Macroinvertebrate communities associated with intertidal and subtidal beds of *Pyura stolonifera* (Heller) (Tunicata: Ascidiacea) on the Natal coast

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The solitary ascidian *Pyura stolonifera* occurs in dense beds on the low intertidal and shallow subtidal rocky shore along the entire South African coastline. The organism is used as bait by fishermen and is also heavily exploited for food in certain areas. The crevices and interstices between individuals in dense beds of *P. stolonifera* provide a safe and stable habitat for a wide variety of benthic macroinvertebrates. Sixty-four and 61 taxa representing 10 phyla, of associated organisms were recorded respectively in an intertidal and a subtidal *P. stolonifera* bed. Forty-two taxa were common to both, but communities of macroinvertebrates associated with intertidal and subtidal *P. stolonifera* beds were different. Numerically, polychaetes (30%) were the dominant group intertidally, and crustaceans (40%) subtidally. Porifera formed 71% of the biomass of associated intertidal organisms, while subtidal biomass was dominated by the bivalves *Striostrea margaritacea* and *Perna perna* (87%). Mean dry biomass of macroinvertebrates was 366 g.m^{-2} (*SD* = 196) intertidally and 670 g.m^{-2} (*SD* = 119) subtidally. These values are between four and eight times higher than those recorded on the southern Cape coast. Recolonization of cleared areas is slow, so considerable secondary production is lost when harvesting practices result in bare patches in *P. stolonifera* beds.

Die alleenlewende bekerdier *Pyura stolonifera*, kom in digte beddings voor in die lae tussengetysone en subgetysone langs die hele Suid-Afrikaanse kusstrook. Hierdie organisme word deur hengelaars gebruik vir aas, en in sekere streke word dit op groot skaal ontgin as voedselsoort. Die skeure en tussenruimtes tussen individue in digte beddings van *Pyura stolonifera* verskaf 'n veilige en stabiele mikrohabitat vir 'n wye verskeidenheid van bentiese makro-invertebrata. Vier-en-sestig en 61 taxa van geassossieerde organismes, verteenwoordigend van 10 filums, is onderskeidelik in die tussen- en subgetysones aangeteken. Twee-en-veertig taxa het in albei gebiede voorgekom, maar gemeenskappe in die tussen- en subgetysones het van mekaar verskil. Numeries was Polychaeta die dominante groep in die tussengetysone (30%), terwyl Crustacea die dominante groep in die subgetysone was (40%). Porifera het 71% van die biomassa gevorm van organismes wat geassosieer was met die tussengetysone *Pyura stolonifera* beddings, terwyl die biomassa in die subgetysone gedomineer was (87%) deur die tweekleppiges *Striostrea margaritacea* en *Perna perna*. Gemiddelde droë biomassa van geassosieerde organismes was 366 g.m^{-2} (*SA* = 196) in die tussengetysone en 670 g.m^{-2} (*SA* = 119) in die subgetysone. Hierdie waardes is tussen vier en agt keer hoër as die wat aan die suidelike Kaapse kus opgeteken was. Hervestiging van gestroopte gebiede is stadig, daarom gaan 'n aansienlike gedeelte van die sekondêre produksie verlore wanneer sekere gebiede deur ongewenste oespraktyke kaalgestroop word.

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Pyura stolonifera is a large solitary ascidian which occurs in dense beds from the low littoral to a depth of about 10 m on rocky reefs along the entire southern African coastline. It is often the dominant species in these areas and prefers locations with maximum exposure to waves and currents. Past studies on *P. stolonifera* have been concerned with ecology (Morgans 1959; Day 1974a), morphology and functional anatomy (Day 1974b), larval development (Griffiths 1976b), biomass and production (Van Driel 1978; Field, Griffiths, Griffiths, Jarman, Zoutendyk, Velimirov & Bowes 1980; Berry 1982) and nutritional ecology (Klumpp 1984; Stuart & Klumpp 1984).

P. stolonifera pods are generally roughly barrel-shaped, although the shape of the test varies to some extent according to the proximity of neighbours. The test of the animal is very tough and represents an advanced protective device against predation and wave action (Day 1974b). Because of the shape of the individual animals, dense beds of closely packed *P. stolonifera* pods contain many interstices and crevices that provide a sheltered habitat for a wide range of fauna. Animals living amongst the *P. stolonifera* pods receive all the benefits of a high energy environment, such as highly oxygenated water, constant replenishment of food and removal of wastes, without being subjected to disadvantages such as exposure to wave action and strong currents. At low tides the interstices retain some water and organisms living among the *P. stolonifera* pods are protected from desiccation and temperature extremes.

