

ONTOGENY OF PHOTOTAXIS DURING LARVAL DEVELOPMENT OF THE SEDENTARY POLYCHAETE, *SERPULA VERMICULARIS* (L.)

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ABSTRACT

Responses of *Serpula vermicularis* larvae to light were studied in the laboratory during all stages from hatching to settlement. Early trochophores swam upward but were indifferent to light until development of an eyespot at three days. After this, and for most of larval life (about 25 days), dark-adapted larvae initially displayed a positive phototaxis when exposed to horizontally directed light. After a period of adaptation, they changed the sign of their response to negative, the time required for the onset of this change being an inverse function of intensity. Trochophores responded to all wavelengths of light from 350 nm to 625 nm, but were most sensitive to those below 525 nm. Metatrochophores, which had two eyespots, were continuously and strongly photonegative. Benthic nectochaete larvae were indifferent to light while crawling on the bottom, but at metamorphosis they generally oriented the primary tube aperture away from the light. Based on laboratory behavior, a twilight migration pattern is predicted for *S. vermicularis* trochophores, and a hypothesis is suggested which could account for the evolution of diel migration in larvae of coastal species.

INTRODUCTION

Quantitative data on responses of invertebrate larvae to environmental stimuli help us understand the often complex interaction of factors influencing larval distribution, and also enable us to predict larval movements for species which are rarely encountered or difficult to sample in the field. Although general patterns of photoresponse have been described for at least some larvae in virtually every phylum (Thorson, 1964), the importance of light intensity, wavelength, and light or dark adaptation remain poorly understood for most common larval forms. For the most part, quantitative studies have been limited to economically important species such as cirripedes (Lang *et al.*, 1979), bivalves (Bayne, 1964) and brachyurans (Forward and Costlow, 1974; Ritz, 1972a), and species with short-lived lecithotrophic larvae such as bryozoans (Ryland, 1960) and compound ascidians (Crisp and Ghobashy, 1973).

In this study, we quantified the ontogenetic changes in photoresponse of lab-reared *Serpula vermicularis*, a species with extended planktotrophic development, with the objective of understanding how behavior might influence vertical distribution of the larvae and, ultimately, recruitment. In the San Juan Islands, Washington state, where our work was carried out, low larval abundance and complex tidal currents make it virtually impossible to study larval distribution by conventional sampling techniques.

S. vermicularis is a common epifaunal species occurring on hard substrata in boreal, temperate and tropical seas throughout the world (Ushakov, 1965). Al-

Received 3 December 1981; accepted 25 March 1982.

though larval behavior of *S. vermicularis* has not been investigated, larvae of related serpulids show several different patterns of photoreponse. For example, *Pomatosceros triqueter* remains photopositive throughout larval life (Segrove, 1941), while *Hydroides norvegica* is indifferent to light at first, only slightly photopositive later, and at settlement may be either photopositive or photonegative (Wisely, 1958).

MATERIALS AND METHODS

Larval culture

Adult specimens were collected from April to August, 1979 to 1981, from the rocky intertidal zone near Pt. Caution, San Juan Island, Washington. Spawning was induced by removing the animals from their tubes. This was accomplished without damaging the animals by carefully breaking the ends of the tubes and blowing the worms out with compressed air, posterior end first (R. L. Fernald, personal communication). Worms were isolated in bowls of seawater where ripe ones generally began spawning within 10 minutes.

Coelomic fluid and immature oocytes were removed by decanting off the seawater after the eggs had settled. The eggs were washed several times in filtered seawater, then fertilized with a small amount of dilute sperm suspension. Excess sperm were removed by rinsing the eggs several more times. Cultures were maintained in 8 liter jars of filtered seawater, stirred continuously by paddles rotating at 60 rpm, and kept cool in running seawater aquaria. After hatching, trochophores were fed daily with the green flagellate, *Dunaliella tertiolacta*. Culture water was changed every three days until the larvae became benthic, after which time only weekly changes were made, since larvae were lost easily during this stage. Overhead fluorescent lights were on for an average of three hours each evening. During the daytime, most light came through large laboratory windows; light intensity in the cultures thus fluctuated in a natural manner. On a typical day, the cultures experienced intensities comparable to those between 5 and 10 m depths in the field (Young and Chia, 1982).

Whenever a larva metamorphosed in culture, we recorded the orientation of its tube relative to the window light, which was predominantly unidirectional.

General experimental techniques

All experiments were carried out at night in a darkened room. The experimental chamber consisted of a rectangular aquarium constructed of microscope slide glass, and measuring 7.5 cm long, 2.5 cm wide, and 2.5 cm deep. The chamber was filled to a depth of 1.0 cm and placed in a wooden box 25 cm long, 10 cm wide, and 10 cm deep, which was painted with mat black paint on all internal surfaces in order to minimize reflections. The lid was lined with black felt to form a light-tight seal. Light was projected through a 3 cm diameter hole in one end of the box, and the intensity was measured with a Li-cor quantum meter (Lambda Instrument Company, Model LI-185) through a similar hole in the opposite end. The light meter was sensitive primarily in the range of the human visual spectrum (400–700 nm) and could detect light at intensities as low as $0.1 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$. During experiments with white light ("intensity experiments") the larvae were observed with the lid of the box removed, while in "wavelength experiments" the lid was left on the box until the experiment was terminated.

The light source was a Bausch and Lomb projecting lamp with a General Electric "CPR" incandescent bulb. Although the projector was fitted with a rhe-

ostat, we always used it at the highest setting and changed light intensity by stopping down the aperture, imposing neutral density filters, or altering the distance between the lamp and the experimental chamber. In this way, changing the spectral characteristics of the emitted light was avoided.

Wavelength experiments

Colored light of discrete wavelengths (10 nm bandwidth) was produced by inserting a Bausch and Lomb diffraction grating monochromator in the projector beam. Ideally, action spectra for behavioral phenomena are derived from "equal response" curves (Forward and Cronin, 1979), in which a particular behavioral level is plotted on a graph of wavelength vs energy. However, since our light meter was relatively insensitive in the infrared and ultraviolet regions, and emitted only very low energy levels near the lower end of the spectrum, we found it impossible to characterize responses at multiple energy levels. Instead, we used the maximum intensity obtainable below 425 nm and held intensity constant at $1.0 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ over the rest of the spectrum, then plotted the degree of the response against wavelength. Although data obtained in this way are not as useful from a physiological standpoint, they do indicate the colors of light which the larvae can sense, and are thus useful for ecological inference.

