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Phototaxis and vertical migration of the queen conch (*Strombus gigas linne*) veliger larvae

Peter J. Barile^{a,*}, Allan W. Stoner^b, Craig M. Young^c

^a Florida Institute of Technology, 150 W. University Blvd., Melbourne, FL 32905, USA

^b Caribbean Marine Research Center, 805 46th Place East, Vero Beach, FL 32963, USA

^c Harbor Branch Oceanographic Institution, ECOS Division, 5600 Old Dixie Highway, Ft. Pierce, FL 34946, USA

Abstract

Ontogenetic changes in phototaxis of queen conch *Strombus gigas* (Linne) veligers were studied in the laboratory and in field mesocosms. In the laboratory, larvae showed a strong positive phototaxis and negative geotaxis during early stages. Positive phototaxis decreased as a function of age from 100% positive response at Day 1 to $\approx 50\%$ at metamorphic competency. In field mesocosm experiments, vertical position correlated significantly with light intensity. Vertical migration patterns were not affected by the presence or absence of solar UV, and did not vary as a function of ontogeny. The overall pattern of vertical distribution in the field appears to be controlled by negative geotaxis moderated by negative phototaxis at high light intensities.

Keywords: Larvae; Phototaxis; *Strombus gigas*; UV light; Vertical migration

1. Introduction

Most zooplankters alter their vertical distribution in the water column on a daily basis (see reviews by Forward, 1976, 1988; Longhurst, 1976; Sulkin, 1984). These migration patterns have generally been described as a function of daylight (i.e. diel or nocturnal migration, twilight migration, and reverse diel migrations; Huchinson, 1967), which is one of the most important stimuli available to marine zooplankton for orientation (Thorson, 1964; reviews by Forward 1976, 1988). The most common pattern of photoresponse among invertebrate larvae is positive phototaxis at lower intensities and negative phototaxis at high intensities (Forward, 1976). Segal (1970) concluded that

* Corresponding author.

high light intensity moderates the attraction of larvae toward the surface even though they may be photopositive.

Ultraviolet light, specifically UV-B (290–320 nm), often effects the behavioral responses of zooplankton. Zooplankton may avoid potentially harmful UV solar radiation by nocturnal migration (Damkaer & Dey, 1982), and Pennington & Emler (1986) concluded that daytime vertical depth distribution of larvae of the sand dollar *Dendraster excentricus* is regulated by solar UV. However, the effects of solar UV on the migration patterns of copepodite larvae of the copepod *Acartia hudsonica* have not been substantiated (Bollens & Frost, 1990).

No information is available on the effects of solar UV on vertical distribution patterns of most other larval forms, including gastropod veligers.

Some novel techniques have recently been employed in the investigation of larval behavior in the field. In addition to direct observation in the field (Olson, 1985; Young, 1986; Olson & McPherson, 1987; Davis, 1987; Bingham & Young, 1991), mesocosm studies have been useful for analyzing larval behavior in situ. Pennington & Emler (1986) used clear, plastic vertical enclosures to study migration patterns of the echinoid larvae *Dendraster excentricus*. A similar apparatus was used by Kaartvedt et al. (1987) to monitor vertical distributions of larval scallops *Pecten maximus*. In this study, we used mesocosm and laboratory experiments to investigate the relative importance of light and gravity in regulating vertical movements of the larvae of queen conch (*Strombus gigas* Linne).

2. Materials and methods

2.1. Subject species

The queen conch is distributed throughout the Caribbean and is the second most important fisheries species in the region (Brownell & Stevely, 1977). Although much is known about the life history of juveniles and adults (Randall, 1964; Appeldoorn & Rodriguez, 1993), very little is known about the ecology of the veliger larvae.

Conch veligers used in this study were cultured at the Keys Marine Laboratory “Experimental Conch Laboratory” on Long Key, Florida by the Florida Department of Natural Resources during the summer of 1992. Veligers used in these experiments were 1-day-old newly hatched larvae which contained embryonic yolk reserves, 4- and 16-day veligers which were fed *Isochrysis galbana* and *Chaetoceros gracilis*, and metamorphically competent veligers, which had pigments (D’Asaro, 1965) indicating competency, at 33 days until induction of settlement.

