Tilapia Invasion Impacts Trophic Position And Resource Use Of Commercially Harvested Piscivorous Fish In The Large Subtropical Pearl River

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Abstract

Species invasions pose a serious threat to native biodiversity and ecosystems. However, quantifying the impacts of invasive species has proven problematic. In this study, we quantified the trophic changes in freshwater food webs invaded by tilapia, using an extensive stable isotope dataset to compare uninvaded and invaded rivers downstream of the Pearl River, China. The trophic position of the widely distributed and locally economically important piscivorous culter fish (*Erythroculter recurviceps*), mandarin fish (*Siniperca kneri*), and catfish (*Pelteobagrus fulvidraco* and *Pelteobagrus vachelli*) decreased significantly in the invaded river compared to the uninvaded river. Our analysis indicated that the decrease in tropic position of these piscivorous fishes reflected a major reduction in the proportion of prey fish biomass as a result of tilapia invasion. Stable isotope mixing models (SIMMs) indicated that small fish in the diet of culter fish from the reference river (32.7% small fish, 17% zooplankton) were replaced by lower trophic level zooplankton prey in the invaded river (35.7% zooplankton, 25.4% small fish), due to the presence of tilapia. Small fish in the diet of mandarin fish in the reference river (46.2% small fish, 10.5% aquatic insects) was replaced by lower trophic level aquatic insect prey in the invaded river (20.3% aquatic insects, 29.9% small fish). Fish eggs in the diet of catfish from the reference river (25.0% fish eggs, 25.2% aquatic insects) were replaced by aquatic insects at a lower trophic level in the invaded river (43.5% aquatic insects, 4.8% fish eggs). The results of this study contributed to a growing body of evidence, showing that tilapia could modify trophic interactions, which had severe consequences in invaded ecosystems.

Introduction

Although freshwater ecosystems cover less than 1% of the earth's surface, they support extremely high levels of biodiversity and provide irreplaceable ecosystem services, including the provision of fish products (Lévéque et al. 2008). Freshwater ecosystems exhibit the highest species richness per unit area of all ecosystems (Balian et al. 2008). However, due to global change and human interference, aquatic ecosystem functioning has declined sharply (Jenkins 2003). Freshwater ecosystems are considered to be one of the most endangered ecosystems (Dudgeon et al. 2006) and have the highest extinction rates on Earth (Michelan et al. 2010).

The introduction of non–native fish, for instance for aquaculture or ornamental use, is widely recognized as a serious threat to the functioning of freshwater ecosystems (as a result of changes in species diversity or the extinction of native species due to competition for food resources) (Ehrenfeld 2010; Marr et al. 2010; Lockwood et al. 2011). A number of studies have reported that fish invasions can destabilize natural communities by altering food web structure and stability (Eby et al. 2006; Attayde et al. 2011; Goto et al. 2020). Although knowledge of how food web structure relates to invasive species establishment and how these disturbances drive changes in the trophic structure of native food webs remains poorly understood, it may potentially be an important aspect of global change (Wainright et al. 2021).

Quantitative predictions of trophic responses to species invasions remains challenging because the structure of food webs is variable and complex. In addition, invasive species often have broad diets, so they have the potential to interact with a wide variety of prey species (Theoharides and Dukes 2007; Polis and Winemiller 2013). Ongoing improvements in stable isotope technology have made it possible to detect the effects of invasive fish species on the structure of food webs, and further understand the subsequent impacts on ecosystem functioning (Cardinale 2012; Thompson et al. 2012; González-Bergonzoni et al. 2020). For instance, using stable isotopes, Vander – Zanden et al. (1999) first documented significant changes in the trophic positions of native lake trout (*Salvelinus namaycush*) after the invasion of two invasive fish species (*Micropterus dolomieu* and *Ambloplites rupestris*), caused by a diet shift from consuming littoral fish to pelagic zooplankton. The invasion of rainbow trout (*Oncorhynchus mykiss*) usurped terrestrial prey that fell into the stream, causing native Dolly Varden charr (*Salvelinus malma*) to shift their diet to insects, which resulted in the restructuring of stream and forest food webs (Baxter et al. 2004). Non–native species invasion has also been shown to increase food chain length in aquatic ecosystems and elevate contaminant levels (such as heavy metals) in top predators, not only reducing the stability of the ecosystem, but also threatening human health (Vörösmarty et al. 2010).

Tilapia, is the general name of all *Tilapia spp.*, which are native to Africa, grow rapidly and show a range of biological responses to environmental conditions, such as disease resistance and increased environmental tolerance (Attayde et al. 2011). Tilapia has been introduced to at least 100 countries and has become one of the most important aquaculture species in the world (Martin et al. 2010; Grammer et al. 2012). However, these species have established viable wild populations in most tropical and subtropical environments (Zengeya et al. 2013). Wild populations were first reported from Australia in the 1970s (Ovenden et al. 2015), and now exist in at least 114 countries (Deines et al. 2016). Tilapia is currently one of the most widely distributed invasive fish, second only to Asian carps (Rutten et al. 2004). In China, tilapia was initially introduced into Guangdong province for aquaculture in 1957, following which, Tilapia culture developed rapidly in south China (Yao and Ye 2014; Fisheries and Fishery Administration Bureau of Ministry of Agriculture 2021).

The subtropical Pearl River is the largest river in south China and is over 2,400 km long. It is characterized by an average annual temperature of 23°C, with very rich aquatic biological resources. The Pearl River supports high levels of biodiversity and is a popular area for global biodiversity research. The Pearl River supports 381 fish species, exhibits high endemism and a diverse gene pool (Lu 1990; Shuai et al. 2017). To restore and maintain fishery stocks, fishing moratoria, such as fishing bans during the spawning season, were introduced in 2010, and since 2018 fishing has not been allowed in the Pearl River Basin from March to June annually. One of the most serious ecological problems in the Pearl River is the invasion of tilapia in some tributaries (Gu et al. 2015; Shuai et al. 2019).

Although the top–down impacts of tilapia invasions on ecosystems has gained a lot of attention in recent years (Attayde et al. 2011; Russell et al. 2012; Córdova–Tapia et al. 2015), to date, it is still not fully understood how tilapia compete with native species for food resources and how this impacts the trophic structure of aquatic ecosystems, despite the ecological importance and urgency of this issue. Trophic position, which represents the food resource utilization characteristics of organisms at the local scale, is a key property linking ecosystem functioning and species invasion (Thompson et al. 2012). In addition, trophic position is the most intuitive and accurately measured ecological index of food web change.

Therefore, in this study, we examined the relative trophic position of native piscivorous fishes to estimate the effects of invasive tilapia on food webs in the downstream sections of the Pearl River, China. Furthermore, we quantified how native piscivorous fish diets changed as tilapia invasion progressed, by using stable isotope mixing models (SIMMs). We selected the widely distributed and locally important commercially harvested culter fish (Hainan culter (*Pelteobagrus vachelli*), pelagic fish), mandarin fish (bigeye mandarin fish (*Siniperca kneri*), mesopelagic fish), and catfish (yellow catfish (*Pelteobagrus fulvidraco*) and darkbarbel catfish (*Erythroculter recurviceps*), demersal fish) as representative native piscivorous fish. By combining long–term abundance monitoring data and stable isotope analyses, we determined how invasion–induced trophic dynamics changed in downstream Pearl River food webs. It is crucial to understand the processes outlined in this study, in order to control non–native aquatic species, conserve the stability of freshwater ecosystems, and improve current conservation strategies in the Pearl River.

