Food Web Perspectives on Studies of Bass Populations in North-Temperate Lakes

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Abstract.—There is growing recognition of the potential contributions of food web and ecosystem-level approaches to lake and fisheries management. Often, these approaches are data intensive and require information on predator–prey interactions and consumer diets. Gut content analysis adequately provides population-level diet information, but is more limited in ability to provide information at finer (intra-population) or coarser (whole food web) organizational scales. In this study, we review three applications of stable isotope techniques to studies of bass trophic ecology. In each case, the approach is used to provide quantitative information at organizational levels that is otherwise difficult to obtain using gut content analysis. In the first example, we examine intra-population trophic variation in young-of-the-year (YOY) smallmouth bass *Micropterus dolomieu*. $\delta^{13}C$ indicated ontogenic trophic habitat shifts from pelagic to benthic prey during first summer. $\delta^{15}N$ was correlated with body size on the final sample date, suggesting that dietary differences might explain intra-population variation in growth rates. The second example demonstrates an application of stable isotope techniques to examine impacts of species invasion at the whole-food web scale. This approach revealed that lake trout *Salvelinus namaycush*, typically viewed as a pelagic predator, can often rely heavily on littoral prey fish. Reduction in littoral prey fish following the invasion of nonnative smallmouth bass and rock bass *Ambloplites rupestris* prompted lake trout to shift towards planktivory. The third example uses stable isotope information to classify lakes according to their sensitivity to bass invasion. Stable isotope evidence indicated that bass and lake trout subsist on separate food chains in lakes that contain pelagic prey fish (cisco, lake whitefish, rainbow smelt). Thus, bass introductions into these lakes is predicted not to affect lake trout populations. Identifying particular lakes and lake-types that are sensitive to bass introductions can guide efforts of lake managers to minimize negative impacts of bass introductions on lake trout.

Introduction

Much of fisheries ecology has traditionally rested on the assumption that individual species could be treated independently, and the primary emphasis has been on the direct effects of stock size and environmental variation on fish recruitment and production (Larkin 1978; Pitcher et al. 1998). Yet no species exists outside of its broader food web context, and there is growing realization of the need for more holistic, ecosystem approaches to fisheries management (Pitcher et al. 1998). Multispecies

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and ecosystem-level approaches are increasingly being applied to lake and fisheries management (Walters et al. 1999; Walters et al. 2000). In fact, this emphasis on predator–prey dynamics is not new to fisheries ecology, as some of the earliest field studies of aquatic food web interactions were Swingle's seminal studies of bass population dynamics and 'balanced' fish communities (Swingle 1950).

The more expansive, ecosystem approach can take many forms. Fundamental is the realization that the amount of primary production controls the potential for production at higher trophic levels, while predation and competition can mediate recruitment, realized production and the distribution of biomass across multiple trophic levels (Lindeman 1942; Carpenter et al. 1985). Ecosystem-level stud-

ies that consider trophic relationships are typically posited upon system-specific knowledge of feeding relationships. This information is almost universally derived from analysis of consumer gut contents, and provides foundational information for bioenergetics models (Kitchell et al. 1977) and more sophisticated, whole-ecosystem mass balance models such as ECOPATH and ECOSIM (Walters et al. 2000).

Gut content analysis reveals the diet of a consumer at a particular place and time, and is often used to infer population-level feeding. The approach can be limited in its capacity for reconstructing energy flow for entire food webs, as the amount of dietary data required for such studies can be prohibitive. Diet analysis is also limited in its ability to capture trophic variability at finer scales of trophic organization, such as intra-population, or individual-level diet specialization. A major challenge of fisheries ecology is to improve our ability to quantify trophic interactions at the desired organizational scales, whether that be individual consumers, populations, or entire food webs.

A number of inferential techniques have the potential to provide information about trophic relationships at a variety of organizational levels. These approaches include, but are not limited to the use of fatty acid biomarkers (Grahl-Nielsen and Mjaavatten 1991), and stable isotope tracers (Minagawa and Wada 1984; Peterson and Fry 1987) (primarily $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios). The use of stable isotopes has emerged as a particularly powerful tool for food web studies, and is currently being used to address a variety of questions concerning trophic interactions that are of relevance to fisheries ecology and management.

The goals of this paper are two-fold. The first is to provide an overview and introduction to the use of stable isotopes in studies of aquatic food webs, with strong emphasis on fisheries-related applications. The second is to present specific examples illustrating the applications of stable isotope techniques, at a variety of food web scales, to studies of bass ecology. Examples range from foraging differences among individual young-of-the-year smallmouth bass (Vander Zanden et al. 1998), to documenting food web shifts following introduction of smallmouth bass and rock bass into northern lake ecosystems (Vander Zanden et al. 1999). We intend to demonstrate some potential applications of stable isotopes to a variety of fisheries-related questions. In particular, we highlight the contribution of this approach to elucidating food web processes at two very different scales that are particularly difficult to study using traditional

techniques: that of whole food webs, and trophic variability occurring at the intra-population level.

Methods

Review of Stable Isotope Techniques and Applications

An overview of the application of carbon and nitrogen stable isotopes techniques to studies of aquatic food webs will be given here. For more general descriptions of stable isotope techniques and applications, a number of excellent reviews are available (Minagawa and Wada 1984; Owens 1987; Peterson and Fry 1987; Michener and Schell 1994; Hecky and Hesslein 1995). A mass spectrometer is used to measure the ratio of heavy to light atoms ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) of a preprepared tissue sample. This is typically muscle for adult fish, and whole organisms for invertebrates and larval fish. The measured isotopic ratio is expressed relative to that of a standard material (atmosphere for nitrogen and PDB limestone for carbon); $\delta^{13}C$ or $\delta^{15}N = ([R_{sample}/R_{standard}] - 1) \times 1{,}000$, where $R = {}^{13}C/{}^{12}C$ or $^{15}N/{}^{14}N$. The delta value or signature of a sample represents the ppt (‰, or per mil) deviation from the standard material.

