



FAU Institutional Repository

<http://purl.fcla.edu/fau/fair>

This paper was submitted by the faculty of [FAU's Harbor Branch Oceanographic Institute](#).

Notice: ©1989 Springer. This manuscript is an author version with the final publication available at <http://www.springerlink.com> and may be cited as: Young, C. M. (1989). Larval depletion by ascidians has little effect on settlement of epifauna. *Marine Biology*, 102(4), 481-489. doi:10.1007/BF00438349

Larval depletion by ascidians has little effect on settlement of epifauna

C.M. Young

Division of Marine Science, Harbor Branch Oceanographic Institution, 5600 Old Dixie Highway, Fort Pierce, Florida 33450, USA

Abstract

Ascidian densities were manipulated while controlling for negative effects of biodeposition and space preemption to examine the effects of ascidian filter-feeding on larval recruitment in St. Joseph Bay and near Turkey Point, Florida (Northern Gulf of Mexico, Florida, USA). Using three different experimental designs during 1984 and 1985, recruitment near living *Styela plicata* or *Molgula occidentalis* was as high as recruitment near ascidian models. Disruption of flow by ascidian bodies had little effect on settlement. Predation rates by ascidians on larvae in six phyla were high in laboratory experiments. The field effects of larval depletion by solitary ascidians are apparently obscured by other factors influencing the abundance of recruiting larvae. Consumption of larvae in the laboratory cannot be used to assume significant inhibitory effects in the field.

Introduction

Several investigators have suggested that filter-feeders should influence settlement distributions and densities of invertebrates by selective or non-selective depletion of larvae (Thorson 1950, Woodin 1976, review by Young and Chia 1987). Experimental tests of this hypothesis on soft bottoms, using clams as the larval predators, have yielded variable results (Best 1978, Williams 1980, Peterson 1982, Commito 1987, Hunt et al. 1987, Black and Peterson 1988, Ertman and Jumars 1988). In epifaunal ("fouling") assemblages, established adults generally inhibit recruitment of new colonists (Goodbody 1961, Sutherland 1974, 1978, Jackson 1977, Osman 1977, Dean and Hurd 1980), but larval predation is only one of several inhibitory mechanisms (e.g. preemption of space, allelopathy, larval avoidance behaviors, modification of the substratum by biodeposition, flow modification by adult bodies) that could be invoked to explain these patterns. The effects of adult bodies have been studied

by the use of physical models (Dean 1981) or dead shells (Bros 1987, Young and Gotelli 1988), and the potential effects of preemption have been controlled by clearing uniform spaces in the midst of filter-feeder patches (Young and Gotelli 1988). Overall, studies of epifaunal recruitment in the presence of adults reveal patterns consistent with larval predation in some species but not in others.

Ascidians, like many other active filter-feeders (Jørgensen 1955), process large volumes of water. Estimates of filtration rates by solitary ascidians range as high as 444 l d^{-1} (for a 13 g dry body-mass individual of *Pyura stolonifera*; Klump 1984), with the highest rates occurring among stolidobranchs, presumably because their plicated branchial baskets allow them to move more water than phlebobranchs or aplousobranchs of comparable body sizes (Randlov and Riisgård 1979). Pumping rates can be modified by numerous environmental factors including food concentration (Fiala-Médioni 1979a, Robbins 1983), temperature (Fiala-Médioni 1978c, Robbins 1983), currents (Young and Braithwaite 1980), and oxygen tension (Fiala-Médioni 1979b). Although ascidians can retain all particles larger than approximately $5 \mu\text{m}$ (Jørgensen and Goldberg 1953, Randlov and Riisgård 1979), they sometimes reduce their retention efficiency behaviorally by expelling inedible particles from the incurrent siphon (Hecht 1918) or by interrupting the secretion of mucus (McGinitie 1939). Most food consumed by ascidians consists of organic seston and phytoplankton, but ascidians also capture many zooplankters, including invertebrate larvae (Cowden et al. 1984, Young 1988).

In this study, I consider the impact of two common subtropical ascidians, *Styela plicata* and *Molgula occidentalis*, on recruitment of sessile invertebrates from several phyla. The filtration rate of the former has been measured in the laboratory; a large individual (1.8 g, dry body mass) can filter over 6 liters per hour (Fiala-Médioni 1978b). In highly productive coastal waters, this is equivalent to ca. 100 mg of food ingested per hour (Fisher 1977). Following the reasoning of earlier authors (Thorson 1950, Woodin

1976), I hypothesized that settlement would be lower on substrata near ascidians or with ascidians attached than on "control" surfaces without ascidians.

Materials and methods

Depletion of larvae in laboratory experiments

I measured clearance rates of *Styela plicata* by incubating individuals in rotating, 1-liter jars (17 cm high, 9 cm wide) of filtered seawater inoculated with aliquots of larvae. Only a single species of larva was used per experiment. The ascidians were attached with cyanoacrylate adhesive ("super glue") to plastic liners on the insides of the jar lids. The jars were filled with 900 ml of seawater (which left a small air space after the predators were added), inoculated, and strapped with velcro on an adjustable-rate 24-position plankton grazing drum similar to those used for studies of planktonic predation rates (Checkley 1980, Dagg and Gill 1980, Landry 1980, Gifford et al. 1981, Yen 1982, Rumrill et al. 1985). The jars were attached to the drum with their long axes parallel to the axis of rotation. They were rotated at 1 rpm until the experiment was terminated after predetermined times ranging from 3 to 24 h. Ascidians generally remained open and fed actively in the jars during the experiments. Grazing drums reduce the probability that prey organisms will concentrate in particular regions of the jar, thereby avoiding or enhancing predation. Quantitative evidence for their effectiveness has been provided by Checkley (1980) and Yen (1982). Depletion was measured by comparing final larval densities between jars with and without ascidians. At the end of each experiment, ascidians were removed quickly, then jars were emptied into plastic beakers and rinsed carefully with a wash bottle of seawater. The contents of each jar was then filtered through Whatman No. 5 filter paper or 0.45 μm Millipore filters. After drying filters in air for at least 24 h, the larvae on them were counted under a dissecting microscope. Where densities were high, eight or ten microscope fields were counted, averaged, and extrapolated to the entire area to give a density estimate.

