

Spatial competition between colonial ascidians: the importance of stand-off

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ABSTRACT: The outcome of 925 encounters between colonies of 4 species of compound ascidians growing on perspex panels were recorded. Of encounters involving *Diplosoma listerianum*, 61 % resulted in stand-off, and almost all the rest in overgrowth by *D. listerianum*. Of encounters involving any two of *Trididemnum tenerum*, *Botryllus schlosseri* and *Botrylloides leachii*, 82 % resulted in stand-off, and the rest in overgrowth by either one of the adjacent pair. These 3 species were competitively equivalent, but subordinate to *D. listerianum*. The very high proportion of stand-offs recorded between these ascidians contrasts sharply with the low proportions previously reported for other taxa.

INTRODUCTION

Spatial competition between sessile organisms on hard substrata has attracted considerable interest over the last decade. Attention has been directed towards the mechanisms whereby some species gain space at the expense of others, and on the outcome for the community of the competitive interactions of its members. Overgrowth, resulting in the death of the underlying organism, is an important form of spatial competition, and success may be achieved by both physical and chemical means (Lang 1973, Stebbing 1973, Jackson 1979, Buss 1980a, b, Rubin 1982). Encrusting communities commonly display a complex network of competitive overgrowth abilities (intransitive relationship) involving reversals and incomplete dominance (Buss & Jackson 1979, Rubin 1982), and this may result in the species richness of the community being maintained through time (Karlson & Jackson 1981). Growth inhibition (stand-off, tie) is another, less frequently recorded process which, despite being apparently defensive, may lead to competitive success (Karlson 1978, 1980, Russ 1982, Sebens 1985).

Jackson (1977) suggested that colonial animals are better suited than solitary animals to succeed in spatial competition because of the indeterminate nature of

their growth and form. Although this view has been challenged (Greene et al. 1983, Rubin 1985), it is nevertheless the case that very many sessile communities are dominated by colonial animals (Jackson 1977, Rubin 1985, Warner 1985). Colonial taxa commonly found in sessile communities include Porifera, Coelenterata (hydroids and corals), Bryozoa and Ascidiacea. Spatial competition between bryozoans and between colonial coelenterates has been extensively investigated (e.g. Jackson 1979, Sheppard 1979, Rubin 1982), but fewer examples of competition between sponges and between species of colonial ascidian have been studied (Kay & Keough 1981, Russ 1982). During the course of a series of experiments using caged panels (Schmidt & Warner 1984 – see 'Materials and Methods'), the opportunity was presented to score the outcome of spatial encounters between 4 species of colonial ascidians at an early stage of community succession.

MATERIALS AND METHODS

Experiments were carried out in Langstone Harbour, Hampshire, England. Four black perspex panels, 0.25 × 0.25 m square and 5 mm thick, were attached to steel frames and submerged from a raft at a depth of 1 m from 1 August to 20 October 1980. Panels were orientated vertically, and parallel to tidal currents, thus each side experienced similar conditions of light

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and water flow. In addition panels were caged with 12.5×12.5 mm galvanised steel mesh (0.8 mm wire diameter); the cage size was $0.19 \times 0.19 \times 0.25$ m (for further details see Schmidt & Warner 1984). Caged panels were used because caging discouraged settlement of otherwise abundantly occurring tubicolous amphipods *Jassa falcata*, and barnacles *Elminius modestus*, but encouraged settlement and rapid growth of colonial ascidians, resulting in high cover values (60 to 80 %, cf. Schmidt 1982). These community changes increased the incidence of encounters between ascidians and facilitated analysis; the changes are due to the physical presence of the cages and not to the exclusion of predators (Schmidt & Warner 1984). Following retrieval, panels were fixed in 5 % formal/seawater and subsequently stored in 70 % industrial methylated spirit until analysis.

Scoring was aided by low power magnification using a Wild M5 stereo-microscope. Colonies consisting of less than 10 zooids were few and were not included in the analysis. All colonies were apparently healthy. The scoring procedure described by Jackson (1979) was used in modified form: no more than 1 encounter was regarded as possible between 2 colonies, thus separate points of contact along a discontinuous contact margin were regarded as parts of the same encounter. Overgrowth was scored if a colony had completely covered at least 1 zooid of the adjacent colony at any point along the contact margin. Stand-off was scored in the case of contact without overgrowth. Each side of a panel was scored separately, giving 8 replicate sets of observations. Statistical analysis was by chi-squared tests.







RESULTS

There was no significant difference between panels regarding the outcome of interactions, data were therefore pooled to test for differences between species pairings.

The results of 925 interspecific encounters are summarised in Table 1. Competitive interactions between the 4 colonial ascidians showed that stand-off between colonies belonging to different species was always more common than overgrowth, and significantly so in encounters between *Trididemnum tenerum* and either *Botryllus schlosseri* or *Botrylloides leachii*. The differences between overgrowth and stand-off in interactions involving *Diplosoma listerianum*, although consistent, were not significant: this species overgrew its opponent in roughly half of its encounters. In stand-off, growth had apparently continued laterally over unoccupied bare panel area and gave rise to a mosaic pattern of irregularly shaped, interlocking colonies. Contact margins were straight, sinuous, or interdigitated like the pieces of a jigsaw puzzle; there was no evidence of colonies gaining space at the expense of others except by overgrowth.

