Reference: *Biol. Bull.* **197:** 309–314. (December 1999)

Swimming and Buoyancy in Ontogenetic Stages of the Cushion Star *Pteraster tesselatus* (Echinodermata: Asteroidea) and Their Implications for Distribution and Movement

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The eggs of some marine fish (1) and benthic invertebrates such as many corals (2, 3) and lecithotrophic echinoderms (4, 5) are positively buoyant at time of release from the parent, and density increases later in ontogeny. How these eggs and larvae are distributed in the water column and eventually reach suitable habitat for settlement will depend, in part, on their vertical velocity and on the turbulence in the water (i.e., *the eddy diffusivity). For eggs and unhatched stages, vertical velocity is passive and depends on egg or embryonic volume and density relative to the seawater (6, 7). For motile stages, vertical velocity depends on relative density, swimming ability, and behavior of the larvae (8, 9). We have measured the vertical velocity of eggs and larvae of the sea star* Pteraster tesselatus *Ives, which spawns floating eggs (1.1 to 1.5 mm diameter) that develop into nonfeeding larvae and spend several weeks in the plankton before settling to the benthos (10). Because of the simple shapes of eggs and larvae, we used force balance equations for drag and buoyant forces to determine the density of eggs and two larval stages. Initially the eggs were positively buoyant and floated upwards at about 1 mm/s. Even formalin-fixed eggs floated in seawater, so concentrations of light ions were not responsible for the buoyancy. The density of the larvae increased in the first 10 to 11 days, but it varied considerably between the three larval cohorts examined. Ten-day-old larvae that were negatively buoyant swam downward at mean speeds as high as 1.7 mm/s, while positively buoyant larvae of the same age swam upward at about 1 mm/s. These patterns of buoyancy and swimming velocity should initially facilitate dispersion and later promote settlement into subtidal habitats.*

Received 24 May 1999; accepted 16 August 1999.

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Position in the water column and relative to the sea bottom will determine the amount of advection and the likelihood of encountering suitable habitat for settlement; variation in vertical position between related propagules will increase the spread of siblings or species (9, 11, 12). Predicting the depth distribution of eggs and larvae and other planktonic organisms requires information on their vertical velocity and on the turbulence structure of the water column (6–9). Alternatively, if the vertical velocity and distribution of propagules are known, one can estimate the turbulence structure (6). Many studies examine the density of fish eggs, and some relate this to their vertical distribution (*e.g.,* 6, 7, 13, 14). For larvae of benthic invertebrates, studies on swimming behavior and responses to environmental cues dominate discussions of vertical distribution (see reviews 15–17). With the exception of numerous studies on crustacean meroplankton (*e.g.,* 18, 19), there are few observations on vertical distribution as a function of stage of development or on density of the eggs and larvae of benthic invertebrates. Medeiros-Bergen *et al.* (20) showed that the lecithotrophic larvae of several sea cucumber species, which are released as positively buoyant eggs, can be distributed to depths exceeding 50 m, though they were most common in the upper 20 m of the water column. Young and Cameron (21) measured the rate of rise of positively buoyant eggs of the bathyl echinoid *Phormosoma placenta,* calculated the density of the eggs, and predicted that these embryos would