Methods

Study area

The tributaries of the Dongjiang River downstream of the Pearl River were selected as the study river, and parallel tributaries of the Beijing River were selected as the reference river. The two parallel tributaries, the Dongjiang River and Beijiang River, have a similar geographical location and it is known from previous investigations and research that the environmental conditions are similar in both tributaries (see Appendix, Table S1 for details). However, there is a serious tilapia invasion in the Dongjiang River as a result of the aquaculture industry (Shuai et al. 2015; Gu et al. 2015), while the tilapia population in the Beijiang River is relatively small due to an underdeveloped aquaculture industry. Therefore, the Dongjiang and Beijiang Rivers provide a natural laboratory to study the impact mechanisms of tilapia invasion on river ecosystem functioning. A total of eight sampling sites (four in the invaded Dongjiang River and four in the reference Beijiang River) were established to provide sufficient samples (Fig. 1, Table 1).

Table 1
The coordinates of sampling sites along the Pearl River basin.

Sites	Name	Coordinates	Width (m)	Subordinate river
S1	Lubao	112°53'23"E, 23°20'53"N	791	Beijiang
S2	Shijiao	112°57'59"E, 23°33'41"N	882	Beijiang
S3	Qingyuan	113°3'49"E, 23°41'50"N	935	Beijiang
S4	Lianjiang	113°18'16"E, 24°1'29"N	635	Beijiang
S5	Hengli	114°36'55"E, 23°10'26"N	770	Dongjiang
S6	Guzhu	114°41'26"E, 23°30'25"N	462	Dongjiang
S7	Heyuan	114°42'45"E, 23°44'18"N	714	Dongjiang
S8	Huangtian	114°59'36"E, 23°53'17"N	341	Dongjiang

Data Collection

As fishing is prohibited in the entire Pearl River basin from March to June every year and there is no obvious winter season in the downstream stretches of the Pearl River basin, fish community samples were collected twice in spring (January and February), summer (July, August, September, and October) and autumn (November and December) at each sampling site from 2013 to 2020. Isotope sample collection was only carried out in the summer, to avoid the differences caused by seasons. Community sampling was carried out using a set of gillnets (length: 10 m, height: 2.5 m; mesh size: 20 mm), fishing hooks (length: 20 m, hooks: 50), and lobster pots (length: 15 m, radius: 18 cm) to overcome selectivity effects. All sampled fish were identified to species level and measured (total length, mm; wet weight, g)

For isotope sample collection, the white muscles of the fish were dissected from the upper side of the body and close to the dorsal fins, and put into a 5–mL centrifuge tube. For the same fish species sampled at different locations, only adult samples were collected to reduce any possible confounding effects of life stage on isotopic values (Rennie et al. 2009). Phytoplankton and zooplankton were collected using a 250–mm zooplankton net. Aquatic insects such as mayflies were collected with a small hand–made net at the bottom of the river. Benthic snails and shrimp were placed in clean water for 24–48 hours, the shell was then removed, and the muscle tissue was placed into a 5–ml centrifuge tube. Any attached benthic algae and the leaves of aquatic plants were collected and washed, along with the attached sediment, in deionized water. Fish eggs and larvae were collected on spawning substrates, such as aquatic plants. All samples were stored in a mobile refrigerator at –20°C and brought to the laboratory, where they were dried to constant weight at 60°C, powdered and stored in a dryer. Each sample had at least six replicates and weighted between 0.5 and 1.0 mg.

Stable Isotope Analyses

Samples were placed in a drying tube and dried in an oven at a constant temperature of 105℃ for 48 h. The sample was weighed using a microbalance (Sartorius Service, Germany) with an accuracy of 0.001 g and wrapped in a tin capsule (volume: 48 μL, Thermo Fisher Scientific, US). The C and N isotope analysis was carried out on a Finnigan Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS, Thermo Fisher Scientific, Inc., Waltham, Massachusetts, U.S.) and a Flash 2000 HT Elemental Analyzer (Thermo Fisher Scientific, Inc., Waltham, Massachusetts, U.S.) via a Conflo IV interface (Thermo Fisher Scientific, Inc., Waltham, Massachusetts, U.S.).

In this study, the trophic position of fishes was estimated relative to a primary "baseline" consumer, as basal trophic levels may vary between seasons and rivers (Cabana and Rasmussen 1996). Consumer trophic position was estimated using the formula: Trophic $position_{consumer}$ = ((δ15$N_{consumer}$ – δ15$N_{baseline}$)/3.4) + 2, where 3.4 is the assumed increase in δ15N per trophic level (Vander–Zanden and Rasmussen 1999). We chose Chironomids (Diptera: Chironomidae, Tabanidae, Stratiomyidae and Ephydridae) as our baseline consumer as they were abundant in all rivers sampled, and were collected in adequate numbers. Chironomids are also one of the main prey species of fish. Our analysis was based on the measurement of δ15N and δ13C signatures from 684 samples from the eight study sites in two rivers.

Stomach contents were used to make preliminarily inferences on the diet of the representative fish. Representative fish individuals (n = 30 per site) were captured alive and measured to the closest 1 cm (total length, TL). Diet analysis was carried out based on the contents in the upper portion of the gut, to the first bend in the digestive tract. The stomach contents were removed from each individual and stored in 70% ethanol, before being analysed by stereomicroscope to check the frequency of occurrence of each source in the digestive tract. The frequency of occurrence is used to determine the composition of diet and the next isotopic analysis.

Changes in δ13C or δ15N of an organism indicate a change in food source (Vander Zanden and Rasmussen 1999; Rennie et al. 2009). To compare the feeding ecology of the three piscivorous fish (culters, mandarin fish and catfish) in different rivers (the invaded Dongjiang River and uninvaded Beijiang River), we estimated the change of the potential contribution of food source using a Bayesian SIMM for R 3.5.3 (R Core Team 2019). SIMM is an upgrade of the SIAR model, which contains a slightly more sophisticated mixing model and uses Just Another Gibbs Sampler (JAGS) to run the model (Parnell et al. 2013). δ13C and δ15N isotope ratios of the three piscivorous fish were put into the model as consumers. Means and SDs of δ13C and δ15N information of small prey fishes, fish eggs, crustaceans, aquatic insects, zooplankton, snails, and aquatic plants were put into the model as source means and source standard deviations data. Other parameters in the model such as concentration and correction coefficients were set as default values (NULL). Gelman–Rubin convergence diagnostics were conducted to test if the model ran properly. The Gelman diagnostic values were all close to 1, indicating that the model ran well. The posterior distribution for each source was reported as 95% credible intervals. The combination netting provided catch–per–unit–effort (CPUE, fish per net per day) estimates of relative densities of the piscivorous culter fish, mandarin fish, catfish, and their prey. All analyses were conducted using R Statistical Software version 3.3.1 (R Core Team 2019).

Results

Fish community structure and variation

A total of 10,623 individual fishes belonging to 74 taxa, 20 families, and seven orders were sampled during the present study in the invaded Dongjiang River. Of these, 66 were native and eight were non–native species. Cyprinids were most abundant, accounting for 59% of all the species caught. Of the eight non–native species, tilapia was the most abundant, accounting for 13.24% of all individuals in the Dongjiang River (Table 2). The abundance of the other non–native species was very low. A total of 10288 individuals belonging to 77 taxa, 17 families and seven orders were sampled in the reference Beijiang River. Of these, 71 were native and six were non–native species. Cyprinids were also the most abundant, accounting for 62% of all the species caught. The abundance of all the non–native species was very low, and tilapia abundance accounted for 4.84% of all individuals (Table 2).

