Biol Invasions (2019) 21:2059–2066
https://doi.org/10.1007/s10530-019-01957-3

ORIGINAL PAPER

Adaptive downsizing in the piscivorous cyprinid fish, *Opsariichthys uncirostris*, facilitates rapid establishment after introduction to a small-scale habitat in Japan

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Received: 13 May 2018 / Accepted: 11 March 2019 / Published online: 18 March 2019

Abstract The three-lips (*Opsariichthys uncirostris*) is a piscivorous cyprinid fish native to the Biwa Lake, central Japan. A recent unintentional introduction of the species has led to its invasion of a novel, small-scale habitat (the Futatsu River) composed of a few riverine stretches connected by irrigation ditches. Comparative observations of fish samples from both habitats provide evidence of disparities in the fish's size at maturity between the two habitats, with fish in the Futatsu River reaching maturity at smaller body sizes. Achieving a large body size at maturation requires a larger habitat offering a sufficient supply of food. Principle component analysis of body-surface morphometric characteristics revealed that the two populations show differences in both their body shape and growth rates. In the Futatsu River, the growth rates of upper jaw length, lower jaw length, eye diameter, predorsal length, and tail length were accelerated, while the growth rates of head depth, body depth, and tail depth were decelerated, leading to the acquisition of a distinctly slender body. It is plausible that small-scale habitats with less abundant food supplies favor sexual maturation at smaller body sizes and that slender bodies improve swimming performance, thus making such disproportional downsizing a consequence of adaptation to a novel environment. Whether this change is due to phenotypic plasticity or rapid evolution remains unknown.

Keywords Invasive alien species · Piscivorous cyprinid · Establishment success · Morphometry · Body shape · Downsizing

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Introduction

Invasive alien species are a major driver of biodiversity loss, urgently requiring the implementation of preventive measures to ensure the sustainability of ecosystems worldwide (Strayer et al. 2006; Dick et al. 2017). Increasing human activity associated with aquaculture, agriculture, recreation, and transportation increases the risks of the intentional or accidental introduction of a species to areas outside of their natural ranges (Seebens et al. 2017). Once an alien species is introduced to a novel environment, they are subject to numerous selective pressures derived from the abiotic and biotic characteristics of the environment which oppose the formation of a nascent alien population (Kolar and Lodge 2001; Hayes and Barry 2008; Ficetola et al. 2009). Unsurprisingly, however, alien species which become invasive often overcome these selective pressures and become established in novel environments. The success of an invasive species in its establishment in a variety of environments results in an expansion in its range, which, in many cases, has negative effects on local biodiversity. The establishment of alien species in a novel habitat can be attributed to a number of factors whose influence eventually results in the establishment of the alien species in its new environment (Heger and Trepel 2003, Williamson 2006; Korsu and Huusko 2009). Understanding how susceptible habitats are to invasion by alien species is critical in the conservation of local biodiversity.

The three-lips (*Opsariichthys uncirostris*) or Hasu in Japanese is a piscivorous fish native to the Biwa Lake, central Japan (Sunaga 1980; Tanaka 2005). Widely regarded as the largest freshwater habitat in Japan (Shiga Prefecture 2013), the lake occupies an area of 670.3 km^2 and has a maximum depth of 103.6 m. The toothless mouth of the three-lips, which is unique to cyprinids, possesses a symphyseal knob on the lower jaw used to hold prey during foraging. Adults can grow up to 300 mm in standard length (SL) and is thus one the largest predatory fish found in Japan.

Ayu (*Plecoglossus altivelis*) from the Biwa Lake have been introduced to most inland waters in Japan for more than two decades to enhance fish stocks (Iguchi et al. 1997). The commercial release of Ayu using fish seed from the Biwa Lake has led to the spread of many lacustrine fishes, including three-lips, into other water bodies across Japan (Onikura et al. 2011; Watanabe 2012). Three-lips from the lake are also transported into other waters as hitchhikers in carrying water tanks on the transport truck. Based on the multiple methods by which the three-lips has been spread throughout Japan, the species should have been thoroughly propagated throughout the Japanese Archipelago; however, the successful establishment of the three-lips depends on similarities between its native habitat and prospective habitats (National Institute for Environmental Studies 2011). The presence of large predators requires a suitably large population of prey organisms, and thus larger water bodies with larger food supplies are more likely to support a nascent population of three-lips. Commonly, lakes—but not ponds—support the immigration of alien species, as exemplified by the second largest lake in Japan, the Kasumigaura Lake (Yanai et al. 2008). Similarly, in running waters, species establishment success depends on the length of the watercourse (Onikura et al. 2013).

