

NOTE

Ontogeny of phototaxis and geotaxis during larval development of the sabellariid polychaete *Phragmatopoma lapidosa*

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ABSTRACT: Thorson generalized that the larvae of intertidal animals should remain photopositive throughout larval life to facilitate encounters with shallow surfaces at settlement. We tested this idea for the sabellariid polychaete *Phragmatopoma lapidosa* by investigating ontogenetic changes in phototaxis and geotaxis of well-fed, laboratory-reared larvae. Larvae at each of 5 age groups were exposed to (1) 8 different light intensities from a directional light source in a horizontal trough and (2) complete darkness in a vertical chamber. Phototaxis changed with age. Half-day old larvae were not responsive to light, 1 d old larvae were positively phototactic, and all older larvae to 28 d age were negatively phototactic. Larvae from 0.5 to 28 d age were positively geotactic with the exception of 5 d old larvae, which lacked a defined response. Consequently, larvae of the predominantly intertidal *P. lapidosa* did not conform to Thorson's suggestion of continuous positive phototaxis in intertidal species.

KEY WORDS: Phototaxis · Geotaxis · Polychaete · Larvae · *Phragmatopoma lapidosa*

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The role of larval swimming in migration, dispersal, and settlement of marine invertebrates has been an area of focus in marine ecology for many years (reviewed in Forward 1976, 1988, Young 1995). Horizontal swimming behavior generally does not affect larval distributions on large spatial scales since most larvae cannot swim against ambient water currents (Mileikovsky 1973, Chia et al. 1984). Vertical swimming behavior may enable larvae to exploit differential horizontal advection because velocity and direction of currents may vary considerably with depth (reviewed in Young & Chia 1987).

Thorson (1964) reviewed the literature on larval responses to light (phototaxis) for 141 invertebrate spe-

cies and concluded that light was the main cue for swimming behavior. Eighty-two percent of the species he considered responded positively to light, 12% were indifferent to light, and 6% responded negatively to light. Thorson (1964) noted that photoresponses generally differ between intertidal and subtidal species. The larvae of the few intertidal species he examined were photopositive throughout their planktonic period. Thorson (1964) suggested that this behavior would position larvae in the upper water column where they would encounter shallow habitats at the end of larval life. In contrast, larvae of most subtidal species were initially photopositive, which is useful for dispersal, but they became photonegative before settlement, presumably to enhance their chances of encountering subtidal adult habitats.

In most of the studies reviewed by Thorson (1964), workers did not attempt to mimic natural light conditions; most used concentrated light beams that induce strong phototactic responses but are not representative of the angular light distribution found in the sea (Forward 1988). Many of the studies also did not measure responses at a range of light intensities. The sign of phototaxis for many marine invertebrate larvae can be affected by light intensity (reviewed by Forward 1976). Because these and other aspects of photobiology were not fully appreciated in Thorson's time, the importance of light in controlling dispersal and transport of larvae to adult habitat remains in question.

An ambiguous aspect of Thorson's generalization is whether light interacts with other cues to stimulate downward swimming or cessation of swimming (Forward 1988, Young 1995). Several theories invoke passive mechanisms in the vertical movement of plankton (Rudjakov 1970, Marszalek 1982, Sulkin 1984, Forward 1989), any of which could apply to settlement. For example, Chia et al. (1984) noted that many larvae

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sink faster as they approach metamorphosis. A larva with negative buoyancy could sink passively rather than actively swimming downwards, thereby preserving valuable energy (Young & Chia 1987). While this might be the case for some larvae, late-stage larvae of the polychaete *Phragmatopoma californica* swim downward in response to increased friction velocity created by moderately high currents (Pawlik et al. 1991, Pawlik & Butman 1993). The potential roles of kinetic or tactic responses to light and gravity are unknown in this species and in other intertidal sabelariids.

Phragmatopoma lapidosa, possibly a synonym of *P. caudata* (Kirtley 1994) and/or a conspecific of *P. californica* (Pawlik 1988), is a reef-building polychaete with a geographic distribution from Brazil to southern Florida (Hartman 1944). Adults live mostly in marine intertidal hard-bottom habitats (Hartman 1944, Eckelbarger 1978), although they sometimes occur subtidally to 10 m (D.A.McC. unpubl., Kirtley 1994). We investigated the ontogenetic changes in phototactic and geotactic responses of *P. lapidosa* larvae to test Thorson's generalization that larvae of intertidal marine organisms are photopositive and remain near the surface of the water column prior to settlement. Laboratory observations were also used to develop a descriptive model that predicts the role of larval behavior and swimming in settlement and dispersal of this species.

