THE ALGAL GARDENS OF *Patella cochlear*

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UCT

For my dad

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ABSTRACT

Most *Patella cochlear* limpets are surrounded by a garden of algae on which they graze. Thus far only two species of foliose or filamentous algae, as well as some crustose forms and corallines, has been recorded in limpet gardens by Branch and Steneck (unpublished). This study focuses on the filamentous or foliose algae in the gardens.

Data was collected from limpet gardens mainly around the Cape peninsula, as well as from the Heads, near Knysna. It was immediately clear that the species diversity of algae in the gardens is much higher than originally expected. 15 Species of foliose / filamentous algae from 7 families have been recorded to occur in the gardens of *P. cochlear* in this study area. No definite pattern has been found in the horizontal distribution of species, for example *Gelidium micropterum*, to make it a "west" or "south" coast species, as was commonly believed. There is vertical zonation of algal species, as well as limpet sizes, in the cochlear zone. In the lower cochlear zone, larger limpets are found with *Herposiphonia heringii* as the dominant garden species there. *Antithamnionella tormentosa* is dominant in the mid-cochlear, and *Gelidium micropterum* is the most common species in the upper cochlear zone, where the limpets are also smaller on average. The smaller gardens of small limpets, their species composition, and the smaller size of *Gelidium micropterum* individuals in them are all correlated with the fact that juvenile limpets have to settle on adults until an empty scar becomes available for them to move down to. There still remains more questions about limpet gardens unanswered than answered, especially about what species the limpets really eat, and how their growth is enhanced by the presence of the limpets.

Grazing by these limpets have a profound effect on the growth of macroalgae in the cochlear zone. McQuaid (1980) documents the dramatic influence of *P. cochlear* on algae. Algal biomass and diversity increases as one goes lower on the shore, but on reaching the cochlear zone, both of these decrease sharply. Steneck (1988) states that increasing herbivory reduces algal biomass and shifts community dominance from macroalgae to turf and ultimately to encrusting corallines. Removal of *Patella cochlear* allows the establishment of a rich algal community, which could exclude the limpets for more than ten years (Branch, 1981).

Nicotri (1977) showed that grazing by three other limpet species had a relatively small effect on diatoms and virtually no effect on blue-green algae. No information on this is available for *P. cochlear*, and this study also does not cover that field.

The gut contents of *P. cochlear* is practically only calcareous material (Steneck, pers com), which led to initial beliefs that they feed mainly on coralline algae. These were identified by Chamberlain (unpublished) to be mainly *Spongites yendoii* and *S. impar*. Crustose corallines survive the most frequent and intense grazing by having a thick epithallus and morphology that resist grazing damage (Steneck 1988). Crustose corallines are often also dependent on limpet grazing to remove epiphytic overgrowth, as well as to regulate crust thickness, and therefore competitive ability (Steneck 1989).

An analysis of the energy budget of *P. cochlear* (Branch 1981) showed that adult limpets cannot survive on crusts alone. That led to his suggestion that the adults mainly depend on *Herposiphonia heringii* for their energy requirements. This will be discussed in more detail later.

INTRODUCTION

Patella cochlear is the dominant limpet in the lower intertidal zone, often known as the cochlear zone (after this species). They are territorial and often "keep" gardens of algae, on which they feed. If the limpets are removed, the gardens initially flourish, but they subsequently die back and are replaced by other algae (Branch,1981). Thus these gardens are clearly dependent on the limpets for their maintenance (Branch 1985a).

The numbers of *P. cochlear* increase with wave intensity (Branch 1975), therefore they occur on exposed, seaward-facing rock surfaces. Populations are normally crowded, so that juveniles only survive if they settle on the shells of adult limpets (Branch, 1981). They will sometimes even have a garden on the shell of an adult, if there is strong competition for space (see plate 1.)

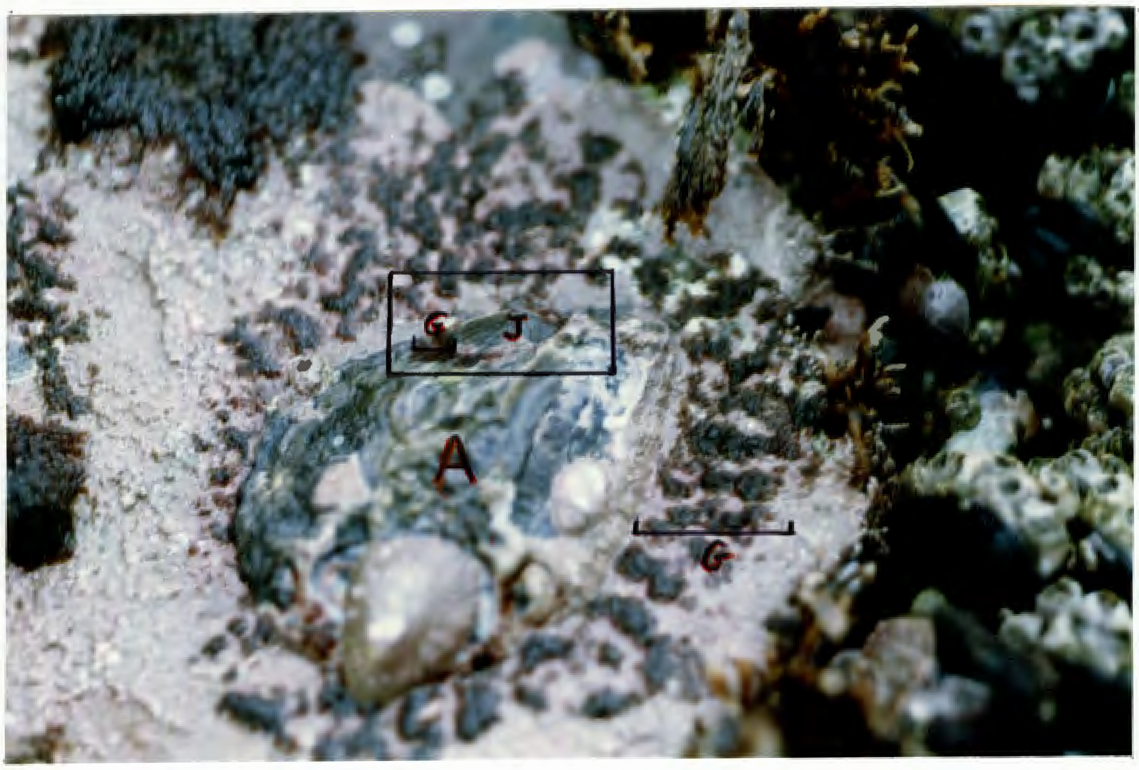


Plate 1. Adult *Patella cochlear* (A) with its garden (G). In small frame: juvenile limpet (J), with its own garden (G) on the shell of the adult.

With growth, a point is reached where the limpets are too large to occupy shells and must descend to the rock. This transition makes the animal vulnerable until they establish a new home scar. High mortality occurs during this period (Branch,1975).

P. cochlear scrapes algae from the substratum by using the radula. Radular muscles pull the radula like a rope over a pulley. In the Patellacea the radula has fewer teeth, allowing the development of a few very strong teeth that can easily excavate even the toughest coralline algae (Branch,1985). The body of each tooth is made of protein and chitin, with a silica skeleton, capped with Goethite, a particularly hard form of iron oxide. The front of the cusps are rich in iron, while the back is richer in silicon. As the back edge is softer and the orientation of fibres is more subject to wear, the tooth acts as a self-sharpening device, keeping the leading edge sharp (Runham 1975).

Plate 2. *Patella cochlear* with paths grazed through its garden.

As can be seen from the above review, there is very little in botanical literature on the algal species in the gardens of *Patella cochlear*.

This will be the first known study to specifically look at the foliose \ filamentous species in *P. cochlear* gardens.

The aim of this study was to answer the following questions:

1. What is the algal species composition of the limpet gardens?
2. Is there a difference in species found in gardens on the coast west of Cape Point, compared to gardens on the coast south of Cape Point?
3. Is there vertical zonation of garden species?
4. Is there a correlation between the size of a limpet and the size of its garden?
5. Is there a correlation between the size of a limpet and the size of *Gelidium micropterum* individuals that occur in its garden?
6. Is there a correlation between the size of a limpet and the distance to its nearest neighbour?
7. Is there vertical zonation of limpet size?
8. Is there a correlation between the size of a limpet and the species of algae that occur in its garden?

METHODS

Study area

The study area includes the west- and False Bay coasts of the Cape peninsula as well as The Heads, near Knysna on the south coast, from where a single sample was collected. For convenience, everywhere east and south of Cape Point will be called "south" coast in this report.

Fig. 1. Map of the coastline of the Cape peninsula, showing sampling sites.

Collecting sites and dates on the west coast were Blouberg (1/8, 15/8 and 12/9/92), Kommetjie (16/6/92), Oliphantsbos (11/9/92) and Platboom (11/9/92).

On the False Bay- and south coast colections were made at Millers Point (3/6/92), Glencairn (3/6/92), Dalebrook (4/5/92), and also Knysna (7/92).

The substrate at Blouberg is predominantly shale, at Millers Point it is granite, and all the other sampling sites are on Table Mountain Sandstone.

Sampling

Due to the cochlear zone's position immediately above the low water mark of spring tides, sampling was difficult in winter, and opportunities were few. Thus complete samples were only taken at three sites, Blouberg, Dalebrook and Kommetjie.

At Blouberg six quadrats of 25cm x 25cm were sampled. Three quadrats were in the upper cochlear zone, all within about 25 cm of the uppermost occurrence of *P. cochlear*, with a total number of 59 limpets. Two samples were taken in the mid-cochlear zone, more or less 50cm lower, with 25 limpets. Due to large swell and bad weather on two sampling excursions, only one quadrat could be sampled in the lower cochlear zone, about 60cm below the mid-zone quadrats, containing 10 limpets. These samples were taken to establish whether the same species of algae occur in the limpet gardens in the upper and lower cochlear zone.

At Dalebrook three 25cm x25cm quadrats were sampled, in the upper cochlear zone, containing a total of 31 limpets.

At Kommetjie three quadrats, with 33 limpets in total, were sampled in the mid- and upper cochlear zone.

In each quadrat, every limpet was given a number and a matched sample bottle for a specimen of its algal garden. Limpet lengths, widths, and nearest neighbour distances were measured with vernier calipers. The average width of each limpet's garden was then estimated by measuring the width of the portion of its garden that represents the average width of the garden. It must be stressed that this is only a visual estimate, since the gardens are often very patchy. The gardens were scraped with a pocket knife and a sample of the algae put in the numbered bottles, containing 5% formalin sea water for preservation.

These were then taken back to the laboratory for identification. The species were identified from Stegenga *et al* (in prep). The percentage occurrence of the different species in each garden was estimated. If the sample contained *Gelidium micropterum*, the size of the largest individual of this species was then measured, using a grid of graph paper and a dissecting microscope.

At Oliphantsbos, Platboom, Millers Point, Glencairn and Knysna, samples of algae were scraped from the gardens of at least 20 limpets. These were preserved and analysed similarly to the quadrat samples back at the laboratory.

