

Patches of the ascidian *Pyura stolonifera* (Heller, 1878): structure of habitat and associated intertidal assemblages

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Abstract

Beds of the ascidian *Pyura stolonifera* on rocky shores around Sydney, Australia, provide an important habitat for many organisms, such as algae, chitons, limpets and snails. Fishermen collect *Pyura* for bait, which can change the structure of those beds. This may, in turn, cause changes in their associated biota. To predict the effects of such disturbances, it is necessary to understand the relationship between the structure of the habitat provided by beds of *Pyura* and their associated assemblages. Beds of *Pyura* can provide two types of habitat: Clumped, with > 50% cover of closely packed individuals or Sparse, with < 50% cover, where individuals are mostly isolated from contact with others. The spaces amongst the *Pyura* can be bare rock or rock covered by numerous species of algae and sessile animals. Nineteen algal species and 45 species of animals were identified in the field in Clumped and Sparse habitats. Assemblages differed significantly between patches of Clumped and Sparse habitat and much of the difference was attributable to relatively few species. In addition, a number of species of algae and animals live on the surface of the *Pyura* themselves. Eighty-four taxa were found at the scale of individual *Pyura*, many of which were relatively small and cryptic. Organisms on *Pyura* differed between individual ascidians that were isolated from other *Pyura* (i.e. a more common situation in Sparse habitat) and those that were surrounded by and in contact with other *Pyura* (i.e. more common in Clumped habitat). These differences were mostly attributed to a few families of small molluscs. It appears that changes in the structure of beds of *Pyura* have the potential to make significant alterations to intertidal assemblages at the scale of individual *Pyura* and at the scale of the habitats formed by beds of *Pyura*. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Patches; *Pyura stolonifera*; Habitat; Molluscs

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1. Introduction

Patch dynamics has long been a focus of ecological studies in different types of habitat and geographical areas (Dayton, 1971; Paine and Levin, 1981; Connell and Keough, 1985; Veblen, 1985; Ramage and Schiel, 1999), but no consistent definition of a “patch” can be found in the literature. According to White and Pickett (1985), any definition of a patch should always make reference to a defined spatial scale and structure and should relate to the system being studied. In forestry, for instance, patches are usually defined as areas dominated by different species of trees or shrubs (Veblen, 1985; Wu and Levin, 1994). On the other hand, in intertidal and subtidal areas, patches are often described as areas of open space that were created by some natural or man-made event (e.g. Connell and Keough, 1985; Sousa, 1985). This makes it impossible to have a general definition of patch that can be applied to all habitats.

Nevertheless, patches have been divided into two general groups: Type I and Type II patches. Type I patches are areas of cleared space in the middle of a matrix of a habitat, i.e. they are surrounded totally or partially by the original habitat. For example, when clumps of mussels are removed from beds of mussels by a disturbance, the patches created are of Type I. Type II patches, on the other hand, are isolated from surrounding assemblages and are the outcome of creation of new substratum. For example, Type II patches are created by organisms such as barnacles, oysters or coralline algae, that can provide additional surfaces for settlement of other organisms (Connell and Keough, 1985; Sousa, 1985).

Most landscapes are composed of Type I and/or Type II patches that differ in age, size, structure, etc. (Veblen, 1985; Mauchamp et al., 1994). As a result, landscapes are often seen as mosaics of different phases (i.e. patches). For example, Montaña (1992) described the alternating densely vegetated patches and bare areas as a two-phase mosaic, characteristic of scrublands in the Southern Chihuahuan Desert.

In rocky intertidal systems, primary substratum is often in short supply (Dayton, 1971; Connell, 1972; Gaines and Roughgarden, 1985; Sousa, 1985) and many organisms live among mussels and other organisms, which can provide additional substratum. Such biologically generated habitat is important in enhancing biodiversity on rocky shores (Lohse, 1993; Seed, 1996; Thompson et al., 1996).

The process of creation or maintenance of habitat, not involving direct trophic interactions among species, was defined by Jones et al. (1994) as ecosystem engineering. Ecosystem engineers are organisms that directly or indirectly control the availability of resources (other than themselves) to other species, by causing changes in biotic or abiotic materials (Jones et al., 1994). Habitats created by living organisms on intertidal shores are structurally more complex than the surrounding rock surface. In addition, the amount of available substratum can be greatly increased by their presence (Lohse, 1993). The structure of habitat influences the composition of species associated with it and different habitats can therefore have different associated assemblages (Ojeda and Dearborn, 1989; Brown, 1991; Lintas and Seed, 1994; Seed, 1996; Thompson et al., 1996).

The structure of habitat can be defined in terms of heterogeneity (the relative abundance per unit area or per unit volume of different structural components; McCoy and Bell, 1991) and complexity (the absolute abundance per unit area or per unit volume of individual structural components; McCoy and Bell, 1991). Each of these elements can

strongly influence the small-scale distribution of species (Bourget et al., 1994; Lemire and Bourget, 1996) and play an important role in structuring marine assemblages (Kohn and Leviten, 1976; Bergeron and Bourget, 1986; Chapman and Underwood, 1994; Lemire and Bourget, 1996). For example, for intertidal organisms, increased structural complexity can alleviate environmental stresses during low tide (Thompson et al., 1996). Invertebrates are protected from dislodgment by strong wave-action, insolation, etc., in mussel beds (Seed, 1996), and clumps of *Fucus* provide shelter for a variety of macro-invertebrates (Thompson et al., 1996). In the early stages of development of a marine epibenthic community in Canada, the small-scale distribution of species was strongly influenced by the heterogeneity (panels with a smooth surface or with crevices of different depths) of the substratum (Bourget et al., 1994).

The spatial and temporal patchiness of the habitat may influence the behaviour of intertidal snails (Underwood and Chapman, 1989), competition (Dayton, 1971), the number of species in assemblages (e.g. Kohn and Leviten, 1976) or structure of populations (e.g. the snail *Littorina unifasciata*, Underwood and Chapman, 1992). The ways in which organisms respond to patchiness can be complex and varied and, among other things, depend on factors, such as the time of creation of the patch (Sousa, 1985), its area (Keough, 1984; Sousa, 1984; Butler, 1991), its shape (Hamazaki, 1996) and the types of organisms present in the patch and surroundings (Keough, 1984; Sousa, 1984; Eggleston et al., 1999). The almost endless number of possible combinations of these elements at a certain point in time and space results in the great patchiness and variability that characterize intertidal rocky shores around the world. It is therefore of utmost importance to be able to describe natural variability as a preliminary to trying to understand what factor(s) cause it.