Van Driel & Steyl (1976) examined the fauna associated with *P. stolonifera* from six subtidal areas in Algoa Bay in the southern Cape, and found species were grouped according to the exposure to wave action. The fauna associated with *P. stolonifera* in areas sheltered from wave action was more diverse than that from exposed areas and estuarine conditions. There are no data on the fauna associated with *P. stolonifera* living in the warmer waters of the Natal coast. The animal is exploited intertidally as a bait organism by fishermen, and between 5–8 t/km of rocky shore (wet unshelled weight) are harvested annually for food by local people living along the Maputaland coast of northern Natal (R. Kyle 1992, unpubl. rep.). Growing concern over the effects of harvesting led to the need for a more detailed description of the animals associated with *P. stolonifera* on the Natal coast. A comparison was made between the fauna associated with subtidal and intertidal beds of *P. stolonifera.*

Study area

Intertidal samples were collected at Pennington 70 km south of Durban. Extensive beds of *P. stolonifera* are present in the lower littoral of a flat rock shelf that is exposed to the full force of wave action. Subtidal samples were collected at a depth of 2 m from the end of Vetch's reef in Durban Bay, using SCUBA. The reef is only subjected to breaking waves during storm conditions but currents and surge are almost always present.

Materials and Methods

Separation of *P. stolonifera* pods and the removal of the associated organisms is extremely time-consuming, so a pilot study was conducted to determine the smallest practical quadrat size that could be used. At Pennington, five replicates were taken in an area of 100% *P. stolonifera* cover, for each of four different quadrat sizes (0,0225 m^2, 0,0625 m^2, 0,1410 m^2 and 0,2500 m^2). Samples were collected and treated as described below. The number of species per sample was plotted against quadrat size (Figure 1). At a quadrat size of 0,1410 m^2, > 90% of the total number of species found were present, and this size quadrat was therefore chosen for further work. Five 0,1410-m^2 quadrats were selectively laid in areas with as near as possible 100% *P. stolonifera* cover, at Pennington and Vetch's reef. There was some variability in the number and size of pods, and the biomass of associated species, in replicates from each site (Table 1), but no further sampling was possible in the time available. Cumulative number of species was plotted against number of replicates (Figure 2). In the fifth replicate the number of new intertidal and subtidal species was 5% and 3% respectively of the number already identified, so most species present in *P. stolonifera* beds from the two sites were represented in the five replicates.

All macroinvertebrates inside the quadrat were collected using scrapers and the area was scraped to bare rock. When only a part of a *P. stolonifera* pod was inside the quadrat, the animal was cut through and the portion inside the quadrat was removed. Samples were stored in a 10% formalin seawater mixture. The pods were then separated and all the macroinvertebrates found between the pods were collected. Organisms attached to the surface of the pods were carefully removed using a scalpel and forceps. The formalin solution in which the sample was originally stored was passed through a 500 μm sieve and the retained animals were collected. Macroinvertebrates were identified to the lowest taxon possible using Barnard (1950), Day (1967), Day (1974a), Griffiths (1976a), Kensley (1978) and Kilburn & Rippey (1982).

The number of *P. stolonifera* pods was counted in each sample and the flesh was removed, dried (80°C for 24 h)

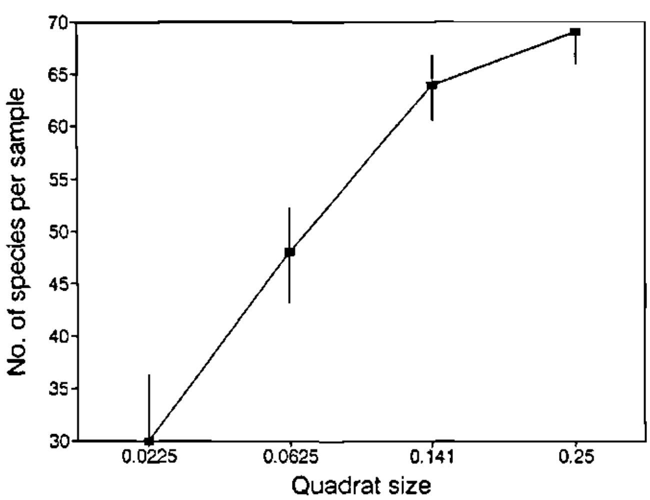

Figure 1 The mean number of macroinvertebrate species per sample associated with intertidal beds of *P. stolonifera* for different quadrat sizes; n = 5 replicates for each quadrat size, error bars = 1 *SD*.

