Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa

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A quantitative description of the fish communities inhabiting rock pools on the Cape Peninsula, South Africa, and the relationships between the physical characteristics of the pools and the distribution, abundance and diversity of the resident fish fauna are given.

A total of 1 541 fish, representing 21 species, were collected from 84 rock pools using the ichthyocide Rotenone. The mean density was 7,42 fish m^{-2} (49,60 g m^{-2}) of pool area or 0,58 fish m^{-2} (3,67 g m^{-2}) of the whole intertidal zone in which the pools were situated. *Clinus superciliosus, C. cottoides* and *Chorisochismus dentex* were the most abundant species, together comprising 75% of the biomass and 60% of the number of fish caught.

The number of species, number of individuals and biomass of fish in the pools all correlated significantly ($P < 0,01$) with pool size and the amount of rock cover available. In addition, the number of species decreased up the shore. These three environmental factors in combination accounted for between 58% and 88% of the observed variance in diversity, number and biomass of fish in the pools. Rock cover was the single most important variable, explaining up to 76% of the variance. Possible reasons for the importance of rock cover and its relationship with pool size, are discussed.

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'n Kwantitatiewe beskrywing van die visgemeenskappe wat in die rotspoele van die Kaapse Skiereiland voorkom, word gegee en die verhoudings tussen die fisiese eienskappe van die poele en die verspreiding, getalsterktes en diversiteit van die visfauna is ondersoek.

'n Totaal van 1 541 visse van 21 spesies is uit 84 rotspoele met behulp van die visgif Rotenone gekollekteer. Die gemiddelde digtheid was 7,42 visse m^{-2} (49,60 g m^{-2}) van die poel-area, of 0,58 visse m^{-2} (3,67 g m^{-2}) van die hele getysone waarin die poele voorkom. *Clinus superciliosus, C. cottoides* en *Chorisochismus dentex* was die volopste spesies en het saam 75% van die biomassa en 60% van die getal visse wat gevang is, gevorm.

Die aantal spesies, aantal individue en biomassa van die visse in die rotspoele het betekenisvol gekorreleer ($P < 0,01$) met poelgrootte en die hoeveelheid rotsbedekking beskikbaar. Daarby het die aantal visse teen die strand op verminder. Hierdie drie omgewingsfaktore saam was verantwoordelik vir tussen 58% en 88% van die variasie wat waargeneem is in die diversiteit, getalle en biomassa van die vis in die poele. Die belangrikste enkele veranderlike was rotsbedekking wat tot 76% van die variasie kon verduidelik. Moontlike redes vir die belangrikheid van rotsbedekking en die verhouding daarvan met poelgrootte word bespreek.

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Existing literature on the biology of intertidal fish has been comprehensively reviewed by Gibson (1969, 1982) who points out that relative to other elements of the intertidal community, fish have received remarkably little attention. Most studies on fish have, moreover, dealt with the northern hemisphere while African, Australian and South American shores remain poorly known.

General information on the species composition, relative abundance and intertidal zonation of fishes inhabiting rock pools in the south-western Cape Province, South Africa, is given by Jackson (1950) and Penrith (1965). Neither report was published, nor provided measures of absolute abundance.

Factors regulating density and species composition of rock-pool fish communities in South Africa and elsewhere remain virtually unknown (Gibson 1982). Seasonal changes in diversity occur and can be correlated with seasonal fluctuations in temperature, wave action and upwelling intensity (Green 1971; Grossman 1982; Thomson & Lehner 1976). South-western Cape rock-pool fish populations remain stable in the long and short term (Jackson 1950; Penrith 1965, 1970) perhaps because there is little seasonal variation in water temperature (Griffiths 1977; Penrith 1970).

In this study, we provide the first quantitative estimates of the abundance and composition of South African intertidal fish communities and elucidate the physical attributes of rock pools that influence the number and species of fish. The feeding habits of the fish collected during this study are reported elsewhere (Bennett, Griffiths & Penrith 1983).

Methods

Samples were collected from six intertidal localities around the Cape Peninsula, South Africa; three in False Bay and three along the West Coast (Figure 1). Each site was visited at low water of spring-tide (LWS) between July and September 1982 and pools representative of the full height and size range were selected. The height (HGHT) and distance (DIST) of each pool from the LWS mark were recorded and its area (AREA), maximum depth (MAXD) and mean depth were measured. Pool volume (VOL) was calculated by multiplying mean depth by area. Subjective ratings of rock (ROCK) and algal (WEED) cover available as shelter to the fish were made on a scale of zero to ten. Total pool area (including pools that were not sampled) in 20 m wide transects was measured and expressed as a percentage of the total area included in each transect.

