STUDIES ON THE INTERTIDAL SANDY-BEACH FAUNA OF THE CAPE PENINSULA

A thesis for the degree of Ph. D.

by

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STUDIES ON THE INTERTIDAL SANDY-BEACH FAUNA OF THE CAPE PENINSULA

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STUDIES ON THE INTERTIDAL SANDY-BEACH
FAUNA OF THE CAPE PENINSULA.

SUMMARY

The thesis comprises six published papers and two papers in manuscript. Five of the publications and the second of the manuscripts deal with the sandy-beach snail, Bullia, while the sixth published paper is a brief account of food-relationships on the Cape Peninsula's sandy beaches. The first manuscript is an introduction to the ecology of the sandy beaches of the Cape Peninsula, the first of a series of papers to be published on this topic. The manuscript on Bullia forms the second part of this series. (Subsequent parts are not presented here but will be published in due course.)

Most of the work presented here therefore concerns the prosobranchiate gastropod, Bullia. The tidal cycle of activity of B. digitalis is described and contrasted with that of B. laevissima. Experiments on the snails' reactions to water currents, to the particle size of the substratum and to other factors are reported, as are various tolerance studies. Burrowing behaviour and the factors affecting it are described. The olfactory function of the osphradium is established and the effect of sulphide pollution on the snails is discussed. Circulatory problems are dealt with, leading to the first consistent theory of pedal expansion and retraction to be put forward for any gastropod mollusc. Investigations which throw light on the snail's sea-water spaces and the origin of its jets are also presented. Experiments on the responses of Bullia to injected foreign particles are reported and the pathways taken by laden macrophages described, supported by radiographs.

The final paper on Bullia (in manuscript) summarizes our present knowledge of the various species of the genus. In addition it presents new information; reproductive behaviour is described

for the first time and experimental work is reported concerning chemoreception and the responses which lead to feeding. Some conclusions are also reached with regard to life-span and growth. The distribution of the species of Bullia is dealt with and the factors responsible for the distribution round the Cape Peninsula are discussed. Attempts to estimate the numbers of Bullia are described and mention is made of water- and heat-relationships, defense mechanisms and parasites.

The paper on the food-relationships of the fauna of sandy beaches is descriptive and no quantitative data are presented. A graphic representation of some of the main food-chains is included and some conclusions are reached regarding the balance of invading and resident species.

The introductory paper (in manuscript) to "the ecology of the sandy beaches of the Cape Peninsula" is largely concerned with describing the beaches and drawing attention to the extremes in physical and chemical conditions which are encountered by the intertidal fauna. Special reference is made to the beaches of Hout Bay, Llundudno, Milnerton and Muizenberg, these having been chosen because they show contrasting conditions and faunistic differences. Tidal conditions, wave action, beach profiles and sand movements are discussed, while attention is also given to the particle-size distribution of the substrata forming the beaches. The organic content of the sand, its permeability and porosity, and the disposition of the water tables are all discussed briefly and some data concerning salinities, temperatures and hydrogen ion concentration are presented. Mention is made of the fauna , and there is some attempt to show how the various physical factors are interrelated.

The work reported in this thesis is original except where otherwise stated and acknowledged in the text. The manuscript on "the mode of life of Bullia" makes use of unpublished reports by two students, working under my direction. This, too, is acknowledged in the text. Two of the published papers presented are joint papers. The paper by Brown & Noble is mainly the work of the first author; Mr Noble, at the time a student working in my laboratory, contributed a single successful test run. The other joint paper, by A.C. Brown & R.J.Brown, contains a statement that the second author was involved only so far as the radiographic techniques were concerned.

1.

PHYSIOLOGICAL-ECOLOGICAL STUDIES ON TWO SANDY-BEACH GASTROPODA FROM SOUTH AFRICA: BULLIA DIGITALIS MEUSCHEN AND BULLIA LAEVISSIMA (GMELIN).

Z. Morph. Okol. Tiere 49, 629 - 657.

Z. Morph. Ökol. Tiere 49, 629—657 (1961)

From the Zoology Department, University of Cape Town

PHYSIOLOGICAL-ECOLOGICAL STUDIES ON TWO SANDY-BEACH GASTROPODA FROM SOUTH AFRICA; *BULLIA DIGITALIS* MEUSCHEN AND *BULLIA LAEVISSIMA* (GMELIN)

By

A. C. BROWN

With 8 Figures in the Text

(Received March 29, 1960)

Contents

A. Introduction and general

South African marine ecology has thus far been concerned mainly with the distribution of animals in the intertidal zone and in estuaries. The physiological aspects of this distribution have been sadly neglected. This is particularly true of sandy beaches, about which little of either ecological or physiological import has been published. During the course of investigations into the ecology of the sandy beaches of the Cape Peninsula our attention was drawn to two very closely related prosobranchiate gastropods, *Bullia digitalis* MEUSCHEN and *Bullia laevissima* (GMELIN). Both species are limited to sandy substrata and the recorded distribution of both is from Port Elizabeth, on the east coast, to beyond Lambert's Bay on the west coast[1]. The bathymetric range of the species is, however, very different. *Bullia digitalis* is essentially an intertidal species, limited to surf-swept beaches. Isolated specimens have been recorded from below tide-marks, the maximum recorded depth being 20 metres, but by far the greatest number of individuals (99%) have been taken from the intertidal zone. *B. laevissima,* on the other hand, is to be found most commonly below tide-marks. Records made by the Fisheries Research Vessel, Africana II, and by

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[1] See addendum.

commercial trawlers indicate that the species reaches its greatest concentrations between 25 and 60 metres depth. It is also found intertidally, but only on very sheltered beaches characterised by waves of such low amplitude that these do not break in calm weather.

Bullia digitalis (Fig. 1b) has an elongate and tapering shell, the average length of which is, in the adult, 3.8 cm. The shell is thin and light, the callus extremely small. The mouth of the shell occupies 19% of the ventral surface while the operculum covers 27% of the shell mouth (average of 25 adult specimens). *B. laevissima* (Fig. 1a) has a thick and heavy shell, approaching an oblong in shape, with an extensive columella callus. The average length of the adult shell is 4.2 cm. The shell mouth covers some 30% of the ventral surface, yet the operculum is ridiculously small and covers barely 2.5% of the shell mouth (average of 25 adult specimens).

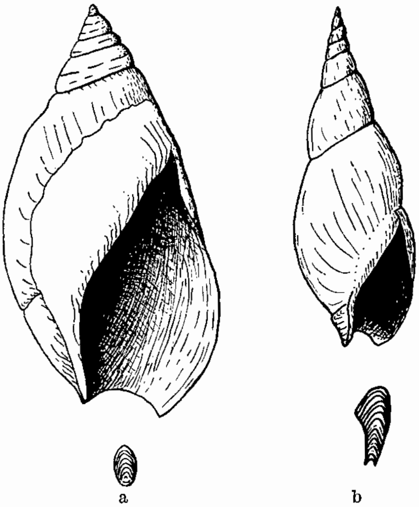

Fig. 1. a Shell and Operculum of *Bullia laevissima* (natural size). b Shell and Operculum of *Bullia digitalis* (natural size)

On exposed sandy beaches, when the water is below mid-tide level, *Bullia digitalis* is to be found in the surf and in the swash-zone, that part of the foreshore alternately covered by water and exposed to air due to the interaction of wave-force and gravity. The animal is rolled over by the waves, the foot fully expanded thus offering a maximum degree of resistance to the water. The shells of this species are clean, smooth and highly polished, obviously resulting from their active life in the surf and constant rubbing against sand grains. As the water rises to mid-tide level they bury themselves in the sand, so that no individuals can be collected from the upper third of the intertidal zone whatever the state of the tide (see also Barnard 1940). They only emerge from the sand when the tide again falls to mid-tide level. The number of individuals in the swash-zone, obtained at different tidal levels, is given in Fig. 2. *B. digitalis* keeps pace with the tide from low- to mid-tide levels. This behaviour is not influenced by daylight and has been observed on several occasions by night. The snails are not bound completely to the sea, but leave the water temporarily and occupy the wet foreshore, this habit being associated with feeding.

On sheltered beaches of the Cape Peninsula, *Bullia laevissima* is to be found intertidally while *B. digitalis* is absent. The former species never leaves the water but follows the entire tidal cycle below the swash-zone. Its distribution under such conditions is shown in Fig. 2, from samples taken immediately below the swash-zone. In contrast to *B. digitalis*, *B. laevissima* is usually found half buried in the sand. Large (and therefore presumably old) individuals commonly have algae growing on their shells, this growth stopping abruptly in a horizontal plane encompassing the shell. This is in full agreement with the observation that they habitually only half bury themselves and that they are not rolled about against the sand as is *B. digitalis*.

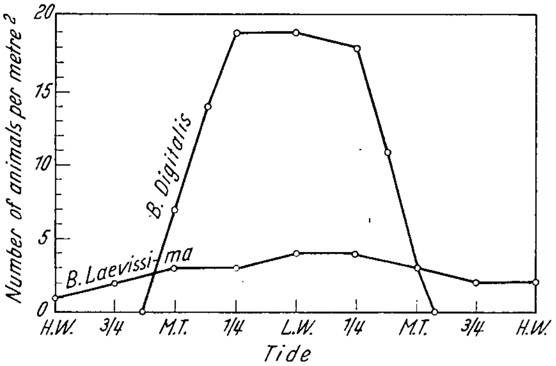

Fig. 2. Temporal distribution of *Bullia* in the intertidal zone. The numbers for *B. digitalis* refer to the maximum numbers found in 1 m² in the swash-zone; those for *B. laevissima* immediately below the swash-zone of a sheltered beach

Though adult specimens of *B. laevissima* are not more than 3 times the volume of adult *B. digitalis*, their average weight is almost 6 times as much (Table 1). It can be seen that this discrepancy is almost entirely due to the more massive shell and not to a marked difference in the tissues. With the foot expanded, the specific gravity of *B. laevissima* is 1.8, while that of *B. digitalis* is 1.1. The latter species will thus be more easily moved by water-currents than will *B. laevissima* and rolling in the surf is more easily accomplished.

We have investigated only intertidal specimens of both species, while bearing in mind that *B. laevissima* is more common below tide-marks and that *B. digitalis* has also been found infratidally. It is, however, worth noting that a third habitat may be invaded by both species — estuaries. *Bullia digitalis* has been found within the mouth of the Great Brak River estuary, while *B. laevissima* has been taken from the sheltered waters of the Bushman's River estuary. Both species also occur in Langebaan Lagoon which displays several estuarine characteristics. *B. digitalis* is found in the more exposed parts of the lagoon; *B. laevissima* occupies the more sheltered sands. That wave-action in this lagoon is the most important factor influencing the distribution of the fauna as a whole has already been suggested (Day 1959).

All species of the genus *Bullia* possess a large ploughing foot, which is unlike the foot of most gastropods in that much of its interior is taken up by a cavity containing sea water. This cavity communicates with the exterior by means of a duct opening below the operculum. When inflated with sea-water the foot of *B. digitalis* covers an area of 13 sq. cm. (average of 10 mature individuals) while the expanded foot of *B. laevissima* covers 36.5 sq. cm. (average of 8 adult specimens).

Both species are scavengers, feeding on medusae, decaying crabs, dead fish — in fact almost any animal material which happens to be available. In the laboratory they can be kept alive on any such food, including the meat of mammals. Even cheese has been accepted. However, they connot be induced to eat plant matter, and no cannibalistic tendencies have been noted even during prolonged starvation.

Considering the difference in habitat between these closely related species, it seemed desirable to study more closely some of the structural and functional adaptations by which they survive in their particular surroundings. An ideal locality for such studies appeared to be Hout Bay, one of the sandy beaches of the Cape Peninsula where both species occur intertidally. This bay is of great ecological interest as neither the environmental conditions nor the fauna are uniform along its length. The beach is semicircular, the eastern segment being exposed to waves which originate from Atlantic rollers and sweep through the mouth of the bay directly onto the beach. The western extremity (Hout Bay Harbour Beach) is, on the other hand, very well sheltered, waves being forced to turn through 180° in order to reach it. Between these two extremes the beach presents a natural gradient as far as wave action is concerned. Waves of a height exceeding 1.5 metres are fairly common on the east beach, while on the Harbour Beach waves seldom break and are usually but a few centimetres in height. The entire beach is barely 4 kilometres long and thus conditions not essentially related to wave action are very similar along its length. Differences in the constitution of the fauna are thus most unlikely to be related to differences in water- or sand-temperatures, humidity, salinity, etc., as these differences are negligible. It may be noted, however, that the Harbour Beach is far richer in organic matter and more dead animals are to be found there, than on the rest of the beach. This is partly a result of decreased wave action but is also to be attributed to the close proximity of fishing vessels in and around the harbour. That it is not these conditions which attract *Bullia laevissima* is, however, indicated by its occurence on beaches where no such pollution occurs.

B. digitalis can be collected from all parts of the Hout Bay beach, with the notable exception of the Harbour Beach. *B. laevissima*, on the other hand, has been recorded intertidally *only* from this stretch of sand and from nowhere else along the beach. It is possible to collect these two species within thirty metres of one another, yet the populations do not normally overlap. In the case of *Bullia digitalis*, very young as well as mature animals are usually found, the shell-lengths ranging from 0.6—4.9 cm. This strengthens the impression that this species is really at home in the intertidal zone. Intertidal individuals of *B. laevissima*, on the other hand, are all large adults, the shell-length varying only between 3.6 and 4.5 cm; juveniles are apparently confined to infratidal levels, only the adults daring to invade tidal regions.

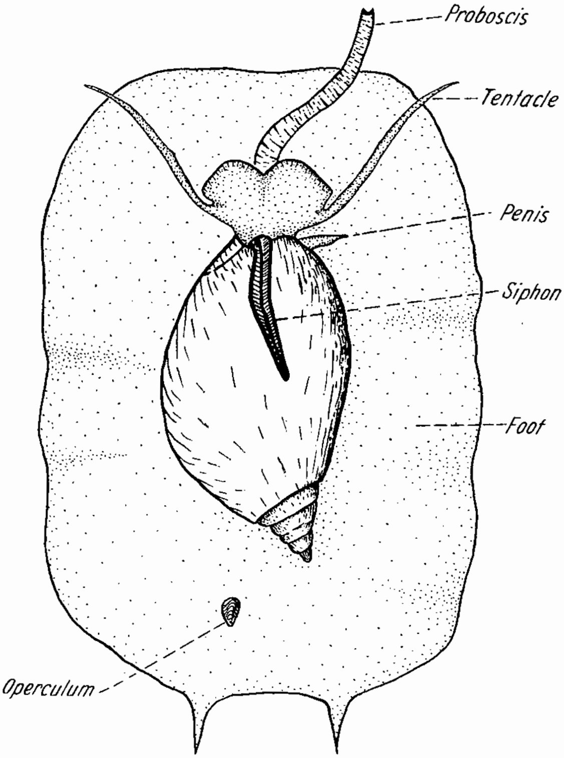

Fig. 3. *Bullia laevissima* with foot expanded, in dorsal view (natural size)

An obvious question to ask is how *B. laevissima* would fare in the environment enjoyed by *B. digitalis*, and vice versa. Consequently certain preliminary field experiments were performed. A number of individuals of *B. laevissima* were collected from the Harbour Beach and placed one by one in the surf in a region of the beach where intermediate conditions prevailed; where the waves averaged 23 centimetres in height. It was observed that *B. laevissima* was not moved to any appreciable extent by these waves, though *B. digitalis*, which naturally occurs in that region, was carried up and down the swash-zone. This shows clearly that the difference in specific gravity measured in the laboratory constitutes a very real factor in the field. However, a difference in the behaviour of the two species was also noted, for the specimens of *B. laevissima* proceeded to bury themselves in the sand while *B. digitalis* showed no such tendency. Later the experimental animals were recovered and transported to the surf-swept east beach, where the waves on this occasion averaged a little over a metre in height. On being placed in the surf they were rolled over and over, the waves giving them no chance to burrow. That they tried to burrow was apparent, but individuals got little purchase on the sand before being swept away. After less than a minute they had ejected the water from the foot (thus increasing the specific gravity and rendering the animals less liable to movements by water-currents). In spite of this some individuals were soon cast upon the foreshore, where they remained immobile and completely helpless as the foot cannot be expanded unless in water.

On a subsequent occasion about fifty *B. digitalis* were transported from their natural habitat to the sheltered Harbour Beach. There they were placed in the calm waters below tide-mark, after having their shells marked with a cross in pencil. Some began crawling over the surface, while others buried themselves at once; a few lay on their backs, waving their extended feet in the water. When revisiting the spot at low tide the following day, no specimens could be recovered either from the surface or buried below low-tide level. However, raking the sand *above* the water-level produced a number of marked specimens. Apparently these individuals had buried themselves during rising or receding tide, but had been left behind as the tide fell. This is, of course, quite contrary to their behaviour on surf-swept beaches.

It is clear that *B. laevissima* cannot adapt itself to surf-swept beaches, while the behaviour of *B. digitalis* is not normal when transferred to calm waters. Further experiments, in which an analysis of certain aspects of their behaviour has been attempted, will throw greater light on this question.

B. Experimental work

I. Experiments on feeding habits

Although both species are scavengers, there are important differences between their feeding-habits. Let us first consider *Bullia digitalis*.

On all of the many occasions on which *B. digitalis* has been seen to feed in the field it has been observed that it does so either completely out of the water (on the wet foreshore) or within the swash-zone. In order to study this habit more closely, dead fish were placed at intervals on the wet foreshore at the time of low water. It was observed that individuals deposited on the foreshore by the waves moved rapidly in the direction of the bait, apparently guided by their chemical sense. Individuals in the swash-zone also tend to move in the direction of the bait, though their course is more erratic due to the intermittent surge of water. However, it was also observed that individuals below the swash-zone, continually covered with water during the experiment, emerged actively from the sand, were carried ashore by the waves and found the food. The animals are apparently attracted by volatile substances emanating from the food and subsequently dissolved in the water. This small concentration seems to be sufficient to cause the animals to emerge, but they do not move *actively* towards the bait until deposited on the foreshore. In the water, which is continuously mixed, a concentration gradient — and thus chemically directed movements — cannot be expected. After feeding the animals bury themselves. It is of interest to note that individuals cannot be attracted to such bait regardless of the state of the tide, for if the bait is placed in the swash-zone when the water is above mid-tide level, *B. digitalis* does not emerge from the sand and the bait is not attacked.

Feeding behaviour was further analysed in the laboratory. A tank was provided with a sandy substratum under sea-water and tilted by means of wedges to an oblique position so that about half the slope of sand was above the waterlevel. Individuals of *B. digitalis* were induced to bury themselves in the submerged sand. Pieces of fish were then placed on the sand above water-level. The animals emerged from the sand within a few minutes, crawled to the artificial shore and found the food. In five experiments with approximately 50 specimens the results were uniform showing firstly that dissolved substances originating from the food were present in the water and secondly that, though below the water, they were able to orientate themselves with regard to the food. In strongly aerated water though activity increased and buried individuals emerged, they showed little or no orientation towards the food. This violent aeration presumably destroyed the concentration gradient and indicates that it was this factor and not the slope of the sand which guided the animals. In the laboratory as in the field the animals buried themselves after feeding and could then no longer be activated by the presence of food.

These laboratory experiments explain certain aspects of the feeding behaviour observed in the field. There is no reason to doubt that, at the beach, all individuals within reasonable distance of the bait, even those submerged and buried, are activated, and once ashore guided by their keen chemical sense. The sense of smell in certain marine gastropods has been studied in some detail by COPELAND (1918) and one of his species, *Alectrion obsoleta* (SAY), appears to be similar in some of its habits to *Bullia digitalis*. This does not, however, mean that its olfactory reactions or chemical sense-organs are of necessity similar and further work on chemo-reception in *Bullia* is undoubtedly necessary.

At present we have the impression that the grade of decomposition of the food is important; it seems to be more atractive the greater its apparent odour. In the laboratory, using stagnant water, conditions do not seem to be always ideal for rapid responses to food which is out of the water. When the animals are kept covered with water on a horizontal layer of sand, and food is placed on the upper ridge of the tank well out of the water, responses are usually slow. A few individuals emerge after some minutes and start to crawl on the surface. When the bait is then placed in the water, however, all buried specimens emerge at once. These slow responses must almost certainly be linked with the lack of movement of the water and consequent slow dissolution of the volatile substances, while on the surf-swept beaches inhabited by these animals solution will occur much more rapidly due to the churning of the water and its mixing with the air.

At the beach, *B. digitalis* is never seen to feed under water. This is not a matter of preference, since in the laboratory they do so without hesitation. Some attempt to solve this anomaly was made in the field. At about low tide a large piece of fish was placed in the waves just below the swash-zone and held there by means of a stake driven through it and into the sand. Numbers of *B. digitalis* were observed to move towards the bait in the periods between breakers. However the waves, averaging some 9—10 seconds apart, swept the animals away and apparently disorientated them. The few individuals which reached the bait did not get any opportunity to feed before being washed away.

After some time the bait was staked in about the middle of the swash-zone, the wave force here being considerably reduced. The food was out of the water between surges. Individuals again moved towards the bait and this time increased markedly in numbers as more and more were brought by the waves from lower down the slope. Within five minutes many snails had commenced feeding. Very few were now swept away by the waves, largely because the proboscis acts as an anchor, being embedded in the food. Later, feeding individuals were removed and the bait placed free in the surf. It was washed up towards the top of the swash-zone and only after having come to rest there was it attacked by snails.

Two factors would therefore seem to contribute towards this aspect of feeding behaviour. Firstly the food, being usually of low density, does not come to rest until washed up onto the beach. Secondly, should any food be present below the swash-zone, the animals tend to be washed away before having a chance to anchor themselves to it. Thus although *B. digitalis* is willing to feed under water it cannot do so under natural conditions.

Bullia laevissima presents a simpler feeding pattern. These animals never leave the water and cannot be induced to feed ashore. Fish bait placed on the wet foreshore in the sheltered region of Hout Bay beach inhabited by *B. laevissima* did not on any occasion attract the animals. Specimens gently removed from the water and placed directly onto the food left the food at once or after a few moments, and either tried to reach the water or buried themselves in the wet sand. These reactions were not due to handling, for when the animals were repalced in the sea and then offered food they readily accepted it. In fact, fish placed in the water invariably attracts hungry individuals. Apparently these animals are guided by a concentration gradient which may well exist in such quiet waters. Their chemical sense is apparently well-developed, for they move towards the bait in a straight line for several metres, sometimes from more than nine metres away. In contrast to *B. digitalis*, *B. laevissima* can be attracted to food regardless of the state of the tide.

After feeding they bury themselves, as could be observed both in the field and in the laboratory. It may be noted that there is no need for *B. laevissima* to enter the the swash-zone in search of food. In the quiet waters in which this animal lives the food is not swept away to the shore and neither is the animal displaced by water-currents.

II. Burrowing activity

Burrowing takes place, in both species, at an angle to the surface of the sand, the alternate contractions and expansions of the foot pushing the animal forwards as well as downwards. *B. digitalis* buries itself completely with only the tip of the anterior (inhalent) siphon above the sand, both in the field and in the laboratory under aerated water or in damp sand. In stagnant water in the laboratory it tends to bury itself less completely. In the field *B. laevissima* is usually found only half buried. In strongly aerated water in the laboratory, however, it buries itself completely. Thus the difference in completeness of burrowing observed in the field is due not so much to a difference between the animals themselves as to differences in the prevailing conditions.

The foot in both species is well suited to burrowing in sand. It is a powerful muscular organ, the high turgor of which is caused not only by pumping blood into it (as in most Gastropoda), but also, as already mentioned, by sea-water introduced into the foot cavities. When the animals retract into their shells this sea-water is expelled under pressure. In *B. digitalis* the resulting jet of water can reach a distance of 30 cm or more, while in *B. laevissima* the ejection is less powerful. The amount of sea-water held in the foot is considerable. It can easily be collected and gives average figures of 1.9 ml for both species (Table 1). From the figures available it can be calculated roughly how much blood is used for the expansion of the foot. The average difference in volume between expanded and retracted animals is 2.1 ml for *B. digitalis* (see Table 1). Most of this difference is made up by water and blood used for expansion. Sindce 1.9 ml of the difference is water, only $2.1 — 1.9 = 0.2$ ml can be blood. Applying the same calculation to *B. laevissima* we find that this species uses ca. 0.5 ml blood to help in keeping the foot expanded. In both species sea-water is obviously the main factor in expansion of the foot.

Retraction of the foot does not seem to occur frequently in nature. *B. laevissima* does not retract its foot when lifted from the water and also fails to do so when the foot itself is stimulated. Even hard pinching of the foot, the application of solid sodium chloride, concentrated alcohol or nitric acid fails to produce a retraction! It was found, however, that the foot is retracted — often very rapidly — when tactile or chemical stimulation is applied to its narrow, apical part where it enters the shell to join the rest of the body.

In *B. digitalis* retraction can be induced by lifting the animal from the sand by means of its shell. Mechanical stimulation of any part of the foot also causes it to be retracted. Under weak stimulation only part of the water is ejected, stronger stimulation causing further ejection and complete retraction. This difference in sensitivity of the foot between the two species may well be related to their modes of life. *B. laevissima* has its foot nearly always buried except when feeding. The foot, therefore, is seldom exposed to enemies and sensory elements in it could hardly help to inform the animal of the chemical and physical conditions of the surrounding water. On the other hand in *B. digitalis*, living a great part of its day in the surf with its expanded foot exposed to enemies and to the water, a good supply of sensory elements to the foot and/or well developed reflex mechanisms for its retraction may be a difinite advantage. When undisturbed under natural conditions *B. laevissima* is never found with retacted foot, *B. digitalis* very seldom and never when out of the water. This would, of course, endanger the animal, for once the sea-water has been expelled it is completely helpless on the shore. The blood-supply to the foot being insufficient to re-inflate it, the animal would be forced to wait until a supply of water was again available. If the tide were falling it might take up to six hours for this to happen and in the meantime the animal would be subjected to the

Table 1. *Average volumes, weights and other measurements of 25 adult specimens*

	B. laevissima	*B. digitalis*
Volume with foot expanded	8.9 ml	4.1 ml
Volume with foot retracted	6.5 ml	2.0 ml
Vol. water in foot.	1.9 ml	1.9 ml
Weight with foot retracted	14.10 gm	2.65 gm
Weight of shell	9.65 gm	0.64 gm
Fresh weight of tissues . .	4.55 gm	2.01 gm
Dry weight of tissues . . .	1.04 gm	0.40 gm
Water content as % of fresh tissue weight . . .	77%	80%
Specific gravity with foot expanded	1.8	1.1

dangers of desiccation, increased temperature, and the attacks of predators.

As observed in the laboratory and in the field, both species can bury themselves in wet sand above the water-level, as well as in submerged sand. Now the sandy beaches of the Cape Peninsula show a wide range of particle-size of the substratum, this particle-size being determined largely by wave-action as well as by the nature of the materials available for deposition. In order to discover whether the species had any preference for sand of a particular grade, experiments were conducted in the laboratory with sand of different particle-size ranges. Sand was sieved under seawater through a series of standard sieves so as to obtain different grades. A glass vessel, 0.5 metres square by 10 cm high, was divided by low diagonal partitions into four equal segments. These segments were filled with sand of four different grades and sea-water added to a depth of some 5 cm above the substratum. Individuals of *Bullia* were then placed in the centre of the tank so that the foot was in contact, with all four grades of sand. The direction taken by the animal and the grade of sand in to which it burrowed were noted. The experiment was repeated approximately 100 times with a number of individuals of both species.

Table 2. *Burrowing ability in different grades of sand. The blanks (—) indicate that the animals were unable to burrow*

Particle size of substratum mm	Averaga time taken to burrow, in seconds	
	B. digitacis	*B. laevissima*
Larger than 3.2	—	—
2.8—3.2	—	25
1.4—2.8	22	18
0.8—1.4	16	15
0.3—0.8	9	13
0.2—0.3	7	11
0.1—0.2	5	10
Smaller than 0.1	3	10

The animals did not show any preference at all with regard to the grades of sand, even when these were vastly different from one another. The number of animals attempting to burrow in each grade also showed no significant differences. While observing the animals in these experiments it became apparent that the individual moved in the direction it happened to be facing and continued more or less in a straight line until it either burrowed or met the wall of the vessel. It was, in fact, possible to cause an individual to attempt to burrow in any one of the grades provided (see Table 2) by placing it facing that direction.

Although they attempted to burrow in all grades of sand they were not always successful. A substratum with a particle size of more than 3.2 mm (gravel) is unsuitable for burrowing in adults of both species. *B. laevissima* can bury itself in somewhat finer grades while *B. digitalis* still fails to do so in particles between 2.8 and 3.2 mm. The finer grades of sand did not provide difficulties for either species, although there are marked differences in the speed with which they burrow (Table 2).

The times listed are averages of those measured from the onset of burrowing activity to its cessation, regardless of whether the shell was completely covered or not. Nevertheless it can be seen that, firstly, both species burrow more quickly in fine than in coarse sand, and secondly *B. laevissima* burrows faster than *B. digitalis* in coarse sand (of particlesize 0.8 to 2.8 mm), whereas the latter species burrows faster in the finer grades.

It is impossible to say, in the present state of our knowledge, whether these differences are of any ecological significance or not. The fact which does emerge clearly from this study is that neither species of *Bullia* shows selective orientation towards any particular range of particle-size; a fact not apparent from field observations as very calm intertidal waters (inhabited only by *B. laevissima*) usually have a substratum composed of finer particles than do surf-swept beaches (inhabited by *B. digitalis*). Yet the laboratory experiments would suggest that *B. laevissima* is more competent to deal with large particles than is *B. digitalis*. Differences in the particle-size of the substratum cannot therefore be an important factor in determining the intertidal distribution of these species. Actually, differences in particle-size and the different distribution of the species would both appear to result from a single fcator — the influence of wave action.

In a further series of experiments the same piece of apparatus was used, but filled with dry sand of various grades. It became clear that neither species was able to burrow successfully in dry sand of the grades provided. This agrees with field observations.

After having considered burrowing activity as such, an attempt was made to find the stimuli which induce burrowing. As previously mentioned, the handling of individuals of either species will induce burrowing; this reaction is obviously an escape mechanism. A second stimulus may be mentioned in the case of *B. digitalis*-exposure to air. When individuals are deposited on the foreshore by waves, they usually crawl around in search of food. If no food is found within a minute or two they commonly bury themselves. It would seem that when exposed to air the burrowing reflex becomes dominant if not suppressed by chemical stimuli produced by the food.

Burrowing after feeding can easily be observed in the field. Both species drop off the food and bury themselves when they have appeased their hunger; *B. digitalis* not only below water but also, as mentioned, in the wet foreshore. In the laboratory, experiments were performed on *B. digitalis* kept in tanks of sea-water over a sandy substratum. Twenty to twenty-five individuals were used in each experiment, Fig. 4 and 5 showing typical results. They confirm that feeding induces mass burrowing.

Finally, some attempt was made to find out more about the mass burrowing which occurs in nature at about mid-tide level. Having, observed that the animals bury themselves without exception after feeding, it was thought that this might be related to their remarkable burrowing-behaviour at rising mid-tide. After emerging at receding mid-tide they have about six hours for feeding; that is until rising mid-tide. Some individuals may find food fairly soon and bury themselves before the six hours have elapsed. By the time of rising mid-tide nearly all individuals may have appeased their hunger and disappear into the sand.

If this explanation is correct, one would expect that very hungry individuals would not bury themselves at mid-tide level but would follow the tide up the beach beyond that level. A number of specimens were therefore removed from Hout Bay beach and kept in the laboratory in an aerated aquarium for 33 hours. They were not fed during this time. The animals were then marked and liberated in the swash-zone of their natural habitat some ten minutes before rising mid-tide. Some proceeded to burrow (perhaps an escape reaction after handling), while others were carried to and fro by the waves. Half an hour after mid-tide several marked specimens were still observed above the sand but numerous unmarked specimens were also seen. By one hour ofter the water had reached mid-tide level, the concentration of *B. digitalis* above the surface had considerably decreased and of the many observed only two were marked snails. The last snail, a marked individual, was seen eight minutes later. The experiment was abandoned about an hour later, no further snails having been seen. These observations cannot be considered to be decisive and more experiments on a larger scale will have to be conducted. Nevertheless, our preliminary results do not strengthen the suggestion that the snails burrow at mid-tide level because they have appeased their hunger. It thus seemed worth-while to investigate the problem further.

In view of the work of WELLS (1945, 1949, 1950) on intrinsic rhythmic mechanisms in *Arenicola*, and of the able summary of rhythmic mechanisms in other marine animals offered by BROWN (1957), it seemed desirable to investigate the possible presence of such rhythms in *Bullia digitalis*. The most likely instrinsic rhythm accounting for mass burrowing was thought to be a mechanism linked either to the tidal period itself or directly to the lunar period. Experiments were performed with over 60 specimens of *B. digitalis*, which were kept alive in the laboratory for approximately three weeks. The animals were housed in tanks with a layer of sand so arranged that its surface presented a natural slope, being some 5 cm below sea-water at its lower end but above the water at its upper extremity. The water was aerated from time to time and the animals were fed regularly. The tanks were kept in a room where both daylight and moonlight had ample opportunity to influence the behaviour of the snails. With wedges placed under each aquarium the slope of the sand could be varied. In spite of the fact that the animals behaved quite normally, and in spite of several different experimental slopes of sand, no indication of rhythmic burrowing activity could be found. Fig. 4 and 5, in which M.T. indicates the time of mid-tide in the sea, show typical examples from this series of experiments. The animals show no inclination to burrow at the time of mid-tide.

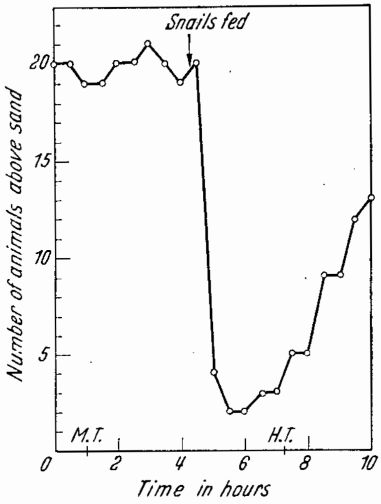

Fig. 4

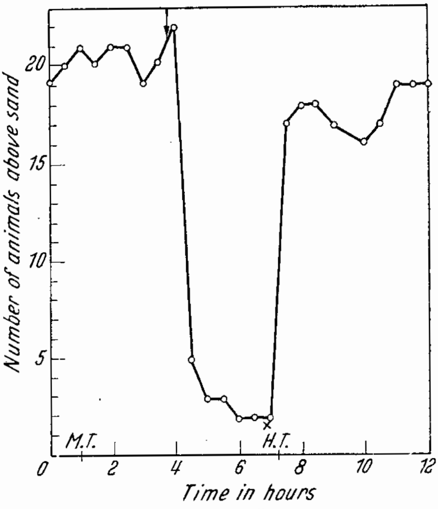

Fig. 5

Fig. 4. Burrowing activity of *Bullia digitalis* in the laboratory, showing burrowing after feeding and lack of inherent burrowing rhythm. M.T. = Time of mid-tide on the shore; H.T. = High Tide

Fig. 5. Burrowing behaviour in *B. digitalis*, showing in particular the response to water currents. Abbreviations as for Fig. 4. Cross indicates time at which strong water-currents were produced for ten minutes

Although one cannot exclude the possibility that such an intrinsic rhythm only becomes manifest in the field when other factors (*e. g.* wave action) are normal, we are bound to express severe doubt as to its existence. We must therefore consider extrinsic factors which may supply the stimulus for the mass mid-tide burrowing. Such a factor would have to be present on all beaches inhabited by *B. digitalis* and would have to be contrasted more or less sharply with conditions below mid-tide level. Field observations suggest that there is only one such factor worth mentioning — the extent to which the sand is saturated with water. At Low Water of Spring Tide the foreshore is always fully saturated with water, the level of the water-table within the beach being higher than that of the free water-level. As the tide rises the water-table (level of ground water) within the beach continues to fall under the influence of gravity and there comes a time when the free water-level rises above the level of the water-table. Until that point is reached the sand of the swash-zone has been fully saturated, but now it contains air-spaces and waves coming up the beach tend to sink into the sand. Though this effect is most apparent at high tide levels, it begins to be apparent on most beaches near mid-tide, the exact level depending on such factors as the slope of the beach, the permeability of the sand, etc. This phenomenon is known not only from South African beaches but has been studied in other parts of the world, *e. g.* see EMERY and FOSTER, 1948. It does not appear to be impossible that in the swash-zone *B. digitalis*, having contact with the substratum while crawling, might be able to perceive the degree of saturation of the sand and that unsaturated sand might initiate burrowing. However, only experimental work can solve this question.

As mentioned previously, *B. laevissima* behaves in a similar way to *B. digitalis* as far as burrowing after handling and feeding is concerned. However there is a third stimulus which induces burrowing in the former species. It was discovered by chance that when the water in a tank is suddenly aerated, individuals of *B. laevissima* crawling on the surface of the sand start to bury themselves at once. Experiments with an electric stirrer confirmed the existence of this response. When the stirrer was at a level high enough above the sand to produce water-currents without moving the particles of the substratum to an observable extent, the animals partly buried themselves; the whole of the foot but only part of the shell was buried, as one so often finds them in the field. Increasing the current by lowering the stirrer, to a point where the sand particles began to move, resulted in deeper burrowing. Still stronger currents caused the animals to bury themselves completely. This activity was found to be quite independent of the direction of the current in relation to the animal. This response to water-currents is in good accordance with the mode of life of the species. Living in quiet waters, half buried for much of the time, *B. laevissima* will respond to temporarily stronger water movements by burrowing deeper and deeper the stronger the currents, thus avoiding being exposed or washed away. This response also explains their pronounced burrowing activity in the field, when they are placed in areas of more marked wave-action.

Having discussed burrowing activity and the stimuli producing it, we now turn our attention to the behaviour and stimuli associated with emergence from the sand. In contrast to burrowing, emergence takes place more or less vertically. In both species the lateral borders of the foot are pushed downwards and inwards, thus forcing the shell upwards through the sand. Repetition of this movement soon brings the entire shell and most of the foot above the surface, from which position the normal crawling movements serve to displace the remainder of the sand. This pattern of emergence was found to be invariable for both species.

Emergence takes place under water but not from wet sand exposed to air. This is probably not of ecological significance in the case of *Bullia laevissima*, which normally does not leave the water, but *B. digitalis* commonly buries itself in the wet sand of the foreshore and does then not emerge until that sand is again covered by the sea. That this is not caused by the suppression of some emergence stimulus but is entirely due to the inability of the animal to extricate itself could be shown experimentally. Animals were kept in a tank on sand covered with sea-water. When they had buried themselves the tank was tilted so that part of the sand was exposed to the air. When food was placed on the damp sand it was interesting to observe that a number of completely buried individuals attempted to emerge from the sand above the water level. This could be seen by the movements of the sand overlying them and in several cases the dorsal surface of the shell became visible, but the snails were unable to escape completely. Water-logged sand weighs very much more in air than in water and, in addition, wet sand-particles have a tendency to stick together in air. The combination of these factors appears to make it impossible for the animals to emerge.

Considering the stimuli which cause emergence, there is firstly a spontaneous emergence shown by both species of *Bullia*. Fig. 4 reflects clearly that some animals which have been fed emerge some 2 hours after burying themselves. Then, gradually, more and more individuals emerge so that 8 hours after feeding most are crawling once more on the surface. No external stimulus was applied which could have initiated their emergence. It seems most probable, therefore, that the stimulus is intrinsic; hunger would be a likely stimulus.

The presence of food causes emergence in both species. This was observed in the field, as already mentioned, and could be shown in the laboratory without difficulty. Substances emanating from the food have, of course, no effect on individuals which have just buried themselves after feeding.

A third type of stimulus causes emergence in *B. digitalis* but not in *B. laevissima*: water currents. As previously indicated, *B. laevissima* burrows when confronted by currents, deeper and deeper as the currents grow stronger. *B. digitalis*, on the contrary, responds to water-currents by emerging. It was observed that individuals of *B. digitalis*, buried below the tube through which the tank water was aerated, emerged from the sand when the air supply was switched on. Specimens buried in other parts of the tank were not affected. Since it could hardly be supposed that changes in oxygen tension had caused this response, more accurate experiments were made with currents produced by an electric stirrer. When the currents are such that no visible displacement of sand-particles takes place, the animals do not respond. It may be assumed, however, that they can perceive the current as part of the anterior siphon always protrudes above the sand. However, when the stirrer is lowered so that the surface of the sand is disturbed, the animals respond promptly by emerging. Apparently either the strong water-current as such or the sand-particles hitting the tip of the siphon initiates the reaction. Fig. 5 gives an example of such an experiment. Animals which were buried for a few hours after feeding showed a mass emergence when a strong current was applied for 10 minutes. As is to be expected, individuals do not respond to any marked extent shortly after feeding.

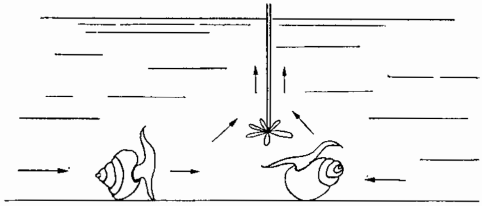

Fig. 6. Response of *B. digitalis* to water currents. Arrows indicate the direction of currents produced by an electric stirrer

The reactions of *B. digitalis* to water currents do not stop once the snail has emerged from the sand. Experiments with a large number of snails have revealed an interesting and uniform further response. After emergence they do not crawl, but turn on their sides, the shell apex facing the current, the side of the shell resting on the sand and the foot expanded as a sail (Fig. 6). This turning over is an active movement; they are not simply turned over by the current. It is easy to prove this in the laboratory by using a pipette to direct a brief jet of water towards a crawling animal; if the jet is strong and brief enough, then turning over is accomplished *after* the momentary current has abated.

The animal's final position with regard to the current is also not passively produced. The emerged animal can often be observed to wait for a few seconds and then suddenly turn round by means of movements of the foot. It then begins to move in the direction of the current, alternately arching and relaxing the foot. On reaching the area immediately below the stirrer, the snail turns onto its back and waves its foot this way and that in the water. When the currents stop the animals usually right themselves and resume normal crawling; when the current is reversed they start to move in the other direction. The movements are always in the direction of the current and, under the prevailing experimental conditions, are very definitely *active* movements. This does not, however, contradict the statement that in nature the wave-action is usually so strong that to a large extent the animals are carried passively, using the foot as a sail. It may be noted that this orientation towards water-currents takes place not only on emergence from the sand but also when the current is applied to individuals which are already crawling on the surface. However, it has not been possible to get snails to *crawl* in the direction of the current; orientated movement only takes place once the snail has turned onto its side.

The presence of food has a profound effect on the response to currents. When individuals are offered food in the course of their orientated progress, they commonly start to feed after which they usually bury themselves, taking no further interest in the current. When a water-current is applied to specimens already feeding they show no reaction and continue to feed, eventually dropping off and burrowing into the sand.

It is clear that the responses of *B. digitalis* to water-currents are related to the mode of life of the animal. Strong water-currents which displace sand occur in and below the swash-zone, causing mass-emergence of the population. The turned-over position, with the foot acting as a sail, perpendicular to the current, favours their being carried up and down by the waves, while active orientated movements may help to bring individuals from regions where the currents are too weak to move them. Both passive and active movements tend to bring the snails towards their food. Our observations that this species is left behind by the tide on very sheltered beaches is also explained. Apparently the wave-action in such localities is insufficiently strong to cause emergence.

III. Resistance to desiccation and other tolerance studies

Having studied certain features and responses which are definitely related to the mode of life of these animals, we now turn our attention to some other factors which may limit their distribution or be of importance to them in their particular environments. Resistance to desiccation is one such factor.

Since under normal conditions *B. laevissima* is never exposed to air, while *B. digitalis* is often found out of the water when feeding, a difference in resistance to desiccation between the two species would not be surprising. Nevertheless, since the operculum does not seal the mouth of the shell completely (Fig. 1) and as *B. laevissima* cannot even retract its foot completely into its shell, both species always present a defenceless naked area to the external environment. Neither species, therefore, was expected to be very resistant to desiccation. The influence of desiccation on a marine animal may be analysed into three parts: the rate of water-loss, the degree of water-loss which proves fatal, and the length of time for which various humidities can be withstood. These aspects vary with temperature. The only previous work attempted on the resistance to desiccation of marine gastropods in South Africa is embodied in papers by BROEKHUYSEN (1940) and BROWN (1960).

Rate of water-loss: In each experiment ten specimens each of *B. laevissima* and *B. digitalis* were stimulated to eject the water from their feet. Pressure was then exerted to ensure that the last drops of water had been eliminated. The animals were dried on blotting-paper before being weighed individually and transferred to desiccators over calcium chloride. Throughout the experiments the temperature was controlled at 19° C (±0.5). At intervals the snails were removed and weighed, and then replaced in the desiccators. At the end of the experiments the snails were dried to constant weight at 105° C, then macerated in water and the tissues completely removed. The shells were then dried to constant weight at the same temperature. This procedure produced the figures for total fresh weight, total dry weight and weight of shell, from which the fresh and dry tissue-weights and the water content of the tissues could be calculated. Table 1 gives the averages of these determinations. Fig. 7 gives graphic examples of the rate of water loss (average of 10 adult individuals of each species).

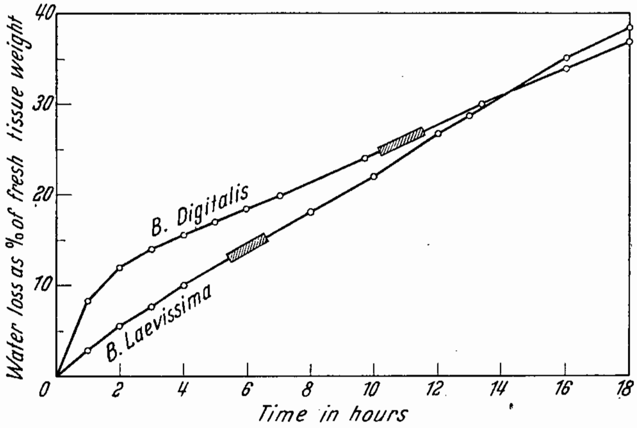

Fig. 7. Rate of water-loss in desiccators at 19° C. The animals died somewhere in the shaded areas of the curves

Certain conclusions can be drawn from the results of these experiments. Firstly there appears to be little difference in the rate of water loss between the two species, *B. digitalis* initially losing water at a slightly higher rate. This despite the smaller operculum, relatively larger shell mouth and incomplete retraction shown by *B. laevissima.* Secondly we must conclude that these animals have no physiological mechanism by which water loss can be controlled. If such a mechanism were present, one would expect that death and the subsequent disintegration of the tissues would lead to an alteration in the rate of water loss.

The percentage of water loss at which death occured, marked in Fig. 7 as a thick shaded portion of each graph, is taken from the results of experiments on fatal water loss (vide infra). The course of the graphs does not show any change after death, indicating that the living animal does not actively interfere with the process of desiccation.

