

Role of early post-settlement mortality in setting the upper depth limit of ascidians in Florida epifaunal communities

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ABSTRACT: At 3 sites in Florida, USA, the communities of marine sessile invertebrates are dominated by oysters (*Crassostrea virginica*) in the mid-intertidal zone, and by ascidians (several species) in the low intertidal and subtidal zones. Our experiments tested the hypotheses that the upper depth limit of ascidians is set by (1) predation by oysters on larvae, (2) larval zonation, and (3) early post-settlement mortality. Hypothesis 1 was tested by monitoring ascidian recruitment on the shells of dead and living oysters placed in both the oyster and ascidian zones. Because recruitment of all ascidian species was confined to oysters placed in the ascidian zone, we concluded that the upper depth limit of these ascidians cannot be due solely to predation on larvae by oysters. Hypotheses 2 and 3 were tested by monitoring the recruitment of ascidians on settling plates fixed in the 2 zones, and on plates floating at 2 depths in the water column. In the 'fixed' experiments, recruitment of all ascidian species was confined to the ascidian zone. In the 'floating' experiments, the number of recruits of *Diplosoma glandulosum* did not differ between shallow and deep plates, and recruitment of *Styela plicata* was confined to shallow plates. Thus, we concluded that early post-settlement mortality is a major factor setting the upper depth limit of these 2 species. We vertically transplanted 2 ascidians (*S. plicata*, *Botryllus planus*) and found that the survivorship of both was greater in the ascidian zone than in the oyster zone. Thus, further support was gained for the post-settlement mortality hypothesis.

INTRODUCTION

One obvious distribution pattern in the marine benthos is the intertidal zonation of sessile invertebrates. Some of the earliest field experiments done in ecology were aimed at identifying the processes that cause zonation. These emphasized the importance of post-settlement events, such as physical factors (Connell 1961a, b), predation (Connell 1961a, Dayton 1971, Paine 1974, Menge 1976, Underwood 1980), and competition (Connell 1961b, Dayton 1971, Menge 1976). More recent experiments provide evidence that intertidal limits are influenced by pre-settlement events, such as larval pre-emption of space (Denley & Underwood 1979), larval zonation (Grosberg 1982), larval predation (Gaines & Roughgarden 1985, 1987), and larval settlement preferences (Raimondi 1988, 1991).

Recent field experiments, aimed at determining the causes of spatial distribution patterns in ascidians, have considered the roles of both pre- and post-settlement events. Some studies highlight the significance of post-settlement events, such as physical factors, predation, and competition (Young & Chia 1984, Young 1985, 1989, Keough & Downes 1986, Davis 1987). Others have found that pre-settlement processes, such as larval transport, larval behavior, and larval predation (Young & Chia 1984, 1987, Olson 1985, Keough & Downes 1986, Davis 1987, Olson & McPherson 1987, Svane 1987, Svane & Young 1989, Stoner 1990, Havenhand & Svane 1991) are significant.

On the coast of Florida, USA, ascidians occur in the subtidal and low intertidal attached to mangrove roots, sea grass blades, mollusc shells, worm tubes, sea walls, or can be found unattached and drifting on the bottom (Rudloe 1971, Odum et al. 1982, Young 1989). Oysters (*Crassostrea virginica*) usually occur at shallower depths on intertidal sand bars, but are also found at the

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same depths and on the same substrata where ascidians live (Menzel & Nichy 1958, Menzel et al. 1958, 1966, Nichy & Menzel 1960, Odum et al. 1982).

What factors set the upper depth limit of ascidians in these communities? Our experiments test the hypotheses that the depth limit is determined by (1) predation by oysters on larvae; (2) larval zonation; or (3) early post-settlement mortality.

Below, 'settlement' refers to the attachment of a larva to a substratum and its concomitant metamorphosis, whereas 'recruitment' is the survival of the early juvenile until seen by an investigator (sensu Keough & Downes 1982).

