Effects of caging on the development of a sessile epifaunal community

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ABSTRACT: In previous published studies on the effects of predation pressure in epibenthic communities, predator exclusion experiments (caging) have generally been employed. In the present study, the effects of caging on a fouling community were examined using experimental panels and several different types of control. The data show that caging *per se*, and not predation, accounts for the observed differences in species composition and abundance between treatments, mainly by affecting the settlement of larvae. Caging dramatically increased abundance of the solitary ascidians *Ciona intestinalis* and *Ascidella aspersa*, while significantly reducing cover of the barnacle *Elminius modestus*. Differing effects on other abundantly occurring species – colonial ascidians, hydroids and tubicolous amphipods – were also determined. We suggest that caging exerts its effects on the contained communities by reducing water movement and light intensity. This was tested by using controls designed to separate these variables. The results indicate that the most important effect on barnacles and hydroids is reduced current speed, whereas solitary ascidians are influenced by current speed, light and the presence of earlier colonists.

INTRODUCTION

It has been suggested that fish and invertebrate grazers often significantly affect epifaunal community structure through selective removal of prey species (Sutherland, 1974; Foster, 1975; Day, 1977; Mook, 1977; Wass and Vail, 1978; Karlson, 1978; Marshall et al., 1980; Russ, 1980). A test of this suggestion is to exclude predators from experimental substrata by caging with wire mesh or fish netting. Such experiments often show a marked increase in the abundance of colonial and solitary ascidians (Sutherland, 1974; Day, 1977; Marshall et al., 1980; Russ, 1980; see Table 3), while settlement of other species may largely be precluded by caging, e.g. *Balanus* spp. (Marshall et al., 1980). However, it is not always clear from these studies whether the observed effects of the experimental treatment were due to predator exclusion or to some other effect of caging.

In the present study, part of a larger investigation into community dynamics using experimental panels (Schmidt, 1983b), 3 field experiments were carried out and several types of control were deployed in order to isolate the various effects of predation (closed *versus* open cages) and also that of caging *per se* (caged *versus* uncaged panels). In Experiment 2, additional

cage types were constructed to distinguish between the consequences of cage-induced current reduction and light attenuation on larval recruitment. Experiment 3 served to determine whether cages provided a structural support for large solitary ascidians. During the course of the study several reports were published on predation effects on fouling communities (Mook, 1981; Smedes and Hurd, 1981; Vail and Wass, 1981; Otsuka and Dauer, 1982); these and the earlier studies are critically discussed in the light of the data presented here.

MATERIALS AND METHODS

Experiments were carried out in Langstone Harbour, Hampshire, UK. The substrate of the harbour is mainly sand and mud, drying out at low tide to leave tidal channels about 6 m deep. Panels were suspended from 1 of 5 rafts belonging to the Ministry of Defence (Navy), Exposure Trials Station. The rafts were moored in the main tidal channel near the harbour mouth. Underwater observations showed that hard substrata in the vicinity of the rafts include gravel and boulders on the channel bed, a small steel wreck, a large concrete structure (Mulberry), and floating structures, such as

buoys and moored yachts. The rafts themselves provided additional floating hard substrata, as did the fronds of *Laminaria saccharina* and *Sargassum muticum* commonly growing on the rafts. The prevailing environmental parameters have been described elsewhere (Schmidt, in prep.).

Black perspex panels, 0.25×0.25 m square and 5 mm thick, were attached to steel frames and submerged at a depth of ca 1 m. The frames were aligned so that the panels were held vertical and parallel to the current. Daylight illumination came from above. Three experiments were carried out, all initiated at the same time of year (Experiment 1, 1 August 1980; Experiments 2 and 3, 1 August 1981), and during peak settlement times of the most abundant species (Schmidt, in prep.).

