

Research Article

Nutrient enrichment alters life-history traits of non-native fish *Pterygoplichthys* spp. in sub-tropical rivers

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Abstract

Nutrient enrichment caused by anthropogenic activities can positively affect biological invasions as novel species can utilize additional resources in the ecosystem for population persistence. Although the effect of resource availability on plant invasions has been well-documented, the impact of nutrient enrichment on fish invasions remains unexplored. In this study, field investigations were conducted to examine the impact of nutrient enrichment on the maturity and reproduction of the invasive detritivorous fish *Pterygoplichthys* spp. A pair-wise greenhouse experiment was carried out to test the impact of nutrient enrichment on the performance of *Pterygoplichthys* spp. and the native fish *Cirrhinus molitorella*. Female *Pterygoplichthys* spp. matured at a larger size when total phosphorus concentration increased, while mean size and age at maturity of males increased with an increase in total nitrogen. Furthermore, total phosphorus concentrations were significantly lower when *Pterygoplichthys* spp. were present relative to those trials with *C. molitorella*. Eutrophication provides empty niches, which may facilitate the invasion of non-native and hypoxia tolerant fish. Thus *Pterygoplichthys* spp. may adjust their life-history traits to maximize fitness in eutrophic ecosystems. They might also benefit from nutrient enrichment due to their abilities to utilize phosphorus. These adaptive responses may help this non-native hybrid swarm to colonize and spread in their introduced range. These findings are instructive for understanding the relationship between biogeochemical changes and fish invasions, which will aid in minimizing the risk of biological invasions when developing management strategies in polluted ecosystems.

Key words: Loricariidae, maturity, phosphorus, stoichiometry, reproduction

Introduction

Fish invasions pose great threats to biodiversity and ecosystem functioning in aquatic ecosystems (Gallardo et al. 2015; Bajer et al. 2016). Fluctuating resource availability theory, which directly links resource availability and community invasibility, suggests that temporal inputs of resources can accelerate non-native species colonization through alleviating resource limitation (Davis et al. 2000). Eutrophication is caused by excessive nitrogen and phosphorus inputs due to

natural and/or anthropogenic activities, resulting in high primary production and abundant detritus in water bodies, which are important food supplies for omnivores and detritivores (Persson 1983; Bajer et al. 2015). Although the effect of resource availability on plant invasions has been well-documented (Davis et al. 2000; Seabloom et al. 2015; Sardans et al. 2016), the impact of nutrient enrichment on fish invasions remains unexplored.

Bottom-up controls have important impacts on species at higher trophic levels in aquatic ecosystems

(Ware and Thomson 2005). An increase of total nitrogen (TN) and total phosphorus (TP) inputs can relax nutrient limitation for phytoplankton or periphyton, resulting in higher primary production (Persson 1983; Maberly et al. 2002; Bajer et al. 2015). For this reason, detritivorous and omnivorous fish, which have a higher tolerance to hypoxia in general, usually dominate fish assemblages in eutrophic water bodies because of abundant food supplies (Lazzaro et al. 2003; SAGRARIO and Ferrero 2013). For example, the population density of roach *Rutilus rutilus* increased in eutrophic lakes due to high algal production caused by excessive nutrient inputs (Persson 1983). However, detritivorous and omnivorous fish are usually limited by food quality as detritus and algae are often poor in nutrient content (e.g. proteins, carbohydrates, etc.), leading to lower nutrient assimilation and slower growth rate (Sterner and Elser 2002; Lujan et al. 2011). However, N and P enrichment can increase detrital quality (i.e. reduced detrital C: P and N: P) (Gulis et al. 2006; Greenwood et al. 2007; Datri et al. 2015; Manning et al. 2016), which means nutrient improvement to food resources could be favorable to detritivorous and omnivorous fish. Along these lines, the performance of detritivorous and omnivorous fish might benefit from nutrient enrichment in natural ecosystems (Hood et al. 2005). Whilst fish growth rate and reproduction are largely affected by dietary nutrient contents, which have been well documented in aquaculture applications (Benstead et al. 2014), the impact of nutrient enrichment on life-history traits of invasive fish under natural conditions is poorly understood.

Native to South America, detritivorous and omnivorous fish of the Genus *Pterygoplichthys* in the Family Loricariidae, have been introduced around the world through the aquarium trade. This non-native fish has become invasive in North America (Fuller et al. 1999; Rueda-Jasso et al. 2013), South Africa (Jones et al. 2013) and in various parts of Asia (Chavez et al. 2006; Chaichana et al. 2011; Ishikawa and Tachihara 2014; Bijukumar et al. 2015). In China, a hybrid swarm of *Pterygoplichthys pardalis* (Castelnau, 1855) × *Pterygoplichthys disjunctivus* (Weber, 1991) (hereafter referred to as *Pterygoplichthys* spp.) has established self-sustaining populations in the main drainages of South China, especially in Guangdong province (Wei et al. 2017).

