Variable effects of ascidian competitors on oysters in a Florida epifaunal community

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Abstract: It is often assumed that sessile animals die when they are overgrown by others. Three settling plate experiments were run to determine whether ascidian overgrowth reduces the survivorship of the oyster, *Ostrea equestris* Say, in a Florida epifaunal community. Each experiment was run under a different set of conditions. Ascidians reduced the number of living oysters in two experiments but enhanced the number in a third. Ascidians had no effect on oyster size in one experiment, but enhanced size in the other two. Thus, there was no consistent effect of ascidians on oysters. At the end of all experiments, many living oysters were found under ascidians. Gaps beneath ascidians permitting water flow to underlying oysters may explain the ability of oysters to survive.

Key words: Ascidian; Competition; Florida; Overgrowth; Oyster

INTRODUCTION

Sessile marine invertebrates compete for space via processes that occur both before and after larval settlement. The former include pre-emption of space by adults, predation by adults on larvae, and avoidance of adults by larvae; the latter include undercutting, crushing, attack by allelochemicals and nematocysts, biodeposition, food depletion, and overgrowth (reviews by Jackson, 1983; Branch, 1984; Connell & Keough, 1985; Buss, 1986; Young & Chia, 1987; Young, 1990).

Perhaps the most common form of competition, overgrowth, generally leads to death of underlying individuals, and it is commonly assumed that overgrown individuals are dead. However, overgrowth does not always lead to death (Todd & Turner, 1988; reviews by Jackson, 1983; Branch, 1984; Connell & Keough, 1985; Buss, 1986).

Among the sessile fauna, ascidians generally kill the sessile animals that they overgrow (review by Jackson, 1983). The only contrary manipulative study we know of is nonlethal overgrowth of bryozoans by colonial ascidians in Scotland (Todd & Turner, 1988).

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Despite an abundant literature on oyster ecology (reviews by Galtsoff, 1964; Andrews, 1979; Abbe, 1986), we are unaware of any field experiments that tested the tolerance of oysters to overgrowth. In fact, we know of only three experimental field studies that investigated oyster competitive ability in general (Bros, 1987; Bushek, 1988; Osman et al., 1989).

In the present paper, we test the tolerance of oysters to ascidian overgrowth in Florida.

Materials and methods

Study period, site and animals. Our study was done in 1987 at Little Jim Bridge in the Indian River Lagoon near Fort Pierce, Florida, USA. The oyster we studied, *Ostrea equestris* Say, was identified by Dr R.W. Menzel (Dept Oceanography, Florida State Univ., Tallahassee, FL, USA). Lists of Indian River fouling species, including ascidians, can be found in Mook (1983), Dalby & Young (1992), and Bingham (in press).

Hypothesis and general design of experiments. We ran three experiments to test the hypothesis that ascidian overgrowth reduces oyster survivorship. Oysters and ascidians were allowed to compete on settling plates in the field. Oysters were present on all plates, whereas ascidians were present on some plates (experimentals) and absent on others (controls). The specific details of Experiments 1, 2 and 3 are described below after more general information is given.

Arrangement of settling plates. Clay settling plates [either full-sized (20 × 145 × 145 mm) or half-sized (20 × 72 × 145 mm) depending upon experiment] were positioned on the sea wall in the low intertidal-shallow subtidal zone. The plates were fastened to nails which we hammered into fissures separating blocks of concrete that together formed the sea wall. The horizontal distance between successive plates was 75 cm.

Occupation of plates by oysters. Oyster spat were obtained by attaching plates to the sea wall and allowing them to be settled on by oyster larvae. Experiments either began with bare plates, which became colonized by oyster spat during the experiment, or with plates already encrusted with oyster spat. Experiments that began with bare plates were intended to represent situations in which sessile organisms colonize patches of unoccupied primary space in the community. Such patches may form when sessile organisms are dislodged by tidal currents, for example. Experiments that began with plates already encrusted with oysters were analogous to situations in which oysters are the first organisms to settle into open space.

