Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement

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Abstract

Newly settled juvenile ascidians were transplanted into shaded and unshaded sites at two subtidal depths to test the hypothesis that photonegative settlement behavior enhances juvenile survival. Silt, filamentous algae and grazing gastropods (*Margarites pupillus*) were identified as sources of mortality associated primarily with non-cryptic microhabitats. Silt inflicted heavy mortality on all six species tested. Algal overgrowth was important in shallow water, where it increased mortality and depressed growth rates over a 14-d period. Laboratory experiments demonstrated that gastropods can remove juvenile ascidians from the substratum. The sources of post-settlement mortality investigated may help determine distributional patterns of ascidians in the San Juan Islands, Washington, USA, and may also represent selective pressures that maintain negative phototaxis in the behavioral repertoires of ascidian tadpoles.

Introduction

The dark undersides of subtidal rocks, coral formations and artificial fouling panels often support populations of sessile invertebrates at higher density and diversity than upward-facing surfaces nearby (Pomerat and Reiner, 1942; Lilly *et al.*, 1953; Buss, 1979; Castric-Fey *et al.*, 1979; Harris and Irons, 1982, etc.). This pattern is commonly attributed to larval behavior since light intensity correlates strongly with surface angle, and since the larvae of most subtidal invertebrates demonstrate negative phototaxis immediately before settlement (Thorson, 1964). In this research, we used ascidians to explore an alternative hypothesis: that the pattern could result from post-settling

mortality occurring before juveniles are large enough to census easily.

Subtidal cryptic habitats in the tropics are often free from several potential sources of mortality, including large predators and water turbulence (Buss, 1979). Preliminary observations in the San Juan Islands, Washington, suggested that silt, filamentous algae and grazing herbivores, all of which occur mostly in non-cryptic habitats, could have detrimental effects on young ascidians. We designed experiments to test the effects of siltation and algal overgrowth in the field and of grazing by the gastropod *Margarites pupillus* in the laboratory on mortality and growth of six species of solitary ascidians.

All of the ascidian species we used are known to exhibit photonegative behavior at settlement (Young, 1982). It is generally assumed that settling responses enhance the likelihood that larvae will select sites where probability of survival is high, and that strong sources of mortality acting differentially in space are selective pressures that fix adaptive behaviors. However, the post-settling fitness data needed to support this viewpoint have been provided in only a few instances for species with documented behavioral repertoires. For example, some bryozoans and other sessile invertebrates demonstrate larval behavior that minimizes the likelihood that the adults will be overgrown by superior spatial competitors (Grosberg, 1981; Young and Chia, 1981) or consumed by predatory fishes (Keough and Downes, 1982). The adaptive value of the photonegative response remains uncertain for most species. The behavior may function in selecting microhabitats at settlement, or it may guide larvae to deep water where adverse effects of UV radiation are minimal (Moore *et al.*, 1963; Jokiel, 1979; Olson, 1983) or appropriate adult habitats are located (Thorson, 1964).

Although many workers have recognized the importance of juvenile dynamics in controlling abundance patterns of adults (Thorson, 1966; Grosberg, 1981; Keough and Downes, 1982; Young and Chia, 1982), and several studies have documented differential survival of juveniles in the

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field (e.g. Connell, 1961; Muus, 1973; Gage and Tyler, 1981; Strathmann *et al.*, 1981), few studies have related larval habitat selection to patterns of juvenile mortality, presumably because juveniles of most invertebrates are too small to observe and manipulate readily in the field.

Material and methods

Six species of solitary ascidians in two orders and four families were used in this study: the phlebobranchs *Corella inflata* (Corellidae), *Ascidia callosa* and *A. paratropa* (Ascidiidae) and the stolidobranchs *Pyura haustor*, *Boltenia villosa* (Pyuridae), and *Styela gibbsii* (Styelidae). Adult ascidians were collected from rocky subtidal sites or floating docks in the San Juan Islands, Washington, and maintained in running seawater aquaria in the laboratory prior to use.