Fatal water loss: Ten specimens of each species, per experiment, were treated as described for the experiments on the rate of water loss. In this series, however, individual snails were removed from the disiccators at intervals and, after weighing, transferred to sea-water. If they showed no signs of life after two hours and failed to respond to mechanical stimulation, they were presumed to be dead. By weighing the empty shells after removal of the tissues, the water loss at which death occurs could be calculated as a percentage of the original fresh tissue weight. As can be seen from Fig. 8, all individuals (100%) of *B. laevissima* survive loss of water up to 12% of their tissue weight. About 50% of those individuals losing 13—14% die, 66% die after loss of 15% water, and individuals which have lost 16% or more all perish. In the case of *B. digitalis,* all individuals which have lost 24% of their tissue weight, or less, survive, death occurs in 25% of the animals which have lost 24%, in half the animals losing 26%, in 60% of the animals losing 27% and in all the animals losing 28% or more.

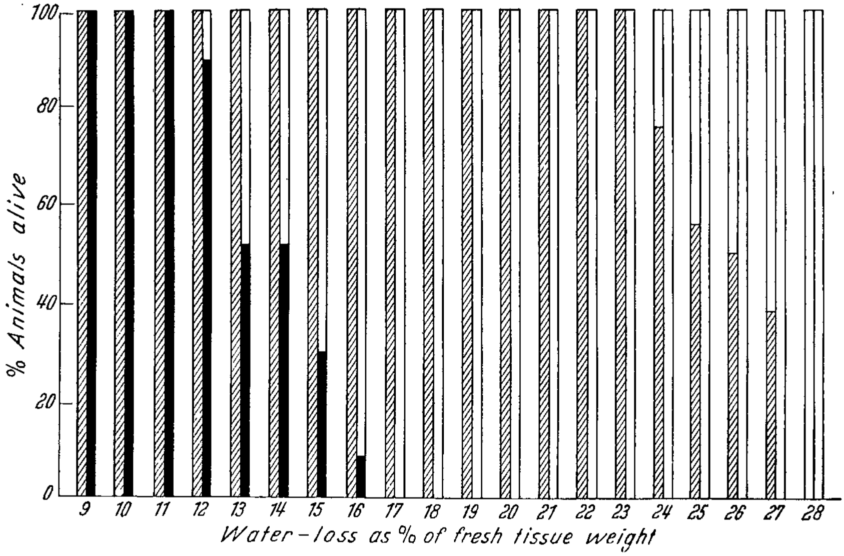

Fig. 8. The Water-loss which proves fatal. Dark columns % living *B. laevissima.* Shaded columns: % living *B. digitalis*

These results show conclusively that *B. digitalis* can withstand a much greater loss of water than *B. laevissima* before it dies; in fact about twice as much. From Fig. 7, into which these results have been introduced, it can be seen that the *period* of desiccation which can be withstood is also much longer in the case of *B. digitalis.* This stands to reason as they lose water at much the same rate.

Nevertheless, a word of caution is necessary, since the problem is not as straightforwards as it would appear at first sight. Though a number of *B. laevissima* is still alive after 10—14% water-loss, their feet are, often irreparably damaged. The foot looks partly brown, as if burnt, and often cannot be inflated completely. Individuals so affected have difficulty in burrowing, and are commonly incapable of doing so. In *B. digitalis* the same phenomenon is apparent between 20 and 25% water-loss. Since such individuals would be likely to perish in nature, the actual fatal water-loss may lie somewhat lower than the observed fatal water-loss found in these calcium chloride experiments.

Table 3. *Average tolerance to various relative humidities at 19° C*

Relative Humidity	Hours of survival	
	B. digitalis	*B. laevissima*
10	15	$13^{1}/_{2}$
31	24	19
56	40	31
78	62	49
91	ca. 100	63

Tolerance to various humidities: The length of time for which various humidities can be withstood may provide a useful set of figures since it reflects conditions in the field by employing a range of humidities. Furthermore, this tolerance must combine the two factors already discussed, fatal water loss and rate of desiccation. The method used was modified after Backlund (1945) and Williamson (1951). Two fresh adult individuals of one or other of the species, collected from the shore on the previous day and kept overnight in sand below sea-water without feeding, were induced to expel the water from the foot-cavity. Pressure was then exerted on the foot and the animal was dried on blotting-paper, before being placed inside a desiccator over a solution of sulphuric acid. The entire apparatus was kept at a temperature of 19° C (±0.5). In different series of experiments, different concentrations of sulphuric acid were used, the resulting humidities being calculated from the International Critical Tables (National Research Council, U.S.A., 1926). After a number of hours the specimens were transferred to sea-water at the same temperature. If they showed no signs of life after 2 hours they were presumed to be dead. Although only two specimens were introduced into the apparatus for each experiment, in order to minimise disturbances of the prevailing equilibrium humidity, the experiments were repeated many times and the average survival times calculated from the figures obtained. Table 3 shows the results for the averages of 25 individuals of each species. *B. digitalis* can survive various degrees of saturation deficiency for longer than *B. laevissima,* this difference becoming more marked at higher humidities.

In the life of *B. laevissima* its low tolerance to desiccation probably has no significance, since the animal is not normally exposed to air. *B. digitalis,* however, leaving the water for short periods of time, is temporarily subjected to saturation deficiencies. It is true that these periods are shorter than those found by experiment to be lethal, but the temperatures on the beach are by no means confined to the vicinity of 19° C as were the experiments. Temperatures of 30° C are common on the intertidal sands, and values as high as 35° C have been recorded. At such temperatures the tolerance to saturation deficiencies may well play a part.

Tolerance to high temperatures. BROEKHUYSEN (1940) has shown that there is a rough correlation between tolerance to high temperatures and the vertical zonation of certain rocky-shore gastropods. Since *B. digitalis* may encounter high temperatures when it leaves the water, while *B. laevissima* is never likely to encounter such conditions, a difference in temperature tolerance between the two species might well be expected. The methods used by BROEKHUYSEN were applied to these sandy-beach snails and were found to be quite suitable.

Ten adult snails of each species were placed in beakers containing sea-water. The beakers were transferred to a large tank with tap water which was heated so that the temperature of the sea-water rose by about 1° C every five minutes. After heating to the required temperature, the water was allowed to cool slowly to 19° C. During both heating and cooling the sea-water in the beakers was stirred from time to time. The snails were then left in aerated sea-water for 2 hours to see if they recovered. By repeating the experiment a number of times, the temperature causing 50% mortality was determined. These figures are 39.0—39.5° C for *B. digitalis* and 35.2—35.8° C in the case of *B. laevissima.* Thus the high temperatures recorded on the beaches of the Cape Peninsula are all below the values which prove lethal to the former species, while on extremely hot days *B. laevissima* would be seriously endangered were it to leave the water.

Tolerance to high and low salinities. Records of both species of *Bullia* from estuaries suggested that these animals might be able to withstand wide ranges of salinity. In addition *B. digitalis* may well encounter salinity variations when buried in the sand above the free water-level, for rain may greatly decrease the salinity of the interstitial water while evaporation will increase it.

Just as in the case of rocky-shore Gastropoda (BROEKHUYSEN 1940), it was found that crawling is only possible between certain limits of salinity. This effect was measured in preference to lethal salinities. Death as a direct result of unsuitable salinity may take many hours under experimental conditions and is therefore not a very accurate yardstick. Moreover, inhibition of the vital functions of the foot must limit survival in the field.

Ten specimens each of *B. digitalis* and *B. laevissima* were placed individually in beakers of sea-water at 19° C. At 10 minute intervals 15 ml distilled water were added to each beaker, the quantity added being later reduced to 10 ml and finally to 5 ml every 10 minutes. The water was stirred after each addition, and the crawling ability of the snail observed after mechanical stimulation. The movements made by the foot became more and more restricted in each case, until the snail was able to move forwards only in short, isolated jerks. At this point distilled water was added drop by drop (with stirring) until the snail no longer moved in response to mechanical stimulation. This was taken as the end-point, though the foot nearly always showed spasmodic localised contractions over its dorsal surface. The end-point salinity of the sea-water was determined by titration against silver nitrate.

At no time during the experiments did either species of snail attempt to retract the foot, which became swollen and smooth, obviously because of the osmotic inflow of water. After the experiment, half the snails of each species were returned to sea-water while the other half were kept at their endpoint salinities for 18 hours before being transferred to sea-water. All the snails showed complete recovery (with the single exception of a snail which is presumed to have died from other causes), which indicates that they can survive for a number of hours at such low salinities though they cannot lead an active life in such conditions. Crawling stopped completely in *B. digitalis* at salinities between 17.7 and $18.5^0/_{00}$, the average being $18.0^0/_{00}$, For *B. laevissima* these figures are 23.0—$24.0^0/_{00}$, the average salinity being $23.4^0/_{00}$. (The salinity of normal sea-water lies between 34.5 and $35.0^0/_{00}$.)

A second series of experiments was performed to find the upper limit of salinity at which crawling stops. The procedure was similar to that followed in the previous experiments, with the difference that instead of being distilled water, the water added was sea-water concentrated by evaporation at 60° C. The foot of each snail was observed to become a little shrunken and wrinkled, due to osmotic outflow, and at a certain point crawling became impossible. All these snails, including those kept at the end-point salinities for some hours, rapidly recoverd when transferred to normal sea-water. The upper limit for *B. laevissima* lies between 45.1 and $45.8^0/_{00}$, with an average of $45.5^0/_{00}$; for *B. digitalis* between 44.5 and $45.6^0/_{00}$, the average upper limit of salinity being $45.0^0/_{00}$

Both species, then, can tolerate a rather wide range of salinity variation, consistent with their occasional occurence in estuaries and — in the case of *B. digitalis* — easily correlated with the normal mode of life of the animal.

C. Discussion and Conclusions

Despite the similarities between the two species of *Bullia*, and the fact that both may occur intertidally, the foregoing studies bring to light a number of very real differences between the two animals. These differences may be summed up in a single generalisation: *B. digitalis* shows adaptations to variable intertidal conditions, while *B. laevissima* is adapted to more stable infratidal life and can thus only penetrate into the intertidal zone where conditions resemble the infratidal region.

The primary factors in the intertidal zone usually necessitating special adaptations are the rise and fall of the tides, and wave action. These primary factors in turn give rise to other problems which may be of importance to the animal. There may be the threat of exposure to the air, a problem much discussed in relation to rocky shores, or wave action may result in instability of the substratum, especially on exposed sandy beaches. If the animal is attached to the substratum it faces desiccation, temperature fluctuations and respiratory problems when the tide falls. If it is not attached to the substratum it risks being carried away by the currents, battered by the waves, and cast upon the beach to suffocate and die.

In *B. digitalis* we see a species completely at home in the intertidal zone. Much has been written about the harshness of the intertidal region and the pressing necessity of animals to either escape from or withstand wave action. Yet here we have a species making full use of these very hazards to perform its biological functions. Instead of trying to escape water-currents, *B. digitalis* is attracted to them. In fact we see that those individuals which have not already emerged driven by hunger, respond to strong currents by actively leaving their shelter in the sand. By using the fully expanded foot as a "sail" and adjusting itself to the direction of the currents, the animal expoits the water movements and uses them to carry it towards the food. The thinness of the shell and consequent low specific gravity of the animal makes this behaviour possible.

Led by its acute chemical sense, it has no further difficulty in finding its food in or just above the swash-zone. Temporary exposure to air does not endanger its life, since it can withstand a certain degree of desiccation and high temperatures for short periods. Nevertheless it avoids unnecessary exposure to air, for when no food is found on the foreshore it buries itself. That it cannot emerge before the water again covers the sand is an advantage, since it protects the animal against undue exposure. Undue exposure both to air and to its enemies in the water is also avoided since the animal buries itself after feeding.

Although *B. digitalis* exploits the waves in this way, surf action may well present other dangers. An animal using the waves to bring it ashore obviously runs the risk of being left behind on the beach when the tide receeds. For *B. digitalis* this might present a grave danger at or near high tide level; the drier sands of these regions make it difficult or impossible for the animal to burrow and, even if it did burrow, desiccation and rapidly increasing or decreasing interstitial salinities might well prove fatal. Also the next high tide might fail to reach it. That these problems are of the utmost importance is suggested by the dramatic way in which they are overcome. The snails avoid the top half of the intertidal beach and bury themselves near mid-tide level. Their subsequent emergence when the tide once more falls to mid-tide level appears to be yet another adaptation making full use of wave-action. The receeding waves of the swash-zone, reaching the buried individuals will disturb the substratum and thus stimulate emergence. Indeed the "harsh" conditions of the surf-swept beach are of primary importance to ensure the normal daily cycle of this species. As has been shown experimentally, on sheltered beaches, where wave-action is too weak to act as a stimulus for emergence, the cycle is profoundly disturbed, the buried animals being left behind by the receeding tide.

B. laevissima presents an altogether different picture. Instead of utilising wave-action, it avoids it and is thus confined to infratidal levels and those parts of the sandy intertidal zone in which infratidal conditions prevail. Far from being adapted to surf-beaten shores its reactions are an adaptation to escape from such an environment. Even such factors as its high specific gravity render it more suited to infratidal life and exclude it from transportation by means of water-currents. Unlike *B. digitalis*, *B. laevissima* buries itself deeper and deeper when confronted by currents or, when this is impossible, retracts its foot, thereby increasing its specific gravity and making it more difficult for movements of water to displace it. If still moved by the water, its weight is likely to favour downhill movement, away from the intertidal zone. Though relatively sensitive to desiccation and to high temperatures, these factors do not normally endanger the life of the animal as its reactions are such as to present little risk of exposure to air.

Nothing is known of the breeding habits of any species of *Bullia*. Indeed the only evidence available is a single egg-ribbon of *Bullia tenuis* (Barnard 1959). However, everything points to the suggestion that *B. laevissima* breeds only infratidally and it may be that *B. digitalis* does likewise. This would explain the infratidal records of the latter species and also our failure to observe any reproductive behaviour in the intertidal zone. However, this would imply *deliberate* off-shore movements on the part of the snails, with reactions quite contrary to those we have discovered. It is therefore tempting to suggest that, in view of the low specific gravity of the animal and its use of water-currents, any off-shore movements of water must inevitably carry snails to infratidal depths.

In addition to these conclusions about the animals themselves, some benefit may be derived from comparing *Bullia* with the snails of nearby rocky shores. Several authors, *e. g.* Erik Dahl (1953), have tended to speak of sandy shores as if the problems confronting the animals are basically the same as those faced by rocky-shore forms, and have even gone so far as to divide intertidal sands into vertical zones corresponding to the well-known zones of intertidal rock. This attitude may be useful in certain specific instances but our studies indicate that as a generalisation it has little to commend it. The environments presented by sand on the one hand and rock on the other are essentially different, and though both may occur in areas showing similar tidal variations and wave action, the effect of these factors on the environment — and hence on the animals — is different in each case.

This essential difference between the two types of environment is strikingly reflected in the modes of life of our intertidal Gastropoda. The sphere of activity of rocky-shore snails might almost be called "two dimensional" in that they are limted in their movements to the surface of the substratum. They cannot penetrate the substratum to escape exposure or wave-action and none, as far as is known, makes use of water-currents as does *Bullia digitalis*. Their defence often consists of clinging to their immovable substratum, a procedure impossible for *Bullia*, and they show a consequent zonation while *Bullia* moves freely up and down the shore. It is apparent, therefore, that wave-action and tidal rhythms do not always have the same significance for sandy-beach gastropods as they do for rocky-shore snails.

Bearing these differences in mind, it is still of interest to discover certain aspects in which the sand and rocky-shore snails resemble one another. In this respect it is worth noting that the resistance to desiccation shown by *Bullia digitalis* is almost identical to that displayed by *Oxystele sinensis*, occupying the lowest zone of Cape Peninsula rocky shores (Brown 1960). *Oxystele sinensis* is exposed to air for short periods by virtue of its position on the shore; *Bullia digitalis* is exposed for short periods in its search for food. *Bullia laevissima*, on the other hand, a species which does not normally leave the water, is less resistant to desiccation than are any of the intertidal rocky-shore snails. The same picture is presented with regard to tolerance of high temperatures.

Zusammenfassung

Die Beziehung zwischen dem Aufenthaltsort einerseits und seiner Struktur und seinen physiologischen Gegebenheiten andererseits werden für 2 *Bullia*-Arten im Freiland und Labor untersucht. Beide Arten leben

von toten Tieren. Sie dehnen ihren Fuß hauptsächlich durch Seewasser aus, das in einen Hohlraum des Fußes aufgenommen wird. Das Blut, welches in den Fuß gepumpt wird, genügt nicht wie bei anderen Gastropoden, um eine Schwellung zu erreichen.

Bullia digitalis lebt in der Gezeitenzone der sandigen Küste; bei Ebbe rollt sie mit gedehntem Fuß in die Brandung. Von den Wellen an den Strand getragen frißt sie dort und gräbt sich ein. Mit steigender Flut graben sich alle Tiere, die vom Wasser überschwemmt sind, ein, um 6 Std später bei fallendem Wasser wieder herauszukommen. Folgende Faktoren stehen in Beziehung zu ihrer Lebensweise:

a) Hungrige Tiere reagieren auf stark strömendes Wasser, indem sie aus dem Sand herauskriechen und sich vom Wasser mit ganz expandiertem Fuß fortbewegen lassen.

b) Ihr niedriges spezifisches Gewicht begünstigt den Transport durch das Wasser.

c) Augenscheinlich werden sie durch den chemischen Sinn aktiviert und zum Futter gelenkt. Selbst Tiere, die unter Wasser eingegraben sind, werden durch Futter aktiviert. Dabei dürften gelöste Stoffe, die vom Futter ausgehen eine Rolle spielen. Weitere Untersuchungen sind im Gange.

d) Die Tiere können eine gewisse Austrocknung, ziemlich hohe Temperaturen und auch ziemliche Salzgehaltsschwankungen ertragen. Das stimmt mit ihrem zeitweiligen Auftreten an der Küste und ihren Vorkommen in den Flußmündungen überein.

e) Das allgemeine Eingraben bei steigender Flut steht nicht mit der Futteraufnahme in Beziehung ~~sondern~~ folgt keinem inneren Rhythmus; H UND darüber laufen weitere Untersuchungen.

Bullia laevissima lebt unterhalb der Gezeitenzone oder in Wasser, das nur schwach von Gezeiten beeinflußt ist. Gewöhnlich nur halb in Sand eingegraben verläßt sie nie das Wasser.

Dementsprechend finden wir:

a) Die Tiere vermeiden starke Strömungen und graben sich, diesen ausgesetzt, tiefer ein.

b) Die schwere Schale ist einem Transport durch Wasser hinderlich.

c) Obgleich diese Tiere augenscheinlich durch ihren chemischen Sinn für Futter unter Wasser geleitet werden, können sie nicht dazu gebracht werden, das Wasser des Futters an der Küste wegen zu verlassen; sie verweigern das Futter am Lande.

d) Sie sind empfindlich gegen Austrocknung und hohe Temperaturen, Faktoren, die ihre Fähigkeiten außerhalb des Wassers zu leben herabsetzen.

e) Gegen Salzgehaltschwankungen sind sie weniger empfindlich, was ihr Vorkommen in Flußmündungen ermöglicht.

Die Arten scheinen weder einen physiologischen Mechanismus, der den Grad der Austrocknung kontrolliert, zu haben, noch zeigen sie Vorliebe für eine bestimmte Sandkorngröße, wenn auch *B. laevissima* sich leichter in gröberen Sand eingräbt.

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Addendum. Since the preparation of this manuscript in February, 1959, further information on Bullia has come to light. Dr. K. H. Barnard, of the South African Museum has reidentified the south coast specimens from exposed beaches as *Bullia rhodostoma (non digitalis)* (*vide* Barnard 1959). Fortunately, all my experimental material was collected at Hout Bay, where *B. rhodostoma* does not occur. Dr. Barnard has kindly examined my preserved material and assures me that only *B. laevissima* and *B. digitalis* are involved. Though difficult to distinguish morphologically, I find interesting physiological and ecological differences between *B. digitalis* and *B. rhodostoma*; these will form the basis of a further communication.

Investigations into the sensory physiology of *Bullia* are proceeding and it has been possible to show that the osphradium is an organ of distance chemoperception in *B. laevissima* (*vide* Krijgsman *and* Brown 1960, and Brown *and* Noble 1960). Results of experiments on feeding behaviour and chemoreception are shortly to be sent to press.

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2.

FUNCTION OF THE OSPHRADIUM IN BULLIA (GASTROPODA).

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3.

EFFECT OF HYDROGEN SULPHIDE
ON BULLIA (GASTROPODA).

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Effect of Hydrogen Sulphide on *Bullia* (Gastropoda)

THE toxicity of hydrogen sulphide to mammals and certain other vertebrate animals is well known, and it is generally considered that the lethal effects of this substance are due in part to direct combination with the animal's hæmoglobin, leading to the formation of choleglobin and sulphæmoglobin, as well as to the inhibition of several enzyme systems associated with heavy metals. Invertebrate animals do not appear to have been investigated in this respect, excepting only *Arenicola marina*, the hæmoglobin of which does not combine with hydrogen sulphide but is a very active catalyst of sulphide oxidation[1]. By means of this, and possibly other, mechanisms, the worm is able to tolerate high concentrations of sulphide for lengthy periods.

The production of sulphides in marine sediments has been examined by Bruce[2], Galliher[3] and other workers, while a review of the subject is provided by Perkins[4]. Marine ecologists have noted the absence of macro-organisms from regions so affected and have tended to link this with the lack of oxygen in the 'black layers'. The present observations on *Bullia* were initiated by the disappearance of *B. laevissima* and *B. digitalis* from the Harbour Beach and the North Beaches respectively of Hout Bay, beaches on which these sand-burrowing prosobranchs were previously abundant (*vide* Brown[5]). The gradual disappearance of these molluscs coincides with the increasing organic pollution from the outlet of a fish-meal factory to which the Hout Bay beaches have been subjected in recent years. At the present time the northern beaches of the bay are virtually devoid of macro-organisms between tide-marks, the sand is blackened and disturbance of the substratum releases small quantities of hydrogen sulphide gas. Conditions are not, however, as extreme as have been observed in many relatively unpolluted South African estuaries[6,7].

Individuals of *B. laevissima* and *B. digitalis* were kept in jars of sea-water through which hydrogen sulphide was bubbled. From time to time individuals were removed and placed in fresh, aerated sea-water. All those removed after 0·5 h or longer of this treatment appeared dead and did not recover. Animals removed within 15 min all recovered, though movement had ceased. Of the animals removed at intermediate stages some recovered completely, others did not, and some appeared to recover but were found dead the next day. In a subsequent series of observations, jars of sea-water were bubbled with hydrogen treated. This was repeated four times (with the same snails) with the identical result. If the entire substratum was treated or if hydrogen sulphide had been briefly bubbled through the water itself, the snails refused to burrow and eventually turned on to their backs and spread their feet, a position which, in the field, encourages transport by waves and water-currents[5]. Such behaviour might well account for the absence of *Bullia* on the beaches mentioned. The detection of hydrogen sulphide is not confined to the osphradium or some other specific chemoreceptory organ, for if a piece of cotton-wool is soaked in sea-water through which hydrogen sulphide has been bubbled, and then applied to any part of the head or foot of a snail which has been removed from the water, violent brushing-off movements are initiated and the proboscis is often everted and extended towards the affected region. The same reactions are used as a defence mechanism against would-be predators, but do not occur if cotton-wool soaked in unadulterated sea-water is applied to the foot.

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4.

BLOOD VOLUMES, BLOOD DISTRIBUTION AND SEA-WATER SPACES IN RELATION TO EXPANSION AND RETRACTION OF THE FOOT IN BULLIA (GASTROPODA).

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BLOOD VOLUMES, BLOOD DISTRIBUTION AND SEA-WATER SPACES IN RELATION TO EXPANSION AND RETRACTION OF THE FOOT IN *BULLIA* (GASTROPODA)

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INTRODUCTION

Bullia is a South African prosobranchiate gastropod, of the family Nassariidae, which burrows in marine sands. So great is the expansion of its ploughing foot that for decades it was believed that this expansion was accomplished largely or entirely by the introduction of sea water into spaces within the foot (Gilchrist, 1916; Clarke, 1951; Brown, 1961 *a*; etc.). However, it has been shown more recently that the jets of water, which appear to issue from the foot when the animal retracts into its shell, in reality originate chiefly from elsewhere and that the foot is expanded in the usual way, by the introduction of blood into the pedal sinus (Brown & Turner, 1962). Pelseneer (1906) appears to have been correct in assuming that the volume of this fluid is quite adequate for expansion of the foot in all gastropods, though no one has measured the blood volumes of snails achieving so remarkable an expansion as does *Bullia.* Indeed the whole subject of retraction and expansion in gastropods has been neglected to such an extent that text-books and review articles seldom mention it except to state that the animal is pulled into its shell by means of the columella muscle.

The work reported in these pages represents an attempt to elucidate this problem in the case of *Bullia*, special attention being paid to movements of blood during retraction and to the sea-water spaces. Measurements of blood volume are also reported as these are relevant to our conclusions.

Though previous writers have drawn attention to the unusually large size of the foot of *Bullia*, no measurements of its degree of expansion have been made except for the few indirect measurements of Brown (1961 *a*). Indeed it has been suggested to me that the apparent degree of expansion may be deceptive if judged only visually; for although the foot covers a large area when fully expanded—13 cm.^{2} in the case of a *B. digitalis* whose retracted volume is only 2 c.c.—it is also very thin indeed, particularly posteriorly and laterally. Some idea of the volume of the foot may be obtained by gently lowering an expanded snail into a graduated cylinder containing sea water until the foot is just submerged, then reading off the volume of water displaced. As the foot is not sharply divided from the rest of the body, some criterion is necessary for deciding just how far the snail should be lowered. I have found it convenient to lower the animal until the head just touches the water. It is found by this method that the volume of the expanded foot of *B. digitalis* is almost two-thirds of the volume of the retracted snail, or one-third of the total volume of the expanded snail. This confirms previous volume measurements (Brown, 1961 *a*) and enables us to calculate that the average thickness of an expanded foot covering an area of 13 cm.^{2} is of the order of 1·0 mm. It is true, then, that the foot is very thin but this does not imply that its degree of expansion is really no greater than in other prosobranchs. I have taken a number of readings of the volume of the foot in local rocky-shore snails, including *Burnupena*, *Thais* and *Oxystele*, and find that their foot volumes are all less than half that of *Bullia*, most being less than one-third. While the method used is admittedly inaccurate and gives very approximate readings, the differences between rocky-shore snails and *Bullia* are so great as to leave no doubt that the degree of expansion in the latter snail is unusually large.

BLOOD VOLUMES

Little work has been done on the blood volumes of the Gastropoda, and much of what has been done would appear to be of doubtful value. Leitsch (1916) and Borden (1931) both calculated the haemolymph volume of the pulmonate *Planorbis*, but obtained results which differ from one another by nearly 100 %. The different methods used would be expected to give somewhat different results, but to know that Leitsch's value of 30 % is too low, while Borden's of 58 % is too high, does not lead to a realistic assessment of the animal's true blood volume. Moreover, most workers have included the weight of the shell in their calculations, an obvious error in view of the fact that it is non-living and is not supplied with blood at any time. Such a procedure renders the final figures virtually meaningless, for not only does the shell commonly weigh very much more than the living tissues but also the shell weight/tissue weight ratio differs both from species to species and among individuals within the species, such differences being correlated with age and the conditions under which the snails have developed (Nolan & von Brand, 1954; etc.). Similar problems have arisen with regard to the study of the resistance to desiccation of rocky-shore snails (see Brown, 1960).

Perhaps the only reliable work on gastropod blood volumes is that of Martin, Harrison, Huston & Stewart (1958) who appear to have taken every possible precaution against error and who do not include the weight of the shell in their calculations. They found the mean blood volumes of *Aplysia californicus*, measured by three different methods, to be 79·3, 76·2 and 73·1 % respectively, results which are lower than those arrived at by Martin & Huston (1950). The blood volume of the nudibranch, *Archidoris*, is given as 65·5 %, while the figure for the pulmonate, *Achatina fulica*, is 40·3 %. The blood volume of *Arion ater* is still lower and shows a mean of 36·6 %.

Measurements of blood volumes in animals in general fall into two groups as far as methods are concerned. Early investigators bled their animals, often extracting the blood pigment from the tissues in addition; they obtained results which were invariably too low. Other methods all rely on the dilution of a known quantity of material injected into the circulating fluid, the readings obtained being higher than the true blood volume due to loss of the injected substance to the tissues and possibly through excretion. A large number of different materials have been used in such dilution studies (see Hopper *et al.* 1944; Yeager & Munson, 1950; Martin *et al.* 1958; Nicol, 1960; Prosser & Brown, 1961; etc.). For the present investigation the amaranth dye-dilution method was used. It, too, gives results which are consistently high, but it appears to involve smaller random errors than many other methods (Yeager & Munson, 1950). An attempt was made to reduce these errors still further by using a more dilute solution of amaranth, injecting more of it and extracting a larger blood sample, than was possible in Yeager & Munson's work on *Periplaneta*. This could be done in view of the fact that the animal, in addition to being much larger, is not enclosed in a hard exoskeleton so that an increase in the volume of haemolymph circulating in the open blood system does not lead to a proportional increase in the pressure of the system.

Material and methods

Only large adults of *Bullia* were used in these experiments. They were obtained from two Cape Town beaches; *B. rhodostoma* from Muizenberg, *B. digitalis* and *B. laevissima* from Hout Bay. The snails were sorted into sexes as well as species, giving six experimental groups in all. They were kept in the laboratory in a large sea-water tank with a sandy substratum, at a temperature of 15° C. (±0·5), the experiments being performed within a few days of capture.

Preliminary experiments showed that 0·5 c.c. of fluid could be injected into a snail without deleterious effects. Even injections of 1 c.c. of sea water or gastropod Ringer appeared to have no affect on the behaviour of the animal, excepting only that the foot could not be pulled completely into the shell on retraction. (The same phenomenon has been observed after snails have taken a heavy meal.) It was assumed that if 0·25 c.c. of dye solution were injected, undue increase in the blood pressure would be avoided while at the same time allowing accurate readings of blood volume to be made. Injection of a concentrated amaranth solution into the pedal sinus showed that there was a circulation of blood in this sinus while the foot was expanded, other parts of the animal turning pink by degrees. However, the length of time taken for the extreme posterior region of the semi-transparent foot to change colour indicated that circulation in this part of the sinus is very poor. This pattern became even more marked when congo red or a carmine suspension was substituted for amaranth, the siphon taking up to 25 sec. to become pink and the posterior part of the foot often showing no colour change until after retraction and re-expansion.

The method used to obtain readings from individual snails were therefore as follows. Snails were placed individually in a series of labelled dishes containing sea water. Each snail in turn was removed, placed on blotting paper with the foot expanded, and then dried. (This procedure raises the threshold for retraction, a threshold which is in any case very high (see Brown, 1961*a*).) 0·25 c.c. of a 0·2% solution of amaranth in saline was injected into the pedal sinus through the blotting paper and the ventral surface of the foot. When injection was completed the animal was caused to retract by pinching it behind the head and then returned to its dish where it was encouraged to re-emerge by rotating the dish so as to produce water-currents. *Bullia* refuses to emerge in air and emergence under water is stimulated by water-currents. The expanded snail was again placed on dry blotting paper and a sample of 0·25 c.c. of its blood drawn off from the pedal sinus and placed in a labelled sodium-fusion tube. As the blood of *Bullia* does not clot it was unnecessary to treat it in any way. After the series was completed the colour of the blood in the tubes was compared visually with a number of standard solutions of amaranth made up in *Bullia* haemolymph and maintained in sealed sodium-fusion tubes. Snails were dried and weighed individually, with feet retracted, and the empty shells were weighed again after removal of the animals. The difference gave the weight of the wet tissues.

A modification of this method, in which 0·25 c.c. of blood was removed from the pedal sinus before injection of the dye solution did not give consistently different results and was thus not applied throughout the series. As the volume (d) and the molar concentration (c') of the injected dye solution and the concentration of the dye in the blood (c'') at the time of sampling were known, the blood volume (V) was obtained from the formula

$$V = \frac{d(c' - c'')}{c''} - d$$

in the majority of cases, but as

$$V = \frac{d(c' - c'')}{c''}$$

where a volume of blood equal to the volume of injected dye solution had previously been withdrawn.

Following the experiments on individual snails, several *B. digitalis* were treated in the same way, but the resulting blood samples were pooled to give an adequate volume of fluid for use in an Eel photo-electric colorimeter. Pooled blood from *B. rhodostoma* was used on a subsequent occasion.

Results

The results of blood-volume analysis are shown in Table 1. They are expressed as millilitres of blood per 100 g. wet tissue weight (i.e. excluding the shell) but as both the blood and the tissues have very nearly the same specific gravity (1·027–1·030), they may be read directly as percentage blood volume. The error involved in this approximation is almost certainly less than discrepancies due to experimental error.

Table 1. *Blood volumes of* Bullia *in millilitres of blood per* 100 *g. wet tissue weight*

(The figure following the ± sign is the standard error of the mean, where this is applicable.)

Species	Sex	Method	No.	Range	Mean	Standard deviation
B. digitalis	Males	Individual	24	56·7–71·0	64·1 ± 0·72	3·55
	Females	Individual	20	52·2–75·3	66·0 ± 0·91	4·10
	Mixed	Pooled	20	—	66·4	—
	Mixed	Pooled	12	—	62·9	—
B. rhodostoma	Males	Individual	20	51·9–71·5	62·8 ± 1·04	4·71
	Females	Individual	18	55·6–71·7	64·2 ± 0·90	3·87
	Males	Pooled	10	—	61·7	—
	Mixed	Pooled	12	—	65·1	—
B. laevissima	Males	Individual	6	49·8–65·3	57·9 ± 2·33	5·70
	Females	Individual	4	49·3–61·7	56·6	—

The differences indicated between males and females in all three species are not statistically significant; nor are the differences between *B. digitalis* and *B. rhodostoma*. The difference between the intertidal snails (individual readings from *B. rhodostoma* and *B. digitalis* combined) and the infratidal *B. laevissima* do, however, show some degree of significance ($P = 0·19$).

It is apparent that, as in all other work on blood volumes, the final results incorporate a number of errors. I believe, however, that these have been reduced to a reasonable level; the ranges of individual haemolymph volumes in each group, and hence the standard deviations, are relatively much smaller than those obtained by Yeager & Munson (1950) using the same dye-solution method on *Periplaneta*, and compare favourably with the measurements of Martin *et al.* (1958) on various molluscs. However, the results may also indicate that my material was, in fact, less variable than Yeager & Munson's. A consistent error, due to loss of dye to the tissues, remains. Attempts to evaluate this error are not described here as they proved fruitless. Unfortunately *Bullia* does not lend itself to the techniques of catheterization described by Martin and his co-authors, and repeated sampling of blood through a hypodermic needle was not a practical possibility. For this reason exponential curves plotted on semi-logarithmic graph-paper and extrapolated back to zero position on the time scale could not be prepared. We can be certain that the figures given for blood volumes are consistently too high.

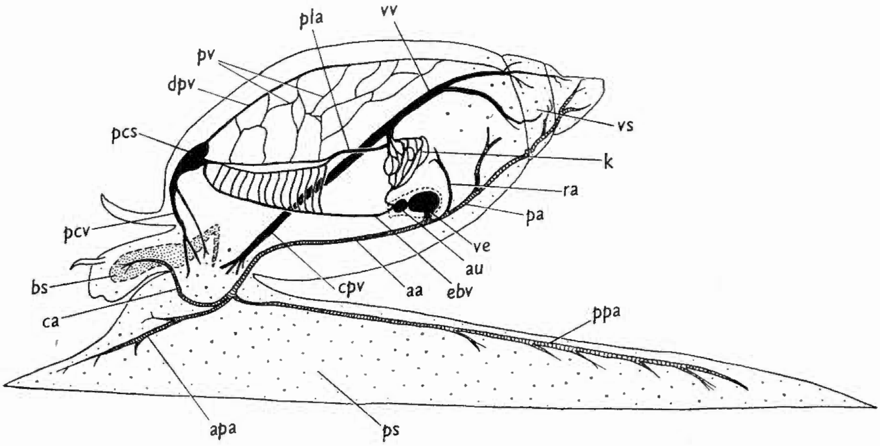
In spite of this, and contrary to what had been expected, it is apparent that *Bullia* does not possess an abnormally high percentage of blood. The means for all groups lie between 56 and 66·5 %. These values are certainly much higher than those determined for arthropods, pelycepods and cephalopods, but are lower than those obtained from the tectibranch gastropod *Aplysia* and of the same order as the percentage blood volume in the nudibranch *Archidoris* (Martin *et al.* 1958). The value obtained by Borden (1931) for *Planorbis* also lies within the range covered by the species of *Bullia*. It is unfortunate that no previous work has been published on the blood volumes of marine prosobranch Gastropoda, for it is thus impossible to compare the blood volumes of *Bullia* with any closely related forms. Our conclusion that blood volumes in this animal are not abnormally high is thus based on comparison with non-prosobranchiate aquatic forms and it is possible that it may have to be revised when a greater body of knowledge is at our disposal. However, the volume is certainly not great enough to be correlated directly with the striking degree of expansion of the foot.

BLOOD MOVEMENTS AND DISTRIBUTION

The mechanism of pedal expansion in gastropods (or in pelycepods) has never been properly worked out. The 'turgor' of the foot is caused by the introduction of blood yet, in *Bullia* at least, this fluid continues to circulate through the pedal sinus while the foot is in the expanded condition. It has also been shown that the volume of blood in *Bullia* is not abnormally large for an aquatic gastropod, despite the unusually extensive expansion of the foot. It might easily follow that the animal is capable of shifting a greater proportion of its total blood volume into the pedal sinus than is the case in most other gastropods, and this in turn might imply greater control over blood movements. The rapid movement of large quantities of blood when the snail retracts or expands might be expected to place a severe burden on the heart, an organ which seems hardly designed to withstand such strains or to maintain the pressure needed for turgor of the foot. However, it seemed possible that the heart might play little part in filling or emptying the pedal sinus; Prosser (1952) has made the statement that 'in all animals in which the blood circulates in sinuses the flow is controlled much more by the activity of the somatic musculature than by heart activity or vessel size'. Nevertheless, it is alleged that in the burrowing pelycepod, *Solen*, blood enters the foot during extension via the heart and pedal artery (Fraenkel, 1927).

Material and methods

Radiographical methods were used to investigate the path taken by the blood leaving the foot of *Bullia* during retraction. In order to understand the results of this study it became necessary to dissect the circulatory system, individuals of *B. laevissima* and *B. digitalis* being pretreated by injecting indian ink or coloured Latex into the heart, efferent branchial vein or cephalic sinus system. Individuals of *Burnupena* (family Buccinidae) were treated in the same way and dissected for comparison.



Text-fig. 1. Diagram of the main blood-vessels of *Bullia*. *aa*, Anterior aorta; *apa*, anterior pedal artery; *au*, auricle; *bs*, buccal sinus-system; *ca*, cephalic artery; *cpv*, cephalopedal vein; *dpv*, dorsal pallial vein; *ebv*, efficient branchial vein; *k*, kidney vessels; *pcs*, pallial collecting sinus; *pcv*, pallial collecting vessels; *pa*, posterior aorta; *pla*, pallial anastamosis; *ppa*, posterior pedal artery; *ps*, pedal sinus; *pv*, pallial vessels; *ra*, renal artery; *ve*, ventricle; *vs*, visceral sinus system; *vv*, visceral vein.

A diagrammatic representation of the main blood vessels of *Bullia* is included as Text-fig. 1. The system greatly resembles that of *Littorina* and differs in several features from the more common monotocardian plan in which there is no direct connexion between the kidney veins and the heart (see Fretter & Graham, 1962). The anterior sinus system, however, differs from the reduced condition found in *Littorina* and resembles that of *Burnupena*, both conforming to the typical prosobranchiate plan. Both dorsal and ventral buccal sinuses are present, the latter being the more extensive; both drain into a ventral cephalic sinus from which the blood can only escape by passing upwards into the dorsal cephalic sinuses which lie above the mid-oesophagus. The subdividing septa of the dorsal cephalic system are incomplete and blood can escape ventrally into an oesophageal system of subdivided sinuses which ultimately link up with the pedal sinus. The pedal sinus, taking up the whole of the foot and part of the head, does not appear to be subdivided by septa though the distribution of muscles running through the sinus is such as to provide numerous spaces and channels. The transverse septum, dividing the anterior system of sinuses from the posterior ones, seems to be very well developed and is muscular in appearance.

There are two routes by which blood may leave the pedal sinus. A large cephalopedal 'vein' drains the central portion of the sinus, while two pallial collecting vessels drain the left side and carry the blood round the mantle collar to a large pallial collecting sinus. From here blood can enter the pallial system of veins and sinuses or pass to the gill. The dorsal pallial vein, the largest of the pallial vessels, enters the visceral sinus system, providing direct vascular communication between anterior and posterior regions of the body. Blood passing up the cephalopedal vein will meet blood coming from the visceral sinus system via the visceral vein, both streams entering the afferent renal vein and draining into the kidney vessels. An alternative route is provided by a vessel which leaves the afferent renal vein where the latter enters the kidney and, after crossing the cephalopedal vein, branches to join the afferent branchial system and the pallial veins. I propose to refer to this vessel as the 'pallial anastomosis', for reasons which will appear later. Blood returning to the heart must thus pass through either the kidney or the gill (but not both as in the majority of prosobranchs); at the same time the vascular system is such that not all the blood leaving the sinus systems must of necessity pass through the heart before recirculating.

The vessels I have referred to as the cephalopedal and visceral veins are, in fact, not veins but sinuses. However, these terms are used by such authorities as Fretter & Graham (1962) in describing the blood system of *Littorina* and are adopted here in preference to the more accurate but somewhat confusing terminology used later by the same authors in their general account of prosobranch anatomy. These vessels in *Bullia* resemble those of *Littorina* in being of fairly uniform bore, while those of *Burnupena* are more irregular and less tube-like. *Bullia* differs from both these snails, however, in the size of the cephalopedal and visceral veins. They are much wider than one imagines from dissection of preserved material and are about twice the width of these structures in *Burnupena*. There are no valves or projections in these vessels, even at their junction, which might impede the flow of blood.

In order to discover the route taken by blood leaving the pedal sinus during retraction, radio-opaque dyes were injected into the haemocoel and radiographs taken both with the foot fully expanded and at various stages of retraction. Two clinical dyes, 'Urografin 76%' and 'Hypaque', proved very toxic to the snails and their injection caused immediate retraction and death; moreover, at exposures of X-rays necessary to penetrate the shell (0·03 sec. at 200 mA. and 66 kV.) these dyes were not sufficiently radio-opaque to cast adequate shadows. Prior removal of the shell would have overcome the latter consideration but would also have partially defeated the aim of the investigation, as the animal would no longer have anything to retract into. For this reason, too, the fluorescent-dye method used by de Graaf (1957) was not attempted.

A third radio-opaque dye, 'Thorotrast', was obtained from the firm of Testagar and Co., Detroit, U.S.A. This is a colloidal suspension of thorium dioxide, extremely opaque to X-rays and chemically unreactive. The dye was originally used in clinical hepatolienography and arterioradiography (Radt, 1929; etc.), but as thorium is radioactive this practice has been largely discontinued. Thorotrast has been used quite extensively, however, in studying vascular systems of the lower vertebrates (Foxon, Griffith & Price, 1956; Foxon & Rowson, 1956; Foxon, 1961*a*, 1961*b*; etc.). Its immediate toxicity is very much lower than that of most other radio-opaque dyes, while its opacity is greater. It does not appear to have been used previously on invertebrate animals, substances such as bismuth oxycarbonate being more popular (e.g. Newell, 1950). I have been unable to trace any reference to X-ray techniques having been previously carried out on Gastropoda.

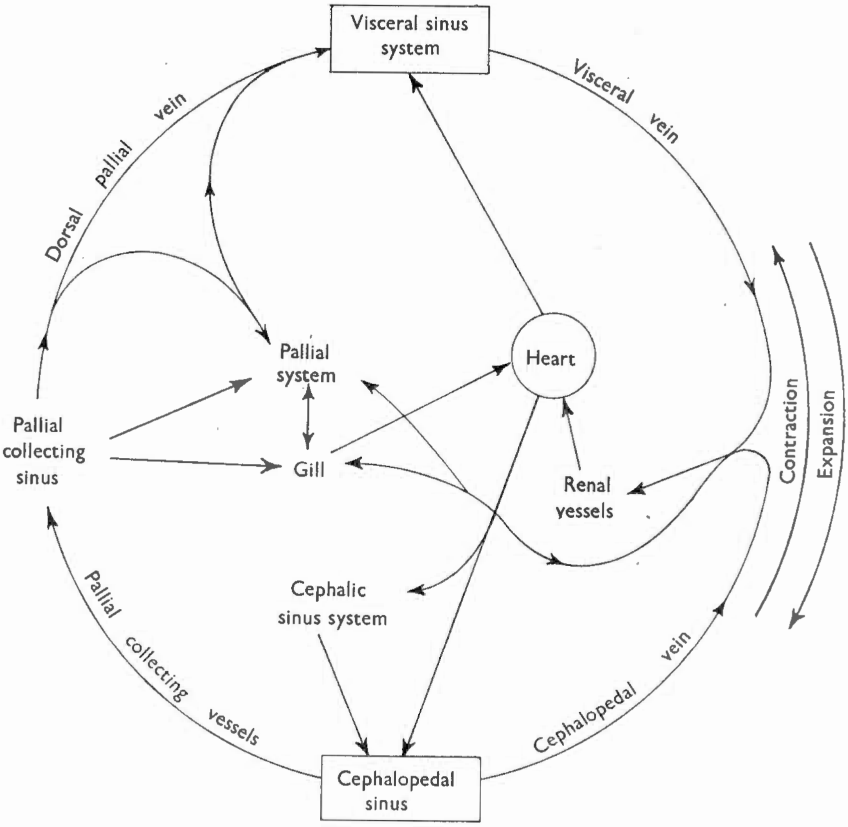
Snails were taken to a local hospital either straight from the sea or from the constant-temperature room in which they had been kept for a day or two at 15° C. They were kept as cool as possible throughout the experiments. Snails were removed from the water and suspended individually in front of a vertically placed X-ray plate. The source of X-rays was a clinical diagnostic machine with horizontal tube and a distance of 100 cm. between shutter and film. The optimal exposure was found to be 0·03 sec. at 200 mA. and 66 kV., this exposure being capable of penetrating both thicknesses of shell as well as the living tissues, while still giving a Thorotrast shadow of reasonable contrast.