Phosphorus content is relatively high in Loricariid fish species because their bony covered armor plates contain abundant Ca-PO₄³⁻ (Capps and Flecker 2013a; Vanni et al. 2002), suggesting that the growth of loricariid fish could be limited by TP availability (Hood et al. 2005). Moreover, P, which largely originates from the weathering of phosphate-bearing

rocks and is patchily distributed (Notholt et al. 1989), is usually limited in most terrestrial and aquatic ecosystems (Grimm et al. 2003). Therefore, in this study we explored whether nutrient enrichment could facilitate the colonization of *Pterygoplichthys* spp. in a novel environment, resulting in a positive impact on fish invasion. Specifically, the goals of this study were to: (1) examine the impact of nutrient enrichment on the maturity and growth of *Pterygoplichthys* spp., and (2) test whether the impact of nutrient addition on the growth of *Pterygoplichthys* spp. differed from that on the native mud carp *Cirrhinus molitorella* (Valenciennes, 1844). Studies suggested that during periods of rapid potential growth or consumption of high-volume and nutrient-poor diets (e.g. detritus and algae) wild fish may experience nutrient-limitations in growth (Hood et al. 2005; Sperfeld et al. 2017). Consequently, we predicted that life-history traits (i.e. maturity and fecundity) of *Pterygoplichthys* spp. would vary with TN and TP concentrations in natural habitats. Although *C. molitorella* share similar dietary habits with *Pterygoplichthys* spp. in the main river drainages of South China (Li et al. 2013; Froese and Pauly 2016), body stoichiometric traits of *C. molitorella* are different from *Pterygoplichthys* spp. (Capps and Flecker 2013a; Mao et al. 1985). As a result, we predicted the performance of *Pterygoplichthys* spp. would differ from that of *C. molitorella* in waters with different N and P concentrations.

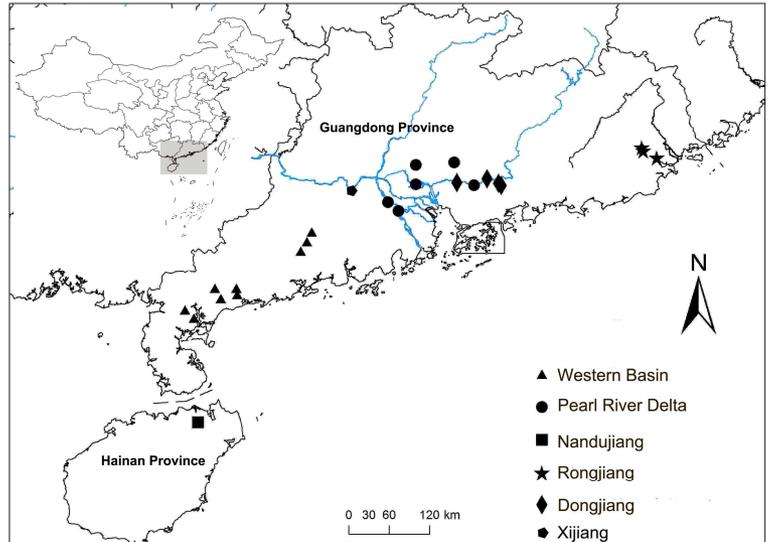
Material and methods

Study species

As benthic fish, *Pterygoplichthys* spp. inhabit in a wide variety of habitats including cool, fast-flowing, oxygen-rich water bodies, as well as warm, slow-flowing, oxygen-poor water bodies (Global Invasive Species Database 2017). The diet of *Pterygoplichthys* spp. consists of detritus, algae and plant materials, as well as bottom dwelling organisms such as worms, fish eggs and small invertebrates (Chaichana et al. 2011; Chaichana and Jongphadungkiet 2012). The invasive *Pterygoplichthys* populations are probably a combination of *P. pardalis*, *P. disjunctivus* and their hybrids, which can be distinguished based on colour pattern on the abdomen (Wu et al. 2011; Nico et al. 2012).

Cirrhinus molitorella inhabits the bottom of slow- or fast-flowing rivers and has a similar diet (i.e. phytoplankton, periphyton and detritus) as *Pterygoplichthys* spp. (Froese and Pauly 2016). *Cirrhinus molitorella* occurs in drainages of subtropical and tropical rivers and is mainly found in South China and the Mekong River (Froese and Pauly 2016) frequently

Figure 1. Sampling locations for *Pterygoplichthys* spp. in the main river drainages of Guangdong and Hainan Provinces (China). Each symbol represents a site where specimens were obtained and used in the current study.



co-occurring with *Pterygoplichthys* spp. in their introduced range (Li et al. 2013). The common size of *Pterygoplichthys* spp. is 189 mm standard length (SL) which is similar to *C. molitorella* (152 mm SL). Thus *C. molitorella* can be compared with *Pterygoplichthys* spp. to test whether the performance of invasive fish differs from native fish in waters with different N and P concentrations.

Impact of nutrient enrichment on life-history traits of wild Pterygoplichthys population

To examine the impact of nutrient enrichment on reproduction and maturity of wild *Pterygoplichthys* populations, field investigations were conducted during Summer and early Autumn from 2014 to 2016 within six river basins in Guangdong Province: including the Dongjiang, Rongjiang and Xijiang river drainages, the Western Basin and the Pearl River Delta, and Nandujiang river drainages in Hainan Province (Figure 1). For each river basin, specimens were sampled at 3–5 locations (28 locations in total). Fish samples were collected using gill nets (mesh size 50–100 mm) and shrimp pots, which were deployed at sampling locations for at least 4 h. Thirty to fifty fish samples were collected in each sampling site and shipped to the laboratory. All fish (1802 specimens in total) were measured for standard length (SL ± 1 mm) and for body mass ($M_t \pm 0.01$ g). Specimens were dissected to remove their gonads, weighed ($M_g \pm 0.01$ g) and visually categorized by gender and maturity stage (after Gibbs et al. 2008). Eviscerated mass ($M_e \pm 0.01$ g) was assessed after

