

## **Spatial and trophic partitioning in cryptic fish communities of shallow subtidal reefs in False Bay, South Africa**

Kim Prochazka

*Zoology Department and Marine Biology Research Institute, University of Cape Town, Rondebosch, 7701, South Africa (e-mail: kprochaz@botzoo.uct.ac.za)*

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### **Synopsis**

Thirty-nine species of cryptic fishes belonging to 16 families were captured on shallow reefs (0–20 m) in False Bay, South Africa using the ichthyocide rotenone. Five samples were collected in each of four depth zones (0–5, 6–10, 11–15 and 16–20 m). The area from which fish were collected in each sample was measured to give an estimate of density. The overall density of cryptic fishes in the area was 3.41 fish m<sup>-2</sup>, with the families Congrogadidae and Clinidae being numerically dominant, representing 27.9% and 22.3% of the total sample respectively. The Clinidae were by far the most diverse group, being represented by 17 species, while no other family was represented by more than three species. Multivariate analysis of numerical density revealed that partitioning of spatial resources did occur, with the shallowest samples (0–5 m) forming a group discrete from the deeper samples (6–20 m). Further analysis indicated that the amount of algal cover present was the most important factor influencing community structure, although the abundance of algae is in turn related to depth. The shallowest samples were dominated by members of the families Clinidae, Gobiessocidae and Bythitidae, while the Cheilodactylidae, Tripterygiidae and Ariidae were more important components of deeper water communities (6–20 m). Analysis of percentage volume of prey items in the diets of 21 species revealed that only two species shared diets that were more than 50% similar, and that partitioning of trophic resources was considerable.

### **Introduction**

The fish communities of shallow subtidal reefs consist of two major groups, namely the suprabenthic and cryptic fishes. The more visible suprabenthic species are often commercially or recreationally important, and have been extensively researched (Alevizon & Brooks 1975, Sonnier et al. 1976, Willan, et al. 1979, Berry et al. 1982, Moreno & Jara 1984, Choat & Ayling 1987, Beckley & Buxton 1989, Ojeda & Dearborn 1990, Cole et al. 1992). By contrast, the smaller, economically insignificant cryptic forms have largely been ignored. Cryptic species

can, however, be abundant in the adjacent intertidal zone (Gibson 1982, Bennett & Griffiths 1984, Prochazka & Griffiths 1992a), and are likely to form an important component of subtidal fish communities as well. Despite this, the relative importance of cryptic versus suprabenthic fishes to reef ecosystems has not previously been investigated. Only six studies could be found in which cryptic fish communities of subtidal reefs have been specifically targeted using appropriate sampling techniques (Williams & Hatcher 1983, Buxton & Smale 1984, Smale & Buxton 1989, Burger 1990, Greenfield & Johnson 1990, Illich & Kotschal 1990), and only two of these

(Greenfield & Johnson 1990, Illich & Kotrschal 1990) attempted to collect quantitative density data.

Studies of sublittoral cryptic fish communities in South Africa have been restricted to the southern and eastern Cape, and have been qualitative in nature (Buxton & Smale 1984, Smale & Buxton 1989, Burger 1990), or have dealt with fish inhabiting sandy substrata only (Prochazka & Griffiths 1992b). This study aims to document the cryptic ichthyofauna of shallow subtidal reefs in False Bay in a semi-quantitative manner. It also examines the influence of depth and reef characteristics on community structure, as well as the apportionment of available food resources between component species.

## Methods

The cryptic ichthyofauna of shallow subtidal reefs at Miller's Point (34°14'S; 18°28'E) in False Bay was sampled using the ichthyocide rotenone. The study area was along the eastern boundary of the Miller's Point Marine Reserve, which extends for three kilometres along the coast and for one nautical mile offshore. The collection of invertebrates from the area is prohibited, and although spearfishing is not allowed, line fishing is permitted within the reserve. Samples were collected when swell and surge action was minimal, which occurred during or shortly after cold-front-associated northwesterly winds. Samples were collected over the year (1994) as follows: February (3); April (1); May (11); June (1); September (1); November (1); December (2). Five samples were collected from each of four pre-determined depth zones, namely 0-5, 6-10, 11-15 and 16-20 m. Care was taken to ensure that samples fell exclusively within one depth zone. The depth at which the samples were collected was measured, and the amount of cover for fishes made up by algae, filter-feeders (including crinoids, sponges, octocorals, bryozoans, hydroids and holothuroids) and rocks was visually rated on a scale of 1-10, based on the method of Bennett & Griffiths (1984) for intertidal pools. Divers manually applied four litres of rotenone resin (dissolved in acetone in the ratio of 100 g rotenone to 1 litre acetone) to the reef during each

sample using squeeze bottles to ensure that the rotenone reached into caves and crevices. Fishes were collected using handnets. Caves, crevices and overhangs were searched thoroughly for fish and divers remained at the site for at least one hour after application of the rotenone, until they were satisfied that all available fishes had been collected. The area covered by the rotenone and searched by divers was estimated visually by the same observer for each sample.

Fish were identified using the volume by Smith & Heemstra (1986), and only cryptic species were used in further analyses. Cryptic fish were defined as those fish that are benthic in their habits and display cryptic colouration and behaviour. Habits described by Smith & Heemstra (1986), as well as personal observations, were used to categorise the lifestyles of individual species.

Total length was measured and the stomach of each individual removed for gut content analysis. Prey items were identified to the lowest possible taxon and, because these were usually small items, their volumes were estimated by counting the number of millimetre squares of graph paper obscured by the prey items, as described by Bennett (1989). Percentage occurrence was calculated as the number of individuals of each fish species which contained a particular prey item in the gut divided by the total number of individuals of that fish species. An index of relative importance was calculated by multiplying the percentage occurrence by the percentage volume.

Diversity indices were calculated after Odum (1971) as follows:

$$\begin{aligned} \text{Margalef species richness index} & d = (S-1)/\ln N, \\ \text{Shannon-Wiener overall index} & H = -\sum(n_i/N)\ln(n_i/N), \\ \text{Pielou evenness index} & e = H/\ln S, \end{aligned}$$

where  $S$  is the number of species present,  $N$  the total number of individuals of all species and  $n_i$  the number of individuals of each species.

Multivariate analyses were performed on fourth root transformed numerical density data using multi-dimensional scaling and group average sorting techniques, based on the Bray-Curtis measure of similarity. A similarity matrix based on the four environmental variables (depth, algal cover, filter-

Table 1. Total number, percent number and density of 39 species of cryptic fish sampled from subtidal reefs in Fasle Bay, in each of four depth zones.