Thorotrast was injected into the pedal sinus through a fine hypodermic needle from a 2 ml. syringe. This seldom stimulated retraction but retraction could be provoked when required by pinching the animal behind the head. The exposure was made either during injection or at a definite time after injection had been completed. For each snail the amount of Thorotrast injected was noted, as well as the injection site, how long afterwards the exposure was made, the state of expansion of the foot and any other relevant information. The radiographs were numbered and developed immediately and later examined through a viewer. Positive contact prints and photographic slides were prepared from many of the plates, the slides being projected onto a screen for detailed examination. This method is suggested by Foxon (1961*b*)

Results

An increase of pressure in the pedal sinus causes blood to flow from this sinus up the cephalopedal vein, past the junction of this vessel with the afferent renal vein and into the visceral vein (see Pl. 1, fig. 3). If this increase of pressure is sufficiently great, blood from the foot passes along the whole length of the visceral vein (in the 'wrong' direction) and enters the visceral sinus system (Pl. 2, fig. 1). At the same time some blood enters the kidney vessels, as it is bound to do if the heart maintains its beat. Such increase of pressure may be brought about artificially by the injection of fluid (including Thorotrast) but will take place under natural conditions when the muscles of the foot contract. The radiographs confirm this fact, for the same result is obtained either if a large quantity of Thorotrast is injected into the pedal sinus or if a smaller volume of dye is followed by retraction of the foot. Moreover, the phenomenon is seen even if the foot only partially contracts. We are bound to conclude that during retraction the heart, gill and kidney are all 'short-circuited', blood being shunted from the pedal sinus to the visceral sinus system via the shortest route. The heart is still supplied via the kidney and efferent branchials but there is nothing to suggest that it deals with a greater volume of blood than usual, as retraction is normally completed without Thorotrast appearing in the anterior aorta. (The possibility of dye appearing in the posterior aorta has not been considered as this vessel is masked by other structures in the retracted snail and Thorotrast in it would pass unnoticed.)

While it is clear that, on retraction, blood flows from the pedal sinus through the cephalopedal and visceral veins into the visceral sinuses, it has not been possible to obtain radiographs showing the reverse procedure when the animal emerges and expands its foot. It is, of course, possible to drill a small hole in the upper whorls of the shell and inject Thorotrast through it into the visceral sinus system. However, snails so treated cannot be induced to emerge even if the hole is plugged immediately. After 10–15 sec. the Thorotrast has entered the pedal sinus through the normal circulation via the heart, making it pointless to continue the experiment.



Text-fig. 2. Diagram of haemolymph flow in *Bullia*.

On many of the radiographs the pallial system of vessels and sinuses shows up diffusely. In most cases it is only the anterior part of the system which contains Thorotrast and it is clear that the dye has entered it by way of the pallial collecting vessels of the mantle skirt. In such cases the pallial collecting sinus casts a heavy shadow. However, where injection has been made into the right side of the foot and particularly if the snail is contracting simultaneously, it is the more posterior part of the pallial system and the afferent branchial vessels which show up. In a few radiographs, all made from snails which were retracting rapidly, there is a vessel in the extreme posterior region of the system which is obviously full of dye (see Pl. 2, fig. 1). In the radiographs the vessel in question appears to originate from the junction between the cephalopedal and visceral veins, that is in the same region as the afferent renal vein. Anatomical considerations deny the existence of such a vessel and the only vessel which could possibly give this erroneous impression on the radiographs is the 'pallial anastamosis' (see Text-fig. 1). I have given it this name as it would appear that one of its functions might be to equalize the pressure in the two systems involved —to act as an escape valve preventing dangerous pressure being exerted on either the kidney or the branchial vessels. This suggestion is borne out by the fact that it only casts a Thorotrast shadow in snails which are retracting rapidly, the blood vessels being presumably subjected to relatively large changes in pressure.

In addition to the cephalopedal-visceral tube, another vessel links the pedal and visceral sinuses. This is the dorsal pallial vein which arises from the pallial collecting sinus and proceeds across the mantle, to the right of the mid-line, eventually entering the visceral sinus system. Though the anterior part of this vessel is often seen in the radiographs, no shadow representing the posterior part has been made out under any circumstances. This leads me to believe that it does not constitute an important pathway for blood leaving the pedal sinus during retraction; its small size compared with the cephalopedal-visceral tube also suggests that it is of little importance as an alternative route. A flow diagram, which incorporates the radiographical findings, is included as Text-fig. 2.

SEA-WATER SPACES OF *BULLIA*

When *Bullia* retracts slowly into its shell, a jet of sea water issues with considerable force from the hind margin of the foot. When retraction is rapid two further jets are often seen, a pair of anterolateral ones being present in addition to the invariable posterior jet. The amount of water released is the same regardless of the number of jets produced. Gilchrist (1916) collected this water and found that it nearly filled the shell of the snail after the animal had been removed. Brown & Turner (1962) showed that about one-third of the water comes from the mantle cavity (or its vicinity), while the contribution of the foot itself—from the 'aquiferous spaces'—is very small indeed. They noted the considerable amount of water contained in the proboscis sheath but were unable to show that it contributed to the jets. They were also not able to extract any water from the 'free space' between the shell and living tissues. An unpublished experiment which they performed was to cut the last whorl off the apex of the shell, wait for the animal to expand its foot, remove it from the water and then cause it to retract. The fact that no water issued from the truncated apex seemed to indicate that no water was present in the top part of the shell.

Radiographs of *B. digitalis* show that the extreme apex of the shell is heavily calcified and careful examination proved that if the top whorl is sawn off, the cavity which becomes visible does not in fact communicate with the main cavity of the shell. It is a small, subspherical space completely surrounded by shell substance. The original experiment was thus repeated, care being taken to penetrate to the main cavity of the shell without damaging the tissues. The five successfully treated individuals of *B. digitalis* which were eventually obtained showed a marked reluctance to emerge, even when emergence-stimulating currents were produced by means of an electric stirrer. Each snail was later fitted with half a gelatin capsule, of suitable size, over the apex, following which they appeared to behave normally, emerging from their shells and crawling over the floor of the dish. When they were taken from the water and their capsules removed, retraction took place at once and water issued from the hole in the apex. The usual jets were completely absent. A number of drops of water fell from the foot as retraction took place but there was no propulsive force behind them; such drops fall also from intact snails in addition to the jets.

Table 2. *Sea-water spaces in four individuals of* Bullia digitalis

(Volumes have been measured correct to 0·05 c.c. as this is approximately equal to one drop of water. Each measurement was carried out four times on each snail, all four readings being shown in the table.)

	Snail no. 1		Snail no. 2		Snail no. 3		Snail no. 4	
Weight with foot retracted (g.) ...	3·17		2·75		2·98		3·20	
Volume with foot retracted (c.c.) ...	2·43		2·08		2·25		2·46	
Total water released on retraction (c.c.)	2·05	1·95	1·90	2·00	2·00	2·05	2·10	2·10
	1·85	2·00	1·90	1·95	1·90	1·95	2·00	1·95
Water collected from jet on retraction (c.c.)	1·70	1·55	1·80	1·65	1·60	1·65	1·75	1·75
	1·60	1·75	1·70	1·55	1·70	1·70	1·80	1·80
Water dripping from foot; capsule in position (c.c.)	0·30	0·35	0·20	0·25	0·35	0·35	0·25	0·30
	0·25	0·30	0·20	0·30	0·25	0·35	0·35	0·25
Water dripping from foot; capsule removed (c.c.)	0·75	0·55	0·60	0·55	0·70	0·60	0·80	0·85
	0·70	0·65	0·45	0·55	0·70	0·65	0·70	0·65
Water issuing from apex when capsule removed (c.c.)	1·35	1·20	1·25	1·15	1·40	1·30	1·35	1·30
	1·25	1·35	1·30	1·25	1·25	1·35	1·45	1·40
Total water present in mantle cavity (c.c.)	0·90	0·85	0·80	0·85	0·90	0·80	1·00	0·90
	0·80	0·85	0·85	0·85	0·80	0·95	0·90	0·95

The jets were restored when the gelatin capsules were left in position during retraction. If they were not held securely over the apex, however, they were dislodged by water welling up from inside the shell. Certain measurements were made on the amount of water escaping from four of the five snails and these are listed in Table 2.

The problem of the origin of the jets, which are such a striking feature of retraction in *Bullia*, is therefore solved. In the expanded snail some two-thirds of this water lies within the shell, above and around the visceral region of the animal. Some of the X-ray pictures of *B. digitalis* and *B. rhodostoma* confirm that there is an extensive downward movement of all the tissues, including the visceral hump, during the emergence, leaving the upper whorls of the shell empty. This movement is made possible by the fact that the columella muscle, the only connexion between the animal and its shell, is attached very low down, being inserted into the columella in the lower part of the second whorl of the shell.

Less than one-third of the water forming the jets comes from the mantle cavity, as indicated previously by Brown & Turner (1962). It has now been possible to show in a more direct manner that water from the mantle cavity does in fact contribute significantly to the jets. A soft arterial catheter is introduced through the siphon and into the mantle cavity of an expanded snail and the water in the cavity sucked out. A pipette containing Thorotrast is then connected to the free end of the catheter and the dye allowed to run down into the mantle cavity. After a little practise this replacement of the sea water by Thorotrast can be accomplished without the snail retracting. It is then caused to retract by pinching it behind the head and, as the jets are produced, a radiograph is made. In some of these pictures the jets cast a shadow, which can only be due to the presence of Thorotrast, while in one it can be clearly seen that the dye is present also in the temporary grooves which run along the margins of the foot (see Pl. 2, fig. 2).

We have only to account, then, for the water which drips from the foot as the animal retracts. The most likely source of this water is the proboscis sheath for if the animal is caused to evert its proboscis drops of water fall from its vicinity. When the animal later retracts the drops appear to be reduced in number. Such observations are not conclusive for if the snail is held out of water for long enough nearly all the water in the free space is found to leak out between the tissues and the shell and to drip from the foot. If, on the other hand, the snail is allowed to crawl over a damp substratum then this leaking does not occur and the jets collected on retraction show no reduction in volume.

A final observation worth mentioning is that it seems as if these sea-water spaces are not completely independent of one another and that transfer of water from one space to another is possible. For instance, if water is removed from the mantle cavity by means of a catheter introduced through the siphon and the snail then placed on a perfectly dry substratum, it is found after ten minutes or so that the cavity is again full of sea water. Is it possible that under normal circumstances there is some exchange of sea water between the mantle cavity, through which there is a continuous flow, and the free space, in which the water would otherwise be stagnant?

OBSERVATIONS ON EXPANSION AND RETRACTION

Expansion and retraction in various species of *Bullia* have been observed in the laboratory and in the field, such activity often being stimulated by appropriate means and timed with a stop-watch. The time taken from the first sign of such activity to its completion varies enormously not only from individual to individual but also in any one snail according to the prevailing conditions and the degree of stimulation. Two phases both of emergence and of retraction may be distinguished.

The first sign that a snail is about to retract is provided by a slight folding of the foot. The ventral surface, normally convex when the animal is not crawling over the substratum, becomes concave, the lateral and posterior parts being drawn inwards and the head pulled back towards the mouth of the shell. There is a reduction in volume during this phase, and radiographs have shown that blood is leaving the pedal sinus; there is, however, no apparent loss of turgor. During this process the extreme lateral margins of the foot curl over against the ventral surface to form the temporary grooves described by Brown & Turner (1962). No jets are produced during this first phase, however, and the animal often unfolds and expands the foot again without retraction entering the second phase.

The movements associated with the phase described above are not always linked with retraction; a similar folding of the foot can be observed during feeding and copulation. It is clear that the undiminished turgor of the foot in these circumstances must be attributed to the tonus of the visceral somatic musculature, which will exert a pressure through the cephalopedal/visceral veins without preventing the rise of blood from the foot into the visceral sinus system.

The onset of the second phase of retraction is marked by the production of jets, while at the same time the foot gradually loses its turgor and becomes wrinkled. As the foot shrinks in size it is drawn into the shell, the whole posterior portion folding over so that the dorsally situated operculum is the last part of the animal to enter the shell. The operculum does not fill the shell mouth and a naked area of foot is always visible around it. In air the second phase appears to be irreversible, this observation being consistent with the view that under no circumstances will the snail draw air into its free space. Under water, however, the snail may re-expand at any stage.

There are obviously two factors involved in retraction—the shunting of blood from the pedal to the visceral sinus system, and the contraction of the columella muscle. This muscle cannot drag the foot into the shell while the foot is fully expanded and turgid for it is many times too large; the first phase of retraction therefore involves a partial deflation of the pedal sinus by means of contraction of the pedal muscles. Blood from the foot must push against the tonus of the visceral musculature and thus turgor of the foot is temporarily maintained. The decrease of turgor which occurs with the onset of the jets implies that the visceral muscles have relaxed, and at the same time the foot begins to be drawn into the shell, being rotated through 90°. This drawing in can only be accomplished by the contraction of the columella muscle for it is the only attachment between the animal and its shell. It is probable that the forcible drawing in of the body by the columella muscle also provides the force necessary for jet production, for the shifting of blood to the visceral sinus (during the first phase) does not cause jets to be produced.

Two phases are again apparent during emergence from the shell and again retraction is possible at any stage. The columella muscle can play no part in emergence, for its relaxation cannot exert an effective force. Emergence must thus rely largely on filling the cephalopedal sinus system with blood. The first sign that emergence is to take place is provided by a partial unfolding of the foot so that the posterior region protrudes through the mouth of the shell. This protrusion, though deflated, is highly mobile and is commonly waved from side to side as if testing the water. If certain substances which are unpleasant to *Bullia* are present, such as γ-buterobetaine (Brown, 1961*b*) or hydrogen sulphide (Brown, 1964), then emergence does not take place and the protruded region is folded back into the shell. This 'testing' phase will also take place in air but is then never followed by emergence.

The second phase of retraction takes place only in fairly unpolluted sea water, and is only certain to take place if water-currents are present. The foot is visibly inflated and as it swells it seems to drag the rest of the animal down to the coiled shell by pressing on the edges of the shell mouth. After emergence of the head, however, the foot no longer presses against the shell, this being supported by the narrow 'neck' region which by no means fills the shell mouth. Nevertheless, the snail is able to hold its shell firmly in position above and not in contact with the foot. The shell can also be moved quite independently of the foot. This control is probably provided by the tissue immediately below the visceral hump fitting tightly against the shell between the first and second whorls. So firm is this contact that a curved seeker or an arterial catheter cannot be pushed beyond this region. This arrangement must also serve to hold the sea water in the free space for there is no other structure which might possibly do so. Emergence can be stopped at any stage and followed by retraction, which is then accompanied by the production of jets. Water must thus be drawn into the free space from the commencement of the second phase of emergence, a conclusion which is supported by the fact that in air the second phase never begins.

DISCUSSION

Combining the conclusions reached in this work with those of Brown (1961 *a*) and Brown & Turner (1962), we are in a position to make the following statements regarding expansion and retraction of the foot in *Bullia*:

(1) The foot is expanded in the usual way, by the introduction of blood into the pedal sinus.

(2) Though the turgor of the foot must be maintained by a pressure of blood, there is a continuous circulation through the pedal sinus while the foot is in the expanded condition. The hydrostatic skeleton is thus in reality dynamic.

(3) The unusually great expansion of the foot in this genus does not depend on an exceptionally high blood volume, the figures obtained being comparable with those calculated for other aquatic gastropods.

(4) The suggestion that *Bullia* must have great control over its blood movements is not refuted by anatomical considerations, which show that there is no reduction of the anterior sinus system. On the other hand, the circulatory system is not more complex than that of a typical prosobranch.

(5) During normal circulation blood leaves the pedal sinus via the pallial collecting vessels and the cephalopedal vein, the latter draining into an afferent renal vessel together with blood coming from the visceral sinuses.

(6) During retraction of the foot blood passes from the pedal sinus up the cephalopedal vein, but then for the most part by-passes the afferent renal vein to flow along the visceral vein and so into the visceral sinus system. This movement takes place over and above the normal circulation.

(7) When contraction is rapid some blood may enter the pallial system and afferent branchials from the afferent renal vein via a 'pallial anastamosis' which may act as a pressure escape valve, receiving blood which might otherwise place a heavy burden on the kidney vessels.

(8) It is postulated in the absence of evidence to the contrary that on expansion of the foot blood flows in the opposite direction to that taken on contraction. No structures are present which might impede such flow.

(9) The essential turgor of the foot while expanded must be attributed to the tonus of the somatic musculature of the visceral sinus system, which will exert a pressure against the rise of blood from the foot.

(10) A rise and fall of blood in the cephalopedal-visceral tube is to be expected during the normal activities of the animal, controlled by contractions and relaxations of the pedal muscles on one hand and the tonus of the visceral musculature on the other.

(11) The jets of water which appear to squirt out of the foot on retraction originate mainly from elsewhere, about two-thirds coming from the free space which exists between the viscera and the shell when the snail is expanded.

(12) Nearly one-third of the water is contributed by the mantle cavity which, however, still retains some water when retraction has been completed. The contribution of the 'aquiferous spaces' of the foot is negligible.

(13) The propulsive force behind the jets is provided by the retraction of the snail into its shell and is thus to be attributed to the contraction of the columella muscle.

(14) Two phases of retraction may be distinguished, the first being characterized by the transfer of blood from the pedal sinus without loss of turgor, the second resulting from the contraction of the columella muscle in addition to transfer of haemolymph, turgor being lost as the visceral muscles relax.

(15) There are two stages of emergence from the shell; a preliminary 'testing' phase followed by inflation of the foot by blood. The columella muscle can play no effective part in emergence.

(16) While retraction will take place both under water and in air, emergence only occurs under water and is stimulated by water-currents. It is suggested that under no circumstances will the animal draw air into its free space.

(17) The water forming the jets is conducted from the free space and mantle cavity by anterolateral flaps of skin which end at the margin of the foot on either side of the head. It is from these points that the anterolateral jets take their origin during rapid retraction. Behind them temporary channels are formed by a folding over of the lateral margins of the foot and these give way to permanent grooves in the posterior region which guide the water forming the posterior jet to the hind margin of the foot between the posterior cirri.

(18) There is no propulsive force behind the water originating from the mantle cavity.

(19) Though water is normally contained in the proboscis sheath this water does not appear to contribute to the jets but drips from the foot when the animal retracts or the proboscis is extruded.

(20) There is some evidence to suggest that the transfer of water from one space to another can take place.

The question arises as to how far any of these conclusions may apply to other prosobranchs or to the Gastropoda as a whole. Unfortunately no previous experimental work appears to have been performed on retraction and expansion in aquatic snails and the occasional observations to be found in the literature are slight and of little value. In fact so poor is the literature that in an excellent 755-page review of the functional anatomy and ecology of British Prosobranchiata, Fretter & Graham (1962) have nothing at all to say on the subject. This is all the more surprising as, if the most obvious feature of a typical prosobranch is the possession of a coiled shell, its next most apparent feature is the ability to retract into this shell.

In assessing how far our conclusions may apply to other marine snails it must be stressed that in some ways *Bullia* is a peculiar animal, especially where its habits and reactions are concerned (see Brown, 1961 *a*). It has no counterpart on the sandy beaches of Europe or Asia, and those carnivorous sandy-beach snails with greatly expanded feet to be found in the Americas and in Australasia are reputed to have very different habits. Jet production appears to be a rare phenomenon though large quantities of water drip from the feet of some snails on retraction (Schiemenz, 1884, 1887; Morris, 1950; etc.). Indeed the retention of water in the free space may be common, for in any marine gastropod which develops such a space on expansion it is apparent that the space must fill with water if the animal is below the surface. *Bullia* may thus have exploited and modified an inevitable occurrence for its own purposes, actively retaining the water in the space and bringing it ashore when it leaves the sea in search of food. The refusal of the animal to emerge from its shell in air points to the importance of this private aquarium. The function of this water and of its production into jets is at present being investigated.

As far as the role of blood in expansion and retraction is concerned it can be asserted that it is of major importance in all Gastropoda. Whether in general the route followed by this blood in leaving and entering the cephalopedal sinus system is the same as in *Bullia*, is a question, however, which cannot be answered with any confidence in view of the variability of the vascular system within the group. Few authors mention or figure a vessel which might be homologous with the 'pallial anastamosis' of *Bullia*, though such a vessel is present in *Littorina*. It is certainly not the same as the 'transverse pallial vein' of *Monodonta* and other prosobranchs, this being a renal efferent vessel.

Attempts to repeat the Thorotrast experiments on other prosobranchs have not met with success. *Bullia* lends itself to such studies in that it will allow the foot to be injected with fluids, can be handled, prodded and suspended in air, yet maintain a fully expanded foot until retraction is required. By comparison the threshold of retraction in rocky-shore snails is extremely low and it has not so far been possible to overcome the difficulties which this implies.

A final matter of interest is the significance of the tonus of the visceral musculature in maintaining the turgor of the expanded foot. There are two questions which must be answered: the nature and degree of development of this musculature, and secondly whether any ancillary structures, such as geodetic fibres, are present. Only then will we be able to erect a working hypothesis.

SUMMARY

1. The expansion and retraction of the foot has been studied in the prosobranchiate sandy-beach gastropod, *Bullia*.

2. In *Bullia* the foot is capable of an unusually great expansion, but this is not dependent upon an unusually large volume of blood.

3. Radiographical investigations have shown that on retraction blood flows direct from the pedal sinus to the visceral sinus system without passing through the heart, kidney or gill.

4. Investigation of the jets of water produced on retraction has shown that in the expanded animal the visceral region within the shell is surrounded by sea water.

5. The roles of blood movement and of contraction of the columella muscle, and also various other aspects of the circulation, are discussed.

I wish to thank my wife, Rosalind, for technical assistance without which this work could not have been undertaken. I am also indebted to Prof. J. H. Day and other members of the staff of the University of Cape Town for their comments, and particularly to Mr Jan Heeg for suggesting certain techniques. The expenses involved were met by a staff research grant generously made available by the University of Cape Town.

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EXPLANATION OF PLATES

Plate 1

Fig. 1. Positive print prepared from radiograph showing injection of Thorotrast into the buccal sinus system of *Bullia laevissima*. While dye passes into associated sinuses and back into the oesophageal sinuses, there is no immediate connexion between these spaces and the pedal sinus. Exposure for this and the following radiographs was 0·03 sec. at 200 mA. and 66 kV. at a focus-film distance of 100 cm.

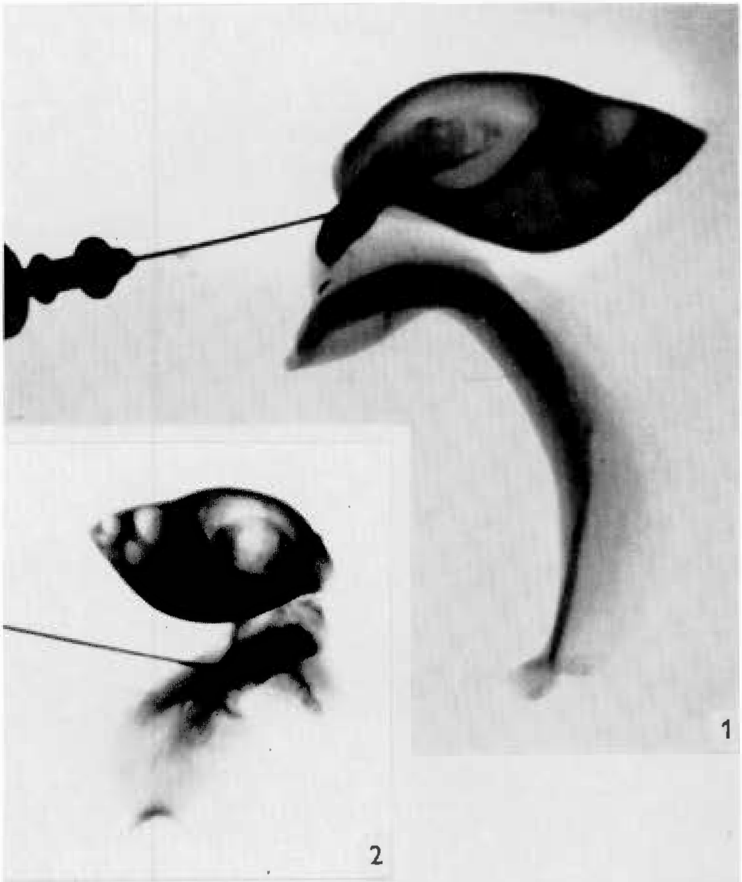
Fig. 2. Thorotrast being injected into the pedal sinus. The injection has been made well back from the 'neck' and on the right side of the foot. The dye has spread out fairly uniformly from the site of injection and can also be seen to have entered the pallial collecting vessels and the cephalopedal vein. It has also passed into the kidney vessels and possibly into the heart. The injection was made slowly and the plate exposed 5 sec. after injection had begun.

Fig. 3. A fast injection of Thorotrast into the pedal sinus of *B. laevissima*. The picture was taken a second after commencement of injection, this being more central than in fig. 2 and almost into the neck itself. The distribution of the dye is less uniform and the most striking features are the cephalopedal vein and the lower part of the visceral vein. Some dye appears to have already passed through this latter vessel and into the visceral sinus system. A little dye has entered the pallial system, which shows up diffusely, and in the foot itself the tendency for Thorotrast to pass backwards from the site of injection, down the dorsal mid-line of the pedal sinus, can be clearly seen.

PLATE 2

Fig. 1. Radiograph of a snail in the first phase of retraction. Injection of Thorotrast was stopped immediately retraction began and the plate was exposed about 1 sec. later. The dye can be seen throughout the cephalopedal and visceral vessels and has entered the visceral sinus system. Some of the Thorotrast has also penetrated into the pallial anastamosis. (*ps*, Pedal sinus; *cp*, cephalopedal vein; *pa*, pallial anastamosis; *vv*, visceral vein; *vs*, visceral sinus.)

Fig. 2. *B. digitalis* in the second phase of retraction. The sea water in the mantle cavity has been partially replaced by Thorotrast, introduced through an arterial catheter (*c*), before the onset of retraction. The dye can be seen in the temporary grooves (*g*) formed by the margins of the foot, and also in the posterior jet (*j*).



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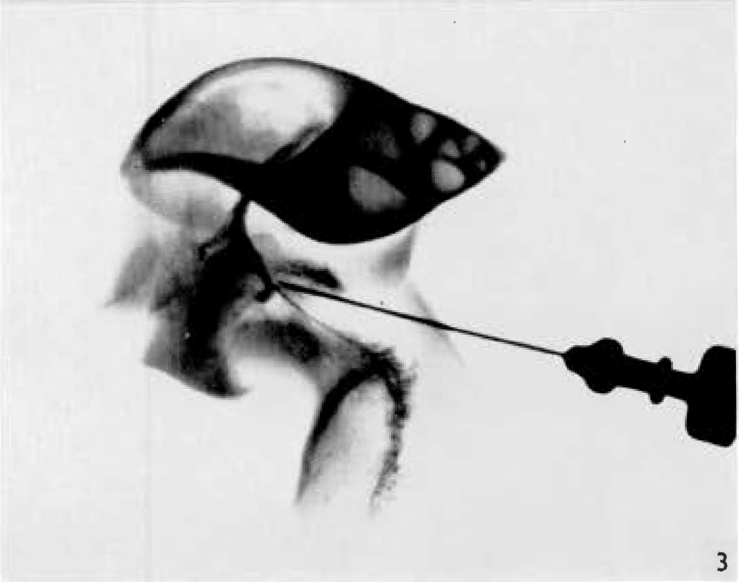

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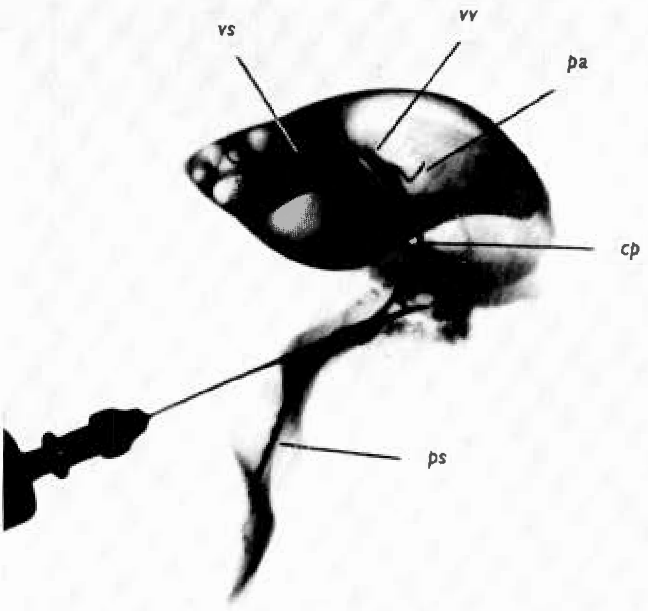

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5.

THE FATE OF THORIUM DIOXIDE INJECTED INTO THE PEDAL SINUS OF <u>BULLIA</u> (GASTROPODA: PROSOBRANCHIATA).

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THE FATE OF THORIUM DIOXIDE INJECTED INTO THE PEDAL SINUS OF *BULLIA* (GASTROPODA: PROSOBRANCHIATA)

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INTRODUCTION

The fate of foreign particulate matter in the haemolymph of gastropods is a subject which has not received a great deal of attention, despite its importance to many different aspects of gastropod physiology, haematology and parasitology. Indeed, apart from a short paper by Tripp (1961) on the snail *Australorbis*, the most closely related work of any consequence appears to be that performed on lamellibranch molluscs, notably species of oyster (Takatsuki, 1934; Ranson, 1936; Stauber, 1950; Tripp, 1958). Cuénot (1914) carried out experiments on a variety of molluscs but was concerned only with the immediate removal of foreign particles from the circulation, paying no attention to their ultimate disposal. The foreign particles injected into the blood-stream by these and other workers have most commonly been indian ink or suspensions of carmine. Such substances have disadvantages in that, first, the aggregations which these particles form in sea water or invertebrate blood are almost certainly much larger than the animals are ever called on to dispose of under natural conditions and, secondly, the animal must be killed and sectioned before even the gross distribution of the injected particles can be assessed. A radio-opaque dye in the form of fine, colloidally suspended particles would overcome both these limitations providing it was non-toxic.

A dye which meets these requirements is Thorotrast, a colloidal suspension of thorium dioxide which is very opaque to X-rays and has consequently been used extensively in clinical arterio-radiography and in studies of the blood-vascular systems of various vertebrate animals (Veal & McFetridge, 1944; Barclay, Franklin & Prichard, 1944; Barclay, 1951; Foxon, Griffith & Price, 1956; Foxon, 1961 *a, b*). It has also been used in studying blood movements in the sandy-beach snail, *Bullia* (Brown, 1964*b*). However, its original use was in clinical hepatolienography (Radt, 1929, 1930; Volicer, 1931), for the thorium particles are taken up from the vertebrate blood stream by the macrophage and reticulo-endothelial system, giving intense shadows in the liver and spleen some days after injection. Thorium dioxide is chemically unreactive and is not excreted to any appreciable extent by the vertebrate body; indeed it is this latter fact that is largely responsible for discontinuing the clinical use of Thorotrast, for it accumulates in the tissues, where its radio-activity causes serious diseases (Schmidt & Herzog, 1950; Prezyna, Ayres & Mulry, 1953). The properties of Thorotrast have, nevertheless, made it an invaluable tool in research on the reticulo-endothelial system in vertebrates other than man (Irwin, 1932; Tripoli, 1934; Foxon & Rowson, 1956;

Foxon, 1961*a*). Such studies do not appear to have been carried out on invertebrate animals.

MATERIAL AND METHODS

Two species of the sandy-beach snail, *Bullia*, were used in our experiments. They were *B. laevissima* (Gmelin) and *B. digitalis* Meuschen, both species being collected from Hout Bay, on the coast of the Cape Peninsula, South Africa. The animals were kept in the laboratory in a large tank of aerated sea water with a substratum of beach sand, at 15° C (± 0·5) but were removed to plastic buckets before injecting, X-raying, etc., and sometimes for feeding. Snails were fed at weekly intervals throughout the series of experiments. While the temperature at which they were kept is consistent with the temperatures the animals experience when submerged in their natural environment, the amount of food they received was quite arbitrary. Their opportunities to feed in their natural habitat are highly irregular and often vary enormously from season to season (Brown, 1961, 1964*a*). In the laboratory they will live for at least 6 weeks without food. These facts are mentioned as it appears likely that the rate of phagocytic uptake of thorium may be influenced both by temperature and by nutritional state. Gordon & Katsh (1952) have shown that the activity of cells of the endothelial system in rats is closely correlated with the nutritional state of the animals.

After 7 days in the laboratory snails were removed from the water and Thorotrast was injected into the cephalopedal sinus under conditions which were made as sterile as possible. They were then X-rayed at intervals, eventually being killed and removed from their shells at appropriate stages. They were X-rayed again after removal from their shells as this allowed the exposure to be greatly reduced, so increasing the degree of contrast in the resulting radiographs. Some of the animals were dissected and the various tissues and organs were X-rayed separately, while others were cut into pieces for embedding in wax and sectioning. Sections were viewed both by dark-ground illumination and by the method of combined dark-ground, phase-contrast and oil immersion suggested by Baxter (1960). Micrographs were prepared from some of the sections and enlarged for more detailed study. Blood was extracted from living snails from time to time in order to study the possible uptake of thorium by the haemocytes.

In a preliminary series of experiments the amount of Thorotrast injected was 0·25 c.c. in the case of *Bullia laevissima* and 0·1 c.c. in the case of the smaller *B. digitalis*. This is proportionately much more than was used by Foxon and his co-workers in their studies of Amphibia and is greatly in excess of the dose of 0·8 c.c. per kilogram of body weight suggested for man and other mammals by Tripoli (1934). Nevertheless, it proved insufficient and in subsequent experiments the dose was increased to 0·5 c.c. for *B. laevissima* and 0·25 c.c. for *B. digitalis*. These large doses were necessary for two reasons. First, the blood volumes of these animals are very much greater than in vertebrates (Brown, 1964*b*) and the blood system is an open one; consequently the Thorotrast becomes greatly diluted shortly after injection so that its effective radio-opacity is much diminished. Secondly, it was necessary to use an exposure of X-rays which would penetrate the shell of the animal as well as its living tissues, the optimum exposure being 0·03 sec. at 200 mA. and 66 kV., at a focus–film distance of approximately 100 cm. At these values low concentrations of the dye cast no visible shadow on the X-ray film.

Following investigations on the uptake and disposal of thorium dioxide particles, a brief study was made of the effect of such foreign matter on the haemocyte population. We were able to revert to lower doses of the dye for this study. Cell counts were made using the haemocytometer techniques usually employed for vertebrate animals, but with the modifications introduced by Yeager & Tauber (1935) for marine invertebrates. The diluting fluid consisted of 20 c.c. boiled and filtered sea water with the addition of three drops of 10% acetic acid and 3 c.c. of 0·01% gentian violet. The dilution pipette was calibrated so as to dilute 1 mm.^{3} of haemolymph 100 times. In addition to total cell counts mitotic indices were calculated, again following the methods of Yeager and Tauber (1933, 1935). The mitotic index is found by counting 2000 cells, taken at random, and noting the number of mitotic figures; the result is then expressed as the number of mitotic figures per thousand haemocytes.

Such counts were made immediately after capture of the snails, after 1 week in the laboratory, and each day after the injection of Thorotrast. Ten marked individuals of *Bullia laevissima* were used, and five control snails of the same species were kept in the same tank. Saline made up in triple-distilled water was injected into these control snails in place of Thorotrast. For this series of tests all haemolymph samples were drawn from the buccal sinus system, though isolated samples were taken from other (untreated) snails from different sites including the heart, the pedal sinus, the anterior aorta and the efferent branchial vein.

RESULTS

(*a*) *Radiographs*

Radiographs show that within 5–10 min. after injection the Thorotrast has been distributed throughout the body of the animal. There is no occlusion of the vessels such as is found after injection of indian ink into lamellibranchs (Stauber, 1950). Comments on the passage of haemolymph from the pedal sinus to other parts of the circulatory system of *Bullia* have been made elsewhere (Brown, 1964*b*). No change can be seen in radiographs taken within 3–4 days of injection, but after that period it is apparent that the distribution of thorium is no longer uniform. Both the posterior part of the mantle and the kidney tissues usually cast a more distinct shadow than other parts of the body and often the gill can be made out, but the most striking change is that the outline of the heart, both auricle and ventricle, can be clearly seen (Pl. 1, fig. 1). Sometimes short lengths of the vessels entering and leaving the heart are also outlined by the dye. These shadows become more intense as time proceeds and after 6 or 7 days it can be seen that the pericardial cavity has also become heavily involved (Pl. 1, fig. 2). While the shadows cast by the heart and pericardial cavity darken, the gill shadow normally fades while the somewhat diffuse shadow cast by the kidney intensifies, its lumen soon becoming as deeply involved as the pericardial cavity (Pl. 1, fig. 3). In a few cases this has been noted sooner than a week after injection of the dye but in others nearly a fortnight elapsed before the lumen of the kidney cast a shadow of comparable intensity. From this stage on the Thorotrast shadows gradually fade, the pericardial shadow being the first to disappear, after which the outline of the heart can again be clearly seen. By this time the shadow cast by the lumen of the kidney has also grown faint, though the diffuse shadow cast by its tissues remains. Fading continues until no shadows appear on the radiographs, the whole process from injection of the dye taking from 4 to 6 weeks under the conditions described.

There appears to be a considerable variation in the uptake of thorium particles by the tissues in different snails. The posterior part of the mantle can be seen in some snails but not in others; in some radiographs the gill can be seen as a faint, though distinct, shadow, while in others, taken at the same time after injection, none of the pallial organs can be made out—this in spite of the uniformity of exposures, focus–film distance and subsequent processing. Care was also taken to maintain all the snails under identical conditions. We can only conclude that the differences seen in the radiographs represent a real variability in the uptake of thorium in the animals themselves. Foxon & Rowson (1956) have found similar differences in the frog, *Rana temporaria*, and state that 'there is therefore some degree of variation in what may take place when the Thorotrast is removed from the blood. Such variation may be correlated with variation in the activity of the cells of the reticulo-endothelial system.' We have not been able to relate the variability in *Bullia* to the sex or the size of individuals. In spite of these differences the most intense shadows always occur in the wall of the heart, the pericardial cavity and the lumen of the kidney, in that time sequence. The period taken for these to develop and regress varies, however, from snail to snail.

In some radiographs, particularly those taken after full development of the kidney shadow, the floor of the pallium could be seen to cast a shadow, especially posteriorly where it is joined by the mantle. Washing out the mantle cavity with sea water introduced through an arterial catheter pushed through the siphon reduced this shadow considerably and in some cases virtually eliminated it. The shadow is largely caused, then, by thorium which has left the body of the snail and accumulated on the floor of the pallium.

(*b*) *Sections*

Sections cut through various regions of snails killed 4, 8 and 21 days after injection of Thorotrast show the changing distribution of thorium dioxide particles in the tissues. Viewed by dark-ground illumination or by the method of Baxter (1960) aggregations of thorium particles in *Bullia* have the same appearance as those studied in other (vertebrate) animals (see Foxon, 1961*a*). Any possible chance that we were viewing particles of some other substance was eliminated by making a 3-week autoradiograph of one of the sections; α-tracks are apparent on the processed microfilm, proving the radio-activity of the particles and showing that they are α-emitters.

In all the sections examined thorium particles were seen only inside amoebocytes, no other type of cell having taken them up; nor could any free particles of thorium be found, even in the snail killed 4 days after injection of the dye. The thorium-containing amoebocytes, however, were found in most of the tissues in one or other of the sections, as well as in the vessels and sinuses. The exceptions were the tissues of the digestive gland and the reproductive organs.

In the 4-day sections virtually all the particle-laden cells were clearly haemocytes which had not yet left the circulatory system, though we gained the impression that most of them were attached to the walls of the vessels or to the sides of the sinuses. Many of those apparently attached, however, may have been free in the living animal. The greatest number of haemocytes was to be found in the heart, clustered against the muscles and filling the small spaces between them; nearly all these haemocytes contained particles of thorium. The gill vessels were also found to be crowded with similar particle-laden cells, as were the blood spaces of the kidney. No migration of these cells through the epithelia or other tissues was, however, encountered.

In sections of the 8-day snail the position was rather different and invasion of the tissues was in evidence. The kidney tissue had been invaded to a considerable extent and some amoebocytes could be seen in the mantle epithelium. However, the most marked invasion was of the heart itself and a very large number of particle-laden cells could be seen between its muscles, in the epithelium and in the pericardial cavity. A few cells were noted in and attached to the pericardial wall—a negligible number compared with those migrating through the heart. No amoeboid cells could be found in the reproductive organs or the digestive gland, though some were present in the associated blood sinuses. Thorium-laden haemocytes were still present in the gill, but no migration of these through the gill epithelium was in evidence.

The 21-day animal gave similar, though not identical, results as far as most of the tissues were concerned, and migrations of haemocytes through the heart wall and mantle epithelia were still apparent. However, very few cells containing thorium particles were seen in the circulatory system; they had disappeared from the gill vessels and from the anterior sinuses and only the arteries and the heart itself still had a few laden cells attached to them. On the other hand very large numbers of haemocytes which did not contain any Thorotrast were seen throughout the vascular system. Both the pericardial cavity and the lumen of the kidney appeared to be nearly choked with a mass containing so much thorium that the entire area showed up a brilliant, opaque white under dark-ground illumination. Under these circumstances it was not possible to be certain that the thorium particles were really confined to amoebocytes.

A few sections cut through an individual of *Bullia laevissima* killed 6 weeks after injection of the dye showed that even at this stage thorium particles were still present in some of the tissues. The circulatory system, pericardial cavity and the lumen of the kidney were, however, quite free of them; nor could any be detected in the mantle epithelia.

(*c*) *Haemocyte counts*

Counts of the blood cells in freshly collected snails give an indication of the variability of the haemocyte population under natural conditions, a variability found also in other invertebrates (see Yeager & Tauber, 1935; Nicol, 1960). Differences between individuals are far less marked after one week in captivity under identical conditions, as shown in Table 1. In addition to this variability between individuals there is also a considerable difference between samples of haemolymph taken from different sites; moreover, these differences are just as marked in snails kept for weeks or months in the laboratory as in those which have been brought straight from the beach. In general, samples from the heart and arteries are richer in haemocytes than those taken from the veins, while the sinuses show a still lower haemocyte population. Samples of haemolymph taken in connexion with the present series were invariably drawn from the buccal sinus.

We were able to distinguish clearly only two types of haemocyte, though many intermediate forms were found to occur. Using the terminology of George & Ferguson (1950) these may be referred to as lymphoid cells and granular macrophages, the latter

Table 1. *The effect of Thorotrast injections on the haemocyte population of* Bullia laevissima

The figures in brackets below the total cell counts are the mitoticindices, Cell counts are expressed in number of cells per mm.^{3} of haemolymph, all samples being drawn from the buccal sinus system.

Snail no.	Within 1 day of capture	7 days after capture	Number of days after injection of Thorotrast												
			1	2	3	4	5	6	7	8	9	10	14	21	28
1	4,100 (<1)	5,000 (<1)	4,800	5,200	—	15,500	—	20,400 (17)	—	18,800	—	16,700 (14)	—	15,000 (11)	12,400 (9)
2	6,400	6,400	6,600	—	6,400	—	15,900	19,000 (18)	—	—	20,500 (17)	—	17,200 (16)	14,800 (14)	11,000 (12)
3	3,800	4,600 (<1)	4,200 (6)	3,400 (10)	—	17,000 (11)	—	20,800	—	19,700 (14)	—	19,800 (13)	19,200 (13)	—	10,700 (9)
4	5,600	5,000	5,600	—	8,400	—	18,000 (14)	22,200	—	22,800	—	—	19,700 (11)	—	17,400 (12)
5	7,000 (<1)	6,200 (<1)	6,000 (6)	6,200 (8)	—	16,700	—	—	17,900	—	—	18,200	—	12,500	—
6	3,800	4,500	4,600	—	7,800	—	16,100	—	—	19,400 (17)	—	19,000	17,000	14,700	—
7	4,800 (<1)	4,800	4,200	4,600	—	13,800	—	16,800 (15)	18,600	—	16,800 (15)	—	16,500 (15)	—	—
8	6,000	5,500	5,600	—	9,600 (14)	—	—	23,000	—	24,200	—	21,600 (15)	—	20,200 (14)	15,200 (11)
9	7,200 (<1)	6,400	5,700 (7)	6,200	—	17,600 (13)	18,100	—	20,300 (18)	—	18,400	—	—	12,800	—
10	4,400	5,800 (1)	5,000 (1)	—	8,200 (12)	—	—	19,800	—	18,700 (17)	—	—	14,800 (14)	—	—

being more numerous and larger than the lymphoid cells. We were not able to distinguish 'eosinophilic granular amoebocytes' as described by George & Ferguson for a variety of gastropods. It was, however, possible to confirm the observations of Kollman (1908) that mitotic divisions may be seen in haemocytes but are confined to the smaller lymphocytes. In samples from freshly collected untreated snails, mitotic figures are seen less frequently than once in 2000 cells (total count), but the mitotic index increases after the injection of Thorotrast. The increase is most marked in the first 3 days after injection, indices of 11 to 14 being common by the fourth day. The index continues to increase, but more slowly, until maxima of 16 to 18 are reached after about a week. The number of mitotic figures then begins to decrease but so slowly that it has not been possible to follow its return to normal. Mitotic indices of 4 to 7 may still be encountered 2½ months after injection of the dye.

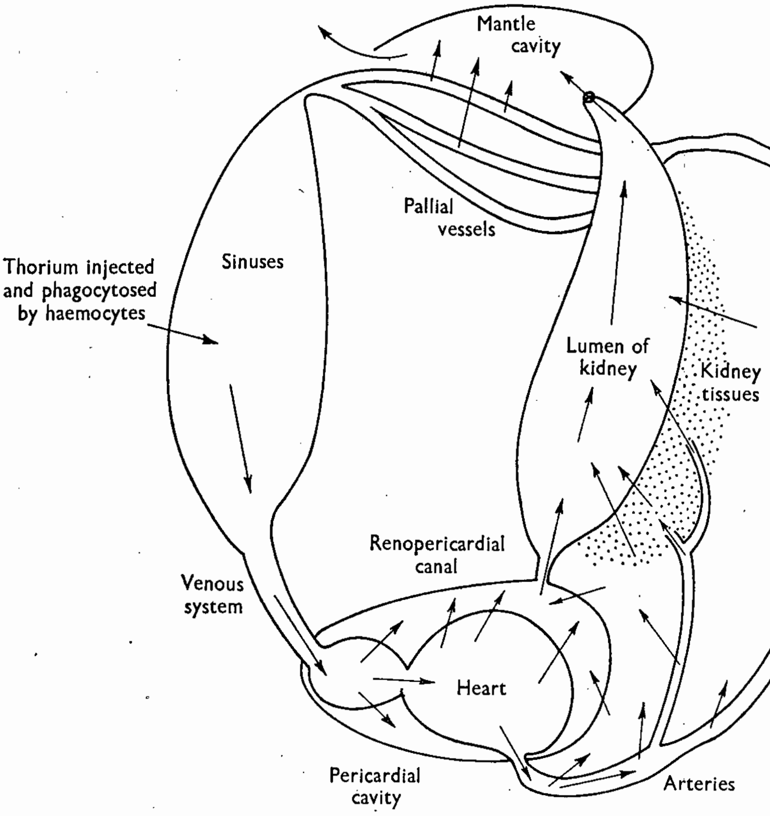
The increase of the haemocyte population following injection of Thorotrast is reflected in Table 1. It can be seen that the apparent increase is far from uniform and that in some cases there appears to be an actual *decrease* in the number of haemocytes during the first day or two. A sharp increase is only found on the fourth or fifth day after injection. Few of the cells extracted at any stage contained thorium dioxide particles and the lymphocytes were invariably free of them.