Table 2 fish community structure in the Dongjiang River and Beijiang River

(E endemic to China; N native species; Non. Non–native species; RS River–sea migratory; RL River–lake migratory; SE Sedentawry; "+" indicates rare species)

Species	English name	Percentage (%)		Feeding Habit	Category
		Beijiang	Dongjian		
CYPRINIFORMES					
Cyprinidae					
Squalidus argentatus	Chub	19.28	8.04	I	N;RL
Hemiculter leucisculus	Common sawbelly	15.05	17.63	O	N;SE
Cirrhinus molitorella	Mud carp	4.06	12.31	H	N;RL
Erythroculter recurviceps	Culter hainan	3.70	0.85	P	N;SE
Pseudohemiculter dispar		3.59	0.37	O	N;SE
Zacco platypus	Pale chub	3.45	0.09	O	N;SE
Squalidus wolterstorffi	Dot chub	3.22	0.08	I	N;RL
Squaliobarbus curriculus	Barbel chub	2.91	1.52	O	N;RL
Abbottina rivularis	Amur false gudgeon	2.62	0.02	O	N;SE
Cyprinus carpio	Carp	1.92	1.51	O	N;SE
Carassius auratus	Crucian	1.82	2.55	O	N;SE
Megalobrama terminalis	black amur bream	1.69	5.47	O	N;RL
Saurogobio dabryi	Longnose gudgeon	1.94	4.79	I	N;RL
Cirrhinus mrigala	Mrigal carp	1.29	1.07	O	NON;SE
Hemibarbus labeo		1.29	0.71	O	N;SE
Hemibarbus maculatus		1.20	1.14	O	N;SE
Hypophthalmichthys molitrix	Silver carp	1.14	1.50	PL.	N;RL
Opsariichthys bidens Günther	Chinese hooksnout carp	1.07	0.93	I	N;SE
Culter dabryi	Dashi culter	1.05		P	N;SE
Sarcocheilichthys parvus		0.91		O	N;SE
Ctenopharyngodon idellus	Grass carp	0.80	0.81	H	N;RL
Aristichthys nobilis	Bighead carp	0.75	0.38	PL.	N;RL
Platysmacheilus exiguus		0.71		I	N;RL
Rhodeus sinensis	Light's bitterling	0.58		O	N;SE
Sinibrama wui	Bigeyes bream	0.40	0.09	O	E;RL
Xenocypris davidi	Yellow tailed xenocypris	0.35	2.28	H	N;RL
Onychostoma gerlachi	Largescale shoveljaw fish	0.29		H	N;SE
Hemiculterella wui		0.28		O	E;SE
Puntius semifasciolatus	Chinese barb	0.26		O	N;SE
Acrossocheilus beijiangensis		0.13		H	N;SE
Osteochilus salsburyi		0.11	1.01	O	N;SE
Parabramis pekinensis	White bream	0.10	0.06	H	N;RL
Xenocypris argentea	silver xenocypris	0.10	0.04		
Culter alburnus	Topmouth culter	0.08	0.57	P	N;SE
Erythroculter hypselonotus	Bigeyse culterfish	0.07	+	p	N;SE
Megalobrama amblycephala	Wuchang fish	0.05	0.02	O	N;RL
Distoechodon tumirostris	Round mouth	0.05	0.02	H	N;RL
Acheilognathus tonkinensis	Vietnamese bitterling	0.03	0.66	O	N;SE
Sinibrama melroseib	Hainan bream	0.02	0.06	O	N;SE
Mylopharyngodon piceus	Black carp	0.02	0.01	I	N;RL

Species	English name	Percentage (%)		Feeding Habit	Category
		Beijiang	Dongjian		
Acrossocheilus parallens		0.02		H	N;SE
Acrossocheilus labiatus		0.02		H	N;SE
Acrossocheilus stenotaeniatus		0.02		H	N;SE
Elopichthys bambusa	Yellow cheek carp	0.02		P	N;RL
Acheilognathus macropterus	Largefin bitterling	0.02		O	N;SE
Rectoris posehensis		0.01		H	N;SE
Cyprinus carpio var.*specularis*	Germany mirror carp	0.01		O	N;SE
Labeo rohita	Roho labeo	0.10		D	NON;SE
Huigobio chenhsienensis	Huigobio gudgeon		+	I	N;RL
Pseudogobio vaillanti			0.08	I	N;RL
Acheilognathus chankaensis	Khanka spiny bitterling		0.26	O	N;SE
Sarcocheilichthys nigripinnis			0.15	O	N;SE
Garra orientalis	Oriental sucking barb		0.04	H	N;SE
Pseudolaubuca sinensis			0.03	PL.	N;SE
Pseudorasbora parva	Stone moroko		0.02	O	N;SE
Tinca tinca	Tench		0.02	O	NON;SE
Spinibarbus denticulatus			0.02	O	N;RL
Gobiobotia meridionalis			0.02	I	E;SE
Rhodeus spinalis Oshima			0.01	O	N;SE
Parasinilabeo assimilis			0.01	H	N;SE
Cobitidae					
Misgurnus anguillicaudatus	Oriental weatherfish	4.06	3.53	D	N;SE
Micronoemacheilus pulcher		0.21	0.08	D	N;SE
Cobitis sinensis	Siberian spiny loach	0.01	0.38	I	N;SE
Homalopteridae					
Vanmanenia hainanensis			0.01	I	E;SE
PERCIFORMES					
Cichlidae					
Tilapia spp.	Tilapia	4.84	13.24	O	NON;SE
Serranidae					
Lateolabrax japonicus	Spotted sea bass	1.20		I	N;RS
Siniperca kneri	Bigeye mandarinfish	0.34	0.05	P	N;SE
Siniperca scherzeri	Spotted mandarinfish	0.16		P	N;SE
Channidae					
Channa asiatica	Chinese snakehead	0.02	0.27	P	N;SE
Channa maculata	Taiwan snakehead	0.01	0.18	P	N;SE
Channa argus	Snakehead	0.01		P	N;SE
Eleotridae					
Eleotris oxycephala	Sharphead sleeper	0.49	0.20	I	N;SE
Hypseleotris hainanensis			0.01	I	N;SE
Gobiidae					
Rhinogobius giurinus	Amur goby	0.17	1.74	I	N;SE

Species	English name	Percentage (%)		Feeding Habit	Category
		Beijiang	Dongjian		
Glossogobius giuris	Tongue goby		2.67	I	N;SE
Anabantidae					
Anabas testudineus	Climbing perch		0.01	O	Non;SE
Mastacembelidae					
Mastacembelus armatus	Tire track eel	0.41	0.55	I	N;SE
SILURIFORMES					
Bagridae					
Pelteobagrus fulvidraco	Yellow catfish	1.43	0.70	I	N;SE
Pelteobagrus vachelli	Darkbarbel catfish	1.27	1.48	I	N;SE
Leiocassis crassilabris	Ussuri catfish	1.07	0.02	I	N;SE
Mystus guttatus	Spotted longbarbel catfish	0.54	0.38	I	N;SE
Leiocassis argentivittatus	Longitudinal catfish	0.25	0.34	I	N;SE
Mystus macropterus	Largefin longbarbel catfish	0.01		I	N;SE
Leiocassis virgatus	Striped catfish		0.37	I	N;SE
Sisoridae					
Glyptothorax fukiensis			0.09	I	N;SE
Ictaluridae					
Ietalurus Punetaus	Channel catfish		0.08	I	NON;SE
Clariidae					
Clarias fuscus	Oriental catfish	0.08	0.65	O	N;SE
Clarias gariepinus	Fuscous catfish	0.01	0.18	O	NON;SE
Siluridae					
Silurus asotus	Catfish	0.36	0.18	P	N;SE
Loricariidae					
Hypostomus plecostomus	Suckermouth catfis	0.05	0.05	O	NON;SE
CLUPEIFORMES					
Clupeidae					
Clupanodon thrissa	Chinese gizzard shad	0.19		PL.	N;RS
Konosirus punctatus	Dotted gizzard shad	0.05		PL.	N;RS
Engraulidae					
Coilia grayii	Gray's grsnadier anchovy	2.60	3.20	I	N;SE
ANGUILLIFORMES					
Anguillidae					
Anguilla japonica	Japanese eel		0.03	P	N;RS
SYNBRANCHIFORMES					
Synbranchidae					
Monopterus albus	Finless eel	0.08	0.06	I	N;RS
CHARACIFORMES					
Anostomidae					
Prochilodus scyofa		0.17	0.01	O	NON;SE
TETRAODONTIFORMES					
Tetraodontidae					

Species	English name	Percentage (%)		Feeding Habit	Category
		Beijiang	Dongjian		
Takifugu ocellatus	Ocellated puffer	+		I	N;RS

The main piscivorous fish in the Dongjiang and Beijiang River are culters, mandarin fish, and catfish. These fish are the most common and widely distributed fish in the current range occupied by tilapia. Moreover, the relative abundance of these three piscivorous fish in the local fish communities has remained stable over time in the Beijiang River, while culter fish (Rs, two–tailed $P < 0.01$, Fig. 2a) and catfish (Rs, two–tailed $P < 0.005$, Fig. 2c) abundance decreased significantly in the invaded Dongjiang River. The number of prey fish species has not changed significantly over time in the invaded or reference rivers (Fig. 2d–2f). The relative densities of prey fish of the three piscivorous fish did not exhibit any significant changes over time in the Beijiang River, while all decreased significantly in the invaded Dongjiang River over time (Rs, two–tailed $P < 0.05$, Fig. 2g–2i).