Stable isotope information is useful for food web studies because the behavior of stable isotope ratios in food chains is relatively well-known. For example, a variety of studies have found that the $\delta^{15}N$ of a consumer's tissue (reflecting the proportional contribution of ^{15}N to the tissue total nitrogen pool) is enriched by an average of 3.4‰ above that of its food, due to preferential excretion of isotopically light (^{14}N) nitrogen atoms (DeNiro and Epstein 1981; Minagawa and Wada 1984). As a result, $\delta^{15}N$ values becomes consistently elevated with each successive trophic step in the food chain. Considering that there is consistent trophic enrichment in $\delta^{15}N$, this value should, in theory, be indicatory of a consumer's trophic position. The term *trophic position* is analogous to the concept of trophic level. The difference is that it is a continuous (rather than discrete) variable that represents the potentially diverse energetic pathways that link a given consumer to the base of the food web (Levine 1980; Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). $\delta^{15}N$ of organisms at the base of the food web (either primary producers or primary consumers) vary widely among lakes (Cabana and Rasmussen 1996), and even among habitats within a lake (Vander Zanden and Rasmussen 1999). Thus, in order for $\delta^{15}N$ to serve as an unbiased measure

of trophic position, we must correct for the underlying, system- or habitat-specific isotopic differences. Rather than using raw $\delta^{15}N$ values as an indicator of trophic position (TP), we use the $\delta^{15}N$ of the consumer and a baseline indicator taxon, in this case, a known primary consumer, to calculate consumer trophic position using the formula:

(1)

$$TP_{consumer} = [(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4] + 2$$

Note that 3.4 is the assumed per trophic level $d^{15}N$ enrichment, and we assume primary producers to be trophic level 1, primary consumers trophic level 2, and so on. TP can be estimated for individual fish, and population- or lake-specific TP is simply the mean value for all individual of the population.

In addition to $\delta^{15}N$, studies commonly use $\delta^{13}C$ information to provide additional and complementary trophic information. The utility of stable carbon isotope ($\delta^{13}C$) information for food web studies in lakes is that $\delta^{13}C$ varies among the major primary producer groups. Benthic algae is generally enriched in ^{13}C relative to phytoplankton, as a result of reduced isotopic discrimination between dissolved inorganic carbon (DIC) and benthic algae relative to phytoplankton (Hecky and Hesslein 1995). These differences in primary producer $\delta^{13}C$ remain relatively unchanged as they pass from prey to predator. Thus, variation in algal $\delta^{13}C$ provides a basis for inferring the relative contributions of littoral and pelagic energy to higher trophic level production (Hecky and Hesslein 1995; Vander Zanden et al. 1999). As with $\delta^{15}N$, the potential of this approach can be fully realized when used in a quantitative context. Provided the $\delta^{13}C$ value of the consumer, littoral prey, and pelagic prey are known, a simple, two-source $\delta^{13}C$ mixing model can be used to quantify consumer energy source (i.e., percent littoral versus pelagic) using the equation:

(2)

$$\% \text{ littoral} = (\delta^{13}C_{lake\,trout} - \delta^{13}C_{pelagic})/(\delta^{13}C_{littoral} - \delta^{13}C_{pelagic}) \times 100$$

The power of the stable isotope approach stems from the capacity to provide time-integrated trophic information at the level of individual consumers. This allows examination of intra-population feeding variation in ways not possible using traditional gut content methods. Yet stable isotopes do not replace gut content information, and there is increasing recognition that these two approaches

provide complementary information. Direct analysis of diets provides immediate and direct evidence for specific feeding relationships, and is critical for evaluating stable isotope model outputs. Gut content studies can be costly and labor-intensive, and adequately characterizing diets requires examination of large numbers of stomachs. While use of stable isotopes do not provide the fine taxonomic resolution of diet analyses, relatively few specimens (generally fewer than 10 individuals of a species) are needed to infer trophic relationships and energy flow pathways. Note that proper isotopic interpretation necessitates isotopic measurement of a variety of organisms and potential prey items from the study system. These auxiliary measurements provide the isotopic context that serves as the basis for interpreting trophic relationships and food web structure. While this increases the number of samples required, analysis costs have decreased in recent years, and are often less than US$10 per sample for both $\delta^{15}N$ and $\delta^{13}C$ in many stable isotope laboratories.

Application of Stable Isotope Techniques to Studies of Bass Ecology

In this section, we demonstrate recent applications of stable isotope techniques to studying food web processes at a variety of organizational levels. The first application examines intra-population and ontogenetic trophic shifts among young-of-the-year (YOY) smallmouth bass (Vander Zanden et al. 1998). Stable isotopes indicated trophic differences among individual YOY bass that correlated with body size and size-at-age. The second application uses stable isotope analysis to quantify changes in food web structure following smallmouth bass and rock bass introductions in a series of Ontario lakes (Vander Zanden et al. 1999). Finally, stable isotope information is used to identify particular lakes that, because of their food web structure, are especially sensitive to bass invasion. This level of information is particularly useful for lake managers, as it can serve as the basis for selecting priority lakes and lake districts for efforts to prevent future bass invasions. By focusing on applications of stable isotopes at organizational scales that are difficult to study using traditional gut content techniques, we highlight areas of research in which stable isotopes can provide particularly useful information.