Larval culturing

Corella inflata isolated in dishes of clean seawater generally spawned each morning. Ripe individuals of *Ascidia paratropa* and *A. callosa* were removed from their tunics. Gametes were then pipetted directly from the gonoducts and fertilized *in vitro*. In *Pyura haustor*, *Styela gibbsii*, and *Boltenia villosa*, hermaphroditic gonads were dissected from several adults and macerated through 253-μm nitex screen into filtered seawater where fertilization occurred. The cultures were then decanted and rinsed repeatedly until the water was clear and free of excess sperm. After hatching, tadpoles were pipetted into small (55-mm diameter; 16-ml) petri dishes of filtered seawater, where they settled. The tadpoles of *A. paratropa* did not settle readily on clean plastic surfaces, so this species alone was allowed to settle in glass dishes. After settlement the juveniles were scraped gently from the dish bottom with a razor blade and placed in plastic dishes, where they reattached within a few days.

Juvenile transplant experiments

We tested for small-scale spatial variation in mortality by transplanting juvenile ascidians to the field under different conditions of light, depth, and surface angle. We reasoned that juveniles transplanted to upward-facing subtidal surfaces would be exposed to both silt and algae, whereas juveniles transplanted to the bottom sides of transparent plates would be subject to algal growth only. Individuals on the bottom sides of opaque plates would serve as controls, being subject to neither silt nor algae. By comparing survival in the two downward-facing dishes, we hoped to get a quantitative estimate of the mortality due to algae. Moreover, by subtracting survival in the upward-facing treatments from that in the downward-facing unshaded ones, and then comparing this difference to survival

in the controls, we expected to obtain values for the effect of silt. These quantitative assessments are only valid if two assumptions hold true: (1) that the mortality processes are additive (that they do not interact either to increase or decrease mortality) and (2) that any mortality processes other than silt and algae act similarly in all three treatments. Transplants were placed at two depths to test the prediction that mortality from both silt and algae would be more intense in shallow water, algae because of favorable light conditions and silt because of greater water turbulence (Schopf *et al.*, 1980).

All transplants were done between March 12 and May 21, 1981. Following settlement, juveniles in petri dishes were maintained in the laboratory in filtered seawater for about a week to assure that they were firmly attached. Thus, the 14-d field experiments terminated when the juveniles were about 21-d-old. Just before transplantation, they were counted under a dissecting microscope with the aid of an underlying grid. Initial densities ranged as follows: *Ascidia callosa*, 4.6 to 34.5 cm^{-2}; *A. paratropa*, 2.4 to 15.9 cm^{-2}; *Boltenia villosa*, 2.8 to 12.8 cm^{-2}; *Corella inflata*, 4.1 to 20.7 cm^{-2}; *Pyura haustor*, 3.7 to 17.1 cm^{-2}; *Styela gibbsii*, 2.7 to 9.2 cm^{-2}. Starting density was significantly correlated with survival only in *P. haustor* ($r=0.686$; $P < 0.05$). Correlation coefficients for the other species ranged from -0.164 (*A. callosa*) to 0.591 (*B. villosa*). Dishes were assigned randomly to one of the six treatments (three conditions at each of two depths), each treatment consisting of duplicate dishes. The dishes were secured with rubber bands to 6.5- by 28-cm strips of 0.5-cm Plexiglas painted black for half their length. Four dishes were attached to one side (ultimately the undersurface), two on the clear half and two on the opaque half, and two more dishes were fastened to the upper surface of the opaque half. To avoid damage to the ascidians during the boat trip to the study site and while they were being carried underwater, the assembled experimental strips were transported in a compartmentalized Plexiglas box filled with seawater. The box was kept cool in a large bucket of seawater while in the boat and was not opened until we had swum to the transplant site.

In each experiment, the sets of dishes were placed at Pt. George, Shaw Island, Washington, one at 4.5 m below MLLW and the other at 21.0 m. The plates were held in a horizontal position on racks (Fig. 1), 10 cm above the substratum. Experiments ran for 14 d, after which we recovered the dishes, transported them to the laboratory, and recounted the cohorts.

