The Supra-Littoral Fringe of New Zealand Sand Beaches

By R. J. MacIntyre,

Division of Fisheries and Oceanography, C.S.I.R.O., Cronulla, Australia.

Abstract

The supra-littoral fringe of sand beaches is described and compared with that of other beach types. This fauna is divided into two groups, *modifiers* and *non-modifiers*: these are air breathers and are separated on the one hand from littoral water breathers and on the other from terrestrial forms which are not tied to the sea. The key environmental factors, substrate, temperature, food, water and salinity are considered in relation to the effect which they exert on the restricted fauna.

Introduction

A sharp line separates the land plants of the sand dunes from a belt of dry, flowing, and often exceedingly hot sand which gives way, at the last tide's debris line, to a damp clean-swept beach, at first soft and spongy, but becoming as hard as a pavement before the wet wave-rippled lower beach joins the water at low tide. Across this narrow beach lies a gradient of conditions ranging from terrestrial to marine, and with it a faunal assemblage running from species wholly dependent on the land, through others relying on both media for one or several of their life processes, to true marine species.

Above the intertidal or littoral region lies the supra-littoral zone. It is both extensive and diffuse, so there is little gained by trying to define its upper margin: in this discussion it is regarded as being no more precise than the term "coastal". An animal of this zone has at least one facet of its ecology governed by the sea. The supra-littoral fringe is defined here as a strip of beach lying between a point slightly below the prevailing high tide, or limit of wave wash, and the rather sharp lower limit of land vegetation. It is unwise to attempt a more rigid definition of the lower limit on a structure as fluid and changeable as a sand beach. Fringe species are air breathers living within the fringe and depending on the sea for food at least. The gradient of environmental conditions and species composition is at its steepest here. It is convenient to subdivide the fringe into three parts. The "upper zone" adjacent to the dunes is covered with dry flowing sand through which burrowers have difficulty in penetrating, except in places where partially buried debris gives them access to the damp underlayer. They are concentrated in these areas; smaller specimens are usually excluded. The "debris zone" embraces the line of recently stranded debris and, as it does not have a deep cover of dry sand, both large and small animals are scattered in their distribution, though there is still a tendency for them to clump under debris. The "lower zone" is washed clean by each tide and is damp at the surface, so that the smaller animals are uniformly scattered throughout in shallow burrows. In calm weather these zones form a wide band, as shown in Fig. 1, but during winter storms the entire supra-littoral fringe is compressed into a very narrow strip at the base of the sand dune grasses.

Throughout the temperate regions of the world (Dahl 1952-53, Bousfield 1957 and Hurley 1959) this fringe is occupied, if not dominated, by amphipods of the family Talitridae, the only amphipod family with terrestrial tendencies: on tropical beaches they are replaced by water-breeding terrestrial crabs. Generally the genera *Talorchestia* and *Orchestoidea* occupy sand beaches, *Orchestia* lives on rock and mud and, in the Indo-Pacific Region, also has fully terrestrial species which inhabit forest litter with a third genus, *Talitrus*.

This account of the supra-littoral fringe as an ecological unit arose from a detailed study (MacIntyre 1954) of one of the dominant New Zealand species, *Talorchestia quoyana*. While the discussion centres on sand beaches, it has been necessary to digress and include comparisons with other beach types. It is hoped that this will serve to define and underline some of the important problems which are awaiting attention in this uniquely convenient field.

Substrate

The physical substrate of a beach can be conveniently classified on the basis of particle size. This method of classification corresponds with the very real division of supra-littoral animals into two major groups here called, *modifiers* and *non-modifiers*. These are, respectively, animals capable of modifying the substrate to suit their own requirements by burrowing, and those which fit passively into whatever shelter is available. The particle sizes range from rock slabs and small stones through fine gravels and sands to mud composed of silts and clays. Rock slabs, stones, and hard dry mud cannot be burrowed into by small animals which must simply seek shelter in the available crevices. Fine gravels and sands, however, can readily be burrowed by a number of species, which can thus survive on the most exposed shores. In both cases stranded organic debris is of the utmost importance.

Rocky shores composed of boulders or pebbles provide some shelter from light, heat and desiccation, but the large air spaces prevent capillary reinforcement of water from below, and there is thorough ventilation with associated drying effects. The major ameliorating factor is the mass of stranded hygroscopic kelp beneath which there is shelter and food. The upper parts of mud flats are similar to rock shores in providing little intrinsic shelter. In some moist areas burrowing staphylinid beetles do occur, but the majority of animals is found in mud cracks, or more commonly, under stranded debris.

The materials intermediate in grain size between rocks and mud retain their plasticity: they can be moulded to the requirements of small animals. Air spaces are small, therefore air circulation is restricted and capillarity is increased, with the result that a fairly uniform region, with respect to temperature, water, light and heat, lies a short distance below the surface.

Shingle particles (say 2–20mm in diameter) are relatively large for a small animal to move, and close packing excludes all but the smallest non-modifying species, so few animals live in shingle. Exceptions are provided by the small but herculean amphipod *Talorchestia cookii,* which is a true modifier capable of literally burrowing through shingle, and the non-modifying amphipod *Orchestia chiliensis* which sometimes insinuates itself between the coarser shingle particles, but it is most abundant under stranded weed.

Sand beaches have several modifier species burrowing in the supra-littoral fringe. Although the sand is extremely loosely packed with a large volume of air in minute spaces its compactness excludes non-modifiers. Ventilation is less and capillarity is greater than in shingle beaches, but again, algal debris with its hygroscopic properties alters local conditions, not only with respect to water and temperature, but also by providing adhesive residues which may contribute to the peculiarly low aggregate density of supra-littoral sand.

