



The behavioral mechanism of competition for food between tilapia (*Oreochromis hybrid*) and crayfish (*Cherax quadricarinatus*)



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ABSTRACT

Studies on polyculture have usually investigated the consequences of this widespread culture method for growth and survival of the cultured species. However, research into the behavioral mechanism underlying competition between co-cultured species is lacking. For the first time in co-cultured fish and crustaceans, this study explored experimentally the behavioral interaction between red tilapia and red-claw crayfish in the context of food competition. The effects of the presence of heterospecifics (absent or present), the size of fish relative to crayfish (larger or smaller) and the number of food patches available for the fish (one- versus two-patch conditions) on the foraging decisions and aggression of fish and crayfish were tested. Time spent by fish in the bottom food patch (accessible for fish and crayfish) was shorter in the presence of crayfish, for small but not large fish and when there was an alternative patch for the fish (accessible only for fish). Time spent by crayfish in the bottom food patch was reduced in the presence of large, but not small, fish and when there was no alternative food patch for the fish. Fish were most aggressive towards conspecifics whereas interspecific aggression was exhibited only by crayfish. At the individual level, the dominant fish and crayfish spent more time in the bottom patch and performed more aggressive actions than the other conspecifics. In fish, this was not altered in the presence of crayfish. In crayfish, the overall reduction in foraging duration and aggression was due to an effect of large fish on the dominant individual. The implication of these findings for fish–crayfish communal culture is discussed.

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1. Introduction

The farming of tilapia is the most widespread type of aquaculture in the world, with more than 135 producer countries and territories worldwide (FAO, 2014). Tilapia are most commonly cultured in semi-intensive polyculture with one or more species of fish and/or crustaceans (Wang and Lu, 2015). The basic idea of polyculture is growing species with complementary or minimal competing feeding habits and different ecological requirements that can utilize different trophic niches in the pond (Milstein, 2005). However, with densities currently applied in polyculture practices, supplementary artificial food is usually added to meet the energetic requirements for optimal growth. This might introduce a resource for which the different cultured species compete. When competition ensues, one species may be more successful than the other, causing a reduction in growth of the inferior species from what might be obtained in monoculture.

Numerous studies over the last 3 decades have investigated polyculture of tilapia with other species, including crustaceans (Wang and Lu, 2015). These studies were conducted under varying degrees of intensification and at different species compositions. For instance, tilapia was investigated as a major species (alongside common carp) in

combination with freshwater prawns in semi-intensive polyculture ponds (Wohlfarth et al., 1985), as a secondary species added to freshwater prawns' periphyton-based ponds (Asaduzzaman et al., 2009) or to marine shrimp intensive culture tanks (Muangkeow et al., 2011; Tian et al., 2001; Yuan et al., 2010), and as a principal species in intensive co-culture with crayfish (Karplus et al., 2001). These studies have investigated effects on growth performance and survival of influencing factors such as species composition, stocking rates, feeding and manure regimes and environmental (water quality) parameters. In contrast to the wealth of studies on these aspects, research into the behavioral mechanism underlying competition between co-cultured fish and crustaceans is lacking.

Unlike tilapia polyculture with freshwater prawns (e.g., Cohen et al., 1983; García-Pérez et al., 2000; Wohlfarth et al., 1985) and marine shrimps (Muangkeow et al., 2011; Tian et al., 2001; Wang et al., 1998), studies on tilapia–crayfish polyculture have usually demonstrated a negative effect on growth and survival of tilapia on crayfish (Karplus et al., 2001; Rouse and Kahn, 1998) or of crayfish on tilapia (Brummet and Alon, 1994). Thus, investigation of the behavioral mechanism of interspecific competition in the context of polyculture is particularly pertinent for tilapia and crayfish.

The current study focused on interspecific competition for food between red tilapia (*Oreochromis hybrid*) and red-claw crayfish (*Cherax quadricarinatus*). Both species are omnivorous, however, while crayfish

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are bottom feeders the red tilapia feeds from both the bottom and the water column. Most studies have considered fish and crayfish in the context of predator–prey relationships (e.g., Stein, 1977; Stein and Magnuson, 1976). However, owing to their large size, hard shell and powerful weapons, crayfish are no easy prey for fish and they may compete directly with bottom feeding fish for food (Carpenter, 2005) and for shelter (Griffiths et al., 2004). Furthermore, under certain circumstances each omnivorous fish and crayfish might harm heterospecifics (Neveu, 2001); fish might harm vulnerable crayfish at molting, and the nocturnal crayfish might harm diurnal fish at night when the fish are less active. Thus, fish–crayfish relationships appear to be complex; it involves both competition and predation (Dorn and Mittelbach, 1999; Reynolds, 2011) and it can be reversed, depending on relative size (Keller and Moore, 2000).

