invaded lakes. In addition, smelt are highly efficient predators and consume large prey items relative to other fish of similar body size. Consequently, smelt can dramatically reduce or even eliminate preferred prey. Smelt also have a broader diet than other forage fish, which commonly includes copepods, cladocerans, *Mysis*, zoobenthos, YOY smelt and other YOY fish (Vander Zanden and Rasmussen, 1996). This broad, generalist diet allows smelt to consume resources opportunistically as they become abundant and to switch to alternative prey when the abundance of preferred prey is reduced. Their generalist and omnivorous feeding behavior allows smelt to avoid food limitation, maintain a large population, and sustain strong predatory impacts on preferred prey (Courchamp et al., 2000).

Which factors might determine smelt impacts on native forage fish? One possibility is that in lakes with a greater diversity of alternative prey, smelt can become more abundant and have greater predatory impacts on preferred prey (i.e., YOY native fish). This suggests that smelt should have greater impacts on native fish in larger lakes in which there are more prey options to exploit. An alternative hypothesis is that the degree of spatial overlap between adult smelt and the vulnerable (YOY) life stage of native fish determines smelt impacts. One might predict that the biota in small, shallow lakes would be more vulnerable to smelt impacts because there is greater potential for spatial overlap between life stages of smelt and native fish. While the link between smelt introductions and declines of native pelagic fish is strong, smelt do not universally have adverse impacts, and the mechanism and magnitude of smelt impact vary widely from system to system. Predicting smelt impacts on native biota is an important area of future research.

A final impact to consider is the potential effect of smelt introduction on concentrations of contaminants in top predators. Smelt are a common prey item of game fish such as lake trout, walleye, and Atlantic salmon (Vander Zanden and Rasmussen, 1996; Vander Zanden et al., 1997). Of concern is the observation that smelt introduction corresponds with increased concentration of mercury and polychlorinated biphenyls (PCBs) in game fish

(Akielaszek and Haines, 1981; MacCrimmon et al., 1983; Mathers and Johansen, 1985; Vander Zanden and Rasmussen, 1996). The presumed explanation is that smelt have a higher trophic position than other forage fish due to their piscivorous diets, and fish that feed on smelt would also have an elevated trophic position and thus a greater scope for contaminant biomagnification. While other factors such as increased growth rates may counter the effects of longer food chains (Evans and Waring, 1987), the available evidence indicates that smelt introduction can lead to increased concentrations of contaminants in top predator fish.

Bythotrephes and *Cercopagis*

The spiny water flea (identified as either *Bythotrephes cederstroemi* or *Bythotrephes longimanus*, hereafter referred to as *Bythotrephes*) is a predatory zooplankter native to northern Europe and Asia. This species was first discovered in North America in Lake Ontario in 1982 and was likely transported to North America via ship ballast water. From Lake Ontario it rapidly spread to the other Great Lakes, then to inland lakes in Ontario, Michigan, Minnesota, and Ohio (Yan et al., 1992). As of 1999, *Bythotrephes* had been identified in 50 North American lakes in the Great Lakes region (MacIsaac et al., 2000; Yan et al., 2002). Little is known about the vector of spread for *Bythotrephes*, although it is likely that they are unintentionally spread via bait buckets, bilge water, live wells, and the use and reuse of anchor ropes by recreational boaters. As with rainbow smelt and bass, any lake with road access and recreational boating traffic should be considered vulnerable to *Bythotrephes* colonists.

