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Starvation and a conspecific competitor influence multiple predator effects in a swimming crab (*Portunus trituberculatus*) - Manila clam (*Ruditapes philippinarum*) foraging system

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ABSTRACT

To investigate the effect of starvation (0–12 days) on multiple predator effects and the mechanisms driving these effects, we established swimming crab (*Portunus trituberculatus*) - Manila clam (*Ruditapes philippinarum*) foraging systems in the laboratory. Specifically, we quantified predation rate, foraging behaviors, and encounter behaviors between predators under different foraging system treatments. The main results were as follows: (1) Changes in multiple predator effects were related to fighting between swimming crab individuals resulting from different starvation regimes. Non-independent multiple predator effects were observed that reduced the foraging success of swimming crabs in short-term starvation treatments. However, independent multiple predator effects were observed in normally fed and long-term starvation treatments, and the foraging success of swimming crabs did not change. (2) Under short-term starvation, a high probability of fighting between swimming crabs significantly increased the proportion of time spent handling clams, while the probability of consumption upon capture of clams significantly decreased. However, the foraging behaviors of swimming crabs were not significantly altered by a low probability of fighting upon encounter under no-starvation and long-term starvation. (3) The pattern of foraging time budget of swimming crabs did not change significantly in the presence of conspecific competitors under any starvation level. The present study provides a foundation for future research on the interaction of conspecific predators, which can be used to improve aquaculture systems.

1. Introduction

It is common for multiple predators to forage for the same prey both in natural and man-made (e.g., aquaculture) systems. Predators may act independently of each other, or they may interact leading to changes in foraging success (Sih et al., 1998; Soluk, 1993). Multiple predator effects are often studied by determining whether the observed predation rate can be predicted by a multiplicative risk model (Sih et al., 1998). Independent multiple predator effects on prey occur when the predation rate does not differ from what is predicted, which occurs when interactions among predators (i.e. competition, interference, and intraguild predation) are negligible or when predator activity does not change prey behaviors (Sih et al., 1998; Vance-Chalcraft et al., 2004; Wong et al., 2010). Non-independent multiple predator effects on prey occur when the proportion of prey consumed differs from predicted values either reducing or enhancing predation risk for prey and/or foraging success for the predator (Wong et al., 2012). If the observed predation rate is less than predicted, this indicates that predator foraging behaviors or prey behaviors have changed thereby having reduced foraging success and/or predation risk, respectively (Soluk, 1993). On the contrary, if the observed predation rate is greater than predicted, this indicates that predator foraging behaviors or prey behaviors have changed and have thereby enhanced foraging and/or increased predation risk, respectively (Griffen, 2006; Mansour and Lipcius, 1991; Soluk, 1993).

Crabs often suffer starvation due to the stress related to molting in addition to changes in the environmental, temporal, and spatial distribution of food (Lixin et al., 2004). Even in aquaculture systems, crabs suffer starvation due to unevenly distributed food. Research has shown that hunger induces changes in the foraging time budgets of swimming crabs (*Portunus trituberculatus*) and Japanese stone crabs (*Charybdis japonica*) (Sun et al., 2015). Flexibility in prey size selection may also be induced by hunger (Micheli, 1995; Smallegange et al., 2008), and with increased hunger, crabs are expected to be less selective (Hughes, 1988). Aggression has also been shown to be affected by starvation (Hazlett, 1966). Behavioral changes in crabs due to starvation, such as

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increased aggression and lower selectivity in the diet, would affect the predator interaction of predation (i.e., competition, interference, and intraguild predation) resulting in variation in multiple predator effects. Studies have shown that predator identity (Vance-Chalcraft et al., 2004; Yeager et al., 2016), predator density (Griffen and Williamson, 2008; Losey and Denno, 1998), predator feeding rhythm (Wong et al., 2012), prey size (Wong et al., 2010), prey density (Soluk and Richardson, 1997; Vance-Chalcraft and Soluk, 2005), substrate type (Swisher et al., 1998; Wong et al., 2010), and spatial scale (Wong et al., 2012) can alter multiple predator effects. However, the influences of starvation on these effects in crabs remains unknown.

The swimming crab (*Portunus trituberculatus*) is widely distributed in India and the West Pacific Ocean (Carpenter and Niem, 1998). This species is one of the most economically important cultured crustaceans in the world (Hamasaki et al., 2006) and is one of the major pond culture and fishing species in China's coastal areas (Chong et al., 2010). Swimming crabs are known to display aggressive behavior, which may be one of the factors that can cause a reduction in its production (Guocheng et al., 2007). In aquaculture systems, it is common that starvation occurs due to the non-uniform distribution of feed and poor feeding management. When prey resources are patchy, predators often aggregate in the patches in proportion to prey density (Holling, 1959; Sutherland, 1983). Starvation could intensify competition for resources resulting in injury, intraguild predation (Mansour and Lipcius, 1991), and a decrease in foraging success (Hines and Ruiz, 1995), and this would decrease aquaculture production. Therefore, it is vital to examine the variation in multiple predator effects under different starvation regimes. We hypothesized that foraging would change less under no-starvation conditions due to the low level of competition for food and that increased competition for food would depress foraging behaviors with prolonged starvation resulting in non-independent multiple predator effects. We recorded and quantified foraging behaviors and predation rates of male swimming crabs foraging on Manila clams under different starvation regimes to test our hypotheses.