	N	%N	Density (fish m <sup>-2</sup> )			
			0–5 m	6–10 m	11–15 m	16–20 m
<b>Ariidae</b>	<b>96</b>	<b>8.1</b>				
<i>Galeichthys ater</i>	96	8.1	0.26	0.60	0.14	0.22
<b>Batrachoididae</b>	<b>18</b>	<b>1.5</b>				
<i>Batrachthys apiatus</i>	2	0.2	–	–	0.01	0.01
<i>Batrachthys felinus</i>	16	1.4	–	0.13	0.05	0.02
<b>Bythitidae</b>	<b>71</b>	<b>6.0</b>				
<i>Bidenichthys capensis</i>	71	6.0	0.48	0.26	0.07	0.13
<b>Cheilodactylidae</b>	<b>91</b>	<b>7.7</b>				
<i>Cheilodactylus fasciatus</i>	90	7.6	0.08	0.54	0.05	0.42
<i>Cheilodactylus pixi</i>	1	0.1	–	–	–	0.01
<b>Clinidae</b>	<b>263</b>	<b>22.3</b>				
<i>Blennioclinus brachycephalus</i>	5	0.4	0.08	–	–	–
<i>Blennophis anguillaris</i>	8	0.7	0.11	–	0.01	–
<i>Blennophis striatus</i>	4	0.3	–	0.01	0.01	0.02
<i>Cirrihibarbis capensis</i>	7	0.6	0.02	0.07	–	0.01
<i>Clinus cottoides</i>	23	1.9	0.35	–	–	–
<i>Clinus nematopterus</i>	10	0.8	–	–	–	0.10
<i>Clinus rotundifrons</i>	19	1.6	0.21	0.01	0.04	–
<i>Clinus superciliosus</i>	17	1.4	0.21	0.04	–	–
<i>Clinus taurus</i>	3	0.3	0.02	0.03	–	–
<i>Clinus venustris</i>	9	0.8	0.09	–	0.03	–
<i>Fucomimus mus</i>	11	0.9	0.14	0.03	–	–
<i>Muraenoclinus dorsalis</i>	7	0.6	0.09	0.01	–	–
<i>Pavoclinus graminis</i>	4	0.3	0.06	–	–	–
<i>Pavoclinus litorafontis</i>	8	0.7	0.12	–	–	–
<i>Pavoclinus myae</i>	69	5.8	–	0.21	0.09	0.45
<i>Pavoclinus pavo</i>	55	4.7	0.59	0.06	0.09	0.02
<i>Pavoclinus profundus</i>	4	0.3	–	–	–	0.04
<b>Congiopodidae</b>	<b>2</b>	<b>0.2</b>				
<i>Congiopodus torvus</i>	2	0.2	–	–	0.02	–
<b>Congrogadidae</b>	<b>330</b>	<b>27.9</b>				
<i>Halidesmus scapularis</i>	330	27.9	0.35	0.99	1.31	0.94
<b>Gadidae</b>	<b>27</b>	<b>2.3</b>				
<i>Gaidropsarus capensis</i>	27	2.3	–	–	0.01	0.26
<b>Gobiesocidae</b>	<b>48</b>	<b>4.1</b>				
<i>Chorisochismus dentex</i>	17	1.4	0.18	0.07	–	–
<i>Eckloniaichthys scylliorhiniceps</i>	22	1.9	0.30	0.03	–	–
Undescribed Gobiesocidae	9	0.8	0.04	0.01	0.05	–
<b>Gobiidae</b>	<b>82</b>	<b>6.9</b>				
<i>Caffrogobius agulhensis</i>	14	1.2	0.03	0.12	0.02	0.02
<i>Caffrogobius saldanha</i>	68	5.8	0.24	0.25	0.08	0.26
<b>Myxinidae</b>	<b>1</b>	<b>0.1</b>				
<i>Eptatretus hexatrema</i>	1	0.1	–	–	–	0.01
<b>Scorpaenidae</b>	<b>1</b>	<b>0.1</b>				
<i>Scorpaena scrofa</i>	1	0.1	–	–	0.01	–
<b>Scylliorhinidae</b>	<b>39</b>	<b>3.3</b>				
<i>Haploblepharus edwardsii</i>	23	1.9	–	0.10	0.05	0.10
<i>Haploblepharus pictus</i>	12	1.0	–	0.13	–	0.03
<i>Poroderma africanum</i>	4	0.3	–	0.02	–	0.03

Table 1. Continued.

	N	%N	Density (fish m <sup>-2</sup> )			
			0–5 m	6–10 m	11–15 m	16–20 m
<b>Syngnathidae</b>	<b>1</b>	<b>0.1</b>				
<i>Syngnathus acus</i>	1	0.1	0.02	–	–	–
<b>Tetrarogidae</b>	<b>2</b>	<b>0.2</b>				
<i>Coccotropsis gymnoderma</i>	2	0.2	–	–	–	0.02
<b>Tripterygiidae</b>	<b>109</b>	<b>9.2</b>				
<i>Cremnochorites capensis</i>	109	9.2	0.06	0.59	0.12	0.51
Area sampled (m <sup>2</sup> )	346		66	68	111	101
Number of species	39		23	23	21	22
Number of individuals	1181		269	297	248	367
Density (fish m <sup>-2</sup> )	3.41		4.08	4.37	2.23	3.63
Margalef species richness	5.37		3.93	3.86	3.63	3.56
ShannonWiener overall	2.06		2.79	2.48	1.78	2.34
Pielou evenness	0.56		0.89	0.79	0.58	0.76

feeder cover and rock cover) was constructed in a similar manner to that of the biotic data. These two similarity matrices were then compared using the harmonic rank correlation coefficient ( $\rho_w$ ) in order to determine which subset of environmental variables contributed most to the understanding of the biotic data. Ordinations of the environmental variables, as suggested by Clarke & Ainsworth (1993), indicated little concordance with the biotic ordination and hence are not presented below.

Separation of trophic resources was investigated by performing multivariate analyses on percentage volume of prey items in the guts, as well as on the index of relative importance. These were performed using multidimensional scaling and group average sorting based on the Bray-Curtis measure of similarity on untransformed data. This was done for each species separately to investigate changes in diet with fish size or depth of capture, and for all fish species combined in order to examine inter-specific differences in diet.

## Results

A total of 1811 cryptic fishes belonging to 39 species and 16 families was captured from subtidal reefs at Miller's Point in False Bay as detailed in Table 1.

This is equivalent to an overall density of 3.41 fish m<sup>-2</sup>. The Margalef species richness index for the whole area was 5.07, while the Shannon-Wiener overall and Pielou evenness indices were 2.06 and 0.56, respectively. By far the most diverse group was the Clinidae (17 species), no other family being represented by more than three species. The families Congrogadidae and Clinidae were numerically dominant, accounting for 27.9 and 22.3% of the total catch, respectively. The families Ariidae, Bythitidae, Cheilodactylidae, Gobiidae and Tripterygiidae each comprised 5–10% of the total number of fishes caught. Only seven species, each from a different family, contributed >5% to the total catch, these being *Halidesmus scapularis* (27.9%), *Cremnochorites capensis* (9.2%), *Galeichthys ater* (8.1%), *Cheilodactylus fasciatus* (7.6%), *Bidenichthys capensis* (6.0%), *Caffrogobius saldanha* (5.8%) and *Pavoclinus myae* (5.8%).

### Community change with depth

The total number of fish species captured in each depth zone remained remarkably constant, varying from 21 to 23 (Table 1). The Margalef species richness, Shannon-Wiener overall and Pielou evenness indices also indicated no depth-related trends. To-

tal density, however, decreased slightly from 4.08 fish m<sup>-2</sup> at 0-5 m to 3.63 fish m<sup>-2</sup> in the deepest zone (16-20 m).

The family Clinidae was numerically dominant in the 0-5 m zone, comprising 50.9% of total fish numbers, but declined in importance in the 6-10 m (11.1%) and 11-15 m (11.7%) zones, before increasing their representation slightly to 17.4% in the 16-20 m zone (Figure 1). This increase may be attributed to the appearance of *Clinus nematopterus* in the 16-20 m zone, as well as to an increase in the density of *P. myae* in this zone (Table 1). The only clinid found in all depth zones was *Pavoclinus pavo*, although the density of this species was greatest in the shallowest zone.

The Gobiesocidae contributed >10% of fish numbers only in the 0-5 m depth zone (Figure 1). *Chorisochismus dentex* and *Eckloniaichthys scylliorhiniceps* were found only in less than 10 m depth, and both attained their highest densities in the 0-5 m zone (Table 1). An undescribed gobiesocid was collected in samples deeper than 5 m.

The Bythitidae, represented by one species, *B. capensis*, made up >10% of the community only in the shallowest samples (Figure 1). Although this species occurred at all depths, its density decreased progressively from 0.48 fish m<sup>-2</sup> in the 0-5 m zone to 0.13 fish m<sup>-2</sup> in the 16-20 m zone (Table 1). The family Congrogadidae, represented by the single species *H. scapularis*, was an important component of the community in the 6-10 m and 16-20 m depth zones (22.6% and 25.9%, respectively), and dominated the 11-15 m zone (58.5%). Of the remaining families only the Cheilodactylidae and Tripterygiidae at 6-10 and 16-20 m, and the Ariidae at 6-10 m made up >10% of the fish fauna.

#### Partitioning of spatial resources

Multivariate analysis of numerical density data suggested that the five 0-5 m samples form a discrete group distinguishable at the 40% similarity level (Figure 2a). The ordination (Figure 2b) indicates a similar result. No other depth related trends were evident, and all stations deeper than 5 m formed a homogenous group.

