The Biotic Community of a Salt Meadow in New Zealand

By Kitty Paviour-Smith
University of Otago

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Summary

The results of seasonal studies of the fauna of a salt meadow on the Otago Peninsula are given. The plant community consisted of 4 species of plants, their average height is about 1 cm, and they form a dense peaty turf about 20 cm deep on the top of pure sand. Faunal samples taken from sea to dry land showed considerable variation. The mesofauna was at its maximum in late summer (February) and at its minimum in winter (July to September). The microfauna changed in the opposite sense. A food web was constructed to indicate the trophic levels in the community. The maximum number of animals found in the salt meadow was approximately 7½ million per square metre, when the microfauna was at its maximum. Zoomasses tended to show an inverse relationship to the pyramid of numbers and the maximum zoomass per square metre, approximately 32 g occurred when the microfauna was at its maximum.

Introduction

This study analyses a simple terrestrial community with reference to its seasonal variations and spatial changes, and particularly to its pyramid of numbers, food web and biomass. The complexities of terrestrial communities are such that it is very difficult indeed to deal thoroughly with them. For this reason previous investigators have selected only a part of their communities, such as arthropods, insects or nematodes. As far as I am aware, only van der Drift (1950) has made any effort to deal with all the animals, but the beech litter with which he was working is itself only part of a community.

The simplest and most uniform terrestrial community available was a salt meadow in Hooper's Inlet, Otago Peninsula, New Zealand. The vegetation consists of four plant species only, whose average height is 1 cm. The plants all multiply vegetatively by means of creeping stolons, and thus an excessively dense turf is formed by the intertwining stolons and roots. The soil is highly organic and peaty, and extends to a depth of about 20 cm, where there is almost pure sand. It was most suitable for this study because of its short vegetation, and uniformly dense and highly organic soil, this in spite of the physical conditions being complicated by periodic covering by the tide, and the difficulty of extracting animals from the dense turf.

Description of the Area

Hooper's Inlet is a shallow tidal inlet, almost cut off from the sea by a wide spit of sandhills. The area under investigation is a flat region on the inlet side of the spit. Nearest the water's edge is a broad area dominated by *Salicornia australis* Soland. This merges gradually into the relatively narrow band of salt meadow, which in its turn gives way to grass and herbs. The ecotone between the salt meadow and the grassy meadow is clearly marked by the presence of scattered tussocks of *Poa caespitosa* Forst. and *Scirpus nodosus* Rottb. A transect was taken to examine the zonation of plants and animals in more detail.

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"Islands" of salt meadow vegetation occur in the *Salicornia* zone, and on some of these "islands" and in the ecotone are some taller plants: the tall juncoid, *Leptocarpus simplex* A. Rich.; the small sedge, *Scirpus nodosus;* and a bushy shrub, *Plagianthus divaricatus* Forst.

The true salt meadow zone in which this study has been concentrated is a belt approximately 20 m in width. The vegetation here consists of four species of plants: *Cotula dioica* Hook., *Selliera radicans* Cav., *Samolus repens* Pers., and *Scirpus cernuus* Vahl. In places a thinly scattered growth of the taller *Scirpus americanus* Pers. occurs, but very little in the region under investigation. In a typical portion of meadow (25 sq cm in area by 20 cm deep) the proportions of the separate species in the total dry weight of live plant material was worked out. Out of a total dry weight of plant material (2·385 gm in this sample—i.e., 954 gm per square metre), the proportions were: *Cotula dioica,* 1 9%; *Samolus repens,* 8 6%; *Selliera radicans,* 31 0%; *Scirpus cernuus,* 35 2%; unidentified roots, 23·3%.

Field observations of relative abundance of each species supported these results. The pin-point analysis was not used, as it was found to be impractical for plants with creeping stolons. *Cotula dioica* seems to prefer the better drained higher parts of the meadow, and so is dominant on scattered hummocks. Attention has been concentrated on the flat salt meadow.

Methods

The area was visited once a fortnight from June. 1952, until June, 1953 Seasonal samples of the animals were taken. physical factors measured. and general observations made. All of the population numbers are given per square metre.

