SOME ASPECTS OF THE ECOLOGY AND ZONATION OF THE FAUNA ON SANDY BEACHES

BY

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1. **Introduction**

The sandy beaches, despite their uniform appearance and their comparative poverty as far as the number of species is concerned, harbour a marine fauna of great ecological diversity. This statement retains its validity even if we do not consider the microfauna to which the vast majority of the species belong.

In day-time or when the tide is out most of the species of the macrofauna are completely hidden from view, or their presence is betrayed only by the openings of their burrows or by heaps of castings. Of the remaining species only a few individuals are generally to be seen, while the majority of them are also hiding below the surface of the sand. The coming of the tide is a signal to renewed activity among most animals reached by its waters. Similarly the fall of darkness brings into action vast numbers of animals living beyond the range of the tide.

Especially in the lower parts of the tidal belt many or even most of the species remain in their burrows also during their periods of activity. Others, however, leave their hiding places to move over the surface of the sand or in the water above it. Most of these species are Crustaceans, and this survey will, on the whole, be devoted to their ecology and its effect on their general distribution. An attempt will be made to trace the occupants of various ecological niches occurring at different levels of the beach and to demonstrate the influence exerted by the main climatic zones. Although there is a good deal of movement of many dominant species up and down the beach most species return for their resting periods to the same more or less well-defined vertical zones. These will be dealt with in the concluding sections of the present paper.

Before embarking on this task I wish, however, to acknowledge my debt to Dr. TH. MORTENSEN whose pioneer work 'Biologiske Studier over Sandstrands-faunaen, særlig ved de danske Kyster' (1923) deserves much more recognition

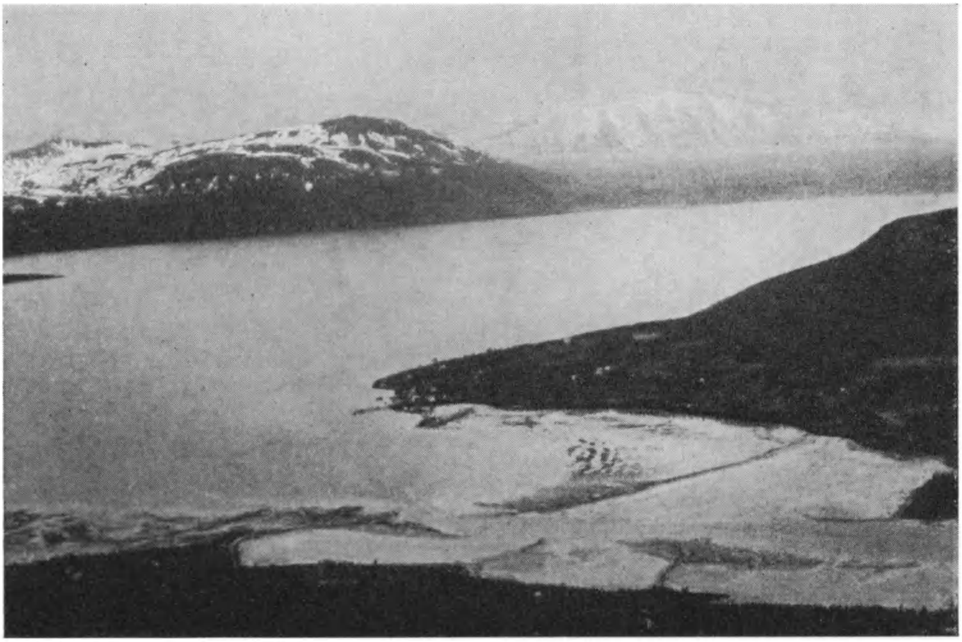


Fig. 1. Sandy beach at Rossfjord in Malangen, Northern Norway, seen from Kraknestind at nearly low tide. (cf. Fig. 5 a).

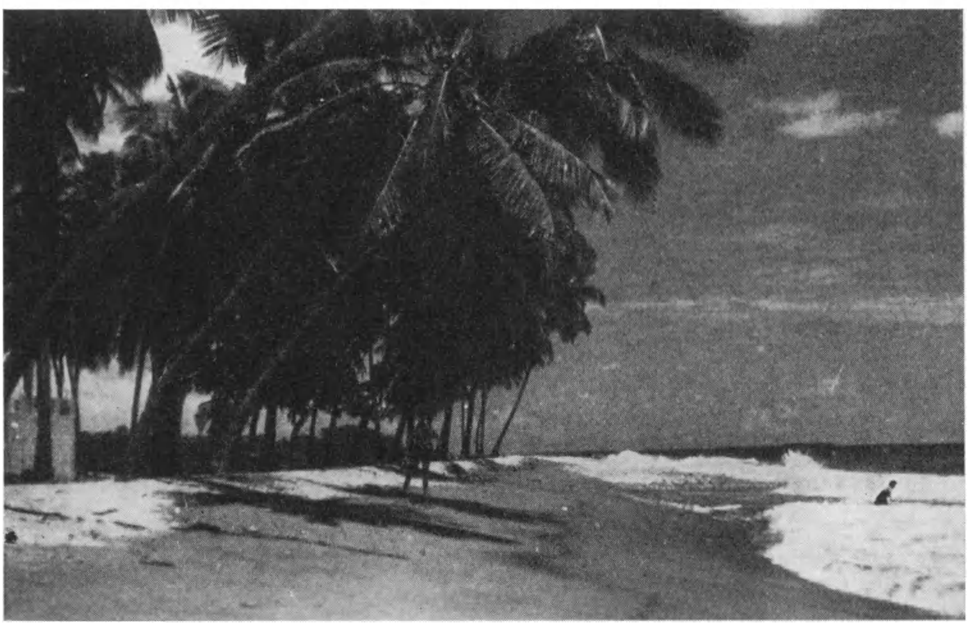


Fig. 2. The beach at Cañango near Puerto Cabello in Venezuela. Note the dark moist line marking the average surf line, and the scattered debris in front of the palms left behind by heavy surf. (cf. Fig. 5 c).

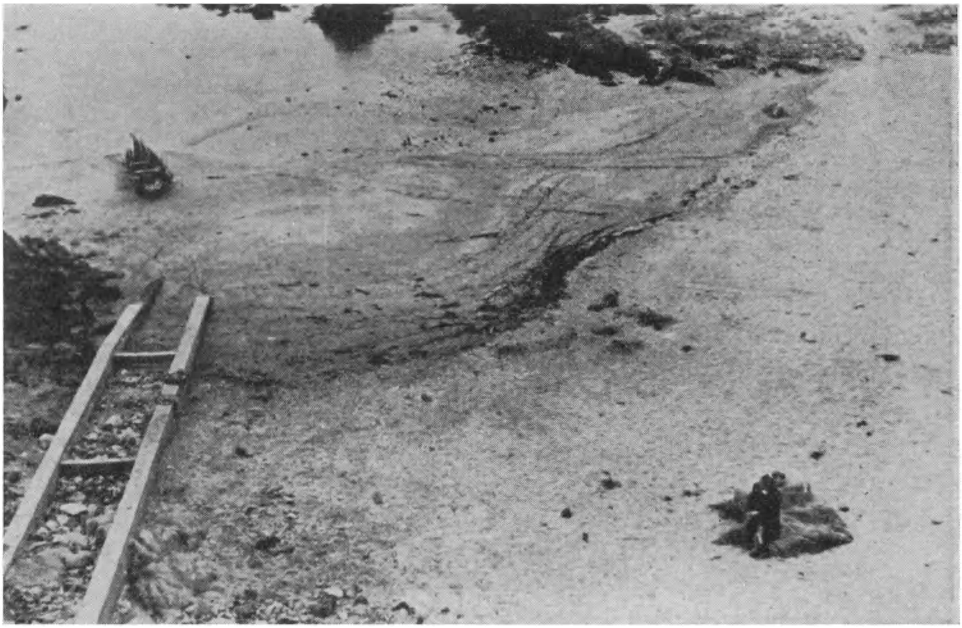


Fig. 3. The beach at Montemar near Valparaiso seen from the roof of the marine biological station. The range of *Orchestoidea tuberculata* lies around the rock on which the lady is seated, and half-way between that and the dark zone of debris further down the local Cirolanids have their maximum. (cf. Fig. 5 d).