Considering the importance of environmental similarity, the recent reports of three-lips inhabiting the Futatsu River (Kyushu Island, southern Japan) is somewhat unexpected (Kurita et al. 2008; Onikura et al. 2008). The Futatsu River is characterized by its narrow width (> 10 m) and shallow depth (> 2 m), and is composed of a small number of riverine stretches connected by irrigation ditches (Nakajima et al. 2008; Sato et al. 2010). Generally, in water bodies, environmental factors such as water temperature, current velocity, substrate material, abundance of prey organisms, and presence of predators are suitable barriers against the invasion of alien species (Kurita et al. 2014). In the Futatsu River, food availability for the three-lips is much lower than in the Biwa Lake (Kurita et al. 2008), and so its persistence there is surprising. The connectivity of different habitat types in the Futatsu River defines the environmental characteristics that facilitate the movement of fishes between lentic and lotic waters (Kurita et al. 2014; Kurita and Onikura 2016). While movement between different microhabitats may be useful in ensuring suitable food availabilities throughout development, how predatory fish such as the three-lips persist in areas with poor food availabilities is unknown.

The introduction of piscivorous fish into a habitat increases the frequency of antagonistic interactions between species and especially in smaller habitats with lower species richness, resulting in community instability (Mougi and Kondoh 2012). The adverse effects caused by the presence of three-lips in the Futatsu River place endangered species at increased risk (Onikura 2016). Therefore, effective measures to prevent its further spread, regardless of habitat size, are required for the conservation of local biodiversity. This study aimed to better understand the process by which three-lips has skipped normal invasion pathways and become established in a small-scale habitat. We hypothesized that three-lips in the Futatsu River would have reacted to the novel habitat conditions (including low food availability and habitat heterogeneity) through adaptive alteration of body shape and growth mode. Two populations were compared using morphometric analysis, one from the original habitat, the Biwa Lake water system (BLWS) and the other from a non-native habitat, the Futatsu River water system (FRWS).

Materials and methods

Sample collection

Sampling of fish from the Futatsu River (representing the non-native habitat) and its connective irrigation ditches (FRWS; 32°10′ N, 130°26′ E) took place in 2006 and 2007. The Futatsu River is a tributary of the Yabe River, running through the northwest region of Kyushu Island, Japan. Cast nets were used to capture fish from different habitat types in order to collect fish of varying body sizes.

The three-lips dwelling in the Biwa Lake and those spawning at the mouth of its inlet streams (BLWS) have been identified as the origin of alien conspecifics in Japan. Because inland fisheries in the Biwa Lake target three-lips at a wide range of developmental stages (Tanaka 1970), fish samples from BLWS were collected from fishery catches in 2008 and 2009.

Morphological analysis

Samples from FRWS comprised fish specimens with SLs ranging from 51.1 to 178.3 mm ($N = 50$), while SLs of fish from BLWS varied between 53.0 and 258.0 mm ($N = 83$). Because sample sizes were limited, morphological analyses in both samples were conducted without consideration for the effects of sex (female/male) and degree of sexual maturation (immature/mature). Morphometry was employed to evaluate body shape numerically (Stower et al. 1960). Fish were fixed in 10% formaldehyde solution and their external traits were measured, including 21 distances between morphological landmarks on the lateral body surface (Fig. 1a) and another seven morphological characteristics (Fig. 1b). Principle component analysis (PCA) provided objectively defined scores that summarized the major components of morphological variation between individuals (Adbi and Williams 2010). Specimens were not uniform in body size, indicating that allometric effects should be taken into account (Gould 1966). Measurements were log-transformed and PCA was performed based on the residuals from a regression line between each morphometric truss and the individual's standard length (SL). Statistical analyses were performed using SPSS software ver. 22.0 (IBM Corporation Japan, Tokyo).