2.2. Photobehavior experiments

To determine if larvae prefer light or dark environments, the veligers were offered a choice between shaded or unshaded regions of a container in the laboratory. A 28 × 35 × 5 cm rectangular plastic container was covered with black plastic to exclude any external light sources. Half of the cover was removed to create a light region. A

Techni-quip T/Q/FOI-1 fiber optic unit was positioned to illuminate the “light” region from above. Filtered seawater was added to the container until the level was about 1–2 cm in depth. Light output was adjusted to mimic midday outdoor light levels (2300–2500 $\mu\text{E}/\text{m}^2/\text{s}$). Two experiments were run, the first with individual larvae, and the second with a group of 10 larvae to test for density effects; the experiments were replicated 10 times. The veligers were added to the center of the container, and, after 5 min, their horizontal positions in the container were recorded on graph paper. Light levels at the final position were measured with a Li-Cor radiometer equipped with a cosine sensor. Photoresponse as a function of larval age and density were tested with two-way ANOVA after variances of means were tested for homogeneity with Cochran’s test at $p = 0.05$.

Phototaxis experiments using horizontal light were run in a plastic container, similar to that described above. Fiber optic light was directed through the end of the container toward the center. Individual veligers were added to the center of the container and tracked for 5 min. Horizontal paths were traced on grided paper and final positions were recorded. Ten runs were performed with 1-, 4-, 16-, and 33-day-old veligers. Directional uniformity of responses to the light stimulus was tested with circular statistics (Zar, 1984). Values were expressed as vectors and mean angles were evaluated for directional significance among age classes.

2.3. Solar UV experiment

The distributions of veligers in the presence and absence of solar UV light were measured in small containers deployed outside at 1215 on 14 August, 1992, in full sunlight. Three replicate 1.5-l beakers were filled with filtered seawater and 50 newly hatched veligers were added to each. Three different treatments were tested: (1) uncovered beakers receiving the full solar light spectrum, (2) beakers covered with UV transparent plexiglass, and (3) beakers covered with UV absorbing plexiglass, which removed > 85% of UV-A and B (290–400 nm) (Fig. 1). Experimental containers were placed in a water bath with flow-through seawater to provide a constant homogeneous

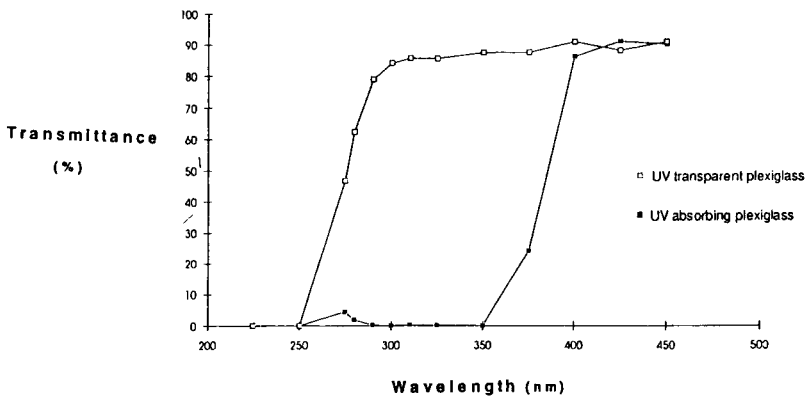


Fig. 1. Transmittance curves for the two Plexiglas materials used in solar UV experiments.

temperature to experimental containers. Numbers of larvae in the upper 1–2 cm of the water were counted after 30 min. Values were tested for homogeneity of variance with Cochran's test and then treatment effect was tested with one-way ANOVA.

2.4. Vertical tube experiments

Two experiments were run in laboratory conditions to evaluate, qualitatively and quantitatively, vertical migration behavior. Two clear acrylic tubes (175 × 6 cm) were filled with filtered seawater and covered with black plastic to block outside light. One was covered at the top to create total darkness, while the other was illuminated from the top with fiber optic light at 400 $\mu\text{E}/\text{m}^2/\text{s}$. Fifty larvae were added to each column. Experiments were replicated three times with 4- and 37-day-old veligers; the latter had morphological features indicating competency. After 30 min, we counted larvae at the surface of each column. Data were compared between treatments and age with a Student's *t*-test, because larval density was not independent of position in the tubes, thus violating the conditions of ANOVA.

2.5. Field mesocosm experiments

Vertical migration behavior was examined in an in situ experiment performed in a leeward embayment at the Keys Marine Laboratory on Long Key, Florida. A floating PVC frame was constructed to suspend nine cylindrical 6-ml polyethylene bags ($L = 3\text{ m}$, $d = 29\text{ cm}$, $V = 139\text{ L}$). Each column was equipped with 0.25 inch airline tubing to collect water and larvae from the surface and from depths of 1, 2, and 3 m inside of each column. At the end of each tube, a funnel with a polyethylene elbow was attached in an upright position to catch veligers which sank in response to the water motion. A hand-held siphon pump was attached to the tubes to withdrawal 1-l samples from each depth in the water column.

The nine bags were filled with filtered seawater and divided into three treatments. Three columns were open at the top to allow penetration of full ambient light. Three were covered with UV absorbing Plexiglas, and three were painted black and covered with black plastic to prevent solar light penetration.