Pyura stolonifera (Heller, 1878) (hereafter referred to as *Pyura*) is a large solitary ascidian that occurs in dense beds on rocky intertidal reefs, from low intertidal habitats to a depth of 10 to 12 m (Edgar, 1997). They are often more abundant in areas of strong wave-action (Paine and Suchanek, 1983; Fielding et al., 1994). In Australia, they can be found from Western Australia to Queensland and in Tasmania (Edgar, 1997). They are also found along the coast of southern Africa (Fielding et al., 1994) and in Chile (Paine and Suchanek, 1983; Edgar, 1997).

Like beds of mussels or kelps, beds of *Pyura* can greatly increase the range and amount of habitat available for other organisms in low-shore areas where they dominate (Fielding et al., 1994). The crevices and interstices among individuals in beds of *Pyura* provide a sheltered environment for a wide variety of organisms. These range from macro-invertebrates, such as chitons (in Australia, *Onithochiton quercinus* and *Plaxiphora albida* tend to be more abundant on *Pyura* than on the surrounding rock), whelks and limpets (Van Driel and Steyl, 1976; Fielding et al., 1994), to micro-invertebrates such as microgastropods, limpets and several species of algae (Van Driel and Steyl, 1976; Otway, 1989; Fielding et al., 1994). Living on and amongst *Pyura* may allow animals and plants to get the benefits of a high energy environment, such as oxygenated water or a continuous flow of food, without being subjected to such potentially destructive variables as strong wave-action or currents (Fielding et al., 1994).

Across their distribution, *Pyura* are used as food and bait for fishing (Otway, 1989; Fairweather, 1991; Chapman and Underwood, 1994). Otway (1989) described beds of *Pyura* (areas of the shore where *Pyura* are dominant) as persistent and conspicuous

elements of low-shore assemblages in NSW, which provided much of the 3D complexity at that level. Sixty-five percent of the loss of *Pyura* observed by Otway (1989) was due to the animals being killed by fishermen. Preliminary observations by Fairweather (1991) around Sydney suggested that collection by fishermen could potentially eliminate or, at least, greatly reduce populations of *Pyura*. The loss of individuals from beds of *Pyura* may lead to changes in the structure provided by those beds. Because the removal of *Pyura* varies in time and space, patches with different types of structure may be present in different areas at any time. At Cape Banks, NSW, Australia, the removal of *Pyura* by fishermen or storms resulted in marked changes to the low-shore assemblage, possibly due to the loss of the additional surface area provided by these animals (Otway, 1989) or to the effects of the storm itself. Patches of bare space and/or patches of basal encrusting coralline algae developed in spaces where *Pyura* were removed (Otway, 1989).

Unquantified observations suggested that beds of *Pyura* around Sydney were comprised of two different structural habitats:

Clumped: areas with large cover of *Pyura* (>50%) and with most *Pyura* in contact or very close together to form large continuous patches of *Pyura* (Fig. 1a).

Sparse: areas with a small cover of *Pyura* (<50%) and with most *Pyura* not in contact with others and therefore forming small patches of *Pyura* (Fig. 1b).

To test the model that these observations reflected natural patterns of structure of the habitats, it was predicted that sampling random patches of *Pyura* on intertidal shores around Sydney (Fig. 2) would show that all patches fall into one or the other of the above categories (i.e. it was predicted that no areas with many isolated *Pyura* covering more than 50% and no areas with very few scattered patches of dense *Pyura* would be found).

Organisms associated with *Pyura* can vary in size from a few millimetres to several centimetres. Individual *Pyura* can form clumps and be surrounded by other *Pyura* or be found standing by themselves separated from other individuals. Animals and plants living on the *Pyura* themselves may vary according to the proximity of surrounding *Pyura*. Therefore, the prediction that different assemblages were associated with different types of

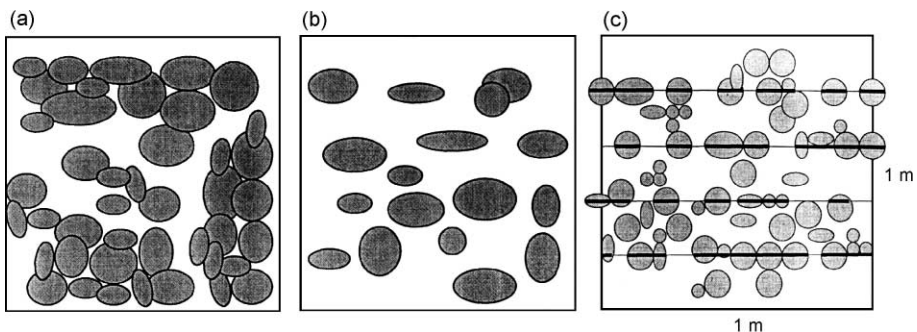


Fig. 1. (a) Clumped habitat; (b) Sparse habitat (circles represent individual *Pyura* and are placed in a way that represents how *Pyura* individuals are organised in the field); (c) example of how the structure of habitats was measured (— substratum not covered by *Pyura*; — substratum covered by *Pyura*).