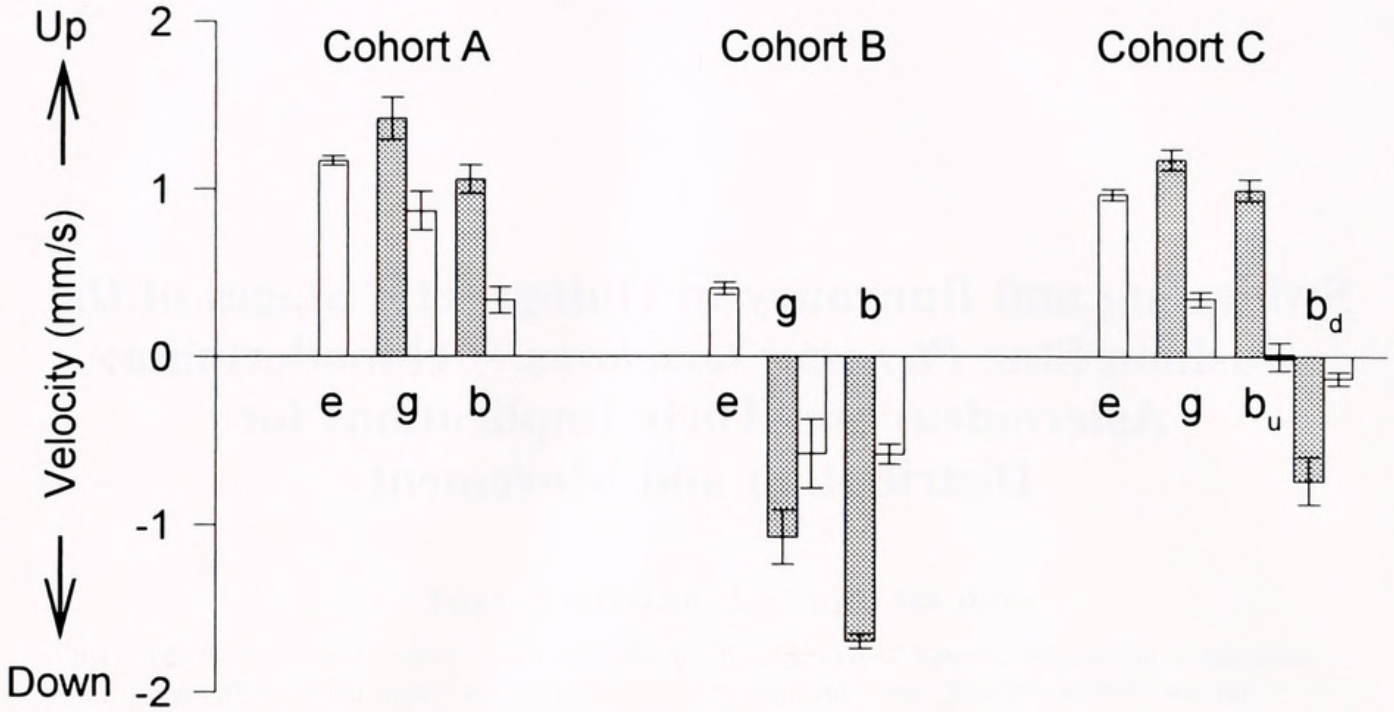

Figure 1. Rising and sinking rates of eggs with jelly coats (e), hatched gastrulae (g), and bilobed larvae (b) from three cohorts of *Pteraster tesselatus*. The open bars represent passive movement of eggs or deciliated larvae, and the shaded bars represent swimming larvae. The value on each bar represents the mean from 10 or 12 eggs, gastrulae, or larvae. Error bars are 1 S.E. b_u, bilobed larvae swimming up; b_d, bilobed larvae swimming down.

We collected adult *Pteraster tesselatus* Ives near San Juan Island, Washington (USA), in May 1998. Adult sea stars were induced to spawn by intracoelomic injection of 2–3 ml of 100 μM 1-methyladenine (4). We collected the spawned eggs from each of three females and washed them in filtered seawater (FSW). Larval stages that we studied were from eggs exposed to sperm at low concentrations. We do not know whether the sperm fertilized the eggs or was necessary for development, as oocytes of this species have been reported to develop without sperm (see Ref. 10).

Vertical speeds were measured in a cylindrical chamber (10 cm in diameter, and 15 cm tall) filled to within 2 cm of the top with 1 liter FSW (salinity, 28‰) and marked with graduations that circled the chamber at 2-cm intervals. The chamber was covered and immersed in an insulated aquarium maintained by a circulating water bath at a temperature of 12.2° (±0.1°C) to minimize convection currents that might affect the movement of the eggs and larvae in the chamber. Positively buoyant eggs and larvae that floated or swam up were introduced to the center of the chamber bottom. Negatively buoyant larvae and those that swam down were released at the surface in the center of the chamber. Rising and sinking times were measured for two successive 2-cm intervals in the middle of the water column where wall effects were minimal. Measurements that differed more than 10% were discarded. The individual was then repositioned at the bottom (or top) and allowed to rise (or sink) again; the new times were recorded. The average time to rise or sink 2 cm was calculated and used to determine speed.

rise into the warmer surface waters where their rate of development would be increased.

Measurement of vertical velocities of invertebrate eggs and swimming larvae is relatively simple and can be used to determine ontogenetic changes in velocity and density as well as to predict distributions of propagules in the field. Measurements on multiple cohorts can reveal variation among offspring from different parents. Among echinoderms, lecithotrophic larval development has evolved repeatedly from planktotrophic larval development (22–24), and many of the lineages with derived, nonfeeding larval development also have large, positively buoyant eggs that have evolved from negatively buoyant ones (5). Shifts in egg and embryonic buoyancy may require functional changes in swimming that are revealed by observations on vertical movement and orientation.