In Experiment 1, panels were either free of cages or individually screened with 12.5×12.5 mm galvanized steel mesh (0.8 mm wire diameter; Fig. 1). A cage size of $0.19 \times 0.19 \times 0.25$ m was chosen so that cages would not restrict growth of the larger solitary ascidian species (cf. Marshall et al., 1980). Cages were complete or cut open at either side parallel to the panel surfaces, leaving windows of 0.227×0.15 m. Cages were constructed to allow an 80 mm lip to protrude from the base between which the panel was secured (Fig. 1). This enabled the cage and panel, as a unit, to be bolted firmly to the frames. Three uncaged controls, and 6 of each caged type were submerged on 1 August 1980. Collecting dates were 2 October 1980, 14 January 1981, and 8 April 1981. Uncaged control panels were collected 1 per sampling date, whereas caged treat-

Fig. 1. Cage construction ('ends open', Experiments 2 and 3). For other types of cage refer to 'Materials and Methods'

Fig. 2. *Elminius modestus*, Experiment 1. Effect of caging on abundance. Given are mean percent cover and standard deviation (bar). Significance levels of differences between treatments included in text. Asterisks: significant change in respective time interval: * $0.05 > P > 0.01$; ** $0.01 > P > 0.001$; *** $P < 0.001$. (a) unscreened control panels; (b) caged panels, opened at sides; (c) caged panels, complete

ments were removed in numbers of 1, 2 and 3 at each consecutive date respectively.

In Experiment 2, 10 panels were used, 2 for each treatment (see below). In addition to the types of cages of Experiment 1, 2 more open cages were constructed. One type had windows of 0.24×0.137 m cut out from the top, allowing more light to reach these panels. The second additional cage type had 0.165×0.165 m windows cut away from both ends to allow a less restricted water flow in the immediate environment of the panel (Fig. 1). Panels were submerged 1 August 1981 and collected 30 October 1981, and 16 December 1981.

In Experiment 3, 4 panels were screened each with a different type of cage, as described above (Experiment 2). After 4 wk of submergence, 1 August 1981 until 28 August 1981, cages were cut off, while panels remained bolted to the frames. Panels were resubmerged and subsequently collected on 16 December 1981. Panels from Experiment 2 served as controls.

Following retrieval, panels were fixed in 5 % formaldehyde/seawater and stored in 70 % IMS until further analysis. Each side of a panel was counted as 1 observation; areas of 0.24×0.18 m were scored for numbers of individuals, and % cover using the point method

Fig. 3. *Botryllus schlosseri*. For explanation see Fig. 2

(Wratten and Fry, 1980) with 432 regularly spaced points (10 mm apart). Data were angular transformed and statistically analysed by ANOVA and Student's t-test on ICL 1904 S, and Nord 100 & 500 computers (Computer Center, University of Reading). For Experiment 1, a 2-way ANOVA program, GLIM (Royal Statistical Society, 1977), took into account the unbalanced format of the data (i.e. numbers of replicates differed between treatments and over time). Species diversity (Quartile Index) was calculated according to Kempton and Taylor (1976). The method is suitable for data in the form of % cover (non-discrete). The Quartile Indices were determined after fitting the data to Gamma distributions using the method of Maximum Likelihood (Ross, 1980).

RESULTS

The most abundant animals on the panels were the barnacle *Elminius modestus*, colonial and solitary ascidians, hydroids, and the tubicolous amphipod *Jassa falcata*. Bryozoans, sponges and actinians were also present but collectively did not cover more than about

Fig. 4. *Diplosoma listerianum*. For explanation see Fig. 2

6 % of the panel surface at any one time. ANOVA tables are deposited in Schmidt (1983b).

Experiment 1

Significance levels between treatments are given in the text, those of changes in abundance over time are included in Fig. 2 to 8.

Fig. 5. *Trididemnum tenerum*. For explanation see Fig. 2

Fig. 6. *Ciona intestinalis* and *Ascidiella aspersa*. Combined cover. In (a) the broken line (O) represents % cover of *Molgula complanata* which scored too low values on caged panels to be represented in (b) or (c). For further explanation see Fig. 2

Elminius modestus (Fig. 2 and 9)

Settlement of *Elminius modestus* was greatly reduced when substrata were screened by cages. The barnacle occupied an insignificant amount of space on

Fig. 7. Hydroids *Tubularia larynx* and *Plumularia setacea* (a); (b) and (c) predominantly *Gonothyrea loveni*. For further explanation see Fig. 2

both open and closed cages throughout the experiment. No significant difference between these 2 treatments was found at any time although initially slightly higher values were recorded on open cages. In contrast, percent cover on uncaged control panels was significantly higher at all 3 sampling dates ($P < 0.001$). Highest mean cover values were recorded after 2 mo of submergence, and at that time *E. modestus* was the

Fig. 8. Mud-tubes of amphipods. Chiefly *Jassa falcata* in (a) and *Corophium acherusicum* in (b) and (c). For further explanation see Fig. 2

most abundant species on control panels. By January the amount of space occupied had decreased sharply. The further decline at the final sampling date, however, was not significant.