In experiments which began with plates occupied by oysters, we first obtained oyster spat by securing full-sized bare plates to the sea wall for several months allowing oyster larvae to settle on them. Next, we returned the encrusted plates to the laboratory and brushed them, using a toothbrush, to remove all soft-bodied sessile organisms (sponges, hydroids, polychaetes, tubicolous amphipods, bryozoans, ascidians, algae). The shells of dead oysters were also removed (incidentally) by this brushing, so our counts of oysters from initial photographs (photographic methods described below) were of living oysters only. Because of the risk of dislodging living oysters, we did not scrape off animals with hard shells (limpets, serpulids, barnacles). We then selected those plates which had enough oyster spat and cut them into halves using a diamond saw to increase the number of replicates. Finally, the plates were ready for use.

Application of ascidian treatments. We subjected oyster spat to the effects of ascidian overgrowth using two methods. In the first method, we allowed ascidians to settle onto our plates (either bare or occupied by oysters) via larval dispersal. These experimental plates were compared to control plates, from which we removed ascidian recruits at ≈2-week intervals by hand or toothbrush.

In the second method, we strapped ascidians onto plates (occupied by oyster spat) using rubber bands. Over time, these ascidians gradually attached to the substratum and grew. (We thought that if oysters could tolerate this sudden experimental smothering by ascidians, then they could probably survive the more gradual overgrowth that occurs naturally.) These experimental plates were compared to control plates to which we added no ascidians. Any soft-bodied sessile organisms that settled from the plankton (listed above) were removed from both experimental and control plates, as ascidians were above. For reasons given previously, we did not remove animals with hard shells.

For both methods, treatments were applied to successive plates along the sea wall in an alternating fashion.

Details of Experiments 1, 2 and 3. The details of each experiment are described below and summarized in Table I. The circumstances of each are different so they are not directly comparable.

TABLE I

Design of Experiments 1, 2 and 3. C, colonial ascidians; S, solitary ascidians.

Experiment	Period	Plate size	Source of ascidians	Experimental plates	Control plates	Plates initially
1	March-September	Full	Larval recruitment	C removed, S removed, none removed	All ascidians removed	Bare
2	July-September	Half	Larval recruitment	No ascidians removed	All ascidians removed	Occupied by oysters
3	September-December	Half	Added manually	Ascidians added	No ascidians added	Occupied by oysters

Experiment 1 began in March when we secured 16 full-sized bare plates to the sea wall. The ascidians used in this experiment settled onto our plates from the plankton. The plates were divided into four groups of four. From one group, only colonial ascidians were removed; from a second group, only solitary ascidians were removed; from a third group, both colonial and solitary ascidians were removed; and from the last group, no ascidians were removed. The experiment was ended in September.

Experiment 2 began in July when we secured 14 half-sized plates to the sea wall. The ascidians used in this experiment settled onto our plates from the plankton. The plates were divided into two groups of seven. From the experimental plates we removed no ascidians; from the controls we removed all ascidians. The experiment was ended in September.

Experiment 3 began in September when we secured 16 half-sized plates to the sea wall. The colonial ascidian *Eudistoma capsulatum* (Van Name) was then fastened to the eight experimental plates; no ascidians were added to the eight controls. We chose this species because we suspected that its tough, thick (up to 4 cm) colonies would easily kill oysters. The ascidians occupied $>2/3$ of each plate at the start. At $\approx$2-week intervals, any ascidian colonies that had died were replaced with new ones. The experiment was ended in December.

Measuring oyster and ascidian abundances. Our plates were photographed at $\approx$2-week intervals in the field to determine the abundance of oysters and ascidians through time. The plates were photographed on Kodachrome film using a Nikonos 5 camera and Whale strobe. To minimize possible edge effects (e.g. those caused by our handling, or by preferential larval settlement), we used a 1:3 framer, which covered only the mid-section of each plate.

To determine percent cover of oysters and ascidians, we projected each color slide on 1 of 8 randomly chosen grids of 100 random points, and recorded which species appeared under each point. Sutherland & Karlson (1977) and Mook (1980) found that 75 and 80 random points, respectively, provided adequate estimates of percent cover of species on plates of similar size.