In Europe, *Bythotrephes* inhabit lakes spanning a wide range of physical, chemical, and biological conditions. MacIsaac et al. (2000) used discriminant function analysis (DFA) to predict *Bythotrephes* distributions and occurrences in Europe and then applied the resulting model to North American lakes. The significant variables in the model were water clarity, lake area, chlorophyll-a concentration, and maximum depth. The model correctly classified lakes according to *Bythotrephes* presence or absence in more than 90% of European lakes. When applied to North America, the model accurately predicted occurrences of *Bythotrephes* in lakes that presently contain the species (82%). More important, the model predicted the occurrence of *Bythotrephes* in many lakes that presently lack *Bythotrephes*. The high frequency of false negatives among North American lakes indicates that many are capable of supporting *Bythotrephes*, but have not yet been colonized. We plotted lake area versus Secchi depth for 1700 Ontario lakes (Figure 13.7) and superimposed the division for *Bythotrephes* presence or absence (estimated from MacIsaac et al., 2000). It is clear from this figure that conditions are favorable for *Bythotrephes* to inhabit the vast majority of Shield lakes, and that thousands of North American lakes appear to provide appropriate habitat for this invader.

Bythotrephes is a voracious predator on other zooplankton. Evidence from North American and European lakes indicates that the introduction of *Bythotrephes* often dramatically restructures the zooplankton community. While laboratory feeding studies indicate preference for large zooplankters (>2.0 mm) (Schulz and Yurista, 1998), field studies indicate that size-selective impacts are highly variable. Introduction of *Bythotrephes* reduced populations of large herbivorous zooplankton (*Daphnia*) in Lake Michigan (Lehman, 1988; Lehman and Caceres, 1993). However, in Harp Lake, Ontario, *Bythotrephes* reduced the abundance of smaller zooplankters such as *Bosmina*, *Chydorus*, and *Diaphanosoma*, while larger zooplankton species (*Holopedium*, *Daphnia*) actually increased in abundance (Yan and Pawson, 1997). While it is clear that *Bythotrephes* impact zooplankton communities through predation, the size-specific impacts on zooplankton communities have been generally unpredictable.

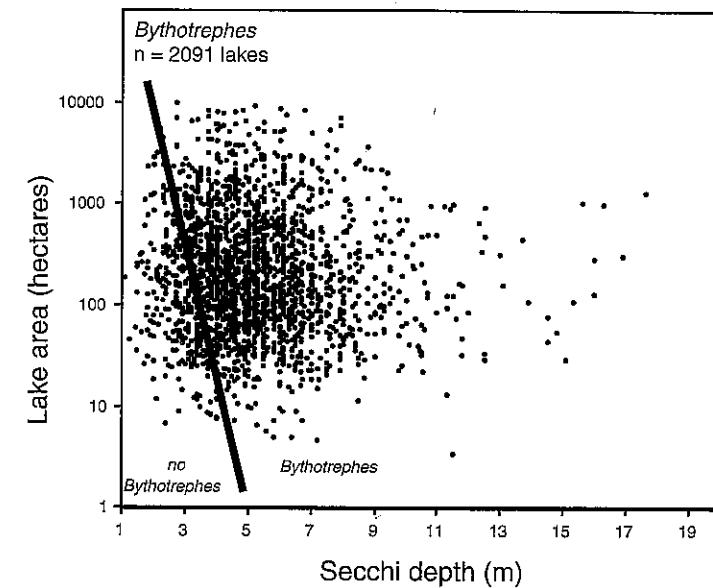


Figure 13.7 Lake area and Secchi depth as factors potentially limiting the distribution of *Bythotrephes* in North American Shield lakes (data from Appendix 2). The diagonal line indicates the predicted cutoff for *Bythotrephes* presence or absence based on the two most important predictor variables from MacIsaac et al. (2000). Lakes to the left of the diagonal line are predicted not to support *Bythotrephes*; lakes to the right are predicted potentially to support this invader.

Bythotrephes are large relative to other zooplankton species and are a preferred prey of zooplanktivorous fish (Mills et al., 1992; Coulas et al., 1998). This suggests that *Bythotrephes* abundances in inland lakes might be controlled by fish predation (Coulas et al., 1998; Yan and Pawson, 1998). While *Bythotrephes* are an important prey of adult planktivores, their large size and long spine likely inhibit consumption by YOY and juvenile fish. The replacement of edible zooplankters by inedible *Bythotrephes* may have negative impacts on growth rates of YOY fish and recruitment (Hoffman et al., 2001), although this question requires further examination in inland lakes.