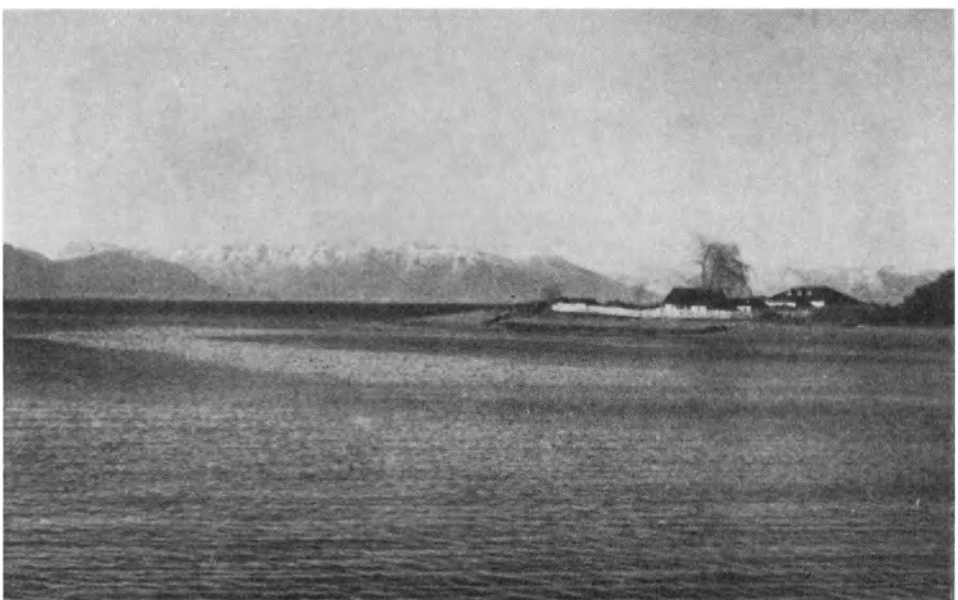


Fig. 4. Beach at the island Tenglo near Puerto Montt in southern Chile. The tidal range is over 7 metres, and at the moment the tide is more than half in, touching the "Cirolana belt". (cf. Fig. 5 e).

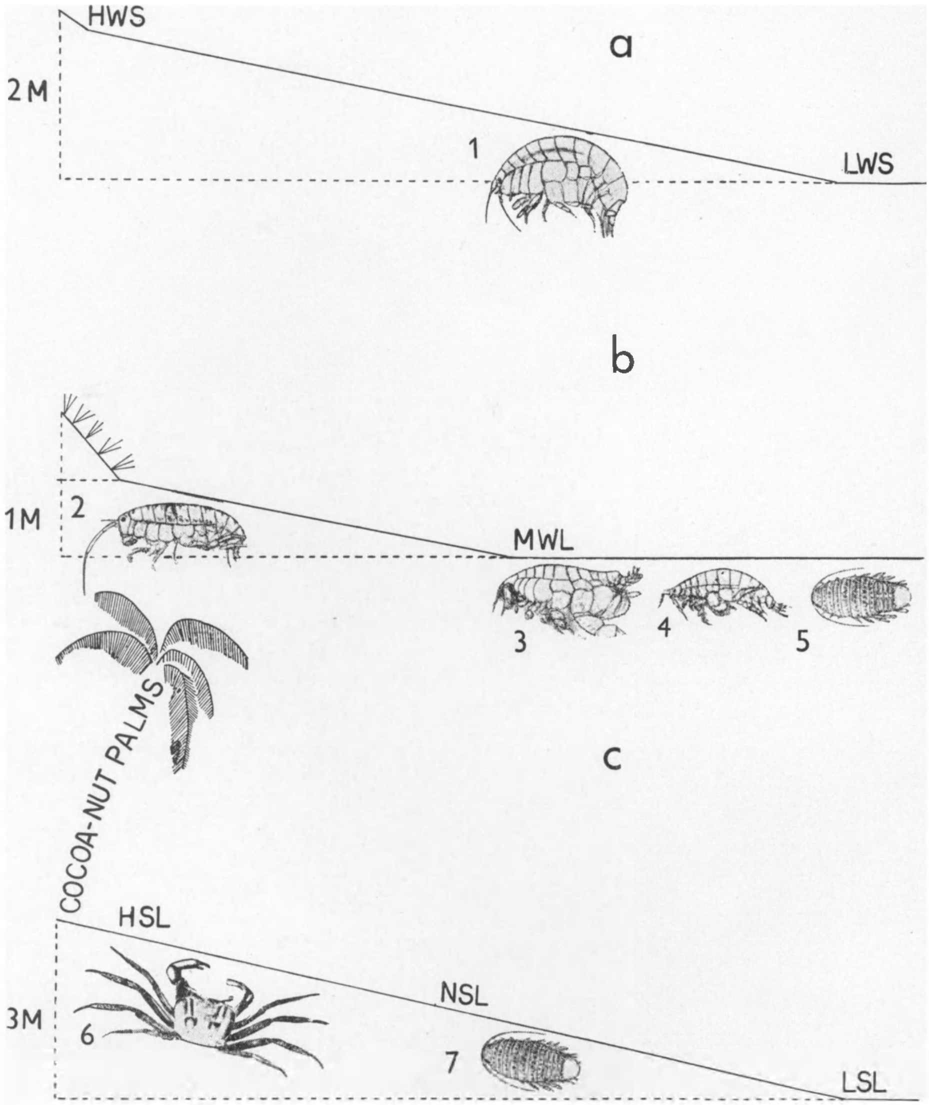
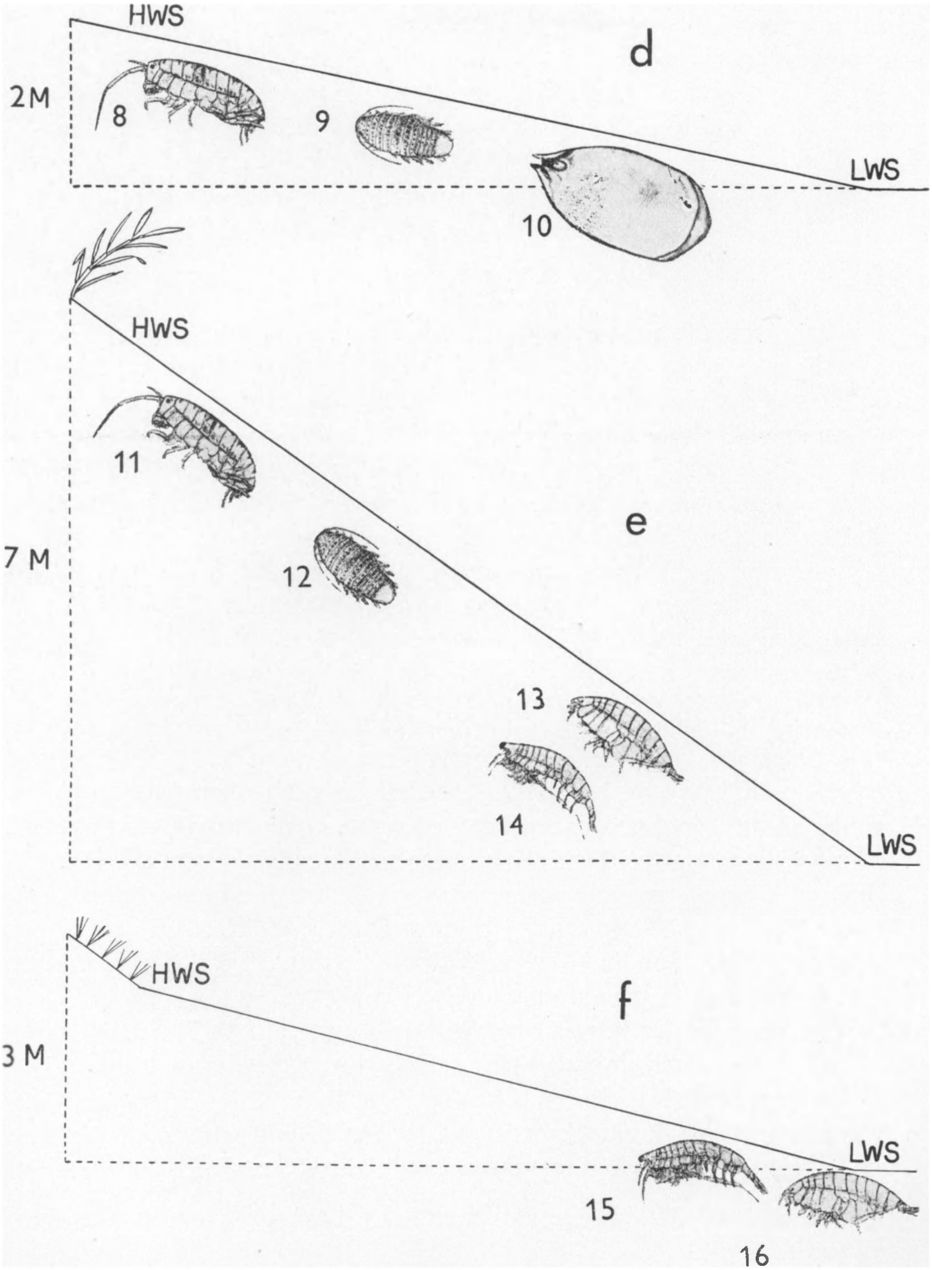


Fig. 5. Diagrams of a series of sandy beaches investigated by the writer. Vertical scale 1:100, horizontal scale varying from diagram to diagram. Tidal and surf levels approximate. Average distribution of Crustacean species represented by photos or drawings of identical or related forms from papers by RATHBUN (no.s 6 and 10) and SARS (all others).