Colonial ascidians (Fig. 3 to 5 and 9 to 11)

Four colonial species were identified. Two occurred infrequently, *Botrylloides leachii* and *Trididemnum tenerum*, occupying an insignificant amount of space. In contrast, *Botryllus schlosseri* and *Diplosoma listerianum* were initially very abundant, highest values being scored after 2 mo, but thereafter generally declining. On closed caged surfaces, however, *B. schlosseri* showed no further decline between January and April (Fig. 3) and consequently covered more space on these than on open caged or uncaged panels ($P < 0.01$). At all other times there was no significant difference between treatments. *D. listerianum* (Fig. 4) differed in that cover values were significantly lower

on closed caged panels at the January sampling date (open/complete cage: $P < 0.05$; uncaged/caged: $P < 0.01$); at the end of the experiment, *D. listerianum* occupied little space on all panels. It was noted that this ascidian often grew extensively on the outside of the cages. Although *T. tenerum* attained comparatively low cover values (Fig. 5), the slight but consistent increase over time on closed caged surfaces resulted in a significantly higher abundance compared to other panels at the final sampling date (open/closed caged: $P < 0.05$; uncaged/caged: $P < 0.01$). *T. tenerum* was the only colonial ascidian to show an increase in cover between the October and January sampling dates.

Solitary ascidians (Fig. 6, 10 and 11)

Five solitary ascidian species were found. *Molgula manhattensis* and *Styela clava* were infrequent and occurred sporadically, differences in time or treatment were not significant. *M. complanata* was more frequent, but only on uncaged control panels where it covered significantly more space after 5½ and 8 mo (Fig. 6; $P < 0.001$). Caging affected markedly the abundance of *Ciona intestinalis* and *Asciidiella aspersa* (Fig. 6). These ascidians scored low cover values on uncaged controls throughout the experiment but they occupied at least half of open and closed caged surfaces after 5½ mo (uncaged/caged: $P < 0.01$), and

Fig. 9. Experiment 1. Uncaged control panel, submerged 1 August 1980 until 2 October 1980. *Elminius modestus* settled heavily, also abundant are *Diplosoma listerianum* and *Botryllus schlosseri*. Note large colony of *Tubularia larynx* and dense growth of *Plumularia setacea*. Abbreviations (Fig. 9 to 11): Aa: *Asciidiella aspersa*; Bs: *Botryllus schlosseri*; Bu: *Bugula* spp. DL: *Diplosoma listerianum*; Em: *Elminius modestus*; Ps: *Plumularia setacea*; TL: *Tubularia larynx*

monopolized the latter after 8 mo (open caged/others: $P < 0.001$; open/closed caged: $P < 0.05$). The increase over time was mainly due to individual growth, the differences between treatments reflected the numbers of animals found. *C. intestinalis* reached sizes of 20 to 30 mm within 2 mo, and had grown to 60 to 80 mm at the end of the experiment; *A. aspersa* was generally 10 to 20 mm smaller.

Hydroids (Fig. 7)

On all panels hydroids attained highest cover values after 2 mo. Thereafter, percent cover was low on caged

treatments while at the January date values recorded on the uncaged control were still relatively high (caged/uncaged: $P < 0.01$). The species composition varied between treatments. Uncaged and open caged surfaces collected mainly *Plumularia setacea*, whereas the most abundant hydroid inside complete cages was *Gonothyrea loveni*. *Tubularia larynx* and *Obelia* spp. occurred infrequently.

