Behavioral basis of internal-wave-induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*

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ABSTRACT: In field experiments, megalopae of the intertidal crab *Pachygrapsus crassipes* Randall, released in the water column at 1 to 5 m depths and observed by a SCUBA diver, swam to the surface. Laboratory experiments on the orientation of megalopae demonstrated a positive phototaxis at 3 light intensities (1240, 690, 70 lux), negative geotaxis, high baro- and photokinesis, and a strong tendency to cling to objects in the water. Spontaneous swimming of megalopae yielded an average speed of 9.5 cm s^{-1}. These observations are consistent with the hypothesis that *P. crassipes* megalopae inhabit the neuston and are transported shoreward by tidally forced internal waves.

INTRODUCTION

In the coastal waters of California (USA), larvae of brachyuran crabs require from 2 to 4 mo for their developmental period (Lough 1974). At the end of this developmental stage the megalopae, if they are to survive, must migrate from their pelagic habitat back to the coast. Because currents at different water-column depths frequently flow at different speeds and directions, a megalopa may enhance its chances of regaining the coast by remaining at a depth where the flow is onshore (Rothlisberg 1982). By timing their vertical migration to the tides, larvae which inhabit estuaries during development or which must migrate up-estuary to reach their juvenile habitat, may utilize tidal currents to control their horizontal movement within the estuary (Christy 1978, Cronin & Forward 1982). Use of wind and tidal currents has also been suggested as a means of onshore transport of megalopae from offshore waters (Boicourt 1982, Johnson 1982, Johnson & Gonor 1982, Epifanio et al. 1984).

Shanks (1983) presented evidence suggesting that crab megalopae and larvae of other coastal invertebrates and fish are transported from offshore plankton to the coastline in surface slicks, generated over tidally forced internal waves. As the ebbing tide flows across bottom relief such as reefs, banks, and the continental shelf break, lee waves are generated on the thermo-

cline (Rattray et al. 1969, Halpern 1976, Maxworthy 1979, Chereskin 1983). Along the continental shelf the lee wave is formed at the seaward edge of the shelf break (Fu & Holt 1982). When the ebbing current goes slack, the lee wave is released and progresses shoreward as a series of large amplitude internal waves (Chereskin 1983). The slicks are surface manifestations of currents generated over the tops of these internal waves (Ewing 1950). They delineate a zone of converging and downwelling currents situated over the trough of the waves (Fig. 7 in Zeldis & Jillet 1982). As the internal waves travel shoreward the wave-generated currents sweep oil and flotsam into the convergence forming a slick (Ewing 1950). Buoyant flotsam will remain at the surface trapped in the convergence and be carried along with the waves (Arthur 1954, Shanks 1983). The proposed mechanism of larval transport suggests that any organism which can maintain itself at the surface in the face of the downwelling currents present at the convergence will, like the flotsam, remain in the slick and be transported ashore (Shanks 1983).

In understanding larval dispersal, a useful complement to field studies is the investigation of species-specific behavior patterns which can contribute to depth regulation (Sulkin 1984) and hence to differential transport by currents. This paper presents a series of laboratory and field observations, and experiments,

investigating the behavior patterns of the megalopae of *Pachygrapsus crassipes* Randall, an organism which is transported by internal waves (Shanks 1983).

METHODS

A supply of *Pachygrapsus crassipes* megalopae was caught using traps consisting of bundles of hemp rope hung from the pier at Scripps Institution of Oceanography (Shanks 1983). Megalopae were removed from the trap daily and used in experiments within 6 h of capture. Seawater at room temperature was used in both holding tanks and laboratory experiments.

To determine the preferred position of megalopae in the water column, field release experiments were conducted on 4 dates: March 1, 8, and 15, 1981, and June 3, 1982. About 20 freshly caught *Pachygrapsus crassipes* megalopae were placed together in each of three 50 ml syringes and immediately transported by a SCUBA diver to the release site in water about 10 m deep and about 150 m from shore. Megalopae were released individually at depths between 1 and 5 m and the direction in which they swam was observed by the diver from distances of 1 to 2 m.

