

Research Article

The distribution, establishment and life-history traits of non-native sailfin catfishes *Pterygoplichthys* spp. in the Guangdong Province of China

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Abstract

In China, the introduction of South American sailfin catfishes of the genus *Pterygoplichthys* are a concern due to the potential risks they pose to native species and ecosystems. The present study reports on the distribution, establishment and maturity of a *Pterygoplichthys* spp. hybrid swarm in Guangdong Province, China. Distribution data demonstrated that *Pterygoplichthys* spp. were widespread in Guangdong Province, whereas only a few records were found in other parts of the country. The presence of mature *Pterygoplichthys* spp. females indicated established self-sustaining populations in most drainages in the study region. While variation in size at maturity and condition was observed among populations established in different drainages, *Pterygoplichthys* spp. in Guangdong Province appeared to mature at a smaller size than in other non-native ranges. National-level legislation with which to prevent and/or mitigate the release of other non-native fishes into the wild is recommended.

Key words: invasive fish, Loricariidae, condition, reproduction, mean size at maturity

Introduction

Numerous fish species have been introduced worldwide following expansion of the global trade in the pet and food industry, with biological invasions being an unintentional outcome of such practices (Gozlan et al. 2010). Native to South America, members of the family Loricariidae, including those of the genus *Pterygoplichthys* (common names include: sailfin catfishes, plecos, armoured catfishes or janitor fish), have been introduced around the world for use in aquaculture and/or the aquarium (pet) fish trade (Liang et al. 2006; Zięba et al. 2010; Nico et al. 2012; Moroni et al. 2015). Following their escape from rearing facilities and/or release by pet fish

owners, *Pterygoplichthys pardalis* (Castelnau, 1855), *Pterygoplichthys disjunctivus* (Weber, 1991) and/or their hybrids have become invasive in North America (e.g. Fuller et al. 1999; Rueda-Jasso et al. 2013), South Africa (Jones et al. 2013) and in various parts of Asia (Ishikawa and Tachihara 2014; Jumawan and Herrera 2014; Bijukumar et al. 2015). The adverse effects of *Pterygoplichthys* spp. associated with these invasions include alteration of ecosystem nutrient dynamics, competition with native species and economic losses to fisheries (Chavez et al. 2006; Pound et al. 2011; Capps and Flecker 2013).

The invasion biology of *Pterygoplichthys* spp., which have been included in the list of invasive taxa, has received little scientific study in China.

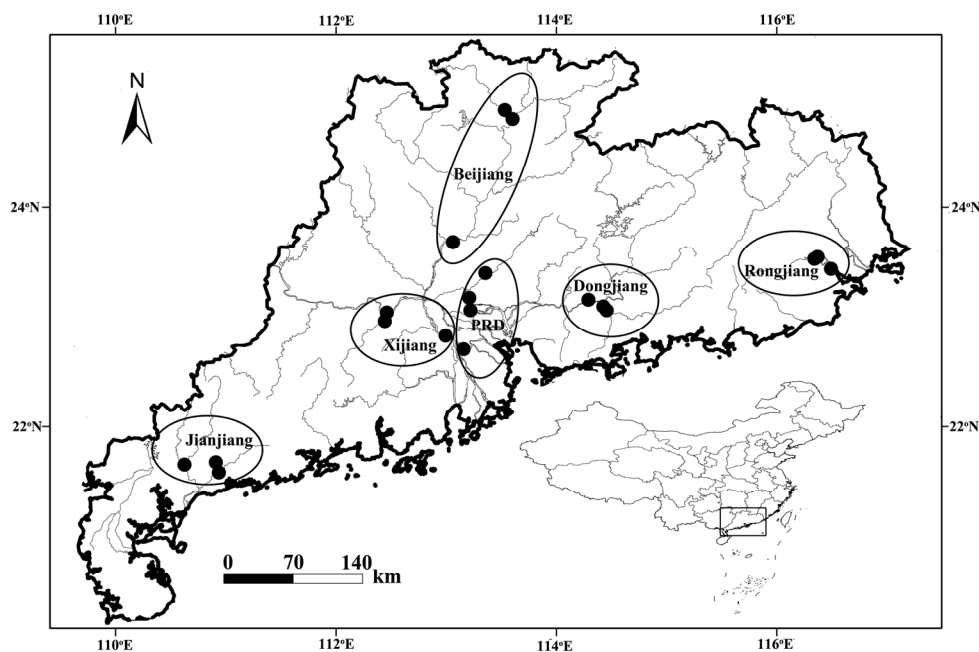


Figure 1. Sampling locations for *Pterygoplichthys* spp. in the main river drainages (PRD = Pearl River Delta) of Guangdong Province (China). Each filled circle represents a site where the specimens used in current study were obtained.

Pterygoplichthys spp. are popular aquarium fish commonly used to control algae in tanks, and were first imported into Guangdong Province in the 1990s (Li et al. 2007). They have been spread via the aquarium trade throughout the country and have probably been present in the wild since the year 2000 (Li et al. 2013). South China, and especially Guangdong Province, provides a suitable environment for *Pterygoplichthys* spp. invasion. This region is characterised by a sub-tropical monsoon climate with mean winter temperature of 13.3 °C, mean summer temperature of 28.5 °C and mean annual rainfall of 1300–2500 mm mainly between April and September (Guangdong Meteorological Service 2013). Similar to the state of Florida in the USA (Lawson et al. 2013), Guangdong Province is likely to be at high risk of being invaded by non-native fishes due to its relatively benign climate, abundance of water courses, a flourishing ornamental fish trade, an extensive sea port, and very high human population densities (Gibbs et al. 2008).