Use of Stable Isotopes to Study Intra-Population Trophic Variability in Bass: Processes occurring during larval and juvenile stages ultimately determine year-class strength, and the factors regulating first-year survival is a central problem in fisheries ecol-

ogy (Ricker 1954; Larkin 1978; Post et al. 1998). Bass typically exhibit substantial variation in size by the end of their first summer, which is significant because the largest age-0 fish at the onset of winter have the highest overwinter survival rates (DeAngelis and Coutant 1979; Miranda and Hubbard 1994). What factors underlie this variation in size-at-age? While fish with an early birth date have been found to be larger by the end of their first summer (Cargnelli and Gross 1996; Cargnelli and Gross 1997), an early birth date will also confer a disadvantage in some years when food availability does not correspond with YOY prey demand. Intra-population dietary differences may also contribute to variation in growth rates and size-at-age for YOY fishes. Individuals that discover new prey items or graduate to piscivory are likely to grow faster. The limitations of gut content studies are readily apparent when examining questions about intra-population dietary differences. While a handful of studies have looked at diet consistency by repeated examination gut contents of individual adult fish (Bryan and Larkin 1972; Schindler et al. 1997), this approach has limited applicability, and for obvious reasons, cannot be extended to young-of-the-year fish. Because stable isotopes offer time-integrated diet information, individual-level dietary specialization can be inferred from isotopic differences occurring within populations (Gu et al. 1997; Vander Zanden et al. 1998; Vander Zanden et al. 2000).

Stable isotope analysis was used to examine trophic shifts among YOY smallmouth bass in Lake Opeongo, Ontario. Among YOY bass collected on the final sample date of the study (24 July), there was a positive relationship between $\delta^{15}N$ and body size (Figure 1), indicating that variation in size-at-age and growth rates corresponded with individual-level dietary differences, and that the largest fish had the highest trophic position. This is consistent with the idea that the largest fish of a cohort are the first to graduate to larger prey items, further accelerating individual growth rates, and producing substantial, diet-based variation in size-at-age by the end of their first summer.

Benthic and pelagic primary producers typically have distinct $\delta^{13}C$ values (Hecky and Hesslein 1995). Thus, $\delta^{13}C$ can be used to discriminate between pelagic and benthic diets. In the study of Lake Opeongo YOY smallmouth bass, $\delta^{13}C$ revealed dietary and trophic habitat shifts during first summer feeding (Figure 2). Premetamorphic smallmouth typically had $\delta^{13}C$ values ranging between –24‰ to –26‰. $\delta^{13}C$ increased over the course of the summer, reaching –21‰ by the time small-mouth bass reached 45 mm in length. These ontogenetic shifts in isotope values provide strong evidence for a trophic shift from pelagic to benthic prey over the course of their first summer.

Nest-specific differences in ontogenetic $\delta^{13}C$ trajectories were also observed for premetamorphic smallmouth bass (< 15 mm total length). The smallest bass had nest-specific $\delta^{13}C$ signatures. This nest-specific variation in $\delta^{13}C$ observed among bass embryos presumably reflects parental $\delta^{13}C$ differences that were passed on to the eggs. $\delta^{13}C$ signatures of bass from all nests converged at around –25‰ when the bass reached 15 mm, presumably as a result of exogenous feeding on a common resource. The source and significance of the parental isotopic variation is unknown, but may ultimately be useful for examining linkages between parental diet, metabolic state, and reproductive success.

Bass Introductions and Food Web Shifts in Ontario Lakes: Adult bass are well-known to be efficient piscivores, and a diverse amount of literature has documented the dramatic impact that bass can have on prey fish diversity, community structure, and abundance in lakes from the northern U.S. and southern Canada (Tonn and Magnuson 1982; Hall and Ehlinger 1989; McQueen et al. 1989; Jackson et al. 1992; Carpenter and Kitchell 1993; Mittelbach et al. 1995; Chapleau et al. 1997; Findlay et al. 2000). These prey fishes in fact represent a diverse assemblage of fishes, but are typically dominated by cyprinids and juvenile centrarchids (most often bluegill) in northern lakes. While these prey fishes have diverse diets, they typically undergo ontogenic diet shifts between zooplankton and zoobenthos. The nature and timing of these trophic shifts vary, depending on the availability of invertebrate prey, refuge availability, and the threat of predation from piscivores (Werner and Gilliam 1984; Werner 1986). Vulnerable-sized bluegill often inhabit the sub-optimal littoral habitats in the presence of predators, returning to the more optimal open-water habitats only after growing to a nonvulnerable size (Werner et al. 1983; Werner and Hall 1988).