The experimental protocol was as follows. Several hundred larvae, dark adapted for at least 10 min, were pipetted into the glass experimental chamber in the dark, and mixed thoroughly by drawing water in and out of the pipette several times. Monochromatic light was shone through the chamber horizontally for 5 min, then extinguished. Samples were then taken immediately and simultaneously from the two ends and the middle of the chamber. The sampling apparatus consisted of three 50 ml hypodermic syringes, fitted with 18 ga needles and held securely in a plexiglass frame. A strip of plexiglass attached to the plungers was lifted quickly in order to withdraw 30 ml samples from all regions at the same time. The samples were discharged into Bogorov plankton counting trays and counted under a dissecting microscope. A fresh group of larvae was used for each wavelength tested.

Intensity experiments

In experiments using white light, we wished to consider the effect of light adaptation by noting changes in larval distribution over time. Since this required that we sample the experimental chamber repeatedly during each run, we needed a sampling procedure which did not remove larvae from the chamber. Initially, we attempted photographing the distributions with high speed film. Although the larvae were easily resolved in the photographs, this method proved unsatisfactory because larvae swarming against the ends of the containers were impossible to count. To avoid this problem, we counted the animals visually through five 2 mm wide slits in a black card resting on top of the chamber. One slit was above each end and the other three were equally spaced. All slits were aligned perpendicular to the light source. At any given sampling time, we began by counting the larvae visible through the slit nearest the light, then proceeded to the opposite end, counting through each slit in turn. The entire procedure took between 45 and 60 seconds, and was carried out at two minute intervals. Larvae from a single culture were used for each experiment. Two subsamples of the culture, containing roughly equal numbers, were placed in separate chambers. These were used for alternate intensity levels in order to expedite the data collection; while one chamber was being exposed

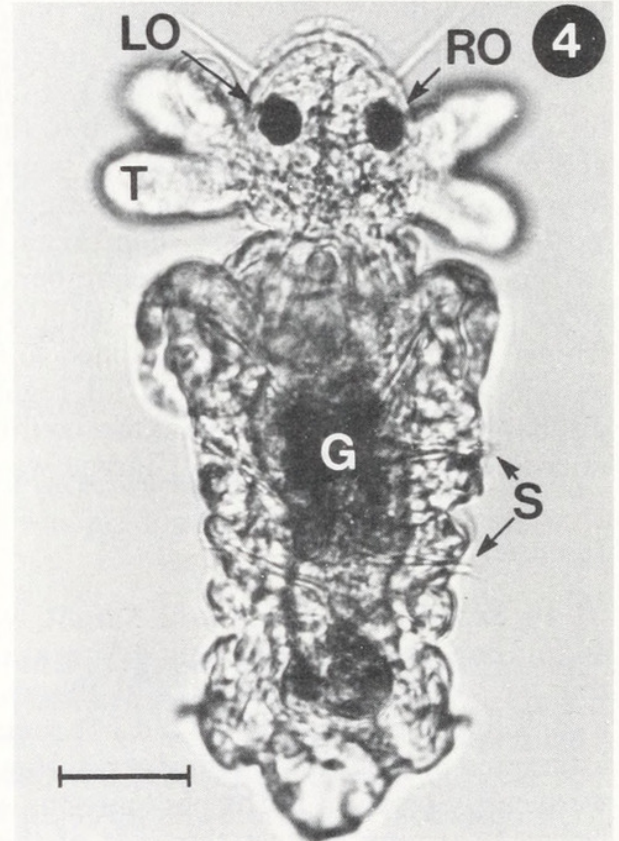
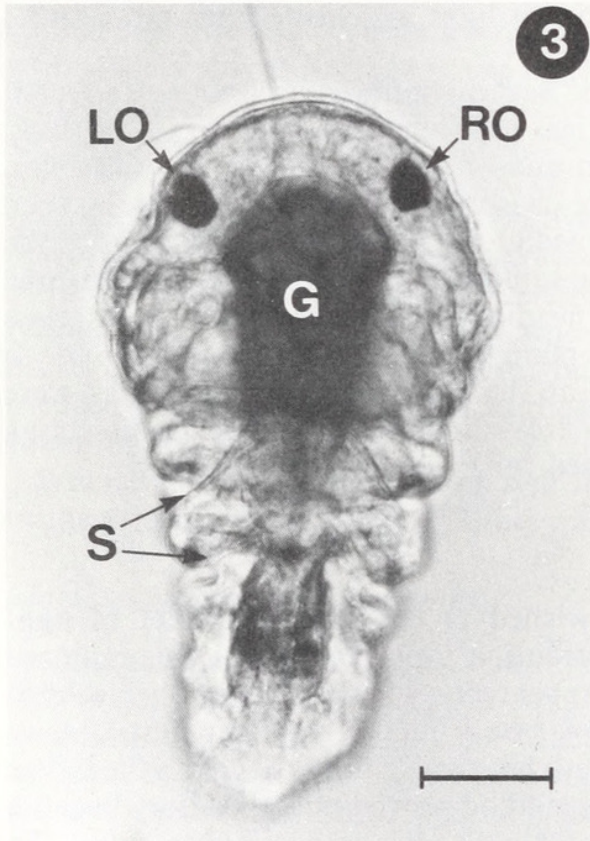
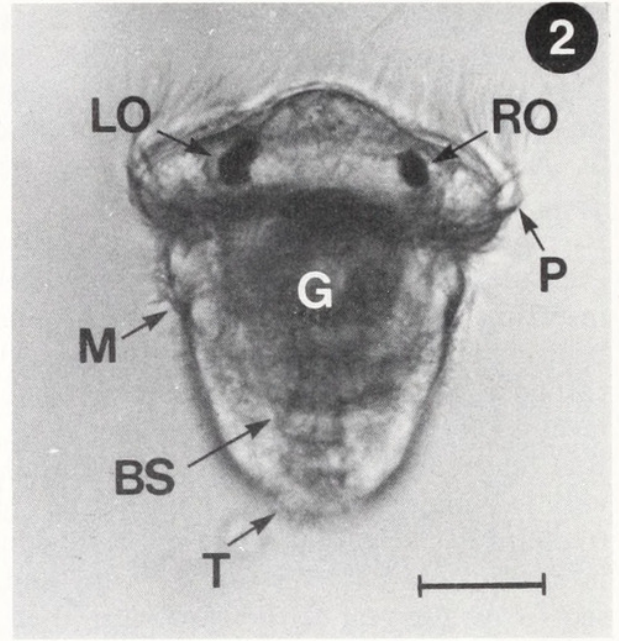
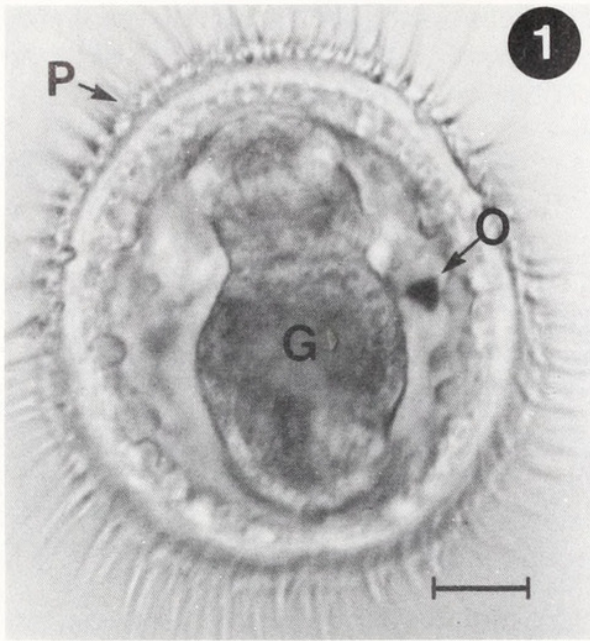