Three separate experiments were run in August and September of 1992 with 1-, 4-, and 16-day-old veligers, held at densities of 25/l, 25/l, and 15/l, respectively. Veligers were introduced to the surface of the columns at midday and were allowed to distribute within the columns for 8 h before sampling. Samples were collected subsequently at 0100, 0700, 1300, and 2000. Light intensity was recorded within the columns at sampling depths after each sampling session using a Li-Cor 1000 quantum meter with a cosine sensor. Temperature and salinity were also measured at sampling depths within the columns using a YSI temperature & salinity meter. Veligers were collected on a sieve and counted with the aid of a dissecting microscope.

Statistical analyses were performed on arcsine-transformed larval position data, with each value expressed as a percentage of the total count. Variances of means were tested for homogeneity with Cochran's test at $p = 0.05$. Three-way ANOVA was used to compare the effects of treatment, depth, and time in each experiment. Multiple com-

parisons of means were made with the Tukey-Kramer method. Mean depth distribution of larvae from experimental mesocosms was calculated by ranking the abundances of larvae by depth.

3. Results

3.1. Photobehavior experiments

Photoresponse in the vertical light experiment was analyzed using percent positive response as the dependent variable (Fig. 2). Two-way ANOVA indicated no significant difference in responses of individual larvae and groups of 10 ($F_{1,72} = 0.214$, $p > 0.05$); however, significant differences in positive responses related to larval age were detected ($F_{3,72} = 12.643$, $p < 0.05$). Tukey's multiple comparison test showed differences ($p < 0.05$) between the responses of Day 1 and Day 16 larvae ($Q = 0.595$), Day 1 and Day 33 larvae ($Q = 0.885$), and Day 4 and Day 33 larvae ($Q = 0.586$). Larvae that responded to the light side of the container always avoided the center of the vertical light beam.

Tracks of veligers responding to horizontal light show that early stage veligers had a much stronger directional orientation than older individuals (Fig. 3). At the end of the experiment, early stage veligers were more likely to be present at the light source than older larvae. The Rayleigh test for circular uniformity indicated that the mean angles for all age groups were significant (Table 1).

3.2. Solar UV experiment

Conch larvae showed no apparent behavioral responses to the presence or absence of solar UV wavelengths during the midday experiment. Larval abundances in the upper 2 cm of the surface water were not significantly different ($F = 5.77$, $p > 0.05$) among open beakers (mean = 7.6 ± 2.1), beakers covered with UV absorbing Plexiglas

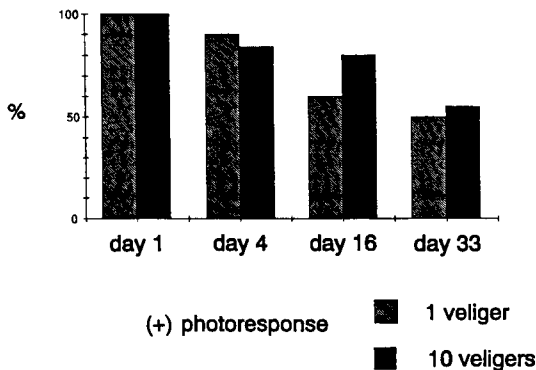


Fig. 2. Percentage of positive photoresponses by veligers as a function of age and density.