The ability of bass and other littoral predators to regulate littoral prey fish is commonly the underlying basis for lake biomanipulation, and the harnessing of trophic cascades as a lake management tool: since predation-driven changes in prey fish populations can have impacts that cascade down to zooplankton and phytoplankton trophic levels. Interestingly, the indirect impacts of piscivores (alteration of prey fish behavior) can rival the direct effects (the actual consumption of prey fish) in initiating trophic cascades (He and
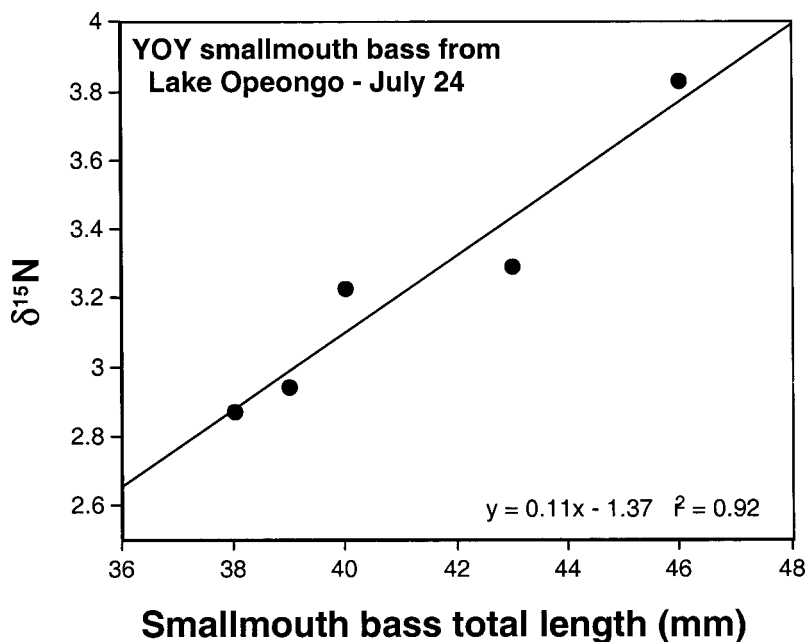
Figure 1. $\delta^{15}N$ of YOY smallmouth bass increases as a function of body size. These specimens were collected on the final sampling date of the study (24 July 1995) in Lake Opeongo, Ontario. Data are from Vander Zanden et al. (1998).
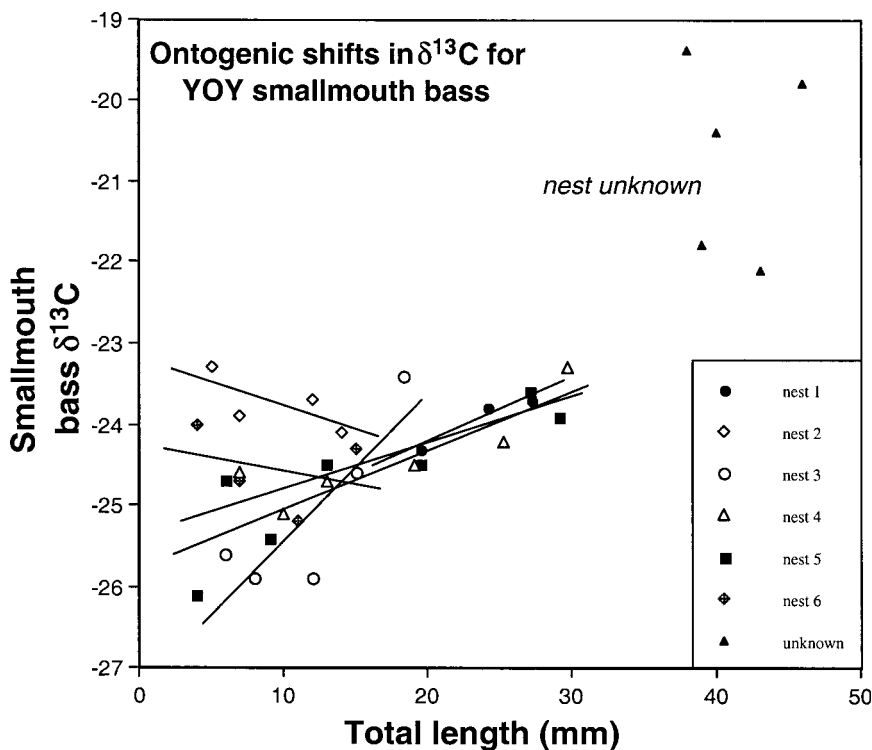

Figure 2. Nest-specific ontogenetic shifts in $\delta^{13}C$ for young-of-the-year (YOY) smallmouth bass from Lake Opeongo, Ontario. $\delta^{13}C$ values converge at 15–20 mm in length. Above 20 mm, there is an increase in $\delta^{13}C$ with size, indicative of a trophic habitat shift from pelagic to benthic prey. Based on data from Vander Zanden et al. (1998).

Kitchell 1990; Kitchell et al. 1994). In effect, bass can serve as keystone predators through their ability to regulate prey fish community biomass, composition, and behavior, with subsequent indirect effects on lower trophic levels (Paine 1980; Schindler et al. 1997).

Smallmouth bass and largemouth bass were historically confined to the Mississippi and Great Lakes drainages. During the past century, they have been widely introduced and now occur throughout much of western North America, in many east coast drainages, and northward into Ontario, Quebec, New Brunswick, Nova Scotia, and western Canada (MacCrimmon and Robbins 1975; Lee et al. 1980; McNeill 1995; Rahel 2000). In addition, largemouth bass and smallmouth bass have been introduced into dozens of countries on nearly every continent, although impacts outside of North America are virtually unknown (McDowall 1968; Robbins and MacCrimmon 1974; Welcomme 1988). The introduction of bass into formerly bass-less waters has traditionally been viewed as a form of fishery enhancement, and until recently, there has been little concern about the ecological consequences on native ecosystems. During recent decades, fishery management agencies in Canada and the U.S. have adopted a more cautious attitude towards intentional piscivore introductions, although bass continue to colonize new aquatic ecosystems at a rapid pace.

In light of the potential keystone role of bass in structuring aquatic food webs, and their dramatic, human-assisted range expansion during the last century, it is important to determine how bass introductions may have altered aquatic food web structure and affected native predator populations. In attempting to address such broad-scale food web-level impacts, possibly on large numbers of lakes, the logistic constraints of gut content analysis become apparent.

Smallmouth bass and rock bass are presently invading headwater lakes of central Ontario. To address the food web consequences of bass introductions, stable isotope techniques have been used to quantify trophic structure of nine lakes; five lakes with bass, and four uninvaded, control lakes (Vander Zanden et al. 1999). All study lakes supported native, self-sustaining lake trout fisheries. Like many inland, headwater lakes, the study lakes lack pelagic prey fish species (rainbow smelt, cisco, lake whitefish), presumably due to restricted postglacial dispersal of these species. The absence of pelagic prey fish is notable because these are the preferred prey species of lake trout. In the absence of pelagic prey fish, lake trout instead rely on a mix of zooplankton, zoobenthos, and littoral prey fish (Martin 1970; Martin and Fry 1972; Vander Zanden and Rasmussen 1996).

