

# Determining the strength of exploitative competition from an introduced fish: roles of density, biomass and body size

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**Abstract** – As species introductions can result in increased resource competition for coexisting species in the receiving ecosystems, the effects of increased exploitative competition for limited food resources from an introduced fish (*Pseudorasbora parva*) on a coexisting fish (*Cyprinus carpio*) were tested experimentally using a substitutive–additive design. Additive treatments revealed that the growth of *C. carpio* was significantly suppressed following the introduction of *P. parva* with the magnitude of growth suppression directly proportional to *P. parva* density and biomass. A substitutive treatment that tested for the effect of intraspecific competition revealed that when *C. carpio* were introduced at a similar biomass to *P. parva*, there was no significant difference in the extent of the suppressed growth. At the same density, however, the effect of *C. carpio* (higher biomass) on growth was significantly above that of *P. parva* (lower biomass). This was independent of the initial body sizes of the introduced fishes. Thus, the interspecific competition imposed by *P. parva* was only as strong as the intraspecific competition of *C. carpio* when present at a similar biomass.

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**Key words:** *Pseudorasbora parva*; *Cyprinus carpio*; growth suppression; introduction; specific growth rate

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## Introduction

Ecological consequences of introduced fishes include the adverse effects of increased competition for resources within the resident communities (Rahel & Olden 2008). These effects include reduced growth and fitness in these coexisting fishes resulting from asymmetric interspecific competition as the introduced fish may exploit common resources more effectively, be a superior competitor or be more numerous (Ruetz et al. 2003). Competitive processes include interference, where aggression excludes competitors with high resource monopolisation, and exploitative, where species with similar feeding modes and/or in the same trophic guild all have access to the resource and exploit it nonaggressively, resulting in reduced resource availability for individuals (Connell 1983; Schoener 1983). In assessing the impacts of introduced fish on the growth of coexisting fishes, the

effects of interference competition have been prevalent; significantly reduced growth has been measured through the consequences of aggressive dominance of the introduced fish (Marchetti 1999), the displacement of coexisting fish into inferior foraging sites (Baxter et al. 2007), reduced foraging behaviour of coexisting species (Lawler et al. 1999) and the disruption of dominance hierarchies (Blanchet et al. 2007a).

Following an introduction, quantifying the effects of the increased interspecific exploitative competition on coexisting fishes requires the assessment of their relative effects in relation to increased intraspecific competition. Previous studies on a range of organisms and systems suggest that interspecific competition is rarely stronger than intraspecific competition. For example, a review by Connell (1983) revealed that where interspecific competition was found in experimental studies, subsequent experiments re-

vealed it was only stronger than intraspecific competition in <25% of cases. Although there have been a number of subsequent studies involving competition in fish, including introduced fishes (e.g. Fausch 1988; Weber & Fausch 2003; Blanchet et al. 2007a), there remains a lack of understanding of the relative effects of inter- and intraspecific exploitative competition, particularly in relation to the body size of the competitors and despite this being a key ecological trait (Schröder et al. 2009). This is because body size ultimately determines whether competing populations comprise of low densities of large-bodied fish or high densities of smaller-bodied fish (Schröder et al. 2009; Arim et al. 2010). Thus, the influence of density, biomass and body size on the strength of inter- and intraspecific exploitative competition remains unclear.

Accordingly, to understand the role of density and biomass on the relative strengths of inter- and intraspecific competition in relation to the body sizes of the competitors, a range of experiments were designed using an introduced species and a coexisting species. These tested the strength of inter- and intraspecific exploitative competition through the analysis of their effects on the growth of the coexisting fish. The introduced species was topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel), a highly invasive, small-bodied 'pest' fish that has the ability to rapidly colonise new waters and establish high-density populations that generally exploit common food resources (Britton et al. 2009a,b). The coexisting species was carp *Cyprinus carpio* L., a larger-bodied, strong exploitative competitor (Koehn 2004; Britton et al. 2010). It is also invasive in many parts of the world (e.g. Zambrano et al. 2006) where populations tend to be less dense but of higher biomass than where *P. parva* is invasive (e.g. Britton et al. 2007). These species are also increasingly occurring in sympatry in European waters (Britton et al. 2009a). Using an extended substitutive-additive experimental design, where additive treatments increased the abundance of introduced *P. parva* and the substitutive treatment introduced *C. carpio* rather than *P. parva* (Underwood 1986), the objectives were to i) test the strength of intra- versus interspecific competition in these two fishes and ii) identify how the different density and biomass of competitors determine the outcome of the intra- and interspecific experimental treatments.