Initially no dimensional measurements of the juveniles were taken. In later experiments, after subjective observations had suggested possible differences in growth rates among treatments, we measured a random subsample of juveniles from selected dishes. A complete comparison of growth rates among treatments was made only for *Boltenia villosa* and *Ascidia callosa*. In the two other species considered, *Pyura haustor* and *Corella inflata*, we only measured shaded and unshaded individuals at 4.5-m depth. Total lengths of juvenile ascidians were taken along
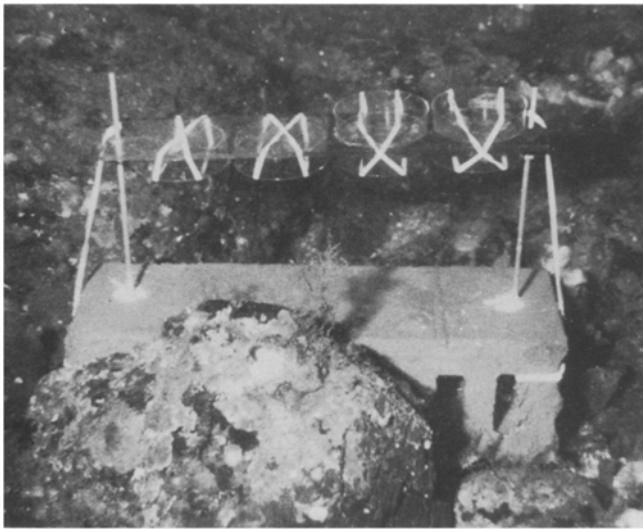
Fig. 1. Juvenile transplant apparatus in place at 21.0-m depth at Pt. George, Shaw Island, Washington, USA

the mid-sagittal plane (line between siphons) using a calibrated ocular micrometer in a Wild M-5 dissecting microscope at 25 X.

Sedimentation was measured with traps deployed at the transplant sites from July 9–14, 1983. Sediment traps consisted of wide-mouth plastic jars (mouth diameter: 7.0 cm; height: 13.0 cm). Gardner (1980a, b) tested such traps in field and laboratory, and noted that they tend to overestimate the actual vertical flux of sediment. Nevertheless, they are adequate for comparing relative siltation between sites. Three replicate traps were deployed at each depth, taking care to keep the trap mouths at least 21 cm away from each other (Gardner, 1980a). The traps were held in place by stacking cobbles around their bases. After 5 d, the jars were capped *in situ* and carried to the laboratory, where the contents of each jar were suction-filtered on pre-tared Whatman No. 40 filter paper, air dried and weighed on a digital Mettler balance sensitive to 0.01 g.

Laboratory experiments

The potential effects of gastropod (*Margarites pupillus*) grazing were investigated in the laboratory. Only snails with shells between 0.8 and 1.3 cm in height were used. Larval ascidians were allowed to settle in polystyrene petri dishes having three built-in compartments (Lab-Tek Tri-Petri 100×15 mm). Four such replicate dishes were used for each of the three ascidian species studied. Within each dish, three treatments were assigned randomly to the compartments: one snail, two snails or no snails (control). The dishes were filled completely with seawater, covered, secured with rubber bands and immersed in a running seawater aquarium for 22 h, at which time the remaining ascidians were counted. With the lids in place, snails were unable to crawl between dish compartments; nevertheless,

any adverse effects of oxygen depletion or snail metabolites were expected to act similarly in all three compartments, since substances could diffuse freely among them.

Field experiments described below suggested that decorator crabs (*Oregonia gracilis*) may have been important agents of mortality in some of our treatments. This possibility was tested by introducing single crabs into glass culture dishes with known numbers of juveniles, immersing the dishes in the water table for 24 h, and comparing survival with control dishes containing no crabs.