Plates were always photographed just before we removed ascidians, except on the last day of each experiment, when another set of photographs was taken after all soft-bodied sessile organisms (listed above) were brushed off the plates to expose the underlying oysters. In the process of brushing the plates, dead oysters were incidentally removed (explained earlier), so our counts of oysters from these final photographs were of living animals only. For reasons given earlier, we did not remove animals with hard shells.

Measuring oyster survivorship. Although our hypothesis was that ascidians reduce oyster survivorship, two logistical problems limited our ability to measure survivorship accurately. The first problem was that we could never be certain of exactly how many oysters died during the experiments. When oysters die, they often fall off the substratum due to dislodgement by water movement or by competitors with hard shells (listed above). Furthermore, all those dead oysters which did not fall off the plates were incidentally removed when we brushed off soft-bodied sessile organisms (listed above). For these reasons, our counts were of living oysters only.

Second, we had no way of stopping settlement of oyster larvae onto our plates throughout the experiments. This in fact occurred in all experiments. Thus, the number of living oysters that we found at the ends of the experiments must have exceeded the number that actually survived from start to finish. A common way of taking this problem into account is to measure background recruitment levels on bare settling plates, and substracting these levels from the number of oysters in the experimentals and controls. However, this method seemed of little use to us since oysters often settle gregariously (Andrews, 1979). This behaviour would have made the level of oyster recruitment on bare plates less than that on plates already occupied by oysters, causing us to underestimate the background level of recruitment by some unknown amount.

Despite these shortcomings in measuring oyster survivorship, our experiments still gave us insights into whether ascidian overgrowth reduces oyster survivorship.

Measuring oyster size.. Oysters were measured in two ways. First, the greatest linear dimension (usually height: Galtsoff, 1964) was used. The smallest oysters that we could detect by naked eye were 3 mm in size.

Second, mean area occupied by an oyster was calculated by dividing percent cover of oysters by number of oysters. We doubt that angular growth of oysters had much of an effect on these calculations since $>95\%$ of oysters were attached directly to settling plates (planar surfaces), and $<5\%$ were attached to conspecifics and barnacles (nonplanar).

RESULTS

Occupation of plates by ascidians and oysters. In Experiment 1, we could not see any solitary ascidians in our photographs, although at some checks in the field we did find 1–2 species; colonial ascidians (7 species) attained mean cover values of 50% (Table II; Dalby, 1988). In Experiment 2, solitary ascidians (3 species) attained mean cover values of 5%, while colonial ones (7 species) reached mean values of 30% (Table II; Dalby, 1988). By the end of Experiment 3, *E. capsulatum* covered $>80\%$ of the surface of each plate. Thus, in all experiments, we attained a sufficient abundance of ascidians to provide an adequate test of our hypothesis.

Oysters were seldom seen until the ends of the experiments when all soft-bodied sessile organisms covering the oysters (listed above) were brushed off the plates. We found many living oysters beneath several taxa of sessile organisms, including ascid-

TABLE II

Ascidians that recruited in Experiments 1 and 2.

Ascidians	Experiments
Colonial	
Botryllus planus	1, 2
Clavelina oblonga	1, 2
Didemnum sp.	1, 2
Diplosoma sp.	1, 2
Eudistoma capsulatum	1
Polyandrocarpa zorritensis	1, 2
Symplegma viride	2
Trididemnum savigny	1, 2
Solitary	
Ascidia curvata	2
Microcosmus exasperatus	1
Molgula occidentalis	2
Styela plicata	1, 2

ians. We suggest that a large fraction of these living oysters were covered specifically by ascidians at some time or other, since our photographs showed that ascidians were present in every square cm of every plate for at least a brief period.

Ascidians were never overgrown by oysters.

Altered number of replicates. During Experiment 1, 4 of the 16 plates became unfastened and fell to the sea bed. These losses reduced sample sizes from $n = 4$ in each treatment to $n = 2$ (colonial ascidians only removed), $n = 3$ (solitary ascidians only removed), $n = 3$ (all ascidians removed), and $n = 4$ (no ascidians removed). Because the level of solitary ascidian recruitment was very low (see above), we ran an ANOVA contrasting treatments with colonial ascidians (removal of solitary ascidians only + removal of none, $n = 7$) against those without colonial ascidians (removal of colonial ascidians only + removal of all, $n = 5$).