Materials and methods. Adult *Phragmatopoma lapidosa* were collected from intertidal worm reefs in Boynton Beach, Florida (26° 32.90' N, 80° 30.20' W). Spawning was induced by excising adults from their tubes and isolating them in bowls of filtered seawater. Worms generally began to spawn within several minutes. The eggs were collected, washed with 0.45 µm filtered seawater, and fertilized with a dilute sperm solution. After hatching, trochophores were fed daily a 1:1 mixture of the algae *Dunaliella tertiolecta* and *Isochrysis galbana* at $\sim 10^{4.7}$ cells ml⁻¹. Developing larvae were reared in 500 ml glass culture bowls with a water change of 0.45 µm filtered seawater (34‰) every other day. Larval cultures were exposed to outdoor ambient light cycles (~13 h light:11 h dark cycle) and seawater temperatures averaging 22 to 23°C. Phototactic and geotactic experiments were conducted independently for larvae of 0.5, 1, 2, 5, and 28 d ages. Twenty-eight day old larvae were competent to settle.

All experiments were conducted between 12:00 h and 15:30 h to reduce variability in behavior due to any biological rhythms. New larvae were used for each trial. Phototaxis experiments began by haphazardly collecting larvae from the culture bowls and dividing them into groups of 10. The larvae were then placed in scintillation vials and dark-adapted for 1 h.

Light stimulation for phototaxis was provided by a slide projector (Viewlex) with a 300 W incandescent lamp. The light was filtered with a hot mirror (Baird Atomic) and an infrared radiation (IR) absorbing filter to remove heat and then was interference-filtered to specific wavelengths (Ditric Optics). Since preliminary experiments determined that larvae detect light between 410 and 510 nm, a 500 nm interference filter (half band pass ≈ 8 nm) was used during each experiment. This wavelength was used because it is near the spectral sensitivity maximum of most zooplankton (Forward 1976, 1988). Light intensity was controlled with neutral density filters and measured with a radiometer (EG&G, model 500).

For each experiment, 10 larvae were placed in the center section of a 15 × 3 × 3 cm (length × width × height) rectangular, horizontal Lucite trough in a dark room. A removable set of partitions divided the trough horizontally into 5 equal sections. The trough was initially immersed in a water bath (to minimize the potential artifact of light reflection off the back wall of the trough) but there were no behavioral differences with or without the water bath. Thus, all experiments were performed without the water bath to facilitate viewing of the larvae. Upon light stimulation, the partitions were lifted, allowing the larvae to swim throughout the trough. After 2 min, the partitions were returned and the larvae in each section were counted. For statistical analyses, larvae in the section closest to the light source were classified as positively phototactic, larvae in the section furthest from the light source were considered negatively phototactic, and larvae in the middle sections of the trough were counted but not included in the analysis. Four replicates were run for larvae at each age at 8 different light intensities (1.89×10^{13} , 1.89×10^{14} , 1.89×10^{15} , 1.89×10^{16} , 6.00×10^{17} , 9.3×10^{17} , 1.30×10^{18} , and 1.86×10^{18} photons m⁻² s⁻¹). In a control group, all test procedures were followed without light stimulation. Results were analyzed by comparing the arcsine-transformed means of positive and negative taxis with values for the dark control using a Dunnett's test (Dunnett 1964). The phototactic threshold was defined as the lowest light intensity that evoked a phototactic response significantly greater than the control level in darkness.

For geotaxis experiments, 10 larvae were placed in an acrylic experimental chamber 3 × 3 × 15 cm (length × width × height) that was positioned vertically in a darkened room. The chamber was marked on the outside to divide it into 5 equally sized vertical sections. One h after being released into the chamber, larvae in each section were counted with the aid of a red light, which did not affect their vertical distribution. For statistical analyses, larvae in the bottom section of the

chamber were recorded as positively geotactic, while those in the section nearest to the top of the chamber were recorded as negatively geotactic. Three replicates were run for each of 5 larval ages: 0.5, 1, 2, 5, and 28 d ages. Results were analyzed using a 2-way

ANOVA with signs of geotaxis and age being the independent factors (Sokal & Rohlf 1995).