DISCUSSION AND CONCLUSIONS

Unlike vertebrate animals, *Bullia* is able to eliminate from its body foreign particles which cannot be metabolized and which are completely insoluble. That such particles are phagocytosed by the haemocytes, which then migrate out of the body, is in keeping with the findings of previous workers on the Mollusca. Both radiographs and sections show that several routes may be followed by such laden haemocytes in reaching the outside of the animal. The chief of these involves the heart, the pericardial cavity, the lumen of the kidney and the mantle cavity, in that sequence; though impossible to observe directly in our experiments, it is logical to suppose that the renopericardial canal and the nephropore are also involved. The chief pathway for migrating haemocytes would thus appear to be from the haemolymph through the wall of the heart (both auricle and ventricle) into the pericardial cavity, then through the renopericardial canal into the lumen of the kidney and out through the nephropore into the mantle cavity. This contrasts with the findings of Tripp (1961) with respect to the gastropod *Australorbis*, in which the haemocytes are said to migrate mainly through the mantle epithelia and adjacent surfaces.

Minor routes in *Bullia* are through the pericardial wall from the surrounding tissue, through the mantle itself from the pallial system of blood spaces, and through the tissues of the kidney—presumably from the associated sinuses. If migration does occur through the branchial epithelia it must be very slight indeed. The absence of migration through the digestive gland and gut is in marked contrast to what occurs in the oyster (Stauber, 1950) though in neither animal is the reproductive system involved. Migratory pathways in *Bullia* are shown graphically in Text-fig. 1.

The migration of haemocytes through the heart wall is probably not as laborious as might at first be supposed. As in other gastropods, there is no endothelium and the muscles are everywhere invaded by blood spaces. In section the entire heart wall has a spongy appearance and it is clear that haemocytes may penetrate almost to the epithelium dividing the heart from the pericardial cavity without being obstructed by the tissues. That a filtration of fluid may occur across this epithelium in some molluscs has been suggested (see Nicol, 1960, etc.). Once in the pericardial cavity the only way out of the system is through the renopericardial canal, whose cilia, beating always away from the heart, may well help to transport the haemocytes into the lumen of the kidney.



Text-fig. 1. Diagram of main routes taken by migrating haemocytes. The chief pathway is through the heart wall into the pericardial cavity, via the renopericardial canal into the lumen of the kidney and out through the nephropore. Other cells join this route by migrating through the pericardial wall while yet others enter the kidney lumen through its tissues. A distinct pathway, shorter yet apparently of secondary importance, is into the mantle cavity from the pallial system of vessels.

Particles of Thorotrast in sea water or invertebrate blood tend to form small, fairly uniform aggregations of a size conveniently phagocytosed. This is doubtless the reason why no fibroblast formation was witnessed, for in *Australorbis* fibroblasts are only formed where the foreign particles are too large for phagocytosis (Tripp, 1961). The size of the particles also probably accounts for the fact that the initial distribution of the dye takes place rapidly, there being no occlusion of the blood vessels as witnessed by Stauber (1950) after injecting indian ink into the oyster.

Though it is apparent that *Bullia* is able to deal with foreign, non-metabolizable particles efficiently and with a minimum of inconvenience or disruption of its normal mode of life, it has been decided not to attempt any comparison with other animals as far as rate of disposal is concerned. As already stated, this rate almost certainly depends on the prevailing temperature and the nutritional state of the animal. It may also depend on the size and nature of the particles and probably varies with the quantity injected. The relationship between this latter factor and rate of disposal is likely to be very complex for it has been shown that the haemocyte count increases after the injection of foreign material; there is no indication that this increase is proportional to the amount of material injected and there must, in any case, be a limit to the possible rate of cytogenesis. A large number of variables is thus involved in the rate of disposal of Thorotrast or other foreign material.

The 'latent period' of 3 or 4 days between injection of the dye and increased haemocyte counts may be explained on the grounds that macrophages laden with foreign particles tend to adhere to surfaces. This is a reasonable assumption in view of their subsequent migrations and is supported by a study of sections. It is also supported by the fact that the majority of haemocytes seen in extracted blood did not contain thorium particles, for if they were attached to the surfaces bounding the blood spaces and vessels they would not be available for extraction with the blood. If this is true then the increase in haemocyte count after 3 or 4 days actually represents the final elimination of free particles of thorium from the circulating fluid and implies that the haemocyte population begins to increase before then.

The origin of the haemocytes has interested several workers on the Mollusca, though little concrete evidence has been presented. Cuénot (1896) reported that the blood cells of gastropods divide by mitosis, mitotic figures sometimes being present in considerable numbers. Kollmann (1908) found division limited to the lymphocytes and considered that these cells give rise to the macrophages and other haemocytes, a view in direct opposition to the earlier theory of Cuénot (1891). The findings of George & Ferguson (1950) tended to support the views of Kollmann. Tanaka, Takasugi & Maoka (1961) working on the oyster, *Gryphea*, obtained a type of cell from the 'liver' from which the five types of haemocyte present in this animal appear to develop.

Our findings on *Bullia* definitely support the theory of Kollmann, postulating the development of the larger macrophages from lymphocytes. The lymphocytes divide while the macrophages do not appear to do so, and intermediate forms occur. More striking evidence is provided by the fact that, although only the macrophages take up thorium particles, the injection of such material causes an increase in the lymphocytic mitotic index as well as in the total cell count. It would be surprising indeed if these events were unrelated. It may be asked why, if the lymphocytic mitotic index increases by more than 1700%, the total haemocyte count increases only four or five times. The answer is quite obviously that enormous numbers of cells are leaving the system, laden with thorium dioxide, so that effectively the rate of mortality of the macrophages has been very greatly increased by the injection of Thorotrast. Increased cytogenesis may thus be seen as necessary not only to increase the number of cells which can remove the foreign particles from the blood but also to replace the cells which have been lost to the body in performing this function.

SUMMARY

1. The removal and ultimate disposal of foreign particles injected into the haemolymph of the sandy-beach snail, *Bullia*, has been studied by using the radio-opaque dye Thorotrast.

2. Particles are removed by phagocytic haemocytes which migrate by various routes to the outside of the body. The main pathway is through the heart wall into the pericardial cavity and via the renopericardial canal into the lumen of the kidney, from which the cells escape into the mantle cavity.

3. The injection of foreign particles stimulates a marked increase in the haemocyte population and also in the mitotic index.

4. The final discussion integrates the available evidence and a comparison is made between *Bullia* and other molluscs. The origin of the macrophages is discussed.

The first author (A. C. B.) takes full responsibility for the planning of this work and the interpretation of the results, the second author being concerned entirely with the radiographic techniques. We are indebted to Dr Spong, of the University of Cape Town, for his advice on the handling, storage and disposal of Thorotrast and to Dr G. J. Broekhuysen for his comments on the preparation of positive radiographs and micrographs. The expenses involved were largely met by a research grant made available by the University of Cape Town.

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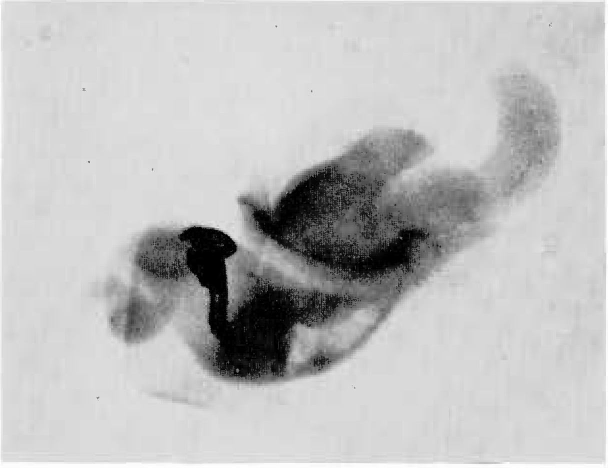

Fig. 3

Fig. 2

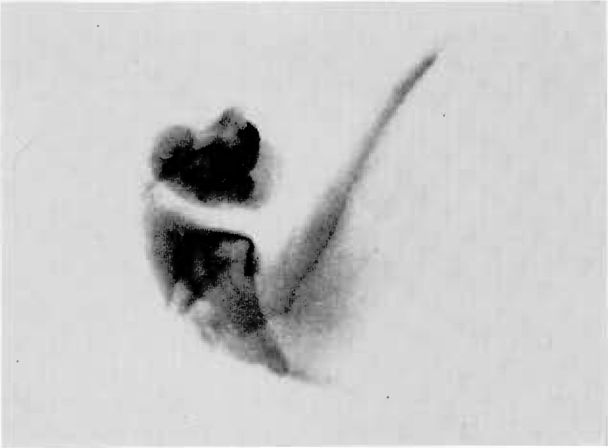

Fig. 1

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EXPLANATION OF PLATE

Plate 1 shows three positive prints made from radiographs of *Bullia laevissima* which had been killed and removed from their shells at different times after the injection of Thorotrast. The exposure in each case was 0·03 sec. at 100 mA. and 55 kV. at a focus–film distance of 100 cm. The figures are slightly larger than natural size.

Fig. 1. Snail in lateral view, killed 4 days after injection of the dye. The lower right-hand shadow is cast by the heart and adjacent parts of the vessels. Above this is a narrow shadow cast by the posterior tissues of the kidney, while on the left another shadow represents part of the mantle ridge and the floor of the pallium.

Fig. 2. Radiograph of another individual of *B. laevissima*, killed seven days after injection of Thorotrast. The only important shadow is that cast by the pericardial cavity.

Fig. 3. Snail killed 9 days after injection, viewed dorso-laterally. The elongate shadow is cast by the lumen of the kidney, while at the right it merges into that of the pericardial cavity.

6.

FOOD RELATIONSHIPS ON THE INTERTIDAL SANDY BEACHES OF THE CAPE PENINSULA.

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FOOD RELATIONSHIPS ON THE INTERTIDAL SANDY BEACHES OF THE CAPE PENINSULA

A. C. Brown

ON MARINE sandy beaches the bionomics of the ecosystem are dominated by two inter-related factors—the unstable nature of the substratum and the absence of attached plants. Both factors are seen in exaggerated degree on the exposed beaches of the Cape Peninsula, particularly those on the Atlantic coast where no photosynthetic organisms of any kind are normally to be found living either in or on the sand. The occasional diatom or unicellular alga discovered on these beaches in isolated cases is believed to have its origin in the marine phytoplankton. Even autotrophic Protozoa are limited to our most sheltered "pocket beaches".

The whole basic structure on which the food-chains of most ecosystems are built is thus virtually absent and the fauna is dependent for its existence on material accumulated by photosynthetic processes in other environments. We may distinguish two sources of such organic material—the sea washing up constantly on to the beach, and the land behind it. The sea accounts for by far the greater bulk of the food-supply, providing detached plants of great variety and dead or dying marine animals, as well as small organic particles derived from organisms which have disintegrated at sea (the "peloglea" and "leptpoel" of Fox *et at* [9]). The supply of macro-debris in the form of intact or recognisable pieces of organisms is clearly very erratic and is to some extent a seasonal occurrence, as it tends to be in other parts of the world also (Hedgpeth[14]). It varies considerably from beach to beach and also from day to day on any one beach. Thus the intertidal sands at Llandudno (below Hout Bay Neck) are normally "clean", almost devoid of organic debris, but after winter storms what remains of the beach is commonly littered with marine plants and animals. Following a violent storm in July, 1957, organic macrodebris was present to the extent of 4.7 kilograms per square metre (between L.W.S. and E.H.W.S., including the upper drift-line); yet five days later most of this material had again been removed by the sea, and the macrodebris amounted to only 6 gms/m^2 as an average for the same area. In mid-summer, 1957/58 and again in 1958/59 values were well under 0.1 gm/m^2.

The nature of the material cast ashore is also extremely variable. The beach at Salt River is noted for the vast quantities of the tunicate *Pyura* which are cast up during rough weather, though it forms only a small part of the macrodebris on other Cape Peninsula beaches. Bodies of Penguins are seldom to be found on the beaches, yet during the winter of 1957 the beaches on both sides of the Peninsula were littered with Penguins which had died from an unknown cause. Perhaps the most constant species to form part of the macrodebris is the sea-bamboo, *Ecklonia maxima*, but it is often absent from our most sheltered sands such as the Hout Bay Harbour Beach, where *Codium fragile* and *Ulva capensis* are the plants most commonly seen. After severe storms both sheltered and exposed beaches are littered with *Porphyra capensis*, *Aeodes orbitosa*, *Gigattina radula* and *Suhria vittata*, though all of these are normally removed by the next tide unless they are out of reach of the water.

It is not only the sea which removes the wealth of food-stuffs it has temporarily provided. Sea-weed is daily being removed from many Cape Peninsula beaches, in some cases to render bathing resorts more attractive, in others to provide the raw material for fertilizers or chemical compounds Large dead animals such as seals and sea-birds are also removed and during the "red tide" of March, 1962, some 50 tons of dead fish were removed each day from the beaches of False Bay.

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While the supply of macrodebris is highly erratic, there is good reason to believe that the supply of small, suspended, organic particles is rather more constant and never entirely absent from the water washing the beach. The transport of such detritus has been studien by several authors, notably Hjulstrom[15], while some aspects of its use by shore animals have been considered by Fox[8]. Much of this detritus settles on the sand only briefly as the tide rises, becoming available to such deposit feeders as *Donax serra* before being removed by the outgoing tide. Some particles, however, become mixed with the sand and permeate slowly through it, their weight being augmented from time to time by particles derived from macrodebris decaying on the beach. It is apparent that small planktonic organisms washed ashore may add considerably to the organic content of the sand, but this aspect of the food-supply has been ignored by previous authors and no figures are available at present.

The organic content of a substratum is normally measured by the Walkely and Black method (*vide* Morgans[19]) and we have used this method extensively on Cape Peninsula beaches. However, we doubt the validity of the figures so obtained, not only because pieces of shell or crustacean carapace in the sample introduce very high errors but also because the corrections applied to the initial readings appear to us to be arbitrary. None of the figures obtained are listed in the present paper. We may state, however, that organic matter has been detected in sand-samples from every beach examined, though only on the polluted beaches of Hout Bay was the value above 0.05% by weight.

The second source of food—the land behind the beach—contributes relatively little to the sandy-beach economy except for rare isolated occurrences such as the coincidence of a strong off-shore wind with the swarming of flying ants as on the west coast of the Peninsula in December, 1960. The beaches at Milnerton and Blouberg were littered witn the tiny bodies of these animals for many days. Sometimes active invaders from the back-beach or the dunes perish on the intertidal sands and thereby add to the potential food-supply. These invaders include not only insects, spiders, millipedes and scorpions, but also small lizards, snakes, birds and mammals. Apart from the birds these invasions are largely nocturnal, though baboons have been seen to invade the beaches near Cape Point during the day. On one occasion a dead baboon was seen on Diaz Beach, being consumed by vast numbers of the beach-flea, *Talorchestia*, while carnivorous polychaets ate into it from below. However, it must be stressed that while the land provides a great variety of potential food, it normally comes only in small quantities.

The permanent inhabitants of our exposed sandy beaches must thus rely on a highly erratic food-supply, if macrophagous, or on an extremely poor though more constant food-supply if microphagous. The latter thus feed for many hours each day, or continuously while covered by the tide while the macrophages are adapted to long periods without food. It is not surprising to find that these macrophagous species are far from specific as to their food-requirements and will accept almost any material within very wide limits. A few, like the sandy-beach "flea", *Talorchestia quadrispinosa*, are omnivorous and will take any plant or animal matter regardless of whether it is freshly dead or in an advanced state of decay. If deprived of other food it will also turn predator and cannibal. More commonly, however, the feeder is restricted to either a plant or animal diet; the sandy-beach snail, *Bullia*, for example, is entirely carnivorous but will consume a living jelly-fish or a still-kicking leg of *Jasus* as ravenously as it attacks an almost decomposed skate or a month-old mess of *Pyura* (*vide* Brown[4]). If deprived of food for some weeks it will eat polychaet worms or living *Callianassa*. Gilchrist[12] observed what was probably *Bullia rhodostoma* (identified by him as *B. digitalis*) eating Amphipods in such numbers that he assumed this to be normal, though in reality it is a rare occurrence and follows a long period of starvation. Unlike most psammodytic carnivores however, *Bullia* does not become a cannibal even when kept in the laboratory for several months without food. Its method of feeding and the way in which it seeks out its food have undoubtedly contributed greatly to its success (Brown and Noble[3]; Brown[4 5]).

The sand isopods, *Eurydice longicornis* and *Exosphaeroma truncatitetson*, show a similar impartiality with regard to their essentially carnivorous diet and do not wait for periods of starvation before attacking the other sand-dwellers or each other. Nevertheless, if isolated from one another in the laboratory they will survive for at least six weeks without food. Similar remarks could be applied to several of the errant sandy-beach Polychaeta. *Nephthys capensis* is particularly impartial and draws the line only at plant material. However, *Glycera convoluta* is said by some investigators to provide an unsolved problem; the worm is equipped with powerful jaws and a poison gland, yet no member of the genus has been shown to be an active predator. It has even been suggested that they are detritus feeders and that this explains their higher concentration in mud than in sand (*vide* Klawe and Dickie[17]). This seems to be improbable for we have found no particles of the substratum in the gut, contrary to what one would expect in a detritus feeder. In general the errant polychaets of intertidal sands are predators or scavengers, usually both, while the sedentary forms rely almost entirely on particulate organic matter.

Between tide-marks our Cape Peninsula beaches cannot boast a single resident species which is confined to a purely plant diet, though herbivores from the dunes and back-beaches often invade the intertidal zone when the tide is out. However, the kelp at and above the tidal limit normally contains a comparatively rich fauna of herbivorous land-isopoda, kelp-fly larvae and beetles such as *Pachyphaleria capensis.* Millipedes swell the numbers of this kelp fauna on the Peninsula's west coast but those found on the eastern beaches are clearly invaders from higher up the shore and not permanent residents.

In general microphagous animals are more common on sheltered than on exposed beaches, a fact to be correlated partly with the higher organic content of the sand and partly with the greater stability of the substratum, for many live in burrows which must be kept open. However, a notable exception is the mysid, *Gastrosaccus psammodytes*, which is most abundant on very exposed beaches. Its method of feeding and mode of life are at present being studied at the University of Cape Town. Deposit-feeders such as *Donax serra* are common on both exposed and sheltered shores, one of the reasons for their success being that they do not compete directly with other sandy-beach forms for a food-supply. *Donax* appears to accept any light particles of suitable size, sucking them in from the surface of the sand like a miniature vacuum-cleaner. Larger objects which are sucked in from time to time are forcibly ejected, apparently by a violent contraction of the inhalent siphon. Occasional sand grains which enter the siphon are dealt with in the same manner. Another bivalve, *Schizodesma*, is a suspension feeder but is a less important than *Donax* to the sandy-beach economy, being uncommon in the intertidal zone and restricted to a very few beaches such as that at Muizenburg.

Other sandy-beach microphages take advantage of organic particles only after they have become trapped in the sand, sometimes together with the living interstitial microfauna. Such a feeder is *Arenicola*, which ingests the sand together with everything that cannot get out of the way quickly enough. In regions where this worm is common, for example the beach at Buffel's Bay, its activities may be of great importance in increasing the amount of detritus which becomes trapped in the sand and in helping to distribute the organic matter (*vide* Wells[24], etc.). A sedentary polychaet found only on very sheltered beaches, *Audouinia*, is very different in its behaviour and, unlike *Arenicola*, does not disturb or mix the substratum to any great extent. It feeds both from the surface and on interstitial organic particles, but it can easily be seen in the laboratory that living micro-organisms are not trapped by the animal and are allowed to escape. This behaviour brings to mind the Sabellid and Serpulid worms studied by Dales[7].

A number of sandy-beach species feed by cleaning organic matter off individual sand-grains. The best-known example of such a feeder is probably the burrowing prawn, *Callianassa*, an animal whose earthworm-like activities are of the utmost importance to all the psammophiles of the lower intertidal zone. The amphipod, *Bathyporeia*, is said to feed in the same way (Watkin[23]). Our sandy-beach Cumacea feed in the manner described by Foxon[10], rolling sand-grains between their mouth-parts while removing the detritus which may coat them.

Extremely little is known of the feeding habits of the interstitial microfauna. Nothing has been published concerning the microfauna of Cape Peninsula beaches and for the most part we do not even know what species are involved, far less what they feed on. Sandy-beach Turbellaria are said to eat autochthonous diatoms (Remane[21]) but it is very difficult to believe that the turbellaria from exposed Cape Peninsula beaches can exist solely or even mainly on diatoms seeing that these are extremely rare. A more definite statement can fortunately be made with regard to the interstitial ciliated Protozoa, for we have observed several species of them under the microscope, congregating in the region of particles of detritus where they ingest bacteria. Flagellates are by far the most abundant of the interstitial Protozoa, though an occasional rhizopod is to be seen. We have not observed the latter to feed.

Nematode worms are very common on the beaches under discussion and, unlike most psammophiles, are to be found both at the surface and at considerable depths, being able to penetrate the anaerobic black layers characterised by the presence of sulphur bacteria (*vide* Bruce[6] and Galliher[11]). Nothing is known of their food-relationships though their numbers are such as to suggest that they play an important part in the bionomics of the ecosystem. A single species of nemertine worm, *Cerebratulus fuscus*, is to be found on the beaches and has been observed to eat the decaying flesh of marine teleosts. It is probable that it feeds on smaller particles as well.

Just as the food-chains of intertidal sands begin in organisms from other environments, so they end in predacious animals not normally resident in the intertidal zone. Chief among these are the fishes notably shallow-water bottom-feeders such as the Galjoen, *Coracinus capensis*, which "eagerly consumes crustacea and most lowly forms of life" (Smith[22]). This fish takes extremely large numbers of *Talorchestia quadrispinosa* as it feeds on the incoming tide; I have examined several with stomachs distended solely by the almost intact bodies of these beach-fleas. It is also said to take *Callianassa* where these are available and I have caught one on a hook baited with the mysid *Gastrosaccus psammodytes*. A fish which certainly does take *Callianassa* regularly is the White Steenbras, *Lithognathus lithognathus*, which is able to send out a powerful jet of water capable of blowing this prawn, and other crustacea, out of their burrows (Smith[22], Brown[2]). *Bullia* is attacked by elasmobranch fishes including skates and rays, while *Donax* and possibly *Schizodesma* are eaten by a large number of predatory fishes (according to the Table Bay Angling Club).

Birds also play a part in reducing the numbers of psammophiles, though certainly not to the extent indicated by Koepcke and Koepcke[18] on South American beaches. The sandy-beach molluscs, including *Bullia*, appear to be quite safe from the avifauna. The Black Oystercatcher, *Haematopus moquini*, will take *Donax* when the latter are exposed, but it has not been seen to dig for them. It may also eat *Arenicola*, as the British Oystercatcher is known to do so (Witherby *et al*[25]) but the bird is in any case relatively rare on intertidal sands, prefering rocky shores. There is, however, one bird which feeds on the cryptic sand-fauna—the Curlew Sandpiper, *Erolia testacea*, as it probes with its curved beak in search of polychaet worms and small crustacea. Sanderlings, *Crocethia alba*, will also probe the sand on occasion but prefer to "devote themselves to picking up the small creatures spilt out of the sand by the receding waves" (Gill[13]). The Sanderling will also take *Talorchestia* now and then, though the only birds seen to consume them in numbers are the White-fronted Sand-plover, *Charadrius marginatus* and, strangely enough, the European Swallow, *Hirundo rustica* (Broekhuysen[1]). Other species of plover and the terns, though common on Cape Peninsula beaches, do

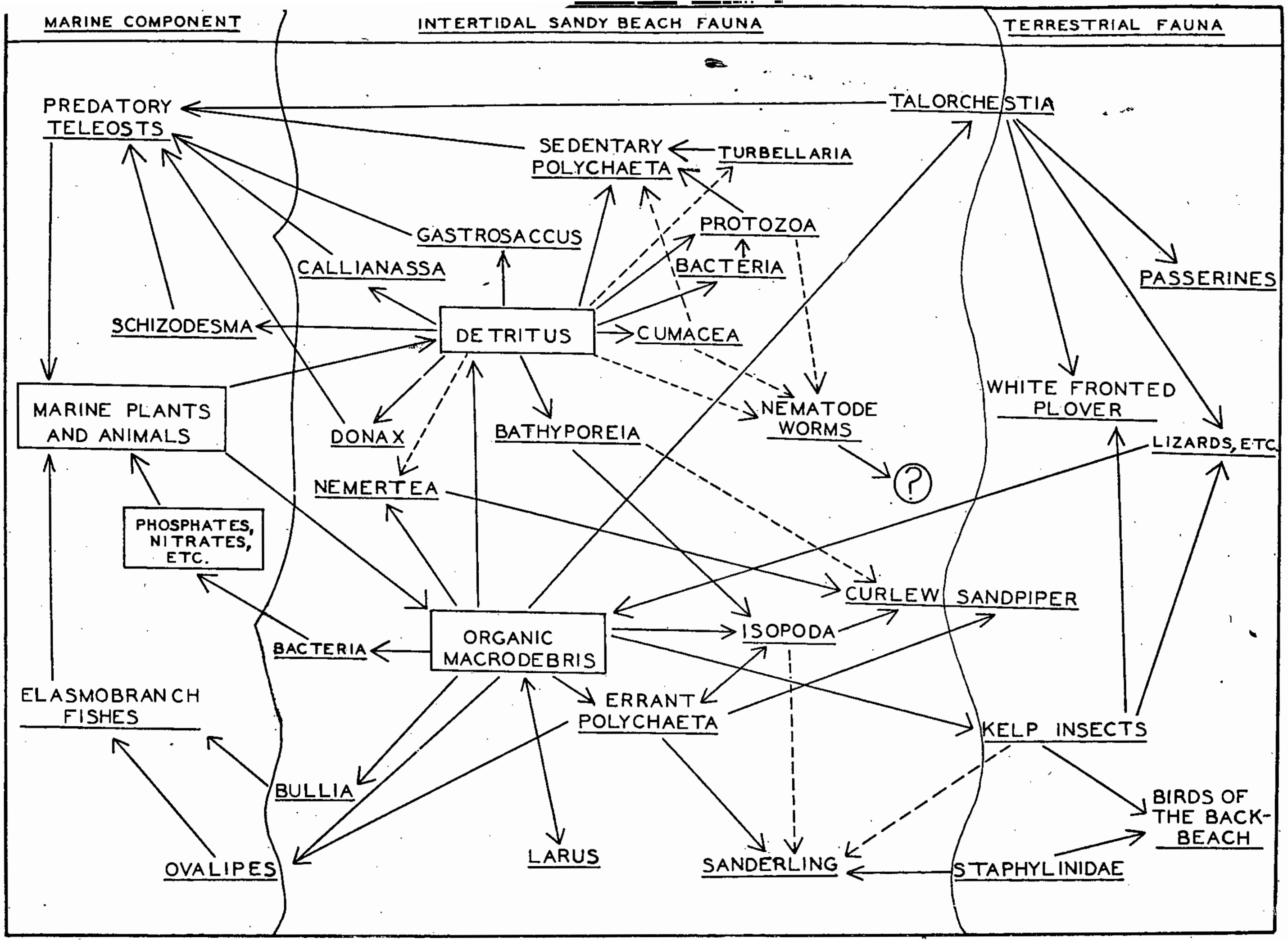

Fig. 1.—Scheme of food-relationships on Cape Peninsula beaches. Unbroken arrows show observed or well-authenticated relationships. Broken arrows indicate inferred or probable relationships.

not appear to feed in the intertidal zone, the plovers feeding mainly on the small insects to be found on the back-beaches and between the dunes, while the terns get their food almost exclusively by fishing. Gulls such as *Larus dominicanus* and *L. hartlaubii* do commonly feed on the intertidal beach but only on organic macrodebris of an animal nature which has been washed up by the sea. In this they compete directly with the sandy-beach scavengers such as *Bullia* and *Eurydice* but, being very messy eaters, they scatter the food over a wide area, a fact which may well benefit the sandy-beach community as a whole. With the exception of the gulls and the White-fronted plover, the above birds are migratory so that their influence on the ecosystem is very much greater in summer than in winter.

To sum up it may be stated that the food relationships of Cape Peninsula intertidal beaches superficially resemble those described from other parts of the world, particularly in the dependence of the fauna on food from other environments and in the price paid to predators from these environments. The details of these relationships are, however, different while the internal relationships appear to be unique, due largely to the complete absence of such crustacea as *Ocypode*, a crab which Koepcke and Koepcke[18] place in a position of central importance with regard to food-relationships. Brown[2] has also stressed its importance on the beaches of the eastern Cape Province of South Africa. Forms such as *Emerita* are also absent from Cape Peninsula beaches, while the giant land-isopod, *Tylos*, is very rare. Instead we find several animals which are limited to southern Africa. Chief among these from a consumer point of view are the gastropods of the genus *Bullia* and that apparently unique sand-burrowing mysid, *Gastrosaccus psammodytes*. Both these animals are very numerous and play a most important part in the economy of our intertidal sands, though neither occupy the ecological niche left vacant by *Ocypode*, a crab which never enters the water. Compared with beaches described from other parts of the world and compared with South African east coast beaches, the centre of gravity of the Cape Peninsula sandy-beach population shows a marked shift towards the sea. The upper half of the intertidal zone is normally devoid of prey and predator alike when the tide is out and, particularly on exposed beaches the greatest turn-over of animal matter and detritus occurs in the region of low water of springs. Plant macrodebris, however, continues to be consumed mainly at and above the upper tidal limit.

The figure attempts to show graphically some of the main food-chains applicable to Cape Peninsula beaches but it must be stressed that the diagram has of necessity been oversimplified. The figure includes one very important aspect which has not yet been mentioned and which, in fact, has been completely ignored by most previous authors. It is that sandy beaches are "great digestive and incubating systems. Bacteria break down organic remains and continually supply the ocean with phosphates, nitrogen compounds, and other valuable materials" (Pearse, Humm *and* Wharton[20]). Thus the debt which the sandy-beach ecosystem owes to the sea is repaid with interest, not only to marine predators but also to the marine photosynthetic organisms and thus to the oceanic community as a whole.

I wish to thank Dr G. J. Broekhuysen, of the University of Cape Town, for his comments and criticism and particularly for his help with the birds. I am also indebted to Professor J. H. Day, who first suggested to me that the sandy beaches of the Cape Peninsula might provide material for interesting and rewarding study.

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Club Facilities at Kelvin House

Members of the Witwatersrand Local Centre are reminded that the renovations and remodelling of Kelvin House are now complete and that the bar has been reopened. Furthermore, buffet luncheons are served daily except on Saturdays, Sundays and Public Holidays, at nominal charges and light refreshments are obtainable in the lounge, where up-to-date reading matter on scientific and general subjects is available.

As the Associated Scientific and Technical Societies of South Africa have provided these facilities for the benefit of members of the constituent bodies, which include the Witwatersrand Local Centre of this Association, it is hoped that members will support the Club and make full use of the excellent facilities that now exist in a building designed and furnished on the most modern lines.

AGRICULTURAL RESEARCH IN THE SUGAR INDUSTRY*

T. G. Cleasby

I AM VERY much the understudy—you were to have had a talk by Mr R. G. T. Watson on low-cost housing; unfortunately this hasn't been possible. I have come into the breach—some of you might rightly say, unfortunately — to tell you something about the agricultural research which is going on in the sugar industry. I hope that there will be enough agriculturists, chemists, botanists and zoologists, etc., present, for what I say to be of academic interest and that those of you who are not so fortunate as to belong to this happy group will at least find it interesting to learn some of the agricultural problems facing our industry. Also, in outline, some of the work which is going on to solve these problems. Some people may say how can an industry like ours which has one crop located in approximately one area still have problems. To these people I will quote what Dr. Bawden said when he addressed the 11th Conference of the International Society of Sugar Cane Technologists held last year in Mauritius:

"The prime purpose of research is to ask questions, and the purpose of experiments is to provide objective answers. Theories are needed, for these pose the questions, but theories have often been accepted as fact and gone into practice without adequate tests. The research worker likely to be of most help to the industry is the sceptic who knows the industry thoroughly and questions its practices, however well established some of them may seem to be. Indeed, often the more hallowed by tradition a practice has become, the more reason there is to question it. Economic and other conditions can change rapidly in agriculture and conclusions drawn validly in one set of conditions may not hold in another. Also, changing circumstances often allow a problem that seemed satisfactorily solved in the past to be solved in a new way that is more efficient than the old one. It is for the research worker to see that the industry is not employing outmoded practices based on experience gained in the past and irrelevant to modern knowledge about crop nutrition and pest control".

Having said this, I think I should at the beginning of my talk admit that it has an ulterior motive. I hope a discussion will follow which may enable you to get answers to questions about things you have seen this morning from experts of the Tongaat Sugar Company. I hope also, that we may get some constructive criticism coming back from your Society, composed as it is of so many distinguished scientists from all parts of the Republic.

I would like to mention some agricultural facts about the sugar industry of which you may or may not have heard. Sugar was first produced in Natal in 1852 by a man called Edmund Morewood, who farmed on the Compensation flats, a little further north of Tongaat. Since that time, and with many ups and downs, the cultivation of sugar cane has grown into an industry which in 1963 expects to produce 1,450,000 tons of sugar from approximately 12,000,000 tons of cane grown on, again approximately, 600,000 acres of land. (Hawaii produces 1,000,000 tons sugar, Australia up to 2,000,000, Cuba, in her heyday, 7,000,000.) The sugar belt, as it is called, stretches from Port Shepstone, about 90 miles south of Durban, into Swaziland. It is principally confined to the coastal strip, with the exception of a few inland areas suitable for cane such as the Wartburg area near Pietermaritzburg and the Pongola irrigation settlement. As I have said already, throughout its 109 years the industry has certainly had its ups and downs. The original varieties grown abounded in delightful names such as Bourbon, Ribbon, Otahati, Creole, Boi Rouge, Purple Green, Rose Bamboo, and so on. They were obtained entirely by private enterprise from Reunion, Mauritius, and also as far afield as Java. As one would expect today, with no control they were soon

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*Address delivered at excursion to the Property of the Tongaat Sugar Company Ltd., July 1963.

7.

THE ECOLOGY OF THE SANDY BEACHES OF THE CAPE PENINSULA, SOUTH AFRICA.

PART 1: GENERAL INTRODUCTION.

THE ECOLOGY OF THE SANDY BEACHES OF THE CAPE PENINSULA, SOUTH AFRICA. PART 1: GENERAL INTRODUCTION.

by

A. C. Brown

(Department of Zoology, University of Cape Town.)

This is the first in a series of papers dealing with the ecology of the intertidal marine sands of the Cape Peninsula, lying at the extreme south-west tip of Africa. The present paper serves to introduce the series and gives some description of the beaches investigated, so as to provide a background against which the activities of several characteristic members of the psammophilic fauna may be viewed. The autecology of each will be discussed separately and a complete list of the fauna and flora given; the series will end with a synthesis of the ecology of the intertidal sands.

The work reported in these pages and in subsequent parts of the series began as a synecological study in 1955, routine analyses of physical and chemical conditions and quantitative sampling of the fauna being continued until the end of 1958. Since then analyses and quantitative measurements have been undertaken only at irregular intervals, attention being focussed on behavioural and physiological aspects of the fauna. Many of these observations and experiments have concerned the prosobranchiate gastropod, Bullia, results being published during the course of the investigation (Brown, 1961a, 1961b, 1964a, 1964b, 1964c; Brown & Brown, 1965; Brown & Noble, 1960; Brown & Turner, 1962; Krijgsman & Brown, 1960). A brief and incomplete account of food relationships on the sandy beaches of the Cape Peninsula has also appeared (Brown, 1964d).

Reference to the ecology of sandy beaches is uncommon in the South African literature, the only paper of note being the survey of Langebaan Lagoon by Day (1959), though Macnae & Kalk (1962) have published an account of the sandy beaches at Inhaca Island, which is relevant to the South African region. Some of the papers on estuaries by J.H.Day and his staff will also be seen to contain data which bear on the present study. In addition information on some of our psammophilic forms, and particularly the cosmopolitan species, has been published from other parts of the world.

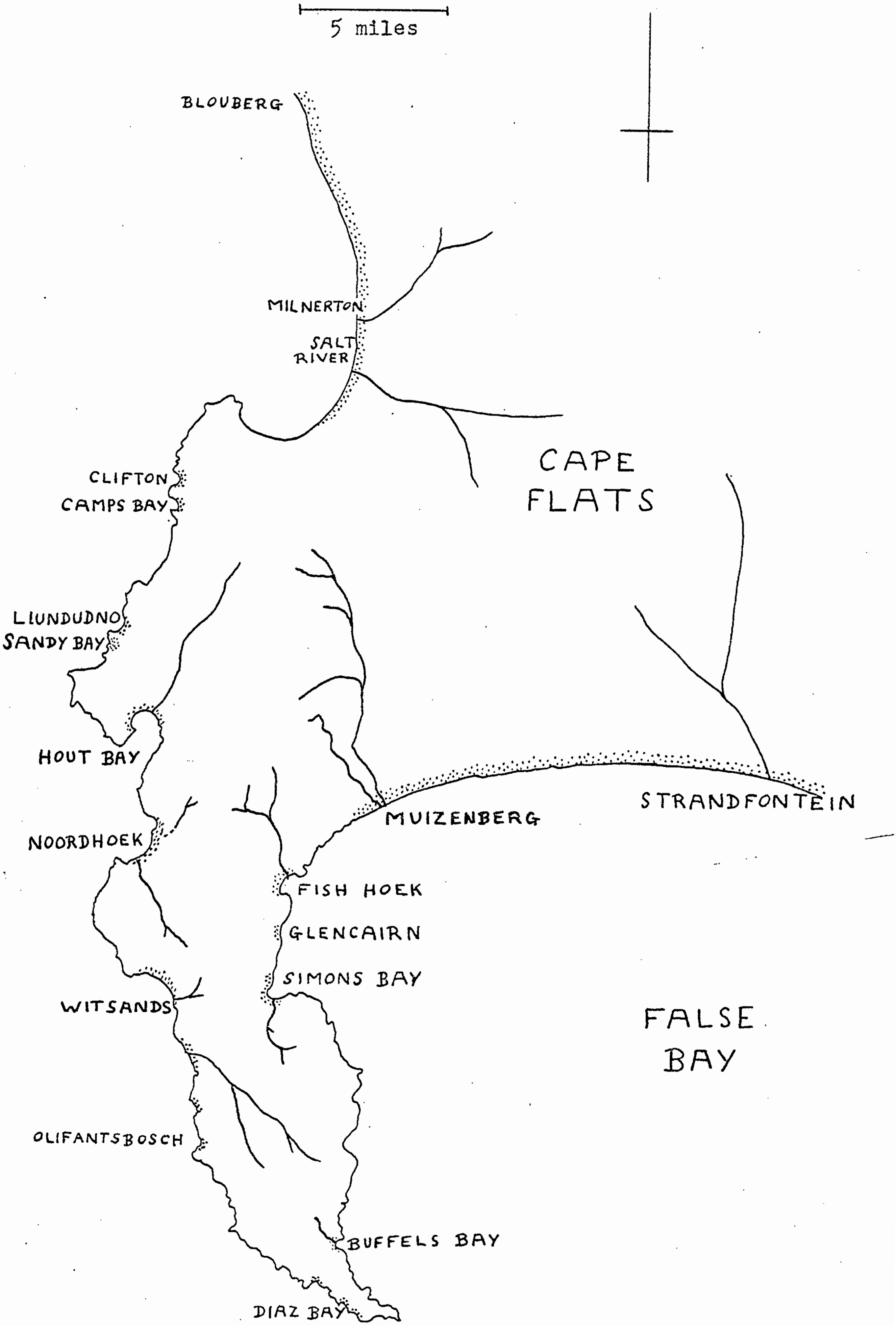


Figure 1

Map of the Cape Peninsula showing the main sandy beaches.

These papers will be referred to where relevant.

THE SANDY BEACHES OF THE PENINSULA

The Cape Peninsula, lying 34° south and 18° 30' east, occupies the south-west tip of Africa. Separated from the mainland by the sands of the Cape Flats, its coast is very steep, particularly in the southern area, where erosion by the waves is predominant, aided by the exposed position of the cliffs and the frequency of storms. These factors render the deposition of material by the sea a relatively unimportant phenomenon along the coasts of the Peninsula and sandy beaches are limited to sheltered bays where the offshore gradient is small. The limited extent of the beaches of the Peninsula proper is in marked contrast to the long, unbroken stretches of sand which adjoin the Peninsula to the north and east, and which mark the seaward boundaries of the Cape Flats.

There are no intertidal muds or muddy sands and, with only one exception of note, the only soft marine substrata between tide-marks consist predominantly of particles of quartz and feldspar, the hard breakdown products of granite, often mixed with material from other sources, such as small pebbles, shell fragments or sponge spicules. To the naked eye, therefore, these beaches present a marked contrast with many European beaches, though they resemble the white, granitic beaches of the west coast of the United States of America and are not inconsistent with the appearance of other sandy beaches around the coasts of southern Africa.

The exception was provided by the most northerly beach investigated during the survey - the beach at Blouberg Village. This is a small, isolated beach between rocky outcrops, immediately north of Bloubergstrand, which differs from all the other beaches studied in consisting, between tide-marks, of smooth, rounded pebbles between 4 and 15 mm in diameter. It is almost devoid of macroscopic life except for large numbers of the collembolan, <u>Anurida</u> <u>maritima</u>, which occur not only at the surface but also between the pebbles, right down to the water table.

Though the other Cape Peninsula beaches may appear superficially similar to one another, it is apparent that no two beaches present identical conditions to the fauna. For example, wave-action varies from conditions in which waves over 7 meters in height may be encountered (e.g. Diaz Beach) to those for which the wave height must normally be measured in centimeters (e.g. Buffel's Bay and the Hout Bay Harbour beach). At Camp's Bay, Llundudno, Sandy Bay and Witsands, the pattern of wave-action is such that long-shore currents and rip-currents are characteristic for much of the year and bathing is therefore forbidden, while Muizenberg, on the other hand, is one of the safest and most popular beaches in southern Africa. Some beaches are thrown into shallow cusps, giving a mildly serrate appearance, for example the long stretch of beach between Muizenberg and Strandfontein, while other beaches, including those at Hout Bay, Fish Hoek and Llundudno, do not show this phenomenon to any appreciable extent. The beaches at Noordhoek and Llundudno, and sometimes that at Muizenberg, display prominent ripple-marks running parallel with the shore, yet at Hout Bay and Fish Hoek the sand was usually perfectly smooth. A few beaches (Llundudno, Diaz Beach) can only be considered semi-permanent, for so much sand is removed from them during the worst storms that at Llundudno the boulders beneath the sand may become exposed, while at Diaz Beach the breakers may encroach on the intertidal zone until they beat against the cliff face.

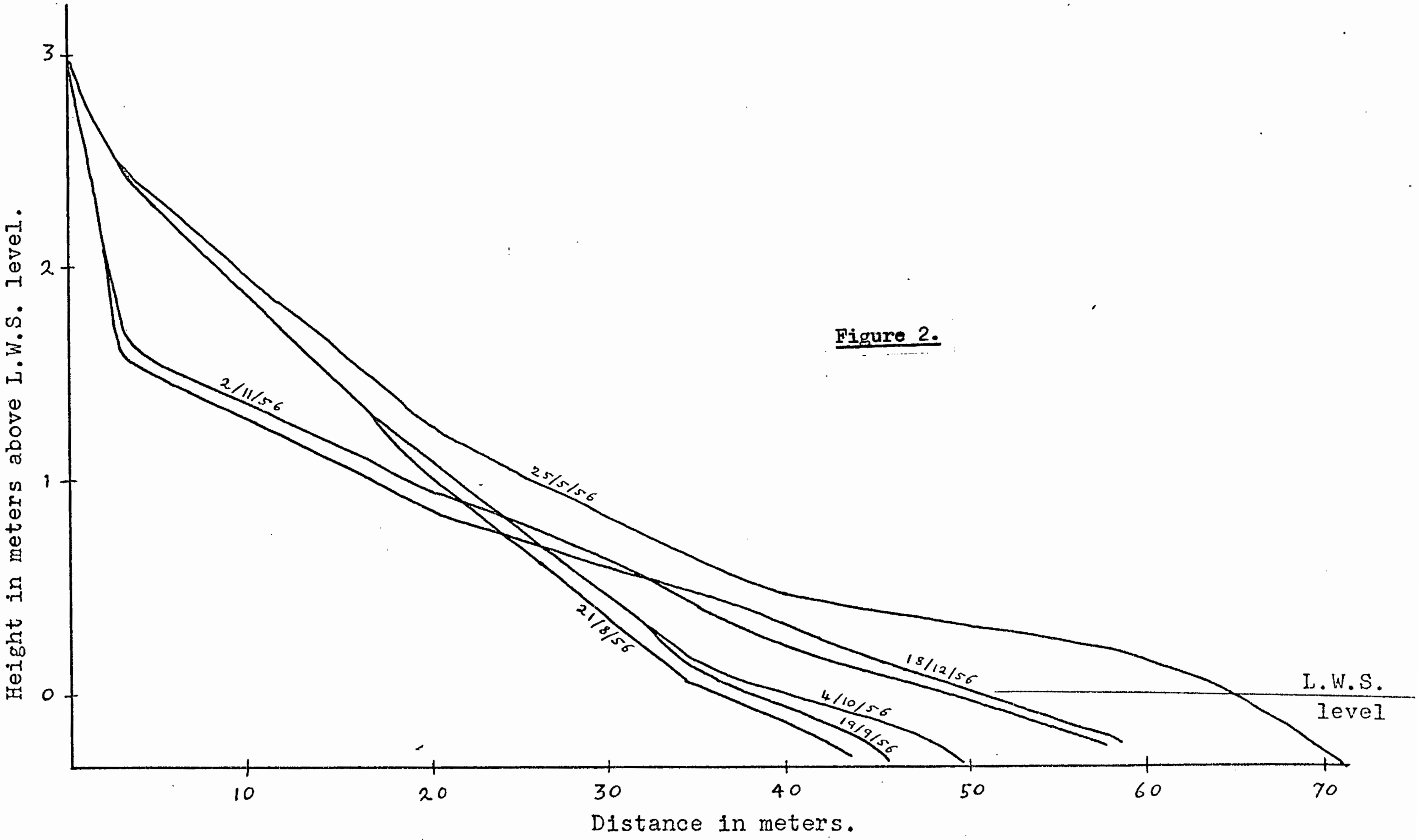
Some beaches, such as those at Fish Hoek, Hout Bay and Muizenberg, are traversed by streams of fresh water running down to the sea, while Noordhoek Beach is permanently under the influence of fresh water in the form of a lake behind the back-beach, which has a water level generally higher than that of the sea. A few beaches, notably those near Cape Point, have very little back-beach, the sands being interrupted by sheer cliffs, while elsewhere the back-beach may be far greater in extent than the intertidal sands and grade imperceptibly into the coast proper (e.g. Noordhoek). Indeed, the Cape Flats may be thought of as providing a giant back-beach to the intertidal sands which mark their seaward boundaries (Bloubergstrand, Milnerton, Muizenberg and Strandfontein) for the Flats have been built up entirely by the deposition of granitic sand and lie at no great height above sea level. That the concept of the Flats as a giant back-beach may be valid in the present context is indicated by the fact that a number of organisms normally associated with back-beaches (such as the pulmonate, Theba pisana) may be found in all parts of the Cape Flats.

