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SUSPENSION FEEDING IN LARVAL CRABS (*CARCINUS MAENAS*)

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First-stage zoeal larvae of the green (shore) crab, *Carcinus maenas* (Crustacea: Brachyura: Portunidae), ingested three types of particles offered in sea-water suspensions. In experiments using two types of fluorescent particles (1-2 μm and 1-7 μm) and living *Dunaliella tertiolecta* cells (5-7 μm), particles were ingested in at least 40% of the zoeae examined with brightfield, darkfield, and epifluorescence microscopy. These results suggest that green crab larvae may be capable of utilizing planktonic particles in the size range of bacteria, small algal cells, and organically-enriched detrital particles in their natural diet.

INTRODUCTION

Decapod larvae reared in laboratory culture to study larval development have often been fed brine shrimp nauplii, but have also been raised on a variety of motile, planktonic animals, such as rotifers, polychaete larvae, and sea urchin larvae and embryos (Costlow & Bookhout, 1959; Sulkin, 1975; Sulkin & Epifanio, 1975; Bookhout & Costlow, 1977). A few decapod larvae have also been shown to feed on non-motile, non-living, particles in the laboratory. While examining nutritional requirements of crustacean larvae, Jones *et al.* (1975) used nylon-protein microcapsules and Levine *et al.* (1983) and Levine & Sulkin (1984a) used microencapsulated nutrients. Levine & Sulkin (1984b) also used microencapsulated fluorescent particles to demonstrate that their large microcapsules (45-180 μm) were indeed ingested by crab larvae.

The possibility that some decapod larvae may remove small particles of food from their planktonic environment has been suggested occasionally in the literature for some time (Gonor & Gonor, 1973, megalopal porcellanids; Herrick, 1895, Williams, 1907, Factor, 1978, larval lobsters; Barshaw, 1989, Lavalli & Barshaw, 1989, postlarval lobsters). Levine & Sulkin (1984b) concluded from a review of the literature that, with rare exceptions, brachyuran larvae reared in the laboratory on microalgae alone do not grow and develop normally. Based on the effect of various diets on successful development of the blue crab (*Callinectes sapidus*), Sulkin (1975) agreed with the earlier assertion of Costlow & Bookhout (1959) that blue crab zoeae can ingest unicellular organisms, but that a diet made up exclusively of these was not adequate.

In the light of these suggestions that crab larvae may be able to feed on unicellular organisms, the present study was conducted to determine if zoeal larvae of the green (shore) crab, *Carcinus maenas* (Linnaeus, 1758), are capable of removing minute, micrometre-sized particles from suspension in sea-water.

MATERIALS AND METHODS

Ovigerous females were collected at the Shoals Marine Laboratory on Appledore Island, Isles of Shoals, in the Gulf of Maine, USA, and transported to the State University of New York at Purchase for experimentation. Upon hatching, first-stage zoeal larvae were transferred to a separate aerated chamber containing filtered sea-water, within the refrigerated aquarium where females were housed, and allowed to acclimate for approximately 24 h.

Suspension-feeding experiments were conducted in a simple apparatus comprising a series of 50-ml test tubes in a rack. In each tube, a single Pasteur pipette was pushed through a two-hole, non-toxic stopper so that the tip was approximately 2 mm from the bottom. An aquarium pump aerated each tube via latex tubing to keep zoeae actively swimming in the water column and to retard settlement of particles. The flow was adjusted to a gentle stream of bubbles that did not visibly disturb behaviour.

Experimental suspensions (Table 1) were prepared using filtered (0·8 μm), autoclaved, Long Island Sound sea-water. Three types of particles were used. 1. Chartreuse fluorescent particles: individual, irregularly-shaped particles measured 1-2 μm; suspension was dominated by single particles with some clumps up to 40 μm. 2. Orange-red fluorescent particles: individual, irregularly-shaped particles measured 1-5 μm; suspension was dominated by single particles with some clumps up to 20 μm. 3. *Dunaliella tertiolecta*: a photosynthetic flagellated protist; individual, live, spherical cells measured 5-7 μm diameter; no clumps. Fluorescent particles were manufactured by Radiant Color Co. (grade JST-300). *Dunaliella tertiolecta* cells were derived from a stock laboratory culture. Concentrations were measured by replicate haemacytometer counts.