Mud-tubes (Fig. 8)

Mud-tubes of amphipods were abundantly found on all panels. On closed caged substrata these were pre-

Fig. 10. Experiment 1. Open caged panel, submerged 1 August 1980 until 2 October 1980, showing large settlement of *Ascidella aspersa* and *Ciona intestinalis* not found on uncaged panels (Fig. 9). *Diplosoma listerianum* and *Botryllus schlosseri* are abundant; *Elminius modestus* and settlement of large hydroids is sparse compared with Fig. 9. Some of the less abundant species were more frequent on caged panels, e.g. *Bugula neritina* (Bu). For abbreviations see Fig. 9

dominantly of *Corophium acherusicum*, and on uncaged controls of *Jassa falcata*. *C. acherusicum* was also present on open caged and uncaged panels but the overall higher cover of mud-tubes on the latter was due to the greater abundance of *J. falcata*. There was no significant difference between the 2 caged treatments. Cover of *J. falcata* mud-tubes on the uncaged controls increased considerably between each sampling date; consequently, the differences between these and either type of caged panel were highly significant in January and April ($P < 0.001$). *J. falcata* also heavily fouled the mesh wire of the cages.

Other species

Other sessile invertebrates collectively covered little space (less than 6 %). Nevertheless, the higher abundance of *Bugula stolonifera*, *B. neritina*, *Cryptosula pallasiana* and *Scypha ciliata* on caged panels was noticeable. Consequently, at the end of the experiment, highest cover values for the sum of these were recorded in closed cages and these were significant ($P < 0.001$). One specimen of a lump-sucker, *Cyclopterus lumpus* (Cyclopteridae, Pisces; 63 mm long), was found entrapped in 1 of the closed cages at the January

Fig. 11. Experiment 1. Closed caged panel, submerged 1 August 1980 until 2 October 1980. The community is similar to the open caged treatment (Fig. 10), but *Asciidiella aspersa* and *Ciona intestinalis* occurred in higher numbers. For abbreviations see Fig. 9

sampling date. There was no apparent difference in the faunistic composition of the panel surface exposed to this fish and other caged substrata.

Diversity (Fig. 12)

Communities on caged treatments were more diverse than on uncaged controls for the first and second sampling dates. The values for both types of caged panels remained comparable until, at the final date, the dense cover of *Ciona intestinalis* and *Ascidiella aspersa* on caged substrata caused the diversity index to decrease to that of uncaged controls.

Fig. 12. Experiment 1. Quartile index of species diversity (see 'Material and Methods'). Bar: standard deviation. ● caged panels, opened at sides; ○ caged panels, complete; ▲ uncaged control panels

Experiment 2

Mean percent cover for species or groups of organisms are given in Tables 1 and 2. For *Ciona intestinalis*, *Ascidiella aspersa* and *Molgula complanata* numbers of individuals are also included. ANOVA show that in most cases there was no interaction between treatment and time (ANOVA Tables deposited in Schmidt, 1983b). Therefore, to show the effect of treatments, time was averaged over treatments (Table 1), and to show the effect of time on abundance

(or densities), treatments were averaged over time (Table 2). The few instances where interaction was significant are listed separately at the bottom of Tables 1 and 2. Levels of significance are included in the Tables.

Effect of treatment

Caging of panels had affected the abundance of most taxa or groups of organisms as compared to uncaged controls (Table 1). Furthermore, the type of cages used did not show a uniform effect on *Elminius modestus*, *Ciona intestinalis*, *Ascidiella aspersa* and the group 'others'.

As in Experiment 1, *Elminius modestus* attained highest cover on uncaged control surfaces where it was the most abundant of all species found, while values for caged panels were all significantly lower. However, with regard to the latter, cages opened at both ends differed significantly from the other caged treatments and had cover values intermediate between those and the uncaged controls.

Abundance of *Trididemnum tenerum*, which was overall greater than in Experiment 1 owing to heavier recruitment, was significantly increased by any type of caging. *Diplosoma listerianum* occupied more space on open caged panels at the first sampling date, but at the second (last) no such difference was found and all panels had low cover values. *Botryllus schlosseri* was, unlike either of the other colonial ascidians, least abundant on closed caged substrata.

For *Ciona intestinalis* and *Ascidiella aspersa* significant differences were found between all treatments, except between uncaged controls and panels opened at both ends. Highest cover values were scored on completely caged surfaces, lowest on panels with cages opened at the top. In contrast to Experiment 1, *C. intestinalis* and *A. aspersa* attained high densities also on uncaged controls.