In recent years, local fishermen have frequently caught *Pterygoplichthys* spp. and noticed a corresponding decline in catches of economically important taxa such as shrimps (H. Wei pers. obs). For this reason, a better understanding of the distribution, establishment and life-history traits of *Pterygoplichthys* spp. is needed to inform national management

strategies for non-native species (cf. Sax and Brown 2000; Hulme 2006). The aims of the present study were to: 1) assess the invasion status of *Pterygoplichthys* spp. in Guangdong Province; and 2) investigate whether life-history traits of *Pterygoplichthys* spp. vary across their non-native ranges.

Methods

Data on the distribution of *Pterygoplichthys* spp. in China and on their environmental biology in their native and introduced ranges were obtained from a review of the peer-reviewed and “grey” literature (i.e. reports, internet resources, field surveys) as well as from interviews with local fishery managers and fishermen. These data were complemented by field-survey data collected during summer and early autumn of 2014 and 2015 from 19 locations within six study areas of Guangdong Province: the Beijiang, Dongjiang, Jianjiang, Rongjiang and Xijiang river drainages and the Pearl River Delta (Figure 1, Supplementary material Table S1).

Fish samples were collected by local fishermen, mainly using gill nets (mesh size 50–100 mm) and shrimp pots, which were deployed at sampling locations for at least 4 h. Three fishermen operated at each sampling location, and the percentage of *Pterygoplichthys* spp. in each catch (relative to all fish captured)

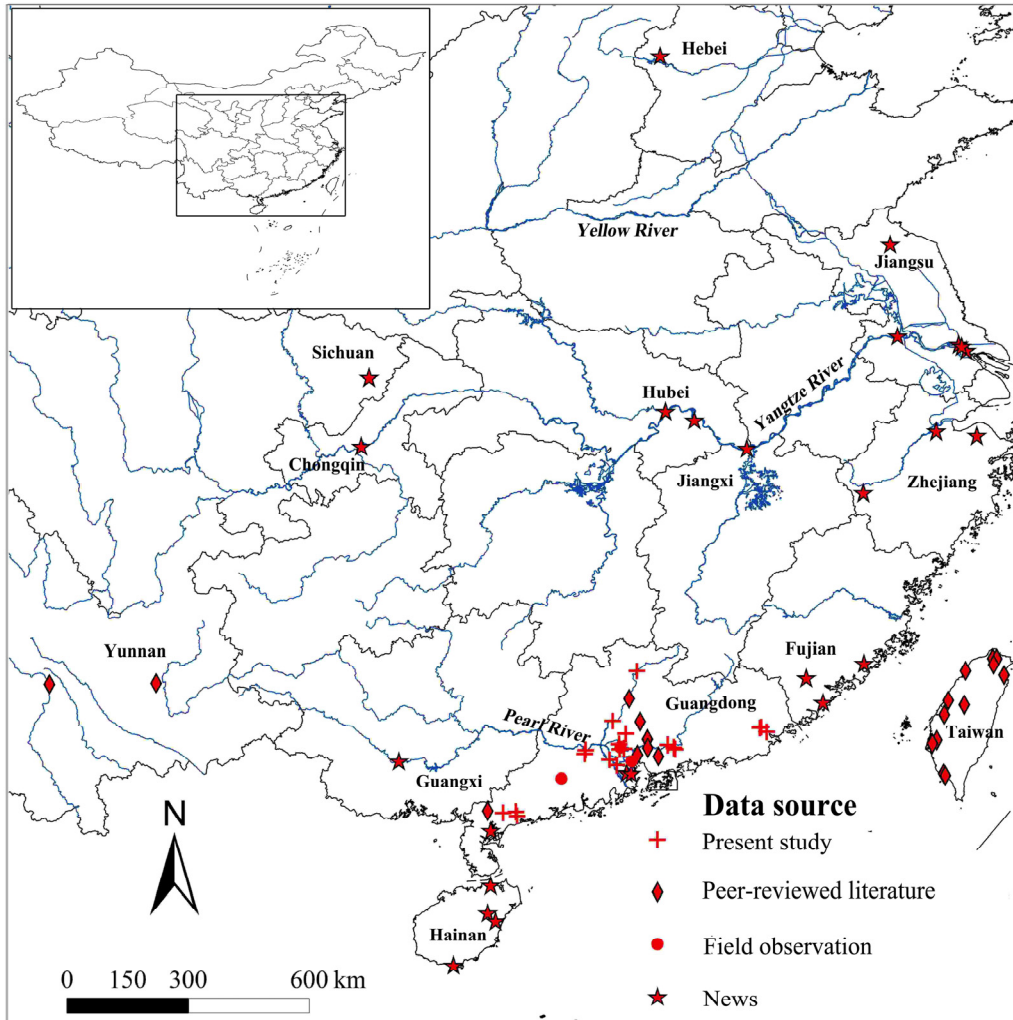


Figure 2. Locations in China where *Pterygoplichthys* spp. have been collected or reported (see Supplementary material Table S1 for coordinates). Major river courses are shown in blue, borders of provinces delineated by black lines.