Some kinds of larvae were not available in sufficient numbers to use in grazing wheel experiments. For these, I videotaped individual encounters between larvae and ascidians using a Panasonic WV-4051 color video camera with a Bausch and Lomb microzoom lens and a Panasonic AG-6010 time-lapse video recorder. Larvae were introduced about 1 cm away from the incurrent siphon through a long syringe positioned by a micromanipulator. Tapes were played back to tabulate the number of acceptances and rejections (Young 1988) of various larval types.

Field experiments on larval depletion effects

Densities of adult ascidians on or near open settlement surfaces were manipulated, and settlement densities compared among high, low, and no ascidian treatments after a given

period of time. Models of ascidians were used to reveal effects of flow alteration by ascidian bodies. Free space was kept constant in all treatments in order to eliminate the confounding effect of preemption.

Ascidians were collected from shallow subtidal habitats near Turkey Point, Florida, USA, in the northern Gulf of Mexico (29°54'N; 84°30'W). Two species of solitary ascidians, *Styela plicata* and *Molgula occidentalis*, occur here in dense, unattached aggregations of up to several hundred individuals. Ascidian aggregations are also found on empty bivalve shells (Mattson 1987) and on shoots of the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in the sandy subtidal and intertidal zones. Besides dock pilings and other man-made substrata, shells and seagrasses are the major available surfaces for settlement of sessile epifauna in this region.

Experiment 1: vertical panels near *Styela plicata* aggregations

I tested depletion effects of large *Styela plicata* aggregations by deploying vertical settlement plates near such aggregations and comparing recruitment between these plates and plates deployed near models of ascidian clumps. The plates were positioned vertically in order to eliminate sedimentation and ascidian biodeposition as factors influencing recruitment. Space preemption by adults was not a confounding factor, since no organisms were present on the plates at the outset, and the experiments were terminated while most space on each plate was still available to settlers. The model ascidians controlled for structural or flow effects due to the presence of adults. By controlling for preemption, sedimentation, and flow in these ways, larval depletion could be invoked with greater confidence to explain any inhibitory effect documented.

The experiments were set up in a sparse bed of *Halodule wrightii* near an intertidal sand spit in the Northern Gulf of Mexico (29°54.8'N; 84°30.7'W). The site was approximately 1.0 m deep at mean lower low water, and was never exposed by low tides during the study. Unglazed, red terracotta Italian floor tiles were secured with aluminum clips and rubber bands between pairs of pressure-treated wooden stakes (Fig. 1). The bottom of each plate rested on the sand. Model ascidian clumps were made of several PVC surgical gloves stuffed with brown plastic garbage bags and bound together with nylon cable ties. The stuffed fingers of the gloves resembled living *Styela plicata* in shape, texture, and color. Natural ascidian clumps were collected from the surrounding areas. Living or model clumps were anchored in the sand immediately in front of the plates with large staples of aluminum tubing (Fig. 1). These staples held the clumps just far enough away (ca. 2 cm) so as to not touch the plates. I deployed ten replicates of each treatment. The experimental plates were arrayed in two rows, 1 m apart, along an east-west isobath. Thus, all replicates were at identical depth, facing the same direction. Living and model treatments were alternated regularly along the two rows; no two replicates of the same treatment were ever adjacent. This regular arrange-

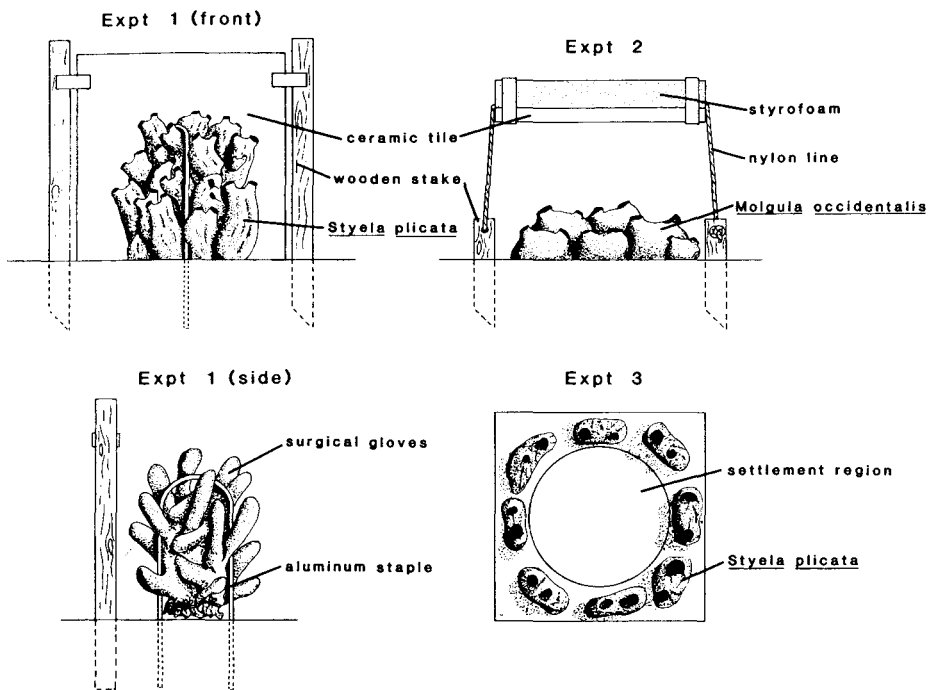


Fig. 1. Experimental set-ups for the three field experiments. Experiment 1 is depicted in two views, one with living ascidians and one with models. All drawings are to the same scale; the ceramic tile is 15 cm wide. (See "Materials and methods - Field experiments on larval depletion effects" for details of experiments)

ment of plates was used instead of a random pattern in order to assure equal sampling of the larval pool by both treatments. The experiment was run twice, each time for two weeks, in April 1984. At the end of each run, the plates were brought into the laboratory where invertebrate recruits were counted under a dissecting microscope. Cochran's test was used to test for homogeneity of variances. Because the variances were significantly heterogeneous in some species, data were analyzed for all species by means of Student's *t*-tests based on the assumption of heteroscedasticity.