After Rotenone (dissolved in acetone) had been added to the pools, fish were collected with hand-nets and immediately transferred to 10% formalin. Each fish was subsequently iden-
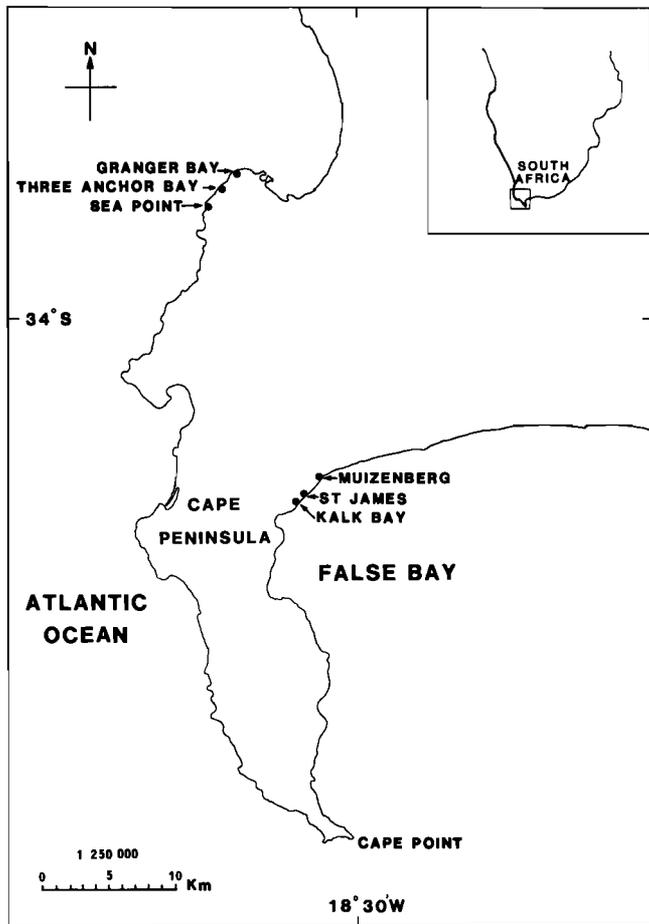
Figure 1 Cape Peninsula, South Africa, showing the six sites from which rock-pool fish were sampled.

tified to species according to Penrith (1969) for clinids and Smith (1965) for other species, measured to the closest millimetre (total length) and weighed to within 0,01 g (wet mass).

Data analysis

Simple linear regression analysis was performed on all possible two-way combinations of dependent variables (number of species, number of fish and biomass) and independent variables (HGHT, DIST, AREA, VOL, MAXD, ROCK and WEED). The respective correlation coefficients were tested for significance ($H_o : r = 0; H_1 : r \neq 0$) and bivariate scatter plots were examined to detect strongly deviating data.

Stepwise multiple regression analyses were used to determine which of the environmental factors significantly contributed to an explanation of the variance in the dependent variables. At each step in the regression, the independent variable with the highest partial correlation coefficient was entered into the equation. Partial correlation coefficients were then recalculated and the procedure repeated until the equation contained all (and only) variables with significant partial correlation coefficients ($P < 0,05$). Significance levels were determined by partial F-value, using a one-sided test and t-value using a two-sided test. The computer program used was STEPREG 1 (Allen 1973) of the STATJOB series.

Multiple coefficients of determination (r^2) were used as an index of predictive value since they are considered to be the amount of variability in the dependent variables accounted for by correlating them with one or more of the independent variables (Zar 1974).

Linear, log-linear (dependent variable transformed), linear-

log (independent variable transformed) and log-log models were used for two reasons: firstly, the data were in some cases not normally distributed and secondly, to detect possible non-linear relationships between the variables.

Unless otherwise stated, where pairs of figures are given in the text, the order is always False Bay : West Coast.

Results and Discussion

The fish communities

A total of 1 541 fish representing 21 species were collected from 84 rock pools (Table 1). Sampling effort was greater on the West Coast where 1 028 fish with a biomass of 6 286 g were collected from 50 pools. In False Bay, 34 pools yielded 513 fish with a mass of 4 021 g. Population densities on the two sides of the Peninsula were very similar, both numerically (6,82 and 7,75 fish m^{-2} pool area) and in terms of biomass (53,45 and 47,41 g m^{-2} pool area). When calculated in terms of the whole shore area in which the pools were situated, densities were again similar: 0,55 and 0,60 fish m^{-2}; 4,30 and 3,20 g m^{-2}.

It is very difficult to compare these figures with any of the previously published information on the densities of rocky shore fish populations elsewhere. Gibson (1982) provides a table of such figures and discusses the problems facing different authors in their choice of units for expressing density. In view of the lack of available information concerning factors as the number of pools per unit shore area, pool size distribution, the proportion of fish inhabiting areas other than rock pools and the proportions of cryptic as opposed to free-swimming species, detailed comparisons are not possible. It suffices to say that Gibson's (1982) observation that 'densities rarely exceed a few individuals per square metre' also holds true for the south-western Cape.

Species distribution and abundance varied considerably between the two sides of the Peninsula. Eight species were common to both sides with eight restricted to False Bay and five to the West Coast (Table 1). The greater number of species in the False Bay sample (despite the smaller sampling effort) reflects the general trend in diversity of intertidal species between the two sides of the Peninsula (Stephenson 1939, 1944, 1948) and has been demonstrated in the Clinidae by Penrith (1970).