Table 1 The mean number of pods.m^{-2}, individual *P. stolonifera* biomass (g dried flesh) and total biomass (g dried flesh.m^{-2}) of *Pyura stolonifera* collected intertidally and subtidally along the Natal coast. The mean biomass (g.m^{-2}) of organisms associated with *P. stolonifera* beds is also shown. n = 5 replicates for each locality, *SD* in parentheses

Area	No. of pods (m^{-2})	Mean individual mass (g)	Total biomass (g.m^{-2})	Biomass ass. organisms (g.m^{-2})
Intertidal	288	1,89	540,25	365,83
	(89)	(0,13)	(150,81)	(195,71)
Subtidal	186	5,22	947,64	670,32
	(36)	(0,79)	(38,40)	(119,28)

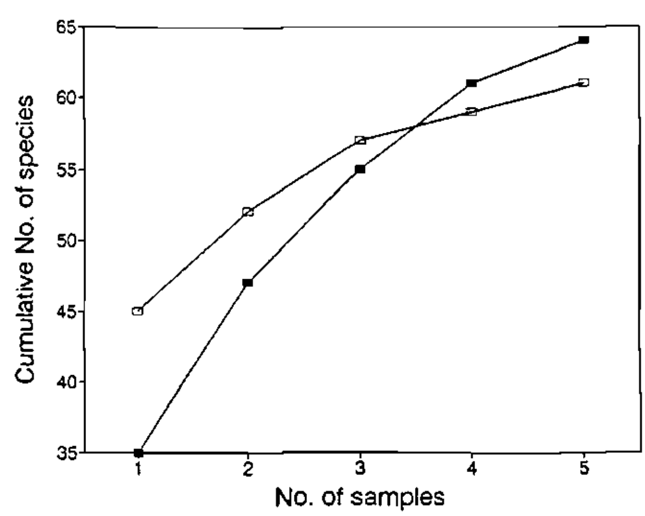

Figure 2 The cumulative number of macroinvertebrate species associated with intertidal (■—■) and subtidal (□—□) beds of *P. stolonifera* at different numbers of replicates of a 0,141-m^2 quadrat.

and weighed. Where neccesary calcareous casings and shells of macroinvertebrates were removed with 5% HCl and all animals were dried and weighed. Species abundance data were root–root transformed (Field, Clark & Warwick 1982). Bray-Curtis dissimilarity indices were calculated for all pair combinations of samples using the root–root transformed data (Field *et al.* 1982) and expressed as percentage similarities. For this analysis the colonial ascidians and sponges were excluded.

Results

The intertidal samples contained significantly smaller *P. stolonifera* individuals, had significantly more pods than the subtidal samples (*t* test, $p < 0,05$) and contained approximately half the flesh weight.m^{-2} (Table 1). Ten phyla were represented in the total of 83 taxa found associated with *P. stolonifera* from the intertidal and subtidal localities (Appendix 1). Crustaceans and polychaetes were the most species rich groups, with 28 and 30 species respectively. (Porifera and Nemertea were not considered because identification to genus or species was not possible). Sixty-four taxa were recorded in the intertidal samples and 61 subtidally, with 42 taxa being common to both localities (Appendix 1). Numerically, crustaceans outnumbered polychaetes subtidally, but polychaetes were the dominant group intertidally. Together these two taxa contributed 51,7% and 60,3% respectively of the numbers of intertidal and subtidal organisms found between the *P. stolonifera* pods (Figures 3a & 3b). Porifera (71,4%) formed the bulk of the biomass of intertidal associated species, while polychaetes (10,8%) made up the next most important group (Figure 4a). In the subtidal samples the bivalves *Perna perna* and *Striostrea margaritaceae* dominated the biomass of associated species (86,9%), and crustaceans (8,3%) and polychaetes (0,9%) were much less important (Figure 4b). The mean dry biomass of associated organisms was 365,83 g.m^{-2} (*SD* = 195,71) intertidally and 670,32 g.m^{-2} (*SD* = 119,28) subtidally. Sixty-six per cent and 69% respectively of the intertidal and subtidal taxa were mobile animals, while 27% of intertidal and 31% of subtidal taxa were attached suspension feeders.

The means and standard deviations of the three sets of Bray-Curtis similarity indices showed that the intertidal and subtidal samples were less similar to each other than they were amongst themselves (Figure 5). This suggests that the two communities were different, although it should be noted that the sponges and colonial ascidians were excluded from the analysis.

Discussion

Natural mortality of *P. stolonifera* larger than about 10 mm is fairly low (Fielding, unpublished data) and the interstices between the tough tests therefore provide a safe and reasonably permanent refuge from larger predators and the heavy wave action that characterizes the Natal coast. The results of this study indicate that *P. stolonifera* beds on the east coast are species-rich systems with a considerable biomass of associated fauna. High species diversities have been recorded in similar structurally complex habitats such as mussel beds and kelp holdfasts (Ojeda & Santelices 1984; Suchanek 1986; Ojeda & Dearborn 1989). Clearly, these types of microhabitat play important roles as spatial refuges from predators, particularly when grazing and predation are the major determinants of community structure (Witman 1985; Branch, Barkai, Hockey & Hutchings 1987; Ojeda & Dearborn 1991). Furthermore, by providing protection from harsh physical conditions, *P. stolonifera* beds greatly increase the range and area of habitat available.