For the three piscivorous fish, there was no significant difference in the number of prey fish species in the invaded Dongjiang River and the reference Beijing River (Fig. 3a). The catch data revealed that there were lower catch rates (fish per net per day) of prey fish for culter fish ($t = 6.705$, d.f. = 62, $P < 0.05$), mandarin fish ($t = 5.009$, d.f. = 62, $P < 0.001$), and catfish ($t = 6.452$, d.f. = 62, $P < 0.05$) in the invaded Dongjiang River compared with the reference Beijiang River (Fig. 3b, Table 3).

Table 3
Prey fish data of three piscivorous fish in invaded Dongjiang River and the reference Beijiang River

Species	River		Total no. of prey species(mean ± sd)	Prey catch rate (grams per net per day, mean ± sd)
	Dongjiang			
		Hengli	5.25 (0.46)	184.00 (63.79)
		Guzhu	6.13 (0.64)	196.75 (65.60)
		Heyuan	6.63 (0.52)	204.88 (48.94)
		Huangtian	5.88 (0.64)	138.00 (50.55)
		Mean	**5.97** (**0.57**)	**180.91** (**60.82**)
	Beijiang			
		Lubao	7.00 (0.93)	317.13 (105.29)
		Shijiao	7.00 (1.19)	302.75 (75.84)
		Qingyuan	6.87 (0.83)	303.50 (65.26)
		Lianjiang	6.75 (0.89)	276.12 (78.25)
		Mean	**6.91** (**0.12**)	**299.88** (**79.84**) *
Mandarin fish				
	Dongjiang			
		Hengli	6.63 (0.52)	243.13 (128.77)
		Guzhu	6.50 (0.76)	175.50 (80.46)
		Heyuan	6.13 (0.35)	229.88 (99.40)
		Huangtian	5.25 (0.46)	213.38 (95.67)
		Mean	**6.42** (**0.26**)	**215.47** (**100.84**)
	Beijiang			
		Lubao	7.00 (0.76)	483.88 (116.46)
		Shijiao	7.25 (0.71)	334.25 (170.95)
		Qingyuan	7.13 (0.83)	315.88 (79.78)
		Lianjiang	6.50 (0.53)	306.88 (125.04)
		Mean	**6.97** (**0.33**)	**369.56** (**141.87**) **
Catfish				
	Dongjiang			
		Hengli	4.5 (0.76)	129.38 (26.65)
		Guzhu	5.25 (0.70)	150.00 (37.99)
		Heyuan	4.88 (0.64)	134.38 (45.34)
		Huangtian	4.5 (0.53)	118.00 (25.42)
		Mean	**4.78** (**0.36**)	**132.94** (**35.11**)
	Beijiang			
		Lubao	5.00 (0.76)	231.38 (95.89)
		Shijiao	5.38 (0.92)	246.12 (55.81)
		Qingyuan	4.88 (0.64)	211.00 (75.08)
		Lianjiang	4.25 (0.46)	221.38 (79.03)
		Mean	**4.88** (**0.47**)	**227.47** (**75.07**)*

Changes In Piscivorous Fish Food Webs After Tilapia Invasion

We further investigated whether the abundance differences in prey fish between the invaded and reference rivers were consistent with differences in food webs between the rivers, as inferred from natural stable isotope distributions in river fish tissues. The trophic position of the three piscivorous fish also declined significantly in the invaded river compared to the reference river (Fig. 4a). The trophic position of culter fish averaged 3.94 in the invaded Dongjiang River, significantly lower than 4.64 in the reference Beijiang River ($t = -4.490$, d.f. = 46, $p < 0.05$). The trophic position of mandarin fish averaged 4.14 in the invaded Dongjiang River, which was significantly lower than 4.93 in the reference Beijiang River ($t = -4.418$, d.f. = 46, $p < 0.01$). The trophic position of catfish averaged 3.51 in the invaded Dongjiang River, which was significantly lower than 4.46 in the reference Beijiang River ($t = -3.977$, d.f. = 46, $p < 0.05$).

Table 4

Trophic position, $\delta^{13}C$ and mixing−model results

Species	**River**	**Trophic position (±sd)**	**Prey fish trophic Position (±1 sd)**	**$\delta^{13}C$ (‰) (±1 sd)**	**Prey fish $\delta^{13}C$ (‰) (±1 sd)**	**Diet(%) (±1 sd)**					
Culter fish						Small fish	Crustacean	Aquatic insects	Zooplankton	Algae	
	Beijiang										
	Lubao	4.48 (0.44)	4.41 (0.14)	–26.08(0.63)	–24.23 (1.83)						
	Shijiao	4.37 (0.28)	2.62 (0.50)	–26.72(0.45)	–25.96 (0.62)						
	Qingyuan	4.68 (0.17)	4.58 (0.34)	–27.19(2.12)	–26.72 (0.97)						
	Lianjiang	4.85 (0.07)	4.27 (0.48)	–25.69(0.96)	–24.86 (0.24)						
	Mean	**4.64 (0.29)**	**4.06 (0.84)**	**–26.95(1.28)**	**–25.16 (1.28)**	32.7(0.21)	20.9(0.15)	13.0(0.10)	17(0.13)	16.5(0.13)	
	Dongjiang										
	Hengli	4.07 (0.14)	4.86 (0.14)	–28.17(0.52)	–25.16 (1.49)						
	Guzhu	3.92 (0.35)	2.59 (0.80)	–28.54(0.93)	–25.51 (3.76)						
	Heyuan	3.96 (0.26)	3.56 (0.02)	–29.72(0.71)	–28.03 (1.17)						
	Huangtian	3.95 (0.14)	4.10 (0.34)	27.88(0.63)	–23.25 (4.10)						
	Mean	**3.94 (0.19)**	**3.81 (0.81)**	**–29.01(0.10)**	**–25.46 (2.87)**	25.5(0.23)	12.7(0.12)	11.9(0.10)	36.3(0.24)	13.6(0.12)	
Mandarin fish						Small fish	Crustacean	Aquatic insects	Zooplankton	Snail	Aquatic plants
	Beijiang										
	Lubao	4.91 (0.05)	3.75 (1.14)	–24.14(1.09)	–23.90 (1.07)						
	Shijiao	5.21 (0.39)	2.71 (0.39)	–27.20(0.31)	–24.62 (0.33)						
	Qingyuan	5.05 (0.62)	4.58 (0.34)	–25.08(1.41)	–23.78 (0.86)						
	Lianjiang	4.68 (0.08)	4.27 (0.48)	–26.28(3.11)	–24.18 (0.01)						
	Mean	**4.93 (0.34)**	**3.83 (0.94)**	**–25.21(2.07)**	**–24.03 (0.78)**	46.7(0.15)	13.6(0.11)	10.4(0.08)	4.5(0.05)	12.1(0.10)	12.8(0.10
	Dongjiang										
	Hengli	4.30 (0.24)	3.86 (0.14)	–26.38(1.72)	–22.82 (3.67)						