FIGURE 1. Anterior view of 3 day old *Serpula vermicularis* trochophore, showing newly developed right ocellus (O), gut (G), prototroch (P). Scale bar equals 10 μm .

FIGURE 2. Twenty-six day old *S. vermicularis* metatrochophore viewed dorsally, showing right ocellus (RO), left ocellus (LO), prototroch (P), metatroch (M), telotroch (T) and body segments (BS). Scale bar equals 50 μm .

FIGURE 3. Thirty day old *S. vermicularis* benthic nectochaete larva, viewed dorsally. Setae (S) are beginning to form; other labels as in Figure 2. Scale bar equals 50 μm .

FIGURE 4. Fifty day old *S. vermicularis* just after the onset of metamorphosis, viewed dorsally and showing newly formed tentacle buds (T). Other labels as in previous figures. Scale bar equals 50 μm .

to light of a given intensity, the other was being cooled and dark adapted in the seawater tables. At some intensities, we repeated the experiment several times with the same group of larvae in order to assure that the general results were repeatable. However, time constraints and limited supplies of larvae prevented us from replicating quantitative trials with animals of any given age.

Photoresponse was tested at seven different intensities ranging from $10 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ to $1450 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$. This range of intensities is realistic in terms of light levels the larvae might encounter during their pelagic phase. Midday light intensities measured on an overcast day in June of 1981 ranged from $1200 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ at the surface to less than $0.5 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ at a depth of 38 m.

RESULTS

Larval development

While early embryonic stages of *Serpula vermicularis* were nearly synchronous, there was considerable temporal variability within and among cultures in later development. Furthermore, the size distribution of larvae within a given dish generally became distinctly bimodal after about two weeks of feeding. Larger animals grew more rapidly and underwent more frequent morphological changes than the smaller ones; the latter never survived to metamorphosis. It is not known whether larvae of the two sizes came from the same or different females, since cultures were of mixed origin. However, it seems unlikely that the bimodality could result from competition for food, since food was always present in excess. The timing of larval development described below is based on the larger larvae, which were the only ones used for behavioral experiments. Figures 1–4 show the major features of larval development and also depict four of the five stages in which we quantified photoresponse.

The embryos hatch as trochophores one day after fertilization, and the trochophores swim for two more days before developing an ocellus. As in other serpulids (Zeleny, 1905; Segrove, 1941; Wisely, 1958), the right ocellus develops first, and is situated on the episphere, slightly nearer the prototroch than the apical organ (Fig. 1). Unlike the ocellus of *Pomatoceros triqueter*, which is black (Segrove, 1941), the photoreceptor of *S. vermicularis* is brilliant red in color. Except for some slight changes in shape (Figs. 2, 3), the ocellus remains essentially the same at the light microscope level during the entire trochophore period. Formation of the left eyespot, which occurs early in the metatrochophore stage (about 20–27 days), coincides with the onset of segmentation (Fig. 2). Both eyespots are retained at least through metamorphosis. Soon after developing the left eye, larvae enter the nectochaeta stage, during which they drop to the bottom and adopt a benthic mode of life (Fig. 3). This stage, which may begin as early as 28 days, is of variable length; some worms remain nectochaetes until at least the 50th day. Although capable of swimming, nectochaetes spend most of their time crawling on the bottom. Just before secreting the primary tube, tentacle buds appear at the sides of the head (Fig. 4). Metamorphosis, which occurs at the 5 setiger stage, took place between 41 and 50 days in our cultures.

Photoresponses of trochophores and metatrochophores

Although early larvae swam actively and swarmed in large numbers at the surface, they demonstrated no response to directional light at any intensity. They became strongly photosensitive as soon as the eyespot appeared. We subjected dark-