removal of viscera. At least one lapillar otolith was removed from each fish. Age was estimated by counting otolith growth band pairs (after Gibbs et al. 2008). All otoliths were read three times by a single reader and the means were used for the age of each fish for further analysis. Mean age and SL at maturity were calculated using the method described in Fox and Crivelli (2001) and Wei et al. (2017). The Gonado-somatic index (GSI) was estimated by $GSI = (M_g/M_e) \times 100$. Females were defined as “mature” when 1) yolky oocytes were present; 2) the ovarian wall was transparent and 3) $GSI \geq 1$ (Jones et al. 2013). The number of mature eggs in both ovaries was counted as a proxy for absolute fecundity (AF). Relative fecundity (RF) was calculated as $RF = AF/M_e$. All sexually mature females were used to estimate fecundity. One hundred eggs in each ovary were randomly selected for size measurement using a vernier caliper (SHRN®, Guilin measuring tool and cutter co., LTD; ± 0.01 mm). Three water samples (approx. 250 ml) were collected using a modified water sampler (similar to a Niskin Bottle) at each sampling site, acidified with 2N H_2SO_4 (pH lower than 2), preserved at 4 °C, then transported to the laboratory for TP and TN analysis. Total phosphorous concentrations were measured as PO_4^{3-} using the ammonium molybdate method after persulfate digestion at 120 °C, 0.098 Mp., while water TN concentrations were measured as NO_3^- using the ultraviolet spectrophotometry method after alkaline persulfate oxidation at 120 °C, 0.098 Mp. (SEPA and Editorial Board of Water and Wastewater Monitoring and Analysis Methods 2002).

Impact of nutrient addition on the performance of *Pterygoplichthys* spp. and *C. molitorella*

To examine the impact of nutrient addition on the invasive fish *Pterygoplichthys* spp., a greenhouse experiment was conducted at the Pearl River Fisheries Research Institute (PRFRI), Chinese Academy of Fishery Sciences, Guangzhou, China (23°04'02.97"N; 113°13'21.93"E) from August 30 to November 6, 2017. The native fish *C. molitorella* was included for comparison. *Pterygoplichthys* spp. and *C. molitorella* were fed with algae to simulate their feeding habits in the wild. The experiment consisted of a 3 × 4 fully factorial design providing 12 unique treatment levels: each of no fish; *Pterygoplichthys* spp.; and *C. molitorella* being assessed with no nutrient addition; medium-level addition; heavy-level addition; and hyper-level addition. Each treatment combination was repeated six times. Treatments that had nutrients and no fish were set up to assess the effects of algae proliferate in the waters. All treatments were randomly assigned to aquariums in the greenhouse.

Juvenile *Pterygoplichthys* spp. and *C. molitorella* were obtained from aquarium vendors near the institute. The gender of juveniles of both fish are difficult to visually identify (*Pterygoplichthys* spp. mature at age 1~2, while *C. molitorella* mature at age 3), so only specimens of similar size were randomly chosen for experiments to ensure females and males were selected with the same probability. Aquariums (10-liter) were filled with 6-liters of aerated tap water which was inoculated with 0.5-liter of algae mixture. The initial mean algae density in the aquariums was 128 ± 2.90 cells ml⁻¹, composed of *Schroederia setigera*, *Raphidiopsis* spp., *Pediastrum* spp., *Chodatella longiseta*, *Oocystis* sp. and *Crucigenia apiculata*. The algae mixture was collected from the aquaculture pond in PRFRI. Algae density was counted using an Optical Plankton Counter (0.5 ml) under an electron microscope (10×) and species were identified following Hu and Wei (2006). The initial TN and TP concentrations were 0.06 mg L⁻¹ and 2.6 mg L⁻¹ respectively. Nutrients consisting of dissolved TN (as NH₄NO₃) and TP (as NaH₂PO₄·H₂O) were added as follows: (1) TN 0 mg L⁻¹ and TP 0 mg L⁻¹ (no nutrient), (2) TN 4 mg L⁻¹ and TP 1.0 mg L⁻¹ (medium-level), (3) TN 6 mg L⁻¹ and TP 1.5 mg L⁻¹ (heavy-level), and (4) TN 10 mg L⁻¹ and TP 2 mg L⁻¹ (hyper-level). These values were selected based on the eutrophication status of lakes in China (Jin 2003). Nutrients were added to maintain eutrophication status throughout the experiment. Thus, the cumulative amounts of nutrient inputs were 8 mg L⁻¹ TN and 2.5 mg L⁻¹ TP in medium eutrophication

treatments, 11 mg L⁻¹ TN and 3.75 mg L⁻¹ TP in heavy eutrophication treatments, and 21 mg L⁻¹ TN and TP: 5 mg L⁻¹ in hyper eutrophication treatments over the course of the experiment.

Algae were grown for 21 days in the experimental aquaria. Then, a single fish of similar size for each fish species (mean weight: *Pterygoplichthys* spp.: 6.51 ± 0.99 g, *C. molitorella*: 4.69 ± 1.21 g; mean length: *Pterygoplichthys* spp. 67.05 ± 0.92 mm SL and *C. molitorella* 67.34 ± 1.25 mm SL) was randomly released into each aquarium and allowed to grow for 45 days. Body mass (M) and standard length (SL) of the fish were measured at the beginning and end of the experiment. Relative specific growth rate (R-SGR) was calculated using $R-SGR = (\ln M_{\text{end}} - \ln M_{\text{initial}}) / t \times M_{\text{initial}}$, and $M_{\text{end}} / M_{\text{initial}}$ indicated fish body mass at the end or beginning of the experiment (Ali et al. 1998). Three algae mixture samples (approx. 15 ml) were stochastically collected from each treatment at the end of the experiment to examine algae densities after fish foraging. Algae cells were counted using the method mentioned above. Three water samples (approx. 250 ml) were randomly collected from each treatment at the end of the experiment, acidified with 2N H₂SO₄ (pH lower than 2) and preserved in 4 °C for TP and TN analysis using the method mentioned above.