Data analysis

The data was entered into Quattro Pro spreadsheets. Averages, frequency distributions and bar charts and were made using this program. Regression analyses and scatterplots were done after importing the data into Statgraphics 5.0.

RESULTS

1. Species composition of the limpet gardens

A total of 15 species of non-crustose algae were found in the gardens of *Patella cochlear*. Almost all the gardens also contained small amounts of a variety of blue-green algae, but these were not identified and could make an interesting study.

The following is a list of all the garden species found, with a short description of each of the four most common species:

Division Rhodophyta

Rhodophyceae

Rhodomelaceae

Herposiphonia heringii (Harvey) Falkenberg

Plants prostrate or with erect filaments up to 5 cm. Prostrate axes attached by several rhizoids per segment. Laterals in two rows, awl-shaped. Number of pericentral cells 14–16; basal segment with 7. Tetrasporangia from the second segment upward.

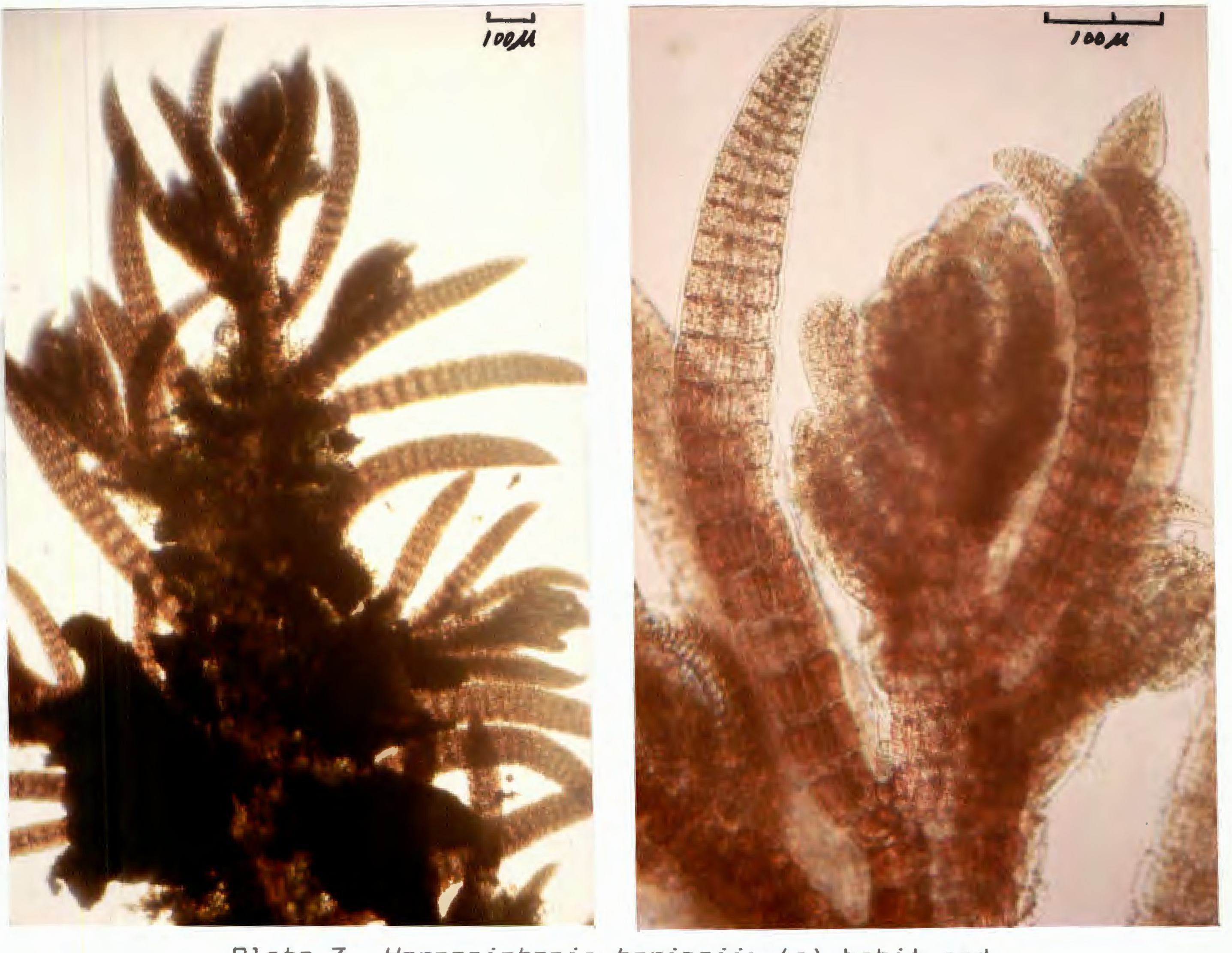
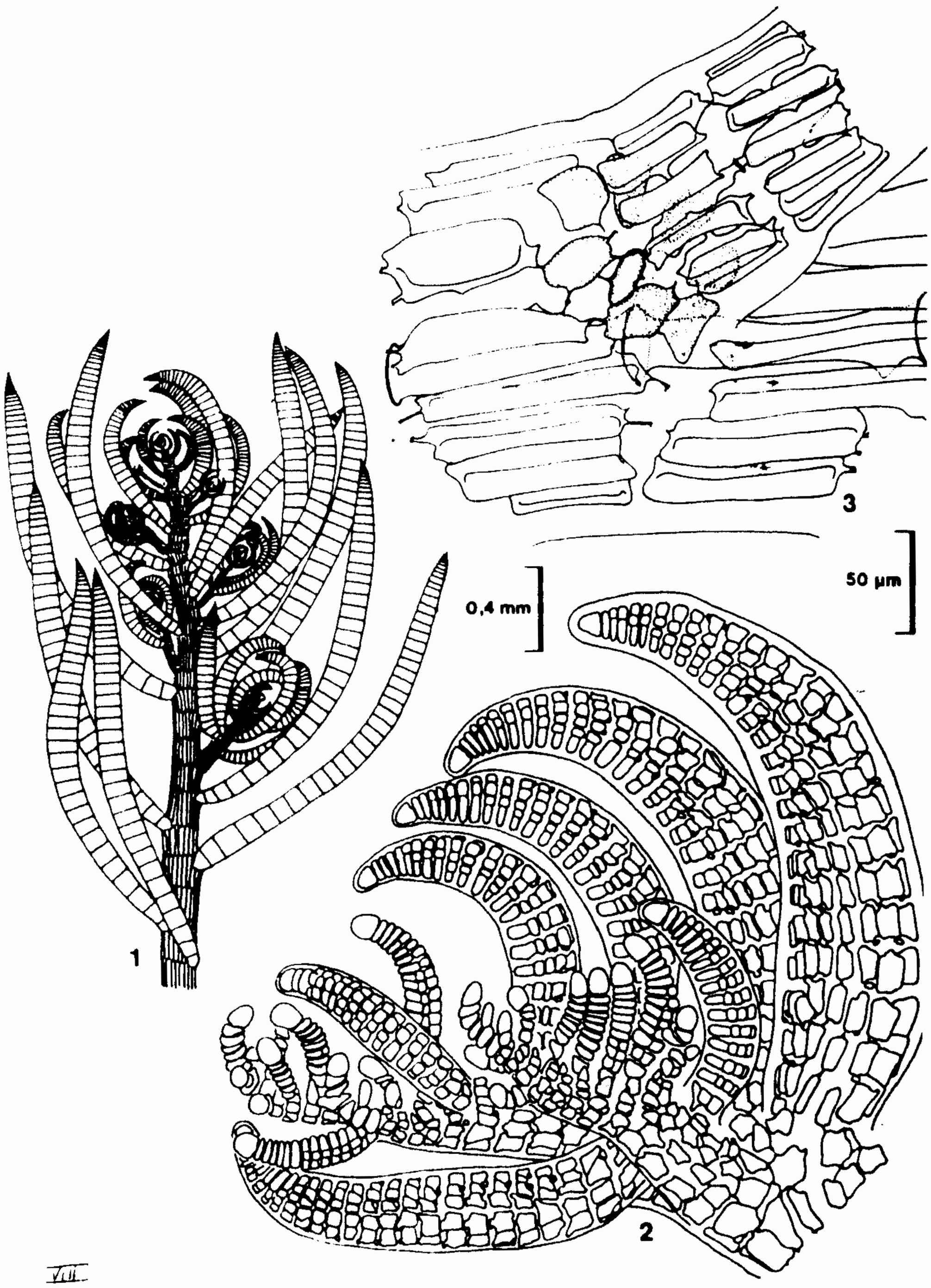


Plate 3. *Herposiphonia heringii*: (a) habit and (b) structure.



(c) structure (from Stegenga, et al (in prep)).

Polysiphonia incompta Harvey

Plants pale brown to black, caespitose, up to several cm high. No clearly defined main axis. Prostrate filaments attached by rhizoids cut off from the pericentral cells. Segments with four pericentral cells without cortication. Radial branching, trichoblasts on every segment, spirally arranged. Tetrasporangia in subapical section.