In a previous study we investigated the consequences of food competition between red tilapia and red-claw crayfish for growth (Barki et al., 2001). We demonstrated that tilapia grew better in the presence of crayfish, possibly by consuming part of the feed ration intended for the crayfish, whereas the growth of crayfish was adversely affected by tilapia. The magnitude of this effect depended on the relative size of the fish. That this was a consequence of food competition was evident by the finding that feeding the crayfish at night, when the fish are less active, reduced the impact of large fish on small crayfish and increased their growth by 32%. In the current study we investigated the foraging decisions and aggressive interactions of the fish and crayfish under intra- and interspecific competition. Specifically, we investigated the interplay of several factors in influencing the foraging decision of fish and crayfish, namely the presence of heterospecific competitors, heterospecific relative size and the number of food patches available for the fish. To the best of our knowledge, this is the first attempt to delve into behavioral details of competition for food between co-cultured crustaceans and fish, up to the individual level.

2. Materials and methods

2.1. Tanks and animals

The experiment was conducted indoors in 32 glass aquaria (25 × 50 × 40 cm). Each aquarium contained an internal biofilter with airstone and a shelter consisting of 4 tubes (10 cm in length, 2 cm in diameter) attached underneath a plastic egg tray. Thermostatically-controlled 60-Watt heaters maintained temperature between 24 and 27 °C. Lighting was provided by timer-controlled ceiling fluorescent tubes on a 12:12 h light:dark daily illumination cycle, in addition to the ambient light. Ammonium level was undetectably low, nitrite level did not exceed 0.1 mg/l, and pH ranged between 7.7 and 8.1.

The experiment was conducted with groups of 3 young red tilapia males (*Oreochromis hybrid*) and 3 redclaw crayfish (*C. quadricarinatus*). The fish were individually identified by their differing color patterns, and the crayfish were individually tagged with color plastic bands glued to the carapace.

2.2. Experimental design and procedure

The experimental design incorporated the following social and environmental factors: i) Relative size – the interspecific relative competitive ability was manipulated by means of the fish size; the 3 fish were either small (mean ± SD, 4.3 ± 1.0 g) or large (20.4 ± 3.8 g), relative to 3 similar-sized crayfish (12.1 ± 3.6 g). ii) Number of food patches – the competitive environment was manipulated by means of the number of food patches in which the food was present. Each aquarium contained two petri dishes (10 cm in diameter) in which the food could be provided through two tubes passing the flexiglass lid and ending approximately 5 cm above the petri dishes. One petri dish was situated in the bottom, attached to the left longitudinal side, and the other was mounted 12 cm above the bottom on the opposite longitudinal

side at the same distance from the frontal glass and was accessible only for the fish (see supplementary video clip). The animals were fed six days a week with commercial feed pellets at a daily ration of 2% of total mass per aquarium. The food was given in either one patch (the bottom petri dish) or two patches (divided evenly between the two petri dishes). iii) Heterospecifics presence – each species was observed both in the absence and in the presence of heterospecifics. Three fish were firstly introduced for 10 days, then 3 crayfish were added for 10 days of cohabitation, and finally the fish were removed and the crayfish stayed alone for 10 days.

Intra- and inter-specific competition for food and aggressive interactions were observed. Each aquarium was video-recorded twice under each competitive condition, over two consecutive days to increase the sampling reliability, and the average values obtained served for the various analyses. The recording sessions were conducted at the end of each stage to ensure that the animals have adjusted to the specific social conditions and feeding regimes. To minimize disturbance, the video camera was located behind a black blind. Video recording lasted for 5 min before and 5 min after food supply. Based on the recorded aggressive interactions, each individual was ranked in a dominance order (see next section) and the rank factor was also included in the analyses.

2.3. Data analysis

We analyzed competitive ability in the context of competition for food by means of three measures: the total time spent in the food patch, the number of visits and the mean time per visit. A fish visit was measured when at least its snout was within the boundaries of the petri dish and approximately 5 cm above it (i.e. the level of the feeding tube opening). A crayfish visit was measured when at least the tips of its chelipeds were inside the petri dish.

Fish aggression measures were the frequencies of the following types of interactions: Overt attack, Displacement, Display and Contest (for details see Barki and Volpato, 1998). The rank order of the 3 fish (dominant, subdominant and subordinate) was determined by the relative number of their retreats in all 3 possible diads. Crayfish aggression measures were the frequencies of the following behavioral acts: Extend, Lunge, Grasp, Escalated-fighting and Displacement (for details see Karplus et al., 2003). The highest ranked crayfish was termed dominant, while the two lower-ranked individuals were similarly termed subordinates because their relative order was usually indiscernible (due to lack of interactions).