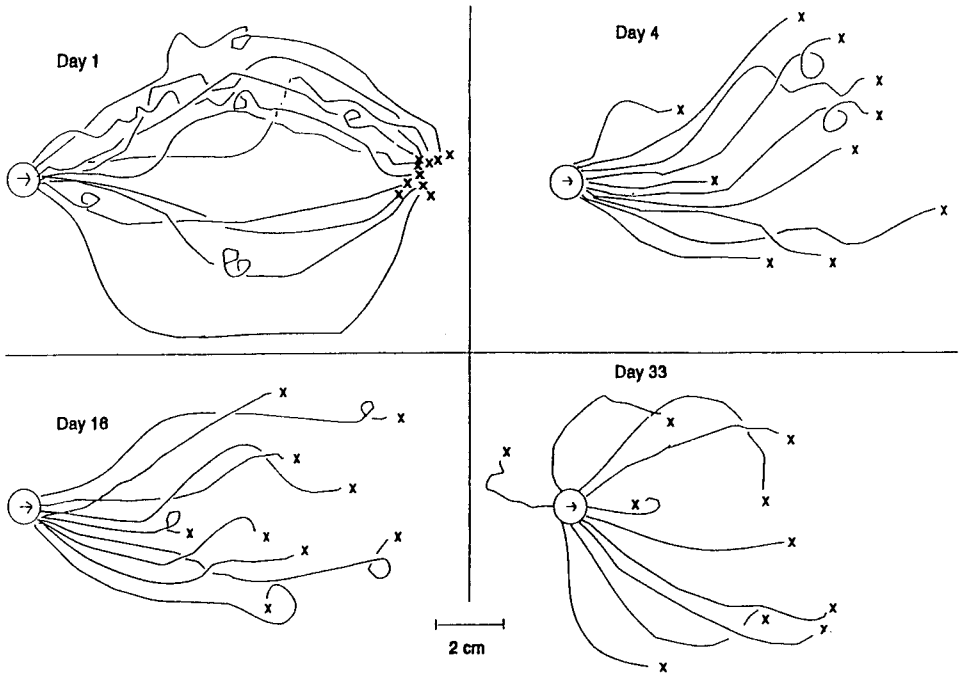


Fig. 3. Paths of veliger phototaxis as a function of age. Light source is from the right of each diagram.

(mean = 8.0 ± 2.0), and beakers with UV transparent Plexiglas covers (mean = 0.6 ± 2.1).

3.3. Vertical tube experiments

The depth distribution of 4- or 37-day veligers between dark and lighted columns was not different (Table 2). However, when age was the dependent variable, a higher proportion of 4-day larvae were at the surface (mean = 83%) than 37-day larvae (mean = 28%), and the difference was significant in both light and dark treatments.

Table 1
Rayleigh's test for significance of the mean angle of phototaxis in four age groups of veligers

Age	R ($\alpha = 2.92$)	Significance of \bar{x} angle
Day 1	10	Yes
Day 4	8.95	Yes
Day 16	9.69	Yes
Day 33	7.99	Yes

Table 2
Student's *t*-test for surface values of veliger abundances in vertical tube experiments

(A)				
Age (days)	Treatment		<i>t</i>	<i>p</i>
	light	dark		
4	42 ± 5	41 ± 6	4.000	0.572
37	6 ± 4	5 ± 1	0.346	0.762

(B)				
Treatment	Age		<i>t</i>	<i>p</i>
	4 days	37 days		
Light	42 ± 5	6 ± 4	7.984	0.015
Dark	41 ± 6	5 ± 1	9.114	0.012

(A) Test of veliger response to treatment within age groups. (B) Veliger response to treatments between age groups. (values = mean ± SD, *n* = 3, significance at *p* < 0.05).

3.4. Field mesocosm experiments

Light values within decreased as a function of depth in experimental mesocosms (Fig. 4). Salinity did not vary within the experimental columns, and temperature did not vary more than 1 °C in the vertical columns.

Newly hatched (1-day) veligers concentrated at the surface during the evening and early morning (Fig. 5). Significant interaction effects occurred between treatment and depth versus time (Table 3). Therefore, the analysis was broken down to compare, individually, the effects of treatment and depth. There were no significant treatment effects in the number of veligers at the surface until the 1300 sample ($F_{2,6} = 7.105$, sig.). The “open” ($p = 0.04$), or uncovered columns, and the “no UV” ($p = 0.03$) columns both differed significantly from the dark columns in surface abundances of veligers. The largest proportions of larvae in both the “open” (61%) and “no UV” (49%) treatments at 1300 were at 2 m, while the largest concentrations in the “dark” columns were at the surface (50%). Ambient light levels at the surface were quite high, reaching almost 2500 $\mu\text{E}/\text{m}^2/\text{s}$. The regression between mean depth distribution and light intensity ($F = 23.276$, $r^2 = 0.85$) was significant (Fig. 6).

Four day larvae concentrated at the surface during 1900, 0100, and 0700 sample sessions (Fig. 7). There were significant differences in surface abundances over time (Table 4). Depth distributions differed significantly according to treatment only at 1300 ($F_{2,6} = 6.500$, $p = 0.031$). The surface abundances in the “open” and “no UV” treatments did not differ from each other, but a Tukey's multiple comparison test showed that the distribution of larvae in the dark treatments was significantly different ($p = 0.03$) than those in the other treatments. The highest abundances of larvae were found at 2