2. Materials and methods

2.1. Animal collection and maintenance

This experiment was conducted in August 2015 at the Aoshanwei Laboratory of the Ocean University of China, Shandong Province, China. Swimming crab individuals were collected from the aquaculture facility in Jiaonan. Predators were held in individual aquaria (40.95 L, 45 × 30 × 30 cm) with filtered seawater (10 mm mesh) at 21 ± 1 °C and salinity 30‰ and allowed to acclimate for 1 week prior to conducting the experiments. The photoperiod was 12 h light:12 h dark. Swimming crabs were fed ad libitum at 08:00 every morning with Manila clams purchased from the local seafood market, and the seawater was exchanged once daily. The aquaria were continuously aerated.

2.2. Experimental design and procedures

The video capture system used to record crab foraging behavior consisted of four infrared cameras (HIKVISION, DS-2CD864; infrared wavelength = 850 nm), a video recorder (HIKVISION, DS-7604N), a monitor (PHILLIP, 233i5), and four experimental aquaria (diameter = 78 cm). The infrared cameras were fixed 0.7 m above the experimental aquaria and recorded in the dark. White fiberglass experimental aquaria were used that were filled with 40 cm of seawater and lacked substrate. We recorded foraging behaviors of swimming crabs in the aquaria with a video capture system. The experiments were conducted in a quiet, undisturbed room beginning at 20:00 and ending at 20:00 the next day. The experimental aquaria were not aerated, but were otherwise maintained under the same conditions as the acclimation tanks were.

Only healthy male swimming crabs (carapace width = 99.45 ± 4.37 mm, mean ± SD, n = 60) in the intermolt stage with all their appendages were chosen for use in the experiments. All permutations of five starvation treatments (0 days, 3 days, 6 days, 9 days, and 12 days without food represented by S_0, S_3, S_6, S_9, and S_{12}, respectively) and two predator treatments (isolated or conspecific pairs of swimming crabs) were applied randomly to the experimental aquaria, and each was replicated four times. Each predator and prey were used only once; thus, in total, we used 60 swimming crabs in our experiment.

A randomly selected focal crab was indicated by a white dot (Liquitex HB, Liquitex Artist Materials) painted on the top of the carapace and was the crab observed (focal crab) in the double predator treatments. In these treatments, the focal crab and one other crab of the same hunger state were placed in opposite sides of a partitioned aquarium. The experiment began when the barrier was lifted after 15 min, and 20 Manila clams (shell length = 32.43 ± 2.16 mm, mean ± SD, n = 800) were added evenly throughout the aquaria. Single predator treatments had one starved swimming crab and no partition in the aquaria but were otherwise the same as the double predator treatments.

The number of clams consumed by 08:00 and 20:00 the next day was recorded for every replicate, and new Manila clams of the same size were added to maintain the density of prey at 20. Furthermore, four additional aquaria without predators were used as controls to monitor natural clam mortality over the course of the experiment. Only results for the full 24-hour experiment were reported and used in analysis.

2.3. Data analysis

2.3.1. Predation rate and multiple predator effects

For both predator treatments, the number of Manila clams consumed was counted in every treatment. Observed predation rate per replicate was calculated as the mean number of clams consumed per day per predator. Because natural mortality observed in the no predator controls was zero, it was not considered when calculating predation rates.

To analyze multiple predator effects, we compared the observed proportion of clams consumed to that predicted by the multiplicative risk model (Wilbur and Fauth, 1990):

$C_{ab} = N(P_a + P_b - P_aP_b)$,where C_{ab} is the predicted proportion of prey consumed by predator a and predator b foraging together; N is the number of prey available; P_a is the observed proportion of prey consumed by predator a in isolation; and P_b is the observed proportion of prey consumed by predator b in isolation. Proportions of prey consumed were calculated as the number eaten divided by the number offered. The P_aP_b term accounts for prey consumed by one predator that could not be consumed by the other predator. To generate predicted values for multiple predator treatments, replicate data from single predator treatments were paired in all possible combinations for each different multiple predator treatment. Each data pair was used in the multiplicative risk model to generate a series of predicted values (Wong et al., 2010, 2012).

2.3.2. Foraging behaviors

A random 60-min period was chosen for analysis of crab foraging behavior during the day (08:00–20:00) and at night (20:00–08:00). Thus, total observation time was 120 min for each treatment combination (Sun et al., 2016, 2015). Only the behavior of the focal crab was analyzed for these periods in the double predator treatments.

We quantified the foraging time budgets of swimming crabs, which included time spent searching for and handling prey. The proportion of foraging time spent searching for prey was calculated as searching time/total observation time. Similarly, the proportion of foraging time spent handling prey was calculated as handling time/total observation time (Nadeau et al., 2009; Wong and Barbeau, 2003).

Predation rate can be analyzed in terms of three components: