Reference: *Biol. Bull.* **165:** 286–304. (August, 1983)

SETTLEMENT AND METAMORPHOSIS OF A TEMPERATE SOFT-CORAL LARVA (*ALCYONIUM SIDERIUM* VERRILL): INDUCTION BY CRUSTOSE ALGAE

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ABSTRACT

The temperate soft-coral *Alcyonium siderium* Verrill has a demersal planula larva which usually settles and metamorphoses on vertical rock surfaces near the parent colony. Such surfaces are covered by a variety of encrusting invertebrate species and by three common crustose algae (*Lithothamnium glaciale, Phymatolithon rugolosum,* and *Waernia mirabilis*). Larvae settle and metamorphose most frequently on these three algal species in the field (Sebens, 1983).

Contact with each of the three crustose algae induced settlement and metamorphosis within 1–5 days in laboratory experiments. Rock or shell fragments, even with naturally filmed surfaces, did not induce metamorphosis in the same time period. A few larvae did metamorphose on the rock, shell, and glass or plastic surfaces of the containers, taking up to 30 days to do so. Larvae were kept alive up to 194 days but their competence to metamorphose declined significantly after ten days. The half-life of larvae that did not metamorphose was approximately 25 days. Larvae presented with coralline algae in darkness delayed metamorphosis by approximately 10–20 days, but most of them did metamorphose by 30 days. Neither sea water incubated with coralline algae, nor coralline algae in close proximity (4–5 mm) to the larvae, but without contact, induced metamorphosis. Induction of settlement and metamorphosis is thus mediated by surface contact with the algae and probably not by a dissolved chemical. Presence of the colonial ascidian, *Aplidium pallidum,* inhibited metamorphosis even when larvae were able to contact coralline algae, and also caused early larval death.

INTRODUCTION

The planulae of octocorals are usually brooded by the adult colony to a swimming stage (Matthews, 1917; Gohar, 1940; Hartnoll, 1975, 1977; Weinberg, 1979; Weinberg and Weinberg, 1979) which settles and crawls on the substratum. They may also be released as demersal crawling larvae (Hartnoll, 1977). The swimming larvae are similar in morphology and behavior to those of certain scleractinian corals (Abe, 1937; Atoda, 1947a, b, 1951a, b, c, 1953; Kawaguti, 1941, 1944; Harrigan, 1972a, b; Lewis 1974), hydroids (Nishihara, 1967a, b, 1968a, b; Donaldson 1974), scyphozoans (Brewer, 1976a, b; Neumann, 1979), and sea anemones (Chia and Spaulding, 1972; Siebert, 1973). Behavior of the demersal planulae is similar to that described for scleractinian corals (Gerrodette, 1981; Fadlallah and Pearse, 1982; Fadlallah, 1983), certain hydroids (Williams, 1965, 1976), and hydrocorals (Ostarello, 1973, 1976). Settlement and substratum choice has been studied for few anthozoans [reviewed by Chia and Bickell (1978)], and for even fewer octocorals (Théodor, 1967; Chia and Crawford, 1973; Weinberg, 1979; Weinberg and Weinberg, 1979).

Received 23 November 1982; accepted 1 April 1983.

The soft-coral *Alcyonium siderium* Verrill is common on vertical rock surfaces at 6–17 m depth along the coast of Northern Massachusetts and further north in the Gulf of Maine. It broods lecithotrophic demersal planulae which are released in late July or August (Feldman, 1976). The released planulae either drift with the current or crawl down the parent colony and onto the nearby substratum. *Alcyonium hibernicum* in the British Isles has a similar demersal larva (Hartnoll, 1977) which differs from the better-known swimming larva of *Alcyonium digitatum* (Hartnoll, 1975, 1977).

I observed larval settlement and metamorphosis of *Alcyonium siderium* planulae in the field during August of 1978, 1979, 1980, and 1981 and quantified availability of substratum types and frequency of larval metamorphosis on all available substrata (Sebens, 1983). Two species of coralline algae (*Lithothamnium glaciale, Phymatolithon rugulosum*) and one fleshy red crustose alga (*Waernia mirabilis* proposed, R. Wilce manuscript) were by far the most common substrata chosen by the larvae. Laboratory studies were then designed to find out if metamorphosis could be induced by the presence of these algae or whether larvae were just attaching to any piece of hard substratum near the parent colony. The following questions were addressed experimentally: 1. Can any of the three algal species induce settlement and metamorphosis?, 2. Is this induction mediated by surface contact or by substances dissolved in sea water?, 3. Can any of the common encrusting larval invertebrates be used as substratum or induce metamorphosis?, and 4. How long can larvae survive, and are they competent to settle and metamorphose if they do not receive the appropriate stimulus within the first few days? There is good evidence that certain bryozoan larvae can avoid settling near colonial ascidians which are known to overgrow established bryozoan colonies (Grosberg, 1981; Young and Chia, 1981). Small *Alcyonium* colonies are overgrown by the ascidian *Aplidium pallidum* in the field (Sebens, 1982). Therefore, additional laboratory experiments were designed to test whether *Alcyonium* larval settlement would be inhibited in the present of *Aplidium*.

Materials and Methods

Fifteen large colonies of *Alcyonium* were collected at the Shag Rocks, Nahant, MA (42°24′50″ N; 70°54′20″ W) from vertical rock surfaces at 6–9 m depth. Corals were scraped off carefully and placed in plastic containers. Only colonies with visible planulae in the anthocodia were taken. Collections were made during August of each year (1980–1982) when ambient temperature ranged from 8–21°C for the month. Larvae were visible in most colonies in early August (1978–1982) but were present in very few colonies by the end of each August. Colonies were maintained in the laboratory in aerated sea water at 11–13°C overnight.

Colonies were slit lengthwise along the lobes with a razor blade, then swished back and forth in filtered (80 μ mesh) sea water to remove the larvae. The larvae and sea water were passed through 80 μ Nitex, followed by two rapid washes in clean filtered sea water. The mesh was then quickly inverted into clean filtered sea water. Larvae, eggs, and some colony fragments settled to the bottom of the dish, from which colony fragments were then removed individually. Elongate crawling planulae (2 mm long) were removed by pipette for each experimental replicate (15 in 1980, 30 in 1981, 1982). This technique probably prevented larvae which were still at early stages of development from being included in the experiment.