For three cohorts (from separate female parents), we measured the vertical velocities of unfertilized eggs, newly hatched gastrulae (5 d), and older, bilobed larvae (10–11 d). After swimming velocities were measured for individual larvae, they were deciliated in hypertonic seawater and their vertical velocity was measured again and used to determine the density of these stages.

Eggs (with intact jelly coats) always floated up, rising at speeds between 0.2 and 1.3 mm/s. The mean rising rates of eggs were 1.2, 0.4, and 1.0 mm/s for cohorts A, B, and C, respectively (Fig. 1). An ANOVA followed by a multiple comparisons test indicated that the rising rates of eggs were

significantly different among cohorts ($F = 135.6$, df 2,27, $P < 0.001$; Tukey HSD test, $p < 0.001$ for all three pairwise comparisons).

Differences in egg rising rates among cohorts were due to differences in egg density and in part to differences in the egg and jelly coat volumes (Fig. 2a). Cohorts had significantly different egg densities (ANOVA, $F = 125.6$, df 2,27, $P < 0.001$; Tukey HSD test, $P < 0.001$ between all three pairwise comparisons). Eggs of cohort A, with the fastest mean rising rate, also had the lowest density (1020.2 kg/m^3); eggs of cohort B, with the slowest rising rate, had the highest density (1021.4 kg/m^3). Comparisons of the egg diameter and jelly coat thickness revealed significant variation among the cohorts in each trait (egg diameter ANOVA, $F = 125.3$, df 2,27, $P < 0.001$; jelly coat ANOVA, $F = 23.02$, df 2,27, $P < 0.001$). However, multiple comparisons (Tukey HSD tests) revealed that cohorts A and B each differed from cohort C in egg diameter ($P < 0.001$) and jelly coat thickness ($P < 0.001$), but A and B were not significantly different from each other in egg diameter ($P = 0.76$) or jelly coat thickness ($P = 0.15$). Thus differences in rising rates between cohorts A and B were due to differences in egg density, whereas differences between cohorts A and C and cohorts B and C were due to both density and dimensions of the eggs. Though eggs of cohort C had an intermediate density, their relatively large diameters and thin jelly coats contributed to their rising rates, which approached those of cohort A.

To determine whether active metabolic concentration of light ions was a possible buoyancy mechanism in the eggs of *Pteraster,* we fixed eggs in 3% formalin in filtered seawater (FSW) for several hours and then transferred them to fresh FSW. Formalin-fixed eggs floated, indicating that their positive buoyancy did not involve the metabolic mechanisms that maintain ion gradients (*e.g.,* 25, 26). Positive buoyancy may also be due to the presence of buoyant lipid reserves. According to Jaeckle (27), lipid content in lecithotrophic eggs of echinoderms ranges between 34% and 50% of total organic weight and is twice that found in planktotrophic eggs. A high lipid content could reduce the densities of the eggs and cause them to float. No data are available on the biochemical composition of *P. tesselatus* eggs and larvae or on the possible importance of lipid content in floating.

For another estimate of egg density, we assumed that the jelly coats were neutrally buoyant in seawater (Fig. 2a). Because the jelly coat has a very high water content, we believe this assumption was reasonable. Furthermore, the jelly coats of eggs of the sand dollar *Dendraster excentricus* are neutrally buoyant (28). The estimated densities of eggs without jelly coats were also significantly different among cohorts (ANOVA, $F = 159.4$, df 2,27, $P < 0.001$; Tukey HSD test, $P < 0.001$ between all three pairwise comparisons). Differences in egg density may be due to variation in biochemical composition and could also reflect variation in egg or maternal nutritional state. The estimated densities of the eggs without jelly coats were lower by 0.4 kg/m^3 (range, 0.7 to 0.2 kg/m^3) than those for the eggs with jelly coats. If the jelly coat is neutrally buoyant, it slows the rising rate of the buoyant egg. We calculated that the mean rising rates of eggs without jelly coats would be 12%, 15%, and 7% faster than those measured for intact eggs of cohorts A, B, and C respectively.