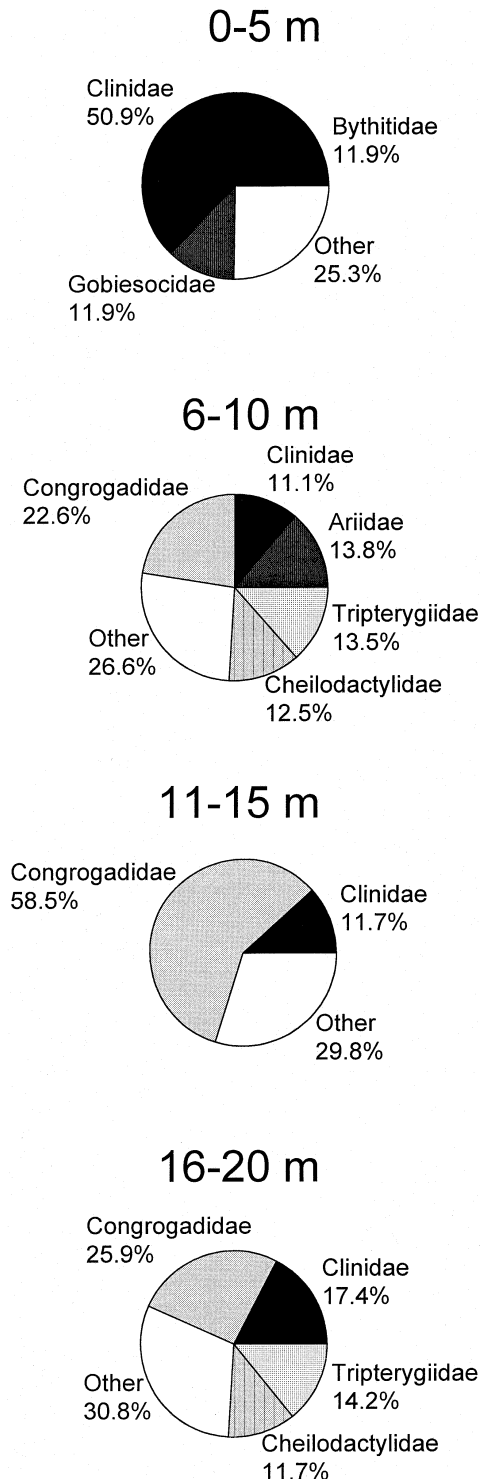


Figure 1. Percent contribution (by numbers) of cryptic fish families in each of four depth zones on subtidal reefs in False Bay. Only families which contributed at least 10% to the community are shown separately.

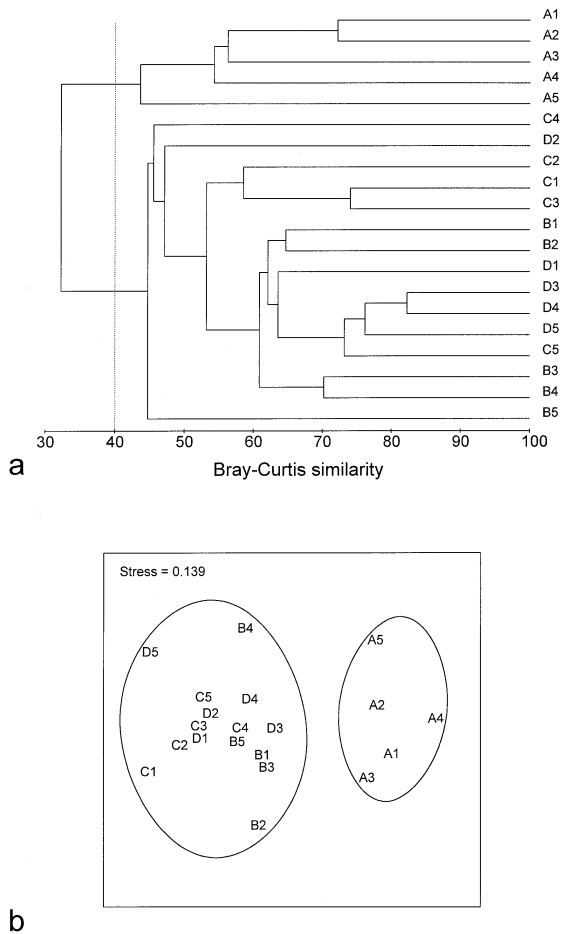


Figure 2. Dendrogram (a) and ordination (b) based on the density of 39 species of cryptic fishes (fish  $m^{-2}$ ) collected in 20 samples from four depth zones in False Bay. Samples are labelled as follows: A = 0–5 m; B = 6–10 m; C = 11–15 m; D = 16–20 m.

The results of linking the density of cryptic fish species to environmental variables using the harmonic rank correlation are presented in Table 2. Correlations between all possible combinations of environmental variables indicated that the amount of algal cover present best explained the biotic similarity matrix ( $\rho_w = 0.52$ ), with depth being a secondary factor ( $\rho_w = 0.44$ ).

### Diets

Multivariate analyses based on percentage volume of prey items revealed no differences in diet with fish size or depth of capture in any of the species

Table 2. Harmonic rank correlation coefficients ( $\rho_w$ ) for all possible combinations of the four environmental variables, namely depth (Depth), algal cover (Algae), filter-feeder cover (Filter) and rock cover (Rock) regressed against the similarity matrix for density of cryptic fishes in False Bay. The best possible correlation is presented in bold type.

Environmental variable(s)	$\rho_w$
<b>Algae</b>	<b>0.52</b>
Depth	0.44
Filter	0.25
Rock	0.13
Algae, Depth	0.50
Algae, Filter	0.47
Algae, Rock	0.36
Depth, Filter	0.35
Depth, Rock	0.31
Filter, Rock	0.18
Algae, Depth, Filter	0.44
Algae, Depth, Rock	0.40
Algae, Filter, Rock	0.35
Depth, Filter, Rock	0.27
Algae, Depth, Filter, Rock	0.38

studied. It should be noted, however, that for several species very few individuals were available, or had identifiable gut contents, and that dietary changes with size may be found if more individuals are examined. This perceived lack of dietary change with size allowed all individuals within a species to be pooled for further analyses. The percentage occurrence and percentage volume of prey items in the guts of 21 species for which at least five individuals had identifiable prey in the guts are presented in Appendix 1, and these will be examined more closely in the following section.

### Partitioning of trophic resources

Only very small differences were evident in the results of the multivariate analyses based on percentage volume data and on the index of relative abundance of prey items in the diets of 21 fish species. Thus only the results based on the index of relative abundance are presented below. The analysis indicated that only two species (*Caffrogobius agulhensis* and *Cirrihibarbis capensis*) had diets which were

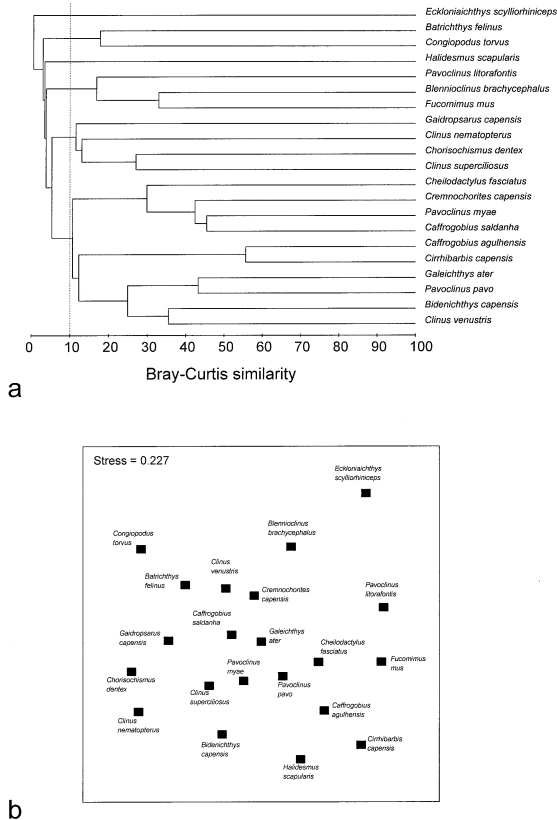


Figure 3. Dendrogram (a) and ordination (b) based on the diets of 21 species of cryptic fishes from shallow subtidal reefs in False Bay.