Settlement experiments were carried out either in a refrigerated chamber (11°C, 1980, 1981) or in a cold room (13°C, 1982). Containers for the 1980 experiments

were glass vials 5 cm tall, 2 cm diameter. Those for the 1981 experiments were plastic Petri dishes 4.5 cm diameter. All vessels had been soaked in flowing sea water for 60 days prior to the experiments, then rinsed in fresh water to remove the organic film. The 1980 and 1981 containers held 6 ml of filtered sea water. The 1982 experiments used wide mouth jars (3 cm tall, 4 cm bottom diameter) containing 12 ml of filtered sea water 1 cm deep. All vessels (1981, 1982) were mounted on a rocking platform that stirred the water by tilting to 15° each 5 seconds. In the 1982 experiments 12 hours of agitation were alternated with 12 hours at rest because the constant agitation in the 1981 experiments caused many larvae to metamorphose without attaching. Water was replaced every 48 hours by pipetting off the old water and adding fresh filtered sea water. Two fluorescent bulbs (40 watt) at 30 cm from the containers were used as the light source. Darkened treatments were kept on the same apparatus in an aluminum foil box with spaces to allow air flow. The 1980 experiments were not continuously agitated, but instead were aerated with an air pump and pipette twice daily. Water was changed daily.

Substrata to be used in treatments were collected from the same site as were the corals, on rock (1982) or mussel (*Modiolus modiolus*) shell (1980, 1981). The rock or shell was fractured and trimmed to produce pieces $\leq 1 \times 1 \times 0.5$ cm with appropriate test substratum on the upper side. Controls were the same rock or shell without algae on the surface. At least one surface of the shell or rock was the original exposed surface but without algae or invertebrates. *Lithothamnium glaciale, Phymatolithon rugulosum,* the red crustose alga *Waernia mirabilis,* the sponge (*Halisarca dujardini*), and colonial tunicates (*Aplidium pallidum*) accounted for most of the space cover on walls with *Alcyonium* (Sebens, 1982, 1983). Each of these organisms was also used as an experimental substratum.

Controls were prepared with only the glass or plastic container as substratum, in both light and darkness. In the 1982 series of experiments, vigorously aerated treatments were also included. Glass tubing from a vibrator aquarium pump was used to bubble air through these containers. This treatment was an attempt to determine whether the oxygen production of crustose algae alone could have induced settlement.

If the presence of any of the experimental substrata induced metamorphosis, it would be of interest to determine whether induction could be mediated by chemicals released by the substratum and dissolved in sea water. In the 1980 experiments, sea water was incubated with each substratum for 24 hours at 11°C (termed 'supernatant') before being poured off and used in the experimental treatment. This would allow metabolic products of the algae or invertebrates to concentrate before being introduced into the larval containers. This treatment was repeated daily with fresh supernatant.

The 1980 experiments indicated that coralline algae could induce metamorphosis. An experiment was thus designed in 1981 to find out whether contact with the alga was necessary. In this experiment, the *Lithothamnium* substratum was suspended by fine monofilament line 4–5 mm above the bottom of the container without touching the walls. This design would allow exudate from the algae to contact the larvae but would prevent contact with the algal surface.

Abalone larvae settle on coralline algae and can be induced to settle by the presence of algal extracts or by the chemical GABA (γ-aminobutyric acid) (Morse *et al.,* 1979). Since coralline algae induced settlement in *Alcyonium siderium* (1980 experiments), it was of interest to test for possible mediation by GABA. Groups of larvae were kept in the light with GABA in sea water (1 μM/l, 50 μM/l, 1 mM/l),

changed daily, since induction of metamorphosis by coralline algae occurred much more rapidly in the light.

Statistical analysis of data (Analysis of variance (ANOVA), Student-Newman-Keuls multiple comparisons test (SNK test) and Chi-squared nonparametric test) were based on methods in Sokal and Rohlf (1969). Table I summarizes the experimental protocol, conditions, and results for all three years.

RESULTS

Survey of potential substrata

The first set of experiments (August 1980–May 1981) pointed out the importance of coralline algae as inducers of metamorphosis. *Lithothamnium* was the only substratum that induced settlement within the first three days, and was certainly the only substratum which caused large numbers of larvae (27 of 45) to metamorphose. The sea water control treatment had three larvae metamorphose between days 3 and 5 and *Waernia* had only one after 49 days (Table II, Fig. 1). *Alcyonium* colonies did not induce settlement and metamorphosis ruling out larval aggregation around adult colonies as a result of adult chemical mediation. *Halisarca* did not induce settlement, but some larvae remained alive until the end of the experiment. *Aplidium* did not induce settlement either, but most larvae died within the first week.

Sea water incubated for 24 hours with each of the substrata (termed 'supernatant') failed to induce metamorphosis. Since *Lithothamnium* supernatant did not have the same effect as *Lithothamnium* itself, it appeared that there was no chemical dissolved in sea water that was mediating the effect of the coralline alga. It was also evident that settlement of the larvae in the presence of corallines did not necessarily occur on the surface of the alga itself. In fact, more larvae metamorphosed on the bottom of the glass vials. There was also no larval swimming or negative geotaxis (*i.e.*, crawling up the walls of the vial). All settlement was on the bottom. A few larvae, however, did crawl to the top surface of the shell fragment and attached directly to the alga or to the shell surface.

This set of larval settlement and metamorphosis experiments had several less than optimal conditions. The temperature ranged from 8–12°C, the water was not agitated constantly, and treatments were kept in darkness most of each day. The temperature range was well within that observed for the August period in the field (8–21°C). However, later experiments pointed out the importance of light in inducing settlement and the short light period may have slowed down the rate of settlement. Agitation of the water did not appear necessary for larval survival, which continued for up to nine months (at 5°C for months 3–9), even without daily aeration.

Mechanism of induction of metamorphosis by coralline algae: effects of contact and light regime

During the August–September 1981 experiments temperature was kept constant (11 ± 1°C), treatments were continuously agitated, and were maintained under constant low irradiance. The percentage of larvae that settled in the presence of coralline algae, and the rapidity with which they metamorphosed, indicated that this set of conditions was more conducive to their substratum selection process. Constant slow agitation did prevent a fairly large percentage (10–40) of the metamorphosed individuals from attaching to any surface during the entire experiment.

