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Miller, SH
Morgan, SG

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SHORT COMMUNICATION

Temporal variation in cannibalistic infanticide by the shore crab *Hemigrapsus oregonensis*: implications for reproductive success

Seth H. Miller[1] & Steven G. Morgan[1,2]

1 Bodega Marine Laboratory, University of California Davis, Bodega Bay, CA, USA
2 Department of Environmental Science and Policy, University of California, Davis, CA, USA

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Correspondence
Seth H. Miller, Bodega Marine Laboratory University of California Davis, 2099 Westside Road, Bodega Bay, CA 94923, USA.
E-mail: shmiller@ucdavis.edu

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Abstract

Larvae of benthic marine organisms are released amid high densities of suspension feeding and predatory adults and are highly subject to being consumed, even by conspecifics or their own parent. During laboratory feeding trials conducted in June 2006, female shore crabs (*Hemigrapsus oregonensis*) from Stege Marsh in San Francisco Bay (37°54.530′ N, 122°19.734′ W) that released their larvae during the previous 24 h ate fewer conspecific larvae than females that had not recently released larvae, though the behavior was not repeated during similar trials in 2007. Additionally, the number of larvae eaten increased with increasing starvation time, and hungrier females showed a trend toward eating more larvae from a different species (*Carcinus maenas*) than larvae of conspecifics. Thus, suppression of suspension feeding may reduce conspecific predation of newly released larvae, but this response partially depends on hunger level. This is the first time crabs have been shown to suppress feeding to reduce cannibalism of larvae, and this behavior could affect reproductive success and population dynamics.

Introduction

Tiny larvae of benthic marine invertebrates are released amid a ‘wall of mouths’ (Emery 1973), navigating a gauntlet of planktonic predators before settling in a suitable adult habitat. In response, many larvae and adults have evolved antipredatory defenses. Some larvae possess chemical defenses that decrease their palatability to predators (Lindquist & Hay 1996 for review; Lopanik *et al.* 2006). Other larvae, particularly those that remain nearshore or in estuaries throughout their development, have evolved morphological defenses, such as spines or large overall size (Wilson 1929; Morgan 1989, 1990), or exhibit defensive behaviors, such as sinking or fleeing when confronted by a predator (Morgan 1987, 1995a,b). Many larvae avoid high densities of planktivorous fishes nearshore by occurring in seaward flowing currents that expedite transport to safer waters offshore (*e.g.* Hovel & Morgan 1997; Gibson 2003; Morgan & Anastasia 2008; Miller & Morgan 2013). In addition to larval defenses, adults of many species release larvae or gametes synchronously when predation is minimized (Johannes 1978; Morgan 1995a,b; Hovel & Morgan 1997; Rasmuson & Morgan 2013) or predators are swamped (Harrison *et al.* 1984). Adults also may migrate to safer locations to release larvae or gametes (Johannes 1978; Warner 1988; Carr *et al.* 2004).

Although it has received limited attention, suspension feeding adults cannibalize their own offspring or consume their neighbors’ offspring during periods of peak release of eggs or larvae (Crisp & Patel 1960; Egloff 1966; Young 1988; Pechenik *et al.* 2004; Alfaro 2006). Facultative suspension feeders, such as many crab species, also exhibit cannibalism. Later stage crab larvae consume earlier stage larvae, postlarval crabs consume larvae in resource-limited environments (Anger 1995; McConaugha 2002), and juvenile crabs frequently cannibalize new settlers or younger juveniles (Moksnes *et al.* 1997; Heck *et al.* 2001; Moksnes 2004; Gimenez 2010). However, the extent of cannibalism by adult crabs on newly hatched larvae is largely unknown (Srikrishnadhas & Ramamoorthi 1976).