Eggs hatched after 3 to 4 d, and by day 5 swimming gastrulae were either at the water surface or at the bottom of their mesh-bottom culture vessels, depending on the female of origin. Gastrulae in cohorts A and C swam up at mean speeds of 1.4 and 1.2 mm/s respectively. When deciliated, all gastrulae in these cohorts were positively buoyant, rising at mean speeds of 0.9 mm/s (cohort A) and 0.3 mm/s (cohort C). In contrast, all gastrulae of cohort B swam down at a mean speed of 1.1 mm/s; when deciliated, 7 of 10 gastrulae were negatively buoyant and three others were slightly positively buoyant. The mean sinking speed of deciliated gastrulae from cohort B was 0.6 mm/s (see Fig. 1).

Larvae swam up or down, usually along a straight, vertical path, and rotated around their anterior-posterior axes as they swam. Regardless of its direction of vertical motion, a gastrula always had its anterior end up and its posterior end, with blastopore, down. Deciliated gastrulae also showed this orientation whether they rose or sank. This posture was assumed as soon as a swimming gastrula was placed in the stable water column and was maintained, without exception, as long as the larva was moving in the water column. This orientation appeared to result from an uneven distribution of buoyancy, with the anterior end being less dense than the posterior end. Because swimming speeds downward exceeded sinking speeds, the cilia must have produced currents that moved water from the posterior end toward the opposite end. The downward movement was sustained and was not likely to result from the transient reversal of ciliary beat that is known for planktotrophic larvae (29; Emlet, pers. obs.). The consistent and sustained downward swimming by gastrulae of cohort B, with the blastopore leading, indicates that the coordination of their cilia was different from that of negatively buoyant gastrulae that swim up, anterior end first, by moving water from anterior to posterior. This change in ciliary coordination from that typical of planktotrophic species has also been observed in downward-swimming, positively buoyant, lecithotrophic larvae of the echinoids *Heliocidaris erythrogramma* and *Holopneustes purpurascens* (Emlet, pers. obs.).

Larvae developed into a bilobed stage, with a circumferential groove that divided the larval body into anterior and posterior regions. By 10–11 d after fertilization, podia were beginning to form within the circumferential groove, but most larvae were still shaped like prolate spheroids and

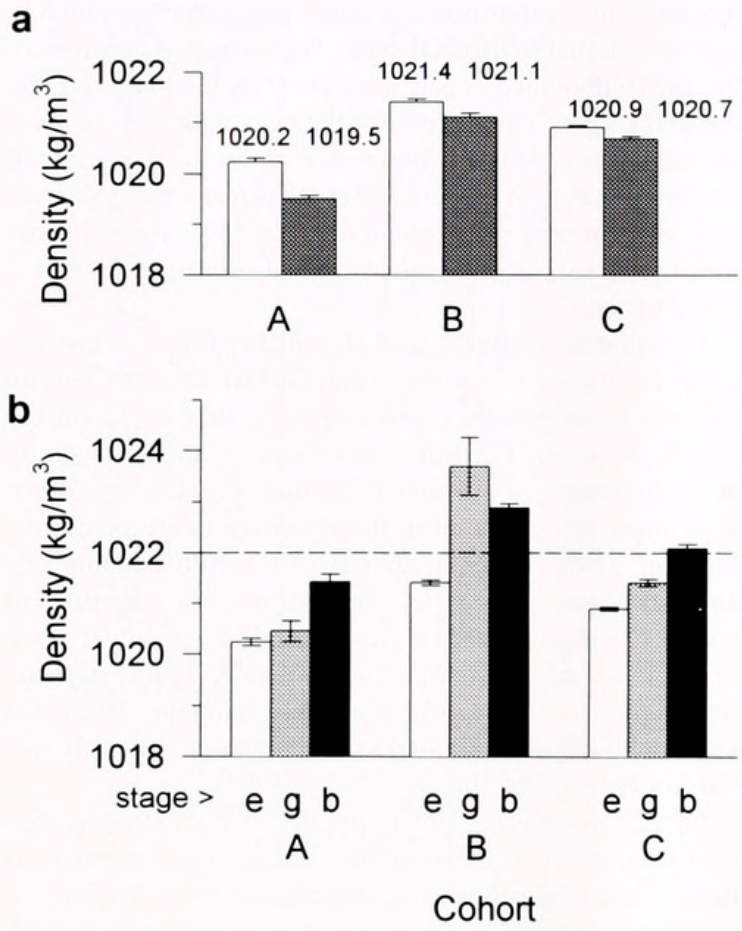

Figure 2. Density of unfertilized eggs (a) and eggs and larvae (b) for three cohorts of *Pteraster tesselatus*. (a) Two estimates of density: open bars are for eggs with jelly coats; dark bars are for eggs only, assuming the jelly to be neutrally buoyant. The value on each bar represents the mean for 10 eggs. Error bars are 1 S.E. (b) Ontogenetic changes in density from eggs and two larval stages for three cohorts. The bars represent the means for eggs with jelly coats (e), hatched gastrulae (g), and bilobed larvae (b). All sample sizes were 10 eggs or 10–12 larvae. Error bars are 1 S.E. The dotted line shows the density of seawater at 12.2°C and 28‰ salinity.

