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Stable isotope evidence for the food web consequences of species invasions in lakes

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Species invasions pose a serious threat to biodiversity and native ecosystems[1,2]; however, predicting and quantifying the impacts of invasive species has proven problematic[3–6]. Here we use stable isotope ratios to document the food-web consequences of the invasion of two non-native predators, smallmouth bass and rock bass, into Canadian lakes. Invaded lakes had lower littoral prey-fish diversity and abundance than uninvaded reference lakes. Consistent with this difference, lake trout from invaded lakes had more negative δ^{13}C values (−29.2‰ versus −27.4‰) and reduced trophic positions (3.3 versus 3.9) than those from reference lakes, indicating differences in food-web structure. Furthermore, a comparison of the pre- and post-invasion food webs of two recently invaded lakes showed that invasion was followed by substantial declines in littoral prey-fish abundance and the trophic position of lake trout, reflecting a shift in the diet of lake trout towards zooplankton and reduced dependence on littoral fish. This study demonstrates the use of stable isotope techniques to detect changes in food-web structure following perturbations; in this instance, bass-induced food-web shifts may have severe consequences for native species and ecosystems.

Human dominance over the Earth's ecosystems has been accompanied by the widespread introduction of exotic species, which has led to the extinction of native species, the collapse of native fisheries and the loss of ecological integrity and ecosystem functioning[1,7,8]. Ecologists are far from being able to predict, detect or measure the ecological impacts of species invasions[3–6]. This is not surprising because natural food webs are variable and complex[9,10], and using traditional methods to examine the impact of species invasions on aquatic food webs would be laborious, difficult and costly.

Natural stable-isotope distributions are increasingly used to provide a time-integrated measure of food-web relationships based on energy flows. Stable nitrogen isotope ratios ($\delta^{15}\mathrm{N} = ({}^{15}\mathrm{N}/{}^{14}\mathrm{N}_{\mathrm{sample}} - {}^{15}\mathrm{N}/{}^{14}\mathrm{N}_{\mathrm{reference}}/{}^{15}\mathrm{N}/{}^{14}\mathrm{N}_{\mathrm{sample}}) \times 1000$) become enriched by 3–4‰ between prey and predator tissues, thereby providing a measure of consumer trophic position[11–13]. Stable carbon isotope ratios (δ^{13}C) exhibit little or no trophic level enrichment ($<$1‰), and are useful for identifying the sources of production for consumers in lakes because benthic algae are typically enriched in δ^{13}C relative to phytoplankton[14,15].

Here we use stable isotope techniques to quantify the food-web consequences of recent invasions of smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) in Canadian lakes. Smallmouth bass have been intentionally introduced (both authorized and unauthorized) into aquatic ecosystems well beyond their native range in North America, and on virtually every continent[16,17]. Furthermore, both bass species may be inadvertently introduced into aquatic ecosystems by the dumping of unused live bait[18], and both are adept at dispersing throughout drainage systems. Consequently, both species have greatly expanded their geographical range over the last century.

These two bass species are presently invading a number of relatively pristine lakes in North America's Northern Hardwood–Boreal Forest transition zone, many of which contain lake trout

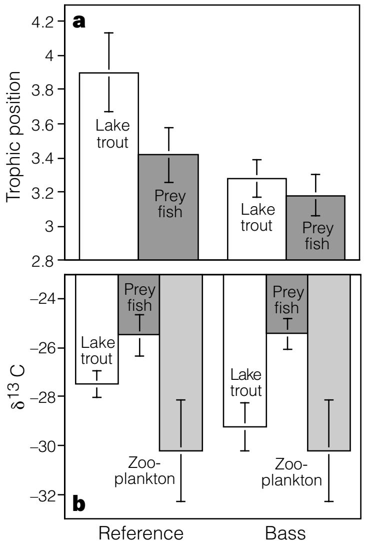

Figure 1 Trophic position and δ^{13}C values. **a**, Comparison of mean trophic position of lake trout and pelagic forage fish from invaded and reference lakes. **b**, Comparison of mean δ^{13}C values of lake trout, littoral prey-fish and zooplankton from invaded and reference lakes. Error bars represent 1 s.e.m. using lake-specific averages.