Competition measures and interspecific aggression were analyzed using PROC GLM (type III SS) of the SAS statistical package. Main and interaction effects of 4 independent variables were tested: relative size, number of food patches, heterospecific presence and dominance rank. We applied a split-plot model of ANOVA, which involved 3 error terms; size and patch were tested over the main plot error term, heterospecific presence was tested over the subplot error term and rank was tested over the residual error (Table 1). In the analysis of interspecific aggression (total number of aggressive actions) we added the feeding factor, i.e. before or after feeding, which was tested over the residual error. Frequencies were $\log(x + 1)$ transformed to increase homoscedasticity of data. In cases of significant effects ($p \leq 0.05$), Tukey–Kramer HSD test was performed for multiple comparisons. Aquaria in which an animal died (due to aggression among fish or cannibalism among crayfish) were not included in the analysis.

3. Results

3.1. Fish competitive ability

Time spent by fish in the bottom food patch was overall shorter in the presence of crayfish than in their absence (main effect of crayfish, $F_{1,19} = 7.57$, $p = 0.013$; Table 1). However, significant interactions of this factor with size and patch ($F_{1,19} = 11.55$, $p = 0.009$ and $F_{1,19} =$

Table 1
F probabilities for the split-plot ANOVAs on total time, number of visits and mean time per visit, spent by fish and crayfish in the bottom and upper food patches (log transformed data). Significant values ($p \leq 0.05$) are in bold. Size = relative size; patch = number of food patches; hetero = heterospecific presence.

Response variable: Factor	df ^c	Fish						Crayfish		
		Bottom patch			Upper patch			Bottom patch		
		Total time	No. of visits	Time visit ⁻¹	Total time	No. of visits	Time visit ⁻¹	Total time	No. of visits	Time visit ⁻¹
Size	1, 1	0.025	0.524	0.010	0.684	0.392	0.962	0.170	0.008	0.325
Patch	1, 1	0.016	0.986	0.050	< 0.001	< 0.001	< 0.001	0.252	0.616	0.365
Size × patch	1, 1	0.154	0.791	0.145	0.684	0.595	0.342	0.171	0.098	0.355
Main-plot error ^a	19,15									
Hetero	1, 1	0.013	0.222	0.035	0.213	0.170	0.328	0.400	0.213	0.136
Size × hetero	1, 1	0.009	0.148	0.094	0.866	0.377	1.000	0.031	0.077	0.031
Patch × hetero	1, 1	0.012	0.182	0.027	0.162	0.125	0.243	0.050	0.971	0.048
Size × patch × hetero	1, 1	0.769	0.557	0.336	0.948	0.741	0.927	0.080	0.535	0.087
Subplot error ^b	19,15									
Rank	2, 1	0.007	< 0.001	0.367	0.026	0.217	0.030	< 0.001	< 0.001	0.002
Size × rank	2, 1	0.739	0.662	0.271	0.028	0.115	0.043	< 0.001	0.005	< 0.001
Patch × rank	2, 1	0.345	0.713	0.119	0.160	0.637	0.183	0.094	0.203	0.053
Hetero × rank	2, 1	0.402	0.063	0.426	0.950	0.869	0.919	0.863	0.127	0.917
Size × patch × rank	2, 1	0.208	0.062	0.150	0.014	0.043	0.017	0.220	0.255	0.399
Size × hetero × rank	2, 1	0.392	0.750	0.276	0.905	0.908	0.828	0.931	0.098	0.710
Patch × hetero × rank	2, 1	0.101	0.465	0.028	0.375	0.364	0.405	0.046	0.389	0.117
Residual error	78, 31									

^a Main-plot error – tank (size, patch).

^b Sub-plot error – tank (size, patch, hetero).

^c df values on the left hand refer to fish and on right hand to crayfish.

10.59, $p = 0.012$, respectively; Table 1) revealed that the presence of crayfish caused small but not large fish to reduce the amount of time feeding in the bottom patch (Fig. 1A) and caused fish to reduce their time feeding in the bottom patch if there was also food in the upper patch but not if the upper patch was empty (Fig. 1B).

The effects of relative size, number of patches and heterospecific presence on the number of visits of fish in the bottom patch were insignificant, but their effect on the mean time per visit was significant, similar to their effect on the total time spent in the bottom patch (Table 1). This indicated that shorter time per visit, rather than the number of visits, accounted for the reduction in the time spent by fish in the bottom food patch.