The Reynolds numbers (Re) were ≤ 0.8 for all eggs and <0.5 for all passively moving larvae, so we used the low-Re equation for terminal velocity and solved for the density of the egg or larva (see *e.g.*, 31, equation 15.11, p. 340). We treated eggs as spheres and larvae as prolate spheroids; in the latter case we included a shape-correction term (see 32). We measured the diameter of each egg and the thickness of the jelly coat on a microscope with a 4× objective, after the egg rising time was measured. A suspension of India ink was added to reveal the edge of the translucent jelly coat. The length and width of gastrulae and larvae at their widest point were measured after larval swimming times were measured. Each larva was then deciliated by placing it in double-strength seawater for 10–15 s, then immediately rinsed three times in normal-strength seawater. This method has been used to collect cilia from echinoderm larvae and does not kill the larva; in fact, cilia are regenerated in a matter of hours (*e.g.*, 33; Emlet, pers. obs.). After the deciliated larvae were equilibrated in seawater at 28‰, we placed them individually in the chamber and measured their passive rising or sinking rates. The seawater in the chamber was at 12.2°C and had a salinity of 28‰; from tables (34) we determined its viscosity to be 0.0013 N s/m^2 and its density to be 1022 kg/m^3.

Sources of error in our calculations of the densities of eggs and larvae include our measurements of dimensions (including jelly coat for eggs) and our assumptions of shape (prolate spheroid or spheres). Measurement errors of 100 μm (7%–10% of egg + jelly diameters) would result in deviations of density of ≤ 0.5 kg/m^3. These errors would be random and should inflate the variation without biasing the means. Our assumption of shape could systematically bias the means through estimates of drag force or volume, but again the magnitude of the error would be about 0.2 kg/m^3. We do not think that any of these biases created erroneous trends in the data.

were not as advanced as the 8-day larva in figure 3 of McEdward (10). The swimming direction and buoyancy of larvae varied among the cohorts (Fig. 1). All larvae of cohort A swam up and were positively buoyant after they were deciliated, and all those of cohort B swam down and were negatively buoyant after they were deciliated. Cohort C was highly variable, with 7 of 12 larvae swimming up and 5 of 12 swimming down. Five of the seven larvae of cohort C that swam up were either positively or neutrally buoyant after being deciliated, whereas all of those that swam down were negatively or neutrally buoyant after being deciliated. The exceptions were two larvae that swam up opposite the direction of their passive motion. Compared to gastrulae, the bilobed larvae swam up at slower speeds or down at higher speeds, reflecting the generally increased density of these later stages (Figs. 1 and 2b). Bilobed larvae showed the same orientation that gastrulae did with larval anterior (adult oral) up and posterior (adult aboral) down regardless of their direction of swimming.

During development, the density of gastrulae and larvae increased relative to that of the eggs, though cohorts varied in the extent and timing of increase (Fig. 2b). Cohorts A and C showed consistent increases in density, with the bilobed larvae of cohort C obtaining a mean density not different from that of seawater (t test, $t = 0.95$, df = 11, $P = 0.362$). In contrast, the mean density of gastrulae of cohort B exceeded that of seawater ($t = 3.0$, df = 9, $P = 0.015$), and some of these individuals had higher densities than any other stages across all cohorts (Fig. 2b).