Experiment 2: horizontal plates above *Molgula occidentalis*

The effect of larval depletion by *Molgula occidentalis* was measured by deploying horizontal, downward-facing plates above naturally occurring individuals on a subtidal sandflat in St. Joseph's Bay, Florida (29°46.2'N; 85°23.8'W). The site was ca. 0.5 km offshore, near the western side of the bay. At this site, *M. occidentalis* were anchored in the sand or attached to dead shells of the mussel *Geukensia demissa*. Four wooden stakes were driven into the sand near each clump of ascidians. Fouling plates attached to blocks of styrofoam with rubber bands were secured to the stakes with nylon line so as to float either 10 or 20 cm above the substratum (Fig. 1). *M. occidentalis* are spherical in shape, up to 6 cm in diameter, and completely covered with a layer of sand. I simulated ascidians by casting concrete balls inside plastic "putting practice" golf balls, then gluing sand over the concrete balls with contact cement. The experiment was set up as a two-factor, completely crossed ANOVA, with factors being "height" (two levels: 10 and 20 cm above substratum) and "ascidians" (three levels: alive, models, no ascidians). The spatial arrangement of the treatments was determined

in part by the locations of natural ascidian aggregations, but treatments were assigned to clumps randomly. Four replicates of each treatment were deployed on 9 August, 1984 and recovered 27 d later.

Experiment 3: *Styela plicata* mounted on plates

I manipulated the density of individuals of *Styela plicata* and models on the settling plates themselves. A compass was used to scribe a 10 cm diam settling region in the center of each plate. Adult ascidians were attached with cyanoacrylate adhesive ("super glue") around the outside of this circle (Fig. 1). Either four or eight ascidians were attached to each plate. In the high-density treatments (eight ascidians), the settlement surface was completely surrounded by ascidians; virtually no open space was present between individuals. The same arrangements were duplicated with model ascidians constructed of stuffed fingers of PVC gloves, sealed with plastic twist ties and glued to the plates. Blank plates (i.e., no ascidians or models) were also deployed. The plates were held face downward on four permanent wooden racks anchored 25 cm above the substratum in a bed of seagrass (*Thalassia testudinum* and *Syringodium filiforme*) on Turkey Point shoal, (29°53.1'N; 84°29.7'W) in the northern Gulf of Mexico. The seagrass blades did not contact the lower surfaces of the plates. The four racks were arranged in a parallel array, 2 m apart, and the plates were assigned randomly to positions on the racks (Young and Gotelli 1988). Because all positions in the entire array were randomized as a single set, all treatments were not represented in every rack. I did not deploy the plates in a randomized block design because block effects at the same site have been considered in a previous study (Young and Gotelli 1988). The

experiment was run from 3 May–3 June 1985, and from 3 June–8 July 1985. The design for analysis was a two-factor ANOVA in which the factors were “density” (two levels: four ascidians and eight ascidians per plate) and “live/model” (two levels). Blank plates were not included in the initial analysis, since it is impossible to completely cross blank plates (i.e., density = 0) with the live/dead factor. The effect of physical structure on settlement was determined in a separate analysis that included only blank plates and plates with model ascidians. In this analysis, the data were heteroscedastic and could not be made homoscedastic by either log or square-root transformation, so they were analyzed by the non-parametric Kruskal-Wallis statistic.

Results

Laboratory depletion of larvae

Six species of larvae in five phyla were offered to *Styela plicata* in rotating grazing-wheel chambers. The densities of five of the six species were significantly depleted by the ascidians (Table 1), but clearance rates were generally about an order of magnitude lower than pumping rates reported for *S. plicata* in the field (Fiala-Médioni 1978a). Larvae of one species, *Polydora* sp., were not consumed in significant numbers. Following runs with echinoplutei of *Arbacia punctulata*, individual ascidians were dissected. Large numbers of pluteus skeletons in the ascidian guts confirmed that larvae were consumed rather than being expelled as pseudofeces.

Individual encounters between larvae and *Styela plicata* were videotaped for two larval species: cyprids of *Balanus*

amphitrite and coronate larvae of the bryozoan *Bugula neritina*. Three adult *S. plicata* consumed 70 of 105 cyprids presented within 1 cm of the incumbent siphon. Virtually all the individuals not consumed swam away from the siphon when released from the pipette. No larvae entering the siphon were expelled by the crossed reflex (Hecht 1918), though four individuals actively swam out of the siphons and escaped. Following the experiments, dissection confirmed the presence of cyprids in the ascidian guts. Six individual larvae of *B. neritina* were introduced into siphons of *S. plicata*. Of these, five were consumed and one swam away.

Field experiments

Four epifaunal species settled in high enough numbers to analyze in Experiment 1 (vertical plates near *Styela plicata* aggregations). Cochran's test demonstrated homogeneity of variances for all recruit species but *Balanus* spp. in Run 1. Barnacle density did not differ significantly (by Student's *t*-tests assuming unequal variances) between plates near ascidian aggregations and plates near model ascidian aggregations (Fig. 2) in either run. Similarly, serpulid, oyster and bryozoan recruitment did not differ significantly between treatments in Run 2 (Fig. 2).

Data from Experiment 2 (*Molgula occidentalis*) indicate generally non-significant differences among live, model, and no ascidian treatments (Fig. 3; Table 2). There was a significant high/low effect on *Balanus* spp. (Table 2), with more recruits settling on high plates than low ones. However, there were not significant differences between living and model treatments (i.e., the “ascidian” main effect), so larval depletion does not explain the significant pattern. Recruit-

Table 1. *Styela plicata*. Consumption of six species of larvae by adult ascidians in plankton grazing-wheel experiments. Clearance rates are calculated as $C = (V/t)(\ln D_1 - \ln D_2)$, where V = volume of seawater, t = duration of experiment, D_1 = initial density and D_2 = final density of prey. Differences between initial and final densities are tested with unpaired Student *t*-tests. Initial densities for all species except *Arbacia punctulata* refer to larval densities in “control” jars (i.e., no *S. plicata*) after experiments were terminated; in *A. punctulata*, initial densities were estimated from aliquots drawn at beginning of experiment. Clearance rates are not calculated for two species: *Polydora* sp., in which initial and final densities of larvae were not significantly different, and *A. punctulata*, in which controls were not corrected for handling loss