It is of interest that the *P. stolonifera* individuals from the intertidal area were considerably smaller than those found subtidally (Table 1). On a wave washed intertidal shore, *P. stolonifera* might devote more energy to thickening their

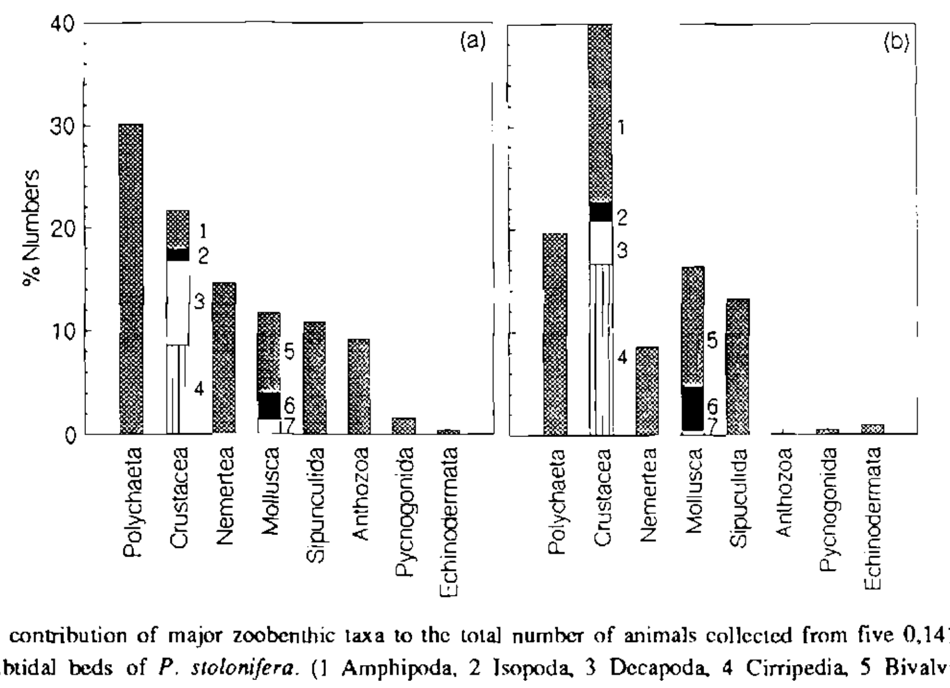

Figure 3 Percentage contribution of major zoobenthic taxa to the total number of animals collected from five 0,141-m^2 quadrats in (a) intertidal and (b) subtidal beds of *P. stolonifera*. (1 Amphipoda, 2 Isopoda, 3 Decapoda, 4 Cirripedia, 5 Bivalvia, 6 Gastropoda, 7 Amphineura.)

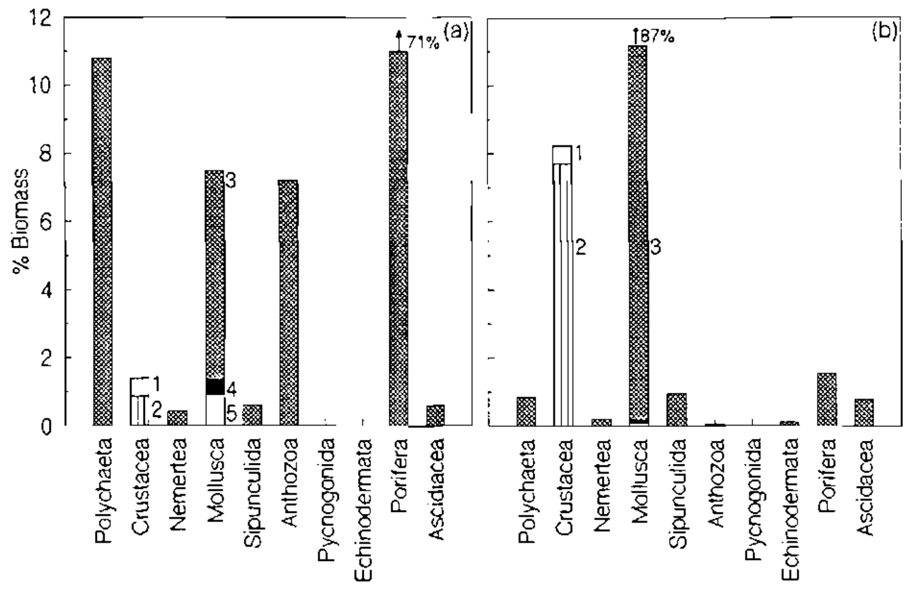

Figure 4 Percentage contribution of major taxa to the total biomass of animals collected from five 0,141-m^2 quadrats in (a) intertidal and (b) subtidal beds of *P. stolonifera*. (1 Decapoda, 2 Cirripedia, 3 Bivalvia, 4 Gastropoda, 5 Amphineura.)