Species	River	Trophic position (±sd)	Prey fish trophic Position (±1 sd)	δ13C (‰) (±1 sd)	Prey fish δ13C (‰) (±1 sd)	Diet(%) (±1 sd)					
	Guzhu	4.17 (0.43)	3.73 (0.69)	–27.33(3.07)	–26.11 (3.98)						
	Heyuan	3.97 (0.14)	2.71 (1.46)	–28.35(1.63)	–26.02 (0.19)						
	Huangtian	4.11 (0.05)	3.10 (0.34)	–29.65(0.71)	–26.27 (0.53)						
	Mean	**4.14 (0.22)**	**3.35 (0.76)**	**–28.13(1.84)**	**–25.21 (3.29)**	29.9(0.22)	8.21(0.07)	20.3(0.17)	17.9(0.18)	8.9(0.08)	14.7(0.13
Catfish						Small fish	Crustacean	Aquatic insects	Fish eggs	Snail	Aquatic plants
	Beijiang										
	Lubao	4.39 (0.11)	3.60 (1.00)	–25.10(1.08)	–23.13 (0.58)						
	Shijiao	4.73 (0.60)	4.13 (0.22)	–26.62(1.25)	–24.96 (0.02)						
	Qingyuan	4.26 (1.27)	3.44 (0.56)	–24.37(0.15)	–23.34 (0.13)						
	Lianjiang	4.20 (1.18)	3.87 (0.05)	–25.95(1.32)	–24.62 (0.33)						
	Mean	**4.46 (0.71)***	**3.75 (0.56)**	**–25.32(0.98)**	**–24.95 (1.09)**	12.9(0.12)	8.9(0.06)	24.8(0.18)	25.1(0.14)	11.4(0.10)	17.1(0.14
	Dongjiang										
	Hengli	3.47 (0.02)	3.22 (0.38)	–27.52(2.00)	–24.64 (2.79)						
	Guzhu	3.49 (0.05)	4.02 (0.21)	–27.08(0.66)	–25.68 (1.50)						
	Heyuan	3.56 (0.05)	3.67 (0.04)	–26.98(0.12)	–24.32 (2.28)						
	Huangtian	3.55 (0.06)	3.64 (0.01)	–27.67(0.18)	–26.01 (2.01)						
	Mean	**3.51 (0.05)**	**3.64 (0.37)**	**–27.43(0.99)**	**–24.10 (1.83)**	9.8(0.07)	12.7(0.11)	43.5(0.17)	4.8(0.03)	13.2(0.11)	15.9(0.14

The δ13C signatures provide additional evidence for differences in food webs between invaded and reference rivers. The δ13C values in culter fish from the reference river averaged –26.95%, indicative of reliance on small prey fish, while δ13C values in culter fish from invaded lakes was –29.01%, indicating greater use of zooplankton prey at lower trophic levels ($t = 3.355$, d.f. = 46, $P < 0.01$, Table 4). The δ13C values in mandarin fish from the reference river averaged –25.21%, indicating that small fish are also their main food source, while δ13C values from the invaded lakes was –28.13%, indicating greater use of zooplankton and aquatic insects ($t = 3.840$, d.f. = 46, $P < 0.05$, Table 4). Similarly, δ13C values in catfish from the reference river averaged –25.32%, while δ13C values in catfish from invaded lakes was –27.43%, also indicating great differences in the use of food resources ($t=6.003$, $P < 0.01$, Table 4).

SIMMs using food source data from observations indicated that the diet of culter fish from the reference river averaged 32.7% small fish, compared with only 25.4% small fish and 36.3% zooplankton for culter fish from the invaded river (Fig. 5a–5b). The diet of mandarin fish from the reference river averaged 46.2% small fish and 10.4% aquatic insects, compared with 29.9% small fish and 20.3% aquatic insects for mandarin fish in the invaded river (Fig. 5c–5d). SIMMs indicated that the diet of catfish from the reference river averaged 25.1% fish eggs and 24.8% aquatic insects, compared with only 4.8% fish eggs and 43.5% aquatic insects in the invaded river (Fig. 5e–5f).

Discussion

Tilapia occur in more than 100 countries outside of their native range after tilapia has been introduced with joy for more than 60 years (Esselman et al. 2013). In 2014, tilapia was officially listed as one of the world's top 100 invasive species in the list of non–native invasive species in China (the third batch). In the present study, we found that tilapia invasion decreased the mean estimated trophic position of native top fish predators. Our analysis clearly demonstrated that this decrease in trophic position was solely due to the decline in prey fish biomass associated with tilapia invasion.

Tilapia have a preference for the same type of habitat as native fish and so the presence of tilapia displaced native fish from their preferred habitats. Tilapia invasion can reduce local biodiversity and result in the extinction of native fish species due to competitive replacement (Starling et al. 2002; Figueredo & Giani 2005). Therefore, the establishment of tilapia has detrimental effects on aquatic food web structure in native habitats (Martin et al. 2010; Attayde et al. 2011; Russell et al. 2012). Fishes which are adapted to consume a diversity of foods often change their diets to overcome increased competition for food following species invasions (McMeans et al 2016; Wainright et al. 2021). These diet changes, such as switching from a specialist to a generalist diet or eating insects instead of fish, are reflected in the trophic structure of food webs.

This is the first study to clarify how the invasion of tilapia affects the feeding habits and trophic position of native species. There was strong evidence of a shift in diet composition and a decline in the trophic position of top fish predators in the invaded Dongjiang River related to changes in prey availability. The trophic position of culter fish, mandarin fish, and catfish in the invaded Dongjiang River, was significantly lower than in the reference Beijiang River. The diet of culter fish shifted from small fish (32.7% small fish, 17% zooplankton) to zooplankton (36.3% zooplankton, 25.5% small fish) in the invaded river. The diet of mandarin fish shifted from small fish (46.7% small fish, 10.4% aquatic insects) to aquatic insects (20.3% aquatic insects, 29.9% small fish) in the invaded river. The diet of catfish changed from fish eggs (25.1% fish eggs, 24.8% aquatic insects) to aquatic insects (43.5% aquatic insects, 4.8% fish eggs) in the invaded river.

This dietary shift was accompanied by a prolonged reduction in the abundance of native fish species. The sampling data showed that the relative densities of native prey fish decreased significantly over time in the invaded Dongjiang River. There has been a great deal of evidence to show that the increase of tilapia in rivers affects the CPUE of the fish community and native fish species (Gu et al. 2015), including the most abundant native species mud carp (*Cirrhinus molitorella*), black amur bream (*Megalobrama terminalis*), barbel chub (*Squaliobarbus curriculus*) and common sawbelly (*Hemiculter leucisculus*) (Shuai et al. 2019). The larvae of these fish are an important food source for top predators. A significant reduction in the CPUE of other commercially important species was also observed after the introduction of Nile tilapia in the North–eastern Brazil reservoir (Attayde et al. 2011). There is substantial overlap in diet between tilapia and native fishes in most tropical and subtropical habitats (Henson et al. 2016). In the current study, which spanned 9 years in the Pearl River, native fish densities decreased with increasing tilapia density. In particular, a progressive decrease in body size, such as fish plumpness, body length, and body weight, of native fishes coincided with the increasing prevalence of Nile tilapia (Shuai et al. 2019), and increased competition from Nile tilapia with local native species for food resources.

Trophic position stability is considered to be an important variable in the structural stability of food webs (Rennie et al. 2011; Thomsen et al. 2014). Analyzing trophic position variation can be helpful in detecting the effects of invasive fish species on the structure of food webs and understanding subsequent impacts on ecosystem functioning (Cardinale 2012; Thompson et al. 2012). Stable trophic positions of predators and prey are one component of stable food webs (Johnson et al. 2014), while trophic dispersion implicitly involves variability in trophic position. Tilapia invasion induced significant trophic dispersion, thereby disrupting trophic positions and destabilizing food webs in the Pearl River. We found that native top fish predators increasingly relied on zooplankton and aquatic insects as invasion progressed, which may have destabilized food webs and promoted their transition to tilapia dominance. Indeed, food web instability is a precursor to ecological state change (Rooney and McCann 2012), and biological invasions are known to yield alternative ecological states (Scheffer and Carpenter 2003), it is likely that these food web changes ultimately produced a new ecological regime (Wainright et al. 2021).