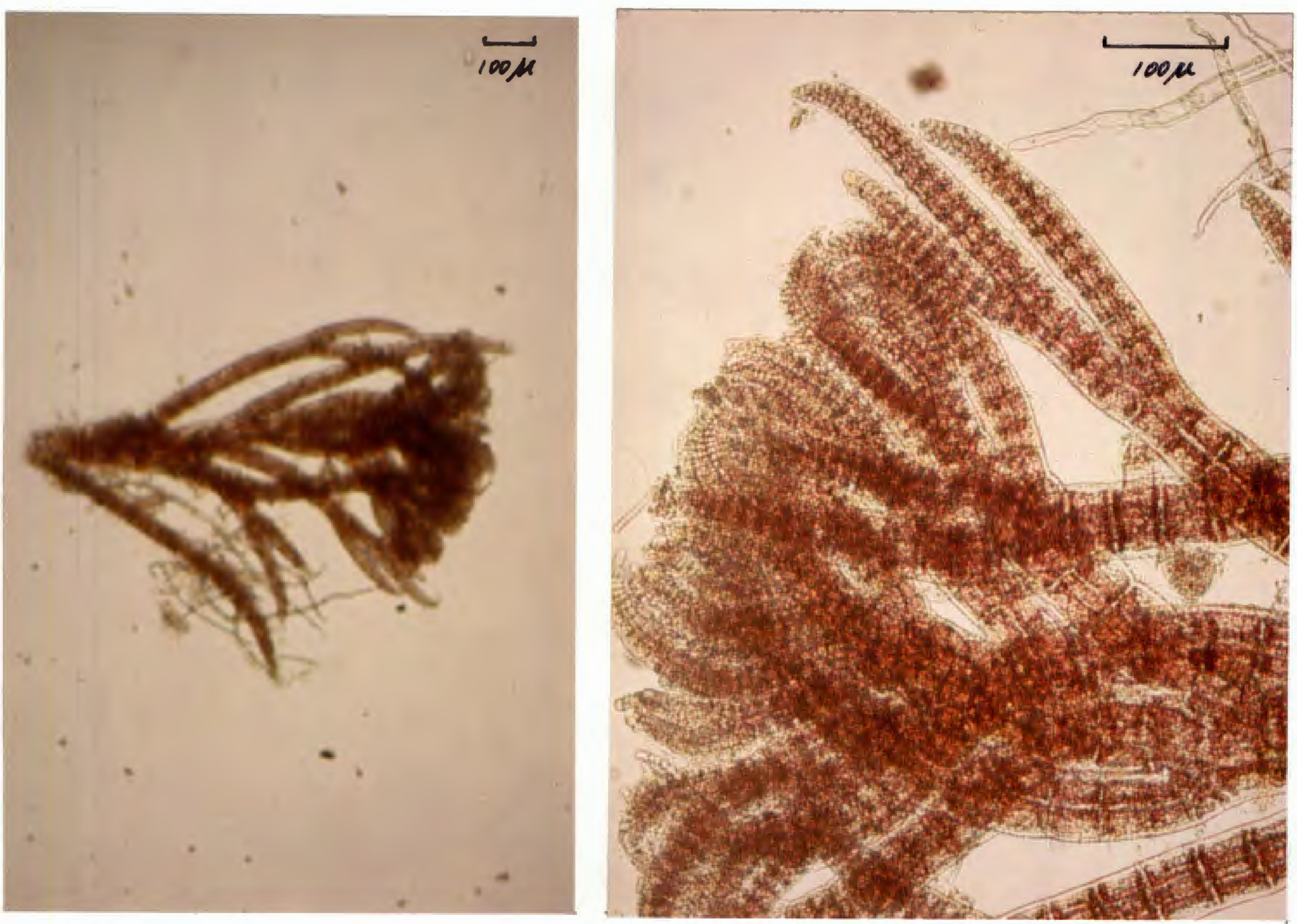
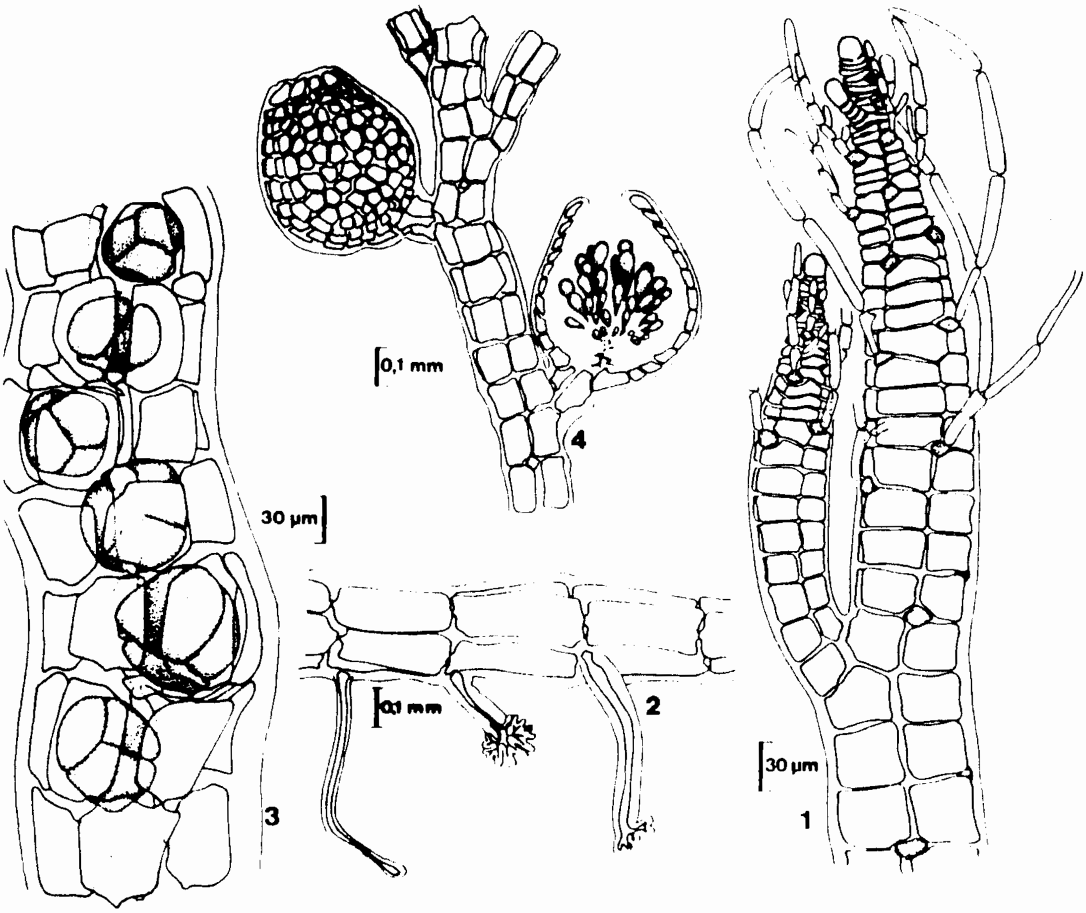


Plate 4. *Polysiphona incompta* : (a) Habit and (b) structure.



(c) structure (from Stegenga et al. (in prep))

Strebloladia camptoclada (Montagne) Falkenberg

Rhodophyceae

Ceramiales

Ceramiaceae

Antithamnionella tormentosa Stegenga

Plants with prostrate basal parts and numerous erect axes. Prostrate filaments attached by unicellular rhizoids growing from the whorl branchlets. Indeterminate laterals grow from alternate segments, with apices crowded, and acute. Gland cells present on the fourth to the seventh cell below the apices. Tetrasporangia sessile or pedicellate on whorl branchlet

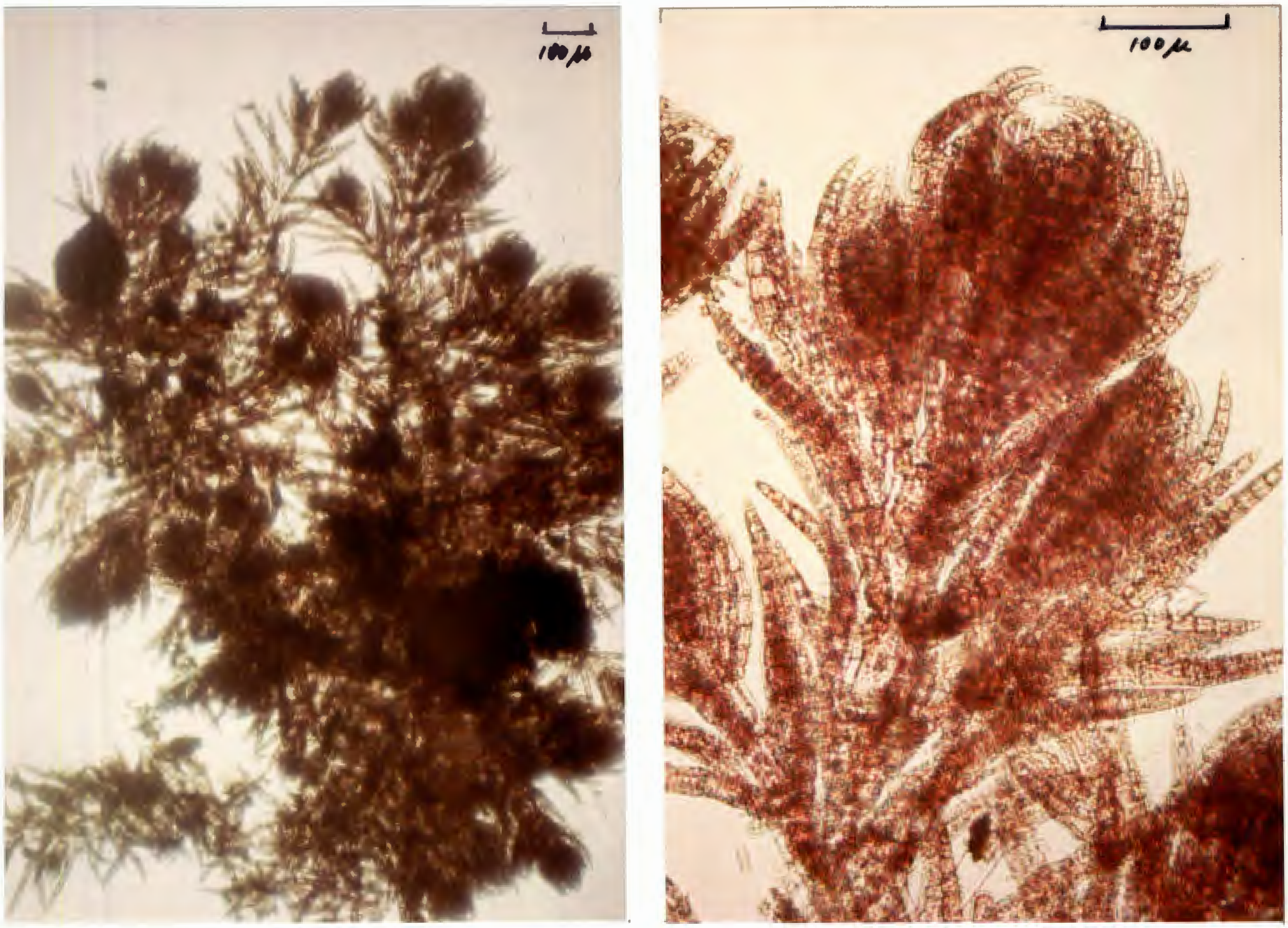
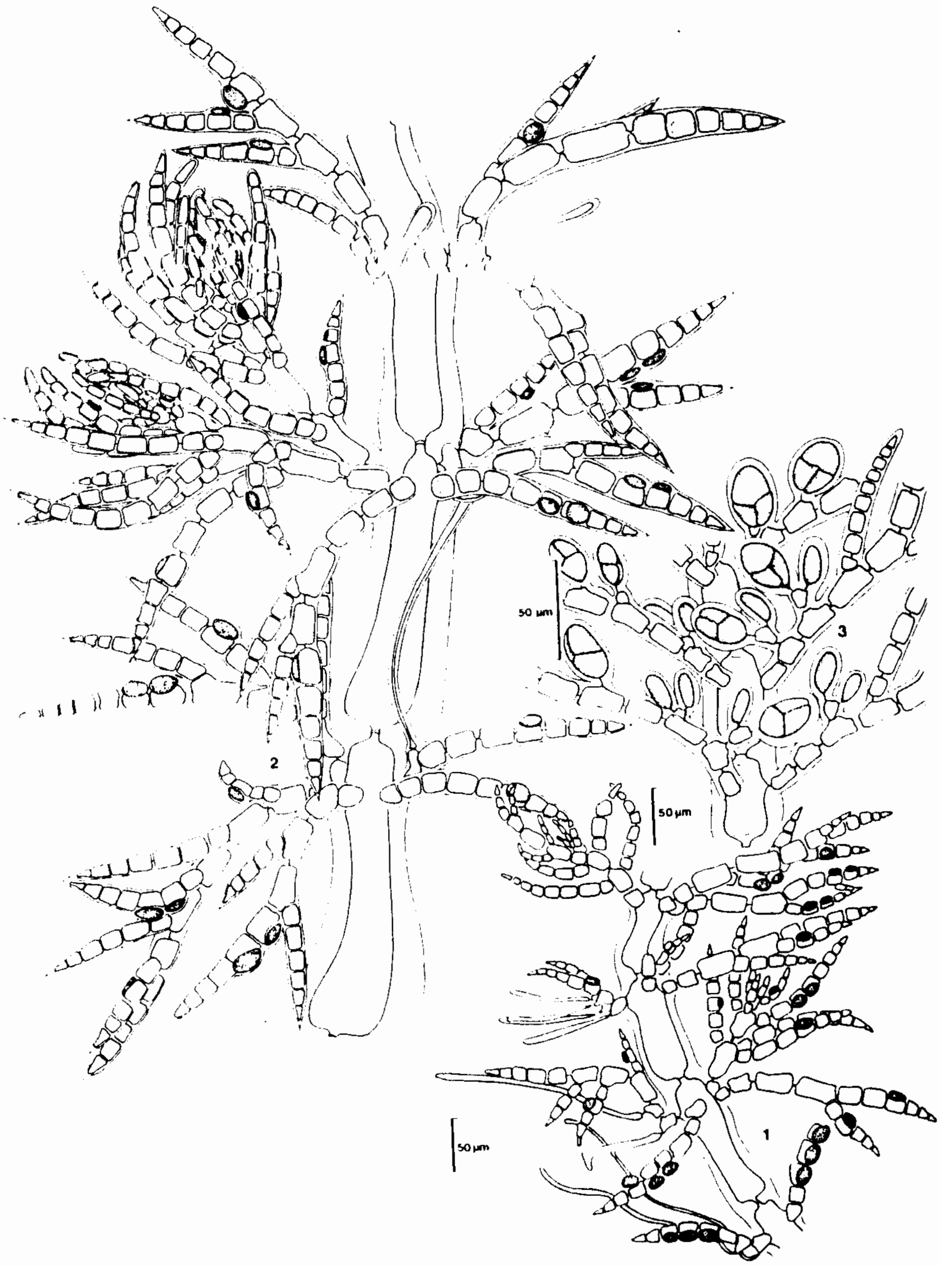