more than 50% similar (Figure 3a). In addition, the 21 species were relatively widely distributed in ordination space (Figure 3b), indicating low levels of similarity between the diets of these fishes. For this reason no groupings have been indicated on the ordination plot (Figure 3b). At the 10% similarity level four groups and two outlying species could be distinguished from the dendrogram (Figure 3a). The congrogadid, *H. scapularis*, had a diet which was unique in that individuals of this species frequently (60.3% Occ) contained large volumes (16.4% Vol) of a minute crustacean that could not be identified even to the level of order (Appendix 1). *Halidesmus scapularis* was the only species which consumed this particular prey item. The weedsucker, *E. scylliorhiniceps*, remained discrete from all other species because its diet consisted chiefly of copepods of the genus *Porcellidium* (85.7% Occ, 74.1% Vol: Appendix 1). *Congopodus torvus* and *Batrachichthys felinus*

shared a similar diet of decapod crustaceans and molluscs. The diets of *C. nematopterus*, *Clinus superciliosus*, *C. dentex* and *Gaidropsarus capensis* were characterised by the presence of fishes and caprellid amphipods. The clinids *Blennioclinus brachycephalus*, *Fucomimus mus* and *Pavoclinus litorafontis* showed a diet that was characterised by relatively large proportions of amphipods of the genus *Laetmatophilus* (46.4% Vol, 42.2% Vol, 17.4% Vol, respectively). None of the groupings above (with the exception of *E. scylliorhiniceps*) are clear from the ordination plot (Figure 3b) because of the large degree of dissimilarity shown in the diets of these fishes.

The remaining ten species formed a large grouping at the 10% similarity level, with diets that were characterised by having a large diversity of amphipod crustaceans. The analysis was therefore re-run with only these species included in order to achieve better definition within this group (Figure 4). At the 20% similarity level these species could be separated into three discrete groups (Figure 4a). The first of these included *C. fasciatus*, *Cr. capensis*, *P. myae* and *C. saldanha*, which shared a diet of the amphipods *Ischyrocerus* spp., Lysianassidae, *Paramoera capensis* and *Podocerus* spp., as well as Tanaidacea (Appendix 1). The diet of *C. fasciatus* was less similar to the other three species as it contained 12 prey items that were consumed by this species only, as well as relatively large amounts of decapod crustaceans. Lysianassid amphipods were the most important component of the diets of *C. agulhensis* and *Ci. capensis* (25.0% Occ, 40.6% Vol and 33.3% Occ, 19.6% Vol, respectively). The third group comprised four species, namely *G. ater*, *P. pavo*, *B. capensis* and *Clinus venustris*, whose diets were characterised by the presence of amphipods of the genus *Ischyrocerus*. Within this group, two sub-groups could be distinguished (Figure 4a). The first of these was a grouping between *G. ater* and *P. pavo* because they shared 16 prey items (Appendix 1). The second sub-group, made up by *B. capensis* and *C. venustris*, appeared to group exclusively as a result of sharing only one prey item, namely *Ischyrocerus* spp. As with Figure 3b, the ordination (Figure 4b) indicated no distinct clustering of species due to the large amount of dissimilarity in the diets of the species studied.

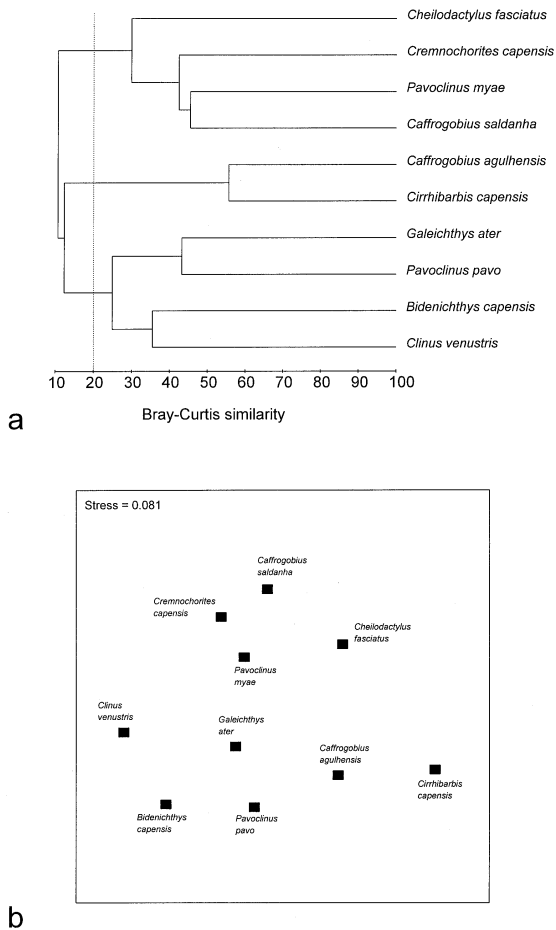


Figure 4. Dendrogram (a) and ordination (b) based on the diets of ten species of cryptic fishes from shallow subtidal reefs in False Bay.

## Discussion

The diversity of the cryptic fish fauna in False Bay (39 species from 16 families) is within the range reported by other workers in South Africa (Buxton & Smale 1984, Smale & Buxton 1989, Burger 1990). One of these studies (Smale & Buxton 1989) was conducted in shallow gulleys near Port Elizabeth on the south coast of South Africa. These authors collected 43 species of cryptic fish belonging to 20 families, and their published diversity indices were all higher than those calculated in the present study. These indices, however, included 'schooling' species, and recalculating the Margalef Species Richness Index using only cryptic species, as defined by Smale & Buxton (1989), gives a value of 4.97, which

is slightly lower than the 5.07 calculated for cryptic fish in False Bay. An interesting point made by these authors was that cryptic species dominated their collections (73%), while schooling species accounted for only 27% of the species present. In terms of numbers, 74% of all fishes captured were cryptic, indicating that cryptic fishes are an important component of subtidal gulley fish communities in this area.

The two other studies of cryptic fishes in South Africa (Buxton & Smale 1984, Burger 1990), were both conducted on the south coast at Tsitsikamma. Buxton & Smale (1984) collected 23 species from 13 families within the Tsitsikamma National Park. This relatively low species richness recorded may be attributed to the preliminary nature of the study, in which only four samples were collected. In a later, more comprehensive survey, Burger (1990) investigated the cryptic fish fauna both within the Tsitsikamma National Park and on exploited reefs just outside its western boundary. The number of species and families (39 species from 15 families) collected within the park were remarkably similar to those found in the present study. Although the Margalef Species Richness Index was slightly lower (4.77) than in False Bay (5.07), the Shannon-Wiener Overall Index (2.51) was higher, while species evenness was greater in the Tsitsikamma National Park (0.70) than in False Bay (0.56), indicating a smaller proportion of common species in the False Bay community. This greater level of dominance was caused primarily by the presence of large numbers of the congrogadid, *H. scapularis*, and the triplefin, *Cr. capensis*.

On exploited reefs outside the Tsitsikamma National Park diversity was lower, with only 25 species from 12 families being captured (Burger 1990). In addition, species evenness was lower on exploited reefs (0.57) and was similar to that found for False Bay. Burger (1990) attributed the discrepancy between the number of species within the marine reserve and on exploited reefs to an inexplicable increase in the abundance of the tripterygiid, *Cr. capensis*, on exploited reefs, which supposedly had a detrimental effect on other cryptic species. It seems more plausible, however, that the smaller number of samples collected on exploited reefs (Tsitsikam-



ma National Park: N=25; exploited reefs: N=13), or differences in reef structure between the two areas, may be responsible for this result.