Results

Distribution of mortality sources

For the duration of the Pt. George transplant experiments, upward-facing dishes contained fine sand and silt, though the absolute amount did not seem to increase over time. We presume that the silt was flushed from and deposited in the dishes on a regular basis by the strong semidiurnal tidal currents. Schopf *et al.* (1980) measured sedimentation rates near our Pt. George site and found that they were inversely correlated with depth. At the precise locations of our transplants, we obtained the opposite result. Following five days of exposure to silt during a spring tide sequence, the three deep sediment traps each contained more silt ($\bar{x} = 3.94$ g $\pm$ 1.73 SE; $n = 3$) than any of the shallow traps ($\bar{x} = 1.978$ g $\pm$ 0.62 SE; $n = 3$). The difference was not significant, however (Student's t-test: 4 d.f., $P > 0.05$). Algal growth was also related to depth, as expected. Following a two-week submersion, diatoms and filamentous algae always blanketed the 4.5-m unshaded treatments, while the 21.0-m treatments were nearly free of algal growth. Control (shaded) dishes were likewise free of algae, though at both depths they sometimes were colonized by stalked ciliates resembling *Vorticella* sp.

The density of *Margarites* spp. near the 21.0-m transplant site was estimated as 49.0 m^{-2} ($\pm$ 11.1 SE) in four haphazardly placed 50×50 cm quadrats on a solid bedrock slope with sparse cover of macroscopic algae. Schroeter (1972) found densities of *M. pupillus* as high as 200 m^{-2} at Cantilever Pt., San Juan Islands, including those individuals in the *Agarum* sp. canopy. In a survey of seven boulders with an average of 9.4 snails per boulder (SE: 2.27) at Pt. George (12.0-m depth), most of the snails occurred on the top sides ($\bar{x} = 95.0\%$; SE: 3.21).

Field survival

Survival data for all species (Fig. 2) were analyzed together in a crossed three-factor ANOVA (Table 1) in which the factors were depth (2 levels), position (3 levels: top, bottom shaded, bottom unshaded) and species (6 levels). Experiments were not all run concurrently so the "species" factor also includes possible temporal variation; species comparisons should be regarded with some caution.
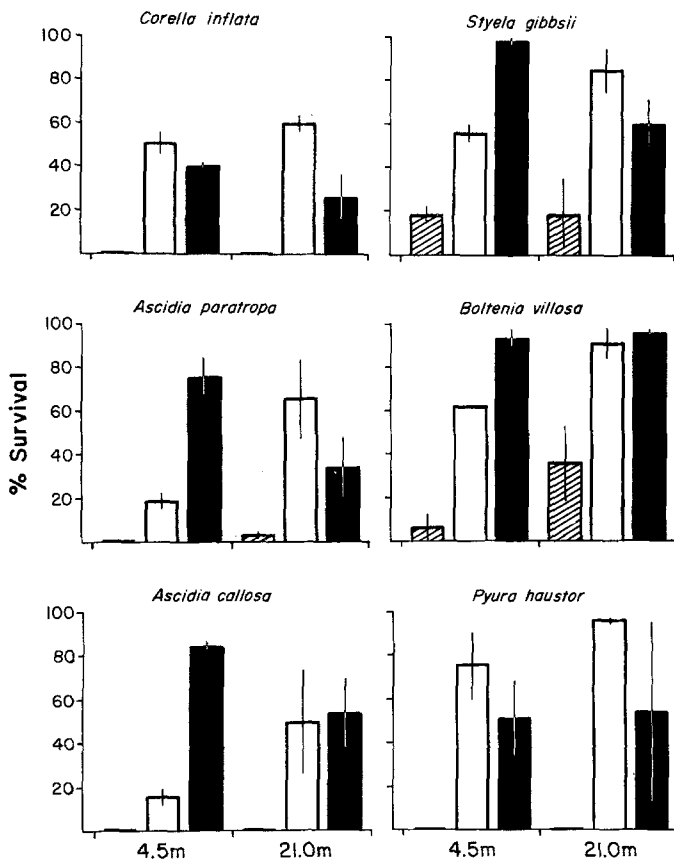
Fig. 2. *Corella inflata, Ascidia paratropa, Ascidia callosa, Styela gibbsii, Boltenia villosa* and *Pyura haustor.* Survival of juvenile ascidians at 4.5- and 21.0-m depths after 2 wk at Pt. George. Solid histogram bars: shaded, downward-facing treatments; open bars: unshaded, downward-facing treatments; crosshatched bars: upward-facing. Each bar represents mean of 2 replicates. Vertical lines are standard errors