Plate 5. *Antithamnionella tormentosa:* (a) Habit and (b) structure.



(c) structure (from Stegenga, 1986)

Centroceras clavulatum (C.Ag.) Montagne

Ceramium sp

Ceramium arenarium Simons

Ceramium obsoletum C. Agardh

Lophosiphonia capensis (Kylin) R.E. Norris comb. nov.

Florideophyceae

Acrochaetiaceae

Rhodothamniella floridula (Dillwyn) Feldmann

Gelideaceae

Gelidium micropterum Kützing

Rarely over 5 cm, brownish red. Texture soft and fleshy. Axes flattened, pinnately branched, branchlets short. Rhizines confined to a narrow strip in the medulla. Bisporangial sori in (pen-)ultimate branchlets of roundish outline. The garden plants are also reproductive, despite their small size, with bisporangial sori.

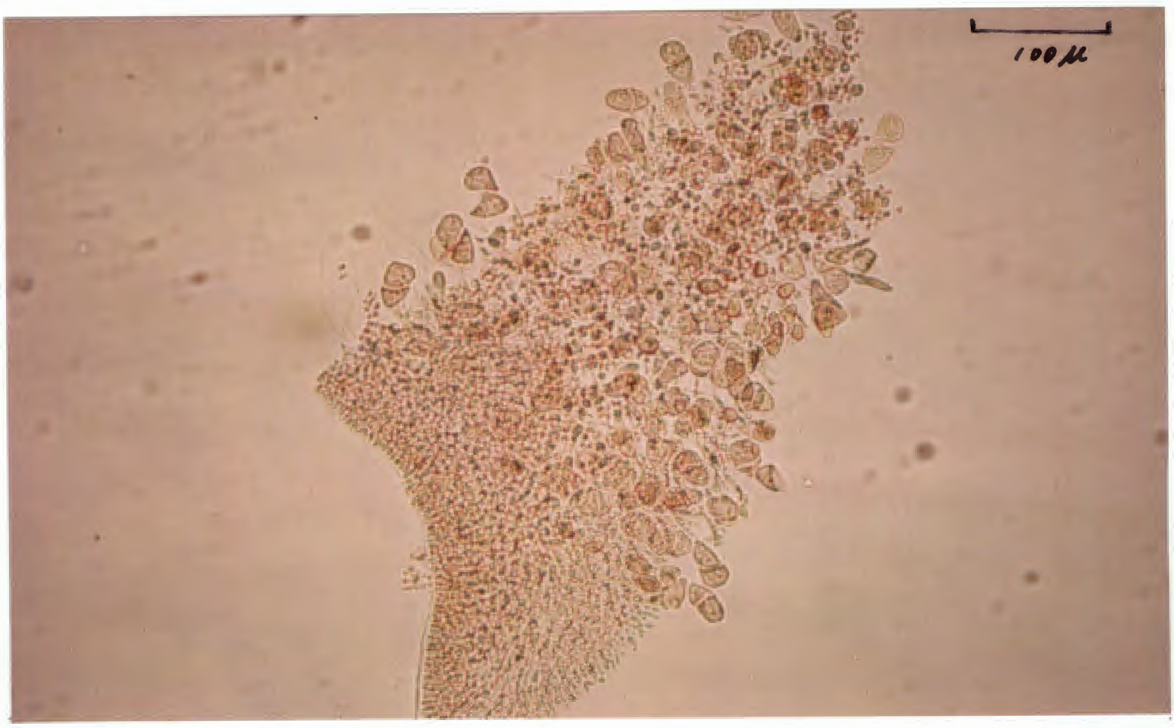


Plate 6. Sorus of *Gelidium micropterum* with bispores.

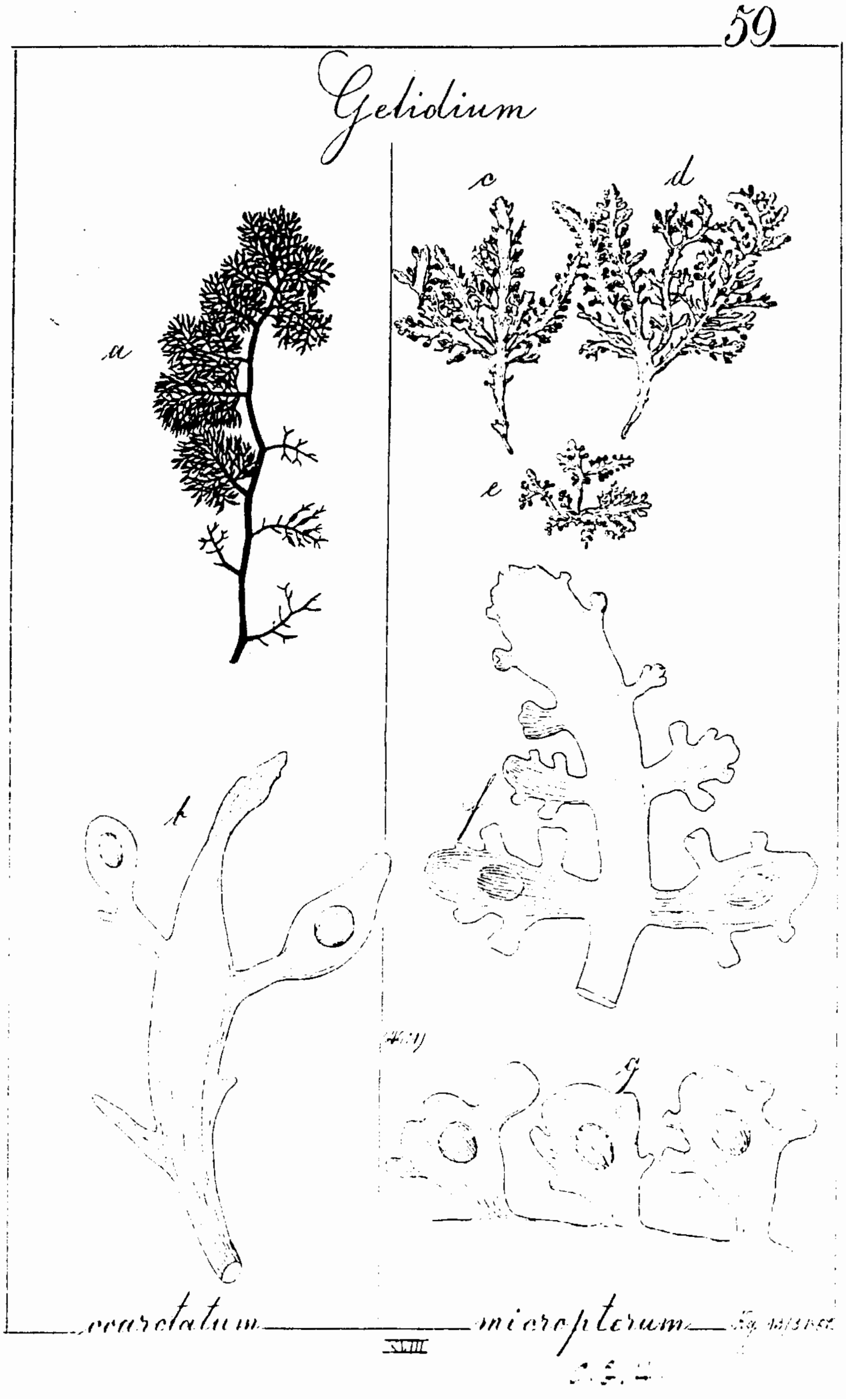
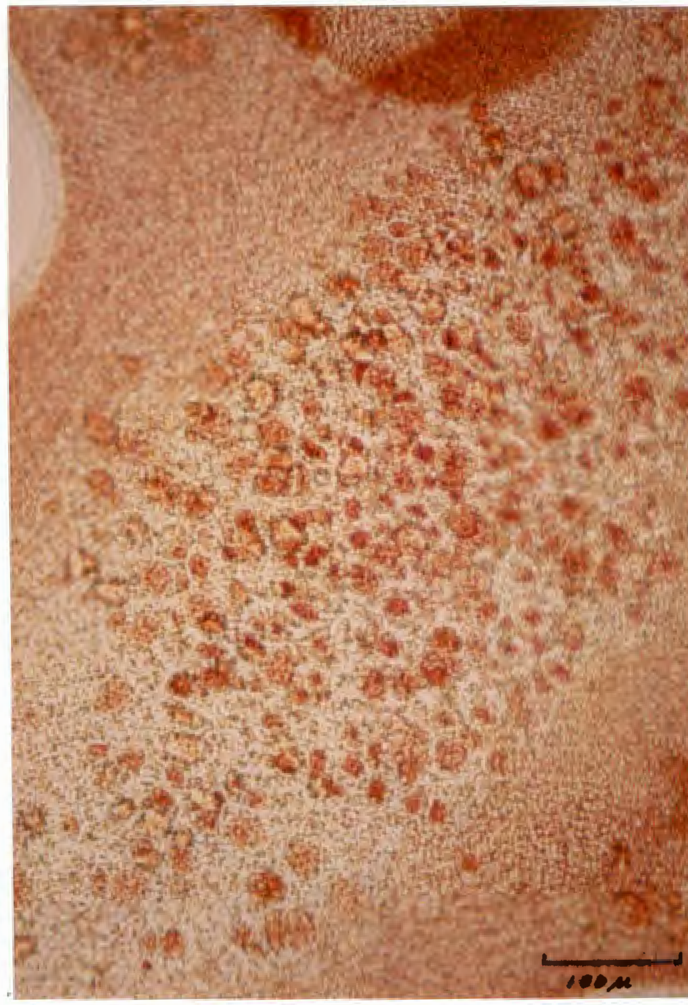


Plate 7. *Gelidium micropterum* : (a) structure (from Kützing, 1868)



(b) habit and (c) structure *of sorus*

Chlorophyta

Cladophorales

Cladophoraceae

Cladophora sp.