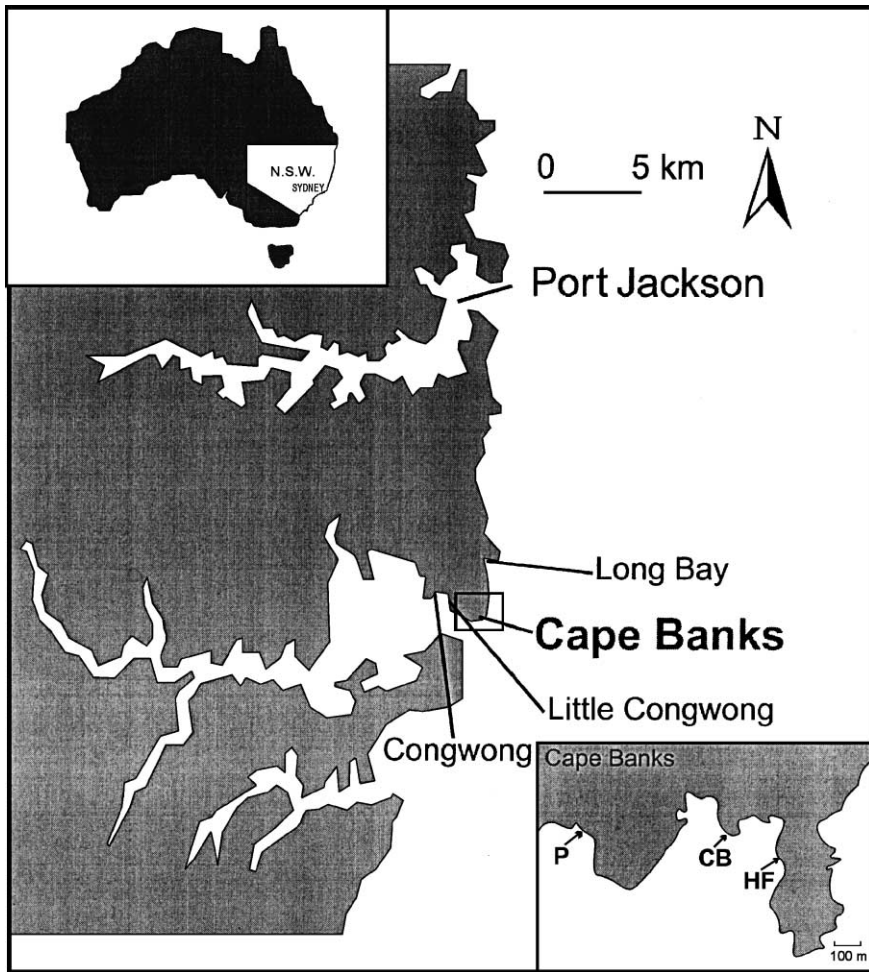


Fig. 2. Map showing all locations and sites sampled.

habitat was tested at two spatial scales: the scale of patches of *Pyura* and that of individual *Pyura*, because when examining the diversity associated with any habitat or assemblage, it is important to use a range of resolutions (e.g. Thompson et al., 1996).

2. Materials and methods

Field work was done at four shores (Cape Banks, Long Bay, Little Congwong and Congwong; Fig. 2) near Sydney, Australia. The experiments relating to the associated assemblages were only done in the Cape Banks Scientific Marine Research Area in Botany Bay, NSW, Australia (Underwood et al., 1983; Fig. 2).

2.1. Patches of *Pyura*

Low intertidal areas of approximately $3\text{ m} \times 3\text{ m}$, where *Pyura* were numerous were randomly chosen from those available at each site and defined a priori to be either Clumped or Sparse habitat, according to the qualitative descriptions given above. In each of these areas, four replicate $1\text{ m} \times 1\text{ m}$ quadrats were randomly placed. Using a 100-cm tape measure, the substratum covered by *Pyura* and the substratum not covered by *Pyura* were measured along four transects set 20 cm from each other (i.e. 20, 40, 60 and 80 cm from the top of the frame of the quadrat; Fig. 1c). When either category extended beyond the frame of the quadrat, the length outside the quadrat was also measured, up to a maximal distance of 1 m away from the frame (distances greater than 1 m were considered to be outside the patch being measured).

These measurements were used to estimate three variables to characterize the structure of each patch of habitat: (i) percentage cover of *Pyura*; (ii) size of patches of substratum covered by *Pyura* and (iii) size of patches of substratum without *Pyura*. Percentage cover was calculated based on the total length of *Pyura* measured in each quadrat and the total possible area (i.e. 400 cm).

To sample the associated assemblages at the scale of patch (i.e. $1\text{ m} \times 1\text{ m}$ quadrat), the cover and diversity of the different species of animals and plants were measured by recording the percentage cover of algae and sessile animals and numbers of mobile animals in four, randomly placed $30\text{ cm} \times 30\text{ cm}$ sub-quadrats. Percentage covers were recorded under 100 points in each sub-quadrat. Any sessile organism present, but not recorded under a point of intersection, was given a cover of 0.5%. Any organism not identified in the field was taken to the laboratory for identification. Organisms were generally identified to species.

2.2. Individual *Pyura*

In order to sample the assemblages at the scale of individual *Pyura*, five Isolated (standing by themselves separated from other individuals) and five Clumped *Pyura* (part of a clump and surrounded by other *Pyura*) were collected from each of two sites (CB and HF; Fig. 2). The individuals collected were randomly selected from those available at each site. Clumped individuals were collected from Sparse or Clumped habitats, whenever possible and from different clumps, so that the widest possible range of individuals was sampled. Isolated individuals were only collected from Sparse habitat (there were no Isolated individuals in Clumped habitat). Each individual was removed from the rock by wedging a knife between the bottom of its test and the substratum and using it as a lever. To avoid the possible loss of any associated animals during collection, a plastic bag was put around each individual prior to removal. The samples were then taken to the laboratory and preserved in 7% formalin.

The covers of algae and sessile animals on the tests of each *Pyura* were estimated using a $3\text{ cm} \times 3\text{ cm}$ quadrat with 10 random points (five replicate quadrats were sampled per *Pyura*; the average area of a typical *Pyura* is 180 cm^2). Mobile animals were removed by placing the *Pyura* in a $500\text{-}\mu\text{m}$ sieve and washing it under running water. When no more animals were found in the sieve, the *Pyura* was examined under

a microscope. Any animals still present were removed with forceps. All animals were then identified and counted. Algae and sessile animals were identified to species, but mobile animals were only identified to family. This taxonomic resolution allowed spatial patterns of these taxa to be identified and saved considerable time during sorting.

