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A PRELIMINARY ACCOUNT OF INVESTIGATIONS INTO THE FALSE BAY SUBLITTORAL BY
THE USE OF A DIVING HELMET.

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I. Profess.

A great deal of work has been done on the ecology of the intertidal zone of South Africa by the Zoology Department of the University of Cape Town under the direction of Professor T.A. Stephenson. As a result of this a number of valuable papers have been published dealing with the plants and animals of the zone, their ecology, lateral and vertical distribution, and so on. Stephenson has, in three papers (1939, 1944, 1947), dealt with the general results and conclusions drawn from this survey. This work dealt entirely with the biota between tide levels, i.e., from the sublittoral fringe upwards. It did not take into account the sublittoral, that part of the shallow coast which is perpetually submerged at all tides.

Because of this there is much that remains unknown about this area which is perpetually submerged. From the point of view of the intertidal survey this region is of interest in several ways. In the first place, many intertidal plants and animals have a well-defined vertical zonation; this zonation has been pointed out in a number of papers dealing with the survey, and two special papers have been written concerning it: Stephenson (1936), on the habits including the zonation of limpets, and Bekenham *et al.* (1938), dealing with the vertical distribution of ~~some~~ certain other marine gastropods. In many cases, however, the distribution of animals between tide-marks does not give a complete picture of their zonation, as the lower limit often lies in the deeper water below the sublittoral fringe; the fringe in some cases is near the lower limit of vertical distribution of the animal, as for instance in the case of the limpet Patella cochlear, and in others near the upper limit, such as in the case of the crinoid Comanthus wahlbergi. It is therefore of interest to determine as far as possible the lower limit of zonation of typ-

ically intertidal animals.

Secondly, Stephenson (1947), makes the point that there has been disagreement among specialists as to the situation of boundaries between various types of littoral faunas, such as the cold-temperate "Cape" fauna and the Indo-Pacific fauna as represented in Natal. Ekman (1934) considers that the disagreement may be due to differences in the extent of the two faunas at different depths within the intertidal region. Stephenson agrees with this, and considers that while the boundary was found during the intertidal survey to be between Port St. Johns and Qokera in the intertidal zone, it may well lie much further to the westward at certain depths "owing", as he says, "to the fact that while the Agulhas current lies close to the coast as far west as Cape Padrone, after that its main body begins to diverge much further offshore round the Agulhas Bank, so that at any given point and depth the nature of the bottom-fauna will be determined by the distance of that point from the coast and its relation to the Agulhas current and/or other water-masses. Consequently, ~~it is possible to find a fauna of a more subtropical type~~ off a locality on the South coast where the warm-temperate fauna is fully established and the Natal fauna has disappeared, it might be possible to find a fauna of a more subtropical type at certain depths; and there seems to be evidence that this is true. Consequently it may be useless to try to fix upon any generally applicable boundary in terms of coastal topography, but when more is known it may be possible to plot a line across the continental shelf reaching the shore near Port St. Johns." (Stephenson 1947, p. 230). Any further work on sublittoral conditions along the coast will probably be of value in this respect.

A good deal of dredging, netting and other investigation of the sea bottom in False bay has been carried out by the Zoology Department under Professor Day. Such work cannot be effective in

fesser Day. Such work cannot, however, be completely effective in areas with rocky bottoms as, apart from the risk of damage to the apparatus, the dredge or trawl cannot remove from the rock such closely adhering organisms as limpets, anemones, algae and many other things, so that an accurate idea cannot be obtained of everything that is present. Therefore, at Professor Day's suggestion, I considered ways and means whereby this work could be amplified by personal investigation of the bottom by means of diving.

One or two attempts to use a home-made diving apparatus in False Bay had already been made, notably by D.H. Davies, who used a gas-mask to which was attached a small oxygen bottle. After experiment with this equipment I came to the conclusion that a diving helmet, as has been used by Beebe (1935) and Kitching (1934) would suit our purpose best. A description of the helmet is given in the following section.

A number of dives were made with this helmet, and our technique in using it has improved. This paper is a preliminary report of the work which is being carried out, and deals mainly with certain common intertidal animals which have been found to extend down into the sublittoral. It is hoped in the future to publish a full account of the sublittoral investigations, including the results obtained from deeper water by dredging and other work.

The author wishes to thank Professor J.H. Day and the staff of the Zoology Department of the University, and would particularly like to thank Mr R. Liversidge of the staff, for their interest and encouragement, and for the constant interest and invaluable technical assistance given by Mr Liversidge.

II. Description of Apparatus.

In essence, the apparatus used consists of a copper helmet, fitted with glass windows in front, which fits over the shoulders. The helmet is con-

ected by means of 60 feet of half-inch garden hose to a double-acting air pump.

1. The Helmet.

The helmet was made out of an old copper hot-water cylinder belonging to a geyser. A scale drawing of the helmet is shown in Fig. 1. The helmet measures 11 inches in diameter by 20 inches in length. Six inches from the bottom an oval space was removed for the helmet to rest on the shoulders. Rubber padding is provided to avoid injury to the shoulders. Air is let in by means of a connection at the top and back and the air travels from this, by means of a copper pipe inside the helmet, to the front where it impinges against the glass windows on the inside. The reason for this is to prevent "misting" of the inside of the glass windows.

The windows are made from two pieces of plate glass measuring 4 inches by 7 inches. These are fitted into brass frames secured in the middle by belts. Putty and paint mixture and various other preparations were tried as an air-tight stuffing. The best preparation was finally found to be "Beetik" sealing compound. The two panes of glass are set obliquely into the helmet, meeting at a point in the centre (Fig. 1c). This makes for better vision.

A stopcock is provided at the top of the helmet. When this is closed the air pumped in bubbles out at the bottom of the helmet, but the amount bubbling out at the bottom can be controlled by opening the stop-cock and allowing the air to escape there. This prevents water splashing into the diver's face from the bottom of the helmet. It has the additional advantage of allowing the warm, used air, which rises to the top, to escape, thus ensuring that there is a continual supply of fresh cold air at the bottom of the helmet.

The helmet without the lead weights attached weighs 18 lb.

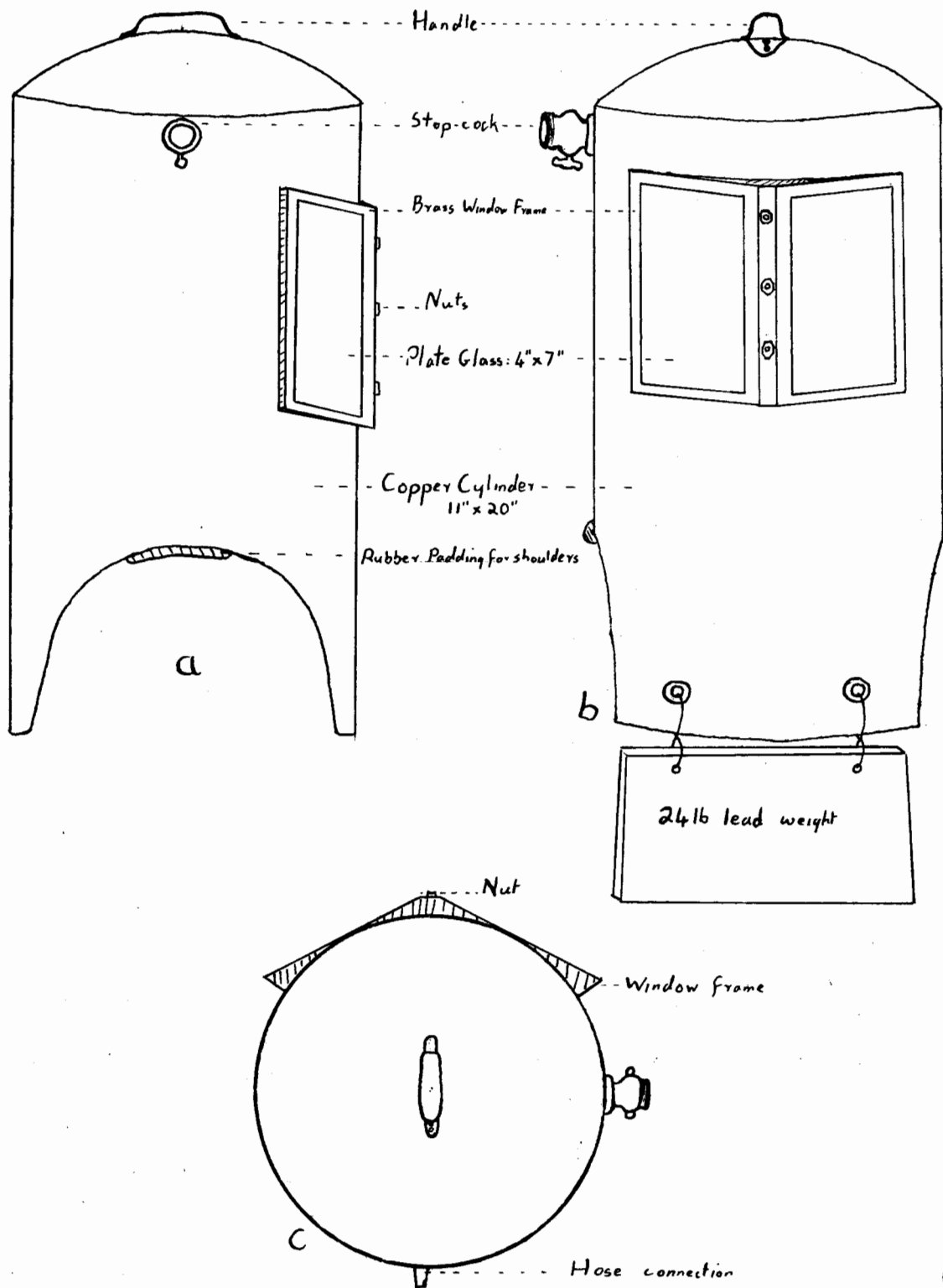


Fig. 1. Scale Plan of Helmet: a) from right side; b) from front; c) from above.

Two rectangular lead weights, weighing 24 lb each, are attached to the front and back of the helmet by means of wire. As the helmet displaces about 60 lb of sea water it can thus be seen that the helmet, when submerged, weighs about 6 lb more than the surrounding water.

The helmet was made by Messrs J.F. Bernards, plumber and tinmith, to my design.

2. The Air Supply.

The pump used for this work is a garage compressor worked by a large vertical lever. It has a double-acting pump, so that compression takes place on both forward and backward strokes. It has a cylinder capacity of 72 cubic inches and is capable of exerting a pressure of 240 lbs/sq. in. This pump is attached to a rubber hose of $\frac{1}{2}$ inch diameter, by means of which air is supplied to the helmet. This supply was found to give an adequate supply of air at all depths thus far worked, to about 32 feet.

III. Method of Work.

Investigation of the sublittoral biota has been carried out both from the shore and from a fishing vessel in shallow water further out to sea. When operating from the shore, the pump is set on a flat rock preferably at low tide, so that the diver does not have to walk very far seaward in order to be in the sublittoral area. Unfortunately for this method to be successful, it is necessary for the sea to be particularly calm, which, in False Bay, means that there has to be no South-Easter wind blowing. Such occasions are comparatively rare during summer. If the sea is at all rough the diver has difficulty in getting into the water with the heavy helmet on, and when once submerged, he is swept back and forth by the swell, which is not only very exhausting but makes it practically impossible for the diver to do any collecting or counting of animals when under water.

Diving can be carried out in deeper water off the shore

Diving can be carried out in deeper water off the shore when the sea is slightly rougher, since at a depth of 25-30 feet the diver is below the depth markedly affected by wave action. It is advisable again, however, to work on a day when the sea is as calm as possible, since the calmer the sea the greater is the visibility, as the water is much clearer and less murky on a calm day than on a rough one.

This means that investigation of the False Bay sublittoral is more or less restricted to very calm days in the summer weather, so that a series of diving expeditions takes some time to complete.

A collecting bag was taken down, and organisms were collected and placed in the bag. Some experience is necessary for collecting under water. In the first place all movements are much slower than they are on land, and collecting takes a long time. In the second place, when an animal such as a limpet is dislodged from the rock with a knife, care must be taken to secure it before it is washed tantalisingly out of reach and away by the waves, particularly in the shallow sublittoral.

As well as collecting, countings of animals in situ on the underwater rocks were made. Certain organisms, such as Pyura stolonifera, Balanus marillaris, Turbo saxatilis (which grows to a very large size in the sublittoral) and others are easily recognised at sight, but others, such as the limpets, have to be dislodged and either collected or examined before their species can be accurately ascertained. Fish were often seen, and sometimes enticed nearer by cutting open a large specimen of the ascidian Pyura stolonifera, when fish of all sizes come and nibble at the flesh. Octopi are often seen in crevices; they are often of a slightly larger size than are those inhabiting the intertidal zone.

IV. The Vertical Distribution of Certain Animals.

1. Preliminary Remarks.

It has already been mentioned that the lower limits of vertical distribution of many intertidal species, where these limits lie below the sublittoral fringes, are not known. During all dives the depths at which various organisms occurred were noted as far as possible with reference to low water of spring tides. The time at which all dives were made was noted and the amount of rise of water since the previous low tide was calculated, on the basis, for spring tides, of one foot rise per hour, and this amount was subtracted from the actual measured level of water above the organism in each case. A degree of accuracy of less than one foot was not aimed at since this would serve no useful purpose in that the depths at which various organisms are found usually vary to a greater extent than that from place to place.

As has already been stressed, this account of diving in False Bay is of a preliminary nature. A great deal more requires to be done and it is hoped that this, together with the results already obtained, will be published in conjunction with the data achieved by dredging in the deeper False Bay waters. In the meantime the following preliminary observations are made, which concern mainly certain forms well-known within tide-marks, but which extend down also into the sublittoral.

2. The Vertical Distribution of Limpets.

Patella cochlear, so characteristic of the lower intertidal levels of temperate South African coasts as to be the dominating organism of the Cochlear zone, has a sharply limited lower area of distribution. At no time was any specimen of *P. cochlear* seen at a lower level than two feet below low spring tide mark. It appears to be an organism primarily affected by wave-action and violent, bubbly water as it sharply decreases in abundance as seen

the region never exposed by low tide is reached, i.e., the lower level of the sublittoral fringe, and, in more sheltered spots, never reaches as low as this. A certain amount of aeration and churning of water appears to be essential for its optimal living conditions, and this would appear to apply also to a good many other intertidal forms.

The only limpets thus far collected at a lower level than P. sochlear are Patella tabularis and P. miniata. P. barbara has also been found down to two feet below low spring tide mark, but not lower than this.

P. tabularis appears to extend slightly further down than does P. miniata, which has not been found at a greater depth than four feet below low spring tide, while one specimen of P. tabularis was collected at seven feet down. From 8 feet down to 32 feet, the lowest depth thus far reached, no Patellid was ever seen. It would thus appear that limpets are gastropods chiefly of the intertidal zone, their extension further down the shore being negligible.

3. Vertical Distribution of Other Gastropods.

Of the three Oxystele species mentioned by Bokenham et al. (1938), in their paper on vertical distribution, namely O. sinensis, O. variegata and O. tigrina, the only one which was commonly found to extend into the sublittoral was O. sinensis. This periwinkle is fairly common 12 feet below low spring tide, 4 being counted on a square yard of vertical rock at this depth, and one or two were found at 17 feet down. At 25 feet, however, no O. sinensis were found despite search for them. The two periwinkles Turbo cidaris and the larger T. sarmaticus both penetrate the sublittoral to a marked extent, but their lower limit of distribution is different for each of the two species. Turbo cidaris was found down to six or eight feet only,

while Turbo sargaticus is well represented at 25 feet below low spring tide mark, without any sign of diminishing in numbers. Two very large specimens of this periwinkle were also seen at 32 feet down.

A very common gastropod at the greater depths was the whelk Argo-buccinum argus. This is one of the few intertidal gastropods which appears to be more abundant deeper down than it is in the intertidal zone, since, on the False Bay coast, more have been found from 15 feet downwards than between tide-marks. It has also been dredged from a sandy bottom in False Bay 45 feet below the surface. In the intertidal zone, this whelk is more common on the west side of the Peninsula than on the east. Another gastropod more common at depths than at the surface is the omer Haliotis sanguinea. This animal is not generally common, but is very abundant in certain areas about 15 feet below low tide mark. There is evidence that it becomes less common again about 35 feet below the surface. It is largely restricted in habitat to vertical ledges, particularly in cracks and crevices in the rocks. It has also been found in the more sheltered waters in Kalk Bay harbour.