Laboratory experiments investigated light and gravity as potential orientation cues, and increased hydrostatic pressure as a kinesis stimulus. Phototaxis was tested at 3 light intensities (1240, 690, and 70 lux, measured with the experimental chamber in a vertical orientation, filled with seawater, and the end plate removed) with the test specimens held in a horizontally oriented cylinder. A cool white fluorescent lamp provided illumination and sets of neutral density filters placed in front of this lamp were used to create the different light intensities. Ten megalopae sealed into the seawater-filled lucite cylinder (7 cm dia × 60 cm long) were dark-adapted for 5 min prior to each experimental series. Before each observation the cylinder was rotated 4 times in the dark, end over end (about 2 s rev^{-1}), to dislodge megalopae clinging to the cylinder walls, and to generate a more or less uniform initial larval distribution. Experimental stimuli were then applied, and after 1 min, individuals in each quarter of the cylinder were counted. Preliminary observations indicated that the response of the megalopae to the illumination occurred in much less than 1 min. Fifteen replicate experiments using 10 fresh megalopae were run for each illumination level. The control consisted of the response of the megalopae in total darkness. Four controls following the protocol outlined above were run interspersed between experimental runs. Counts on controls were made by sighting down the chamber toward a dim white light (70 lux) positioned at one end of the tube. Only 5 to 10 s of illumination

was required for the counts. The control was repeated if during the counts megalopae were observed to move into a new quarter section of the cylinder (1 repeat/5 attempts).

Next, experiments were conducted to test the effects of light, gravity, and hydrostatic pressure in various combinations on the distribution of megalopae in a vertical tube. The first experiment examined the combined effects of all 3 variables; increasing hydrostatic pressure, 0.0 to 1.2 atm above ambient, was applied to a vertically oriented chamber with overhead illumination of 690 lux. The second experiment tested the combined effects of gravity and increased pressure on orientation. In this experiment, a pressure increase from 0.0 to 1.2 atm above ambient was administered to individuals in a vertical cylinder in the dark. Counts were made following the procedure described above for the horizontal-chamber controls. The third experiment tested the relative importance of gravity *versus* light as orientation cues for the response to a pressure increase. The vertical cylinder was illuminated (690 lux) from below, and hydrostatic pressure was increased sequentially. Experimental protocol for these experiments was similar to that used in the phototaxis experiments: 10 megalopae were placed in a seawater-filled cylinder, dark-adapted for 5 min, the cylinder was rotated in the dark, the rotation stopped with the cylinder vertical, the experimental stimuli were applied, and after 1 min the megalopae in each quarter section of the cylinder were counted. Five replicate experiments using 10 fresh megalopae were run for each pattern of illumination.

To test for thigmo-kinesis (Fraenkel & Gunn 1961) the response of groups of *Pachygrapsus crassipes* megalopae held in a seawater-filled bowl to a bundle of eelgrass *Phyllospadix* spp. suspended in the center of the bowl was observed for 10 min periods. The bowl (20 cm dia × 8 cm deep) was illuminated from above by fluorescent light. At the end of the experiment, the total number of megalopae on the eelgrass was recorded. Seven separate groups of 20 individuals were observed. Low thigmo-kinesis (little movement when in contact with an object; Fraenkel & Gunn 1961) was arbitrarily defined as greater than 50 % of the megalopae clinging to the eelgrass at the end of the experiment.

Two different techniques were employed to estimate the swimming speed of *Pachygrapsus crassipes* megalopae. The first method made use of the positive phototaxis exhibited by the megalopae. Megalopae were released at one end of a long horizontal lucite tube (5 cm dia × 184 cm long), and the time they required to swim the length of this tube toward a light positioned at the opposite end was measured with a stop watch. The large size of *P. crassipes* megalopae

(9 mm length) made this a simple operation. For the second technique, observations were made of spontaneous swimming activity. The experiments were designed so as to remove the possible effects of high photokinesis and, because the larvae were allowed to swim greater distances (at least 4.4 m), it was hoped that the measurements would represent an estimate of the sustainable cruising speed of the megalopae. When a number of megalopae were placed in a bucket of sea water with illumination from directly above, it was observed that there were always a few megalopae spontaneously swimming laps about the perimeter of the bucket (88 cm cir). The lap speed (s lap^{-1}) of selected, active individuals which swam at least 5 laps was recorded.

RESULTS

Of the megalopae released in the sea 51 were successfully observed and followed by the diver. All tumbled about for several seconds until they became oriented and then swam rapidly to the surface where they swam horizontally, maintaining a depth of less than 1 m.

Experiments in the horizontal chamber indicated that *Pachygrapsus crassipes* are positively phototactic (Table 1). At all 3 light intensities, more than 80 % of the megalopae were in the quarter of the tube nearest the light. These distributions were significantly different from the controls (Chi-squared > 62 in all cases, P < 0.005). Most of the megalopae responded immediately to illumination by swimming rapidly toward the light until they actually bumped against the end plate of the chamber. During these and the following experiments at times a megalopa would wedge itself into the orifice connecting the chamber to the pressure reg-

ulator and not respond to any stimuli. This was a minor source of error in all experiments using this apparatus.