Tubularia larynx had recruited heavily (Schmidt, in prep.) reaching high cover on uncaged controls, but being sparse on caged panels. It had also extensively fouled the wire mesh. Mud-tubes of amphipods scored lowest values on closed caged panels and attained highest cover on uncaged surfaces. There was no significant difference between any of the open caged treatments. The distribution of *Corophium acherusicum* and *Jassa falcata* was as described above (Experiment 1). Other sessile invertebrates ('others') covered little space (> 5 %), least on uncaged panels.

Effect of time

Table 2 shows that, within the 1½ mo between the sampling dates, cover of *Tubularia larynx* had

Table 1. Experiment 2. Effect of different types of caging (treatments) on species abundance. For species names see text. Values are mean % cover, or numbers of individuals (bottom entries), averaged over time. Where interaction between treatment and time was found, values for each time are given (T1, 27 October 1981; T2, 16 December 1981). Non-significance ($P > 0.05$) indicated by underlining the appropriate values. * $0.05 > P > 0.01$; ** $0.01 > P > 0.001$; *** $P < 0.001$; these levels refer to differences between values underlined and not underlined; other combinations were as follows: *Elminius*: C/E***; Solitary ascidians: A/B or D***, B/D***; Mud-tubes: A/E***; 'Others': B/E; *Ascidella* (numbers): C/D*

Species/group	caged complete (A)	caged open sides (B)	Treatment caged open ends (C)	caged open top (D)	uncaged control (E)
% cover					
<i>Elminius</i>	14.13	15.60	33.47**	20.33	66.28***
<i>Botryllus</i>	2.68**	6.88	10.23	11.03	6.43
<i>Trididemnum</i>	16.33	17.28	18.85	18.85	1.83***
<i>Diplosoma</i> T1	6.45***	17.20	16.55	13.85	4.80***
T2	2.95	3.20	5.35	1.80	5.90
Solitary ascidians	38.88***	24.33*	15.48	9.25**	18.25
<i>Molgula/Styela</i>	0.23	0.20	0.40	0.33	1.83***
<i>Tubularia</i>	1.48	1.43	4.78	1.93	17.65***
Mud-tubes (<i>Jassa/Corophium</i>)	4.73***	10.40	11.23	10.40	21.05***
'Others'	2.83	4.22***	1.93	2.45	1.08***
Numbers of individuals					
<i>Ciona</i>	44.5	36	22.25**	15.75**	37.25
<i>Ascidella</i> T1	79.5***	18.5	33	17	34
T2	64	70.5	37.5***	11***	54
<i>Molgula</i>	1	2.5	5	2.25	34.5***

Table 2. Effect of time (Experiment 2, first 2 columns) and of cage removal (Experiment 3, right column) on species abundance. *Tubularia*: 4.7/0.1***. For further explanation see Table 1

Species/group	Experiment 2		Experiment 3
	7/10/81	Date 16/12/81	16/12/81 (caged removed after 4 weeks)
% cover			
<i>Elminius</i>	23.65	18.11	6.93**
<i>Botryllus</i>	11.00***	4.4	6.6
<i>Trididemnum</i>	16.44	19.21	20.29
<i>Diplosoma</i>	13.46***	3.33	3.78
<i>Ciona/Ascidella</i>	11.10***	34.44	31.33
<i>Molgula/Styela</i>	0.26	0.38	0.55
<i>Tubularia</i>	4.7**	0.1**	1.64**
Mud-tubes (<i>Jassa/Corophium</i>)	9.0	9.38	13.20**
'Others'	1.89	3.83***	2.29
Numbers of individuals			
<i>Ciona</i>	21.63**	37.63	35.13
<i>Molgula</i>	3.5	1.88**	4.13
<i>Ascidella</i> complete	79.5*	64	59
side open	18.5***	70.5	76
ends open	33	37.5	72.5***
top open	17	20	11**

decreased while the solitary ascidians *Ciona intestinalis* and *Asciidiella aspersa*, and the group 'others' had increased in abundance. The 3 colonial ascidians differed with regard to their changes in coverage over time. Values for *Botryllus schlosseri* decreased, while those for *Trididemnum tenerum* had not changed significantly. *Diplosoma listerianum* showed interaction between time and treatment, cover values declining on open caged panels but remaining similar (and low) on closed caged and uncaged control surfaces. Cover of *Elminius modestus*, mud-tubes (principally *Jassa falcata*), and the solitary ascidians *Molgula complanata*, *M. manhattensis* and *Styela clava* showed little change, the latter 3 ascidians together only attaining cover values of < 2 %.