for each boat was evaluated immediately after capture. In total, 1257 specimens were sampled across the six study areas. All fish were brought back to the laboratory where they were taxonomically classified based on the number of dorsal fin rays and on the colour pattern of the ventral region (Armbruster and Page 2006; Jumawan et al. 2011; Wu et al. 2011; Nico et al. 2012; Jones et al. 2013) and measured for standard length (SL) and total length (TL) to the nearest 1 mm and for body mass (M_b) to the nearest 0.01 g. Specimens were then dissected to remove their gonads, which were weighed (M_g) to the nearest 0.01 g and visually categorised by gender and maturity stage (after Gibbs et al. 2008).

Mean SL at maturity (SL_M) was calculated from the percentage of mature females and males in each

10 mm SL class interval using the Trippel and Harvey (1987) modified version of DeMaster's (1978) formula (after Fox and Crivelli 2001). Published data on *Pterygoplichthys* spp. included female SL at first maturity (in mm), minimum and maximum SL (in mm), introduction history, sampling gear used and time of sampling. These data were collected to examine whether maturity of *Pterygoplichthys* spp. varied across their introduced range. When TL was given in a study, it was converted to SL using the relationship between TL and SL obtained in the present study. Note that in the course of sampling, mature males and females included both individuals that would be able to produce eggs or sperm and individuals that had achieved reproductive maturity (but with quiescent gonads). The paired two-tailed Students' *t*-test was

Table 1. Total number of *Pterygoplichthys* spp. specimens, juveniles, males and females, with indication of the number of mature (Mat.) individuals and minimum (Min) and maximum (Max) standard length (SL, mm) of mature specimens (by sex), sex ratio (females : males) and their mean SL at maturity (SL_M) sampled across six drainages of Guangdong Province (south China).

Drainage	Total	Juv	Sex ratio	Males		Females		Min SL(mm)		Max SL(mm)		SL _M (mm)	
				<i>n</i>	Mat	<i>n</i>	Mat	M	F	M	F	M	F
Beijiang	3	0	0.5:1	2	0	1	0	–	–	–	–	–	–
Dongjiang	417	52	1.6:1	113	92	185	119	160	175	342	367	204	229
Jianjiang	350	34	3:1	42	21	124	55	185	160	316	331	261	211
Pearl River Delta	215	9	1.1:1	84	55	89	61	170	150	310	368	226	261
Rongjiang	237	122	4.7:1	19	16	90	24	200	193	339	300	253	210
Xijiang	35	1	6.5:1	2	1	13	3	249	223	249	245	250	230

Table 2. Information on size at first maturity, size range (minimum and maximum SL) and introduction history of *Pterygoplichthys* spp. in its invasive ranges, including sampling gears and timing in each study.

Site	Size at first maturity (SL mm)	Size range (SL mm)	Introduced history	Sampling gear	Sampling time	Reference
Florida (USA)	260–300	210–450	late 1950s	cast net and turtle grabbers	overnight	Gibbs et al. (2008)
Michoacán – Guerrero (Mexico)	192	78–398	before 1990s	gill net	evening	Rueda-Jasso et al. (2013)
Peninsular Malaysia	130	108–360	before 1990s	cast net	-	Samat et al. (2016)
Philippines	260	50–450	1950s	cast net	daytime	Jumawan and Herrera (2014)
South Africa	198	7.7–370	late 1970s	monofilament gill nets, valve traps, 6 double-ended fyke nets, electrofishing	overnight	Jones et al. (2013)
Taiwan	250	125–437	1970s	gill net, cast net	overnight and daytime	Liang et al. (2005)
Guangdong (China)	150–223	27–368	1990s	shrimp pot, gill net	overnight and daytime	Present study

employed to examine the differences of SL_M between males and females. Spatial variation in sex ratios was examined using the Chi-square (χ^2) test.

The relationship between SL and TL was assessed using simple regression analysis. Growth patterns were evaluated based on the length-weight relationship $M_i = aSL^b$, where a and b are growth parameters, and with the value of the slope parameter b (all specimens combined) used as a measure of generalised condition (Pitcher and Hart 1992), which is effectively an estimator of “plumpness” (e.g. Cassani and Caton 1986; Springer and Murphy 1990; Copp and Mann 1993), for each drainage separately. Data analyses were performed with SAS v. 8.1 (SAS Institute Inc., Cary, NC, USA).

Gonado-somatic index (I_G) in females was calculated using the formula $I_G = 100 \times (M_g \times M_f^{-1})$ after Gibbs et al. (2008), and females were defined as “mature” whenever yolky oocytes were present, the ovarian wall was transparent and $I_G \geq 1$. Relationships between I_G and SL were assessed across drainages (except for Beijiang, where $n = 1$) by linear mixed effects (LME) modelling (Bates 2010). In the model, I_G (log-transformed to stabilise variance) was the response variable, SL the fixed effect (covariate), and drainage the random effect. The resulting random intercept model (fitted under the assumption that I_G varies depending on SL though at the same rate across drainages) was as follows:

$$I_G \sim SL + (1 | \text{Drainage})$$

where the term outside the parentheses is the fixed effect, and the one inside is the random effect. Note that a model also was preliminarily fitted with both a random intercept and slope, i.e. under the assumption that I_G would vary not only depending on SL but also at different rates across drainages, but no convergence was achieved. The statistical significance of the model was then tested relative to a “null” model (i.e. no random effects) to see whether inclusion of a random intercept was justified. Fitting of the LME model was in R with the package “lme4” (Bates et al. 2014), and the AIC-based comparison between the random effect and the null model was with the package “bbmle” (Ben Bolker and R Development Core Team 2014).

Results

Pterygoplichthys spp. were present at multiple locations throughout southern China, whereas only a few records were available for the other parts of the country (Figure 2). In Guangdong Province, the contribution of *Pterygoplichthys* spp. to catch composition was 31.7% in both the Rongjiang and Jianjiang drainages, 20% in the Dongjiang, 10.8% in the Pearl River Delta, 0.3% in the Xijiang and <0.01% in the Beijiang drainage.

Table 3. Generalised condition (regression slope b values) for *Pterygoplichthys* spp. (all specimens combined) in six drainages of Guangdong Province (south China). Statistically significant P values in bold ($\alpha = 0.05$).

Drainage	b	Intercept	r^2	df	F	P
Beijiang	2.515	-3.650	0.976	2	41.54	0.098
Dongjiang	2.837	-4.347	0.978	416	18301.12	< 0.001
Pearl River Delta	2.804	-4.231	0.967	214	6179.98	< 0.001
Rongjiang	2.845	-4.389	0.987	236	18517.97	< 0.001
Jianjiang	2.973	-4.640	0.972	349	12129.47	< 0.001
Xijiang	2.667	-3.939	0.967	34	952.14	< 0.001

Identification to species level was difficult. The number of dorsal fin rays ranged from 11 to 13 and most of the specimens had 12. Three types of colour pattern on the abdomen of the specimens were identified: 1) discrete ventral spots, 2) ventral vermiculation, and 3) intermediate forms between the former two types. Specimens could be identified as either *P. pardalis* (6.2%), *P. disjunctivus* (17.8%) or as *P. pardalis* \times *P. disjunctivus* hybrids (76%). This identification was consistent with morphological analyses on invasive *Pterygoplichthys* populations elsewhere (e.g. Wu et al. 2011; Nico et al. 2012; Jones et al. 2013), and indicates that invasions in China are most likely the result of a hybrid swarm of *P. pardalis* \times *P. disjunctivus*. As genetic analysis was not conducted in the current study, the populations of the study organism are hereafter referred to as *Pterygoplichthys* spp.

There was considerable variation in minimum and maximum SL for both juveniles (27–120 mm SL) and mature individuals (Table 1). The overall relationship of TL vs. SL (all specimens from all drainages) was $TL = 21.657 + 1.253SL$ ($r^2 = 0.979$, $F_{1,1256} = 58063.96$, $P < 0.001$). Mean SL at maturity of females was slightly smaller (mean \pm SE: 228.20 ± 9.36 mm) than in males (mean \pm SE: 238.60 ± 10.49 mm), with the shortest female SL_M occurring in Rongjiang and the shortest male in Dongjiang, although this difference was not statistically significant (paired two-tailed Student's $t = 0.76$, $P = 0.45$). *Pterygoplichthys* spp. were capable of spawning in all sampled drainages ($I_G \geq 1$) except for Beijiang ($I_G = 0.259$). Sex ratios were female-biased in most drainages and differed significantly amongst drainages ($\chi^2 = 40.25$, $df = 5$, $P < 0.01$), with the highest ratio found in Xijiang (Table 1). Size at first maturity ranged from 150 to 223 mm SL for females and from 160 to 249 mm SL for males (Table 1). At a more global scale (Table 2), female *Pterygoplichthys* spp. matured at smaller sizes in Guangdong Province relative to Taiwan, KwaZulu-Natal in South Africa, the southern US state of Florida, Michoacán-Guerrero in Mexico and the River Marikina, Philippines, whereas

Table 4. Fixed and random effects coefficients for a linear mixed effect model describing variation in I_G relative to standard length (SL) for *Pterygoplichthys* spp. across five drainages of Guangdong Province (see also Figure 3).

Drainage	Fixed effects		Random effects
	Intercept	SL	
All	-5.33052	0.02454	
Dongjiang	-5.49117	0.02454	-0.16065
Jianjiang	-5.41174	0.02454	-0.08122
Pearl River Delta	-5.36270	0.02454	-0.03218
Rongjiang	-5.39565	0.02454	-0.06512
Xijiang	-4.99134	0.02454	0.33918

they matured at a larger size relative to peninsular Malaysia.

There was a positive correlation between M_t and SL, and similar growth patterns were found across Guangdong drainages (Table 3). Generalised condition varied amongst drainages, with the plumpest fish found in Jianjiang and the thinnest in Xijiang, and with specimens from the other three drainages having similar condition (Table 3). Statistically, exclusion of a drainage as a random effect in the null model resulted in a slight improvement only (as indicated by AIC: $\Delta = 12.3$), as this was due to the three vs. four degrees of freedom relative to the random effects model. For this reason, the latter model was retained as a better descriptor of the relationships between I_G and SL across drainages (Table 4). Overall, there was an increase (occurring at a similar rate) in I_G at all drainages, even though Xijiang stood out for the higher I_G values relative to SL (Figure 3).

Discussion

The widespread occurrence and presence of several mature individuals are evidence for the establishment of *Pterygoplichthys* spp. populations in most drainages of Guangdong Province. This might be attributed to the relatively warmer temperatures in that region, where mean temperature is 13.3 °C during

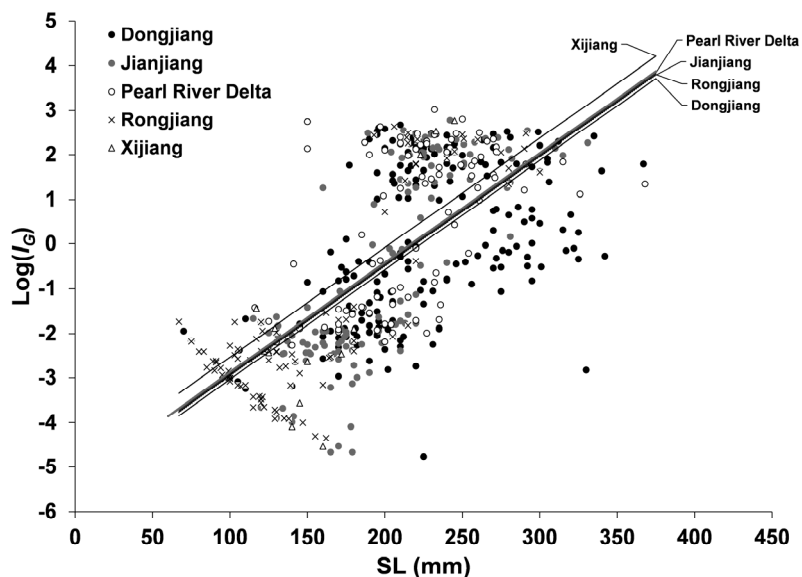


Figure 3. Relationships between the log of the gonado-somatic index (I_G) and standard length (SL) of *Pterygoplichthys* spp. across five major drainages of Guangdong Province (Beijiang omitted because of low sample sizes). For each drainage, the fitted linear relationship between I_G and SL according to a mixed effects model (Table 2) is indicated together with the overall relationship across all drainages (grey line).

the coldest season (Guangdong Meteorological Service 2013). While only a few specimens were recorded further north in China, this suggests tolerance of *Pterygoplichthys* spp. to relatively low temperatures. Presumably, the distribution range of *Pterygoplichthys* spp. in China could expand further north, especially under future climate warming scenarios (e.g. Britton et al. 2010). Under such a scenario, abiotic habitat variables related to hydrology, connectivity and nutrient availability in China could facilitate dispersal and colonisation of *Pterygoplichthys* spp. at small geographical scales (cf. Sato et al. 2010). However, further investigation is needed to assess the potential for establishment of this non-native catfish beyond southern China.

Life-history traits of non-native fish can shift across native and invaded regions as an adaptation to local biotic and abiotic environments, allowing them to colonise new areas and ultimately expand their distribution ranges (Fox and Copp 2014; Masson et al. 2016). In the case of *Pterygoplichthys* spp. in Guangdong Province, inter-drainage variation in mean size at maturity was observed. For example, in the Rongjiang drainage, where the smallest female size at maturity was recorded, total phosphorous and nitrogen levels are elevated and accompanied by lower overall biodiversity and elevated water pollution levels (Li et al. 2013; H. Wei, unpublished data). *Pterygoplichthys* spp. are expected to benefit from the environmental conditions (e.g. abundant food supply and low competition) found in this drainage. Life-history theory predicts that organisms

mature later when faced with environmental stressors and earlier when encountering favourable conditions (Stearns and Koella 1986). *Pterygoplichthys* spp. are known to mature at larger size in their invasive regions relative to their congener *P. ambrosetti* (88 SL mm) in the Amazon Basin (Garcia et al. 2014). A possible cause may be greater availability of food resources during the wet season and presence of various predators, which may contribute to increased juvenile growth rate and decreased size at maturity (Abrams and Rowe 1996; de Mérona and Rankin-de-Mérona 2004; Nico 2010). Similarly, variation in size at first maturity amongst invasive populations may be ascribed to different environmental conditions. For example, *P. pardalis* in Malaysia were reported to mature at a smaller size than in other non-native populations, and this has been attributed to the warmer and more stable water temperatures of the tropical rivers in that region (Samat et al. 2016). On the other hand, a shorter invasion history in Guangdong Province, relative to other invaded regions, may explain the variation found in SL at maturity, since life histories of recently-established invasive populations can be more variable than those observed in the species' native range (Bøhn et al. 2004). For example, recently-established populations of introduced pumpkinseed *Lepomis gibbosus* in Europe were reported to invest more into reproduction than longer-established populations (Copp and Fox 2007).