Grain size in sands was shown by Dahl (1946) to define the distribution of two European talitrid amphipods and in the present investigation it was found to have a clear-cut effect on the distribution limits of *Orchestia* and two species of *Talorchestia.* Two factors determine the size-distribution of beach sand: the upper size limit of the particles is determined by the source of supply of the material, and the lower limit depends on the intensity of sorting and removal of fine lighter material by wave action.

Most of the ocean beaches examined had sand grains between 0.3 to 0.1mm in diameter, but an examination of Canterbury beaches showed some interesting variations, not only between shingle, sand and mud but between various types of sand. Banks Peninsula is a mass of basaltic rock which joins the alluvial plain of Canterbury, but its soil mantle is largely composed of loess, of which only 25% is fine sand (Alley 1948). As its bays are isolated by deep water from sediment sources to the north and south the beaches are composed of local materials sorted out according to the degree of wave exposure. The following four beach types are recognisable.

1. Short inlets with severe wave action where the shore is composed of basaltic stones and boulders.

2. Longer inlets with strong wave action and rather coarse and dense (s.g. 3.30) black basaltic sand (e.g., Taylor's Mistake and Gough's Bay).

3. Long and moderately stable inlets with quartz sand derived from the coarser fraction of the local loess soil (e.g., Okain's Bay and Peraki).

4. Very long inlets where ocean waves have almost no effect and extensive mud flats are found. Here there is sometimes a secondary shell sand derived from the shells of mud dwelling molluscs (e.g., Lyttelton and Akaroa).

The extensive beaches north and south of the peninsula are different from one another. On the exposed southern side the Rakaia River carries all particles up to shingle sizes to the sea, and strong wave action leaves a shingle beach: at Taumutu wave action is so strong that the supra-littoral fringe fauna is eliminated. Northwards, in the lee of the peninsula, the Waimakariri River does not carry shingle to its mouth and the beach is sandy. Further north again at Leithfield and Amberley sand is replaced by shingle, and *Talorchestia quoyana* is replaced by *T. cookii* (Fig. 2). The results of sieve analysis of beach material is shown in Fig. 3, where it is seen that quartz sands generally lie within group 5 (0.3–0.1mm) while the mode of shingle beaches is in group 1 (> 2mm); the two exposed basaltic sand beaches are slightly coarser. Finer analysis shows that the loess sands contain much more fine material than do the river sands.

The compressible spongy structure of sand in the supra-littoral fringe is most important to the life of burrowing species. This is due to the peculiar property of sand which causes it to have a minimum bulk density when it is partially saturated with water. In this condition sand grains stick together, leaving large numbers of air spaces, whereas completely dry sand and water-saturated sand grains tend to pack more closely.

To illustrate this effect a traverse was made of the sand spit enclosing the estuary of the Avon and Heathcote Rivers at New Brighton. Fig. 4 shows an analysis of the sand structure in terms of solids, water, and air: in the same traverse the salinity of the soil moisture was measured. Samples of undisturbed sand were taken with a thin-walled steel tube of one square decimetre cross-

sectional area which was inserted to a depth of two decimetres. The samples were weighed immediately, dried to constant weight in the laboratory at 120° C. and reweighed. The specific gravity of the quartz sand was determined at 2.65 in a specific gravity bottle. From the values of wet volume, wet weight, dry weight and specific gravity the method of Taylor (1948) was used to obtain the parameters bulk density, porosity, void ratio and degree of saturation shown in Fig. 5.

Void ratios and porosity do not vary greatly, but the bulk densities show clear minima in both supra-littoral fringes, and the degree to which the existing voids are filled with water varies from 10% towards 100% in both directions as the low tide mark is approached. The regions of high saturation correspond with very firm sand where footprints leave a very slight impression. On the estuarine beach this corresponds with the upper limit of crab burrows, while on the ocean beach this is the rather barren intermediate zone which separates the wet marine zone with its abundant water breathing fauna from the air breathing fauna of the supra-littoral fringe. In the centre of the fringe, the debris zone has minimum saturation and maximum compressibility so that footprints are deep and burrowing is easy.

In warmer climates where species are more numerous Pearse (1950) has suggested that there is a continuous range of animals from the upper littoral zone to the dry land. In New Zealand, however, especially on sand beaches where there are few species, there is a sharp discontinuity in the intermediate zone between air and water breathers.

Temperature

Conditions in the sea are much more conservative or stable than those in the air. Below the surface of a damp soil, fluctuations are of an intermediate order. In summer the surface of dry sand presents a very special and very lethal environment which was measured at up to 55° C. and which prohibits the life of all but the specialised deep-burrowing fauna. Below the surface the moist, spongy sand opposes temperature change, both by insulation and by evaporation. At a standard depth of six inches in the debris zone the maximum recording was 23° C. The 32° temperature difference over this small depth is reduced to zero in winter when the temperatures converge: in fact there are times when the underlying sand is appreciably warmer than the surface. Comparison with figures from Knox (1953) show the maximum diurnal and mean seasonal changes for sea, sand, and air in the Christchurch area.

TEMPERATURE RANGES IN °C.

	Sea*	Sand	Air*
Maximum diurnal change	5	9	18
Mean seasonal change	6	9	12

* Knox (1953).

Unlike the Woods Hole region described by Smallwood (1903) and Edwards and Irving (1943) New Zealand sand beaches do not undergo a marked winter freeze and *Talorchestia* does not hibernate, though it is less active in winter.

Away from the shore the sea modifies coastal climate. In an extended sense those land species, particularly plants, in which distribution depends on this moderated costal climate, might be regarded as supra-littoral.