Unlike obligate suspension feeders, facultative suspension feeders have the option of switching to a different feeding mode during peak release of eggs or larvae. For example, many adult hermit and brachyuran crabs are capable of switching between suspension feeding and their primary feeding modes when food is scarce (Schembri 1982; Depledge 1989; Whitman *et al.* 2001), and copepods decrease cannibalism on conspecific larvae when alternative food sources are abundant (Daan *et al.* 1988). Additionally, some species decrease or stop suspension feeding near the time of larval release, perhaps reducing cannibalism of larvae (Thorson 1966; Brun 1972). However, hungry crabs may suspension feed during peak larval release, given that many species forage less selectively when food is scarce (Kislalioglu & Gibson 1976; Pastorok 1980; Williamson 1980).

Reproductive success and metapopulation dynamics should be influenced by the ability of suspension feeders to detect and avoid consuming their own offspring or their neighbor's offspring. We determined whether female crabs ate newly hatched larvae of (i) their own, (ii) a conspecific female, and (iii) a different species, as well as whether (iv) hunger level or (v) how recently larvae were released affected these results.

Material and Methods

We collected ovigerous and nonovigerous females of the yellow shore crab *Hemigrapsus oregonensis* from a single population in the lower intertidal zone of Stege Marsh in San Francisco Bay, California (37°54.530′ N, 122°19.734′ W) in 2006 and 2007 at the height of their reproductive period in June. We also collected ovigerous females of the European green crab *Carcinus maenas* from Bodega Harbor, California (38°19.019′ N, 123°02.386′ W) in 2007. This species was introduced to San Francisco Bay in approximately 1989 and rapidly expanded its range to cover much of the West Coast (Grosholz *et al.* 2000). Crabs were transported to the laboratory and held individually in mesh containers (17 × 10 cm) in simulated diel (14 h light :10 h dark) and tidal cycles (timed patterns of high and low tide to ambient tidal cycles). Upon hatching, all larvae were separated from the female crab and held in labeled containers identifying their parent.

Twelve newly hatched *H. oregonensis* larvae were added to replicate bowls (15 cm diameter × 5 cm tall) with clean seawater containing (i) the female that had released those larvae (n = 6 in 2006, n = 4 in 2007) or (ii) an unrelated conspecific female that had released larvae within 24 h (n = 12 in 2006, n = 4 in 2007), to test for the effect of relatedness on cannibalism. In a second experiment, larvae were placed with an unrelated conspecific female that released larvae within 24 h (n = 18 in 2006, n = 8 in 2007) or (ii) a conspecific female that had not recently released larvae (n = 11 in 2006, n = 13 in 2007), to test for the effect of recentness of larval release on cannibalism.

Feeding trials were conducted in a temperature-controlled room at 11 °C with a natural diel cycle to approximate conditions experienced by natural populations releasing larvae on nocturnal ebb tides. Females were removed the next morning after 16 h, and the number of larvae remaining in each container was recorded. The low numbers of larvae in our trials allowed us to record conservative estimates of cannibalism because crabs would be exposed to hundreds of thousands of larvae during a natural spawning event. The duration of the trials was chosen to mimic the duration of a natural spawning event, during which numerous females in the population release larvae over the course of the night. All experimental methods were identical in both years.

We added a new experiment in 2007 to determine whether females eat more larvae of a different species than of a congener and whether the results depended on hunger level. Seventeen *H. oregonensis* females were held individually in bowls and were each fed 12 newly hatched *C. maenas* larvae (larvae of these two species are approximately the same size). Females had not released larvae within 24 h to eliminate any potential effect of recent larval release on suspension feeding. We conducted two trials to determine the effect of hunger level on cannibalism. In the first trial, females were starved for 1 day. Immediately after the first trial concluded, these same females were starved for 22 more days and then the experiment was repeated. Using the same crabs in both trials allowed us to eliminate any potential effect of individual variation on the results. All statistical comparisons were made using arcsine-transformed data to meet the assumptions of analysis of variance (ANOVA) with the JMP 9 software package (SAS Institute, Cary, NC, USA).