Prey item	Duration	Initial density [mean ± SD (n)]	Final density [mean ± SD (n)]	Clearance rate (liters h ⁻¹)	<i>t</i> (<i>p</i>)
Nauplii of <i>Balanus eberneus</i>	6 h	202.5 ± 45.94 (7)	75.7 ± 28.19 (8)	0.162	6.14 (<0.001) ^a
Tadpoles of <i>Molgula occidentalis</i>	3 h	92.3 ± 28.36 (4)	11.0 ± 5.35 (4)	0.703	8.14 (<0.001) ^a
Müllers larvae of unidentified flatworm	12 h	133.2 ± 47.93 (4)	29.1 ± 9.47 (5)	0.126	6.78 (<0.001) ^a
Setiger larvae of <i>Polydora</i> sp.	12 h	7.9 ± 1.47 (4)	5.3 ± 2.65 (5)	–	1.93 (NS)
Echinoplutei of <i>Arbacia punctulata</i>	12 h	1 778.6 ± 282.24 (3)	397.8 ± 283.52 (3)	–	5.35 (<0.01)
Trochophores of <i>Pomatoceros</i> sp.	20 h	1 256.1 ± 638.55 (4)	347.5 ± 275.04 (5)	0.064	3.28 (<0.05) ^a

^a Log-transformed prior to analysis to correct heteroscedasticity

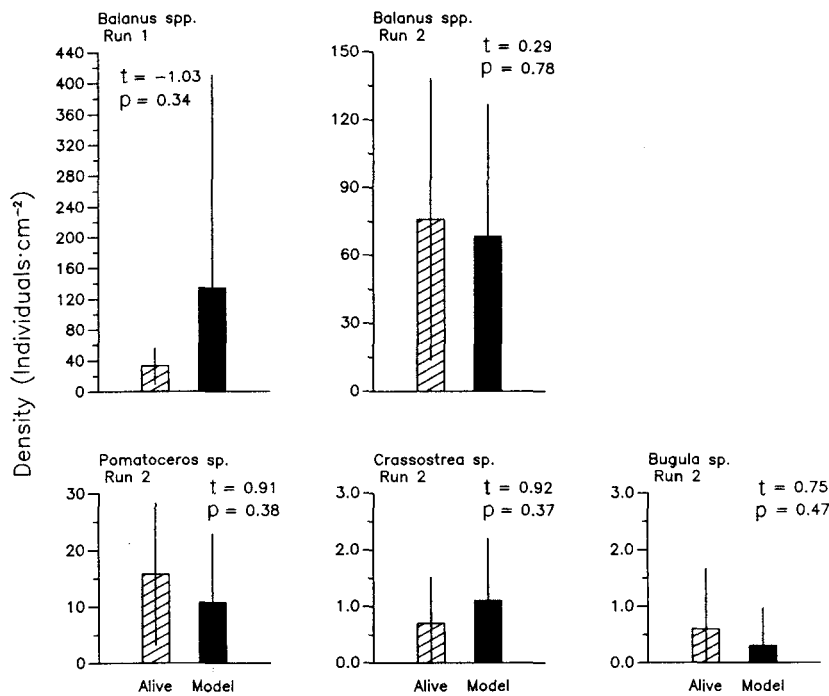


Fig. 2. *Styela plicata*. Mean densities of epifaunal recruits on vertical plates near ascidians and models in Experiment 1. Error bars in this and subsequent figures are standard deviations

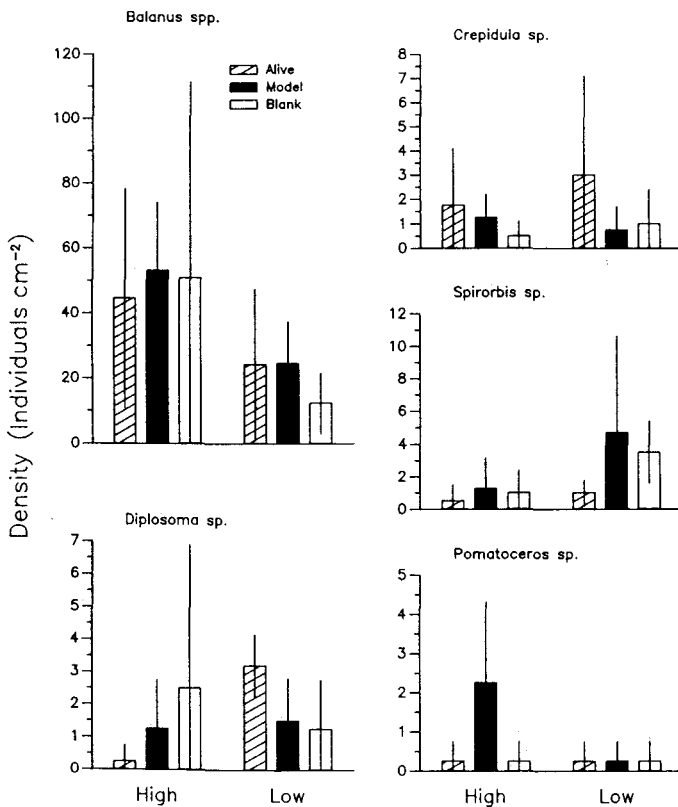


Fig. 3. *Molgula occidentalis*. Mean recruit densities of five epifaunal invertebrates on horizontal plates at two distances above living ascidians, model ascidians, or bare sand (Experiment 2). Analysis in Table 2

Table 2. *Molgula occidentalis*. Two-way fixed analyses of variance comparing settlement densities among plates suspended at two heights above living *M. occidentalis*, models, or bare sand (Fig. 3). All data were rendered homoscedastic (as determined by Cochran's test) by square-root transformation. MS: mean square