Table 1. Three-factor analysis of variance for survival of juvenile ascidians (6 species) in transplants to 2 depths and 3 "positions" (facing up, light facing down, dark facing down). Data were arcsine transformed for the analysis

Source of variation	df	SS	MS	F	P
Mean	1	19.360	19.360	348.52	0.0000
Depth	1	0.745	0.074	1.34	0.2545
Position	2	7.397	3.698	66.59	0.0000
Species	5	2.429	0.486	8.75	0.0000
Depth × position	2	1.355	0.677	12.19	0.0001
Depth × species	5	0.346	0.693	1.25	0.3083
Position × species	10	1.727	0.173	3.11	0.0062
Depth × position × species	10	0.556	0.056	1.00	0.4616
Error	35	1.944	0.055	–	–

The main effects of position and species were highly significant, while that of depth was not (Table 1). The three-way interaction was not significant, but since all three main effects were involved in two-way interactions, each must be interpreted with respect to at least one of the others. Of the two-way interactions, only depth × species was not significant.

After 14 d, all six species had experienced heavy mortality in upward-facing dishes at both depths (Fig. 2). The species × position interaction can be explained in part by the fact that only three species had any survivors at all in the upward-facing treatments. Additionally, within the other two levels of "position" (bottom shaded, bottom unshaded), there were very large quantitative differences between most pairs of species. These differences become apparent when means and standard errors among species for any of the treatments (positions) are compared. Because of the significant species × position interaction, the effects of silt and algae must be considered separately for each species. Two species, *Ascidia callosa* and *Boltenia villosa*, survived equally well in light and dark downward-facing dishes at 21.0 m. *Corella inflata, A. paratropa, Styela*

gibbsii and *Pyura haustor*, however, survived much better in unshaded than shaded dishes at the same depth. This unexpected pattern invalidated our initial assumption of additivity, making it impossible to assign quantitative values to the relative importances of silt and algae. It also suggested that we should seek an important source of mortality associated with shaded dishes. On three different occasions, we observed decorator crabs, *Oregonia gracilis*, residing in the "control" dishes. By wedging their legs into the corners of the dishes, crabs were able to cling securely and hang upside down. We suspected that the sharp dactyls of the crabs damaged the ascidians, causing the observed high mortality. This possibility is supported by laboratory experiments in which crabs were allowed to occupy dishes with ascidian juveniles. In each of the three species tested, mortality in the crab dishes was substantial (*C. inflata*, 72,9%; *A. paratropa*, 97,0%; *S. gibbsii*, 30.1%) after 22 h. No mortality was observed in control dishes maintained simultaneously.

In downward-facing (silt-free) dishes in shallow water, mortality was significantly higher in unshaded than shaded dishes for *Styela gibbsii, Boltenia villosa, Ascidia paratropa* and *A. callosa*. This difference is attributable to algal growth in the unshaded dishes. In the remaining two species, the reverse pattern was seen, though the differences between light and dark were probably not significant. It is possible that crabs or other vagile colonists interfered with the shaded individuals here as they did in deeper water.

Several explanations for the depth × position interaction are apparent from the graphs (Fig. 2). First, survival on upward-facing (silted) surfaces was higher at 21-m depth than at 4.5-m depth for *Boltenia villosa* and *Ascidia paratropa*, two of the three species with survivors in the upward-facing treatments. Second, in all species, there were more survivors in downward-facing light treatments in deep water than in shallow water. This is the pattern that would be predicted if algal growth were an important source of mortality. Finally, in four of the six species (*Corella inflata, A. paratropa, A. callosa, Styela gibbsii*), there were more survivors in shallow shaded treatments than in deep shaded treatments.