Results

Hemigrapsus oregonensis females that released larvae within the previous 24 h cannibalized 32% of the larvae presented over both years. They ate similar percentages of their own larvae and larvae of a conspecific female in both years (ANOVA, $F_{1,24} = 0.0022$, P = 0.9633, Fig. 1), and there was no interaction between year and relationship to larvae, indicating that mothers did not distinguish

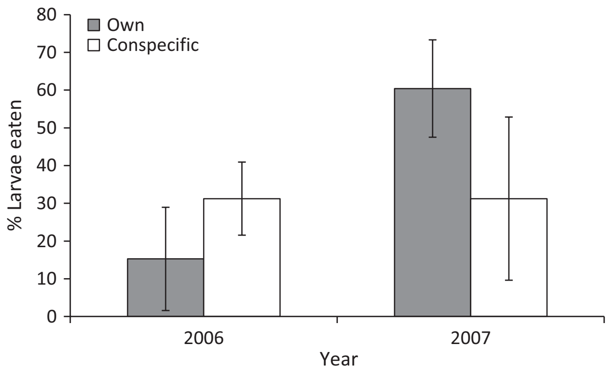

Fig. 1. Percentage of 12 larvae eaten (±1 SE) in 16 h by females that released their larvae within the previous 24 h when presented with their own larvae (dark bars; n = 6 in 2006, n = 4 in 2007) compared with when they were presented with larvae that were released by a conspecific female (light bars; n = 12 in 2006, n = 4 in 2007). Females ate similar percentages of their own larvae (31% overall) and larvae of conspecific females (33% overall) (P = 0.8859).

Table 1. Results of analyses of variance for two multifactor comparisons. (A) The interannual comparison tested whether year (2006 *versus* 2007) or release state (released larvae within 24 h *versus* not recently ovigerous) affected crab feeding behavior. (B) The interspecific comparison tested whether the species of larvae presented to the crab (conspecific *versus Carcinus maenas*) or hunger (starved 1 day *versus* 22 days) affected crab feeding.

Source	df	F-ratio	P-value
(A) Interannual comparison			
Whole Model	3	10.9365	<0.0001
Year	1	2.3664	0.1308
Release State	1	12.7695	0.0008
Year*Release State	1	14.4173	0.0004
(B) Interspecific comparison			
Whole Model	3	4.0370	0.0118
Species of Larvae	1	0.5737	0.4522
Time Starved	1	8.1386	0.0062
Species*Time Starved	1	2.5688	0.1150

their own larvae from those of conspecific females. Therefore, these treatments were combined in subsequent analyses.

Hemigrapsus oregonensis females that released larvae within the previous 24 h cannibalized fewer larvae than females that were not recently ovigerous in 2006 but not in 2007 (Table 1, Fig. 2), and there was a significant interaction between year and release state (P = 0.0004). Thus, only females that recently released larvae appeared to suppress feeding on conspecific larvae, but they did not do so both years.

Hemigrapsus oregonensis females ate more larvae when they were starved for 22 days rather than 1 day, regardless of whether they were fed conspecific or *C. maenas* larvae (Table 1, Fig. 3). However, hungry females tended (P = 0.1150) to eat more *C. maenas* than conspecific larvae.

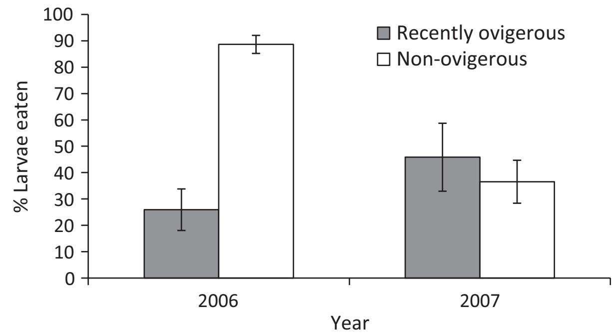

Fig. 2. *Hemigrapsus oregonensis*. Percentage of 12 larvae eaten (±1 SE) in 16 h by females that released larvae within the previous 24 h (dark bars; n = 18 in 2006, n = 8 in 2007) compared with females that were not ovigerous recently (light bars; n = 11 in 2006, n = 13 in 2007) in 2006 and 2007. In 2006 but not 2007, females that recently released larvae ate fewer larvae than did females that were not ovigerous recently (Table 1).