Data analysis

For the field study, Pearson correlations were performed to determine the relationships between nutrient concentrations (i.e. TN and TP) and life-history traits (i.e. AF, egg size, gonad mass, mean age and SL at maturity, GSI and RF) (see Supplementary material Table S1). Absolute fecundity was log₁₀ transformed and mean SL at maturity of both genders was ln transformed to meet the assumption of normality. The means for water and fish samples from each sampling site were used for correlation analyses. Linear regression analysis was employed to fit the variables when the correlations were significant. A path analysis using AMOS (IBM® SPSS® AMOS 21.00.00) was developed to explore the relationship among nutrient concentrations (i.e. TN and TP), mean age and SL at maturity for females, and reproduction traits (i.e. AF, egg size, GSI, and RF) (Goulet et al. 2017). All variables were standardized using the Z-score method to reduce dimension and intrinsic variation of variables. A residual covariance path was added between absolute and relative fecundity to improve model fit.

The model was estimated using the maximum likelihood estimation method. Multiple model fit indicators were assessed including chi-square (χ^2),

Table 1. Correlation coefficients and p-values for Pearson correlation analyses describing the relationships between nutrient concentrations (total phosphorus and total nitrogen) in drainages and life-history traits of *Pterygoplichthys* spp. [egg size (mm), Gonad mass (g), Gonadosomatic index (GSI), Absolute fecundity (lg transformed), relative fecundity, mean standard length at maturity (ln transformed) for female (MatslF) and for male (MatslM), mean age at maturity for female (MatageF) and for male (MatageM), as well as relative fecundity]. Significant effects are indicated in bold.

Nutrient	Life-history traits	Mean	r	p-value
Total phosphorus	Egg size (cm)	1.84	-0.02	0.90
	Gonad mass (g)	24.04	0.08	0.68
	GSI	8.01	0.04	0.84
	Absolute fecundity (grain)	3.19	0.06	0.77
	MatageF (years)	1.46	0.20	0.30
	ln (MatslF) (mm)	5.42	0.50	0.007
	MatageM (years)	1.63	0.08	0.7
	ln (MatslM) (mm)	5.47	0.12	0.53
Total nitrogen	Relative fecundity (grain/g)	8.04	0.20	0.30
	Egg size (cm)	1.84	-0.05	0.81
	Gonad mass (g)	24.04	-0.19	0.33
	GSI	8.01	0.30	0.13
	Absolute fecundity (grain)	3.19	-0.30	0.12
	MatageF (years)	1.46	0.15	0.45
	ln (MatslF) (mm)	5.42	0.20	0.31
	MatageM (years)	1.63	0.54	0.003
	ln (MatslM) (mm)	5.47	0.53	0.004
	Relative fecundity (grain/g)	8.038	-0.17	0.38

the comparative fit index (CFI), goodness-of-fit index (GFI), a root-mean-square error of approximation (RMSEA) and Tucker-Lewis Index (TLI). Values that were greater than 0.95 for the CFI, greater than 0.9 for the GFI, less than 0.06 for the RMSEA, and greater than 0.95 for TLI indicate a good fit of the data to the model (Hu and Bentler 1999).

For the greenhouse study, a General Linear Model (GLM) was employed to assess the effect of fish species, nutrient addition and their interaction on R-SGR and algae density, as well as TN and TP concentrations and nutrient ratio (N:P) at the end of the experiment. Algae density, as well as TN and TP concentrations and N:P were standardized using Z-score which can be used directly for testing the changes in fish performance between different species (Cheadle et al. 2003). When the GLM indicated a significant effect Bonferroni post-hoc multiple comparison tests were used to examine the differences among treatments. When the interactive effects were significantly different, the differences among treatment combinations were examined using adjusted means partial difference tests. All data analyses were carried out using SAS 8.1 (SAS Institute 2000). Figures were created using ArcMap 10.0 (Environment System Research Institute 2010) and SigmaPlot 12.0 (Systat Software Inc 2011).

Results

The impact of nutrient enrichment on life-history traits of wild Pterygoplichthys populations

Total phosphorus and TN concentrations had no significant impact on AF, egg size, gonad mass, GSI or RF of *Pterygoplichthys* spp. (Table 1, Table S1). Total phosphorus showed no significant correlation with mean age at maturity of male and female *Pterygoplichthys* spp. (Figure 2a). Mean SL at maturity of female *Pterygoplichthys* spp. was positively affected by TP concentration at sampling sites, while mean SL at maturity of males showed no significant correlation with TP (Figure 2b). Mean age and SL at maturity of male *Pterygoplichthys* spp. were positively affected by TN, while mean age and SL at maturity of females showed no significant correlation with TN (Figure 2c, d). The structure equation model gave a good fit ($\chi^2 = 12.17$, $df = 12$, $p = 0.43$, CFI = 0.99, GFI = 0.92, RMSEA = 0.00 and TLI = 0.99). Higher TP concentrations led to a larger size at maturity for females ($\beta = 0.52$, $p = 0.001$) and mean SL at maturity increased 0.52 units with every 1 unit increase of TP (Figure 3, Table S2). A positive effect of mean SL at maturity on GSI was noted ($\beta = 0.44$, $p = 0.01$), while