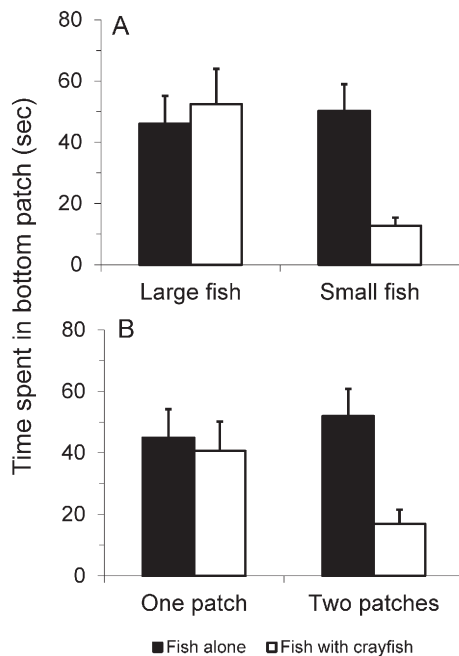


Fig. 1. Time spent by fish in the bottom patch in the absence (fish alone) and presence of crayfish (fish with crayfish) during 5 min following food supply. (A) Small fish versus large fish; (B) one food patch versus two food patches. Error bars indicate SEM.

Relative size and heterospecific presence had no effect on the total time spent by fish in the upper patch, mean time per visit and the number of visits. The number of patches, as expected, had highly significant effects on these response variables ($F_{1,19} = 50.1, 45.8$ and 127.9 , respectively, $p < 0.001$; Table 1) because the food was available in the upper patch only in two-patch treatments.

The dominant fish spent significantly more time ($F_{2,78} = 5.27$, $p = 0.007$, followed by Tukey–Kramer test; Fig. 2) and visited more times ($F_{2,78} = 13.99$, $p < 0.001$) in the bottom food patch than the two other fish types (Table 1). Concomitantly, the dominant fish spent less time in the upper patch than the two other fish ($F_{2,78} = 3.81$, $p = 0.026$; Fig. 2), but a significant relative size × rank interaction ($F_{2,78} = 3.74$, $p = 0.028$; Table 1) indicated that among large fish it differed from the subordinate fish, whereas among small fish it differed from the subordinate fish (Tukey–Kramer HSD, $p < 0.05$).

3.2. Crayfish competitive ability

A significant size × heterospecific presence interaction ($F_{1,15} = 5.67$, $p = 0.031$; Table 1) revealed that crayfish spent reduced time in the bottom patch in the presence of large fish, but not in the presence of small fish (Fig. 3A). In addition, a significant patch × heterospecific presence interaction ($F_{1,15} = 4.47$, $p = 0.05$; Table 1) revealed that crayfish

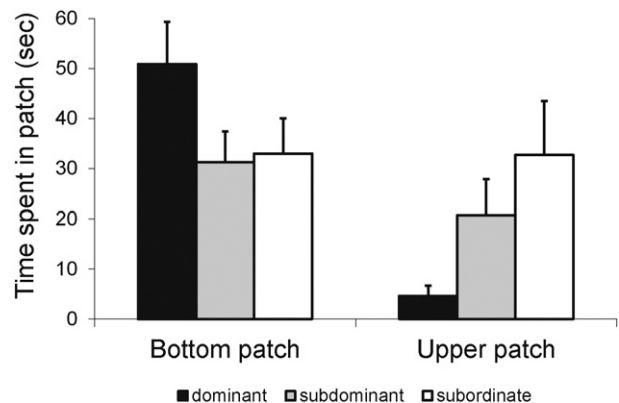


Fig. 2. Time spent by the dominant, subdominant and subordinate fish in the bottom and upper patches during 5 min following food supply.

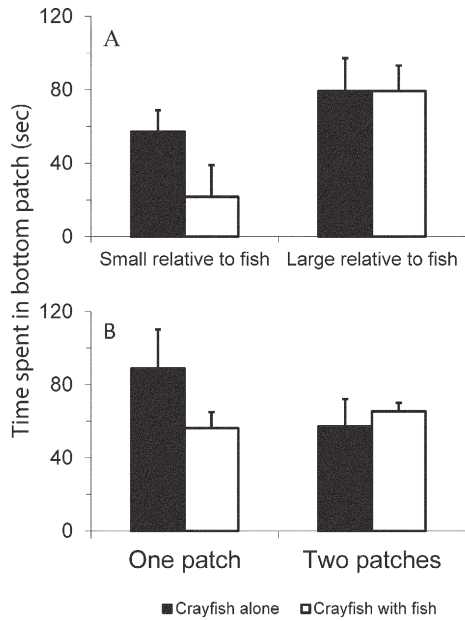


Fig. 3. Time spent by crayfish in the bottom patch in the absence (crayfish alone) and presence of fish (crayfish with fish) during 5 min following food supply. (A) Small versus large relative to fish; (B) one food patch versus two food patches.

reduced the time spent in the bottom patch in the presence of fish only when the feed was supplied exclusively in that patch (Fig. 3B). The results for mean time per visit were similar to those for total time spent in the bottom patch (Table 1).

The dominant crayfish spent longer time in the bottom patch than the subordinates, however only in the presence of small fish (size × rank interaction, $F_{1,31} = 14.87, p < 0.001$) (Fig. 4). Similar highly significant effects of rank were obtained for the other response variables (Table 1).