Cladophora capensis Kützing

Ulvaceae

Enteromorpha sp.

Phaeophyta

Phaeophyceae

Chordariales

Encoeliaceae

Colpomenia sinuosa (Roth) Derbes et Solier

2. *Species composition of west coast, compared to south coast gardens*

Table 1. Percentage cover of species at different sites along the coast west- and south of Cape Point. (BB = Blouberg, KM = Kommetjie, OB = Oliphantsbos, PB = Platboom, MP = Millerspoint, GC = Glencairn, DB = Dalebrook, KN = Knysna). (sh= shale, tm = table mountain sandstone, gr = granite).(N = no. of gardens sampled, including all samples at Blouberg)

	WEST COAST				SOUTH COAST			
SAMPLING SITES	BB	KM	OB	PB	MP	GC	DB	KN
SUBSTRATE	sh	tm	tm	tm	gr	tm	tm	tm
N	60	29	≥20	≥20	≥30	≥20	27	≥20
Antithamn. tormentosa	31							
Centroceras clavulatum		1						
Ceramium sp	1	1	1	1			1	
Ceramium arenarium								1
Ceramium obsoletum		1						
Cladophora sp.					1	25	1	
Cladophora capensis		1						
Colpomenia sinuosa							1	
Enteromorpha sp.		1						
Gelidium micropterum	56	80	50	50	90	70	95	98
Herposiphonia heringii	13	20				1		
Lophosiphonia capensis							1	
Polysiphonia incompta			50	50	10			
Rhodothamniella floridula					1			
Streblocladia camptoclada	1							

The horizontal distribution of individual species will be treated in the discussion.

3. Vertical zonation of garden species

A definite pattern was found in the zonation of garden species at Blouberg. *Gelidium micropterum* is the dominant species in the upper cochlear zone, *Antithamnionella tormentosa* dominates the mid- cochlear and *Herposiphonia heringii* is the dominant species in the lower cochlear zone.

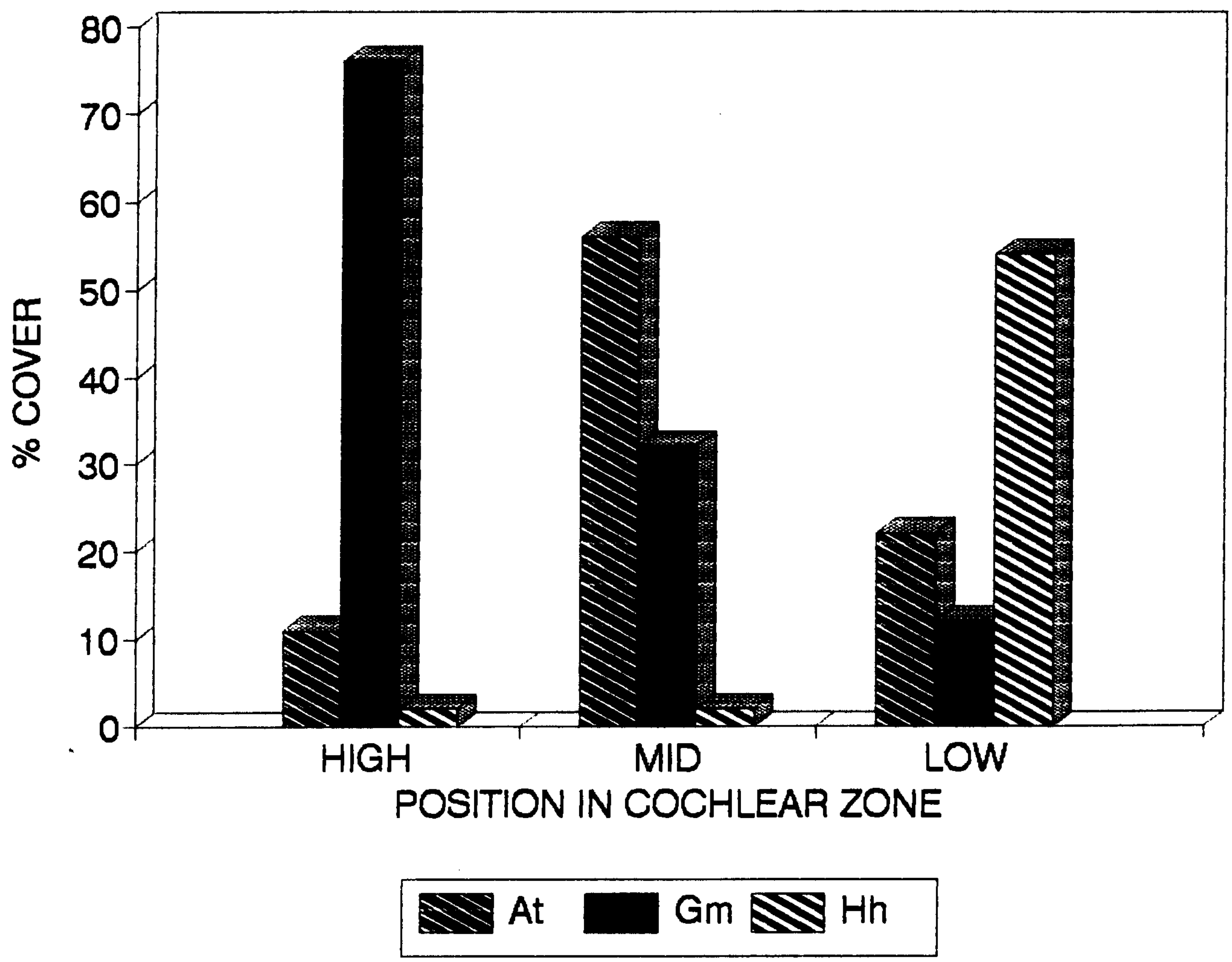


Fig. 2. Vertical zonation of the three dominant species of algae in the gardens of *Patella cochlear* at Blouberg.
(At = *Antithamnionella tormentosa*, Gm = *Gelidium micropterum*, Hh = *Herposiphonia heringii*). (Number of gardens sampled per zone: High = 26, Mid = 25, Low = 9)

According to Stegenga et al (in prep) *Antithamnionella tormentosa* is a subtidal species. However, in this study it has been collected from limpet gardens over the whole cochlear zone at Blouberg, with an estimated average percentage cover of 31%. It is interesting to note that it is the dominant species in the mid-cochlear zone, with a percentage cover of 56%, and not in the lower cochlear (Fig.2.).

Gelidium micropterum is the dominant species in the higher cochlear zone at Blouberg, but its abundance decreases rapidly towards the lower cochlear, where its cover is only 12% (Fig.2). It would be interesting to compare the zonation of the limpet garden populations of Blouberg with those of Oliphantsbos and Platboom, to see if there is a similar trend in the presence of the two co-dominant species, *Herposiphonia heringii* and *Polysiphonia incompta*, respectively.

The collection at Blouberg confirms Stegengas records that *Herposiphonia heringii* is a lower intertidal to sublittoral species. Figure 2 shows that it is the dominant species in the lower cochlear zone.

4. Relationship between limpet size and garden size

Although a few large limpets were found with small gardens, there were no small limpets with large gardens. Variation in limpet size accounted for 50.52 percent of the variation in garden size. (See table 2 for summary of statistics.) Figure 3 shows clearly that the size of the garden increases with limpet size.

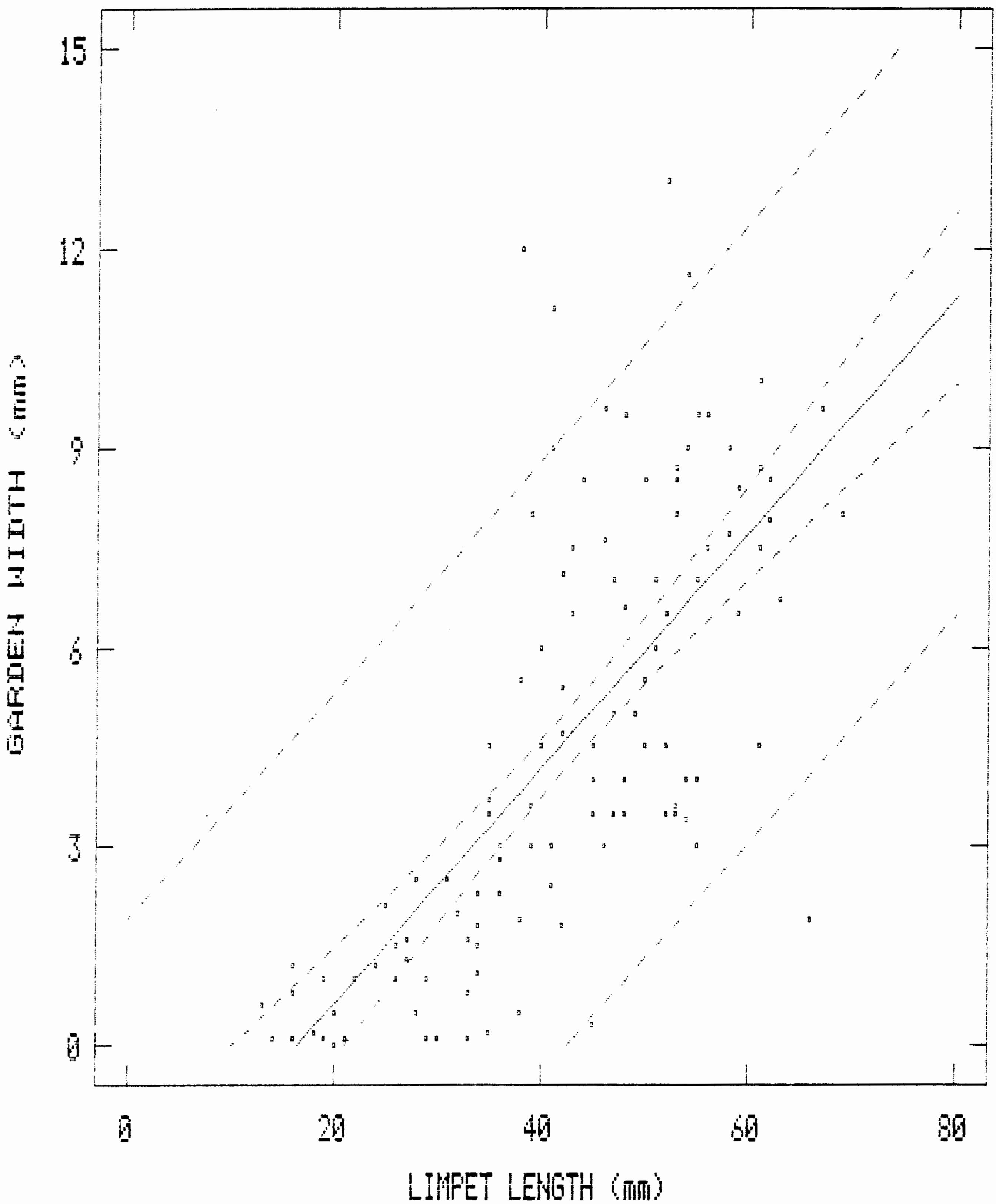


Fig. 3. Regression of the correlation between limpet size and garden size.