In Experiment 2, the number of replicates never changed. In Experiment 3, *E. capsulatum* never affixed themselves on 3 of the 8 experimental plates so these three were ignored.

Effects of ascidians on number of oysters. At the end of Experiment 1, the number of oysters was significantly less in treatments with colonial ascidians than in treatments without colonial ascidians (Fig. 1a, ANOVA: $df = 1,8$; $p = 0.031$). In Experiment 2, the increase in number of oysters when ascidians were present was significantly less than that when they were absent (Fig. 1b, t-test: $df = 12$, $p = 0.001$). In Experiment 3, the increase in number of oysters when ascidians were present differed significantly from the decrease when they were absent (Fig. 1c, t-test: $df = 11$, $p = 0.026$).

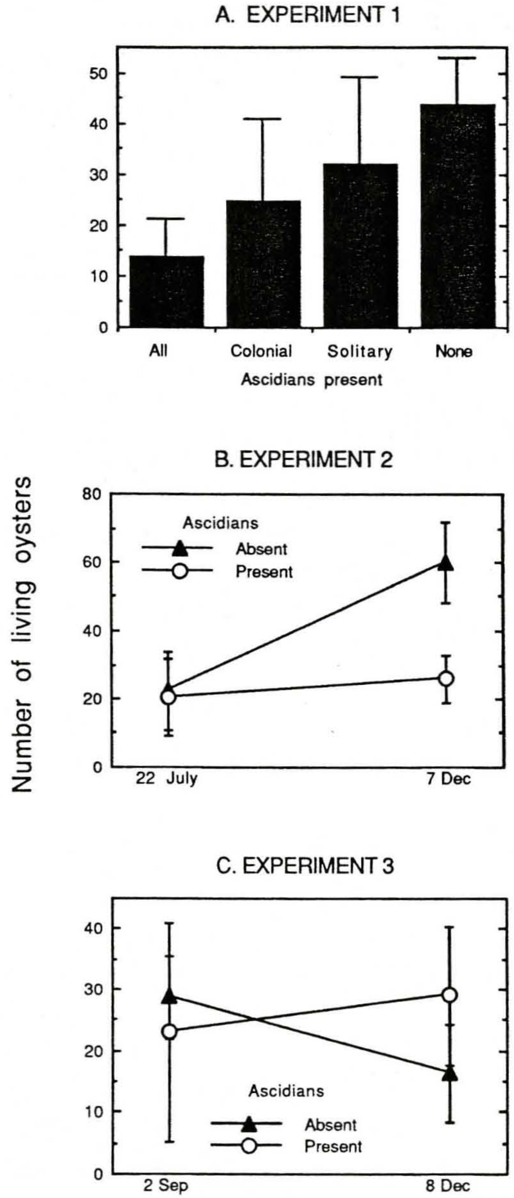

Fig. 1. Effect of ascidians on number of living oysters (mean ± SD). See text for statistics.

Effects of ascidians on oyster size. At the end of Experiment 1, the difference in size between treatments with and without colonial ascidians was nonsignificant (Fig. 2a, ANOVA: $df = 1,8$; $p = 0.324$). In Experiment 2, the size increase when ascidians were present differed significantly from the decrease when ascidians were absent (Fig. 2b,