Results and discussion. *Phragmatopoma lapidosa* trochophores developed within 0.5 d of fertilization and generally swam upward while rotating around their longitudinal axes. Early larvae were randomly distributed throughout the 5 sections of the test trough upon stimulation with all light intensities tested (Fig. 1A). By 1 d, larvae developed a single, reddish eyespot and a complete digestive system. They exhibited a positive phototaxis at all test light intensities $>10^{16}$ photons $m^{-2} s^{-1}$ ($n = 4$, $p < 0.01$; Fig. 1B) with a threshold at 1.9×10^{16} photons $m^{-2} s^{-1}$. Although 7 to 20% of larvae were photonegative, the mean percentage of photonegative larvae did not differ significantly from the mean number of larvae in the comparable compartment of the dark control treatments ($n = 4$, $p > 0.05$). By 2 d, larvae had developed 2 eyes and switched to negative phototaxis for light intensities of 1.9×10^{15} to 1.9×10^{19} photons $m^{-2} s^{-1}$ ($n = 4$, $p < 0.05$ to 0.01 ; Fig. 1C). The mean percentage of photopositive larvae (7 to 22%) did not differ significantly from the mean percentage of larvae in the corresponding compartment of the dark controls ($n = 4$, $p > 0.05$).

The percentage of larvae displaying a negative phototactic response increased to 60 to 80% by 5 d (Fig. 1D). Larvae at this age responded to all stimulus light intensities $> 1.9 \times 10^{15}$ photons $m^{-2} s^{-1}$ ($n = 4$, $p < 0.01$). Most of the mean values for positive phototaxis were not significantly different from the control mean except at 1.9×10^{16} and 6.0×10^{18} photons $m^{-2} s^{-1}$, where the number of larvae responding was significantly less than that of the control ($n = 4$, $p < 0.05$).

Twenty-eight day old larvae continued to be negatively phototactic with mean responses ranging from 60 to 75% ($n = 4$, $p < 0.01$; Fig. 1E). A light intensity of 2×10^{18} photons $m^{-2} s^{-1}$ induced a mean positive response that was significantly less than the control. They were 1 order of magnitude less sensitive to light (threshold: 1.9×10^{16} photons $m^{-2} s^{-1}$) than 5.0 d old larvae (threshold: 1.9×10^{15} photons $m^{-2} s^{-1}$; Fig. 1E).