## Materials and methods

### Experimental design

Experiments were completed in 45-l tank aquaria arranged randomly on shelving with three tiers (top,

middle and bottom shelves) and completed at 20 °C under a 16:8-h light:dark regime. A control and four treatments were designed, each being replicated three times and starting with seven *C. carpio* (total mass: 68.1–74.5 g). The control had no *P. parva* added, whereas the additive treatments had *P. parva* introduced at varying abundances. These treatments were termed the 'low abundance treatment' ( $N = 3$ , 9.2–10.1 g), 'medium abundance treatment' ( $N = 15$ , 32.6–33.4 g) and 'high abundance treatment' ( $N = 30$ , 49.2–52.5 g). The final treatment was substitutive, introducing *C. carpio* (intraspecific treatment,  $N = 3$ , 32.9–33.9 g) to test the effect of adding the same number of individuals as the low abundance treatment and similar biomass as the medium abundance treatment and to test the differential effects of inter- and intraspecific competition.

The experimental procedure required *C. carpio* to be individually tagged using passive integrated transponder tags, measured (fork length  $L$ , nearest mm) and weighed ( $W$ , nearest 0.1 g) at the start of the experiment (M0). Feeding was then once per day using floating pellets (1.5 mm diameter; 28% protein, 3.5% oil) at fixed rations of 1.5% mean starting body mass per day. These pellets were chosen as although *C. carpio* is generally a benthic feeder, a preliminary feeding trial revealed their high capability to feed on these pellets. Moreover, the pellets were capable of being ingested by both species across their size ranges. The experiment then ran for 80 days to enable the growth of *C. carpio* to be determined in the absence of other competitors; at the end of the period, the fish were identified by their tag number, measured and weighed again (M1). The fish introductions into the relevant treatments were then undertaken, followed by maintenance of the fixed feeding rations, and the experiment concluded after 60 days to allow re-measurement (M2).

### Statistical analyses

The effect of the treatments on *C. carpio* growth in the time intervals between M0 and M1 and between M1 and M2 was characterised using two growth indices: specific growth rate (SGR) and incremental fork lengths (IL). SGR was determined from  $[(\ln W_{t+1} - \ln W_t)/t] \times 100$ , where  $W_t$  = total starting weight of *C. carpio* in the tank,  $W_{t+1}$  = total finishing weight of *C. carpio* in the tank and  $t$  = number of days between  $W_t$  and  $W_{t+1}$ . IL was determined from  $(L_{t+1} - L_t)/t$ , where  $L_t$  was the starting fork length,  $L_{t+1}$  the finishing fork length and  $t$  the number of days between  $L_t$  and  $L_{t+1}$ . For the two indices, values were determined for each fish per treatment and the mean per treatment with 95% confidence limits.

Prior to testing the effects of the treatments on the growth of *C. carpio*, the relationship between growth in the period M0–M1 and M1–M2 was assessed using linear regression to test whether growth between these periods was independent. The effects of the treatments on SGR and IL for each period were then tested using linear regression (to test for any relationship in growth between the periods) and ANCOVA (to test for differences in growth between treatments), where the effects of the *C. carpio* starting *W* and *L* (as measured at M0), and tank position, were controlled. A secondary analysis was then used to investigate the individual growth rates of *C. carpio* in the treatments, as their size distribution may have influenced growth through enabling the larger fish to compete more effectively for the food resources. Correspondingly, the analysis was designed to test whether *C. carpio* of greater than the mean size experienced higher growth within each replicated treatment, with the converse for those individuals below the mean. As per Seiler & Keeley (2009), the first step was to calculate the relative initial mass of each fish according to their initial mass (M0) divided by the mean mass (M0) of the fish in their tank. ANCOVA was then used to compare the growth (SGR) of the individual fish in the two periods with their initial relative mass, where the effects of the treatments were controlled in the model. All statistics were completed in SPSS v.16.0 (SPSS Inc., Chicago, IL, USA) with significance evaluated at  $\alpha = 0.05$ .

