The intertidal fish fauna of the west coast of South Africa — species, community and biogeographic patterns

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In the first quantitative survey of intertidal fish from the South African west coast 62 intertidal rock pools were sampled at two sites, using the ichthyocide rotenone. A total of 2 022 fish representing 14 species belonging to only two families — the Clinidae (88–98% by number) and the Gobiesocidae (12–2%) — were caught. *Clinus superciliosus, C. heterodon* and the gobiesocid *Chorisochismus dentex* were the most abundant species in terms of both numbers and biomass. Vertical zonation of individual species on the shore indicated little separation of the habitat between species, although some species exhibited size-specific partitioning of the shore. Relationships between fish distribution and abundance and rock pool characteristics were elucidated by means of stepwise multiple regression, both at the whole community and individual species levels. The abundances of individual species were best predicted by pool size, although some species also showed an association with weed cover. For the community as a whole, the number of species present, the total number of fish and the total biomass in any pool were all dependent on pool size, height above LWS and amount of available cover. Relative to other South African sites the west coast has a low diversity of intertidal fish, combined with a high degree of dominance and a low level of habitat separation.

Tussengety-visspesies aan die Suid-Afrikaanse weskus is vir die eerste keer kwantitatief versamel uit 62 getypoele in twee areas met behulp van die visdoder rotenone. 'n Totaal van 2 022 visse wat 14 spesies, maar slegs twee families verteenwoordig — die Clinidae (88–98% van die totale aantal) en die Gobiesocidae (12–2%) — is gevang. *Clinus superciliosus, C. heterodon* en die suiervis, *Chorisochismus dentex,* was die mees talryke spesies beide met betrekking tot getalle en biomassa. Vertikale indeling van individuele spesies in die tussen getysone het op min verdeling van die habitat tussen spesies gedui, alhoewel sommige spesies 'n verdeling in terme van grootte vertoon het. Verwantskappe tussen die verspreiding en talrykheid van visse, en die kenmerke van rotspoele is blootgelê deur middel van stapsgewyse veelfaktor-regressie vir die hele gemeenskap sowel as vir individuele spesies. Die talrykheid van individuele spesies is die beste voorspel deur poelgrootte, alhoewel sommige spesies ook geassosier is met die wierbedekking. Vir die hele gemeenskap was die getal visspesies en induvidue en die totale biomassa in enige poel almal afhanklik van poelgrootte, hoogte bo LWS en die hoeveelheid skuiling. In vergelyking met ander gebiede in Suid-Afrika het die Weskus 'n lae diversitiet van getypoelvissoorte, tesame met 'n hoë vlak van dominansie en relatief min verdeling van die habitat.

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Although the intertidal fish fauna of southern Africa is rich in species and exhibits a high degree of endemism, research on these communities has been limited. The first community-level studies were descriptive in nature and concerned purely with presence/absence, or relative abundance data (Jackson 1950; Penrith 1965, 1970; Penrith & Kensley 1970a,b; Kensley & Penrith 1973). More recent studies have been based on quantitative collections (Marsh, Crowe & Siegfried 1978; Christensen & Winterbottom 1981; Bennett & Griffiths 1984; Beckley 1985; Bennett 1987; Burger 1988; 1991), although only three papers (Marsh *et al.* 1978; Bennett & Griffiths 1984; Bennett 1987) have related fish abundance to rock pool size.

Of the South African studies listed, all sampled areas on the southern coast of the country between the Cape Peninsula (33°59′S/18°01′E) and Port Alfred (33°36′S/26°54′E). They thus encompass only some 1000 km, or 37% of the total coastline of South Africa. The west coast in particular, remains almost completely unsampled, although it is both extensive (800 km or 30% of the total coastline) and a biogeographically distinct region of the South African coastline (Stephenson 1939, 1944, 1948). It also includes the northern limits of the ranges of many endemic and other temperate species, as well as the southern limits of some subtropical Atlantic forms (Penrith 1970).

This study aims to provide a first quantitative survey of the intertidal ichthyofauna of the Cape west coast, with a view to elucidating patterns of habitat subdivision at species, community and biogeographical levels.