TABLE I

Summary of experiments for induction of settlement and metamorphosis of Alcyonium *planulae*

Experiment	Date	H Light	H Dark	Purpose	Significant Settlement
Lithothamnium on shell	1980	3	21	Test for possible induction by this substratum	Y
Waernia on shell	1980	3	21	Test for possible induction by this substratum	N
Halisarca on shell	1980	3	21	Test for possible induction by this substratum	N
Aplidium on shell	1980	3	21	Test for possible induction by this substratum	N
Alcyonium on shell	1980	3	21	Test for possible induction by this substratum	N
Shell substrate alone	1980	3	21	Control for effects of other substrata	N
Lithothamnium supernatant	1980	3	21	Test for possible induction by soluble chemicals released by this substratum	N
Waernia supernatant	1980	3	21	Test for possible induction by soluble chemicals released by this substratum	N
Halisarca supernatant	1980	3	21	Test for possible induction by soluble chemicals released by this substratum	N
Aplidium supernatant	1980	3	21	Test for possible induction by soluble chemicals released by this substratum	N
Alcyonium supernatant	1980	3	21	Test for possible induction by soluble chemicals released by this substratum	N
Lithothamnium on shell	1981	24	0	Test for induction by this substratum in light	Y
Lithothamnium on shell	1981	0	24	Test for induction by this substratum in dark	Y
Lithothamnium on shell	1981	12	12	Test for induction by this substratum in light/dark cycle	Y
Lithothamnium on shell suspended	1981	24	0	Test for induction by this substratum without direct contact	N
Lithothamnium on shell using old larvae	1981	24	0	Test for competence of larvae denied induction stimulus for 10 days	N
Lithothamnium on shell with *Aplidium*	1981	24	0	Test for inhibition of induction by *Aplidium*	N
Phymatolithon on shell	1981	24	0	Test for induction by this substrate in light	Y

TABLE I (*Continued*)

Experiment	Date	H Light	H Dark	Purpose	Significant Settlement
Shell substratum alone	1981	24	0	Control for effects of other substrata in light	N
Shell substratum alone	1981	0	24	Control for effects of other substrata in dark	
Sea water alone	1981	24	0	Control for effects of shell substratum in light	N
Sea water alone	1981	0	24	Control for effects of shell substratum in dark	N
GABA in sea water, 3 concentrations	1981	24	0	Test for induction by GABA	N
Lithothamnium on rock	1982	24	0	Test for induction by this substratum in light (repeat of 1981 treatment)	Y
Lithothamnium on rock	1982	0	24	Test for induction by this substratum in dark (repeat of 1981 treatment)	Y
Phymatolithon on rock	1982	24	0	Test for induction by this substratum in light (repeat of 1981 treatment)	Y
Waernia on rock	1982	24	0	Test for induction by this substratum in light (conditions different than in 1980)	Y
Rock substratum alone	1982	24	0	Control for effects of other substrata	N
Lithothamnium on rock with *Aplidium*	1982	24	0	Test for inhibition of settlement by *Aplidium*	N
Sea water alone, aerated	1982	24	0	Test for induction of settlement by increased oxygen tension alone, asmight occur with crustose algae in the light	N

Lithothamnium again induced metamorphosis of the greatest numbers of larvae (Table III, Fig. 2). *Phymatolithon,* the other coralline alga, also induced a large proportion of larvae to metamorphose. Note that there was a great difference between two subsequent sets of three replicate groups with both *Lithothamnium* and *Phymatolithon* (A and B in Table III). In a light/dark cycle (12h each), metamorphosis in the presence of *Lithothamnium* was comparable to that with constant light (Fig. 3). In constant darkness, most larvae did not metamorphose until after 10 days (Fig. 3). However, almost all larvae did metamorphose by 30 days.

When *Lithothamnium* was separated from the larvae by 4–5 mm, metamorphosis was drastically reduced (not statistically different from the control, Fig. 3). This agrees with the previous year's results that indicated that the induction was not mediated by a chemical diffused through sea water, and that contact with the

TABLE II

Alcyonium *larval metamorphosis experiments conducted during August 1980 to May 1981*

	Lithothamnium	*Waernia*	Sea Water Control
Days			
1	0	0	0
2	1.0 ± 1.0	0	0
3	3.0 ± 1.0**	0	0
5	5.0 ± 2.6	0	1.0 ± 1.7
10	6.3 ± 2.3**	0	1.0 ± 1.7
49	8.3 ± 4.7**	0	0
194	8.3 ± 4.7**	0.3 ± 0.6	0

Treatments without metamorphosis: *Halisarca* (sponge), *Aplidium* (tunicate), *Alcyonium*, *Lithothamnium* supernatant, *Waernia* supernatant, *Halisarca* supernatant, *Aplidium* supernatant, *Alcyonium* supernatant. All treatments were given 2–3 hours light per day at 8–12°C, then 5°C after day 49. Values are mean number of larvae metamorphosed, out of an initial 15, ±S.D. for three replicates.

** Denotes treatments significantly different than the control (ANOVA, $P < 0.05$ at least).

coralline alga was necessary. Constant aeration of sea water alone (1982) did not induce metamorphosis. Therefore, it is unlikely that the addition of oxygen to the water by the crustose algae could, by itself, be the factor mediating induction of metamorphosis. I considered using dead coralline algal skeletons to see if the induction was mediated by surface texture rather than by contact chemoreception. However, this would not differentiate the potential role of surface texture of the live

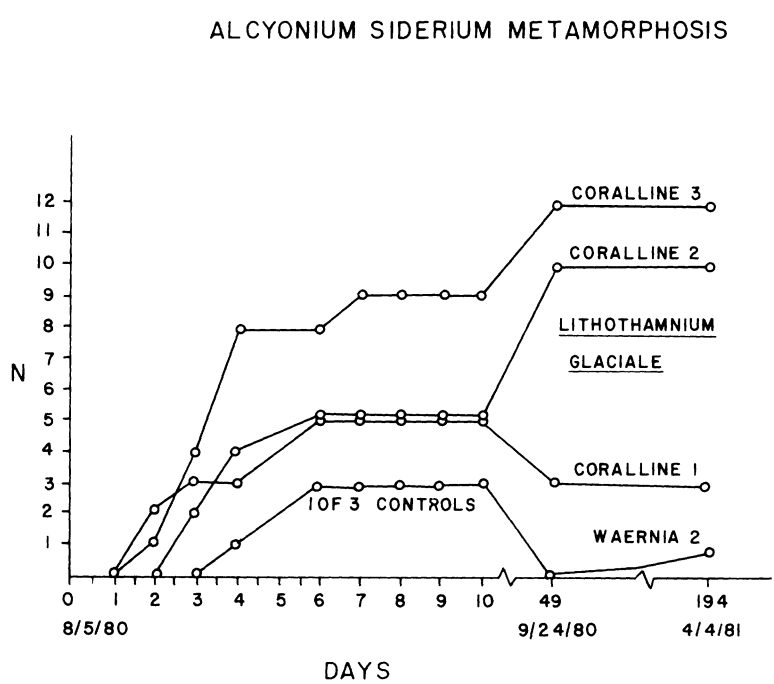

FIGURE 1. Number of larvae that had metamorphosed (of initial 15), during the 1980 experiments, on each of the three coralline algae replicates (*Lithothamnium glaciale*), and on the crustose red alga *Waernia mirabilis*. One of the 3 replicates in the control group also had some metamorphosis.