**Results**

The growth of *C. carpio* in each tank between M1 and M2 was not significantly related to that between M0 and M1 (SGR:  $r^2 = 0.06$ ;  $F_{1,13} = 0.77$ ,  $P > 0.05$ ; IL:  $r^2 = 0.05$ ;  $F_{1,13} = 0.68$ ,  $P > 0.05$ ); thus, the growth was independent between the two periods. At M1, there was no significant difference in SGR and IL between the control and treatments (Fig. 1a,b). Between M1 and M2, the overall effect of the treatments on the SGR and IL of *C. carpio* was significant (Fig. 1c,d), but not the effects of the initial mean weight and length of the introduced fish and tank position (Table 1). In the additive treatments, linear regression revealed that the magnitude of growth suppression was significantly proportional to *P. parva* abundance (SGR:  $r^2 = 0.98$ ;  $F_{1,2} = 871.1$ ,  $P < 0.01$ ; IL:  $r^2 = 0.98$ ;  $F_{1,2} = 260.7$ ,  $P < 0.01$ ; Fig. 1). The pairwise comparisons with Bonferroni adjustments for multiple comparisons from ANCOVA revealed that the differences in SGR and IL between the control and the medium and high abundance treatments were significant (Table 1). In the model, the interaction term between the initial length mass of *C. carpio* and the experimental treatments was not significant ( $F_{1,4} = 0.21$ ,  $P > 0.05$ ).

The intraspecific competition treatment revealed that the effects of additional carp on growth were not significantly different to the medium abundance