Results

PCA was performed for all basic variables to produce new principle components. The first three principal components (PC1, PC2, and PC3) accounted for 56.9% of variance in the original data (Table 1). According to loading weights, eigenvectors such as d–e, e–f, g–h, c–j, d–i, and e–i were represented by PC1 and c–d and b–k were represented by PC2. No conspicuous eigenvector was found in PC3. Samples differed in mean PC scores in both PC1 (Fig. 2a; Student's t test, $t_{131} = 11.72$, $P < 0.001$) and PC 2 (Fig. 2b; $t_{131} = -5.69$, $P < 0.001$), but did not differ significantly in PC3 (Fig. 2c; $t_{131} = -0.797$, $P = 0.427$). Significant relationships were found between PC1 and PC2 scores when the two samples were analyzed separately (Fig. 3; Pearson's correlation coefficient, FRWS, $r_{48} = 0.570$, $P < 0.001$; BLWS, $r_{81} = 0.499$, $P < 0.001$). Characteristics that showed higher eigenvectors in the PCA were analyzed using ANCOVA to examine allometric regressions between log-transformed measurements and log-transformed SL (Table 2). The gradient of these regression lines often differed between samples: FRWS > BLWS for upper jaw length (UJL), lower jaw length (a–l), eye diameter (ED), predorsal length (PDL) and tail length (e–f); FRWS < BLWS for head depth (b–k), body depth (c–j), and tail depth (e–h). No significant differences were found in snout length (SnL), head length (a–b), pectoral fin length (PectFL), and pelvic fin length (PelFL) between the two samples.

Discussion

The two populations of three-lips, one native to the Biwa Lake water system (BLWS) and the other alien