We found that invasive tilapia forced other fishes to increasingly rely on zooplankton and aquatic insect resources in the tropical river. These results demonstrated how invasive tilapia initiated disruption of native food webs via trophic displacement, and the study provided clear evidence that invasive predators can influence the dominant energy pathways of native predators, ultimately destroying ecosystem stability. The results of this study provided a basis for understanding and predicting the directional effects of invasive species on recipient food webs. Trophic changes due to fish invasion can also exhibit biotic homogenization with trophic downgrading (Singh 2021). For example, the invasion of lake trout (*Salvelinus namaycush*) increased fish diet variability, disrupted food webs by reorganizing macroinvertebrate communities, and displaced native fishes from their reference diets in the northern Rocky Mountains, USA (Wainright et al. 2021). The invasion of Dreissenid mussels, including the zebra mussel (*Dreissena polymorpha*) and quagga (*Dreissena rostiformus bugensis*) in the Great Lakes, caused commercially harvested native whitefish (*Coregonus clupeaformis*) to become more reliant on nearshore benthic production, changing the fundamental energy pathways in the lakes (Fear et al. 2017).

Therefore, the invasion of tilapia is bound to have a serious impact on the trophic position of native fish populations, and the negative impact of tilapia on native fisheries and ecosystems in southern China should not be underestimated. Protecting native fish populations often involves stopping the intentional introduction of non–native fish. The potential damage associated with invasive species has prompted recent efforts to predict the vulnerability of ecosystems to species invasions and prioritize them for management (Strassburg et al. 2020; McDonald–Madden et al. 2016). Ultimately, protecting entire landscapes from biological invasions may be required to sustain native biodiversity and ecosystems. This strategy may require stopping the introduction of invasive species, including non–native fish–stocking programs, and using innovative bio–surveillance monitoring techniques, such as environmental DNA (Evans et al. 2017), for early detection of potential invaders.

However, tilapia plays a very important role in the international market, ranking second in the global freshwater fish trade, second only to salmon and trout. Tilapia is one of the most internationally competitive aquaculture varieties in China, and it is also the species with the most potential for industrial development (Yao and ye 2014). In 2020, the global culture output of tilapia reached about 6.93 million tons. The huge demand for tilapia in the international market has further expanded the breeding scale of tilapia in China. The production of tilapia in aquaculture in China reached 1.66 million tons in 2020 (Fisheries and Fishery Administration Bureau of Ministry of Agriculture 2021). For many years, China has been the world's largest tilapia producer and leading tilapia exporter (more than 60% of global tilapia exports), exporting to 80 countries or regions every year (Liao et al. 2020).

In spite of available regulatory approaches and guidelines to manage aquatic invasive species, fish invasions are increasing. The importance of the tilapia breeding industry, makes it difficult to control tilapia invasion, and it is neither realistic nor desirable to completely eradicate tilapia. To date, at least 10 tilapia species have been recorded in China, including New *tilapia zillii*, *tilapia zillii*, Mossambica tilapia (*Oreochromis mossambicus*), Nile tilapia (*Oreochromis niloticus*), Fushou tilapia (Mossambica tilapia × Nile tilapia), aureus tilapia (*Oreochromis aureus*), O'nei tilapia (aureus tilapia × Nile tilapia), blackchin tilapia (*Sarotherodon melanotheron*), *Sarotherodon galilaeus* and *Tilapia rendalli* (Yao and Ye 2014). As a result, feral tilapia have hybridized and introgressed in aquaculture settings before escaping to the wild. Reproductively viable hybrids have resulted, facilitating tilapia invasion. In order to better develop the aquaculture industry, germplasm improvement of tilapia is progressing rapidly. It is fairly well understood that hybrids, mixed hybrids and breeding, will lead to a general invasion success for most tilapia species. Therefore, after the serious ecological consequences caused by tilapia, the prevention and control of tilapia invasion is still a difficult problem.

In recent years, local governments have invested a lot of human and financial resources to protect and repair of the decline of fishery resources in rivers, such as annual proliferation and release activities, but these attempts have not been particularly successful. This was largely due to a lack of understanding regarding the mechanisms driving the decline in fishery resources. The results of the current study provided an initial insight into the decline of fishery resources in the Pearl River following tilapia invasion. At present, the most effective way to prevent invasion impacting fishery resources in the Dongjiang River is to be stringent regarding environmental isolation in pond culture, avoiding tilapia for release activities, and strictly controlling the growth range of this species. More stringent regulation of aquaculture activities and proactive fisheries management are required to avoid additional releases and further spread of tilapia in the region.

Understanding the consequences of invasive species on ecosystem functioning through changes in trophic interactions among species has received considerable interest over the past decade (Thébault 2003). Most of these studies have used stable isotopes to quantify changes in the trophic structure of communities (Cucherousset et al. 2012), as carbon (δ13C) and nitrogen (δ15N) can provide an accurate quantitative method for the study of the changes of nutritional structure in aquatic ecosystems (Bearhop et al. 2004). Recent methodological developments have facilitated the quantification of multiple facets of the trophic structure of communities, such as isotopic diversity metrics, i.e. trophic niche width (TA), isotopic richness (IRic), isotopic evenness (IEve), isotopic divergence (IDiv), isotopic dispersion (IDis), and isotopic uniqueness (IUni) (Jackson et al. 2011; Cucherousset and Villéger 2015). These metrics were widely used to assess the effects of biological invasions on a multitude facets of food webs and ecosystem functioning at both local and global scales (Zambrano et al. 2010; Walsworth et al. 2013; Spurgeon et al. 2014; Sagouis et al. 2015).

While theoretical and methodological approaches have been recently developed, empirical studies are still needed to assess the effects of biological invasions on the trophic structure of recipient communities. The changes in food webs described in the current study have serious implications for native fish populations and food resources. An increased understanding of the interactions between tilapia and native fish is necessary for fishery management in many regions. Our findings emphasized the need to implement proactive control efforts to restore invaded ecosystems, particularly during colonization and early stages of establishment, to avoid food web disruptions that may be difficult to reverse. As tilapia is a commercially important species, its introduction cannot be banned, and so the strictest supervision of this species is required.