Experiments in the vertical chamber demonstrated that the megalopae are positively phototactic, negatively geotactic, and display both high baro- and photokinesis (Fig. 1). Results of these experiments were analyzed using a 2-way analysis of variance on the arcsin transformed data (Sokal & Rohlf 1969). Effects of both pressure and lighting regime were significant (Table 2). In all lighting regimes, with increasing pressure a greater percentage of the megalopae were present at the top of the cylinder (Fig. 1): a behavior indicative of high barokinesis (i.e. more rapid swimming following a pressure increase). At all pressures tested the greatest percentages of the megalopae were at the top of the chamber when illumination was from above. Larvae were next most responsive, again at all pressures, when illumination was from below. The smallest percentage of
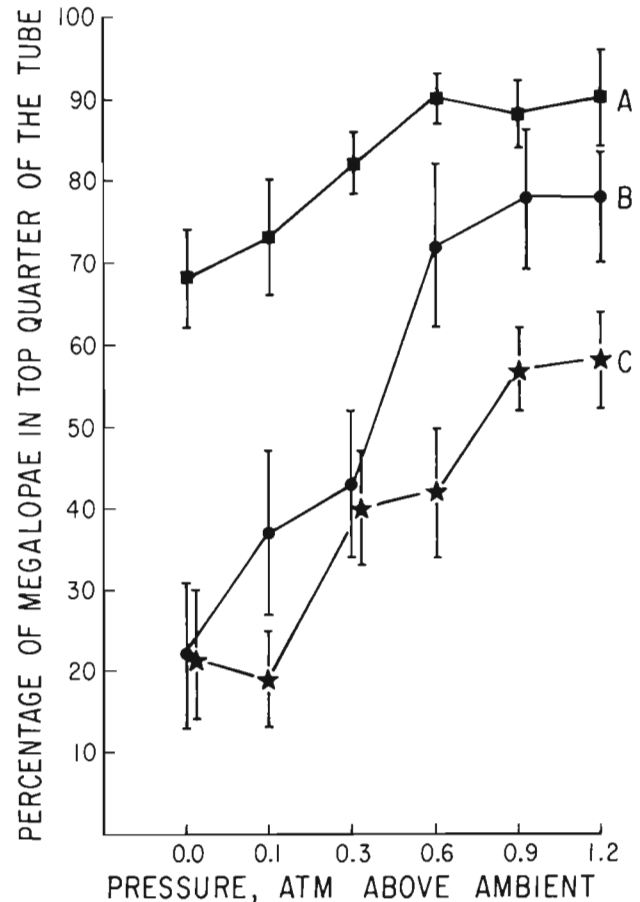
Table 1. *Pachygrapsus crassipes*. Percentage (mean, SE) of megalopae in each quarter section of a horizontal chamber down which light was directed from Section 1. For the 'no light' (control) experiments n = 4; for the 'low' (70 lux), 'medium' (690 lux), and 'high' (1240 lux) light experiments n = 15

Condition	Section			
	1	2	3	4
No light (control)	28.7 (4.3)	10.8 (4.2)	37.0 (8.5)	23.8 (4.7)
Low light	81.4 (2.2)	5.8 (1.7)	3.2 (1.6)	8.9 (1.8)
Medium light	83.8 (2.7)	3.3 (1.6)	4.2 (1.5)	8.7 (2.4)
High light	83.7 (3.4)	1.7 (1.2)	2.5 (1.1)	12.1 (3.2)

Fig. 1. *Pachygrapsus crassipes*. Results of vertical cylinder experiments: percentage (mean ± SE) of megalopae in the top quarter of the chamber at 6 different pressures, 0.0, 0.1, 0.3, 0.6, 0.9, and 1.2 atm above ambient, and 3 lighting regimes: (A) medium light (690 lux) from above; (B) medium light from below; (C) no light. Each point represents the results of 5 experiments with 10 megalopae

Table 2. Results of a 2-way analysis of variance applied to the arcsin-transformed data from the vertical cylinder experiment (Fig. 1)

Source of variation	df	SS	MS	F	Signifi-cance
Pressure	5	10,827	2,165	13.20	$P < 0.001$
Light regime	2	12,919	6,460	39.39	$P < 0.001$
Pressure × light regime	10	1,339	134	0.82	NS
Error	72	11,816	164		
Total	89				

NS not significant

megalopae were at the surface when the chamber was in the dark, but even in the dark > 50 % of the larvae were at the surface at pressures greater than 0.9 atm above ambient. The fact that more individuals were swimming at the surface in both experiments with illumination, even when illumination was from below, than in those in the dark suggests that the megalopae were displaying high photokinesis.