TABLE III

Alcyonium *larval metamorphosis experiments conducted during August to September 1981*

DAYS	LITHO LIGHT A	LITHO LIGHT B	LITHO LT/DK	LITHO LIGHT SEP.	LITHO DARK	LITHO APLID	LITHO OLD LARVAE	PHYM LIGHT A	PHYM LIGHT B	CONTROL LIGHT	CONTROL DARK	SEA WATER LIGHT	SEA WATER DARK
1	1.3 ± 1.1	0	1.0 ± 1.7	0	0	0.3 ± 0.7	0	0.3 ± 0.7	0	0	0	0	1.0 ± 1.7
2	12.3 ± 2.1 **	0	2.0 ± 2.6	0	0	0.3 ± 0.7	0.7 ± 1.2	1.3 ± 1.5	0.3 ± 0.7	0.3 ± 0.7	0	0.7 ± 1.2	0
5	20.0 ± 1.7 **	4.5 ± 2.1 **	6.0 ± 9.5	0.3 ± 0.7	1.3 ± 0.6	0.7 ± 1.2	0.3 ± 0.7	1.0 ± 1.7	1.6 ± 0.6	0.3 ± 0.7	0.5 ± 0.7	0.7 ± 1.2	0
10	20.0 ± 1.1 **	16.0 ± 12.7	12.0 ± 11.3	1.7 ± 0.6	3.3 ± 5.8	1.0 ± 1.7	0	0.7 ± 1.2	4.7 ± 2.3 **	0.7 ± 0.6	0.5 ± 0.7	0.7 ± 1.2	0
36	21.0 ± 3.8 **	10.5 ± 3.5 **	17.0 ± 10.4 *	6.0 ± 6.1	29.0 ± 0.6 **	0	1.3 ± 2.3	1.3 ± 2.3	9.7 ± 6.1 **	4.6 ± 4.0	2.0 ± 1.4	0.7 ± 1.2	0 **

Treatments had constant low light (11° ± 1°C). Values are mean number of larvae metamorphosed ±S.D., of an initial 30, for 3 replicates per treatment.

** Denotes treatments significantly different than the control (light) (ANOVA, $P \leq 0.05$ at least).

* Denotes treatments different from the control at the $P \leq 0.10$ confidence level (ANOVA).

LITHO (*Lithothamnium*) A, B refers to two subsequent treatments (3 replicates each), as does PHYM (*Phymatolithon*) A, B. 'OLD LARVAE' were kept without substratum for 10 before contact with *Lithothamnium*.

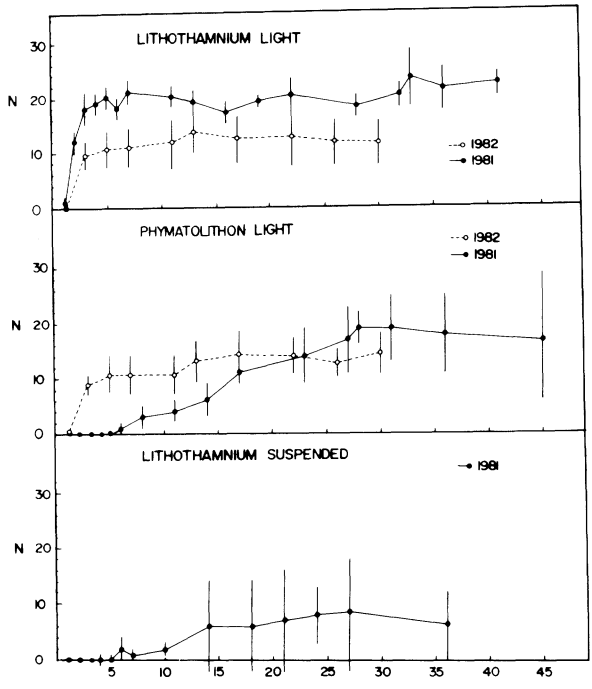

FIGURE 2. Cumulative number of larvae metamorphosed (of initial N = 30 planulae) in treatments with *Lithothamnium* (in light and suspended in light) and *Phymatolithon* (in light). Values are mean number of metamorphosed larvae ± S.D. for three replicates of each treatment (1981 or 1982).

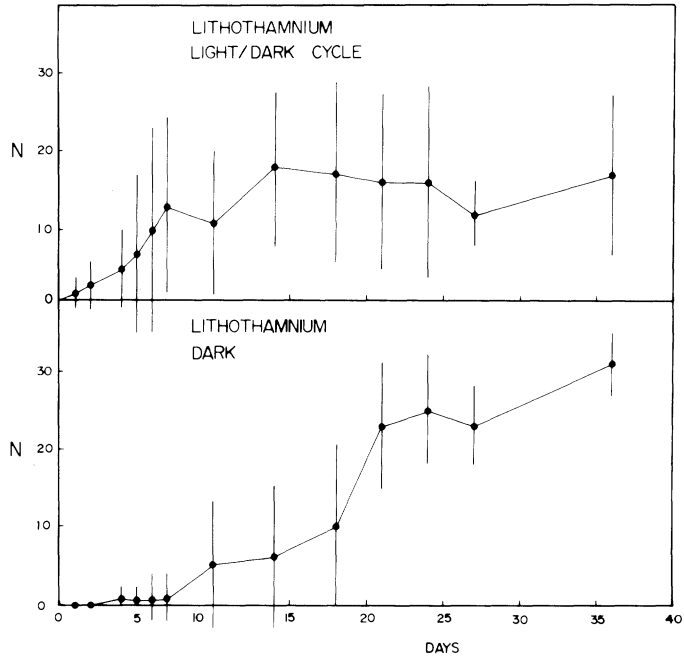

FIGURE 3. Cumulative number of larvae metamorphosed (of initial N = 30 planulae) in treatments with *Lithothamnium* (in light/dark cycle, and in the dark). Values are mean number of metamorphosed larvae ± S.D. for three replicates of each treatment (1982).

alga. The surface contacted by the larva is living cell surface, not the carbonate skeleton.