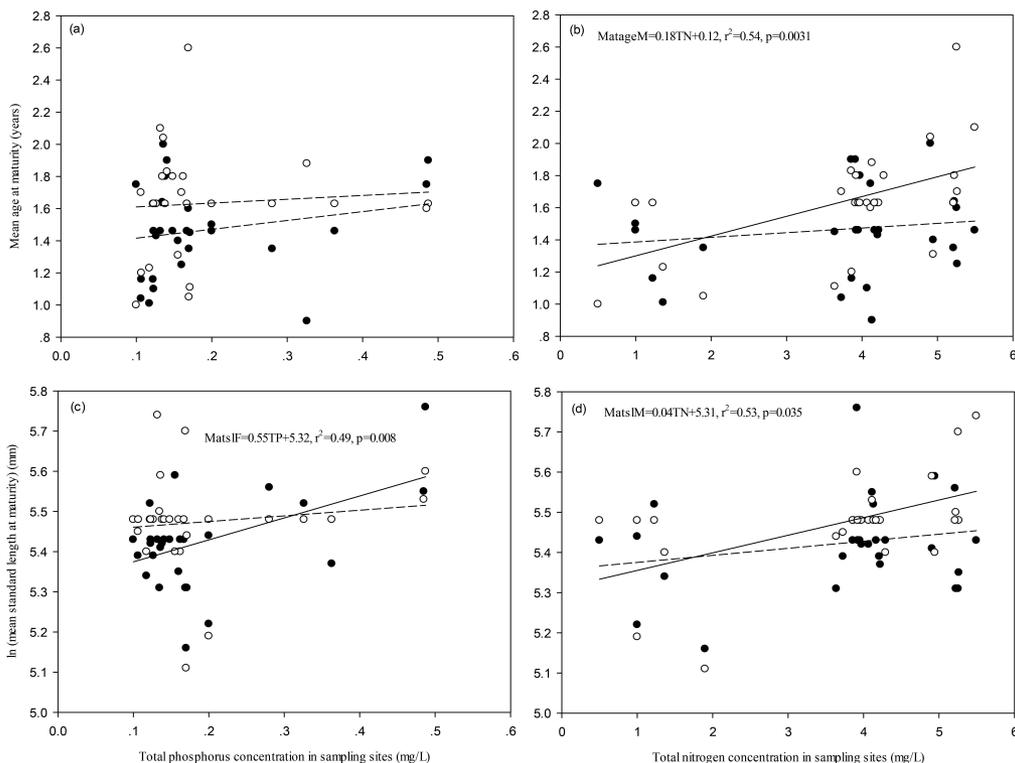


Figure 2. The impact of nutrient concentration on maturity of *Pterygoplichthys* spp.: (a) total phosphorus (TP) vs mean age at maturity of females (MatageF) and males (MatageM); (b) total nitrogen (TN) vs MatageF and MatageM; (c) TP vs mean standard length at maturity of females (MatsIF) and males (MatsIM) and (d) TN vs MatsIF and MatsIM. Points represent means of individual samples from each sampling site. Black points indicate female fish, and white points represent male fish. Solid trend lines indicate significant relationships: (b) $MatageM = 0.18TN + 0.12, r^2 = 0.54, p = 0.0031$, (c) $MatsIF = 0.55TP + 5.32, r^2 = 0.49, p = 0.008$, and (d) $MatsIM = 0.04TN + 5.31, r^2 = 0.53, p = 0.035$, while dashed trend lines indicate non-significant relationships.

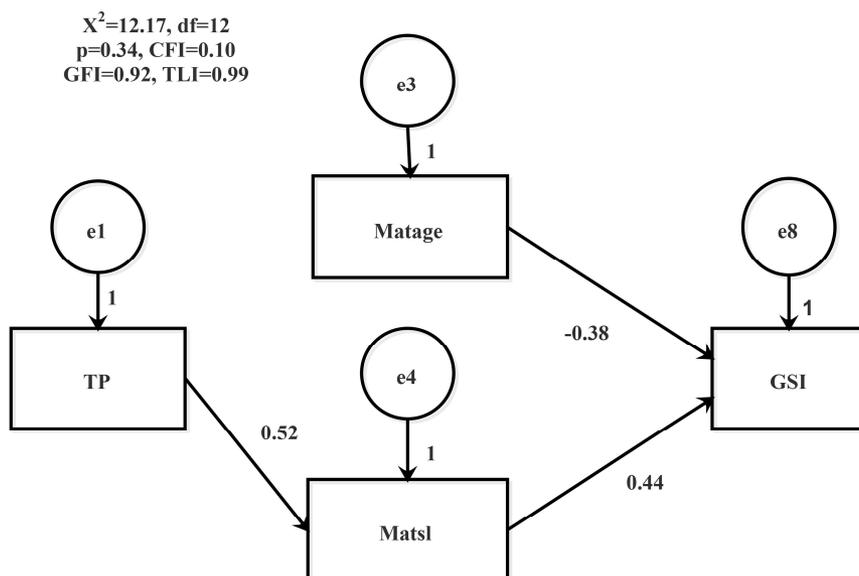


Figure 3. Pathway analysis showing the significant effect of nutrient concentration on reproductive traits of *Pterygoplichthys* spp. ($P < 0.05$). The abbreviations indicate: Matage = mean age at maturity, Matsl = mean standard length at maturity, GSI = gonado-somatic index.