MATERIALS AND METHODS

Study sites. This study was carried out in Florida, USA, at 2 sites in the Indian River Lagoon near Fort Pierce (Little Jim Bridge = LJB, Harbor Branch Oceanographic Institution marina = HBM), and at 1 site in the northern Gulf of Mexico near Carrabelle (Florida State University Marine Laboratory boat basin = FSU). Fort Pierce and Carrabelle are 550 km apart; the 2 Fort Pierce sites are separated by 7 km.

Photography. Sessile organisms (including ascidians) occupying sea walls and settling plates were photographed on Kodachrome color slide film (ASA 64) using a Nikonos 5 camera and Whale strobe. To calculate the percent cover occupied by each species, we projected each slide on 1 of 8 randomly chosen grids of 100 random points, and recorded the species which appeared under each point. Sutherland & Karlson (1977) and Mook (1980) found that 75 and 80 random points, respectively, provided adequate estimates of the percent cover of species on plates of similar size. Because many species are epizoic, it was possible to have more than 100% cover for a given slide.

Zonation. To document zonation of oysters and ascidians at LJB, we took 5 photoquadrats in a vertical line at each of 7 locations along the sea wall, using a 1:6 close-up lens and framer and 28 mm lens (field of view 144×216 mm). At FSU, we took 3 photoquadrats in a vertical line at each of 10 locations along the sea wall, using a 1:3 extension ring and framer with a 35 mm lens (field of view 71×106 mm). Photos were taken in June 1986 (LJB) and April 1988 (FSU). We deemed it unnecessary to photograph zonation at HBM, since the pattern at this site was no different from that at the other Fort Pierce site, LJB.

Placement of settling plates. In the experiments described below, plates were mounted on nails hammered into sea wall fissures (LJB); or suspended along a cement dock from PVC pipes (HBM), or wooden beams (FSU). An arbitrary datum was estab-

lished at both Fort Pierce sites since, unlike FSU, neither had tidal gauges. Plates were mounted in the oyster and ascidian zones such that their upper edges were positioned at tidal heights of +63 and 0 cm (LJB), +75 and 0 cm (HBM), and +42 and -70 cm (FSU). Each plate positioned in the oyster zone was paired with a plate in the same vertical line in the ascidian zone.

Larval predation experiment. To test the hypothesis that the upper depth limit of ascidians at LJB is due to predation by *Crassostrea virginica* on larvae, we monitored ascidian recruitment on the shells of living and dead oysters placed in the oyster and ascidian zones.

We haphazardly collected 72 oysters (mean height \pm SD = 83 ± 18 mm) from HBM, removed all epibiotia from their shells, and randomly divided them into 2 groups of 36. We then removed the bodies from the shells of all individuals of 1 group, and replaced them with cement. Next, the dead oysters were randomly divided into 6 groups of 6, as were the living ones. Each group of 6 oysters was then cemented onto a cement plate ($18 \times 20 \times 2$ cm) in a 2×3 array. Each oyster was haphazardly oriented with its lower valve closest to the plate.

The 12 plates (each occupied by a group of 6 oysters) were then mounted on the sea wall fissures at LJB. Three of the 6 living groups were set in the oyster zone, and the other 3 were placed in the ascidian zone. The 6 dead groups were distributed in the same way. Vertical pairs of living and dead groups were horizontally interspersed.

Ascidians that recruited on oyster shells were counted at the end of the 18 d experiment. We checked the oysters daily to see if they were feeding.

Fixed experiments. To determine whether the absence of ascidians in the oyster zone is due to a lack of recruitment, we monitored recruitment on clay tiles ($14.5 \times 14.5 \times 2$ cm) secured in the 2 zones. The smooth surface of each plate faced away from the sea wall, and was the surface we monitored for ascidian recruitment. To minimize possible edge effects, we used a 1:3 framer (which covered only the mid-section of each plate) when photographing ascidians on plates. The same framer was also used to outline the area in which ascidians were counted.