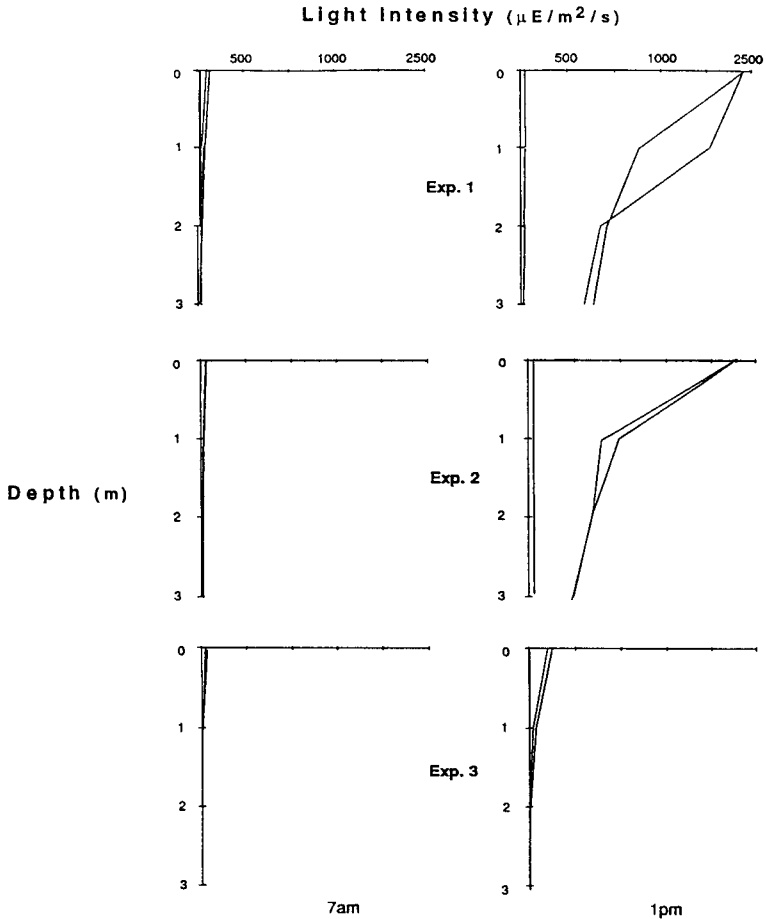


Fig. 4. Light ($\mu\text{E}/\text{m}^2/\text{s}$) profiles as a function of depth (m) in experimental columns for the three mesocosm experiments.

m in both the “open” (39%) and “no UV” (43%) treatments. The regression between mean depth distribution and light intensity was marginally significant ($F = 9.437$, $r^2 = 0.054$) (Fig. 8).

The 16-day veligers behaved in the same manner as younger veligers. While significant differences did not exist between surface abundances in 1900 and 0100 treatments, vertical distribution patterns at 0700 and 1300 warrant specific attention (Fig. 9). At the 0700 sampling session, stormy conditions disturbed the experimental array. Veligers were not present in the samples at 0700. By the 1300 session, with improved weather conditions, veligers were again present in the samples. Although conditions were overcast, light was measured ($800 \mu\text{E}/\text{m}^2/\text{s}$), and significant differences in surface abundances were detected between treatments (Table 5). Significant treatment effects occurred only at 1300 ($F_{2,6} = 7.43$, $p = 0.021$). The “dark” treatment differed ($p = 0.013$) from the other treatments as indicated by Tukey’s multiple comparison. The largest

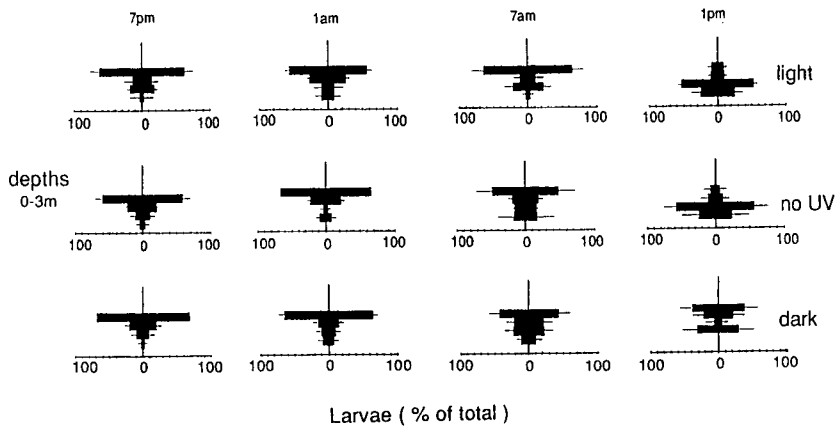


Fig. 5. Vertical depth profiles (m) of 1-day veliger abundances (% of total) in the three treatments as a function of time.

proportions of veligers in the “open” (42%) and “no UV”(51%) treatments were measured at 1m, but in the “dark” treatment, the highest proportion was at the surface (59%).