Experiment 3: cage removal

Coverage of neither colonial nor solitary ascidians was affected by the removal of cages after 4 wk of submergence (Table 2); any difference in abundance caused by the type of cages used (Experiment 2) was also observed on panels where cages had been taken off. Other species or groups of taxa were affected by the experimental procedure: *Tubularia larynx* and *Jassa falcata* (mud-tubes) increased in abundance, whereas *Elminius modestus* and 'others' decreased (Table 2).

DISCUSSION

Predation

The ascidians *Ciona intestinalis*, *Asciidiella aspersa*, *Molgula manhattensis*, *Botryllus schlosseri* and *Diplosoma listerianum* have been reported as prey items of fish and invertebrates, including flatworms, molluscs, crabs and starfish (see Millar, 1971 for review; Gulliksen, 1972, 1980; Gulliksen and Skjæveland, 1973; Day, 1977; Russ, 1980; Smedes and Hurd, 1981). In the present study an unidentified species of flatworm was frequently observed associated with *B. schlosseri*, the crabs *Cancer pagurus* and *Carcinus maenas* (< 5 cm carapace width) were frequently observed on the holding frames and panels, caged as well as uncaged. Fish were occasionally seen swimming between panels and a small lump-sucker (*Cyclopterus lumpus*) was once found entrapped in a closed cage. Over 50 species of fish have been recorded in Langstone Harbour (Culley and Palmer, 1978). Thus potential predators were present and had access to uncaged and open caged panels; small predators also had access to closed caged panels. However, the similarity between the communities on all types of caged

panels, irrespective of whether they were open or closed (Fig. 10 and 11; Tables 1 and 2) and the differences between these and the uncaged controls, suggests that the most important effects of caging were *not* due to the exclusion of predators.

In several other studies, abundance of solitary ascidians increased when surfaces were screened by cages (Table 3), and this was usually attributed to the exclusion of predators. The experiments, however, always involved a combination of either caged and open caged, or caged and uncaged panels. The conclusions of Smedes and Hurd (1981) were supported by laboratory studies and predator inclusion experiments, and those of Russ (1980) by direct observations and fish stomach content analysis, but the remaining studies lacked adequate controls to distinguish between predation and the effects caused by cages *per se* (cf. Arntz, 1981; Otsuka and Dauer, 1982).

Cage effects

The main effects of caging on the physical environment are probably on light intensity and water current velocity. Even though a narrow wire diameter was chosen for the present cages (0.8 mm), light and current inside would have been reduced, particularly when the outsides of cages became fouled by mud-tubes of *Jassa falcata*, red algae, colonies of *Diplosoma listerianum* and – in the second year (Experiment 2) – by dense growth of *Tubularia larynx* (see below). In Experiment 1, fouling of cages was not prominent during the initial months of exposure (August–October), i.e. during the peak settlement time of ascidians and *Elminius modestus* (Schmidt, in prep.). However, the wire mesh was not cleaned, and fouling increased, subsequently occluding the cage mesh by 40 to 50 % towards the end of the study. This probably reduced the food supply to animals inside cages and may have caused the decline of the *Ciona intestinalis*/*Asciidiella aspersa* assemblage over time on closed caged surfaces. The decrease was noticeable earlier in *A. aspersa* than *C. intestinalis*, the former species being generally smaller, less extensible and more slowly growing.

Otsuka and Dauer (1982) suggested that cages primarily provided a structural support preventing the sloughing-off of *Molgula manhattensis* from panels in their study. Smedes and Hurd (1981) reported on dislodging of *M. manhattensis* through the activity of fish. Experiment 3 showed that large solitary ascidians retained substrate stability in the absence of cages. Therefore, at least for the duration of the experiment (5½ mo), this suggested cage effect had little influence on the species composition. Results from horizontally

aligned, uncaged panels which had collected a dense assemblage of *Ciona intestinalis* and *Ascidella aspersa* support this conclusion (Schmidt, 1983a). In the present study, cages primarily affected the species composition by influencing the settlement of their larvae.