Abundance values for False Bay, for the West Coast and for the combined data are shown in Table 1. *Clinus cottoides* was numerically the most important species on the False Bay coast, followed by *Caffrogobius caffer, Clinus superciliosus* and then *Chorisochismus dentex*. In terms of biomass, however, *Clinus superciliosus* dominated the catches followed by *Caffrogobius caffer, Clinus cottoides* and then *Chorisochismus dentex*. On the West Coast, the abundance hierarchy was different. *Clinus superciliosus* dominated in terms of both numbers and biomass with *Clinus cottoides* and *Chorisochismus dentex* being the second and third most important species numerically. The same two species also filled the second and third places in terms of biomass, but in the reverse order. When the West Coast and False Bay data are combined, *Clinus superciliosus, Clinus cottoides* and *Chorisochismus dentex* are the most abundant species, together comprising 75% of the total biomass and 60% of the total number of fish caught.

Zonation

The intertidal distribution and abundance of the various species occurring on each side of the Cape Peninsula are shown in Figures 2 and 3. In the case of those species which occur on

Table 1 The abundance and biomass of fish collected from intertidal rock pools around the Cape Peninsula

	False Bay		West Coast		Combined data	
	$N\,\mathrm{m}^{-2}$	$\mathrm{g\,m}^{-2}$	$N\,\mathrm{m}^{-2}$	$\mathrm{g\,m}^{-2}$	$N\,\mathrm{m}^{-2}$	$\mathrm{g\,m}^{-2}$
Ariidae (sea catfishes)						
Galeichthyes feliceps (Valenciennes)	0,05	0,40	–	–	0,02	0,14
Cheilodactylidae (fingerfins)						
Cheilodactylus fasciatus Lacépède	0,01	0,42	–	–	<0,01	0,15
Congrogadidae (snakelets)						
Halidesmus scapularis Günther	0,24	0,74	–	–	0,09	0,27
Clinidae (klipfishes)						
Blennioclinus brachycephalus (Valenciennes)	0,03	0,09	0,02	0,07	0,02	0,08
Clinus acuminatus Bloch-Schneider	0,12	2,13	0,71	1,60	0,50	1,79
C. agilis Smith	–	–	0,65	1,70	0,41	1,08
C. anguillaris (Valenciennes)	0,12	3,07	0,06	0,70	0,08	1,56
C. berrisfordi Penrith	0,08	0,83	–	–	0,03	0,30
C. brevicristatus Gilchrist & Thompson	–	–	0,01	0,03	<0,01	0,02
C. capensis (Valenciennes)	0,21	1,68	–	–	0,08	0,61
C. cottoides Valenciennes	2,37	10,72	1,09	6,46	1,55	7,96
C. dorsalis Castelnau	0,19	0,30	0,84	0,53	0,60	0,45
C. heterodon Valenciennes	–	–	0,47	1,49	0,30	0,95
C. superciliosus (Linnaeus)	1,34	15,44	2,61	22,08	2,15	19,68
C. taurus Gilchrist & Thompson	0,01	0,16	–	–	<0,01	0,06
C. venustris Gilchrist & Thompson	–	–	0,12	0,27	0,08	0,17
Pavoclinus mus (Gilchrist & Thompson)	0,03	0,22	–	–	0,01	0,08
P. pavo (Gilchrist & Thompson)	0,04	0,28	–	–	0,01	0,10
Gobiesocidae (clingfishes)						
Chorisochismus dentex (Pallas)	0,55	4,74	1,00	12,07	0,83	9,42
Eckloniaichthys scylliorhiniceps Smith	–	–	0,02	0,01	0,01	0,01
Gobiidae (gobies)						
Caffrogobius caffer (Günther)	1,44	12,23	0,14	0,40	0,61	4,68
Total number of fish	513,00		1028,00		1541,00	
Total biomass (g)	4020,51		6285,96		10306,47	
Pool area sampled (m^{-2})	75,22		132,60		207,82	
Pool area % shore area	8,05		9,91		9,12	
Number of fish (m^{-2} pool area)	6,82		7,75		7,42	
Biomass (m^{-2} pool area)	53,45		47,41		49,60	
Number of fish (m^{-2} shore area)	0,55		0,60		0,58	
Biomass (m^{-2} shore area)	4,30		3,20		3,67	

both coasts, their vertical distribution patterns are similar on the two coasts, although on the West Coast they usually extend slightly higher (about 30 cm) up the shore.

Three groups of species may be recognized according to the zones that they occupy on the shore. The first group occurs mainly at high levels, primarily from mean tide level (ML) upwards to the highest pools. Species of the second group are distributed throughout the intertidal zone, while the third group of species occupies lower levels, usually below mean low water of neap-tides (MLWN). This division of intertidal species into three groups is essentially the same as that described by other authors (see Gibson 1982).

Clinus acuminatus was the only species found exclusively high on the shore on both sides of the Peninsula. *Caffrogobius caffer* occurred only in high shore pools on the West Coast, but in False Bay it was distributed throughout the intertidal zone, although more abundant above ML. Two other species, *Clinus cottoides* and *C. superciliosus* occupied the whole shore in False Bay, the former being more abundant between MLWN and ML and the latter below MLWN. Four species were distributed throughout the intertidal zone on the West Coast, namely *Clinus superciliosus, C. heterodon, C. cottoides*

and *C. dorsalis. Clinus heterodon* was captured only on the West Coast, where it was most abundant between MLWN and MHWN. *Clinus cottoides* was most abundant at similar levels as in False Bay, whereas *C. superciliosus* was abundant at all levels, not only low on the shore as on the False Bay coast. *Clinus dorsalis* occurred only below MHWN in False Bay. The remaining species, 12 in False Bay and seven on the West Coast, were group three species, occurring in greatest abundance below MLWN.