Control treatments included the same rock or shell material that the algae were growing on, with its natural surface. This surface was probably covered with a bacterial film, known to induce settlement in several invertebrate larvae (Crisp and Ryland, 1960) including bryozoans (Mihm *et al.,* 1981; Brancato and Woollacott, 1982), polychaetes (Kirchman *et al.,* 1982), hydroids (Spindler and Müller, 1972), and scyphozoans (Brewer, 1976b; Neumann, 1979). Treatments with naturally filmed rock or shell surfaces alone did not cause more larvae to metamorphose than sea water controls with only the cleaned glass or plastic surfaces available (Table III, Fig. 5). However, bacterial films can develop in a matter of hours and the artificial surfaces were probably also covered with bacteria since the experiments lasted for many days. Neither rock, shell, nor the artificial surfaces ever had the rapid effects of the crustose algae, and it is unlikely that bacteria alone are inducing settlement in the *Alcyonium* larvae, unless there are specific bacteria associated with the algal surface that are being recognized.

Larvae that were kept for 10 days in filtered sea water (old larvae, Table III) had very low rates of metamorphosis even with *Lithothamnium* present. This is surprising since many of the larvae kept with *Lithothamnium* in the light metamorphosed between days 5 and 20 (B, Table III) and most of those in the dark metamorphosed between days 10 and 36. The results of the 1980 experiments indicated that some larvae remained competent even after 49 days. Clearly there is some reduction in the larvae's ability to metamorphose given increased time without a stimulus.

There was no induction of settlement (attachment) or metamorphosis by GABA at any of the experimental concentrations. The only visible effect of GABA at the highest concentration (1 m*M*/l) was that the planulae were thin and extremely elongate, up to twice as long as normal. Crawling was discerned at the 1 μM/l and 50 μM/l concentrations but not at 1 m*M*/l. The lack of attachment or metamorphosis in the presence of GABA argues for a different mediation by corallines from that suggested for abalones (Morse *et al.,* 1979) or for chitons (Rumrill and Cameron, 1983). It is possible that introduction of GABA occurred before larvae were competent. This sometimes prevents larvae from ever responding to the stimulus (*e.g.,* gastropods, Hadfield, 1977). However, presence of the known inducer, *Lithothamnium,* did induce metamorphosis in larvae from the same batch (Table III). The attachment and initial change from elongate to rounded morphology takes many hours and some larvae had completed this process within the first 24 hours. Larvae were thus competent initially or became so rapidly during the first day.

Experiments with Waernia

The experiments conducted during August–September 1982 (13° ± 1°C, constant low light) introduced intermittent agitation so that metamorphosing larvae had time to become firmly attached. In fact, only 0–20 percent of metamorphosed individuals in each treatment were unattached by the end of the experiment. As in the previous year's experiments, *Lithothamnium* and *Phymatolithon* were strong inducers of metamorphosis (Table IV, Fig. 2). *Waernia* was tested again because many larvae in the field metamorphosed on it (Sebens, 1983). This time *Waernia* was as successful in inducing settlement as were the corallines (Fig. 4). The control had slightly more metamorphosis this year than previously (Fig. 5). The lit control had more larvae metamorphose than did *Lithothamnium* in the dark, but the differences were not significant.

TABLE IV

Alcyonium *larval metamorphosis experiments conducted during August to September 1982*

DAYS	PHYM LIGHT	WAER LIGHT	LITHO LIGHT	LIGHT CONTROL	LITHO DARK	APLIDIUM + LITHO	AERATED SEAWATER
1	0.7 ± 1.2	0.3 ± 0.6	0	0	0	0	0
3	9.0 ± 1.7*	9.0 ± 3.0*	9.7 ± 2.5*	4.3 ± 2.5	1.7 ± 2.1	1.7 ± 2.0	0**
5	10.7 ± 3.2*	9.3 ± 3.1*	10.3 ± 3.5*	5.3 ± 2.3	2.3 ± 3.2	1.7 ± 2.1	0**
11	10.7 ± 3.2	11.0 ± 2.7*	11.7 ± 4.7*	7.3 ± 2.5	3.0 ± 3.6	1.7 ± 2.1**	0**
30	14.0 ± 3.5**	11.6 ± 2.1*	11.3 ± 4.0*	7.0 ± 2.5	4.7 ± 3.8	0**	0**

Experiments were run at 13°C with low light levels and intermittent slow stirring. Values are mean number of larvae metamorphosed, out of an initial 30, ±S.D. of 3 replicates in each treatment.

** Denotes treatments significantly different than the light control (ANOVA, $P \leq 0.05$ at least).

* Denotes treatments different from the light control at the $P \leq 0.10$ confidence level (ANOVA).

LITHO = *Lithothamnium*, PHYM = *Phymatolithon*, WAER = *Waernia*.

Effects of Aplidium

The 1980 experiments had no settlement in treatments with the tunicate *Aplidium*, with the sponge *Halisarca* or with the *Alcyonium* colonies present. Field experiments (Sebens, 1983) showed that settlement did not occur on sponge or

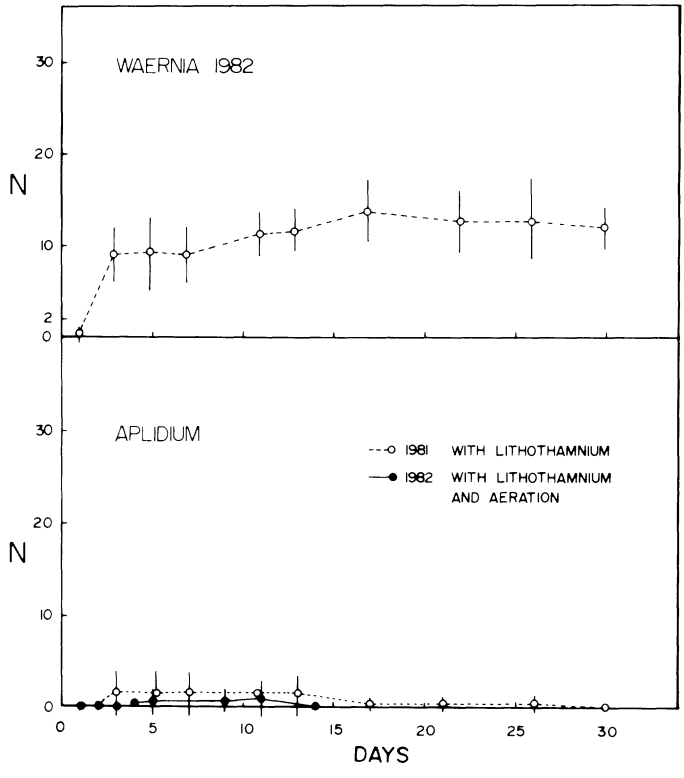

FIGURE 4. Cumulative number of larvae metamorphosed (of initial N = 30 planulae) in treatments with *Waernia* (in light 1982) and *Aplidium* plus *Lithothamnium* (in light 1981, in light with aeration 1982). Values are mean numbers of metamorphosed larvae ± S.D. for three replicates of each treatment.