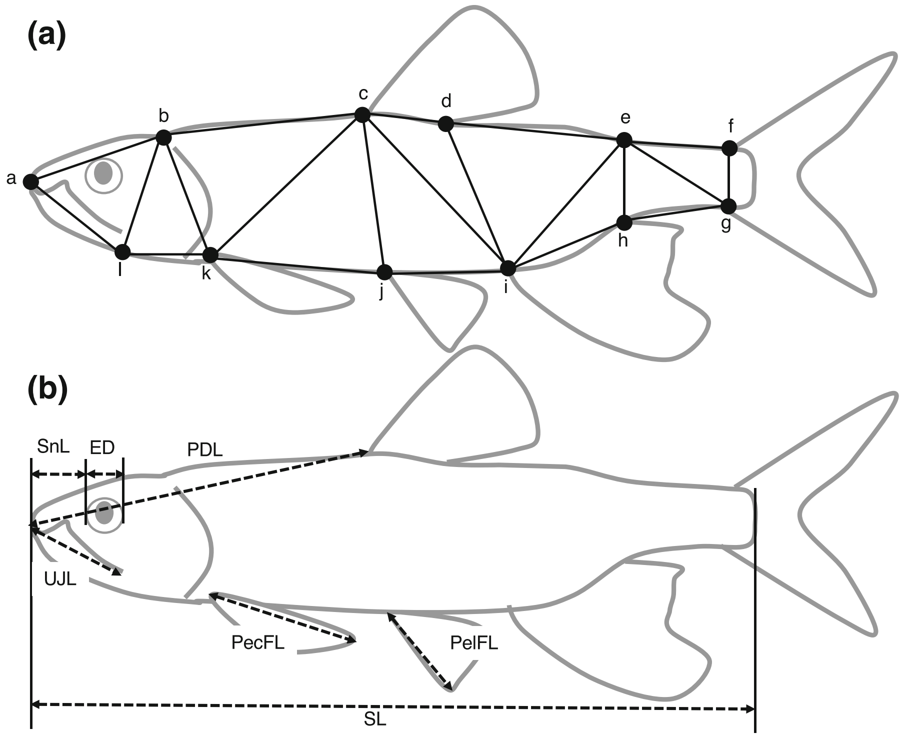

Fig. 1 **a** Morphological landmarks and truss networks used to describe the body shape of three-lips (*Opsariichthys uncirostris*): a: snout, b: dorsal head-body transition, c: anterior dorsal fin base, d: posterior dorsal fin base, e: dorsal point above posterior anal fin, f: dorsal caudal fin base, g: ventral caudal fin base, h: anterior anal fin base, i: posterior anal fin base, j: pelvic fin base, k: pectoral fin base, l: ventral head-body transition. **b** Other measured morphological characteristics. *SnL* snout length, *UJL* upper jaw length, *ED* eye diameter, *PDL* predorsal length, *PecFL* pectoral fin length, *PelFL* pelvic fin length, *SL* standard length

to the Futatsu River water system (FRWS), showed differences in their growth modes. In BLSW, three-lips are thought to reach sexual maturation upon reaching standard lengths greater than 160 mm in males and greater than 140 mm in females (Tanaka 1970), while in FRWS sexual maturity is reach at standard lengths of around 155 and 118 mm for males and females, respectively (Kurita and Onikura 2016). The observed size ranges in both samples that we examined indicate that both include young and adult fish, confirming that the three-lips in FRWS become sexually mature at smaller body sizes relative to the native fish in BLWS (Kurita and Onikura 2016). In terms of fish size, the translocation of fish from BLWS into FRWS in the 1980's resulted in a decrease in adult body size. Three-lips require 2–3 years to reach maturity in FRWS (Kurita and Onikura 2016) and thus it can be estimated that such changes in body size occurred at most within 20 generations.

Food supply is determinant of body size at maturation (Rosenweig 1968; Denys 2016). Another native three-lips population inhabits the Mikata Lake, a much smaller water body located approximately 50 km north of the Biwa Lake; however, it seems to have already become extinct (Fukui Prefecture 2016). Three-lips in the Mikata Lake had slightly smaller body sizes, possibly due to their inhabitance of such a small habitat, which measures less than 1% of the size of the Biwa Lake (Tanaka 2005). An empirical rule known as insular dwarfism states that large animals become smaller over multiple generations after inhabiting a small habitat such as an island (Foster 1964; Prothero and Sereno 1982). The underlying idea of this process is that smaller habitats contain less food which leads to the eventual evolution of smaller adult body sizes (Whittaker 1998; Raia and Meiri 2006). The Ayu is one of the dominant fish species in BLWS where the three-lips preys on it almost exclusively, hunting them at high speed (Tanaka 2005). BLWS is thus a promising habitat containing an abundance of prey species to sustain healthy three-lip populations. Conversely, in FRWS the narrow range of prey species limits the three-lips' food supply. Life history theory based on bioenergetics predicts that fewer and lower quality food items lead to low growth deficiencies and stunted growth, resulting in so-called dwarfism in extreme cases (Juncos et al. 2011; Shuter et al. 2016). The small adult body sizes of three-lips in FRWS can thus be reasonably attributed to limitations in food availability. A fundamental assumption in invasion

Table 1 Eigenvectors, eigenvalues, and cumulative contribution of variance for the first three principal components (PC1, PC2, and PC3)

	PC1	PC2	PC3
Eigenvectors			
a–b	− 0.166	− 0.229	0.537
b–c	− 0.360	0.263	0.274
c–d	0.015	0.737	− 0.330
d–e	0.712	− 0.266	0.119
e–f	− 0.779	− 0.100	− 0.065
g–h	− 0.731	− 0.216	− 0.098
i–j	0.609	0.470	− 0.344
h–i	− 0.027	− 0.264	0.332
j–k	0.086	0.157	0.575
k–l	− 0.467	0.198	− 0.416
a–l	− 0.653	0.434	0.303
b–l	− 0.286	0.560	0.376
b–k	− 0.125	0.796	0.324
c–k	0.618	0.121	0.493
c–j	0.883	0.013	0.084
c–i	0.624	0.358	− 0.060
d–i	0.860	0.085	− 0.002
e–i	0.877	0.261	− 0.150
e–h	0.676	0.079	0.067
e–g	− 0.657	0.009	− 0.008
f–g	− 0.491	0.677	− 0.097
Eigenvalues	7.116	2.964	1.861
Cumulative contribution (%)	33.9	48.0	56.9

