FOOD RELATIONSHIPS ON THE INTERTIDAL SANDY BEACHES OF THE CAPE PENINSULA

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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 "pelo-glea" 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[9]. 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 with 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 earth-worm-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 tnem.

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[16] 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

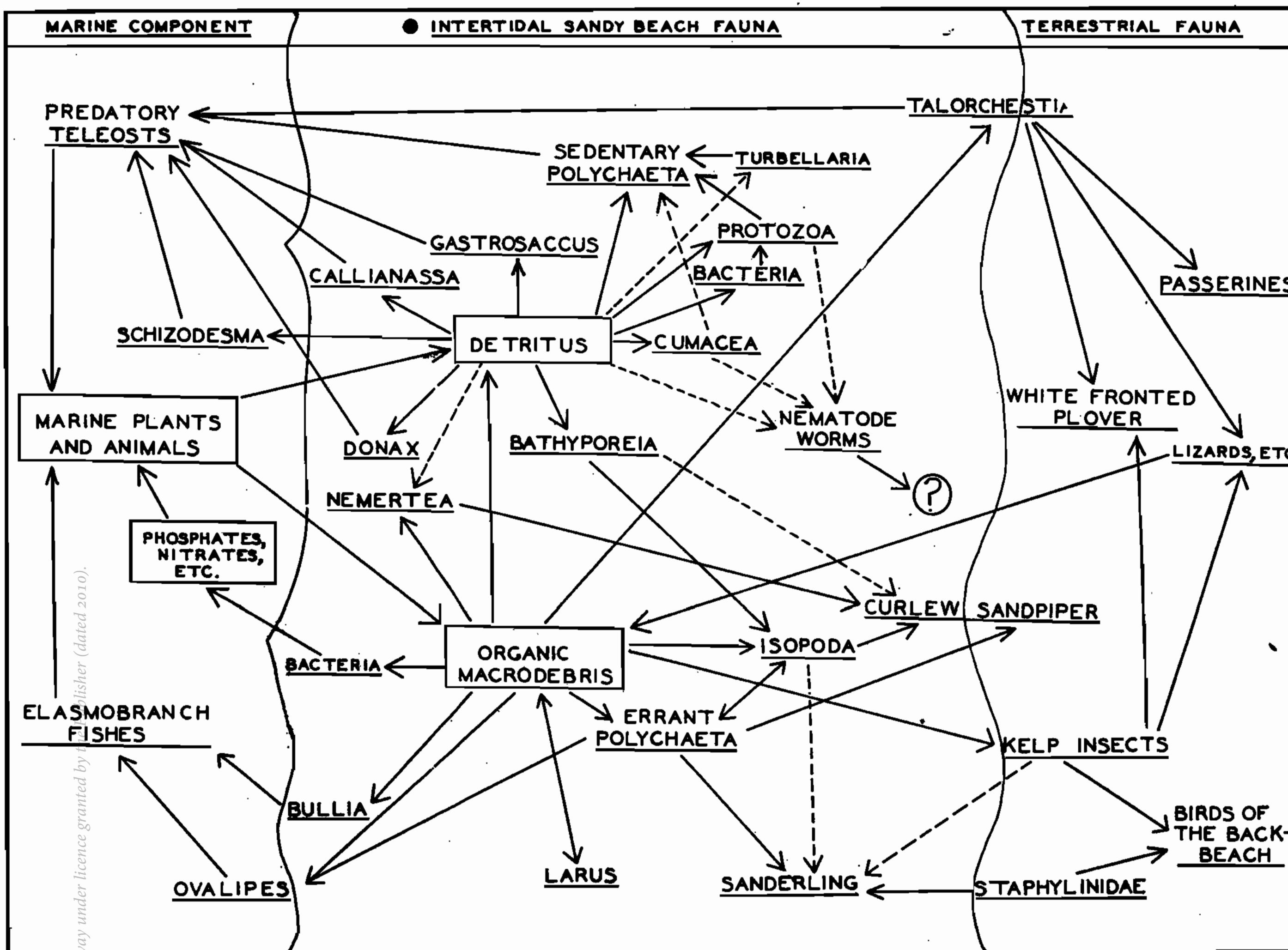

Fig. 1.—Scheme of food-relationships on Cape Peninsula beaches. Unbroken arrows show observed or well-authenticated relationships. Broken arrows indicate inferred or probable relationships.

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.

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