A similar zooplankter, the fishhook water flea *Cercopagis pengoi*, native to the Ponto-Caspian region, was discovered in Lake Ontario in the summer of 1998 (MacIsaac et al., 1999). *Cercopagis* has since spread to Lake Michigan and the Finger Lakes in New York (Charlebois et al., 2001). This species probably has dispersal capabilities similar to that of *Bythotrephes* and is likely to spread to more inland lakes with recreational watercraft. *Cercopagis* have invaded aquatic ecosystems well beyond its native range in Europe (MacIsaac et al., 1999) and can thrive across a broad range of environmental conditions, indicating that this species may thrive in North American lakes (Ricciardi and Rasmussen, 1998). Projected impacts are similar to that for *Bythotrephes*.

Dreissenid mussels

Dreissenid mussel invaders to North America include zebra mussels and quagga mussels. *Dreissenid* mussels established in the Great Lakes in the 1980s and have since colonized large portions of North America. Much has been written about zebra mussels in North America, and a number of excellent reviews are available (Neary and Leach, 1992; MacIsaac, 1996; Strayer et al., 1999). Despite the rapid spread and widespread distribution of *dreissenids* in North America, most Shield lakes are not expected to support thriving

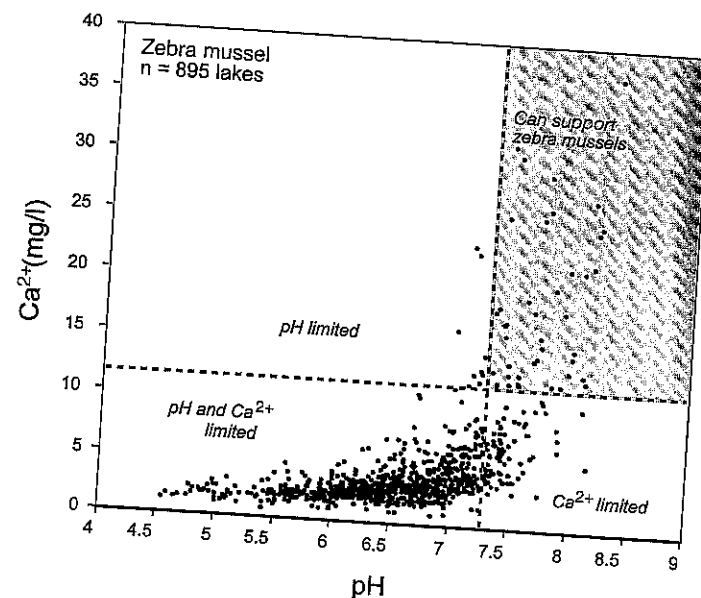


Figure 13.8 Thresholds potentially limiting the distribution of zebra mussels *Dreissena polymorpha* in North American lake trout lakes (data from Appendix 2). The vertical line indicates the pH threshold of 7.3, below which they do not survive (Ramcharan et al., 1992). The horizontal line indicates a Ca^{2+} threshold of 12 mg/l (Sprung, 1987), below which they are not likely to persist.

dreissenid populations. The presence of zebra mussels is limited primarily by low Ca^{2+} concentrations and low pH. In Europe, zebra mussels do not occur below a pH 7.3 threshold (Ramcharan et al., 1992). Several threshold values for Ca^{2+} have been reported: 12 mg/l (Sprung, 1987), 15 mg/l (Mellina and Rasmussen, 1994), and 28.3 mg/l (Ramcharan et al., 1992). Other potentially limiting factors such as oxygen concentrations, upper temperature, and salinity would not limit the distribution of dreissenids in Shield lakes (Karatayev et al., 1998). Using data from Appendix 2, we plotted Ca^{2+} versus pH for North American lake trout lakes ($n = 895$ lakes; Figure 13.8). The pH 7.3 threshold and the lowest right section of Figure 13.8 have the potential to support zebra mussels (i.e., both Ca^{2+} and pH threshold values are exceeded). Furthermore, Ca^{2+} concentrations in Shield lakes have been declining during the past two decades in correspondence with recovery from acidification (Keller et al., 2001). While this indicates that a small proportion of Shield lakes is capable of supporting dreissenids, this species typically has dramatic impacts on lake ecosystems where it occurs (MacIsaac, 1996), and the potential impacts of zebra mussels in select Shield lakes should not be neglected.