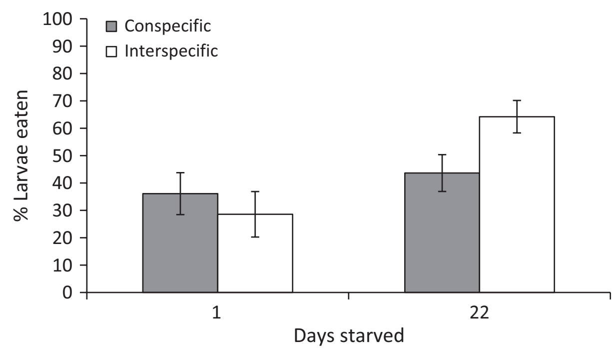

Fig. 3. *Hemigrapsus oregonensis* and *Carcinus maenas*. Percentage of 12 larvae eaten (±1 SE) in 16 h by 17 females presented individually with conspecific larvae (dark bars) or non-native larvae (light bars) that were starved for 1 day or 22 days in 2007. Hungry females (starved for 22 days) ate more larvae, and they tended (P = 0.1150) to eat more non-native larvae (Table 1).

Discussion

Hemigrapsus oregonensis females overall cannibalized 46% of larvae presented during feeding trials, indicating that cannibalism may reduce reproductive success. Cannibalism of newly hatched larvae by conspecific females is not simply an artifact of confining them in a small volume of seawater in the laboratory because substantial numbers of larvae are consumed by conspecific adults in natural populations of other benthic invertebrates (*e.g.* Navarrete &

Wieters 2000), and the larval densities in our experiment were several orders of magnitude lower than they would be in the field.

Cannibalism and predation by benthic species has long been thought to be reduced by widespread swimming of larvae toward the surface upon hatching (Thorson 1964). It now appears that cannibalism also is reduced by the suppression of suspension feeding while females are releasing larvae. To our knowledge, this is the first time that adult invertebrates have been shown to alter their feeding behavior to avoid consuming their offspring.

Larvae, however, were consumed by females that had not released larvae within the last 24 h, indicating that they would be cannibalized by other crabs in the population. Like most shore crabs worldwide, peak larval release by *H. oregonensis* occurs for several consecutive days near spring tides while other females are not ovigerous (Thurman 2004; Morgan 2005; Morgan *et al.* 2011) and so a substantial portion of the population could cannibalize larvae. Males also likely cannibalize larvae, though this remains to be determined.

Unexpectedly, the suppression of suspension feeding on recently released larvae did not occur during the second year of the study. The protocol for the experiment was identical during both years, including feeding females the same diet and holding them in the laboratory the same length of time before larvae were released. Only environmental conditions experienced by crabs before collection may have differed during the 2 years. We propose that crabs were food-limited during the second year, and these hungry females did not suppress feeding on recently released larvae. Although *H. oregonensis* augment their diets by suspension feeding on plankton, they primarily scrape benthic diatoms from mudflats and opportunistically feed on macroalgae, small invertebrates and carrion (Morris *et al.* 1980). Crabs that endure food limitation in the field could consume larvae when their primary food sources are limited, as has been shown in several crustaceans (Wolcott & Wolcott 1984; Daan *et al.* 1988; Sparrevik & Leonardsson 1998; Duarte *et al.* 2010).

The frequency and cause of food limitation in crabs should be more fully investigated to evaluate the impact of cannibalism on newly hatched larvae in reducing reproductive success in natural populations. This is consequential, because food limitation reduces the allocation of resources to reproduction, and if it also increases cannibalization of newly hatched larvae, its effect on the reproductive output of populations would be magnified. Therefore, although the term 'maternal effects' is usually applied to the effect of the variable allocation of parental resources and traits on offspring survival (*e.g.* McEdward 1996; Marshall & Morgan 2011; Pernet *et al.* 2012), we propose that it be expanded to include variation in cannibalistic behavior of the parents as well, since cannibalism also has a strong effect on offspring survival.

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