Food

Scavengers and carnivores comprise the fauna of the fringe. Almost any organic material is eaten: dead birds, horse manure, fish and insects are rapidly consumed and at night the foam lines or swash marks are foraged for the small stranded planktonic animals which they contain. However the diet of the scavengers is governed by supply, so that by far the greater part of it consists of plant matter in the form of stranded seaweed, particularly the kelps *Macrocystis* and *Durvillea*. This algal material is most important to the fauna. The piles of hygroscopic weed provide moist sheltered oases which teem with animals sheltering from the lethal temperatures of the sand surface, while the decay products provide more hygrophilic, foam-forming, adhesive material which no doubt contributes to the peculiarly spongy sand structure which is so vital to these burrowing animals. The chemical composition of some algal species from various sources is listed in Fig. 6. The alginic acid composition is important for this substance can absorb 200 to 300% of its weight of water (Chapman 1950). As food this material is low in protein (2%) and fat (1%), but it is high in free water (80%) and nitrogen-free compounds (16%) which yield water on oxidation. This high water/nitrogen ratio is important to those animals which lack the terrestrial excretory system of the insects. In this highly saline environment it is difficult for the crustaceans in particular to find sufficient water for their excretion, and it has been suggested by Dresel and Moyle (1950) that terrestrial crustaceans have adapted themselves by lowering their nitrogen metabolism.

Water

The environment below the surface of a sand beach is similar to that of the forest leaf-mould which has protected the unspecialised primitive insects for so long: both are damp. They are intermediate between aquatic and truly terrestrial environments, for although the inhabitants are air breathers, and are not immersed in water, they are surrounded by an atmosphere more or less saturated with water vapour which almost eliminates evaporative loss of body water.

The relative humidity, measured on a hair hygrometer, is always 95% to 100% below the surface, whereas on the surface it varies widely, like temperature, from less than 40% to 70% on fine days up to saturation when dew is forming at night.

The sources of water available to the beach fauna are: 1, the sea; 2, rivers and streamlets; 3, rainfall and dew; 4, groundwater; and 5, food. Whenever the tide covers the beach, sea water with its prevailing salinity is by far the most important influence; this, combined with the effect of evaporation, produces hypersaline water. For *Talorchestia*, at least, it is necessary that there is an additional source of less saline water. On the open beach away from river mouths the rainfall has no significant effect on the overall salt content of the interstitial water, but both rain and dew serve to lower the salt content of the stranded hygroscopic seaweed which serves as food. As has already been mentioned, this also provides a ready source of carbohydrate for conversion to water.

The crustacean element of the fauna is more susceptible to desiccation than the almost impervious insects (Edney 1954), but their habits of burrowing and nocturnal activity protect them, while the ability to lose water rapidly can be a positive advantage during brief periods of exposure to such extremely high temperatures as occur on the sand surface. Provided the humidity is not high the evaporative loss of water prevents thermal death over short periods (Edney 1951).

Salinity

The sources of water for supra-littoral sand species and its loss have been discussed. One most important feature of the film of moisture which coats the grains of the spongy sand is its content of dissolved salts, particularly sodium chloride. To obtain this value samples were first weighed and dried to obtain the water content, then the salts were redissolved in a known volume of water and determined by Harvey's (1928) short silver nitrate titration. This value, together with the determined water content, gives the salinity of the moisture.

The salinity profile of the sand spit enclosing the estuary at New Brighton, Christchurch, shown in Fig. 4, reveals drastic fluctuation of salinity in the supra-littoral fringe. Open ocean water has a salinity of about 35‰ (parts per thousand) but the onshore water in this area usually varies between 30‰ and 33‰. Within the estuary there is a complicated mass of mixing waters of various salinities. Bruce (1953) gives figures during a tidal cycle at the South Brighton bridge where the salinities range from zero to 24‰ and average 10‰.

The samples were as follows:

A1. The ocean dune face amongst the land plants and above the maximum tide level.

A2. The "Debris Zone" above the preceding high tide.

A3. The "Lower Zone" which had been swept clean by the preceding tide.

A4. The hard-packed and rather barren "Intermediate Zone" which separates the wet marine flat from the spongy supra-littoral fringe.

B. This single sample represents the stabilised centre of the spit where several grasses thrive.

C1. The narrow sandy estuarine supra-littoral fringe.
C2 and C3. The estuarine Flat.

At B. and at A1. the salinity is low because the only source of salt is the wind-blown spray which is diluted by rainfall. The evaporative increase at A2, which led to a value equal to twice that of the local sea water, could be much higher in hot weather if the tide did not cover the area for several days. A3. approximates the value of the sea, but A4. appeared low until it was found to lie at the level where the local water table intersected the beach. On the estuarine side at C1. the salinity rose but no peak was detected, while the values at C2. and C3. rose towards the estuarine mean. An explanation of the lack of an estuarine peak would require detailed study: it may be that during the period of high tide this area receives surface water of lower-than-average salinity.

On an extensive scale this pattern is repeated with highly saline sands (30‰ or more) on ocean beaches and less saline sands (24‰–0‰) in estuaries and at river mouths, or even where tiny streams cross the beach. These two habitats house the two common species of *Talorchestia*. Even in small areas, wherever there is a patch of less saline sand the smaller *T. telluris* replaces *T. quoyana*. (See Fig. 7.)

Fauna

It is both realistic and convenient to divide the fauna into "modifiers" and "non-modifiers": species which construct burrows and those which hide where they can.

1. Modifiers

These largely constitute the fauna of sand and shingle beaches where natural shelter is scarce and where the dangers of desiccation and predation by birds are high.

The Genus Talorchestia

The first and most prominent species in this group is the common sandhopper, the amphipod *Talorchestia quoyana*. Its habitat is oceanic sand beaches throughout New Zealand from Spirits Bay in the north to Oreti Beach in the south. It is tied to the sea by its requirement for salt, and to the sand by its need and ability to burrow to a moderate environment saturated with water vapour. The giant kelp *Macrocystis* is the main item of its diet, but it is quite omnivorous and also eats dead birds, boot laces and live insects. *Talorchestia* species differ from species of the closely related talitrid genus *Orchestia*, which move through forest litter or piles of rotting seaweed by shuffling in an almost random manner on their sides. To species of the bare open sand beach, the capacity to recognise direction and move rapidly in a linear fashion from food to safety is of the utmost importance: it is not surprising therefore to find that a displaced *Talorchestia* rapidly moves up or down the beach to the soft sand by a close approximation of the shortest possible route, in a linear series of leaps. The animal invariably lands back to front and turns through a precise 180° before proceeding to the next leap.