Methods

Intertidal fish were collected from 30 rock pools at Groenrivier (30°51′S/17°33′E) and 32 pools at Cape St Martin (32°40′S/17°56′E) during January and April 1991 respectively. Pools were visited at low water of spring tide (LWS) and were selected to represent the full range of pool parameters measured. These included height above (HEIGHT), and distance from (DISTANCE) low water springs (LWS), surface area (AREA) and mean depth. Pool volume (VOLUME) was calculated by multiplying surface area by mean depth, and an index of isolation from the sea, or exposure (EXP), was calculated as the product of pool height and distance from LWS. In addition, the amount of rock (ROCK) and weed (WEED) cover or shelter available was rated subjectively on a scale of 1–10 as described by Bennett & Griffiths (1984).

The ichthyocide rotenone, dissolved in acetone in the ratio 1 : 10, was introduced into the pools and all comatose fish were collected with handnets and placed in 10% formalin for two days before being transferred to 70% ethanol for permanent preservation. The fish from each pool were kept separately and were identified, counted, measured to the nearest millimetre and weighed to the nearest 0,1 g.

At Cape St Martin pools were baled after catching all fish that came to the surface, and the pool bottom searched for fish that may have remained in crevices or under seaweed. These fish were kept separately and treated as above, although they were excluded from further analysis for the purpose of inter-site comparisons, as other authors had not baled their study pools.

The data were analysed by performing stepwise multiple regressions using the number of species, the total number of fish and the total mass of fish caught as dependent variables and the pool parameters detailed above as independent variables. The procedure was repeated using the abundances of those individual species which made up more than 5% of the total numbers or biomass caught as dependent variables.

Species diversity indices were calculated after Odum (1971) as follows:

Margalef species richness index: $d = (S-1) / \ln N$
Shannon-Wiener overall index: $H = -\Sigma(n_i / N)\ln(n_i / N)$
Pielou evenness index: $e = H / \ln S$

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

Results and Discussion

The fish communities

The number of fish species recorded, the total number of individuals and the total fish biomass, shown in Table 1, were all considerably greater at Cape St Martin (12; 1417; 5318,6 g respectively) than at Groenrivier (9; 605; 3876,0 g respectively). The total pool area sampled was 110,2 m^2 and 174,7 m^2 at Groenrivier and Cape St Martin respectively. Thus although the overall numerical fish density was greater at Cape St Martin (8,11 fish m^{-2}) than at Groenrivier (5,49 fish m^{-2}), biomass showed the opposite tendency (30,45 and 35,16 g m^{-2} respectively). This result may be explained by the presence of larger numbers of juveniles at Cape St Martin, which was sampled in late summer (April), than at Groenrivier, which was sampled in January. Although Veith (1979) stated that *Clinus superciliosus* breeds throughout the year, his conclusions were based on gonadal mass data, and did not take differential recruitment into account. A summer peak in recruitment of juvenile clinids has been demonstrated by Beckley (1985).

The above numerical densities are similar to those reported for False Bay (6,82 fish m^{-2}) and the Cape Peninsula west coast (7,75 fish m^{-2}) by Bennett & Griffiths (1984), and fall within the range cited by Gibson (1982) for intertidal fish on rocky substrata in other areas around the world. Biomass figures of 35,16 and 30,45 g m^{-2}, however, were lower than the 47,41 and 53,45 g m^{-2} reported for the Cape Peninsula by Bennett & Griffiths (1984).

Both west coast sites were represented by two families only, namely the Clinidae and the Gobiesocidae, the clinids making up 88,1% and 98,5% of the total number of fish caught at Groenrivier and Cape St Martin respectively. *Clinus superciliosus* and *C. heterodon* together constituted the bulk of the total catch in terms of both numbers (61,3% and 74,5%) and biomass (56,9% and 83,3%) at Groenrivier and Cape St Martin respectively. Also of importance were *Chorisochismus dentex*, *Clinus acuminatus* and *C. agilis* at Groenrivier and *C. dentex*, *Muraenoclinus dorsalis* and *C. agilis* at Cape St Martin. The five most abundant species

Table 1 The composition of the intertidal ichthyofauna of 30 rock pools totalling 110,2 m^2 at Groenrivier and of 32 pools totalling 174,7 m^2 at Cape St Martin on the west coast of South Africa. *N* denotes numbers and *M* biomass