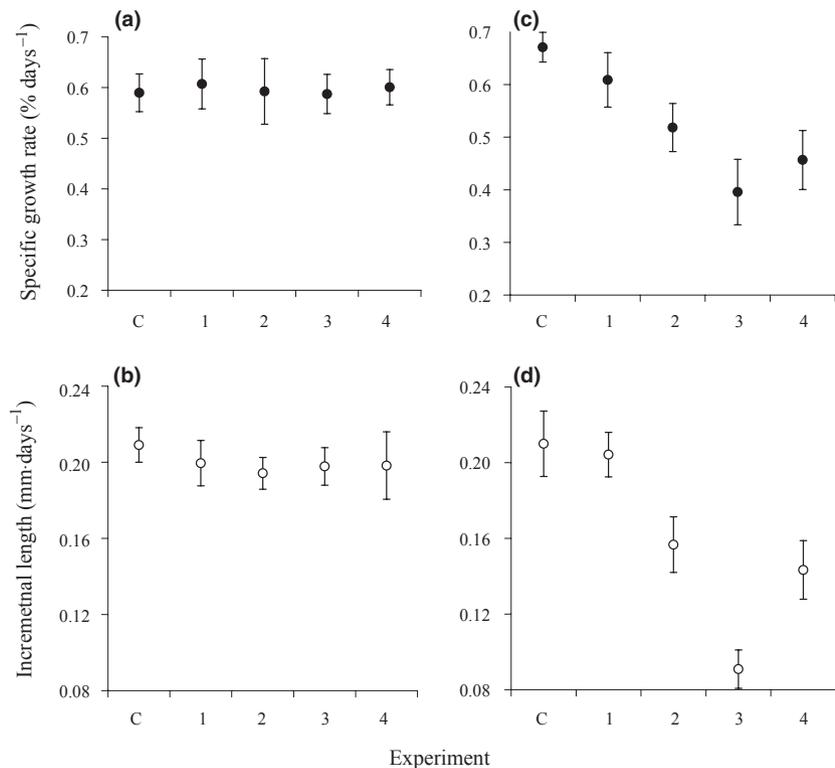


Fig. 1. Mean specific growth rate (% weight gain per day; ●) and incremental fork length (length gain per day, mm; ○) of *Cyprinus carpio* in the control and treatments in the intervals between M0 and M1 (a, b) and M1 and M2 (c, d). Error bars represent 95% confidence limits. Key to x-axis: C = control, 1 = low abundance treatment, 2 = medium abundance treatment, 3 = high abundance treatment, 4 = intraspecific competition treatment.

Table 1. Effect of tank position, starting weight and length, and the experimental treatments on the specific growth rate (% day<sup>-1</sup>) and incremental fork lengths (mm day<sup>-1</sup>) of *Cyprinus carpio* between M1 and M2 (ANCOVAs).

Effect	SGR	Incremental fork length
Tank position	$F_{3,11} = 0.52$ , $P > 0.05$	$F_{3,11} = 1.74$ , $P > 0.05$
Starting weight/length	$F_{1,14} = 0.55$ , $P > 0.05$	$F_{1,14} = 0.20$ , $P > 0.05$
Treatment	$F_{4,10} = 11.87$ , $P < 0.05$	$F_{4,10} = 21.29$ , $P < 0.01$
<i>Difference between treatments (mean ± SE)</i>		
Control		
Low abundance treatment	0.08 ± 0.05	0.02 ± 0.02
Medium abundance treatment	0.16 ± 0.05*	0.09 ± 0.02*
High abundance treatment	0.30 ± 0.05**	0.15 ± 0.02**
Intraspecific competition treatment	0.22 ± 0.05*	0.11 ± 0.02**
Intraspecific competition treatment		
Control	-0.23 ± 0.05**	-0.11 ± 0.02**
Low abundance treatment	-0.20 ± 0.05*	-0.09 ± 0.02**
Medium abundance treatment	-0.62 ± 0.05	-0.02 ± 0.02
High abundance treatment	0.08 ± 0.05	0.04 ± 0.02

The corresponding differences, indicated by pairwise comparisons with Bonferroni adjustments for multiple comparisons, between the control and the intraspecific competition treatment and the other treatments are displayed. SGR, specific growth rate.

\* $P < 0.05$ ; \*\* $P < 0.01$ .

treatment where a similar additional biomass of *P. parva* was added (Table 1; Fig. 1). It was, however, significantly different from the low abundance treatment where the same number of *P. parva* was added (Table 1; Fig. 1). Hence, adding a similar biomass of *C. carpio* and *P. parva* had similar adverse growth effects on *C. carpio*, but not adding the same density.

There was no effect of the initial relative mass on the growth rate of *C. carpio* (M0–M1:  $F_{1,97} = 0.87$ ,  $P > 0.05$ ; M1–M2:  $F_{1,97} = 2.13$ ,  $P > 0.05$ ), indicating that *C. carpio* that were smaller than the mean at the commencement of the experiments generally did not grow any less. There was also no influence of the treatments on this relationship (interaction term: M0–M1:  $F_{1,97} = 0.04$ ,  $P > 0.05$ ; M1–M2:  $F_{1,97} = 0.25$ ,  $P > 0.05$ ).

## Discussion

The additive treatments revealed that the consequence for *C. carpio* of *P. parva* introduction under limited food resources was suppressed growth through exploitative competition. Although the extent of the suppressed growth was proportional with *P. parva* abundance, the medium abundance and substitutive treatments revealed that there were no significant differences in its extent when a similar biomass of *P. parva* and *C. carpio* was introduced. By contrast,

when identical densities of *P. parva* and *C. carpio* were introduced (low abundance and the substitutive treatments), significantly different growth effects were detected. Thus, the interspecific competition imposed by *P. parva* was only as strong as the intraspecific competition of *C. carpio* when present at a similar biomass. These growth consequences were independent of the mean initial body lengths and mass sizes of the released fish.