Genus of recruits and source of variation	DF	MS	F	p
<i>Balanus</i>				
ascidians	2	3.41	0.56	NS
height	1	31.59	5.21	<0.05
interaction	2	0.40	0.06	NS
error	18	6.06	—	
<i>Crepidula</i>				
ascidians	2	0.60	0.75	NS
height	1	0.05	0.06	NS
interaction	2	0.33	0.41	NS
error	18	0.79	—	
<i>Spirorbis</i>				
ascidians	2	1.07	1.22	NS
height	1	4.43	5.05	NS
interaction	2	0.21	0.23	NS
error	18	0.88	—	
<i>Diplosoma</i>				
ascidians	2	0.15	0.19	NS
height	1	1.17	1.50	NS
interaction	2	1.18	1.52	NS
error	18	0.78	—	
<i>Pomatoceros</i>				
ascidians	2	1.17	1.06	NS
height	1	0.12	0.11	NS
interaction	2	0.21	0.19	NS
error	18	1.10	—	

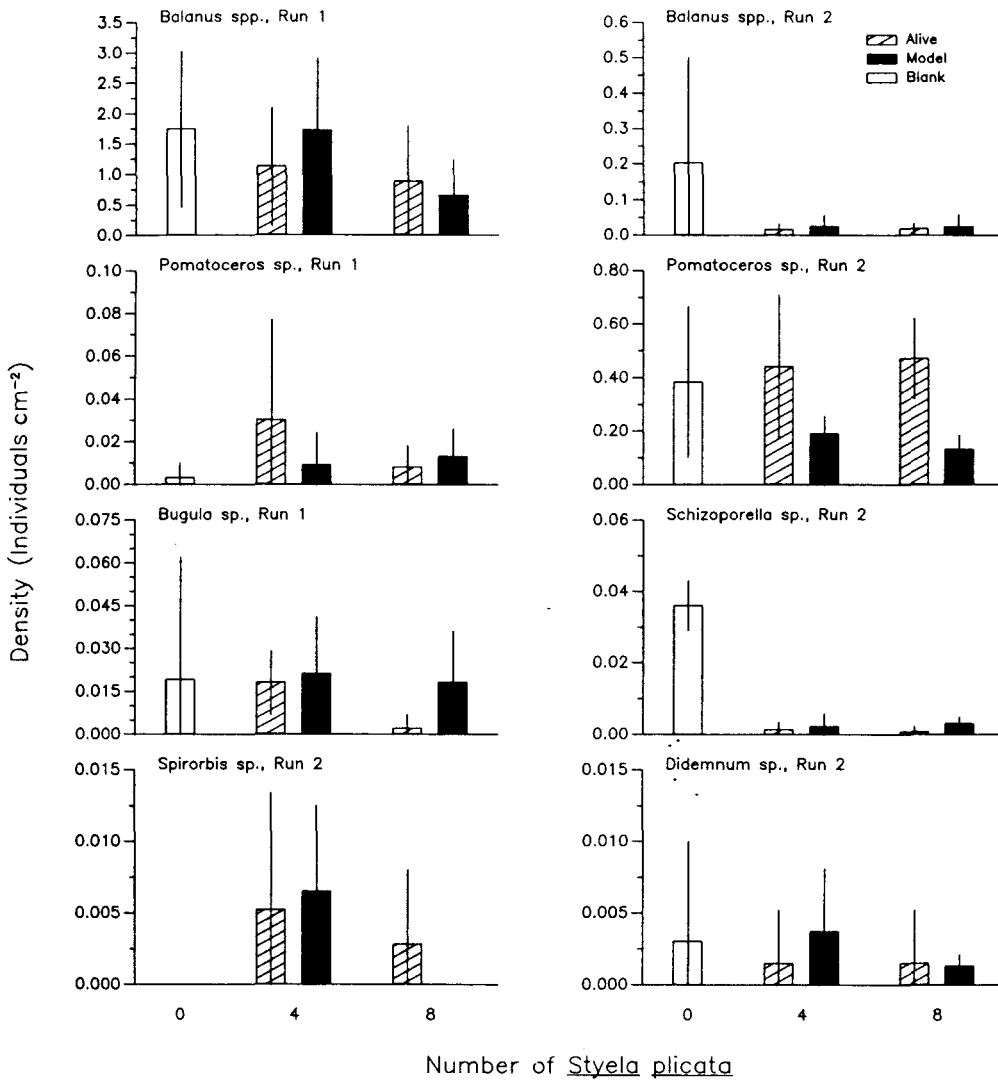


Fig. 4. *Styela plicata*. Mean recruit densities of four most common epifaunal species in two runs of Experiment 3. Data analyses in Tables 3 and 4

ment was not related to either ascidian presence or height for any of the other species that colonized the plates.

In Experiment 3 (*Styela plicata* and models glued to the faces of settlement panels), the data (Fig. 4) were analyzed as a two-factor ANOVA without inclusion of the blank-plate data. Ascidian density was not significant in any species (Table 3). The only significant alive/model effect occurred with *Pomatoceros* sp. in Run 2. However, the direction of the difference was the reverse of that expected for a larval predation effect (Fig. 4).

To determine the possible effect of physical structure on recruitment, the model treatments (eight model ascidians, four model ascidians) were compared with the blank-plate treatments. There was no significant difference among treatments for any species in Run 1. Structure apparently had a significant impact on settlement of species of *Balanus*, *Pomatoceros*, and *Spirorbis* (Table 4). In the first two, the ordering of the rank sums was identical; more settled on blank plates than on plates with models. By contrast, more *Spirorbis* sp. settled on plates with eight models than on the other treatments.