At both LJB and FSU, 16 plates were positioned in the oyster zone, and 16 in the ascidian zone; at HBM there were 5 in each zone. The horizontal distance between successive plates was 75 (LJB), 4.5 (HBM), and 62 cm (FSU).

At LJB and FSU, the 16 plates within each zone were divided equally into 4 treatments: (1) removal of compound ascidians only, (2) removal of solitary ascidians only, (3) removal of all ascidians, and (4) no removals

(control). These treatments were part of a concurrent study designed to test the tolerance of oysters to ascidian overgrowth (Dalby 1988).

Experiments were run in March to September 1987 (LJB), August to September 1987 (HBM), and October 1986 to August 1987 (FSU). At LJB, plates were photographed and ascidians removed every 2 to 4 wk. At HBM, plates were examined once at the end of the 16 d experiment. At FSU, ascidians were counted and removed every 1 to 2 wk and photos taken every 3 to 5 wk. Photos were always taken prior to ascidian removal.

Floating experiments. In the fixed experiments, we observed that ascidian recruitment was confined to the ascidian zone. The lack of recruitment in the oyster zone may be due to larval zonation (i.e. larvae are present only at low depths) or early post-settlement mortality (i.e. larvae are present at all depths but die after settlement in the oyster zone). To test these hypotheses, we monitored ascidian recruitment on clay tiles (14.5 × 14.5 × 2 cm) floating at 2 depths.

Plates were attached to rectangular racks (100 cm wide, 75 cm tall) made of PVC pipe (25 mm diameter). On each rack, 5 plates were hung along the upper pipe, and 5 along the lower pipe. The horizontal distance between successive plates was 45 mm.

Each rack was held afloat by 6 styrofoam floats (15 cm diameter) attached along the upper pipe; each rack was connected by a rope to a cement block on the bottom. Ropes were slack enough to allow free vertical movement of racks with tidal flux. When the surface of the water was still, the upper edges of the shallow and deep plates were 21 and 96 cm from the surface, respectively. During low tides, the deep plates never came within 1 m of the bottom, and were thus inaccessible to benthic predators. The average depths in which the experiments were run were 3 m (HBM) and 4 m (FSU). At HBM, 5 racks were deployed for 16 d in August-September 1987. At FSU, 6 racks were deployed for 34 d in May-June 1987.

At HBM, ascidians were counted after plates were recovered and dried out; at FSU, counts were made from photographs taken *in situ*. For the HBM experiment, we counted only those colonies that appeared on the smooth surface of each plate, as those on the rough surface were not easily discerned. For the FSU experiment, there was no such difficulty, so both plate surfaces were considered.

Transplant experiments. To test the hypothesis that ascidians are absent from the oyster zone because they cannot survive there, we transplanted individuals of 2 ascidian species to the oyster zone with control individuals in the ascidian zone.

***Styela plicata*:** We haphazardly collected 54 specimens of *S. plicata* (mean height ± SD = 45 ± 7 mm)

from LJB and randomly divided them into 6 groups of 9 individuals. Each group was glued (Krazy Glue) to a cement plate (18 × 20 × 2 cm) in a 3 × 3 array. Three plates were then mounted in each zone at LJB. The distance between successive plates within each zone was 75 cm. Ascidians were monitored daily over a 41 d period in June-July 1986.

At FSU, *Styela plicata* were obtained by hanging 8 clay tiles (14.5 × 14.5 × 2 cm) at the level of the ascidian zone in November 1987. Once plates became fouled by *S. plicata* (3 to 10 mm tall), 4 plates were suspended at the level of the oyster zone, and the other 4 were left in the ascidian zone where they served as controls. The distance between successive plates within each zone was 1 to 3 m. The experiment began in December, and individuals on all plate surfaces (smooth side, rough side, edges) were checked monthly until March 1988.

In both experiments, we counted the number of living and dead ascidians at each check. Dead individuals were recognized when necrotic tissue appeared or when the ascidians did not contract when poked.