Superimosed on the zonation patterns described above are intraspecific differences in size distribution of different fish. Very small *Chorisochismus dentex* (<20 mm) were, for example, found only below MLWN, those of intermediate size (20 – 60 mm) occurred throughout the tidal range of the species but larger individuals (>100 mm) were again found only below MLWN. *Clinus superciliosus* of <75 mm occurred at all intertidal levels, but larger individuals (>110 mm) seldom occurred above ML. *Clinus cottoides* displayed a similar pattern, with individuals longer than 60 mm seldom occurring above MHWN. The reverse trend was shown by *Clinus acuminatus*, an upper shore species, and *C. heterodon*, a primarily midshore species; larger individuals of both these species occurring
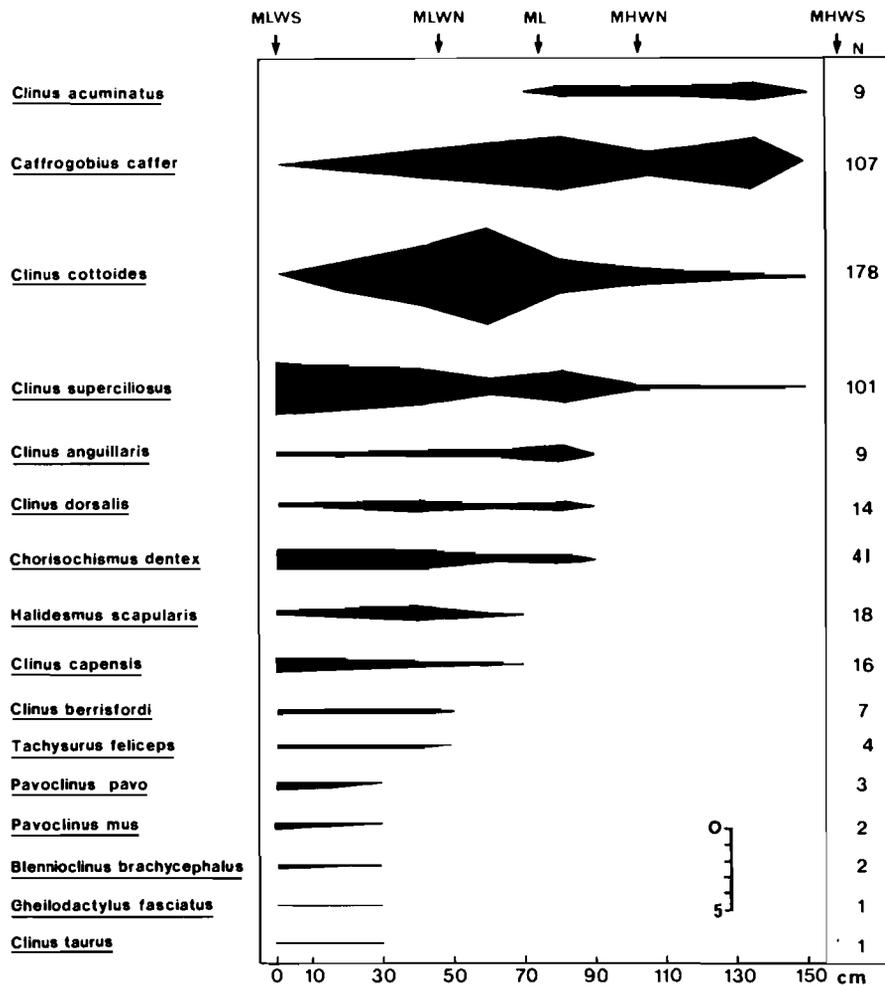
Figure 2 Zonation and abundance (m^{-2} pool area) of rock-pool fish species on the False Bay coast of the Cape Peninsula.

only near the upper distribution limits of the species.

Vertical zonation of rocky shore intertidal fish has been described by a number of other workers (see Gibson 1969, 1982). Although experimental work on factors imposing upper and lower distribution limits is limited, there is some evidence to suggest that they are similar to those influencing the distribution of intertidal invertebrates and algae (Gibson 1972). For a review of these factors, see Newell (1979).

There are two descriptive accounts of the vertical zonation patterns of intertidal fish on the south-western Cape coast of South Africa. Jackson (1950) provides a diagram showing heights on the shore at which 16 species may most frequently be found on the Cape Peninsula and Penrith (1965) provides information on the relative abundance of clinids in four vertical zones at 'typical' west and south coast localities. The abundance of the different species is quantified in this report but the zonation patterns are similar to those described previously.

One additional aspect of zonation evident from this study is that the vertical distribution of species on the more exposed West Coast is noticeably higher than that on the False Bay coast. This is contrary to Gibson's (1982) proposal that fish on rocky shores usually shift their distribution downwards in response to increased wave action. The upshore shift evident here may be a result of the larger waves flushing high-shore pools more often, thus reducing physical stress and increasing feeding time. This type of argument has often been used to explain the upshore shift of sessile invertebrates and algae (Newell 1979). The profiles of the localities sampled on the West Coast were also less steep than at the sites in False Bay. It is therefore possible that, even though the waves are larger

on the West Coast, the less steep shore causes wave action to be attenuated at higher levels. Thus the direct effects of turbulence on West Coast fish may actually be less than indicated by offshore measurements of swell height.