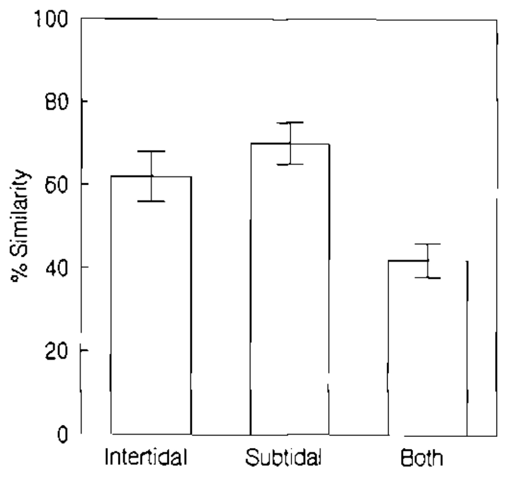

Figure 5 The mean Bray-Curtis similarity indices of intertidal and subtidal samples of organisms found associated with *P. stolonifera* beds on the Natal coast (n = 5 samples at each locality, error bars represent 1 *SD*). Indices were calculated using root–root transformed density data. The bar labelled 'Both' represents the mean similarity index of intertidal and subtidal samples (n = 10).

tests and improving their hold on the rocks than subtidal animals would. Flesh weights of intertidal animals would therefore be smaller than subtidal animals and a difference in the flesh weight : test weight ratio of intertidal and subtidal animals might be expected. However, there was no significant difference (p > 0,99, n = 156) in the slopes of flesh weight / test weight regressions for intertidal and subtidal animals from Pennington and Vetch's reef respectively. Growth studies on *P. stolonifera* have shown that L_∞ = 97 mm for intertidal animals and 104 mm for subtidal animals (Fielding, unpublished data), but this does not fully explain the difference in size of intertidal and subtidal animals shown in Table 1.

Apart from providing a safe and stable microhabitat, the interstices in *P. stolonifera* beds, like those in mussel beds (Ojeda & Dearborn 1989), may represent optimal feeding grounds for infaunal and epifaunal species. Food particles probably become trapped between the pods and are then available for consumption by mobile epifauna, and sediment and detritus accumulate at the base of *P. stolonifera* beds, providing a habitat for infaunal organisms. In mussel beds, soft-bodied suspension feeders take advantage of the turbulences and the reduced water flows created by currents and waves washing over individual mussels (Connel 1972; Wainwright & Koehl 1976), and a similar situation is likely to exist in *P. stolonifera* beds.

Numerically, the major difference in the intertidal and subtidal faunas resulted from the change in dominance of polychaetes intertidally to crustaceans subtidally (Figures 3a & 3b). The bulk of the intertidal polychaete numbers was made up of *Arabella mutans*, *A. caerulea* and *Marphysa corallina*, while subtidally *Nereis* spp. were most common. The change in subtidal crustacean numbers was due mainly to an increase in the numbers of amphipods (*Maera* spp., *Urothoe* spp. and *Ceradocus natalensis*) and barnacles (*Balanus* spp.; Appendix 1). In biomass terms, intertidal polychaetes were also more important than crustaceans, while the reverse was true in the subtidal samples (Figure 4a & 4b). The change in the relative biomass of these two taxa was a result of the increase in the biomass of subtidal barnacles, whereas amphipods caused crustacean numerical dominance subtidally. However, both these taxa were overwhelmingly dominated by the biomass of Porifera intertidally and the bivalves *P. perna* and *S. margaritacea* subtidally. Clearly the subtidal *P. stolonifera* beds form suitable settlement sites for these bivalves, presumably because they provide protection for the vulnerable new recruits. However, the number of *P. perna* and *S. margaritacea* per m^2 in the *P. stolonifera* beds is low when compared to areas outside the beds (Berry 1982), and many empty shells are found between and beneath the *P. stolonifera* pods. The bivalves that survive are generally large (shell length > 90 mm for *P. perna* and > 49 mm for *S. margaritacea*). These animals produce large numbers of gametes (Berry 1978; Schleyer pers. comm.) and may provide spawning reservoirs for exploited bivalve stocks.

That the fauna of the intertidal and subtidal beds of *P. stolonifera* should be different (Figure 5) is not surprising, because of the different physical conditions of an intertidal and subtidal habitat. As factors determining the types of organisms present in the *P. stolonifera* beds, desiccation and temperature tolerance are likely to be secondary to differences in the degree of turbulence at the two sites, because in Natal intertidal *P. stolonifera* occur only very low down on the shore and beds are only exposed at spring low tides on calm days. Calm conditions seldom occur along the Natal coastline and even during exposure the microhabitat between the densely packed *P. stolonifera* pods is unlikely to experience temperature extremes or desiccation. The differences demonstrated between the two communities should be treated with some caution because, for practical reasons, the sampling locations were 70 km apart. The two locations may therefore be different in ways other than their position on the littoral/sublittoral slope. However, observations on intertidal and subtidal *P. stolonifera* samples taken for gonad analyses at two other locations, indicated that polychaetes were more numerous intertidally than subtidally, that intertidal *P. stolonifera* were frequently overgrown by sponges, and that large *P. perna* and *S. margaritacea* often occurred in subtidal samples but seldom in intertidal samples.