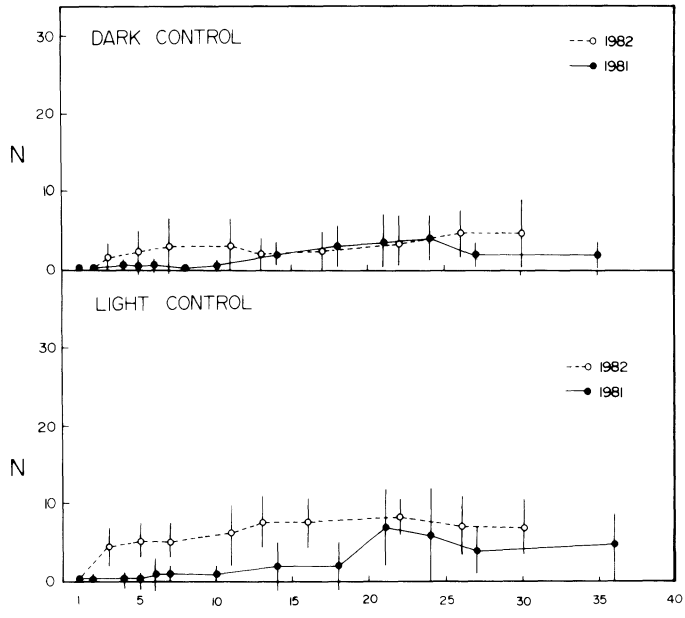

FIGURE 5. Cumulative number of larvae metamorphosed (of initial N = 30 planulae) in control treatments with only rock (1982) or *Modiolus* shell (1981) substratum. Values are mean number of metamorphosed larvae ± S.D. for three replicates of each treatment.

tunicate surfaces. Since there seemed to be a negative effect of *Aplidium* on larvae in 1980, I examined its effect in the presence of a known inducer of metamorphosis (*Lithothamnium*).

When *Aplidium* was present with *Lithothamnium,* larval metamorphosis and survivorship were again poor (Table IV, Fig. 4). This time the treatments were constantly aerated to reduce the possibility that the *Aplidium* was depleting available oxygen during the experiments. Colonies of *Aplidium* remained alive and apparently healthy throughout this set of experiments. However, all such experiments were within containers, allowing maximum concentration of released metabolites or other chemicals.

Substratum orientation by larvae

In all three years of experiments, many larvae metamorphosed on the bottoms of the glass or plastic containers, but never on the walls. Larvae never swam (as suggested by Feldman, 1976) after removal from adult colonies or during natural release. The corner where the bottom met the wall was the most common site of attachment but there was no evidence of aggregation. When the number of metamorphosed larvae on the rock or shell surface was compared to that on the bottom of the container (corrected for surface area), there was no difference in treatments with *Phymatolithon* or *Waernia* in the light, or in the lit controls (1981, 1982 combined) (Table V). However, there was significant preference for the rock or shell substratum in the *Lithothamnium* (light or dark) and dark control treatments (Table V). When there was a preference shown, it was always for the natural substratum. The large number of larvae metamorphosing on the glass or plastic argues against

TABLE V

Metamorphosis of Alcyonium *larvae after 30 days, on the container bottom (plastic or glass) and on the rock or shell material used as substratum (1981 and 1982)*

TREATMENT	ON CONTAINER (9.6 cm^2)	ON CONTAINER (CORRECTED) (3.0 cm^2)	ON ROCK OR SHELL (3.0 cm^2)	χ^2	P
LITHOTHAMNIUM (light)	84	26	57	20.5	<0.01
PHYMATOLITHON (light)	47	15	22	1.95	>0.05
WAERNIA (light)	23	7	5	0.76	>0.05
LITHOTHAMNIUM (dark)	9	3	64	156.03	<0.01
LIGHT CONTROL	22	7	12	2.61	>0.05
DARK CONTROL	10	3	35	69.30	<0.01

Top (with crustose algae) and bottom of the rock (without) were combined for this comparison. The number of larvae on the container bottom (9.6 cm^2) was corrected to 3.0 cm^2.

χ^2 = chi-squared statistic, P = significance level.

thigmotaxis for coralline or other algal surfaces, although surface texture recognition by the larvae is certainly possible.

There were several treatments in which it appeared that larvae were primarily on the bottom, or the top, of the substratum offered. When *Phymatolithon* covered the upper surface of the rock or shell, significantly more larvae settled on the bottom and sides than on the top (algal) surface in the lit treatments (Table VI). There was also less attachment on the top surface of *Waernia* and *Lithothamnium* (light or light/dark cycle). Only *Lithothamnium* is darkness had more settlement on the top (algal surface) than expected by its area. In the lit controls, most settlement was on the top surface. This indicates that while contact with the crustose algae induces settlement, the algae may also be able to deter settlement directly onto their living surfaces.

Larval survivorship

It was clear from the 1980 experiments that long-term survival of actively crawling planulae was possible (to at least nine months). Survivorship was better in

TABLE VI

Metamorphosis of Alcyonium *larvae on the top or bottom of the rock or shell substratum after 30 days (1981 and 1982)*

TREATMENT	SUBSTRATE		χ^2	P
	TOP	BOTTOM		
LITHOTHAMNIUM (light)	16	41	0.9	>0.05
LITHOTHAMNIUM (light/dark)	8	14	2.1	>0.05
LITHOTHAMNIUM (dark)	32	30	8.9	<0.05
WAERNIA	2	5	0	>0.05
PHYMATOLITHON	9	47	8.0	<0.05
LIGHT CONTROL	11	1	8.3	<0.05
DARK CONTROL	18	15	0.3	>0.05

The top of the rock was covered with the encrusting algae in the first 5 treatments.