***Botryllus planus*:** At HBM, we collected 54 colonies of *B. planus* (< 30 mm diameter) and randomly divided them into 6 groups of 9. Each group was then strapped to a cement plate (18 × 20 × 2 cm) in a 3 × 3 array using rubber bands. The 6 plates were then mounted in the ascidian zone for 1 wk to allow colonies to secure themselves to plates.

Next, 3 of the 6 plates were moved up to the oyster zone. Within each zone, the distance between successive plates was 75 cm. The experiment was run in July 1986 and ended after 24 h when the colonies were checked for the first time. Dead colonies were identified by their blackened appearance.

RESULTS

Zonation

At both LJB and FSU, an oyster (*Crassostrea virginica*) zone was found above an ascidian zone (Fig. 1). We saw the same pattern at HBM.

Bingham (1990) identified 32 species of ascidians at our Fort Pierce sites. We found 6 species at FSU (Table 1). Many other sessile taxa are present at the 2 Fort Pierce sites (Mook 1983a) and at FSU (Menzel 1971).

Larval predation experiment

Ascidians did not recruit on the shells of either dead or living oysters placed in the oyster zone. However, 3 species (*Botryllus planus*, *Didemnum* sp., *Polyan-*

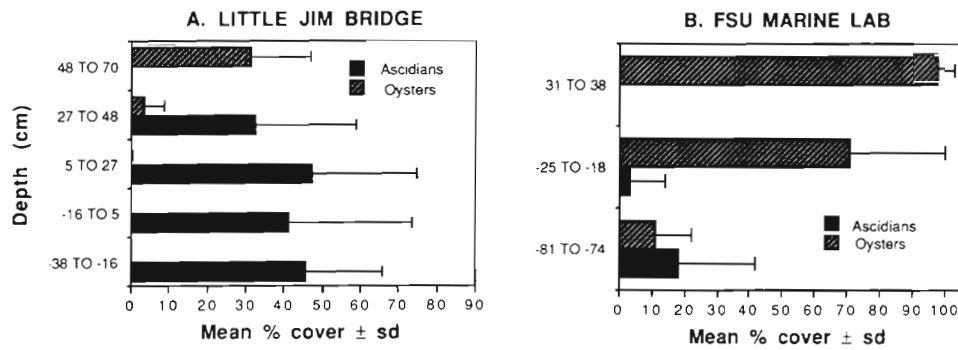


Fig. 1. Vertical zonation of oysters and ascidians on sea walls at (A) LJB and (B) FSU

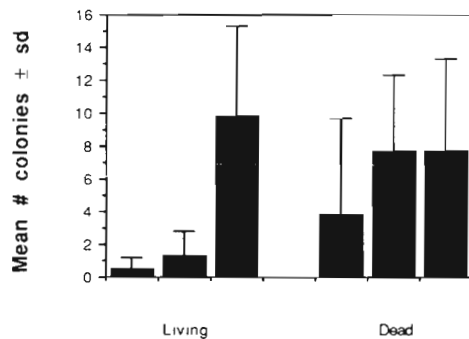


Fig. 2. *Didemnum* sp. Recruitment on shells of dead and living oysters in the ascidian zone at LJB. Each bar represents a group of oysters on a plate. The difference between dead and living oysters was nonsignificant (t -test: $df = 4$, $p = 0.479$)

drocarpa zorriventis) recruited on oysters placed in the ascidian zone.

Some of the living oysters placed in the ascidian zone were not used in analyses because we never saw them feeding (i.e. valves were always closed) during the experiment. As a result, instead of analyzing data for 6 oysters per plate, we analyzed data for 2 oysters on 1 plate, 4 on the second, and 5 on the third.

The difference in the number of *Didemnum* sp. recruits (2 to 10 mm colonies) between dead and living oysters in the ascidian zone was nonsignificant (Fig. 2). The amount of recruitment of *Botryllus planus* and *Polyandrocarpa zorriventis* was inadequate (mean no. colonies oyster⁻¹ < 1) for analyses.

Fixed experiments

Ascidians never recruited on plates set in the oyster zone at any of the 3 sites. The numbers of ascidian species that recruited on plates in the ascidian zone were 14 at LJB, 1 at HMB, and 6 at FSU (Table 1).