Most of the larger gastropods are in general of a much larger size in the sublittoral than they are in the intertidal zone. This is probably due to the fact that they are protected in the perpetually submerged sublittoral from the depredations of the many beachcombers who collect them for eating.

4. Vertical Distribution of Echinoderms.

Echinoderms do not appear, in general, to be as restricted to zones as are other animals, and the common intertidal species extend downwards generally much further than do other intertidal animals.

The sea urchin Paraschizus angulosus is the most common echinoderm occurring in the sublittoral. They are abundant at all levels down to 32

feet, occurring usually where they can get no lower, i.e., at the bottom of crevices and ledges and in depressions in flat rocks. They also occur, though not so commonly, on the sides and tops of rocks.

Starfish are very common, occurring generally in ledges, holes and crevices. Harrisia ornatus and Patiria ballula have both been collected at 25 feet, but the lowest record of Marthasterias glacialis seen during diving operations has been 17 feet. It has thus far escaped detection at greater depths, but must certainly occur among rocks lower down since it has been dredged from a sandy bottom in False Bay at a depth of 7 fathoms. The sea-star Asterina grima has been found 6 feet below low spring tide mark, but has not yet been taken lower down, though in all probability it does occur in deeper water.

The crinoid Comanthus wahlbergi is very common at certain places, having been found at all levels to 32 feet, and has been dredged from greater depths. The only Holothurian collected was Cucumaria insolens, which was not found, despite search, higher up the shore than about 20 feet. At 25 feet and below it is common, its orange colour contrasting vividly with the dark shadowy ledges and caves which it frequents.

5. Other Animals.

Of the other sublittoral animals the most abundant is undoubtedly Pyura stolonifera. This ascidian, which is not normally found higher up the shore than the sublittoral fringe, is extremely abundant and grows to a large size in the sublittoral. At no place visited with the helmet was it found to be absent, and in many places it occurs in great numbers. It does not occur in the naked solid banks characteristic of the wave-washed rocks in the sublittoral fringe at St. James, as illustrated by Eyre (1939) Pl. XIX, but in the perpetually submerged sublittoral the animals are generally of very large size and a few inches apart from each other. Other sessile and sedentary animals

live on the rocks between them, as well as a good growth of sea-weed. The leathery tests of the animals themselves are not naked, as is generally the case on the wave-beaten rocks of the sublittoral fringe, but are thickly covered with a dense mass of algae, hydroids and small mussels. Crabs, small fish, burrowing and errant polychaets, echinoderms and other animals inhabit this growth. This ascidian shows no sign of decrease of abundance at 32 feet, the greatest depth thus far attained in this work. Michaelson (1934) records Pyura stolonifera as occurring at 100 metres.

The only barnacles thus far taken in the sublittoral are Balanus trigonus and B. maxillaris, both of which are abundant down to 32 feet. B. trigonus often occur on the tests of Pyura stolonifera. Balanus maxillaris is invariably found on rock. It is a solitary animal, as contrasted with B. trigonus, and grows to a large size. Its shell is often covered with a growth of algae and I have not infrequently mistaken one for a small Pyura stolonifera. The crab Plagusia shabrus was often seen to a depth of 12 feet below low spring tide mark but has not yet been recorded as occurring lower down than this. Dehaanius dentatus, on the other hand, has been found among Sargassum longifolium at 25 feet. The Brachiopod Kraussina rubra has also been observed at 25 feet but does not appear to be very common.

V. The Occurrence of Algae.

The algae of the Cochlear Zone and sublittoral fringe of False Bay form a mixed sward of a number of different species, some of the more important and abundant of these being Gigartina rubra and G. stictica, Hypnea epispifera, Galidium pristoides, Lourussia obtusa and L. flexosa, Sargassum heterophyllum, S. alexand., S. incisifolium and S. longifolium, Floeridianum corallorhiza, Chondria canaliculata and Caulerpa ligulata. There is thus a wide variety of abundantly occurring algae in the sublittoral fringe, but nearly

all disappear markedly in the sublittoral proper, until at 6 feet below the surface the dominating algae belong to two or three genera only. These are Laurencia, Sargassum and certain genera of coralline algae such as Jania and Corallina.

Six feet below low spring tide mark, Laurencia species, such as Laurencia flammosa and L. glomerata are still abundant, forming often thick banks or else growing freely on or between the tests of P. stolonifera. It may also occur in what Stephenson (1944) describes as "algal turf" with, as well as Laurencia species, Sargassum heterophyllum and coralline algae belonging to the genera Corallina and Jania. At other points at this depth nearly all algae apart from the corallines are absent or occur in isolated tufts. Here the corallines form thick banks of purplish-brown weed, harbouring a large community of epiphytes and growing frequently on and among the tests of Pura stolonifera and the shells of Balanus maxillaris. Such banks are particularly thick on the vertical faces of rocks.

As one proceeds lower down the shore all the above-mentioned algae are present, but the emphasis begins to shift to the genus Sargassum until, at 20 feet below low spring tide mark, this genus is undoubtedly dominant among the algae present. The dark brown Sargassum longifolium is particularly well represented, growing often to two feet or more in length, while the closely allied yellowish-brown forms Sargassum heterophyllum, S. glomerum and S. incisifolium are also present in varying amounts. The sea bed Strophodontophora takes on a brownish appearance from the waving fronds of the Sargassum, which grows to a good length particularly on the vertical faces of the rocks and underwater cliffs. The growth is not as thick and generally much shorter on the horizontal faces such as the substratum and flat tops of rocks. On sandy or shingly areas on the sea bottom it does

not occur at all. All tests of *Pyura stolonifera* bear a good growth of this algae; naked ascidians are seldom or never seen at this depth.

VI. A Note on Fish.

Fish are commonly seen when diving; they do not display any timidity and frequently swim close to the diver. They were chiefly of small size; though larger ones were seen, these appeared to be fewer in number than even the natural preponderance of young fish over older would lead one to expect. This is probably accounted for by the fact that the area in False Bay where the diving was done ~~was~~, between Simonstown and Kalk Bay, is one where a great deal of angling is done. As Smith (1949) remarks, littoral fish which do not move about much from place to place tend to become "fished out" in a heavily fished area.

A certain amount of vertical zonation appears to be present in some of these littoral fish. From 0 - 8 feet below the sublittoral fringe the commonest fish seen is the Blacktail, Diplodus sargus. A few small specimens only of the Roman (Chryseblennius laticeps) occur. However, as one proceeds deeper down the position becomes reversed, until at 25 feet C. laticeps is very abundant in all sizes, whereas very few specimens of D. sargus are seen, and these are chiefly of large size, a foot or more in length. No Diplodus sargus of under about eight inches in length was ever seen at 25 feet.

Some species of the family Clinidae are very common, particularly in the shallow sublittoral, though Clinus superciliosus has been seen at 30 feet. They can often be seen crawling about on the rocks, disappearing if alarmed into a crevice. The crawling habit of these fish can be well observed when a Pyura stolonifera is cut open, when numerous fish congregate round the delicacy. While other fish swim to the spot and remain suspended in the water round about, Clinus superciliosus and Pagrus heterodon approach over the rock like mice, and swim only if disturbed, never remaining

suspended in the water round the ascidian.

Other fish observed were the Zebra (Diplodus trifasciatus) a Chirocentrid, probably Palanopsis grandis, the Hottentot (Pachymetopus blehii) the Milk-fish (Parascorpa tytus) and the sucker-fish (Choriacanthus detax.) None of these, however, were commonly seen except for Pachymetopus blehii, one or two specimens of the others at most being seen on a dive.

VII. A Note on the Animals of Sheltered Water.

There are in many ways a striking difference between faunas inhabiting waters which are sheltered from wave action and those which live on the open coast, battered by waves, in waters constantly churned and disturbed by wave action. Again, the fauna of the shore below the effect of wave action, while including many intertidal species, is yet different in many ways from a typical intertidal fauna. It is hoped in the future to go into this question of the fauna of calmer waters, and, as a preliminary, some dives were made in the sheltered water of Kalk Bay harbour, and the fauna attached to the vertical inside wall of the pier examined.

At low tide there is about 16 feet of water against this pier, and as it presents a perfectly flat and undifferentiated environment, the zonation, particularly of the intertidal portion, is band-like. From about half-tide there is a band of Ulva lactuca extending for about eighteen inches downwards. Below this there is an intermediate zone where the commonest animals are the fanworm Sabellastarte longa and the anemone Eunosema japonica. From approximately low tide mark there commences a band of Laurencia species, which begins to fade out about three feet below low tide mark. Pyura stellerifera begins to occur at this point, at first scarcely but more abundantly about six feet below low tide mark, and it is then abundant to the bottom of the wall.

The whole wall and everything growing on it is thickly covered with dirt and sediment, while, when walking on the bottom, thick clouds of sediment are churned up at every step. This sediment probably accumulates through the lack of wave action.

The following intertidal animals were noticed in the sublittoral area. Three specimens of Halictis sanguinea were taken from the crack where two of the concrete slabs of the wall join at 12 feet below low spring tide.

These were the only gastropods thus far found on the sublittoral area on the wall. Also present in the crack were Plagusia chabrus, Cocanthis wahlbarki were quite common, and other echinoderms noticed were Henricia ornatus and Parachinus anulus. The only barnacle seen was Balanus trigonus. The anemone Bufoanus canchalis was fairly common.

VIII. Discussion.

The helmet as described above, used last summer, while very satisfactory in every way under the water, suffered from one defect on dry land. The copper from which it was made was too thin and without any adequate strengthening, so that, if handled in the slightest degree carelessly, particularly with the heavy weights attached, bent and buckled. The result was that uneven stresses were set up in the glass window panes, which cracked. Because of this the glass in both windows cracked and had to be patched to prevent undue leakage.

When the result of this series of dives is examined certain interesting facts come to light. These are firstly the relative paucity of species at some depths below the intertidal zone compared with the zone itself, secondly, the common occurrence of certain west coast species, rare or absent from the east coast intertidal zone, at some depths below the surface of the east coast shore, and thirdly, the similarity in many ways of the fauna of

the deeper water of Kalk Bay harbour and the open coast, as contrasted with the dissimilarity of the intertidal zone of the harbour wall and that of the open coast.

To take these points in order, one is first struck, on a dive twenty feet below the surface at, say, Fish Hoek, by the fact that there is little of the variety of life in the intertidal zone to be seen at that depth, and that this want is made up by the much increased numbers of the species that do occur. Mention has already been made of the abundance of Pyura stolonifera at that depth, and of the fact that the whole area looks brown because of the abundance of Sargassum. There are large quantities of echinoderms such as Parachinus annulosus and, to a lesser extent, Harrisia ornatus. Molluscs, of which there are so many species in the intertidal zone, are reduced to a few species only, and these never occur in such large quantities such as the banks of mussels and hundreds of periwinkles in the intertidal zone. Fan-worms are entirely absent. There are only two species of barnacles present. Anacrus lose their variety and abundance, the only common one occurring being Bunocoma capensis. On the other hand colour is provided by the bright red gorgonians and crinoids, which are but occasionally represented in the sublittoral fringe.

One of the main reasons for this appears to be that many intertidal species find the deeper water too calm and still, and possibly insufficiently aerated for their ~~purpose~~ way of life. On a moderately calm day only a very slight wave motion is felt at 20 feet, while bubbles produced by wave action seldom penetrate lower than 6 feet below the surface.

It is interesting in this respect to notice that there is a striking similarity between the animals found in the deeper water of the shore and the deeper water of Kalk Bay harbour. Pyura stolonifera, Halictis sanguinea

Henricia ornatus, Parachinus ancolonus, Comanthus wahlbergi, Plagusia chabrus and Balanus trigonus are all common to both localities, as are certain epizoa of P. stolonifera such as Adornia filigera and Kirohansauria pinnata. It is also significant to notice that the most successful species of the sheltered intertidal zone of the Kalk Bay pier, such as Sabellastarte longa, Bunerosa capensis and Parachinus ancolonus, are all listed by Eyre (1939) as occurring as cryptofauna in waves, ledges, and other sheltered spots in the False Bay intertidal zone. Those intertidal species living on open rock on the coast, such as most limpets and mussels, are either absent or poorly represented in the pier's intertidal zone.

While it is known that the north-west corner of False Bay has a higher average temperature than the rest of the Bay (Isaac 1937), it is possible that the difference in temperature found twenty or thirty feet down makes it impossible for some of the warm-temperate forms established in this corner to live at that depth. It is certainly a fact that certain cold-temperate west coast forms, never found in the intertidal zone of the east coast, are well established twenty feet down. Examples of these are the whelk Argo-buccinum argus and the holothurian Cucumaria insolens, both commonly found in the west coast intertidal zone but seldom or never in the east coast intertidal zone. This appears to lend weight to Stephenson's theory mentioned above that some intertidal faunas may extend their range beneath the surface. In view of these considerations, the South African sublittoral promises to be an interesting field of study for some time to come.

IX. Summary.

1. The design of a diving helmet for study of the False Bay sublittoral is described.

2. The method of use of the helmet is described.
3. Certain intertidal species have a well-marked zonation extending beneath the surface. Their sublittoral vertical distribution is discussed.
4. Some observations are made concerning sublittoral algae and fishes.
5. Some considerations arising from the diving work on the sublittoral occurrence of intertidal species is discussed.

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5) Crustacea.

Cirripedia

Balanus saxillaris.'

Balanus tricornis.'

Brachyura

Dehaenius dentatus.'

Flacusia chabrus.'

6) Echinodermata.

Asteroides

Asterias exilis.

Henricia ornatus.'

Marthasterias glacialis.'

Patiria bellula.'

Echinoidea

Parachinus angulosus.'

Holothuroidea

Cucumaria inoleus.'

Crinoidea

Gomanthus vahibergi.'

7) Ascidiaceae

Pyura stolonifera.

8) Pisces.

Diplodus sargus.'

D. fasciatus.'

Pachymetopon blochii.'

Palunelaps grandis.'

Parascorpus typus.'

Olinus superciliosus.'

Paveolimus heterodon.

Ghorisochisma dentex!

APPENDIX

L List of plants and animals mentioned in the text. ' denotes "has been found at 30 feet below low water of spring tide".

I ALGAE.

1) Phaeophyceae.

Sargassum elegans.'
S. heterophyllum.'
S. longifolia.'

2) Chlorophyceae.

Caulerpa ligulata
Ulva lactuca.

3) Rhodophyceae.

Galidium pristoides.
Gigartina striata.
G. radula.
Hypnea spicifera.
Laurencia flexuosa.'
L. glomerata.'
Plocamium cerallorhiza.

4 Corallinaceae

Cerallina sp.
Jania sp.

II. ANIMALS.

1) Ccelenterata.

Hydrozoa.

Kirchensteueria pinnata.'

Actinaria

Eunosema capensis.

2) Polychaeta.

Aduinia filigera.'
Sabellastarte longa.

3) Mollusca.

Prosobranchiata.

Arxobuccinum arxus.'
Haliothis sanguinea.'
Oxystele sinensis.
O. tigrina.
O. variegata.
Patella barbara.
P. cochlear.
P. miniata.
P. tabularis.
Turbo sidaris.
T. sarmaticus.'

4) Brachiopoda.

Kraussina rubra.'

**THE FISHES OF THE INTERTIDAL
ZONE OF THE CAPE PENINSULA.**

Thesis presented for

M.Sc. degree

by

P. B. H. Jackson

June, 1950.

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PREFACE

The Zoology Department of the University of Cape Town, under the direction of Professor T.A. Stephenson and later Professor J.H. Day, has for long been concerned with the ecology of South African Coast. The very valuable results gained from this extensive work have been set forth in a number of papers, and the conclusions arising therefrom form the basis of three papers by Stephenson (1939, 1944, 1947), dealing with the survey as a whole. The workers during the course of the course of the survey did not have the time to enter into the study of the intertidal fishes to any great detail. There was a great deal to be done and fish are elusive and difficult to capture so that their study would have taken more time than was warranted on a survey of that scale.

Nevertheless, fishes form an important and interesting part of the intertidal population, and their ecology is interwoven with that of the other biota of the rock pools to a considerable extent, so that this paper represents a contribution to the ecological knowledge of the South African intertidal zone by a study of the fishes in one area of the coast; it deals also with points, mainly of a systematic nature, arising out of this ecological study of the fish.

The author wishes to express his thanks to Professor J.H. Day of the Zoology Department of the University of Cape Town for constant help and encouragement, to the staff of the Department for their willingness to assist in every way, and to Dr K.H. Barnard of the South African Museum for allowing the author the use of the Museum library.

NOTE.

The Scientific names of fishes in this paper are those given by Smith (1949), with the exception only of the Family Glinidae. The members of this family are named according to the revised genera given in Part II of this paper.