4. Discussion

In the laboratory, queen conch larvae responded similarly to vertical and horizontal light fields. Veligers were most strongly attracted to light early in development, and the attraction decreased with age, with competent veligers showing the weakest response. This was also the most common pattern of photoreponse identified in invertebrate larvae by Thorson’s (1964) extensive literature search. Thorson also stated that “geonegativity and photopositivity often combine to place early stage pelagic invertebrate larvae in the surface waters which may help keep the young larvae close to the surface even during dark hours and so further support the spreading of the species.” The queen conch veliger appears to behave in a similar manner. In laboratory vertical

Table 3
Three-way ANOVA for the effects of treatment and time on depth positioning of 1-day veligers

Source	df	MS	F	p
Treatment	2	0.000	0.004	0.996
Time	3	0.000	0.003	0.998
Depth	3	1.214	61.603	<0.001
Depth × time	9	0.279	13.899	<0.001
Treatment × time	6	0.359	25.034	<0.001
Treatment × time × depth	18	0.050	2.524	0.002
Error	96	0.020		

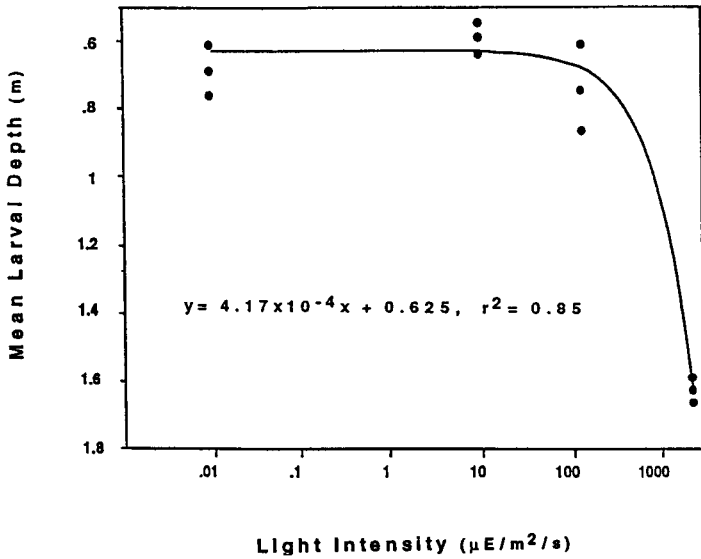


Fig. 6. Curvilinear regression between mean depth distribution and light intensity for 1-day veligers.

tube experiments, early staged veligers swarmed at the surface in both light and dark treatments, indicating that negative geotaxis is also important in the early stages.

All early stage veligers swam toward the light. Based on qualitative observations, older veligers appear to sink faster, and, if upward swimming has been disrupted, they must spend more time orienting themselves upward in the column to return to the surface. Cragg (1980) observed similar sinking responses in *Pecten* veligers. Ontogenetic

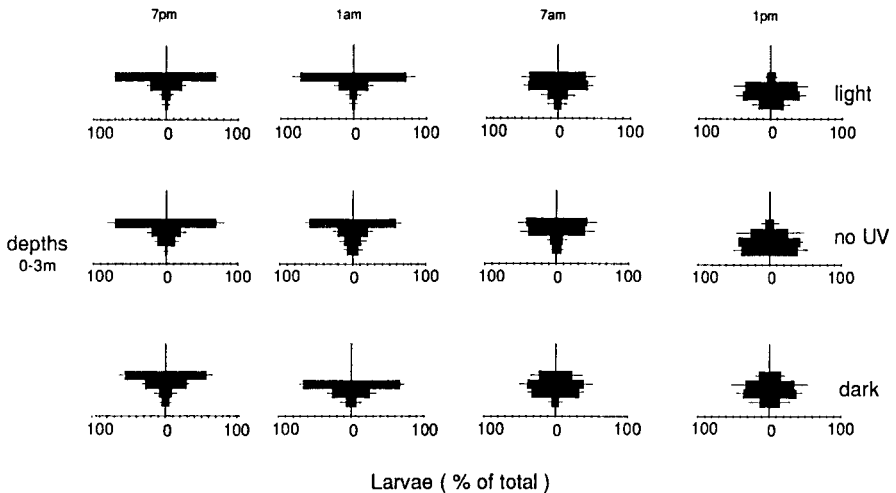


Fig. 7. Vertical depth profiles (m) of 4-day veliger abundances (% of total) in the three treatments as a function of time.

Table 4

Two-way ANOVA for the effects of treatment on surface densities of 4-day veligers verses time

Source	df	MS	F	p
Treatment	2	0.022	1.658	0.212
Time	3	0.881	67.747	<0.001
Treatment × time	6	0.025	1.913	0.120
Error	24	0.013		

changes in phototaxis have been reported in other molluscan veliger larvae. Bayne (1964) described extreme fluctuations in the presence or absence of phototaxis of *Mytilus edulis* veligers before settlement. The gastropod veliger *Phestilla sibogae* (Nudibranchia) showed a strong phototaxis during early stages which then became more indifferent to light with age (Miller & Hadfield, 1986). Miller & Hadfield's high light intensity treatment was the same ($400 \mu\text{E}/\text{m}^2/\text{s}$) as that used in this study. More importantly, they found no difference in positive photoresponses at high light intensities relative to medium or low light intensities. This nudibranch larvae became increasingly photoindifferent with age and the swimming behavior during later stages was characterized by an increase in the number of stops, and circles, and the lack of directional attraction to the light. As *Strombus gigas* veligers become older their swimming speeds become lower and changes in the mean direction of their responses to the light source may be due to this decrease in swimming velocity. However, swimming behavior, in terms of stops and circles, did not differ as a function of age.