χ^2 = chi-squared statistic, P = significance level.

Area of top surface = 34%, area of bottom and sides combined = 64% of total area.

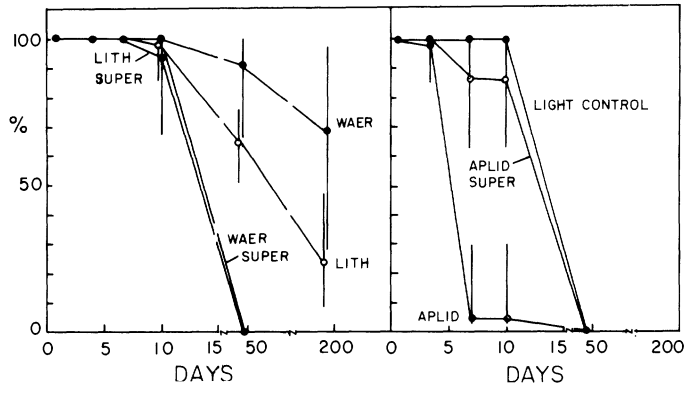

FIGURE 6. Survivorship of planulae during the 1980 experiments expressed as the percentage of all initial larvae that did not go on to metamorphose. Values are mean ± S.D. for arcsine transformed data, backtransformed for the graph. At days 1 and 3 treatments were statistically indistinguishable. At days 7 and 10 the *Aplidium* treatment was significantly different than all others ($P \leq 0.05$, ANOVA and Student-Newman-Keuls (SNK) multiple comparisons test). At days 49 and 194 the *Lithothamnium* and *Waernia* treatments were different from the rest (SNK test). All other combinations of treatments at each time were indistinguishable (statistical analysis from Sokal and Rohlf 1969). Abbreviations as follows: LITH = *Lithothamnium*, light, WAER = *Waernia*, *LITH SUPER* = *Lithothamnium* supernatant, WAER SUPER = *Waernia* supernatant, APLID = *Aplidium*, APLID SUPER = *Aplidium* supernatant.

treatments with crustose algae than in treatments with other substrata or in controls. Survivorship was worst in treatments with *Aplidium* (Fig. 6). Data on numbers of live planulae were not taken regularly during 1981. During the 1982 experiments, live planulae were again counted every other day. In this set of experiments mean survivorship was between 11 and 39 percent for 30 days for larvae that never did metamorphose (Fig. 7). 28 percent of the light control group, and 61 percent of the

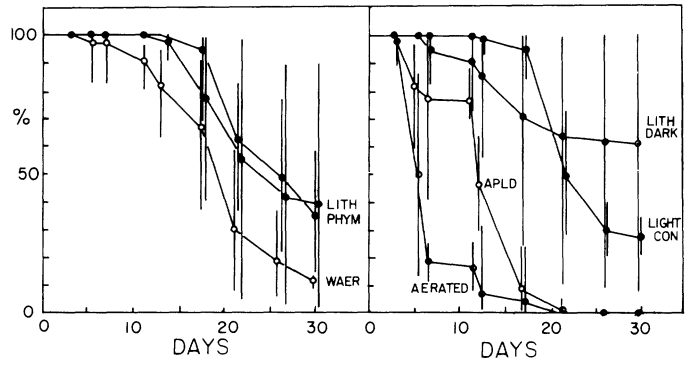

FIGURE 7. Survivorship of planula larvae during the 1982 experiments expressed as percentage of all initial larvae that did not go on to metamorphose. Values are mean ± S.D. for arcsine transformed data, backtransformed for the graph. At days 1 and 3 all treatments were statistically indistinguishable. At days 5, 7, and 11 the aerated treatment was different from the rest ($P \leq 0.05$, ANOVA and SNK test). At days 17 and 22 the *Aplidium* and aerated treatments were indistinguishable but different from all but the dark control group (on day 17) and the *Lithothamnium* and *Waernia* treatments (on day 22); all other treatments were indistinguishable from each other. At day 30 the 5 treatments that still had living larvae (all but aerated and *Aplidium* treatments) were indistinguishable (statistical treatment based on methods in Sokal and Rohlf (1969). Abbreviations as follows: LITH = *Lithothamnium*, PHYM = *Phymatolithon*, WAER = *Waernia*, APLD = *Aplidium*, LITH DARK = *Lithothamnium* in darkness, LIGHT CON = control, in light.

dark control group were still alive after 30 days. All larvae in the aerated treatments and in the treatments with *Aplidium* died within the 30 day period. Aeration may have increased the larvae's metabolism causing them to lose their energy reserves rapidly. On the other hand, the agitation itself may have caused the larvae to damage themselves by hitting the walls of the container.

Discussion

The crustose coralline algae, *Lithothamnium glaciale* and *Phymatolithon rugulosum,* as well as the fleshy red crustose alga *Waernia mirabilis,* induced settlement of *Alcyonium siderium* planulae in laboratory experiments. Rock surfaces around *Alcyonium* colonies in the field are covered with colonial invertebrates (tunicates, sponges, hydroids) and the three crustose algae used in this experiment (Sebens, 1982, 1983). Field studies of larval settlement (Sebens, 1983) showed significant metamorphosis only on these algae and on adjacent bare rock, although settlement on *Lithothamnium* was less than expected by its percent cover and settlement on *Waernia* was greater.

Any of the three algae, but not the common encrusting invertebrates *Aplidium pallidum, Halisarca dujardini,* or the mussel shell (*Modiolus modiolus*), can induce metamorphosis in laboratory experiments. Once the inducing substratum has been contacted metamorphosis can then occur on nearby rock surfaces, but not necessarily on the algal surface itself. Even so, there was no field settlement of planulae on any of the encrusting invertebrates adjacent to algal crusts (Sebens, 1983). In a few vertical rock wall community samples collected by scraping rock surfaces, I have noted single polyps of *Alcyonium* attached to erect bryozoans, small red algal fronds, or to the sides of *Aplidium* colonies that were encrusted with detritus (unpublished observations). In the field studies, some larvae settled in the mat of small polychaete tubes, amphipod tubes, and bound detritus that sometimes covers the encrusting algae (Sebens, 1983). These individuals were probably attached directly to the algal surface beneath.