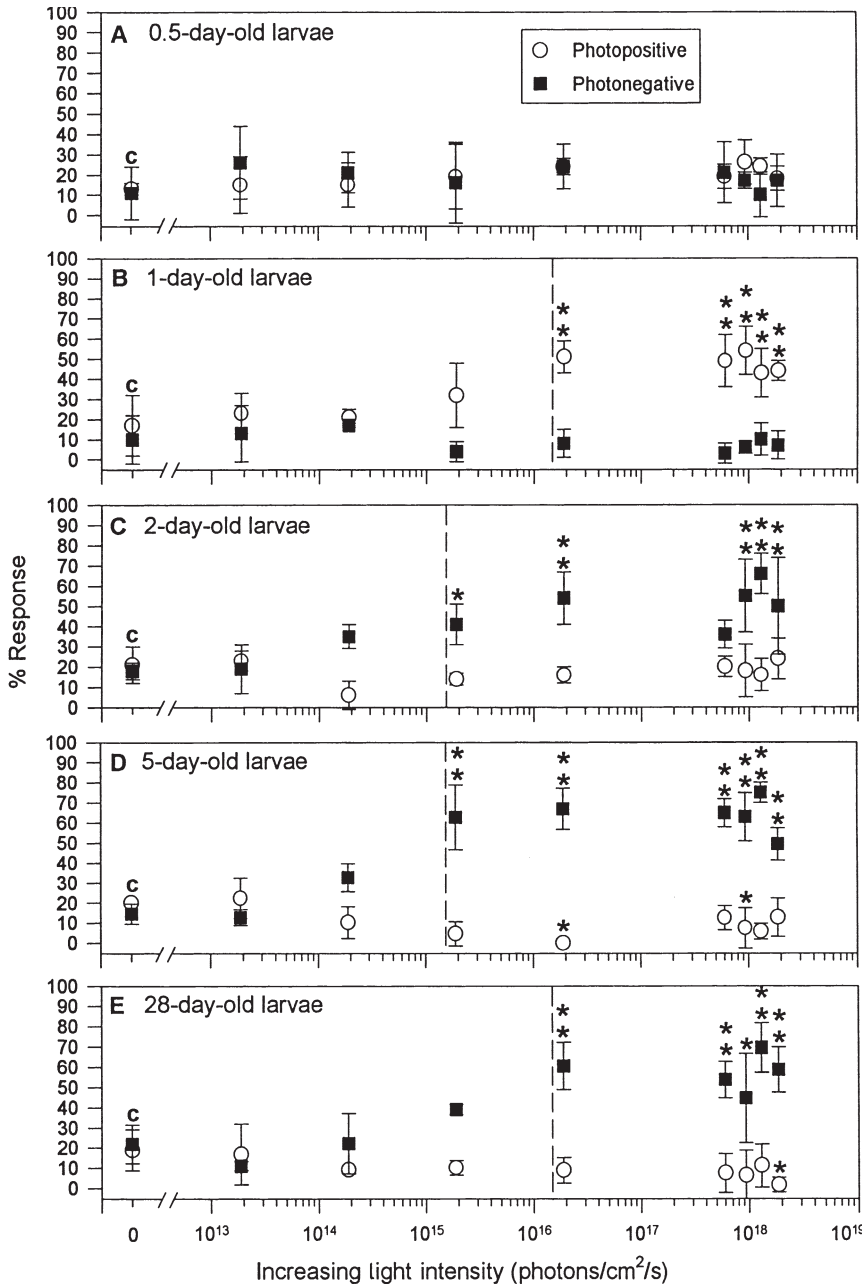


Fig. 1. Mean percentage (± 1 SD) positive (O) and negative (●) phototaxis for dark-adapted larvae (A) 0.5 (no eyes), (B) 1.0 (1 eye), (C) 2.0 (2 eyes), (D) 5.0 (4 eyes), and (E) 28.0 (4 eyes) d old. A 'c' indicates the control level of swimming in the positive and negative directions in the absence of light stimulation. Asterisks indicate that the mean phototactic response is significantly different from the control level (t -test; *: $p < 0.05$; **: $p < 0.01$). The threshold intensity of 500 nm light for phototaxis is indicated by a vertical dashed line. (Four replicates with 10 larvae replicate⁻¹; seawater temperature $\sim 23^{\circ}C$; salinity $\sim 34\%$)

Table 1. *Phragmatopoma lapidosa*. Analysis of ontogenetic changes in the geotactic response. (A) Two-way ANOVA ($n = 3$) with the independent factors of sign of response (2 levels) and age (5 levels). The dependent factor was the percentage response. Data were arcsine-transformed to meet ANOVA assumptions. (B) Tukey p -values comparing positive (P) and negative (N) geotactic responses for each age

(A) Source	SS	df	MS	F-ratio	p-value
Sign	11436.769	1	11436.769	94.348	0.001
Age	669.649	4	167.412	1.381	0.276
Sign \times age	6442.423	4	1610.606	13.287	0.001
Error	2424.377	20	121.219		
(B) Age (d)	p-value	Result			
0.5	0.001	P > N			
1.0	0.036	P > N			
2.0	0.001	P > N			
5.0	0.765	P = N			
28.0	0.001	P > N			

The minimum light intensities that induced a phototactic response (threshold) in *Phragmatopoma lapidosa* changed with development. It was 1.9×10^{16} photons $m^{-2} s^{-1}$ for 1 and 28 d old larvae but 1 log unit lower at 1.9×10^{15} photons $m^{-2} s^{-1}$ for 2 and 5 d old larvae. The latter threshold is about 7 orders of magnitude below surface sunlight intensity (about 10^{21} photons $m^{-2} s^{-1}$). *P. lapidosa* larvae are not as sensitive as crustacean larvae, which respond behaviorally to light intensities as low as 10^{11} to 10^{13} photons $m^{-2} s^{-1}$ (Forward et al. 1984).