3. Results

3.1. Two habitats

Clumped and Sparse habitats were compared, using analysis of variance, in terms of percentage cover of *Pyura* and sizes of patches covered by *Pyura* or covered by other

Table 1

Summary of analyses comparing (a) the average percentage cover of *Pyura* at three sites, at Cape Banks; variances were homogenous (Cochran's test, $p > 0.05$); (b) the mean size of patch of substratum not covered by *Pyura* at three sites, at Cape Banks. Variances were heterogeneous, so data were transformed to $\text{Ln}(x+1)$; (c) the mean size of patch of *Pyura* at three sites, at Cape Banks. Variances were heterogeneous, so data were transformed to $\text{Ln}(x+1)$

Source of variation	df	Mean squares	F-ratio	P
(a)				
S	2	45.55	1.68	ns
H	1	2375.06	13.39	ns
Q(S × H)	18	27.05	1.43	ns
S × H	2	177.43	6.56	*
Residual	72	18.86		
(b)				
S	2	2.92	2.74	ns
H	1	25.35	10.33	ns
Q(S × H)	18	1.07	2.50	**
S × H	2	2.45	2.30	ns
Residual	72	0.43		
(c)				
S	2	2.19	2.81	ns
H	1	1.85	0.08	ns
Q(S × H)	18	0.78	1.55	ns
S × H	2	22.24	28.51	***
Residual	72	0.50		

SNK tests ("=" not significant at $P = 0.05$); Site 1: C ≠ S; Site 2: C ≠ S; Site 3: C ≠ S

SNK tests ("=" not significant at $P = 0.05$); Site 1: C = S; Site 2: C ≠ S; Site 3: C ≠ S

S = Site (three levels; random), H = Habitat, i.e. Clumped versus Sparse (two levels; fixed), Q(S × H) = Quadrats (four levels in each habitat at each site; random). $n = 4$ replicate transects.

ns, $p > 0.05$; * $p < 0.05$; ** $p > 0.01$; *** $p > 0.001$.

substratum. In cases where Cochran's tests were significant, data were transformed (Tables 1 and 2). The hypothesis that patches of *Pyura* would fall into two structural groups was tested at three sites in Cape Banks (HF, CB and P, see Fig. 2). The generality of the findings was then tested at the three other locations around Cape Banks (Fig. 2).

Even though the difference varied among sites ($S \times H$ interactions in Tables 1a and 2a), the cover of *Pyura* was greater in Clumped than in Sparse habitat at all sites sampled at Cape Banks and at all other locations. Across all locations, the cover of *Pyura* was always greater in Clumped habitat (Fig. 3a,e). The size of patch of *Pyura* in Clumped habitat varied more from site to site and from location to location. At two out of three sites at Cape Banks, patches of *Pyura* were larger in Clumped habitat (Fig. 3b,e), but this was not significant (Table 1b). At all other locations sampled, there were significant differences between habitats (Table 2b). The size of patches of substratum other than *Pyura* was consistently greater in Sparse habitat (Fig. 3c,f). At Cape Banks, there was a site $\times$ habitat interaction. Patches without *Pyura* were smaller in Clumped than in Sparse habitats at two

Table 2

Summary of the analyses comparing (a) the average percentage cover of *Pyura* at three locations; variances were homogenous (Cochran's test, $p > 0.05$); (b) the mean size of patch of substratum not covered by *Pyura* at three locations. Variances were heterogeneous, but data could not be transformed; (c) the mean size of patch of *Pyura* at three locations. Variances were heterogeneous, so data were transformed to $\sqrt{x}$

Source of variation	<i>df</i>	Mean squares	<i>F</i> -ratio	<i>P</i>
(a)				
L	2	622.17	1.49	ns
H	1	22330.89	53.5	***
Q(L $\times$ H)	12	417.42	1.81	ns
L $\times$ H	2	1764.39	4.23	*
Residual	54	230.13		

SNK tests ("=" not significant at $P=0.05$); Loc 1: C=S; Loc 2: C $\neq$ S; Loc 3: C $\neq$ S

(b)				
L	2	6.05	1.72	ns
H	1	78.12	22.17	**
Q(L $\times$ H)	12	3.52	2.42	*
L $\times$ H	2	10.39	2.95	ns
Residual	54	1.45		

(c)				
L	2	1217.06	2.10	ns
H	1	8975.95	15.52	**
Q(L $\times$ H)	12	578.44	2.41	*
L $\times$ H	2	1463.03	2.53	ns
Residual	54	240.12		

L=Locations (three levels; random), H=Habitat, i.e. Clumped versus Sparse (two levels; fixed), Q(L $\times$ H)=Quadrats (three levels; random). $n = 4$ replicate transects.