Styela plicata numbers on control plates at FSU peaked in May 1987 and crashed in July 1987 (Fig. 3), the latter occurring during a time of high water temperatures (Dalby 1988).

Table 1. Ascidians (C = colonial, S = solitary) that recruited on fixed plates at LJB, HBM, and FSU

Taxa	C/S	LJB	HBM	FSU
Order Aplousobranchia				
<i>Clavelina oblonga</i>	C	x		
<i>Didemnum conchyliatum</i>	C	x		
<i>Didemnum</i> sp.	C	x		
<i>Diplosoma glandulosum</i>	C	x	x	
<i>Diplosoma macdonaldii</i>	C	x		
<i>Diplosoma</i> sp.	C			x
<i>Eudistoma capsulatum</i>	C	x		
<i>Trididemnum savignii</i>	C	x		
Order Phlebobranchia				
<i>Ascidia curvata</i>	S	x		
<i>Ecteinascidia turbinata</i>	C			x
<i>Perophora viridis</i>	C			x
Order Stolidobranchia				
<i>Botryllus planus</i>	C	x		
<i>Microcosmus exasperatus</i>	S	x		
<i>Molgula occidentalis</i>	S	x		x
<i>Polyandrocarpa zorriventis</i>	C	x		
<i>Styela partita</i>	S			x
<i>Styela plicata</i>	S	x		x
<i>Symplegma viride</i>	C	x		

Floating experiments

The only ascidian species to appear on floating plates at HBM was *Diplosoma glandulosum*. After 16 d, the difference in the number of colonies (2 to 5 mm) between shallow and deep plates was nonsignificant (Fig. 4A).

Styela plicata was the only ascidian species to recruit on floating plates at FSU. Twenty-five days into the experiment, ascidians were present only on the shallow plates. The same pattern was observed when the experiment was ended on Day 34 (Fig. 4B). At this time, ascidians were ≤ 10 mm in size. Because the ascidians were so crowded, it was difficult to distinguish individuals in photographs, so siphons were counted instead.

Transplant experiments

***Styela plicata*, LJB.** The data that we analyzed were the number of days that each individual survived. One individual disappeared before the end of the experiment in the oyster zone, as did 7 in the ascidian zone. Since we noticed that the grip of these 8 individuals was weakening with each inspection, we believe these individuals fell off the plates as a result of glue dissolution. We doubt that fish preyed on them since only juvenile *S. plicata* are known to be vulnerable (Mook 1983b); our experiment used adult animals only. For these 8 individuals, we took the number of days of survival to be the number of days present.

Thirteen of the 27 ascidians placed in the ascidian zone were still alive at the end of the 41 d experiment, so for these individuals we took the number of days of survival to be 41. None of those placed in the oyster zone were alive after 41 d.

The mean number of days that *Styela plicata* survived in the ascidian zone was significantly greater than that in the oyster zone (Fig. 5A).

***Styela plicata*, FSU.** The number of young *S. plicata* remaining in the oyster zone after 3 mo was 0; in the ascidian zone, there was a dramatic increase in abundance due to recruitment (Fig. 5B). Dead individuals were never seen. It is probable that the loss of young

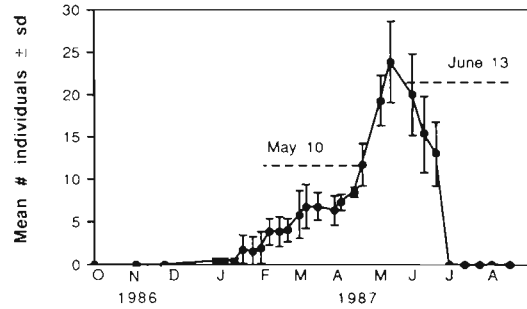


Fig. 3. *Styela plicata* abundance in the ascidian zone at FSU in 1986–87. (The concurrent floating experiment ran from May 10 to June 13)

ascidians in the oyster zone was due to death rather than detachment, since individuals are known to detach only when under the weight of dense aggregations of large conspecifics (Sutherland 1978).