Littoral prey fish catch rates and species richness were significantly ($p < 0.05$) lower in bass lakes relative to lakes without bass (Table 1). Corresponding with the depressed littoral prey fish populations in bass lakes, lake trout trophic position (based on $\delta^{15}N$) was reduced, indicating consumption of invertebrates rather than fish. $\delta^{13}C$ indicated that lake trout relied primarily on littoral prey in lakes without bass, and pelagic prey in lakes with bass (Table 1). Two of the study lakes, MacDonald Lake and Clean Lake, have been the subject of long-term studies that predate bass introductions. Electrofishing catch data spanning a 15 year period show dramatic declines in littoral prey fish following bass establishment in MacDonald Lake. Analysis of freezer-archived muscle tissue revealed a concurrent decline in lake trout trophic position (Figure 3). Less dramatic shifts were observed in Clean Lake. Smallmouth and rock bass established in Clean Lake six years later than in MacDonald Lake, and the full impact of bass introductions may not have been realized at the time that stable isotope samples were

Table 1. Prey fish communities and lake trout trophic variables from Ontario lakes with and without bass. Variables provided are: number of lakes, mean prey fish catch rates (number of prey fish/trap/day, and grams of prey fish/trap/day), mean cyprinid species richness, mean prey fish species richness, mean lake trout trophic position (baseline-corrected $\delta^{15}N$ values), and percent consumption of littoral-derived carbon (based on $\delta^{13}C$ values). Using one tailed t-tests, all comparisons between lakes with and without bass were significant at $p < 0.05$. Values taken from Vander Zanden et al. (1999a). Errors represent 1 SD of mean of lake-specific means.

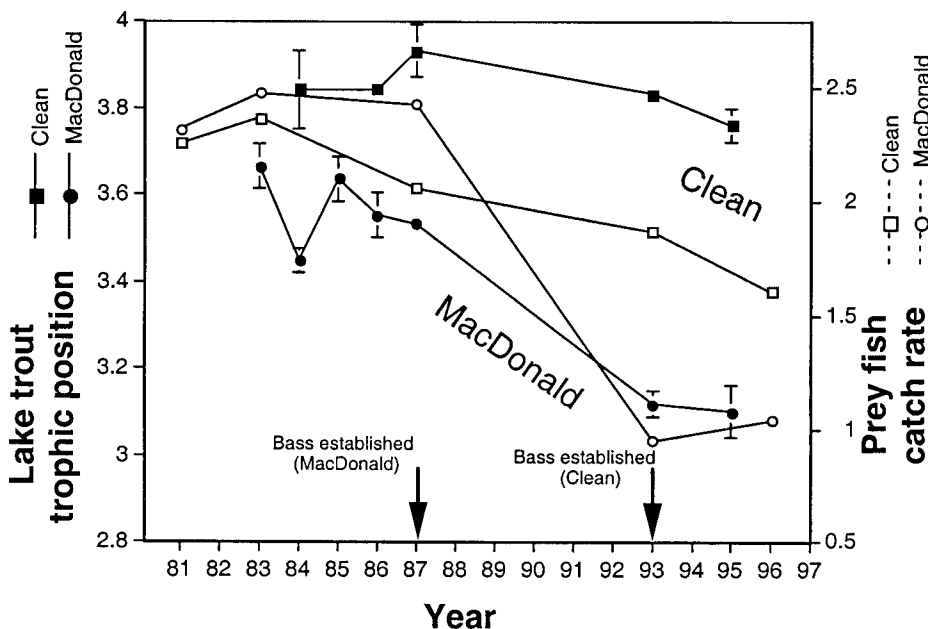|	Number of lakes	Fish/ trap	Grams/ trap	Cyprinid species	Prey fish species	Trophic position	Littoral carbon
Bass	5	0.9	6.6	0.4	2.4	3.28	27%
		± 0.6	± 4.7	± 0.25	± 0.4	± 0.25	
No bass	4	5.9	35.8	5.3	8.2	3.90	62%
		± 2.0	± 11.3	± 1.0	± 1.1	± 0.52	

Figure 3. Long-term trends in lake trout trophic position and prey fish catch rates (from quantitative electrofishing transects) in MacDonald and Clean lakes. Bass invaded MacDonald Lake in 1987 and Clean Lake in 1993. Figure adapted from Vander Zanden et al. (1999).

collected. Recent work on Clean Lake indicates that trophic changes similar to those observed in MacDonald have since occurred (J.M. Casselman and D. Brown, unpublished data).

Stable isotope evidence was used to depict the food web shifts in response to bass introduction (Figure 4). Use of stable isotope techniques allowed quantification of the impacts of bass introductions on food web structure using both cross-lake and long-term analyses. This study would have been prohibitively labor-intensive and costly using dietary analysis alone. Furthermore, discerning the contributions of littoral versus pelagic energy reliance would not have been possible using traditional techniques, short of detailed and lake-specific diet analysis of each of the prey fish species consumed by lake trout. Still, much of our understanding of food web interactions in these lakes was derived from examination of gut contents, highlighting the value of combined use of isotopic and dietary techniques to characterize aquatic food webs.