Discussion

The filtration rates of adult *Styela plicata* estimated using thermistor probes in the field and laboratory averaged about 4 liters h⁻¹ (Fiala-Médioni 1978 a, b), whereas closed-container techniques (Randlov and Riisgård 1979, Robbins 1983, and others) gave lower values. Because pumping by *S. plicata* is more or less constant throughout the day (Fiala-Médioni 1978 a, b), we can calculate from literature values an approximate daily clearance rate of 96 liters/d. In the experiments with horizontal plates, each replicate of the high-density treatment held eight individuals and the runs lasted 14 d. Thus, over the course of the run, approximately 10 752 liters of water should have been filtered by ascidians in each high-density treatment. In light of these prodigious clearance values, the consistent absence of density-dependent effects on recruitment requires an explanation. However, the importance of filtration rates cannot be evaluated in an ecological context without knowing how much water actually passed by the plates during the experiment. Even enormous numbers of larvae removed by ascidians

Table 3. *Styela plicata*. Two-factor fixed analyses of variance for Field Experiment 3 (*S. plicata* horizontal plates). Dependent variable is settlement density (Fig. 4). Very small mean squares are shown as exponents (e.g. "2E-3" = "2 × 10⁻³")

Genus of recruits and source of variation	DF	MS	F	p
Run No. 1				
<i>Balanus</i>				
alive/model density	1	0.1933	0.23	0.638
interaction	1	2.4723	2.91	0.104
error	19	1.0093	1.19	0.289
<i>Pomatoceros</i> ^a				
alive/model density	1	0.24 E-2	0.30	0.589
interaction	1	0.26 E-2	0.33	0.570
error	19	0.0142	1.78	0.197
<i>Bugula</i>				
alive/model density	1	0.52 E-3	2.45	0.134
interaction	1	0.52 E-3	2.45	0.134
error	19	0.20 E-3	0.97	0.337
Run No. 2				
<i>Balanus</i>				
alive/model density	1	0.32 E-3	0.46	0.507
interaction	1	0.34 E-7	0.00	0.945
error	20	0.15 E-4	0.02	0.884
<i>Pomatoceros</i> ^b				
alive/model density	1	0.4265	27.00	0.000
interaction	1	0.13 E-2	0.08	0.778
error	20	0.0200	1.27	0.273
<i>Schizoporella</i>				
alive/model density	1	0.15 E-4	1.42	0.247
interaction	1	0.42 E-7	0.00	0.951
error	20	0.34 E-5	0.32	0.578
<i>Didemnum</i>				
alive/model density	1	0.10 E-4	—	—
interaction	1	0.60 E-5	0.47	0.499
error	20	0.82 E-5	0.64	0.432
<i>Spirorbis</i>				
alive/model density	1	0.82 E-5	0.64	0.432
interaction	1	0.26 E-4	0.80	0.382
error	20	0.32 E-4	—	—

^a Heterogeneous variances (as detected by Cochran's test) rendered homoscedastic by square-root transformation

^b Heterogeneous variances improved by square-root transformation, but remain significantly different (Cochran's test: $p < 0.05$)

could represent only a tiny proportion of the total larvae to which the plates were exposed.

The most parsimonious explanation for non-significant differences between ascidian and model treatments is that larvae are not removed from the water column by *Styela plicata* or *Molgula occidentalis*. Three pieces of evidence argue against this possibility. First, *S. plicata* consumed all but one species of larvae offered in laboratory grazing-wheel experiments. Second, larvae introduced into the incurrent

Table 4. *Styela plicata*. Results of Kruskal-Wallis (*H*) tests comparing settlement densities among plates with eight model ascidians, plates with four models and blank plates

Genus of recruits	Sum of ranks			<i>H</i>	<i>p</i>
	8 models	4 models	blank		
Run No. 1					
<i>Balanus</i>	56.0	34.0	63.0	4.09	0.129
<i>Pomatoceros</i>	46.0	65.0	42.0	1.95	0.377
<i>Bugula</i>	50.0	58.5	44.5	1.03	0.598
Run No. 2					
<i>Balanus</i>	39.0	25.0	72.0	6.19	0.045
<i>Pomatoceros</i>	46.5	19.5	70.0	7.49	0.024
<i>Schizoporella</i>	35.0	42.5	58.5	1.21	0.546
<i>Didemnum</i>	52.0	40.5	43.5	1.66	0.436
<i>Spirorbis</i>	59.0	35.0	42.0	7.54	0.023

siphon did not elicit the crossed reflex (Hecht 1918), a response used by virtually all ascidians for expelling unsuitable particles, and by some species for expelling larvae (Young 1988). Finally, analysis of gut contents from both *S. plicata* and *M. occidentalis* demonstrates that these species consume many kinds of larvae in the field (Bingham and Walters in press).

Some data from the laboratory feeding experiments suggest that two kinds of larvae (cyprids of *Balanus amphitrite* and setigers of *Polydora* sp.) might be capable of escaping the incurrent siphons of ascidians. Some larvae, notably polychaete setigers, escape suction-feeders by negative rheotactic behavior (Singarajah 1969). Although the present results with setigers of *Polydora* sp. support this idea, the non-significant depletion effect observed could also have resulted from small sample size.

A lack of larval predation effects in the field might be expected if ascidians remove water from a different larval subpopulation than that which supplies individuals for settlement. Consider a hypothetical situation where a 5 cm-tall ascidian lives on a flat substratum in a gentle current. Assume also that larval distribution is uniform throughout the water column. The larvae that encounter the settlement surface would be primarily those transported in streamlines near the substratum and those residing in the boundary layer (Butman 1987). The ascidian, with its siphons directed upward, would therefore remove larvae not from the recruiting, near-bottom subpopulation, but from a portion of the water column hundreds of larval-body diameters away. In theory, this effect could be studied by microscale sampling of plankton at different heights upstream and downstream from ascidians. Ertman and Jumars (1988) demonstrated, using a flume, that the flow fields produced by siphons of individual cockles play little role in either increasing or decreasing deposition of larvae on the sea floor. Instead, the dominant effect is increasing variability in downstream particle deposition. This pattern results primarily from vortices shed by the excurrent siphon (Ertman and Jumars 1988).

Analysis of variance compares the within-treatment variation to the between-treatment variation in order to

estimate the relative importance of the latter. Thus, in the field experiments, any process that increases the patchiness of settling larvae could also obscure the effects of treatments. Even if depletion of larvae is high, the effect on the larval pool could be negligible in comparison to other factors influencing larval density. Examination of the treatment variances in the field experiments demonstrates extremely high spatial variation in settlement, presumably because of patchiness in planktonic larval abundances. Factors that could produce such uneven larval distributions include diffusive and advective dispersal of larvae, spatial patterns of spawning adults, larval swimming behavior, and patchiness in planktonic mortality. Patchiness in recruitment can also occur because of gregarious behavior at the time of settlement.