The depth of the water table below the sand differs from beach to beach, and while on the Hout Bay Harbour and north beaches it was never far below the surface, in the upper parts of the intertidal zone at Witsands, Sandy Bay and Diaz Beach it is beyond most people's ability to dig down to it. Noordhoek Beach has an exceptionally high water table, which at high tide rises above the sand of the far back-beach, presenting conditions not found elsewhere in the Cape Peninsula.

Other factors, though less immediately apparent than those mentioned above, may be of equal or greater importance to the organisms inhabiting the sand. These include the particle-size distribution of the sand, the rate of deposition or erosion of particles, the permeability and porosity of the sand, its organic content, the amount of debris lying on the beach, the oxygen content of the interstitial water and the temperature range which the animals may encounter. These and other factors of possible importance to the fauna will be discussed in this series of papers.

Though every sandy beach from Blouberg Village, round the Peninsula to Strandfontein, was visited during the survey, it was not possible to devote equal attention to all, or even to most, of them. Consequently a few were chosen for intensive study which seemed to cover the wide range of conditions found on our beaches. Permanent transects were established on these beaches, the surveying of the beach profile being undertaken by the method described by Day (1959). The transects were made permanent by sinking long stakes into the sand at surveyed points and by incorporating permanent objects, such as life-saving boxes, into the transect wherever possible. Where feasible, the transects were surveyed back to bench-marks and so related to tidal datum. The transect sites were visited regularly, both during the day and at night, in fine weather and in foul, and at various states of the tide, though the time of Low Water of Springs was favoured. Whenever convenient,

Figure 2.



Beach profiles at Milnerton, mid-winter to mid-summer, 1956.

the beach profile was resurveyed, readings of chemical and physical conditions taken at fixed points along the transect line, and quantitative sampling of the fauna undertaken. The beaches accorded this special attention were:-

(1) Milnerton. This was the only beach in Table Bay selected for detailed study. The site was chosen as lying well inside the bay but not close enough to the Cape Town docks to suffer the pollution to which Salt River Beach, for example, is subjected. Wave-action is moderate to strong and large quantities of sand are moved by the wind and the waves. Figure 2 shows beach profiles along the permanent transect-line for part of 1956. It is a relatively unfrequented beach and bathing is unsafe for much of the year due to long-shore currents.

The common intertidal animals are a variety of errant Polychaeta, the nemertine Cerebratulus fuscus, the psammophilic mysid Gastrosaccus psammodytes, the isopod Eurydice longicornis and the pelecypod Donax serra. Bullia digitalis is present in the swash-zone of the low-tide terrace for much of the year but is absent at times during summer. An occasional individual of Echinocardium may be found buried in the sand near low water-mark. The drift-line is dominated by the talitrid amphipod Talorchestia quadrispinosa, which is also to be found under debris on the back-beach together with a variety of insect species.

(2) Llundudno. This is a small, restricted beach on the west coast of the Peninsula, exposed to heavy wave-action and subject to severe changes in profile. The intertidal slope becomes steeper and steeper during the summer and early winter; winter storms, however, flatten it to such a degree that the horizontal distance between low and high water-marks may be more than trebled. These changes in profile are accompanied by changes in the pattern of water-currents, for when the slope is steep long-shore currents, and sometimes rip-currents, are in evidence but when the slope is gentle these currents are very greatly diminished.

Figure 3

Llundudno Beach on a calm day in summer (2/12/56).

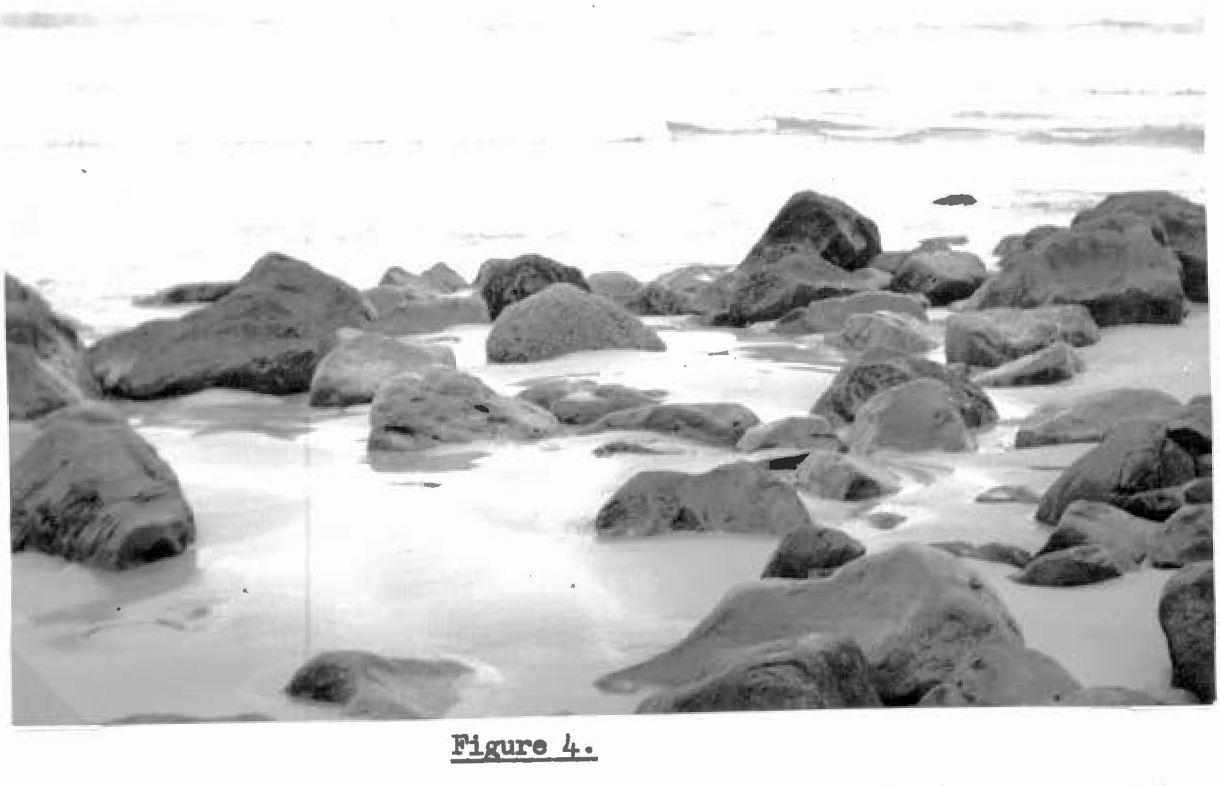


Figure 4.

Part of Llundudno Beach after a winter storm (4/8/56), showing rocks previously covered now exposed through the erosion of sand.

The flattening of the beach is also followed by a marked change in the fauna. This is normally poor both in species and in numbers, the only common animals in or near the surface of the sand being the mysid, Gastrosaccus psammodytes, with occasional patches of the isopod, Eurydice longicornis. However, within a few days of the beach being flattened, the numbers of Eurydice greatly exceed those of Gastrosaccus, while the sandy-beach prosobranch, Bullia digitalis, which is normally completely absent, invades the beach in force. Even the crab Ovalipes punctatus, which is not usually found on exposed beaches, has been taken at Llundudno within a week or two of the flattening of the profile.

The northern part of the beach is only semi-permanent for the winter storms which flatten the beach as a whole here cause rocks, previously covered by the sand, to be exposed. Severe storms have been known to remove all the sand from this region so that the sandy shore becomes a rocky shore. Anthozoa (sea-anemones) are to be found attached to some of these rocks - the ones most liable to exposure - despite the fact that they are buried under the sand for much, or even most, of the year.

(3) The beaches of Hout Bay. Before the end of 1958, the sandy beaches of Hout Bay offered, more than any other locality in the Cape Peninsula, an opportunity of studying both the relationships between various physical conditions and the effect of these conditions on the constitution of the fauna. To speak of Hout Bay's "sandy beaches" is, perhaps, misleading for though the local inhabitants spoke of their beaches in the plural, there was in fact only one beach, continuous in the region of L.W.S. level and below but broken above this by rocky outcrops towards its western extremity and by a small river about half way along its length. The beach was thus divided into the "Harbour Beach", "North Beach" and the "East Beach" respectively. These largely artificial divisions have been retained in the present work for the sake of convenience and beacause it so happens that the three stretches of sand differed from one another faunistically. A permenent transect

Figure 5

The transect-site on the north beach at Hout Bay, in mid-winter, 1957. The extremely gentle slope of the beach and the extensive area over which the water table lies at the surface can be clearly seen. At the left of the picture is a permanent stake marking the upper limit of the L.W.S. swash-zone, while towards the right and somewhat nearer the camera is a small rock heavily colonised by black mussels.

was established on each of the beaches. The east beach, which is the only remaining beach of Hout Bay, is to some extent sheltered from the full force of the Atlantic rollers by the disposition of the mouth of the bay. Wave-action decreased gradually as one proceded along the beach towards the west, waves being forced to turn through an ever-increasing angle in order to reach the shore. The slope of the beach also tended to decrease from east to west.

The east beach of Hout Bay was for many years the best collecting ground for *Bullia digitalis*; other common animals included *Eurydice longicornis* and *Gastrosaccus psammodytes*, errant Polychaeta such as *Glycera convoluta*, *Nephtys capensis* and *Nerine cirratulus*, the nemertine worm, *Cerebratulus fuscus* and the pelecypod *Donax serra*. The drift-line was dominated by *Talorchestia quadrispinosa* and a staphylinid beetle of the genus *Philonthus*, while the giant isopod *Tylos granulatus* was present in some numbers on the back-beach.

The north beach showed a decrease in the numbers of most of these and other species, though not of *Glycera* or *Cerebratulus*, and towards its western end other species were to be found in addition to those typical of the east beach. The most conspicuous of these additional species were the burrowing prawn, *Callianassa kraussi* and the polychaet, *Arenicola loveni*, which occured in small numbers.

On the tiny, sheltered Harbour Beach, however, the fauna was completely different from that of the east beach, *Eurydice* being replaced by *Exosphaeroma truncatitelson* and *Bullia digitalis* by *Bullia laevissima*. Though errant Polychaeta were still to be found in considerable numbers, representing more species than on the east or north beaches, sedentary forms were much in evidence, including not only *Arenicola loveni* but also *Abarenicola* and, at and below the lower tidal limit, two species of *Cirriformia*. The Harbour Beach was both the most sheltered and the richest of all the sandy beaches of the Cape Peninsula. The beach had for some years been subject to some organic pollution from the adjacent fishing harbour and from the effluents of fish factories in the area. In 1958 the beach became part of an

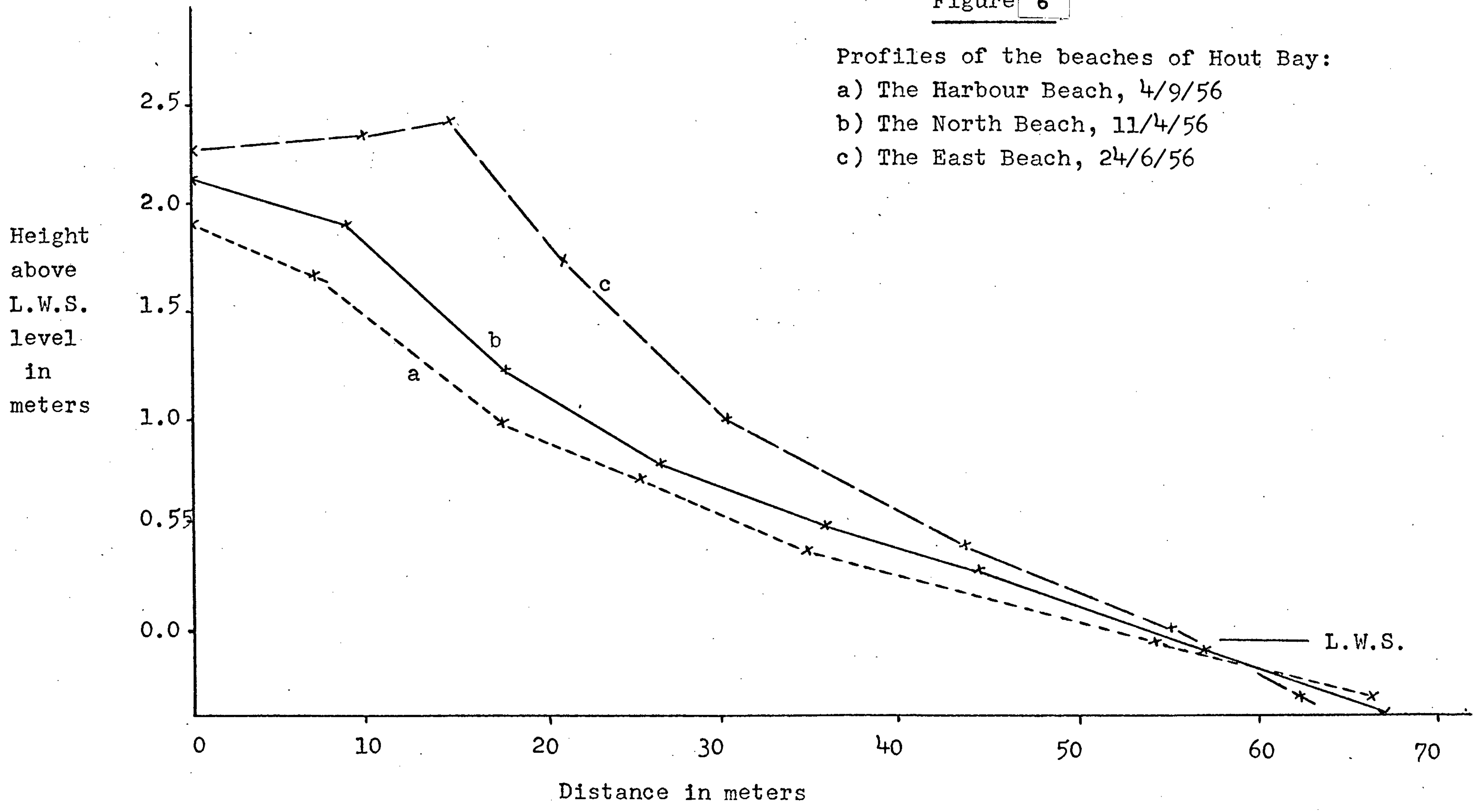


Figure 6

Profiles of the beaches of Hout Bay:
a) The Harbour Beach, 4/9/56
b) The North Beach, 11/4/56
c) The East Beach, 24/6/56

area taken over by a new fish factory, the preparations for which changed the shape, slope and extent of the beach, while the subsequent pollution virtually eliminated its fauna, nematode worms being the only macroscopic forms remaining for any length of time. The pollution took longer to affect the north beach and still longer to influence the east beach. Nevertheless, by 1964 no animals could be found on the north beach and a number of species had disappeared from the east beach. These included not only Gastrosaccus and Donax serra but also Bullia digitalis, once so abundant. The only remaining sign of this former abundance was the number of empty Bullia shells encountered; indeed they were sometimes so numerous that they formed a carpet, completely hiding the sand from view. Between 1964 and 1969 no living individuals of Bullia were to be found in Hout Bay; however, at the time of going to press there are indications that B. digitalis may be returning to the bay. While none have yet been taken intertidally, they have been seen below L.W.S. off the east beach.

(4) Sunrise Beach, Muizenberg. The False Bay beaches selected for special study were the beach in Simon's Bay and Sunrise Beach at Muizenberg; the former because of its shelter from wave-action and the latter because it seemed to present conditions typical of False Bay beaches. The transect on Simon's Bay beach will not be discussed here as it soon became apparent that conditions were abnormal due to the dumping of large quantities of wind-blown sand in the intertidal zone by municipal workers, during the summer months.

Muizenberg beach forms part of the southern boundary of the Cape Flats. It has an extensive back-beach which, like that at Milnerton, gradually merges with the coast. Wave-action is moderate and presents excellent conditions for both bathing and surfing. Though sand-movements occur, the intertidal profile is relatively stable, being steep above mid-tide level but very gentle (only about 1 in 40) at L.W.N. and below.

This gently-sloping low-water terrace supports a sparse population of Arenicola loveni and Callianassa kraussi, though the most abundant intertidal forms are Bullia rhodostoma, Eurydice longicornis, Donax serra and such polychaet worms as Scolelepis squamata and Glycera convoluta. The pelecypod, Schizodesma spengleri Linn., has been recorded only from the stretch of beach between Muizenberg and Strandfontein, where it occurs in considerable numbers, and from nowhere else in the world. Talorchestia quadrispinosa again dominates the drift line, with an occasional Tylos capensis, staphylinid beetles and various other insects.

Though permanent transects were established only on the beaches described above, transects were surveyed from time to time on other beaches. Considerable attention was given to Fish Hoek beach and the beach at Buffel's Bay, while Diaz Beach was visited on a number of occasions, as it is the most exposed beach of the Peninsula. Particular aspects of interest were also studied repeatedly at Noordhoek, Witsands and Strandfontein. On the other hand, Clifton, Camps Bay, Blouberg, Salt River and Glencairn beaches were visited only rarely.

CONDITIONS IN THE INTERTIDAL ZONE

It is not proposed, in this introductory paper, to present the details of the physical and chemical conditions studied on all the Cape Peninsula's sandy beaches but rather to give a general picture of conditions in the intertidal zone, pointing out the trends that exist. The various factors will be dealt with in turn, a high percentage of the data naturally coming from those beaches selected for intensive study. This section of the work will end with a comparison of these special beaches.

Most attention was paid during the survey to beach profiles, the particle-size distribution of the sand, the disposition of the water table and the salinity of the interstitial water. Measurements were also made of the permeability and porosity of the substratum, its organic content, the hydrogen ion concentration of the water and several other factors. Wherever possible the measurements were made at surveyed points along transect lines previously established on the beach. However, it is necessary at the outset, before discussing these factors, to say something about tidal conditions around the Peninsula.

Tides and Waves

Tidal rise and fall around the Cape Peninsula may be described as moderate compared with other parts of the world and is usually given as approximately 2 meters. Bokenham, Neugebauer and Stephenson (1938) give the following figures for Simon's Bay, based on tide-gauge records over a 3-year period: extreme range of springs - 7.0 feet (2.13 meters); mean range of springs - 5.4 feet (1.65 meters); mean range of neaps - 1.1 feet (0.34 meters). The above authors considered these figures applicable to sites further north in False Bay without modification, an assumption which is almost certainly valid and one which, in the present absence of other tidal gauges in False Bay, will be made in the present series of papers also. Tidal records available from Gordon's Bay (on False Bay's west coast) for part of the period differ only very slightly from the records made in Simon's Bay and may well be less reliable (Shipley, personal communication). In Table Bay the extreme range of springs is given as 2.17 meters, while the mean range of springs is 1.67 meters. The mean range of neaps is 0.35 meters. Differences in tidal range between False Bay and Table Bay are thus very slight and may probably be disregarded as far as the present work is concerned.

For practical purposes, Mean Sea Level may be considered constant, despite evidence of former levels higher than that which exists at present (Krige, 1926). While there is an appreciable seasonal variation in this level along the coast of South West Africa, it is small enough to be disregarded further south, while along the coasts of the Cape Peninsula it is not measurable by normal means. Apparent small changes in sea-level recorded on the tide gauge in Table Bay are meaningless as by 1967 this gauge had not been calibrated or adjusted since its installation, many years before (Shipley, personal communication).

The system of deriving the times of high and low water for a particular place by reference to time differences from a standard point is, of course, not accurate. However, where places are very close together the error is insignificant. Thus the times of high and low water from Blouberg Village to Hout Bay may be referred to predictions and records for Table Bay, while all False Bay beaches may be referred to the tide gauge in Simon's Bay. In Hout Bay itself, however, some tidal lag is to be expected due to the comparatively restricted opening of the bay. Field observations of the time of low water on the northern beaches of

Hout Bay, prior to 1966, indicated that this lag was not more than five minutes as compared with recorded low water in Table Bay, this observation being supported by tide-gauge records from Hout Bay Harbour, which are available for part of the period of the survey. Low water in Simon's Bay is approximately five minutes later than low water in Table Bay. As expected, field measurements at Noordhoek and at Witsands show that the time of low water at these places is intermediate between those recorded in Table Bay and in Simon's Bay. All the beaches investigated, then, show tidal cycles which correspond to within about five, and certainly not more than six, minutes of one another.

Under exceptional circumstances, the recorded time of low or high water may differ from the predicted time, usually due to sudden changes in wind direction. For practical purposes, however, the predicted times for the Cape Peninsula have been found to compare very closely indeed with the actual recorded times. During the greater part of the survey the only time-predictions available were forecasts made at the Liverpool Observatory and Tidal Institute, though predictions are now being made by the South African Naval Hydrographic Office. Hourly predictions for Table Bay and for False Bay for the whole of 1956 (when I established transects on many of the beaches) were hindcast especially for the present work, using the method described by Shipley (1966).

Abnormal meteorological conditions sometimes cause differences between predicted and observed tidal levels. However, at least during 1956, these differences were surprisingly small - never more than 5 cm. "High seas" around the Peninsula, including such occurrences as the inundation by sea-water of the road behind the back-beach at Camp's Bay, must therefore be due to an increase in the size of waves rather than to an abnormally high tidal level.

A fact which may be relevant to the intertidal ecology is that Low Water of Springs always occurs between 9 a.m. and 10 a.m. and between 9 p.m. and 10 p.m. This means that the lowest part of the intertidal zone is never exposed to the full heat of the day and during the morning low tide is quite frequently sheltered from the direct rays of the sun by overcast conditions, fog or mist, which are more common in the early morning than later in the day. This is particularly true of the Peninsula's west coast; Cape Town can expect to have 25 full days of fog during the year, compared with only 5 at Simonstown (Schaffer, 1952).

The west coast of the Peninsula, facing the Atlantic rollers, tends to be more exposed to wave-action than the False Bay coast. This is not to say that there are no sheltered beaches on the west coast; on the contrary, the Hout Bay Harbour beach was the most sheltered of the whole Peninsula. Nevertheless all the beaches subjected to heavy wave-action (Diaz Beach, Noordhoek, Llundudno, Sandy Bay, Witsands) lie on the Peninsula's west coast. Not only are the east coast beaches more sheltered from wave-action but they show a gradient of increasing shelter from north to south, Strandfontein and Muizenberg being the most exposed, while Fish Hoek is generally exposed to somewhat smaller waves. Glencairn is very much more sheltered than Fish Hoek, as is the beach at Simon's Bay, and Buffel's Bay was exceeded in shelter only by the Hout Bay Harbour beach.

Initially wave-height was measured against a long stick in one-third of a meter of water or, to be more accurate, where the troughs of the waves were approximately one third of a meter from the sea bed. However, this standard condition meant that where the off-shore slope was gentle the wave-height was measured much further from the shore than where the slope was relatively steep, thus seriously under-estimating the real difference in wave height between sheltered and exposed beaches. The alternative - measurement of wave height a standard distance from the shore - proved equally misleading, however. On the most exposed beaches it was not possible to take direct readings at all, due to the force of the waves, though the height of waves could often be estimated by throwing objects of known size into the breakers. Occasionally the presence of surfers made the estimation of wave height relatively easy.

Measurements made by these methods, though they must be treated with caution, do at least allow one to arrange the beaches in order with respect to wave-action (see Table 1) and also lead to some conclusions of interest. One of these is that beaches facing north and east are subjected to their highest waves during winter storms, when the typical north-west wind reinforces them, while beaches facing south or west are not so affected by winter storms, the north-west wind tending to flatten and retard the waves. Waves impinging on these beaches are reinforced by the south-east wind of summer. As a result of this a beach such as Llundudno often has smaller waves than Muizenberg when the south-easter blows, though there can be no doubt that Llundudno is in general the more exposed to wave-action.

As the slope of the intertidal beach, and in particular the changes which the profile may undergo, are clearly related to wave-action, this is the next factor to be discussed.

Beach Profiles

The steepest slope surveyed was that of the beach at Blouberg Village, which had an overall intertidal slope of 1 in 8. As already mentioned, this beach consists of pebbles rather than sand. The beach at Simon's Bay also proved exceptional in having a convex, instead of a concave, profile and an overall slope of 1 in 13. These conditions were found to be due to the dumping of sand in the intertidal zone during summer.

The other beaches of the Peninsula showed a consistently concave shape, the slope in the upper part of the intertidal zone being steeper than that in the lower part. The difference between upper and lower regions was often found to be greatest on moderately exposed beaches, particularly Muizenberg and Fish Hoek. Indeed the upper part of the intertidal zone at Muizenberg commonly had a slope of about 1 in 10, while the slope of the lower part was only 1 in 40 or even 1 in 45.

There is generally stated to be a relationship between the slope of the beach, exposure to wave action and the average particle size of the sand (Bascom, 1951; Hedgpeth, 1957). This is sometimes interpreted as meaning that exposed beaches may be expected to show a greater slope than sheltered ones because they tend to be composed of larger particles. However, as far as Cape Peninsula beaches are concerned, my records indicate that any such generalisation oversimplifies the real conditions to a degree and is in certain cases badly misleading. It is true that if the beaches are arranged in order of increasing exposure to wave action, this is also their approximate order with regard to increasing <u>average</u> overall slope. However, the picture is very different if one

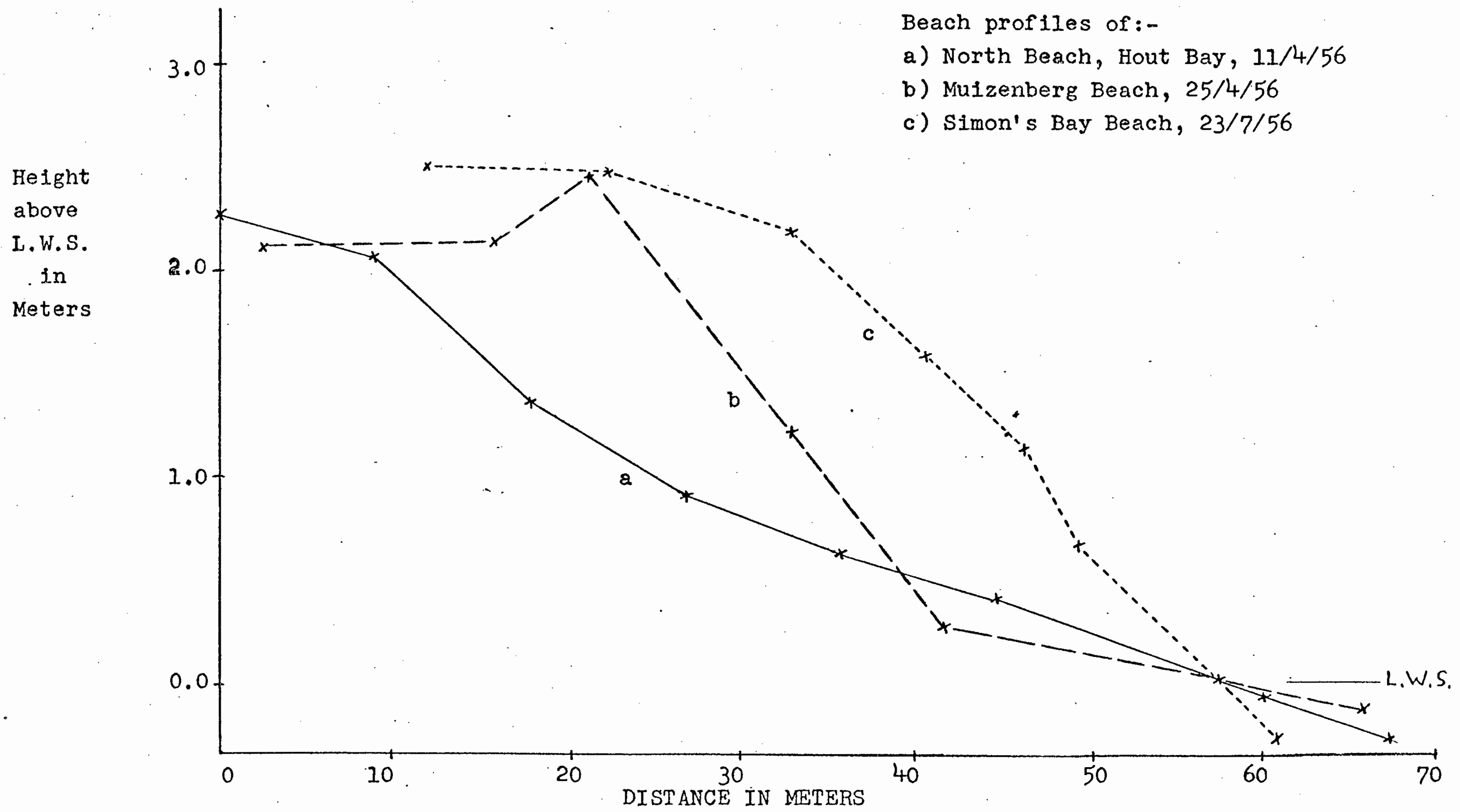


Figure 7

Beach profiles of:-
a) North Beach, Hout Bay, 11/4/56
b) Muizenberg Beach, 25/4/56
c) Simon's Bay Beach, 23/7/56

compares the profiles of beaches for a given month of the year, exposed beaches often showing a gentler slope than sheltered ones. This is because periods of high waves, during storms, flatten and cut back the exposed beach, while leaving the sheltered beach relatively unaffected. Also, as already mentioned, the effect of a storm depends to some extent on the direction the beach faces. In general the beaches on the False Bay side of the Peninsula, being less exposed to wave action, suffer less change in profile due to storms than do the beaches of the west coast.

It has been stated above that average overall slopes tend to be steeper the greater the exposure to wave action but this statement does not always hold true for specific regions of the intertidal zone. Attention has already been drawn to the fact that the upper part of the slope is invariably steeper than the lower part and that this difference is more marked on some beaches than on others. This leads to a state of affairs in which the average lower intertidal slope of a moderately exposed beach, such as that at Muizenberg, actually has a more gentle slope than that of any sheltered beach, including even the Hout Bay Harbour beach, while the upper slope is, on the average, steeper than that of many exposed beaches.

The extent of the slope which comes under tidal influence is, of course, greater than the tidal range and increases with increasing exposure to wave action, the water surging higher up the beach and retreating further down the slope the higher the waves. It is thus not surprising to find that on Cape Peninsula beaches the crest of the berm is better developed the greater the exposure to wave action. Indeed, for sandy beaches in general, it is known that the height of the berm crest above mid-tide level is approximately 1.3 times the height of the waves which formed it (Bagnold, 1940; Bascom, 1954). Thus on the most sheltered Cape Peninsula beaches, no crest is distinguishable, while on the most exposed beaches the crest normally rises well above the surrounding sand and is the highest point of the beach, seaward of the dunes or the coast proper. The berm of Noordhoek Beach is remarkable in that it often has two crests, of about equal height, one immediately behind the other with a deep trough between. As a result of the high water table,

BEACH	Steepest slope surveyed	Gentlest slope surveyed	Average summer slope	Average winter slope	Average overall slope	Number of surveys	Maximum diff. in X-sectional area
Hout Bay Harbour	1/28	1/28	1/28	1/28	1/28	14	Negligible
Buffel's Bay	1/26	1/26	-	-	1/26	2	-
Simon's Bay	1/12	1/14	-	-	1/13	4	-
Hout Bay north beach	1/25	1/27	1/27	1/26	1/26	10	4 sq. m.
Salt River	-	-	-	-	1/22	1	-
Glencairn	-	-	-	-	1/21	1	-
Fish Hoek	1/14	1/23	-	-	1/19	4	15 sq. m.
Hout Bay east beach	1/16	1/20	1/17	1/19	1/18	8	15 sq. m.
Muizenberg	1/15	1/19	1/16	1/17	1/17	12	17 sq. m.
Milnerton	1/13	1/24	1/20	1/15	1/16	14	74 sq. m.
Llundudno	1/15	1/25	1/18	1/20	1/19	10	133 sq. m.
Sandy Bay	-	-	-	-	1/15	1	-
Witsands	1/14	1/20	-	-	1/17	2	150 sq. m.
Noordhoek	1/12	1/14	-	-	1/13	2	-
Diaz Beach	-	-	-	-	1/13	1	-

Table 1.

Summary of some of the slopes surveyed intertidally on Cape Peninsula beaches. The beaches are listed in the approximate order of increasing exposure to wave action. The final column shows the difference in cross-sectional area of the beach between the two most extreme profiles.

Simon's Bay has been included for the sake of completeness but it should be noted that this does not represent a natural profile. Abnormal slopes on other beaches, due to the dumping of sand, have been excluded from the summary.

this trough often contains a pool of water, even at the time of low tide. The reason for the formation of such double crests is not clear.

Interesting as the examination and comparison of individual profiles may be, changes in beach profile - both in extent and in rate of change - must be considered of greater importance, both to the fauna and in any appreciation of the dynamic character of the beach. The extent of the changes in profile of some of our sandy beaches is shown in Table 1, where change in profile is expressed as a change in the cross-sectional area between L.W.S. and H.W.S. levels.

Sand movements

Changes in beach profile are the result of sand movements due mainly to the action of waves and water-currents on one hand and to wind on the other. However, quantities of sand may be eroded or deposited without marked changes in slope taking place; the whole profile may simply be pushed seawards or shorewards. It is for this reason that I have found the assessment of changes in cross-sectional area particularly valuable, though such assessments can, of course, only be made where a permanent transect has been established or at least where one of the surveyed points is represented by a permanent object.

Unfortunately changes in cross-sectional area do not tell one the whole story about erosion and deposition; they would only do so under conditions where either erosion or deposition occurred exclusively. Such conditions may be encountered during certain storms but are certainly not the rule. Undoubtedly the proper way to study sand movements is to label the particles in such a way that the labelling may be detected in samples collected at a later date. Neutron-irradiated quartz has been used for this purpose (Goldberg & Inman, 1955); however permission to carry out such experiments could not be gained during the present work.

Nevertheless, simple experiments and direct visual observation throw a certain amount of light on sand movements. For example, planks of wood placed at right-angles to the shore-line and nailed to stakes driven into the sand, collected sand along one side on all the moderately exposed beaches tested (Muizenberg, Strandfontein, Fish Hoek) and also on the Hout Bay north beach, which must be considered sheltered.

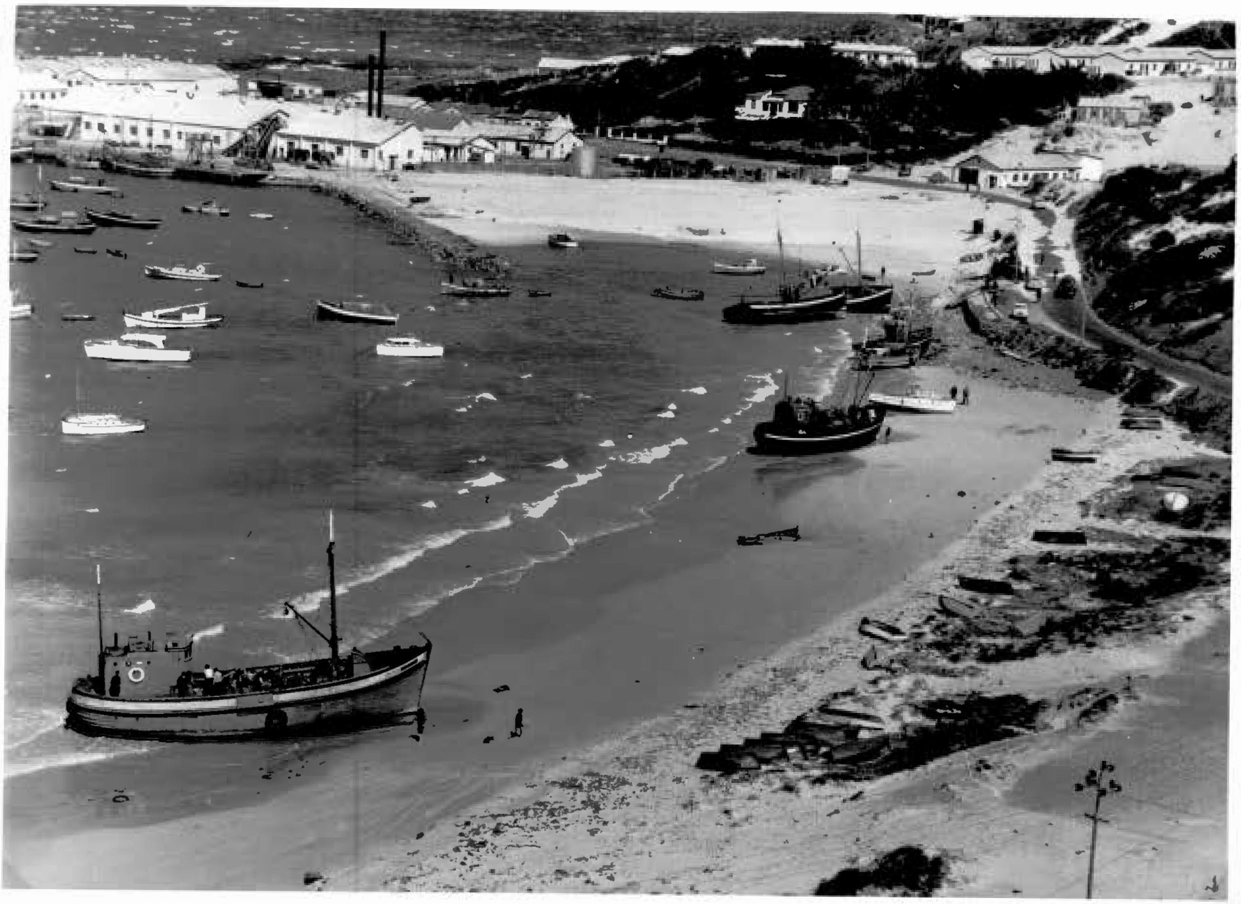


Figure 8.

Boats washed up at Hout Bay, following the most violent storm recorded for many years (16/9/58). The western part of the north beach is in the foreground, while the Harbour beach is to be seen in the background.

However, the process took much longer on this beach than on the moderately exposed ones. These miniature break-waters collected no sand at Simon's Bay, Buffel's Bay or the Hout Bay Harbour beach, even though in the latter case they were left in position for several tidal cycles.

Lack of water-induced sand movements on the most sheltered beaches was confirmed not only by direct visual observation of the inability of the waves to move sand grains, but also by the fact that wind-blown sand deposited by human agency in the intertidal zones of Simon's Bay beach and, in 1958, the Hout Bay Harbour beach, in such quantities as to completely alter the intertidal profiles, was not removed under normal conditions; only after a particularly violent storm (on 16/9/58) was the profile found to have changed. One therefore comes to the conclusion that, while the profiles of the moderately exposed beaches represent an equilibrium between deposition and erosion, the profiles of the most sheltered beaches represent static conditions established by, and only altered by, abnormally heavy wave-action during storms.

Water may also move small quantities of sand by flotation (Emery, 1945a), though observation indicates that this is not an important process on Cape Peninsula beaches. Only at the Hout Bay Harbour beach have I seen a few grains of sand floating on the surface of the water. Some of these eventually drifted ashore, while the majority sank. Erosion due to run-off after rain is undoubtedly more significant than sand movement by flotation.and may be seen on most of our beaches, though it varies with the rainfall and with the topography of the coast. Its effect is most obvious, however, on beaches whose profiles are very concave, so that rainwater which has sunk down through the sand emerges abruptly where the water table meets the surface of the sand. Figure 9 shows such erosion taking place on Muizenberg beach, where the difference between upper and lower slopes was particularly marked. Indeed, on such beaches this type of erosion may take place even in the absence of rain, "weeping " from the marine water-table occurring at low tide.

Water is not the only agency responsible for sand movements and the wind is by no means a negligible factor in this respect, though its effects are not as dramatic as those induced by wave action during storms. On Cape Peninsula beaches a great deal more sand is moved

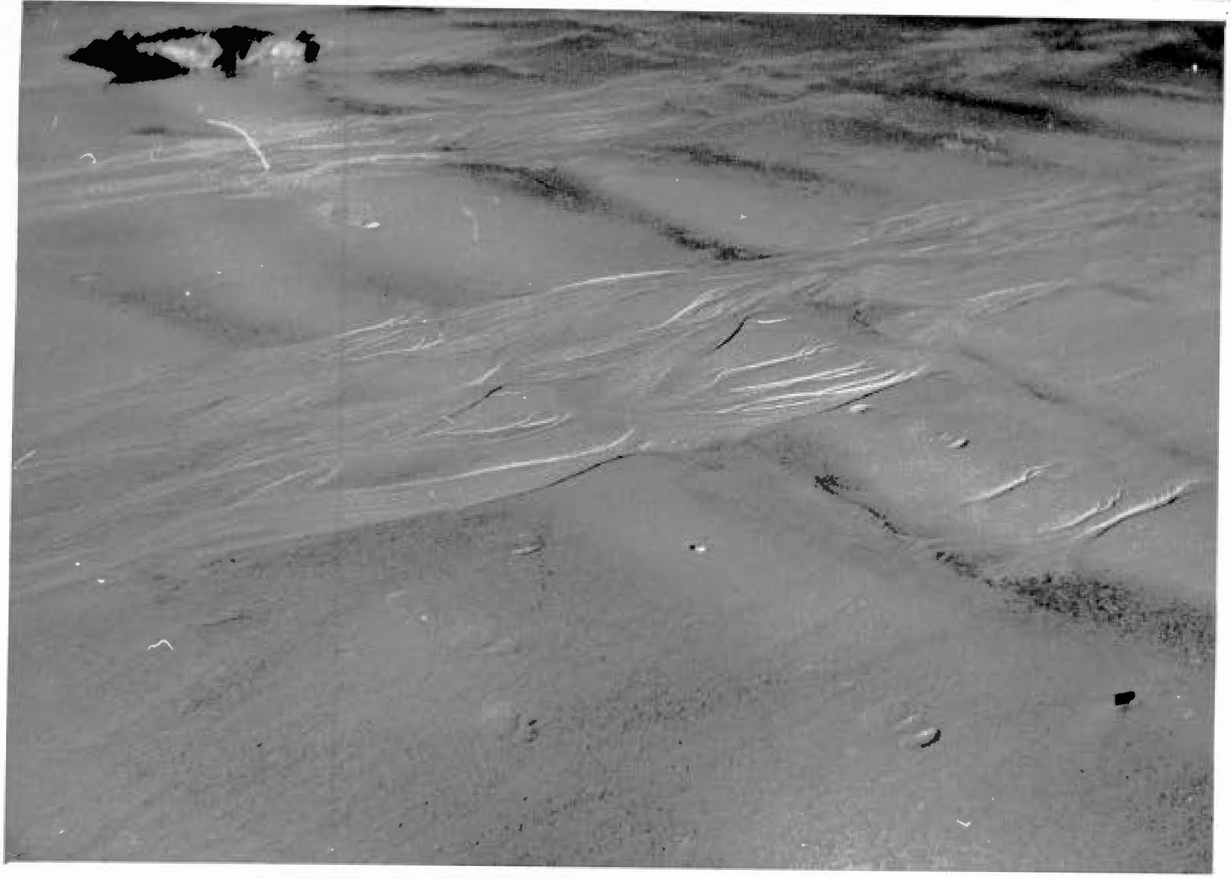


Figure 9.

Erosion due to run-off after rain. The picture was taken on the lower part of the saturated intertidal zone of Muizenberg beach, immediately after a winter thunderstorm. The rivulets of fresh water emerged from the sand where the water table met the surface and then pursued their course down to the sea, cutting through the longitudinal ripple-marks as they flowed.

by the wind during the summer than during winter. This is partly because the south-east wind, which is the prevailing wind of summer, tends to be stronger than the north-west wind of winter, often reaching gale force; it also tends to blow for longer periods. It is also due to the fact that winter is the rainy season; wet sand is not moved to any appreciable extent by the wind, however strong it is. For this reason also, wind tends to remove sand predominantly from the upper part of the intertidal zone and notably from the crest of the berm, while the lower half of the intertidal zone, being permanently wet, is an area of deposition.

These facts result in interesting differences between the beaches. South-facing beaches such as Muizenberg, as well as east-facing beaches such as Fish Hoek, suffer relatively little intertidal deposition of wind-blown sand, for the south-easter of summer erodes sand from the berm and carries it onto the back beach, while the north-wester of winter is only very occasionally capable of carrying sand in the opposite direction, to be deposited in the intertidal zone. On the other hand considerable intertidal deposition occurs on north- and west-facing beaches exposed to the south-east wind. Moreover this deposition takes place mainly in summer; it is most apparent where extensive back-beach and dune systems occur, such as at Milnerton and Noordhoek. Some beaches, of course, are relatively sheltered from one or other of the prevailing winds and this clearly affects the issue. Llundudno Beach, for example, is sheltered from the south-easter by high cliffs, so that relatively little intertidal deposition of wind-blown sand takes place, even though the beach faces north.

As the forces determining erosion and deposition also play a part in determining the particle-size distribution of the substratum, this is logically the next factor to be discussed.

Particle-size distribution of the sand

Much attention was paid during the early part of the survey to the sizes of the particles comprising the various beaches. Untreated sand samples were returned to the laboratory and sieved through a series of standard sieves, using a method modified after Morgans (1956). Results were plotted as phi cumulative curves, from which median phi

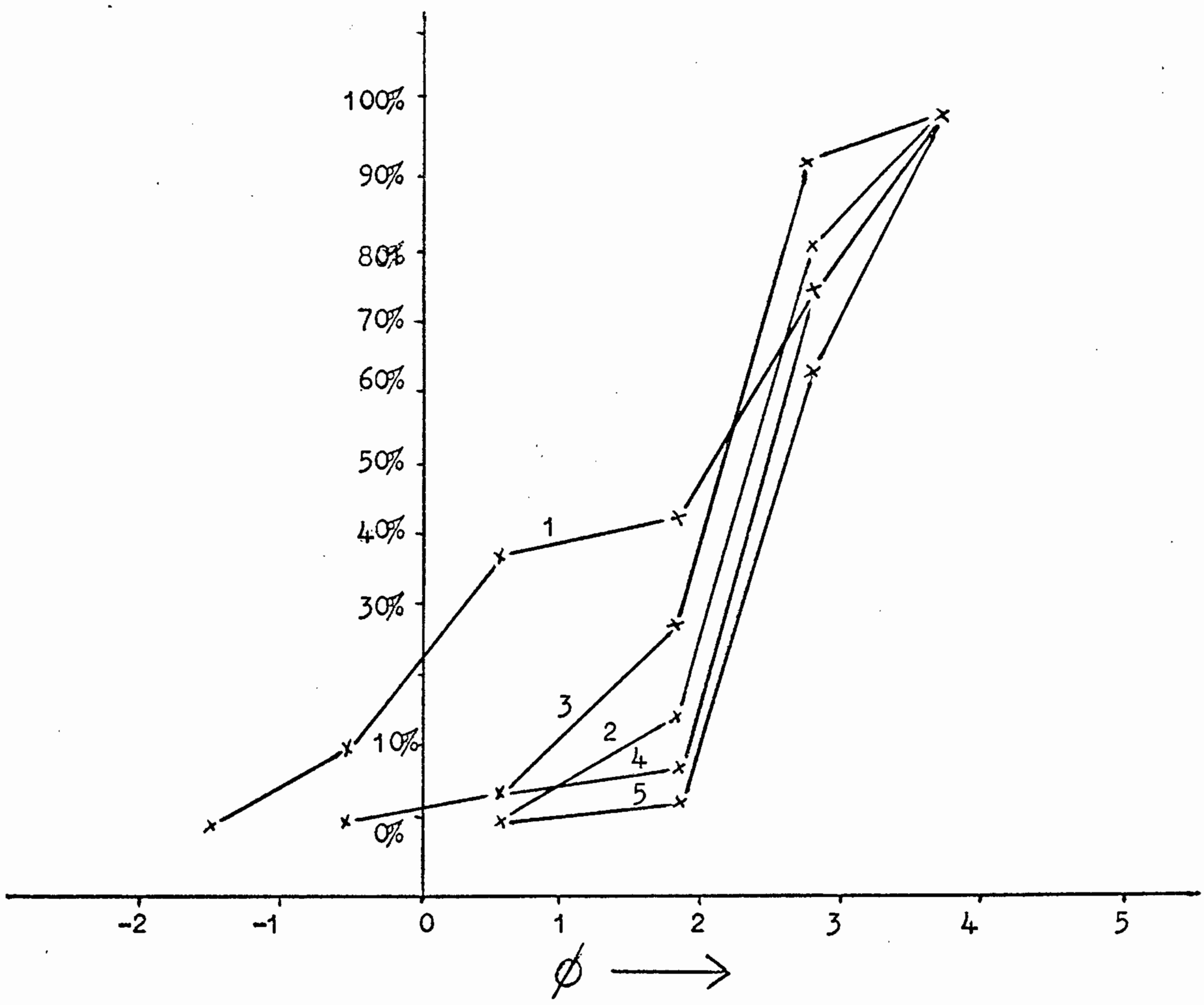


FIGURE 10

Phi cumulative curves of sand samples from Hout Bay north beach, 10/4/56. 1 = sand from the "toe" of the beach, just below L.W.S. 2 = sand from the low-tide swash-zone. 3 = sand from mid-tide level. 4 = sand from H.W.N. 5 = sand from the berm, just above extreme high water-mark.

values, quartile deviation and the phi quartile skewness could be read off. It is not intended in this introduction to present a detailed analysis of the results gained, though it is possible that this will be done in a later paper. However, it is necessary to report here certain general findings which are relevant to the papers on the sandy-beach fauna which follow this introductory one.