Table 2. Summary of statistics of regression analysis of the relationship between limpet size and garden size.

Regression Analysis - Linear model: Y = a+bX

Dependent variable: TSORT.Gar — Independent variable: TSORT

Parameter	Estimate	Standard Error	T Value	Prob. Level
Intercept	-2.90435	0.7281	-3.98894	.00012
Slope	0.176978	0.0164055	10.7878	.00000

Analysis of Variance

Source	Sum of Squares	Df	Mean Square	F-Ratio	Prob. Level
Model	631.16470	1	631.16470	116.3758	.00000
Residual	618.27971	114	5.42351		
Lack-of-fit	182.25918	46	3.96216	.6179	.95756
Pure error	436.02053	68	6.41207		
Total (Corr.)	1249.4444	115			

Correlation Coefficient = 0.710743 R-squared = 50.52 percent
Stnd. Error of Est. = 2.32884

5. Relationship between limpet size and the size of algal plants in its garden

Since *Gelidium micropterum* was the most common garden species, it was chosen to be measured for size comparison. Table 3 shows that only 19.23 percent of the variation in the size of *Gelidium micropterum* individuals can be explained by variance in the size of limpets, but it is clear from the graph in figure 4 that there are no small limpets with large plants in their gardens, while there are quite a few large limpets with plants smaller than 2mm in their gardens.

Table 3. Summary of regression of *Gelidium micropterum* size and limpet size.

Regression Analysis - Linear model: Y = a+bX

Dependent variable: TSORT.GmSize   Independent variable: TSOR

Parameter	Estimate	Standard Error	T Value	Prob. Level
Intercept	1.12023	0.407794	2.74704	.00719
Slope	0.0420519	8.84153E-3	4.75618	.00001

Analysis of Variance

Source	Sum of Squares	Df	Mean Square	F-Ratio	Prob. Level
Model	25.142996	1	25.142996	22.62123	.00001
Residual	105.59041	95	1.11148		
Lack-of-fit	37.814573	40	.945364	.76716	.80899
Pure error	67.775833	55	1.232288		
Total (Corr.)	130.73340	96			

Correlation Coefficient = 0.438546   R-squared = 19.23 percent

Stnd. Error of Est. = 1.05427

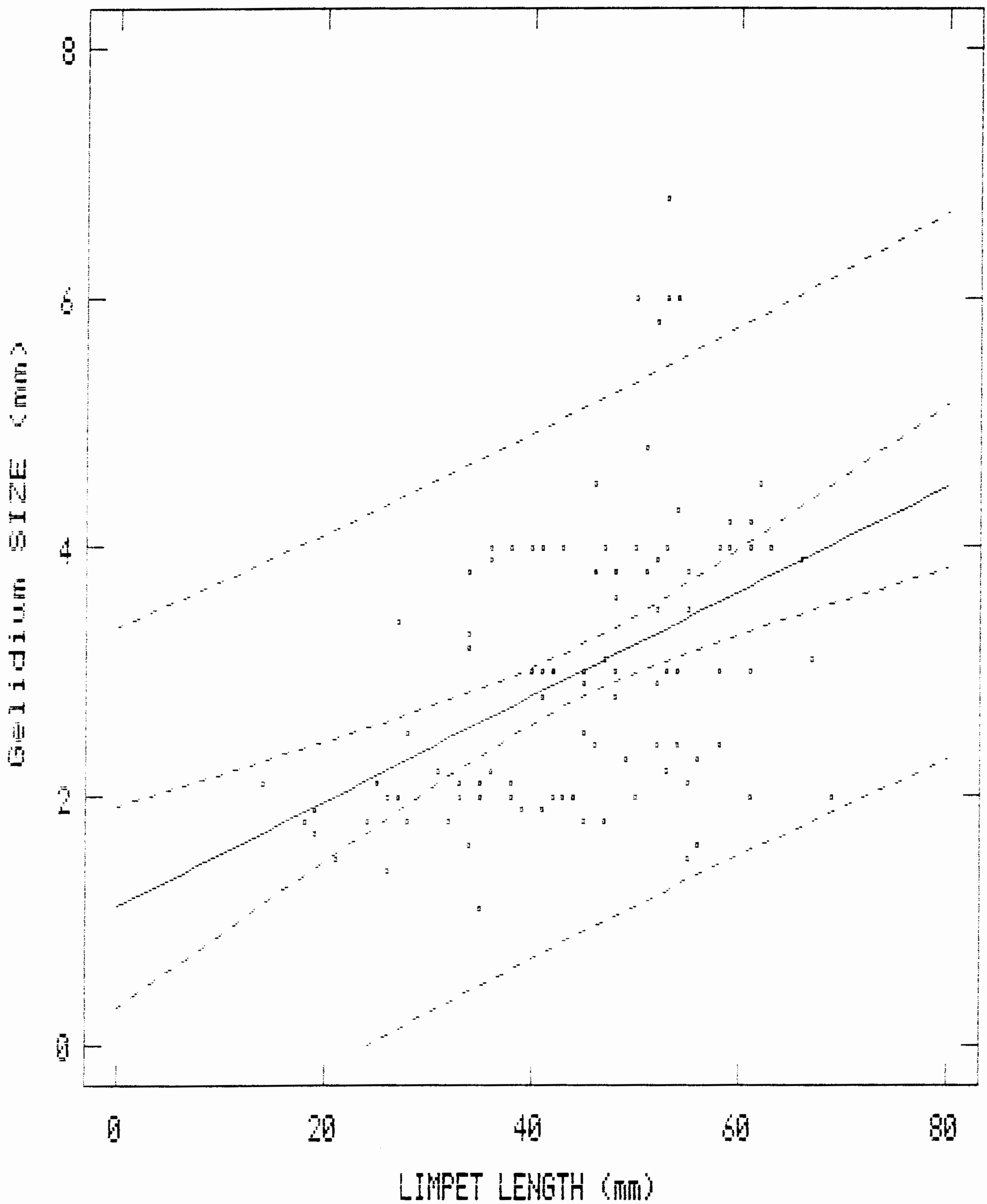


Fig. 4. Regression of limpet size and the size of *Gelidium micropterum* individuals in their gardens.

6. Relationship between the size of a limpet and the distance to its nearest neighbour

Table 4 and Figure 5 shows a weak relationship between the size of a limpet and the distance to its nearest neighbour. Only 26.78 percent of the variation in measured nearest neighbour distances can be explained by variation in limpet size. In other words, there is a tendency for limpets to have larger territories with increased size, but there are many exceptions to the rule, as shown by figure 5.

Table 4. Summary of regression analysis of limpet length and nearest neighbour distance.

Regression Analysis - Linear model: Y = a+bX

Dependent variable: TSORT.Nrd Independent variable: TSORT

Parameter	Estimate	Standard Error	T Value	Prob. Level
Intercept	5.52102	1.31148	4.20975	.00004
Slope	0.240628	0.0321696	7.48	.00000

Analysis of Variance

Source	Sum of Squares	Df	Mean Square	F-Ratio	Prob. Level
Model	1811.0576	1	1811.0576	55.950	.00000
Residual	4952.4521	153	32.3690		
Lack-of-fit	1373.7283	49	28.0353	.815	.78616
Pure error	3578.7238	104	34.4108		
Total (Corr.)	6763.5097	154			

Correlation Coefficient = 0.517464 R-squared = 26.78 percent
Stnd. Error of Est. = 5.68937

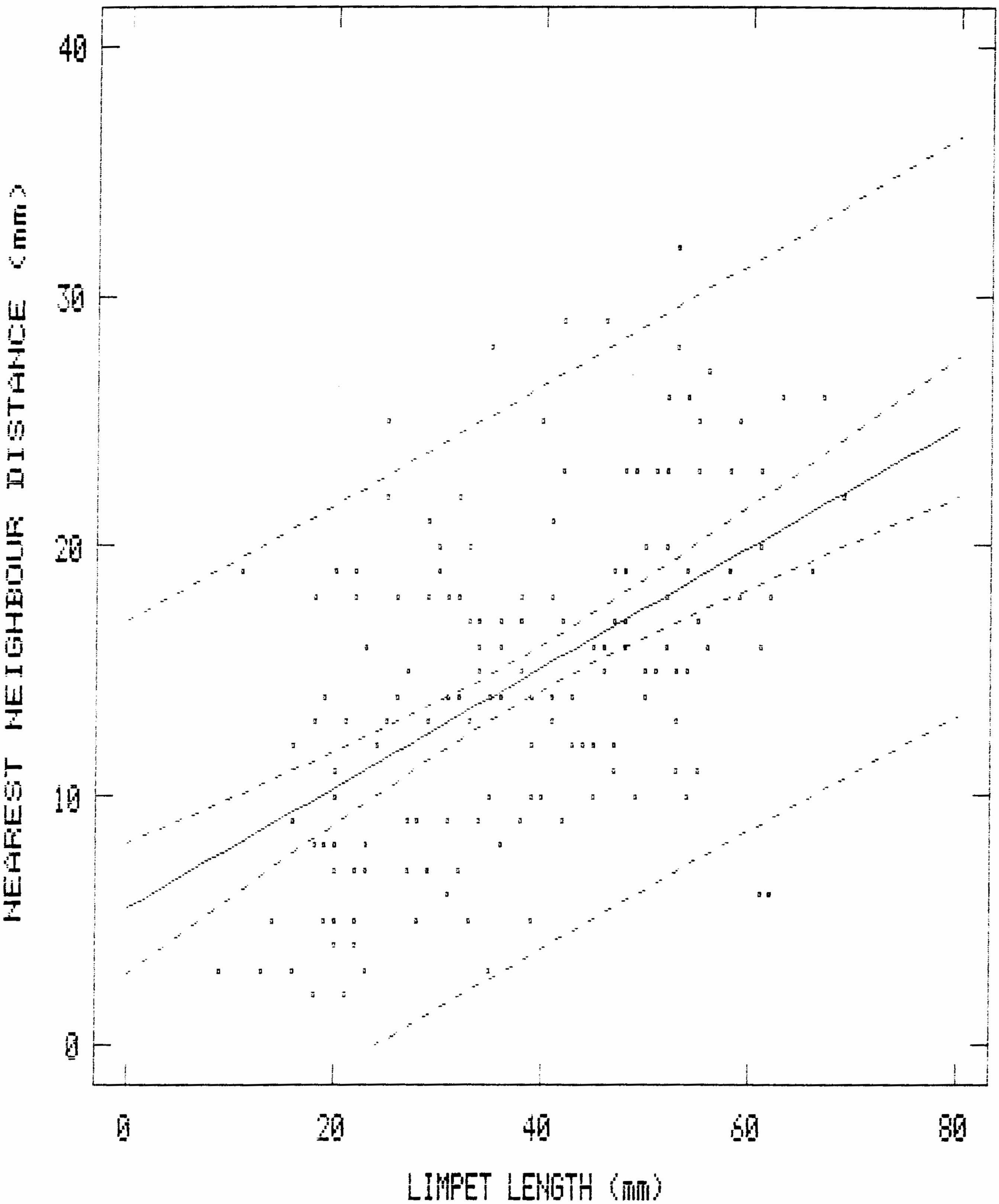


Fig. 5. Best fit line of correlation between limpet size and nearest neighbour distance.