See Fig. 1 for positions of landmarks a–l

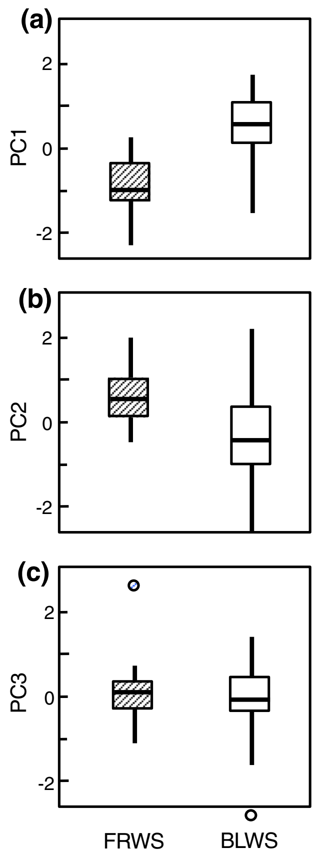

Fig. 2 Box plots comparing principle component scores between samples from the Futatsu River water system (FRWS) and the Biwa Lake (BLWS). Principle component analysis was conducted for the lengths between landmarks shown in Fig. 1. **a–c** Correspond to scores in PC1, PC2, and PC3, respectively

biology is that the most invasive species exhibit enhanced performance in novel habitats relative to their home ranges (Parker et al. 2013). The downsizing effect observed in this study may appear to be an anomaly, however, our understanding is that flexible transitions to small body size may be beneficial, as downsizing has made it possible for three-lips to exploit a novel niche and become a successfully invasive species.

Fish body shape is affected by both abiotic and biotic factors including water condition, diet, and predation (Wimberger 1992). PCA using the measured morphometric characteristics produced newly summarized variables. The samples from the two populations differed in the distribution of their PC1 and PC2 scores, indicating that three-lips in FRWS and BLWS can be distinguished from one another by their overall body proportions. Independent correlations between PC1 and PC2 in the two samples indicate that each population displays unique variation in their body proportions. It is important to note, however, that the smaller body size of FRWS three-lips is not attained simply by the ceasing of further growth which might otherwise be expected to occur in BLWS three-lips. The distinctive growth rates of compatible morphometric characteristics contribute to the specific overall body shape of FRWS three-lips. More specifically, in fish from FRWS variations in the growth rates of upper jaw length, lower jaw length, eye diameter, predorsal length, and tail length are accelerated while changes in head depth, body depth, and tail depth are decelerated (relative to those in BLWS). These changes in the growth rates of surface body parts can be summarized

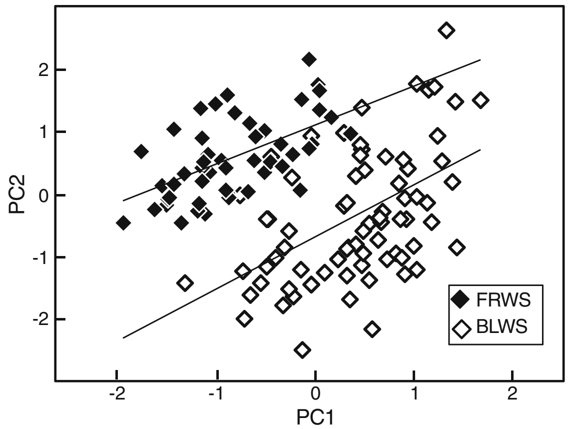

Fig. 3 Relationships between principle component scores for PC1 and PC2 in samples from the Futatsu River water system (FRWS) and the Biwa Lake (BLWS). Principle component analysis was conducted for lengths between landmarks as shown in Fig. 1