Burger (1990) suggested that the removal of top predators, especially the red steenbras, *Petrus rupestris*, from exploited reefs may have been responsible for the observed greater abundance of cryptic fishes, and particularly *Cr. capensis*, in these areas. This suggestion was based on the fact that the diet of *P. rupestris* is comprised mostly of small fishes, with cryptic fishes accounting for a large proportion of the prey consumed (Smale 1986). Although this paper is not intended to be a comment on marine reserves, it is interesting to note that the fish community at Miller's Point in False Bay (where the removal of top predators by angling continues) bears stronger resemblance to that on exploited reefs at Tsitsikamma than to the community within the Tsitsikamma National Park. This is highly suggestive, and remains to be tested with careful field controls.

No comparative numerical density figures for cryptic fishes exist for other sites within South Africa. The total density of cryptic fishes on subtidal reefs in False Bay (3.41 fish m<sup>-2</sup>) is, however, an order of magnitude higher than reported by Greenfield & Johnson (1990) for the western Caribbean (0.44 fish m<sup>-2</sup>), and only slightly less than reported by Illich & Kotrschal (1990) for blennioid fish in the northern Adriatic (4.0 fish m<sup>-2</sup>). These densities should, however, be viewed with caution due to the problems inherent in collecting fishes subtidally with the use of rotenone. These include the fact that the rotenone affects different species and sizes of fish in different ways, and that these effects may vary according to concentration of the rotenone and water temperature (Randall 1963, Gilderhus et al. 1986). In the present study water temperature was between 12°C and 16°C on all sampling occasions, and collections were carried out under conditions of minimal surge in an attempt to keep diffusion of the rotenone to a minimum. Another problem with rotenone collections is the movement of fish in and out of the sampling area. This may only be counteracted by the use of an enclosure, such as employed by Smale & Buxton (1989) and Prochazka & Griffiths (1992b). Such a structure was, how-

ever, deemed impractical for the present study due to the irregular reef profile, abundance of kelp, *Ecklonia maxima*, in the shallow stations, and relatively large sampling areas. By their nature, cryptic fishes are closely associated with the reef surface or interstices; most are relatively small, many lack swim bladders, and while they are capable of rapid 'sprints', they are unable to sustain high-speed swimming for long periods. Thus, their defence is their camouflage, and their response to threats is to hide rather than to swim away (personal observations). Thus emigration out of the sampling area is considered to cause relatively small errors for most species. The exceptions are large specimens of *C. superciliosus* and the scylliorhinids. In addition, although other authors have experienced problems with larger predatory fishes consuming narcotised specimens (Burger 1990), these problems were not encountered in the present study. Hottentot, *Pachymetopon blochii*, were abundant, but tended to stay away from the sampling area after the rotenone was released.

Total density of cryptic fishes subtidally (3.41 fish m<sup>-2</sup>) was approximately half that reported for intertidal rock pools in False Bay (6.82 fish m<sup>-2</sup>) by Bennett & Griffiths (1984). This suggests that intertidal fishes may indeed be 'concentrated' in rock pools during low tide, as suggested by Gibson (1982) and Bennett et al. (1983). The number of species and families in the subtidal zone (39 species from 16 families) was far greater than the 16 species from six families found in the adjacent intertidal zone (Bennett & Griffiths 1984). Three of the species collected from the intertidal zone were absent from the subtidal surveys. These were *Caffrogobius caffer*, *Clinus acuminatus* and *Clinus berrisfordi*. The former two typically inhabit intertidal pools high on the shore, while the latter reaches peak abundance below mean low water of neap tides (Bennett & Griffiths 1984). Twenty-six species occurred subtidally only, while 13 species were common to both subtidal and intertidal habitats. Of these, seven were at least an order of magnitude more abundant in the intertidal zone than in subtidal areas, suggesting that they are predominantly intertidal forms. They included the clinids *Blennophis anguillaris*, *Ci. capensis*, *Clinus cottoides*, *C. superciliosus*, *Cli-*

*nus taurus* and *Muraenoclinus dorsalis*, and the gobiesocid *C. dentex*. With the exceptions of *C. cotoides* and *M. dorsalis*, however, individuals of these species collected subtidally were almost all larger than recorded in the intertidal zone (unpublished data). Of the remaining six species, two (*B. brachycephalus* and *F. mus*) were only slightly more abundant in the intertidal zone, while four (*G. ater*, *C. fasciatus*, *P. pavo* and *H. scapularis*) had similar densities in both zones. Yoshiyama et al. (1986) stated that the fish assemblages of intertidal and subtidal habitats in California were essentially distinct; however, they also found that several species occurred in both habitats, although most were considerably more abundant in one or the other of the two habitats.

Contrary to the findings of Burger (1990), the number of species recorded during the present study did not increase with depth. Total density, however, appeared to decline with depth. Unfortunately, no data exist with which to compare this finding. Multivariate analysis of numerical density (Figure 2) indicated that the shallowest reefs (0–5 m) supported fish communities that were distinct from those of deeper reefs (6–20 m). These shallowest reefs were dominated by fishes of the families Clinidae (50.9%), Bythitidae (11.9%) and Gobiesocidae (11.9%), while deeper reefs supported communities dominated by the families Congrogadidae (22.6–58.5%), Ariidae (13.8%), Tripterygiidae (13.5–14.2%) and Cheilodactylidae (11.7–12.5%). These results are similar to those for the Tsitsikamma National Park (Burger 1990), where members of the family Clinidae were found to be numerically dominant on the shallowest reefs, but decreased their representation with depth, whereas members of the family Tripterygiidae increased their representation with depth. Of the remaining families that contributed at least 5% to the numbers caught in the present study, only the Congrogadidae achieved this level in the Tsitsikamma National Park (Burger 1990). Burger (1990) considered the cheilodactylids *C. fasciatus* and *C. pixi* to be suprabenthic rather than cryptic species; however, recent visual censusing of suprabenthic fish in False Bay indicates that *C. fasciatus* is sampled more accurately using rotenone than by visual counts (Lechanteur unpub-

lished data). This is because these fish spend most of their time in caves and are thus often overlooked by conventional counts. Because *C. fasciatus* and *C. pixi* are similar in morphology and habits, it is likely that the same would hold true for the latter species. Data in Burger (1990) indicate that the Cheilodactylidae do indeed increase their representation with depth, as shown in the present study. In addition, there is a positive relationship between depth and fish size, with larger individuals occurring in deeper water (Lechanteur unpublished data).

The influence of reef characteristics on fish community structure has been examined by several authors (Stephens & Zerba 1981, Williams & Hatcher 1983, Choat & Ayling 1987, Burger 1990). In the present study the amount of algal cover was found to be the most important factor influencing the density of cryptic fish species (Table 2). Algal cover and depth are, however, closely related, because algae need light to photosynthesise. In addition, wave energy is also related to depth, being greatest in the shallowest areas. However, wave energy was not measured during the course of the work and thus its effect on community structure cannot be assessed here. The shallowest reefs (0–5 m) were characterised by dense and structurally complex algal cover, consisting largely of *Bifurcaria brassicaeformis*, *Sargassum heterophyllum* and the kelp, *Ecklonia maxima*. Deeper reefs, on the other hand, were characterised by beds of filter-feeders, which provided a short (approximately 10 cm in height), very dense, but structurally simple covering to the reef surface. These filter-feeders consisted predominantly of crinoids (mostly *Comanthus wahlbergi*), a variety of sponges, octocorals, bryozoans and hydroids, and the holothurian *Pseudocnella insolens*. Only small patches of structurally simple algae occurred on these deeper reefs, mostly *Codium stephensiae* and short coralline turfs. This is consistent with the higher density of fishes found in the shallowest zone, because positive relationships between the amount of algal cover and the abundance of several cryptic fish species have been shown previously (Marsh et al. 1978, Wheeler 1980, Bennett & Griffiths 1984, Prochazka & Griffiths 1992a). In addition, Larson & DeMartini (1984) and Choat & Ayling (1987), working on reefs in California and New

Zealand respectively, both found a positive relationship between algal cover and the abundance of small fishes.