In the absence of light, larvae displayed an ontogenetic change in geotaxis (Table 1A). Approximately 70 to 90% of 0.5, 1, and 2 d old larvae were geopositive

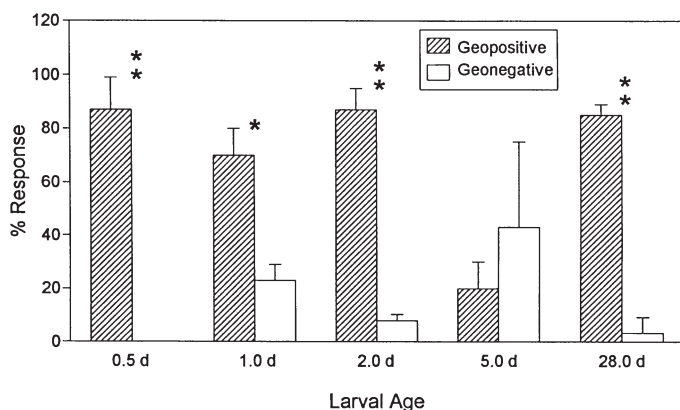


Fig. 2. *Phragmatopoma lapidosa*. Percentage (mean \pm 1 SD) of different-aged larvae that were positively geotactic (cross-hatched histogram) and negatively geotactic (open histogram). Asterisks indicate that the mean phototactic response is significantly different from the control level (t -test, *: $p < 0.05$; **: $p < 0.01$). (Three replicates with 10 larvae replicate $^{-1}$; seawater temperature $\approx 23^\circ C$; salinity $\approx 34\text{‰}$)

($n = 3$, $p < 0.04$ to 0.001) and were observed crawling at the bottom of the experimental chamber (Fig. 2, Table 1B) after 1 h in darkness. The remaining 10 to 30% appeared to move randomly throughout the water in the chamber. Five d old larvae did not have a statistically significant ($n = 3$, $p < 0.765$) geotactic response (Fig. 2, Table 1B). At this age, 40% of the larvae were geonegative (swimming in the top portion of the water column), 40% were swimming in the center sections of the chamber, and the remaining 20% were on the bottom. In contrast, 28 d old larvae became strongly geopositive again.

The observed ontogenetic changes in phototaxis are in contrast to Thorson's (1964) generalization that larvae of an intertidal species should remain photo-

topositive throughout larval development to maximize the chances of encountering intertidal adult habitat. Nevertheless, there is an ontogenetic change in responses to light and gravity that could affect larval dispersal and settlement. However, ecological inferences from our phototaxis and geotaxis results must be considered with caution because of potential experimental artifacts.

Phototaxis was measured in a horizontal trough with a directional light source that was not designed to mimic the angular light distribution in the sea. The problems associated with measuring phototaxis in an unnatural light field are reviewed by Forward (1988). In some studies the sign of phototaxis changes in different light regimens, while in other cases it does not (Forward et al. 1984, Forward 1988). Ideally, the sign of phototaxis at different light intensities should be measured in both kinds of light fields to verify that natural responses occur in a narrow light field. This comparison was not done in the present study, which limits the certainty that laboratory-observed phototactic responses actually occur *in situ*. However, the threshold light intensity that induces phototaxis generally is not affected by the nature of the light field.

In addition, our experiments did not rigorously test for geotactic response as in experiments by Pires & Woollacott (1983). The observed positive geotaxis may have been related to factors such as the geomagnetic field or partial pressure gradient of dissolved gases in the experimental chambers (Pires & Woollacott 1983). Further, it is not clear whether phototaxis overrides geotaxis when these taxes are antagonistic. In the field, positive phototaxis might override the observed positive geotaxis of 1 d old larvae (Fig. 2), because

early larvae of *Phragmatopoma lapidosa* have been observed to swim at the water's surface during the day (Eckelbarger 1976, Pawlik 1988). The observed positive geotaxis in the absence of light suggests that larvae descend at night, thereby undergoing reverse diel vertical migration. Positive phototaxis during early (~1 d old) development would bring larvae of *P. lapidosa* into surface waters during the day, which might enhance horizontal transport and dispersal because surface waters generally move faster relative to waters near the substratum (Denny & Wetthey 2001). Also, surface waters typically have more phytoplankton for food, which may accelerate development times (Harris 1953).

Negative phototaxis and positive geotaxis observed in 2 d old larvae of *Phragmatopoma lapidosa* suggest they would be deep in the water column during both day and night. This position should reduce the risk to visual predators and harmful UV light (Forward 1988). In contrast, at 5 d, larvae were negatively phototactic and geotactically neutral. This behavior predicts a diel vertical migration pattern, with larvae descending at sunrise in response to light and dispersing in the water column at night.