Declarations

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Figures

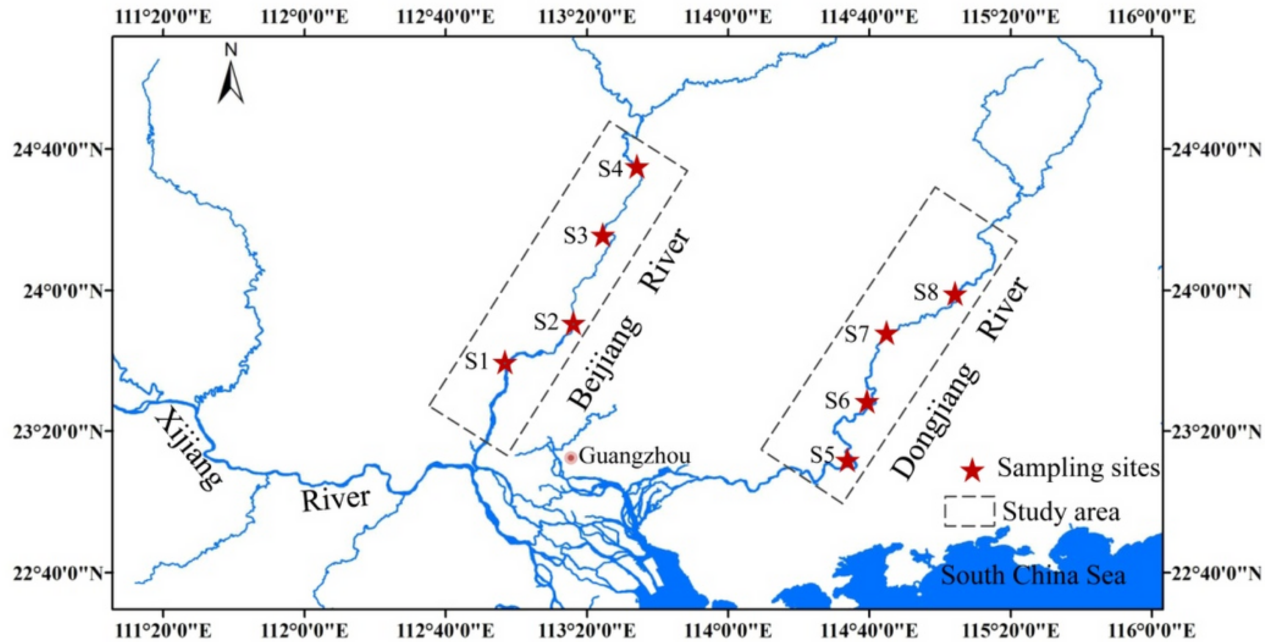

Figure 1

Sampling sites.

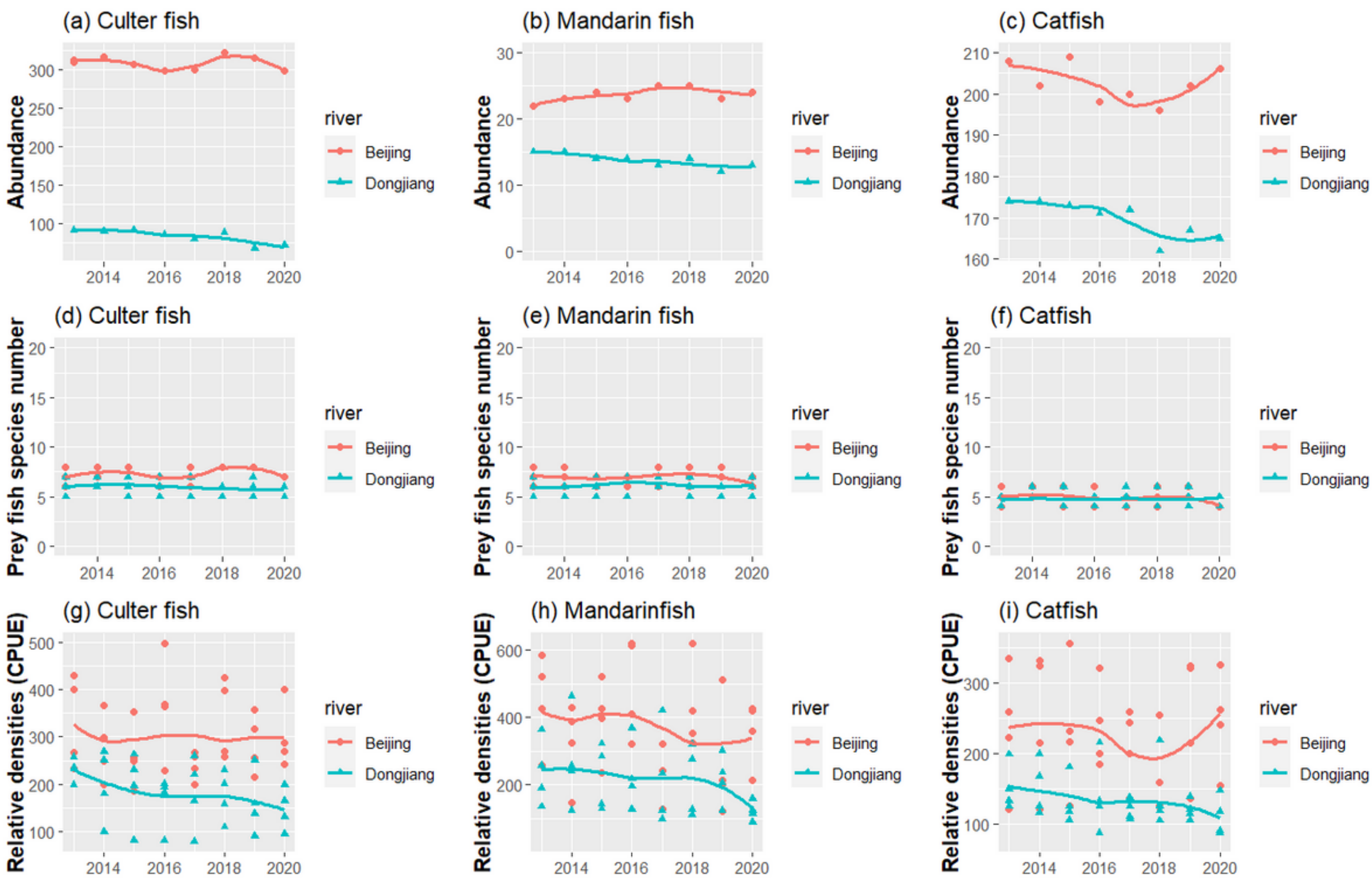

Figure 2

Temporal dynamics of three piscivorous fish and their prey fish. (a) abundance of culter fish, (b) abundance of mandarin fish, (c) abundance of catfish, (d) species number of prey fish of culter fish (e) species number of prey fish of mandarin fish, (f) species number of prey fish of catfish, (g) relative densities (CPUE, g per net per day) of prey fish of culter fish, (h) relative densities (CPUE) of prey fish of mandarin fish, (i) relative densities (CPUE) of prey fish of catfish in the Dongjiang River and Beijiang River from 2013 to 2020 (culter fish *Erythroculter recurviceps*, mandarin fish *Siniperca kneri*, catfish *Pelteobagrus fulvidraco* and *Pelteobagrus vachell*).

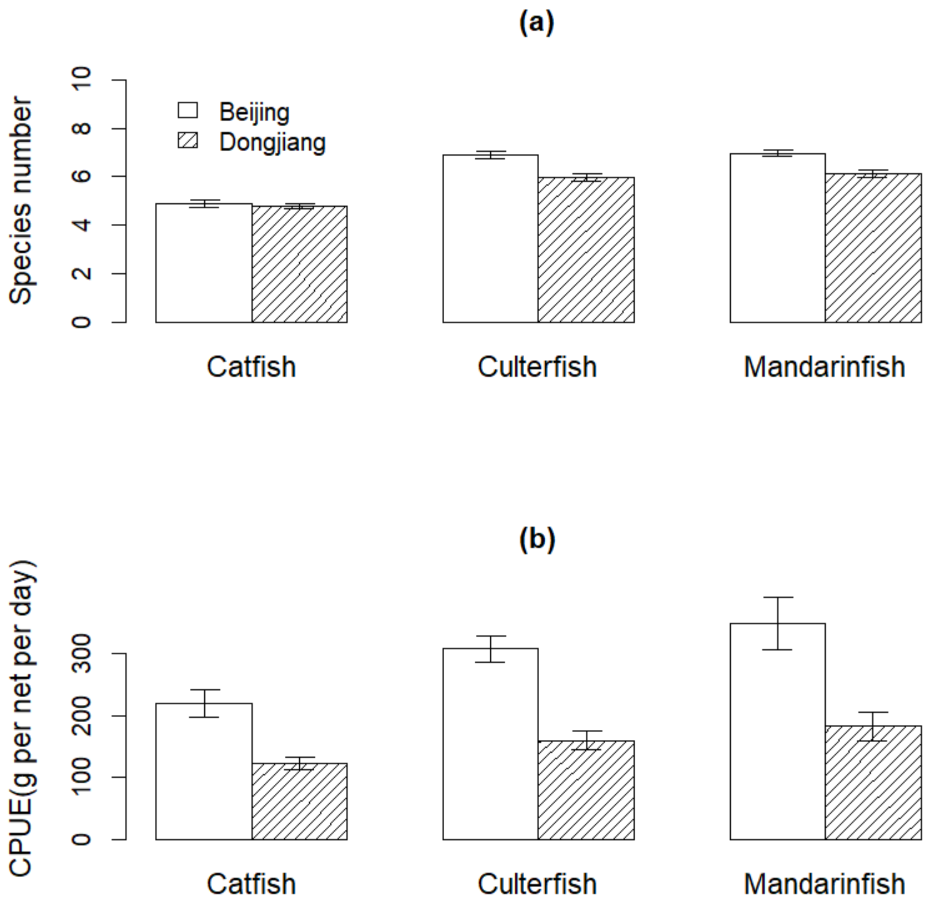

Figure 3

Prey fish data of the three piscivorous fish from the invaded and reference rivers. (a) Comparison the number of prey fish species, (b) Comparison of the relative densities (CPUE, g) of prey fish caught in each net each day.