ns, $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

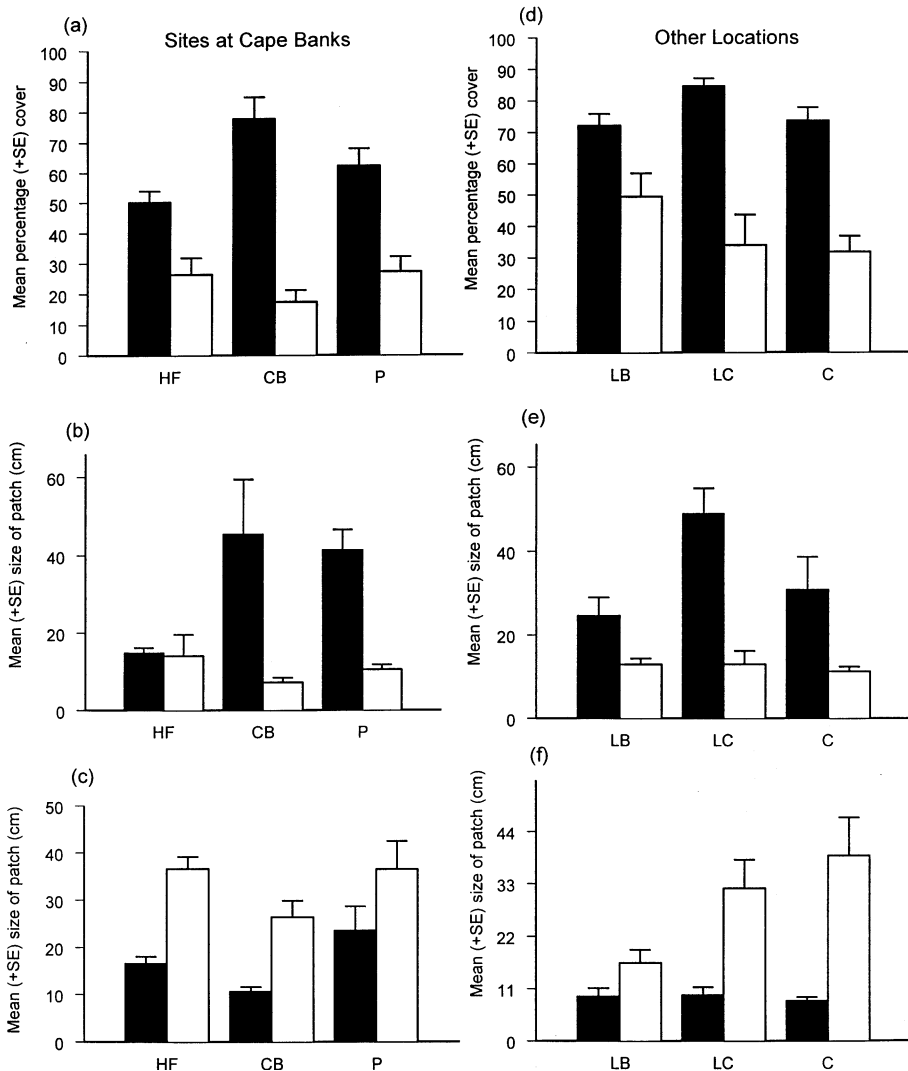


Fig. 3. Mean (+SE): (a,d) percentage cover of *Pyura*; (b,e) size of patches of substratum covered by *Pyura*; (c,f) size of patches of substratum not covered by *Pyura*, (■ = Clumped, □ = Sparse). HF, CB and P are three sites at Cape Banks (a–c); LB (Long Bay), LC (Little Congwong) and C (Congwong) are three other shores.

out of three sites (SNK tests and Table 1c). At all remaining locations, the patches of substratum not covered by *Pyura* were smaller. Using just one of these variables to classify habitats would not be useful, but combining all three variables makes the distinction between Clumped and Sparse habitats easier. The cover of *Pyura* and the sizes of patches of *Pyura* were greater in Clumped habitat, while the sizes of patches of other substratum were greater in Sparse habitat.

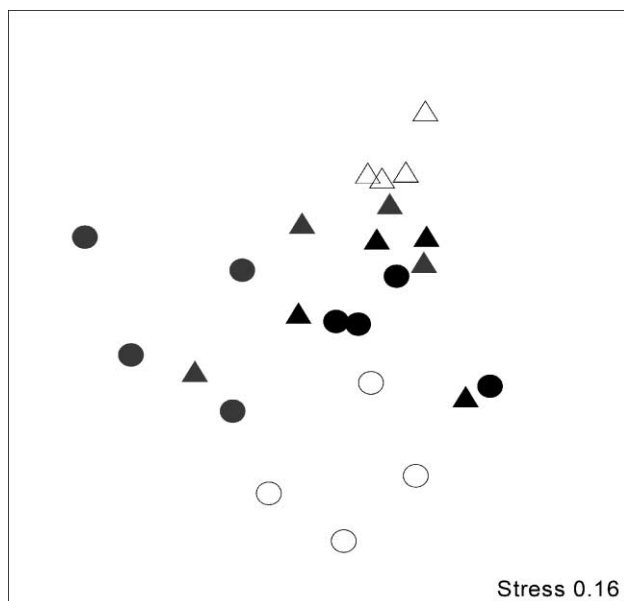


Fig. 4. nMDS plot of assemblages associated with *Pyura stolonifera* at the scale of patch, from the three sites at Cape Banks combined (circles, Clumped habitat; triangles, Sparse habitat). There were four quadrats in three patches of each type of habitat (different shading of symbols represents the three sites).

3.2. Assemblages in the two habitats

Assemblages associated with the two habitats were different at all sites at Cape Banks, but this difference was only significant in ANOSIM tests (on ranked Bray–Curtis dissimilarities, Clarke, 1993; $P < 0.06$) at two of the sites (HF: ANOSIM $R = 0.08$, $P < 0.06$; CB: $R = 0.27$, $P < 0.0005$; P: $R = 0.53$, $P < 0.0005$). To test the generality of these

Table 3

The contribution towards Bray–Curtis measures of dissimilarity for the most important species in each site, between assemblages in Clumped versus Sparse habitats

		Dissimilarity			
		Clumped versus Sparse habitat			
		Site 1	Site 2	Site 3	All sites
Bare	% (Rank)	2 (13)	0.3 (10)	7 (5)	3 (6)
<i>Corallina officinalis</i>	% (Rank)	21 (1=)	26 (1)	42 (1)	29 (1)
Non-geniculate <i>Corallina</i>	% (Rank)	6 (3=)	20 (2)	4 (7)	11 (=3)
<i>Sargassum</i> sp.	% (Rank)	4 (5)	2 (7=)	1 (9)	2 (7=)
<i>Hildenbrandia rubra</i>	% (Rank)	21 (1=)	7 (4)	9 (3)	13 (2)
<i>Ralfsia verrucosa</i>	% (Rank)	13 (2)	16 (3)	8 (4)	11(=3)
<i>Laurencia</i> sp.	% (Rank)	1 (14=)	4 (5=)	0.1 (27)	2 (7=)
<i>Tessieropora rosea</i>	% (Rank)	1 (14=)	2 (7=)	12 (2)	5 (5)
<i>Montfortula rugosa</i>	% (Rank)	6 (3=)	4 (5=)	6 (6)	6 (4)
Small black siphonarians	% (Rank)	4 (4)	3 (6)	0 (36)	2 (7=)

patterns across Cape Banks, the data from all three sites were combined. Assemblages associated with Clumped and Sparse habitats were significantly different ($R=0.19$, $P<0.0005$; Fig. 4). Cover of *Pyura* was not included in these analyses because *Pyura* was considered the provider of habitat. Percentage covers of algae and sessile animals were corrected after the removal of the cover of *Pyura*. Where significant patterns were detected, SimDiss (an equivalent procedure to SIMPER, Primer package, Clarke and Warwick, 1994) was used to determine the contribution of different species to those patterns.