T. telluris differs from *T. quoyana* in one respect: it can tolerate lowered salinity, so that this small species occurs where *T. quoyana* is absent. It can be found in sand, sometimes in remarkably small patches, wherever a stream or river

cuts through a sand beach. It occurs most extensively in lagoons and behind sand spits where rivers meet the sea.

T. cookii is a much more robust species; it is a powerfully rounded form which lives on oceanic beaches, but differs from *T. quoyana* in occupying beaches composed of coarse sand and shingle.

A similar large species, *T. tumida*, burrows inland among sand dunes beyond the zone of *T. quoyana*. Both these latter species are restricted in their distribution to the southern part of the South Island of New Zealand.

On the Chatham Islands the genus *Talorchestia* has evolved to produce different species to fill the available niches. There are no rivers, and there are no shingle beaches although some of the sands are rather coarse, so the shingle-hopper niche and the estuarine sand-hopper niche are absent. The oceanic sand-hopper is *T. chathamensis*, and the sand dune-hopper is *T. kirki*.

The niches occupied by the New Zealand species of *Talorchestia* can be summarised as follows:

T. quoyana.   Oceanic sand hopper.

T. telluris.   Estuarine sand hopper.

T. chathamensis.   Oceanic sand hopper (Chatham Islands).

T. cookii.   Oceanic shingle hopper.

T. tumida.   Sand dune hopper.

T. kirki.   Sand dune hopper (Chatham Islands).

There remain two species listed by Hurley (1956) which were not encountered during the present investigation: *T. dentata* from Kapiti Island, and *T. spadix*, which was sought but not found near the mouth of the Waimakariri River.

Scyphax ornatus is a very large isopod which burrows with *T. quoyana* in the debris zone constructing a truly cylindrical vertical shaft of 20–30cm depth: this can be readily distinguished from the precisely oval burrow of the amphipod which is usually blocked with spoil. The young isopods live further down the beach in the wet sand of the lower zone where they may be seen active during the day, in sharp contrast to the adults, which are nocturnal scavengers: these young animals are readily confused with the adults of another isopod *Actoecia euchroa*, which occupies the same habitat in different areas, but the two have not been found to co-exist. The distribution of *S. ornatus* covers the North Island and the north-west coast of the South Island.

Actoecia euchroa is a very small isopod which makes shallow burrows in the lower zone where the sand is kept moist by each high tide: this fact together with its very small size enable the species to remain active during the day despite the heat of the sun and the watchful eyes of shore birds. Generally *Actoecia* is present where *Scyphax* is absent, but one exception was found at Raglan, where *Scyphax* was collected on the ocean side of a spit while *Actoecia* occupied the inlet side. Apart from this occurrence *Actoecia* was found from the east round to the south-west coast of the South Island, but was not found in the north-west or in the North Island, which territories are so very thoroughly occupied by *Scyphax* and the burrowing beetle *Chaerodes*.

Chaerodes trachyscelides is most abundant on some beaches: sometimes it is as numerous as *Talorchestia*, with which it burrows in the sand. It is distributed,

like *Scyphax*, in the North Island and the north-west coast of the South Island: its colour varies from yellow on the golden sand at Waimarama to dark brown on the ironsand at New Plymouth. This beetle has powerful digging limbs, but no wings; there is an air space under the elytra which are lightly fused together. The mouth parts are generalised and the gut contents indicate a generalised diet like that of *T. quoyana*. There is some doubt about the systematics of the genus. Hudson (1934) says that *C. trachyscelides* occurs in the North Island, while in the South Island its place "Seems to be taken by the very similar *C. concolour*". He also mentions the smaller *C. laetus* as occurring in the far north. The present work showed *C. trachyscelides* to be distributed through the North Island and the north-west coast of the South Island: there was an exception on the Otago Peninsula, where a very small and probably separate species was found. Conversely a single sample from Waimarama, Hawkes Bay, when compared with specimens in the Canterbury Museum, showed forms corresponding with both *C. trachyscelides* and *C. laetus*. It is clear that here, as with many other species, there is a need for a systematic examination of material from all parts of the country.

Geophilus xylophagus

This small centipede is found throughout New Zealand in the upper zone of both ocean and estuarine beaches as well as among the intervening sand dunes. Despite its specific name, there is no indication that this species is anything but carnivorous; there are many young amphipods and isopods to provide its food. In fact a recent study on a similar littoral geophilomorph in Britain (Lewis 1961) shows it to be a sucking carnivore. See Archey 1936.

Anabarhynchus bilineatus

The adults of this robber fly species are not a conspicuous element of the beach fauna, though they have been taken in copulation in the sand dunes during summer. The larva, however, is an unusual and most striking component of most beach collections. It reaches about 40mm in length and is an exception among the Diptera in having twenty instead of the usual sixteen body segments. On segments one and seventeen there are pairs of protracted stigmata which join two great longitudinal trunk tracheae. Examination of gut contents did not reveal the nature of its diet, but Hudson (1950) considers that it is "almost certainly carnivorous". The most striking feature of the larva is the speed with which it moves and burrows.

Pericoptus

Both the larvae and adults of two species of this large nocturnal beetle are found in the sand of the upper beach and the dunes of both North and South Island beaches. The adults reach 25mm and the larvae 50mm in length. The larvae feed on dead vegetable matter. A detailed account of these species, *P. truncatus* and *P. punctatus* has been given by Dale (1956). *P. truncatus* is a beach species: its distribution is limited to beaches, particularly in areas where driftwood is abundant, and it is more tolerant of saline conditions than *P. punctatus* which is not restricted to the coast and also occurs inland where sandy soil is available.