Wheeler (1980) emphasised the importance of colouration and protective resemblance of fishes associated with algae. It is clear from this study that members of the family Clinidae dominated the shallowest areas (0–5 m). All the southern African clinids show adaptive colouration, and several have developed protective resemblance. A striking example is *F. mus* which, along with several other clinids, has evolved transparent 'windows' in the fin membranes which break up the harsh outline of the fish and make it resemble a frond of algae. The Tripterygiidae and Cheilodactylidae, which inhabit deeper reefs, have mottled colouration which matches that of the filter-feeder community that predominates at these depths. However, the limited amount of cover provided by the filter-feeders means that the fish must either be small, as in the case of the triplefin *Cr. capensis*, or must spend a large proportion of their time in caves, as with *C. fasciatus*. Members of other families, such as the Congrogadidae, Bythitidae and Ariidae, primarily inhabit small rocky crevices, the spaces under boulders, or the deep recesses of relatively large caves and lack adaptive colouration or protective resemblance.

The diets of component species showed distinct partitioning of available food resources, with only two species (*C. agulhensis* and *Ci. capensis*) having diets more than 50% similar (Figures 3, 4). At the 10% similarity level four groups and two outlying species were distinguishable (Figure 3). The diets of five of these could be characterised by the predominance of certain prey items. These included the clingfish, *E. scylliorhiniceps*, which took mostly copepods of the genus *Porcellidium*. These copepods cling to blades of algae, which in turn are the preferred habitat of this fish. Similarly, the congrogadid, *H. scapularis*, also appeared as a specialist, consuming mainly an unidentified crustacean: however, nothing is known of the habits of this prey item. One group fed primarily on decapod crustaceans and molluscs (*B. felinus* and *C. torvus*). The diets of *C. nematopterus*, *C. superciliosus*, *C. dentex* and *G. capensis* were characterised by the presence

of fishes and caprellid amphipods. The clinids *B. brachycephalus*, *F. mus* and *P. litorafontis* fed on relatively large amounts of the amphipods *Laetmophilus* spp. The last group, containing 10 species, consumed a mixture of prey items, mostly amphipod crustaceans. Treating this group in isolation (Figure 4) indicated that these species could be subdivided into a further three groups at the 20% similarity level, each characterised by the presence and relative abundance of particular prey species in the diet. Again, within this group, only two species shared a diet that was more than 50% similar. Both the analyses of diet presented here, and the unanalysed data of Bennett et al. (1983) point to extensive dietary segregation between cryptic fish species. This highlights the importance of identifying prey to the species level. If identifications are not resolved below the level of order of family, it would be easy to reach the erroneous conclusion that the diets of these fishes overlap extensively.

This study has shown that a diverse community of cryptic fishes exists on shallow reefs in False Bay, South Africa. It has further shown that a degree of depth partitioning occurs between component species and that the amount of algal cover present, which is itself closely related to depth, plays an important role in determining both community structure and density of cryptic reef fishes. The degree of spatial segregation, however, is nowhere near as marked as the degree of dietary segregation, and the latter thus probably plays a major role in allowing the co-existence of such a diversity of cryptic fish species. Because these cryptic fishes exist in parallel with the suprabenthic fish fauna, this new knowledge will make it possible to assess the relative roles that these two groups play in the ecology of temperate reefs. Studies of the suprabenthic fishes in the False Bay area are currently underway, and a later paper will investigate the interactions between the two fish groups, and examine to what extent they overlap in their use of available resources.

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*Appendix 1.* Percentage occurrence and percent volume of prey items in the diets of 21 species of cryptic fish from shallow subtidal reefs in False Bay. Only species in which at least five individuals had identifiable contents in the guts are included, with the exception of *Congiopus torvus*.

	<i>Galeichthys ater</i> N=50		<i>Batrachthys felinus</i> N=12		<i>Bidenichthys capensis</i> N=18		<i>Cheilodactylus fasciatus</i> N=19		<i>Blennioclinus brachycephalus capensis</i> N=5		<i>Cirrhibarbis capensis</i> N=5		<i>Clinus nematopterus</i> N=7	
	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol
<b>Algae</b>														
Coralline	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fleshy	2.0	<1	–	–	11.1	2.2	–	–	–	–	–	–	–	–
<b>Cnidaria</b>														
<b>Octocorallia</b>	–	–	8.3	7.1	–	–	–	–	–	–	–	–	–	–
<b>Polychaeta</b>														
Unid. Errantia	30.0	4.4	8.3	1.0	–	–	5.3	<1	–	–	–	–	–	–
<i>Eunice</i> sp.	–	–	8.3	4.0	–	–	–	–	–	–	–	–	–	–
<i>Euphrosine capensis</i>	–	–	–	–	–	–	5.3	1.5	–	–	–	–	–	–
<i>Lepidonotus</i> sp.	–	–	8.3	1.0	–	–	–	–	–	–	–	–	–	–
Unid. Sedentaria	8.0	1.0	–	–	–	–	–	–	–	–	–	–	–	–
<b>Crustacea</b>														
<b>Amphipoda</b>														
<i>Amaryllis macrophthalma</i>	24.0	1.6	8.3	<1	–	–	–	–	–	–	–	–	–	–
<i>Ampelisca palmata</i>	–	–	–	–	–	–	10.5	<1	–	–	–	–	–	–
<i>Ampelisca</i> sp.	14.0	<1	–	–	–	–	10.5	2.6	–	–	–	–	–	–
<i>Amphilocheus</i> sp.	4.0	<1	–	–	–	–	–	–	–	–	–	–	–	–
<i>Amphilocheus neopolitanus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ampithoe</i> sp.	8.0	1.0	–	–	–	–	–	–	–	–	–	–	–	–
<i>Aora</i> spp.	28.0	2.7	–	–	–	–	–	–	–	–	–	–	–	–
<i>Argissa hamatipes</i>	2.0	<1	–	–	–	–	21.1	6.4	–	–	–	–	–	–
<i>Caprella cicur</i>	–	–	–	–	–	–	36.8	8.1	–	–	–	–	–	–
<i>Caprella penantis</i>	–	–	–	–	–	–	5.3	<1	–	–	–	–	–	–
Unid. Caprellidea	54.0	7.2	8.3	10.6	–	–	5.3	3.4	40.0	5.8	–	–	14.3	3.3
<i>Caprellina longicollis</i>	2.0	<1	–	–	–	–	10.5	2.3	–	–	–	–	–	–
<i>Ceradocus rubromaculatus</i>	4.0	<1	–	–	–	–	–	–	–	–	25.0	1.5	–	–
<i>Ceradocus</i> sp.	2.0	<1	8.3	<1	11.1	10.4	–	–	–	–	–	–	14.3	11.7
<i>Chevalia aviculae</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cyproidea ornata</i>	–	–	25.0	1.1	–	–	5.3	<1	–	–	25.0	<1	14.3	3.3
<i>Cypsiphimeda gibba</i>	–	–	–	–	–	–	5.3	1.0	–	–	–	–	–	–
<i>Erichthonius brasiliensis</i>	–	–	–	–	–	–	–	–	20.0	5.8	–	–	–	–
<i>Euonyx conicurus</i>	2.0	<1	–	–	–	–	10.5	1.0	–	–	–	–	–	–
<i>Euonyx</i> spp.	–	–	–	–	–	–	21.1	2.8	–	–	–	–	–	–
<i>Gammaropsis</i> spp.	18.0	1.1	–	–	5.6	3.1	–	–	–	–	–	–	–	–
<i>Grandidirella</i> sp.	2.0	<1	–	–	–	–	10.5	1.8	–	–	–	–	–	–
<i>Hyale</i> sp.	4.0	<1	–	–	–	–	–	–	20.0	11.6	–	–	–	–
Unid. Hyperiidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ischyrocerus anguipes</i>	4.0	<1	–	–	–	–	15.8	6.1	–	–	–	–	–	–
<i>Ischyrocerus</i> spp.	38.0	3.3	–	–	16.7	2.6	31.6	7.0	–	–	–	–	–	–
<i>Jassa falcata</i>	12.0	<1	8.3	<1	5.6	1.6	–	–	–	–	–	–	–	–
<i>Laetmatophilus</i> spp.	4.0	1.2	–	–	–	–	–	–	20.0	46.4	–	–	–	–
<i>Lembooides crenatipalma</i>	–	–	–	–	–	–	5.3	<1	–	–	–	–	–	–
<i>Lembooides</i> spp.	–	–	–	–	–	–	5.3	1.0	–	–	–	–	–	–
<i>Liljeborgia</i> sp.	–	–	–	–	5.6	1.6	–	–	–	–	–	–	–	–
<i>Lysianassa</i> spp.	6.0	<1	–	–	–	–	–	–	–	–	–	–	–	–
Unid. Lysianassidae	34.0	1.2	–	–	–	–	31.6	7.6	–	–	25.0	40.6	–	–