3.3. Interspecific aggression

Fish practically performed no aggressive actions towards crayfish (only 6 recorded events of overt attack) whereas they frequently exhibited aggression towards conspecifics (3090 aggressive actions during all recording sessions, mainly overt attacks). Crayfish performed 212 aggressive actions interspecifically (mainly cheliped extending). Intra-specific aggression among crayfish was almost as frequent, totaling 186 actions. Interspecific aggression was more commonly addressed towards small fish, mainly by the dominant (size × rank interaction $F_{1,49} = 6.3, p = 0.016$; Fig. 5A). The vast majority of aggressive actions

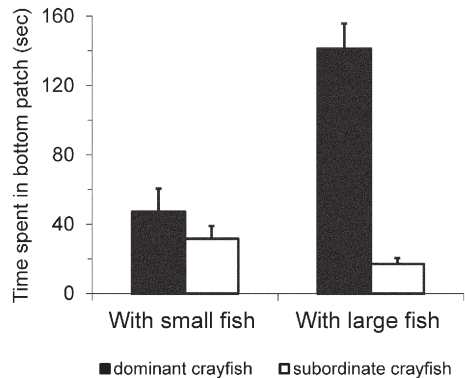


Fig. 4. Time spent by the dominant and subordinate crayfish in the bottom food patch during 5 min following food supply, in the presence of small and large fish.

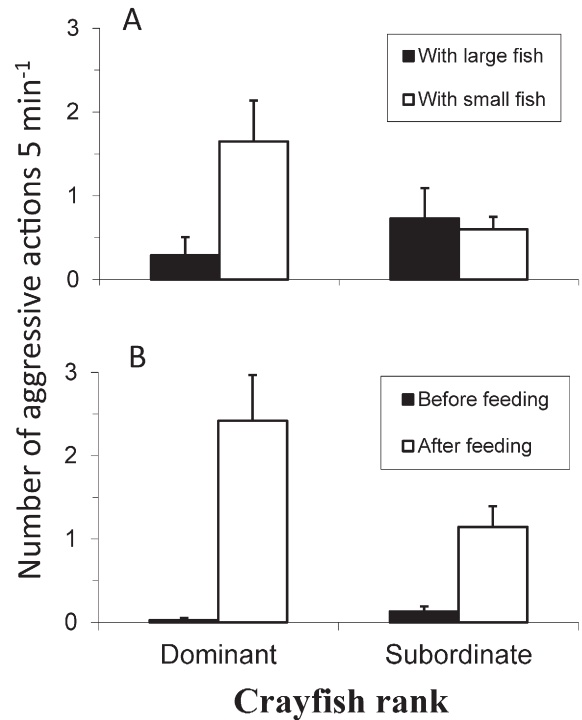


Fig. 5. The number of aggressive actions addressed by dominant and subordinate crayfish during 5 min. (A) Towards large and small fish; (B) before and after food supply.

were performed after feeding (feeding × rank interaction, $F_{1,49} = 5.0, p = 0.03$; Fig. 5B).

4. Discussion

This study sheds light on the behavioral mechanism underlying the competitive relationships between red tilapia and red-claw crayfish. The results suggested that the fish and crayfish foraging decisions are based on various relevant factors. Among these factors, interspecific competition seemed to play a central role, since most of the tested effects have been revealed only in the presence of heterospecific competitors.

Interspecific competition was clearly size-dependent. While large and small fish exhibited similar foraging behavior in the absence of crayfish, only small fish decreased the time spent in the bottom patch following the introduction of crayfish, over which interspecific competition occurred. Likewise, crayfish decreased the time spent in the bottom patch only in the presence of large fish, but not in the presence of small fish. Our results are consistent with previous studies, demonstrating that the intensity as well as the outcome of interactions between heterospecific individuals may change with relative size (e.g., in fish–fish interaction, Persson, 1988; Mills et al., 2004; Young, 2004; Schröder et al., 2009, in fish–crayfish interaction, Bondar et al., 2006; Hirsch and Fischer, 2008).

As in the case of relative size, the effect of the number of food patches on the time spent by fish in the bottom patch was revealed only in the presence of crayfish. Under increased competitive pressure and risk in the bottom patch following the introduction of crayfish, the fish decreased their foraging duration in the bottom patch more readily when an alternative food patch was available. However, since intraspecific competition occurred as well, we could expect a similar result also in the absence of crayfish. Furthermore, although overall the fish spent significantly longer time in the upper patch under two-patch conditions, no significant interaction between the number of patches and crayfish presence was found for the upper patch. This indicated that the significant reduction in foraging time in the bottom patch in the

presence of crayfish was not accompanied by an increase in the time spent by fish in the upper patch, suggesting that the fish preferred the bottom patch over the upper one. This preference is further supported by the fact that the dominant fish spent longer time in the bottom patch compared to the other fish, assuming that competitive rank should be correlated with percentage of time spent in the better (preferred) patch (Sutherland and Parker, 1992; Tregenza and Thompson, 1998). A possible explanation may stem from the finding that the reduction in the time spent in the bottom patch was due to shorter time per visit rather than to less visits. That is, instead of allocating more feeding time in the less preferred patch in the presence of crayfish, fish continued to feed in the bottom patch but changed their foraging tactic and snatched pellets from the bottom patch, taking advantage of their quickness relative to the crayfish. The fish persistence in the bottom patch in the lack of an alternative patch induced reduction in feeding time of crayfish in that patch, which was not evident when the food was supplied in two feed patches (Fig. 3).