Marked differences are apparent between *P. stolonifera* beds in Algoa Bay on the southern Cape coast (Van Driel & Steyl 1976) and those on the Natal coast. The dried flesh weight of subtidal *P. stolonifera* in Natal was approximately half that of similar sites in Algoa Bay. Generally, *P. stolonifera* individuals are considerably larger in the Cape than in Natal (pers. obs.) and this accounts for the difference in biomass. In Algoa Bay, a maximum of 25 species of macroinvertebrates were found in three shallow subtidal *P. stolonifera* beds exposed to direct wave action, and 29 species occurred in three more sheltered subtidal habitats (Van Driel & Steyl 1976). Sixty-one taxa were recorded in subtidal *P. stolonifera* beds in Natal (Appendix 1). Algoa Bay and the Natal coast are parts of different biogeographic provinces on the South African coast, and this may partly account for the differences in the number of species. However, Suchanek (1986) showed that the structural complexity of a matrix such as a mussel bed was correlated with species richness. In a dense *P. stolonifera* bed the smaller animals on the Natal coast would result in a structurally more complex matrix with many more interstices and crevices than would occur in a bed of large individuals such as those on the Cape south coast. This may also play a part in the difference in the number of taxa recorded from the two areas.

On the Natal coast the biomass of macroinvertebrates associated with subtidal beds of *P. stolonifera* was almost an order of magnitude greater than in Algoa Bay. Van Driel & Steyl (1976) recorded macroinvertebrate biomasses of between 75 and 98 $g.m^{-2}$ at exposed and moderately sheltered subtidal sites. Subtidally a mean of 670 $g.m^{-2}$ of associated fauna was found at Vetch's reef, and even in the harsh intertidal zone, biomass (366 $g.m^{-2}$) was approximately four times that in Algoa Bay. The larger macroinveterbrate biomass associated with the Natal coast *P. stolonifera* beds may also be partly a function of the increased number of interstices available between smaller individuals.

Actiniaria and Echinodermata were the most important invertebrates in both biomass and abundance terms in Algoa Bay, and *S. margaritacea* and *P. perna* were poorly represented (Van Driel & Steyl 1976). These two bivalves accounted for 87% of the biomass of associated species in Natal subtidal *P. stolonifera* beds, while numerically, crustaceans and polychaetes were most important (Figures 3 & 4).

P/B ratios for invertebrates vary widely (Burke & Mann 1974; Chambers & Milne 1975). A P/B ratio of 2 : 1 appears to be a fairly conservative estimate for the kinds of organism found associated with *P. stolonifera* (Appendix 1; Burke & Mann 1974). With an average dry weight of associated organisms of 366 $g.m^{-2}$ intertidally and 670 $g.m^{-2}$ subtidally, an estimated secondary production of 732 $g.m^{-2}$ intertidally and 1340 $g.m^{-2}$ subtidally is lost when areas are cleared of *P. stolonifera*. Between 1988 and 1991, an average of 26,91 t (*SD* = 7,61; wet unshelled weight) or about 7 t/k of rocky shore of *P. stolonifera* was removed annually from the northern Maputaland intertidal area (R. Kyle 1992, unpubl. rep.). Harvesting is generally by means of a sharpened vehicle spring blade and clumps of *P. stolonifera* are hacked off the rocks. Patches ranging in size from approximately 0,02 m^2 to 0,25 m^2 are cleared in this manner. Both in Australia and locally, recolonization by *P. stolonifera* of 0,025 m^2 and 0,25 m^2 cleared intertidal patches is extremely slow, ranging from 0–15% recovery after two years (Fairweather 1991; Fielding, unpubl. data). Because the recolonization of cleared patches is so slow, the secondary production lost through this harvesting practice must be considerable. *P. stolonifera* is also occasionally used as a bait organism by fishermen along the Natal coast but legislation forbids the removal of the whole *P. stolonifera* pod. The pod must be left in place and only the top may be cut off to extract the flesh. Although the empty pod decays fairly rapidly (2–4 weeks, Fairweather 1991; Fielding, unpubl. data), this harvesting practice probably allows the mobile organisms which make up nearly 70% of the fauna associated with the *P. stolonifera* beds, time to relocate themselves, and the harvesting method should be encouraged in other areas. Because *P. stolonifera* is not a popular bait organism in Natal, fishermen seldom cut more than three or four scattered animals, and cleared patches are not created. Thus the secondary production lost is probably minimal.