That the consequent growth impacts in the coexisting fish were independent of the introduced species and dependent only on their biomass suggests that impacts from exploitative competitors may be subject to general rules that exclude the influence of body size. Indeed, the influence of starting size of *C. carpio* on their subsequent growth was not significant – a contrast to the output of many studies on salmonid fishes (generally interference competitors) that demonstrates that body size confers a significant competitive advantage to larger fish, often through dominance, leading to higher growth rates (Seiler & Keeley 2009). This then shapes the life history of individuals, particularly their reproductive tactics (e.g. Blanchet et al. 2007a; Seiler & Keeley 2009). Thus, these profound individual influences of body size in salmonids may be relatively insignificant for exploitative competitors.

Whilst body size did not influence competitive strength in this study, in natural situations it remains a key determinant of population size (and hence biomass) through its influence on individual energetic demands and feeding rates, trophic position and life-history traits (Schröder et al. 2009; Arim et al. 2010). Correspondingly, the introduction of a small-bodied fish that has *r*-selected life-history traits, such as *P. parva*, has substantial life-history advantages for their rapid establishment and the formation of abundant populations when compared to larger-bodied fish such as *C. carpio* (Garcia-Berthou 2007; Britton et al. 2010; Gozlan et al. 2010a,b). Thus, body size may still play a significant role in determining the impacts on the growth of coexisting fishes, although it is likely to be an indirect influence that regulates the population growth and biomass of the introduced fish. It is therefore recommended that future work on the relative strengths of intra- and interspecific exploitative competition involving introduced fish incorporates the role of body size in determining their rates of establishment and population growth and subsequent competition strength.

Recent field investigations on invasive *P. parva* populations have demonstrated that when their highly abundant populations share trophic space with roach *Rutilus rutilus* and *C. carpio*, suppressed growth occurs (Britton et al. 2009a,b). However, these field studies were conducted without replication and were

likely to have been subject to some stochastic environmental variables, i.e. conditions were unable to be controlled. Correspondingly, the design of these experiments using replication and highly controlled conditions (e.g. fixed daylight length, temperature, space, food supply) enabled the collection of complementary experimental data on the ecological effects of invasive *P. parva*. Thus, the consistency in the outputs of the experiments and field studies in revealing the effects of invasive species on native species (e.g. Blanchet et al. 2007b) is another important outcome given that studies on the effects of competition from invasive fish often find experimental data do not necessarily match field observations. This is generally because of experimental spatial constraints resulting in unnaturally intense interactions and issues relating to scaling up experimental data to represent more complex natural situations (Korsu et al. 2009).

In summary, the interspecific competition imposed by *P. parva* was only as strong as the intraspecific competition of *C. carpio* when they were present at a similar biomass. Notwithstanding, the introduction of such small-bodied fishes remains of great concern because of their increased ability to rapidly establish and form pest populations of high biomass when compared with larger-bodied fishes.