Rusty crayfish

Rusty crayfish *Orconectes rusticus* are native to the Ohio River Basin and since the 1960s have spread northward into Wisconsin, Michigan, Iowa, New York, Minnesota, Ontario, and all of the New England states. Although now banned for use as live bait in most states, rusty crayfish were once common live bait, and bait bucket releases are believed to have been introduced to control nuisance aquatic vegetation (Magnuson et al., 1975). In northern Wisconsin lakes, Capelli and Magnuson (1983) found that, unlike the native

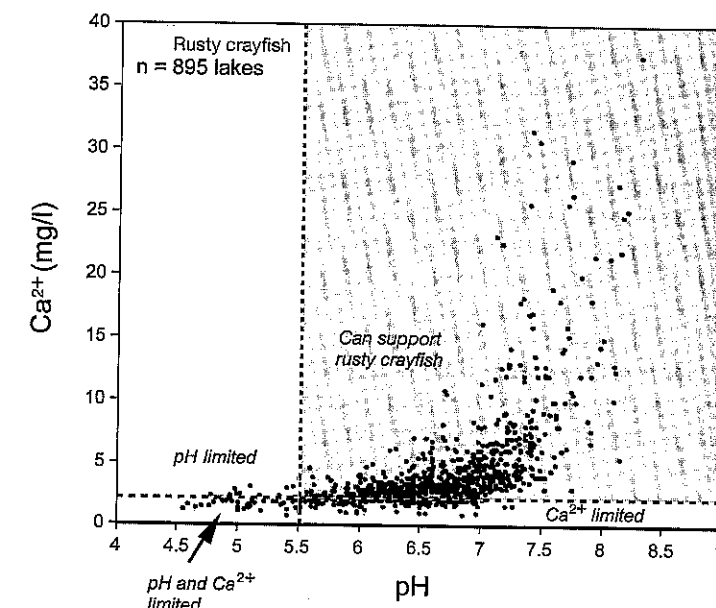


Figure 13.9 Thresholds potentially limiting the distribution of rusty crayfish *Orconectes rusticus* in North American lake trout lakes (data from Appendix 2). The vertical line is the pH threshold of 5.5, below which rusty crayfish tend not to occur in lakes (Berrill et al., 1985). The horizontal line indicates the Ca^{2+} threshold of 2.5 mg/l (Capelli and Magnuson, 1983), below which rusty crayfish are not observed.

crayfish *O. virilis* and *O. propinquus*, the distribution of rusty crayfish among suitable lakes was positively correlated with human activity and proximity to major roads. Once in a drainage system, rusty crayfish use natural waterways to spread along rivers and from lake to lake. However, natural dispersal is slow relative to other aquatic invaders because rusty crayfish do not have a pelagic larval stage. Colonization around the littoral zone of a single lake can take many years (Wilson, 2002; Wilson and Magnuson, in review).

Rusty crayfish distribution is likely limited by physiochemical factors, particularly dissolved calcium and pH. Berrill et al. (1985) rarely found rusty crayfish in lakes with a pH less than 5.5. In laboratory experiments, rusty crayfish stage III juveniles do not survive at pH 5.0 or lower, while adults do not survive at pH 4.7 or lower. Dissolved calcium is another limiting factor; lakes with dissolved Ca^{2+} concentrations less than 2.5 mg/l do not support rusty crayfish populations (Capelli and Magnuson, 1983). Based on these threshold values for pH and calcium, over 70% of Shield lakes are considered suitable for rusty crayfish colonization (Figure 13.9).