	Groenrivier				Cape St Martin			
Species	*N*	*M*	%*N*	%*M*	*N*	*M*	%*N*	%*M*
Clinidae	**533**	**2843,8**	**88,1**	**73,4**	**1396**	**4988,5**	**98,5**	**93,8**
Clinus superciliosus	208	1706,9	34,4	44,0	689	2702,6	48,6	50,9
Clinus heterodon	163	498,3	26,9	12,9	367	1730,5	25,9	32,5
Clinus agilis	65	161,8	10,7	4,2	113	226,8	8,0	4,3
Clinus acuminatus	72	386,5	11,9	10,0	16	63,7	1,1	1,2
Blennophis anguillaris	15	36,0	2,5	0,9	4	7,2	0,3	0,1
Clinus venustris	8	49,6	1,3	1,3	–	–	–	–
Clinus taurus	1	4,5	0,2	0,1	–	–	–	–
Muraenoclinus dorsalis	1	0,2	0,2	<0,1	150	108,0	10,6	2,0
Clinus cottoides	–	–	–	–	53	144,8	3,7	2,7
Pavoclinus pavo	–	–	–	–	2	3,7	0,1	0,1
Clinus rotundifrons	–	–	–	–	1	0,2	0,1	<0,1
Xenopoclinus leprosus	–	–	–	–	1	1,0	0,1	<0,1
Gobiesocidae	**72**	**1032,2**	**11,9**	**26,6**	**21**	**330,1**	**1,5**	**6,2**
Chorisochismus dentex	72	1032,2	11,9	26,6	20	329,6	1,4	6,2
Eckloniaichthys scylliorhiniceps	–	–	–	–	1	0,5	0,1	<0,1
Totals	**605**	**3876,0**			**1417**	**5318,6**		
Densities per m²	**5,49**	**35,16**			**8,11**	**30,45**		

thus together made up 95,8% and 94,5%*N* and 97,7% and 95,8%*M* at Groenrivier and Cape St Martin respectively.

Capture efficiency

Bottom searches of the pools sampled at Cape St Martin revealed that surface capture may be inefficient, at least for some species (Table 2). Seven species were found during the bottom searches. Of these, four had been captured efficiently at the surface, with only an additional 1,9–3,2% being found on the bottom. However, for three species (*Clinus agilis*, *C. acuminatus* and *Chorisochismus dentex*) the proportion found on the bottom was greater than 10% of the total catch. Indeed, 35,5% of all the *C. dentex* captured were found during bottom searches. It thus appears that conventional rotenone samples in which only surface recoveries are made, may result in underestimates of the abundance of some species.

Table 2 The total number of individuals of different fish species caught in intertidal rock pools and the number found during bottom searches, as well as the per cent of each species found on the bottom

Species	Total number	Number on bottom	% On bottom
Chorisochismus dentex	31	11	35,5
Clinus acuminatus	18	2	11,1
Clinus agilis	127	14	11,0
Clinus heterodon	379	12	3,2
Muraenoclinus dorsalis	155	5	3,2
Clinus superciliosus	706	17	2,4
Clinus cottoides	54	1	1,9

Intraspecific distribution patterns

The most abundant species, *Clinus superciliosus*, showed 'bi- and tri-modal' vertical zonation patterns at Groenrivier and Cape St Martin respectively (Figure 1). Dividing the fish into three size classes (juveniles = < 1 g; small adults = 1–5 g; large adults = > 5 g) indicated that, although all three size classes were present at all tidal levels, large individuals were more abundant lower in the intertidal, while small ones were more prevalent at higher levels. Thus, at Groenrivier, the low-shore was dominated by adults (83%), while the high-shore had a more even mixture of sizes, with juveniles contributing 47% to the total numbers present. Similarly, at Cape St Martin juveniles comprised only 42% of low-shore and 83% of high-shore populations (Figure 1). Although Bennett & Griffiths (1984) also showed a 'bimodal' vertical zonation of this species, they did not present data on the size distribution of individuals in the two modes. Habitat separation by different size classes has been demonstrated previously by Gibson (1972) for intertidal fish on the Atlantic coast of France, although this occurred on the basis of both pool size and vertical height on the shore. Stepwise multiple regression results for *C. superciliosus* indicated positive relationships between abundance and pool area at both sites (Table 4), while the exposure index contributed weakly to explaining variance in abundance.

