

## Letter

# Invasion of stream fishes into low trophic positions

Gido KB, Franssen NR. Invasion of stream fishes into low trophic positions.  
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**Abstract** – In the absence of other life-history constraints, fishes that can feed at low trophic levels (i.e., omnivores/detritivores) are predicted to be successful invaders because their food resources during the colonization and integration phases of the invasion are rarely limiting. Accordingly, we hypothesized that trophic position of non-native fishes in five mid-western and south-western U.S. river systems would be lower than native fishes. By standardizing  $\delta^{15}\text{N}$  values with a common invertebrate (chironomids) across sites, we were able to evaluate differences in trophic position between natives and non-natives across sample locations and years. Our data tend to support this hypothesis, but there was notable spatial and temporal variation in this pattern. Moreover, three of four species generally fed at lower trophic positions in their introduced ranges than their native ranges. Although many factors influence the success of introduced species, our data suggest that the ability to forage on low-quality resources is a favourable trait for invasive fishes in lotic systems. Because these fishes feed at low trophic positions, it is important to consider how they will influence invaded systems, in contrast to invaders that feed at higher trophic positions. Future studies that evaluate the resistance of communities to invaders from different trophic positions would help understand the mechanisms that control the establishment and spread of species with different life-history traits.

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## Introduction

The field of invasion biology has gained considerable attention in recent years. In particular, there is a growing body of literature that describes the consequences of alien invasions on ecosystems (e.g., Townsend 2003) and characteristics of invaders that successfully colonize foreign habitats (e.g., Fausch et al. 2001; Kolar & Lodge 2001, 2002; Fisher & Owens 2004; Jeschke & Strayer 2006). Alien fish predators can alter prey assemblage structure by killing or altering the behaviour of their prey (e.g., Ross 1991; Turner et al. 1999; Harvey et al. 2004). Introduced fishes that feed at lower trophic levels can competitively displace species that feed on similar resources (e.g., Douglas et al. 1994; Taniguchi et al. 2002) or exploit resources used by native fishes

(Flecker & Townsend 1994). Finally, introduced species that forage on producers or alter nutrient pathways also can affect the ecosystem structure and function of streams (e.g., Baxter et al. 2004). These examples suggest a linkage between the effect of introduced species on aquatic ecosystems and the trophic level of those invaders.

The trophic ecology of organisms also can influence their probability of establishment. For example, Jeschke & Strayer (2006) found that carnivorous mammals and birds had lower invasion success than herbivores, and that species with greater diet breadth were more successful invaders in Europe. In contrast, Forsyth et al. (2004) found that carnivorous or omnivorous mammals were more likely than herbivores to spread, once established in Australia. Studies of introduced species in California streams provide a

basis for predicting the success of fish invaders from different trophic levels (Moyle & Light 1996; Marchetti et al. 2004a,b). Moyle & Light (1996) hypothesized that in the absence of other life-history constraints on invasion, the success of an invader should be related to the availability of food during the establishment phase of the invasion. Thus, they predicted that top predators and omnivores/detritivores are most likely to be successful invaders because they use a food resource that is rarely limiting in aquatic systems. A subsequent study by Marchetti et al. (2004a) showed that trophic status was an important variable in a model to predict establishment of alien fishes in California. Marchetti et al. (2004b) further noted that herbivores were not as likely to have widespread invasions as other trophic groups, and invertivores were less likely to become integrated (i.e., have high average abundance) than fishes from other trophic groups. Given the importance of food resources in both the establishment and integration phases of a species invasion, trophic position is likely to be a key factor in the success of an invader. However, the importance of trophic position will likely vary across systems with different levels of resource limitation and assemblage composition.

We used stable isotopes to examine the relative trophic position of non-native fish species in lotic systems of the western and mid-western USA. In particular, the ratio of  $^{15}\text{N}/^{14}\text{N}$ , which is a good indication of trophic position (Vander Zanden & Rasmussen 2001), was used to compare trophic position of native and non-native fishes from six river systems. We also evaluated literature-based reports of diet for fish species used in our isotope analysis to show that non-native fishes, when established in lotic systems in this region, foraged at lower trophic levels than native fishes. Because the trophic position of alien invaders will largely dictate their impact on the invaded ecosystem, our findings should help predict the consequences of species invasions in lotic habitats.