Field growth

Growth data were collected for only four of the six species. In each species, individuals reared in shallow water grew less in unshaded than in shaded treatments over a two-week period (Fig. 3). There was no such difference between light and dark treatments in the 21.0-m transplants for either *Ascidia callosa* or *Boltenia villosa*. *A. callosa,* though not *B. villosa,* were significantly smaller in the 4.5-m dark treatment than in either deep treatment. On upward-facing surfaces, growth of *B. villosa* was depressed in shallow water but not in deep water. This finding suggests that, while silt and algae both cause mortality, algal overgrowth alone has the effect of depressing growth rates. We noted at times that mats of algae in the shallow dishes appeared to obstruct the siphons of young juveniles, suggesting a possible mechanism for this reduction in growth.

Grazing by gastropods

Data from laboratory experiments on grazing by *Margarites pupillus* (Fig. 4) were analyzed with a randomized complete block ANOVA in which each dish represented a block, and the treatments were different snail densities (Sokal and Rohlf, 1969). *Corella inflata* and *Boltenia villosa* showed significant treatment effects resulting from higher survival in the control chambers than in the presence of snails (Table 2). In addition, the block (dish) effect was significant in the latter. In *Styela gibbsii,* one replicate was discarded because snails entered the control chamber. As a result, the significance level for the snail effect was just over 0.05. The data (Fig. 4) suggest a strong
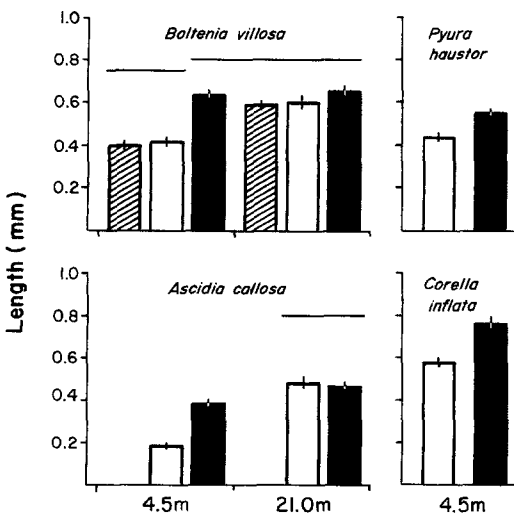

No. of *Margarites pupillus*

Fig. 4. *Corella inflata, Boltenia villosa* and *Styela gibbsii.* The relationships between *Margarites pupillus* density and ascidian survival in 22-h laboratory experiments. Each point shows mean of 4 (*C. inflata; B. villosa*) or 3 (*S. gibbsii*) replicates ±1 SE. *C. inflata:* ▲ ; *B. villosa:* ● ; *S. gibbsii:* ■

Table 2. Two-factor randomized block analyses of variance for arcsine-transformed data on grazing by *Margarites pupillus* (Fig. 4)

Species	Source of variation	df	SS	MS	FS	P
Corella inflata	dishes	3	301.130	100.377	1.484	ns
	snails	2	11 657.168	5 828.584	86.184	< 0.001
	error	6	405.775	67.629	–	–
Boltenia villosa	dishes	3	2 790.780	930.260	12.924	< 0.005
	snails	2	1 817.686	908.843	12.626	< 0.01
	error	6	431.844	71.979	–	–
Styela gibbsii	dishes	2	840.382	420.191	1.369	ns
	snails	2	2 977.152	1 488.576	4.851	ns
	error	4	1 227.502	306.875	–	–

snail effect nonetheless. By observing ascidian/snail encounters through the sides of transparent dishes, we concluded that *M. pupillus* can kill juvenile ascidians either by rasping them off with the radula, or by dragging the shell across them. The former method seems to be more common. Ascidians crossed by snails opened their siphons and resumed normal pumping behavior within a few minutes. Thus, juveniles were apparently not harmed by mucus trails left by the snails as they passed over.