Extremes of particle size are not generally encountered on Cape Peninsula beaches, with the single exception of the pebble beach at Blouberg Village. Leaving this beach aside, the 310 sand samples analyses during the survey varied in median particle size between 0.175 mm and 0.850 mm. The highest median size values were in general gained from samples collected on the beaches most exposed to wave-action, but the lowest values (between 0.175 and 0.2 mm) were by no means confined to the most sheltered beaches. On the contrary, surface sand-samples collected from all the beaches at one time or another had median sizes between these two values and there was often no demonstrable difference in median particle size or degree of sorting between the surface sand of a very sheltered beach such as that at Hout Bay Harbour and the surface particles of exposed beaches such as Noordhoek, the phi cumulative curves superimposing on one another. However, while the sand of the Hout Bay Harbour beach displayed no significant variation with the seasons, the median particle size lying consistently around 0.180 mm (2.40 phi), the more exposed beaches showed a variation which could be correlated with the direction of the prevailing wind. Thus the intertidal surface sands of beaches such as those at Noordhoek and Milnerton had median values between 0.18 and 0.2 mm for much of the summer, while beaches facing south or east (including Muizenberg and Fish Hoek) had maximum median values during the second half of summer.

The conclusion that the sand showing these relatively low values was wind-blown sand was confirmed by analysing surface sand from the back-beaches at Noordhoek, Muizenberg and Buffel's Bay and also by analysing wind-blown sand collected in receptacles placed on the back-beaches during south-east winds of strengths varying between 10 and 50 knots. All these samples had median values between 0.170 and 0.195 mm and phi quartile deviations very similar to one another and to those of

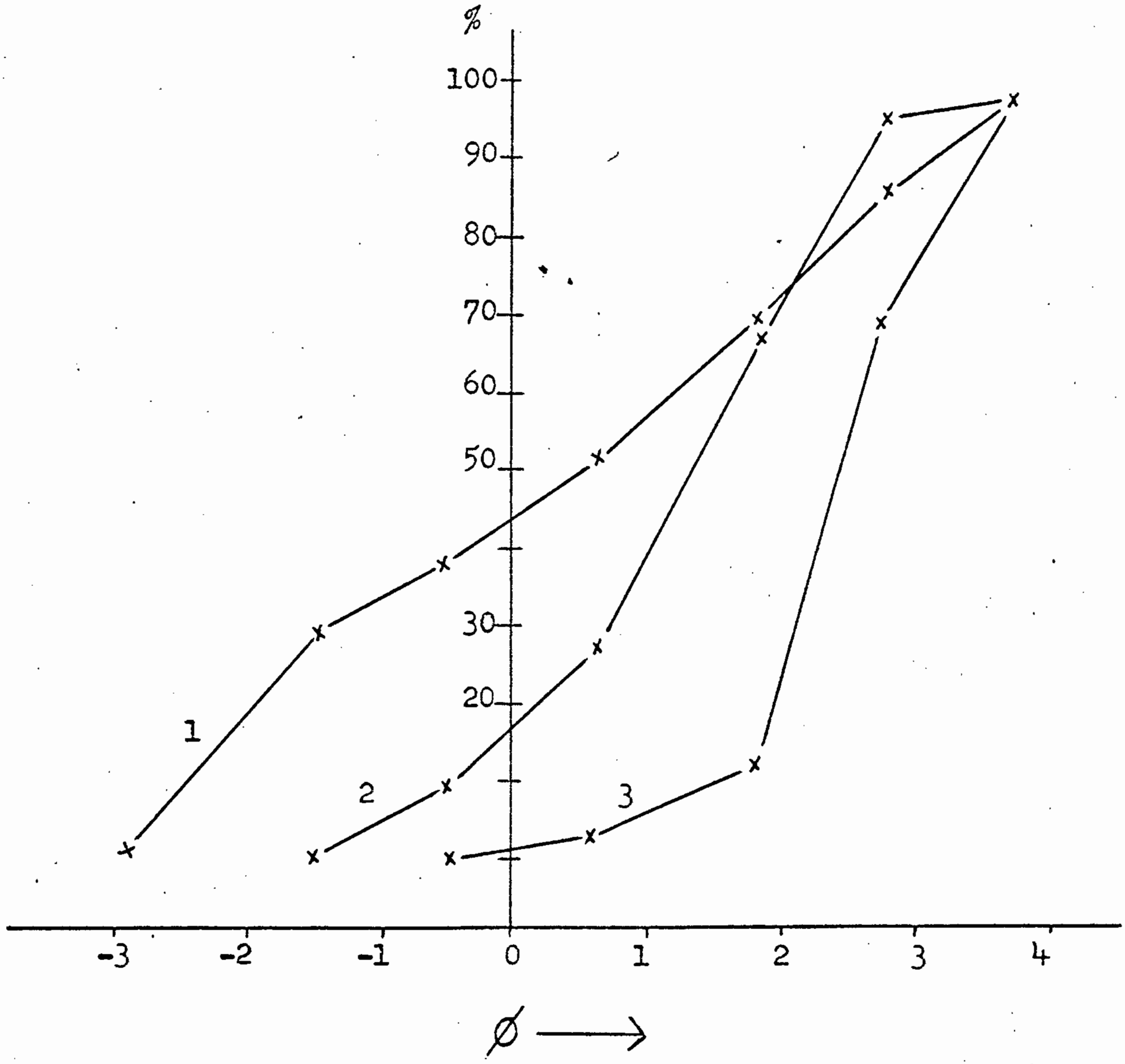


Figure 11

Phi cumulative curves resulting from analysis of sand samples from Milnerton Beach, 21/8/56.

1) Sand from Low Water of Springs level.

2) Sand from approx. mid-tide level.

3) Sand from just below high water-mark.

the fine intertidal sands.

Sand samples collected from various depths below the surface in the intertidal zone also proved of considerable interest for, while the most sheltered beaches (Hout Bay Harbour, Simon's Bay, Buffel's Bay) showed no significant variation with depth, all the more exposed beaches showed alternate layers of relatively coarse and relatively fine sand. On beaches such as those at Muizenberg, Diaz Bay and Noordhoek, this stratification was obvious to the naked eye, while on more sheltered beaches, such as the Hout Bay east beach, only particle-size analysis revealed the layering. As the fine layers from all beaches and from all depths displayed values similar to those obtained from the fine surface sands and from the back-beach sands, it is probable that they consist predominantly of wind-blown particles, while the coarser layers must be largely water-deposited. However, while the fine layers were always relatively free of large particles, the coarse layers almost invariably consisted of relatively large particles mixed with fine sand. Phi cumulative curves prepared from analysis of these relatively coarse layers usually displayed two (or more) log-normal components, one of which corresponded to curves prepared from samples of the fine layers. This is therefore also almost certainly wind-blown sand which has mixed with the water-deposited particles either at the time of deposition or subsequently.

The layers differed considerably in thickness from beach to beach, south-facing beaches displaying very thin layers of fine sand, while north- and west-facing beaches (notably Noordhoek) had relatively thick layers of fine sand. This is consistent with what has already been said about the prevailing winds and the fact that the south-easter moves much more sand than the north-wester. The layers were not found to be the same thickness throughout the intertidal zone of a particular beach and, in addition to local variation along the length of a beach, tended to increase in thickness with increasing distance from L.W.S. The crest of the berm and the upper part of the intertidal zone nearly always had a thick layer of fine surface sand, even when the surface layer further down the slope was coarse.

On some beaches, and particularly where the alternate strata are relatively thin, the sub-surface layer may reach the surface in some areas. This has been noticed particularly on Muizenberg beach, where examination of the surface often reveals areas of fine sand alternating with areas of coarse sand. On such occasions digging has invariably shown that the coarse layer is continuous, the fine sand overlying it having presumably been eroded away by the waves in those areas where the coarse layer is exposed.

Over and above those aspects of grain size already mentioned, the surface sand often shows differences in different parts of the intertidal zone. The coarsest sand is usually to be found on the "toe" of the beach, near L.W.S. level; this is the region of maximum turbulence and, as it is seldom exposed by the receeding tide, fine particles get little chance to settle. Median size values are generally lower higher up the slope, these showing either no significant difference from one another (e.g. Hout Bay north beach, fig. 10) or a gradient up the slope, the finest particles occuring towards the crest of the berm. Such a gradient is typical of the more exposed beaches, particularly during the season when wind-blown sand is not being deposited in quantity in the intertidal zone (e.g. **Milnerton** beach, fig. 11).

Organic content of the sand

Many food-chains begin from small organic particles trapped in the sand. It thus becomes important to be able to assess the concentration of this organic matter if quantitative ecological work is to be attempted. Moreover, the organic content can play a part in determining the physical environment, particularly of the microfauna, for it influences the degree of aggregation of the particles, affects the permeability of the sand and alters the nature of the surfaces with which the animals come into contact.

On unpolluted Cape Peninsula beaches, however, the organic content is so low that it has not been possible to make satisfactorily accurate measurements of it. Initially all sand samples subjected to particle-size analysis were also assessed for organic content, using the Walkley & Black method described by Morgans (1956) and incorporating the corrections introduced by Trask (1939). However, having analysed 198 samples from various beaches in this way, it was apparent that most of the figures were so low that their variation lay well within the limits of experimental error. 167 of the 198 samples tested gave readings of available organic matter which lay below 0.04% by weight. These included all samples from all the surf-swept beaches, including Muizenberg, Milnerton, Noordhoek, Camp's Bay and Fish Hoek. The organic content of Llundudno, Diaz Beach and Witsands was **barely detected** by the Walkley & Black method.

Samples from Simon's Bay showed values ranging from 0.04% to 0.06%, while a single surface sample from Buffel's Bay gave a reading of 0.045%. Only on the Hout Bay Harbour beach did values approach 0.1% prior to 1958, a condition attributable to the proximity of the fishing harbour and several fish-factories, as well as to the sheltered nature of the beach, while after 1958 the establishment of a new fish-factory factory virtually on the beach itself pushed the organic content of the surface sand up to 0.3%. By this stage the only organisms which could be found in the sand were bacteria and nematode worms.

Methods other than the Walkley & Black technique were considered but rejected for one reason or another. A number of these was discussed by Piper (1947), who nevertheless also favoured the Walkley & Black method. A.O.Fuller (personal communication) is of the opinion that no method has yet been developed whereby values for organic content below 0.04% can be assessed accurately.

Permeability, porosity and water tables

A suitable method for measuring the permeability of sand has been developed by Fireman (1944). It consists of obtaining a core of sand and passing a known quantity of water through it, noting the time taken. The permeability is then given by an equation derived from Darcy's Law:

$P = \frac{Ql}{AhT}$, where P = permeability in darcys, Q is the quantity of water, l the length of the column of sand, A its cross-sectional area, h the hydrostatic head and T the time required for the water to pass through the sand.

Values so gained may be somewhat low due to the introduction of air into the sand while collecting the columns (Christiansen, 1944), though Emery (1945b) has pointed out that air is also trapped in the sand <u>in situ</u>, thus decreasing the permeability of the sand in nature. It is therefore important for the sand in the column to be as close as possible to the state in which it occurred before collection; failure to do this is undoubtedly the chief source of error involved in the experiment. It must also be remembered that the measured permeability is based on vertical movements of the water, whereas under natural conditions the water may move both vertically and horizontally. Emery & Foster (1948) state that horizontal permeability may under certain conditions be much greater than the vertical permeability, due to an alternation of fine and coarse layers in some beaches. Such stratification has already been shown to exist on the majority of Cape Peninsula beaches.

The lowest permeability recorded during the survey was 20 darcys, for the Hout Bay Harbour beach. This figure must be considered low for a sandy beach (as opposed to a beach consisting of mud or muddy sand). This low figure must be attributed not only to the prevailing particle sizes of the substratum but also to its relatively high organic content. Emery & Foster (1948) recorded a permeability of 20 darcys for sand with a median diameter of 0.18 mm, which is about the same as the value for the Hout Bay Harbour beach, but their sand was less well sorted.

Figures for the more exposed beaches are considerably higher, though none approached the value of 114 darcys obtained by Emery & Foster for a well-sorted substrate composed of large particles. (The pebble beach at Blouberg Village was not tested for permeability.) Values ranged from 30 (Hout Bay north beach) to 58 (Diaz Beach). Both Noordhoek and Llundudno had the surprisingly rather low value of 42, while Muizenberg gave readings of 40 and 48 (from the upper and lower intertidal zone respectively. These permeabilities, though lower than had been expected, should lead to reasonable drainage, particularly when horizontal drainage through the coarse strata can occur. The resistance measured in the laboratory was undoubtedly due mainly to the fine strata which all these beaches possess. The difference between upper and lower slopes at Muizenberg can also be attributed to the fact that the fine layers tend to be thicker higher up the beach, as already mentioned.

The few readings of porosity taken at the same time as the permeability measurements are sufficient to show that there is no clear relationship between porosity and permeability. This may appear strange until one realises that while the figures for porosity indicate the total size of the interstitial space, they give no indication as to how that space is divided; a large number of small grains with small spaces inbetween may give the same reading for porosity as a small number of large spaces between large grains, yet the permeability may be expected to be higher in the latter case than in the former.

Figures for porosity were gained by returning water-saturated sand samples to the laboratory, weighing them after the careful removal of visible organisms, and then drying to constant weight at 105°C. The difference in weight gave the amount of water contained in the sand and this was assumed, for practical purposes, to equal the total interstitial space. This was expressed as a percentage of the original sample by volume. 18 readings of porosity were gained in this way, all lying between 25% and 27%. As samples from the most exposed as well as the most sheltered beaches had been included, it was felt that further measurements did not justify the time involved. It is clear that porosity does not vary markedly from beach to beach.

Measurements of the depth of the water table below the surface of the sand were made on numerous occasions, using the method outlined by Emery & Foster (1948). It will be demonstrated in a later paper that the disposition of the water table is a major factor in determining the zonation of the intertidal fauna, the point at which it meets the surface being critical. It may be noted here, however, that the depth of the water table below the surface and the distance over which it lies at the surface clearly depend on the state of the tide, the slope of the beach and the permeability of the sand. Thus on the Hout Bay Harbour beach, the gentle slope of the beach and the

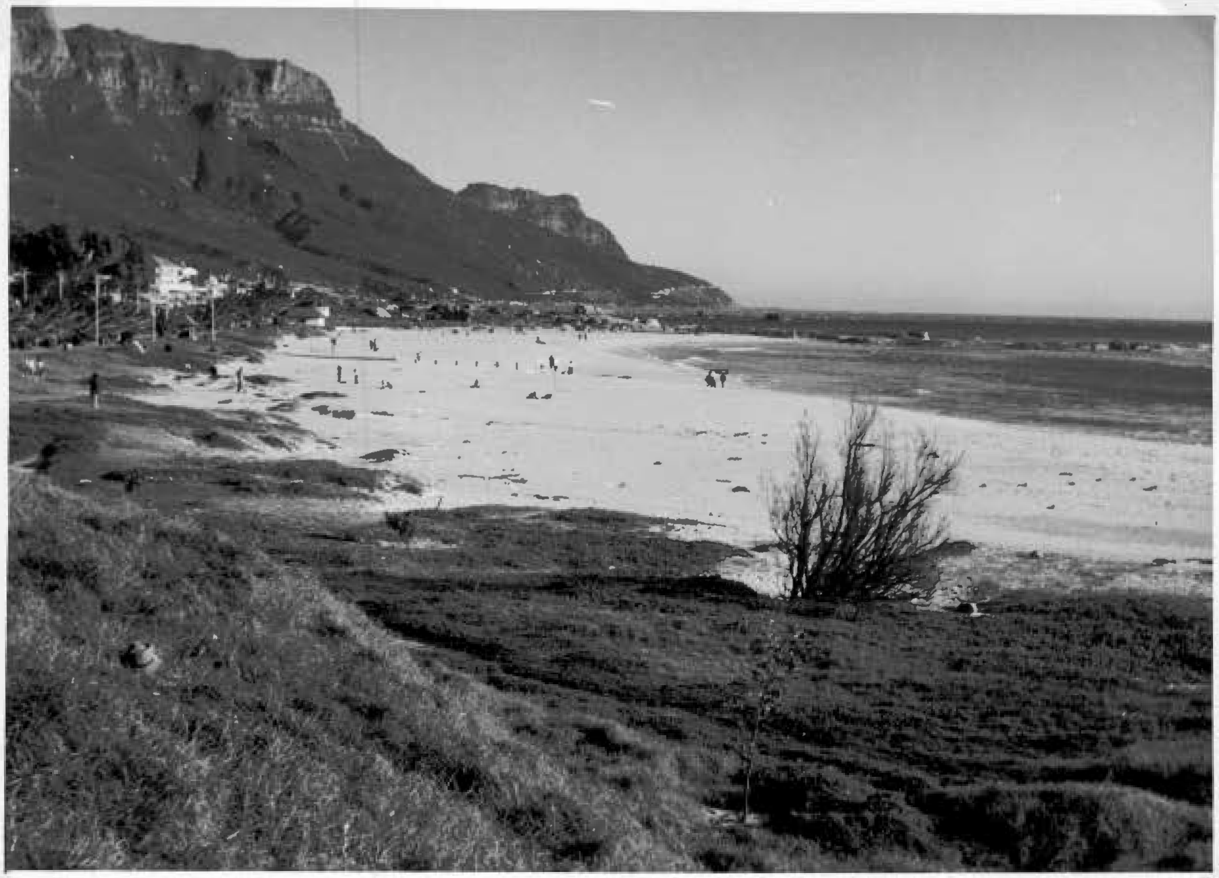


Figure 12.

The beach at Camp's Bay. Bathing is dangerous due to long-shore and rip currents; however, these are not as strong as those encountered at Llundudno and the beach is comparatively stable.

relatively low permeability of the sand resulted in the highest water table measured, the water never sinking below the surface of the sand in the lower half of the intertidal zone. The other extreme was encountered on the steeply-sloping pebble beach at Blouberg Village, where the level of the water table was effectively the same as the level of the tide on the three occasions when it was measured. Other Cape Peninsula beaches were intermediate between these extremes, the water table rising and falling with the tides but to a lesser extent, the degree of rise and fall becoming less and less as one proceeded away from the sea. A time lag was also apparent, the water table continuing to fall after the tide had begun to rise and continuing to rise after the tide had started to fall. Moreover the lag increased with increasing distance from the sea. This resulted in the water table sloping seawards at the time of low water but sloping coastwards at high tide. Naturally the slope was steeper during spring tides than at neaps.

The fact that at low tide the water table is at the surface for some distance from the sea means that at this time virtually all the water surging up the slope returns down it, while at high tide the abrupt descent of the water table allows most - and sometimes all - of the upsurging water to sink into the sand and be carried coastwards. Under these conditions there is nothing to prevent even the lightest water-borne particles from being deposited, while at low tide they have little chance to settle. As the proportion of water sinking into the sand shows a gradient up the beach, this factor clearly accounts for the gradient in particle size of the surface sand encountered on some beaches at certain seasons of the year. It is also a prime factor in establishing the concave shape of the beach.

Salinity

Many sandy-beach workers have measured the salt content of intertidal sands, usually by washing the salt out of the sand, evaporating to dryness, and expressing their results as a percentage by weight. Some workers, including Emery & Foster (1948), apply this method even to water collected from below the water table. This procedure is quite unrealistic as the results are related to the weight of sand and water and have little bearing on the actual salinities to which the fauna will be subjected. Ralph Smith (1956), on the other hand, offers a much more suitable method in that he measures the actual salinity, in parts per thousand, of the interstitial water contained in the sand. The figures gained are thus directly comparable with salinity measurements for the sea and give a true reflection of a natural condition which is likely to affect the fauna and flora.

Smith's method was therefore used in the present investigation, sand samples being collected by pressing a jar into the sand and immediately closing it with an air-tight lid to prevent evaporation. Samples were returned to the laboratory, where the salinity of the interstitial water was determined. Where samples from below the water table were required, they were drawn up through a narrow brass tube from the required depth.

The great majority of salinity readings from below the water table showed very little variation from the salinity of the sea, and need not be discussed here in any detail. Most of these readings were taken along transect lines which had deliberately been established in areas free from contamination by fresh-water streams. Under these conditions, and in the absence of rain or hail, the salinity of the water overlying the sand, sampled from just below the swash-zone, varied between 34.8‰ and 36.0‰ (39 readings between 1956 and 1959), while the water sampled from below the water table up the length of the transects varied between 34.0‰ and 37.2‰ (87 readings taken on the same occasions). Though the variation in salinity was somewhat greater than that of the sea, there was no indication of clearly-defined salinity gradients. However, there was a slight tendency for summer salinities (average 35.8‰) to be higher than the readings taken during winter (average 35.0‰). Such seasonal differences are not altogether unexpected and Marchand (1932) showed that during 1930 the salinity of the surface water at St James (on the east coast of the Peninsula) varied from 36.66‰ in January to 34.99‰ in July.

Of greater interest as far as the sandy-beach fauna is concerned are the extremes of salinity encountered during rain or hail or under abnormal conditions. Winter is the rainy season for the

Cape Peninsula, though it does rain occasionally during summer. The actual rainfall varies considerably between different parts of the Peninsula and is to be correlated largely with the proximity to the mountains which form its central area. The rain-gauge at Maclear's Beacon (on Table Mountain) may record a total rainfall for the year of 100 inches, while Faure, on the Capo Flats, may receive under 5 inches for the same period. Thus beaches such as those at Blouberg, Milnerton, Muizenberg and Strandfontein receive much less direct precipitation than do beaches such as Llundudno or Camp's Bay, where the coast rises more or less steeply to above the 1000 ft contour. The beaches forming the boundaries of the Cape Flats also receive far less run-off from the land than do those of the Peninsula proper, and for the same reasons.

Reid (1930, 1932) contributed pioneer work on the influence of fresh water flowing over the intertidal beach at the time of low water. He concluded that such fresh water has very little effect on the salinity of the water at any great depth below the water table and stated that "at a depth of 10 inches the salinity will be similar to that of the sea." Thus psammophilic burrowers may enjoy reasonably constant conditions of salinity providing they can burrow to something less than a third of a meter below the water table. While my own measurements of salinity support those of Reid (and later workers) in this respect, it should be noted that on Cape Peninsula beaches few of the dominant forms are capable of burrowing to such a depth.

Samples taken from the surface of the water table after a prolonged period of heavy rain often had very low salinities (down to less than 5‰) and it was apparent that there was little tendency for the water derived from rain to mix with the sea-water underlying it. Rain-water tends to be carried coastwards at the time of high tide, along the coastward-sloping water table, but is carried towards the sea at low tide. There is a tendency for the rain-water to stagnate in certain areas round about mid-tide, when the water table is more or less horizontal and indeed "pools" of fresh water within the sand may sometimes be detected at other states of the tide, for the slope of the water table is seldom uniform and may provide troughs in which rain-water can collect.

Thus, while the deep burrowers may be largely unaffected by heavy rain, those animals living at or just below the water table will have to tolerate a decrease in salinity, while the air-breathers such as *Talorchestia* and *Tylos*, living above the water table, will be subjected to virtually fresh water. The position is complicated by the fact that many animals do not occupy the same situation, relative to the water table, all the time but change their position according to the state of the tide or the time of the day. Thus at high tide the intertidal species of *Bullia*, lying buried in the sand at some depth below the surface of the sea, will not be faced with a decrease in salinity; but during low tide they come ashore to feed, regardless of weather conditions, and are thus exposed to the elements, the rain beating down directly onto the dorsal surface of the foot, while the thin film of water bathing the foot's ventral surface may become considerably diluted or even be composed of virtually fresh water.

If animals situated above the water table, and particularly those restricted to the sand surface, must tolerate very low salinities during rain, they must face saturated salt conditions during hot days in summer. Evaporation commonly dries out the surface of the sand almost completely, leaving a deposit of crystalline salt which is often sufficient to bind the sand grains together. This is especially noticeable immediately above high-water mark, where spray from the waves has fallen on the sand and evaporated, but may also be marked in other areas, where water has been drawn up by capillary action from the water table, to evaporate at the surface of the sand. In addition to its direct effect on the fauna, the binding of the sand particles by precipitated salt may be expected significantly to decrease their erosion by wind and on tropical beaches it is claimed that such binding prevents the formation of back-beach dunes (*vide* Callan, 1964).

Temperatures

The Cape Peninsula is said to enjoy a Mediterranean climate. Winter temperatures rarely fall to freezing point and snow and frost are seldom encountered. Temperatures in summer sometimes reach 90°F in the shade but higher values are rare, largely due to the summer's typical south-east wind blowing from the sea. The marked contrast between summer and winter found in some parts of Africa does not apply to the Cape Peninsula, there being a relatively steady increase or decrease in temperature with the seasons.

Temperatures of the sea around the Peninsula have received much attention and have been considered to play a large part in determining the distribution of the fauna, particularly with regard to faunistic differences between the east and west coasts (Gilchrist, 1905; Stephenson, 1944; Ekman, 1953; Day, 1964). In general the Peninsula's west coast is influenced by the relatively cold waters of the Benguella current, while False Bay is warmed by the Agulhas current. Stephenson, Stephenson & du Toit (1937) have written that "the meeting places of warm and cold water-masses ..... vary in position with season and weather. It is, nevertheless, correct to say that during the summer the northern part of the False Bay coast of the Peninsula is chiefly affected by the warmer water and the northern part of its Atlantic coast by the colder; and the difference between the temperature of the sea at specific localities on opposite sides, on the same day, may exceed 8°C." In the opinion of these authors, "possibly there is no small area in the world where water of such different temperature is separated by so little land." It may be noted in passing that the high summer temperatures of False Bay are not to be attributed solely to the influence of the Agulhas current and are, in fact, unusually high for a locality so far west along the southern coast.

During the course of the present survey, temperatures of the air, water and sand were taken by means of mercury-bulb thermometers, reading to 0.25°C, the lower ends of the thermometers being equipped with spikes for penetrating the sand. Each thermometer was twice standardized in the laboratory. Temperatures of the sea were taken immediately below the swash-zone; the highest average obtained was that of the sea at Muizenberg - a value of 16.5°C (average of 98 readings). This figure agrees very closely with the mean annual temperature of the sea as given by the Muizenberg Municipality (16,7°C). Mean temperatures were lower further south and the average for Simon's Bay and Buffel's combined was 15.5°C (52 readings); it may be noted that Isaac (1937) gives a figure of 15.3°C for the mean annual temperature of the water off Simonstown.

Temperatures of the water taken on the Peninsula's west coast beaches were invariably lower than those taken in False Bay at the same time of year. The average difference between east and west coast readings was 3.25°C, the mean for Milnerton being 13.0°C and for the beaches of Hout Bay 13.75°C. Differences between east and west coasts were considerably greater during summer than winter, the seasonal variation in temperature being much larger in False Bay than off the Peninsula's west coast. The fact that False Bay's seasonal variation is abnormally large has been recognised ever since the graphic representation of this variation by Stephenson et al (1937).

Temperatures recorded from below the water table on beaches on both sides of the Peninsula agreed very closely with those of the sea, the only significant variation being found in the top two centimeters. Where differences were found, they were most marked where the water table lay at the surface of the sand, above the swash zone. Even here, however, the temperature seldom differed by more than 1.5°C from that of the sea. Above the water table the picture was, of course, different and at the surface of the sand temperatures tended to be close to the temperature of the air, even where the sand was damp. On very hot days the surface temperature of dry sand, particularly near the crest of the berm, was sometimes higher than that of the air and surface temperatures of up to 50°C have been recorded on the back-beaches.

Other factors

Other factors of the chemical and physical environment studied during the survey included oxygen levels, hydrogen ion concentration, the relative humidity of the habitats enjoyed by the terrestrial and semi-terrestrial organisms and the extent of the cover provided by attached plants and washed-up debris at and above the drift line. Humidity and cover will not be dealt with in this paper but will be presented at a later time, when the back-beach fauna is discussed.

Discussion of the oxygen concentrations of the interstitial water is also postponed, because an investigation of this factor is at present being carried out under my supervision. It may be stated here, however, that on the beaches so far investigated the decrease of oxygen tension with depth below the water table is less than that recorded by Brafield (1964) on European beaches, using similar techniques. This may be correlated with the better drainage of existing Cape Peninsula beaches and their low content of organic matter. (It is unfortunate that the Hout Bay Harbour beach ceased to exist before a suitable method for determining oxygen concentration had been developed, for this beach might well have given different readings from the others.) It is very relevant to the generally high oxygen tensions that, although the presence of ferrous sulphide "black layers" below the surface of the sand is one of the best-known phenomena associated with marine sandy beaches, such black layers have not been noted on the majority of Cape Peninsula beaches. This does not mean that they do not exist but rather that they begin below the depth to which investigations were normally conducted, i.e. half to one meter in the lowest part of the intertidal zone increasing to up to three meters in the upper part of the slope. The beaches sheltered from wave action were, however, exceptions to this rule, a black layer being encountered on Buffel's Bay beach some 40 to 50 cm below the surface of the low-tide terrace, though in the upper part of the intertidal region it was well over a meter below the surface. On the Hout Bay north beach it was somewhat closer to the surface, being about 35 cm deep near the level of L.W.N., while on the Harbour beach it was never far from the surface and disturbing the sand to only 4 or 5 cm released hydrogen sulphide gas. The ferrous sulphide black layers may be expected to be poor, though not completely lacking, in oxygen (Brafield, 1964) and begin closer to the surface in beaches which are poorly oxygenated.

Marchand (1932) has presented data for the daily variation in hydrogen ion concentration at St. James (between Muizenberg and Fish Hoek) for the year 1930, while Morgans (1959) gives a table summarising the monthly means. Marchand demonstrated a marked seasonal variation in pH at this station and associated the higher pH values of summer with a dense phytoplankton population, which reduced the level of CO_2 in the water. Hogben & Zoond (1928) studied the surface pH about two miles off-shore around the Peninsula from well inside False Bay to Table Bay. They were unable to show any statistically significant difference in pH between the surface water on either side of the Peninsula, despite the fact that two very different bodies of water were involved, differing in temperature by over 5°C. These authors came to the conclusion that differences in hydrogen ion concentration around the coast constituted an unimportant factor as far as the local distribution of marine plants and animals was concerned and that the effect of pH was in general negligible compared with the effect of temperature. This conclusion has been accepted and supported by later workers. Nevertheless a few readings of pH were made during the present survey in view of the fact that the free CO_2 content of a sandy beach may vary from 1 to 12.6 parts per thousand at a depth of 8 cm (Pennak, 1942). Such concentrations might be expected to lower the pH quite considerably.

The values actually obtained, however, were disappointing in that, though water drawn from below the water table sometimes had a lower pH than that of the sea, these differences were small. The greatest differences were encountered on Hout Bay Harbour beach (13/4/57 and 7/12/57) when the water drawn from a depth of 20 cm below the water table, which was at the surface of the sand, had a pH about 0.25 lower than that of the sea. However on Muizenberg beach (6/1/62 and 20/7/62) it was necessary to draw water from a depth of nearly 40 cm before a pH reading 0.1 lower than that of the sea was obtained. Bruce (1928) suggested that the calcareous matter present in a sandy beach may provide a buffer system which effectively stabilizes the hydrogen ion concentration. My results possibly lend support to this view.

Greater pH changes may be encountered during rain, for rainwater commonly has a pH slightly on the acid side of neutral, whereas all my values for sea-water, including those from below the water table, have been alkaline. However, it is mainly the surface fauna which will be subjected to such changes.

		Hout Bay				
	Milnerton	East	North	Harbour	Llundudno	Muizenberg
Wave height - trough to crest	1.3 - 3.2 meters	0.5-1.7 meters	0.1-0.7 meters	0.02-0.07 meters	1.5 - 5.1 meters	0.75 - 3.0 meters
Max. overall slope	1/13	1/16	1/25	1/28	1/15	1/15
Min. overall slope	1/24	1/20	1/27	1/28	1/25	1/19
Median size coarsest sand	0.710 mm	0.485mm	0.300mm	0.190mm	0.735 mm	0.695 mm
Median size finest sand	0.185 mm	0.185mm	0.180mm	0.175mm	0.185mm	0.185 mm
Permeability	48d	-	30d	20d	42d	40-48d
Porosity	25.9%	26.1%	25.7%	25.1%	-	26.5%
Development of berm crest	Good	Fair	None	None	Good	Good
Extent of back beach	Vast	Large	Small	Minute	Small	Vast
Shelter from south-easter	None	Little	Little	Little	Good	None
Beach faces	west	south-west	north	east	north-west	south
Mean temp. of water	13.0°C	13.75°C combined average			-	16.5°C
Approx. ann. Rainfall	30 cm	between 50 and 70 cm			85 cm	40 cm
Organic cont. of sand	<0.04%	<0.04%	0.05%	0.1%	barely detectable	< 0.04%

Table 2.

Summary of some of the physical factors encountered on those Cape Peninsula beaches accorded special attention. (Figures for Hout Bay beaches prior to 1958.)

THE FAUNA

Though this paper has been almost entirely concerned with introducing the physical and chemical conditions encountered on Cape Peninsula sandy beaches, it must not be forgotten that our chief concern in this series of papers will be the fauna. It would, of course, be premature in this introduction to enter into any detailed description of the fauna or of the modes of life of the species comprising it. Nevertheless, it is considered desirable at this stage to say something about the sandy-beach animals, particularly those occurring on the six beaches accorded the most regular and intensive sampling. To this end, Table 3 has been prepared, listing those animals collected regularly from the six beaches, with some indication of their abundance. Animals collected only rarely have been omitted from this list, as have the invaders from the sea and the back-beaches. We are left with a list of some 27 species of the macrofauna which are characteristic not only for the six special beaches but also for Cape Peninsula sandy beaches as a whole. The microfauna is not represented because it has not yet been possible to identify or make a detailed study of the majority of them.

Of the 27 species of macrofauna listed, only 9 are to be found on virtually all Cape Peninsula beaches; 7 favour beaches sheltered from wave action, being limited to, or reaching maximum density on, beaches such as that at Hout Bay Harbour; and 6 favour beaches moderately exposed to the waves. Not a single species is limited to beaches with a high degree of exposure to wave action. The species may also be grouped according to their occurrence on either side of the Peninsula; no less than 21 of the 27 species listed occur on both the east and the west coasts, though some, such as <u>Bullia</u> <u>digitalis</u>, are much more common on one side thanthe other. Of the remaining 6 species, 4 are limited to the east coast of the Peninsula and only 2 to the west coast.

The macrofauna of all the beaches is clearly dominated by annelid worms, gastropod and lamellibranch Mollusca, and Crustacea, though, as pointed out elsewhere (Brown, 1964d) the food chains start and terminate in organisms not resident on the intertidal beach and invading predators almost certainly outweigh the resident predators. Fish are

SPECIES	Milner-ton	Hout Bay			Llun-dudno	Muizen-berg
		East	North	Harbour		
NEMERTEA:						
Cerebratulus fuscus	C	FC	FC	FC	P	C
NEMATODA (unidentified)	C	C	VC	A	P	C
ANNELIDA:						
Abarenicola gilchristi	-	-	-	FC	-	-
Arenicola loveni	-	-	P	C	-	FC
Cirriformia tentaculata	-	-	-	VC	-	-
Dispio magna	P	P	P	P	P	P
Glycera convoluta	FC	C	C	VC	P	C
Nephtys capensis	C	C	P	P	P	VC
Nephtys hombergii	-	-	P	FC	-	-
Nerine cirratulus	C	VC	FC	FC	P	VC
Scolelepis squamata	-	-	-	-	-	A
MOLLUSCA:						
Bullia digitalis	FC	A	FC	-	FC	P
Bullia rhodostoma	-	-	-	-	-	A
Bullia laevissima	-	-	-	C	-	P
Donax sorra	FC	C	C	C	-	C
Schizodesma spengleri	-	-	-	-	-	VC
ARTHROPODA: CRUSTACEA:						
Gastrosaccus psammodytes	C	C	P	-	VC	C
Pontogeloides latipes	P	P	P	P	P	P
Eurydice longicornis	C	A	P	-	C	C
Exosphaeroma truncatitelson	-	-	P	A	-	P
Tylos granulatus	P	FC	-	-	-	-
Tylos capensis	-	-	-	-	-	P
Bathyporeia gracilis	P	FC	C	P	-	FC
Urothoe elegans	P	P	P	P	P	P
Talorchestia quadrispinosa	A	A	C	P	C	A
Callianassa kraussi	-	-	P	C	-	P
ECHINODERMATA:						
Echinocardium cordatum	P	-	-	-	-	-

Table 3.

Occurrence of intertidal faunistic species on those Cape Peninsula beaches to which special attention was accorded. Only species collected with some regularity are listed. (P = Present, FC = Fairly common, C = Common, VC = Very common, A = Abundant.) Hout Bay records are those made before June, 1958.

probably the most important of these invaders, supported by birds and a few Crustacea. However the division between resident and invading species is not as clear cut as it is for many other ecosystems. There are two reasons for this - the comparatively narrow width of the environment, so that no part of the intertidal zone is more than a few meters from an adjacent ecosystem, and the fact that a large part of the fauna is very mobile, not only tending to move up and down the beach with the tides but also exchanging intertidal for infratidal life from time to time. Thus of the twenty-seven "permanent residents" listed in Table 3, only thirteen are, as adults, confined to the intertidal sands or their immediate vicinity. Some, such as Bullia laevissima, do not breed in the intertidal zone and are generally more common below tide-marks than intertidally; nevertheless as they are always present on those beaches on which they occur, they are clearly a permanent part of the intertidal ecosystem. Even Bullia digitalis and B. rhodostoma, which must be considered essentially intertidal forms, are to be found in quite deep water from time to time and on certain beaches (Milnerton, Llundudno) occur intertidally for only part of the year. Exosphaeroma deserts its beaches for long periods as part of a seasonal cycle of activity which will be discussed in a subsequent paper. Even the giant air-breathing isopod, Tylos, moves all over the back-beach and may, where conditions are suitable, be found over a kilometer inland, though it has a strong tendency to return to the upper part of the intertidal region.

The ecosystem is thus a singularly open one, whose fauna is in general characterised by a high degree of mobility and the ability to burrow into sand. Most of the resident species show adaptations to intertidal psammophilic life; an investigation of these will provide much of the data presented in subsequent papers.

DISCUSSION

Though it is tempting - and indeed rewarding - to pursue the inter-relationships between the various physical and chemical factors of sandy beaches for their own sake, in the present context it is far more relevant to consider these factors as contingencies to be faced by the organisms within the ecosystem. It is for this reason that I have been content, in this introduction, to describe the environment in rather general terms, pointing out the extremes in conditions rather than analysing them in detail or attempting to present all the data collected.

Intertidal sandy beaches are usually considered to offer a harsh environment for potential colonisers and the beaches of the Cape Peninsula are no exception to this rule. Nevertheless a wide range of conditions is encountered and not all the beaches are equally hazardous to living organisms. Exposure to wave action, which plays such a large part in determining other parameters of the physical environment, varies considerably from beach to beach; it is doubtful whether there are many sandy beaches in the world more exposed to wave action than is Diaz Beach, while Hout Bay Harbour beach was extremely sheltered in this respect. The other Cape Peninsula beaches show degrees of exposure intermediate between these extremes, so that a whole range of conditions is presented. Wave action itself may, of course, be a limiting factor as far as the distribution of certain species is concerned; this means not only that there is an upper limit of wave action which can be tolerated by some animals but also that certain forms actually require a certain degree of wave action to undertake successfully their cycles of activity, as has already been shown in the case of the sandy-beach snail, Bullia digitalis (Brown, 1961a). Other species may be limited not by wave action itself but by factors dependent on the degree of wave action, such as the stability of the sand or the size of the particles comprising the substrate.

The Cape was not once called "The Cape of Storms" for nothing and it is particularly during the Cape's winter storms that the aquatic psammophilic fauna must meet its most adverse conditions. Not only does wave action itself increase dramatically during these storms but the resultant erosion may destroy in a single forty-eight hour period a profile which has taken all summer to build up, reducing it to its pre-aestral condition. This is particularly true of the beaches of the Peninsula's west coast, including Llundudno and, to a lesser extent, Milnerton. Even the semi-terrestrial fauna (Tylos, Talorchestia and the staphylinid beetle, Philonthus, etc.) are not safe from such erosion, for storms commonly remove that part of the beach where they are most abundant - the drift line, the crest of the berm and the near back-beach.

The slope of the beach and the particle-size distribution of the sand, with its attendant variation in permeability and porosity, are determined by the equilibrium which exists for a longer or shorter period between erosion and deposition, these sand movements being due to the complex action of both the waves and the wind. Except where sand movements due to the water are usually negligible (Hout Bay Harbour beach) these factors result in a stratification of the sand, relatively fine sand alternating with layers of relatively coarse sand. While the particle-size distribution of the fine layers varies very little from beach to beach, and is consistent with the view that this is wind-blown sand, the coarse layers increase in coarseness with increasing exposure to wave action. This leads us to the conclusion that the inhabitants of exposed beaches must tolerate a wider range of particle size than must the animals of sheltered beaches, while the fauna of the most sheltered beaches will encounter an almost uniform size distribution at all depths and at all seasons of the year. I believe this to be a far more realistic statement than the usual assumption that the particle size of the substrate increases with exposure to wave action. It may be of some importance, however, to note that even the coarse layers of Cape Peninsula beaches normally contain a certain percentage of fine, wind-blown sand, for ever since the work of Allen (1899) it has been generally accepted that, where coarse and fine grades of sand are mixed, it is the fine sand which predominantly determines the environmental characteristics of the substratum and consequently the species which will colonise it. Animals requiring a relatively fine sand may, in other words, be able to populate such a mixture, while forms restricted to coarse sand may have difficulty doing so.

The low organic content of the majority of Cape Peninsula beaches must reflect on the food relationships of the community and also leads to a higher vertical permeability than would otherwise be the case. With the exception of the Hout Bay Harbour beach, permeability measurements were largely dependent on the coarseness of the coarse layers and the thickness of the thin strata. Adequate permeability leads to adequate drainage, as reflected in the tidal movements of the water table within the beach. Such movements may be of considerable importance to the fauna as well as helping to determine other conditions, such as the oxygen tension.

Temperatures cannot be considered extreme, though the west coast beaches are subjected to lower temperatures than are those on the east coast. This difference in temperature has been shown to influence the distribution of rocky-shore forms and it would be surprising if it were not important in the distribution of sandy-beach animals as well. In this respect it has been noted that several species are confined to the sandy beaches of one coast or the other, while certain other species are dominant forms along one coast but not along the other. It would be difficult to find a factor other than temperature to account for this distribution.

The range of salinity which must be tolerated clearly depends on the habits of the individual species. Deep burrowers may enjoy relative freedom from salinity changes, though the possibility of burrowers such as Arenicola and Callianassa drawing water of low salinity into their burrows due to their pumping activities may be born in mind. Animals living at the surface of the water table or confined to the surface of saturated sand will certainly have to withstand low salinities, while the semi-terrestrial forms, such as the amphipod, Talorchestia, may expect to meet conditions ranging from virtually fresh water to super-saturated salt solutions and crystalline salt itself. pH, on the other hand, is unlikely to constitute an important ecological factor.

These, then, are some of the conditions which must be tolerated or avoided by the organisms living on Cape Peninsula beaches. Subsequent papers will show how the dominant species manage to come to terms with them and even exploit them, while at the same time coping with a multitude of biological factors which may, in some instances, be equally harsh and forbidding.

SUMMARY

This is the first in a series of papers devoted to the ecology of the sandy beaches of the Cape Peninsula. Conditions on these beaches are described, with special reference to the beaches of Hout Bay, Llundudno, Milnerton and Muizenberg. Tidal conditions, wave action, beach profiles and sand movements are discussed, while attention is also given to the particle-size distribution of the substrata forming the beaches. The organic content of the sand, its permeability and porosity, and the disposition of the water tables are all discussed briefly and some data concerning salinities, temperature and pH are presented. Mention is made of the fauna and a list of the more important members of the resident fauna of the beaches accorded special attention is given. There is some attempt to show how the physical factors are interrelated.

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8.

THE ECOLOGY OF THE SANDY BEACHES OF THE CAPE PENINSULA, SOUTH AFRICA.

PART 2: THE MODE OF LIFE OF *BULLIA*.

THE ECOLOGY OF THE SANDY BEACHES OF THE CAPE PENINSULA, SOUTH AFRICA. PART 2: THE MODE OF LIFE OF BULLIA (GASTROPODA: PROSOBRANCHIATA).

by

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INTRODUCTION

The decision to devote a separate paper to Bullia in this series arises partly from this animal's importance to the sandy-beach ecology - as indicated by its abundance and by its position in the food cycle - and partly from the desire to present at this stage a picture of the animal's activities which may serve as a basis for future research. This paper therefore presents new observations and experiments and attempts to integrate the conclusions reached from these with conclusions already arrived at in previous publications on this sandy-beach snail.