We cannot declare that survivorship was greater in the ascidian zone than in the oyster zone because we could not distinguish transplanted individuals from ones that recruited during the experiment. Nevertheless, the observation that there were no survivors beyond 3 mo in the oyster zone is consistent with our notion of differential survivorship.

***Botryllus planus*.** After 1 d, all 27 *B. planus* colonies placed in the oyster zone at LJB died, whereas all 27 of those in the ascidian zone survived beyond 3 wk.

Fig. 4. Recruitment of (A) *Diplosoma glandulosum* at HBM, and (B) *Styela plicata* at FSU, on floating plates. In (A), the difference in recruitment between shallow and deep plates was nonsignificant (Paired *t*-test: *df* = 4, *p* = 0.215)

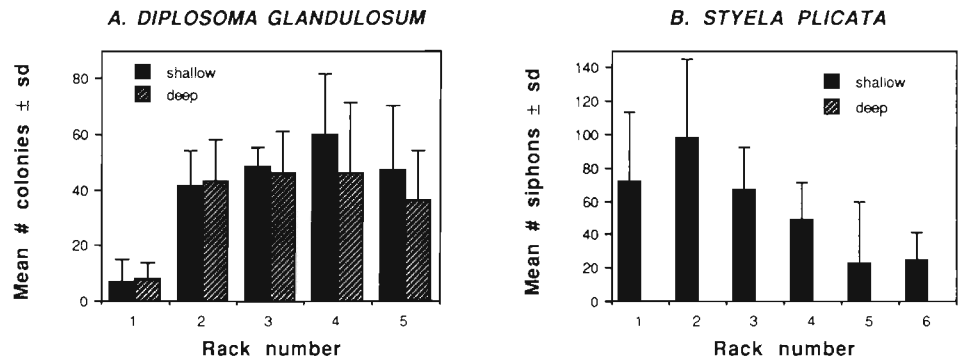
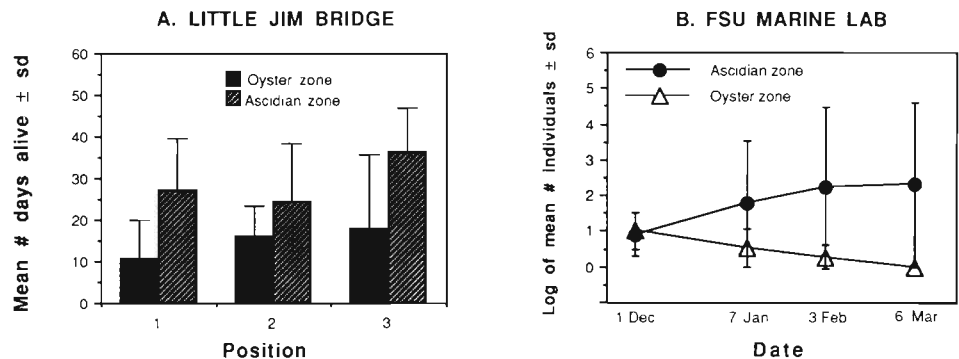


Fig. 5. *Styela plicata*. (A) Survivorship when transplanted to the oyster and ascidian zones at LJB. Survivorship in the ascidian zone was significantly greater than that in the oyster zone (Paired *t*-test: *df* = 2, *p* = 0.04). (B) Change in abundance when transplanted to the 2 zones at FSU



DISCUSSION

When experimental surfaces (oyster shells, settling plates) were placed in the oyster and ascidian zones at our 3 study sites, recruitment of all ascidians was confined to surfaces set in the ascidian zone. Thus, there is no evidence that the absence of ascidians in the oyster zone is purely the result of predation on larvae by oysters. At HBM, the difference in the number of *Didemnum* sp. recruits between dead and living oysters in the ascidian zone was nonsignificant. Thus, there is no reason to believe that predation on larvae by oysters contributes to the absence of *Didemnum* sp. in the oyster zone at HBM. Young (1990) discusses problems in detecting larval predation effects.