7. Is there vertical zonation in limpet size?

At Blouberg, the difference in sizes of limpets in the upper and lower cochlear zone were clearly visible in some areas, as shown in plates 8, 9. and 10. Unfortunately it was not possible to sample in the area shown in plate 8, since it was on a vertical, very exposed rock face, but figure 6 shows clearly that there are definitely more large limpets in the lower cochlear zone than near the top.

Plate 8. Rock face at Blouberg, showing vertical zonation of different sizes of *Patella cochlear*.

Plate 9. 25cm x25cm Quadrat in the upper cochlear zone, showing many individuals of small size.

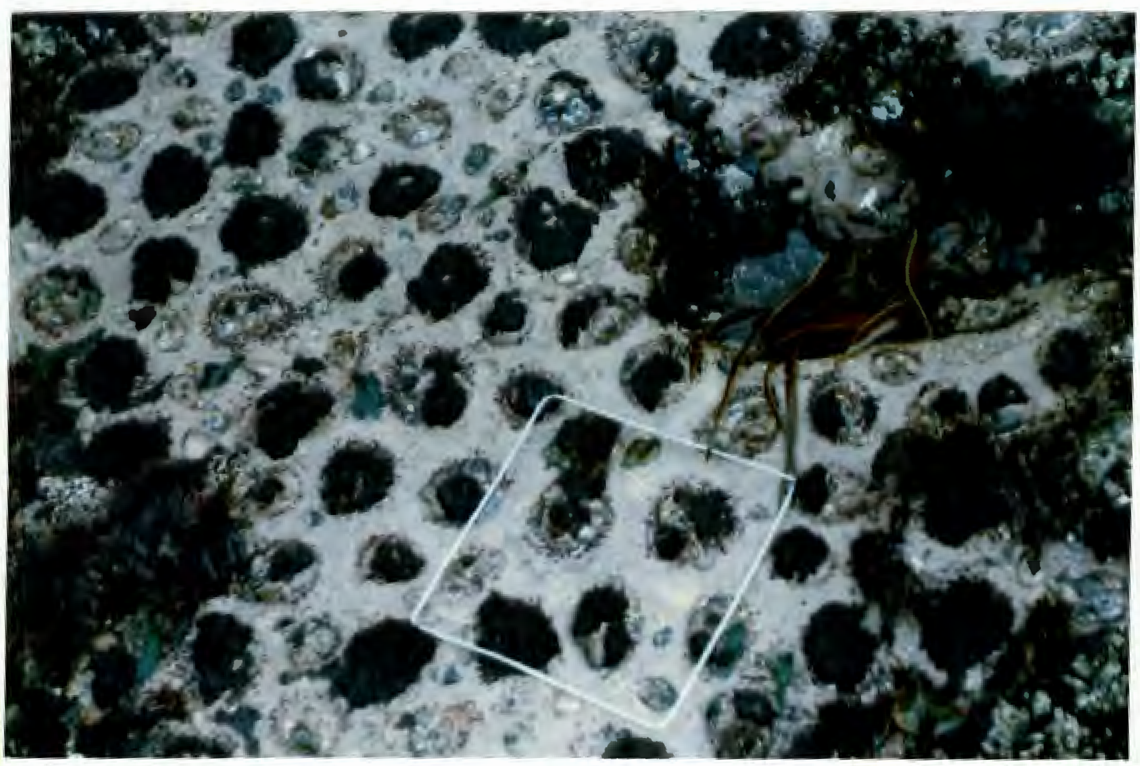


Plate 10. 25cm x 25cm Quadrat in the lower cochlear zone, showing fewer, large-sized individuals.

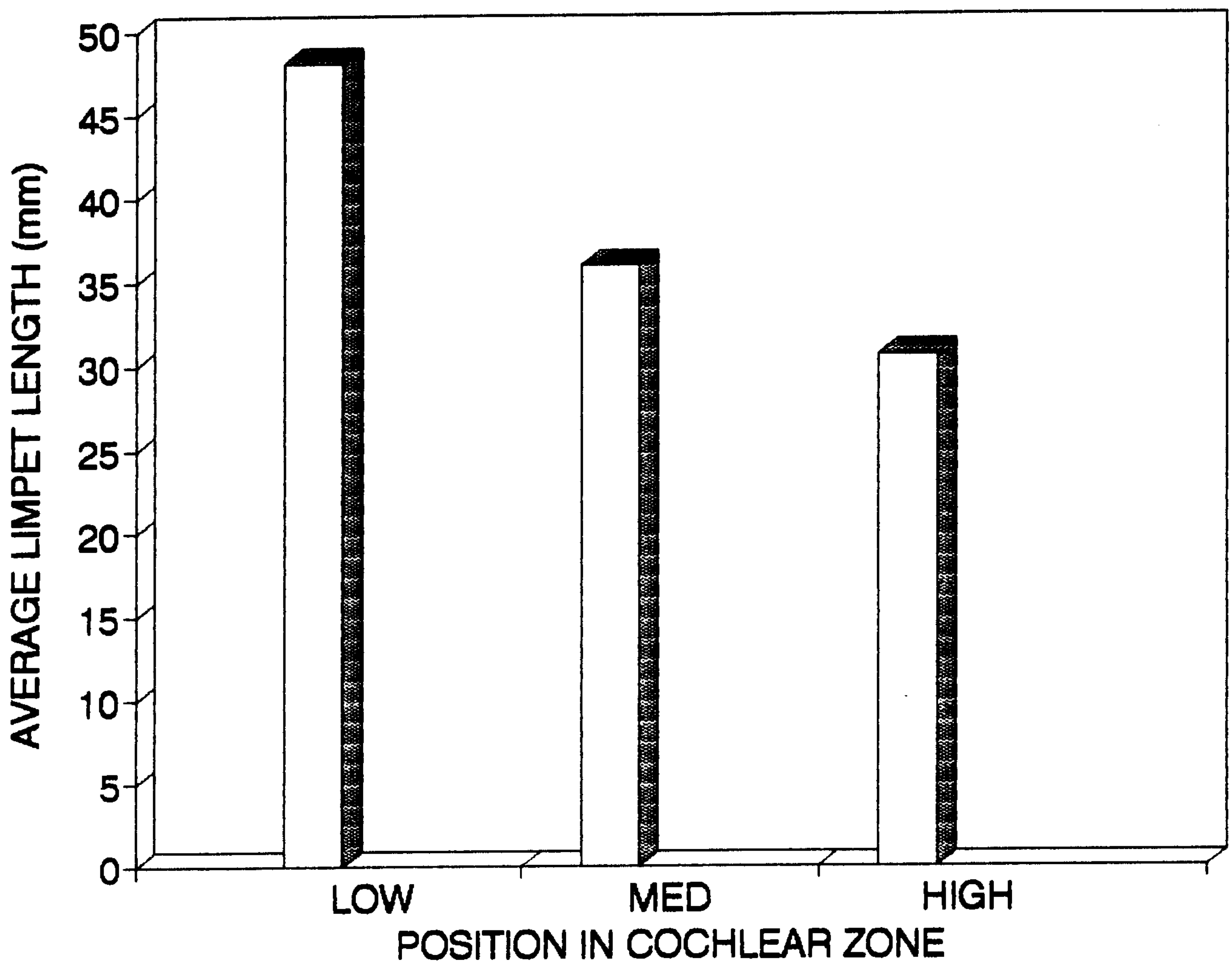


Figure 6. Average limpet sizes in the three parts of the cochlear zone at Blouberg to show vertical zonation. (Number of samples per zone: Low=9, Med=25, High=26)

8. Relationship between limpet size and the species of algae occuring in its garden

Gelidium micropterum was found in gardens of all limpet sizes in all three sampling sites, and in many gardens it was the only algal species, apart from the ever-present, but relatively unimportant, blue-greens.

Antithamnionella tormentosa also occurred in all size classes of limpets, but only at Blouberg.

In figures 7 and 8 it can be seen that *Herposiphonia heringii* only occur in the gardens of limpets that are longer than 30mm. Unfortunately a similar size distibution could not be done for *Polysiphonia incompta*, since the samples at Oliphantsbos, Platboom and Millers Point were mixed collections from several limpet gardens.