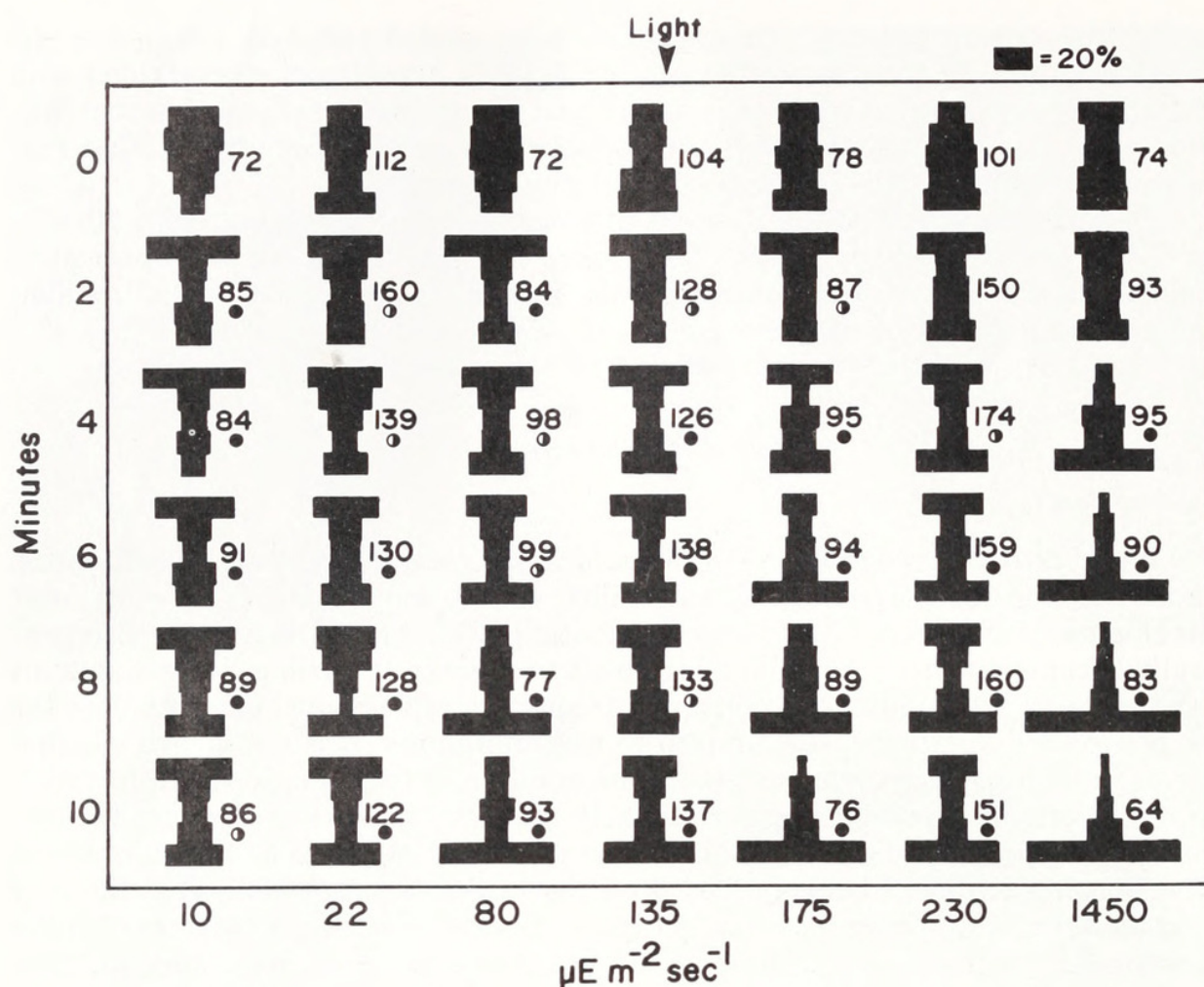


FIGURE 5. Distributions of 17 day old *S. vermicularis* trochophores exposed to different intensities of light and following various periods of light adaptation. Histogram bars show the percentages of larvae in five regions of the experimental container. Each column of graphs represents a single experiment, monitored at progressive time intervals, so the effect of light adaptation can be seen by noting changes in distribution while reading down a column. Number of larvae sampled is indicated to the right of each graph together with a symbol showing significance level, as determined by Chi-Square test for goodness of fit to a uniform distribution. Open circle: $P < 0.05$. Half-closed circle: $P < 0.01$. Closed circle: $P < 0.001$. No symbol: not significant.

adapted one-eyed trochophores to horizontal light at approximately two-day intervals. Multiple light levels were used at 6, 11, and 17 days; qualitative observations were made on the other days at a single intensity. Since the basic response did not change throughout this period, we present data from a single typical experiment (Fig. 5). Following dark adaptation, larvae responded to light of low intensity by swimming toward it. After swarming against the light side of the chamber for several minutes, they were invariably light adapted and changed the sign of their response. The time required for light adaptation was an inverse function of intensity. Indeed, at very high intensities, no photopositive period was apparent at all, though this may be because the change from positive to negative phototaxis occurred faster than the time lag inherent in our counting procedure. The overall strength of the response, as measured by the percentage of larvae responding, was also influenced by intensity. At $10 \mu E \cdot m^{-2} \cdot sec^{-1}$, only about 40% of the larvae occupied the darkest region after 10 minutes of exposure to light, while at the highest intensity, over 70% responded. It is apparent from the graph that two different samples of