## Study area

Fish assemblages were sampled from six river systems (Fig. 1) to evaluate the stable isotope signatures and diet of native and non-native fishes. These systems represented a range of climatic, geomorphological and faunal characteristics. Wildcat Creek, Kansas, is a medium-sized stream having a mean discharge of  $0.06 \text{ m}^3 \text{ s}^{-1}$  with typically moderate increases in discharge during spring and erratic flooding throughout the year. The catchment encompasses approximately  $190 \text{ km}^2$  and the stream substrate is comprised of limestone bedrock and large cobbles. The Kansas, Arkansas, Cimarron and Canadian rivers all flow west to east across the Great Plains. Substrates are dominated by shifting sand, and similar to Wildcat Creek, discharge typically increases moderately in the spring. The San Juan River has a slightly higher gradient than the rivers in Kansas and Oklahoma with substrates a mixture of sand and cobbles. Discharge in the San Juan River is strongly linked to snowmelt in the spring and to rainstorms in late summer. Introduced species were collected in all river systems except the Cimarron River. Nevertheless, we included the Cimarron River to compare the trophic position of fish species native to this system but introduced in the other systems we sampled.

## Methods

Collections were made from Wildcat Creek in October 2002, the Kansas River in October 2003 and May 2005, the Arkansas River and Canadian River in March 2003 and April 2005, the Cimarron River in April 2005 and the San Juan River in July 2003 and June 2005. All fishes were collected with a  $4.6 \text{ m} \times 1.2 \text{ m}$  (3.2-mm mesh) seine and frozen on site on dry ice. Each site was sampled intensively for approximately 1 h or until no new species were encountered. Because we only sampled wadeable habitats, we only included small-bodied fishes

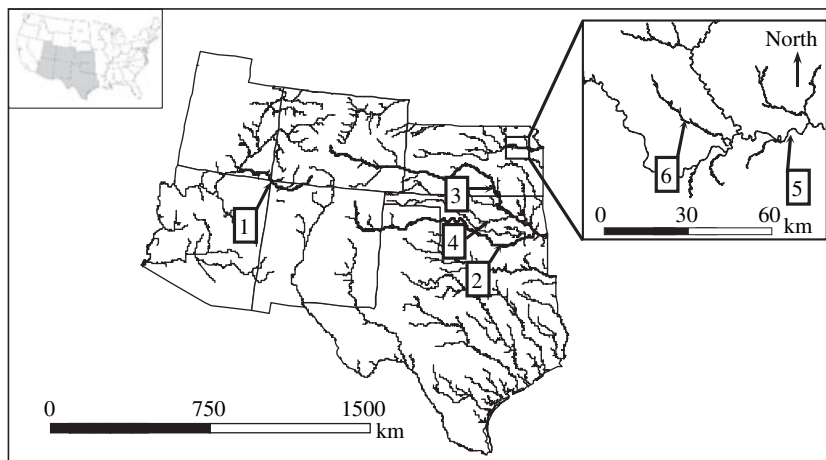


Fig. 1. Sample locations on six rivers where fish and chironomids were collected to assess trophic classifications of native and non-native fishes. The numbered squares indicate: 1 = San Juan River, 2 = Canadian River, 3 = Arkansas River, 4 = Cimarron River, 5 = Kansas River and 6 = Wildcat Creek.

(<100 mm standard length), as larger fishes that occupy deeper habitat were not effectively sampled.

**Stable isotope analysis**

Dorsal muscle tissues were taken from a minimum of three individuals from each fish species and were analysed for  $\delta^{15}\text{N}$  signatures. The use of white muscle tissue of fishes for stable isotope analysis showed the lowest variability of  $\delta^{15}\text{N}$  compared with other tissues, and does not require acidification to remove inorganic carbonates (Pinnegar & Polunin 1999). Samples were dried at a constant temperature (60 °C) for 48 h before grinding into powder with a mortar and pestle. Samples ( $\cong 2.5$  mg) were analysed for  $\delta^{15}\text{N}$  in the Stable Isotope Mass Spectrometry Laboratory (SIMSL) at Kansas State University with a Thermo-Finnigan Delta Plus mass spectrometer with a CE 1110 elemental analyser and ConFlo II interface in continuous flow mode (CF-IRMS). Stable isotope ratios were calculated in the standard notation:

$$\delta^{15}\text{N} = (\delta^{15}\text{N}/^{14}\text{N}_{\text{sample}} / ^{15}\text{N}/^{14}\text{N}_{\text{standard}}) - 1 \times 1000$$