The availability of suitable habitat and the presence of predators, particularly fish, may also influence the establishment and abundance of rusty crayfish in lakes. Rusty crayfish prefer firm substrates (cobble or sand) over mucky substrates (Kershner and Lodge, 1995), and shelter in the form of logs or cobble is required for egg or young-carrying females and molting individuals. Rusty crayfish are consumed by several fish species, but quickly reach a size refuge from all but the largest predators (Stein and Magnuson, 1976). This species is also highly omnivorous, foraging opportunistically on aquatic plants, benthic invertebrates, fish eggs, detritus, and small fish (Momot, 1995), indicating a limited potential for resource limitation.

Once established in lakes and rivers, rusty crayfish tend to displace native crayfish (primarily *O. propinquus* and *O. virilis*) (e.g., Berrill, 1978; Capelli, 1982), sometimes

reaching densities 20 times greater than that of the native crayfish (Wilson and Magnuson, in review). Rusty crayfish introduction is associated with declines in aquatic plant biomass and species richness, low densities of snails, and overall reductions in littoral fish abundance (Lodge and Lorman, 1987; Olsen et al., 1991; Lodge et al., 2000; Wilson, 2002). In summary, while rusty crayfish are no longer used as live bait and are a relatively slow natural disperser, the majority of Shield lakes are potentially vulnerable to rusty crayfish colonization. Furthermore, rusty crayfish tend to have dramatic, ecosystem-altering impacts and as such should be of high concern for lake managers.

Daphnia lumholtzi

This large, spiny cladoceran zooplankton species first appeared in North America in 1989 and has spread extremely rapidly through reservoirs in the southern and midwestern United States (Havel and Hebert, 1993), reaching Lake Erie by 1999 (Muzinic, 2000). The live wells, bait buckets, and bilge water of recreational anglers are thought to be the major transport vector for this exotic zooplankton (Dzialowski et al., 2000; Havel and Stelzleni-Schwent, 2000).

Feeding trials with juvenile bluegill sunfish indicated that *D. lumholtzi* were far less edible due to their spiny morphology than native *Daphnia* of the same size (Swaffar and O'Brien, 1996). The effect was particularly evident among the smallest bluegill (20 to 25 mm), indicating potential impacts on growth and survivorship of YOY fish. *Daphnia lumholtzi* prefers warm waters and is often abundant during middle-to-late summer in southern reservoirs (Havel et al., 1995; Kolar et al., 1997; East et al., 1999; Lennon et al., 2001). In laboratory studies, *D. lumholtzi* outperforms other *Daphnia* species in water between 25° and 30°C, although they can survive and reproduce at much cooler temperatures (Lennon et al., 2001) and are occasionally found in Missouri reservoirs during late fall (J. Havel, October, 2002, personal communication). These findings suggest that while some Shield lakes may support *D. lumholtzi* populations, they are not likely to thrive or dominate the zooplankton community in the cold waters of Shield lakes.

Other exotics

Another concern is that the Laurentian Great Lakes presently harbor a number of nonnative fish such as ruffe *Gymnocephalus cernuus*, round goby *Neogobius melanostomus*, and tubenose goby *Proterorhinus marmoratus* (Jude et al., 1992). While there is certainly potential for these fish species to be transported to inland lakes via angler's bait buckets (Litvak and Mandrak, 1993; Litvak and Mandrak, 1999) or even through natural dispersal, such occurrences are expected to be rare, and these species should spread at a slow rate. There are very few occurrences of these species in inland lakes, and we do not consider further the occurrences and impacts of these nonnative fish.