Factors affecting abundance and diversity

Interpretation of the abundance and diversity patterns of the fish populations on the two coasts requires some comparisons of the physical characteristics of the pools sampled (Table 2).

The intertidal zone at the West Coast sites was on average wider (maximum 83 m) than that in False Bay (maximum 37 m), resulting in a difference in the mean distance of the pools from LWS. (The greater width of the intertidal zone is the main reason that more pools were sampled on the West Coast.) Average rock and algal cover and mean pool area were similar on both sides of the Peninsula, whereas mean height of the pools above LWS and mean pool volume were greater on the West Coast, although not significantly so ($P > 0,05$) owing to the large variances. The only physical parameter that did differ significantly ($P < 0,005$) was the maximum depths of the pools, pools on the West Coast being on average deeper.

Correlations between all possible pairs of environmental variables are shown in Table 3. The height of pools increased significantly with increasisng distance from LWS on the West Coast, but not in False Bay because, although intertidal topography was uneven on both coasts, the intertidal zone on the West Coast was wider, allowing greater resolution. Pool area, volume and depth were all significantly correlated with each other on both coasts but these cross correlations are not surprising considering the way in which volume was calculated.
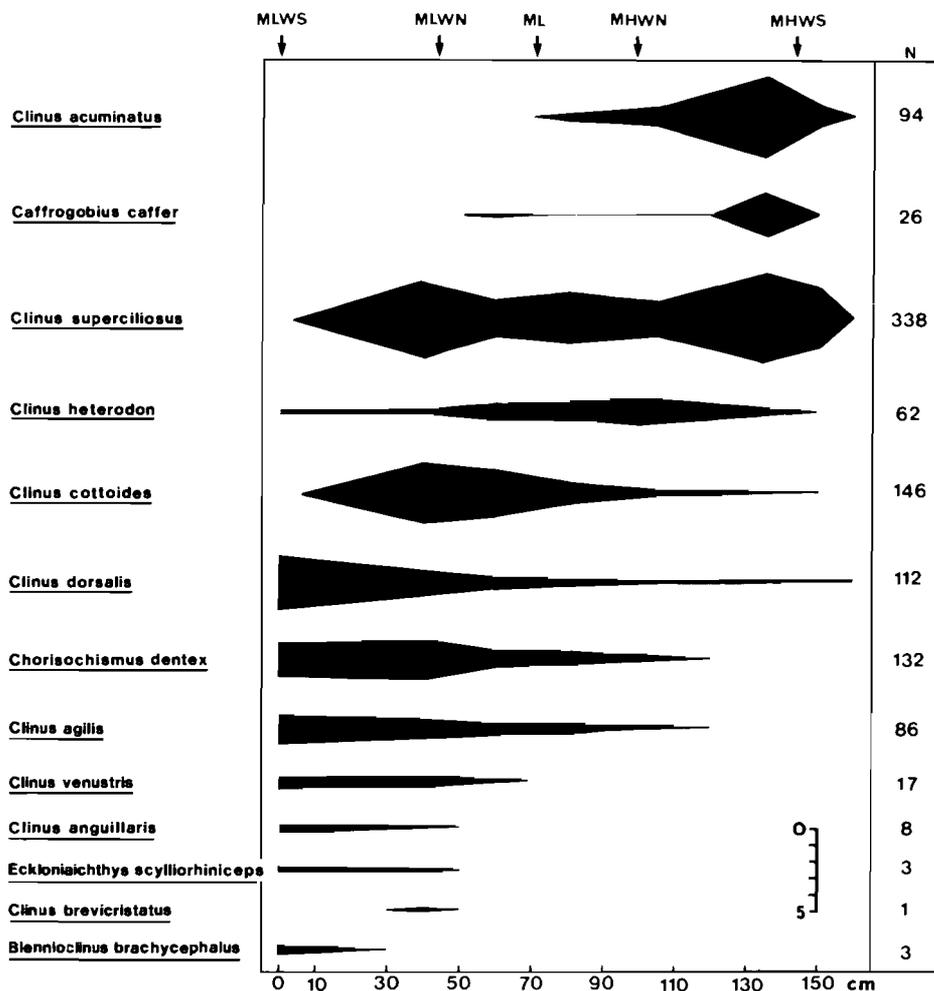
Figure 3 Zonation and abundance (m^{-2} pool area) of rock-pool fish species on the West Coast of the Cape Peninsula.