Ascidians

In Experiment 1, settlement of *Ciona intestinalis* and *Ascidella aspersa* was greatly enhanced on caged surfaces while *Diplosoma listerianum* and *Botryllus schlosseri* became equally abundant on caged and uncaged panels. The difference between solitary and colonial ascidians in response to treatments may be attributed to a difference in response to interacting physical factors, particularly light regime and current velocity. Experiment 2 showed that *C. intestinalis* and *A. aspersa* occupied significantly less space when panels were screened with cages opened at the top (thereby allowing higher light levels to reach the panel surfaces). *D. listerianum* and *B. schlosseri* did not show this, suggesting that at the time of attachment *C. intestinalis* and *A. aspersa* were more strongly photonegative than the two colonial species. Results from settlement experiments (Schmidt, in prep.) support this idea.

In Experiment 2, *Diplosoma listerianum* and *Botryllus schlosseri* attained comparatively low cover values on closed caged panels, probably due to heavy fouling of the mesh by *Tubularia larynx* in that year, preventing these 2 ascidians from densely colonizing closed caged surfaces. This was not the case, however, with *Ciona intestinalis* and *Ascidella aspersa*. A difference in postsettlement mortality is a less likely explanation of these results as data from Experiment 1 suggest that solitary ascidians were more affected by the fouling of these cages than were colonial ascidians (Fig. 4, 5 and 6). However, the results suggest that larvae of *D. listerianum* and *B. schlosseri* invade already colonized surfaces less successfully (or avoid such substrata) than *C. intestinalis* and *A. aspersa*; in this case, it is suggested that the dense *T. larynx* growth on the wire mesh signalled occupied substratum. A parallel series of panel experiments showed that *T. larynx* may greatly enhance settlement of *C. intestinalis* and *A. aspersa* (Schmidt, 1983a). The initial abundance of *T. larynx* in Experiment 2 therefore also explains the high cover of *C. intestinalis* and *A. aspersa* on uncaged panels. Different settlement intensities in the two years of study (Schmidt, in prep.) account for the observed year-to-year differences in abundance of *Trididemnum tenerum* and *T. larynx*, both species settling heavily in the second but not in the first year.

Molgula complanata was the only ascidian to occur more frequently on uncaged panels. Since the larva of

this species lacks light receptive organs (Berrill, 1950), settlement preferences for environments with unrestricted water flow would best explain the observed distribution. *M. complanata* did not avoid attaching to substrata largely occupied by other ascidian species (cf. Young, 1980; Grosberg, 1981).

Crustaceans

Settlement of *Elminius modestus* was greatly inhibited by screening. Marshall et al. (1980) reported similar findings for *Balanus* spp. Cages opened at both ends (allowing faster current flow past the panel surfaces) scored cover values intermediate between other types of cages and uncaged controls (Experiment 2) indicating that reduction of water velocity is the main factor accounting for the observed differences in abundance between uncaged and caged panels. *E. modestus* and other species of barnacles are stimulated to settle in rapidly flowing water (Crisp, 1976). The occurrence of *Jassa falcata* tubes support the conclusion that the amphipod favours fast current velocities (Nair and Anger, 1979).

Hydroids

Enhanced hydroid settlement on caged substrata, as found for *Gonothyrea loveni*, has not been reported previously. The hydroids *Tubularia larynx* and *Plumularia setacea* were largely confined to the outside mesh of the cages and to uncaged controls – environments with more rapid water flow favourable for growth of passive suspension feeders. Similar findings have been reported for *T. crocea* (Sutherland, 1974), *T. larynx* (Marshall et al., 1980) and *Obelia* sp. (Otsuka and Dauer, 1982). As was expected, *T. larynx* covered more space on panels having cages opened at both ends than with other cages, although due to variability in the data these differences were not significant.