a. Rossfjord in northern Norway (69°20′N). HWS high water springs, LWS low water springs. 1 *Pseudalibrotus littoralis.*
b. Haverdal, Swedish West Coast (56°45′N). MWL mean water level. 2*Talitrus saltator*, 3 *Haustorius arenarius*, 4 *Bathyporeia pilosa*, 5 *Eurydice pulchra.*
c. Cañango in Venezuela (10°30′N). HSL highest surf line, NSL normal surf line, LSL lowest level laid bare by surf. 6 *Ocypode arenarius*, 7 *Cirolana* sp.



d. Montemar near Valparaiso, Chile (33°S). HWS high water springs, LWS low water springs. 8 *Orchestoidea tuberculata*, 9 Cirolanid isopod, probably *Exocirolana* sp., 10 *Emerita* sp.

e. Isla Tenglo near Puerto Montt, Chile (41°30'S). HWS high water springs, LWS low water springs. 11 *Orchestoidea tuberculata*, 12 Cirolanid isopod, probably *Exocirolana* sp., 13 Phoxocephalid amphipods (*Metharpinia cornuta, Pontharpinia fuegiensis*), 14 Oedocerotid amphipods (*Bathyporeiapus magellanicus, Monoculodes* sp.).

f. Near Punta Arenas on the Straits of Magellan (53°S). HWS high water springs, LWS low water springs. 15 Oedocerotid amphipods (*Monoculopsis vallentini, Metoediceros fuegiensis*) 16 *Pontoharpinia fuegiensis* (fam. Phoxocephalidae).

than it has received for having, for the first time, called attention to many of the problems concerned.

I am also indebted to Professor JOHN DAY of Capetown University who read my manuscript and made many valuable suggestions.

Miss CHRISTINE BLANK kindly helped me with the diagrams.

2. **Material examined**

As a basis for the following discussions I have chosen a series of sandy beaches the crustacean fauna of which, in the course of the years, I have had the opportunity of examining, and which, despite the fact that they are situated widely apart and along the shores of two different oceans, have nevertheless turned out to be fairly significant and to conform with the results obtained by previous authors. In most of the areas concerned I had the opportunity of examining many different beaches, and those discussed here are chosen as typical examples, being representative of their respective areas. An exception to this rule is the coast of Venezuela, for in that region I had occasion to investigate only one typical sandy beach.

The position and general type of the beaches investigated are as follows:

1. Northern Norway, Rossfjord in the Malangen Fjord (lat. 69°20'N.). Tidal
2. SW. Sweden, Haverdal Beach on the Kattegatt (lat. 56°45'N.). Tidal difference small, wave exposure great, beach sloping rather steeply.
   range about 2 m, wave exposure moderate, beach sloping gently (Fig. 1).
3. Venezuela, Cañango Beach near Puerto Cabello (lat. 10°30'N.). Tidal difference small, wave exposure very great, beach sloping rather steeply (Fig. 2).
4. Central Chile, Montemar N. of Valparaiso (lat. 33°S.). Tidal amplitude 1.8 m, exposed, beach sloping gently (Fig. 3).
5. Southern Chile, Isla Tenglo near Puerto Montt (lat. 41°30'S.). Tidal range 7.2 m. Upper beach sloping rather steeply, lower beach sloping very gently. Rather exposed (Fig. 4).
6. Magellan Strait, Punta Arenas (lat. 53°S.). Tidal range 2 m. Exposure rather great. Beach sloping gently.

The localities nos. 3–6 were investigated in the course of the Lund University Expedition to Chile.

The diagram Fig. 5a–f illustrates the distribution of the Crustacea Malacostraca met with on the various beaches. It should be pointed out that on most of them the Malacostraca constituted the bulk of the macrofauna, on some of them they were the only forms observed. As a result of the heavy surf and the short time at my disposal at Cañango my investigations of the lowest reaches of the beach laid bare by the surf were too superficial. No animals whatever were observed there, but some forms of life, e. g. Hippid crabs, probably occur, although they were overlooked by me.

3. Crustacea Malacostraca of sandy beaches

The uppermost reaches of sandy shores are inhabited mainly by two types of Crustacea, viz. crabs of the genus *Ocypode* and Amphipoda of the family Talitridae. According to MORTENSEN (1923, p. 33) a small terrestrial Isopod of the genus *Scyphax* from New Zealand has a similar ecology, but I have not found any further data on the life history of this species. Other forms, e. g. hermit crabs of the genus *Coenobita* and prosobranch snails of the genus *Bullia* are found in the same zone on many beaches but are not confined to it.

The species of *Ocypode* and the sand-burrowing Talitridae are all of them scavengers, living principally on the plant and animal debris thrown up on the beach, especially its higher levels. According to notes made by HERBERT LANG on the species *Ocypode ippeus* and *O. africana* (published by RATHBUN 1921, p. 464) they prefer "decaying animal and plant matter; under certain circumstances, especially at night, they may come in numbers to remains of fish, but they are not really gregarious and shift for themselves". Occasionally the species of *Ocypode* kill and devour other animals, instances have been quoted of young birds and even a young rabbit killed by ghost crabs. According to MAYER (1905, p. 105) *O. albicans* on North American shores occasionally preys on terrestrial amphipods, an observation with a certain bearing on the problems which are to be dealt with below.

The choice of food of the sand-burrowing beach fleas very closely resembles that of the ghost crabs (cf. SCHELLENBERG 1928 a). Their predatory tendencies appear to be less pronounced, but *Talitrus saltator* of the European West Coast has been accused of killing and devouring its own kind, at least in captivity.

The ecological resemblances between the ghost crabs and the beach fleas are not restricted to the general range on the beach and the choice of food. It might be added that they all of them hide in burrows made by themselves, though with the difference that while those of the ghost crabs are more or less permanent, those of the beach fleas are not used more than once. Further, both types are largely nocturnal in their habits. However, this tendency is less pronounced in the ghost crabs. BALSS (1927, p. 926) even maintains that the *Ocypode* species prefer to search for their food by daylight, and CRANE (1947) notes that on the west coast of tropical America *O. gaudichaudii* from sheltered beaches is mainly diurnal, while *O. occidentalis* of exposed beaches is nocturnal.

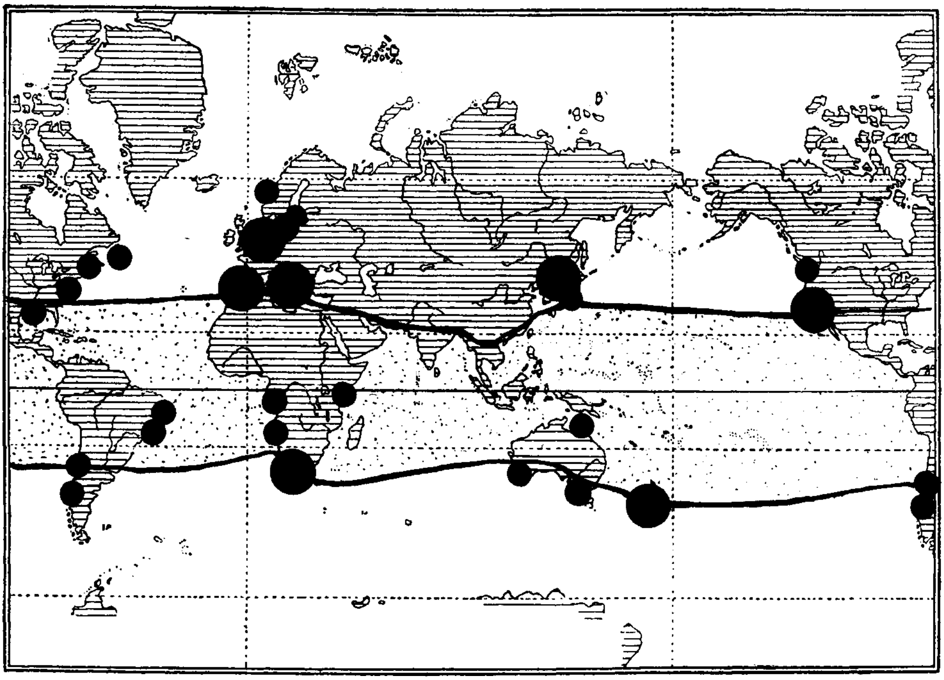


Fig. 6. Map showing the distribution of Talitrid amphipods digging in sandy beaches (black circles indicating number of species, 1–4, with this ecology in the respective areas) and the distribution of the crab genus *Ocypode* (dotted area between black lines).