Twenty-eight d old larvae became negatively phototactic and positively geotactic like 2 d old larvae, which suggests that competent larvae descend in the water column during both day and night. Thus, if phototaxis- and geotaxis-mediated vertical migratory behavior is responsible for the onshore transport of sabellariid larvae, transport must occur before competency (i.e. 14 to 28 d old larvae).

Phototactic responses of other polychaetes also may move late-stage larvae to deeper waters for settlement. Young & Chia (1982) observed that light-adapted metatrochophores of the serpulid polychaete *Serpula vermicularis* were negatively geotactic in darkness but negatively phototactic when light was present. *Phyllodoce maculata*, *Polydora* sp., *Owenia fusiformes*, and *Pectinaria koreni* have all been found in higher abundance in the bottom layer in the Bay of Seine in the English Channel (Lagadeuc 1992, Theibaut et al. 1992, 1995). Late-stage larvae of these species may be negatively phototactic and may descend in response to lower salinity surface waters that come into the bay. It is possible that a similar behavioral mechanism keeps larvae of the sabellariid *Sabellaria vulgaris* in bottom waters of the Delaware Bay, where they have been sampled by Curtis (1978).

The relative importance of light versus other exogenous factors in controlling dispersal and transport of larvae to their settlement sites is still not clear. Other exogenous factors such as pressure, temperature, salinity, chemical cues, and turbulence induce behavioral responses that affect larval swimming (reviewed in

Chia et al. 1984, Marsden 1994, Young 1995, Welch et al. 1999). For example, behavioral responses to water currents and chemotaxis may also be important in the transport and settlement of *Phragmatopoma lapidosa* larvae. There are numerous observations of competent larvae of this species crawling on the substratum before metamorphosis (Eckelbarger 1976, Pawlik 1988) in the absence of flow. Pawlik et al. (1991) showed that competent larvae ascend to the surface of the water column in low flow conditions, a behavior that could facilitate transport to intertidal areas. In higher water flows, such as those that might occur in a turbulent intertidal area, competent larvae swim downward, crawl on the bottom, and settle at higher numbers on substrates with chemicals found in the tubes of conspecifics. Pawlik & Butman (1993) observed reduced settlement in the presence of very high flow conditions, possibly because of enhanced turbulent mixing.

It is likely that the nutritional state of competent larvae of *Phragmatopoma lapidosa* affects tactic behaviors. Pawlik & Mense (1994) demonstrated that *P. californica* undergo a reversible reversion to a precompetent condition in response to starvation. J. R. Pawlik (pers. comm.) observed that competent larvae would go from the bottom of a jar to the top after only 1 d of starvation. Theoretically, there should be more phytoplankton for larvae in surface waters *in situ*. Because larvae in the marine environment probably encounter fluctuating levels of food, it is likely that the nutritional state interacts with light and gravity to determine the vertical movements of larvae.

Young & Chia (1987) suggest that light might be most important in the search for settlement sites on small spatial scales. Settlement sites that are either shaded or darker are known to have higher numbers of invertebrate settlers than substrates that are exposed to higher intensities of light. These types of substrata are more cryptic and would better serve as a refuge from predation (Buss 1979, Young & Chia 1982), siltation, algal overgrowth and other sources of mortality (Young & Chia 1982).

Larvae of *Phragmatopoma lapidosa* do not remain photopositive throughout larval life as suggested by Thorson (1964) for an intertidal species. Instead, precompetent larvae (>1.0 d old) display negative phototaxis that results in diel vertical migration that should facilitate dispersal. At the end of development, positive geotaxis, negative phototaxis, and responses to currents (Pawlik et al. 1991) should bring competent larvae near the bottom, where chemotaxis (Pawlik et al. 1991) can mediate selection of a suitable habitat for settlement on or near conspecifics. Work that combines laboratory behavior experiments with direct observations of the vertical distribution of *P. lapidosa* larvae in

the water column is required to determine the importance of tactic behaviors in the transport of larvae to adult habitats. If competent *P. lapidosa* swim on the bottom, then higher intertidal abundances may result from preferences for topographical, chemical, or light conditions that are more common intertidally than subtidally.

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