Table 2 Comparison of the physical characteristics of the rock pools that were sampled on the False Bay and western costs of the Cape Peninsula

	False Bay Range	False Bay Mean	West Coast Range	West Coast Mean	Significance ($P < 0,01$)
Distance from LWS (m)	1,5 – 37,0	14,68	1,0 – 88,0	22,06	$P < 0,001$
Height above LWS (cm)	12 – 147	69,18	5 – 287	87,37	NS
Area (m^2)	0,13 – 11,13	2,82	0,17 – 12,40	2,60	NS
Volume (1)	7 – 2617	293,85	16 – 2240	467,41	NS
Maximum depth (cm)	9 – 75	22,50	7 – 67	31,30	$p < 0,005$
Rock cover	0 – 9	3,21	0 – 8	2,90	NS
Weed cover	0 – 9	2,82	0 – 8	2,96	NS

Table 3 Coefficients of correlation within the environmental variables of the pools sampled on the False Bay (FB) and western coasts (WC) of the Cape Peninsula (*$P < 0,01$)

	HGHT FB	HGHT WC	DIST FB	DIST WC	AREA FB	AREA WC	VOL FB	VOL WC	MAXD FB	MAXD WC	ROCK FB	ROCK WC
DIST	0,27	0,50*										
AREA	−0,23	−0,12	0,38	0,33								
VOL	−0,39	−0,05	0,35	−0,01	0,83*	0,75*						
MAXD	−0,44	0,32	0,31	0,01	0,55*	0,36*	0,78*	0,47*				
ROCK	−0,36	−0,35	0,35	0,09	0,37*	0,36*	0,40	0,44*	0,28	0,09		
WEED	−0,22	−0,06	0,40	0,15	−0,27	0,08	−0,18	0,01	0,01	−0,19	−0,19	0,03

Two significant correlations that are of importance in later analysis are those between the two measurements of pool size (area and volume) and rock cover for the West Coast data.

Correlations between the fish community and aspects of the pool environment

On the False Bay coast, the number of species, total number of fish and biomass per pool all exhibited highly significant positive correlations ($P < 0,001$) with the amount of rock cover present in the pools (Table 4). Pool size, as measured by both surface area and volume, was also significantly correlated ($P < 0,01$) with these three dependent variables. Pool depth seemed to be somewhat less important, while height above LWS showed a significant negative correlation only with the number of species per pool. No correlation was apparent between any of the dependent variables and distance from LWS or the amount of algal cover present.

Very similar relationships between the dependent variables and environmental factors were evident on the West Coast (Table 4). Highly significant positive correlations ($P < 0,001$) were recorded between all three dependent variables and both rock cover and pool volume. The number of species and number of fish both showed significant positive correlations with area, but the correlation between this variable and biomass was not significant. Only the number of species per pool correlated (negatively) with height above LWS. No other correlations were significant.

Table 4 Correlation of number of species (SPNO), total biomass (MASS) and total number of fish (TOTNO) in rock pools sampled on the False Bay and west coasts of the Cape Peninsula with environmental variables measured in the pools (* denotes significance $P < 0,01$)

	SPNO		TOTNO		MASS	
	FB	WC	FB	WC	FB	WC
HGHT	−0,53*	−0,47*	−0,33	−0,26	−0,36	−0,20
DIST	−0,25	−0,26	−0,10	−0,03	−0,14	−0,17
AREA	0,53*	0,60*	0,65*	0,84*	0,63*	0,20
VOL	0,63*	0,45*	0,55*	0,75*	0,65*	0,50*
MAXD	0,51*	0,38	0,36	0,25	0,51*	0,23
ROCK	0,81*	0,55*	0,66*	0,57*	0,75*	0,51*
WEED	−0,27	0,06	−0,16	0,02	−0,21	−0,13

The results of the stepwise multiple regression analyses are shown in Table 5 (False Bay) and Table 6 (West Coast). In summary, at least 58% and up to 88% of the variance in the rock pool fish populations on both sides of the Peninsula can be explained by the environmental factors measured.

In the False Bay sites, variance in the number of species per pool is best explained by a linear model; the total number of fish per pool by a log-linear model and biomass is almost equally well explained by log-linear or log-log models. In each case, the relationship between the dependent variable and rock cover is positive and highly significant ($P < 0,001$) and accounts for between 65% and 76% of the variance. Measurements of pool size also contribute significantly ($P < 0,05$); volume explaining 11% of the variance in the number of species and 9% or 15% in biomass (depending on the model chosen), and area 19% in the number of fish per pool. The only other significant independent variable is height above LWS which

Table 5 Coefficients of determination for different models of stepwise multiple regression on the False Bay data. Dependent variables are SPNO, TOTNO and MASS and independent variables are environmental factors. Only those environmental factors contributing significantly ($P < 0,05$ F-test) to an explanation of the variance are included

Model	SPNO		TOTNO		MASS	
Lin −	ROCK	0,65	ROCK	0,44	ROCK	0,57
lin	VOL	0,11	AREA	0,19	VOL	0,15
	HGHT	0,03				
Log −	ROCK	0,55	ROCK	0,69	ROCK	0,70
lin	VOL	0,09	AREA	0,19	VOL	0,15
Lin −	ROCK	0,56	VOL	0,44	VOL	0,52
log	VOL	0,09			ROCK	0,08
	HGHT	0,06				
Log −	ROCK	0,55	ROCK	0,70	ROCK	0,76
log	VOL	0,67	VOL	0,11	VOL	0,09

explains 3% of the variance in the number of species inhabiting the pools.