PART I. THE ECOLOGY OF THE INTERTIDAL FISH.

I. Introductory.

1. The Intertidal Region.

The concept of the "intertidal region" adopted here is the same as that defined by Stephenson (1937) during work on the South African coast. It embraces that section of the coast-line from the uppermost level of the shore splashed by the waves at high spring tide to the lowest part exposed by the sea at low spring tide. This region is divided into four sub-regions or zones. Progressing downwards from the top, the uppermost of these zones is called the Littorina Zone, due to fact that it is characterised by the presence of numerous periwinkles of the genus Littorina. The lower level of this zone only is submerged during the highest tides, but the whole zone receives a certain amount of splash from the waves at high tides, depending on the calmness of the sea at the time. Immediately below this sub-region is the Balanoid zone, so called because the dominating organism in this zone are barnacles of the genus Balanus and others. This zone is ordinarily submerged at high water of ordinary tides and left bare at low water of these tides. The zone just below this is known as the Cochlear zone, The dominating organism in this zone is the limpet Patella cochlear. The Cochlear zone is exposed completely only during low

water of spring tides, and may even then be partly covered if the sea is rough. The final, lowest zone is the sublittoral fringe, which is almost perpetually covered with water, but which may be exposed if a low spring tide coincides with a calm day. The region below this is called by Stephenson the sublittoral, and it is the highest region of the sea bottom which is perpetually submerged.

(1) The Rock Pools.

During the course of the present work attention was paid chiefly to the rock pools in the intertidal zone, as these form the home of all the fish to be found in the intertidal zone. The pools in this area vary in size from saucer-like depressions in the rocks to large and deep pools and gullies, the lower end of which are frequently in connection with the sea even at the lowest tides.

The frequency with which these pools are replenished with fresh sea-water depends almost entirely on their position on the shore. Pools in the Littorina zone are nearly always stagnant, new water arriving from the sea only for a short while at the top of each high tide; on a rough day when the waves splash high up the shore they receive more water than they would on a day when the weather is calm. These pools are often discoloured and dirty, with a greenish scum floating on them. Yet all but the very highest pools, which are apt to dry up completely between spring tides, contain a fish

population. The pools are usually bare with a sandy or rocky bottom; of the few sea-weeds which grow there the commonest, on both sides of the peninsula, is Porphyra capensis.

Balanoid pools are replenished with new sea-water to a far greater extent than are the Littorina pools. While they are usually cut off from the sea for long periods at low tide, they are completely covered at high tide, and the water in them is always fresh. On the False Bay side of the Peninsula the bottom of these pools is chiefly rocky, although sandy pools do occur to some extent, especially in certain localities. At Sea Point and other places on the West Coast a great many shallow pools are found in the lower Balanoid region which have sandy bottoms and rocky walls. They contain a plentiful growth of algae of which Ulva lactuca is the most common. Isaac(1937) considers that Ulva lactuca is a dominant species in the upper rock pools. Other common algae in these pools include various species of Gigartina and Codium. Beneath these algae are concealed numbers of fish.

The pools of the cochlear zone and sublittoral fringe, if they are of any size, usually have an opening into the sea even at low spring tide. Many of these pools are more correctly gullies, which cut across the zones even as far up the shore as the lower Balanoid zone, so that often no hard and fast line can be drawn between the various zones. They support a rich

and varied plant and animal community, details of which are given in papers by Eyre (1939) and Bright (1938), of the East and West sides of the Cape Peninsula respectively. These papers form part of the work done under the direction of Professor T.A. Stephenson(1939), (1944), (1947), on the intertidal zone of the South African coast.

2. Method of Work.

Fish, from a collector's point of view, differ sharply from practically all the other members^{of} an intertidal community in that they are very mobile and do not stay in the same place to nearly the same extent as other intertidal organisms do. In addition, they are very elusive and always more or less difficult to catch when seen; they also possess in most instances a nearly perfect system of camouflage and an ability to hide themselves to a remarkably successful degree. The worker therefore can never satisfy himself in the course of a collecting trip that, firstly, he has obtained specimens of all the species present, and in the second place that what he does possess is a fair sample of the fish fauna, with regard to size, sex and numbers, which are present in that locality at that time.

Consequently the method of work adopted was to select two points on either side of the Cape Peninsula and collect there at regular intervals, obtaining by this means a fairly

representative sample of the fish fauna at each of the two places throughout the year, and, in addition, visits were made to various other points within the area limited by these points, with a view to obtaining information as to the distribution of various species, both in False Bay and in the colder Atlantic waters on the western side of the Cape Peninsula. Information of this nature is presented chiefly in the form of records, as the area in question is a very critical one, and many of the species considered have very sharp limits of distribution on either the "cold water" or the "warm water" side of the Cape Peninsula.

Collecting was chiefly done by means of hand nets, in rock pools and sublittoral gullies. A few fish were caught in this area on rod and line, notably larger specimens of Gobius nudiceps. This voracious inhabitant of the intertidal zone is a characteristic frequenter of large pools high up on the shore, where several specimens of all sizes make their headquarters under a particularly large and immovable rock, or in intricate underwater tunnels and small caves formed by piles of large broken rock, to this inaccessible refuge the larger and wilier specimens make an instant retreat at the slightest sign of danger, so that it is practically impossible to net any but the smaller specimens. But a baited hook left in the water near the mouth of the hide-out will often entice the larger fish, and in this way several of the bigger speci-

mens can be caught during the course of a morning.

Several experiments were made with baited fish traps, but these were seldom successful; they had to be heavily weighted and securely fastened down to prevent them being washed away by the tide, and, if they survived until the next day, generally caught little more than large quantities of Comminella and other carnivorous whelks.

Colour notes and any peculiarities of live fish were noted, and other remarks of interest were made in a note-book on the spot. The fish were usually put into a bottle of sea-water and brought back to the laboratory for identification alive. They were then killed by being dropped into a jar of 60% alcohol, in which they died very soon and set themselves, i.e. expanded their dorsal and other fins, in a satisfactory manner.

3. The Scope of the Work.

The object of the present survey has been to inquire into the ecology of the fish population of the intertidal zone. From this point of view the following aspects of the fish-life have been examined: the abundance of the fish population as a whole, and the relative abundance of different species comprising the population, their habitats, food and the zonation which they exhibit. Their reproduction has been studied and finally their place in the intertidal community is discussed.

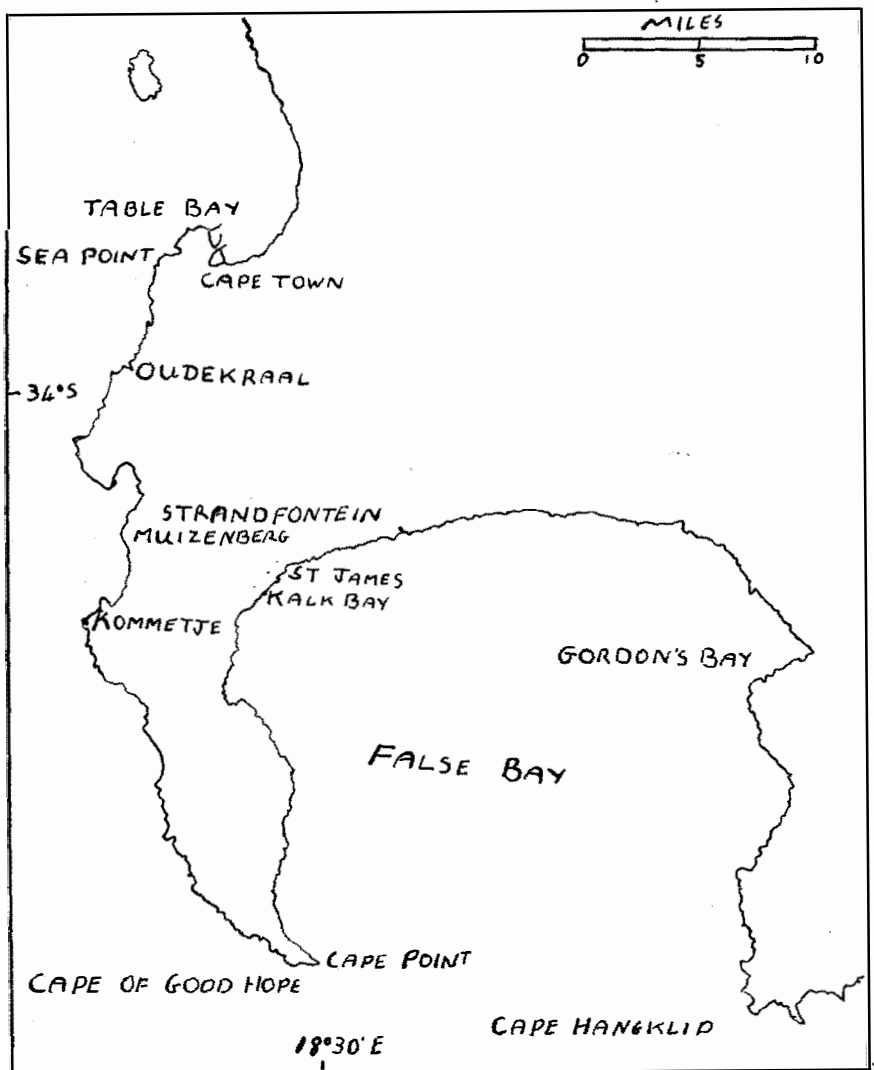


Fig The Cape Peninsula and False Bay. After Stephenson (1966).

II. General Account of the Survey.

I. Localities Visited.

The two places where most of the collecting was done were the rocks at St. James, in False Bay, and the rocks at Sea Point below La Rochelle boarding house.

An account of the intertidal zone at St. James, with full notes on all the marine biota except fish, and a description of the rocks, is given by Eysse (1939). Similarly a description of the conditions prevailing at Oudekraal, a place typical of the West coast of the Peninsula, is given by Bright (1938).

In addition various other places on the Peninsula, such as Rooikrantz, Cape Point and Bantry Bay were visited. (Fig. 1).

Each of these places possesses a characteristic fish fauna. On the False Bay side, fish occur which are not to be found on the West Coast, and similarly there are several species at Sea Point which do not occur in False Bay. In addition, there is a large component of the fish fauna which is common to both sides, and some of the commonest species can be numbered among these. Others, however, while fairly common on one side, are scarce on the other. Such a species is Clinus squamatus, which has been captured on several occasions at Sea Point, but only once at St. James.

In general the characteristic warm water forms tend

to die out at Cape Point is approached, to be replaced by the characteristic cold water forms. This is what is to be expected, but no exact spot was found, however, where a hard and fast line could be drawn with warm water forms on the one side and cold water forms on the other. Seen in the perspective of the South African coast as a whole the division between cold water and warm water is very marked in the region of the survey, but the distinctness falls away to some extent when seen at close quarters, and no exact point of difference has been ascertained.

2. Components of the Fish Fauna of Intertidal Zone.

(1) The Position at Low Tide

The facts given throughout this paper with reference to distribution, zonation, habitats etc., refer solely to the position as it occurs in the intertidal zone at low tide only. The reasons for this are threefold:

a) The whole of the zone is ordinarily accessible at low tide only.

b) All the previous work which has been done on the South African coast on the intertidal zone has been done at low tide.

c) There is every reason to suppose that the whole picture, with regard to fish, changes to a marked degree at high tide. Not only are the fish able to move about when the zone is completely covered with water, but forms which inhabit

the sublittoral and which are seldom or never found in the rock pools at low tide, often come up with the high water and hunt about for food, retreating again as the water recedes.

(ii) The Components of Fish Population.

Taking the intertidal zone as it is at low tide as a basis, then, it was noticed at both main collecting areas that the fishes to be found there appeared to fall naturally into three subdivisions:

a) Fishes which inhabit the intertidal zone permanently.

b) Fishes which inhabit the intertidal zone for some portion of their lives only.

c) Fishes which cannot correctly be called inhabitants of the intertidal zone, and whose presence there is caused by abnormal conditions, such as the onset of cold currents, storms etc.

3. The Permanent Component

These include the typical inhabitants of the intertidal rock pools. In general they are comparatively small, sluggish forms, living in rock crevices and caves and among sea-weed. They are almost without exception brilliantly coloured, usually in rich shades of brown, russet and green, and have elaborately developed concealing coloration to blend with the colours of their environment. The fins are often irregular and have transparent patches to suggest the fronds of sea-weed, and there are darker lines and patches about the eye for the purpose of con-

cealing that organ. Many of them are also, capable of changing their colour to suit their background. They are nearly all carnivorous, and are not given to migrating or wandering to any extent, preferring, at low tide at least, to stay in in one crevice or weedy rock. When they do move, this is usually a dash from one rock or patch of algae to the next.

Chiefly among this type on the Cape coast are the members of the family Clinidae. They are of particular interest since they include a great many endemic forms among them. This is what would be expected, since fish of the habits described above are the type among which it is most probable that endemic forms would be found.

Of the twenty-one species of fish captured and examined during this survey, thirteen or over 60% belong to this family.

They are:

Table I

Species	Where Found on this Survey
<i>Clinus superciliosus</i>	Ubiquitous
<i>Clinus cottoides</i>	Ubiquitous
<i>Clinus robustus</i>	West coast
<i>Clinus anne</i>	West coast
<i>Clinus venustis</i>	West coast
<i>Elinus acuminatus</i>	Ubiquitous (rare on E. coast)
<i>Clinus brevicristatus</i>	West coast
<i>Clinus dorsalis</i>	Ubiquitous
<i>Clinus capensis</i>	East Coast

Species	Where found on Survey
<i>Myxodes fucorum</i>	East coast
<i>Myxodes mus</i>	East coast
<i>Myxodes branchy^ccephalus</i>	East coast
<i>Myxodes heterodon</i>	East coast

It will be seen that of the thirteen Clinids listed *five* here were found only in False Bay, four were found on both sides of the Peninsula and four were found only at Sea Point some species, such as *Clinus robustus*, ^c*C. capensis* and *Myxodes heterodon*, are probably present on both sides of the Peninsula but escaped capture except as stated. Otherwise this list confirms the lateral distribution given by Smith (1949), with the exception of *brevicristatus*, hitherto found only in False Bay. It is perhaps noteworthy that while *Clinus* species in general occur on both sides of the Peninsula or else on the West coast only, *Myxodes* species were found only in the warmer waters of the East coast (see remarks on Lateral Distributions). Of the 28 species of South African Clinids twenty-one have been found in this area (Smith 1949). Of these five are extremely rare, having only been found on a few occasions. These five species are *Clinus navalis*, *Clinus brevicristatus*, *Clinus latipennis*, *Gymnocylinus rotundifrons* and *Clinoporus biporosus*. None of these were seen or caught with the exception of *Clinus brevicristatus*, one specimen of which was caught in a Cochlear pool at Sea Point. This curiously localized species was previ-

ously known only from "False Bay, from Kalk Bay to Simonstown."
(Smith 1949, p. 358).

Of the remaining 16 species listed by Smith, 12 have been found in the present survey. Those which have not been found are: Clinus anguillaris, Clinus striatus, Clinus taurus and Myxodes nava. The first three are listed by Smith as "not abundant", "not often seen" and "not abundant", respectively while the last is called by him "not uncommon".

The Clinidae constitute the majority of species which make up the permanent component, but three other fish, belonging to three different families, were caught which are members of this component.

These were:

Family Gobiesocidae

Choriothianus dentax

Family Gobiidae

Gobius nudicens

Family Blenniidae

Blennius cornutus

These, in colour, size and habits are typical members of

** It is possible that Blennius cornutus is a summer migrant, since it has been caught

~~in False Bay~~ and in False Bay were caught only in False Bay.**

* * only in the summer months while other species were regularly

caught the whole year round. One species which was expected

would be found which has not been caught is Gymnabatrachus apiatus, which is known from Sea Point.

4. The Temporary Component.

These fish consist chiefly of those whose young are to be found at the upper levels but which do not live there all their lives. They are among those which are described as typical littoral fish, but which in their adult condition invade the intertidal zone only at high water, when the zone is more or less covered with water, and which are seldom or never to be found in the low tide rock pools except in their juvenile condition. This category embraces most of the shallow water rock-frequenting types; species caught in this survey are:

Family Sparidae

Pachymetopon blochii

Diplodus sargus

Family Coracinidae

Coracinus capensis

Family Tachysuridae

Tachysurus feliceps

Family Mugilidae

Mugil sp. (probably Liza ramada)

All these make their appearance (as juveniles) during the summer months, and, when the tide receds, are frequently to be found, often in little shoals, in the larger rock pools, where they form a characteristic part of the summer fish fauna. Judg-
ing

from an examination of the stomach contents of specimens from this category, their diet, at this time of life at least, is predominately vegetarian, although in later life many, such as Diplodus sargus, are omnivorous. These juveniles often form part of the food of fish permanent to this zone; small Mugil up to 4 cm long have been found among the stomach contents of both Clinus superciliosus and Clinus cottoides.