2. Non-modifiers

By definition these forms cannot make their own shelter, so they are not conspicuous elements of sand beach faunas, except in areas of mixed rock and sand or in very large and stable deposits of plant debris.

Orchestia chiliensis

Just as *Talorchestia quoyana* is the most obvious and abundant animal on the supra-littoral fringe of a sand beach, so orange-brown masses of *O. chiliensis*, a closely related talitrid, dominate the scavenging fauna on rock and mud shores in both oceanic and estuarine conditions. *Paviour-Smith* (1956) describes it in salt marsh. It is potentially amphibious, being able to tolerate submersion in sea water for at least 90 hours and in 20% sea water for 28 to 40 hours. This genus has retained the typical lateral flattening of aquatic amphipods with the result that movement on land appears awkward. There are three forms of locomotion: in water the body is extended and the pleopods are used for swimming while on land the peraeopods are used for slow and cumbersome walking, but a rapid though erratic form of emergency locomotion is achieved by abdominal flicking. In the Indo-Pacific Region *Orchestia* has evolved to occupy litter niches ranging from semi-marine forms living in rotting seaweed to fully terrestrial forms living away from water in forest litter. Here shelter is profuse and the environment is more uniform than that of a sand beach, so that rapid hopping over long distances is not important.

O. chiliensis could be thought of as a stem-type from which the other members of the genus diverged in the move to terrestrial conditions. Its ecology corresponds almost exactly with that of the salt-marsh species *O. palustris* described from North America by Smallwood (1905), and it is also similar to European species which are described by British authors as "Shore Hoppers" to distinguish them from *Talorchestia* species which occupy the world-wide role of "Sand Hoppers". See Hurley 1957.

Ligia novaezelandiae

This large, swift-running isopod is restricted to rocky shores, and does not extend to mud flats. Unlike *Orchestia* this species does not survive submersion in sea water at any salinity for more than three hours, so that it is truly restricted to the shore. It is active at night, but like its European counterpart *L. oceanica* (Edney 1951, 1952 and 1953) it is sometimes seen on the surface of stones during extremely hot weather. This habit allows the animal to lower its body temperature by water loss, for, while the air under the stones may be cooler, it is usually saturated with moisture so that water loss by evaporation is impossible. See Hurley 1950.

Cyclograpsus whitei

Richardson (1949) lists two species of this crab: *C. lavauxi* from the lower tidal zone of the rocky shore, and *C. whitei* from the upper part. On the shores examined, particularly round Banks Peninsula, the latter species was abundant above high tide, while the former was not seen. This rather terrestrial crab lives for 3 or 4 weeks in a damp jar without food: it can survive submersion in sea water for over 90 hours, but it is less tolerant of low salinities (15–25 hours in 20% sea water) than *O. chiliensis*. In tests of high temperature tolerance at 35° C. it survived 2 to 3 hours compared with 1 hour for the smaller amphipods and isopods. See Chilton and Bennett 1928.

Porcellio scaber

The common cosmopolitan wood-louse does not belong to the beach: it is closely associated with human dwellings and has followed man in his travels. Only moderately resistant to desiccation by isopod standards, and unable to burrow for shelter, it is nevertheless, an extremely abundant and successful species. It

is mentioned here because it can be found above the supra-littoral fringe on rocky shores, and in the early morning it has been seen returning from the beach through the dunes at New Brighton, Christchurch. See Hurley 1950.

Anisolabis littorea

This large earwig is one of the few supra-littoral species which has been ecologically described (Giles 1953). It is distributed with *Ligia* on rocky shores and is not usually found on sand, but on one occasion it was found on an estuarine sand beach under heavy driftwood where it had eaten large numbers of *Talorchestia telluris*.

Coelopa Species

Kelp flies are extremely conspicuous at night on a rocky shore for they are attracted in dense swarms by lights; their larvae are no less abundant, and piles of half-rotten kelp are often seething masses of maggots. Besides the small *Coelopa littoralis* there is a larger species. Neither form is common on sand beaches at any great distance from rocky shores.

Seagulls

These are very important predators of the beach fauna. At low tide the large Black-Backed Gull *Larus dominicanus* is found at the water's edge feeding on the "Pipi" *Amphidesima subtriangulatum*, while the smaller Black, and Red-Billed Gulls probe the sand of the upper beach and watch for amphipods. A sand-hopper liberated on hard sand within 50 yards of a group of gulls rarely lasts for more than a minute.

Other Species

The list of species given covers the more obvious forms, but it is by no means comprehensive. Obviously the large microfauna in the interstices of sand grains on the wet lower beach has not been mentioned; there are large earthworms burrowing at the edge of the sand dunes; Collembola and staphylinid beetles are abundant on upper mud flats, and a machilid species is common in clay banks above rocky shores. Spiders are also present in the sand dunes.

CONCLUSION

It is hoped that this account of the supra-littoral fringe will explain some of the extremes of environment which operate to filter out all but a very narrow spectrum of animals which live out of water, and yet avoid competition from fully terrestrial species. This simple fauna, like a desert or an Arctic fauna, is ideal for the study of population numbers, for species are few and numbers are large. There is a distinct faunal association based on the plant litter cast up by the sea and running through omnivorous scavengers to a series of parasites and carnivores. The structure of this web and the detailed ecology of most of the species remain to be described.

LITERATURE

ALLEY, P. J., 1948. Loess in soil cement mixtures. *Proc. N.Z. Inst. of Engineers*, 34: 140–166.

ARCHEY, G., 1936. A revision of the New Zealand Chilopoda. *Rec. Auckland Mus.*, 2, (1): 43–70.

BACKLUND, H. O., 1945. Wrack fauna of Sweden and Finland, ecology and chorology. Opuscula entomologica supplementum, Lund.