The extent of trophic interactions between lake trout and bass were not anticipated because bass reside in the littoral zone, while lake trout occupy deep-water and pelagic habitats (Martin and Fry 1972; Scott and Crossman 1973). Yet despite these clear differences in habitat, bass and
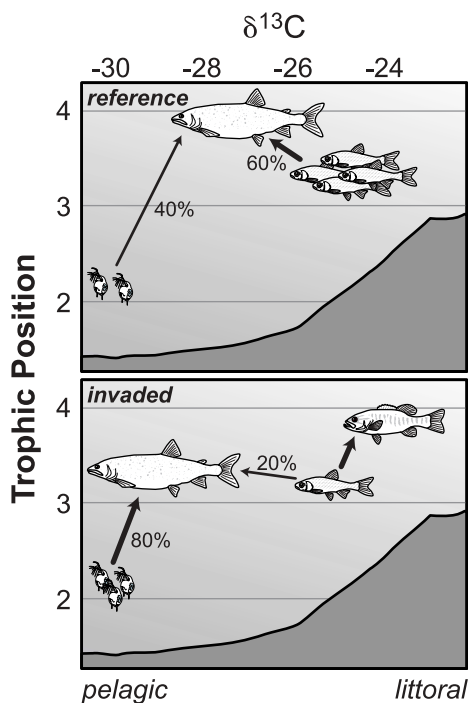

Figure 4. A summary of the trophic pathways supporting lake trout based on stable isotope information for lakes without bass (reference) and lakes invaded by bass (invaded). Copied with permission from *Nature* magazines, Vander Zanden et al. 1999a.
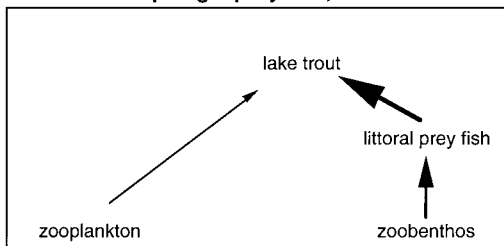
lake trout often rely on a common resource: that of littoral prey fish. While lake trout appear not to significantly reduce littoral prey fish populations, bass are a more efficient predator and often regulate littoral prey fish populations, thus reducing the food base that would otherwise be available for lake trout. Because this interaction involves lake trout foraging across traditionally recognized habitat boundaries(Lodge et al. 1988; France 1996), these trophic linkages have not been recognized and it is assumed that bass introductions have no effect on lake trout populations (Martin and Fry 1972; Scott and Crossman 1973; Carlander 1975; Olver et al. 1991), although long-term studies of lake trout population in MacDonald Lake and Clean Lake indicates otherwise (J. M. Casselman, personal communication).

Using Food Web Information to Predict the Sensitivity of Lakes to Bass Invasion: The lakes discussed in the previous section were noteworthy in their absence of pelagic prey fish species (cisco, lake whitefish, and rainbow smelt). In central Ontario, many lake trout lakes contain at least one, and often multiple species of pelagic prey fish. Their presence/absence is determined by a combination of variatiability in postglacial dispersal, and more recently, introductions by humans. In fact, if pelagic prey fish are present, they typically comprise the vast majority of lake trout diet (Martin 1970; Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996). How might this influence the strength of bass –lake trout interactions? We predicted that in lakes containing pelagic prey fish, lake trout would be linked to the pelagic food web, and that only in the absence of pelagic prey fish would lake trout rely on littoral prey fish. And as discussed in the previous section, the availability of littoral prey fish depends on whether bass are present—the presence of bass reduces littoral prey fish availability, relegating lake trout to a diet comprised primarily of invertebrates. A diagrammatic representation of the three food web types is presented (Figure 5).
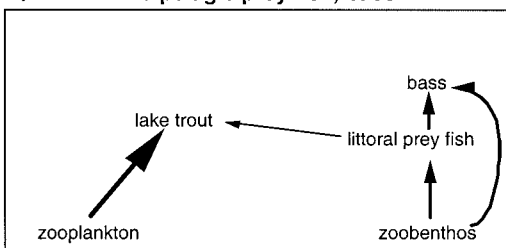
Our heuristic model of how pelagic forage fish mediate bass-lake trout interactions can be tested using stable isotope information. Stable isotope food web diagrams have been built for each of 17 central Ontario lakes, which span a wide range of community composition. Each lake was classified as either: *NB*, lakes with no bass and no pelagic prey fish; *B*, lakes with bass and no pelagic prey fish; or *PPF*, lakes containing pelagic prey fish (with or without bass). A composite stable isotope food web diagram was built using lake-specific averages for each of the three lake types (Figure 6). The com-

posite food web diagrams reveal clear difference in trophic structure among the three lake-types. In *NB* lakes, lake trout rely heavily on littoral prey fish (Figure 6a). Lake trout from *B* lakes consume pelagic prey and have a depressed trophic position, while bass occupy the trophic niche of a littoral predator (Figure 6b). In *PPF* lakes, lake trout
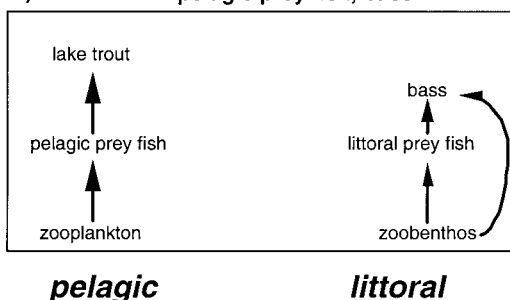

Figure 5. A diagramatic representation of a lake classification scheme that reflects the food web structure dependence of bass-lake trout interactions. A) NB, lakes lacking both pelagic prey fish and bass. Lake trout rely primarily on littoral prey fish. B) B, pelagic prey fish are absent and bass are present. Lake trout rely primarily on zooplankton. C) PPF, pelagic prey fish are present. Bass and lake trout are on different food chains, and the presence of pelagic prey fish buffers lake trout from the potential top down impacts of bass on littoral prey fish.

and bass are top predators atop largely separate pelagic and littoral-based food chains (Figure 6c).