The data show that *Diplosoma listerianum* responded in a similar way to encounters with any of the other 3 species (Table 1, indicated by brackets marked NS), and that there was consistency in the outcome of encounters involving any 2 of the latter. Therefore competitive abilities measured by overgrowth frequencies may be expressed in a plexus diagram (Fig. 1) which shows that the 4 species were not evenly balanced in terms of competitive ability. *D.*

Table 1. Outcome of encounters between *Diplosoma listerianum*, *Trididemnum tenerum*, *Botryllus schlosseri* and *Botrylloides leachii*. Lack of a significant difference ($p < 0.05$) is indicated within species pairings by underlining values, and between species pairings by NS (data for *B. schlosseri*/*B. leachii* encounters were too few for statistical analysis). Arrows show the direction of overgrowth

Species pairing		Overgrowth	Stand-off	Total encounters	
NS	<i>Diplosoma-Botryllus</i>		<u>128</u> 1	<u>181</u>	310
	<i>Diplosoma-Trididemnum</i>		<u>123</u> 1	<u>199</u>	323
	<i>Diplosoma-Botrylloides</i>		<u>12</u> 0	<u>38</u>	50
NS	<i>Trididemnum-Botryllus</i>		<u>17</u> <u>21</u>	177	215
	<i>Trididemnum-Botrylloides</i>		<u>2</u> <u>2</u>	20	24
	<i>Botryllus-Botrylloides</i>		0 0	3	3

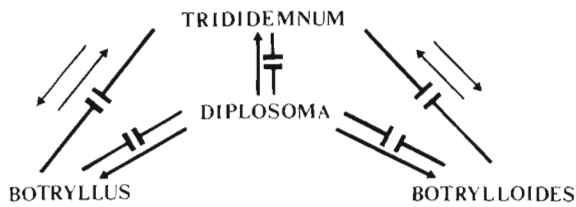


Fig. 1. Overgrowth relations between *Diplosoma listerianum*, *Trididemnum tenerum*, *Botryllus schlosseri* and *Botrylloides leachii*. Although stand-off was the most frequent outcome, the dominant position of *D. listerianum* is apparent, the other 3 species being competitively equivalent. *B. schlosseri*/*B. leachii* encounters were too few to include. Arrows show direction of overgrowth, T-bars indicate stand-off; thickness of both arrows and T-bars indicates relative frequency (cf. Table 1.)

listerianum was the species most frequently overgrowing others, itself being overgrown in only 2 out of 673 encounters. *Botryllus schlosseri* and *Trididemnum tenerum* overgrew each other at similar frequencies indicating competitive equivalence between them. Overgrowth between conspecifics did not occur.

DISCUSSION

The proportion of stand-offs recorded in this intraphyletic study (67 % of all encounters) is higher than that reported by Russ (1982) for encounters between 4 species of colonial ascidian (33 %). However, both Russ (1982) and Sebens (1985) commented on the high frequency of stand-offs in the encrusting communities they studied. Proportions of stand-offs in these 2 communities, including all inter- and intraphyletic encounters, were 26 and 41 % respectively (Russ 1982, Sebens 1985).

Karlson (1980) suggested that stand-off, combined with opportunistic growth over adjacent bare substrata, might be a successful means of exploiting disturbed habitats: bare substratum is generated by physical disturbance or grazing, providing growth opportunities for species relying on a stand-off strategy. In contrast, the only way to grow in an undisturbed habitat is to overgrow, since there is no bare substratum. It can therefore be argued that the 4 species of ascidians considered here are adapted to life in disturbed habitats. In support of this suggestion, both *Botryllus schlosseri* and *Diplosoma listerianum* have been recorded as primary colonists on bare surfaces (e.g. Brunetti 1974, Anger 1978, Grosberg 1981, Schmidt 1982), indicating that the settlement preferences of their larvae may favour the colonisation of disturbed habitats.

An attempt was made to apply Rubin's (1982) index of intransitivity to our ascidian data. The index

depends upon a comparison of the probabilities of the various species in the community winning spatial encounters with each other, and ranges from 1, perfectly intransitive, to more than 4 (community of 4 species), perfectly transitive. The index was developed from studies on encounters between encrusting bryozoans in which stand-off is infrequent (Jackson 1979), and there is no provision for stand-off in the formula. If stand-off is ignored, the resulting index is about 40, perfectly transitive and much higher than quoted by Rubin (1982). This is due to the very small number of wins by any species over the dominant *D. listerianum*. However, if stand-off is treated as a win for both sides, the resulting index is 1.03, almost perfectly intransitive. The contrast between these 2 results illustrates the difference (pointed out by Russ 1982) between communities in which stand-off is frequent, and those better known cases in which competitive networks based on overgrowth (*sensu* Buss & Jackson 1979) are observed.

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