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Table 1 Lake and prey-fish data

Lake	Location		Lake area (ha)	Average secchi depth (m)	Total no. of prey species	No. of prey species (in traps)	Prey catch rate (fish per trap per day)	Prey catch rate (grams per trap per day)
	North latitude	West longitude						
Unimpacted								
Louisa	45° 28′	79° 29′	489	7.7	11	7	5.5	36.6
Havelock	45° 17′	78° 37′	175	9.8	5	4	2.6	14.5
Source	45° 33′	78° 39′	271	7.6	8	7	9.8	56.3
MacDonald (1980s)	45° 14′	78° 34′	138	9.8	9	n.d.	n.d.	n.d.
Clean	45° 15′	78° 02′	160	11.7	8	3	0.6	6.5
Mean			268	8.7	8.2	5.3	5.9	35.8
Impacted								
MacDonald (1990s)	45° 14′	78° 34′	138	9.8	2	0	0.0	0.0
Dickie	44° 47′	77° 45′	208	5.9	4	1	1.7	8.9
Johnson	45° 16′	78° 37′	151	7.6	2	0	0.0	0.0
Kelly	45° 15′	78° 37′	99	7.2	2	0	0.0	0.0
Hapy Isle	45° 45′	78° 30′	536	9.9	2	2	3.0	24.4
Mean			226	8.1	2.4**	0.6**	0.9*	6.6*

Background data for the study lakes: lake area (ha), mean summer secchi disk transparency (m), total number of prey-fish species recorded, number of prey-fish species collected in quantitative minnow trapping, prey-fish catch rate, expressed as fish per trap per day and grams per trap per day. Clean lake is undergoing bass invasion at present and is treated as an unimpacted lake as it has not yet undergone a complete invasion.

* $P < 0.05$ between invaded and reference lakes (one-tailed t-test, 7 d.f.).

** $P < 0.001$ between invaded and reference lakes (one-tailed t-test, 7 d.f.).

(*Salvelinus namaycush*) as the native top predator. Although lake trout are generally considered to be a cold-water, pelagic piscivore[19], populations from lakes lacking pelagic prey-fish can consume substantial amounts of fish from littoral habitats[20,21]. Considering the potential top-down impacts of warm-water predators such as bass on littoral prey-fish communities[22,23], we set out to examine the impact of bass invasion on food-web structure; in particular, the impact on the pathways of energy flow leading to the native top predator, lake trout.

Lakes invaded by bass contained fewer prey-fish species than reference lakes in which bass have not become established (Table 1; one-tailed t-test, $t = 5.53$, $P < 0.0005$). Similarly, our minnow-trapping efforts in invaded lakes produced fewer prey-fish species ($t = 4.59$, $P < 0.0025$) and lower prey-fish catch rates (fish per trap per day, $t = 1.95$, $P < 0.05$; grams per trap per day, $t = 1.94$, $P < 0.05$) than in reference lakes.

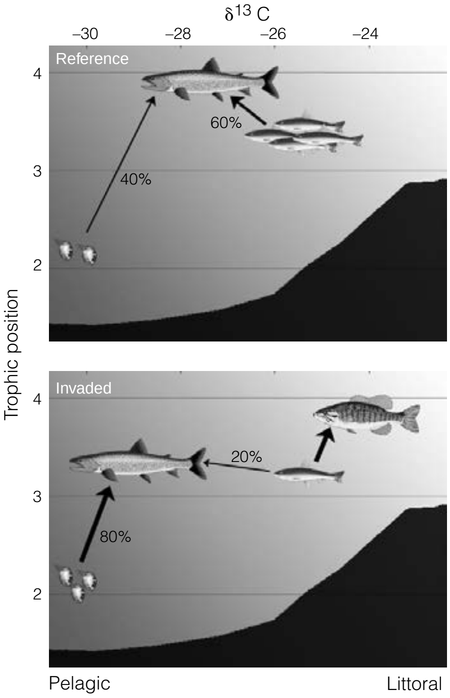

Figure 2 The pathways of energy flow through food webs of reference lakes (lakes in which bass have not become established) and lakes invaded by smallmouth bass and rock bass, based on δ^{15}N and δ^{13}C information.

We investigated whether these differences in the prey-fish communities between invaded and reference lakes are consistent with food-web differences among lakes, as inferred from natural stable-isotope distributions in lake trout tissues. Habitat- and lake-specific differences in δ^{15}N values at the base of the food web preclude the use of consumer δ^{15}N values as an absolute measure of consumer trophic position. Instead, the trophic position of consumers can be estimated by interpreting consumer tissue δ^{15}N values relative to the δ^{15}N of primary consumers, which are used as indicators of 'baseline' isotopic values[13,24].