In each of the 7 thigmo-kinesis experiments, over 50 % (Mean = 71 %, SD = 8 %, Range = 60 to 85 %, n = 7) of the megalopae were clinging to the bundle of eelgrass at the end of the observation period. Of the megalopae which contacted the bundle, 81 % (SD = 8 %) stopped swimming and clung to it, and of these megalopae 88 % (SD = 7 %) remained on the eelgrass until the end of the experiment. Megalopae swimming within about 3 cm of the eelgrass frequently turned sharply from their path to swim to the bundle and settle. Once on the bundle, most of the megalopae worked their way in amongst the blades of eelgrass until they were completely surrounded and hidden. These observations indicate that *Pachygrapsus crassipes* megalopae display low thigmo-kinesis (Fraenkel & Gunn 1961).

The swimming speed of *Pachygrapsus crassipes* megalopae released in the long tube ranged from 1.8 to 16.2 cm s^{-1} with an average speed of 9.1 cm s^{-1} (SD = 2.7 cm s^{-1}, SE = 0.3 cm s^{-1}, n = 76) or 10.1 body lengths s^{-1}. The spontaneous swimming speed of megalopae swimming laps in the bucket ranged from 7.4 to 12.4 cm s^{-1} with an average speed of 9.5 cm s^{-1} (SD = 1.7 cm s^{-1}, SE = 0.4 cm s^{-1}, n = 18) or 10.6 body lengths s^{-1}. The lap speed of individual megalopae was fairly constant, the standard deviation in speed between laps ranged from 0.6 to 2.8 cm s^{-1}. These swimming velocities were maintained over distances of from 4.4 to 71.2 m. The excursions were usually terminated when a swimming megalopa bumped into another individual, causing the swimmer to stop and cling to the wall of the bucket. However, the individual which swam farthest (71.2 m) was still

swimming after the 80 laps. There was no significant difference (2-sample T-test, T = −0.62, P = 0.54) between the swimming speeds measured by the 2 techniques.

DISCUSSION

The surface layer of coastal waters is the habitat of *Pachygrapsus crassipes* megalopae. In the field-release experiments all larvae successfully observed swam immediately to the surface. In day and night plankton samples collected in the Southern California Bight, *P. crassipes* megalopae were 10 times more numerous in neuston than in oblique plankton tows (Shanks pers. obs.). Furthermore, in a vertical array of traps (0, 1.5, and 6 m depth) hung from the end of the Scripps Institution of Oceanography pier 91 % of the megalopae were caught at the surface (Shanks 1983).

The laboratory experiments demonstrate a combination of positive phototaxis, negative geotaxis, high baro- and photokinesis; behavioral patterns which help to maintain the *Pachygrapsus crassipes* megalopae at the ocean surface. Movements in response to a pressure increase were, in all cases, oriented negatively with respect to gravity even in the experimental situation where illumination in the vertical tube was from below. This combination of behavioral pattern was observed by Rice (1964) in the megalopae of the shore crab *Carcinus maenas* (Linneaus). The megalopae of *Callinectes sapidus* (Rathbun) also display many of these same patterns (Naylor & Isaac 1973, Sulkin & Van Heukelem 1981).

The terminal larval stages of many coastal decapods, i.e. the stages which migrate back to the coast, often inhabit the neuston. Larval stage IV of *Homarus americanus* (Milne Edwards) (Harding et al. 1982, Cobb et al. 1983), the megalopae of *Cancer magister* (Dana) (Wickham 1979, Johnson et al. 1983, Reilly 1983) as well as the megalopae of other California coastal crabs (Shanks in prep.), and the megalopae of several species of crab from the East Coast of North America including *Callinectes sapidus* (Smyth 1980, McConaugha et al. 1981) are highly concentrated in the neuston. Swarms of megalopae swimming at the surface have been observed on several occasions in Caribbean waters (Chace & Barnish 1976, Rice & Kristensen 1982). The puerulus stages of the spiny lobsters *Panulirus argus* (Latreille), *P. interruptus* (Randall), and *P. cygnus* (George) have all been observed to swim just below the ocean's surface (Phillips & Olsen 1975, Serfling & Ford 1975, Calinski & Lyons 1983). The post-larval stage of *Munida gregaria* (Fabricius) has been observed in dense surface swarms which at times appeared to be associated with internal wave slicks (Zeldis & Jillett 1982). Like *Pachygrapsus crassipes*

megalopae, Stage IV *H. americanus* and post-larval *M. gregaria* swim to the surface when released in the water column (Ennis 1975, Zeldis & Jillett 1982, Cobb et al. 1983).