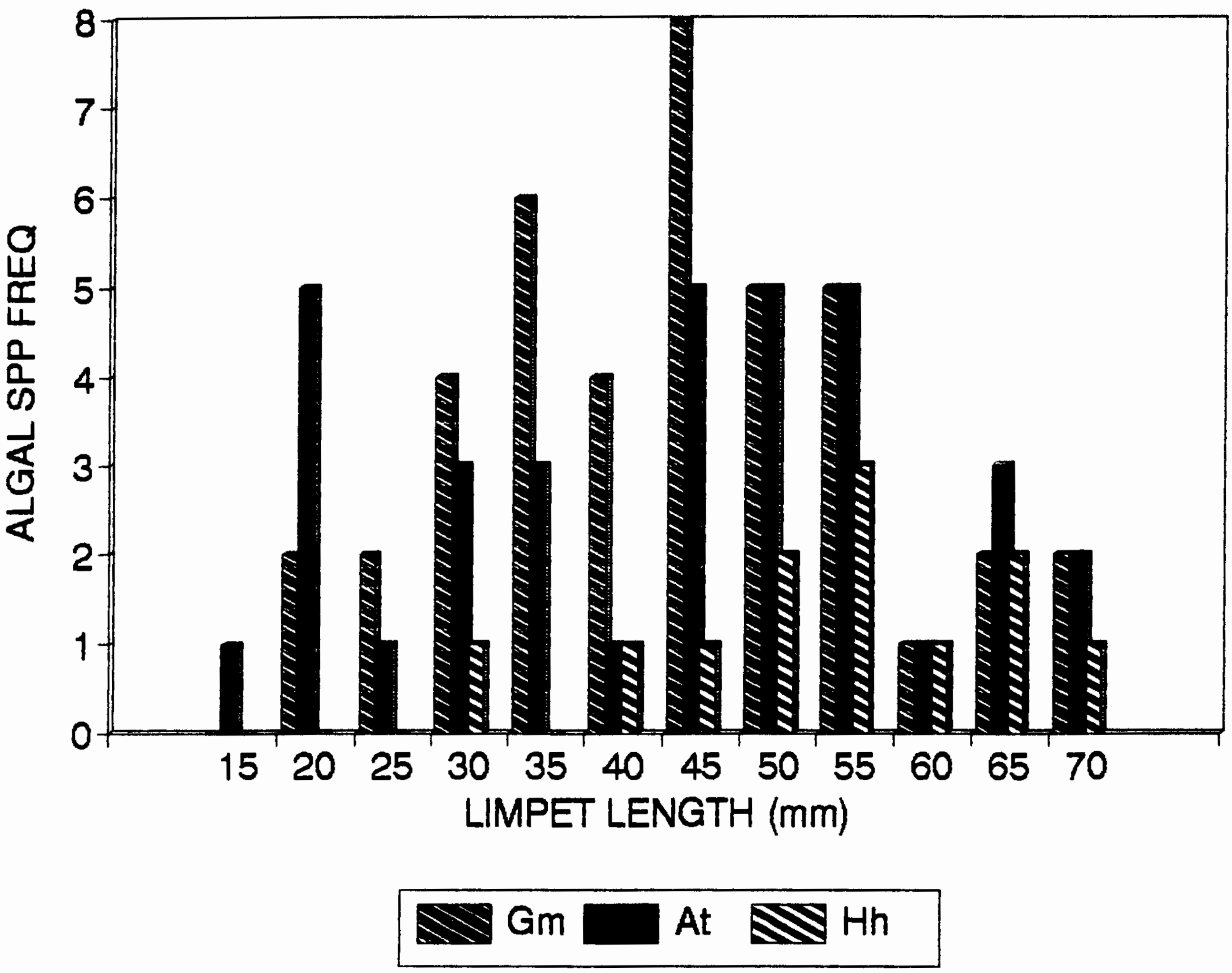


Fig.7. Distribution of *Gelidium micropterum* (Gm), *Antithamnionella tormentosa* (At), and *Herposiphonia heringii* (Hh), in different limpet size classes at Blouberg (N = 60).

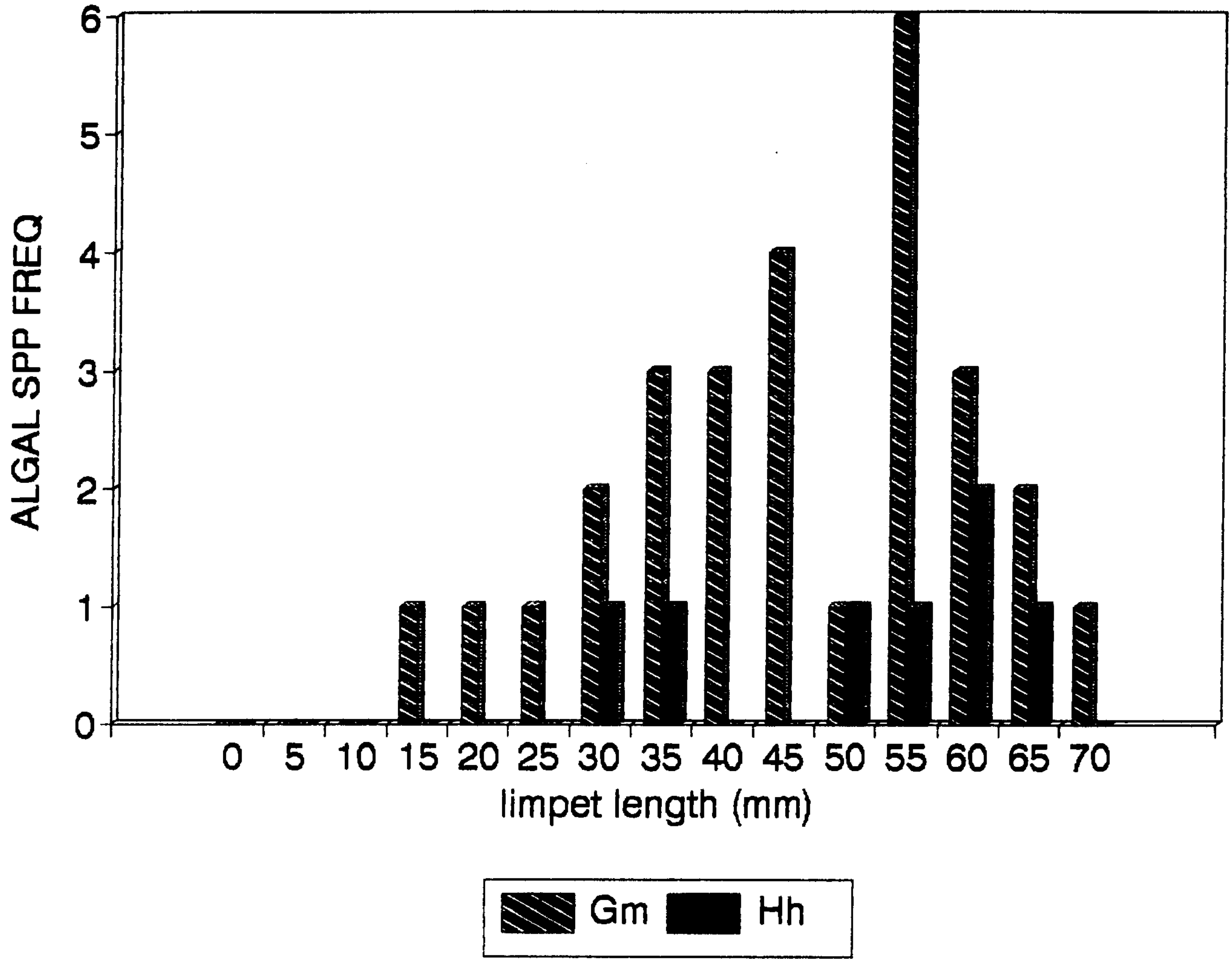


Fig. 8. Distribution of *Gelidium micropterum* (Gm) and *Herposiphonia heringii* (Hh), in different limpet size classes at Kommetjie (N = 29).

DISCUSSION

1. Species composition

This study shows that the composition of the *Patella cochlear* gardens is far more diverse than was previously known. 15 Species were recorded in the samples taken and this number is probably much higher. More localities need to be collected for a more complete list of garden species.

2. Horizontal distribution of algae

It is immediately clear that *Gelidium micropterum* is definitely not a "west coast species", as was commonly accepted. It actually appears to be more abundant in south coast gardens (see table 1). Also, contrary to Branch (1981), this species is not confined to *P. cochlear* gardens , but grows up to 5 cm tall outside gardens.

In this study the single collection of *Herposiphonia heringii* at Glencairn on the False Bay coast is probably an under-estimate of this species, since no samples were taken at the spring low tide mark on that side. (According to Stegenga *et al* (in prep), it occurs from Hondeklipbaai to St James). From the results it can be seen that *H. heringii* occurs in great numbers in the gardens of the lower cochlear zone on the west coast. (Fig.1.) This only became clear after, at Blouberg, one quadrat out of six could be sampled in this zone. Therefore percentage cover of 13% at Blouberg and 10% at Kommetjie for *H. heringii* could be a poor reflection of the potentially much higher percentage cover of this species in gardens, especially if taken into account that *P. cochlear* gardens extend down into the infratidal zone, where *H. heringii* is the dominant species, at least in some of the west coast sites. Also, according to Branch (1971), *Herposiphonia* is "notorious" to disappear for months from localities, indicating that there might be some environmental factor influencing their growth.

The unexpectedly high percentage (25%) of an unidentified species of *Cladophora* found in limpet gardens at Glencairn could be the result of pollution. According to Bolton (pers com) these species often benefit from pollution high in nitrogen. This might well be possible in such a heavily utilised area. Even runoff from the at spring low tide with a low swell, as was experienced during sampling.

4. Limpet size \ garden size

The fact that no small limpets had large gardens is indicative of the fact that small limpets stay on the back of the large ones, where some may even have their own gardens (Branch 1971, plate 1). From here they move down if an adult dies to leave an empty scar. Therefore many of the small individuals have only been on the rock for a short period, not allowing much time for growth of a garden. The smallest limpet that had just the beginnings of a garden was 13 mm long, while the smallest individual on rock was 9 mm. It seems reasonable to accept that that is more or less the smallest size of limpet that can take over an adult scar succesfully. The largest limpet found without a garden was 61 mm, but this must be an unusual individual with a mysterious past, because, of 87 limpets of 35mm or longer, only four did not have gardens. On the other hand, of 68 limpets smaller than 35mm, 35 did not have gardens. This shows that the juvenile limpets simply have to wait it out until an adult is removed before it can invade its scar.

5. Limpet size \ size of G. micropterum *individuals*

A limpet have to wait until it has grown to a considerable size, before it might get the opportunity to move down onto the rock, then starting a new garden there. Examination of the *G. micropterum* individuals in the samples showed that, although they were all prostrate and small, the fronds were largely intact and seldom cropped. This supports evidence in Branch (1971) that *P. cochlear* gut very seldom contain this species. It is interesting that *Gelidium pristoides* often grows on the shells of the limpets, but it has not been found in one sample of a garden. It therefore seems as if the prostrate form of *G. micropterum* has developed to exist in the protected territory of *P. cochlear*, were it will not be grazed or overshaded by other algae. A few limpets with a thick, overhanging growth of algae on the shell have been observed to have a very patchy garden, which might indicate that *G. micropterum* had been shaded out.

6. Limpet size \ nearest neighbour distance

According to Branch (1981), dispersion of *P. cochlear* becomes more uniform as density increases, with slightly smaller distances between them. That was not found in this study, because quadrats were not sampled in different density zones as such.

7. Vertical zonation of limpet size

The higer number of large limpets in the lower cochlear zone could be due to them being competitively superior to the smaller ones in the more competitive lower cochlear and subtidal zone. Grazing pressure by other gastropods will be more intense here, which will make it more difficult for a limpet to defend its territory, and maybe impossible if it is too small (Stimson 1970).

It could also be that these limpets have the benefit of *Herposiphonia* gardens, which the ones in the upper zone do not have. Dessication could be a detrimental factor both to the limpet itself and its food source. Therefore these limpets might remain small, because they have to live mainly off corallines.

Steneck (1982) argued that tightly linked associations and coevolution is most likely to develop where the grazer is small and sedentary, has a low energy requirement, and does little damage to its algal partner and when the alga is relatively large and long-lived and is a low-quality food. Although the crustose corallines in the cochlear zone do fit into this description, there is little, if any supporting evidence for this phenomenon in limpet gardens.

Thus there remains a lot to be learned about the algae in limpet gardens and their relationships with their "keepers". I hope that this study will lead to more research on this subject.

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