But on the whole, and although it is a well-known fact that specimens may be found roving on the beach at any hour of the day, most authors put down the ghost crabs as nocturnal or at least with a predilection for the hours around dawn and dusk. The beach fleas are more strictly nocturnal; adult specimens are rarely seen on the beach at day. An exception from this rule is *Orchestoidea benedicti* (RICKETS and CALVIN 1939, p. 112), which species "can be found at will by day". On the other hand, young specimens a few millimetres in length may frequently be seen by thousands on the moist sand near the water's edge; apparently, they do not burrow, and it is doubtful whether they could work their way through the hard, moist sand. This behaviour is probably more or less universal for I have seen it in species of all three genera of Talitridae burrowing in sand, viz. *Talitrus saltator*, *Talorchestia deshayesii*, and *Orchestoidea tuberculata*. Both ghost crabs and beach fleas have a very acute sense of vision. The ghost crabs will discover an observer at a distance of several metres and disappear as quick as lightning while according to the very interesting observations recently published by WILLIAMSON (1951, p. 92) a specimen of *Talitrus saltator* can see a human being at a distance of 3 m. The same writer has definitely proved that *Talitrus* orientates itself by the sight. The observations made by SMALLWOOD (1903) on *Talorchestia longicornis* point in the same direction, although the question was not discussed in detail by Miss SMALLWOOD.

In view of the great ecological similarity between the ghost crabs and the sand-burrowing beach fleas, the general distribution of the two groups is of considerable interest. In the map Fig. 6 an attempt has been made to compare the general distribution of the genus *Ocypode* with that of Talitrid amphipods which are definitely known to burrow in sandy beaches. The map calls for some comments, for while most ghost crabs of the genus *Ocypode* are confined to tropical or warm-temperate areas and appear to have more or less the same ecology this is not the case with the genera of Talitridae. Species burrowing in sand on the beaches are known to occur within the genera *Talitrus*, *Talorchestia*, and *Orchestoidea*. Some species of *Orchestia* are also to be found dug into sandy beaches, but in all cases known to me they also occur elsewhere, e. g. in wrack beds, which is not the case with the typical burrowers. Unfortunately, the ecological data contained in the literature are far too scanty in the case of many species, especially within the genus *Talorchestia*.

The genus *Talitrus* in the sense used by STEBBING (1906, p. 524) has been split into two, *Talitrus* s. str., and *Talitroides*. If we accept this division, the genus *Talitrus* becomes probably monotypic, comprising only the well-known European *T. saltator* (MONT.), the classical example of a burrowing beach flea. The species of *Talitroides* are tropical forest forms and have become notorius as hot-house pests in Europe and the United States.

The genus *Orchestoidea*, is almost exclusively American, having representatives along the west coast of both Americas and on the coast of Brazil. One species has been recorded from the South Sea, and also from Greece, which latter record is probably wrong. Finally one species is known from the Sea of Japan. At least the American species *O. californiana*, *O. tuberculata*, *O. benedicti*, *O. corniculata*, and *O. brasiliensis* are true inhabitants of sandy beaches. Within the large genus *Talorchestia*, practically cosmopolitic in warm and temperate areas, conditions are more complicated. It would carry too far to discuss here in detail the ecology of all the species (for a survey of most of them cf. STEPHENSEN 1935). However, the case seems to be that in temperate areas most or all of the species are true sand forms (e. g. in eastern North America, in Europe, in Japan and adjacent areas, further in South Africa, South Australia and New Zealand) while in the tropics the vast majority of the species either live among wrack on the shores or frequent the shores of fresh waters or other damp places in the forests. This rule is by no means without exceptions. Thus to name a few instances *T. tricornuta* lives on the sandy beaches around the Congo estuary (SHOEMAKER 1920, p. 373, LANG in RATHBUN 1921, p. 465), and *T. spinipalma* has been recorded from a sandy beach at Port Denison in Queensland (STEBBING 1906, p. 552). Despite this fact and the circumstance that many tropical species are only known from one single locality, there is no doubt about the general tendency, as illustrated by the map in Fig. 6.

Thus it seems safe to conclude that the ghost crabs and beach fleas are, on the whole, forms which replace each other and which occupy the same part of the sandy beaches, the ghost crabs in tropical and subtropical areas, the beach fleas in temperate areas.

The reason for this different distribution is probably to be found in ecological properties others than those dealt with above. In the first place, the small and comparatively thin shelled Amphipoda are much more sensitive to desiccation than the more róbust ghost crabs. It is further to be noted that the crabs escape the direct effect of the sun during their most sensitive phase by passing their larval stages in the water. This possibility does not exist in the case of the Amphipoda, the brood of which develops in the marsupium of the female, and the recently emerged young dry up and die very easily. It is noteworthy in this connexion that, as already mentioned, the young of *Talitrus saltator* and *Talorchestia deshayeesi* in Scandinavia and those of *Orchestoidea tuberculata* in central and southern Chile have been observed to occur in the first place in the lower reaches of the beach where the sand surface holds more moisture, while the adults prefer the higher levels where they have to dig through layers of dry sand before reaching the moister strata in which they spend the day.

The very few reliable data published on the occurrence of burrowing amphipods on tropical sand beaches show that in the tropics they occur further downwards on the beach than in temperate regions, a fact which is in good agreement with the general pattern of the distribution of plants and animals on tropical beaches as compared with conditions in temperate areas. Thus SCHELLENBERG (1938, p. 209) notes that at Recife in Brazil *Orchestoidea brasiliensis* occurs "in der nassen, von den auflaufenden Flutwellen bespülten Zone" and LANG in RATHBUN (l. c.) obviously with reference to *Talorchestia tricornuta* in the Congo estuary speaks of "the streak of moist sand just above the surf-line, where countless tiny burrows of sand fleas (amphipods) give the surface a rough, pitted aspect." As has been repeatedly stated the typical habitat of burrowing amphipods in cooler areas is the drier sand around high water mark, and this, in its turn, is the area occupied by the ghost crabs of subtropical and tropical shores.

Thus in the tropics the burrowing amphipods, on the beaches where they do occur, do not occupy the same niche as the ghost crabs. Direct evidence of this has been produced by LANG in RATHBUN (l. c.) who states that on the sands in the Congo estuary the burrows of *Ocypode africana* commence a little way below the uppermost drift line, while those of *O. ippeus* were found a little way further down and those of *Talorchestia tricornuta* in the moist area. Similarly Dr. HEEGAARD kindly informed me that in Mexico he saw ghost crabs in the upper part of the beach and beach fleas in the moister areas further down. Dr. BACKLUND has put at my disposal a similar observation from East Africa. On the Cañango Beach in Venezuela there were no Talitrids despite the fact that the beach seemed ideal for them, and the same seems to be the case on many tropical shores.

Thus it would seem probable that the predominance of ghost crabs in hot areas and of beach fleas in temperate zones is at least partly due to the greater drought-resistance of the former. There is hardly any need to assume a direct competition between the two types, nor does it appear that the fact stated by MAYER (1905, p. 105) that the ghost crabs occasionally catch beach fleas should have any greater significance.

Another feature in the ecology of ghost crabs and beach fleas and in fact of crabs and amphipods in general bearing on their distribution is also connected with their reproduction. Various writers, (especially THORSON 1936, 1946, 1950) dealing with the general aspects of the reproduction of marine animals, demonstrated the prevalence of small broods with brood protection or large ova with non-pelagic development in cold areas and of large broods hatching from small ova and with pelagic development in warm areas. The reproduction of amphipods and crabs respectively represent the extremes in this respect, for, as has already been pointed out, the crabs have pelagic larvae while the amphipod ova develop in the marsupium of the female. Female crabs generally produce broods consisting of many thousand eggs, while in most Amphipoda the number of ova in each brood for most species lies between 10 and 50 and rarely exceeds 100.

The enormous increase in number of species and individuals of crabs is one of the most striking and well-known features of the warm seas as compared with those of temperate regions, while it is equally well-known that the amphipod fauna attains its highest quantitative and qualitative development in colder areas and in somewhat deeper waters. This is most probably due to the different reproductive biology of the two groups.

As shown in Fig. 6 the range of the burrowing *Talitridae* does not nearly cover the whole of the boreal and antiboreal regions. In the northern hemisphere their northern limits are Puget Sound (*Orchestoidea pugettensis*), Gulf of St. Lawrence (*Talorchestia longicornis*), SW Norway (*Talitrus saltator*), the Sea of Japan (*Talorchestia spp.*). Of the southern continents only South America reaches south of the range of the burrowing Talitrids; on the west coast the southern limit appears to be Chiloé Island (*Orchestoidea tuberculata*), while no burrowing beach fleas have been recorded from the antiboreal part of the east coast.

In the colder parts of the boreal and antiboreal regions and in the arctic and antarctic areas no animal of a marine ancestry occupies the same level and the same mode of life as the ghost crabs and the burrowing Talitridae (cf. surveys of literature by MADSEN 1936, 1940; MANN 1948).

It is evident from the diagram Fig. 5a–f that on all the beaches investigated by the present writer, with the exception of the northernmost and southernmost ones, isopods of the subfamily Cirolaninae occurred at levels somewhat further down than those inhabited by Talitrids and ghost crabs. It should be noted in this connexion that the beach at Haverdal included in the diagram is representative in this respect of a great number of similar beaches on the Swedish and Danish coasts investigated by MORTENSEN (1923) and the present writer, and apparently also of the British Isles (cf. ELMHIRST 1931, Fig. 1, p. 170).