Values are expressed on a per million (‰) basis. Overall, there was little variability in  $^{15}\text{N}$  among individual fishes taken from the same collection site; mean coefficient of variation (CV) =  $5.6 \pm 3.1\%$ . Because basal trophic levels may vary spatially and temporally in  $\delta^{15}\text{N}$  (Velinsky et al. 1989; Paerl & Vogel 1994), the trophic position of fishes was calculated relative to a primary consumer (Cabana & Rasmussen 1996). We chose chironomids as our primary consumer because they were abundant in all river systems sampled, and their  $\delta^{15}\text{N}$  was similar to other dominant primary consumers (i.e., mayflies) in systems where adequate numbers of both were collected. Thus, trophic position was calculated according to Cabana & Rasmussen (1996) as:

$$\text{Trophic position} = [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{chironomids}}) / 3.4] + 2$$

**Diet analysis**

In addition to analysis of isotopic signatures, we also evaluated diet of individuals from these collections as well as trophic classification based on diet accounts in current literature. Diet was based on the contents in the upper portion of the gut to the first bend in the digestive tract (Bowen 1996). Contents were spread on a 0.8-mm grid in a Petri dish, and per cent area for each food item was recorded. The area each diet item

occupied was assumed to be proportional to its volume (Hellawell & Abel 1971). The mean per cent area occupied by each diet item was calculated for each fish species in all systems. Although gut contents were identified to the lowest possible taxonomic group, diet items were placed into two categories (invertebrates and algae/detritus) to assess the trophic level of the prey items. Trophic positions of fishes were inferred from the mean per cent area of food items in the gut; omnivores were classified as having on average >25% of invertebrates and algae/detritus, invertivores having >75% invertebrates and algae/detritivores having >75% algae/detritus in their gut (Adams & Kimmel 1983; Franssen & Gido 2006). Therefore, diet data represented a coarse evaluation of food habits that was used to classify species into trophic groups.

We compiled literature descriptions of diet for the species used in our analysis from regional species accounts (Table 1). To simplify analyses, species were classified into one of three groups, algae/detritivores, omnivores or invertivores following Franssen & Gido (2006). If literature sources differed in their classification of a species, we selected the classification that was used in the majority of cases. Most food habit descriptions were based on the diet of adults. However, additional sources were used for largemouth bass *Micropterus salmoides*, flannelmouth sucker *Catostomus latipinnis*, river carpsucker *Carpionodes carpio* and channel catfish *Ictalurus punctatus* because  $\delta^{15}\text{N}$  values only were obtained from juveniles of these species.

**Data analysis**

We used a one-tailed paired *t*-test to test the hypothesis that mean trophic position (as calculated above) of non-native species was lower than native species across our sample sites. This analysis was based on grand mean trophic position, averaged across species, for each site ( $n = 5$ ). Because we had data from 2 years for the San Juan, Arkansas and Kansas River, we averaged mean trophic position of natives and non-natives between years. We used ANOVA with Tukey's HSD for *post hoc* comparisons to test for differences in trophic position of species across sample sites. Specifically, we were interested if species fed at lower trophic positions at sites where they were non-native, thus we restricted this analysis to four species that had both native and non-native occurrences across our sample sites. We pooled data from multiple years for species that we had isotope data for more than 1 year. Analyses were performed in SPSS version 11.0.

**Results**

Mean trophic position of introduced species was lower than native fishes in four of the five lotic systems with

Table 1. List of stream fishes sampled from six river systems in the western and south-western USA, status (I = introduced, N = native), number of guts analysed, trophic classifications based on literature review, trophic classifications based on observed diet, mean per cent invertebrates found in the diet and trophic position based on  $\delta^{15}\text{N}$  values in muscle tissue.