Clinus heterodon showed a trend of decreasing abundance up the shore at Groenrivier, reaching a maximum height of 180 cm above LWS (Figure 1). This is in accordance with the result of the stepwise multiple regression (Table 3), which indicated a negative relationship between number of fish and height on the shore. By contrast, Bennett & Griffiths (1984) found that this species reached peak abundance on the mid- to high-shore on the Cape Peninsula west coast. The lack of correlation with any pool parameter at Cape St

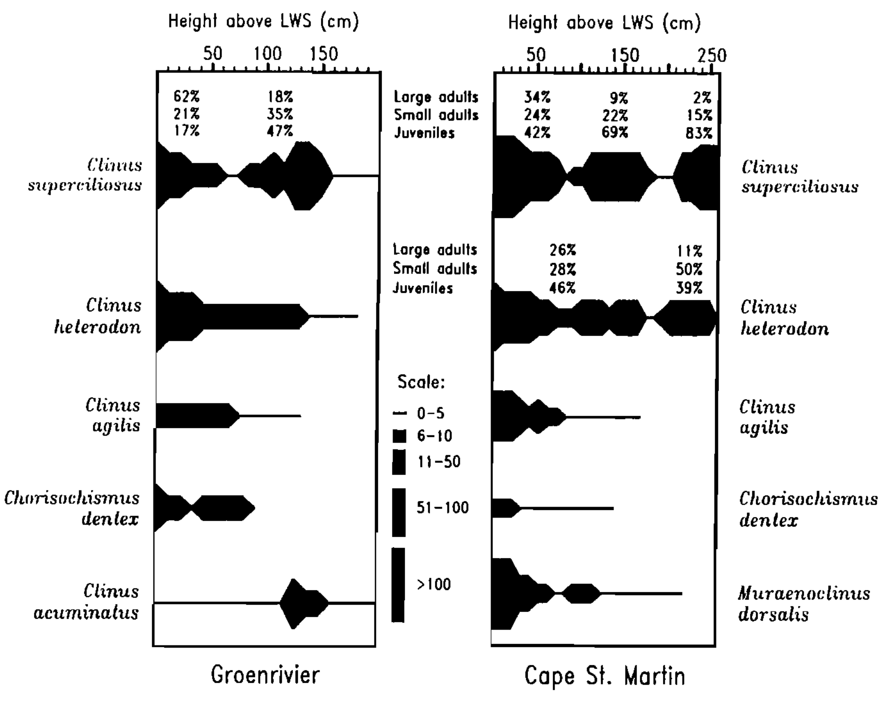

Figure 1 Vertical zonation of the five most abundant intertidal fish species at Groenrivier and Cape St Martin on the Cape west coast.

Table 3 Correlation coefficients obtained by stepwise multiple regression relating the abundance of rock pool fish species to pool parameters at Groenrivier and Cape St Martin on the South African west coast. Dash denotes a lack of correlation

Species	Groenrivier		Cape St Martin	
Clinus superciliosus	AREA	+0,50	AREA	+0,46
	Whole reg.	0,50	EXP	+0,19
			Whole reg.	0,55
Clinus heterodon	HEIGHT	–0,28	–	
	Whole reg.	0,28		
Clinus agilis	VOLUME	+0,60	WEED	+0,29
	AREA	+0,22	Whole reg,	0,29
	Whole reg.	0,71		
Clinus acuminatus	AREA	+0,23		
	WEED	+0,06		
	VOLUME	+0,02		
	Whole reg.	0,56		
Muraenoclinus dorsalis			WEED	+0,32
			Whole reg.	0,32
Chorisochismus dentex	AREA	+0,27	VOLUME	+0,68
	WEED	+0,22	Whole reg.	0,68
	Whole reg.	0,35		

Table 4 Results of stepwise multiple regression relating species number, number of individuals and total mass of fish caught to rock pool parameters at Groenrivier and Cape St Martin on the South African west coast