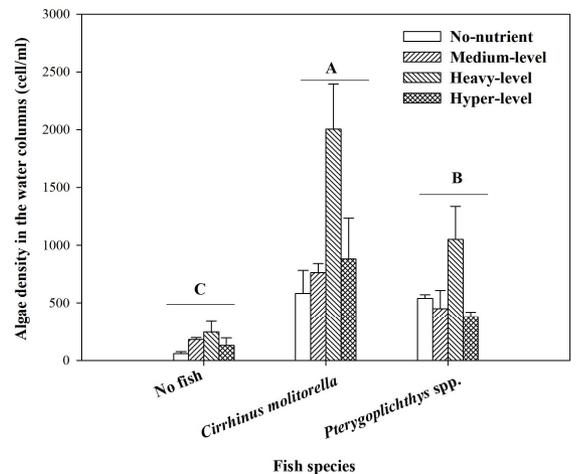
Table 2. General linear model (GLM) results for the impact of fish species (*C. molitorella* and *Pterygoplichthys* spp.), nutrient addition and their interaction on relative specific-growth rate (R-SGR), algae density (AD), and total phosphorus (TP) and nitrogen (TN) concentration, and nutrient ratio (N:P) in water columns. Significant effects are indicated in bold.

Variable	Species(S)			Nutrient(N)			S × N		
	df	F	P	df	F	P	df	F	P
R-SGR	1	0.04	0.84	3	0.39	0.76	3	0.91	0.45
AD	2	22.11	< 0.0001	3	8.87	0.0004	6	2.46	0.05
TP	2	4.63	0.020	3	12.44	< 0.0001	6	2.25	0.07
TN	2	3.46	0.048	3	1.07	0.38	6	1.40	0.26
N:P	2	24.66	< 0.0001	3	44	< 0.0001	6	23.19	< 0.0001

a negative effect of mean age at maturity on GSI was observed ($\beta = -0.38$, $p = 0.02$) (Figure 3, Table S2). This means reproduction allocation increased 0.44 units with every 1 unit increase in mean SL at maturity, while it decreased 0.38 units with every 1 unit increase of mean age at maturity. The direct effect of TP on mean SL at maturity is 0.519, while the direct effect on GIS is 0.445. The indirect effect of TP on GSI is 0.161, which might be mediated by mean size at maturity (Table S3). No standardized regression weights of the path with nutrient concentration (TP and TN) to fecundity related traits (Table S2) were significant.

Impact of nutrient addition on the growth of *C. molitorella* and *Pterygoplichthys* spp.

The R-SGRs of *C. molitorella* and *Pterygoplichthys* spp. were not affected by nutrient addition (Table 2) and decreased by the end of the experiment. Algae densities were significantly different among nutrient treatments after 21 days growth ($F_{3,35} = 320.48$, $p < .0001$; no nutrient: 1092.67 ± 37.34 cell ml^{-1} ; medium-level: 1504.00 ± 23.84 cell ml^{-1} ; heavy-level: 1769.78 ± 8.36 cell ml^{-1} ; hyper-level: 2267.56 ± 31.52 cell ml^{-1}), and the presence of fishes significantly decreased algae densities by the end of the experiment (Figure 4). Algae densities in waters with *C. molitorella* were higher than those with *Pterygoplichthys* spp., indicating that *Pterygoplichthys* spp. consume more algae than *C. molitorella*, while algae densities in waters without fish decreased sharply by the end of the experiment (Figure 4). Algae densities were higher in heavy nutrient addition treatments relative to the other three nutrient treatments (Table 2, Figure 4). Fish species and nutrient additions had significant impacts on TP concentrations and nutrient ratios. In this respect, the lowest TP concentrations were observed in the control treatments, while TP concentrations were significantly lower in waters where

**Figure 4.** The impact of fish species and nutrient addition on algae densities. Data were collected at the end of the experiment. Algae proliferate was assessed using data from no fish treatment.

Pterygoplichthys spp. were present (mean \pm SE, 3.31 ± 1.02 mg L^{-1}) than *C. molitorella* (mean \pm SE, 6.35 ± 1.02 mg L^{-1}) (Figure 5a). Total nitrogen concentrations were significantly higher in water without fish relative to that with *Pterygoplichthys* spp. and *C. molitorella* (mean \pm SE, 16.71 ± 0.49 mg L^{-1}) (Figure 5b). Nutrient ratios (N:P) were higher in waters with *Pterygoplichthys* spp. than that with *C. molitorella*. The highest nutrient ratios were observed in the control treatment (nutrient ratio: 33.95 ± 4.40), while the lowest nutrient ratios were found in heavy nutrient addition treatments (Figure 5c). Nutrient ratios were higher in heavy nutrient addition treatments where *Pterygoplichthys* spp. were present than that with *C. molitorella* (Figure 5c).