This component, though forming a well-defined and stable element of the fish of the intertidal zone, is none the less somewhat more fluid and variable than the first. It does not exist, for instance, in the same proportion the whole year round, being greater in number and species during the summer months, though specimens of Diplodus sargus have been seen in the pools once or twice during winter. They are not nearly as abundant as they are in summer, and are generally of larger size, indicating probably that these are fish spawned during late summer which have stayed in this zone longer than their companions before finally leaving the rock pools for the sublittoral.

(1) Differences in the Fish Population at Night.

In the second place, there is a greater number of larger fish present in the intertidal zone at low water at night. Fairly large specimens of Diplodus sargus and other typical fish of the rocky sublittoral make their way up gullies and pools in the cochlear zone and sublittoral fringe at night, provided

that such gullies and pools hav^e immediate access to the open sea. These have at no time been observed in the same gullies and pools during the day. For instance, in an often visited pool, the top end of which is in the upper Cochlear zone and with lower end open to the sea even at low spring tide, a specimen of Diplodus sargus 235 mm in length was captured by hand net at about 9 p.m. of the night of 24th June, 1949, and several others of the same size and larger were observed in the pool. Fish of this size have never been seen in the pool during the day, the largest Diplodus caught here (on a tiny hook) during the daytime measuring about 100 mm.

In general, there are many more bigger fish, belonging to both the intertidal components, seen at night in the intertidal zone ^{there} during the day. With regard to the permanent component, this is particularly true of those fish which, while well represented in the intertidal zone, have a range of vertical distribution the lower limit which is well below the sublittoral (see remarks on Zonation). Such fishes are for instance, Clinus superciliosus and Chorichismus dentex.^{xx} The larger

✱✱ The larger specimens of these are seen and captured during the night than during the day.

There are probably several reasons for the fact that larger fish appear to be more common in the intertidal zone at night than they are during the day. In the first place, fish, be-

longing especially to the second, impermanent category, are encouraged by the darkness and quietness to remain much higher up the shore during low tide at night than they would during the day. Possibly they cannot see at night how narrow the confines of the pools are in which they are remaining. Secondly, many larger fish, even if they are always present in the intertidal zone, do not immediately vanish into a hiding place or into the open sea at night as they do during the day at the approach of danger, but remain where they are, often dazzled by the light of a torch, and are thus more often seen and more easily caught than they are during the day. Many of the larger Clinids especially are frequently very wary during the day and are much less so at night.

5. The Rare Visitors to the Intertidal Zone.

This category is unimportant from the point of view of the survey of the fish of the intertidal zone. Par definition it embraces practically every type of fish life in the sea which may be a very occasional visitor to the intertidal zone, the visits usually being caused by rough weather or other abnormal cause.

Excluding fish which have been washed up in an obviously sick or dying condition, only two healthy fish which should be classified under this heading have been caught. These were a White Stumpnose (Rhabdosargus globiceps), measuring 398 mm in length, and a Shark (Mustelus punctulatus). The Stumpnose was

found in a cochlear gully at low tide and the Shark was stranded by a wave in a shallow pool in the same area. Both these fish, as far as could be observed, were in a healthy condition with no parasites or marks of violence upon them. The shark was stranded on a very rough day with a particularly violent South Easterly gale blowing.

III. Special Aspects of the Survey.

I. Abundance.

Mention has already been made of the fact that accurate counts of the fish population in any area at low tide between the sublittoral fringe and the Balanoid zone cannot be accomplished with the same facility with which counts of limpets or other more or less sessile inhabitants of the intertidal zone can be made. Moreover, the numbers of the population, although relatively stable over any period of time, do in fact vary to some degree between one day and another and even between one spring tide and the next, as even the most sluggish Clinid or Goby is far more mobile than the average mollusc, and is capable of travelling fair distances. Thus in a pool in which on one occasion 13 small Clinus cottoides were counted ^{contained} only 7 Clinus cottoides a fortnight later.

In addition the numbers of fish taken both of specimens and species cannot be considered to reflect an accurate view of the species and numbers obtaining ^m a locality, since certain species are relatively sluggish, easy to catch and conspicuous,

in contrast to others which, besides being well camouflaged, are most elusive and agile when danger threatens.

Therefore, while it is perfectly simple in some cases to notice that certain species are very common and others very rare in most intermediate cases it is difficult to determine the relative abundance or scarcity of intertidal fish and epithets such as "relatively scarce" or "comparatively common" should be used with caution. In the following table an attempt has been made to list the intertidal fish of the permanent component in a decreasing order of abundance, with the commonest at the head of the list, and, while it is hoped that this reflects the position as accurately as possible, future work may well alter the positions of many species on the list.

Table II

1. Clinus cottoides
2. Gobius nudiceps
3. Clinus superciliosus
4. Clinus dorsalis
5. Myxodes mus
6. Choriochismus dentex
7. Clinus acuminatus
8. Clinus anne
9. Clinus capensis
10. Myxodes fucorum
11. Myxodes heterodon

12. Clinus robustus
13. Blennius cornutus
14. Myxodes brachycephalus
15. Clinus venustria
16. Clinus brevicristatus

It should be noticed that this list has been drawn up with the emphasis on the number of individuals present in the fish population rather than the different species which occur. The two are not always proportional. For instance Clinus capensis is relatively abundant as a species, as one or two may be found, in the appropriate habitat under stones, at most places along the coast. Yet the pool which holds one or two specimens of this fish will probably have a dozen Clinus superciliosus in it, with a like number of Clinus cottoides, and a smaller neighbouring pool will contain eight of these species and five Muraenoclinus dorsalis, but no Clinus capensis. Throughout the survey it has been noticed a given area in the appropriate zone contains three to four times as many Clinus superciliosus as Clinus capensis, though both species commonly occur in that area. It therefore follows that, other factors being equal, the ecological effect of Clinus superciliosus on the environment will be proportionately greater than is that of Clinus capensis. This, of course applies to the area of the shore where C. capensis occurs most abundantly, since the vertical distribution of this fish is more limited than is that of Clinus

superciliosus, which occurs over the whole intertidal zone with the exception of the highest levels.

Statistics on the abundance of fish in the intertidal zone are likely to be least accurate in the case of those whose upper levels of vertical distribution are in the levels of the low tide mark. A cunning fish which lives in or about the sublittoral fringe and which seldom or never penetrates the regions above this (see remarks on Zonation), can easily slip off into deeper water un-noticed by the collector, who is apt to get a mistaken impression about the numbers of this species which are present. A case in point is that of the two fish Myxodes mus and Myxodes heterodon, both stated to be common inhabitants of the Cochlear zone and below. They are both brilliantly coloured in rich browns, reds and silver, as are all Clinids which are frequenters of seaweeds in the lower intertidal zone.

Yet far more Myxodes mus were caught on this survey than were Myxodes heterodon. While M. heterodon is probably the less abundant of the two the large discrepancy in the numbers caught is probably due to the fact that Myxodes heterodon is by far the most agile of the two and it therefore escapes capture easier than does Myxodes mus. On visiting the perpetually submerged sublittoral, just below low tide mark, with a diving helmet, specimens of M. heterodon were occasionally seen crawling about on the rocks near seaweed by means of their pectoral fins. On danger they darted into the weed (Laurencia^{ca} gloriosata^{ca}) and vanished. Myxodes pass, stated to be common, has entirely escaped capture.

It is, however, probably relatively scarce as far to the south of False Bay. It is not an easy matter to determine exactly the relative population strength of the fish.

The abundance of the fluctuating component is strictly seasonal, arriving at a climax during the summer months and dwindling almost to zero in the winter. These fish are also not confined to one locality to nearly the same extent as the first component is, being influenced by the tide and to a great extent, at least in their very early life, by the current. They also disperse over a wide area of the shore at high tide, the number that are left in pools at low tide being probably a matter of accident to a large extent. Though these fish do, in their juvenile stadia, make their home in the tide-pools almost to the same extent as the first component does, they are not solely confined to the upper levels, apart from the effect of the tide and current on their dispersal.

Because of this, counts of the number of these juvenile fish present in the intertidal zone at low tide are useful only in that they may give an indication of the commonest species which make up this component, and cannot give any idea of the actual numbers of fish present and of their effect on the intertidal community. Matters are also complicated by the fact that though these fish are generally much easier to identify at sight than are most Clinids they are usually difficult to catch as, added to the fact that they are extremely speedy and elusive,

they are usually found in pools lower down the shore the lower end of which is open to the sea, and low tide, and fish readily escape through these openings into the sublittoral when hunted.

In addition to the species listed in the section on the Temporary Component the following two species were noticed as being present but specimens of them were not caught:

Family Sparidae

Diplodus trifasciatus

Family Tetraodontidae

Amblyrhynchotes honkeni

Of these seven fish the two species most likely to be present in the rock pools at any time during the summer months are the Blacktail (Diplodus sargus) and the Zebra (D. fasciatus). These are the most abundant and regular element, often occurring in small shoals in the proportion of 10-15 Blacktail to one Zebra. The others are more periodic in their occurrences, but becoming very abundant on certain days, particularly in the case of the mullet, small individuals of which occurring in large shoals at certain times. Juvenile Galjoen (Coracinus capensis), and Hottentot (Pachymetopon blochi) were never abundant in the intertidal zone but were often present in fair numbers in the immediate sublittoral fringe, young barbel (Tachysurus feliceps) were often to be seen in the intertidal zone, sometimes quite high up the shore. They were, however, very shy and wary, remaining in underwater caves and ledges and seldom showing themselves. They were more easily seen and were less timid at night.

2. Reproduction.

The data accumulated in this section refers only to fish found in the first component of intertidal fishes, i.e. those which are to be found in this area at all life stadia. Of these the predominant group in the area in question are those fishes of the family Clinidae, many members of which occur fairly commonly on both sides of the Peninsula.

(1) The Family Clinidae

All members of this family are viviparous, and fertilization is by copulation, for which purpose the males have a distinctive intromittent organ which provides a ready means of telling sexes apart.

The amount of young produced at a time varies in the different genera and also with the age of the fish. Each species has a different minimum size at which spawning takes place for first time. Judging from an examination of specimens of all sizes at different times of the year, the first spawning appears to take place during the second year of growth. The following list tabulates the minimum size at which gravid fish of various species were found, the largest gravid females that were caught, and the weight of the ovaries in each case.

GRAVID FEMALES.

Species	Minimum size (mm)	Gonad wt (mg)	Maximum size (mm)	Gonad wt (mg)
<u>C. superciliosus</u>	112	165	158	6975
<u>C. cottoides</u>	61	100	88	970
<u>M. mus</u>	65	80	79	630

In each fish examined it was noticed that the eggs and embryos were not all in the same state of development, but there appeared to be two or three different stages of growth in the ovaries of each fish. Thus in the smallest Clinus cottoides, mentioned above, there were 21 small fish with yolk-sacs nearly absorbed, and in addition there were a number of large yolky eggs with embryo fish just visible in them. The largest C. cottoides had ovaries which contained about 70 small transparent fish, with yolk-sacs attached in various stages of absorption, ranging in size from 1 to 15 mm in length, the largest having ^{no} yolk-sacs attached. In addition, the ovaries contained about 100 eggs of various sizes, ranging from small black dots to yellow globes about the size of pin's head. A Clinus superciliosus 145 mm long with gonads weighing 775 mg contained 38 well-developed young fish from 9 to 11 mm in length, as well as about 80 eggs and very young fish. The largest C. superciliosus, mentioned above, contained about a hundred young fish, the largest of which, 16 mm long, was transparent yet marked with faint brown bars and blotches like its parent. A similar state of affairs was observed in the case of Myxodes mus, except that in this case the young fish and eggs, though large in size, were fewer in number, there being usually about 20 embryo fish and about 60 eggs. The largest unborn fish found here measured 20½ mm in length, and though transparent, was faintly pigmented with brown in typical F. mus style. Several of these fish had ovaries in which were one or two fish 20-21 mm in length. These young, if removed from the ovary of a freshly

killed female and liberated in a bowl of sea water would swim about in a perfectly normal fashion. If they had been left undisturbed, these fish would undoubtedly ^{have} spawned these larger fish within a few days, long before the other fish in the ovary were sufficiently mature for birth.

This evidence points to the fact that the Clinidae do not have only one spawning period, but give birth to their young a few or one at a time at intervals. The number of young born at a time is probably eight to ten in the case of Clinus superciliosus, perhaps a few less in the case of Clinus cottoides, but ^{Myxodes} ~~Eusomus~~ rus, in all probability, gives birth to only one or two young at a time. Gilchrist and Thompson(1910) record that 24 young Clinus superciliosus were born in the aquarium at St. James. In the case of the less common Clinids sufficient data was not collected for any pronouncements to be made, but it is probable that the same applies to them, since they are all viviparous. This interesting aspect of the breeding habits of the Clinidae could easily be verified in an aquarium.

Times of Spawning.

Very small Clinids are scarce or absent from the rock pools during the colder months of the year, but fair quantities were seen from about November onwards. In the summer months there are large numbers of small juveniles, ranging in the case of Clinus superciliosus from about 45-60 mm in length. Gilchrist and Thompson(1910) noticed the small, transparent young of Clinids

in the rock pools from October onwards.

This in

This indicates that the spawning period of these fish commences in late winter or early spring. The following list gives the months in which gravid females of the three species mentioned above were caught:

Table IV.

<u>Clinus superciliosus</u>	<u>Clinus setteides</u>	<u>Myxodes mas</u>
M		
March (1 specimen)	-	-
May	-	-
June	-	-
(No fish caught in July)	(Ditto)	(Ditto)
August	-	-
September	September	September
October	October	October
--	November	November

This table confirms to some extent the fact that the chief spawning months are these in the early winter and late spring. No figures were obtained for July and few for August; these are probably critical months in this respect.

Of the fish that were caught the percentage of males with ripe gonads were insufficient to draw any but the most general conclusions about the times of maturity of testes. In general, however, it was found that the greatest proportion of male fish with mature testes were caught in winter and spring, as shown in Table V:

TABLE V

<u>Glinus superciliosus</u>			<u>Glinus octoides</u>			<u>Myxodes mus</u>		
Date	Length of fish	Gonad wgt.	Date	Length of fish	Gonad Wgt	Date	Lgt of fish	Gonad Wgt
March	147 mm	710 mg	March	65mm	140 mg	May	62mm	60mg
March	167	270	May	91	200	May	67	120
May	168	310	May	94	210	May	55	70
May	195	555	June	89	160	Dec	98	250
May	170	240	Nov	88	140			
June	190	465						
June	200	290						
June	211	610						
Aug	121	425						
Oct	138	760						

The results from this table indicate that sexual maturity in male Clinids occurs most often in winter; e.g. 10 records of maturity in male C. superciliosus six occur during May and June. No collecting would be done during July and little in August; unfortunately these months are probably the most important from this point of view. Breeding, however, probably continues, though to a lesser extent, well into the summer, as witness the exceptionally large Myxodes mus with ripe testes caught in December.

This data is not sufficiently comprehensive for definite conclusions as to time of breeding to be drawn from them, as in-

sufficiently sexually mature specimens of both sexes were obtained, but the general trend of breeding times in the Clinidae is probably that copulation takes place a month or two before spawning occurs, throughout the year except possibly for the late summer months, rising to a peak in spring, diminishing during the summer, with a second probably smaller season in autumn. The work on the breeding habits of Clinids done by Gilchrist and Thompson(1910) and Smith(1949) confirms this.

(ii) Other Members of the Permanent Component.

No specific data was compiled concerning intertidal fish other than the Family Clinidae. It is known, however, that gobies and blennies are oviparous, and lay their eggs in clusters under stones and rocks, or in empty shells. Less appears to be known of the breeding habits of Choriochismus dentex. The eggs have been found attached firmly to stones in deeper water of 9 to 20 fathoms during November and December(Gilchrist 1904, 1905). In a later publication(1916), Gilchrist describes the eggs and larvae of this species. A related genus of the same family(Eckloniaichthys) lays its eggs on the stipes of seaweeds in shallow water (Smith 1949). It would thus seem that Choriochismus moves into deeper water to lay its eggs, although one or two have been found in the intertidal zone with ripe or nearly ripe eggs. The following list gives the lengths, gonad weight and date captures of some females found in the intertidal zone;

Date	Length (mm)	Ovary Weight (mg)
May	180	2100
Feb.	131	1990
Feb.	224	6120

Thus of the other members of the permanent component Choriochismus dentex for one probably always moves into deeper water to spawn. Another which probably also does so, in this area at least, is Blennius crenatus, since eggs of this species are recorded by Gilchrist (1916) to have been dredged up in the shell of a barnacle, (probably Balanus maxillaris) in nine fathoms in the month of November. Gobius nudiceps has never been recorded from deeper water, and it is probable that the eggs are laid in the underwater caves which this species frequents high up the shore. The eggs have been described by Gilchrist (1916) from specimens deposited on the glass front of an aquarium tank.