Strikingly, the fish exhibited aggression only towards conspecifics. Large fish imposed strong restriction on crayfish foraging in the bottom patch without overt aggression, indicating interference through intimidation. Small fish, which were affected by interference of crayfish in the bottom patch, adopted an alternative non-aggressive competitive strategy which seemed to involve rapid snatching of food. It thus appears that the fish aggressive actions served mainly for maintaining a status of dominance and for interference competition with conspecifics. Crayfish aggression towards fish was mainly evident after the administration of feed pellets and was as likely to be addressed towards conspecifics, reflecting its general use for interference competition for food.

Difference in aggression at the individual level was observed among differently ranked fish and crayfish, with dominants exhibiting the highest, and subordinates the lowest, rate of aggressive actions. In fish, this difference between individuals, as well as the longer time spent by dominant fish compared to the two other fish in the bottom food patch, were not influenced by the presence of crayfish, relative size or the number of patches (no significant interaction effect of rank with these factors). Apparently, interspecific competition in the bottom patch did not affect individual fish differentially, by changing their relative competitive ability and aggression, thus the interspecific effect on fish could be revealed at the group level. The lack of crayfish influence on fish aggression does not conform the prediction of individual-based models that aggressiveness should increase with competitors density (Stillman et al., 1997, 2002; Sirot, 2000). It also does not correspond with studies on competition between fish species that did show interspecific effects on dominance relations within groups, including differential effects on behavioral strategies (Blanchet et al., 2007; Harwood et al., 2002) as well as on brain gene transcription patterns of dominant and subordinate individuals (Roberge et al., 2008). In crayfish on the other hand, the reduction in foraging duration at the bottom patch in the presence of large fish, which was evident at the group level (Fig. 3A), was in fact due to an effect on the dominant individual (Fig. 4). Similarly, the presence of large fish altered the level of aggression of the dominant crayfish but not of the subordinates (Fig. 5A). It thus appears that the superiority of the dominant crayfish, but not of the dominant fish, over conspecifics in the context of food competition is diminished in the presence of superior heterospecifics.

The aforementioned interspecific effects of relative size on the foraging behavior may eventually be expressed in growth performance if the behavioral alteration imposed on the inferior species are associated with reduced food intake. Although small fish overall spent less time in the bottom food patch in the presence of crayfish, our observations revealed that they responded rapidly to the arrival of feed pellets and consumed part of the ration before the arrival of crayfish and afterwards continued snatching food while decreasing the time per visit (see supplementary video clip). It is not known whether this tactical change resulted in higher food intake, since it was impossible to quantify food

intake when all the pellets were provided together rather than one by one. However, Barki et al. (2001) revealed no adverse effect of red-claw crayfish on red tilapia growth, for both large and small fish. Moreover, the fish grew better in the presence of crayfish, possibly because they benefited from the feed ration intended for the crayfish. In contrast, crayfish growth was adversely affected by tilapia, and the magnitude of this effect was dependent on their size relative to the fish. Using a bio-economic model, Ponce-Marbán et al. (2006) analyzed three time horizons and three production densities in co-culture of Nile tilapia and redclaw crayfish. The simulation results demonstrated improved economic profitability, particularly over a 5-year time horizon and with an optimum stocking combination of 33 tilapia m^{-3} and 10 crayfish m^{-2} . However, stocking size combinations were not modeled. The effect of relative size should be taken into account in determining the stocking size of the fish and crayfish and the duration of communal culture according to the size gap that may develop with time between the fish and crayfish. Despite the potentially negative effect of fish on crayfish growth, a positive outcome may arise from the fact that the competitive pressure of the fish particularly influenced the dominant (i.e. large) individual. Consequently, size variation among crayfish may decline under co-culture condition, yielding more uniformly-sized crayfish.