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## References

- Arim, M., Abades, S.R., Laufer, G., Loureiro, M. & Marquet, P.A. 2010. Food web structure and body size: trophic position and resource acquisition. *Oikos* 119: 147–153.
- Baxter, C.V., Fausch, K.D., Murakami, M. & Chapman, P.L. 2007. Invading rainbow trout usurp a terrestrial prey subsidy from native charr and reduce their growth and abundance. *Oecologia* 153: 461–470.
- Blanchet, S., Loot, G., Bernatchez, L. & Dodson, J.J. 2007a. The disruption of dominance hierarchies by a non-native species: an individual based analysis. *Oecologia* 152: 569–581.
- Blanchet, S., Loot, G., Grenouillet, G. & Brosse, S. 2007b. Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. *Ecology of Freshwater Fish* 16: 133–143.
- Britton, J.R., Boar, R.R., Grey, J., Foster, J., Lugonzo, J. & Harper, D. 2007. From introduction to fishery dominance: the initial impacts of the invasive carp *Cyprinus carpio* in Lake Naivasha, Kenya, 1999 to 2006. *Journal of Fish Biology* 71(Suppl. D): 239–257.
- Britton, J.R., Davies, G.D. & Harrod, C. 2009a. Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: a field investigation in the UK. *Biological Invasions* 12: 1533–1542.
- Britton, J.R., Davies, G.D. & Brazier, M. 2009b. Eradication of the invasive *Pseudorasbora parva* results in increased growth and production of native fishes. *Ecology of Freshwater Fish* 18: 8–14.
- Britton, J.R., Cucherousset, J., Davies, G.D., Godard, M. & Copp, G.H. 2010. Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. *Freshwater Biology* 55: 1130–1141.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122: 661–696.
- Fausch, K. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? *Canadian Journal of Fisheries and Aquatic Sciences* 45: 2238–2246.
- Garcia-Berthou, E. 2007. The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology* 71: 33–55.
- Gozlan, R.E., Britton, J.R., Cowx, I.G. & Copp, G.H. 2010a. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76: 751–786.
- Gozlan, R.E., Andreou, D., Asaeda, T., Beyer, K., Bouhadad, R., Burnard, D., Caiola, N., Cakic, P., Djikanovic, V., Esmaili, R., Falka, I., Golicher, D., Harka, A., Jeney, G., Kováč, V., Musil, J., Povz, M., Nocita, A., Poulet, N., Virbickas, T., Wolter, C., Tarkan, A., Tricarico, E., Trichkova, T., Verreycken, H., Witkowski, A., Zhang, C., Zweimueller, I. & Britton, J.R. 2010b. Pan-continental invasion of *Pseudorasbora parva*: towards a better understanding of freshwater fish invasions. *Fish and Fisheries* DOI: 10.1111/j.1467-2979.2010.00361.x.
- Koehn, J. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* 49: 882–894.
- Korsu, K., Huusko, A. & Muotka, T. 2009. Does the introduced brook trout (*Salvelinus fontinalis*) affect the growth of the native brown trout (*Salmo trutta*)? *Naturwissenschaften* 96: 347–353.
- Lawler, S.P., Dritz, D., Strange, T. & Holyoak, M. 1999. Effects of introduced mosquitofish and bullfrogs on the threatened California Red-legged frog. *Conservation Biology* 13: 613–622.
- Marchetti, M.P. 1999. An experimental study of competition between the native Sacramento perch (*Archoplites interruptus*) and introduced bluegill (*Lepomis macrochirus*). *Biological Invasions* 1: 55–65.
- Rahel, F.J. & Olden, J.D. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22: 521–533.
- Ruetz, C.R., Hurford, A.L. & Vondracek, B. 2003. Interspecific interactions between brown trout and slimy sculpin in stream enclosures. *Transactions of the American Fisheries Society* 132: 611–618.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *The American Naturalist* 122: 240–285.
- Schröder, A., Nilsson, K.A., Persson, L., van Kooten, T. & Reichstein, B. 2009. Invasion success depends on invader body size in a size-structured mixed predation-competition community. *Journal of Animal Ecology* 78: 1152–1162.

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- Seiler, S.M. & Keeley, E.R. 2009. Competition between native and introduced salmonid fishes: cutthroat trout have lower growth rate in the presence of cutthroat-rainbow trout hybrids. *Canadian Journal of Fisheries and Aquatic Sciences* 66: 133–141.
- Underwood, T. 1986. The analysis of competition by field experiments. In: Kikkawa, J. & Anderson, D.J., eds. *Community ecology: pattern and process*. Melbourne, Australia: Blackwell Scientific, pp. 240–268.
- Weber, E.D. & Fausch, K.D. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1018–1036.
- Zambrano, L., Martinez-Meyer, E., Menezes, N. & Townsend Peterson, A. 2006. Invasive potential of common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) in American freshwater systems. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1903–1910.