For each treatment 8-10 zoeae were placed in each of two 50-ml test tubes containing 40 ml of the experimental suspension. Control test tubes each contained 10 zoeae in filtered, autoclaved sea-water without particles to determine that the apparatus did not harm larvae or visibly alter behaviour. At the end of the 24-h experiment all zoeae were removed from the test tubes, rinsed in distilled water, and preserved in 70% ethanol. Presence or absence of particles in the gut was first determined using brightfield microscopy. Because it was sometimes difficult to discern particles with brightfield alone, specimens were also examined using darkfield and fluorescence microscopy.

RESULTS

First-stage zoeal larvae of the green crab ingested all three types of artificial and living particles that were offered in sea-water suspensions (Table 1). Combining results from all experimental treatments, a total of 45 zoeae were examined; of these, 40% of the zoeae clearly had particles in their stomachs and/or intestines. These figures are considered to be conservative estimates of particle ingestion for three reasons: the scoring system counted as positive only those zoeae seen to contain particles by both authors independently and questionable specimens were scored as negatives; the distilled-water rinse and/or preservation in ethanol may have caused regurgitation in some larvae, causing

Table 1. *Results of suspension-feeding experiments with first-stage zoeal larvae of* Carcinus maenas

Particle type	Concentrationof suspension		No. of zoeae inspected	No. of zoeae ingesting particles	% zoeae ingesting particles
Orange-red fluorescent particles (1-5μm)	Initial: Final: Average:	0.66×10^6 ml^{-1} 0.35×10^6 ml^{-1} 0.51×10^6 ml^{-1}	16	5	31.3
Dunaliella tertiolecta cells (5-7 μm)	Initial: Final: Average:	1.16×10^6 ml^{-1} 0.68×10^6 ml^{-1} 1.17×10^6 ml^{-1}	16	6	37.5
Chartreuse fluorescent particles (1-2 μm)	Initial: Final: Average:	3.35×10^6 ml^{-1} 1.56×10^6 ml^{-1} 2.46×10^6 ml^{-1}	13	7	53.8
Totals			45	18	40.0

them to appear negative; and some larvae may have ingested and completely passed particles by the end of the 24-h experiment.

A typical darkfield microscopic view of a zoea that ingested suspended particles is illustrated in Figure 1A. Even when the brightfield image showed little evidence of ingested particles (Figure 1B), the epifluorescence microscopy yielded very clear evidence of particles in the stomach and/or intestine (Figure 1C). Strings of particles were also commonly seen in the anterior portion of the intestine, sometimes separated by the peristaltic constrictions of the intestine.

Particle concentrations in the experimental test tubes decreased by approximately 41-53% (average 47%) over the course of the experiment (Table 1), primarily as a result of settling. Despite this, final concentrations were still quite high and more closely approximated natural concentrations of planktonic particles. Microscopic examination of subsamples indicated that most or all of the larger clumps of particles settled out during