Species	SJR	Can	Cim	Ark	Kan	WC	Number of guts analysed	Literature classification <sup>†</sup>	Our classification	Per cent inverts in diet	Mean and range of trophic position
<i>Camptostoma anomalum</i>	–	–	–	–	–	N	5	ALG	ALG	0	2.9 (2.8–3.0)
<i>Cyprinella lutrensis</i>	I	N	N	N	N	N	94	OMN	OMN	49	2.9 (1.7–4.1)
<i>Cyprinus carpio</i>	I	–	–	I	–	–	8	OMN	OMN	64	3.0 (2.6–3.5)
<i>Hybognathus placitus</i>	–	N	N	–	–	–	9	ALG	ALG	0	2.6 (2.3–2.9)
<i>Lythrurus umbratilis</i>	–	–	–	–	–	N	9	OMN	OMN	67	3.1 (2.8–3.3)
<i>Notropis atherinoides</i>	–	N	N	–	N	–	18	OMN	OMN	31	3.1 (2.5–4.1)
<i>Notropis stramineus</i>	–	–	–	–	N	N	18	OMN	INV	80	3.2 (2.7–3.7)
<i>Rhinichthys osculus</i>	N	–	–	–	–	–	43	INV	INV	96	3.3 (2.4–3.8)
<i>Pimephales notatus</i>	–	–	–	–	–	N	5	OMN	ALG	0	3.4 (3.3–3.5)
<i>Pimephales promelas</i>	I	–	–	–	–	–	20	OMN	OMN	25	2.9 (2.1–4.3)
<i>Pimephales vigilax</i>	–	N	N	N	I	–	39	OMN	OMN	40	3.2 (2.1–3.8)
<i>Semotilus atromaculatus</i>	–	–	–	–	–	N	6	INV	INV	73	3.0 (3.0–3.1)
<i>Carpoides carpio</i>	–	–	–	–	N	–	7	OMN	ALG	0	2.8 (2.0–3.4)
<i>Catostomus discobolus</i>	N	–	–	–	–	–	n/a	ALG	–	n/a	3.0 (2.5–3.7)
<i>Catostomus latipinnis</i>	N	–	–	–	–	–	33	OMN	OMN	58	2.9 (2.2–4.1)
<i>Ictalurus punctatus</i>	I	N	N	N	N	–	30	INV	INV	84	3.4 (2.7–3.9)
<i>Noturus exilis</i>	–	–	–	–	–	N	8	INV	INV	77	3.5 (3.2–3.7)
<i>Cyprinodon rubrofluviatilis</i>	–	I	–	–	–	–	n/a	INV	–	n/a	3.2 (3.2–3.3)
<i>Gambusia affinis</i>	I	N	–	N	I	I	29	INV	OMN	60	2.9 (1.4–3.9)
<i>Fundulus zebrinus</i>	I	N	–	N	–	–	9	INV	ALG	0.1	3.5 (3.1–3.7)
<i>Lepomis humilis</i>	–	N	N	N	N	N	41	INV	INV	94	3.4 (2.8–3.9)
<i>Micropterus salmoides</i>	I	–	–	–	–	–	9	INV	INV	100	2.9 (2.3–3.5)
<i>Etheostoma spectabile</i>	–	–	–	–	–	N	8	INV	INV	100	3.6 (3.4–3.8)

<sup>†</sup>Trophic classification based on the following references: Smith (1979), Robison & Buchanan (1984), Sublette et al. (1990), Cross & Collins (1995), Pflieger (1997), Ross (2001) and Miller & Robison (2004).

introduced species present (Fig. 2). However, this difference was not statistically significant (one-tailed, paired *t*-test; d.f. = 4, *t* = 1.34, *P* = 0.13). The mean trophic position of non-natives was 2.9 and natives

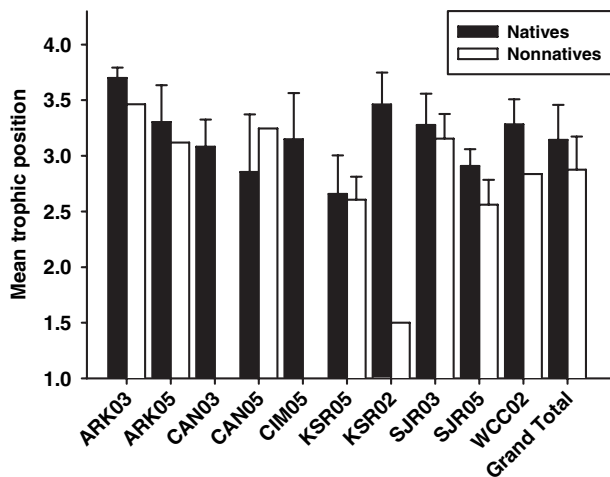


Fig. 2. Mean ( $\pm$ SE) trophic position, averaged across species, of native and non-native fish species collected from six river systems in the mid-western and south-western USA. *y*-axis labels indicate river system (ARK = Arkansas, CAN = Canadian, CIM = Cimarron, KSR = Kansas and SJR = San Juan rivers). The last two digits of the abbreviations indicate the year of sampling (02 = 2002, 03 = 2003 and 05 = 2005).

was 3.1, suggesting fishes on average fed at approximately one trophic level above chironomids, the primary consumer we used as a reference.