If high within-treatment variances obscure the effects of larval predators in the analysis, then one might argue that insufficient replication was used to detect the effects. Power analysis can tell us the approximate level of replication needed. However, in order to run a power analysis, one must define initially the magnitude of the treatment difference that would be of interest. The difficulty arises in doing this impartially. In the present study, the prediction that recruitment should be related inversely to predator density might seem useful in generating an effect size for use in the analysis. However, without knowing the quantitative effect of a single ascidian, it is impossible to estimate the effect size that would be expected in comparing high- and low-density treatments. If one wishes to demonstrate an effect (i.e., low " p "), then a bias toward small effect size will maximize the likelihood of so doing. Conversely, setting a large effect size will reduce the number of replicates required to show that two treatments are the same. If we set an arbitrary effect size of 0.50 (e.g. 50% more settlement on control than ascidian treatments), the power of Experiment 3 (horizontal-plate experiment) in testing the alive/model main effect is 0.29 at $p < 0.05$ (Cohen 1977). Seventeen replicates would be required per treatment in order to accept the null hypothesis of no difference between treatments at $\beta = 0.20$, which has been tentatively recommended as an appropriate critical value for a powerful test (Underwood 1981). This would involve the simultaneous deployment (and subsequent counting) of 204 living ascidians and a similar number of models on 68 plates. Logistics constrain experiments of this magnitude in the present system. This same problem has been encountered in other ecological studies producing negative results (Doherty and Sale 1985, Young and Gotelli 1988).

Biological interactions among sessile species have received much attention as structuring forces in epifaunal communities (reviewed by Underwood and Denley 1984, Jackson 1983, Connell and Keough 1985). Most studies acknowledge that post-settlement demography and community composition can be influenced significantly by the composition of the larval pool (Keough 1983, Connell 1985, Gaines et al. 1985, Gaines and Roughgarden 1985), which itself is influenced by reproductive seasons, larval mortality, larval behavior, and oceanographic processes. The present

study suggests that one class of biological interactions, larval predation by benthic suspension-feeders, may not be important in determining initial community composition or settlement density in dense ascidian assemblages. Further work is needed on the control of small-scale distribution of larvae in the plankton, emphasizing the factors that influence plankton patchiness, before we understand fully the role of benthic larval predators in the recruitment process.

Low recruitment and negative associations among species have been attributed to larval depletion by benthic filter-feeders (reviewed by Thorson 1950, Woodin 1976, Young and Chia 1987). Most evidence for larval predation effects comes from laboratory studies and analysis of gut contents. While the evidence shows that larvae are consumed, this study and several others (e.g. Black and Peterson 1988, Ertman and Jumars 1988, Young and Gotelli 1988) suggest that extrapolations to population or community phenomena (e.g. Thorson 1950, Woodin 1976) may be unwarranted. High laboratory predation rates cannot be used to assume field effects at the population level.

Acknowledgements. I thank Florida State University Marine Laboratory for making laboratory space and facilities available for this study. J. Schmitt, N. Gotelli, and R. Menendez assisted in the field. Barnacle cyprids were supplied by D. Rittschoff. M. Keough, L. Cameron, B. Bingham, R. Olson and N. Gotelli provided stimulating conversations or comments on the manuscript. Supported by NSF Grants OCE-8400406 and OCE-8544845. This is HBOI Contribution No. 695.

Literature cited

- Best, B. (1978). The effects of suspension feeding by the bivalve, *Mercenaria mercenaria*, on community structure. M.S. thesis, University of Florida
- Bingham, B. L., Walters, L. J. (1989). Solitary ascidians as predators of invertebrate larvae: evidence from gut analyses and plankton samples. *J. exp. mar. Biol. Ecol.* (in press)
- Black, R., Peterson, C. H. (1988). Absence of preemption and interference competition for space between large suspension-feeding bivalves and smaller infaunal macroinvertebrates. *J. exp. mar. Biol. Ecol.* 120: 183–198
- Bros, W. E. (1987). Effects of removing or adding structure (barnacle shells) on recruitment to a fouling community in Tampa Bay, Florida. *J. exp. mar. Biol. Ecol.* 105: 275–296
- Butman, C. A. (1987). Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. mar. Biol. A. Rev.* 25: 113–165
- Checkley, D. M., Jr. (1980). The egg production of a marine planktonic copepod in relation to its food supply: laboratory studies. *Limnol. Oceanogr.* 25: 430–436
- Cohen, J. (1977). *Statistical power analysis for the behavioral sciences.* Academic Press, New York and London
- Commito, J. A. (1987). Adult-larval interactions: predictions, mussels and cocoons. *Estuar. cstl Shelf Sci.* 25: 599–606
- Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. exp. mar. Biol. Ecol.* 93: 11–45
- Connell, J. H., Keough, M. J. (1985). Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: Pickett, S. T., White, P. S. (eds.) *The ecology of natural disturbance and patch dynamics.* Academic Press, New York and London, p. 125–151