At HBM, the number of colonies of *Diplosoma glandulosum* that appeared on plates floating near the surface did not differ from the number on plates floating at a lower depth. This result supports the idea that early post-settlement mortality is a factor responsible for the absence of this ascidian in the oyster zone. It also suggests that the absence is partly due to reduced settlement: the oyster zone is exposed for longer periods than the ascidian zone, and thus there is less opportunity for settlement in the former than in the latter.

At FSU, *Styela plicata* recruited on plates floating near the surface and not on ones floating at a lower depth. This result suggests that the absence of this ascidian in the oyster zone is due to early post-settlement mortality. It also suggests that *S. plicata* settle in the ascidian zone when the tide is low.

The lack of *Styela plicata* recruitment on the deep floating plates could have been due to suppressed growth and/or survivorship rather than reduced settlement. At low depths, fish predation could be more intense, and there might be less phytoplankton food available. However, these possibilities are unlikely since *S. plicata* living on plates fixed in the ascidian zone were at peak levels of abundance during the floating experiment (Fig. 3).

Based on the literature, we did not expect the recruitment of *Styela plicata* on floating plates to be confined to the shallow level. Yamaguchi (1970) found that settlement of this species in Japan on floating glass slides did not differ between 0 and 2 m depth. In Italy, *S. plicata* colonized shaded surfaces of settling plates more readily than unshaded ones (Tursi & Mataresse 1981). From this observation, one might predict less recruitment on shallow (more insolated) plates than deep ones.

Our experiments have not addressed the possible role of larval settlement preferences in setting ascidian depth distributions. For example, the settlement of some barnacle species is induced by algae and inver-

tebrates that occupy the same zone (Strathmann et al. 1981, Raimondi 1988). Perhaps the larvae of *Diplosoma glandulosum* and *Styela plicata* cue on certain organisms that reside in the ascidian zone.

Survivorship of *Styela plicata* and *Botryllus planus* transplanted to the oyster zone was less than that in the ascidian zone. Processes that kill ascidians at shallow depths include desiccation, insolation, exposure to freshwater, freezing, and predation (Millar 1971, Jokiel 1980, Olson 1983, Dalby 1989, Young 1989). By contrast, the ascidian *Pyura stolonifera*, which forms a band in the intertidal zone on some shores in the southern hemisphere (Stephenson & Stephenson 1972, Dakin 1987), is thought to suffer greater mortality in the subtidal than in the intertidal zone because of subtidal predators (Paine & Suchanek 1983, but see Underwood & Fairweather 1986).

Styela plicata transplanted to the oyster zone at FSU probably froze to death. In winter at this site, tides reach their lowest annual heights (NOAA Tide Tables). In addition, northerly cold fronts depress tides below their predicted levels, and cause air temperatures to drop below the freezing point. Likewise, the ascidian *Molgula occidentalis*, which occurs on intertidal sand bars near FSU, freezes to death during winter low tides (Young 1989). Fresh water may have also killed *S. plicata*, as surface salinities occasionally dropped to 7 ppt at this site (Dalby 1988). Although the snail *Melongena corona* preys on *S. plicata* in the intertidal zone of sandy shores (Dalby 1989), we doubt that it contributed to the mortality that we observed in our transplant experiment since we have never seen this snail on sea walls at FSU.

Given that our transplanted adult/juvenile ascidians were unable to survive in the oyster zone, it seems even less likely that newly settled larvae (of the same species) would survive either. The higher surface area to volume ratio of newly settled larvae (due to their smaller size but similar shape) leaves them more vulnerable to physical stresses such as desiccation.

Our study has examined both pre- and post-settlement events in setting depth limits of intertidal/subtidal invertebrates. While a recent wave of studies emphasize the importance of pre-settlement events in determining these limits (see 'Introduction'), in our case we find that post-settlement events are of major significance.

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