BOUSFIELD, E. L., 1956. Distributional ecology of the terrestrial Talitridae (Crustacea: Amphipoda) of Canada. *Proc. 10th Internat. Congr. Entomology*, 1: 883–898.

BRUCE, A., 1953. A report on a biological and chemical investigation of the waters in the estuary. Presented by E. F. Scott to the Christchurch Drainage Board.

CHAPMAN, V. J., 1950. *Seaweeds and Their Uses*. London, Methven.

DAHL, E., 1946. The Amphipoda of the Sound. Part I—Terrestrial Amphipoda. Unders. over Oresund, XXIX. Lunds University, Arsskr., N.F., Avd. 2, Bd. 42, Nr. 6.
——— 1952-53. Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos* 4 (1): 1–27.

DALE, P. S., 1956. The sand scarab, *Pericoptus*. M.Sc. Thesis, Canterbury University, Christchurch, N.Z.

DRESEL, E., and MOYLE, V., 1950. Nitrogenous excretions of amphipods and isopods. *J. Exp. Biol.* 27 (2): 201–225.

EDNEY, E. B., 1951. Evaporation of water from wood lice and the millipede *Glomeris*. *J. Exp. Biol.* 28 (1): 91–115.

——— 1951. The body temperature of wood lice. *J. Exp. Biol.* 28 (3): 271–280.
——— 1952. Body temperature of arthropods. *Nature* 170: 586.
——— 1953. The temperature of wool lice in the sun. *J. Exp. Biol.* 30 (3): 331–349.
——— 1954. Wood lice and the land habitat. *Biol. Rev.* 29 (2): 185–219.

EDWARDS, G. A., and IRVING, L., 1943. The influence of season and temperature upon the oxygen consumption of the beach flea, *Talorchestia megalopthalma*. *J. Cell. Comp. Physiol.* 21: 183–189.

GILES, E. T., 1953. The biology of *Anisolabis littorea* (White). (Dermaptera: Labiduridae.) *Trans. Roy. Soc. N.Z.*, 80 (3 + 4): 383–394.

HARVEY, H. W., 1928. *Biological Chemistry of Sea Water*. Cambridge University Press.

HUDSON, G. V., 1934. *New Zealand Beetles and Their Larvae*. Ferguson and Osborn Ltd., Wellington.

——— 1950. *Fragments of New Zealand Entomology*. Ferguson and Osborn Ltd., Wellington.

HURLEY, D. E., 1950. New Zealand Terrestrial Isopods. *Tuatara*, 3 (3): 115–127.
——— 1956. Studies on the New Zealand amphipodan fauna. No. 13. Sandhoppers of the genus *Talorchestia*. *Trans. Roy. Soc. N.Z.*, 84 (2): 359–398.
——— 1957. Terrestrial and littoral amphipods of the genus *Orchestia*, family Talitridae. *Trans. Roy. Soc. N.Z.*, 85 (1): 149–199.
——— 1959. Notes on the Ecology and Environmental Adaptations of the Terrestrial Amphipoda. *Pacif. Sci.* 13 (2): 107–129.

KNOX, G., 1953. Intertidal ecology of Taylor's Mistake, Banks Peninsula. *Trans. Roy. Soc. N.Z.*, 81 (2): 189–220.

LEWIS, J. G. E., 1961. The Life History and Ecology of the Littoral Centipede *Strigamia* (*Scolioplanes*) *maritima* (Leach). *Proc. Roy. Soc. Lond.* 137 (2): 221–248.

PAVIOUR-SMITH, K., 1956. The biotic community of a salt meadow in New Zealand. *Trans. Roy. Soc. N.Z.*, 83 (3): 525–554.

PEARSE, A. S., 1950. *The Emigrations of Animals from the Sea*. The Sherwood Press, Dryden, N.Y.

MACINTYRE, R. J., 1954. A Common Sand-hopper. M.Sc. Thesis, Canterbury University, Christchurch, N.Z.

MOSS, B., and NAYLOR, M., 1954. Chemical Composition of Two New Zealand Species of *Durvillea*. *Trans. Roy. Soc. N.Z.*, 81 (4): 473–478.

SMALLWOOD, M. E., 1903. *Talorchestia longicornis*. Cold Spring Harbour Monographs, No. 1, pp. 1–27.

——— 1905. The Salt Marsh Amphipod *Orchestia pallustris*. Cold Spring Harbour Monograph No. 3, pp. 1–21.

TAYLOR, D. W., 1948. *Fundamentals of Soil Mechanics*. New York, Wiley.