Physical Factors

Records from the N.Z Official Year Book indicate the type of climate in this region. The records are for Dunedin, 8 miles west of the area

CLIMATOLOGICAL AVERAGES AT DUNEDIN (ALTITUDE = 5 FEET) OVER A PERIOD OF YEARS

Average Annual Rainfall. ins.	Average Number of Rain Days.	Average Bright Sunshine. hrs	Temperature in Shade, Degrees Fahrenheit					
			Mean Daily Maximum.			Mean Daily Minimum.		
			Jan	July	Year	Jan	July	Year
29.74	161	1.715	65.2	49 3	59 0	51.2	36 2	44 3

The temperature at the time of sampling was measured in the vegetation and in the soil at a depth of 10 cm. The soil temperature showed seasonal variation between 5° C in August and 20° C. in January.

A rain gauge showed that 17 34 inches of rain fell from July 1, 1952, to July 1, 1953 The minimum monthly rainfall was 18 inch for September, 1952, and the maximum 2 56 inches for April, 1953.

The water content of the soil was found by drying samples at 110° C. for 48 hours, and a well was sunk and the level of the water table measured It was found that the water table in the sand below the turf fluctuated, being highest in April and May, and lowest in January. In spite of this the turf maintained a fairly high and constant water content throughout the year, averaging 70% weight of wet soil.

The salt content of the soil was found by means of Mohr's titration, and though it fluctuated rather erratically it did show a tendency to be more salt in summer (3·5% on 8/1/53 in air-dried soil) and less salt in winter (only 1·2% on 10/7/52). This agrees with the results of Evans (1953) working on halophytic vegetation at Lake Ellesmere, New Zealand, although his highest values in summer were about 6%. It was found that only the spring tides came over the salt meadow, while the highest springs reached the inland edge of the ecotone.

Soil

The organic content of the soil to a depth of 20 cm was examined. below which there is almost pure sand. From a typical sod 25 sq cm in area and 20 cm deep, all the plants and live roots were separated out. The organic content of the remaining soil was found by drying and incineration. 25 5% dry weight of the soil was organic matter. Vertical distribution of organic matter including plant material was found to be·

Depth.	Percentage of Organic Matter.
2 cm	53 %
5 cm	42 %
10 cm	37.2%
15 cm	23.5%
20 cm	3 3%

The Biome. For the purposes of sampling extraction and counting of organisms, it was found convenient to divide the organisms in this way·

1. Soil Microbiota: Bacteria. protozoa, diatoms. and algae.
2. Soil Microfauna Nematodes, rotifers, tardigrades, harpacticoid copepods and haplotaxid oligochaetes.
3. Mesofauna: Arthropods and larger oligochaetes
4. Macrofauna· Birds and Mammals
5. Macroflora.

1. *Soil Microbiota.* Dilution techniques were used, giving a mean result for 26/6/53 of 25,000 moulds and 968,000 bacteria (aerobic heterotrophs) and yeasts per cc of soil. On an area basis these are per square metre 255,000,000 moulds, and 9,880,000,000 bacteria and yeasts.

For protozoa, diatoms and algae. these methods were highly unsatisfactory owing to the very large amount of fine organic matter in this soil. For the protozoa, experiments indicated merely their rarity on the salt meadow, an average result being 2,500 protozoa per sq m.

2. *Soil Microfauna.* A cylindrical brass sampler was used for taking soil samples. 1 sq cm in area and 10 cm deep Each sample consisted of 5 such borings Seasonal samples were taken to a depth of 10 cm because experiments on vertical distribution of the soil microfauna showed that most of the fauna was present in the upper 10 cm of turf.

Depth.	Percentage of Soil Microfauna
2 cm	78 57%
5 cm	16 18%
10 cm	5 16%
15 cm	0 09%
20 cm	0 00%

For extraction of the fauna the funnel technique of Overgaard (1948) was used, but five large funnels were used instead of nine small ones, the shredded soil being placed in wire gauze trays, 7 cm in diameter. The electric light was adjusted to keep the temperature constant at 30° C. After 15 hours in the apparatus, 10 ccs were run off from each funnel, and, after being centrifuged and heated, stored in Goodey's fixative. To facilitate counting, the supernatant liquid was poured off, and lactophenol + a few drops of lactophenol cotton blue were added, and the tube allowed to stand for at least an hour. It was found that all of the microfauna except for one species of harpacticoid, stained readily by this method, and could then be easily counted.

The efficiency of this time for extraction was tested by running the apparatus as usual for 15 hours, then tapping off 10 ccs from each funnel, and running it for a further 13½ hours. It was found to have this efficiency:

85% for nematodes
91% for haplotaxid oligochaetes
96% for harpacticoid copepods
90% for nauplii.