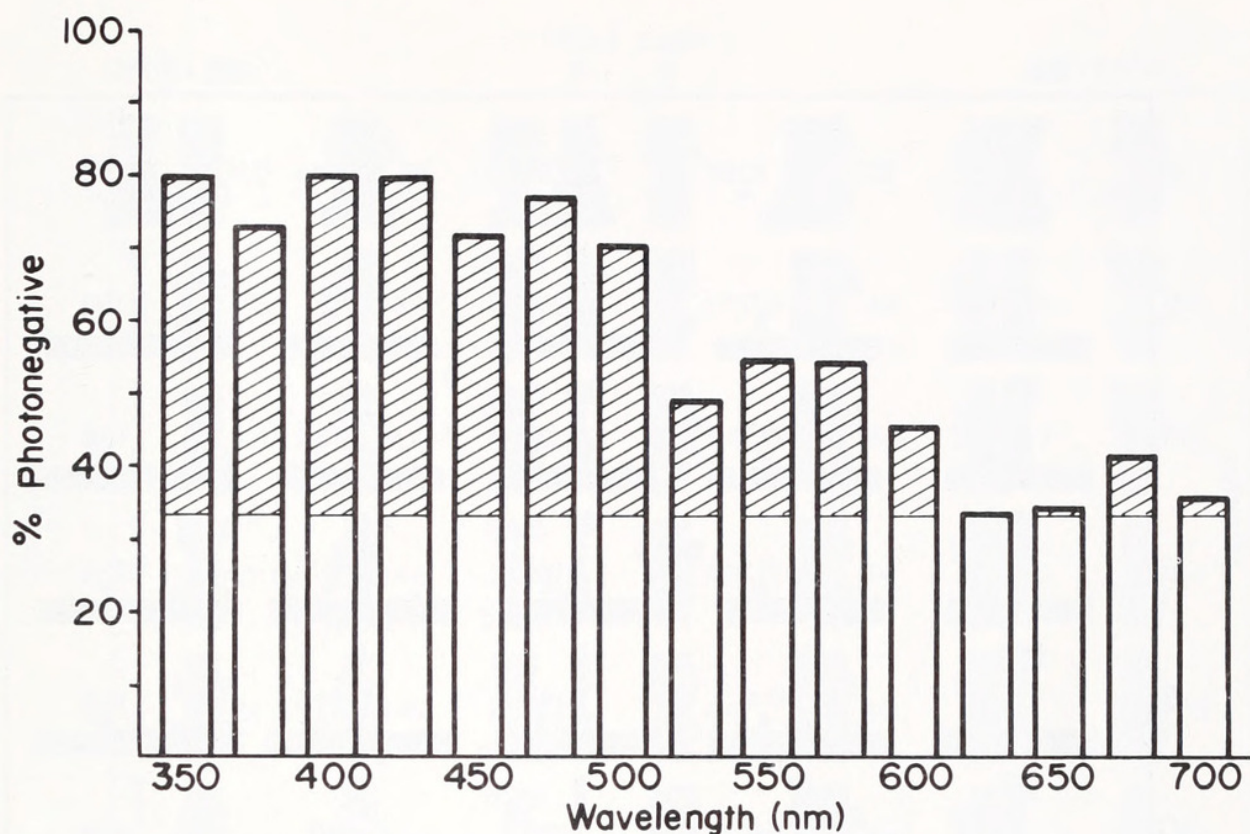


FIGURE 6. Mean ($n = 2$) percentages of *S. vermicularis* trochophores (4 days old) at the dark end of the experimental chamber following five minute exposure to monochromatic light of various wavelengths. Shaded segment of each bar is that portion exceeding the expected value of 33%.

larvae were used for alternate intensity levels, as the overall strength of the response differed slightly between samples. Nevertheless, the same basic trend was demonstrated by both, and the results were repeatable at a given intensity level.

Although the action spectrum for phototaxis in *Serpula vermicularis* shows a slight mode between 500 and 600 nm (Fig. 6), the highest peak is very broad, spanning all wavelengths from 350 nm (ultraviolet) to 500 nm (green). As expected, wavelengths longer than 600 nm, which penetrate to only shallow depths in the sea, were the only ones to which larvae did not respond.

With the development of the left eye, metatrochophores retained their overall negative phototaxis, but lost the initial photopositive phase of the response (Fig. 7). Phototaxis was very strong at all intensity levels tested.

Nectochaete photoresponses

After the setigerous larvae went to the bottom, they showed no response to light at any level of intensity (Fig. 8). The main behavior displayed by larvae during the creeping stage appeared to have the dual function of substratum exploration and feeding. Larvae crept about on the bottom, moving the head slowly from side to side, and apparently tasting the bottom with the mouth. Occasionally, they ingested small benthic algae.

Of several hundred larvae which survived to the nectochaete stage in our cultures, only 11 underwent metamorphosis. These larvae did not seek out and settle in the darker regions of the dishes; however, they showed a remarkable similarity in the way they oriented their tubes. Seven pointed the aperture of the primary