R. J. McIntyre,
Div. Fisheries and Oceanography,
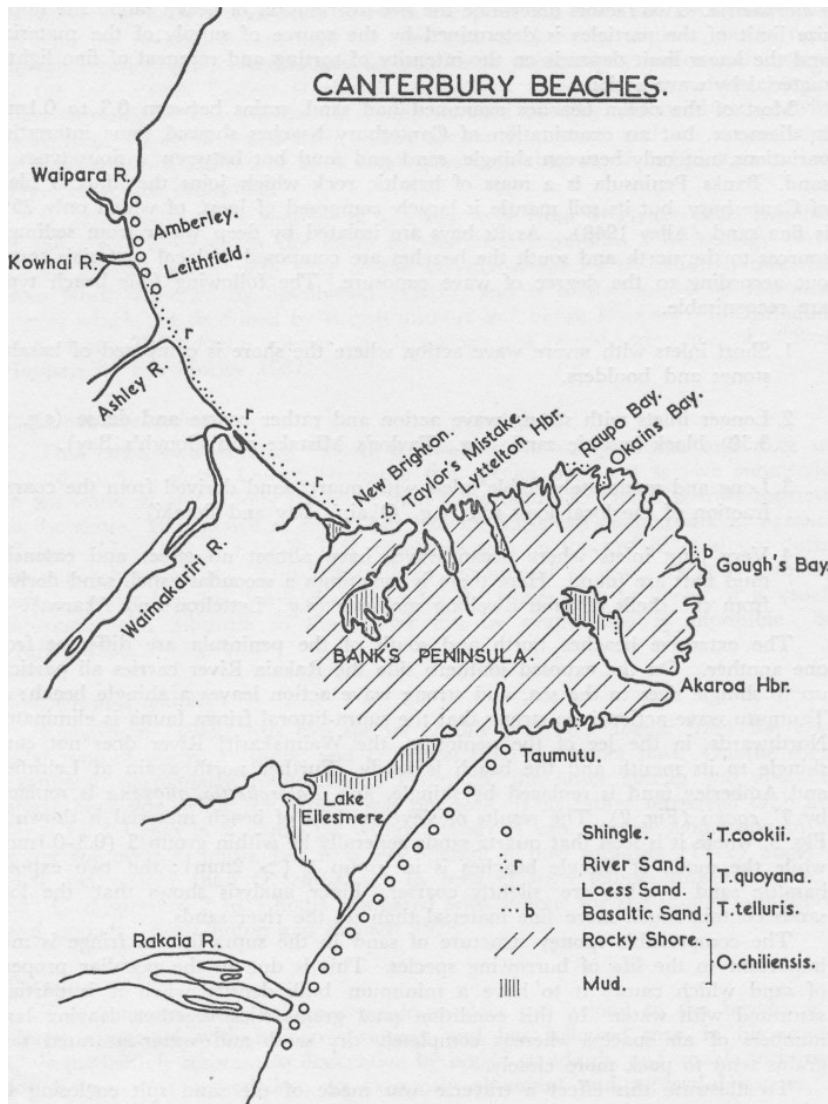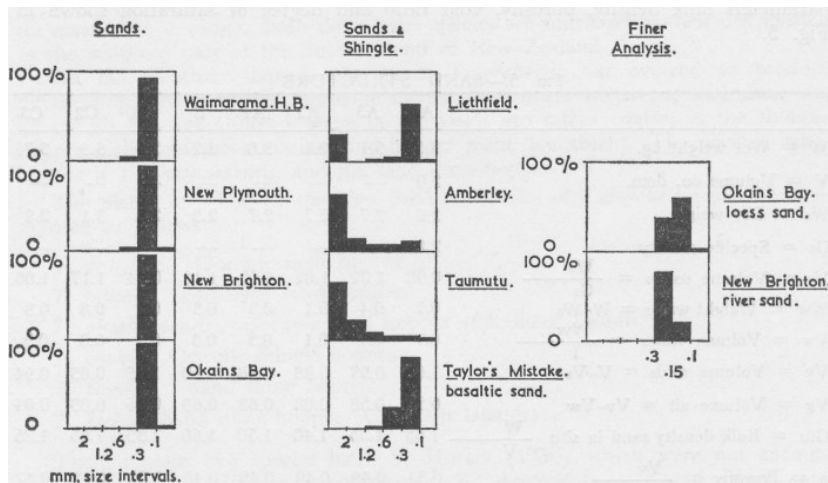C.S.I.R.O.,
Cronulla, N.S.W., Australia.

CANTERBURY BEACHES.

Fig. 2

CANTERBURY BEACHES.

FIG. 3
PARTICLE SIZE ANALYSES.
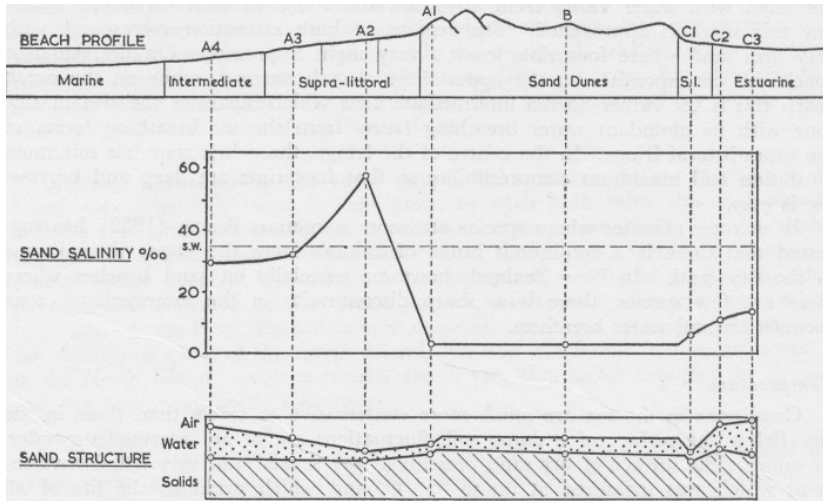

FIG. 4
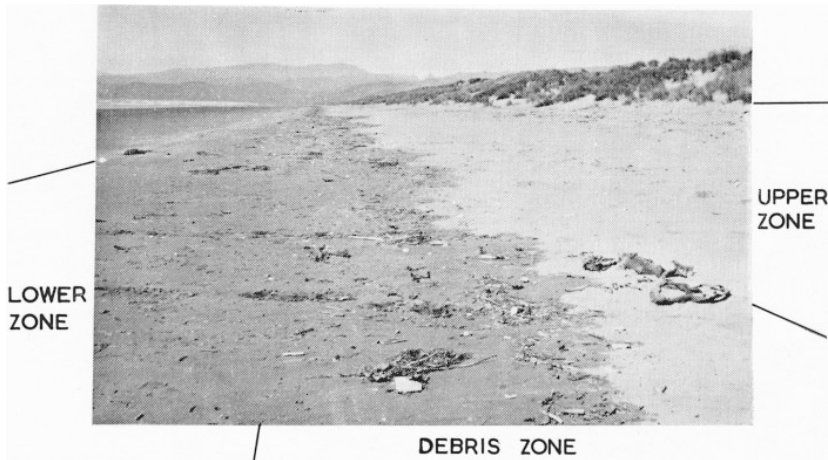# SECTION THROUGH SAND SPIT.