Body condition (or plumpness), which reflects foraging success and tolerance of environmental

pressure, is a good predictor of fitness and ultimately affects reproduction (Jakob et al. 1996). In the present study, the lower condition found in Xijiang drainage, where total phosphorous and nitrogen levels are lower, appears to reflect limited food resources relative to the other Guangdong drainages (Li et al. 2013; H. Wei, unpublished data). By contrast, the higher condition value observed in Jianjiang drainage probably reflects the elevated temperatures and food supplies present in this more southerly drainage, which is characterized by moderate-to-high concentrations of total phosphorous and nitrogen (Li et al. 2013; H. Wei, unpublished data). Overall, *Pterygoplichthys* spp. in China had generally higher (generalised) body condition values (Table 3) than in other invaded regions of the Northern Hemisphere, although these values may also have been affected by different sampling dates (Liang et al. 2005; Gibbs et al. 2008; Rueda-Jasso et al. 2013; Jumawan and Herrera 2014). Sampling for *Pterygoplichthys* spp. in the present study was conducted in summer and early autumn, when temperatures are favourably warm. Conversely, *Pterygoplichthys* spp. were sampled throughout the year in the other parts of its introduced range, where temperatures are known to be less favourable (i.e. lower) than in Guangdong Province.

While growth allocated to reproduction increased with female size (i.e. I_G in relation to SL), this increase occurred at a similar rate in all Guangdong drainages. Also, I_G was higher relative to female SL in Xijiang compared to other drainages, but this was likely due to smaller sample sizes. Whilst Gibbs et al. (2013) found a similar relationship between I_G and female length in Florida, no such relationship was reported for Taiwan (Liang et al. 2005). Overall, there seems to be a trend of increasing I_G with increasing female length in these invaded regions, which potentially facilitates resource exploitation, predator avoidance and greater energy allocation to reproduction (Roff 1983; Auer et al. 2010).

Although *Pterygoplichthys* spp. have been reported to be invasive in several countries, the present study is the first to report on their invasion biology in China. The results suggest that *Pterygoplichthys* spp. are “fully invasive” (sensu Blackburn et al. 2011) as the species have established self-sustaining populations in most drainages of Guangdong Province. *Pterygoplichthys* spp. are therefore very likely to expand its current range in China, facilitated by their ability to adapt to novel environments (Gibbs et al. 2008, 2013). Further studies on *Pterygoplichthys* spp. are needed in China and elsewhere to investigate their rapid adaptation to novel environments, and this is of particular relevance with regard to predicted future climate conditions. In light of the extant,

albeit limited, evidence of adverse environmental impacts exerted by *Pterygoplichthys* spp. (Capps et al. 2015), it is recommended that national-level legislation be implemented to prevent and/or mitigate the release of this and other non-native fishes into the wild.

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References

- Abrams PA, Rowe L (1996) The effects of predation on the age and size of maturity of prey. *Evolution* 50: 1052–1061, <https://doi.org/10.2307/2410646>
- Armbruster JW, Page LM (2006) Redescription of *Pterygoplichthys punctatus* and description of a new species of *Pterygoplichthys* (Siluriformes: Loricariidae). *Neotropical Ichthyology* 4: 401–410, <https://doi.org/10.1590/S1679-62252006000400003>
- Auer SK, Arendt JD, Chandramouli R, Reznick DN (2010) Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*). *Ecology Letters* 13: 998–1007, <https://doi.org/10.1111/j.1461-0248.2010.01491.x>
- Bates DM (2010) lme4: Mixed-effects modeling with R. Springer, Berlin
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7
- Ben Bolker and R Development Core Team (2014) bbmle: Tools for general maximum likelihood estimation. R package version 1.0.16
- Bøhn T, Terje Sandlund O, Amundsen PA, Primicerio R (2004) Rapidly changing life history during invasion. *Oikos* 106: 138–150, <https://doi.org/10.1111/j.0030-1299.2004.13022.x>
- Bijukumar A, Smrithy R, Sureshkumar U, George S (2015) Invasion of South American suckermouth armoured catfishes *Pterygoplichthys* spp. (Loricariidae) in Kerala, India: a case study. *Journal of Threatened Taxa* 7: 6987–6995, <https://doi.org/10.11609/JoTT.o4133.6987-95>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339, <https://doi.org/10.1016/j.tree.2011.03.023>
- Britton JR, Cucherousset J, Davies GD, Godard MJ, Copp GH (2010) Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. *Freshwater Biology* 55: 1130–1141, <https://doi.org/10.1111/j.1365-2427.2010.02396.x>
- Capps KA, Flecker AS (2013) Invasive aquarium fish transform ecosystem nutrient dynamics. *Proceedings of the Royal Society B – Biological Sciences* 280: 20131520, <https://doi.org/10.1098/rspb.2013.1520>