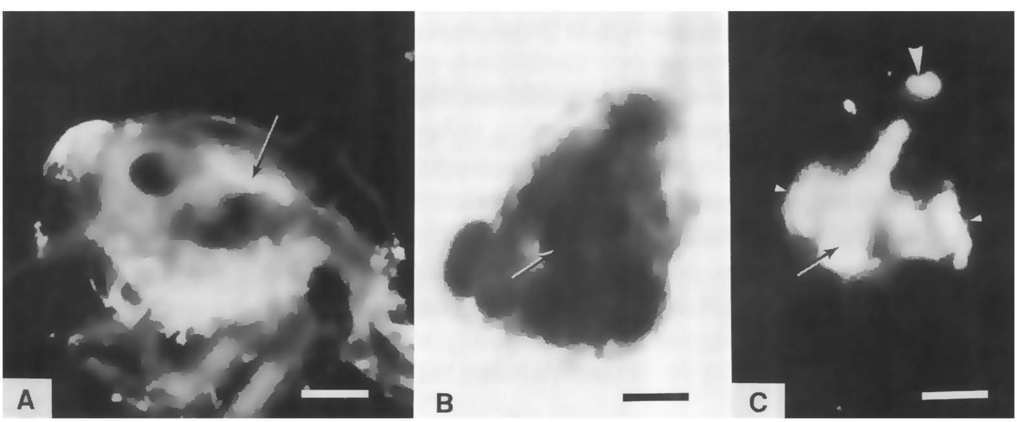

Figure 1. (A) Darkfield image of ingested particles in the stomach of a first-stage zoea, lateral view. Arrow indicates a bolus of particles. (B) Brightfield and (C) fluorescence images of ingested fluorescent particles (chartreuse type) in the stomach of a first-stage zoea, dorsal views. Arrows indicate particles in the stomach; large arrowhead indicates particles in the anterior, downturned portion of the intestine; small arrowheads indicate particles in the gill chambers. Photomicrographs. Scale bars: 0·1 mm.

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the experiment, but that individual artificial particles and small clumps and *Dunaliella tertiolecta* cells all remained in suspension. Ingested particles appeared to be overwhelmingly single; there was no evidence of the ingestion of large clumps, as determined by microscopic comparison with the clumps seen in suspensions. The zoeae in all groups remained in the water column throughout the experiment and there was no mortality among either control or experimental larvae.

DISCUSSION

Results of this laboratory experiment demonstrate that first-stage zoeal larvae of *Carcinus maenas* can remove small, living and non-living particles from suspension. These results are consistent with the findings of Costlow & Bookhout (1959) and Sulkin (1975), who suggested that larvae of the blue crab (*Callinectes sapidus*) may feed on unicellular organisms.

Levine & Sulkin (1984b) showed that zoeal larvae of *Eurypanopeus depressus* ingested microcapsules in the range of 45-180 µm, but they did not suggest the mechanism of capture. While it is at least possible that the largest of their capsules could have been captured raptorially, Sulkin (personal communication) does not think that crab larvae visually seek out particles. The unidentified diatoms found in the stomachs of larval lobsters by Herrick (1895) and Williams (1907) could have been quite large, as diatoms may range up to 1000 µm in size, making raptorial capture possible.

In the present study, experimental suspensions were dominated by individual particles in the 1-7 µm range and their ingestion suggests that the *Carcinus maenas* zoeae used some type of suspension-feeding mechanism to remove such small particles from the water. Although the mechanism of suspension feeding is not known, it is likely to involve the setose mouthparts and/or thoracic appendages, which have been described and illustrated by Rice & Ingle (1975). The percentage of larvae ingesting particles increased at higher particle concentration, with an apparently linear relationship, suggesting that suspension feeding is non-selective, is based on encounter rates, and is independent of particle form or quality.

Many small crustaceans and other planktonic organisms are not simply passive 'filter feeders', but possess a broad range of feeding styles and selection capabilities (reviewed by Price *et al.*, 1988). Some copepods are non-selective during early larval life, but become very selective at later stages; others are non-selective throughout (Dexter, 1984). Larger planktonic organisms, traditionally thought to feed primarily by raptorial capture of individual items, may also possess a range of feeding capabilities that allows them more effectively to exploit a variable planktonic food resource.

Despite the simple design of the present study, results suggest that green crab larvae may be capable of utilizing planktonic particles in the size range of bacteria, small algal cells, and organically-enriched detrital particles (1-10 µm) in their natural diet. The precise mechanism of capture and the nutritional role of particulate food in the natural diet remain subjects for further investigation.

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