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Appendix 1 — See next page

Appendix 1 Mean density and biomass of macroinvertebrate taxa in five quadrats cleared in *P. stolonifera* beds in the intertidal and subtidal zones along the Natal coast. *SD* in brackets

	Intertidal		Subtidal	
Species	Mean density (m^{-2})	Mean biomass ($g.m^{-2}$)	Mean density (m^{-2})	Mean biomass ($g.m^{-2}$)
Porifera	–	254,275 (214,651)	–	10,294 (8,191)
Anthozoa				
Actinaria spp,	134,8 (30,9)	25,656 (7,363)	4,3 (9,5)	0,418 (0,934)
Nemertea	214,2 (25,3)	1,486 (0,069)	180,1 (18,5)	1,465 (0,037)
Sipunculida	158,9(86,5)	2,156 (1,599)	279,4 (123,7)	6,347 (1,724)
Polychaeta				
Arabella iricolor caerula	35,5 (41,0)	0,388 (0,646)	2,8 (3,9)	0,021 (0,030)
Arabella mutans	42,6 (61,6)	0,692 (0,965)	15,6 (27,7)	0,363 (0,546)
Eunice antennata	1,4 (3,2)	0,006 (0,014)	4,3 (6,3)	0,228 (0,478)
Eunice aphroditois	2,8 (6,3)	0,047 (0,106)	2,8 (6,3)	0,120 (0,268)
Eunice tubifex	2,8 (6,3)	0,129 (0,289)	8,5 (12,7)	0,745 (1,444)
Glycera sp.	–	–	1,4 (3,2)	0,002 (0,003)
Harmothoe spp.	–	–	1,4 (3,2)	0,009 (0,020)
Leocrates sp.	–	–	28,4 (25,1)	0,104 (0,096)
Lepidonotus sp.	5,7 (3,23)	0,066 (0,042)	39,7 (11,9)	0,717 (0,387)
Lumbrinereis coccinea	5,7 (12,7)	0,101 (0,226)	–	–
Lumbrinereis tetraura	2,8 (3,9)	0,040 (0,059)	1,4 (3,2)	0,005 (0,011)
Lumbrinereis spp.	–	–	13,45 (21,8)	0,047 (0,065)
Lysidice natalensis	1,4 (3,2)	0,101 (0,225)	11,3 (9,5)	0,169 (0,055)
Marphysa corallina	195,7 (43,3)	33,773 (6,456)	14,2 (5,0)	0,879 (0,428)
Marphysa sp.	15,6 (17,7)	0,357 (0,644)	–	–
Nereis spp.	2,1 (6,7)	0,018 (0,057)	71,7 (89,9)	0,441 (0,695)
Onuphidinae sp.	–	–	1,4 (3,2)	0,006 (0,012)
Perinereis capensis	1,4 (3,2)	0,052 (0,117)	–	–
Syllis variegata	15,6 (23,7)	0,029 (0,049)	2,8 (3,9)	0,011 (0,016)
Trypanosyllis gemmulifera	7,1 (12,3)	0,004 (0,007)	–	–
Chone sp.	1,4 (3,2)	0,040 (0,088)	21,3 (20,1)	0,379 (0,346)
Cirrformia capensis	8,5 (12,7)	0,071 (0,125)	–	–
Cirriformia punctata	25,5 (19,8)	2,184 (2,828)	4,3 (6,3)	0,181 (0,272)
Gunnarea capensis	1,4 (3,2)	0,144 (0,254)	2,8 (3,9)	0,024 (0,034)
Gyptis capensis	–	–	1,4 (3,2)	0,004 (0,010)
Hydroides sp.	22,7 (20,3)	0,020 (0,018)	–	–
Megalomma quadrioculatum	11,3 (10,8)	0,086 (0,087)	35,5 (25,1)	0,182 (0,145)
Pherusa sp.	–	–	2,8 (3,9)	0,035 (0,050)
Pomatoleios sp.	21,3 (15,0)	0,015 (0,014)	–	–
Terebellid sp.	2,8 (1,9)	0,023 (0,016)	13,2 (11,6)	0,155 (0,122)
Crustacea: Cirripedia				
Balanus amphitrite	–	–	11,3 (10,8)	0,005 (0,004)
Balanus trigonus	12,8 (21,5)	1,535 (3,099)	222,7 (76,5)	49,488 (10,945)
Balanus venustus	76,6 (40,6)	1,482 (0,719)	116,3 (64,7)	1,411 (0,546)
Chthalamus dentatus	18,4 (37,4)	0,004 (0,005)	–	–
Octomeris angulosa	18,4 (19,8)	0,031 (0,039	–	–
Crustacea: Isopoda				
Cirolana sp.	1,4 (3,2)	0,002 (0,003)	–	–
Cymodocella sp.	4,3 (3,9)	0,008 (0,007)	–	–
Lanociro gardineri	5,7 (12,7)	0,035 (0,077)	–	–
Leptanthura laevigata	–	–	7,1 (12,3)	0,059 (0,099)
Mesanthura catenula	1,4 (3,2)	0,002 (0,005)	15,6 (19,7)	0,022 (0,029)
Parisocladus sp.	1,4 (3,2)	0,003 (0,006)	7,1 (12,3)	0,012 (0,021)
(Isopod) sp.	–	–	11,3 (18,5)	0,010 (0,018)
Crustacea: Amphipoda				
Ceradocus natalensis	14,2 (8,7)	0,005 (0,004)	117,7 (39,7)	0,046 (0,017)
Hyale grandicornis	1,4 (3,2)	0,001 (0,003)	12,8 (13,6)	0,032 (0,028)
Lysianassa sp.	2,8 (6,3)	0,002 (0,003)	–	–
Maera spp.	9,3 (10,7)	0,004 (0,006)	61,0 (31,1)	0,053 (0,024)
Talorchesta australis	8,5 (19,0)	0,020 (0,046)	–	–
Urothoe sp.	1,4 (3,2)	0,001 (0,003)	110,6 (20,4)	0,013 (0,002)
(Amphipod) sp.	4,3 (6,3)	0,004 (0,005)	–	–
Crustacea: Decapoda				
Actea sp.	–	–	2,8 (3,9)	0,009 (0,934)
Alpheus crassimanus	4,3 (6,3)	0,049 (0,070)	8,5 (7,8)	0,033 (0,044)
Charybdis orientalis	1,4 (3,2)	0,098 (0,219)	21,3 (15,0)	1,329 (0,987)
Dehaanius quadridentatus	2,8 (6,3)	1,258 (2,812)	5,7 (5,9)	1,169 (1,583)
Hippolyte sp.	–	–	7,1 (10,0)	0,010 (0,013)