- Capps KA, Ulseth A, Flecker AS (2015) Quantifying the top-down and bottom-up effects of a non-native grazer in freshwaters. *Biological Invasions* 17: 1253–1266, <https://doi.org/10.1007/s10530-014-0793-z>
- Cassani JR, Caton WE (1986) Growth comparisons of diploid and triploid grass carp under varying conditions. *The Progressive Fish-Culturist* 48: 184–187, [https://doi.org/10.1577/1548-8640\(1986\)48<184:GCODAT>2.0.CO;2](https://doi.org/10.1577/1548-8640(1986)48<184:GCODAT>2.0.CO;2)
- Chavez JM, de la Paz RM, Manohar SK, Pagulayan RC, Carandang J (2006) New Philippine record of South American sailfin catfishes (Pisces: Loricariidae). *Zootaxa* 1109: 57–68
- Copp GH, Fox MG (2007) Growth and life history traits of introduced pumpkinseed (*Lepomis gibbosus*) in Europe, and the relevance to invasiveness potential. In: Gherardi F (ed), *Freshwater Bioinvasers: Profiles, Distribution, and Threats*. Springer, Berlin, pp 289–306, https://doi.org/10.1007/978-1-4020-6029-8_15
- Copp GH, Mann RHK (1993) Comparative growth and diet of tench *Tinca tinca* (L.) larvae and juveniles in river floodplain biotopes in France and England. *Ecology of Freshwater Fish* 2: 58–66, <https://doi.org/10.1111/j.1600-0633.1993.tb00084.x>
- DeMaster DP (1978) Calculation of the average age of sexual maturity in marine mammals. *Journal of the Fisheries Board of Canada* 35: 912–915, <https://doi.org/10.1139/f78-148>
- Fox MG, Copp GH (2014) Old world vs new world – Life history alterations in a successful invader introduced across Europe. *Oecologia* 174: 435–446, <https://doi.org/10.1007/s00442-013-2776-7>
- Fox MG, Crivelli AJ (2001) Life history traits of pumpkinseed (*Lepomis gibbosus*) populations introduced into warm thermal environments. *Archiv für Hydrobiologie* 150: 561–580, <https://doi.org/10.1127/archiv-hydrobiol/150/2001/561>
- Fuller PL, Nico LG, Williams JD (1999) Nonindigenous fishes introduced to inland waters of the United States. American Fisheries Society, Bethesda, Maryland, 613 pp
- Garcia DAZ, Almeida FS, Silva e. Souza AT, Britton JR, Orsi ML (2014) Invasion characteristics of *Pterygoplichthys ambrosietii* (Holmberg, 1893) in the lower Paranapanema River, Brazil. *Journal of Applied Ichthyology* 30: 1041–1044, <https://doi.org/10.1111/jai.12468>
- Gibbs MA, Shields JH, Lock DW, Talmadge KM, Farrell TM (2008) Reproduction in an invasive exotic catfish *Pterygoplichthys disjunctivus* in Volusia Blue Spring, Florida, U.S.A. *Journal of Fish Biology* 73: 1562–1572, <https://doi.org/10.1111/j.1095-8649.2008.02031.x>
- Gibbs MA, Kurth BN, Bridges CD (2013) Age and growth of the loricariid catfish *Pterygoplichthys disjunctivus* in Volusia Blue Spring, Florida. *Aquatic Invasions* 8: 207–218, <https://doi.org/10.3391/ai.2013.8.2.08>
- Gozlan RE, Britton JR, Cowx IG, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76: 751–786, <https://doi.org/10.1111/j.1095-8649.2010.02566.x>
- Guangdong Meteorological Service (2013) Climate characteristics of Guangdong Province. http://www.grmc.gov.cn/qxgk/tjsj/201310/t20131022_21888.html (accessed 22 October 2013)
- Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology* 43: 835–847, <https://doi.org/10.1111/j.1365-2664.2006.01227.x>
- Ishikawa T, Tachihara K (2014) Introduction history of non-native freshwater fish in Okinawa-jima Island: ornamental aquarium fish pose the greatest risk for future invasions. *Ichthyological Research* 61: 17–26, <https://doi.org/10.1007/s10228-013-0367-6>
- Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. *Oikos* 77: 61–67, <https://doi.org/10.2307/3545585>
- Jones RW, Weyl OL, Swartz ER, Hill MP (2013) Using a unified invasion framework to characterize Africa's first loricariid catfish invasion. *Biology Invasions* 15: 2139–2145, <https://doi.org/10.1007/s10530-013-0438-7>
- Jumawan JC, Herrera AA (2014) Ovary morphology and reproductive features of the female suckermouth sailfin catfish, *Pterygoplichthys disjunctivus* (Weber 1991) from Marikina River, Philippines. *Asian Fisheries Science* 27: 75–89
- Jumawan JC, Vallejo BM, Herrera AA, Buerano CC, Fontanilla IK (2011) DNA barcodes of the suckermouth sailfin catfish *Pterygoplichthys* (Siluriformes: Loricariidae) in the Marikina River system, Philippines: Molecular perspective of an invasive alien fish species. *Journal of Materials Science Letters* 4: 103–113
- Lawson LL Jr, Hill JE, Vilizzi L, Hardin S, Copp GH (2013) Revisions of the Fish Invasiveness Screening Kit (FISK) for its application in warmer climatic zones, with particular reference to Peninsular Florida. *Risk Analysis* 33: 1414–1431, <https://doi.org/10.1111/j.1539-6924.2012.01896.x>
- Li G, Zhao J, Zhu X, Zhang J, Zhao H, Liu L (2013) Investigation and Research on Freshwater Fish Resources of Guangdong. Science Press, Beijing, China, 272 pp
- Li J, Dong Z, Li Y, Wang C (2007) Alien aquatic animals and plants in China. Shanghai Scientific and Technical Publishers, Shanghai, China, 57 pp
- Liang S, Chuang L, Chang M (2006) The pet trade as a source of invasive fish in Taiwan. *Taiwania* 51: 93–98
- Liang S, Wu H, Shieh B (2005) Size structure, reproductive phenology, and sex ratio of an exotic armored catfish (*Liposarcus multiradiatus*) in the Kaoping River of southern Taiwan. *Zoological Studies* 44: 252–259
- Masson L, Brownscombe JW, Fox MG (2016) Fine scale spatio-temporal life history shifts in an invasive species at its expansion front. *Biological Invasions* 18: 775–792, <https://doi.org/10.1007/s10530-015-1047-4>
- de Mérona B, Rankin-de-Mérona J (2004) Food resource partitioning in a fish community of the central Amazon floodplain. *Neotropical Ichthyology* 2: 75–84, <https://doi.org/10.1590/S1679-62252004000200004>
- Moroni FT, Ortega AC, Moroni RB, Mayag B, Jesus RSD, Lessi E (2015) Limitations in decision context for selection of amazonian armoured catfish acari-bod (*Pterygoplichthys pardalis*) as candidate species for aquaculture. *International Journal of Fisheries and Aquaculture* 7: 142–150, <https://doi.org/10.5897/IJFA15.0480>
- Nico LG (2010) Nocturnal and diurnal activity of armored suckermouth catfish (Loricariidae: *Pterygoplichthys*) associated with wintering Florida manatees (*Trichechus manatus latirostris*). *Neotropical Ichthyology* 8: 893–898, <https://doi.org/10.1590/S1679-62252010005000014>
- Nico LG, Butt PL, Johnston GR, Jelks HL, Kail M, Walsh SJ (2012) Discovery of South American suckermouth armored catfishes (Loricariidae, *Pterygoplichthys* spp.) in the Santa Fe River drainage, Suwannee River basin, USA. *Bioinvasions Records* 1: 179–200, <https://doi.org/10.3391/bir.2012.1.3.04>
- Pitcher TJ, Hart PJB (1992) *Fisheries Ecology*. Chapman and Hall, London, 414 pp
- Pound KL, Nowlin WH, Huffman DG, Bonner TH (2011) Trophic ecology of a nonnative population of suckermouth catfish (*Hypostomus plecostomus*) in a central Texas spring-fed stream. *Environmental Biology of Fishes* 90: 277–285, <https://doi.org/10.1007/s10641-010-9741-7>
- Roff DA (1983) An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1395–1404, <https://doi.org/10.1139/f83-161>
- Rueda-Jasso RA, Campos-Mendoza A, Arreguin-Sánchez F, Diaz-Pardo E, Antonio Martínez-Palacios C (2013) The biological and reproductive parameters of the invasive armored catfish *Pterygoplichthys disjunctivus* from Adolfo López Mateos El Infiernillo Reservoir, Michoacan-Guerrero, Mexico. *Revista Mexicana de Biodiversidad* 84: 318–326, <https://doi.org/10.7550/rmb.26091>
- Samat A, Yusoff FM, Arshad A, Ghaffar AM, Nor SM, Magalhaes ALB, Das SK (2016) Reproductive biology of the introduced sailfin catfish *Pterygoplichthys pardalis* (Pisces: Loricariidae) in Peninsular Malaysia. *Indian Journal of Fisheries* 63: 35–41