The sub-family Cirolaninae is cosmopolitan, and many species of several genera occur in the tidal zone. Unfortunately, it is very difficult to obtain exact data from the literature on the habitats frequented by many of these intertidal species. However, at least the following areas harbour species of Cirolaninae living on sandy beaches in more or less the same manner as those recorded in Fig. 5, viz. California (*Exocirolana linguifrons*, G. E. and N. MAC GINITIE 1949), the Galapagos Islands (*Cirolana mayana*, VAN NAME 1924), eastern North America and Caribbean Sea (probably various species, RICHARDSON 1905), Congo Estuary (*Eurydice carangis*, VAN NAME 1920), South Africa (*Pontogeloides latipes*, and probably *Cirolana bovina*, BARNARD 1940), British East Africa (verbal information by Mr. T. WOLFF), and South Australia (*Cirolana* spp., HALE 1929) (cf. Fig. 7). Most probably several species, especially from the Indo-Pacific areas (cf. NIERSTRASZ 1931), should be ranged into the same category, although detailed information on their ecology is still wanting.

The Cirolaninae are scavengers or ectoparasites on fishes. Those living on the beaches probably eat all kinds of dead and dying animals thrown up on the shore or used as bait for catching them. Among dead invertebrates devoured by them some forms have been especially mentioned by various authors, e. g. the Anomuran crab *Emerita* (the staple food of *Exocirolana linguifrons* according to G. E. and N. MACGINITIE 1949, p. 264), sea-stars (VAN NAME 1920, p. 53), and an ascidian (STEBBING 1910, pp. 421–422). However, they apparently attack anything coming their way including warm-blooded animals. In August 1937, on Anholt a small island in the Kattegatt, Professor B. HANSTRÖM and the present writer were watching numerous specimens of *Eurydice pulchra*, feeding on weak and dying young *Pleuronectes* in a small lagoon on the sandy beach, when we were ourselves suddenly attacked by the isopods. Despite the small size of our agressors their bites were quite painful. Of the Californian *E. linguifrons* G. E. and N. MACGINITIE (l. c., p. 264) write that it "often starts biting ones toes if one stands in the water too long in one place. It begins its meal on the tender skin between the toes. The bite causes a stinging sensation that is rather uncomfortable". Professor T. GISLÉN has told me that in California he

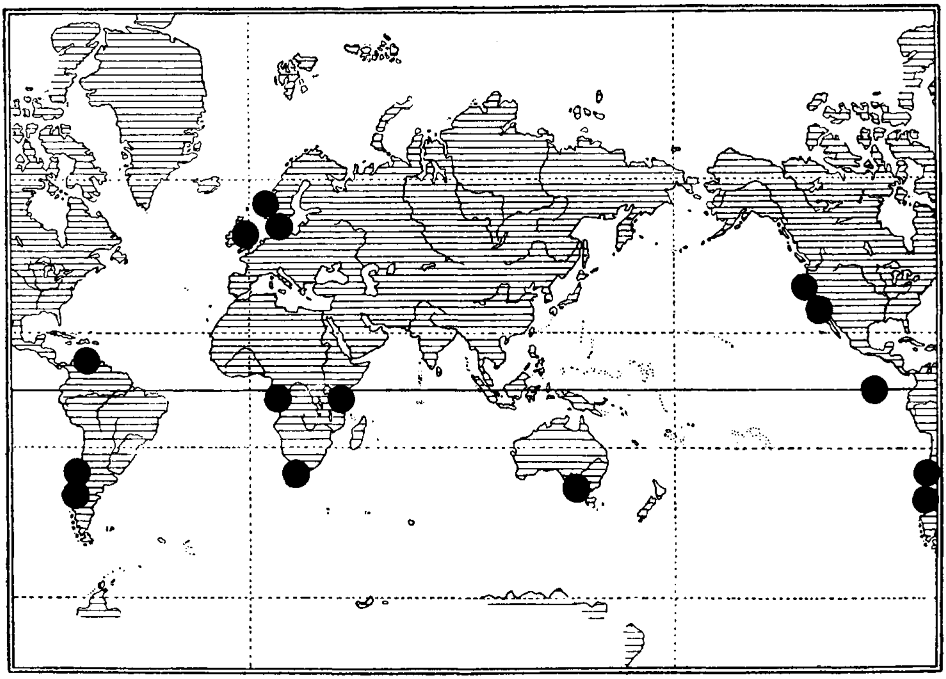


Fig. 7. Documented distribution of Cirolanid isopods living as scavengers, predators, and sometimes facultative ectoparasites in tidal zone of sandy beaches.

was attacked by a "*Cirolana*", probably the same species. Similarly the species occurring on the beaches in central and southern Chile has a bad reputation among the local fishermen, and I was bitten by it once or twice. Although it did not seek out "the tender skin between the toes" its attentions were rather unpleasant. Mr. WOLFF (verbatim) and HALE (1929) have reported similar observations.

I have dwelt at some length on these matters because in my opinion they illustrate so clearly the similarity in behaviour of related forms living at approximately the same levels on the same type of beach in localities separated by whole oceans and continents. It should be noted that although these species all belong to the subfamily Cirolaninae they have been referred to several different genera.

A further ecological similarity between the Cirolaninae of the sandy beaches might be mentioned viz. that their period of activity falls in the period when they are covered by the tide. Then they swim about very rapidly or rest on or in the bottom. When the beach is uncovered at ebb-tide they hide in the sand, but they never dig deep and they keep to the areas that are never completely dry. On the Swedish west coast where there are no tides *Eurydice pulchra* is, with very few exceptions, never to be found above the water line, but on the

British Isles it occurs in the tidal zone (cf. e. g. ELMHIRST l. c.). On the Cañango Beach in Venezuela, where the tidal difference is very small but the surf violent, the local "*Cirolana*" was found only in an area moistened by each wave. On the small sandy beach at the biological station at Montemar near Valparaiso, where the tidal difference at spring is nearly two metres but the daily fluctuations of the surf accounts for water movements on a much larger scale up and down the beach, the specimens of "*Cirolana*" after a period of heavy surf were always to be found higher up, the upper part of their range then occasionally coinciding with the lower reaches of the zone inhabited by *Orchestoidea tuberculata*. On the Tenglo beach near Puerto Montt the tidal range was about seven metres, and at spring the areas occupied by *Orchestoidea* and the *Cirolana* sp. partly overlapped, although otherwise the Isopoda were found lower down on the beach.

The evidence brought forward here, although unfortunately by no means complete, tends to show that on sandy beaches throughout the tropical and not too cool areas of the temperate regions, below the level occupied by the scavenging and more or less omnivorous ghost crabs and beach fleas there follows a belt inhabited by Isopoda of the sub-family Cirolaninae. These forms are carnivorous, living on dead, injured, or even healthy animals. At low tide during the night, ghost crabs and terrestrial amphipods feed in the area inhabited by these isopods.

As was the case with the previous ecological group the Cirolaninae, too, are absent from the sandy beaches of the cold-temperate and cold areas, all representatives of the sub-family in arctic and antarctic waters being confined to large or moderate depths. There seems to be no marine animal which can be said definitely to replace them. In his survey of the littoral fauna of the Arctic MADSEN (1936, p. 60) in his discussion of the general distribution of intertidal species claims that "*Mesidothea entomon* occurs on Novaya Zemlya and along the north coast of Sibiria and Arctic America (GURJANOVA 1930, p. 239; BIRNSTEIN 1933; BOONE 1920, p. 20)". Could it be demonstrated that species of *Mesidothea* were widely distributed on the Arctic sandy beaches they might provide a very interesting parallel to the Cirolaninae of warmer areas, the more so as the *Mesidothea* spp. are known to be scavengers (in the Baltic *M. entomon* makes itself a nuisance, devouring the bait on fishing lines) and also to attach themselves to live fishes. However, their occurrence on the marine sandy beaches is hardly typical. *M. entomon* is confined to localities with a reduced salinity, according to GURJANOVA (1933) it is in fact rather an estuarine than a marine species. When MADSEN (l. c.) states that the *Pseudalibrotus* species—widespread on sandy and clayey beaches throughout the Arctic—has a mode of living similar to that of *M. entomon* this should not be taken to include its feeding habits, for all evidence tends to show that the amphipod

Pseudalibrotus in this respect more resembles the beach fleas. As far as the evidence goes the Antarctic beaches also do not possess any species with the same ecology as the Cirolaninae dealt with above.