There was distinct inhibition of metamorphosis in darkness, even with *Lithothamnium* present. It is possible that *Lithothamnium* does not produce or release the stimulus in the dark. It is more likely that the larvae are inhibited from receiving, or responding to, the stimulus in darkness. This mechanism would allow them to discriminate between deep crevices, underhangs, and open vertical rock surfaces, especially since they often crawl for several days before metamorphosis. Inhibition of settlement in darkness may keep them out of microhabitats that are likely to be far from the greatest water flow thereby allowing the best chance of capturing zooplankton prey. Weinberg (1979) found a positive photokinesis in a Mediterranean gorgonian coral planula (*Eunicella singularis*), and a total lack of light-related response in that of a second species (*Corallium rubrum*). It is not clear that *Alcyonium* shows either a phototaxis or photokinesis, but instead simply fails to attach and metamorphose in the dark. Although *Alcyonium siderium* has a similar habitat distribution (vertical walls) to *Corallium rubrum* (Weinberg, 1979), it does not appear to share a negative geotaxis that would lead the planula up walls or to the undersides of rock ledges. Release of larvae directly onto the substratum surrounding the parent colony may alleviate any need for this behavior.

Larvae did not settle significantly, nor survive well, in the presence of the compound ascidian *Aplidium pallidum,* even when treatments were aerated intermittently (1980) or continuously (1982). Field studies (Sebens, 1982) indicate that *Aplidium* overgrows, and probably kills, small colonies of *Alcyonium.* Larvae will,

however, settle near *Aplidium* in the field (Sebens, 1983). Grosberg (1981) demonstrated that swimming bryozoan larvae avoid settling on experimental plates with the compound ascidians *Botryllus schlosseri* and *Botrylloides leachi.* Both ascidians overgrew established bryozoan colonies. Young and Chia (1981) found a similar result in laboratory studies of bryozoan larvae in the presence of other compound ascidians. In both the present study and that of Young and Chia (1981), larvae were confined with the ascidians in relatively small volumes of water. In Grosberg's study, settling plates were suspended in the relatively still water of the Eel Pond, Woods Hole, MA. In all such cases ascidian metabolites or other exuded chemicals could concentrate at levels that would not be found in more turbulent conditions such as the field sites where *Alcyonium* has been studied (Sebens, 1982, 1983). Bryozoan larvae can swim away if they contact the ascidians; the *Alcyonium* planulae can only crawl. Thus, *Alcyonium* is probably not absolutely restricted from settling near *Aplidium* in the field, thereby avoiding overgrowth. If there is a chemical recognition of the ascidian by the larva, it probably keeps the planula from crawling onto the ascidian rather than preventing nearby settlement.

The vertical rock wall community is in constant spatial flux. Invertebrates are often observed overgrowing coralline algae, *Waernia,* and sometimes small *Alcyonium* colonies. The presence of uncovered algal crusts indicates either that a grazer (*e.g.,* the sea urchin *Strongylocentrotus droebachiensis*) has recently cleared off the tunicates, sponges, or hydroids, or that those encrusting organisms have receded on their own (after reproduction or starvation). On vertical walls, such algae are ideal settlement sites for the soft-coral in that they are hard, stable surfaces that will persist for long periods of time. Horizontal surfaces adjacent to the vertical walls are completely covered by *Lithothamnium, Phymatolithon,* and other corallines but are constantly grazed by sea urchins. Nothing that settles on these algae survives such grazing very long. On vertical surfaces, grazers are much less common and *Alcyonium* can probably grow to a size sufficient to be avoided before the area is grazed. Planulae would probably be induced to metamorphose if they were to drift onto horizontal surfaces with corallines, but they would not survive.

Coralline algae induce settlement in mollusks which later graze the algal surface (chitons, Barnes and Gonor, 1973; Rumrill and Cameron, 1983; abalone Morse *et al.,* 1979). Harrigan (1972a, b) found that *Pocillopora damicornis* planulae would settle on coral rubble with coralline algae on its surface. Breitburg (1983), however, found that settlement of a variety of invertebrates and algae in the field was less successful on the surface of corallines than on scraped rock areas. She notes that corallines are easily overgrown by invertebrate colonies expanding laterally onto them rather than by direct settlement onto their living surface. *Alcyonium* will certainly settle on coralline surfaces under both field and laboratory conditions. However, there is some evidence that it prefers to settle on the rock, shell, or glass adjacent to the coralline algae rather than on the algal surfaces after having contacted the algae in the laboratory. This agrees with field evidence that bare rock is preferred to corallines (Sebens, 1983).

Alcyonium larvae leave the parent colony and crawl across the substratum for periods up to several days (Sebens, 1983). However, it appears that most larvae settle within a few centimeters of the adult colonies. They probably do not have a chance to leave the local habitat unless they are washed off the colony by wave surge as they emerge. Similar local dispersal by crawling demersal planulae has been shown for the temperate Pacific coral *Balanophyllia elegans* (Gerrodette, 1981; Fadlallah, 1983). Substratum choice is not a matter of settlement, testing and then swimming away as in barnacle cyprids (Crisp, 1965, 1974), polychaete larvae (Wilson, 1948,

1952, 1954, 1968), hydroid planulae (Nishihara, 1967a, b; 1968a, b; Spindler and Müller, 1972, Müller, 1973), and many other invertebrate larvae (reviewed by Mileikowsky, 1971; Meadows and Campbell, 1972). Crawling larvae are in constant substratum contact and must respond by either settlement, continued crawling, or active avoidance of each substratum type. Substrata may be either suitable surfaces for metamorphosis, or less suitable attachment sites but still inducers of metamorphosis. Larvae will settle on non-inducing substrata (rock, shell, glass) after having contacted *Lithothamnium, Phymatolithon,* or *Waernia.* These algae serve as indicators of suitable habitat for the larva rather than as necessary attachment sites.

ACKNOWLEDGMENTS

I thank the following for their field and laboratory assistance: M. Ashenfelter, D. Denninger, D. Levitan, S. Norton, R. Olson, M. Patterson, J. Sigda, D. Smith, W. Stotz, and T. VanWey. Edward Elbers and JoAnn Resing helped set up and monitor substantial portions of the laboratory experiments. I also thank R. Olson for reading and commenting on the manuscript and R. Steneck and R. Wilce for algal identification.

The Marine Sciences and Maritime Studies Center of Northeastern University, the Museum of Comparative Zoology and the Biological Laboratories of Harvard University provided laboratory space and equipment. The research was supported by NSF grants OCE 78 08482 and OCE 80 07923 and the Milton Fund of Harvard University. This is M.S.M.S.C. Contribution no. 117.

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