- Sato M, Kawaguchi Y, Yamanaka H, Okunaka T, Nakajima J, Mitani Y, Shimatani Y, Mukai T, Onikura N (2010) Predicting the spatial distribution of the invasive piscivorous chub (*Opsariichthys uncirostris uncirostris*) in the irrigation ditches of Kyushu, Japan: a tool for the risk management of biological invasions. *Biological Invasions* 12: 3677–3686, <https://doi.org/10.1007/s10530-010-9762-3>
- Sax DF, Brown JH (2000) The paradox of invasion. *Global Ecology and Biogeography* 9: 363–371, <https://doi.org/10.1046/j.1365-2699.2000.00217.x>
- Springer TA, Murphy BR (1990) Properties of relative weight and other condition indices. *Transactions of the American Fisheries Society* 119: 1048–1058, <https://doi.org/10.1577/1548-8659-119.6.1048>
- Stearns SC, Koella JC (1986) The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40: 893–913, <https://doi.org/10.2307/2408752>
- Trippel EA, Harvey HH (1987) Reproductive responses of five white sucker (*Catostomus commersoni*) populations in relation to lake acidity. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1018–1023, <https://doi.org/10.1139/f87-119>
- Wu L, Liu C, Lin S (2011) Identification of exotic sailfin catfish species (*Pterygoplichthys*, Loricariidae) in Taiwan based on morphology and mtDNA sequences. *Zoological Studies* 50: 235–246
- Zięba G, Copp GH, Davies GD, Stebbing PD, Wesley KJ, Britton JR (2010) Recent releases and dispersal of non-native fishes in England and Wales, with emphasis on sunbleak *Leucaspius delineatus*. *Aquatic Invasions* 5: 155–161, <https://doi.org/10.3391/ai.2010.5.2.04>

Supplementary material

The following supplementary material is available for this article:

Table S1. Records of *Pterygoplichthys* spp. in inland waters of China.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2017/Supplements/AI_2017_Wei_etal_TableS1.xls