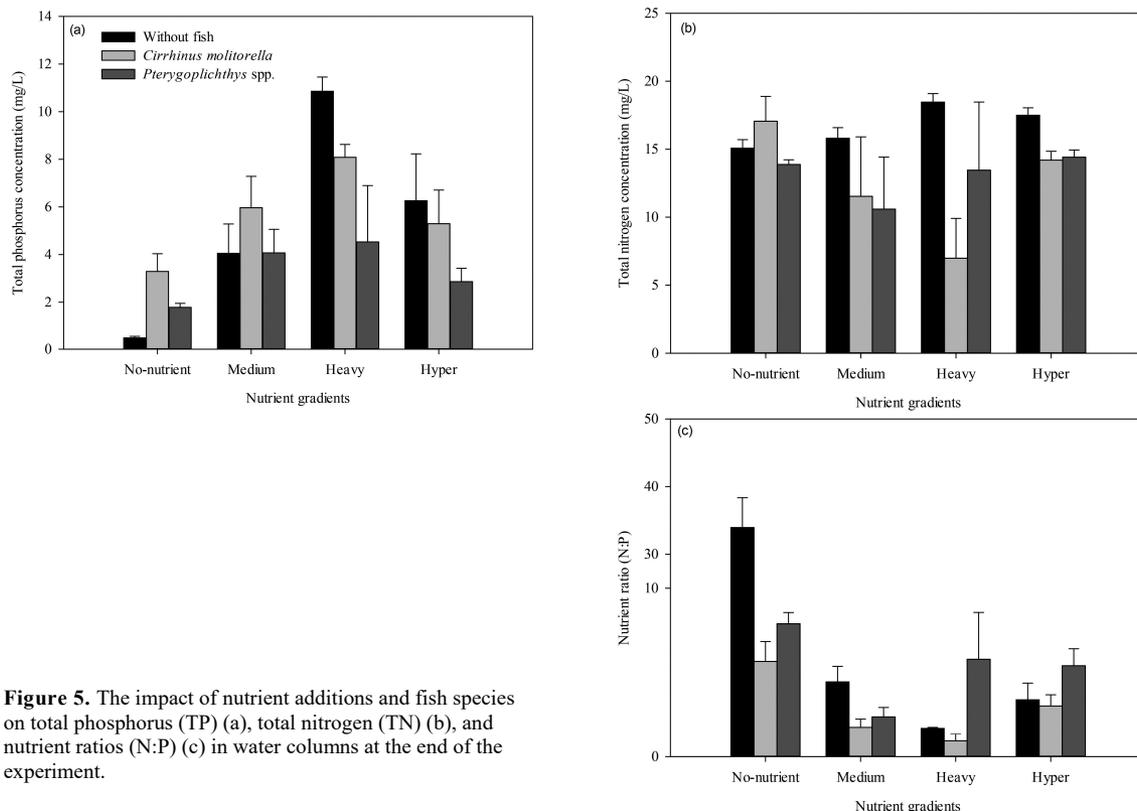


Figure 5. The impact of nutrient additions and fish species on total phosphorus (TP) (a), total nitrogen (TN) (b), and nutrient ratios (N:P) (c) in water columns at the end of the experiment.

Discussion

Life-history traits can display plasticity across different environments (Stearns and Koella 1986). Animals enter mature stages at an earlier age and a larger size, and with higher growth rates, when encountering good environments, whereas life-history traits will exhibit various patterns when animals suffer from stressful environments (Stearns and Koella 1986): they 1) mature later at a smaller size, 2) mature later at the same size, 3) mature later at a larger size, 4) mature earlier at a smaller size, or 5) mature at a smaller size. The results of the present study suggest that life history traits of *Pterygoplichthys* spp. could be affected by nutrient concentrations in the drainages. In this respect, female *Pterygoplichthys* spp. matured at larger size when TP concentrations increased in the drainages, while age at maturity of female was not affected by TP concentrations. Mean size and age at maturity of males increased with an increase in TN concentrations. These results suggest nutrient enrichment is likely to affect the colonization and population expansion of *Pterygoplichthys* spp. by altering the maturity of both males and females.

Characterized by a sub-tropical monsoon climate with warm mean winter (13.3 °C) and summer temperatures (28.5 °C) (Guangdong Meteorological Service 2013), southern China may be favorable for the spread of *Pterygoplichthys* spp. due to lack of predators, stable water levels and a benign climate (Li et al. 2013). However, as a detritivorous fish, *Pterygoplichthys* spp. could be limited by food quality in invaded habitats, due to their unique stoichiometric traits (Hood et al. 2005). Although nutrients can vary temporally and fish can move, which means fish are not always exposed to the same nutrient concentrations during their entire life, water chemical conditions remain relatively stable (Environmental Protection of Guangdong Province 2014–2017). In this respect, extra nutrient input by natural/anthropogenic disturbance is expected to relax nutrient limitation for omnivores or detritivores through trophic cascades (Datri et al. 2015; Biggs et al. 2011). Moreover, *Pterygoplichthys* spp. can tolerate hypoxia, since their guts can act as air-breathing organs (Fosha and Dzialowski 2009). Thus, *Pterygoplichthys* spp. are likely to benefit from eutrophication which can provide “windows” (i.e. abundant food supply, high-quality food and less competition) for *Pterygoplich-*

thys spp. to colonize (Davis et al. 2000). Similar results have been found in the invasive fish *Cyprinus carpio* in which abundance increased nonlinearly with increasing surface water TP across the Brazos and Trinity River basins within the Cross Timbers ecoregion (Taylor et al. 2014).

Detritivorous and omnivorous fish can indirectly benefit from nutrients by consuming food (e.g. plankton, detritus etc.) stimulated by the increase in nutrients. Additionally, the nutrient contents of these food resources vary with nutrient concentrations in the water (Hemmi and Jormalainen 2002; Datri et al. 2015; Manning et al. 2016). Phosphorus and nitrogen are essential elements in growth and reproduction of fish species, so restricted diet nutrition can delay their maturity (Jonsson et al. 2013). Individual fish have different nutrient requirements during their life cycles due to differences in stoichiometric traits and physiological activities between juveniles and adults, mature and immature fish, and between sexes (Stearns and Koella 1986; Sterner and Elser 2002). For *Pterygoplichthys* spp., mean size and age at maturity of males were larger than in females (Wei et al. 2017), suggesting that the sexes may have different nutrition requirements for sexual maturity. High growth rates are usually related to high P content in food, especially for invertebrates and vertebrates in the juvenile stage, because P is essential to the synthesis of energy substances (i.e. phospholipids, ATP and nucleic acids) (Sterner and Elser 2002). Also, the demand for P will increase during the development of oocytes (Craik and Harvey 1984) because P is the major constituent of yolk, suggesting that females have a higher TP demand for reproduction. For this reason, female *Pterygoplichthys* spp. are likely to grow rapidly at the juvenile stage and mature at a larger size to produce more and viable eggs when TP concentrations increase in invaded habitats. On the other hand, as a major constituent of protein, TN is likely to affect spermatozoa and sperm motility of males (Cheah and Yang 2011). Moreover, nutrition chemical traits are effective cues in fish species for sexual selection. Giaquinto et al. (2010) reported that female *Oreochromis niloticus* preferred males at high protein states. For this reason, males may have a high TN demand for growth, sexual selection and reproduction, resulting in higher growth rates and larger sizes at maturity. Although *Pterygoplichthys* spp. can tolerate poor water quality, excessive N in the form of ammonia and nitrate is harmful for the performance of fish species (El-Shafai et al. 2004). Thus, the positive impact of increased N in water columns on the fitness of *Pterygoplichthys* spp. might be reduced when TN concentration is within a certain range. In