If from the belt inhabited by the Cirolaninae we advance a little further seawards the number of marine species and the degree of ecological variability increase very rapidly. While among marine animals the Crustacea are in more or less sole possession of the uppermost reaches of the beach, numerous classes, e. g. Mollusca, Polychaeta and Echinoderma, are represented at the lower levels. It would be beyond the scope of the present paper and the power of the writer to give a survey of all the ecological types. I shall confine myself to those forms which, like those dealt with above, more or less regularly leave their hiding places in search of their food on the surface of the sand or in the water above it. Besides microscopical forms which are not considered in this paper, the animals with such an ecology are practically all Crustacea Malacostraca, or fishes such as the sand-eels (*Ammodytes*), which may occasionally be found dug in near the low-water mark, and hardly belong to the true sandy beach fauna.

If we revert to the diagram Fig. 5 we see that most of the species of Malacostraca encountered in the lower parts of the beaches in temperate areas are Amphipoda. On the Cañango beach, on the other hand, no amphipods were found, and on the whole amphipods are apparently not common in the lower reaches of sandy beaches in the tropics. The tropical and warm-temperate beaches, however, harbour another type of Crustacea lacking in the boreal and antiboreal regions proper, viz. Anomuran crabs of the group Hippidea.

However, despite the wide distribution of similar and closely related types of Crustacea occurring near the low-water mark over vast areas, one should be very careful in drawing ecological parallels. For in the lower reaches of the beach the opposite conditions of those encountered in the upper parts are found. Round the high-water mark conditions are so strenuous as to leave only little room for ecological variation in marine or "ex-marine" animals. But the more we approach the low-water mark, and the better the environment meets the claims of a marine fauna, the greater become the possibilities for ecological variation. Thus round high-water mark on sandy beaches practically all the marine animals have the same ecology (*Ocypode* spp. several genera of Amphipoda), while near low-water mark closely related forms may be very different from an ecological point of view.

On the next few pages some of the convergences and divergences in structure, mode of living and choice of food in the lower reaches of the sandy shores are discussed. Among the most typical inhabitants of those levels in tropical, subtropical, and, to a certain extent, warm-temperate areas are the Anomuran crabs af the tribus Hippidea. Best known of all is the West American species

Emerita analoga. The *Emeritas* are suspension feeders, straining edible particles from the water by means of their setose antennae, which are kept extended over the sand and at intervals are drawn through their mouth-parts (cf. JONES 1936). They swim and dig backwards with great dexterity; also when crawling they move their hind end foremost. Of their movements over the beach the MACGINITIE's (l. c., p. 301) give the following description: "As the tides come in or recede the crabs move up and down the beach, remaining in a zone that provides maximum feeding opportunities or where the receding water from the breaking waves flows by them the maximum length of time. This movement up and down the beach with the waves occurs en masse. As a wave travels shoreward the crabs issue from the sand, allow themselves to be carried by the water until the force of the water slackens, then hastily dig into the sand again. In the course of an incoming tide such a movement may take place several times."

On the same beaches as *Emerita analoga* but generally somewhat further downwards another representative of the same tribe, *Blepharipoda occidentalis*, will generally be found around the low-water mark or somewhat further down. Although considerably larger it closely resembles *Emerita* in general appearance. It is not a plankton feeder, though, but a scavenger, feeding on dead animals, very often *Emeritas*. The *Blepharipoda* are accomplished burrowers. In Chile I have often seen solitary specimens crawling over the sand in shallow water in broad day-light in search of food. They have been accused of being beasts of prey, but this was denied by the MACGINITIE's (l. c., p. 304) who could not induce them to take living food.

Of an Australian species of *Hippa* (s. str.?) MORTENSEN (1923, p. 34) tells us that it lives dug in the breaker zone on sandy beaches. "If a small fish is thrown up and left behind by the waves, it will within a moment be pulled down into the sand and devoured. If one digs into the sand where the fish disappeared, he will find it surrounded by handfuls of the Crustaceans."

On shores of less violent exposure the Californian *Lepidopa myops* and the Mediterranean *Albunea symnista* burrow deeply into the sand, by means of their long and setose antennulae forming a tube through which a water current can be maintained.

These instances may illustrate the ecological diversity of this group of Decapoda, so uniform in general appearance and frequenting on the whole the same levels of sandy beaches.

As has already been mentioned the range of the Hippidea is limited to warm or fairly warm waters, and it might be interesting to find out what animals replace them in colder areas. Here again it is repeated that the species replacing them must not necessarily be found among the Crustacea, or at least Crustacea need only replace them as far as part of their ecology is concerned. Thus a suspension feeder such as *Emerita* may, for practical purposes, be replaced not by another Crustacean but by a mussel with the technical difference that *Emerita* strains its food particles from the water by means of its extended antennae, while the mussels pump a current of water over the blades of their gills.

As a North European equivalent to the tropical Hippidea various authors (MORTENSEN l. c., p. 35, YOUNGE 1949, p. 227) call attention to the burrowing Brachyuran crab *Corystes cassivelaunus* from the Mediterranean and Atlantic coasts. Here again the ecological resemblance is "composite", for *Corystes* rather corresponds to the Hippidea in general than to any particular species. In general appearance it fairly closely resembles a Hippid crab, and like the Hippidea it burrows backwards. By day it remains hidden below the surface of the sand, breathing after the mode of *Lepidopa* and *Albunea* through a tube formed by the antenna. During night it comes out to search for food on the surface of the sand. It appears to be, at least mainly, rapacious. According to HUNT (1925) its food consists in the first place of small molluscs, worms and Crustacea. It is interesting to compare its mouth-parts with those of the suspension feeder *Emerita*, especially its strong, ivory white mandibles contrast sharply with the thin, transparent, and setose plate forming the same appendage in the latter species. As in *Blepharipoda* most of its range lies below the tidal area.

MORTENSEN (l. c.) in his search for ecological equivalents to the Hippidea on the Scandinavian shores, where *Corystes*, too, is very scarce, mentions the burrowing amphipods of the family Haustoriidae, i. e. *Bathyporeia* spp. and, in the first place, *Haustorius arenarius*. To these should be added *Urothoë grimaldii* from the coasts of western Europe and also members of the family Oedocerotidae, especially *Pontocrates arenarius*.

It is very interesting indeed to find that once more as we proceed from warmer to colder areas the Decapoda of a certain habitat are replaced by Amphipoda (cf. p. 10). It should however be remembered that the replacement is in the first place one of space, not necessarily comprising all ecological details.

Most interesting among the above mentioned Amphipoda is *Haustorius arenarius*, which is also by far the largest. Although it swims and burrows forwards it is not unlike a small *Emerita*; moreover, it is often found in its greatest numbers where the waves are pounding on the shore (cf. SCHELLENBERG 1940, p. 171), just as is generally the case with *Emerita analoga*. At Haverdal beach on the coast of the Kattegatt I have found it especially plentiful just below the belt of coarse sand denoting the normal water line (the *Otoplana* zone of REMANE 1940). Similarly *Emerita* at low tide was generally found in a great concentration in and below a corresponding shelf of coarse sand near the low-water mark in the bay at the Marine Biological Station near Valparaiso.

It is difficult at present to tell whether the similarity with *Emerita analoga* also includes its feeding habits. According to DENNEL (fide SCHELLENBERG 1940, p. 172) this might be the case, for he claims that *Haustorius* is a suspension feeder, straining small detritus particles (and plankton?) from a water current caused by the rotation of the maxillae and passing through the long hairs of the mouth parts. According to REMANE (1940, p. 69), however, it is a "Sandlecker", i. e. it rotates sand grains between its mouth-parts, gnawing off any organic matter covering them. It is difficult at present to decide which of these interpretations is the most correct, for although the shape and armature of the maxillulae, maxillae and maxillipeds seem to be excellently adapted to straining, the mandibles are, nevertheless, distinctly biting.

In the case of the *Bathyporeia* species, also claimed by REMANE (l. c.) to be "Sandleckers" the structure of the mouth parts decidedly support such a view.

Like most of the burrowing Crustacea also the amphipods mentioned here are active at night, when they are to be found in numbers swimming in the water (cf. WATKIN 1939).

On the east coast of North America another Haustoriid amphipod, *Amphiporeia virginiana*, was reported by SHOEMAKER (1933) under circumstances which makes it probable that it leads a life similar to the European genera just mentioned.

I found it interesting that the antiboreal coasts of Chile south of the zone inhabited by *Emerita* also harbours a number of amphipods burrowing in the lower part of the tidal zone of sandy beaches. The species encountered under such circumstances during the Lund University Expedition to Chile all belong to the two families Oedocerotidae and Phoxocephalidae. Of Haustoriidae there were none in this zone, the southern representatives of this group being on the whole absent from the tidal area. Ecologically they are replaced by the Phoxocephalidae, and it is interesting to note that the difference between these two families, as pointed out by SCHELLENBERG (1931), is distinct in the northern hemisphere but tends to become obliterated in the south. It seems significant that series of intertidal sand samples from the lower parts of the beach collected at Coquimbo (about 30°S), Valparaiso (about 33°S), and the Talcahuano area (about 37°S) yielded no amphipods, while on a beach near Puerto Montt (41°30'S) four species were found, two Oedocerotidae (*Bathyporeiapus magellanicus*, ? *Monoculodes* sp.) and two Phoxocephalidae (*Metharpinia cornuta*, *Pontharpinia fuegiensis*). On the Punta Arenas beach (about 53°S) I found only *Monoculopsis vallentini* (Oedocerotidae), but another beach at Tierra del Fuego (about 54°30'S) was inhabited by the last-mentioned species and besides by *Pontharpinia fuegiensis* and *Metoediceros fuegiensis* (Oedocerotidae). All the three last species were recorded from beaches in the same area by SCHELLENBERG (1931). *Monoculopsis vallentini* was recorded by STEBBING (1914) from a beach on the Falkland Islands, and *Pontharpinia fuegiensis* by STEPHENSEN

(1949) from the tidal zone at Tristan da Cunha. It was also recorded by SCHELLENBERG (l. c.) from South Georgia but only from below the tidal belt. *Exoediceros fossor* (Oedocerotidae) was reported from sandy beaches in E. Australia (STEBBING 1906).