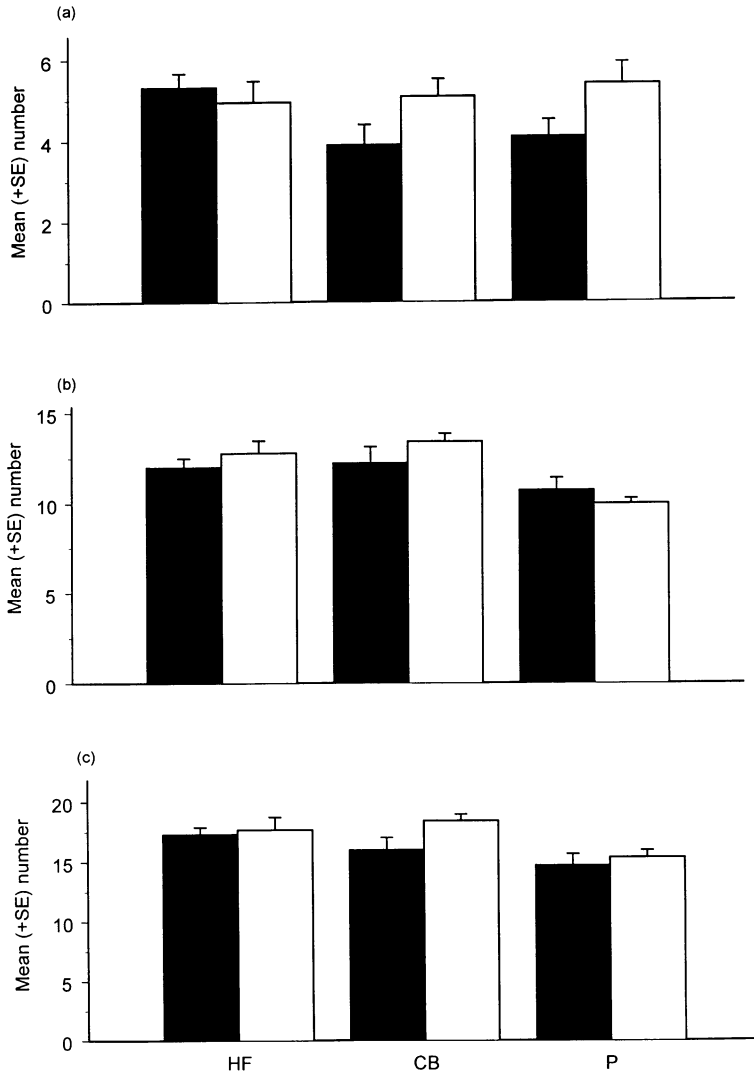


Fig. 5. Mean (+SE): (a) number of mobile species; (b) mean number of sessile species; (c) mean total number of species associated with habitats of *Pyura*, at the three sites sampled at Cape Banks (■ = Clumped, □ = Sparse).

Nineteen species of algae and 45 species of animals were found in the habitats provided by *Pyura*, across the three sites. Molluscs were the dominant group. Others included sponges, echinoderms, anemones and crustaceans. Of the 64 taxa, only a small group was responsible for the majority of the dissimilarities between assemblages (Table 3). Across all sites, *Corallina* contributed most to the differences. Others included the encrusting algae *Hildenbrandia* and *Ralfsia*. All these taxa are generally associated with the space among *Pyura* and tended to be more common in Sparse habitat. The fissurellid limpet *Montfortula rugosa* was the only mobile animal that contributed more than 5% to the

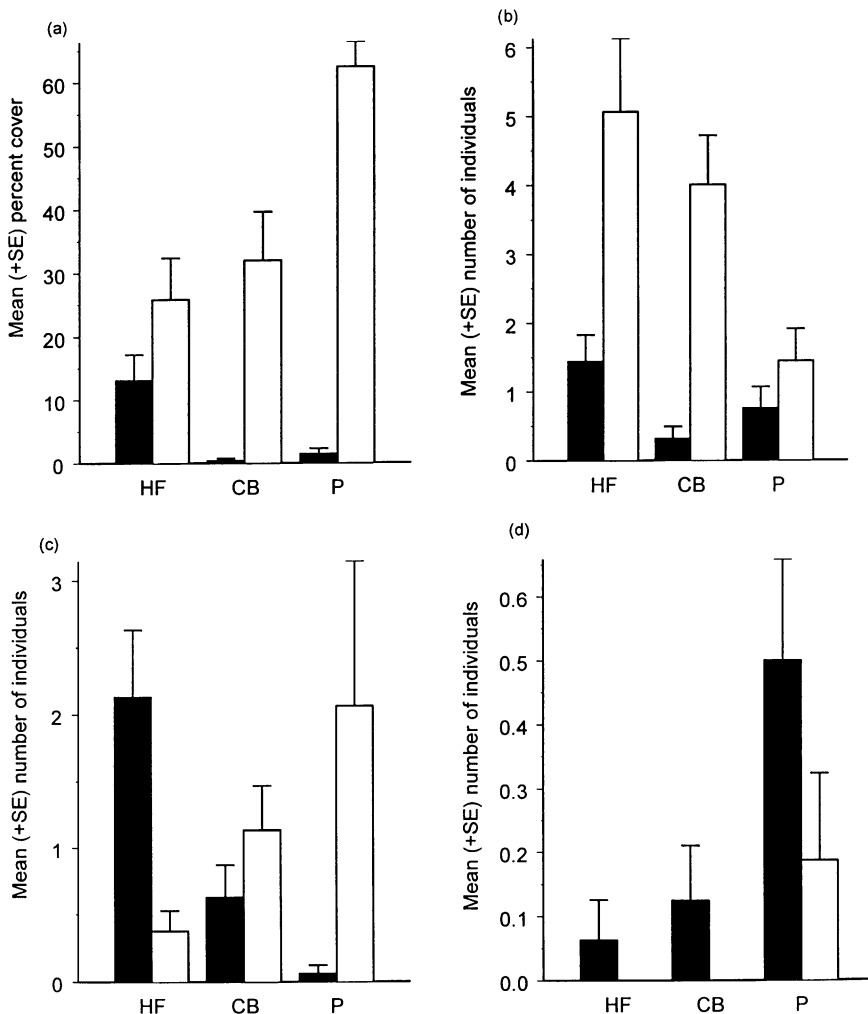


Fig. 6. Mean (+SE): (a) percent cover of *Corallina officinalis*; (b) number of *Cellana tramoserica*; (c) number of *Thais orbita*; (d) number of *Cabestana spengleri* found in habitats of *Pyura*, at the three sites sampled at Cape Banks (■ = Clumped, □ = Sparse).

differences between assemblages. This species was present in both habitats and found on *Pyura* and on the surrounding area.