Appendix 1 Continued

Species	Intertidal		Subtidal	
	Mean density (m^{-2})	Mean biomass ($g.m^{-2}$)	Mean density (m^{-2})	Mean biomass ($g.m^{-2}$)
Pachycheles natalensis	–	–	2,8 (3,9)	0,438 (0,709)
Pacidea dehaania	39,7 (27,3)	0,407 (0,231)	32,6 (32,3)	0,333 (0,132)
Pilumnus longicornis	–	–	2,8 (3,9)	0,043 (0,058)
Rhyncoplax bovis	4,3 (6,9)	0,040 (0,062)	2,8 (6,9)	0,072 (0,161)
Pycnogonida				
Quebus jamesanus	24,1 (11,9)	0,079 (0,034)	9,9 (22,2)	0,018 (0,040)
Polyplacophora				
Acanthochitonia garnoti	19,9 (13,6)	3,160 (2,367)	9,9 (6,3)	0,684 (1,225)
Bivalvia				
Arcopsis gibba	–	–	31,2 (33,5)	6,069 (6,475)
Barbatia obliquata	19,9 (20,9)	3,483 (4,494)	17,0 (17,8)	6,966 (8,087)
Perna perna	19,9 (10,5)	8,901 (2,194)	178,7 (83,5)	353,854 (72,169)
Septifer bilocularis	73,8 (23,8)	9,485 (5,826)	17,0 (10,8)	10,911 (12,817)
Striostrea margaritacea	–	–	68,1 (56,0)	197,531 (130,069)
(Bivalve) sp.	4,3 (9,5)	1,130 (2,527)	7,1 (8,7)	1,487 (2,598)
Gastropoda				
Diodora crucifer	2,8 (6,3)	0,008 (0,018)	–	–
Diodora spreta	1,4 (3,2)	0,007 (0,015)	–	–
Engina natalensis	2,8 (3,9)	0,011 (0,015)	–	–
Fissurella mutabilis	–	–	7,1 (8,7)	0,016 (0,022)
Gibbula tryoni	2,8 (3,9)	0,023 (0,033)	–	–
Helcion dunkeri	4,3 (9,5)	0,053 (0,118)	–	–
Oxystele tabularis	14,2 (10,0)	0,304 (0,329)	–	–
Patella minuata	1,4 (3,2)	0,002 (0,005)	–	–
Serpulorbis natalensis	4,3 (6,3)	0,130 (0,286)	7,1 (7,1)	3,468 (3,340)
Ophiuroidea				
Macrophiothrix hirsuta cheyena	5,7 (12,7)	0,130 (0,290)	19,9 (7,8)	1,346 (0,791)
Ophiactus savignyi	–	–	58,2 (43,8)	1,035 (0,707)
Crinoidea				
Comanthus wahlbergi	–	–	2,8 (3,9)	0,646 (1,037)
Ascidiaceae	–	1,085 (2,003)	–	2,709 (3,811)