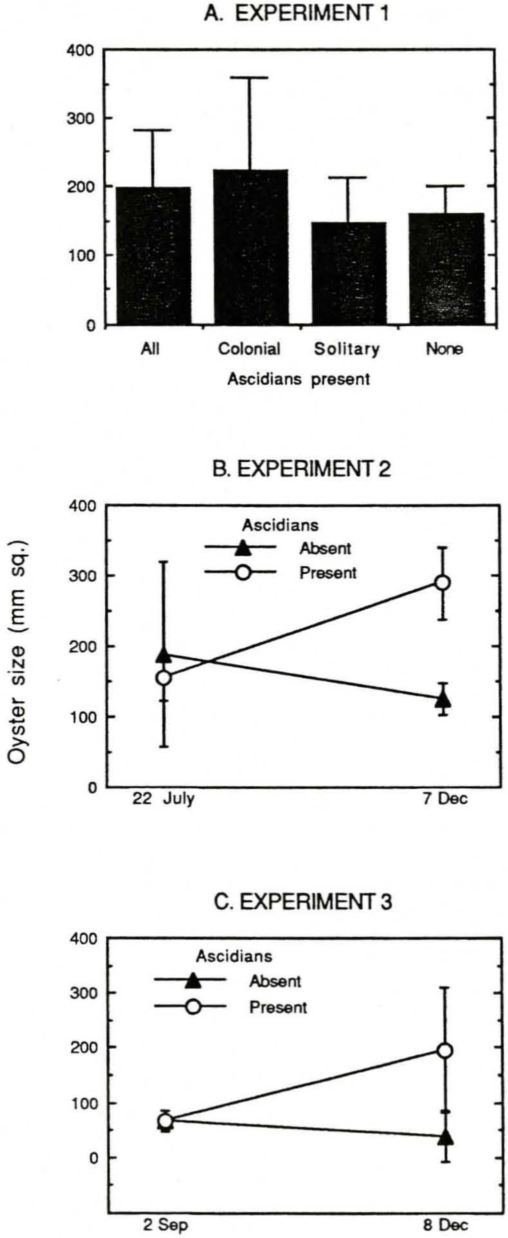

Fig. 2. Effect of ascidians on oyster size (mean ± SD). See text for statistics.

t-test: d*f* = 12, $p = 0.001$). In Experiment 3, the size increase when ascidians were present differed significantly from the decrease when they were absent (Fig. 2c, *t*-test: d*f* = 11, $p = 0.047$).

DISCUSSION

Although ascidians affected the number of living oysters in all experiments, the directions of the effects were inconsistent: the number of oysters was suppressed in the presence of ascidians in Experiments 1 and 2, and enhanced in Experiment 3. We do not know which of the different conditions under which the experiments were run (Table I) may have led to these variable outcomes.

In all of our experiments, oysters were overgrown by ascidians. The reduction in number of oysters that occurred in Experiments 1 and 2 may have been due to death by this overgrowth. However, ascidians may have killed oysters through several other mechanisms, including food depletion, biodeposition and allelopathy (Young, 1990). Furthermore, because larval oysters settled onto the plates during both of these experiments, the reduced number of oysters may have been due to an effect of ascidians on settling larval oysters. These include larval avoidance, pre-emption of space and larval predation (Young, 1990). Our experiments would have required many additional treatments to distinguish all of these mechanisms.

We cannot explain the puzzling result in Experiment 3 in which ascidians enhanced the number of oysters. To our knowledge, only two field studies have shown an enhancement by ascidians of the abundance of other sessile taxa: *Molgula manhattensis* enhanced mussels in Connecticut (Dean & Hurd, 1980), and *Styela plicata* enhanced serpulids in Florida (Young, 1989). The mechanisms of enhancement in these studies were unclear. In any case, our Experiment 3 provided no evidence that ascidian overgrowth reduces oyster survivorship.

We will never be certain of the exact mechanism(s) by which ascidians caused changes in numbers of oysters in our experiments. However, knowledge of these mechanisms is of only secondary interest. Of primary interest was the observation that, in all experiments, many living oysters were found beneath ascidians after months of overgrowth. We suspect that the ability of oysters to survive beneath ascidians was due to the fact that some parts of ascidian colonies were not attached to the substratum, leaving gaps where water flow could reach underlying oysters. This possibility pertains especially to the surviving oysters in Experiment 3; the bases of *E. capsulatum* colonies often assume an undulating shape in lateral view. Some sponge species can withstand overgrowth of other sponge species via structural modifications that facilitate water flow to the underlying animal (Rutzler, 1970). In other studies showing prolonged survival of one sessile species beneath another (Todd & Turner, 1988; reviews by Jackson, 1983; Connell & Keough, 1985; Buss, 1986), mechanisms of survival are not explained.

Oyster size was unaffected by ascidians in Experiment 1, but was enhanced in Experiments 2 and 3. The latter effect may have occurred either through increased oyster growth, reduced survival of small oysters, or reduced settlement of larval oysters. The designs of our experiments prevent us from inferring which mechanism was responsible.

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