One of the characteristic behavior patterns of *Pachygrapsus crassipes* megalopae is their tendency to cling to objects in the water (low thigmo-kinesis). This behavior was observed repeatedly during the free-release experiments; many of the megalopae actually settled on the diver. The laboratory experiments which demonstrated low thigmo-kinesis are consistent with these observations. Observations of low thigmo-kinesis in crab megalopae are rare. Laboratory measurements are not available to compare with those made in the present study, but field observations of apparent low thigmo-kinesis by megalopae and other larval forms have been reported in the literature. The megalopae of *Cancer magister* have been observed clinging to jellyfish (Weymouth 1918, Shanks pers. obs.), the neustonic siphonophore *Velella velella* (Wickham 1979, Reilly 1983), and flotsam (Poole 1966, Wickham 1979). Gooding & Magnuson (1967) observed megalopae of unknown tropical crabs settling on a raft and even on juvenile fish associated with the raft. During this study a large variety of megalopae and other larval forms, even fish, were found clinging to the hemp rope trap. Similar traps have been used for years in different areas of the world to catch pueruli of spiny lobsters (Phillips 1975, Serfling & Ford 1975, Little & Milano 1980) suggesting that these larvae may also display low thigmo-kinesis. The post-larvae of *Munida gregaria* have been observed to cling to a variety of flotsam (Williams 1980, Zeldis & Jillett 1982).

The megalopae of *Pachygrapsus crassipes* is an example of a larva which migrates from the offshore plankton back to the coast in slicks over tidally forced internal waves (Shanks 1983). Utilization of this mode of onshore transport requires that the organisms remain at the ocean surface. Larvae which reside in the water column or near the bottom will not be transported by this mechanism. The evidence presented in this paper demonstrates that the megalopae of *P. crassipes* exhibit behavioral traits that will promote maintenance of their position in the surface layers. The later larval stages of other species of decapods appear to have similar behavior patterns. However, in order to be actually transported by an internal wave, an organism must swim strongly enough to avoid being washed down and out of the surface waters by the downwelling currents present under the surface slick (Ewing 1950). An estimate of the vertical current speeds which the larvae must overcome can be made by calculating the velocity of vertical deformation of the thermocline on which the internal wave is propagating (Zeldis & Jillett 1982). Calculations using data from LaFond's (1959) description of numerous slicks and associated internal waves off the southern California coast indicate that the average rate of vertical deformation was 4.9 cm s^{-1} (SD = 2.6 cm s^{-1}, range 1.5 to 13.3 cm s^{-1}, N = 67). This speed is well within the swimming capability of *P. crassipes* megalopae as well as many other larval decapods (Table 3). Megalopae which are able to find and cling to positively buoyant flotsam can maintain themselves at the surface without swimming, and when the flotsam is eventually caught up by a slick will be transported shoreward. The cover provided by the flotsam may also assist the megalopae in hiding from predators (Mitchell & Hunter 1970).

Shoreward transport by internal waves is a mechanism for the onshore migration of the planktonic larvae of coastal organisms. Experimental analysis of the behavior patterns of post-larval decapods and observations of their vertical distribution in the field suggest many forms occupy the near-surface zone. By occupying this stratum in the water column, post-larval decapods place themselves in an ideal location for transport by internal waves, and they thus may be

Table 3. Swimming speeds of various larval and post-larval decapods

Decapods	Swimming speeds (cm s^{-1})	Source
Cancer magister	4.2 to 17.4	Jacoby (1982), MacKay (1943)
Callinectes sapidus	8 to 11	Sulkin & Van Heukelem (1981)
Pachygrapsus crassipes	7.4 to 11.8	This study
Munida gregaria	17.5	Zeldis & Jillett (1982)
Lobsters		
Panulirus argus	7.7 to 10	Calinski & Lyons (1983)
P. cynus	15 to 46	Phillips & Olsen (1975)
P. interruptes	6 to 9	Serfling & Ford (1975)
Homarus americanus	6.2	Ennis (1975)

prime examples of organisms which utilize this mechanism of onshore transport.

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