Diet of native and non-native fishes based on reports in the literature show that the majority of successful invaders have the ability to forage at lower trophic levels. Five of eight (63%) introduced species collected from the five river systems with introduced species were classified as omnivores, in contrast to only 10 of 22 (45%) species classified as omnivores from the total pool of species evaluated; however, the difference in these proportions between introduced and native species is not significant ( $\chi^2 = 1.628$ , *P* = 0.20). Moreover, the per cent invertebrates in guts of introduced species varied from 25% to 100%, suggesting that all introduced fishes at least partly relied on invertebrate prey, which is consistent with a mean trophic position around 3.0.

Trophic position for three of the four species that had both native and non-native occurrences at our sites, *Cyprinella lutrensis*, *Gambusia affinis* and *Pimephales vigilax*, varied significantly across those sites (all *P* < 0.001). In general, mean trophic position was lower where these species were non-native (Fig. 3). *Post hoc* comparisons suggested *C. lutrensis* trophic position in the San Juan River, where it is non-native, was significantly lower than where they are native in the Arkansas River. Trophic position of both

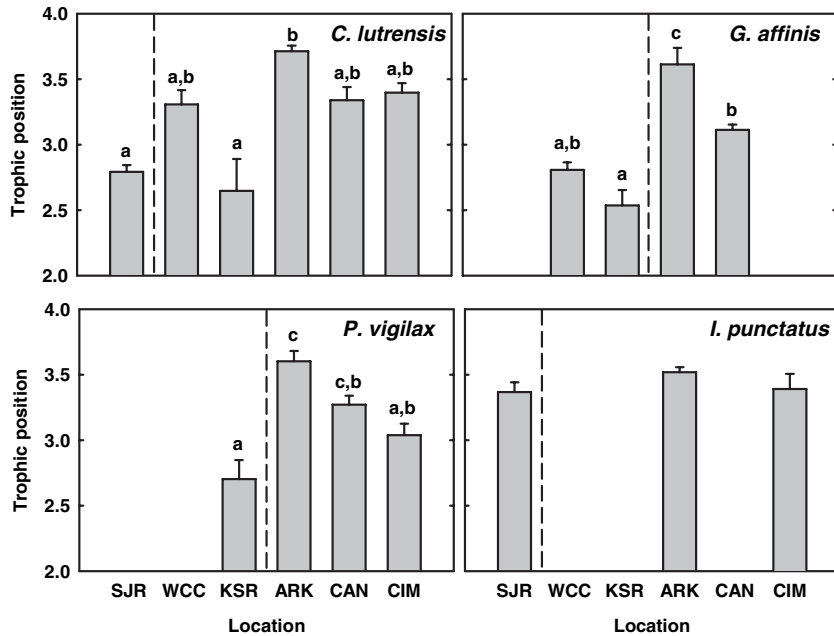


Fig. 3. Mean trophic position ( $\pm$ SE) of four fish species in river systems that had native (right of dashed line) and non-native (left of dashed line) occurrences. Shared letters above error bars indicate homogeneous subsets based on ANOVA with Tukey HSD *post hoc* comparisons.

*G. affinis* and *P. vigilax* was significantly lower in the Kansas River, where they are non-native, than the Arkansas and Canadian rivers. Trophic position of *I. punctatus* was generally high and not significantly different ( $F = 1.14$ ,  $P = 0.343$ ) among the three sites at which this species was captured.

## Discussion

The above results suggest that non-native fishes that are established in these western and mid-western streams tend to forage at lower trophic positions than native fishes, a pattern that is consistent with the prediction by Moyle & Light (1996). Whereas our data revealed only marginally significant results, it is likely that this pattern applies to other streams and rivers in the Great Plains. A previous study (Gido et al. 2004), which documented the occurrence and abundance of non-native fishes in this region, also supports the hypothesis that fishes from lower trophic levels are successful invaders. Of the seven introduced fish species that occurred in moderate to high abundance (>10 individuals per collection) in Oklahoma and Kansas streams, four were omnivores (*Cyprinus carpio* common carp, *Carassius auratus* goldfish, *Pimephales vigilax* bullhead minnow and *Oreochromis aureus* blue tilapia), and the other three were open-water planktivores/predators (white perch *Morone americana*, bluegill *Lepomis macrochirus* and inland silverside *Menidia beryllina*). Whereas the high incidence of fishes specializing on planktivory contrasts the prediction by Moyle & Light (1996),

these fishes can be highly abundant in reservoirs and their surrounding tributaries (Falke & Gido 2006). Thus, the success of these seven species may be associated with the distribution of reservoirs in this region as well as their ability to forage at lower trophic positions.