Recent attention has been given to the effects of solar UV radiation on marine zooplankton (Damker et al., 1980), particularly with the prospects of increased UV-B

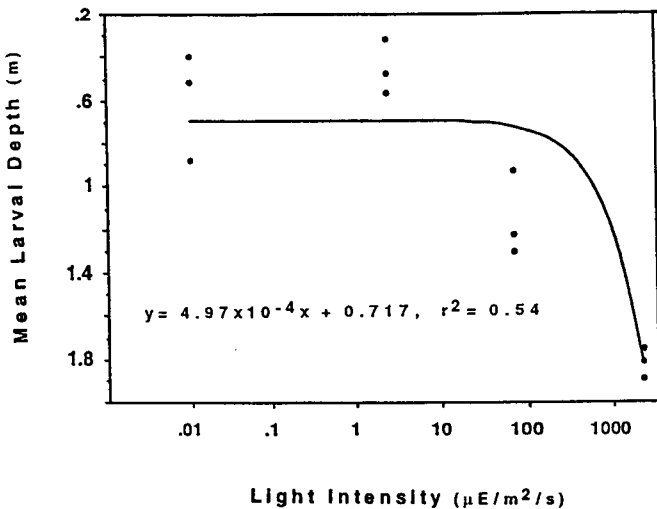


Fig. 8. Curvilinear regression between mean depth distribution and light intensity with 4-day veligers.

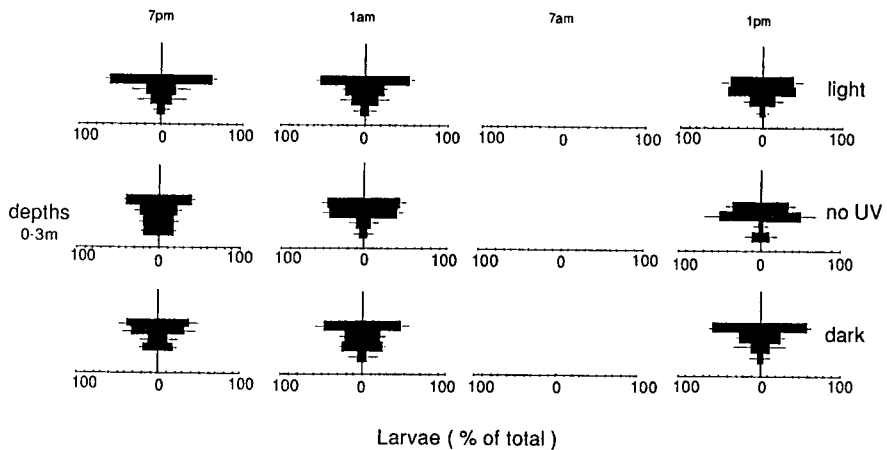


Fig. 9. Vertical depth profiles (m) of 16-day veliger abundances (% of total) in the three treatments as a function of time.

penetration into the atmosphere as the earth's ozone layer is degraded. The conch veliger, with its attraction to the upper water column as well as the exposure of its soft velar lobes, would seem to be susceptible to damage by UV wavelengths. The potential of this effect would be particularly important in tropical marine systems where UV penetration can reach several meters (Smith & Baker, 1979). In laboratory conditions, conch veligers showed negative behavioral responses to UV-B irradiation (J. Regan, pers. comm.). However, the UV exposure was artificial and probably does not represent the natural level of exposure in the field. The lower, ambient solar UV light used in this study elicited no significant behavioral responses. Furthermore, no effect was detected in field vertical migration experiments where UV radiation was manipulated. Of the invertebrate larval forms evaluated for sensitivity to UV, only echinoid plutei have shown behavioral responses in field conditions (Pennington & Emler, 1986). Copepodites (Bollens & Frost, 1990) and other crustacean larvae (Damkaer & Dey, 1982) showed negligible behavioral responses to solar UV. Larvae affected by UV wavelengths may not show behavioral responses, but may instead possess screening pigments or repair mechanisms that could be in equilibrium with destructive UV (Damkaer et al., 1980).