Stepwise multiple regression analysis of the West Coast data shows somewhat different results (Table 6). In general, less of the total variance is explained by the environmental factors measured than was the case for the False Bay data. Nevertheless, between 58% and 80% of the variance in the fish populations can be accounted for. Linear models give the highest coefficients of determination for both the number of species and total number of individuals per pool, whereas the variance in biomass is best explained by a log-log model.

On the West Coast pool surface area is the environmental variable explaining the highest percentage of the variance in all three dependent variables, as opposed to rock cover in False Bay. Rock cover is of secondary importance, accounting for between 6% and 12%, height above LWS (16%) is significant only in an explanation of the variance in the number of species, and distance from LWS (4%) only in biomass.

In False Bay, rock cover is the critical variable controlling the fish community whereas on the West Coast, pool area is

Table 6 Coefficients of determination for different models of stepwise multiple regression on the West Coast data

Model	SPNO		TOTNO		MASS	
Lin −	AREA	0,36	AREA	0,71	ROCK	0,26
lin −	HGHT	0,16	ROCK	0,08	VOL	0,09
	ROCK	0,06			AREA	0,07
Log −	ROCK	0,28	AREA	0,52	ROCK	0,47
lin	AREA	0,11	ROCK	0,16	AREA	0,14
	DIST	0,09				
Lin −	AREA	0,32	AREA	0,51	ROCK	0,17
log	HGHT	0,18	ROCK	0,04	DIST	0,09
Log −	ROCK	0,27	AREA	0,59	AREA	0,49
log	AREA	0,10	ROCK	0,07	ROCK	0,13
	DIST	0,08			DIST	0,04

more important, posing the question as to why there should be a difference between the two coasts. Before attempting to answer this question, our results should be compared with those of two previous studies.

Marsh, Crowe & Siegfried (1978) reported total cover (a combined measure of rock and algal cover) to account for approximately 70% of the variance in the abundance of clinids per pool. Rock cover alone, as well as depth, were of secondary importance and no significant relationship with pool size was obtained. Their study was conducted at Bailey's Cottage, very close to one of our transect sites in False Bay. However, since they concentrated on small pools, formed mainly in crevices and depressions in solid bedrock, both pool size and the amount of rock cover were small and fairly uniform. All size and cover readings fell within a fairly narrow range and hence these two variables did not correlate significantly with the fish populations inhabiting the pools.

For the effects of pool size to be detected, it is essential that enough pools encompassing a wide range of physical factors, are analysed. The way in which rock cover is estimated is also important. If rock cover is calculated as a percentage of pool area, then small pools can have values as high as larger ones, although considerably less cover is available in absolute terms. This method of estimation was used by Marsh et al. (1978) and Gibson (1972), who analysed rock pool fish populations in exposed and sheltered areas on the coast of France. Gibson's multiple regression analyses showed that level and area are significant in accounting for variance in the number of fish in pools on sheltered shores, whereas cover (also rock and algae combined) was not significant. On' exposed shores, none of the environmental factors that he measured were significant.

In this study, estimates of cover were based not on a relative but an absolute scale of amount of cover in the pools, such that very small pools could not have high cover ratings. For this reason, rock cover on the West Coast increased significantly with increasing pool size. The size distribution of False Bay pools was skewed to the left (i.e. a predominance of smaller pools was sampled), so that the size range of pools was inadequate to show a significant relationship between pool size and rock cover. To illustrate this point, it can be shown that if only those pools on the West Coast within the limited range of $2,0 - 3,2$ m^2 ($N = 14$) are re-analysed, the abundance of fish present is significantly correlated ($P < 0,01$) with rock cover, but not with pool area or volume.

The amount of rock cover is the most important factor regulating the abundance of fish in rock pools around the Cape Peninsula whereas size is significant only because larger pools can incorporate more cover.

Reasons for the relationship between rock cover and abundance

Correlations alone cannot establish cause and effect relationships so more fundamental reasons should be sought for why the abundance of rock-pool fish is related to rock cover. All species collected were small, cryptic and with the exception of Caffrogobius caffer, carnivorous (Bennett et al. 1983). Some proportion of the populations of these species are resident in rock pools and, with the exception of Pavoclinus mus, P. pavo, Clinus brevicristatus and Eckloniaichthys scylliorhiniceps which are not found in rock pools devoid of algae (Penrith 1965; pers. obs.), spend most of the low tide period concealed in rocky cover. The few small individuals of Clinus superciliosus and Caffrogobius caffer which may be seen in the open rapidly take refuge when approached (Marsh et al. 1978; pers. obs.). Bennett et al. 1983 calculated that probably not enough food

is available in the pools to sustain resident fish populations. A proportion of the food must therefore come from outside the pools. The importance of dislodged food washed into the pools during high tide relative to food actively sought by fish emigrating from the pools to forage over areas which are only covered at high tide is unknown. Some species, such as Clinus superciliosus, C. cottoides and Chorisochismus dentex leave pools at high tide. The guts of these species contain items which do not normally occur in pools, such as the cirri of barnacles.

Penrith (1965) and Marsh et al. (1978) observe that cover for fish is also cover for some of their prey species such as amphipods, isopods, molluscs and decapods. Thus fish remain in the same areas as their prey. The relative scarcity of fish in areas peripheral to cover, suggests however that fish gain other direct benefits from cover.