LOWER
ZONE

UPPER
ZONE

DEBRIS ZONE

FIG. 1.—Supra-littoral fringe at New Brighton, Christchurch. (a) View along upper, debris and lower zones. (b) Core sampling for animals of the three zones.
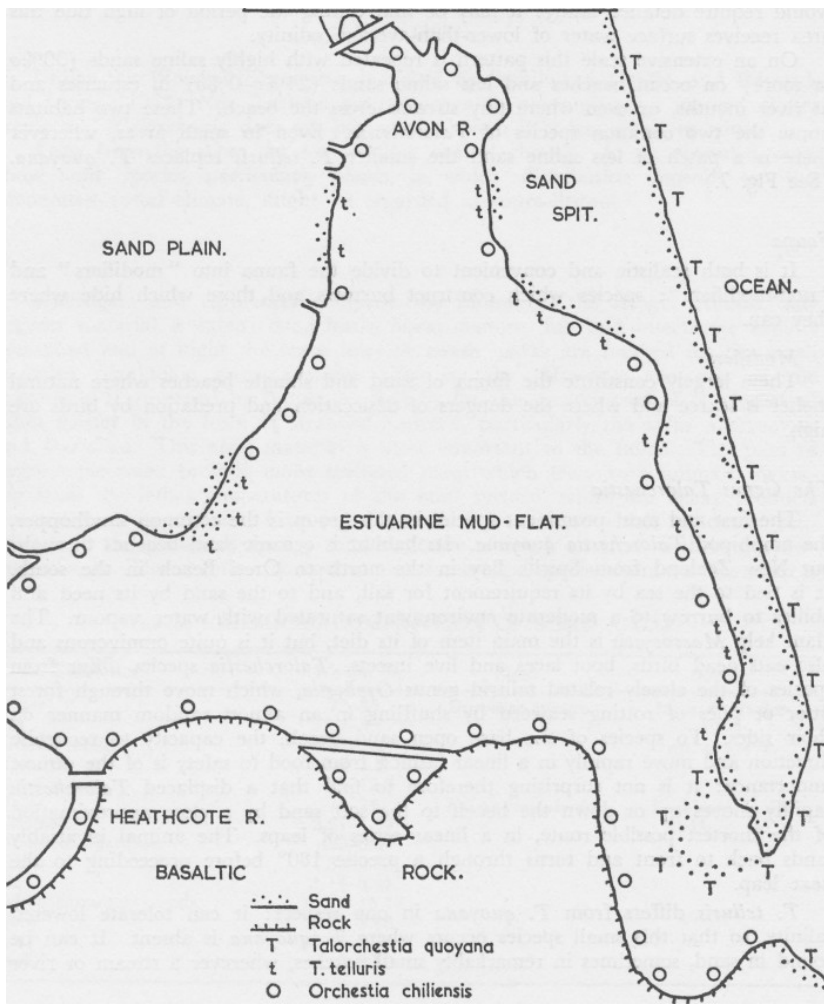
AVON R.

SAND SPIT.

SAND PLAIN.

OCEAN.

ESTUARINE MUD-FLAT.

HEATHCOTE R.

BASALTIC ROCK.

Legend:
- ∴ Sand
- ⊥⊥⊥ Rock
- T Talorchestia quoyana
- t T. telluris
- O Orchestia chiliensis

FIG. 7

ESTUARY - NEW BRIGHTON

	A4	A3	A2	A1	B	C1	C2	C3
W = Wet weight kg.	3.3	3.1	2.8	3.0	3.2	2.7	3.9	3.7
V = Volume cu. dcm.	2.0	—	—	—	—	—	—	—
Ws = Dry weight	2.6	2.7	2.7	2.7	2.9	2.5	3.1	2.8
Gs = Specific gravity	2.65	—	—	—	—	—	—	—
$Vs = \text{Volume solids} = \dfrac{Ws}{Gs}$	0.98	1.02	1.02	1.02	1.10	0.94	1.17	1.06
Ww = Weight water = W–Ws	0.7	0.4	0.1	0.3	0.3	0.2	0.8	0.9
$Vw = \text{Volume water} = \dfrac{Ww}{1}$	0.7	0.4	0.1	0.3	0.3	0.2	0.8	0.9
Vv = Volume voids = V–Vs	1.02	0.98	0.98	0.98	0.90	1.06	0.83	0.94
Vg = Volume air = Vv–Vw	0.32	0.58	0.88	0.68	0.60	0.86	0.03	0.04
$Gm = \text{Bulk density sand in situ } \dfrac{W}{V}$	1.65	1.55	1.40	1.50	1.60	1.35	1.95	1.85
$n = \text{Porosity} = \dfrac{Vv}{V}$	0.51	0.49	0.49	0.49	0.45	0.53	0.42	0.47
$e = \text{Void ratio} = \dfrac{Vv}{Vs}$	1.04	0.96	0.96	0.96	0.82	1.13	0.71	0.89
$s = \text{Saturation} = \dfrac{Vw}{Vv}$	0.69	0.41	0.10	0.31	0.33	0.19	0.97	0.96

FIG. 5.—SAND STRUCTURE

Substance	Weight %	Plant	Source
Water	73–85	*Durvillea* species	Moss & Naylor
Ash	3.2–5.7		1954
Crude Protein	0.07–2.2		pp. 473–478
Mannitol	1.2–2.9		
Alginic acid	4.5–12.2		
Water	74–74	*Fucus vesiculosus*	Backlund H. O.
Albumen	2.81–1.98		1945, p. 47
Albumen digestible	0.0–0.0		
Amids	1.30–0.42		
Fat	1.14–0.41		
N-free extractable cpds.	15.60–16 26		
Fibre	0.75–1.48		
Ash	3 93–5.09		
Sand	0.47–0.36		

FIG. 6.—CHEMICAL COMPOSITION OF SOME ALGAE.