Some species varied from one habitat to the other, but the numbers of taxa in each habitat appeared to be similar. In light of this, the hypotheses that the number of mobile, sessile and the total number of taxa were similar between the habitat were tested. The numbers of mobile and sessile species and the total number of species were similar in each habitat (Fig. 5a–c). Some species, such as *C. officinalis* and the limpet *Cellana tramoserica* were usually associated with the spaces amongst *Pyura* and were more abundant in Sparse habitat (Fig. 6a,b). The whelks *Thais orbita* and *Cabestana spengleri* were generally found attached to *Pyura*. *Thais* was found in both habitats and had no specific pattern of abundance (Fig. 6c). *Cabestana*, on the other hand, were mostly found in Clumped habitat (Fig. 6d).

3.3. Assemblages on individual *Pyura*

Eighty-four taxa were found living on the tests of individual *Pyura*. Again, molluscs were the dominant group, although several species of algae, polychaetes and isopods were also present. The differences (Fig. 7) between the types of *Pyura* (for HF and CB, respectively, ANOSIM $R=0.60$, $P<0.0008$; $R=0.59$, $P<0.008$) were mainly due to limpets of the families Siphonariidae and Acmaeidae, bivalves of the family Erycinidae and micro-gastropods of the family Eatoniellidae. Analysis of variance was initially used to test the hypothesis that abundances of these taxa differed between Isolated and Clumped

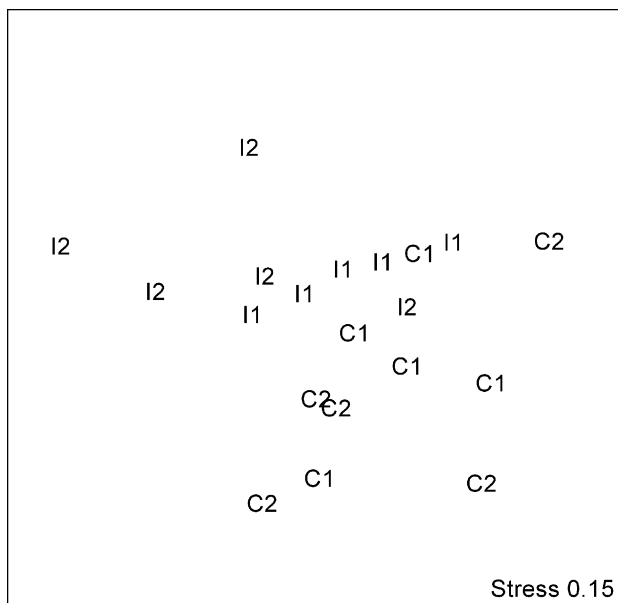


Fig. 7. nMDS plot of assemblages on individual *Pyura*. Five individuals were collected from Clumped or Sparse habitat at each of the two sites (C=Clumped *Pyura*; I=isolated *Pyura*) to close square.

Table 4
Analyses of numbers and frequencies of occurrence of types of gastropods on *Pyura*

Taxon	Site	Individual <i>Pyura</i>		Clumped <i>Pyura</i>		χ^2 ^(a) (1 df)	P	χ^2 ^(b) (1 df)	P	Fi	Fc
		No. occupied	No. individuals	No. occupied	No. individuals						
Siphonaridae	1	4	99	1	13	1.8	ns	66.0	***		
	2	5	144	0	0	5.0		144.0	***		
	1 + 2									0.5	1.00
Acmaeidae	1	4	77	2	5	0.7	ns	63.2	***		
	2	5	88	3	5	0.5	ns	74.1	*		
	1 + 2									0.66	0.5
Erycinidae	1	5	557	5	127	0.0	ns	270.3	***		
	2	5	173	5	142	0.0	ns	3.0	ns		
	1 + 2									0.67	0.5
Eatonieillidae	1	5	280	5	102	0.0	ns	82.9	***		
	2	4	54	5	22	0.1	ns	13.5	***		
	1 + 2									0.59	0.67

For each family of gastropods, at each site, χ^2 ^(a) tested the null hypothesis that the frequencies of Isolated and Clumped *Pyura* occupied by that family were equal; χ^2 ^(b) tested the null hypothesis that the total number of that family on 10 Isolated *Pyura* equals the total number on 10 Clumped *Pyura*. Fi is the probability from Fisher's exact test of the null hypothesis that the proportion of Isolated *Pyura* occupied by that family in site 1 equals the proportion occupied in site 2; Fc is the same test for Clumped individuals.
* $p < 0.05$; *** $p < 0.001$.

Pyura, but the heterogeneity of the data did not allow conclusive results and the transformation of data did not solve this problem. To overcome this difficulty, three different hypotheses were tested: (i) the proportion of Isolated *Pyura* occupied by taxon $i \neq$ proportion of Clumped *Pyura* occupied by taxon i ; (ii) the proportion of taxon i on Isolated *Pyura* $\neq$ proportion of taxon i on Clumped *Pyura*; (iii) the proportion of Clumped or Isolated *Pyura* with taxon i at site 1 = proportion of Clumped or Isolated *Pyura* with taxon i at site 2. In the cases, where the expected values (under the null hypothesis of no difference) were smaller than 5, Fisher's exact tests were used. The tests were done for the taxa (chosen on the basis of SIMDISS results) that accounted for most of the differences between the types of *Pyura*.