A possible means for minimizing interspecific food competition could be partitioning the feed in time and space between the cultured species. The results indicated that the availability of an additional food patch for the fish relaxed competition for food between fish and crayfish in the bottom patch, as revealed by the reduction in time spent by fish in the bottom patch (Fig. 1B) and by the lack of change in the time spent by crayfish in that patch in the presence of heterospecifics, unlike in the one-patch condition (Fig. 3B). Supplying feed pellets in two patches vs. one patch in the current study is analogous to feeding with sinking and floating pellets (both accessible for the fish but only the sinking pellets for the crayfish) vs. feeding only with sinking pellets, which was tested by Barki et al. (2001) in small tanks. However, there was no effect of spatially separating the feed on growth of small fish or small crayfish, unlike the effect on their behavior found in the current study. In contrast, temporally separating the feed by feeding the nocturnal crayfish at night and the diurnal fish during the day did improve the growth of small crayfish (Barki et al., 2001). Spatially separating the feed might be effective in larger or deeper tanks where the distance between the two feed patches and, consequently, separation between the species would be greater, but this remains to be established.

In conclusion, this study provides insights regarding the behavioral aspect of interspecific competition for food between co-cultured tilapia and red-claw crayfish and important factors that might influence it. Such knowledge is fundamental for finding useful means for improving feeding management and optimizing growth performance, to be tested under controlled conditions and verified under real pond situation.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.aquaculture.2015.07.031>.

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References

- Asaduzzaman, M., Wahab, M.A., Verdegem, M.C.J., Mondal, M.N., Azim, M.E., 2009. Effects of stocking density of freshwater prawn *Macrobrachium rosenbergii* and addition of different levels of tilapia *Oreochromis niloticus* on production in C/N controlled periphyton based system. *Aquaculture* 286, 72–79.
- Barki, A., Volpato, G.L., 1998. Early social environment and the fighting behaviour of young *Oreochromis niloticus* (Pisces, Cichlidae). *Behaviour* 135, 913–929.