The lower parts of the sandy beaches harbour amphipods also in arctic and subarctic areas. Here as so often in cold waters a genus of the family Lysianassidae is the typical representative, in this case *Pseudalibrotus, P. littoralis* and *P. birulai* being the most common species. With respect to the substratum their range is greater than that of the intertidal Haustoriidae, for they also frequent beaches where a certain amount of clay and mud is present in the sand. Apparently, their diet is also different, for in the stomach and intestine of specimens of *P. littoralis* from N. Norway I only found a finely granulated, brownish mass, which gives the impression of finely triturated plant remains. The rather powerful mouth parts are excellently suited for such a diet but are poor in setae and bristles and certainly inadequate for straining small particles from the water. As regards their nutrition they apparently correspond rather to the burrowing Talitrids than to the Haustoriids with the difference, however, that their period of activity falls when the tide is in.

Apparently, the beaches of the cool area in the south also have a burrowing Lysianassid amphipod, *Stephensenia haematopus*. Unfortunately it has been found only once, in the gullet of an oyster-catcher shot on the west coast of Tierra del Fuego, but the structure of its limbs, to a much higher degree than those of *Pseudalibrotus*, are adapted to burrowing in sand (SCHELLENBERG 1928b, 1931).

Thus as in the case of the upper beach we have also here near the low-water mark a zone which in tropical and warm waters is inhabited by various Decapoda, some instances of which have been quoted above, while in cool and even cold areas, as far as investigated, it harbours Amphipods of the families Haustoriidae (northern hemisphere), Phoxocephalidae (especially southern hemisphere), Oedocerotidae and Lysianassidae (cold areas). It should, however, be emphasized once more that there is a strict replacement only in space. In other respects the ecological variation within this zone is considerable. To get a complete concept of the ecological interplay and the partial or complete replacement of certain forms by others not only such more or less sedentary Crustacea as the Thalassinidea of the *Calianassa* type, but also many representatives of widely different groups should be included. In this zone we find also many species, such as *Crangon crangon*, which do not belong to the beach proper but migrate inwards with the rising tide.

4. Sources of food and feeding methods

A good deal has already been said of this in connection with the distribution and habits of the individual species, and this section will only give a brief summary and underline that there is a certain vertical zonation of the main types of food and the feeding methods.

Available food:

1. Organic débris (animal and vegetable).
2. Dead and dying animals.
3. Suspension of plankton and organic detritus.
4. Diatoms and other living or dead minute organic particles on or in the sand.
5. Animals preyed upon by rapacious or ectoparasitic forms.

Of these principal sources of food the organic débris predominates on the upper beach.

Somewhat further down dead and dying animals left stranded by the tides are sought out by Ocypodids but still more by the Cirolaninae, especially when the tide is in, although the isopods often remain attached to their prey when the tide recedes. They are in many cases also facultative ectoparasites and attach themselves to the fishes which enter the zone to feed during high tide. Certain suspension feeders (*Emerita*) also enter this zone at high tide, seeking out the level of the greatest water movement.

Further down we enter a zone where the danger of desiccation has diminished to such an extent as to permit the development of a microfauna and microflora in the surface strata of the sand. These sources of nutrition become utilized by the "Sandlecker" type (*Haustorius*, *Bathyporeia*, probably the beach-dwelling Phoxocephalids of the southern hemisphere). In this area, exposed to the air only during comparatively short periods, suspension feeders and deposit feeders find more favourable conditions and become resident. The comparatively rich fauna of these levels provides good opportunities for predators and scavengers ("Gross-Stückräuber").

5. Limiting factors

To a very large extent the limiting factors are the same as those encountered on rocky shores, about which an extensive literature exists (cf. e. g. surveys by Gislén 1943, 1944 and Stephenson 1943 et. al.). Some of those which seem to have a direct bearing on the composition and zonation of the fauna are summarized below, though it should be borne in mind that certain other factors may exist, especially biotic ones, the influence of which are at present liable to escape our notice.

1. Ice action. The effect of ice action on arctic and antarctic shores is so great as to completely prevent a marine littoral fauna from establishing itself.

2. Air temperature. Desiccation. Low air temperature is most probably the factor which limits the penetration of burrowing Talitrids both towards the north and the south. How it works is difficult to say, but probably it is through an abbreviation of the yearly period of activity below an endurable minimum. On Swedish beaches the activity of burrowing Talitrids generally seems to come to an end in October and start again during April or early in May. During the winter they lie buried deep in the sand.

The question of the bearing of temperature limits on the distribution of Ocypodid crabs is much more complicated; a shortening of the activity period may contribute to the northern and southern limits of their range, but it is quite as likely that water temperature and other factors influencing the life of their pelagic offspring are of greater importance.

High air temperatures combined with strong insolation may expose small Crustacea, such as Talitrids and other amphipods and isopods and especially their young, to a great risk of desiccation.When present on tropical shores the Talitrids occur further downwards on the beach, below the zone inhabited by the better protected Ocypodids. The danger of desiccation forces the recently hatched young of Talitrids further downwards on the beach than the adults also on temperate shores.

3. Temperature of water. The species of *Pseudalitrotus* are essentially arctic forms which do not thrive on temperate coasts—in Northern Norway they do not even penetrate nearly as far southwards as to the Arctic Circle. Whether any competitive factor in the border areas contributes to the limitation of their range cannot be decided at present.

It was already mentioned that the water temperature in warm and temperate regions exerts a considerable influence on the general composition of the sandy beach fauna. The cool and temperate areas are largely occupied by amphipods, the warm-temperate and tropical ones by Decapoda. It was also suggested that this fact is connected with the breeding biology of the two groups, the brood protection of small litters as found in the Amphipoda being advantageous in cool waters and adjusted to the food production there, while the large quantities of pelagic offspring typical of Decapods (particulary crabs) is favourable in warm waters. This corresponds perfectly to conditions found in other groups.

4. Food conditions. Lack of suitable food will hardly ever be a limiting factor to the fauna on the sandy beaches, for generally nourishment seems to be present in adequate amounts, at least if algae grow anywhere near the beaches. When e. g. in the Arctic and Antarctic a marine sandy beach fauna is lacking this is due to other factors especially ice and low air temperature. In the preceding paragraph attention was drawn to the connection between food

production in the sea and the type of reproduction which is reflected in the composition of the fauna.

5. Interspecific competition. As always this question is so complicated that any definite conclusions and any indisputable instances are difficult to find. I should believe it is safe to say that where interspecific competition appears to limit the distribution of a species it is at least very often acting in connection with environmental factors tending to favour one and hamper the other of the competitors.

6. Substratum. The nature and composition of the substratum is of very great importance to the fauna of the sand. As has repeatedly been stressed above the present survey takes into account only beaches of more and less pure sand, i. e. such with a low content of organic substances and a low percentage of very fine particles.

As has been shown by various investigators the particle size composition of the sand is very important to animals living in the sea. The same apparently applies to the beach animals dealt with in the present survey. Thus the present writer (1945) demonstrated that on the Swedish coast *Talitrus saltator* avoids certain beaches with fine sand where *Talorchestia deshayesii* still occurs in great numbers. Similar adaptations to the mechanical composition of the sand are certainly to be found also among other species. If small minerogenic particles are added to such an extent that the general structure of the beach begins to approach that of clay, a sandy beach fauna of the type dealt with here no longer exists on it. *Pseudalibrotus litoralis* constitutes an exception for it thrives also on beaches with a considerable admixture of clay.

A profound influence is excersised also by an admixture of organic matter. On beaches where plenty of seaweed is imbedded in the sand a true sand fauna generally does not exist, and in the lower reaches of a silty beach the true sand forms gradually become replaced by more mud-loving forms. On north European shores e. g. the appearance of the Polychaets *Arenicola marina* and *Nereis diversicolor* indicates that the sand is no longer pure, and similarly the occurrence of the Thalassinid genus *Callianassa* as a rule points in the same direction.