	Groenrivier		Cape St Martin	
No. species	VOLUME	+0,43	WEED	+0,54
	HEIGHT	–0,39	AREA	+0,53
	ROCK	+0,28	Whole reg.	0,61
	Whole reg.	0,63		
No. fish	AREA	+0,67	VOLUME	+0,85
	HEIGHT	–0,26	AREA	+0,50
	Whole reg.	0,70	Whole reg.	0,94
Total mass	AREA	+0,58	ROCK	+0,69
	HEIGHT	–0,29	WEED	+0,39
	ROCK	+0,27	Whole reg.	0,74
	Whole reg.	0,68		

Martin (Table 3) is a result of the 'bimodal' vertical distribution illustrated in Figure 1. Here it may be seen that although the percentages of adults and juveniles were similar in both 'modes', both juveniles and large adults were more prevalent on the lower shore, while small adults dominated the higher shore populations, extending to a height of 260 cm above LWS.

Clinus agilis declined in abundance with increasing shore height at both sites, reaching 130 cm and 170 cm above LWS at Groenrivier and Cape St Martin respectively. The positive relationships with pool volume (+0,60) and surface area (+0,22) at Groenrivier indicate a 'preference' for large pools. This phenomenon appears to be consistent with a low-shore species, since large pools may effectively simulate the subtidal situation. Stepwise multiple regression with number of *C. agilis* at Cape St Martin indicated that the amount of weed cover present was an important factor governing the abundance of this species. Indeed, behavioural observations by the senior author confirm that this species is primarily a weed dweller.

The giant clingfish, *Chorisochismus dentex*, was also most abundant lower on the shore, and although it only reached a height of 90 cm above LWS at Groenrivier (Figure 1), it extended to 140 cm at Cape St Martin (Figure 1). This is consistent with the positive regression relationships (Table 3) with pool area (+0,27) and volume (+0,68). The positive correlation with the amount of weed cover present at Groenrivier (Table 4) indicates the tendency of this species to 'hide' under patches of weed, or for small individuals to cling to the undersides of kelp fronds (pers. obs.).

Clinus acuminatus, which was rare at Cape St Martin, was the only species more abundant at mid- to high tidal levels than on the low-shore, a similar result to that found by Bennett & Griffiths (1984). At Groenrivier (Figure 1), it was most abundant between 120 cm and 160 cm above LWS, although some individuals were present throughout the tidal range. Unfortunately simple regression is an inappropriate technique for statistically testing this relationship, and thus the correlation coefficients do not reflect this relationship (Table 3).

Muraenoclinus dorsalis decreased in abundance with increasing elevation at Cape St Martin (Figure 1), although some individuals extended as far as 220 cm above LWS. However, no correlation between abundance and shore height was found, and only the amount of weed cover could be used to explain abundance (+0,32).

Diets

The diets of several South African intertidal fish species have been studied previously (Stobbs 1980; Bennett, Griffiths & Penrith 1983; Burger 1991). The most obvious differences in diet occur between the clinids and the gobiesocids, with *Chorisochismus dentex* consuming a largely limpet-based diet, and the clinids eating mostly a variety of amphipod and isopod crustaceans. All the clinids appear to have similar diets, the only exception being *Clinus agilis*, which has a 'restricted diet' (Bennett, Griffiths & Penrith 1983), with the amphipod *Paramoera capensis* occuring in 58% of stomachs. However, this prey item may also contribute large proportions to the diets of other species (Bennett, Griffiths & Penrith 1983). Thus data from dietary studies suggest little partitioning of the available food resources by South African intertidal fish.