Discussion

Our data strongly support the idea that shaded substrata are refuges for juvenile ascidians and furthermore implicate siltation, overgrowth by microscopic algae and grazing by herbivorous gastropods as potentially important sources of mortality associated with unshaded substrata. In the rocky subtidal zone of the San Juan Islands, silt appears to have a more important effect on mortality than algae at both deep and shallow sites. Assuming our

Fig. 3. *Boltenia villosa, Ascidia callosa, Corella inflata* and *Pyura haustor.* Mid-sagittal lengths of juveniles following 2-wk transplant at Pt. George. Shading of bars as in previous figure. Vertical lines are standard errors. Horizontal lines indicate all non-significant differences, determined by Student-Newman-Keuls test following one-way Analysis of Variance in *B. villosa* and *A. callosa* and unpaired Student's *t*-test in *P. haustor* and *C. inflata*
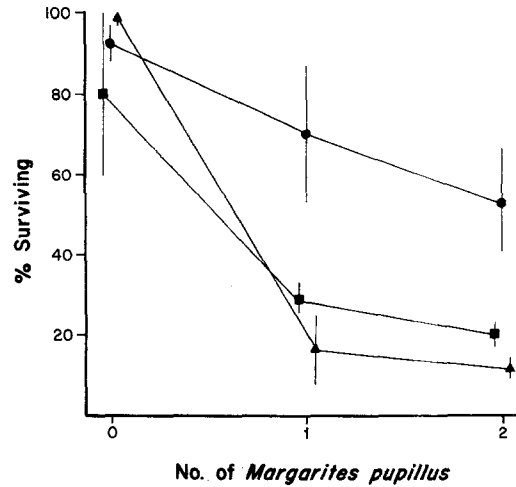
upward-facing petri dishes roughly mimic upward-facing rock surfaces, we would predict virtually no survival on such surfaces. This prediction is supported by quantitative observations on the distributional patterns of adult ascidians in the San Juans, which show that nearly all individuals of most species occupy cracks, holes, the sides and bottoms of rocks, or vertical rock walls (Young, 1982).

Heavy silt loads are often correlated negatively with abundance of benthic animals (reviewed by Moore, 1977). For example, Mayer (1918) considered silt to be the major factor limiting distribution of corals on the Great Barrier Reef, an opinion that is supported by recent work on juvenile corals by Bak and Engel (1979). In the shallow subtidal of Lough Ine, Scotland, Round et al. (1961) demonstrated experimentally that the hydroid *Sertularia operculata* is unable to survive in areas where suspended or resting silt loads are heavy. Working with boulders in this same region, however, Lilly et al. (1953) did not consider silt an important limiting factor, despite the fact that nearly all species occurred more abundantly on the sides and bottoms of boulders than on the tops. Their rationale was that species occurring predominantly on the bottoms of rocks in sheltered, silty areas would be expected to occur atop boulders in rapidly moving water if silt were important; this pattern was not seen. Unfortunately, the authors failed to consider the possible distinction between silt as an "ultimate factor" and silt as a "proximate factor". It seems possible that while the adults may survive on upward-facing surfaces in areas free of silt, larvae still prefer to settle on the undersides, since, overall, selection has always favored the latter habitat as a refuge from silt. Observational studies have also implicated silt as an important limiting factor for numerous subtidal organisms, including ascidians, hydroids and sponges occurring on rock (Kitching et al., 1934; Evans et al., 1979) and epifaunal organisms occurring on algae (Norton, 1971; Boaden et al., 1975) and hydroids (Hughes, 1975). The present study supports and extends these general conclusions. By monitoring cohorts of known size, we have identified the early juvenile stage as a vulnerable period when silt is an important source of mortality. To our knowledge, such data have not been previously available for any species.