The genus Bullia was erected by Gray (in Griffith, 1833) for the purpose of distinguishing a group of species intermediate between Buccinum and Terebra and characterised in the living animal by the remarkably wide expansion of the foot. From the chaos of gastropod systematics which prevailed during the latter half of the nineteenth century emerged the family Nassidae (Nassariidae), containing, among others, the genera Nassa and Bullia, the latter being considered distinct from the genus Dorsanum in being blind. Large numbers of Bullia species were described, mostly from southern Africa but some from other parts of the world, empty shells, often beach-worn, being accepted as sufficient evidence for the erection of a new type. Shell pattern was held to be a specific criterion and colour-varieties were legion. Though several authors attempted to resolve the resulting confusion, this was only achieved comparatively recently by the late K.H.Barnard (1959). From this study, Bullia emerges as a genus of twelve, or at most thirteen, species, limited to the coast and shallow waters of southern Africa. There remain certain fossil prosobranchs, attributed to the genus Bullia from other parts of the world (vide Wenz, 1938). However, it is difficult enough to be sure that these fossils belong to the family Nassariidae, and to attribute them to a genus within that family appears to be the merest guess-work. There is, in fact, good evidence, which I hope to present later, that Bullia arose from a primitive Nassarid ancestor in the South African intertidal zone, from where it has shown adaptive radiation along the coast and into deeper water, and that it has never occurred in other parts of the world.

All snails of the genus occur on sandy substrata, into which they burrow by means of the widely expanded ploughing foot. Four species are relevant to the ecology of the sandy beaches of the Cape Peninsula, though only two of these, B. rhodostoma and B. digitalis, may be described as typically intertidal. B. laevissima, though an infratidal form, invades the intertidal zone where wave-action is slight and conditions resemble those in the infratidal shallows (Brown, 1961a), while B. annulata occasionally invades the beaches of False Bay in small numbers, possibly in order to breed. A fifth species, B. tenuis, while present off-shore, has never been recorded intertidally.

LOCOMOTION AND BURROWING

Though the expanded foot of Bullia is very thin, averaging only about 1 mm in thickness in a medium-sized B. digitalis, the degree of expansion in terms of volume is very much greater than in rocky-shore snails (Brown, 1964c). Nevertheless the foot is expanded in the usual way, by the introduction of haemolymph into the pedal sinus (Brown & Turner, 1962). In this it differs from sandy-beach naticid snails such as Polinices, in which the foot is expanded largely by the introduction of sea-water (Bernard, 1968). The total volume of the haemolymph is not abnormally large for an aquatic gastropod and this implies that Bullia is capable of shifting a greater proportion of its haemolymph into the pedal sinus than is possible in most gastropods and that the animal may have greater control over haemolymph movements (Brown, 1964c).

The expanded foot is very agile and may be turned and twisted rapidly in any direction, folded over or drawn back around the shell. The apparent independence of movement of different regions of the foot is unusual in a gastropod and is aided by its thinness and wide expanse. Nevertheless, during normal locomotion over a damp substratum, the locomotory wave-pattern analysed by Lissman (1945, 1946) is in evidence. Most of the forward propulsive force is provided, however, by the lobular antero-lateral

Figure 1.

An individual of Bullia rhodostoma commencing to burrow. The characteristic track left by the animal while progressing over wet sand can be seen.

(Photo: G.J.Broekhuysen)

regions of the foot, which swell out, at the same time pushing downwards and backwards against the sand. Consequently the animal moves forwards in a series of jerks, the resulting tracks left in the sand being completely characteristic. The progress achieved by this method of locomotion is rapid and speeds of about four meters per minute are not unusual. Very much higher speeds may be attained over short distances by adult individuals in search of food and an adult B. digitalis was once clocked at a speed of ten meters per minute, over a distance of approximately half a meter. However, this individual could not be induced to repeat its performance.

The necessary turgor of the foot during these and other movements is apparently provided by the tonus of the visceral somatic musculature, which exerts a pressure on the haemolymph through that part of the sinus system which links the visceral sinus with the cephalopedal sinus; the system also allows for rapid changes in the volume of the foot without placing a strain on the heart, kidney or gill (Brown, 1964c).

The entire sole of the foot is rich in mucus-producing cells, which lubricate the under surface of the foot during locomotion and in addition there is a pedal gland which can pour mucus into the pedal groove which separates the propodium from the metapodium. Not only does this mucus lubricate; it can also act as an adhesive, allowing the animal to crawl up the vertical side of a glass tank or plastic bucket to well above the water-level. In stationary animals a suction pressure is developed against dislodgement. It is difficult to see what significance either adhesion or suction might have during normal locomotion over a sandy substratum, but they probably play a part during copulation and may also be important at times during feeding, particularly when the food is being moved around in the swash zone of the beach.

As in many other burrowing prosobranchs, it appears from observation that submergence into the sand is a continuation of normal surface locomotion, "the propodium being inserted as a mobile, freely progressing wedge" (Morton, 1964). This view is probably correct as Trueman (1968), having intensively studied burrowing in naticid snails by analysing cinematographic and electronic recordings, concludes that in gastropods "burrowing is an adaptation of normal surface locomotion." Bullia will attempt to burrow in all grades of sand but is not able to do so successfully in gravel (diameter of particles 3.2 mm and above), while the time taken to complete burrowing decreases with decreasing particle size (Brown, 1961a). Repeating these experiments with snails in different size ranges, it is found that juveniles have more difficulty burrowing in the larger grades than do the adults. Individuals of *B. digitalis* with a shell length of about 0.5 cm are unable to burrow among particles of more than 1.4 mm diameter. If particle size is ever a limiting factor with regard to distribution, it must therefore be more limiting to the juveniles than to the adults. A certain proportion of large particles in a sand of mixed grades can, however, be tolerated and even the smallest individuals of *B. rhodostoma* appear to have little difficulty in burrowing on a beach such as that at Muizenberg, where the percentage of particles over 1.4 mm is sometimes quite high (Brown, 1969~~a~~).

The animals are not able to burrow successfully into dry sand or even into damp sand if the water-table lies below the surface. Sand saturated with water presents no difficulty and snails which have been handled will bury themselves immediately in the saturated sand of the foreshore or in the laboratory. Field observations of snails which have not been disturbed, however, show a more complex pattern of events. In the first place the burrowing of undisturbed snails in the field is much more leisurely than that of handled snails, commonly taking twice or three times as long as the times listed by Brown (1961a) for handled snails in the laboratory. Secondly, there is a tendency for undisturbed snails in the swash zone to burrow only while covered by water. It is very common for snails to commence burrowing while covered by the swash from one wave, and then lie partially buried when the water has retreated, awaiting the swash from the next wave, in which burrowing is completed.

Emergence from the sand usually takes place vertically, the lateral margins of the foot pushing downwards and forcing the shell upwards through the sand (Brown, 1961a). In deeply buried animals, however, these vertical movements do not free the shell but serve to loosen the sand around and above the animal; final emergence then takes place by normal locomotory movements, at an angle to the sand surface. *Bullia* is unable to emerge from sand from which the water has been drained. In the case of *B. digitalis* and *B. rhodostoma*, the two typically intertidal species, emergence is stimulated by water-currents or the presence of food, while in the predominantly infratidal *B. laevissima* it is possible to inhibit emergence by creating water-currents (Brown, 1961a). The few individuals of Bullia annulata which have been tested in this respect gave somewhat ambiguous results; in general an increase in turbulence appeared to stimulate emergence in snails kept in well-aerated sea water while the production of water currents inhibited emergence in snails which had been kept for a few days in stagnant water.

REPRODUCTION

As in most prosobranch Mollusca, the sexes are separate. Sexual dimorphism is not obvious superficially but may be determined by the presence or absence of a penis. The females also tend to be slightly broader than males of the same length. Females are more numerous than males in all adult populations examined, though this difference is not apparent among juveniles. The proportion between the sexes is reasonably constant and shows no seasonal fluctuation. The disparity is probably due to the early death of the males, a conclusion already reached in the case of certain other prosobranchs (Fretter & Graham, 1964).

In my earlier account of the behaviour of Bullia (Brown, 1961a) it was necessary to admit that little was known about reproduction in this genus, the only relevant evidence being **four** egg-cases of B. tenuis (Barnard, 1959). However, copulation has now been witnessed both in B. digitalis and B. rhodostoma and the egg cases of both have been discovered. Credit for the discovery of the egg cases of B. rhodostoma should go to Professor J. Omer-Cooper (personal communication) and to Clarke (1951).

In both the intertidal species of Bullia, copulation most commonly takes place in late autumn. In B. rhodostoma copulating pairs have been taken from below the surface of the sand on Muizenberg beach and at Strandfontein; they have only been found below L.W.S. level on a rising tide. Wave action makes copulation difficult to study under such circumstances and when the pair is removed from the sand they invariably separate; neither has it been found possible to induce copulation in captive snails in the laboratory. Courtship has not been witnessed but is known to be brief and sometimes hardly recognisable in aquatic gastropods (Webb, 1950; Fretter & Graham, 1964).

There appear to be two positions in which copulation

Locality	Species	Date	Max. No. per m^2		Adults		Juveniles	
			Feeding	-	%♂	%♀	%♂	%♀
North Beach, Hout Bay	*B. digitalis*	11/4/56	36	14	37	63	0	0
Milnerton	*B. digitalis*	25/5/56	171	31	41	59	0	0
Milnerton	*B. digitalis*	21/8/56	90	-	33	67	0	0
Milnerton	*B. digitalis*	4/10/56	-	11	11	27	33	29
Milnerton	*B. digitalis*	18/12/56	117	23	17	30	25	28
Milnerton	-	3/3/57	0	0	-	-	-	-
Fish Hoek	*B. rhodostoma*	20/8/56	27	-	40	60	0	0
Muizenberg	*B. rhodostoma*	29/1/57	-	10	20	40	22	18
Muizenberg	*B. rhodostoma*	2/3/57	73	-	21	39	19	21
Muizenberg	*B. rhodostoma*	15/3/60	-	-	26	59	8	7
Muizenberg	*B. rhodostoma*	6/1/62	-	14	7	26	31	36
Harbour Beach, Hout Bay	*B. laevissima*	16/11/56	-	-	36	64	0	0
Buffel's Bay	*B. laevissima*	-	-	-	34	66	0	0
Simon's Bay	*B. laevissima*	-	-	-	30	70	0	0

Table 1.

The constitution of some populations of *Bullia* in the swash zones of Cape Peninsula beaches. The last two analyses were made on material collected from the beaches in question on several different dates. Under "maximum number per square meter", the first column lists maximum numbers in areas where *Bullia* was feeding on stranded medusae or other material, while the second column lists maximum numbers in areas where no such activity was obvious.

may take place in *B. rhodostoma*. In one, the snails lie side by side, facing opposite directions, with the right side of the male's foot overlapping that of the female so that the shells almost touch, allowing the penis to be pushed into the shell mouth of the female. The proboscis of one or other of the partners and sometimes both may be extruded and brought into contact with the foot or head of the other snail. It is known that some pulmonates enhance copulatory excitement by bodily contacts and by gnawing the partner's body (Webb, 1950), though I can find no record of such activities among prosobranchs. A second copulatory position, which has only been seen twice, involves the male mounting the shell of the female so that it is almost completely hidden by his foot. Part of the foot is drawn back on the right side, however, to permit entry of the penis. In this position the partners face the same direction. Copulation may last at least half an hour but as its onset has never been witnessed, it is not possible to allocate a more definite period to this activity.

B. digitalis also displays two methods of copulation, one being identical with the first position described for *B. rhodostoma*, the snails lying side by side and facing opposite directions. This is accomplished a few centimeters below the surface of the sand. The second position witnessed in *B. digitalis*, however, is accomplished in the surf. Under these circumstances the male is mounted on the shell of the female, facing the same direction. The pair is washed backwards and forwards and rolled over and over on the sand by the waves; it is under these conditions that the adhesive properties of the foot of the male must undoubtedly play a part in keeping the partners attached to one another. Pairs copulating in the surf on Hout Bay East Beach have been carefully removed to a plastic bucket for examination, sometimes without causing a cessation of copulatory activity. The male may then be seen to gnaw the female repeatedly on the head and anterior parts of the foot, while she twists her foot from side to side, brushing her operculum strongly over the dorsal surface of his metapodium. This activity has been observed for up to fifteen minutes before the partners finally separated. A presumably fertilised female, removed to the laboratory, laid eggs contained in a capsule, six days after copulation. The capsule was situated only two to three centimeters below the surface of the sand and was deserted at once. None of the eggs hatched under these circumstances.

In the field, egg cases of both species are to be found during late autumn and early winter, four to twelve centimeters below the sand surface below low water-mark. In a surprising number of cases a snail is to be found alongside the eggs and this animal has invariably been found to be female. J. Omer-Cooper (personal communication) has written that "the eggs (of *B. rhodostoma*) are difficult to find until one has acquired the knack, but when one finds them there is always a large female with them. I think they stay with the eggs all winter and look after them." Parental care is not unknown among gastropods, and *Hipponyx* is known to brood over eggs laid external to the body (Yonge, 1953).

The egg cases of both intertidal species of *Bullia* measure from 2 to 2.5 cm in length and 1.2 to 1.6 cm in width. They appear normally to contain between 1,500 and 2,500 eggs, the eggs lying in clumps of 50 to 100. However, egg cases containing fewer eggs have been found, one (of *B. rhodostoma*) having only 24 eggs. Some of the eggs may be food eggs. The eggs hatch as miniature adults, there being complete suppression of free-living larval stages. It is of interest to note that the European species of the closely-related genus, *Nassa* (*Nassarius*), all have planktonic larvae and produce egg cases very different from those of *Bullia* (Lebour, 1931; Thorson, 1946). It is also worth recalling that the only egg cases of *Bullia tenuis* which have been found contained only a single individual each, with the exception of a single egg case containing "numerous eggs" (Barnard, 1959). Egg cases of other species of *Bullia* have never been discovered.

Newly hatched snails are to be found intertidally on the beaches of the Peninsula from late winter to late spring. However, only *B. rhodostoma* and *B. digitalis* are involved. Juveniles of *B. annulata* or *B. laevissima* have not been found in the intertidal zone of Peninsula beaches, though juveniles of *B. laevissima* have been taken intertidally in Langebaan Lagoon. Mating behaviour has not been seen in either *B. laevissima* or *B. annulata*.

Though both *B. digitalis* and *B. rhodostoma* normally appear to copulate during autumn, a large number of individuals of *Bullia digitalis* was found copulating in the surf on Hout Bay East Beach in the spring of 1963. As this has not been observed elsewhere along the coast, two possible explanations present themselves. Firstly, it is known that warm water from the east coast may on occasion sweep round Cape Point and influence the temperature in the shallow bays of the Peninsula's west coast. After some while the conditions change and the temperature drops back to a more normal level. If reproduction depends partly on temperature, as it well may do in view of its seasonal nature, then reproductive behaviour is likely to be upset by such fluctuations in temperature as have been mentioned. The second possibility is that the behaviour of Bullia in Hout Bay had been thrown out of gear by the increasing pollution of the area. This is not unlikely as it is known that certain behaviour patterns in B. laevissima were profoundly disturbed by this pollution. It should also be mentioned here that Mrs C.M.Connolly, of Fish Hoek, discovered an egg case apparently produced by B. digitalis, on Fish Hoek beach on 5/11/61 (i.e. well into summer). It was lying on the surface of the sand, which must be considered abnormal, but was nevertheless accompanied by a large female B. digitalis. It was found to contain approximately 2,000 eggs, which were nearing the end of their development.

GROWTH AND LIFE-SPAN

The difficulties of studying growth-rates in the Mollusca are legion. The allometric nature of their growth makes linear measurement an unreliable index of growth and weight remains the most accurate assessment (Wilbur & Owen, 1964). However, the difficulty with weight measurements in a prosobranch gastropod is that the shell commonly weighs far more than the living tissues, so that a marked increase in weight does not necessarily imply a great increase in tissue weight; nor are the two related to one another in any simple manner. A further difficulty arises from the fact that the rate of food intake greatly influences the growth rate, though it may not be related to the ultimate size achieved by the individual. Nutritional aspects have been but little studied, though Yuki (in Wilbur & Owen, 1964) has developed an equation which describes the growth of young pearl oysters and uses the transparency of the water as a measure of the food supply. Such an equation is hardly applicable to prosobranchs such as Bullia, which have the opportunity to feed only at irregular intervals and will survive for periods up to several months in the laboratory without food.

Preliminary laboratory experiments have shown that newly hatched snails can reach a weight of up to 2 gm (with foot retracted) in twenty weeks, if offered food twice a day. This approaches the adult weight, though examination of the reproductive organs of such individuals indicates that they are not yet mature. Snails fed between once and twice a week reached only between 0.7 and 1.1 gm in twenty weeks, while newly hatched snails fed once a fortnight did not survive.

The differences between field and laboratory conditions are such that no definite conclusions can be drawn from the above results. The range of sizes of snails collected in the field shows a discontinuity from the end of winter, when "babies" and "adults" may be distinguished, right through to mid-winter, by which time it is often not possible to place a given individual in either the juvenile or the adult group. Young snails examined in autumn were apparently not sexually mature. It thus appears that snails hatching at the end of winter will not breed until the autumn of the following year, though they may reach adult size well before then.

During February, 1960, large numbers of individuals of <u>Bullia</u> <u>digitalis</u> and <u>B</u>. <u>rhodostoma</u> were marked, some with "Necol" anti-fouling paint and some by cutting a small notch in the mouth of the shell, as part of a capture-recapture programme for assessing the size of the populations. As it was not intended at that time to study growth or life-span, no record was kept of the size or sex of marked snails. However, a marked female of <u>B</u>. <u>rhodostoma</u> was recaptured on Muizenberg beach as late as March, 1964, while two marked females of <u>B</u>. <u>digitalis</u> were recovered from Hout Bay in December, 1963, in the normal course of collecting. The female life-span in these species is thus at least four years, and probably considerably longer. A life-span of fifteen to twenty years would appear to be unexceptional for an intertidal prosobranch (<u>vide</u> Altman & Dittmer, 1964).

WATER AND HEAT RELATIONSHIPS

Osmotic relationships in <u>Bullia</u> have been studied under my supervision by K. Tresselt and H. Kahn (unpublished student projects, 1963 & 1964). Haemolymph was extracted from the cephalopedal sinuses of snails immediately after removal from the beach and regularly after their immersion in various concentrations of sea water. The freezing point depressions of these haemolymph samples were determined. Changes in the weight of the snails were also plotted. In a subsequent series of experiments, the concentrations of various ions in the haemolymph of snails placed under osmotic stress were compared with those of the surrounding water.

I do not intend to report here the details of the methods used or the results gained. Suffice it to say that, as expected, Bullia is a poikilosmotic animal, whose internal concentration of solutes varies closely with that of the surrounding water. When removed from its natural habitat and placed in either diluted or concentrated sea water, it reaches osmotic equilibrium within two hours, decreasing or increasing in weight and volume as it does so. If the animal survives this change, its weight and volume slowly tend towards normal once more, its osmotic pressure remaining constant. If in a dilute medium, the weight may overshoot the zero value, so that for an hour or two the animal actually weighs less than it did originally. None of these results is unexpected in view of the work of Krogh (1939) and more recent investigators.

However, the lack of osmoregulatory ability in these animals does not imply that they are unable to tolerate wide changes in the osmotic pressure of their environment. On the contrary, Krijgsman & Brown (1960) found that although Bullia digitalis ceases to crawl about when the salinity is lowered slowly to 18‰, the snails can be kept for some hours at this reduced salinity without permanent ill-effects, for they recover completely when returned to normal sea water. Brown (1961a) also reported cessation of crawling activity at high salinities, the critical value lying between 45.1 and 45.8‰ in the case of B. laevissima and between 44.5 and 45.6‰ in the case of B. digitalis. All the snails recovered when returned to fresh sea water. Since then I have kept individuals of B. digitalis and B. rhodostoma at salinities of 10.0‰ and 50.0‰ for one hour and obtained one hundred percent recovery. However, the range of tolerance is less if the period involved is increased and Tresselt has found that at a salinity of approximately 20‰, half the snails are dead after 125 hours.

In the field, snails may be subjected to quite considerable short-term fluctuations in salinity (Brown, 1969). The lowest salinities encountered will be at low tide during rain, for the snails still come ashore in search of food and crawl around on the wet foreshore, the rain beating directly onto them and diluting the surface film of water in which the ventral side of the foot is submersed. However, such conditions do not have to be tolerated for long, for the snails soon burrow into the sand or re-enter the surf. I have on occasion found a "stranded" snail lying on the sand during heavy rain, its foot swollen and apparently incapable of movement; however, as they seldom venture far above the swash zone, the rising tide soon reaches such snails and they will presumably recover in the majority of cases.

Though there is no osmoregulatory ability in Bullia, the animals show some regulatory ability as far as the proportions of ions in their fluids are concerned. This ionic regulation decreases when the animals are placed under osmotic stress but reasserts itself once osmotic equilibrium has been reached.

If the intertidal species of Bullia must face greatly decreased salinities during rainy weather, they meet other hazards on hot, sunny days. Rocky-shore snails generally retract into their shells and remain inactive while exposed by the tide, but it is just during this period that B. digitalis and B. rhodostoma are most active and come ashore to feed, exposing their broad, thin feet to whatever conditions the environment has to offer. The rate of evaporation from the dorsal surface of the foot has not yet been measured but it is clear that it must be considerable on the hottest, windiest days, once the snail has wandered above the swash zone. Brown (1961a) studied the rate of water-loss of individuals of B. digitalis and B. rhodostoma placed in desiccators over calcium chloride at 19°C and also investigated the tolerance to various saturation deficits. Unfortunately, while there is no good reason to doubt the accuracy of the results gained, or even their validity under the particular conditions described, it is not possible to draw conclusions from them which will be applicable to the animals under field conditions. The main reason for this is that when Bullia is subjected to desiccation in the laboratory, it soon retracts into its shell and remains there until it dies, while on the beach, animals exposed to the atmosphere are invariably fully expanded, exposing the whole dorsal surface of the foot to the wind and sun. Under these conditions evaporation must be very much more rapid. However, the snails confine their activities to the lower part of the beach and specifically to that area in which at least a thin film of water overlies the sand. It is thus possible that water lost through the dorsal surface of the foot may be replaced through the ventral surface. Moreover, the siphon is held down, in front of the head, in this surface film, water being continuously siphoned through the mantle cavity. This stream of water is only allowed to cease during feeding and sometimes when the animals are suddenly disturbed.

In addition the animal brings ashore a sizeable reservoir of sea water in its free space and there is some evidence to suggest that an interchange of water between this space and the mantle cavity can take place (Brown, 1964c). An indication of the importance of the water in the free space is provided by the fact that snails will on no account draw air into this cavity instead of water. However, this reservoir subserves other functions as well, so that it is not possible at the present time to assess its significance in the water- or heat-relationships of the animals.

The most significant cooling effect is likely to be provided by evaporation from the dorsal surface of the foot. This is invariably moist, even on the hottest day. As the foot is very thin and there is a continuous circulation of haemolymph through it at all times, it may well act in the same way as the radiator of a motor car in helping to cool the entire body. It is evident that some such cooling device is essential as *B. digitalis* cannot tolerate high temperatures.

DEFENCE MECHANISMS

Like other prosobranchs, *Bullia* is capable of retracting rapidly into its coiled shell. It does not do so frequently, however, and it is very rare to find a retracted snail in the field. In the laboratory, the foot may be stimulated in a variety of ways without causing retraction (Brown, 1961a) and, after practice, haemolymph may be withdrawn from the pedal sinus or substances injected into it while the

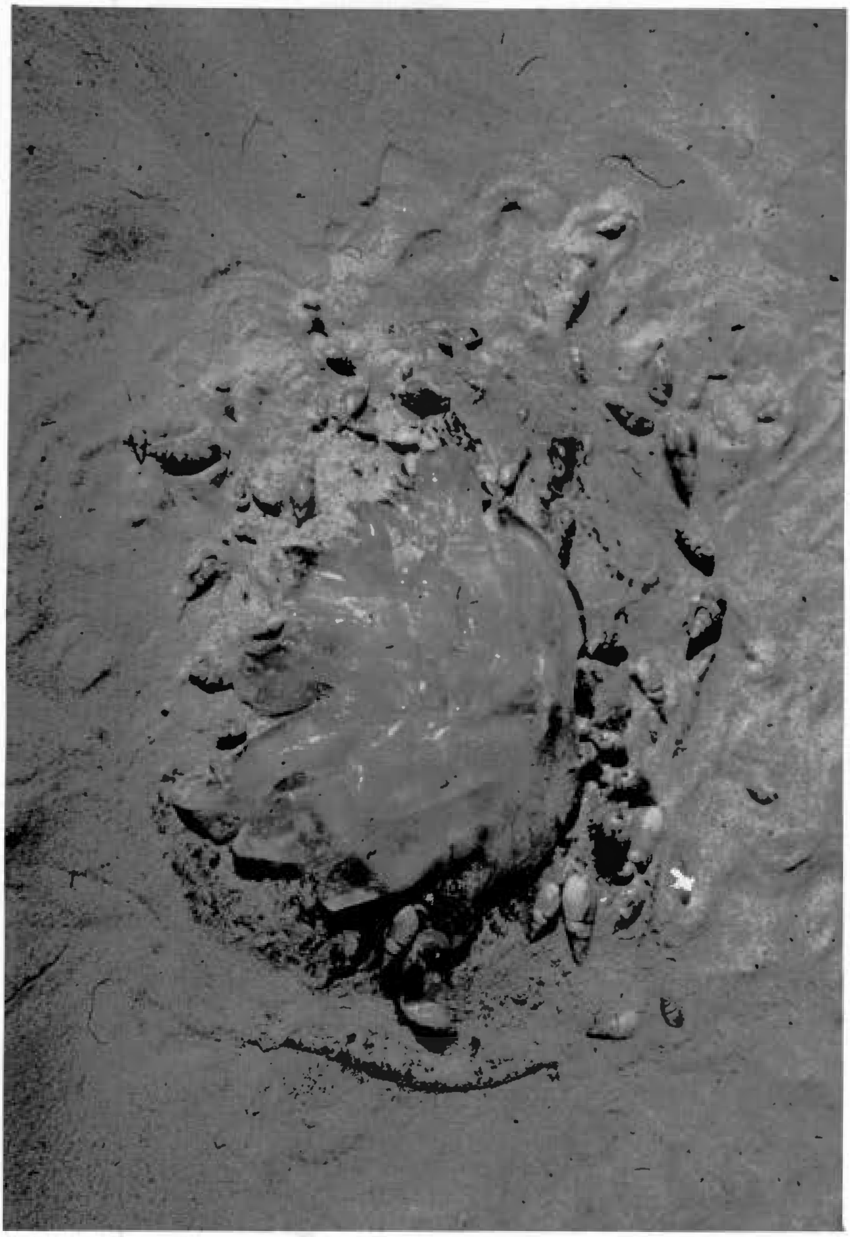

Figure 2.

A typical sight on False Bay beaches: Bullia rhodostoma clustered round a stranded jelly-fish. Some snails are still feeding, while others have dropped off and are burying themselves.

(Photo: R.H.Simons)

foot remains expanded. On the other hand, tactile stimulation of the region behind the shell, where the body enters the shell, usually results in rapid retraction. It may be significant that this is the region most likely to be stimulated if the snail is seized by a sizeable predator. Retraction into the shell does not protect the snail from very small enemies such as isopods, for these are capable of crawling into the shell mouth and attacking the naked tissues of the foot, the operculum being of an almost vestigial nature. The threshold for retraction seems to be raised once the animal leaves the water and is increased still further if the foot is dried (Brown, 1964c).

As the animal retracts into its shell, jets of water issue from the foot (Gilchrist, 1916; Brown, 1961a). This water is drawn from the free space and from the mantle cavity, the jets deriving their force from the contraction of the columella muscle (Brown, 1964c). At first sight it would appear that these jets might constitute a useful defence mechanism against land predators. However, while it can certainly be an alarming experience for an uninitiated observor to receive a jet of water full in the face while examining a Bullia, a would-be predator might surely learn to ignore so harmless a phenomenon. Moreover, attempts to show the addition of some poisonous or highly unpleasant substance to these jets have proved fruitless. Jets collected from snails which have been handled and "teased" have a pH which is not significantly different from that of the sea water they have been allowed to draw in during expansion. Unlike the snails studied by Thompson (1959, 1961) Bullia is not a secreter of acid. It is possible to demonstrate the presence of traces of ammonia in the fluid expelled from some snails; however, this is inevitable in an ammoniotelic animal and the quantities added are insufficient to alter significantly either the pH or the total osmotic pressure as determined by a cryoscope. In view of the lack of increase in the osmotic pressure, there remains only the possibility of the addition of some substance effective in minute quantities.

Tests for protein are completely negative (Brown & Turner, 1962) as are tests for cyanide, tetramethylammonium hydroxide, histamine and a variety of less likely substances. Not surprisingly, traces of mucopolysaccharide may be demonstrated in the fluid, but this is certainly not what we are looking for. A little of the fluid applied to a freshly-made cut on the back of the hand causes no greater reaction than ordinary sea water and no undue inflammation of the tissues is observed. The fluid tastes like sea water to the human palate and no ill-effects result on drinking it. While this evidence is not conclusive, it now appears rather unlikely that the jets contain any substance which might deter a predator. Moreover, it seems improbable that a predator such as a bird, attacking a snail from above while it is crawling over the sand, would be struck by the jets, as these are directed downwards.

Nevertheless, the fact remains that none of the birds of Cape Peninsula beaches will attack Bullia (Brown, 1964a), though the snails take no action to hide themselves. On several occasions I have seen a snail bump into the foot of a waiting sea-gull, and once a snail crawled onto the foot of a resting Larus dominicanus, to be shaken off with obvious distaste. Moreover the size and coloration of the snails, and the fact that they move about rapidly on the surface of the sand, make them by far the most conspicuous invertebrates in the intertidal zones of those beaches on which they occur. The most plausible explanation for their safety from land predators is thus unpalatability of the flesh. This unpalatability certainly extends to the human sense of taste, the tissues tasting metallic and sour both in the cooked and uncooked conditions. Nevertheless, the flesh is not poisonous, nor does its unpalatability extend to the vertebrates as a whole, for Bullia is eagerly consumed by the Galjoen, Coracinus and by adults of the holocephalian, Callorhynchus, as well as by elasmobranch fishes.

It is against aquatic predators, then, that Bullia may be expected to require special defence mechanisms. One obvious and effective means of escape is burrowing into the sand. However, with each tide the intertidal species of Bullia are committed to passive transport by the waves and it is surely then that they must be most vulnerable. It is worth considering whether the jets could in any way help to protect the animal as it is carried backwards and forwards by the waves, sometimes at a considerable height above the surface of the sand and in an inverted position. It is clear that jet-production under water would be even less effective in frightening a predator than it would on land. However, there emerge possible functions for the jets under water which would be quite inapplicable to the terrestrial phase of the snail's cycle.

One of these possibilities is that when a submerged snail, in contact with the substratum, retracts and produces its jets of water, these stir up the sand and divert the interest of the predator. While this idea was thought to be promising at first, I feel it does not stand up to simple experiment and observation. It is true that when a snail is crawling over the submerged sand of a laboratory tank and is caused suddenly to retract, the resulting jets do stir up the sand on either side of the animal as well as behind it. However, the difficulty is to make the snail behave in the appropriate way to begin with. Snails which are disturbed while crawling over the sand normally bury themselves, whether the disturbance is mechanical or chemical. On the rare occasions when a snail has been seen to retract into its shell instead of burying itself, it has invariably turned over onto its back first so that the jets, instead of being directed downwards into the sand are directed up into the water, with no effect at all on the substratum. In fact to observe the stirring up of sand by the jets I have found it necessary to prevent the snail from burrowing or turning over by actually holding it in position. It seems most unlikely, therefore, that this possibility is realised in the field.

A second possible function for the jets is jet propulsion. Far fetched as this seems, it may be worth discussing it briefly. If a snail is suspended upside down in a tank of sea water, it can be caused to retract by the addition of various substances to the water, though the same substances elicit the burrowing response if the foot is in contact with the substratum. These substances include γ-buterobetaine, a compound which occurs in high concentration in the bodies of elasmobranch fishes. It is soluble in water so that the possibility of this substance warning *Bullia* of the approach of an enemy cannot be ignored. Escape by burrowing is not immediately open to the snail while it is being transported by the waves or while it is suspended in a tank. In the former case, retraction allows the animal to sink towards the substratum. Whether this is an effective defence or not must partly depend on the rate of sinking through the water. Unless increased by other means, this rate of sinking cannot be expected to be fast, for the snail has a specific gravity only a little higher than that of sea water (Brown, 1961a). The rate of descent might be increased, however, by the production of jets. When the animal is in its inverted position, as it always is while being passively transported, then the jets of water will be directed upwards and the resulting force will act downwards on the falling snail.

Preliminary work in the laboratory indicates that during the most rapid retractions the thrust of the jets is considerable, but there is a great deal of variation. Furthermore, while this thrust exists, it may be only coincidental to the real function of the jets. There are several objections to this theory of jet propulsion, quite apart from the fact that it doesn't "feel" right. One obvious objection is that the elasmobranch fishes are mainly bottom feeders, as presumably _Callorhynchus_ is also. Another difficulty is that after its descent to the substrate the snail would have to expand its foot again before it could bury itself; it would thus be quite helpless for a moment if the predator followed it down to the sea floor.

As no other possible functions for the jets seriously present themselves, we may ask whether, perhaps, the jets as such have any function other than simply getting rid of the water in the free space and the excess water in the mantle cavity. However, the production of this water into jets - instead of just letting it drip out of the shell - requires both morphological and behavioural adaptations (Brown & Turner, 1962; Brown, 1964c). I am therefore fully convinced that these jets have a function of their own, though what that function is cannot yet be determined. In this respect it may be noted that _Bullia_ _laevissima_ and _Bullia_ _annulata_ as well as the intertidal species produce jets.

THE COLOURS OF _BULLIA_

Attention has already been drawn to the conspicuousness of the intertidal populations of _Bullia_. This is partly due to their behaviour, partly due to their size and partly due to their colours, which range from pure white through cream to brown, and from the lightest of blues to dark purple. Some snails have a fairly uniform, homogeneous shell colour, without obvious pattern, except that the colour tends to be darkest between the whorls. Other shells show several colours which may occur on different parts of the shell or may be arranged in more or less complex patterns, including various arrangements of banding and/or stripes. Many shells show flecks of one colour in another. B. digitalis, for example, is often silvery blue with flecks of orange or gold. At least two shades of green occur both in B. digitalis and B. rhodostoma. The lighter of these is clearly due to the presence of a photosynthetic organism, for the colour fades when the animal is kept in the dark, which the darker green does not. Moreover, the light green colour is found predominantly on the upper surface of the shell, where it is more likely to receive light than if it occurred elsewhere, while this distribution is not apparent for other colours, including the dark green. However, the nature of the organism responsible for the light green colour is not apparent from simple microscopic examination for no algal mat or filaments are visible and the texture of the shell appears identical with that in regions lacking the green colour. Scraping the shell gently with a sharp scalpel partially removes the green colour as well as the surface of the shell. This is in contrast to the green algal mat which commonly covers the upper surfaces of the shells of Bullia laevissima, a species which seldom buries itself completely in the sand and thus encourages the growth of an epiflora (Brown, 1961a).

Attempts to group the shell patterns of the intertidal species convincingly for further analysis has not met with success, owing to the bewildering array of patterns presented. Indeed it seems most unlikely that the colours and patterns are dictated by genetic criteria alone and it is to be expected that dietary considerations play a large, or even a major,part. However, certain patterns and colours are to be found predominantly or even exclusively in one or other of the intertidal species.

SENSE ORGANS

Not only is Bullia without eyes but it has not been possible to demonstrate any reaction whatsoever with regard to light, either in the field or in the laboratory. The animals also fail to react to mechanical vibrations, including thumping on the side of their aquarium and stamping around them on the intertidal sands. (I have not been able to confirm reports that the snails can detect the approach of an observor while he is still some distance away.) Under these circumstances it is clear that the chemical senses and the animal's sense of touch must play major roles in the successful orientation of the snail towards environmental changes and in the maintenance of its tidal cycle of activity. Gibbons (1878) noted the sensitivity to touch of B. rhodostoma and assumed an "acute sense of smell" to be present to compensate for the lack of eyes. Brown & Noble (1960) have shown that the osphradium is an organ of chemoreception, the sensitivity of which indicates that it is specifically olfactory. It has been shown to be particularly sensitive to trimethylamine and other volatile amines (Brown, 1961b). Further experiments on this olfactory sense are described below. In addition to the osphradium there is a well-developed sub-radula organ which is probably chemoreceptory in function. The cephalic tentacles may also be sensitive to chemical stimuli, as the snail commonly touches the food with them before feeding, and they are certainly very sensitive to touch. However, their amputation causes no abnormality in the chain of events which leads to feeding. The pair of posterior cirri may well have a sensory function, for the animal "tests" the water with the posterior part of the foot before emerging from its shell and refuses to do so if the water is polluted with substances such as hydrogen sulphide (Brown, 1964b, 1964c). Early suggestions that the cirri act as rudders are certainly incorrect. In addition the animal possesses a general chemical sense over the entire exposed surface of the body, though the sole of the foot is remarkably insensitive both to chemical stimulation and to touch (Brown, 1961a).

Bullia has a pair of statocysts, lying on either side of the pedal ganglia. Each statocyst consists of a nearly spherical envelope enclosing a cavity which contains calcareous matter. In this it closely resembles the genus Buccinum (Dakin, 1912). It is also possible that the shell acts as a giant statolith, as it is known to do in some Gastropoda, and sensitivity to forces acting on the shell may partly account for the snail's ability to detect the strength and direction of water currents. However, the animal can detect the presence of water currents when buried beneath the sand, with only the tip of the siphon showing. Amputation of the siphon results in failure to emerge from the sand in response to currents, though the snails still react to such currents when crawling over the substratum. This sensitivity to water currents and the animal's reactions towards them constitute one of the most remarkable features of the mode of life of Bullia and one of the major adaptations to intertidal life in B. digitalis and B. rhodostoma.

CHEMORECEPTION IN THE LIFE OF BULLIA

The reactions of aquatic gastropods to chemical substances have received scant attention. Copeland (1918), working on the carnivorous snails Nassarius and Busycon, showed that both these animals were guided to their food by means of chemoreception, being capable of orientation towards a food source and possessing both olfactory and contact chemical senses. Copeland used food extracts in his experiments and was not concerned with the chemical substances initiating responses. Henschel (1932) recorded that the herbivorous gastropod, Nassarius reticulatus, can perceive both starch and glycogen in the respiratory water which is drawn through the mantle cavity; this snail also reacts positively to glucose, maltose, saccharose, glycol, aminobenzoic acid, lactic acid and skatol. However, it is noted that if lactic acid solutions stronger than 0.055mg/100 cc are pipetted close to the siphon, the animal retreats. Avoidance and escape reactions in Nassarius have been studied by several authors, including Weber (1924), who states that contact chemoreceptors seem to be located at the hind end of the foot. The gastropod shows escape behaviour if touched by a starfish and also in the presence of a number of pure chemicals, including picric acid, alkalis and chloroform. Escape reactions in certain intertidal gastropods have been observed by Bullock (1953), while Burke (1964) has made a brief study of chemoreception in the prosobranch, Tegula. The reactions of gastropod scavengers to chemicals appear to have been entirely neglected.

As already noted (Brown, 1961a, 1964a), Bullia is essentially a scavenger limited to animal matter, though it will turn predator after a period of starvation. Snails react to food placed at a considerable distance from them and it is not always necessary for there to be contact between the food and the water for the appropriate responses to be initiated. In the field, spoiled fish or a fresh coelenterate medusa left on the dry sand well above the swash zone soon attracts swarms of Bullia up out of the water, though they refuse to cross the barrier from wet to dry sand and simply mill around in that part of the swash zone nearest

Figure 3.

Bullia rhodostoma feeding on a jelly-fish. The snail near the centre of the picture has its proboscis thrust deeply into the medusa; the remarkable length of the organ when fully extended is clearly seen.

the food. In the laboratory the snails may be caused to emerge from the sand in which they lie buried by placing decaying fish, pieces of the tunicate Pyura and other food material out of the water, on a corner of the tank. This is not the case with all potential food, however; perfectly fresh teleost muscle placed on a corner of the tank produced no response from 54 individuals of B. rhodostoma. Nevertheless, 23 snails emerged from the sand when this food was placed in the water.

Many observations both in the field and in the laboratory suggested that in the case of teleost fish, spoiled flesh was more effective in attracting snails than was unspoiled flesh. This was not the case, however, with coelenterate medusae. The tunicate, Pyura, remains the most effective "bait" for attracting the animals from a distance, regardless of whether it is fresh or in an advanced state of decay. So attractive is Pyura to Bullia that if a small piece of it be simply dragged rapidly across the beach on a piece of string, large numbers of the snails are commonly stimulated to emerge from the water and to congregate on the track left by its passage.

Various substances were introduced into a small tank containing about 4 litres of fresh sea-water, a sandy substratum and individuals of B. rhodostoma. The reactions of the snails were then carefully observed. From time to time small pieces of spoiled fish were introduced into a second tank, also containing individuals of B. rhodostoma collected at the same time and kept under identical conditions. The tests for a particular day were disregarded if the food placed in this control tank failed to stimulate 50% emergence of the buried snails. However, in the entire series of experiments this happened only twice. On both occasions the animals were replaced with freshly collected material before testing was resumed. Throughout the series the sea water in both tanks was changed daily and also after any test to which the snails responded.

During a period of about six months, approximately 150 snails were subjected to the various substances, most being tested with the same substance more than once. However, experiments with a few very unlikely substances, such as protamine sulphate, were not repeated. In the first instance, solutions of the substances were introduced on pieces of cotton-wool, but in a later series of tests they were added drop-wise from a pipette, sometimes close to the siphons of buried snails.

Where the snails reacted at all they were found to do so in one of three ways. They either emerged actively from the sand after moving their siphons from side to side, or they withdrew their siphons into the sand, or they reacted by actively digging themselves deeper into the sand. A fourth possible reaction - the movement of the siphon from side to side without actual emergence from the sand - was ignored, firstly because many snails wave their siphons in the absence of any apparent stimulus, and secondly because slight movements of the siphon are easily overlooked when several snails are being observed at the same time.

In Table 2 the percentages of snails reacting to each substance tested, in each of the three ways, are listed. The emergence of a very small percentage of snails may be taken as coincidental, as snails do emerge from time to time in the absence of apparent external stimuli. This is not the case, however, with deeper burrowing, which has never been observed outside of these and similar experiments. The amino-acid mixture referred to in Table 2 was kindly provided by Mr G. Turner, formerly of the Virus Research Institute, University of Cape Town. It was a saturated solution containing Arginine (21.0 mgm/100 ml solution), Cystine (12.0 mgm), Histidine (4.2 mgm), Isoleucine (13.1 mgm), Leucine (13.1 mgm), Lysine (18.4 mgm), Methionine (7.5 mgm), Phenylalinine (8.2 mgm), Threonine (11.9 mgm), Tryptophan (2.0 mgm), Tyrosine (18.1 mgm) and Valine (11.7 mgm). A certain amount of hydrochloric acid was present in the solution, so that its pH was 2.5. Neutralisation could not be undertaken without precipitation of the amino acids. In a preliminary test run, cotton wool was impregnated directly with the mixture; in subsequent tests, however, the mixture was diluted 10 times, and later 100 times, before being partially neutralised with sodium bicarbonate. On no occasion did the snails respond. Nevertheless, the constitution of this amino-acid mixture and the pretreatment it was given before use are considered to be of some importance in view of its use in other tests to be described later.

To judge from Table 2, the substances which appear to be attractive to _Bullia rhodostoma_ are urea, trimethylamine, skatole, indole and taurine. Of these trimethylamine is the most effective in

Substance	Number of observations	% Snails emerging	% Siphons withdrawn	% Deeper burrowing	% No reaction
Plant extract (Marmite)	104	0	0	0	100
Meat extract (Bovril)	104	1	0	0	99
Bacto-beef extract	158	0	20	0	80
Arginine (sat.)	132	0	0	0	100
Tyrosine (sat.)	132	0	0	0	100
Casein (sat.)	140	1	0	0	99
Amino-acid mixture	287	2	0	0	98
1 to 10% Sucrose	154	0	0	0	100
1 to 10% Maltose	140	0	0	0	100
1 to 10% Glucose	140	0	0	0	100
0.1% Urea	244	4	0	0	96
5% Urea	130	48	0	0	52
1% Ammonia	130	2	4	0	94
5% Ammonia	202	0	30	2	68
0.0001% Trimethylamine	154	89	0	0	11
0.00001% Trimethylamine	154	73	0	0	27
0.01% Skatole	104	71	0	0	29
0.1% Indole	200	49	7	0	44
0.01% Taurine	200	27	0	0	73
0.1% Taurine	200	38	14	1	47
N-Betaine-choline bitartrate	244	0	21	79	0
γ-Buterobetaine (N)	200	0	2	98	0
1% Betaine hydrochloride	244	0	45	3	52
5% Betaine hydrochloride	244	0	48	52	0
1% Cadaverine	104	10	5	0	85
5% Methyl alcohol	132	4	0	0	96
5% Ethyl alcohol	101	0	9	1	90
1% Ethyl alcohol	100	0	0	0	100
1% Acetic acid	154	0	60	5	35
Cholesterol	52	0	0	0	100
Protamine sulphate	52	0	0	0	100

TABLE 2

Reactions of *Bullia rhodostoma* to various substances.

See text for details of amino-acid mixture.

producing a positive response. The betaines, however, appear to repel the animal. A further series of tests was designed to elucidate the reactions of Bullia to these substances.

A trough, 1 meter in length and 10 cm wide, was filled to the brim with sea water over a shallow substratum of beach sand. Five snails were then placed in the centre of the trough and allowed to bury themselves. A glass sheet was placed over the trough, touching the water but leaving each end of the trough uncovered for a distance of 5 or 6 cm. A small piece of cotton-wool was then soaked in the substance to be tested and dropped into the water at one end of the trough, a piece of cotton-wool soaked in sea water being dropped into the other end. The "active" and "control" ends of the trough were reversed after each test, after changing the sea water. The direction taken by emerging snails was noted, as well as their subsequent behaviour. The water in the trough was not aerated or disturbed in any way, as water-currents are known to influence the direction taken by emerging snails (Brown, 1961a). The experiment was repeated several times with the same snails and later with different snails. A full series of tests was also made with B. digitalis; as the responses of this species appeared identical with those of B. rhodostoma the results may be considered together.

5% Urea: This solution caused only about 50% emergence, as indicated in Table 2. The total number of snails whose post-emergence behaviour was studied was thus 69 out of a total of 149 animals. After emerging, the snails did not protrude their proboscides, as they tend to do when seeking food, but crawled over the sand in a seemingly random fashion, eventually burying themselves again. Twenty-five (16%) subsequently re-emerged temporarily. The direction taken by the emerging snails showed no relationship to the source of urea. It was considered pointless to increase the strength of the solution beyond 5% and it had already been shown that weaker solutions of urea produced weaker responses (Table 2). Thus although Bullia would seem to detect urea it is most improbable that this substance can play any great part in the normal life of these animals, for while they might conceivably encounter urea in low concentrations, they apparently respond only to concentrations very much higher than any they could meet in the field.