Table 5

Two-way ANOVA for the effects of treatment on surface densities of 16-day veligers verses time

Source	df	MS	F	p
Treatment	2	0.062	9.663	0.007
Time	3	0.375	68.061	<0.001
Treatment × time	6	0.019	3.008	0.061
Error	16	0.006		

In this study, conch veligers responded to light intensity gradients in photoresponse experiments. Light intensity has been identified as the primary stimulus for vertical depth regulation in many invertebrate meroplankton, particularly crustacean larvae (Forward et al., 1984). However, little information is available on what stimuli control vertical migration in non-decapod forms, especially gastropod larvae (Young & Chia, 1987). Data on the vertical distributions of bivalve larvae in the field are available (Carriker, 1951; Mann & Wolf, 1983; Tremblay & Sinclair, 1990). Although laboratory studies indicate that vertical depth regulation probably occurs, there has been no physical evidence presented to date that shows behavior is responsible for depth distribution in molluscan veligers. Our mesocosm data suggest that the veligers undergo a diel or nocturnal migration pattern. Several other studies have noted veligers in the upper portion of the water column during the night (Quayle, 1952; Scrope-Howe & Jones, 1985; Tremblay and Sinclair, 1990). In all age classes, *Strombus* larvae concentrated at the surface at night. As in some other veligers (Cragg, 1980), negative geotaxis appears to place conch veligers in the upper portion of the water column during dark and low light conditions. High light intensity caused a negative phototaxis which moderates the effect of negative geotaxis. An increase in mean depth during periods of high light intensity was also observed in the vertical depth regulation of the scallop larvae *Pecten maximus* in a similar type of mesocosm experiment (Kaartvedt et al., 1987). Convincing evidence for light intensity effects on vertical positioning was found in the experiment with 16-day-old veligers. During cloudy conditions where light intensity was low, veligers distributed themselves higher in the column than in trials run in full sunlight. The correlation of mean depth with light intensity was significant as in *Pecten* veligers.

The effects of turbulence may play a role in vertical positioning behavior of the veligers. Stormy conditions shook the experimental array during the morning of the last experiment, and no veligers were found in the experimental columns during this period. It is quite likely that the veligers sank to the bottom in response to turbulence within the bag. After turbulent conditions subsided, veligers were again present in the upper portions of the column. Tremblay & Sinclair (1990) concluded that turbulence in field conditions limits the swimming abilities of veligers of different stages, especially in tidally energetic areas. Simulation models produced by Smith & Stoner (1993) corroborate the significance of vertical turbulence in vertical migration and horizontal transport.

Mesocosm experiments have certain limitations for use in making inferences to natural field conditions. For example, the lack of predators (Ohman, 1988; Bollens & Frost, 1989), could affect the distribution of the veligers. Another consideration is the effect of food resources on swimming behavior. Early stage *Strombus* veligers contain embryonic food reserves and should not be affected by the lack of dietary supplements. Distribution of non-feeding veligers did not differ from the later staged planktotrophic larvae. In addition, all larvae used in experiments were well fed before being treated and it is unlikely that they lacked ample food resources for normal behavior or became starved during the 24-h treatment. Despite certain limitations, experimental mesocosms can be a valuable technique for understanding mechanisms of distribution in the field.

While hydrographic factors are probably the most important considerations in lar-

val transport, most marine benthic invertebrate larvae are capable of regulating their position in the water column (Mileikovsky, 1973) and this behavior can place larvae in vertical strata moving in different directions and at different velocities. Negative geotaxis and positive phototaxis throughout most of the larval period probably keeps the veligers of queen conch close to the ocean surface where current velocities are the greatest. This makes estimation of potential dispersal of the conch relatively simple in comparison to strong migrators such as decapod larvae. Davis et al. (1993) calculated that queen conch larvae could be transported 900 km during the 3-wk larval stage in typical 0.5 m/s surface currents of the Caribbean Sea. The hypothesis of long distance dispersal of queen conch larvae in the Caribbean is supported by genetic data which indicate a high degree of homogeneity among most adult populations (Mitton et al., 1989). On the other hand, conch veligers have been found at 30 m depth and upcurrent from the most eastern islands of the Caribbean (Posada & Appeldoorn, 1993). Posada & Appeldoorn speculated that veligers, collected upstream from nearest adult populations, were transported on island eddies, strong tidal currents, and upwelling systems. It is clear that transport models for species with strongly photopositive larvae will depend upon detailed information on the interactions between larval behavior, swimming capabilities, horizontal advection, and vertical turbulence.

Acknowledgements

This research was supported by grants from the Florida Institute of Oceanography and the Astronaut Shell Club. Additional support was provided by the National Undersea Research Program of NOAA (U.S. Department of Commerce), the Florida Department of Natural Resources, and Florida Sea Grant. Also, special thanks to Dr. K.B. Clark and NSF Grant BIR 8951326 for computer use at Florida Tech.

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