This chapter focuses on animal invaders in Shield lakes and as such does not consider invasive aquatic plants such as Eurasian watermilfoil *Myriophyllum spicatum* invasions. Invasive aquatic plants have the potential to alter the physical structure of the littoral zone and represent potentially large perturbations to lake ecosystems (Carpenter and Lodge, 1986). Eurasian watermilfoil has recently become problematic in acid lakes of eastern New England (Les and Mehrhoff, 1999; Crow and Hellquist, 2000) and central and northern Ontario and may continue to spread among Shield lakes. Eurasian watermilfoil can reproduce via fragments and winterbud — as well as seed and expansion — enabling easy transport via boats, boat trailers, and live wells.

Conclusions

Perhaps with the exception of *D. lumholtzi*, the invasive species highlighted in this chapter all have potential for dramatic impacts on Shield lake ecosystems. The first three invaders (bass, rainbow smelt, and *Bythotrephes*) are already a problem and are almost certain to continue to colonize new systems in the future, particularly in light of predicted global climate change scenarios. In addition to the handful of invaders considered here, there will undoubtedly be new waves of invaders that will establish in the future, and prediction of their identity is an important goal (Ricciardi and Rasmussen, 1998; Kolar and Lodge, 2001). For the exotic species it is critical to recognize that colonization of the Laurentian Great Lakes serves as a stepping stone for the eventual colonization of inland lakes. The Great Lakes can thus be viewed as source populations from which the species disperse outward to the smaller inland lakes. If the past is any predictor of the future, subsequent invaders of Shield lakes will continue to be a subset of the Great Lakes invader pool.

At timescales of decades to centuries, the identity and rates of nonnative invasions in Shield lakes will depend on a number of factors: the establishment of invaders in the Great Lakes, the trajectory of climate change, patterns of residential development and recreational boating (Padilla et al., 1996), educational and outreach efforts, and the development of legislation restricting the transport and introduction of nonnative species. In this chapter we have emphasized the importance of developing models to predict the occurrences and impacts of specific invaders in individual lakes. These predictions will ultimately derive from an understanding of the biology and physiological tolerances of the invader, attributes of the receiving community and ecosystem, and the often-subtle interactions between them. This approach can yield models to predict the location and impacts of invaders (Ramcharan et al., 1992; Koutnik and Padilla, 1994; Buchan and Padilla, 2000; MacIsaac et al., 2000; Vander Zanden et al., in press). By identifying vulnerable lakes and regions, management efforts aimed at preventing future invasions can be most efficiently focused. Indeed, prevention of nonnative introductions remains the most effective invasive management strategy because once an aquatic invader becomes established elimination of the invader is difficult, and further colonization of surrounding systems commonly follows (Hrabik and Magnuson, 1999). While prevention is imperative to stem the tide of invasions, we also note that serious research effort has not yet been invested into methods for controlling or eliminating aquatic invaders.

Shield lakes and their watersheds are subject to a diverse range of anthropogenic impacts, many of which are documented elsewhere in this volume. Introductions of nonnative species are clearly among the leading threats to lake ecosystems and in fact were recently noted as the leading threat to biodiversity in lakes (Sala et al., 2000). The diversity of threats and their potential interactions pose difficult management challenges that require adaptation to our increasing understanding and the ever-changing nature of the threats.

An understanding of some of the interactions between these diverse impacts is starting to emerge. Climate warming is predicted to promote further bass introductions, with potentially massive impacts on minnow diversity in Shield lakes (e.g., Jackson and Mandrak, 2002). Climate change, increased ultraviolet radiation, and acid deposition have cumulative and perhaps synergistic effects on boreal landscapes (D.W. Schindler, 1998). While a single species introduction may or may not be sufficient to cause an observable adverse impact on a Shield lake ecosystem, addition of multiple invaders, along with a variety of other simultaneous stressors, expands the scope for impacts dramatically. It becomes rapidly apparent that the greatest gap in our understanding is that of cumulative impacts and the potential interactions among multiple stressors. Addressing this issue is the greatest challenge for the future management of Shield lake ecosystems.

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