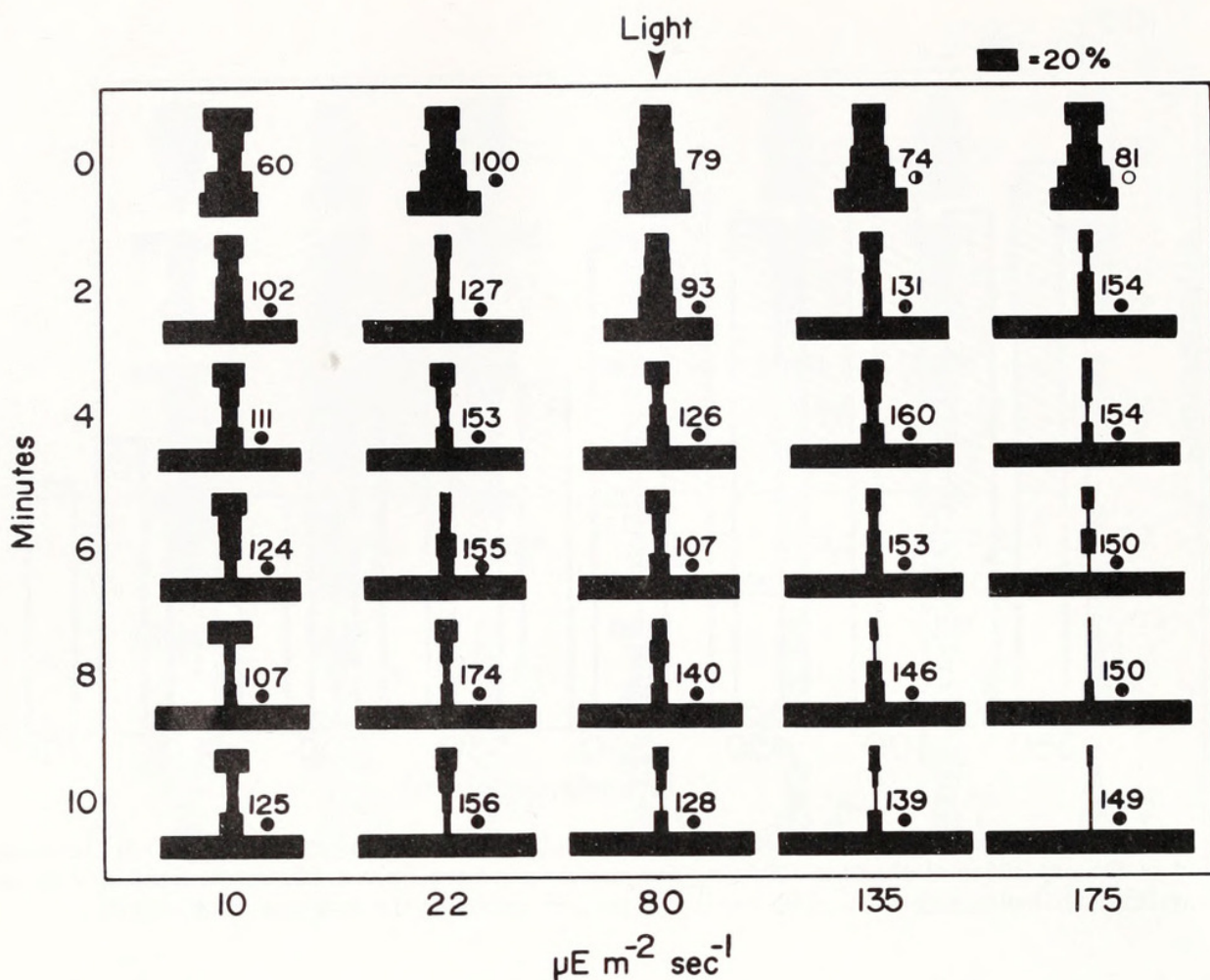


FIGURE 7. Percentage distributions of 27 day old *S. vermicularis* metatrochophores exposed to different light intensities and following different periods of light adaptation. For complete explanation, see Figure 5 legend.

tube directly away from the window, one directed it toward the light, one was angled about 45 degrees away from the light, and the remaining two tubes were roughly perpendicular to the light. If tube orientation at settlement has survival value to the juvenile worms, perhaps two ocelli function more efficiently than one in determining the light direction.

DISCUSSION

Based on laboratory observations, we predict the following movements of *Serpula vermicularis* in the field. Newly hatched trochophore larvae, which lack an eye, are indifferent to light. Nevertheless, they swim directly up, and swarm at the surface, where they remain for about a day. As this upward swimming occurs in both presence and absence of light, we assume it is a negative geotaxis. Unlike the larvae of *Hydroides norvegica*, which remain indifferent to light even after the ocellus is formed (Wisely, 1958), *S. vermicularis* larvae become strongly photosensitive as soon as the eyespot appears. These trochophores probably use light as a cue for making diel vertical migrations. The migration pattern we hypothesize resembles the "twilight" type (Cushing, 1951). Larvae swim toward the surface early in the morning, become light adapted after a short time, then swim or sink into deeper water, where they remain for most of the day. At night, low light levels

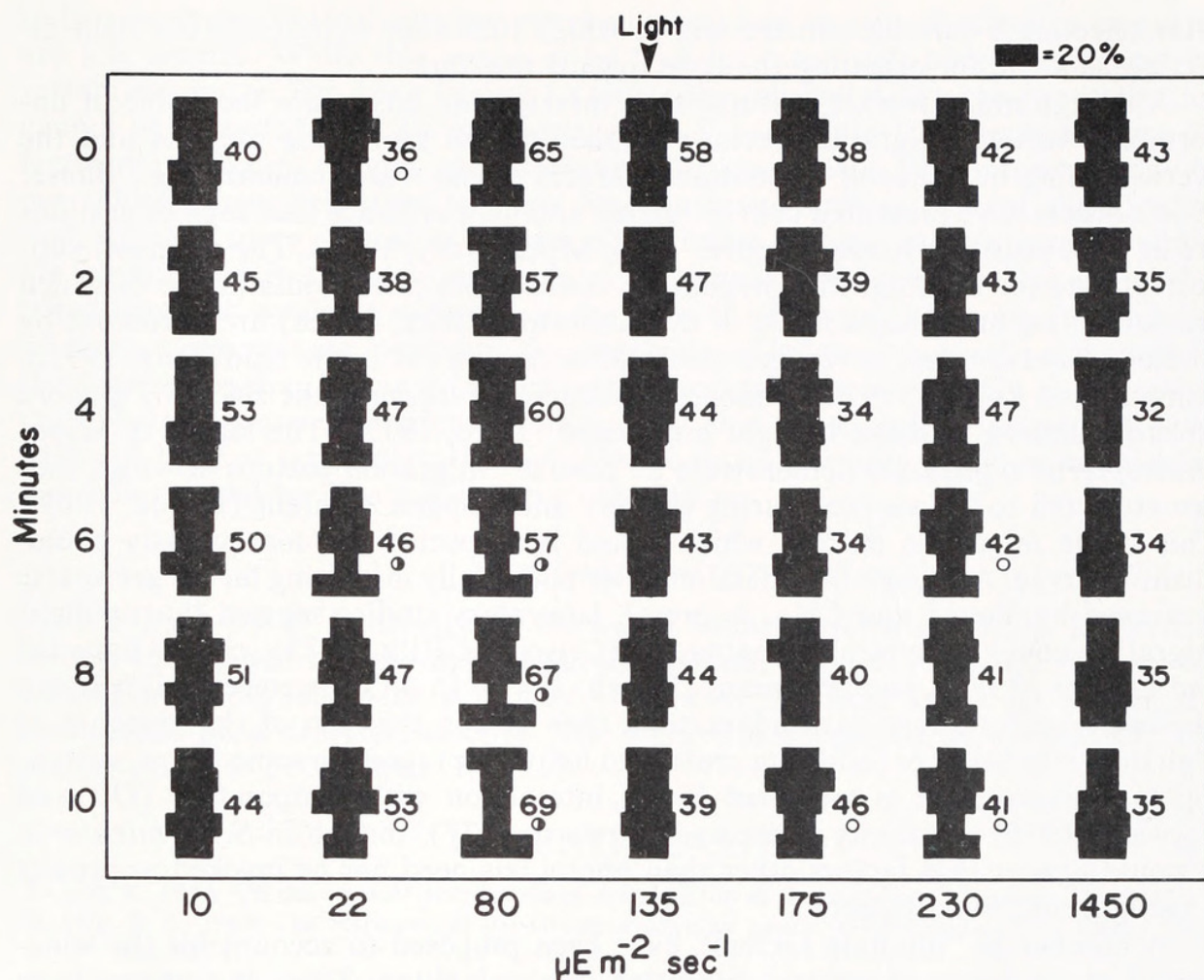


FIGURE 8. Percentage distributions of 38 day old *S. vermicularis* nectochaetes exposed to different intensities of white light and following different periods of light adaptation. For explanation, see legend in Figure 5.

may cause the larvae to disperse throughout the water column. We have no reason to suppose that there is an early evening migration to the surface, as would be predicted by Cushing's twilight migration paradigm, though evidence for this would have to come from much longer observations of light-adapted animals than we made in this study.