The accumulation of organic matter in the sand is in itself dependent on various factors—e. g. the degree of wave exposure, the prevailing currents, the inclination of the beach, the coarseness of the sand itself, the content of detritus of the water and the amount of vegetation in the vicinity. Like the accumulation of organic detritus on growing algae it is thus a complicated matter. Wave action is, perhaps, the most important factor but by no means omnipotent. On several Chilenian beaches where the upper beach slopes steeply and the lower beach is more flat, there is just below the zone of inflection a narrow belt of *Calianassa* burrows. This naturally is a zone very likely to become somewhat silty.

7. Wave action. Certain aspects of the influence of wave action were mentioned in the section dealing with the sediment. On the whole a fairly great exposure to wave action is absolutely necessary to keep the beach sufficiently clean for a true sand fauna to thrive on it. A great amount of wave action also directly favours such forms as *Emerita* which, when feeding, constantly seek out the zone with the greatest water movement.

General conclusions

Professor and Mrs. STEPHENSON (1948, pp. 7 ff.) demonstrated that the zonation on rocky shores all over the world can probably in the ultimate analysis be reduced to three belts, viz.:

1. The Littorina zone ("subterrestrial fringe").
2. The Balanoid zone ("midlittoral zone").
3. The sublittoral fringe.

It appears to me to be a matter of profound interest that the sandy beaches obviously lend themselves to a similar tripartition. In fact, conditions are perhaps even more schematical there, owing to the much greater poverty of the fauna. On the other hand, the sandy beaches have the disadvantage of providing less sessile forms (as the barnacles and sea-weeds) or slow-moving species (as the littorinas). The fast-running or swimming crustacea, which alone among marine animals are at home in the higher reaches of the sandy shores, extend their foraging excursions, the timing of which is regulated by the rhythm of day and night and the pulsation of the tides, to cover almost the whole of the beach. But if we use for our comparisons the areas where the respective species rest, the zonation stands out clearly enough.

If using the terms suggested above, the sandy shores present the following zones, viz.:

1. The subterrestrial fringe, ("Talitrid-Ocypodid belt") which, like the same zone on the rocky shores, is devoid of a marine fauna in the true arctic and antarctic areas. In temperate regions it harbours mainly Talitrid amphipods, in warm areas Ocypodid crabs.

2. For the midlittoral zone ("Cirolana belt"), it is more difficult to give a universal definition. It would seem probable that its most characteristic elements are the Cirolaninae and that this can be universally applied in warm and temperate areas, but there are certain complications. Thus on the Swedish west coast, where there are no tides, the midlittoral zone merges with the sublittoral fringe and the Cirolanid isopod of the region, *Eurydice pulchra*, occurs

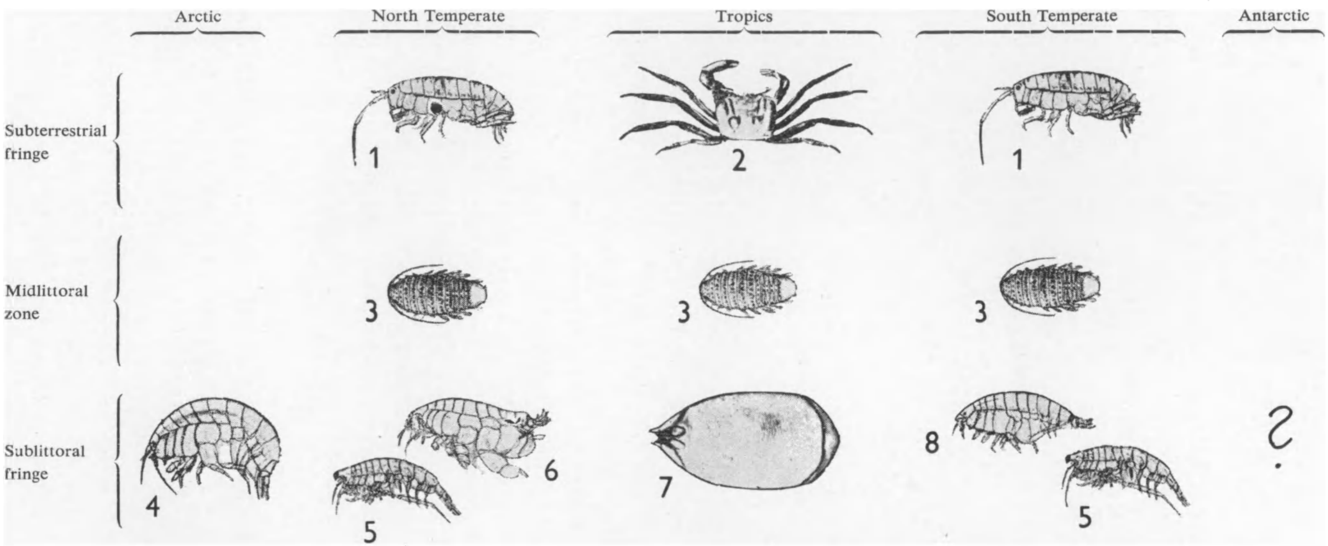


Fig. 8. Generalized diagram showing zonation of sandy beach Crustacea in main climatic zones of the earth. 1 Talitrid amphipods, 2 Ocypodid crabs, 3 Cirolanid isopods, 4 Lysianassid amphipods (genus *Pseudalibrotus*), 5 Oedocerotid amphipods, 6 Haustoriid amphipods, 7 Hippid crabs, 8 Phoxocephalid amphipods. Further discussion in text.

together with the Haustoriid amphipods. On the British coasts, too, *E. pulchra* occurs together with some of the amphipods. Within the genus *Bathyporeia* there are considerable differences in the range on the beach, and especially *B. pilosa*, which in Britain occurs "above the high-water mark of neap spring tides" (WATKIN 1938, p. 231), definitely has part of its normal range in the midlittoral zone. The same applies to a certain extent to *Haustorius arenarius*, which is often very common just below the *Otoplana* zone on Swedish beaches, and inhabits "the upper half of the intertidal area" (ELMHIRST 1931, p. 171) in Britain. Thus on the tide-less shores of Sweden the "midlittoral zone" on sandy beaches is normally covered by water, which is but natural from an ecological point of view, since it is inhabited by animals which are active when covered with water. Similarly on Swedish coasts without great wave exposure the *Balanus*-belt lies around the average water line. With changing winds and barometric pressure great parts of the "midlittoral zone" are occasionally laid bare also on tide-less coasts, often for considerable periods.

In Chile the Oedocerotid and Phoxocephalid amphipods ecologically replacing the Haustoriidae are generally more strictly confined to the sublittoral fringe, as are also certain species of *Bathyporeia* and *Urothoë* in NW Europe, where also *Pontocrates norvegius* belongs to the same category. Thus in Chile between 30° and 43°S the local Cirolanid isopod is the only typical "midlittoral" form on sandy shores. The same was the case on the beach investigated in Venezuela and apparently conforms with the observations of the American Museum Congo Expedition 1909–1915.

3. The sublittoral fringe. As on the rocky shores the sublittoral fringe of sandy beaches harbours a great variety of animals. The Crustacea no longer dominate to the same extent as further upwards, but they still play a very considerable part, the more pronounced the cleaner the sand. In cold and cold temperate areas amphipods (*Pseudalibrotus*, Haustoriidae, Phoxocephalidae and Oedocerotidae) dominate, towards warmer waters they are gradually becoming replaced by Decapod Crustacea, above all of the tribus Hippidea.

In the diagram Fig. 8 an attempt is made to give a survey of the outlines of the zonation on sandy beaches in different climatic zones, based on a combination of literature records and the writer's own observations. Conditions in the southern temperate regions as depicted here represent almost exclusively observations made by the writer in Chile, it being practically impossible to find ecological information in other comparable areas.

Summary

1. The fauna of non-microscopic Crustacea inhabiting a number of sandy beaches in Europe and South America is described.

2. The most important larger Crustacea inhabiting different levels on pure sandy beaches in different climatic zones are surveyed. It is demonstrated that the upper beach is largely inhabited by Talitrid amphipods in temperate zones, by Ocypodid crabs in hot areas. Further downwards Cirolanid isopods are often abundant, and it would seem as if this was an universal phenomenon. Certain aquatic amphipods also extend their range fairly high up on the beach. In the lower reaches of the beach numerous animal groups are represented. In temperate and cold areas Amphipoda are the dominating Crustacea, and in the warm areas Decapoda (Hippidea etc.).

3. It is suggested that the predominance of Decapoda in warm waters and of Amphipoda in cold and cool waters is due to differences in the mode of reproduction typical of the two groups.

4. The different factors influencing the distribution of Crustacea on the sandy beaches are surveyed.

5. A zonation seems to occur which is comparable with that observed on rocky shores by STEPHENSON and it is suggested that the macrofauna of the sand, too, can be sub-divided into three horizontal belts, viz.:

a. The subterrestrial fringe ("Talitrid-Ocypodid belt").
b. The midlittoral zone ("Cirolana belt").
c. The sublittoral fringe (Rich and varied fauna).

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