Competition between solitary and colonial ascidians

Abundant growth of ascidians on caged substrata made it possible to collect data on overgrowth interactions between species of this group. Data for the colonial species will be presented elsewhere (Schmidt, in prep.). Jackson (1977) noted that solitary sessile species may avoid being overgrown by colonial forms through 'escape in size'. *Ciona intestinalis* and *Ascidella aspersa* grew rapidly in size enabling them to monopolize caged substrata after several months of

Table 3. Summary of panel studies in which cages were employed to assess the predation pressure on panel communities. Despite some large differences in experimental design – including caging materials, mesh size, and duration of experiments – most studies showed comparable results, i.e. increased abundance of ascidians on caged substrata

Author (Year)	Study site	Type of experiments	Material; Size of cages	Mesh size (mm)	Duration of experiments	Effect of caging	
						Increased abundance of (on caged sub- strata unless otherwise stated)	Interpretation
Sutherland (1974)	Beaufort, North Carolina, USA	20 panels enclosed together; uncaged control	Nylon fish netting	1/4 inch	9 mo (monthly sampling)	<i>Styela</i>	Fish predation
Forster (1975)	Santa Cruz Island, California, USA	Sets of 3 concrete blocks caged; uncaged control	Galvanized wire cleaned every 2 mo, replaced every 6–8 mo	127	584 d	Primarily bryozoans	Fish predation/ seastar grazing
Day (1977)	Heron Island, Queensland, Australia	Caged; uncaged control	Not specified	20	3 mo	Colonial ascidians	Fish predation
Mook (1977)	Indian River Lagoon, Fort Pierce, Florida, USA	5 panels enclosed together; uncaged control	Nylon hardware cloth 200 × 200 cm cleaned daily	12	6 wk	<i>Balanus</i> (2 species) <i>Spirorbis</i>	Fish predation
Osman (1977)	Sheep Pen Harbour, Nonamesset Island, USA	Caged glass slides; uncaged controls	Galvanized wire	0.75 cm ²	1 yr	No effect	Predation absent
Russ (1980)	Portsea Pier, Victoria, Australia	Closed cages (cc); open cages (oc); open complex cages (occ)	Galvanized steel (.8 mm); 20 × 20 × 10 cm (high)	12.5 × 12.5	4 mo and 7 mo	cc: <i>Distaplia</i> <i>Botrylloides</i> oc: bryozoa, occ: <i>Distaplia</i> , <i>Botrylloides</i> sponges	Fish predation
							Fish predation Shading, water flow
Marshall et al. (1980)	Gunnamatta Bay, NSW, Australia	Screened (sc); unscreened controls (uc); screen removed (scr)	Nylon cloth 1 cm above panel, covering 400 cm ²	1	1 wk, 4 wk, 7½ mo	sc: <i>Diplosoma</i> <i>Pyura</i> , <i>Styela</i> , uc: <i>Balanus</i> (2 species), scr: decrease of <i>Styela</i>	Predation Physical restriction by cages
Mook (1981)	Indian River Lagoon, Fort Pierce, Florida, USA	5 panels enclosed together	Fish net; changed every month	30	23 mo (monthly sampling)	<i>Styela</i>	Predation Predation
Smedes & Hurd (1981)	Broad Rill River Estuary at Lewes, Delaware, USA	Cages containing 48 panels; cages with 3 toad fish included for 4 mo	Mesh welded wire fencing 90 × 90 × 80 cm; mesh cleaned	25 × 50	16 mo and 7 mo (monthly sampling)	<i>Mytilus</i> <i>Molgula</i>	Predation; dislodging by toad fish
Vail & Wass (1981)	Port Hacking, Sydney, Australia	Screened; unscreened; screens removed	Nylon mesh	1	34 wk weekly (non-destructive scoring)	Bryozoa	Probably predation
Wass & Vail (1978)	Port Hacking, Sydney, Australia	Screened only	Nylon mesh	1	12 wk	Bryozoa	Predation
Otsuka & Dauer (1982)	Lynnhaven Bay, Virginia, USA	Caged; uncaged (uc) control	Hardware cloth 25 × 25 × 5 cm	5.6	23 mo (weekly or monthly or bimonthly non- destructive observation)	<i>Molgula</i> , <i>Bot- ryllus</i> uc: Hydroids, Hydroids on cages	Predation Probably also cage effect (cage effect: current differentials; lar- val entrapment)
		cages removed after 11 mo			10 mo	Occupants (<i>Bot- ryllus/Sabella</i>) gradually fell off	Cages act as structural support

submergence, despite colonial ascidians initially covering much of the panel surfaces. The latter did not overgrow recently settled *C. intestinalis* and *A. aspersa* which, through their upright growth, probably gained a feeding advantage over the sheet-like colonial species.

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