3. Feeding habits.

(1) The Permanent Component

With very few exceptions the specimens of all the species of this component were found to be macroscopic feeders and carnivorous. The chief exception to this was that Ulva, probably U. lactuca, was found to be present in the stomach of specimens of Gobius nudiceps on several occasions.

Gobius nudiceps.

It is not known whether the Ulva found in the stomach

of this species was swallowed as food or for the sake of the microscopic organisms which may have been adhering to it. This species when caught, usually had nothing in its stomach and on the other occasions had a mass of unidentifiable remains. Though many of the intertidal fish will eat practically anything that comes their way, *Gobius nudiceps* appears to be more of a scavenger than most. More amphipods were found among the stomachs contents than any other ~~animal~~ ^{animal} food, but one animal had swallowed a fresh leg of *Cyclograpsus punctatus*. This fish was caught in a pool in the *Littorina* zone in which several specimens of this crab were also present. It had never been observed, however, that Gobies attack healthy specimens of *Cyclograpsus punctatus* or the shrimp *Leander pacificus*, both of which occur in the same pools as these fish.

Family Clinidae

All members of the Clinid family are practically completely carnivorous, but, possibly because they do not usually occur so high up the shore as the gobies do, their diet appears to consist of fresher food. Practically all types of animal food is acceptable to these fish, but much of the flesh that is eagerly eaten can seldom or never be obtained in the natural state, such as ascidians protected by their thick leathery tests. From observations made on the stomach contents of these fish it can safely be said that their main natural food consists of amphipods and Isopods.

The following table gives a list of the commones amphipods and isopods found in Clinid fish:

Table VII

Amphipods

Species	Found in:
<i>Lymanassa</i> sp.	<i>Clinus dorsalis</i>
<i>Paramoera capensis</i>	Most species
<i>Ceradocus rubromaculatus</i>	<i>Clinus superciliosus</i> , <i>C. cottoides</i>
<i>Cymadusa anstralis</i>	<i>Clinus superciliosus</i>
<i>Hyale</i> spp.	<i>Myxodes mus</i> , <i>Myxodes</i> spp.
Caprellids	<i>Myxodes</i> spp.

Isopods

<i>Cirolana</i> spp.	<i>Clinus acuminatus</i> <i>C. dorsalis</i> <i>C. cottoides</i>
<i>Exosphaeroma</i> spp.	<i>C. acuminatus</i> <i>C. cottoides</i> <i>C. superciliosus</i>
<i>Paridotea</i> spp.	Particularly <i>Myxodes</i> spp. <i>Clinus superciliosus</i>

Chorisochismus dentex

This is also a common fish and a varied collection of organisms were found among the stomach contents. No amphipods were ever found, but all of the specimens which had any food in their stomachs contained molluscs, so that it appears that various

kinds of molluscs form the main food of this species. The teeth of this fish are much larger and stronger than of any other species of the ^{permanent} intertidal component and they can therefore deal with hard shelled animals better than other members of this component.

The table on pages 33, 34 & 35 gives a list of the stomach contents of 60 fish examined of 4 species. Not all the fish examined are listed since a great many had empty stomachs:

Species	Date	Amphipods	Isopods	Fish	Worms	Molluscs	Barnacles	Other.
		no.	no.				no.	
<u>G. der-</u>	May					<u>Siphonaria</u>		
<u>tex</u>								
"	June					<u>Diodora & P.</u>		<u>Parachinus</u>
						<u>oculus</u>		<u>angulosus</u>
"	Sept.				<u>Gur-</u>	<u>Siphonaria</u>		
"	Feb.				<u>nares</u>	<u>2 Patella</u>		
"	Feb.			<u>2 G. der-</u>	<u>1</u>	<u>H. brui-</u>		
				<u>salis.</u>	<u>neroid</u>	<u>egg.</u>		
<u>M. mus</u>	May	x	x					
"	May	x						
"	Sept.	x						
"	Oct.	x						
"	Nov.	x						

Species	Date	Amphi- pods	Isopods	Fish	Worms	Molluscs	Barnacle legs	Other
<u>E. set- toides</u>	Mar.			April 28 mm				
"	Mar.	X	X					
"	May	X						
"	May	X						
"	May		X			Limpet	X	
"	May	X					X	
"	June	X					X	
"	Sept.		X					
"	Sept.	X					X	
"	Sept.	X					X	
"	Sept.	X					X	
"	Sept.	X	X				X	
"	Sept.		X			Limpet	X	
"	Oct.	X					X	
"	Nov.	X	X					
"	Nov.	X	X					
"	Nov.	X						
"	Nov.		X					
"	Feb.		X		X			
"	Feb.	X	X					
"	Feb.		X					
"	Feb.	X	X					
"	Feb.	X	X			Limpet		
"	Feb.	X						
"	Feb.	X	X					
"	Feb.	X	X					
"	Feb.	X						X
"	Feb.	X	X					X

Species	Date	Amphi- pods	Iso- pods	Fish	Worms	Molluscs	Barnacle legs	Other
<u>G. subar- silicosa</u>	May.	x		<u>G. sub- 62 mm</u>				
"	"	x			<u>Starlet Diadema</u>			
"	Apr.	x						
"	May			<u>Mugil 30mm.</u>				
"	"	x						
"	"		x					
"	"				x			
"	June							<u>Flaccaria shab- ing (leg.)</u>
"	"							<u>Parachinus analicus</u>
"	Sept.	x				<u>Gastropod</u>		
"	"					<u>Helcion</u>		
"	"	x						
"	"	x	x		<u>Nereid</u>			
"	Oct.	x	x					
"	"	x	x					
"	Nov.	x	x					
"	"	x	x					
"	Feb.	x	x					
"	"	x	x					
"	"	x						
"	"	x						
"	"	x						
"	Apr.		x					<u>Parachinus analicus.</u>
"	"		x					
TOTALs		40	22	4	5	11	10	4
(For all 4 species).								

It will be seen from the preceding list that of the 68 fish examined, 40 had amphipods in their stomachs. The only species from which amphipods were consistently absent was Chorisochismus dentex. Isopods were present in 22 of the fish, C. dentex again being the sole exception. In 4 cases fish were present among the stomach contents, while 5 of the fish examined had worms present among the stomach contents. Molluscs were present in 11 cases; all five of the Chorisochismus dentex listed, which were the only ones whose stomachs were not empty, contained mollusc remains. In 10 cases the thoracic appendages of barnacles were found, but these all occurred in a single species, viz. C. cottoides. These appendages were all solid and fresh, and did not appear to be casts, so it seems that C. cottoides has the rather unpleasant habit of biting off the limbs of barnacles as these are protruded out of the shell into the sea. Other animals found among the stomach contents of these fish were small specimens of the sea-urchin Paranichinus angulosus in two specimens of C. superciliosus and one of C. dentex and in one case a leg of the crab Plagusia charbrus.

Other species of the permanent component examined, though the specimens whose stomachs were not empty were not sufficient in numbers to add to this list, showed no difference from those already mentioned, and amphipods, isopods and molluscs predominated in their stomach contents.

The four species dealt with here are fairly typical of the zone as a whole, and the three Clinid species indicate well the

relative difference in the feeding habits of the genus Clinus and the genus Myxodes, the former having a much more varied diet than the latter which, with sluggish habits and gape mouth, is specialised to an environment where the prey is abundant though not varied, consisting solely of amphipods and isopods. The food of the four species as a whole as represented by the 62 specimens listed is analysed graphically in Fig. 1a, and it is probable that the same proportions of food is to be found in any other cross-section of the permanent component. The proportions of various types making up the food of each individual species, as shown in the list, is graphically indicated in Fig. 1b-e. If the food histories of all the species making up the permanent intertidal fish population were known and washed out the results in general, would probably be very similar to these, with the only exception the fact that Gobius rudiens is known to eat seaweed on occasion.

a) The Size, Habits Etc. of the Prey.

In general the size of the animals eaten varies with the size of the fish. This is partly due to the size of mouth and stomach of the predator; while the mouth is large the stomach is relatively small. It is probably due to a greater extent to the fact that larger prey, especially in the case of fish and molluscs, is too difficult to catch in the one case and too difficult to remove from the rocks in the other, for a fish of a given size. Of the fish that were eaten one C. superciliosus 62 mm in length

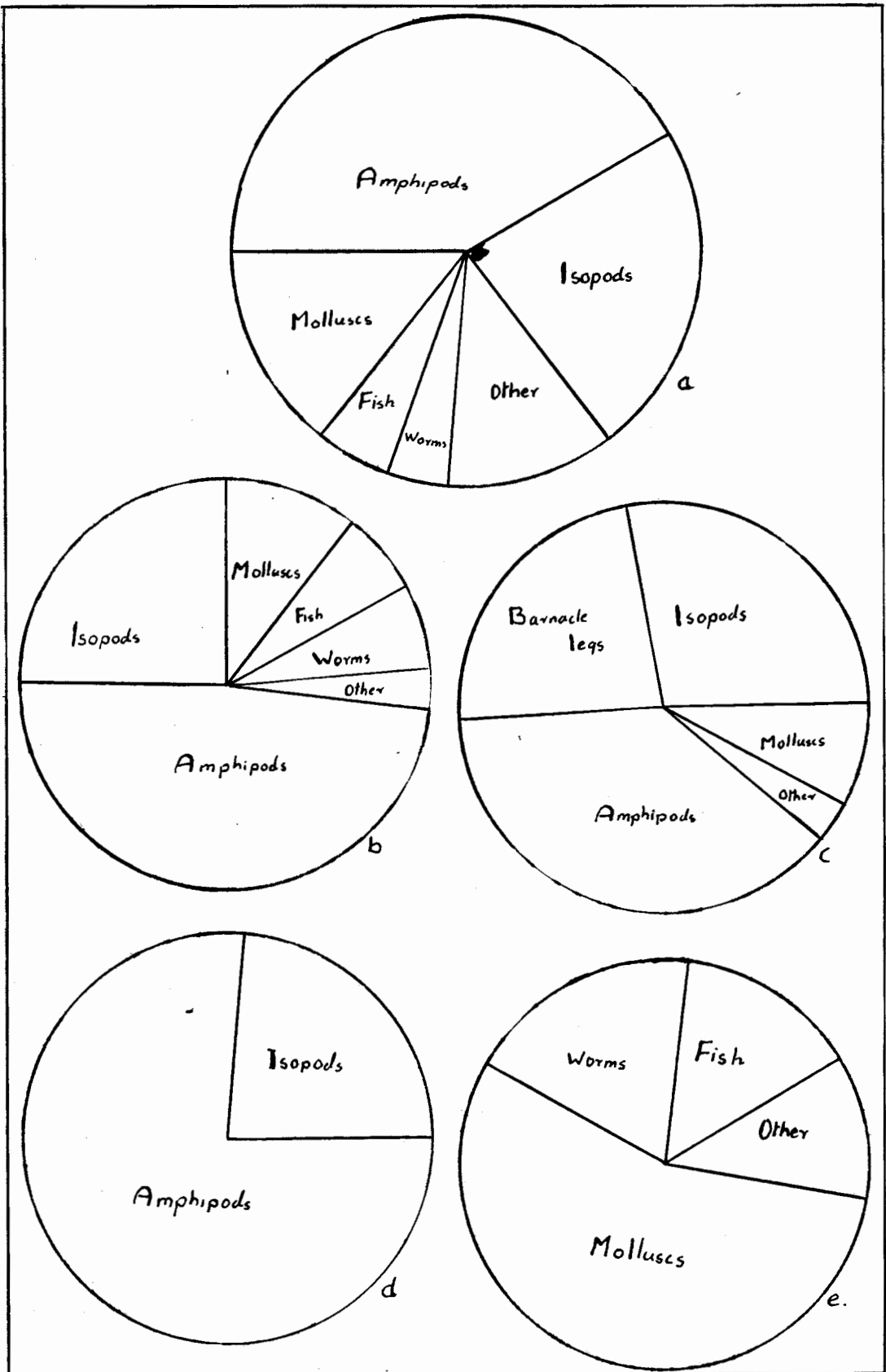


Fig. 1. The relative proportions of the food eaten by four typical intertidal fish. a) Analysis of the four fish as a whole; b)... e) analyses of the food of *Clinus superciliosus* (b), *C. coltoides* (c), *Myxodes mus* (d), *Chorisoichismus dentex* (e).

was found inside another which was 189 mm in length, the only case of cannibalism found. Another Clinus superciliosus 95 mm long contained two small Mugil sp. 32 and 28 mm in length. A B. cottoides caught on the same day, measuring 91 mm, contained on Mugil sp. 28 mm long. Finally a Chorisochismus dentex, 224 mm long, contained two Muraenoclinus dorsalis each about 40 mm in length.

The staple diet of C. dentex appears to be molluscs, which are usually swallowed whole with the shell uncrushed. They are usually limpets of small size, the largest being ^aSiphonaria deflexa 14 mm long. It is probable that this fish, though it has fairly strong teeth, has difficulty in removing limpets of larger size from the rocks. The largest limpet found in other fish was three specimens of Diodora mutabilis 12 mm long found in a Clinus superciliosus 168 mm in length.

Only five worms were found among the prey of the fish listed, four being found in Clinids and in Chorisochismus dentex. Of the five worms caught two were errant forms, one being Platynereis dumererili. The other three were tubicolous forms, including one Gunnarea capensis found in the sucker-fish. Occasionally a worm of some length was found to have been swallowed, such as a nereid, possibly Platynereis, of 69 mm length, which was found in an ^{Clinus} Syngnathus acuminatus of total length of 86mm. This was of course possible because the worm was coiled up in the stomach in a manner impossible for a fish or a gastropod.

Sea-urchins were found only on three occasions and ^{all} both

were very small, the largest measuring 7 mm in diameter across the disc.

In general, with the exception of normally small forms such as amphipods, most of the animals found to form the food of the permanent component of the intertidal fish were juveniles, and the smaller the fish the smaller was its prey. Juvenile specimens of Myxodes mus and other Clinids were found to have the stomach packed with tiny amphipods, most of microscopic size.

(11) The Temporary Component

Not so much data on the feeding habits has been accumulated with regard to these fish. All the Sparids caught classified when adult as omnivorous, have been found in their juvenile stadia to be chiefly vegetarian, as far as could be judged from their stomach contents, since these were invariably packed with sea-weed, some species of Ulva predominating. No form of animal life was found in these stomachs, although these little fish bite eagerly at the flesh of Pyura stolonifer^a and molluscs if this is thrown among them in a rock pool. Two specimens of Tachysurus feliceps, however, 92 and 95 mm long, were found to contain numerous small amphipods and isopods, and in the smaller the unrecognisable remains of a segmented worm. No trace of algae was found in their stomachs.

4. Zonation.

Stephenson(1936) discussed the zonation of limpets and Bokenham and Neugebauer(1938) wrote a paper on the zonation of cer-

tain gastropods, but nowhere during the intertidal coastline survey is any reference made to the vertical distribution of intertidal fish with the exception of Eyre(1939) who gave the subject brief mention. She wrote:

"The channels and rock-pools at St. James are abundantly supplied with small fish. In this survey little attention has been given to them, but so far as I have seen, three species are commoner than others, and exhibit a certain zonation. The mottled Gobius nudigena frequents shallow sandy-floored pools, inshore or at fairly high levels; the variegated Clinus superciliosus occupies pools at lower levels; and the sucker-fish Chorisochisma dentex is often to be found adhering to rock surfaces in the lowest regions." (p.299).

Eyre was right; at low tide a definite zonation can be observed, not only of the three fishes that she mentions, but also of most of the other members of the permanent component of the intertidal fish. To some extent only the upper limit of vertical distribution can be observed: C. superciliosus, although it is to be found at "lower levels" as indicated by Eyre, also occurs at low tide mark and to some considerable distance below. It is not known where the lower limit of vertical distribution is for this species, but it has been seen at a depth of 12 feet below extreme low water of spring tides and very probably occurs still deeper than this. This species, incidentally, appears to have a wider range of vertical distribution than any other member of

this component.