The stable isotope-based food web reconstructions revealed that the presence of pelagic prey fish mediates the strength of bass-lake trout interactions. In other words, bass-lake trout interactions are predictable from lake food web structure, as inferred from species composition. If pelagic prey fish are present, lake trout are, in effect, buffered from the impacts of bass on the littoral prey fish community, provided that lake trout do not rely on littoral prey fish during their trophic ontogeny. Only in the absence of pelagic prey fish are lake trout expected to be sensitive to bass impacts. The idea that food web structure determines the sensitivity of lake trout populations to bass introductions has clear implications for efforts to minimize the potential impacts of bass introductions on native lake trout fisheries.

Summary

Much of classical fisheries biology has considered the dynamics of individual species with little or no regard to biotic interactions (Larkin 1978; Pitcher et al. 1998). In fact, all species are embedded within a network of predator–prey relationships, and there is growing recognition that the strength of these biotic interactions can determine the abundance and productivity of species and trophic levels (Carpenter et al. 1985). Interestingly, the importance of predator–prey dynamics has long been recognized for bass populations, and has provided the basis for bass management programs in the southeastern U.S. (Swingle 1950; Stroud and Clepper 1975). A movement towards ecosystem-based approaches for understanding and managing fish populations is emerging (Kitchell et al. 1994; Stow et al. 1995, Walters et al. 2000). Yet use of food web and ecosystem based approaches have unique information needs; specifically, information about the trophic relationships among species, which are often complex and variable in both space and time. While the requisite information can sometimes be obtained through gut content analysis, inferential approaches are particularly applicable at broader (whole food web) and narrower (individual-level) organizational levels. It is at these scales that the limitations of traditional gut content methods for inferring trophic relationships become apparent.

The examples presented here demonstrate how stable isotope techniques can be used to elucidate trophic processes at two scales that are problematic using gut content analysis: examination of whole food web structure, and analysis of intrapopulation diet variation. Specifically, the food web interactions that linked lake trout and bass populations were unexpected as these two species inhabit different parts of the lake, but were found to rely on a common resource. Similarly, stable iso-
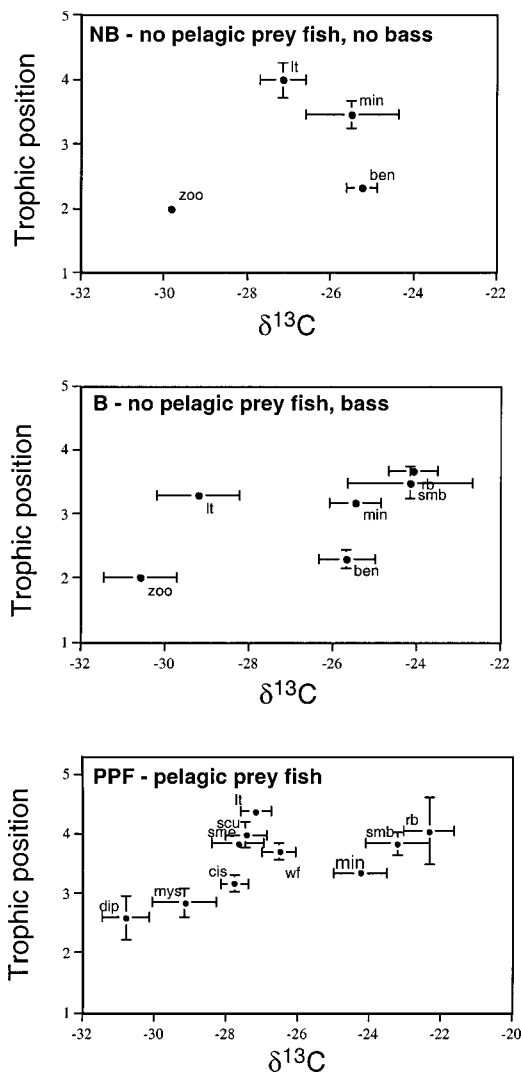

Figure 6. Trophic position - $\delta^{13}C$ food web diagrams of the three food web types of Figure 5. lt = lake trout, min = minnows, ben = benthic invertebrates, zoo = zooplankton, rb = rock bass, smb = smallmouth bass, dip = diporeia, mys = mysis, cis = cisco, wf = whitefish, sme = rainbow smelt, scu = sculpin.

topes revealed diet shifts and differences among YOY bass that may relate to differences in fish growth rates and size-at-age. Application of stable isotope techniques creates tremendous potential for exploring how variation in diet and food web structure, both within and among populations, are manifested in other forms of ecological variability, ranging from fish growth to ecosystem-level responses to perturbation.

Acknowledgments

References

Bryan, J. E., and P. A. Larkin. 1972. Food specialization by individual trout. Journal of the Fisheries Research Board of Canada 29:1615–1624.

Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences (U.S.A.) 93: 10844–10847.

Cargnelli, L. M., and M. R. Gross. 1996. The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). Canadian Journal of Fisheries and Aquatic Sciences 53:360–367.

Cargnelli, L. M., and M. R. Gross. 1997. Fish energetics: larger individuals emerge from winter in better condition. Transactions of the American Fisheries Society 126:153–156.

Carlander, K. D. 1975. Community relations of bass: Large natural lakes. *In* R.H. Stroud & H. Klepper, editor. Black bass biology and management, Sport Fishing Institute, Washington, D.C.

Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, England.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.

Chapleau, F., C. S. 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.

DeAngelis, D. L., and C. C. Coutant. 1979. Growth rates and size distribution of first-year smallmouth bass populations: Some conclusions from experiments and a model. Transactions of the American Fisheries Society 108:137–141.

DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341–351.

Findlay, C. S., D. G. Bert, and L. Zheng. 2000. Effect of introduced piscivores on native minnow communities in Adirondack lakes. Canadian Journal of Fisheries, and Aquatic Sciences 57: 570–580.

France, R. L. 1996. Energy provenance for juvenile lake trout in small Canadian Shield lakes as shown by stable isotopes. Transactions of the American Fisheries Society 125:512–518.