Morphological adaptations that enable intertidal fish to resist turbulence have been reviewed by Gibson (1969, 1982). Many of these adaptations are evident amongst the species examined here. Gibson also reviews work suggesting that fish largely avoid turbulence by remaining in holes and crevices amongst rocks. Observations on the reactions of South African species to turbulence are available only for Caffrogobius caffer. This species is probably the least 'cover dependent' examined in this study since, relative to their abundance, they were most frequently observed in the pools at low tide. Butler (1981) showed that this species took to cover when water flow reached a critical rate. Movement out of pools only occurred during early stages of the rising and late stages of the ebbing tide when water movement was below the critical rate. The fact that all the other species spend almost all their time under cover in pools at low tide when they are not subject to any turbulence, suggests that, at low tide at least, there are additional reasons for the high correlations with rock cover.

The most obvious direct benefit that can be gained from remaining under cover is protection from predators. The major predators on intertidal fish around the Cape Peninsula are probably birds, other fish and humans. Six of the species investigated in this study feed on other fish (Bennett et al. 1983); birds such as little egrets (Egretta grazetta), kelp gulls (Larus dominicanus) and cormorants (Phalacocorax spp.) forage in rock pools at low tide (Biden 1930; Skead 1966; pers. obs.); and children armed with hand-nets frequently pursued fish in rock pools in the study areas. The intensity of predation by birds and other fish on rock-pool species is unknown, but a low intensity of predation might be sufficient for cryptic behaviour to be advantageous in evolutionary terms.

Reasons for the relationships between rock cover, height and diversity

The number of species of fish recorded in each pool was significantly correlated with rock cover, pool size ($\equiv$ rock cover) and the height of the pools above LWS. Together, these three variables accounted for 58% and 85% of the variance in species diversity on the West Coast and in False Bay respectively. In their multiple regression analyses, Marsh et al. (1978) found only weed cover to be significant and Gibson (1972) showed that the number of species decreased with shore level, although apparently no attempt to correlate diversity with other environmental parameters was made.

Decreasing diversity up the shore has been documented by previous workers (see Gibson 1969, 1982 for review), and may occur because of the progressively more variable and extreme physical conditions in high shore pools (Newell 1979).

Gibson (1972) observes that where species overlap in ver-

tical distribution the microhabitats occupied by each are different and Critchlow (1972, in Gibson 1982) found that microhabitat specialization was greater where species diversity is high. In this study, three or more species were found in 54% of the pools sampled, six or more in 12%, while 10 species occurred in three pools. Some qualitive information concerning the habitat preferences of South African species is available (Jackson 1950; Penrith 1965; Butler 1981; Bennett *et al.* 1983), but it is not sufficiently detailed to resolve the manner in which the rock-pool habitat is subdivided. The rock-dwelling species, show substantial interspecific variation of body form (see Penrith 1969; Smith 1965 for illustrations and measurements) suggesting that they are morphologically adapted to using different microhabitats. If this is the case and it is assumed that more rock cover results in greater habitat diversity, then the correlation between species diversity and rock cover follows.

Marsh *et al.* (1978) found weed cover to be the only variable significantly correlated with species diversity. This is somewhat surprising since they caught no typically weed-dwelling species, over half their pools contained only one species, and the distribution of weed cover was heavily skewed to the left. For these reasons, their result may well be an artefact of sampling. It would only require a few of the pools containing more than one species to be low on the shore, to be larger or to have more rock cover, to enable weed cover to appear significantly correlated with species diversity.

Conclusions

Three lines of evidence support the hypothesis that physical characteristics of rock pools are critical factors limiting the abundance and diversity of intertidal fish communities in the south-western Cape. Firstly, there is no significant difference in the numbers of fish inhabiting similar pools between areas where the number of pools per unit shore area is different. The carrying capacity of the pools is therefore likely to be limited. Secondly, the population structure of the rock-pool fish is stable both seasonally and for longer periods, indicating that their numbers and diversity are limited by factors that remain constant. Finally, there is not enough food available in the pools to sustain the resident populations — some food must therefore be obtained outside the pools. Since none of the species are found intertidally other than in rock pools, it may be assusmed that the fish are 'concentrated' in the pools at low tide.

The amount of rock cover available was the most important of the environmental variables accounting for observed variance in the abundance and diversity of the fish populations. The importance of rock cover is attributed to the protection it provides from predators and wave turbulence. Increased rock cover may also increase the number of microhabitats available for different species. Microhabitat specialization can, however, only be inferred from the morphological diversity within this group of species, since no detailed observations of habitat preferences are available. Similarly, the relative importance of protection provided from predators and wave action cannot be evaluated since very little is known of predation pressure, high tide movements and the reaction of the species to waves during high tide.

Finally, Penrith (1970) found that after the pools are cleared of fish they remain unoccupied for at least six months before recolonization commences. Marsh *et al.* (1978) and Butler (1981) using mark-recapture techniques, also found that individual fish exhibit a high fidelity to particular pools. These last two points provide additional indirect evidence of the importance of rock cover. Recolonization is slow because of pool fidelity which may have evolved because of the necessity of regaining rock cover during tidal exposure.

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