The vertical distribution is also linked up to some extent with the habitat preferred by different species. For instance, the two fish Clinus dorsalis and Clinus capensis are found only under stones and among coarse gravel and broken shells in the bottom of pools, and specimens of this fish occur in pools which offer this type of shelter even though the pools may be situated quite high up the shore. Since shingle of this nature is commonly cast by wave action fairly high up the shore, and pools in the Cochlear and below have a bottom composed either of solid rock or with one or stones large enough not to be affected by waves, it follows that these fishes are most commonly found in the Balanoid zone, where a substratum most to their liking is most generally found. The lower limit of the vertical distribution of C. dorsalis appears to be a little higher than is that of C. capensis, which has also been found in the upper Cochlear, but not lower. It is stated (Smith 1949) to occur also in deeper water.

In the third place, it has commonly been found that the upper limit of distribution of a species is likely to contain a bigger proportion of younger fish than the areas lower down. The whole area does contain adults of the species but these are most plentiful, relative to the amount of juveniles present, lower down the vertical range of species. This is especially noticeably in species with a wide range of vertical distribution, such as Clinus superciliosus. Most of the largest specimens of this species frequent the sublittoral, or deep weedy gullies and

channels at low tide mark, ready to slip into the sea if danger threatens.

The following is a brief account of the zonation which was found to occur with sixteen different species belonging to the permanent component of the intertidal fish, starting with the pools highest up the shore. It must again be remembered that this position applies at low tide only.

A graphical idea of the position is given in Fig. 3 for 16 of the fish. The graphs for three of the fish, namely Myxodes heterodon, Clinus venustris and Clinus brevicristatus, are based on records of one specimen only, and therefore cannot be regarded as definite. It is unlikely, however, that the fish habitually occur higher up the shore than the localities given. The highest point at which Clinus robustus was found is given; this species was not again found in the intertidal zone but has been caught several times from the sublittoral.

It can be seen from the graph that the highest occurring fish is Gobius nudiceps. This fish occupies all pools in the Littorina zone which are periodically refilled with sea water, even though these may not be reached (except by splash) by the high water of neap tides. Occurring nearly as high as Clinus cottoides, but the lower limit of this fish occurs slightly lower down, in the lower Balanoid, but it reaches its greatest abundance in the lower Balanoid and continues downwards in numbers throughout the intertidal zone. Clinus capensis and Clinus dorsalis is

The uppermost limit of Clinus superciliosus is in the upper Balanoid,
are found only slightly lower down, but, while C. dorsalis

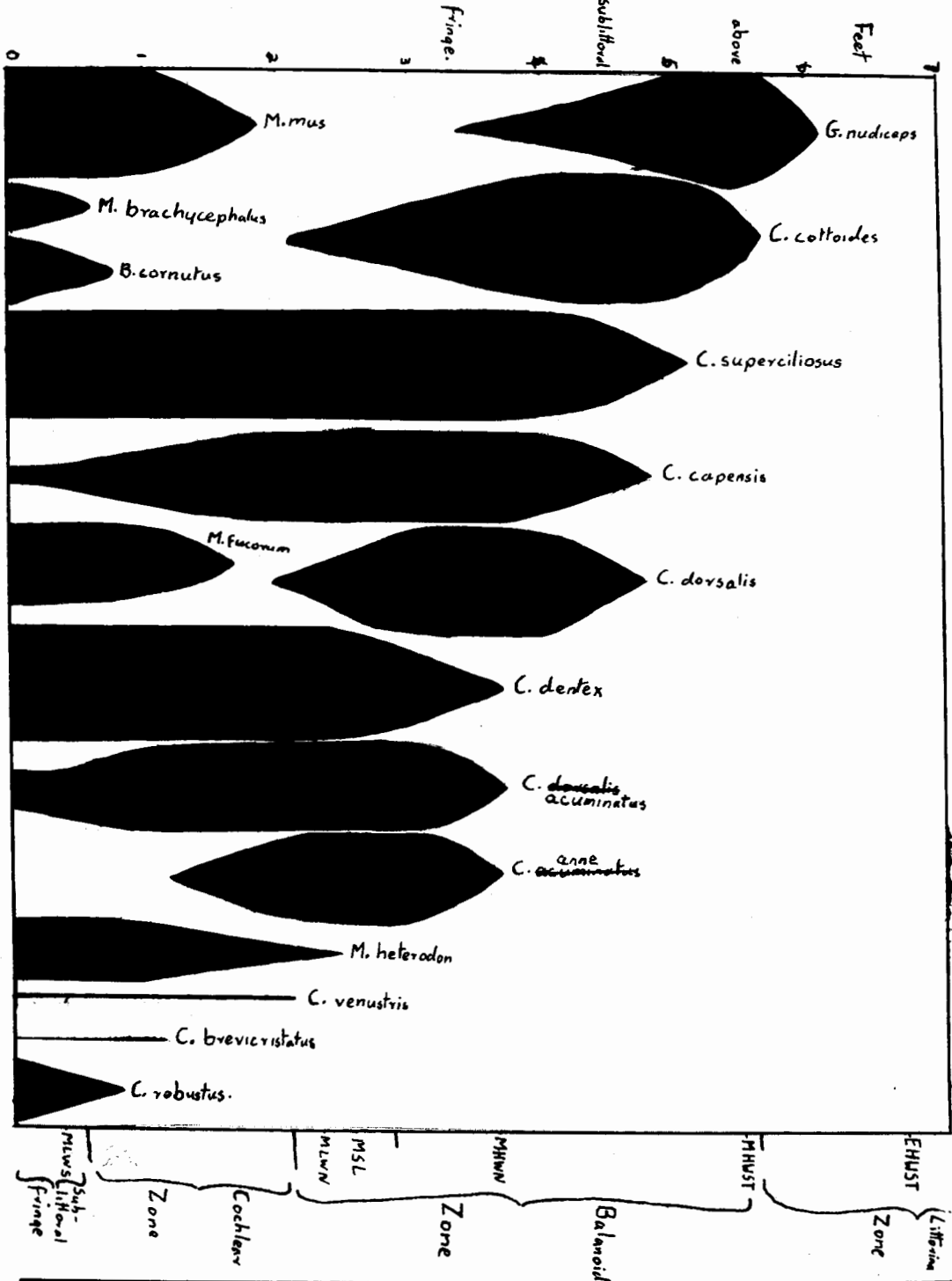


Fig. Zonation chart of 16 intertidal fish. Tide levels from Bokenham, et al., 1938.

considerably more abundant in its zone, C. capensis has a greater vertical distribution. It has never been found below the upper Cochlear in this survey, but its range has been extended into the sublittoral following observations by Smith (1949). Chorisochismus dentex occurs next highest on the shore, but this suckerfish is uncommon until the Cochlear is reached, where it occurs with uniform abundance to the sublittoral. Clinus acuminatus and C. anne are frequenters of the mid Balanoid to upper Cochlear regions, chiefly in the flat, shallow sandy-bottomed pools of the Balanoid at Sea Point, though C. acuminatus has been found below this.

The fish next in order after this are all fish of the Cochlear gullies and below, seldom occurring except where the lower end of their pool or channel is open to the sea, and most abundant on the seaward side of ledges of rock in the sublittoral fringe, they all occur also below this level in the sublittoral, so that their lower limits of distribution cannot be determined. The highest of these is Myxodes heterodon, specimen of which was found in an upper Cochlear pool. The most abundant of these is Myxodes mus, which is commonly found in the Cochlear and below. Myxodes mucorum and Clinus brevicristatus have also been found fairly high in the Cochlear, but Clinus brachycephalus, Blennius cornutus and Clinus robustus have only been found in the sublittoral fringe.

As has already been mentioned, the zonation of these fish in practically all cases closely bound up with the habits of the fish

and the habitats it frequents, and this aspect of the ecology of the intertidal fish will be discussed in the next section.

IV. The Ecological Position of Fish in the Intertidal Zone.

1. Habitats.

The fish of the permanent component of the intertidal zone have shown themselves to occupy a variety of different habitats comprising almost every imaginable type of ecological niche. There are at the Cape no species which hop or skip out of water or which are commensal in Holothurians or other animals, otherwise the list would be complete.

The highest pools in which fish life occurs are populated solely with G. nudiceps; these pools are bare and rocky, with a bottom either sandy or consisting of stones of various sizes. Very large gobies are found only in those pools where adequate shelter is provided by caves and spaces under large rocks. If such pools are of good size and fairly deep a population of B. cottoides and C. superciliosus may occur with the gobies, particularly if the pool extends down into the Balanoid. These three species inhabit the underwater caves and rocky crevices at the sides of the pool or of large rocks in the pool. If the pool is floored with a mass of broken rock, small stones and coarse shingle, C. dorsalis will occur in large numbers, the eel-like body of this fish coiling up comfortably in this habitat, slightly lower down the shore C. capensis occupies the same habitat, but this fish has never been observed in the same pool as G. nudiceps, though Clinus cottoides, C. superciliosus and

have, these four species often occurring together in a rocky upper Balanoid pool.

Of the 5 species mentioned, G. superciliosus and G. cottoides also frequent the rocks under weed; the other three seldom occur near weed, and have colours to resemble rock not weed. Where G. superciliosus and G. cottoides occur in weedy pools they are often camouflaged with brown and olivegreen patches so that they are difficult to see among the algae. They do not however, live among the algae as other of these fish do, but in this environment their home is on a ledge or in a crevice in the rock with the seaweed growing over the rock or crevice and concealing them. Thus the habitat of these fish is always basically rocky; they either shelter under the bare rock or live on the rock sheltered by sea-weed. They are the true "klipfish" of the Cape coast.

Another type of rocky habitat is used by Chorisochismus dentex, the suckerefish, which clings on to rocky faces by means of its powerful ventral sucker. This sucker is sufficiently powerful to prevent its being dislodged by the most powerful waves and thus it is often found adhering to the naked rock in the lower intertidal zones. In these cases it is wonderfully camouflaged with mottled brownish colours to resemble its substratum. This fish also sometimes found in pools under sea-weed but again the algae is merely incidental to the pool and fish is always adhering to the rock beneath. In the lower wave-washed area a suckerefish is often washed on to a rock by a wave, where it clings for a while, finally returning to the sea by another wave/^{or} dropping off from the rock back into the sea. It can live for a long while out of the water, as much as the interval between two tides (Smith 1949).

Other fish which live in chiefly rocky habitats at points from the lower Balanoid downwards are Clinus acuminatus and

C. anne, and to a lesser extent as seen in this survey, Blennius cornutus and Clinus robustus. The two first mentioned are quite often found among stones at the bottoms of pools or in sandy pools along the West side of the Peninsula. The last two are inhabitants of deeper water, but it is probable that they, too, live among rocky environment.

The other members of the permanent component are forms which live among weeds, frequently at some distance from the rocks, provided that the algae is thick enough to conceal them adequately. They are the most brilliantly coloured of the Cape intertidal fish and often have transparent patches in the fins to enable them to resemble sea-weed more efficiently. They are usually very sluggish, and live almost exclusively on those very small animals which abound in the sea-weed which they frequent, such as amphipods and isopods. As far as their vertical distribution is concerned, they are exclusively to be found in the weedy pools, channels and ledges of the Cochlear zone and sublittoral fringe.

Such fish, at the Cape Peninsula, are Myxodes heterodon, ^{Myxodes} ~~Tucemius~~ mus, Myxodes fucorum, ^{Clinus} ~~Petrastes~~ brevicristatus and Myxodes brachycephalus. Only one specimen of Myxodes heterodon (syn. Clinus graminis) was found in a pool in the lower Cochlear containing chiefly Hypnea spicifera. Gilchrist and Thompson (1910-, however, record this species as to be found "in weedy tidal pools, especially those in which the green, 'sea-grass'

occurs." (p. 222). The green "sea grass" referred to is probably Caulerpa ligulata. This species was found to be very agile. Myxodes mus lives almost entirely among the fronds and branches of Laurencia glomerata, and is also found among Gigartina radula and other Gigartina species. When removed from these its colour was found to resemble the alga in every detail. Gigartina and Laurencia is very abundant around low tide mark, Laurencia species extending to well below low tide mark, and apart from the above species, Myxodes fucorum and Myxodes brachycephalus were found among it. Myxodes fucorum has also been found sheltering in the fronds of Sargassum longifolium. M. brachycephalus has been found in Gigartina beds in the sublittoral fringe.

It can thus be seen that among the permanent intertidal fish populations there exist a wide range of different habitats. It is well known that in any biocoenosis there exist a number of different biotopes which are normally all occupied and for which there is normally a good deal of competition. In the biocoenosis of the sea shore the fish form a distinctive though by no means an entire part of the population. While it was not possible in this survey to go into all the biological factors affecting the ecological position of the fish their position as intermediates, forming both predators and prey, is interesting and may be remarked upon.

2. Predatory Forms.

In principle, these intertidal fish form an intermediate

group, preying upon smaller animals in the intertidal zone and themselves being preyed on by larger forms, not belonging to the intertidal zone proper, but coming in from the deeper waters off-shore when the tide is high.

It is probable that most of the intertidal fish, and particularly the Clinids, are eaten by bigger fish and birds when opportunity arises; the duikers (Phalacrocorax) are stated by Biden (1930) to eat klipfish on occasion, and no doubt they are the prey of other sea birds as well. Many fish feed on Clinids; Biden (loc. cit.) states that one of the best baits for the Red Steenbras (Petrus rupestris) are klipfish such as Clinus superciliosus.

The Clinids and other intertidal fish are themselves predators of many smaller animals, as has been seen, and as they are very numerous they must be a very important element in the control of the numbers of their chief food animals, i.e., amphipods and isopods, and of many of the other small animals of the intertidal zone. They are probably the chief predators of amphipods and isopods, since these appear to be the staple diet of all juveniles of these species with the solitary exception of Gobiosochismus dentex. They form a large percentage of the food of most of the adult fish, while the adults of Myxodes species, such as Myxodes mus and Myxodes fucorum, appear to eat practically nothing else.

In this respect it is probable that the protective coloration

so characteristic of these little fish serves two purposes, that of concealing the fish from its enemies, which are numerous and varied, and also of concealing it from its food. In the case of Myxodes mus for example, the fish lives among the branches and fronds of sea weed and it is so skilfully camouflaged that it must appear to be a part of the weed not only to large fish and others enemies constantly in its vicinity in the sublittoral, but also to the very numerous amphipods and isopods that crawl on the algae and which form the almost exclusive food of this species. (Fig. 1d).

The most abundant single species of intertidal fish in the Balanoid zone is probably the rock-frequenting ^{Clinus} Blennioides cottoidea, and since over a quarter of the food found in the stomach of this fish consists of bitten-off barnacle legs it is likely that this species exerts a considerable influence over the numbers of barnacles present, and must be one of its chief enemies, as, even if the barnacle does not die from shock or starvation before the legs are regenerated, its normal activities such as rate of reproduction and rate of growth must be considerably retarded.

Perhaps to a lesser degree the sucker-fish and larger Clinids have some influence over the numbers of gastropods in their area, and Clinus superciliosus and ^{Clinus} Blennioides cottoidea must be added to the already numerous predators of juvenile mullet and other young fish.

Lateral Distribution.