Of the six most widespread introduced species in this region (i.e., those that occurred at >30 of the 949 sample sites), only common carp and western mosquitofish *G. affinis* were classified as omnivores. The other widespread species were top predators associated with sportfishing (e.g., largemouth bass *M. salmoides* and white bass *Morone chrysops*). Again, sport fishes that are associated with reservoirs also were common invaders in this region, further illustrating the importance of reservoirs in mediating the distribution of introduced species (Havel et al. 2005).

The ability of a fish to acquire energy from basal trophic groups should increase their success in a novel environment. Although many omnivores can sustain basal metabolic demands foraging on low-quality food (e.g., detritus), high-quality food is necessary to support growth and reproduction (Ahlgren 1990; Bowen et al. 1995). Thus, omnivory would be advantageous during the invasion stage by allowing those propagules to successfully find food. Nevertheless, those species that are able to sustain growth and reproduction on a low-quality diet should have a greater capacity to become integrated into a local assemblage. Accordingly, we would expect such fishes to be opportunistic and only forage on low-quality food items when necessary. The presence of

invertebrates in the diet of all these species suggest they do consume, and likely prefer invertebrate prey, but also can sustain themselves on lower trophic groups.

When contrasting the trophic position of species in both their native and non-native ranges, it was interesting to note that three of the four species generally fed at higher trophic positions in their native range (Fig. 3). There are several hypotheses why these fish might forage at lower trophic levels where they are introduced. Presumably native fishes are adapted to local conditions and are likely better able to efficiently use food resources. As an example, native fishes in the San Juan River spawn earlier than non-natives (Gido & Propst 1999), thus young-of-the-year (YOY) fishes presumably have access to a different, and potentially more plentiful, suite of prey than do non-natives, which spawn later in the year when water temperature is higher and discharge is lower. In the Great Plains, the general pattern of invasion has been from southern to northern drainages (e.g., from the Arkansas to the Kansas River basin; Gido et al. 2004). Thus, non-native fishes potentially experience cooler water temperatures than in their native range, which may delay spawning relative to native fishes. Although this is largely speculative, it is possible the emergence of non-native YOY fishes may not be synchronized with major pulses of invertebrate prey (e.g., Noble 1986) and they are forced to forage on lower quality prey items. Given the potential for both spatial and temporal variabilities in  $\delta^{15}\text{N}$  signatures, further work is necessary to better quantify this pattern and evaluate factors involved in determining diet of non-native fishes.

It is important to note that a majority of stream fishes are opportunistic feeders that can typically consume a variety of prey, given that gape is not limiting consumption (Gerking 1994). Nevertheless, stream fishes likely vary in their ability to acquire energy from algae and detritus. Our  $\delta^{15}\text{N}$  data suggest that species that feed efficiently at lower trophic levels are more successful invaders. In addition to the examples provided by Moyle & Light (1996), non-native fishes from other regions also support this hypothesis. For example, common carp are not only widespread in North America (Fuller et al. 1999), but also have proliferated in Australia (Koehn 2004). In Korea, the introduced pale chub *Zacco platypus*, which feeds on benthic algae, was the most dominant fish in the Urano River system (Katano et al. 2004); albeit this result contrasts the findings by Marchetti et al. (2004b), which suggested that herbivorous fishes were less likely to have widespread invasions than other trophic groups. There are still many examples of large predators, such as largemouth bass *M. salmoides*, and planktivorous fishes associated with sport fishing that have become widespread. However, these fishes

are widely introduced and are somewhat dependent on source populations in nearby impoundments. Thus, in warmwater streams and rivers, the generalist feeding strategy appears to be a favourable trait of successful invaders.

Current efforts to prevent species invasions are stymied by insufficient biological knowledge (Simberloff et al. 2005). Our study provides evidence to support the predictions of Moyle & Light (1996) that fishes feeding at low trophic levels in warm-water lotic systems in the mid-western and south-western USA tend to be successful invaders. Because these species can forage on detritus and algae, we might expect their populations to be relatively stable, as these food resources are rarely limiting. Moreover, the effects of these omnivores on ecosystem processes may have different consequences for native fish assemblages than would be predicted for non-native fishes that feed at higher trophic levels. Rather, algivory and detritivory may have a series of indirect effects that could have a resounding affect in stream food webs (e.g., Matthews 1998; Flecker & Taylor 2004). Further studies on introduced stream fishes should focus on the resistance of communities to invaders with different foraging strategies as well as on a more thorough understanding of the ecosystem impacts of invaders from these different feeding guilds.

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