For all four taxa tested, with the exception of Siphonariidae at CB, the proportions of Isolated and Clumped *Pyura* occupied by taxon were similar (Table 4). At each site, however, more individuals were found on Isolated than on Clumped *Pyura*. The only exception to this trend was Erycinidae at CB. The proportions of Isolated and Clumped *Pyura* occupied by each taxon were similar at the two sites.

4. Discussion

Pyura are a conspicuous and abundant component of rocky shores across its area of distribution in Australia (Kott, 1985; Otway, 1989; Edgar, 1997). Their presence provides added surface area for the settlement of other organisms, and by ameliorating environmental conditions they may provide different microhabitats for those organisms. Living on and amongst *P. stolonifera* may allow animals and plants to get the benefits of a high energy environment, such as oxygenated water or continuous flow of food, without being subjected to potentially destructive variables as strong wave-action or currents (Fielding et al., 1994). *Pyura* may therefore be considered an example of an intertidal ecosystem engineer (Jones et al., 1994).

Patches of other substratum (generally occupied by different species of foliose and/or encrusting algae) in habitats of *Pyura* fall under the category of Type I patches — areas of habitat surrounded by a matrix of some other habitat (Connell and Keough, 1985), in this case *Pyura*. Patches of *Pyura* can, on the other hand, be considered Type II patches because they are a different substratum and provide an additional area for the settlement of other organisms (Connell and Keough, 1985).

As originally predicted, habitats in beds of *Pyura* separated into two different structural types based on a combination of percentage cover and relative sizes of patches of *Pyura* and patches of other substratum. Samples were randomly chosen, at all sites and locations so that the widest possible range of patches was sampled. This also assured that if there were any overlapping between the two types of habitat, it would be identified in the analyses. There was only a handful of cases where a patch could have possibly been considered intermediate but in every such case statistical analyses showed them to be either Clumped or Sparse and not intermediate.

Clumped habitats were characterized by a large cover of *Pyura* and by larger patches of *Pyura* in relation to those of other substratum. Sparse habitats, on the other hand, were characterized by a small cover of *Pyura*, with patches of other substratum being on

average larger than those of *Pyura*. These patterns were consistent across all locations sampled. The fact that no intermediate areas were found and the generality of the patterns observed support the original idea that areas of the shore where *Pyura* is found can be classified either as Clumped or Sparse habitat. The differences between Clumped and Sparse habitats are presumably the result of combinations of differences in dispersal, rates of settlement or post-settlement mortality, including differences due to disturbances.

Assemblages can vary at different spatial scales and the type of patterns observed at one scale may or may not be present at a different one emphasizing the need to sample at different spatial scales in order to reach a better assessment of the diversity in a given area (Thompson et al., 1996). In the present study, the scales chosen were patches of *Pyura* and individual *Pyura*.

Various studies have shown that different intertidal habitats are associated with different assemblages (e.g. Hawkins, 1981; Lohse, 1993; Thompson et al., 1996). This was also the case for the habitats of *Pyura* at Cape Banks. Assemblages were different at all three sites. When the data from all sites were combined, the assemblages were significantly different. Species normally associated with bare spaces, such as the algae *Corallina* and *Hildenbrandia*, were responsible for most of the differences between the assemblages in the two habitats. The algae *Corallina* and the limpet *Cellana* were more abundant in Sparse habitat, which can possibly be explained by the greater availability of substratum not covered by *Pyura*. *Corallina* may settle and grow better on rock (at all sites *Corallina* was mostly found on the space between *Pyura* rather than on the *Pyura* themselves). *C. tramoserica* are grazers and the algae they tend to feed on are more common on the substratum that surrounds the *Pyura*. Species like the whelks *T. orbita* and *C. spengleri* were generally found attached to *Pyura* and were more frequent in Clumped habitat.

As was the case at the scale of patch, the assemblages were different at the scale of individual *Pyura*, supporting the idea that two different habitats were present in the beds of *Pyura*. Differences at this scale were mostly due to differences in the abundances of organisms rather than the number or types of taxa. What varied between Isolated and Clumped *Pyura* were the numbers of animals present and the proportions of *Pyura* occupied by those organisms rather than the types of animals. In this case, contrary to what happened at the scale of patch, where differences were mainly due to algae, the taxa responsible for most of the differences were mobile molluscs (three families of gastropods and one family of bivalves).

The results of this study suggest that the variables used, percentage cover of *Pyura*, the size of the patches of substratum covered and not covered by *Pyura*, and whether *Pyura* are isolated or in clumps were appropriate for identifying patterns in the structure of habitat and assemblages associated with the beds of *Pyura* around Sydney.

Pyura is commonly killed and used as bait by recreational fishermen (Underwood and Kennelly, 1990) in Australia. Fishermen usually cut off the top of the test and use the insides as bait. The portion still left attached to the rock usually disappears after about two weeks. This type of collection can be selective; larger or more readily accessible individuals are preferred. The numbers of *Pyura* can be seriously reduced by this type of collection (Fairweather, 1991) and the structure of the patches of *Pyura* can also be affected. A reduction in the number and cover of *Pyura* may lead to changes in the structure of the habitat available for other organisms. Removal of *Pyura* at Cape Banks, by

fishermen or storms, has been shown to result in marked changes to the assemblages in low-shore areas (Otway, pers. comm.).

Changes in the structure of a habitat may affect the associated assemblages in different ways, so, in order to be able to predict the possible effects of such changes, it is important to know the underlying natural patterns in those assemblages. Possible responses of the assemblages to changes in the structure of the habitat can include decreases or increases in abundances of some or all species and/or increases or decreases in the number of species. Some species can disappear and new ones can replace them or be added to an assemblage. In the case of habitats provided by *Pyura*, there are differences in the associated assemblages, depending on whether the ascidians are clumped or sparsely scattered on the shore. To determine the extent to which changing the arrangement of the *Pyura* themselves may lead to changes in associated assemblages requires manipulative experiments. In order to be able to plan and design such experiments, the natural patterns of occurrence of the assemblages associated with *Pyura* must be known. Describing those patterns quantitatively is the important first step in that understanding.

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