Some remarks on the lateral distribution of the intertidal fish found in this survey are in place here, since this distribution is of interest in two respects. First, the question arises as to how the distribution of the intertidal fish, the permanent component of this paper, fits in with what is known about the lateral distribution of the intertidal fauna. Secondly, it has been shown in Part II of this paper that the Clinidae, forming a major portion of the Cape intertidal fish, are clearly divided into ecological sub-genera, the question arises as to whether there is any geographical replacement of species groups (Artenkreise) or of subspecies (Rassenkreise). A great deal more, however, has to be known about the relative abundance of individuals of different species, and of the ecology of intertidal fishes, before these questions, particularly the second, can be answered with accuracy. As Stephenson, (1944) points out, the extreme distribution of a species does not give a complete idea of the ecological effectiveness of the species, since this effect will be greatest where the species is most abundant, and, as it dies out towards the end of its range, a few individuals of a species may be recorded from a locality but its ecological effect on the population as a whole at that point will be negligible. Its place in the ecological scheme of things will have been taken by another species. Further, the study of a number of species in one area gives no idea of their distribution round the coast, so that this paper, dealing entirely with the Cape Peninsula, is almost useless from

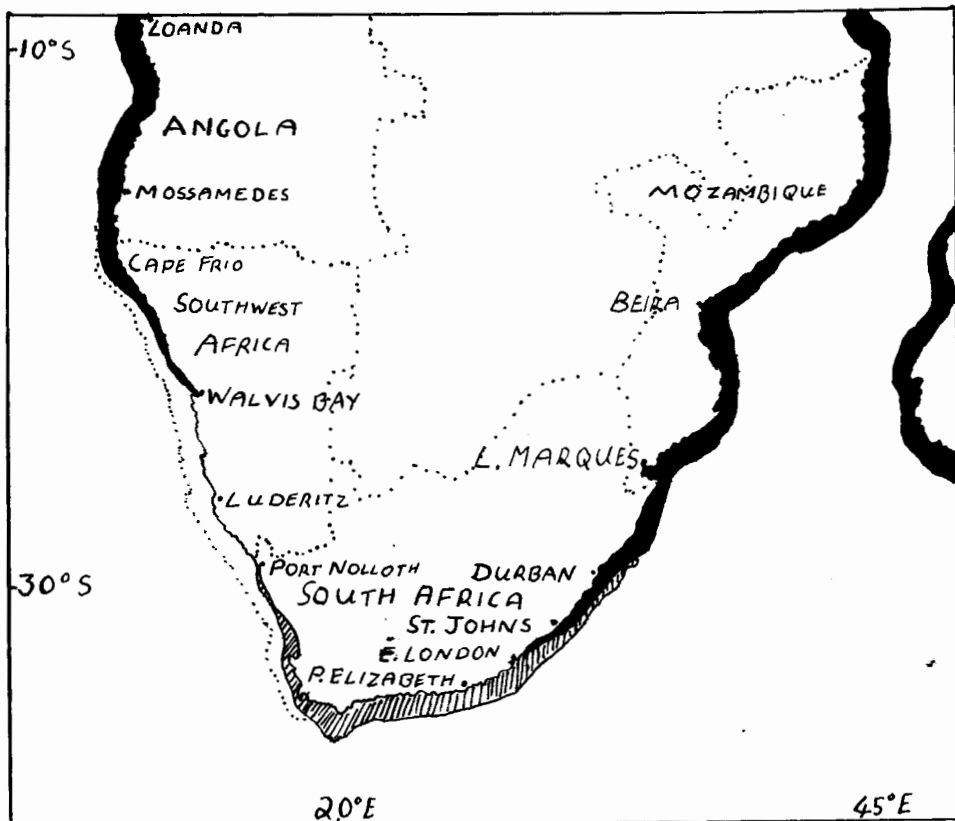


Fig. A map of Southern Africa showing the approximate distribution of the coastal faunas. The two tropical faunas are shown in black. The cold-temperate fauna is surrounded by a dotted line; the warm-temperate fauna is shaded. After Stephenson (1967.)

the point of view of the lateral distribution of the intertidal fish. However, some remarks can be added to the observations already made on the subject.

As a result of the extensive work done on the intertidal region of the South African coast as a whole, Stephenson (1947) arrives at the result that the intertidal population may be divided into four regions (Fig. 4):

- 1) A subtropical population of Natal, including many Indo-Pacific species from the North, and a few endemics. This section goes down the coast almost as far as East London.
- 2) A warm-temperate section of the South Coast, overlapping the first section to the North of its range, and with its purest form between Cape Agulhas and Algoa Bay. Some representatives occur on the South-West side.
- 3) A cold-temperate section with its headquarters on the South-West coast, finally overlapping on the tropical West African fauna, and extending in diminished form East of the Cape approximately to Cape Agulhas.
- 4) A certain number of species occur round the whole coast and are thus common to all three of the above populations.

The intertidal population of the Cape Peninsula occupies in many ways an intermediate position. The western part in the main belongs to category 3, which also is well represented in False Bay to the East of the Peninsula. Warm-temperate species are also to be found in False Bay, particularly in the North-Western corner

of it, between Muizenberg and Kalk Bay, which, because of winds and currents, has a higher average temperature than the rest of the bay (Issac 1937a). Here the cold-temperate forms receive a severe check and warm-temperate species are found. Here also was done most of the collecting of fishes during the present survey.

Smith (1946) has collected Clinids and other intertidal fish very extensively round the South African coast, and the very valuable results from this work have been commented on by Stephenson (1947), who show how well the lateral distribution of the Clinidae agrees with the above concept of the South African intertidal region. Further work by Smith (1949) has modified the 1946 position to some extent and the data of Clinid distribution as given by Smith (loc. cit.) is: 8 are known from short stretches of coast only (mainly South-East coast); These are: Clinus brevibristatus, C. agilis, C. helenae, D. latipennis, Myxodes stella, Gynuteclinus rotundifrons, Clinoporus biporosus and Xenopoclinus kochi. During the present work it has been found that Clinus brevibristatus: previously only known from False Bay occurs also in Table Bay. 2 occur solely in the cold-temperate zone, viz, Clinus anne and C. acuminatus. 3 are subtropical, namely Clinus woodi, Myxodes mentalis and M. laurentii. Of the remainder 3 occur almost right round the coast and thus belong to category 4. These are Clinus superciliosus, C. dorsalis and Myxodes heterodon. The remaining 12 belong to the South-East component, namely:

Clinus capensis, C. navalis, C. anguillaris, C. striatus, C. taurus
C. cottoides, C. robustus, C. venustis, Myxodes brachycephalus
M. fucorum, M. mus and M. pavo.

When these Clinid distributions are examined as a whole, this being incidentally greatly facilitated by the excellent distribution chart given by Smith, some interesting general facts become apparent. Smith (1947, 1949) that the Clinidae came to South Africa as a result of invasions from the South and South-west, during a colder geological age than the present. While this supposition is probably correct, the present day South African Clinidae have undoubtedly colonized the warm-temperate and warmer coasts rather than the colder South-west coast. Of the 20 widely distributed species 12 belong to this warm temperate fauna, as against only 2 cold-temperate forms. 3 are ubiquitous and 3 sub-tropical. Of the 8 known from short stretches of coast only one (Xenopoclinus kochi) is found in the cold water to the West of Cape Point, all the others being found around the Cape Peninsula or well to the East of it.

Another interesting point is that the trend in the genus Myxodes is towards the tropical. Only one of the 8 members of this genus penetrates to the West past Cape Point; this is Myxodes heterodon which has been recorded from Port Nolloth (Smith 1949) It is significant that this fish has also the greatest geographical range of any South African Clinid, being found also beyond Lourenco Marques. Unfortunately little is known about its relative abundance at any point. I have not found it common in

False Bay and have never taken it in Table Bay. Its "headquarters", to borrow an expression from Stephenson are probably along the East coast. Two Myxodes species, M. mentalis and M. laurentii, both in the subgenus (Labroclinus), are subtropical category 1 forms, while only one Clinus species, (C. woodi) is known to have penetrated North of Durban.

Thus the South African Clinidae are mainly cold-temperate forms, extending to a small extent up the West coast and to a greater extent up the East Coast, particularly in the case of the genus Myxodes. None are recorded from Beira, the reason probably being that penetration into the tropics becomes increasingly difficult as increasing competition from Indo-Pacific intertidal forms such as Blennies and Chromids, is found.

The replacement of one species by another in the same ecological niche within the range of the Clinidae probably occurs to some extent, but insufficient is known about the ecology of the group for any definite pronouncement to be made.

With reference to the non-Clinid intertidal fish found during the survey, namely Chorisochismus dentex, Gobius nudiceps and Blennius cornutus, these are all endemic species and are widespread, belonging to Stephenson's 4th category. They have all be found from well up the West coast right around to Durban and beyond (Smith 1949).

PART II. A Generic Revision of the Family Clinidae.

Introductory.

The Clinidae have recently been systematically revised by Smith (1946), who, by a study purely of the morphological differences exhibited by the various species of the group, has divided them into a number of different genera. The separation of this highly specialised family of littoral fish into such a large number of different genera is, in my view^{un} justified.

It is unnecessary in that the polymorphism exhibited by every member of this closely related group is so wide from species to species that most of the differences are not worthy of generic distinction. As Norman(1931) puts it: "The value of a particular morphological character, whether it be the form of the fins, the structure of the scales, or the colour pattern, differs enormously in different families or orders, and a character which serves to distinguish two species of, say, Cyprinids, may be of sufficient importance to separate two genera of Cichlids." (p. 367). As I shall show, the only morphological characters of generic importance link up extremely well with the ecology of the group, and form a broad natural cleavage within the family into two main genera, with the exception of one or two rare and little-known species.

Fine generic splitting is also unjustified because it tends to minimize the natural relationships which exist between various groups of animals. The science of systematics has a very real

importance apart from its classificatory value, which is to indicate the relations between animals. This is of extreme importance in ecological, physiological, genetical and evolutionary aspects of biology. To discover that two obviously very closely related animals have two entirely different specific names adds difficulties to workers in these fields, who, by the nature of their work, cannot expect to have specialist knowledge of all the animals with which they have to deal. This point will be returned to later.

Earlier Generic Differentiation.

The Glinidae have not been neglected by systematists. During the past forty years no less than three attempts at classifications the South African members of the group have been made, none of which are entirely satisfactory. The reason for this lies in the fact that they are among the most polymorphich of fishes, and that hitherto very little has been known of their ecology. Very similar in the main, they possess nevertheless a host of minor differences in their external features which makes them a very puzzling group to deal with systematically. The number of dorsal spines, for instance, ususally so very constant within genera and even families, here varies to such an extent even between individuals of the same species as to make it quite useless characteristic on which to base generic differences. The same applies to scale counts, relative body measurements, numbers of anal and dorsal rays, teeth, the presence of absence of a dorsal crest and lateral line details. All these vary so

much in our 28 species that they cannot individually be taken to represent differences of generic rank.

As a result of this bewildering morphological complexity of the Clinids the history of the systematics of the South African group has been one of the progressive splitting of the species into more and more genera. The first systematic description of the South African forms, that of Gilchrist and Thompson(1908), ignored genera proposed by earlier workers, such as Cirrhibarbus Cuvier(1817) and Petraites Ogilby(1885), and grouped them all in the genus Clinus Cuvier(1817) of the family Blennidae, with the single exception of Cristiceps mentalis, which they separated as Cristiceps Risso on account of the crest formed by the first three dorsal spines.

The separation of the group into a family away from the Blennidae, well justified by the structure of the teeth, and the viviparity of the Clinidae as distinct from the oviparity of the Blennies, as well as other features, was done by Barnard(1927) who divided the Clinidae into three genera and grouped them, with three less closely related genera, into the family Clinidae. The three latter genera have been quite justifiably been given family rank by Smith(1949) and do not concern the present discussion. Barnard's three Clinid genera were: Clinus Cuv., including most of the forms, Petraites Ogilby, including three crested species, and Clinoporus Barnard(loc. cit.). Barnard created this latter genus to accomodate Clinoporus biporosus(G & T), with a lateral

line of alternate double pores. Barnard removes Cristiceps mentalis G. & T. into Petraites, which he remarks is "scarcely distinct from Clinus." He makes a point, which will be mentioned again, that the membrane from the 3rd spine reaches the base of the 4th; it is therefore questionable whether the crest can be described as really separate from the rest of the fin. In Cristiceps the first three spines are clearly separate from the rest. His genus Clinoporus, based on lateral line differences, appears difficult to uphold considering the variety of form to be found in the lateral line of other species placed by him all in the one genus Clinus. As Smith(1937) remarks there are grounds for generic distinction between Clinid species at least as valid as those accepted by Barnard for genera such as Clinoporus and Petraites. In my view all these grounds merit subgeneric distinction at the most. Barnard later(1935) placed a newly discovered species(Climacoporus navalis Barnard) into a new genus (Climacoporus) also by virtue of lateral line differences.

The group was again revised by Smith(1946) who has differentiated 28 South African species about the validity of which there is no question. Smith makes the point that Barnard's 4 genera are arbitrarily defined that there are other genera equally as valid which have been neglected by him. Smith revived 5 genera proposed by older workers, namely: Cirrhibarbus Cuvier (1817), Blenniopsis Swainson, (1839), Ophthalmolepis Gill (1860), Blennioclinis Gill (1860) and Myxodes Cuvier(1829), out of the

50 odd genera that have been proposed for this family in the past (Jordan 1923), and proposes 7 new ones of his own. The seven new ones are: Muraenoclinus, Blenniomimus, Eucomimus, Labroclinus, Pavoclinus, Gynutoclinus and Xenopoclinus. Adding Barnard's 4 genera to this total, Smith thus subdivides the 28 species of the family into 16 genera, of which no less than 8 are monotypic.

The characteristics on which Smith bases his generic differences do not appear to be as clear-cut as he assumes. While certain groups in the family may fall together to some degree, such as similarity of body shape or the presence of a crest or incised membrane, these differences do not appear to be of generic rank, but to be at most sub-generic, because such variations are in small morphological details, not consistent through the group, and not as important as the morphological and ecological differences that divided the family into two main groups. This is the more striking when the family is examined as a whole, when their fundamental similarities are at once obvious. Such differences as the possession of a dorsal crest are progressive from one to the other throughout the group. The matter of the dorsal crest is really a question of the elongation of the first three spines and/or the depth of the incision behind the third spine. At the greatest depth of the incision the first three spines are separate from the rest of the fin; the best example of complete separation in our Clinids is seen in the new species Xenopoclinus kochi. In other species there is such variation between complete separation and

different degrees of connection from species to species, such as in Clinus robustus and Clinus superciliosus, Ophthalmolophis latipennis, O. anne and O. agilis and Blenniomimus taurus and B. cottoides, and indeed between individuals of the same species, such as Clinus superciliosus, which possesses so variable a crest as to induce Gilchrist and Thompson to differentiate one type of crest as a new species (Clinus ornatus), that this should not in any case be taken as being of generic significance. There are no consistent morphological differences throughout the group save only to, the presence of absence of an orbital tentacle and the size of the mouth, whether broad, with relatively massive jaws, or narrow and frail with relatively delicate jaws. A few examples from Smith's general will illustrate this.

For example, the genus Cirribarbus was held to be generically distinct by Cuvier because Cirribarbus capensis possesses barbels round the mouth, but it agrees so closely with other Clinidae in other respects that this feature alone is not of generic value. Labroclinus mentalis has a long skinny flap on the lower lip, which differentiates it from Labroclinus laurentii but Smith has correctly not considered this to be a generic difference between these two species. In the same way, the barbels of Cirribarbus capensis are also not of generic importance, when the similarities between this fish and other Clinus species, such as Blenniophis anguillaris, Clinus superciliosus and Muraenoclinus dorsalis are considered.

The characters of the genus Clinus Cuvier as given by Smith (1946) are: "A tentacle over the eye. A marked anterior crest in dorsal fin, not detached, the membrane between the 3rd and 4th spines incised. Genotype Clinus superciliosus (Linn.)"

This description could apply equally well to Blenniomimus taurus. The lateral line in B. taurus and Clinus robustus agree very well. The crest mentioned is very marked (though very variable) in Clinus superciliosus, but is not developed to nearly the same extent in Clinus robustus. A specimen of the latter in my possession, 15 inches long, has scarcely any crest, a small incision in the membrane only being present, as it is in Blenniomimus taurus and in numerous other Clinid species. For instance, Ophthalmolophis anne possesses a well-marked incision, while O. acuminatus has none. The supraorbital ridge is at least as strongly developed in Clinus robustus as it is in the Blenniomimus cottoides, yet it is mentioned as being of generic importance in the genus Blenniomimus, but ignored in the specific description of Clinus robustus. In the massiveness of the head Clinus robustus resembles Blenniomimus species far more than it does Clinus superciliosus. Again, the 3-rayed ventral fins of Clinus robustus is found also in both species of Blenniomimus, never in C. superciliosus. In spite of all this, the resemblance between Clinus robustus and C. superciliosus are so marked as to induce Smith to put them into the same genus and Blenniomimus taurus and B. cottoides into another. The habitat of all four

species is identical, though each species varies in its zonation on the shore and its lateral distribution. In my view the differences between the four are not worthy of differentiation into two separate genera.

The genus Muraenoclinus Smith is separated from Blenniophis Swainson only because the latter possesses scaly cheeks and the former has only one dorsal ray. Though these differences are constant they, considering the polymorphism of the group, scarcely warrant generic rank. The habits of all three species of both genera, living under stones and amongst rubble at the bottom of pools, are identical. The genus Blenniophis as originally described by Swainson(1839), for Blenniophis anguillaris, viz: "Oviparous, anguilliform; body lengthened, subcylindrical; dorsal and anal fins low and equal; profile nearly rectilinear; head crested; teeth velvet-like, the exterior strongest, dorsal fin attached to the caudal, which is rounded; ventrals of 3 rays nearly as long as the pectorals." (p. 276), fits Muraenoclinus dorsalis just as well as it does Blenniophis anguillaris and B. striatus; it applies exactly to none of the three. In my view, however, there is no real justification for separating any of these forms with orbital tentacles from the genus Clinus. A progressive elongation of form can be traced through this sub-family of Smith's from the thicker and robust shape of Clinus robustus on the one hand, through taurus, cottoides, superciliosus, anne, acuminatus, brevicristatus, capensis and so on to the extreme length and

flattening of Muraenoclinus dorsalis and Blenniopsis anguillaris on the other, without being able to draw a clear dividing line anywhere. This, with the virtual impossibility of finding large, clear-cut and consistent morphological and ecological differences in the group, inclines one to the view that here we have a series of species, progressively varying ⁱⁿ matters of external shape, size of crest, etc, within a single large genus. Within this genus there may occur groups the morphological and ecological differences between which being subgeneric in value.