Like most invertebrate larvae studied to date (Forward, 1976), *S. vermicularis* larvae are sensitive to light between 500 and 600 nm, corresponding to the wavelengths which penetrate to the greatest depths in coastal waters. However, they are also capable of detecting and responding to wavelengths as short as 350 nm, which are in the ultraviolet range of the spectrum.

With the development of a second eye in the metatrochophore stage, diel migrations probably cease. The strong and constant negative phototaxis exhibited by these larvae may help them locate the bottom, as in other late stage invertebrate larvae (Thorson, 1964). Although nectochaete larvae, which are benthic, retain both eyespots, they demonstrate no phototactic response. While it may seem paradoxical that two well-developed photoreceptors would not be used during this exploratory stage, Zeleny (1905) has suggested that ocelli may be present during this period so that the juvenile shadow response, in which worms withdraw into the tube in response to an abrupt decrease in light intensity, can begin shortly after the primary tube is secreted. The setigerous larvae remain indifferent to light until

after selecting a suitable substratum, at which time they apparently use light direction as a cue for orienting the tube toward the dark.

Although many workers assume that invertebrate larvae are incapable of undertaking vertical migration because of their feeble swimming abilities and the overwhelming influence of discontinuity layers in the water column (e.g., Banse, 1964), others have presented convincing lab and field evidence that such migrations are at least possible (Konstantinova, 1966; Mileikovsky, 1973). The strongest support to date for the migration hypothesis comes from phyllosoma larvae in which predictions on movements made in the laboratory (Ritz, 1972a) are borne out by studies of diel changes in vertical distribution carried out in the field (Ritz, 1972b; Rimmer and Phillips, 1979). Among polychaete larvae, only the spionid *Polydora ciliata* is known to make twilight migrations (Daro, 1973). The larvae of *Mesochaetopterus sagittarius* demonstrate a "reverse" migration pattern in which they are attracted to the surface during the day and disperse at night (Bhaud, 1969). This is the migration pattern which would be expected for continuously photopositive larvae. Although field data on other potentially migrating larvae are sparse (reviewed by Young and Chia, in press), laboratory studies suggest that twilight migration could be typical of barnacles (Crisp and Ritz, 1973), crabs (Forward and Costlow, 1974), and bryozoans (Lynch, 1947). In all these species, larvae are photopositive following dark adaptation, then switch the sign of the response at high light intensities or following prolonged light adaptation. In some forms, switching to photonegative is mediated by an interaction with temperature (Ott and Forward, 1976) or salinity (Latz and Forward, 1977), though in *S. vermicularis*, it would appear that factors other than phototaxis need not be invoked to predict a twilight migration pattern.

A number of "ultimate factors" have been proposed to account for the widespread phenomenon of vertical migration in zooplankton. These hypotheses have been reviewed by McLaren (1963) and include maximizing dispersal (Hardy and Gunther, 1935), minimizing predation (Hutchinson, 1967), and optimizing feeding (Harris, 1953). McLaren (1963) added to these his own hypothesis, later expanded by Enright (1977), which ascribes a metabolic advantage to feeding in warm surface waters and digesting at a lower temperature in deep water. In the San Juan Islands, strong currents mix the water during every tidal cycle, preventing the establishment of strong thermoclines and distributing food more or less evenly through the water column (Thompson and Phifer, 1937). Thus, of the above hypotheses, only Hutchinson's idea that larvae stay deep to avoid visual predators would seem to apply to the presumed migration of *S. vermicularis* larvae. Selective pressures favoring a very brief daily excursion to the surface are harder to envision. One factor which seems not to have been considered as a selective pressure on larvae in coastal waters is the high probability of encountering the bottom. Larvae reaching the substratum before becoming competent to metamorphose, whether because of currents or their own photoresponses, are likely to become trapped in the "dead spaces" between, behind, and under rocks, or in the boundary layer where water flow is negligible. Entrapment on the bottom would effectively nullify whatever advantage the larvae accrue by dispersing in the plankton for several weeks, and would also expose larvae to hazards associated with the benthos, including benthic predators, silt, attached bacteria, and possibly lower food concentrations. A short photopositive stage each day would help resuspend trapped larvae in the water column. The fact that the response is absent in the bottom-seeking metatrochophore stage is consistent with this hypothesis.

Buss (1979) has suggested that many larvae may rely on negative phototaxis

to locate cryptic settlement sites where physical and biological selective pressures are less intense. While this seems to be true for many soft-bodied epifaunal invertebrates in the San Juan Islands (Young, unpublished data), the generalization cannot be extended to *S. vermicularis*, since *S. vermicularis* nectochaetes are effectively indifferent to light while seeking a settlement site. Photoresponse may be overridden during this stage by some other behavior such as contact chemoreception, which is more critical to the worm's ultimate success. *S. vermicularis* adults are often found in the open on subtidal rock walls and boulders; this is the distribution which would be expected on the basis of laboratory behavior. Intertidally, where most animals are located on the undersides of ledges or in cracks and crevices, the distribution may be caused by differential mortality or substratum choice rather than photoresponse. Preliminary data suggest that larvae orient their tubes away from the light at settlement; this behavior could conceivably function in reducing mortality caused by siltation or some other factor.

ACKNOWLEDGMENTS

We thank Dr. D. D. Beatty for the use of a monochromator, Dr. R. L. Fernald for providing algal culture and helpful discussions, and Dr. A. O. D. Willows for making available lab space at Friday Harbor. R. A. Koss and J. T. Pennington commented on a draft manuscript. The work was supported by an NSERC operating grant to F. S. Chia.