<u>0.0001% Trimethylamine</u>: Reactions to this solution were in marked contrast to those occasioned by solutions of urea. 121 snails were stimulated to emerge of a total of 140 (87%), and of these at least 90 protruded the proboscis on or shortly after emerging. Furthermore, most of the snails set off at once towards the source of the trimethylamine, only a very few taking the opposite direction. These few generally turned back before they had gone very far (see Table 3). The snails attempted to thrust their proboscides into any object they happened to encounter. This object was frequently the piece of cotton-wool carrying the trimethylamine, but was sometimes a small stone left lying in the trough or even the glass walls themselves. Occasionally a snail would thrust its proboscis against the foot or shell of another snail. Pieces of fresh, unimpregnated cotton-wool introduced into the tank were also attacked. However, on no occasion did snails persistently attempt to feed on any of these objects. The cotton-wool soaked in trimethylamine was rejected as firmly as untreated cotton-wool and other objects.

<u>0.00001% Trimethylamine</u>: This solution stimulated somewhat fewer snails to emerge than did the ten-times stronger solution. However, those animals which did emerge showed a reaction which was not less marked, nor were their directional powers markedly diminished (Table 3). There can be little doubt that trimethylamine in the order of concentration used here must be a common occurrence in <u>Bullia</u>'s natural environment. Moreover, this is a substance which emanates from the most commonly eaten food of the snail. Poller & Linnewek (1926) appear to have been the first workers to isolate trimethylamine oxide from teleost tissues (herring muscle) and to show that under normal conditions bacteria quickly reduce it to trimethylamine, which accounts for the large production of this substance after the death of the animal. This is now known to be true of all marine teleosts, though different species are somewhat variable as far as the actual content of these substances in the tissues is concerned. Jakobsen (1947) and Dyer (1952) state that trimethylamine oxide also occurs in most marine invertebrates, including Crustacea and Cephalopoda, though clams are said to contain no detectable amounts of the oxide.

SUBSTANCE	No. of snails used	No. of snails emerging	No. of snails in "active" arm of trough; minute readings:									
			1	2	3	4	5	6	7	8	9	10
0.0001% Trimethylamine	140	121	61	113	105	112	109	97	94	100	108	91
0.00001% Trimethylamine	115	75	48	49	57	54	58	67	61	65	62	62
0.01% Skatole	140	78	22	35	27	13	18	17	14	14	9	7
0.001% Skatole	140	40	9	9	16	10	6	8	5	4	0	1
0.0001%Skatole	100	2	0	1	0	0	0	0	0	0	0	0
1.0% Indole	75	9	2	4	4	1	0	0	0	0	0	0
0.5% Indole	100	21	6	9	15	10	9	4	1	1	0	0
0.1% Indole	100	43	14	19	17	20	19	21	15	10	9	9
0.01% Indole	75	4	0	0	0	2	1	1	0	0	0	0
0.01% Taurine	100	30	8	14	12	8	8	9	6	2	0	0
0.001% Buterobetaine + 0.0001% Trimethylamine	70	57	31	40	47	46	39	42	42	41	36	41
0.1% Buterobetaine + 0.0001% Trimethylamine	70	12	5	7	11	10	6	7	9	2	2	1
0.1% Buterobetaine + 0.00001% Trimethylamine	43	0	0	0	0	0	0	0	0	0	0	0

Table 3.

Orientation of *Bullia* to different concentrations of some stimulating substances.

0.000001% Trimethylamine: Concentrations as low as this do not appear to stmulate the snails to emerge in the absence of water currents. However, if they are caused to emerge by turning on an electric stirrer or by aerating the water so as to produce currents, they can still orientate themselves towards the trimethylamine source (once the stirrer or air pump has been switched off).

0.01% Skatole: As noted in Table 2, this solution causes an emergence of *Bullia* which is comparable with that occasioned by 0.00001% trimethylamine. However, the reactions of the snails after emergence are different. Few snails extrude their proboscides and their directional responses are comparatively poor. Many bury themselves again before long. Dilution of the skatole solution results in progressively weaker responses, 0.0001% skatole having no apparent affect on the snails at all.

0.1% Indole: This substance is rather similar in its effect to skatole, except that some snails appear to find it unpleasant. Siphonal withdrawal becomes much more marked at a concentration of 0.5% and fewer snails emerge, while a solution of 1% stimulates avoidance behaviour in the form of deeper burrowing into the sand. Dilution to 0.01% destroys its effect as a stimulant, the snails showing no response of any kind (though this does not, of course, mean that they cannot detect it).

Taurine: As in the case of urea, emerging snails do not appear to move towards a taurine source. The proportion emerging is not high and their proboscides are not, as a rule, extruded. Moreover, the snails do not attempt to feed on cotton-wool "blanks" or on other objects in the trough.

γ-Buterobetaine: This substance, more than any other tested, provokes deeper burrowing on the part of the animals, as shown in Table 2. In order to test other possible reactions, a number of *B. rhodostoma* was tested in the trough already described but with the substratum of sand removed, so as to prevent the animals burrowing. It was hoped that the animals might move away from the source of the substance. This did not, in fact, occur. The addition of 0.1% γ-buterobetaine to

end of the trough resulted at first in increased locomotory activity on the part of the snails, some animals making repeated attempts to burrow into the metal floor of the trough. They did not, however, show any directional behaviour and after seeming to become more and more "agitated", they withdrew one by one into their shells.

It has already been noted that trimethylamine is liberated from most of the normal food of *Bullia*. However, it can never be the *only* substance released. Allison (1948) has found that the substances liberated in highest concentrations from spoiling teleostean tissues are ammonia, tyrosine, indole, ethyl alcohol, trimethylamine, hydrogen sulphide and histamine, together with certain unspecified volatile amines and acids. The list includes at least one - hydrogen sulphide - which is definitely repellent to *Bullia*, at least in high concentration (Brown, 1964b). However, the *combination* of substances listed as emanating from the food of *Bullia* is clearly attractive to the snails; either hydrogen sulphide is no longer repulsive when certain other substances are also present, or it is "masked" by these other substances so that the animal no longer detects it. The reactions of *B. rhodostoma* to various combinations of substances were therefore tested. The results will not be reported here in detail as the number of tests was too small to lead to convincing conclusions. One of the combinations, however, proved so interesting that a relatively large number of snails was tested with it; this was a combination of γ-buterobetaine with trimethylamine. In this case it was found that the response of the snails depended on the *proportion* between the two substances. Thus a combination of 0.001% buterobetaine and 0.0001% trimethylamine in equal quantities, attracted 82% of snails placed in the experimental trough, while 0.0001% trimethylamine with 0.1% buterobetaine (again in equal quantities) was found to attract only 17% and caused at least the same percentage to withdraw their siphons and/or burrow deeper into the substratum. In the case of 0.1% buterobetaine and 0.00001% trimethylamine there were no conflicting responses, all the snails refusing to emerge, while most withdrew their siphons or burrowed deeper. For a possible explanation of the importance of this behaviour in the field we must turn to the work of Shewan (1953):

Shewan examined extracts of various fresh fish muscles chromatographically, his main concern being the presence of nitrogenous substances. In a series of tables, he compares the composition of teleost fishes (various species of the whiting, *Gadus*) with that of the muscles of elasmobranchs (*Raja*, *Acanthias* and *Mustelus*). He shows a number of differences in free amino acid content, etc, between the two groups, but what is of far greater interest in the present context is the presence in the flesh of elasmobranch fishes of extremely high concentrations of betaines, substances which Shewan's methods could not even detect in teleost muscle. We now, perhaps, have the reason why *Bullia* is unwilling to eat perfectly fresh elasmobranch flesh, but will eagerly consume it after it has lain in the sun for an hour or two; the amount of trimethylamine liberated increases rapidly as the flesh spoils, so that it soon masks the unpleasant betaines. Shewan's observations also suggested to me that the responses of *Bullia* to animal betaines might constitute an escape reaction, for the elasmobranchs are among the most important predators of the snail. It has not yet been possible to test this theory in detail, though it is easy to demonstrate that a small elasmobranch, killed by means of an electric shock and immediately placed in a tank containing *Bullia*, stimulates virtually all the snails to burrow deeper into the sand. A live elasmobranch appears to elicit the same reactions, though small marine teleosts, collected from rock pools, do not.

It has already been mentioned that while snails are attracted to various test substances, they do not attempt to feed on the objects from which they emanate. A short series of experiments was carried out in which cotton-wool, and later agar gel, was impregnated with both trimethylamine and a non-volatile substance before being offered to the snails. No account of directional behaviour was taken, attention being focussed on the number of snails feeding or attempting to feed on the preparation. It was found that the addition of solutions of sucrose, glucose, maltose or lactose to the cotton-wool had no effect on the behaviour of snails attracted to it by trimethylamine. Amino acids, on the other hand, had a marked effect. The amino-acid mixture already described was diluted X 100 and neutralised with sodium bicarbonate. To this was added an equal volume of 0.0001% trimethylamine. A piece of dry cotton-wool was dipped into this mixture and offered to 57 individuals of Bullia rhodostoma contained in a large tank. After two minutes, 21 snails were clustered around and on the cotton-wool, with their proboscides thrust into it. A few of the snails soon dropped off but were replaced by others. The length of time for which each snail attempted to feed varied considerably; some appeared to find the "food" unsatisfactory and soon moved away or buried themselves, while others continued to attack it for five minutes or more. This is in marked contrast to their behaviour towards cotton-wool soaked in trimethylamine solution only.

In an experiment conducted the following day, the same preparation was presented to the same snails, but three "blanks" in the form of untreated pieces of cotton-wool were introduced at the same time. Again it was noted that snails thrust their proboscides into any of the pieces of cotton-wool with which they came into contact; however, the blanks were at once rejected while the impregnated preparation continued to interest the snails for over ten minutes. Twenty-six snails were attempting to feed on it after two minutes, the number dropping to nineteen during the fifth minute. Eight snails were still "feeding" after ten minutes.

Further experiments, as described above but using impregnated agar gels instead of cotton-wool, produced similar but more convincing results. The attraction of the snails appeared to take somewhat longer, presumably because the trimethylamine was released more slowly, but once the snails found the agar they fed on it for much longer than they had on the cotton-wool preparations. Moreover, it was apparent at the end of each test that quantities of the agar had actually been ingested by the snails.

In the absence of detailed observations on related gastropods, the positive reactions of Bullia are found to parallel quite closely the reactions of a completely different group of animals occupying a very different habitat - namely the blood-sucking Diptera (Insecta). The feeding reactions of this group have been carefully studied by the late B.J.Krijgsman (1930, 1936, 1937) and by Krijgsman & Windred (1930, 1931). Krijgsman distinguishes four phases in a chain of feeding reactions in these flies:-

(1) Distance perception by means of chemoreception, leading to positive taxis.

(2) Contact perception after reaching the food, causing extrusion of the proboscis. (In some cases extrusion takes place before contact with the food.)

(3) Piercing movements of the proboscis, initiated by contact perception.

(4) As a result of these piercing movements, the proboscis comes into contact with the food-substances (blood) and the fly begins to feed.

It is noted that ingestion does not take place unless perception by the proboscis adds a new stimulus. If this is lacking, the piercing movements simply continue, while if the added stimulus turns out to be "unpleasant" to the fly, it is repelled and the piercing movements cease. In each phase a new stimulus, produced by the food, is necessary to initiate the next link in the reaction-chain which leads to feeding.

The above analysis might be written with little modification to describe the feeding reactions of Bullia in the laboratory. Under field conditions the analysis is complicated by the fact that the animals may be led to exchange the medium of sea water for that of air during the chain of reactions. Combining the evidence of the present research with that of Brown (1961a), we may analyse the feeding reactions of the intertidal species of Bullia in the following way:-

(1) Distance perception by means of chemoreception. In the laboratory, under water, this leads to emergence from the sand followed by positive taxis, the snail crawling towards the food over the surface of the sand. In the field, under natural conditions of wave action on a surf-swept sandy beach, a different reaction is evidenced; the snail turns onto its back after emergence from the sand and is brought ashore by the waves. Active, positive taxis during this phase would in any case be impossible due to the destruction of chemical gradients by turbulence. Transport of the snails by waves and water currents is facilitated by their low specific gravity and by the fact that the fully-expanded foot offers considerable resistence. The substances capable of initiating this first phase include volatile amines, notably trimethylamine,

to which the snails are remarkably sensitive, and possibly other volatile substances not yet identified. The presence of water currents greatly lowers the threshold of stimulation necessary to cause the snails to emerge and, if strong enough, water currents alone will initiate the whole of the first phase in the absence of volatile substances emanating from potential food. The real food-substances - proteins, fats, carbohydrates and their break-down products - appear to play no part in distance chemoreception, while certain other substances, such as high concentrations of buterobetaine, inhibit emergence.

(2) Having reached the swash zone, the snail rights itself and crawls in the direction of the food, at the same time often extruding its proboscis. The siphon is held horizontally in the surface film of water which is invariably present on the low-tide terrace; thus water continues to enter the mantle cavity, allowing the osphradium to sample dissolved substances. The relative straightness of the path taken by the snail depends on conditions; where the food lies directly up-shore from the snail, the animal usually goes towards it in an almost straight line but where the food lies to one side of the animal it does not always take the shortest possible route but appears to start by crawling around almost at random, its orientation becoming improved, however, so that it soon crawls in the general direction of the food. Some degree of trial and error is, of course, unavoidable in an animal relying on a single chemoreceptor placed in a cavity which samples the water through a single siphonal tube. Nevertheless, snails normally find their food with remarkable rapidity and this is partly due to the fact that they will not willingly roam above the saturated foreshore, nor do they commonly re-enter the water without having fed. Their movements, once ashore, are thus limited to a relatively narrow strip of beach - precisely that area in which washed-up animal remains are most likely to come to rest.

(3) Piercing or thrusting movements of the proboscis initiated by contact perception. That these thrusting movements do not rely on any chemical stimulus is apparent from the fact that snails will react in this way to any object touched, once the first two links in the chain of reactions have been completed. Where the proboscis has not been

extruded during phase (2), it is extruded as soon as contact is made with the object, as a preliminary to the thrusting movements. Another common preliminary is the "feeling" of the object with the cephalic tentacles; however, I have never seen an object rejected after such contact alone, so that the function of this behaviour remains obscure. Moreover amputation of the tentacles does not lead to any disruption of the reaction chain which leads to feeding.

(4) Feeding. The thrusting movements soon cease if the object is anything other than potential food and the object seems to be rejected at once if it is very hard (stones, the shell of another snail, etc). An exception to the latter observation, however, is provided by washed-up individuals of the pelycepod, Schizodesma spengleri, for when the snails encounter these they do not reject them but seek an opening between the valves into which they may thrust their proboscides. In order for feeding to take place, the object must contain substances which add a further stmulus, presumably acting through a chemoreceptor situated in or near the anterior end of the alimentary canal, possibly the sub-radula organ. The volatile amines which attracted the snails to the food in the first place will not suffice to initiate feeding. Amino acids are, however, effective in stimulating the snails to feed and to continue feeding. Sugars, on the other hand, do not provide the necessary stimulus.

Thus in the absence of organs of sight in Bullia, the olfactory sense has become very highly developed, this being quite obviously of great advantage in an environment where food is likely to be scarce for long periods and may often lie at some distance from the area occupied by the snails. The fact that the snails are aquatic, while their food is usually washed up onto the beach and exposed to the air, presents another problem which the snails have overcome by virtue of their acute olfactory sense combined with an appropriate chain of behavioural responses.

The division of this reaction-chain into four phases is by no means arbitrary, for each phase demands a new stimulus to be present before it will be initiated. Once initiated, however, the phase will go to completion. Should the chain be broken by the absence of the appropriate stimulus, the snail's behaviour must be considered perfectly consistent with the circumstances and conducive to its survival. Thus should phase (1) be completed but phase (2) not initiated due to the absence of volatile amines, the snail will bury itself in the wet sand, often in the swash zone. It thus protects itself, does not use up energy unnecessarily, but is close at hand should it be restimulated to enter the chain. Similarly, if during phase (3) the stimuli which would promote phase (4) - feeding - are absent, the snail does not waste time continuing with phase (3) behaviour but will abandon the object and return to phase (2) - actively seeking the food. It is also of some interest to note that, while the pattern may be disrupted if the stimulus initiating the next phase is absent, the later phases are not dependent on the completion of the earlier phases and the latter may at times be omitted altogether. Thus a snail which has had its osphradial nerve cut cannot receive the stimuli which would initiate phase (1), yet will make thrusting movements with its proboscis and commence to feed if it is placed directly onto the food, even though the first two phases have been entirely left out (Brown & Noble, 1960).

PARASITES AND DISEASE

Though no special study has been made of the parasites of Bullia, it is clear that they are fairly free of them. I have not found a single ectoparasite on any individual and have only found an epifauna growing on the upper part of the shells of B. laevissima, a species which does not usually bury itself completely. It may be noted here that Millard (1966) has recorded abundant colonies of the hydroid Leuckartiara octona (Pandeidae) growing on the shells of living Bullia annulata. As far as internal parasites are concerned, the only forms I have come across with any regularity have been the larvae of digenetic trematodes. These are found as miracidia, sporocysts and rediae in the blood-spaces associated with the digestive gland and gonad. In snails kept in the laboratory for some months, post-mortem examination has sometimes shown damage to these organs together with the presence of large numbers of the larvae. However, in no case could the cause of death be attributed directly to this condition. Where the snails had not been killed deliberately they were usually the victims of some unforeseen change in laboratory conditions. Examination of freshly-collected snails has never revealed macroscopic damage to any of the organs, though the preparation of smears from the digestive gland and gonad has repeatedly shown the presence of the parasites. It seems unlikely, then, that the presence of trematodes in these organs is a major cause of mortality among Bullia populations under normal conditions, though the parasites are bound to account for some of the energy intake of their hosts. They may sap the vitality of the snails and the possibility of parasitic castration cannot be overlooked.

Although Bullia does not appear capable of removing or immobilising these trematodes, there is reason to believe that other invaders, probably including bacteria and viruses, may be dealt with efficiently. Brown & Brown (1965) have shown that thorium dioxide suspensions, injected into the pedal sinus, are phagocytosed by macrophagic amoebocytes which migrate with the particles through various tissues and organs, eventually leaving the body altogether. Though this elimination is not as rapid as that displayed by some other prosobranchs (Brown, 1967), it is at least efficient and does not disrupt the normal activities of the animal in any way. Recent work in this connection has shown that certain other substances, notably foreign protein in the form of bovine haemoglobin, is eliminated from the body very much faster than is thorium dioxide. However, explants of various Bullia tissues, including the foot, digestive gland, kidney and haemolymph, do not retard the growth of those bacterial cultures which have been tested.

On three occasions I have found a small nematode worm in the mid-gut. Only one individual was present in each case. As it was alive and completely undamaged in one case and appeared to be completely intact in the other two cases, the snails having previously been preserved in formalin, it is improbable that they had been eaten by the snails and I have assumed that they were parasites. Several small cysts were found in the pericardium of one individual of Bullia rhodostoma; unfortunately this specimen had been poorly preserved in alcohol for some time and the condition of the cysts was not suitable for detailed study. Despite a lengthy search they have not been found in other snails of this or other species.

One individual of B. digitalis was found to have a large lump at the posterior end of the mantle cavity. Frozen sections stained with aceto-carmine revealed that the lump consisted of a mass of cells without any specialised morphological features. A large number of these cells showed mitotic figures. The mass involved part of the mantle epithelium, the distal end of the ureter, the floor of the pallium, and extended downwards into the haemocoel to press on the gut. The above evidence would suggest that the growth was malignant. Little work has been done on malignancies among the invertebrates, but carcinomas are not entirely unknown among the Mollusca (Smith, 1934).

A strange condition was found in some individuals of Bullia digitalis collected from Hout Bay between 1959 and 1964; the ventral surface of the foot, normally very smooth and uniform in colour, was seen to contain numerous, circular, white areas, each about the size of a pin's head. These areas were slightly raised above the surface and were hard to the touch so that the whole surface of the foot felt rough. Crude sections cut through such areas showed that the condition was relatively superficial and involved only the outermost layer of cells. The objects themselves were not cellular and were easily fragmented, though firmly attached to the tissues. They dissolved slowly in hydrochloric acid and very readily in nitric acid. A drop of hydrochloric acid which had dissolved several of the objects gave a positive result on testing for the presence of calcium. It is strange that this condition has never been found in snails collected from other beaches, nor was it noticed in snails collected from Hout Bay before 1959. It is tempting to link the condition with the pollution to which the Hout Bay beaches had been subjected since 1958; however the nature of such a possible relationship remains obscure.

THE DISTRIBUTION OF BULLIA

Though it is intended to discuss in these pages only the details of the distribution of those species of Bullia which are of importance to the ecology of the sandy beaches of the Cape Peninsula, it is nevertheless convenient to at least state the known distribution of all the species, particularly as the genus is limited to southern Africa.

The distribution list which follows has been compiled from records made by the University of Cape Town Ecological Survey and from records in the library of the South African Museum, as well as from published records. The only records used have been those in which the living animals have been collected. Records of empty shells have been ignored.

Bullia annulata (Lamarck): From Saldanha Bay, on South Africa's west coast to Port Elizabeth, on the east coast. Recorded both intertidally and from shallow water to a depth of 62 meters. Also recorded from east coast estuaries.

Bullia callosa Wood: So far recorded only from Mossel Bay, Port Elizabeth and the Great Fish River mouth, in shallow water.

Bullia digitalis Meuschen: The common intertidal and shallow-water *Bullia* of the west coast, from Luderitz in South West Africa, to Cape Point. Also recorded in small numbers from False Bay and allegedly as far east as Port Elizabeth.

Bullia laevissima (Gmelin): Recorded from Luderitz, in South West Africa, round the coast to the mouth of the Great Fish River, in the eastern Cape Province. A shallow-water form (down to 65 meters), but intertidal where wave-action is slight. Also recorded from estuaries.

Bullia diluta (Krauss): An east coast species recorded from False Bay to Delagoa Bay in Portuguese East Africa. There are numerous records in the literature and Barnard (1959) describes it as a common species, a statement which, however, has not been confirmed by the University of Cape Town Ecological Survey.

Bullia natalensis Krauss; An intertidal species recorded from the sandy beaches of Natal and Portuguese East Africa.

Bullia osculata (Sowerby): A poorly-known species, recorded with certainty only from the East London area in 60 meters of water.

Bullia pura Melville: The only living specimens of this species have been taken in False Bay.

Bullia rhodostoma (Gray): The common intertidal *Bullia* of South Africa's south and east coasts, recorded from False Bay to Delagoa Bay.

Bullia similis Sowerby: From East London to St, Lucia, in shallow water.

Bullia tenuis Gray: Recorded alive from False Bay to the mouth of the Great Fish River, in depths of water ranging from 25 to 200 meters.

Bullia trifasciata Smith: So poorly known that Barnard (1959) reported that the animal itself, as distinct from the empty shell, had never been seen. However the University of Cape Town Ecological Survey has collected living animals from off the Great Fish River mouth, in shallow water.

Bullia mozambicensis Smith: The only living individuals have been taken from the mouth of the Zambesi River.

It is apparent that the distribution of most of the species of Bullia is still but poorly known and it is to be expected that the ranges of many species will be greatly extended in the future.

Some aspects of the distribution of the Cape Peninsula species of Bullia have already been discussed elsewhere (Brown, 1961a). It has been shown, for instance, that the occurrence of B. laevissima in the intertidal zones of very sheltered beaches only, is directly linked with its behaviour towards water currents, a behaviour which is in marked contrast to that of B. digitalis, a species which exploits water currents and requires a certain minimum degree of wave action in order to maintain its rhythmic pattern of behaviour. The behaviour of B. laevissima, on the other hand, shows no adaptation to intertidal life and it can only live intertidally where the conditions at high tide closely resemble those in the infratidal zone. Just as too-sheltered conditions lead to the disruption of the tidally-orientated behaviour of B. digitalis, so B. laevissima is normally unable to cope with any degree of wave action which will move it over the sand. Moreover, the behaviour of these two species is such that each is able to avoid conditions of wave action unfavourable to it.

Bullia digitalis is the common sandy-beach snail of the west coast of the Peninsula, but is largely replaced in False Bay by B. rhodostoma, a species which resembles it morphologically, anatomically, physiologically and behaviourly. However, while Bullia rhodostoma has never been recorded west of Cape Point, adults of B. digitalis may be taken in small numbers in False Bay, from the same areas as those occupied by B. rhodostoma. The reactions to water currents and surf displayed by B. rhodostoma are identical with those of B. digitalis and in fact it occupies the same ecological niche on the Peninsula's east coast that B. digitalis fills on the west coast. The difference in distribution between these two species must therefore be attributed to some difference in conditions between the two coasts. The only factor which would appear to meet the case is temperature. However, it has not yet been possible to prove this point conclusively. Adults of both species can tolerate temperatures of up to 38°C for very short periods, under the conditions described by Brown (1961a); at the other end of the scale, it has been found that a temperature of 4°C soon kills adults of B. rhodostoma, while leaving B. digitalis apparently unharmed. However, it must be noted that neither species will be subjected to such low water temperatures; moreover, while low temperatures may be encountered at night when the snails come ashore to feed, this applies to both coasts of the Peninsula. Under these circumstances it seems probable that, if temperature is of primary importance in determining the distribution of these two surf-loving species, it is limiting during the development of the egg rather than at a later stage. This idea is supported by the work of Hall (1964), who states that for shallow-water molluscs in general "the critical factor that probably determines the limits of marine shallow-water climates is the number of consecutive days or months that shallow sea water is at a temperature required for reproduction and early growth."

There is a number of sandy beaches around the Cape Peninsula where no sandy-beach snails occur. These beaches include Witsands, Diaz Beach and Noordhoek. Snails are also absent from Llundudno for most of the year, while only a single individual of B. digitalis is recorded from Camp's Bay. One tends to think of all the beaches mentioned as being very exposed to wave action and indeed Diaz Beach and Noordhoek are subject to higher waves than are other beaches in the Peninsula. However, the waves at Llundudno are often smaller than those at Milnerton or even Muizenberg, where the snails are abundant. Thus, though there may well be a limit to the degree of wave action which even the surf-loving species of *Bullia* can tolerate, I decided to look for a different factor which all the beaches lacking in *Bullia* share and in which they differ from the beaches on which *Bullia* is common. I have only been able to find one such factor; on all those beaches on which *Bullia* is absent for all or most of the year, the municipal or provincial authorities have caused notices to be raised, warning the public that bathing is dangerous. And in all cases the bathing is dangerous because of the presence of strong long-shore and/or rip-currents for at least part of the year.

In order to test whether this relationship had any validity, fifteen sandy beaches were visited along the coast east of the Peninsula. On seven of these bathing was stated to be dangerous and on none of them could any individuals of *Bullia* be found. *B. rhodostoma* was found to occur in some numbers on six of the remaining eight beaches, *B. laevissima* and a single individual of *B. digitalis* being encountered on the seventh. On the eighth beach no snails could be found, but this was not surprising as it was nearly high tide; local inhabitants, on being shown specimens of *Bullia*, said that the snails did in fact occur on the beach, and this statements was confirmed by the presence of empty *Bullia* shells near the drift line. It seems quite possible, then, that the snails are limited in their distribution by the presence of long-shore and rip-currents (and that they might even conveniently be used as an "indicator species" to judge whether or not it is safe to swim).

It is easy to see how the presence of such currents would disrupt the normal behaviour pattern of either *B. rhodostoma* or *B. digitalis*. These species rely on being brought ashore by the waves and have no mechanism to prevent being carried along the coast or out to sea. Strong swimmers have little to fear from long-shore currents or even from rip-currents, a relatively puny swimmer such as man being able to escape from a rip-current by swimming a short distance parallel to the beach; but *Bullia* cannot swim at all and is carried passively by waves and currents. The most it could do would be to avoid being carried by retracting into its shell or burying itself if in contact with the substrate. However, such a reaction would presumably follow a perception of being carried in the wrong direction and there is nothing to suggest that the snails are capable of such perception. On the contrary, laboratory work has shown that the surf-loving species of Bullia react to all types of water currents, both weak and strong, continuous and intermittant, regular and irregular, by emerging from the sand and spreading the foot, thus facilitating transport. The possibility that long-shore and rip-currents limit distribution and that the snails are very much at the mercy of strong currents in general, receives support from the numerous infratidal records of B. digitalis from South Africa's west coast. As these snails copulate, lay their eggs, develop and feed in, or just below, the intertidal zone, and as they show so many clear adaptations to intertidal life, it is inconceivable that some of them should wander voluntarily below tide-marks to a depth of twenty meters or more. It seems to me that these movements are, in fact, passive and are the unavoidable result of transport by currents along and away from the shore. The question of whether such snails ever manage to regain the intertidal zone would then become of some importance, for if they can do so then the phenomenon may be considered advantageous as far as distributing the species is concerned.

The seasonal cycle of events on Llundudno beach is particularly relevant to this discussion. Bullia is completely absent from this beach throughout summer and often for much of the winter; nevertheless, within a week or two of the beach being flattened by a winter storm, B. digitalis is to be found intertidally, sometimes in considerable numbers (Brown, 1969). This flattening of the beach results in a marked decrease in the strength of the long-shore currents and rip-currents seem to disappear altogether (though the change in profile can hardly affect the original height of the waves). In spring, as the beach slope becomes steeper again, the currents increase in force and there soon comes a day when Bullia is no longer to be found. They have either migrated out to sea, which does not appear to happen on other beaches, or they have been removed passively by the increased currents. This example not only serves to support the theory that such currents limit the distribution of B. digitalis, but also shows that a shorewards migration of individuals from deeper water can, and does, take place.

We have seen that the fact that different Cape

Peninsula beaches support different species of *Bullia* depends on differences in wave action and possibly on differences in the temperature of the water, while the absence of *Bullia* on certain beaches may well be due to the prevelance of long-shore and rip-currents. However, before leaving the subject of distribution, it may be noted here that the distribution of *Bullia* along any one beach is seldom uniform, except possibly in the case of *Bullia laevissima* on the most sheltered beaches. On a few beaches, such as that at Fish Hoek, I have noted a tendency for the snails to collect towards one end of the beach; in the case of Fish Hoek this is the northern end. While there do not appear to be marked differences in wave action, beach profiles or other physical factors along the length of Fish Hoek beach, the snails' tendency to congregate at one end is easily explained in terms of food-supply and water currents. The system of currents in Fish Hoek Bay is such that debris of all kinds is washed up on the northern part of the beach, while the southern part remains relatively "clean." This debris naturally includes food for *Bullia*, in the form of large medusae, dead fish and other animal matter. In view of the snail's keen olfactory sense and rapid mode of locomotion, it would be surprising if the animals did *not* congregate at that end of the beach, particularly as the snails may be aided by the same currents which determined the distribution of the food.

On most beaches the distribution of *Bullia* is patchy, stretches of beach abundant in snails alternating with stretches in which none is to be found. I suggest that this discontinuity may also be related to the food-supply and to currents. Food tends to be scarce, but what there is of it often occurs as a relatively large lump on which many snails can, and do, feed at the same time. Snails within a certain area converge on the washed-up fish or medusa even before it comes to rest, concentrating the population and denuding the outer regions of the area. After the meal the snails bury themselves and remain buried while the tide rises. When they emerge at the next low tide they are still in a compact group, though the food which brought them together has probably washed away hours before. If no new food has washed up in the immediate vicinity, members of the group may tend to disperse again, both through crawling around over the sand and through passive transport in the surf, unless they tend to remain together due to mutual attraction. However, the arrival of another piece of food will tend to congregate them once more.

Water currents may be expected to aid rather than disrupt this behaviour for it is clear that, on any given occasion, food is more likely to wash up at some points than at others. A common event in summer, for example, is for large numbers of the "blue-bottle", *Physalia*, to wash up on Muizenberg beach. Even the most superficial observation of these blue-bottles is enough to demonstrate that their distribution along the beach is not uniform; a ten-meter stretch of the swash zone may contain over a hundred of the coelenterates, only to be followed by a ten-meter stretch in which only one or two occur. It is apparent that the distribution of this washed-up food is largely determined by currents produced by the interaction of the waves and the beach slope, so that in some areas the water is moving predominantly towards the shore and in other areas predominantly away from the shore. The fact that *Bullia* is moved passively in the water for part of its cycle may thus mean that it is most likely to be brought into the swash zone at the very places where its food is most likely to wash up.

While I believe that the discontinuous distribution of *B. digitalis* and *B. rhodostoma* along the beach may be accounted for by the above arguments, the possibility of other factors playing a part cannot be ignored. The most interesting of these possibilities - and one for which there is, perhaps, some evidence - is that the snails tend to be gregarious, being attracted to one another by some chemical sense. Early in my investigation of the mode of life of *Bullia* I noted the presence on Muizenberg beach, during spring and early summer, of groups of juvenile *Bullia rhodostoma*, which for the most part occupied different areas from the adult groups. A most remarkable aspect of these juvenile groups was that all the snails within the group seemed to be of very much the same size. This subjective impression was later confirmed by measuring the shell lengths of individuals within the groups. In any one group the fact that the shell lengths were all rpughly the same might well be due to chance, particularly as the number of snails in the group is sometimes quite small. However, the fact that juvenile groups repeatedly show this phenomenon can only mean that the members of the group are all roughly the same age and have enjoyed the same opportunities of feeding. The inference may be that all members of the group hatched from the same egg case and have remained together since hatching, being subjected to the same conditions and eating the same food.

However, it must be stated that the picture is not always so simple. Larger groups of individuals occur in which the shell length is not uniform. It is then often possible to sort the animals into two or more groups, each showing a very narrow range of size, but in some cases this is not possible. Juvenile groups also occur within the adult populations, but often tend to be less widely dispersed, so that the uniformity of the group is still apparent. It should be made clear, however, that these observations have only been made with respect to B. rhodostoma and only on the long stretch of beach between Muizenberg and Strandfontein. No such groupings have been found on the beach at Fish Hoek, where the entire population often tends to congregate at one end, nor were well-defined juvenile groups encountered among the population of B. digitalis at Hout Bay. However, this aspect of the mode of life of Bullia was only considered after Hout Bay had become heavily polluted and the snails were dying in large numbers.

Whether the adults of B. rhodostoma are gregarious or not must for the moment remain an open question. It must be reported that individuals kept in the laboratory in a large tank of sea water over a substratum of beach sand show no tendency whatsoever to be gregarious. However, one hesitates to admit as evidence the lack of social behaviour on the part of animals kept under such abnormal conditions. Members of opposite sex must be attracted to one another for purposes of copulation, and this attraction is almost certainly chemical. Is it perhaps possible that there is a chemical attractant which is species and/or group specific in the juvenile but becomes sex specific in the adult?

Finally, one is bound to ask whether there is any conceivable advantage either to the juveniles or to the adults in being gregarious. One possible advantage stands out above all others; if it is true, as has been suggested earlier, that the flesh of Bullia is distasteful to birds and to certain other potential predators, then gregariousness will subtend the survival of the population by encouraging the predator to learn quickly that the snails do not constitute suitable prey. However for this mechanism to be effective the only requirement would seem to be that the snails should occur in dense groups, as indeed they do. Whether gregariousness contributes to the formation of such groups or not does not affect the issue.

It is clear that definite conclusions on this problem will only be reached after intensive experiments on the dispersal and mixing of marked snails in the field. Until then gregariousness can only be offered as an interesting possibility in the life of these snails.

THE NUMBERS OF BULLIA

While it is a relatively easy matter to count the number of snails in a given area of exposed or partially exposed sand at low tide, it is apparent that such counts give no indication of the total size of the population. Apart from the fact that the distribution of Bullia is patchy along the length of the beach, there is the probability that only a fraction of the total population enters the intertidal zone at each low tide. Even the most casual observation suggests that this is so and that the actual percentage to come ashore varies considerably. In general, more snails may be found at low Spring Tides than at Neaps, but there are other factors concerned in this phenomenon as the numbers encountered on the beach vary greatly even between Spring Tides. In view of the fact that these animals live for at least four years and appear to breed only once a year, the recorded fluctuations cannot represent real fluctuations in the population and can only mean that the proportion of the population available for sampling varies. Under these circumstances, more sophisticated methods for assessing the total population of Bullia were required.

Methods for estimating the size of populations have been described by a large number of workers and some of the best methods are discussed by Dowdeswell (1959) and by Hairston et al (1958). In view of the problems peculiar to Bullia, it was apparent that the only technique which might lead to reproducible results was the capture-recapture method. In this method a number of individuals is captured and marked so that the animals may be recognised again. They are then released. The population is calculated as the total number of individuals taken on a later visit, multiplied by the total number marked and released on the first visit, divided by the number of marked animals retaken. According to Hairston _et al_ (1958), this method is capable of great accuracy providing that the mixing of marked and unmarked snails is complete, that the mortality rates of marked and unmarked individuals are equal, and that the rate of reproduction is either known or is negligible for the period between release and capture. Because of these qualifications the authors conclude that the technique is impracticable for assessing populations of the bilharzia-carrying snail, _Oncomelania quadrasi_. However, in the case of _Bullia_ the reproduction rate may be ignored unless very long periods are involved, and there is nothing to suggest that there might be a difference in the mortality rate between marked and unmarked individuals if an appropriate marking method was chosen. The only important factor to be considered was thus the rate of mixing of the marked snails with the rest of the population.

In a preliminary experiment on Muizenberg beach, 100 adults of _B. rhodostoma_ were marked with "Necol" anti-fouling paint and released at the points of capture after the paint had dried. The beach was revisited at low tide, 14 days later, and every snail which could be found in the original area was examined. About 15% of these were marked individuals but in many cases most of the paint had already worn off and it was often difficult to tell whether a given snail was a marked individual or not. It was concluded that the method of marking was unsatisfactory and the experiment was abandoned.

In a second experiment, on February 7th, 1960, every snail found on the surface of the sand in and above the swash zone, over a distance of approximately 300 meters, was marked by means of a small notch cut in the mouth of the shell. The notch was cut well back from the anterior edge so as not to interfere with the normal activities of the snail. It was attempted to make each notch triangular and about 3 mm deep. This proved a very effective method of marking, recaptured snails being readily identified as marked individuals. Moreover, even after the notch has been filled in and the shell increased in size, marked snails can be recognised from the small triangular blemish which remains in the shell.

Altogether, 268 individuals of B. rhodostoma were marked in this way. At first they were collected at low tide and placed in a series of plastic buckets, filled with sea water, high up the beach. When all the snails in a bucket had been marked, they were returned to the approximate stretch of beach from which they had been collected. As the tide rose, later in the day, buckets of marked snails were carried well out into the water before being deposited. The distance of 300 meters was simply paced out along the beach, 150 meters on either side of the permanent transect-line which had been established on Muizenberg beach (see Brown, 1969).

The same area was revisited at the time of low water on February 30th and all the snails observed in and above the swash zone were placed in buckets of sea water for examination. 103 snails were collected from the 150-meter stretch of beach west of the transect and of these only one was a marked individual. From the 150-meter stretch east of the transect line, 196 snails were collected (not counting a few individuals of B. digitalis) and 21 of these were found to be marked. It was then decided to continue the investigation eastward for a further 100 meters. Over this distance 92 snails were found and 14 of these were marked individuals. The study was continued still further east but by now the tide had risen considerably and it was necessary to wade into the water and dig in the sand in order to collect the snails. 56 snails were collected in this way but only two of them turned out to be marked.

On March 15th I revisited the beach, accompanied by a group of advanced students, thus making it possible to collect systematically over a distance of 1.5 kilometers. 762 individuals of Bullia rhodostoma were collected of which 71 were marked. However, with only a single exception, all the marked individuals were captured within 500 meters east of the transect line, the total number of snails taken over this distance being 379.

Two important points arise from this study; firstly it is apparent that the rate of dispersal along Muizenberg beach, under the conditions prevelant during the investigation, is slow. There is evidence that during the period studied the population tended to move

Figure 4.

Bullia rhodostoma in the swash zone. At the extreme bottom of the picture a snail is burying itself, while above and to the right a snail is having difficulty extricating itself from the sand.

eastward but that it moved as a unit, with relatively little spreading out. Secondly it would seem that the assumption that only a part of the population comes ashore with each low tide is completely justified. However, attempts to calculate the actual numbers of Bullia from the figures gained must of necessity be treated with caution.

If we assume that between the date of marking and the first date of recapture a negligible amount of spreading took place but that the whole population moved consistently east, then we can calculate the total population of B. rhodostoma for a 300-meter stretch of beach as:

$$\frac{(196 + 92) \times 268 \times 3}{(21 + 14) \times 2.5} = 2,646$$

This would in turn mean that only about 12% of the total population was actually collected. This does not seem unreasonable in view of the fact that it is quite impossible to collect all the animals in a given area; it implies that considerably more than 12% of the population is present in the swash zone at low tide.

On the second date of recapture the marked snails had dispersed over a distance of something more than 500 meters. According to our figures, therefore, the number of snails present along this stretch of beach should be:

$$\frac{379 \times 268}{70} = 1,448$$

It would seem likely from these two results that the method as applied to Bullia involves a considerable error. The most likely source of error is that the qualification that there should be complete mixing between marked and unmarked populations within the area studied has not been fulfilled. Such lack of mixing would be easily explained if, as has been tentatively suggested, the snails tend to keep together in rather well-defined groups. Moreover, if this is so, then the programme described above did not involve the random marking of individuals but consisted largely of marking all or virtually all of the snails in a relatively few groups of individuals. In other words the valid unit for this study would be the group instead of the individual. The number of units marked would thus not by 268, as originally stated, but this number divided by a factor of at least 20. The marking of only 13 units might well lead to widely different results on different occasions.

DISCUSSION AND CONCLUSIONS

The work which has thus far been completed on *Bullia* ranges through a number of fields, including anatomy, parasitology, pathology, sensory physiology, haematology, locomotion, circulatory physiology, behaviour and a number of aspects of autecology. These fields are often thought of as being quite distinct from another. However, I am inclined to take the opposite view and believe that one can only discuss the ecology of a species or group of species with confidence once one has an intimate acquaintance with all aspects of its life processes. This is not to say that such a stage has now been reached with regard to *Bullia*. On the contrary, I have tried to point out in this paper how much remains to be discovered, even with regard to *B. digitalis* and *B. rhodostoma*, and how poor is our knowledge of other species of the genus. Nevertheless I hope that a beginning has now been made to understanding these snails and the factors which are of importance to them.

From these studies *Bullia* emerges as an animal singularly well adapted to a harsh and demanding environment. While other intertidal forms retreat from the waves, or hide from them in deep burrows, *Bullia* exploits them, using waves and water currents to bring it ashore, probably to just those regions where its food is most likely to be waiting. Food is scarce but the animal's acute and highly specialised chemical senses, combined with a beautifully appropriate chain of reactions, ensures that what food there is will not be overlooked. If food is, indeed, absent, the animal can wait for several weeks, if necessary, for its next meal, conserving its energy in the meantime. When the next meal does arrive, however, it may eat up to a third of its own body weight (excluding shell), not only making up for lost time but also ensuring its survival during a subsequent period of fasting.

Temporary exposure to the air does not endanger it, since it can withstand a certain degree of desiccation and high temperatures for short periods. Neither do short-term fluctuations in salinity, such as it may encounter during rain, usually disrupt its activities for any length of time. Nevertheless it avoids unnecessary exposure to the elements, for when not actively concerned in finding food it buries itself in the sand. Its behaviour is also such that it rigorously avoids the upper part of the beach, thus obviating the danger of being left stranded by a retreating tide. Indeed the whole tidal cycle of activity in the intertidal species of Bullia displays a simple effectiveness which it would be hard to better, despite the fact that this cycle does not seem to be regulated by any internal pacemaker rhythm.

Bullia is not without its natural enemies, but these are almost entirely restricted to the aquatic phase of its cycle. On land it appears to have little to fear in the way of predators and even man has thus far failed to exploit it, though he has killed it with pollution and by destroying the beaches on which it lives. Its defense mechanisms against aquatic predators remain obscure, unfortunately, though certain possibilities have been presented. One of the reasons for the success of the snails may be that, while there are only a few animals which eat Bullia, there are a lot of things which Bullia will eat. It will consume nearly all animal flesh, from coelenterates to mammals, though it does not appear to favour the latter, and will even turn predator if very hungry. How it is attracted to live food (such as Callianassa and amphipods) remains to be investigated, however. It has not been seen to eat plant material though J.R.Grindley (personal communication) has found during recent studies of a toxic "red tide" in Algoa Bay, that Bullia had become toxic. The toxicity tests employed were the standard Sommer & Meyer tests for mussel poison, which depend on injecting alcoholic extracts into mice. This result is puzzling as there is evidence that mussel toxin is only accumulated at first hand; for example, crawfish which have fed on poisonous mussels do not themselves become poisonous. The possibility of Bullia consuming washed-up phytoplankton, remote as it seems, is to be investigated.

The life-cycle of Bullia, though only partly known, provides several points of interest, not the least of which is the suggestion of parental care of the eggs. It is certainly not unusual among intertidal psammophiles to find that the eggs are cared for by being retained in brood-pouches or even by being attached to the body but it would appear to be very uncommon indeed for a marine invertebrate to brood over eggs or egg-masses laid completely external to the body. Such a phenomenon may constitute a logical evolutionary step, but it is a step which involves the acquisition of patterns of behaviour with which the marine Prosobranchiata are not generally credited. The suppression of larval stages may possibly be seen as an adaptation to intertidal life in view of the fact that closely related genera have free-swimming larvae. An objection might be made that the infratidal species of Bullia, as far as is known, also show a suppression of larval forms; however, this argument falls away if, as I believe, the existing species of Bullia evolved from an essentially intertidal ancestor.

The distribution of the Cape Peninsula species of Bullia may be influenced by a number of factors, though temperature and wave action stand out as being the most important. There can be little doubt that it is the difference in temperature between the east and west coasts which limits B. rhodostoma to the region east of Cape Point, though the effect of temperature is probably more subtle than a simple direct influence on the adult. B. digitalis, the common species of the west coast, does not appear to be limited by the higher temperatures of the east coast, as it occurs in False Bay. Perhaps it is prevented from becoming a dominant species there because of competition with B. rhodostoma, for the habits of these two species are nearly identical. The picture is clearer with regard to the influence of wave action, for it has been shown that these species require a certain degree of wave action in order to undertake their tidal cycle of activity (Brown, 1961a), while too great a degree of exposure to waves leads to conditions in which the animals are carried away from the beach, along the coast or out to sea. They are thus in general limited to moderately exposed beaches. B. laevissima, on the other hand, cannot tolerate even the degree of wave action which is minimal for B. digitalis or B. rhodostoma, for it has no behavioural adaptations to intertidal life and wave action disrupts its pattern of activity. It is thus limited to very sheltered beaches, where it does not have to compete with either of the surf-loving species.

Bullia has proved a most rewarding animal to study, being easy to collect and to study both in the field and the laboratory.

It is easily maintained, requiring no special attention, and is robust, responding well to various experimental techniques and recovering rapidly from surgery. It is, moreover, a convenient size and has a relatively uncomplex anatomy. These characteristics have enabled a considerable amount of work to be done on the animal and are likely to facilitate further discoveries in the future.

SUMMARY

This paper gives an account of the present state of our knowledge of the sandy-beach snail, Bullia, on the beaches of the Cape Peninsula. The work deals mainly with the two surf-loving species, B. digitalis and B. rhodostoma, though mention is made of B. laevissima, a species found in quiet waters. Reproductive behaviour is described for the first time. Much of the work reported concernes chemoreception and the responses which lead to feeding. Some conclusions are reached with regard to growth and life-span. The distribution of the three species is dealt with, and the factors responsible for this distribution are discussed. Attempts to estimate the numbers of Bullia on Muizenberg beach are described. Some mention is made of water- and heat-relationships, defense mechanisms and parasites.

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