The same is found when examining the genera in Smith's subfamily the Myxodinae. Here again generic criteria are based on slight morphological differences. Blennioclinus Gill is separated from similar forms simply because of the fact that the dorsal rays are much longer than the spines immediately anterior to them, this being the only criterion in Smith's description of the genus which differs from other genera. This lengthening of the dorsal rays is undoubtedly very striking when a specimen of Blennioclinus stella is examined alone, but a similar state of affairs exists, albeit to a lesser extent, in Fucominus, Myxodes, Labreclinus and Favoclinus. Myxodes and Fucominus are separated only by ^{the} fact that Fucominus has 2 bands of teeth in each jaw, Myxodes only one. The only generic characteristics given by Smith are exactly identical. Both his genera are monotypic in this country. Smith mentions the existence of other Myxodes species presumably M. viridis

Cuv., in South America, but he can, with his fine splitting of genera, scarcely expect to find representatives of the same genus an ocean away when he separates two such closely allied forms living side by side. I doubt also whether the teeth differences are worthy to rank as criteria of generic significance. The teeth of Clinus superciliosus and Clinus robustus, are practically as different. According to Barnard (1927) C. robustus has "a broad row of smaller teeth behind the front row in both jaws and a broad band on the vomer", while C. superciliosus has "an outer row of strong teeth on both jaws with smaller ones behind, a curved band on vomer". Both Fucominus mus and Myxodes fuorum have no teeth on the vomer; they are the only Clinid fish with no vomerine teeth. The common lack of vomerine teeth in these two species is as valid a reason for placing them in one genus by themselves as are the maxillary teeth differences on which they are separated into two genera by Smith.

This illustrates the futility of attempting to divide the Clinidae by morphological characteristics alone. Any attempt to divide any large assemblage of the innumerable organisms of Nature into watertight compartments purely on museum characteristics must necessarily be unsatisfactory, since certain groups within that assemblage inevitably have characteristics resisting such arbitrary division based ~~purely~~ on morphological differences. Smith's monograph of the South African fishes (1949), excellent though it is in nearly every way, is unsatisfactory in this res-

pect. Though museum characteristics in most cases answer well, in some cases they do not, as for instance in the Clinidae.

The Clinidae provide a good example of relationship in a natural group; their similarities are overwhelming, and yet they exhibit a high degree of individual differentiation throughout the group. The answer to the problem is to be found by considering the group from the evolutionary aspect. They are obviously a group on which natural selection has acted and is acting intensely in separating them into special niches in their environment. This environmental pressure has resulted in the specialisation of species to different environments, often amazingly restricted. The habitat of Fucomimus mus is almost completely restricted to the fronds and branches of the algae Gigartina and particularly Laurencia; its zonation, in False Bay corresponds very closely with that of the latter weed. It is probable that the habitats of other species is equally restricted.

Environmental pressure has thus differentiated these forms into distinct and highly specialised species, occupying many biotopes on the shore. They are a group naturally divided, not into subspecies as are many birds and insects, but into groups of subgenera. Rensch (1938) has called Artenkreise those groups of species which replace each other geographically. Huxley (1940) has translated this term to mean a geographical subgenus. While our Clinids do not, as far as is known, form geographical subgenera they certainly do form ecological subgenera. They do

replace each other ecologically, each to its own habitat, forming subgeneric groups which, in turn, are united under two broad types of habitat., forming subgeneric groups which, in turn, are united under two broad types of habitat, weed-haunting forms and rock-haunting forms. As these two ecological general differences are strikingly correlated with the two major morphologic-al differences, large or small mouth and presence or absence of orbital tentacles, this appears to be an excellent generic distinction.

Some of the species will, I feel confident, be revealed by further work to possess within the specific group what Huxley (1938) has called clines, or the progressive variation of some character of characters with geographical distribution. Such a cline almost certainly exists with reference to the dorsal crest of Glinus superciliosus. Smith(1935) mentions that the crest grows progressively longer the further along the East coast the species is found. A cline relating to the dorsal crest is probably also present in estuarine forms, depending on the salinity of the habitat.

Evolution of these forms has probably resulted in the formation of subgenera in the group; all through the group certain small differences can be seen behind the obvious relationship. It is these differences that have exercised the minds of systematists, leading them to the vain attempt to subdivide the family morphologically, without reference to the ecological, physiological and genetical characters which are probably in the background. It is of

no practical use to fasten on to these differences and elevate them to generic importance. As Huxley (1940) puts it.

"The all-too-common practice of splitting genera until many are ^{no}typic defeats one of the main aims of Linnaeus' great invention. The subgenus..... is the proper category for such detailed classification. We thus should normally recognise as our ideal a quadrinomial system. Genus and species will be the categories normally used by the general zoologist, while subgenus and subspecies are needed for full accuracy and are essential for certain purposes. Subgenera indicate affinities of species within genera, while subspecies define geographical or physiological differentiations, and are all-important for certain studies, including genetical and ecological analysis as well as zoogeographical and faunistic problems. As already noted, for certain special cases a further supraspecific category would appear to be desirable." (p. 26)

The Present Generic Differentiation.

Physiologically and genetically, nothing whatever is known about the group. What ecological knowledge there is has been summed up earlier in this paper. The Clinidae are obviously a group upon which natural selection has acted relatively recently, because of the comparative slightness of the differences of the differences between these closely related forms, and strongly, because of the high specialisation of form and habit to definite ecological niches found among them. Bearing in mind their essen-

resemblances rather than their essential

tial differences, I propose to group most of the Clinidae under two genera, Clinus and Myxodes, both of Cuvier.

Clinus will include all forms which have an orbital tentacle. These are rock-haunting forms, and all their habitats are fundamentally rocky, though of different types. Some, such as Clinus superciliosus, C. robustus, C. taurus and C. cottoides, live on rocky ledges and in crevices in rock. Others, such as Clinus acuminatus, C. anne and C. brevicristatus, live on flat rock sheltered by the weed which is above the rock. They do not live among the branches of the weed as Myxodes species do. Still others, such as Clinus capensis, C. dorsalis, C. striatus and C. anguillaris live chiefly among the small rocks, shells and other debris on the substratum. Such forms are generally elongate, with narrow heads; this is an environmental adaption to enable them to wriggle among the pebbles and shells the more easily. In the forms mentioned above we probably have subgenera, distinguished by morphological and ecological similarities in the species comprising the subgenus.

The members of this genus, in general, have large mouth with strong jaws and a wide gape; this ^{is} probably correlated with a more general habit of feeding than the other genus. Certain exceptions occur; some have less well developed jaws, but the general trend particularly with increase of size, is towards the large mouth that goes with voracity of feeding habits. The shape of the fishes is correlated with their habitat; the trend is towards concealment from above. None of these forms show the irregularity of outline, when seen from the side, found so often in the genus

Myxodes. The anguilliform species, living among shingle, often have a stripe on top of the head between the eyes as a disruptive colour pattern. The broader headed forms often have dark stripes leading from the eye to break up the shape of this organ, readily seen from above.

The genus *Myxodes* includes those typical forms without tentacles above the eye. These primarily weed-haunting forms, living, not against the rock under the weeds, as the *etheredae*, but actually in the branches of the seaweed, from which they seldom move. I was first struck by the preference of these forms to branches away from the substratum during a visit some years ago to the East London aquarium, where several *Clinidae* were displayed in a tank. The tank has a number of rocks artistically arranged on the bottom, among which lurked a number of *Clinus* species including *C. superciliosus*. The tank also contained a single bare stick of coral with a number of slender bare branches. Round these was coiled a single specimen of *Myxodes* (*Labroclinus*) *nan-talis*, a dirty grey in colour, and glaringly unconcealed. It had had chosen the nearest thing that there was to its natural habitat to be found in the tank. Later I collected other specimens of this species from rock pools on the Wild Coast, a beautiful deep green in colour to match the weed among which they were living. During field work recently on the False Bay coast I have been repeatedly struck by the way in which *Myxodes nua*, *M. fusorum* and *M. branchycephalus* resemble the algae among the branches and

fronds of which they were living. Species of this genus have a tendency towards an irregular outline as part of their disruptive concealment against being seen from the side. The difference between Clinus and Myxodes has been very well shown in the excellent illustrations on Plate 79, p. 352, of Smith's recent monograph (1949). Here the contrast between the large mouth and solid outlines of Clinus species, and the small mouth and irregular outline of the Myxodes species can clearly be seen in the species illustrated.

Myxodes, then, is a sluggish genus living among weed, and its principal food, at least of the False Bay forms, appears to be the amphipods and isopods which abound in enormous numbers in the seaweed. Nothing else was ever found among the stomach contents of Myxodes mus and M. fucorum. Such small and easily obtained prey requires only a small mouth to deal with it.

There are only three species of Clinidae that do not fit the requirement for either of the above genera, and it is noteworthy that these species are all extremely rare; in two cases only the type specimens have so far ever been found. These three forms I propose to leave in the genera given them by Smith. Two of these have no tentacles: Gymnoclinus rotundifrons (Barnard), which has a large mouth extending to behind the eye and a solid body shape with none of the irregularities found in Myxodes species, and Clinoporus biporosus Barnard, which has a regular body shape and a moderate mouth. The third is Xenoclinus kochi

Smith, which differs from all other Clinids in possessing a small fleshy papilla above each orbit. The shape of the head is characteristic and also unique. A single specimen from Lambert's Bay has been described by Smith (1947).

The family Clinidae is thus composed of five genera, of which three are monotypic:

Family Clinidae.

Carnivorous weakly swimming fishing living either among rocks or seaweed in shallow water, a few extending to deeper water. Elongate body usually with small scales. A long dorsal and anal fin with a highly variable number of spines and rays; occasionally the first three dorsal spines are elongated to form a crest, the amount of separation of the crest from the rest of the dorsal fin being highly variable. Teeth conical and villiform on both jaws, often also on vomer and palatine. An upturned hook-like projection always present on the inner margin of the shoulder girdle. All viviparous. Type genus *Clinus* Cuvier (1817).

Genus *Clinus* Cuv. (1817).

A fringed tentacle present over the eye. Face generally blunt, with a large mouth and wide gape. Jaws relatively massive. Habitat under rocks or in crevices or against rock under seaweed. Voracious carnivores with a varied diet. Genotype *Clinus superciliosus* (Linn) (*Blennius superciliosus* L.)

Clinus (*Clinus*) *superciliosus* (Linn.)

Clinus (*Clinus*) *settoidea* Cuv.

- Clinus (Clinus) taurus G. & T.
Clinus (Clinus) robustus G. & T.
Clinus (Ophthalmolophus) agilis (Smith)
Clinus (Ophthalmolophus) anne (Smith)
Clinus (Ophthalmolophus) venustis G. & T.
Clinus (Ophthalmolophus) acuminatus Cuv.
Clinus (Ophthalmolophus) helenae (Smith)
Clinus (Ophthalmolophus) latinennis Cuv.
Clinus (Climacopomus) navalis (Barnard)
Clinus (Petraites) woodi (Smith)
Clinus (Petraites) brevicristatus G. & T.
Clinus (Blenniopsis) dorsalis Bleeker
Clinus (Blenniopsis) anguillarum C. & V.
Clinus (Blenniopsis) striatus G. & T.
Clinus (Cirribarbus) capensis (Cuv.)

Genus Myxodes Cuv. (1829)

Orbital tentacles invariably absent. Face pointed with a small mouth with a narrow gape and weak jaws. Habitat amongst branches and fronds of seaweed, disruptive colour-patterns and irregular outlines usually present to break up the form in the weed. Diet less varied than in Clinus, the Cape forms living practically entirely on amphipods and isopods. Genotype Myxodes viridis Cuv.

- Myxodes (Myxodes) fucorum (G. & T.)
Myxodes (Myxodes) mus (G. & T.)
Myxodes (Myxodes) pavo (G. & T.)

Myxodes (Myxodes) heterodon (C. & V.)

Myxodes (Blennioclinus) stella (Smith)

Myxodes (Blennioclinus) brachycephalus (C. & V)

Myxodes (Labroclinus) mentalis (G. & T.)

Myxodes (Labroclinus) laurentii (G. & T.)

Genus Gynutoclinus Smith (1946).

No tentacle above the eye, Snouth rather blunt. Mouth
ex-
large/tending to behind eye. Shape solid and regular. Genotype
Gynutoclinus rotundifrons (Barnard).

Gynutoclinus rotundifrons (Barnard)

Genus Xenopoclinus Smith (1947)

A fleshy papilla above eye. Head anteriorly depressed and
constricted, eyes in anterior fifth. Pelvic 3-rayed, resembling
a webbed foot. Genotype Xenopoclinus kochi Smith.

Xenopoclinus kochi Smith.

Genus Clinoporus Barnard (1927)

No tentacle above eye. Scales entirely absent. Head
blunt, mouth moderate. Shape regular. Lateral line with alter-
nate branches above and below opening each by a pore. Genotype
Clinoporus biporosus Barnard.

Clinoporus biporosus Barnard.

V. Conclusion

During the course of this work an endeavour was made to
collect as much information as possible about the life and habits of
the fish that are to be found in the intertidal zone of the Cape

Peninsula at low tide. It was soon noticed that a large proportion of the fish present were to be found at all stages of maturity and at all times of the year, while there was in addition a "floating population" of fish which could not be relied upon always to be presnet, but were to be found in the rock pools on occasion, especially during the summer months, and which were nearly always juvenile forms of common sublittoral species. Most of the information collected refers to the first or permanent sedation of the population.

Literature on the subject indicated that there were about 25 species which may have been found, some of which, however, were extremely rare and had been seen only on one or two occasions. Finally 16 species were found, and data pertaining to the habits of these was accumulated. Of these 16 species of intertidal fish 13 belonged to the family Clinidae.

It was found that there was a considerable variation in the fish population at high and at low tide, and also, to a lesser extent, between low tide during the day and low tide at night. The position at high water was ignored and the work is presented on the basis of the position in the intertidal zone during low water.

The data accumulated with respect to these fish was then reviewed. Certain difficulties, mentioned in the text, were encountered in assessing the relative abundance of the different species, but a list has been drawn up indicating the relative abundance of the various fish which is believed to be accurate.

Reproduction in these fish was then discussed and data with reference to the spawning time, number of young spawned, and sizes at which sexual maturity is reached is presented. It was found that several of the viviparous Clinids do not spawn their young all at once, but may have two or more separate spawning periods some considerable time apart.

Data with reference to feeding habits was collected and presented in the cases of several of the individual species. It was found that the major food of most of the Clinids, particularly in their younger stadia, consists of amphipods, and, to a lesser extent, isopods.

At low tides a marked zonation was found in the case of the permanent intertidal fish, and this is discussed and a graph given which shows the relative positions in the intertidal zones that these fish live in, and the highest and lowest points in the zone that individual fish of each species were captured.

It was found that the question of zonation was closely bound up with that of habitat and that many of the fish had distinct habitats correlated with their ecological niche in the biocoenosis of the shore. Their habitat, zone, prey and enemies are integrated in accordance with their ecological position.

As a result/^{of} the ecological study of the Clinidae, broad ecological differences in the group were noticed, and these, correlated with the only constant large morphological differences, divided the groups so well that the group was systematically revised in accordance with modern systematic practice. The numerous rather

fine genera to which they had been relegated were reduced to the status of sub-genera. The Clinidae are thus considered to be composed of five genera, as against the sixteen into which they had previously been placed.

SUMMARY.

1. The intertidal fish form groups, permanent and temporary.
2. The fish population varies between high and low tide, so the position at low tide only is considered.
3. The relative abundance of different species in the zone is given.
4. Data concerning the reproduction of the fish is given.
5. The chief food of most of the fish, particularly of the genus Myxodes, is amphipods and isopods. Other details of the food are also given.
6. The fish were seen to possess a definite zonation.
7. The fish occupy definite habitats.
8. Some discussion of the position of the fish as predators and prey, and of their effect on the community as a whole, is given.
9. The genera of the family Clinidae are revised.

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