another words, male *Pterygoplichthys* spp. might adjust maturity to maximum fitness when encounter stressful environments. Delaying maturity can decrease juvenile mortality rates, while larger sizes at maturity increases the life expectancy of offspring (Stearns and Koella 1986).

Reproductive traits of *Pterygoplichthys* spp. were not affected by TN or TP enrichment in these drainages, which could be ascribed to intrinsic trade-offs among life-history traits (i.e. growth, reproduction and maintenance) (Stearns 1989). Female *Pterygoplichthys* spp. allocated more energy to reproduction when they matured at a larger size, while less energy was allocated to reproduction when females matured later. The present study suggests a weak positive relationship between TP and GSI, which might be mediated by mean size at maturity. Life history traits can be influenced by a combination of environmental factors, such as temperature, hydrology, water quality and food supply (Stearns 1989), implying that the impact of nutrient enrichment on fish life-history traits may be complex. Further research is needed to investigate how intrinsic and extrinsic factors interactively affect variation in fish life-history traits across drainages.

Nutrient enrichment can improve the quality of phytoplankton in aquatic ecosystems (Greenwood et al. 2007; Manning et al. 2016). Hemmi and Jormalainen (2002) demonstrated that eutrophication changed the carbohydrate metabolism of the brown alga *Fucus vesiculosus*, which increased insoluble sugars and decreased total carbon content in tissue, resulting in higher growth rates and increased food consumption of *Idotea baltica* in a nutrient-rich environment. Although *Pterygoplichthys* spp. consumed more algae relative to *C. molitorella*, the growths of both fish species were not affected by N and P additions. Datri et al. (2015) reported similar results in that growth rate, lipid and nutrient content of *Pterygoplichthys* spp. were not different between nutrient enriched and unenriched streams. Interestingly, water TP concentration decreased in the aquarium where *Pterygoplichthys* spp. were present when compared with that when *C. molitorella* were present, suggesting higher P sequestration rate and lower P excretion rate for *Pterygoplichthys* spp. This hybrid swarm could modify nutrient cycling by altering nutrient storage and remineralization rates (Capps and Flecker 2013a, b). Less N and P may be excreted by *Pterygoplichthys* spp. than by native fish (e.g. characid, molly, pimeleodid etc.) and the excretion of this hybrid swarm could satisfy greater N and P demand in the Chacamax River relative to that of native fishes (Capps and Flecker 2013a). Thus *Pterygoplichthys* spp. were recognized as a net

remineralizer of N and a net sink of P (Capps and Flecker 2013a). A decrease in P excretion might thus be ascribed to higher P allocation to the P-rich bony tissues of *Pterygoplichthys* spp., thereby enhancing growth when other environmental factors were favorable and maintaining growth when encountering less favourable environments (Liess and Hillebrand 2006; Benstead et al. 2014). Phosphorus enrichment may thus accelerate *Pterygoplichthys* spp. invasion due to their ability to utilize P.

Biogeochemical cycle change (e.g. N and P) which mainly results from eutrophication caused by overpopulation or agricultural discharge is an important component of global change (Elser et al. 2009). These changes can affect trophic interactions by altering habitat quality and food webs in freshwater or marine ecosystems (Smith and Schindler 2009; Glibert et al. 2011). Studies also suggest that frequent invasions along with eutrophication can promote additional invasion, especially for non-native aquatic species which can tolerate poor water quality (Simberloff 2006; Glibert et al. 2011; Havel et al. 2015). While nutrient enrichment can exert positive impacts on the performance of invasive plants (Gonzalez et al. 2010; Seabloom et al. 2015; Sardans et al. 2016), the impact of nutrient enrichment on fish invasions has rarely been investigated. Eutrophication provides empty niches, which is likely to facilitate the invasion of non-native hypoxia tolerant fishes. Thus, *Pterygoplichthys* spp. could adjust their life-history traits to maximum fitness in eutrophic ecosystems. They may also benefit from nutrient enrichment due to their ability to utilize P. These adaptive responses might help this non-native fish to colonize and spread in novel aquatic ecosystems. Further study is needed to explore the underlying mechanisms for the impact of nutrient enrichment on aquatic invasions, i.e. by altering food quality or fish stoichiometric plasticity (Leal et al. 2016). These findings may be instructive for understanding the relationship between biogeochemical changes and fish invasions, which would aid in minimizing the risk of biological invasions when developing management strategies in polluted ecosystems.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Means of life-history traits and water nutrient concentrations in each sampling sites.

Table S2. Regression weights of variables in maximum likelihood estimation.

Table S3. Direct and indirect effects among variables in maximum likelihood estimation.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Wei_et_al_SupplementaryTables.xlsx