LITERATURE CITED

- BANSE, K. 1964. On the vertical distribution of zooplankton in the sea. *Prog. Oceanogr.* **2**: 53-125.
- BAYNE, B. L. 1964. The responses of the larvae of *Mytilus edulis* to light and gravity. *Oikos* **15**(1): 162-174.
- BHAUD, M. 1969. Etude de la migration verticale quotidienne des larves de *Mesochaetopterus sagittarius* a Nosy-Be (Madagascar). *Mar. Biol.* **4**: 28-35.
- BUSS, L. W. 1979. Habitat selection, directional growth and spatial refuges: why colonial animals have more hiding places. Pp. 459-497 in G. Larwood and B. R. Rosen, Eds., *Biology and Systematics of Colonial Organisms*. Academic Press, New York and London.
- CRISP, D. J., AND A. F. A. GHOBASHY. 1973. Responses of the larvae of *Diplosoma listerianum* to light and gravity. Pp. 443-465 in D. J. Crisp, Ed., *Fourth European Marine Biology Symposium*. Cambridge Press, Cambridge.
- CRISP, D. J., AND D. A. RITZ, 1973. Responses of cirripede larvae to light. I. Experiments with white light. *Mar. Biol.* **23**: 327-335.
- CUSHING, D. H. 1951. The vertical migration of planktonic crustacea. *Biol. Rev.* **26**: 158-192.
- DARO, M. H. 1973. Etude des migrations nycthemerales du zooplankton dans un milieu marin peu profond. *Hydrobiologia* **44**(2-3): 149-160.
- ENRIGHT, J. T. 1977. Diurnal vertical migration: adaptive significance and timing. Part I. Selective advantage: a metabolic model. *Limn. Oceanogr.* **22**: 856-872.
- FORWARD, R. B., JR. 1976. Light and diurnal vertical migration: photobehavior and photophysiology of plankton. *Photochemical and Photobiological Reviews* **1**: 157-209.
- FORWARD, R. B., JR., AND J. D. COSTLOW JR. 1974. The ontogeny of phototaxis by larvae of the crab *Rhithropanopeus harrisi*. *Mar. Biol.* **26**: 27-33.
- FORWARD, R. B., JR., AND T. W. CRONIN. 1979. Spectral sensitivity of larvae from intertidal crustaceans. *J. Comp. Physiol. A. Sens. Neural Behav. Physiol.* **133**(4): 311-316.
- HARDY, A. C., AND E. R. GUNTHER. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. *Discovery Reports* No. 11: 456 pp.
- HARRIS, J. E. 1953. Physical factors involved in the vertical migration of plankton. *Q. J. Microsc. Sci.* **94**: 537-550.
- HUTCHINSON, G. E. 1967. *A treatise on Limnology*, Vol. II Wiley, N. Y. 1115 pp.
- KONSTANTINOVA, M. I. 1966. Characteristics of motion of pelagic larvae of marine invertebrates. *Dokl. Akad. Nauk SSSR* **170**(3): 726-729.
- LANG, W. H., R. B. FORWARD, JR., AND D. C. MILLER. 1979. Behavioral responses of *Balanus improvisus* nauplii to light intensity and spectrum. *Biol. Bull.* **157**(1): 166-181.

- LATZ, M. I., AND R. B. FORWARD, JR. 1977. The effect of salinity upon phototaxis and geotaxis in a larval crustacean. *Biol. Bull.* **153**: 163-179.
- LYNCH, W. F. 1947. The behavior and metamorphosis of the larva of *Bugula neritina* (Linnaeus): experimental modification of the length of the free-swimming period and the responses of the larvae to light and gravity. *Biol. Bull.* **92**: 115-150.
- MCLAREN, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *J. Fish. Res. Bd., Canada* **20**: 685-727.
- MILEIKOVSKY, S. A. 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Mar. Biol.* **23**: 11-17.
- OTT, F. S., AND R. B. FORWARD, JR. 1976. The effect of temperature on phototaxis and geotaxis by larvae of the crab *Rhithropanopeus harrisii* (Gould). *J. Exp. Mar. Biol. Ecol.* **23**: 97-107.
- RIMMER, D. W., AND B. F. PHILLIPS. 1979. Diurnal migration and vertical distribution of phyllosoma larvae of the western rock lobster *Panulirus cygnus*. *Mar. Biol.* **54**: 109-124.
- RITZ, D. A. 1972a. Behavioral response to light of the newly hatched phyllosoma larvae of *Panulirus longipes cygnus* George (Crustacea: Decapoda: Panuliridae). *J. Exp. Mar. Biol. Ecol.* **10**: 105-114.
- RITZ, D. A. 1972b. Factors affecting the distribution of rock lobster larvae (*Panulirus longipes cygnus*) with reference to variability of plankton net catches. *Mar. Biol.* **13**: 309-317.
- RYLAND, J. S. 1960. Experiments on the influence of light on the behavior of polyzoan larvae. *J. Exp. Biol.* **37**: 783-800.
- SEGRIVE, F. 1941. The development of the serpulid *Pomatoceros triqueter* L. *Quart. J. Microsc. Sci.* **82**: 467-540.
- THOMPSON, T. G., AND L. D. PHIFER. 1937. Seasonal variations in the surface waters of San Juan Channel during the five year period, January 1931 to December 30, 1935. *J. Mar. Res.* **1**: 34-59.
- THORSON, G. 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. *Ophelia* **1**: 167-208.
- USHAKOV, P. V. 1965. *Polychaeta of the Far Eastern Seas of the U. S. S. R.* Israel Program for Scientific Translations, Jerusalem. 419 pp.
- WISELY, B. 1958. The development and settling of a serpulid worm, *Hydroides norvegica* Gunnerus (Polychaeta). *Aust. J. Mar. Freshw. Res.* **9**: 351-361.
- YOUNG, C. M., AND F. S. CHIA. 1982. Factors controlling spatial distribution of the sea cucumber, *Psolus chitonoides*: settling and post-settling behavior. *Mar. Biol.* in press.
- YOUNG, C. M., AND F. S. CHIA. In press. Abundance and distribution of pelagic larvae as influenced by predatory, behavioral and hydrographic factors. In A. C. Giese and J. S. Pearse, Eds., *Reproduction of Marine Invertebrates* Vol. **9**. Academic Press, N. Y. and London.
- ZELENY, C. 1905. The rearing of serpulid larvae with notes on the behavior of the young animals. *Biol. Bull.* **8**: 308-312.



Young, Craig M. and Chia, Fu-Shiang. 1982. "ONTOGENY OF PHOTOTAXIS DURING LARVAL DEVELOPMENT OF THE SEDENTARY POLYCHAETE, SERPULA VERMICULARIS (L.)." *The Biological bulletin* 162, 457-468.

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