The trophic position of lake trout averaged 3.3 in invaded lakes, indicating a plankton-based diet, compared with 3.9 in reference lakes, indicative of a primarily fish-based diet (t-test, $n = 10$, $t = 2.40$, d.f. = 8, $P < 0.025$; Fig. 1a). A two-source mixing model[25] using lake-specific mean trophic-position data and the zooplankton trophic-position endpoint of 2.0 (estimate based on 30 zooplankton samples) indicated that the diet of lake trout from reference lakes was, on average, 62% fish, compared to 22% in invaded lakes (Table 2).

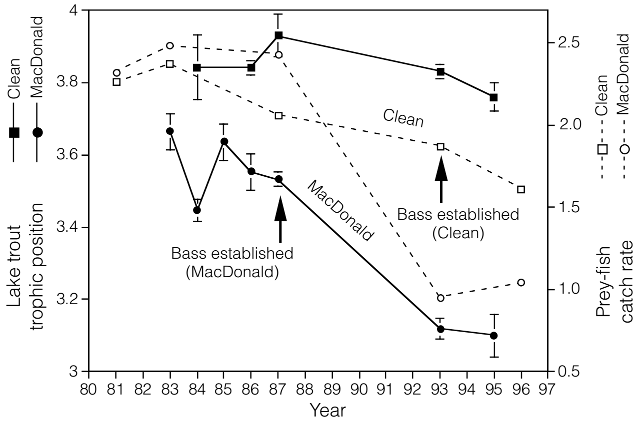

Figure 3 Temporal changes in the trophic position of lake trout (left axis) and log-transformed littoral prey-fish catch rate from quantitative electrofishing transects (right axis) in MacDonald Lake (circles) and Clean Lake (squares) for the period 1981–1996. Arrows indicate the year in which both smallmouth bass and rock bass were fully established in MacDonald and Clean lakes.

Table 2 Trophic position, δ^{13}C and mixing-model results

Lake	Lake trout trophic position (±1 s.d.)	Prey fish trophic position (±1 s.d.)	Lake trout diet		Lake trout δ^{13}C (‰) (±1 s.d.)	Prey fish δ^{13}C (‰) (±1 s.d.)	Pelagic δ^{13}C (‰)	Lake trout diet	
			% Fish	% Zooplankton				% littoral	% pelagic
Unimpacted									
Louisa	4.82 (0.25)	3.84 (0.52)	99	1	–25.82 (0.35)	–25.31 (2.15)	–29.70	88	12
Havelock	3.73 (0.07)	3.01 (0.30)	70	30	–27.77 (0.60)	–27.63 (1.41)	–29.99	93	7
Source	3.60 (0.26)	3.21 (0.22)	46	54	–28.26 (1.12)	–26.54 (0.87)	–29.99	50	50
MacDonald (1980s)	3.55 (0.14)	3.26 (0.22)	40	60	–28.79 (1.25)	–25.60 (4.24)	–30.92	40	60
Clean	3.82 (0.18)	3.76 (0.26)	44	56	–26.75 (0.98)	–22.45 (1.33)	–29.58	40	60
Mean	3.90	3.42	64	36	–27.48	–25.50	–30.04	62	38
Impacted									
MacDonald (1990s)	3.11 (0.21)	3.26 (0.22)	3	97	–29.55 (1.02)	–25.60 (4.24)	–30.92	26	74
Dickie	3.18 (0.39)	2.92 (0.07)	12	88	–32.59 (1.43)	–27.49 (0.90)	–33.59	16	84
Johnson	3.71 (0.29)	3.55 (–)	43	57	–26.62 (1.26)	–23.65 (–)	–28.36	37	63
Kelly	3.29 (0.34)	3.23 (0.30)	18	82	–28.83 (0.93)	–25.40 (2.32)	–28.36	31	69
Happy Isle	3.12 (0.33)	2.93 (0.01)	5	95	–28.39 (1.49)	–25.02 (0.41)	–30.39	26	74
Mean	3.28	3.18	16	84	–29.20	–25.43	–30.32	27	73

Stable isotope-based estimates of trophic position of lake trout and littoral prey fish are shown. Two-source mixing models use the average zooplankton trophic position of 2.0 and lake-specific mean trophic position values to estimate the % fish and % zooplankton contributions to lake trout diet. Mean lake trout, littoral prey fish and pelagic (zooplankton and unionid mussel) δ^{13}C are also presented. Mixing models were used to estimate the % contribution of littoral and pelagic prey to lake trout diet. The δ^{13}C mixing models for Havelock and Source lakes use the cross-lake mean pelagic δ^{13}C value as the pelagic endpoint owing to the lack of lake-specific data.