The technique of allowing larval ascidians to settle on artificial substrata in the laboratory, and then transplanting them to the field has often been used to study ascidian growth (Lambert, 1968; Goodbody and Gibson, 1974; Nomaguchi, 1974; Yamaguchi, 1975). In the only previous controlled experiments using this technique, shading of *Ascidia nigra* juveniles in Jamaica suggested that diatoms could significantly depress the growth rates of young ascidians (Goodbody, 1963). Our experiments demonstrated that overgrowth by filamentous algae causes mortality, as well as depressing growth rate of ascidians early in the post-settling period. In our experiments, algal colonization began only when the already settled ascidians were transplanted to the field. Thus, under natural conditions where algal mats are already established at the time

of ascidian settlement, algal overgrowth may be an even stronger selective agent; algae may inhibit settlement altogether. The effect of algae, as expected, shows a strong negative relationship with depth. In the Pt. George transplants, ascidians in the 4.5-m treatments (which were even shallower at low tide) in the light grew significantly less and showed much greater mortality than comparable ascidians maintained at 21.0 m.

In designing subtidal transplants, we did not anticipate that crabs and other vagrant animals would use the dark dishes as hiding places. In several instances, mortality was higher in the dark "control" dishes than in certain other treatments, apparently because the decorator crabs colonized the controls preferentially. We presume that these crabs killed the young ascidians by scraping them off with their sharp dactyls. Crustaceans could conceivably represent a selective pressure that favors settlement in noncryptic habitats. That so many sessile animals seek out cryptic sites at settlement, however, argues strongly that this factor is not as important as algae or silt, that its effect is less predictable in time, that many cryptic sites are inaccessible to crabs, or that the phenomenon is an artifact of introducing unoccupied habitat into the environment.

Incidental grazing and bulldozing by gastropods and sea urchins has been implicated as an important factor controlling dynamics of juvenile barnacles in the intertidal zone (Connell, 1961; Stimpson, 1970; Hawkins, 1983) and of encrusting animals, including ascidians (Vance, 1979; Ayling, 1981) subtidally. Because the distributions of snails and other herbivorous animals tend to correlate inversely with the distributions of largely cryptic ascidians, we might suspect that the herbivores help exclude ascidians from the tops of rocks. Our laboratory experiments lend some credence to this possibility by showing that *Margarites pupillus* can kill juvenile ascidians. However, in the field, silt and algae, both of which are present in the same microhabitat as *M. pupillus*, kill most ascidians within a short time, so gastropod grazing may be an infrequent occurrence by comparison.

Fouling studies have shown that larvae of many benthic invertebrate species, including some ascidians (Dybern, 1962), settle primarily on the bottom or darker portions of panels, rocks, and other substrata in the sea (Pomerat and Reiner, 1942; Meadows and Campbell, 1972). Buss (1979) and others have suggested that this behavior is adaptive because animals occupying cryptic habitats are probably less subject to certain sources of mortality associated with exposed habitats. Two additional functions of the photonegative settling response have been proposed. Of these, Thorson's generalization that photonegative behavior allows larvae of benthic species to find the bottom (Thorson, 1964) has enjoyed the widest acceptance (Forward, 1979; Young and Chia, in press). Dybern (1962) also suggested that sunlight itself, and especially the ultraviolet component, may be directly damaging to adult ascidians. Recent controlled experiments with ascidians and other invertebrates (Jokiel, 1980; Olson, 1983) confirm the importance of this factor in shallow tropical systems.

In the San Juan Islands, the distribution of subtidal ascidians is controlled by a number of different factors, including predation (Young, 1980, 1982) and larval settlement (Young and Braithwaite, 1980). The tendency for most animals to occupy cryptic habitats seems to result in part from mortality in unshaded areas and in part from the photonegative responses of the larvae at settlement (Young, 1982). It is difficult to distinguish these two factors, since in an ultimate sense selective pressure associated with unshaded areas probably favor evolution of the "proximate" behavioral response.

In summary, photonegative behavior by ascidian larvae has two possible consequences relating to distribution: (1) greater probability of settling at depth and (2) greater probability of settlement in cryptic microhabitats. Both of these consequences are favorable from the standpoint of juvenile survival.

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