- Barki, A., Gur, N., Karplus, I., 2001. Management of interspecific food competition in fish–crayfish communal culture: the effects of the spatial and temporal separation of feed. *Aquaculture* 201, 343–354.
- Blanchet, S., Loot, G., Bernatchez, L., Dodson, J.J., 2007. The disruption of dominance hierarchies by a non-native species: an individual-based analysis. *Oecologia* 152, 569–581.
- Bondar, C.A., Zeron, K., Richardson, J.S., 2006. Risk-sensitive foraging by juvenile signal crayfish (*Pacifastacus leniusculus*). *Can. J. Zool.* 84, 1693–1697.
- Brummet, R.E., Alon, N.C., 1994. Polyculture of Nile tilapia (*Oreochromis niloticus*) and Australian red claw (*Cherax quadricarinatus*) in earthen ponds. *Aquaculture* 122, 47–54.
- Carpenter, J., 2005. Competition for food between an introduced crayfish and two fishes endemic to the Colorado River basin. *Environ. Biol. Fish* 72, 335–342.
- Cohen, D., Ra'anan, Z., Barnes, A., 1983. Production of freshwater prawn *Macrobrachium rosenbergii* in Israel I. Integration into fish polyculture system. *Aquaculture* 31, 67–76.
- Dorn, N.J., Mittelbach, G.G., 1999. More than predator and prey: a review of interactions between fish and crayfish. *Vie Milieu* 49, 229–237.
- FAO, 2014. The State of World Fisheries and Aquaculture. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
- García-Pérez, A., Alston, D.E., Cortés-Maldonado, R., 2000. Growth, survival, yield, and size distributions of freshwater prawn *Macrobrachium rosenbergii* and tilapia *Oreochromis niloticus* in polyculture and monoculture systems in Puerto Rico. *J. World Aquacult. Soc.* 31, 446–451.
- Griffiths, S.W., Collen, P., Armstrong, J.D., 2004. Competition for shelter among overwintering signal crayfish and juvenile Atlantic salmon. *J. Fish Biol.* 65, 436–447.
- Harwood, A.J., Armstrong, J.D., Griffiths, S.W., Metcalfe, N.B., 2002. Sympatric association influences within-species dominance relations among juvenile Atlantic salmon and brown trout. *Anim. Behav.* 64, 85–95.
- Hirsch, P.E., Fischer, P., 2008. Interactions between native juvenile burbot (*Lota lota*) and the invasive spinycheek crayfish (*Orconectes limosus*) in a large European lake. *Can. J. Fish. Aquat. Sci.* 65, 2636–2643.
- Karplus, I., Harpaz, S., Hulata, G., Segev, R., Barki, A., 2001. Culture of the Australian red-claw crayfish (*Cherax quadricarinatus*): IV. Crayfish incorporation into intensive tilapia production units. *Isr. J. Aquacult. Bamidgah* 53, 23–33.
- Karplus, I., Sagi, A., Khalaila, I., Barki, A., 2003. The influence of androgenic gland implantation on the agonistic behavior of female crayfish (*Cherax quadricarinatus*) in interactions with males. *Behaviour* 140, 649–663.
- Keller, T.A., Moore, P.A., 2000. Context-specific behavior: crayfish size influences crayfish–fish interactions. *J. N. Am. Benthol. Soc.* 19, 344–351.
- Mills, M.D., Rader, R.B., Belk, M.C., 2004. Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. *Oecologia* 141, 713–721.
- Milstein, A., 2005. Polyculture in aquaculture. *Anim. Breed. Abstr.* 73, 15N–41N.
- Muangkeow, B., Ikejima, K., Powtongsook, S., Gallardo, W., 2011. Growth and nutrient conversion of white shrimp *Litopenaeus vannamei* (Boone) and Nile tilapia *Oreochromis niloticus* L. in an integrated closed recirculating system. *Aquac. Res.* 42, 1246–1260.
- Neveu, A., 2001. Confrontation expérimentale entre des poissons omnivores autochtones (11 espèces) et des écrevisses étrangères introduites (2 espèces). *Bull. Fr. Peche Piscic.* 361, 705–735.
- Persson, L., 1988. Asymmetries in competitive and predatory interactions in fish populations. In: Ebenman, B., Persson, L. (Eds.), *Size-structured populations*. Springer-Verlag, Berlin Heidelberg, pp. 203–218.
- Ponce-Marbán, D., Hernández, J.M., Gasca-Leyva, E., 2006. Simulating the economic viability of Nile tilapia and Australian redclaw crayfish polyculture in Yucatan, Mexico. *Aquaculture* 261, 151–159.
- Reynolds, J.D., 2011. A review of ecological interactions between crayfish and fish, indigenous and introduced. *Knowl. Manag. Aquat. Ecosyst.* 401, 10. <http://dx.doi.org/10.1051/kmae/2011024>.
- Roberge, C., Blanchet, S., Dodson, J.J., Guderley, H., Bernatchez, L., 2008. Disturbance of social hierarchy by an invasive species: a gene transcription study. *PLoS ONE* 3, e2408. <http://dx.doi.org/10.1371/journal.pone.0002408>.
- Rouse, D.B., Kahn, B.M., 1998. Production of Australian red claw *Cherax quadricarinatus* in polyculture with Nile tilapia *Oreochromis niloticus*. *J. World Aquacult. Soc.* 29, 340–344.
- 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. *J. Anim. Ecol.* 78, 1152–1162.
- Siro, E., 2000. An evolutionary stable strategy for aggressiveness in feeding groups. *Behav. Ecol.* 11, 351–356.
- Stein, R.A., 1977. Selective predation, optimal foraging, and the predator–prey interaction between fish and crayfish. *Ecology* 58, 1237–1253.
- Stein, R.A., Magnuson, J.J., 1976. Behavioral response of crayfish to a fish predator. *Ecology* 57, 751–761.
- Stillman, R.A., Goss-Custard, J.D., Caldow, R.W.G., 1997. Modelling interference from basic foraging behaviour. *J. Anim. Ecol.* 66, 692–703.
- Stillman, R.A., Bautista, L.M., Alonso, J.C., Alonso, J.A., 2002. Modelling state-dependent interference in common cranes. *J. Anim. Ecol.* 71, 874–882.
- Sutherland, W.J., Parker, G.A., 1992. The relationship between input and interference models of deal free distributions with unequal competitors. *Anim. Behav.* 44, 345–355.
- Tian, X., Li, D., Dong, S., Yan, X., Qi, Z., Liu, G., Lu, J., 2001. An experimental study on closed-polyculture of penaeid shrimp with tilapia and constricted tagelus. *Aquaculture* 202, 57–71.
- Tregenza, T., Thompson, D.J., 1998. Unequal competitor ideal free distribution in fish? *Evol. Ecol.* 12, 655–666.
- Wang, M., Lu, M., 2015. Tilapia polyculture: a global review. *Aquac. Res.* <http://dx.doi.org/10.1111/are.12708>.
- Wang, J.-Q., Li, D., Dong, S., Wang, K., Tian, X., 1998. Experimental studies on polyculture in closed shrimp ponds I. Intensive polyculture of Chinese shrimp *Penaeus chinensis*/with tilapia hybrids. *Aquaculture* 163, 11–27.
- Wohlfarth, G.W., Hulata, G., Karplus, I., Havery, A., 1985. Polyculture of the freshwater prawn *Macrobrachium rosenbergii* in intensively manured ponds, and the effect of stocking rate of prawns and fish on their production characteristics. *Aquaculture* 46, 143–156.
- Young, K.A., 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology* 85, 134–149.
- Yuan, D., Yi, Y., Yakupitiyage, A., Fitzimmons, K., Diana, J.S., 2010. Effects of addition of red tilapia (*Oreochromis* spp.) at different densities and sizes on production, water quality and nutrient recovery of intensive culture of white shrimp (*Litopenaeus vannamei*) in cement tanks. *Aquaculture* 298, 226–238.