δ^{13}C signatures of lake trout muscle tissues provide additional evidence for food-web differences between invaded and reference lakes. δ^{13}C in lake trout from reference lakes averaged −27.5‰, indicative of reliance on littoral prey, while δ^{13}C in lake trout from invaded lakes was −29.2‰, indicating greater use of pelagic prey (t-test, $n = 10$, $t = 1.55$, d.f. $= 8$, $P < 0.10$; Fig. 1b). Two-source mixing models using lake-specific pelagic (mean of zooplankton and unionid mussel) and littoral prey-fish δ^{13}C endpoints indicated that lake trout from reference lakes averaged 62% littoral prey, compared with only 27% for lake trout from invaded lakes (Table 2). Because differences in '% fish' and '% littoral' were so closely coupled (% littoral $= 9.69 + 0.85 \times$ % fish, $n = 10$, $P < 0.001$, $r^2 = 0.84$), both lines of evidence were used simultaneously to summarize the differences in food-web structure between invaded and reference lakes (Fig. 2).

Our comparison of invaded and reference lakes is complemented by long-term studies of MacDonald and Clean Lakes. These two lakes are close to each other (<200 m), and were nearly identical in lake area, morphometry, littoral habitat and fish species composition before bass invasion. Both lakes have now been invaded by the two bass species, although the chronology of bass establishment differs for the two lakes. In MacDonald lake, both bass species were fully established by 1987, after which littoral prey-fish catch rates declined markedly (Fig. 3). Corresponding with this decline in the littoral prey-fish community, lake trout from MacDonald Lake exhibited a marked decline in trophic position following bass establishment. In Clean Lake, smallmouth bass were found in small numbers during the 1980s, although it was not until 1993 that both bass species had become fully established. The data from Clean Lake indicate that a reduction in the littoral prey-fish community and the trophic position of lake trout has begun (Fig. 3).

Pelagic and littoral habitats are often treated as separate components of lake ecosystems[26]. In this study, a native top predator generally considered to be pelagic[19] was sustained primarily by littoral resources, thereby linking these two habitats. Furthermore, the magnitude of this littoral–pelagic habitat coupling was mediated by strong top-down effects of invasive predators, resulting in an unexpected interaction between cold-water and warm-water fish species. Our findings contribute to a growing body of evidence that subsidies of resources from other systems or habitats can be both energetically significant and important in food-web dynamics[10].

The food-web changes described here have severe implications for native lake trout populations (D. M. Brown and J.M.C., unpublished data). However, not all lake trout populations are expected to be affected similarly by bass invasions, and the extent to which an invasion affects lake trout should depend on the structure of the pre-invasion food web. Specifically, bass–trout interactions should be minimal in lakes containing pelagic prey fish (such as cisco, smelt and alewife) because pelagic prey-fish species are generally not consumed by bass, but are a major prey item of lake trout[20]. It is lakes lacking pelagic forage fish, such as those examined here, that are particularly affected by invasive predators.

Increased understanding of lake trout–bass interactions might have implications for fishery management in the many other regions in which non-native predators are deliberately introduced into aquatic ecosystems. Contrary to the prevalent belief that introduction of bass and other predators represents a form of fishery enhancement, our data draw attention to the adverse competitive impacts of introduced predators upon native fish populations. Protecting native fish populations will often necessitate halting the intentional introduction of bass and other predators, and limiting the use of live bait by anglers.

Predicting the impact of perturbations such as species invasions in natural food webs presents a formidable challenge to ecology. It is increasingly recognized that broad-scale, ecosystem-level approaches (both experimental and comparative) are crucial, and even uniquely required to understand and predict ecosystem-level processes[27,28]. This study demonstrates how the use of stable isotopes can provide time-integrated and energy-based depictions of food-web structure. In fact, this isotopic approach provides a very sensitive indicator of environmental change that can be used to quantify the impacts of a broad range of anthropogenic activities on food-web structure and the pathways of energy flow in natural ecosystems. ☐

Methods

All field sampling was conducted from 1995 to 1997. Lake trout and littoral prey-fish were collected using gill nets, minnow traps, beach seines and from anglers. Zooplankton were collected using a 250-μm zooplankton net. Details of the isotopic analysis are presented elsewhere[13]. The trophic position of each fish was estimated using muscle tissue δ^{15}N and δ^{13}C data and a baseline correction method that interprets the fish δ^{15}N value relative to that of the lake- and habitat-specific primary consumer δ^{15}N; this value is used as the 'baseline' for estimating trophic position[13]. Consumer trophic position is estimated using the formula: Trophic $\text{position}_{\text{consumer}} = ((\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/3.4) + 2$, where 3.4 is the assumed per trophic level increase in δ^{15}N; primary producers = trophic level 1, primary consumers = trophic level 2, and so on. Trophic position estimates for lake trout 1983–93 rely on the 1995 baseline data. Our analysis is based on the measurement of δ^{15}N and δ^{13}C signatures from 433 samples from the nine study lakes.