Community patterns

Stepwise multiple regression results for whole communities at Groenrivier and Cape St Martin are presented in Table 4. The total number of species present at Groenrivier was positively correlated with pool volume (+0,43) and to a lesser extent with amount of rock cover (+0,28). Height on the shore had a negative effect on number of species present (–0,39). At Cape St Martin pool area explained 53% of the variance in species number, while the amount of weed cover present explained 54%. Thus, the variance in species number was explained primarily by a function of pool size (area and/or volume), available cover (rock and/or weed) and pool height. This result is similar to that obtained by Bennett & Griffiths (1984) using linear-linear stepwise

Table 5 Diversity indices for intertidal fish at Groenrivier and Cape St Martin on the South African west coast, and for other sites around the coast. Data for Cape Peninsula and False Bay from Bennett & Griffiths (1984), data for Tsitsikamma from Burger (1991), and data for Port Elizabeth from Beckley (1985)

	Margalef species richness	Shannon-Wiener overall	Pielou evenness
Groenrivier	1,21	1,64	0,75
Cape St Martin	1,52	1,41	0,57
Cape Peninsula	1,73	2,59	1,01
False Bay	2,40	3,19	1,15
Tsitsikamma	2,00	1,40	0,50
Port Elizabeth	4,36	2,67	0,75

multiple regression for the west coast of the Cape Peninsula.

The total number of fish present was positively correlated with pool area (+0,67) and negatively correlated with height (–0,26) at Groenrivier, and positively correlated with both volume (+0,85) and area (+0,50) at Cape St Martin. Once again this is similar to the results obtained for the Cape Peninsula west coast by Bennett & Griffiths (1984). However, these authors also found a positive correlation between number of fish present and available rock cover, although this relationship could only explain 8% of the variance in the total number of fish caught.

The total mass of fish caught at Groenrivier was positively correlated with pool area (+0,58) and rock cover (+0,27), and negatively correlated with height (–0,29). However, at Cape St Martin, variance in the total mass of fish caught was correlated only with cover (ROCK +0,69; WEED +0,39), and not with any pool size parameter. Similarly, the results of Bennett & Griffiths (1984) indicate that on the Cape Peninsula west coast rock cover contributed to explaining 26% of the variance in total mass, while the pool size parameters of volume and area could only explain 9% and 7% of the variance respectively.

Biogeographical patterns

Both the number of species and the number of families of intertidal fish were lower at both the west coast sites than at other sites around the South African coast (Figure 2). While west coast communities are dominated by members of the families Clinidae and Gobiesocidae, these families constitute progressively smaller proportions of the total communities in more eastern areas (Figure 3). Instead, more easterly communities become increasingly dominated by members of the family Sparidae, with the Gobiidae, Blenniidae, Mugilidae and Cheilodactylidae each also contributing more than 5% of the numbers of fish present. This shift in familial composition is accompanied by a shift from cryptic-dominated to non-cryptic-dominated communities. The reasons for this remain obscure.

Species richness (Table 5) was low on the west coast, rising to the east, while species evenness (Table 5) appeared to be lower towards both the west and east coasts, and highest in the Cape Peninsula/False Bay area, suggesting that the west coast is dominated by large numbers of indivi-

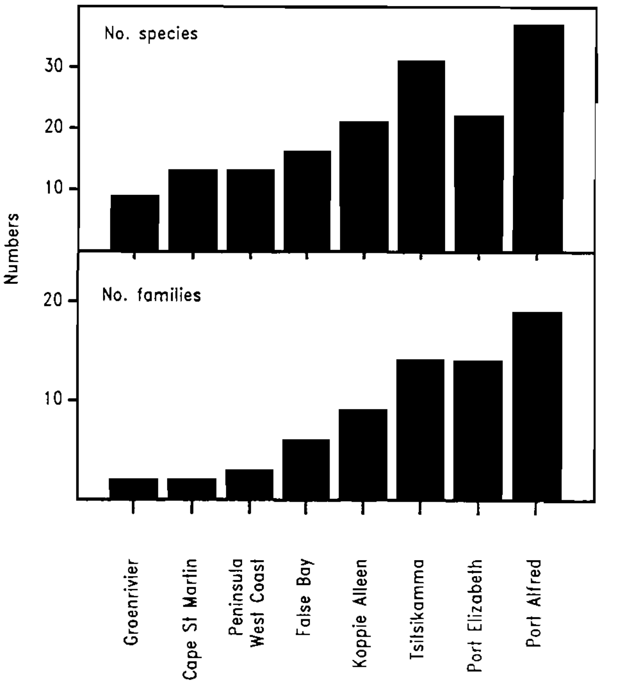

Figure 2 The number of species and families of intertidal fish represented at eight sites around the South African coast. Data for the Cape Peninsula and False Bay from Bennett & Griffiths (1984), for Koppie Alleen from Bennett (1987), for Tsitsikamma from Burger (1991), for Port Elizabeth from Beckley (1985), and data for Port Alfred from Christensen & Winterbottom (1981).