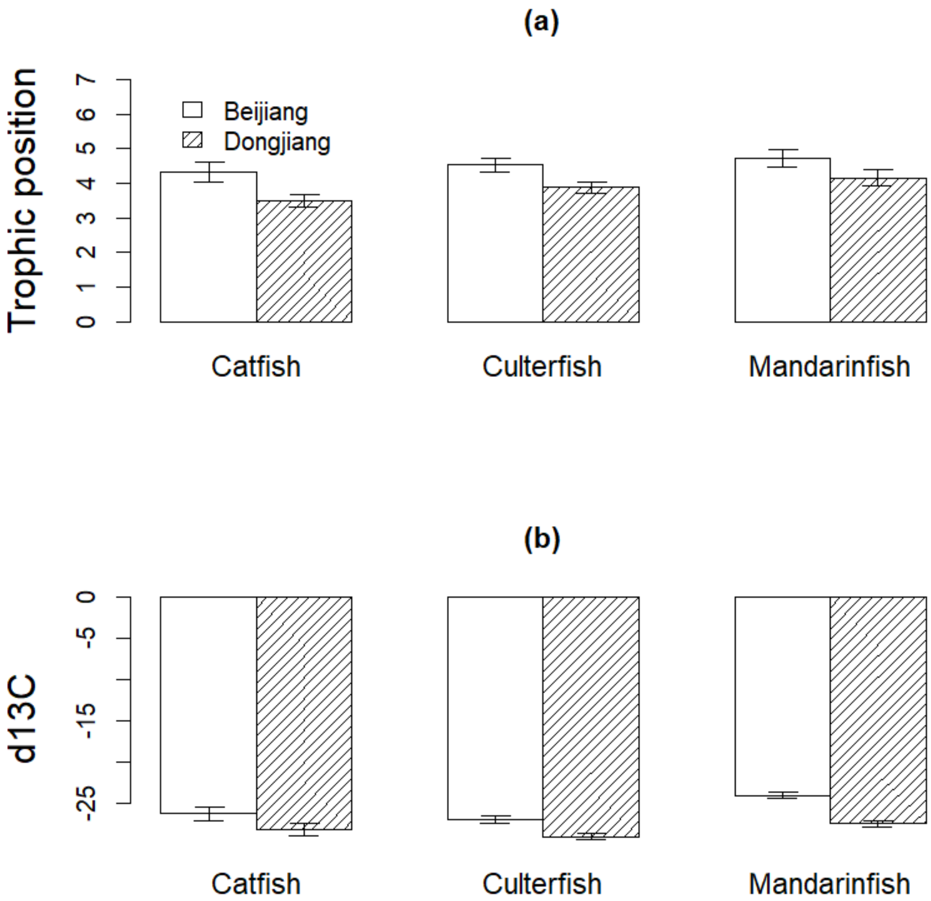

Figure 4

Trophic position and $\delta^{13}C$ values. (a) Comparison of mean trophic position of piscivorous culter fish, mandarin fish, and catfish from invaded and reference lakes. (b) Comparison of mean $\delta 13C$ values of piscivorous culter fish, mandarin fish, and catfish from invaded and reference rivers.

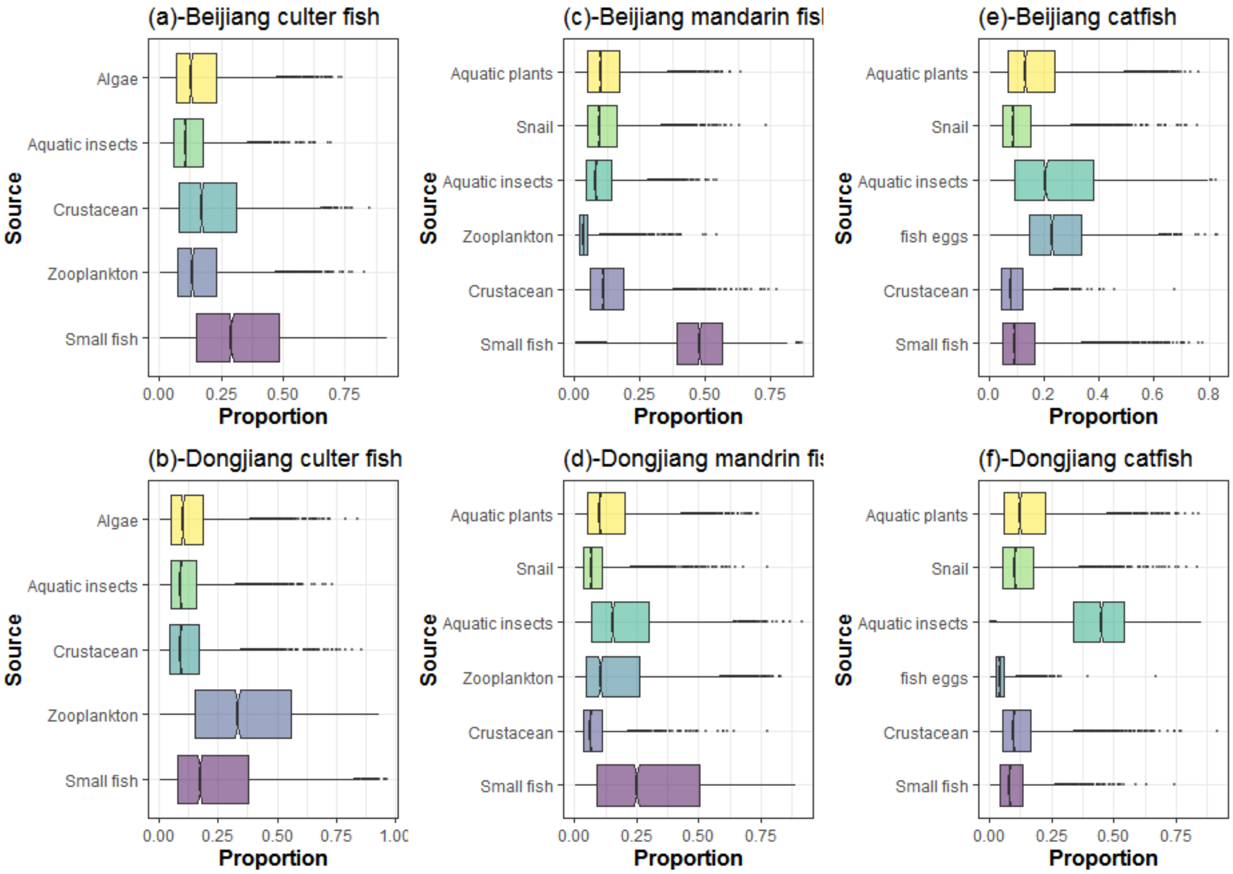

Figure 5

Food resource structure of uninvaded and invaded rivers.

Supplementary Files

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- AppendixTableS1.docx