Species were considered to be littoral prey-fish if they have been found to be, or are likely to be, consumed by lake trout[20]. Littoral prey-fish catch rates (Table 1) are expressed as number per trap per day and grams per trap per day, and were estimated from 24-h sets of baited minnow traps (15–40 traps per lake) during 1996 and 1997. The littoral prey-fish catch rate shown in Fig. 3 is the log-transformed catch rate (biomass) from 100-m quantitative electrofishing transects.

Counts of littoral prey-fish species are based on our field sampling efforts, unpublished Ontario Ministry of Natural Resources documents and quantitative electrofishing excursions on MacDonald and Clean lakes. Owing to the higher efficiency of electrofishing for detecting species, only the littoral prey-fish species that make up more than 1% of the electrofishing catch were retained in the species lists of these two lakes[29].

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Stable isotopes reveal strong marine and El Niño effects on island food webs

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Stable isotope analysis is a powerful tool for unravelling the complex structure of food webs[1–3]. This technique is particularly well suited for studies at ecosystem boundaries, where physical processes and mobile consumers link the dynamics of seemingly disparate systems[4–6]. In coastal and insular environments, seabirds play a crucial role in transporting marine-based energy and nutrients to islands[7–9]. Here we show using stable isotopes that nutrients from the ocean drive the dynamics of terrestrial food webs on small islands. The indirect effects of seabird-derived nutrients on plant productivity are particularly prominent during wet El Niño Southern Oscillation years on our Gulf of California study sites. During dry years that characterize the region, many terrestrial consumers are subsidized by carrion and prey from the ocean. Shifts in trophic structure related to El Niño Southern Oscillation could only be elucidated because of the distinct nitrogen isotope ratios associated with seabird islands. The contributions of seabirds and other marine sources are reflected in the isotope signatures of terrestrial consumers in ways that challenge conventional interpretations of stable isotope results in studies of food webs.

For the last 10 years, we have studied the effects of allochthonous resources from the ocean on terrestrial communities of islands off Baja California, Mexico (28° 55′ N, 113° 30′ W)[10–14]. These islands are situated in one of the driest and most barren regions of North America (mean annual precipitation, 59 mm), and marine inputs are an important source of energy and nutrients. These inputs take two forms. First, tens of kilograms of detrital algae and carrion wash ashore per metre of shoreline each year, supporting a rich intertidal community and abundant terrestrial scavengers, detritivores and predators at and above the supralittoral zone[10]. Second, seabirds that roost or nest on smaller islands provide food for terrestrial scavengers in the form of food scraps and carcasses. Seabirds also deposit large amounts of guano, which fertilizes the soil and stimulates primary productivity[7,14–16]. Growth of plants, especially annuals, is particularly striking on seabird islands during periodic El Niño Southern Oscillation (ENSO) events that bring heavy precipitation. This flush of vegetation seems to switch the system from one that is dependent primarily on allochthonous input from the ocean to one that is driven more by *in situ* terrestrial productivity. Terrestrial arthropods track these changes: in dry years, aerial insect assemblages are dominated by taxa associated with the ocean (kelp, carrion and parasitic flies)[10], but herbivores, which depend on terrestrial plants, increase 40–190-fold during ENSO years[11].

Stable isotope analysis is increasingly used to examine the exchange of energy and nutrients between ecosystems, especially at the ocean–land interface[1,17,18]. Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), expressed as the ratio of heavy-to-light carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) relative to Peedee belemnite limestone and atmospheric N standards, respectively, are the most widely used. $\delta^{13}C$ values of consumers in marine phytoplankton food webs are significantly enriched (that is, higher in ^{13}C) compared with those in food webs based on plants with C3 photosynthesis, but usually less enriched than consumers in C4 and CAM (crassulacean acid metabolism) plant-dominated environments[1]. Because relatively little (≲1‰) fractionation of C isotopes occurs between a consumer and its prey, a consumer's $\delta^{13}C$ signature is similar to that of its diet. In contrast, $\delta^{15}N$ is thought to