Table 2 Gradients of regression lines between log-transformed trait measurements and log SL based on fish from the Futatsu River water system (left) and the Biwa Lake water system (right)

	Slope	$F_{1,130}$	P
a–b	1.059/0.966	0.382	0.528
a–l	1.208/1.171	184.85	< 0.001
b–k	1.147/1.165	47.35	< 0.001
c–j	1.144/1.222	98.17	< 0.001
e–h	1.029/1.051	36.35	< 0.001
e–f	0.970/0.716	66.37	< 0.001
SnL	1.306/1.219	0.32	0.575
UJL	1.286/1.138	32.90	< 0.001
PDL	1.030/1.002	63.82	< 0.001
ED	0.595/0.565	110.63	< 0.001
PecFL	1.079/1.033	3.50	0.064
PelFL	1.035/1.081	0.094	0.760

ANCOVA was performed to detect significant differences between samples

See Fig. 1 for positions of landmarks and abbreviations of traits

as the acquisition of a slenderer body. It follows that decreases in adult body size and the alteration of growth rates in body parts occurred synchronously after invasion of FRWS. Thus, the environmental conditions of FRWS play an important role in the formation of a unique body shape in the resident three-lips population.

The slender body of three-lips in FRWS likely provides some selective advantage. Foraging sites in the original habitat of BLWS allows three-lips to exploit a wide range of food types ranging from copepods to bait fish dependent upon developmental stage (Sunaga 1980; Tanaka 2005). Although the habitat size of FRWS is much smaller than BLWS, it contains a variety of microhabitats. The three-lips exploits the microhabitats of irrigation ditches during its early development before travelling to the main water body to grow (Kurita et al. 2014), and movement between microhabitats likely mirrors developmental changes in food requirements. The functional significance of fish body design has been previously studied in significant detail (Blake 2004). Fish swimming speed is highly dependent on body length (Bainbridge 1958), and a streamlined body shape is effective in reducing drag as the fish swims (Fletcher et al. 2014). The associations between body shape and swimming ability support the idea that the slender body acquired by three-lips in FRWS mitigates the deleterious effects of a smaller body size on swimming speed to ensure the fish is able to swim at high speeds. Larger jaws expand the range of available food items (Kishida et al. 2011), and larger eyes improve the visual acuity of fish in turbid water (Dugas and Franssen 2012). Both of these characteristics are observed in the FRWS specimens and likely help them hunt for prey and avoid predators

The downsizing observed in three-lips in FRWS over its 40 years of inhabitance remains controversial. *Opsariichthys uncirostris* (three-lips) stems from the lineage of *Opsariichthys bidens*, which has a cosmopolitan distribution across East Asia (Lin et al. 2016). *Opsariichthys bidens* can be found in some irrigation ditches and streams in China and has an adult body size smaller than that of *O. uncirostris* in BLWS (Iguchi et al. 1999). This suggests that the ancestral inhabitation of the Biwa Lake by three-lips has enabled it to grow to large sizes. The rapid downsizing of three-lips in FRWS raises concerns around the basis of this change, be it phenotypic plasticity or an inherited genotype (Chapman et al. 2000; Wund et al. 2008). Evolutionary change can occur within a short period of time when selection pressures are strong (Stuart et al. 2014). However, the driving forces behind the adaptive change that occurred in the three-lips in FRWS remains enigmatic. Further studies are needed to understand the relative contributions of environmental effects and genetic effects to this change, commonly known as a common garden experiment (Villemereuil et al. 2016). To conclude, it is understood that three-lips is flexible in its responses to a given environment thanks to its ability to make rapid changes to its mode of growth, allowing it to overcome the usual limitations imposed by habitat size on establishing species. Thus, extreme care should be taken in preventing the further spread of this species both within and outside of Japan to preserve native biodiversity.

Acknowledgements We thank N. Onikura and the members of the Fishery Research Laboratory, Kyushu University for their assistance in collecting fish from the Futatsu River water system (FRWS). We also thank members of the Laboratory of Animal Ecology, Kyoto University for their assistance in collecting fish from the Biwa Lake water system (BLWS).

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