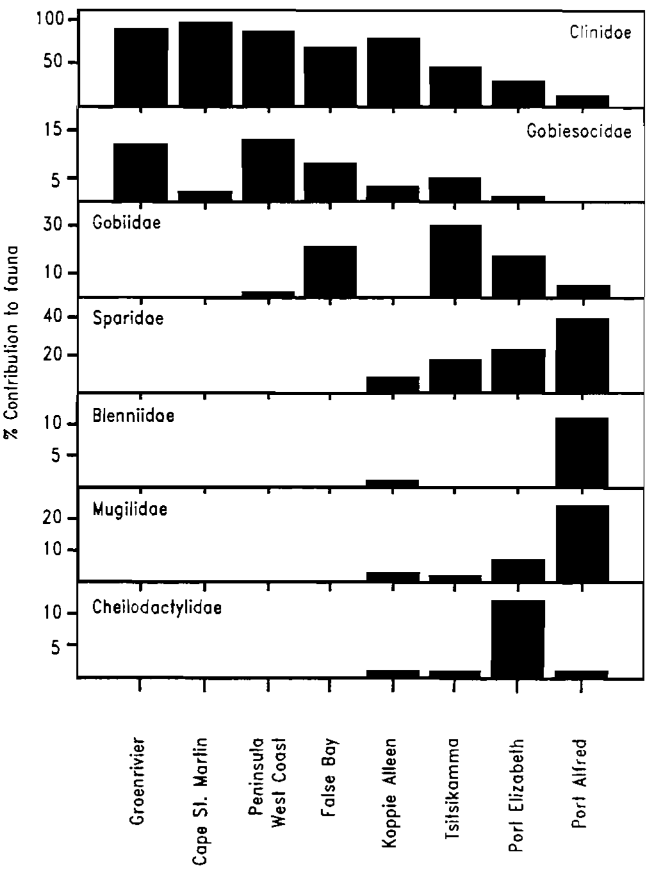

Figure 3 The per cent contribution of seven families by numbers to the intertidal ichthyofauna at eight sites around the South African coast. Sources of data as in Figure 2.

duals of a few species, while on the east coast, although many species are present, only a few dominate in terms of numbers. In the Cape Peninsula/False Bay area many species are represented, but with minimal dominance of individual species. This issue of dominance and species richness is a confused one. MacArthur (1969) stated that, for terrestrial environments, the degree of dominance decreases in more species-rich communities, while Birch (1981) found the opposite relationship in the marine environment. The present study clearly indicates a trend similar to that found by MacArthur (1969). Why the two predictions oppose one another is unclear, and may be a result of the different types of organisms studied in the two analyses.

Conclusions

This study has shown that South African west coast intertidal fish communities are comprised of only two families and relatively few species. Only small differences in vertical zonation and 'pool preferences' appear to exist between the species, with the most abundant forms overlapping greatly in these respects. In his review of intertidal fish biology, Gibson (1982) stated that there is evidence to suggest that, although species overlap in vertical distribution, they may differ in terms of their microhabitat preferences. Other workers have found that microhabitat specialization is less distinct in areas of low species richness (MacArthur 1955, 1965, 1969; Critchlow 1972 in Gibson 1982). Thus the apparent lack of habitat separation by west coast intertidal fish communities may be linked to the low species richness in the area.

Contrary to the above findings, this study has shown that individual species may separate the shore vertically according to size. This phenomenon has been noted previously (Gibson 1982), although Gibson states that the mechanisms of this intraspecific habitat separation remain unknown. It is hypothesized that size-specific partitioning of the shore by the species studied here is a result of territoriality and aggressive behaviour by adults occupying pools at more 'favourable' tidal heights. Although Marsh *et al.* (1978) present some evidence to substantiate this, the hypothesis remains speculative and bears out the conclusion of Peters (1983) that '...quantitative study of community size structure needs and merits further study'.

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