Differences in density among eggs (without jelly), gastrulae, and bilobed larvae were analyzed separately for each cohort because of significant heterogeneity of variances within cohorts A and B but not cohort C (Cochran's C tests, $P < 0.01$ for cohort A, $P < 0.001$ for cohort B, $P = 0.11$ for cohort C). Cohorts A and C had significantly different densities among all stages. (Cohort A: Kruskal-Wallis test, $H = 21.8$; multiple comparisons with a nonparametric equivalent of the Tukey test (Ref. 30), $P < 0.05$; cohort C: ANOVA, $F = 91.9$ df 2,29, $P < 0.001$; Tukey HSD, $P \leq 0.002$ for all comparisons). Cohort B also had significant differences in density among stages (Kruskal-Wallis test, $H = 19.9$, $P < 0.001$). Nonparametric pairwise comparisons indicated that density differed significantly between eggs and gastrulae ($P < 0.001$), between eggs and bilobed larvae ($P < 0.005$), but not between gastrulae and bilobed larvae ($P > 0.5$).

McEdward (10) observed that eggs and embryos of *P. tesselatus* were positively buoyant until the time close to

settlement, when larvae swam near the bottom. The present study confirms that observation for two cohorts, but a third cohort was negatively buoyant soon after hatching. The rising speeds of eggs and the swimming speeds of gastrulae and larvae of *Pteraster* usually exceeded 1 mm/s. Although still slow, these rates are about five times the sinking speeds of planktotrophic eggs and two to three times the swimming speeds of planktotrophic larvae of echinoderms (5). Our measurements showed significant increases in density as development progressed (Fig. 2b), with bilobed larvae approaching or exceeding the density of seawater. Becoming less positively buoyant or negatively buoyant may increase downward swimming speed and assist larvae in the search for suitable settlement habitats.

The mean downward swimming speed of 1.7 mm/s for bilobed larvae of cohort B should allow them to overcome resuspension by turbulent mixing during some parts of the tidal cycle. Gross *et al.* (8) modeled larval settlement in tidally dominated flows found in estuarine and shelf conditions, exploring how larval swimming speed influenced the probability of settlement. For a water depth of 50 m, the model predicted that a doubling of fall velocity from 0.8 to 1.6 mm/s resulted in a 12-fold increase in the probability of contacting the bottom throughout the entire tidal cycle. During periods of weak tidal flows, the model predicted that up to 40% of larvae swimming at 1.6 mm/s could interact with the bottom and possibly settle, while 1% to 4% of those swimming at 0.8 mm/s would be capable of settling (8).

Our studies were conducted at a salinity of 28‰ and a temperature of 12.2°C, conditions typical of the surface waters near San Juan Island, Washington. Though seawater higher in salinity (and hence more dense) is found in other coastal settings, we believe that our results are applicable to these regions as well. Preliminary observations showed that when deciliated larvae of *Pteraster* that were negatively buoyant at 28‰ were placed in water with a salinity of 30‰, they would initially float for a few minutes before sinking at constant speed. A possible explanation is that the osmotic difference resulted in water loss and salt gain by larvae, restoring the relative density of the larvae in seawater. Further studies that vary salinity would be necessary to determine if the absolute magnitude of the differences between the density of the larvae and the seawater are the same when the salinity changes. Other studies (Emlet, unpub. data) of buoyancy and swimming in ontogenetic stages of two echinoids at a salinity of 35‰ found patterns similar to those reported here.

This study has documented ontogenetic changes in buoyancy from positive to either neutral or negative buoyancy and found changes in swimming direction and speed that correlate with buoyancy for one species of sea star with positively buoyant eggs. The eggs and larvae exceeded 1 mm in diameter and departed from the density of seawater by as much as 2.0 kg/m^3. (For comparison, the density of seawater changes by 2 kg/m^3 for each 10°C change in temperature.) Though small, the resulting difference in density caused the eggs and larvae to rise or sink relatively rapidly compared to planktotrophic larvae, and rates of movement were augmented later in development by ciliary swimming. These patterns should initially facilitate dispersion from the site of egg release and then promote settlement. Buoyancy and swimming for specific stages were also found to vary within and between cohorts, which should increase the spread of siblings as well as offspring of conspecifics (12). Finally, the swimming orientation of anterior up, posterior down that was maintained during development suggests that the ciliary coordination of positively buoyant larvae has been changed from that of planktotrophic ancestors.

Acknowledgments

A. O. D. Willows, Director, provided space and facilities at the Friday Harbor Laboratories. We thank R. Strathmann and J. Hoffman for contributing ideas throughout this study and for valuable comments that improved the manuscript. The manuscript was also improved with helpful comments by O. Mokady and anonymous reviewers. Funding was provided by the Friday Harbor Laboratories Marine Science fund (# 63-3972), an Aharon Katzir Foundation travel grant to D.K, and NSF grant OCE-9416590 to R.B.E.

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