## Appendix 1. Continued.

	<i>Clinus superciliosus</i> N=9		<i>Clinus venustris</i> N=5		<i>Fucomimus mus</i> N=8		<i>Pavoclinus litorafontis</i> N=5		<i>Pavoclinus myae</i> N=27		<i>Pavoclinus pavo</i> N=14		<i>Congiopodus torvus</i> N=2	
	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol
<i>Euphrosine capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lepidonotus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Sedentaria	-	-	-	-	-	-	-	-	-	-	7.1	1.0	-	-
<b>Crustacea</b>														
<b>Amphipoda</b>														
<i>Amaryllis macrophthalmia</i>	-	-	-	-	-	-	-	-	-	-	7.1	1.4	-	-
<i>Ampelisca palmata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ampelisca</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Amphilocheus</i> sp.	-	-	-	-	-	-	-	-	3.7	1.0	-	-	-	-
<i>Amphilocheus neopolitanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ampithoe</i> sp.	11.1	<1	-	-	-	-	-	-	3.7	1.8	-	-	-	-
<i>Aora</i> spp.	-	-	-	-	-	-	-	-	14.8	2.1	21.4	5.0	-	-
<i>Argissa hamatipes</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Caprella cicur</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Caprella penantis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Caprellidea	22.2	1.0	40.0	3.3	-	-	-	-	7.4	1.2	7.14	1.0	50.0	<1
<i>Ceradocus rubromaculatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ceradocus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chevalia aviculae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyproidea ornata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cypsiphimeda gibba</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Erichthonius brasiliensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euonyx conicurus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euonyx</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gammaropsis</i> spp.	-	-	-	-	-	-	-	-	3.7	1.2	-	-	-	-
<i>Granditirella</i> sp.	-	-	-	-	-	-	-	-	3.7	1.0	-	-	-	-
<i>Hyalie</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Hyperiidea	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ischyrocerus anguipes</i>	-	-	-	-	12.5	2.1	-	-	-	-	-	-	-	-
<i>Ischyrocerus</i> spp.	-	-	40.0	1.7	-	-	100.0	43.5	18.5	4.6	14.3	2.7	-	-
<i>Jassa falcata</i>	-	-	-	-	-	-	-	-	7.4	4.9	7.1	1.0	-	-
<i>Laetmatophilus</i> spp.	11.1	5.1	-	-	12.5	42.2	33.3	17.4	-	-	7.1	<1	-	-
<i>Lembooides crenatipalma</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lembooides</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Liljeborgia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lysianassa</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Lysianassidae	-	-	-	-	25.0	8.4	-	-	3.7	1.2	7.1	3.6	-	-
<i>Melita</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Metaleptamphopus membrisetata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ochlesis levetzowi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paramoera capensis</i>	22.2	6.1	-	-	-	-	-	-	18.5	6.4	14.3	15.0	-	-
<i>Paraphoxus oculatus</i>	11.1	4.9	-	-	12.5	2.1	-	-	-	-	7.1	2.0	-	-
<i>Parelasomopus suluensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Photis</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Podocerus brasiliensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Podocerus</i> spp.	11.1	<1	-	-	-	-	-	-	44.4	22.1	-	-	50.0	1.1
<i>Temnophilias capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Temnophilias</i> spp.	-	-	-	-	-	-	-	-	14.8	2.7	-	-	-	-
<b>Copepoda</b>														
Unid. Copepoda	-	-	-	-	25.0	7.4	-	-	-	-	-	-	-	-
<i>Porcellidium</i> spp.	-	-	-	-	37.5	5.6	-	-	-	-	7.1	<1	-	-
<b>Cumaceam</b>														
<b>Decapoda</b>														
<i>Cryptodromiopsis spongiosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diogenes costatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dromidia hirsutissima</i> -	-	-	-	-	-	-	-	-	-	-	-	50.0	2.5	-
Unid. Anomura	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hymenosoma orbiculare</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Decapoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paguristes gamianus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paguristes</i> sp.	11.1	3.4	-	-	-	-	-	-	-	-	-	-	50.0	5.1



## Appendix 1. Continued.

	<i>Clinus superciliosus</i> N=9		<i>Clinus venustris</i> N=5		<i>Fucomimus mus</i> N=8		<i>Pavoclinus litorafontis</i> N=5		<i>Pavoclinus myae</i> N=27		<i>Pavoclinus pavo</i> N=14		<i>Congiopodus torvus</i> N=2	
	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol
<i>Pilumnus hirsutus</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	1.0
<i>Plagusia chabrus</i>	11.1	2.0	-	-	-	-	-	-	-	-	-	-	50.0	3.5
<b>Isopoda</b>														
Unid. Arcturidae	-	-	-	-	-	-	-	-	7.4	2.1	-	-	-	-
<i>Cirolana</i> sp.	11.1	<1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cirolana venusticauda</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymodoce falcata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymodoce valida</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymodocella magna</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymodocella pustulata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymodocella</i> sp.	-	-	-	-	-	-	-	-	3.7	<1	-	-	-	-
<i>Dynamanella macrocephala</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dynamanella</i> sp.	22.2	<1	-	-	12.5	1.1	-	-	-	-	14.3	2.0	-	-
<i>Exosphaeroma porrectum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Exosphaeroma</i> sp.	-	-	-	-	-	-	-	-	-	-	7.1	<1	50.0	1.5
<i>Exosphaeroma truncatitelson</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Exosphaeroma varicolor</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Glyptidotea lichtensteini</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gnathia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Jaeropsidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Jaeropsis</i> sp.	-	-	-	-	12.5	6.3	-	-	-	-	-	-	-	-
Unid. Janiridae	-	-	-	-	-	-	-	-	7.4	1.5	21.4	1.6	-	-
<i>Lanocira gardenii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Munna</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Neastacilla longispina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Neastacilla</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Notasellus capensis</i>	-	-	-	-	-	-	-	-	-	-	7.1	1.0	-	-
<i>Parisocladus perforatus</i>	-	-	-	-	-	-	-	-	-	-	7.1	1.0	-	-
<i>Parisocladus</i> sp.	-	-	20.0	4.4	-	-	-	-	-	-	7.1	1.0	-	-
<i>Stenetrium</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Leptostraca</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Mysidacea</b>	-	-	40.0	6.6	-	-	-	-	-	-	-	-	50.0	<1
<b>Ostracoda</b>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<b>Tanaidacea</b>	-	-	-	-	25.0	3.2	-	-	3.7	<1	-	-	-	-
<b>Unid. Crustacea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Bryozoa</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Mollusca</b>														
<b>Bivalvia</b>														
<i>Aulacomya ater</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	1.0
<i>Carditella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Cardium turtoni</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Chlamys tincta</i>	-	-	-	-	-	-	-	-	-	-	-	-	100.0	5.9
<i>Macoma</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Tellina gilchristi</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<b>Cephalopoda</b>														
<i>Sepia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Gastropoda</b>														
<i>Balcis algoensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	1.0
<i>Cerithidea decollata</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Clionella rosaria</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Crepidula capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Crepidula porcellana</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	2.2
<i>Dendrofiurella scutella</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fissurella mutabilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	1.0
<i>Fissurella</i> sp.	11.1	4.5	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gibbula capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Gibbula zonata</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<i>Haliotis spadicea</i>	11.1	1.0	-	-	-	-	-	-	-	-	-	-	50.0	1.8
<i>Helcion pruinosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Marginella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	50.0	4.1
<i>Nassarius capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1