Grahl-Nielsen, O., and O. Mjaavatten. 1991. Dietary influence on fatty acid composition of blubber fat of seals as determined by biopsy: a multivariate approach. Marine Biology 110:59–63.

Gu, B., C. L. Schelske, and M. V. Hoyer. 1997. Intrapopulation feeding diversity in blue tilapia: Evidence from stable-isotope analyses. Ecology 78:2263–2266.

Hall, D. J., and T. J. Ehlinger. 1989. Perturbation, planktivory, and pelagic community structure: the consequence of winterkill in a small lake. Canadian Journal of Fisheries and Aquatic Sciences 46:2203–2209.

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.

Hecky, R. E., and R. H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. Journal of the North American Benthological Society 14: 631–653.

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.

Kitchell, J. F., L. A. Eby, X. He, D. E. Schindler, and R. A. Wright. 1994. Predator-prey dynamics in an ecosystem context. Journal of Fish Biology 45:209–226.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*). Journal of the Fisheries Research Board of Canada 34:1922–1935.

Larkin, P. A. 1978. Fisheries management-An essay for ecologists. Annual Review of Ecology and Systematics 9:57–73.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAlister, and J. R. Stauffer. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, North Carolina.

Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. Journal of Theoretical Biology 83:195–207.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.

Lodge, D. M., J. W. Barko, D. Strayer, J. M. Melack, G. G. Mittelbach, R. W. Howarth, B. Menge, and J. E. Titus. 1988. Spatial heterogeneity and habitat interactions in lake communities. pp. 181-208. *in* S.R. Carpenter (editor.) Complex interactions in lake communities, Springer-Verlag, New York, New York.

MacCrimmon, H. R., and W. H. Robbins. 1975. Distribution of the black basses in North America Black bass biology and management, Sport Fishing Institute, Washington, D.C.

Martin, N. V. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. Journal of the Fisheries Research Board of Canada 27:125–146.

Martin, N. V., and F. E. J. Fry. 1972. Lake Opeongo: Effects of exploitation and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29:795–805.

McDowall, R. M. 1968. The proposed introduction of the largemouth bass *Micropterus salmoides* (Lacepede) into New Zealand. New Zealand Journal of Marine and Freshwater Research 2: 149–161.

McNeill, A. J. 1995. An overview of the smallmouth bass in Nova Scotia. North American Journal of Fisheries Management 15:680–687.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59:289–309.

Michener, R. H., and D. M. Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. Pages 138-157 *in* R.H. Michener and K. Lathja, editors. Stable Isotopes in Ecology and Environmental Science, Blackwell Scientific Publications, Oxford, England.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Miranda, L. E., and W. D. Hubbard. 1994. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Transactions of the American Fisheries Society 123:80–87.

Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. Ecology 76:2347–2360.

Olver, C. H., R. L. DesJardine, C. I. Goddard, M. J. Powell, H. J. Rietveld, and P. D. Waring. 1991. Lake trout in Ontario: management strategies. Page 86 *in* Lake Trout Synthesis, Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Owens, N. J. P. 1987. Natural variation in 15N in the marine environment. Advances in Marine Biology 24:390–451.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667–685.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Pitcher, T. J., P. J. B. Hart, and D. Pauly. 1998. Reinventing fisheries management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. Canadian Journal of Fisheries and Aquatic Sciences 55:2588–2600.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288: 854–856.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Robbins, W. H., and H. R. MacCrimmon. 1974. The black bass in America and overseas. Biomanagement and Research Enterprises, Sault Ste. Marie, Ontario, Canada.

Schindler, D. E., J. R. Hodgson, and J. F. Kitchell. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia 110:592–600.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin Number 184. Fisheries Research Board of Canada.

Stow, C. A., S. R. Carpenter, C. P. Madenjian, L. A. Eby, and L. J. Jackson. 1995. Fisheries management to reduce contaminant consumption. BioScience 45:752–758.

Stroud, R. H., and H. Clepper. 1975. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Swingle, H. S. 1950. Relationships and dynamics of balanced and unbalanced fish populations. pp. 74, Alabama Agricultural Experimental Station, Auburn University.

Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149–1166.

Trippel, E. A., and F. W. H. Beamish. 1993. Multiple trophic level structuring in Salvelinus-Coregonus assemblages in boreal forest lakes. Canadian Journal of Fisheries and Aquatic Sciences 50:1442–1455.

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature (London) 401:464–467.

Vander Zanden, M. J., M. Hulshof, M. S. Ridgway, and J. B. Rasmussen. 1998. Application of stable isotope techniques to trophic studies of age-0 smallmouth bass. Transactions of the American Fisheries Society 127:729–739.

Vander Zanden, M. J., and J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. Ecological Monographs 66:451–477.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer δ^{15}N and δ^{13}C and the trophic position of aquatic consumers. Ecology 80:1395–1404.

Vander Zanden, M. J., B. J. Shuter, N. P. Lester, and J. B. Rasmussen. 2000. Within- and among-population variation in the trophic position of the aquatic top predator, lake trout. Canadian Journal of Fisheries, and Aquatic Sciences 57: 725–731.

Walters, C., D. Pauly, and V. Christensen. 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2:539–554.

Walters, C., D. Pauly, V. Christensen, and J. F. Kitchell. 2000. Representing density dependent conse-quences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems. 3: 70–83.

Welcomme, R. L. 1988. International introduction of inland aquatic species, FAO.

Werner, E. E. 1986. Species interactions in freshwater communities. In J. Diamond and T.J. Case, editors. Community Ecology, Harper and Row, New York, New York.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–426.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

Werner, E. E., and D. J. Hall. 1988. Ontogenic habitat shifts in bluegill: The foraging rate-predation risk trade-off. Ecology 69:1352–1366.