- Cowden, C., Young, C. M., Chia, F. S. (1984). Differential predation on marine invertebrate larvae by two benthic predators. *Mar. Ecol. Prog. Ser.* 14: 145–149
- Dagg, M. J., Gill, D. W. (1980). Natural feeding rates of *Centropages typicus* females in the New York Bight. *Limnol. Oceanogr.* 25: 597–609
- Dean, T. A. (1981). Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *J. exp. mar. Biol. Ecol.* 53: 163–180
- Dean, T. A., Hurd, L. E. (1980). Development in an estuarine fouling community: the influence of early colonists on late arrivals. *Oecologia* 46: 295–301
- Doherty, P. J., Sale, P. F. (1985). Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* 4: 225–234
- Ertman, S. C., Jumars, P. A. (1988). Effects of bivalve siphonal currents on the settlement of inert particles and larvae. *J. mar. Res.* 46: 797–813
- Fiala-Médioni, A. (1978 a). Filter-feeding ethology of benthic invertebrates (ascidians). III. Recording of water current *in situ* – rate and rhythm of pumping. *Mar. Biol.* 45: 185–190
- Fiala-Médioni, A. (1978 b). Filter-feeding ethology of benthic invertebrates (ascidians). IV. Pumping rate, filtration rate, filtration efficiency. *Mar. Biol.* 48: 243–249
- Fiala-Médioni, A. (1978 c). Filter-feeding ethology of benthic invertebrates (ascidians). V. Influence of temperature on pumping, filtration and digestion rates and rhythms in *Phallusia mamillata*. *Mar. Biol.* 48: 251–259
- Fiala-Médioni, A. (1979 a). Influence de la concentration algale du milieu sur le pompage, la filtration et l'absorption de *Phallusia mamillata* (Cuvier, 1815) (ascidie simple). *Annls Inst. océanogr.*, Paris (N.S.) 55: 155–162
- Fiala-Médioni, A. (1979 b). Effects of oxygen tension on pumping, filtration and oxygen uptake in the ascidian *Phallusia mamillata*. *Mar. Ecol. Prog. Ser.* 1: 49–53
- Fisher, T. R. (1977). Metabolic maintenance costs of the suspension feeder *Styela plicata*. *Mar. Biol.* 41: 361–369
- Gaines, S., Brown, S., Roughgarden, J. (1985). Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67: 267–272
- Gaines, S., Roughgarden, J. (1985). Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. natn. Acad. Sci. U.S.A.* 82: 3707–3711
- Gifford, D. J., Bohrer, R. N., Boyd, C. M. (1981). Spines on diatoms: do copepods care? *Limnol. Oceanogr.* 26: 1057–1061
- Goodbody, I. (1961). Inhibition of the development of a marine sessile community. *Nature, Lond.* 190: 282–283
- Hecht, S. (1918). The physiology of *Ascidia atra* Lesueur II. Sensory physiology. *J. exp. Zool.* 25: 261–299
- Hunt, J. H., Ambrose, W. G., Jr., Peterson, C. H. (1987). Effects of the gastropod, *Ilyanassa obsoleta* (Say), and the bivalve, *Mercentaria mercenaria* (L.), on larval settlement and juvenile recruitment of infauna. *J. exp. mar. Biol. Ecol.* 108: 229–240
- Jackson, J. B. C. (1977). Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am. Nat.* 111: 743–767
- Jackson, J. B. C. (1983). Biological determinants of present and past sessile animal distributions. In: Tvesz, M. J. S., McCail, P. L. (eds.) *Biotic interactions in recent and fossil benthic communities*. Plenum Press, New York and London, p. 39–120
- Jørgensen, C. B. (1955). Quantitative aspects of filter feeding in invertebrates. *Biol. Rev.* 30: 391–454
- Jørgensen, C. B., Goldberg, E. D. (1953). Particle filtration in some ascidians and lamellibranchs. *Biol. Bull. mar. biol. Lab., Woods Hole* 105: 477–489
- Keough, M. J. (1983). Patterns of recruitment of sessile invertebrates in two subtidal habitats. *J. exp. mar. Biol. Ecol.* 66: 213–245
- Klump, D. W. (1984). Nutritional ecology of the ascidian *Pyura stolonifera*: influence of body size, food quantity and quality on filter-feeding, respiration, assimilation efficiency and energy balance. *Mar. Ecol. Prog. Ser.* 19: 269–284
- Landry, R. M. (1980). Detection of prey by *Calanus pacificus*: implications of the first antennae. *Limnol. Oceanogr.* 25: 545–549
- Mattson, S. A. (1987). The impact of predation on species richness and percent cover of epifauna after recruitment to cockle shells. M.S. thesis, Florida State University
- McGinitie, G. E. (1939). The method of feeding of tunicates. *Biol. Bull. mar. biol. Lab., Woods Hole* 77: 443–447
- Osman, R. W. (1977). The establishment and development of a marine epifaunal community. *Ecol. Monogr.* 47: 37–63
- Peterson, C. H. (1982). The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecol. Monogr.* 52: 437–475
- Randlov, A., Riisgård, H. U. (1979). Efficiency of particle retention and filtration rate in four species of ascidians. *Mar. Ecol. Prog. Ser.* 1: 55–59
- Robbins, I. J. (1983). The effects of body size, temperature, and suspension feeding density on the filtration and ingestion of inorganic particulate suspensions by ascidians. *J. exp. mar. Biol. Ecol.* 70: 65–78
- Rumrill, S. S., Pennington, J. T., Chia, F. S. (1985). Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar, *Dendraster excentricus* (Eschscholtz), embryos and larvae by zoeae of the red crab, *Cancer productus* Randall. *J. exp. mar. Biol. Ecol.* 90: 193–208
- Singarajah, K. V. (1969). Escape reactions of zooplankton: the avoidance of a pursuing siphon tube. *J. exp. mar. Biol. Ecol.* 3: 171–178
- Sutherland, J. P. (1974). Multiple stable points in natural communities. *Am. Nat.* 108: 859–873
- Sutherland, J. P. (1978). Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, North Carolina. *Ecology* 59: 257–264
- Thorson, G. (1950). Reproduction and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25: 1–45
- Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. mar. Biol. A. Rev.* 19: 513–605
- Underwood, A. J., Denley, E. J. (1984). Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong, D., Simberloff, D., Abele, L. G., Thistle, A. B. (eds.) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, p. 151–180
- Williams, J. G. (1980). The influence of adults on the settlement of spat of the clam, *Tapes japonica*. *J. mar. Res.* 38: 729–741
- Woodin, S. A. (1976). Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *J. mar. Res.* 34: 25–41
- Yen, J. (1982). Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. *J. exp. mar. Biol. Ecol.* 63: 105–117
- Young, C. M. (1988). Ascidian cannibalism correlates with larval behavior and adult distribution. *J. exp. mar. Biol. Ecol.* 117: 9–26
- Young, C. M., Braithwaite, L. F. (1980). Orientation and current-induced flow in the stalked ascidian *Styela montereyensis*. *Biol. Bull. mar. biol. Lab., Woods Hole* 159: 428–440
- Young, C. M., Chia, F. S. (1987). Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. In: Giese, A. C., Pearse, J. S., Pearse, V. B. (eds.) *Reproduction of marine invertebrates. Vol. 9. General aspects: seeking unity in diversity*. Blackwell, Palo Alto, and Boxwood Press, Pacific Grove, p. 385–463
- Young, C. M., Gotelli, N. J. (1988). Larval predation by barnacles: effects on patch colonization in a shallow subtidal community. *Ecology* 69: 624–634