## Appendix 1. Continued.

	<i>Clinus superciliosus</i> N=9		<i>Clinus venustris</i> N=5		<i>Fucomimus mus</i> N=8		<i>Pavoclinus litorafontis</i> N=5		<i>Pavoclinus myae</i> N=27		<i>Pavoclinus pavo</i> N=14		<i>Congiopodus torvus</i> N=2	
	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol
<i>Tricolia kochi</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	2.3
<i>Tricolia</i> sp.	11.1	<1	-	-	25.0	1.5	-	-	-	-	21.4	<1	-	-
<i>Turbo</i> sp.	11.1	<1	-	-	-	-	-	-	-	-	-	-	-	-
<b>Opisthobranchia</b>														
<i>Tambja capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Echinodermata</b>														
<b>Crinoidea</b>														
<i>Annametra occidentalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Comanthus wahlbergi</i>	-	-	-	-	-	-	-	-	-	-	-	-	50.0	26.4
Unid. Crinoidea	-	-	20.0	2.2	-	-	-	-	-	-	-	-	50.0	22.7
<b>Echinoidea</b>														
<i>Parechinus angulosus</i>	11.1	10.2	-	-	-	-	-	-	-	-	-	-	-	-
<b>Ophiuroidea</b>														
	-	-	-	-	-	-	-	-	-	-	-	-	50.0	<1
<b>Ascideacea</b>														
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Pisces</b>														
	22.2	8.0	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Halidesmus scapularis</i> N=78		<i>Gaidropsarus capensis</i> N=12		<i>Chorisochismus dentex</i> N=11		<i>Eckloniaichthys scylliorhiniceps</i> N=14		<i>Caffrogobius agulhensis</i> N=6		<i>Caffrogobius saldanha</i> N=47		<i>Cremnochorites capensis</i> N=7	
	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol
<b>Algae</b>														
Coralline	-	-	-	-	9.1	3.9	-	-	-	-	-	-	-	-
Fleshy	-	-	-	-	9.1	1.6	-	-	-	-	4.3	<1	-	-
<b>Cnidaria</b>														
<b>Octocorallia</b>														
<b>Polychaeta</b>														
Unid. Errantia	-	-	8.3	<1	-	-	-	-	-	-	4.3	4.3	11.1	<1
<i>Eunice</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euphrosine capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lepidonotus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Sedentaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Crustacea</b>														
<b>Amphipoda</b>														
<i>Amaryllis macrophthalma</i>	2.6	<1	-	-	9.1	<1	-	-	-	-	-	-	3.7	<1
<i>Ampelisca palmata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ampelisca</i> sp.	-	-	-	-	-	-	-	-	-	-	4.3	3.6	-	-
<i>Amphilocheus</i> sp.	-	-	-	-	9.1	<1	-	-	-	-	-	-	-	-
<i>Amphilocheus neopolitanus</i>	-	-	-	-	-	-	7.1	1.0	-	-	-	-	-	-
<i>Ampithoe</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aora</i> spp.	-	-	-	-	-	-	-	-	16.7	4.9	2.1	<1	-	-
<i>Argissa hamatipes</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Caprella cicur</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Caprella penantis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Caprellidea	1.3	1.0	25.0	3.0	9.1	<1	-	-	-	-	17.0	2.1	81.5	11.3
<i>Caprellina longicollis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ceradocus rubromaculatus</i>	-	-	8.3	5.5	-	-	-	-	-	-	2.1	1.0	3.7	1.3
<i>Ceradocus</i> sp.	2.6	1.4	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chevalia aviculae</i>	1.3	<1	-	-	-	-	-	-	-	-	-	-	7.4	<1
<i>Cyproidea ornata</i>	-	-	8.3	<1	-	-	-	-	-	-	8.5	1.0	14.8	<1
<i>Cypsiphimedia gibba</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Erichthonius brasiliensis</i>	-	-	-	-	-	-	-	-	-	-	2.1	<1	-	-
<i>Euonyx conicurus</i>	1.3	<1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euonyx</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	3.7	<1
<i>Gammaropsis</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	7.4	<1
<i>Granditirella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyale</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Hyperiidea	6.4	1.0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ischyrocerus anguipes</i>	3.8	1.8	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ischyrocerus</i> spp.	1.3	<1	-	-	18.2	1.0	7.1	1.2	16.7	17.2	4.3	1.0	22.2	2.4



## Appendix 1. Continued.

	<i>Halidesmus scapularis</i> N=78		<i>Gaidropsarus capensis</i> N=12		<i>Chorisochismus dentex</i> N=11		<i>Eckloniaichthys scylliorhiniceps</i> N=14		<i>Caffrogobius agulhensis</i> N=6		<i>Caffrogobius saldanha</i> N=47		<i>Cremnochorites capensis</i> N=7	
	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol	% occ	% vol
<i>Neastacilla longispina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Neastacilla</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	11.1	1.0
<i>Notasellus capensis</i>	12.8	7.0	-	-	-	-	-	-	-	-	-	-	18.5	1.0
<i>Parisocladus perforatus</i>	-	-	-	-	9.1	1.0	-	-	-	-	-	-	-	-
<i>Parisocladus</i> sp.	-	-	-	-	9.1	<1	-	-	-	-	2.1	<1	-	-
<i>Stenetrium</i> sp.	6.4	3.0	-	-	-	-	-	-	-	-	-	-	7.4	1.0
<b>Leptostraca</b>	1.3	<1	-	-	-	-	-	-	16.7	2.5	14.9	2.7	-	-
<b>Mysidacea</b>	-	-	8.3	3.3	-	-	-	-	-	-	2.1	-	-	-
<b>Ostracoda</b>	10.3	1.0	16.7	1.0	-	-	-	-	-	-	4.3	<1	7.4	<1
<b>Tanaidacea</b>	11.5	1.6	-	-	9.1	<1	-	-	-	-	2.1	<1	3.7	<1
<b>Unid. Crustacea</b>	60.3	16.4	-	-	-	-	-	-	-	-	-	-	-	-
<b>Bryozoa</b>	-	-	33.3	13.8	-	-	-	-	-	-	-	-	-	-
<b>Molluscam</b>														
<b>Bivalvia</b>														
<i>Aulacomya ater</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Carditellasp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cardium turtoni</i>	-	-	-	-	9.1	<1	-	-	-	-	-	-	-	-
<i>Chlamys tincta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macoma</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tellina gilchristi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Cephalopoda</b>														
<i>Sepia</i> sp.	-	-	-	-	9.1	1.6	-	-	-	-	-	-	-	-
<b>Gastropoda</b>														
<i>Balcis algoensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cerithidea decollata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Clionella rosaria</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Crepidula capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Crepidula porcellana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dendrofissurella scutella</i>	-	-	-	-	9.1	6.7	-	-	-	-	-	-	-	-
<i>Fissurella mutabilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fissurella</i> sp.	-	-	-	-	18.2	13.8	-	-	-	-	-	-	-	-
<i>Gibbula capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gibbula zonata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Haliotis spadicea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Helcion pruinosus</i>	-	-	-	-	9.1	2.1	-	-	-	-	-	-	-	-
<i>Marginella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nassarius capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nassarius speciosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Natica tecta</i>	1.3	<1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Patella compressa</i>	-	-	-	-	18.2	11.7	-	-	-	-	-	-	-	-
<i>Patella concolor</i>	-	-	-	-	9.1	2.1	-	-	-	-	-	-	-	-
<i>Patella miniata</i>	-	-	-	-	9.1	19.1	-	-	-	-	-	-	-	-
<i>Patella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tricolia kochi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tricolia</i> sp.	1.3	<1	-	-	18.2	<1	-	-	16.7	0.6	2.1	<1	-	-
<i>Turbo</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	11.1	<1
<b>Opisthobranchia</b>														
<i>Tambja capensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Echinodermata</b>														
<b>Crinoidea</b>														
<i>Annametra occidentalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Comanthus wahlbergi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Crinoideam	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Echinoidea</b>														
<i>Parechinus angulosus</i>	-	-	-	-	9.1	10.1	-	-	-	-	-	-	-	-
<b>Ophiuroidea</b>	3.8	2.3	-	-	-	-	-	-	-	-	-	-	-	-
<b>Ascideacea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Pisces</b>	-	-	16.7	4.1	9.1	14.9	-	-	-	-	10.6	1.3	-	-