Only 1 rotifer was found, so that no conclusions have been drawn about them. Overgaard estimated 90% efficiency for nematodes and rotifers from moss samples.

3. *Mesofauna.* For full-time arthropod members of the community, bucket-sampling was found to give consistent results. Cylindrical samplers (10 cm in height x ½ sq dm in area), made from galvanised iron, had one end sharpened and toothed into a cutting edge. 1 cm from this edge, a band of thick wire was soldered around the cylinder, so that the effective depth of the sampler was 1 cm. Over the blunt end of the sampler a square of dentist's rubber dam was fastened with a rubber band. To sample. the cylinder, complete with the rubber over the blunt end, was forced into the ground up to the level of the wire. The soil was cut round and then cut off flush with the sharp end of the sampler. A second rubber dam was fastened over the sharp end, and the cylinder carried home with vegetation uppermost. Five such samples were taken each time.

Samples were taken to a depth of 1 cm. Experiments showed that most of the mesofauna occurred in this layer:

Depth.	Percentage of Mesofauna.
0–1 cm	93.8%
1–2 cm	5.9%—only coccids and mites.
2–3 cm	3%—only 2 mites in 2½ sq dm, probably due to unavoidable handling of samples.

This does not, unfortunately, include caterpillars of the moth, *Scoparia tetracycla* Meyr, which did not occur in the experimental samples but are found commonly on the salt meadow, burrowing to a depth of about 8 cm.

The apparatus for extraction of the mesofauna was a modified version of Salmon's hotplate + funnel method. Instead of the hotplate at 80° C. (Salmon, 1946), an electrically heated waterbath was used. The temperature at the bottom of the tank, whose under surface was in contact with the inverted samples (soil surface uppermost), was raised in 1¾ hours to 65° C., and was maintained at this temperature for 15 hours. by which time no more animals came down. The waterbath was a convenient method of subjecting samples from three different areas to the same extraction conditions. The air-gap (Haarlov, 1947) was not allowed for as ants and spiders easily escaped. However, sometimes oligochaetes lay on the sides of the funnel These were washed through with alcohol, or, if too desiccated, were merely counted and added to the number in the jar. Macfadyen (personal communication) suggests that the use of vertical-sided samplers, without funnels but with the air-gap, overcomes many of these difficulties.

The high temperature was used partly to hasten extraction of the animals and partly because of Salmon's success with high temperature funnels. The last seasonal sampling was just being done when Macfadyen's paper describing his low-temperature funnels appeared (1953). Trials were then made with lower temperatures on the salt meadow mesofauna. It was found that the low temperature, 35° C for seven days, was certainly very much more efficient in extracting coccids and mites, and probably also for collemboles and dipterous larvae, although these groups are so erratically distributed on the salt meadow that only by taking a large number of samples could this be proved. However, in spite of its shortcomings, the method described here has been used consistently throughout the work in this study so that all the results are comparable, though probably too low.

Some idea of which were the most active animals of the mesofauna was gained by the use of Fichter alcohol pitfall traps (Fichter, 1941). This apparatus was successful throughout the year in the grassy meadow, but was flooded out at times by the tide covering the salt meadow. Therefore, although it does give some information about the active animals of the community, its results cannot be used quantitatively. Sweeping with a special net with one flat side (20 cm in length), and a long handle, was attempted in order to sample flying and jumping animals rarely caught in the bucket samples. However, the weather and tide did not often permit successful sweeping to be carried out, and qualitative but no quantitative information was gained.

Van der Drift (1950) seems to be the only other worker using automatic extraction methods to have studied nematodes and rotifers as well as the arthropod fauna, and has also used trapping techniques. His study also was carried out on the simplest most uniform community available to him, the litter of a beech forest floor. This is strictly speaking only part of the beech forest community, and he did not examine the trees themselves.

4. *Macrofauna* Visual observations were made on the birds and mammals. Black-backed gulls, *Larus dominicanus* Lichtenstein, pied oystercatchers, *Haematopus ostralegus finchi* Martens, pied stilts, *Himantopus himantopus leucocephalus* Gould, bar-tailed godwit, *Limosa lapponia baueri* Naumann, and rarely red-billed gulls, *Larus novaehollandiae scopulinus* Forster, were occasionally present on the meadow feeding and sheltering behind *Leptocarpus* and *Scirpus nodosus* when there was a very strong wind and a high tide. A flock of banded dotterel, *Charadrius bicinctus* Jardine and Selby winters on the area.

Harrier hawks, *Circus approximans gouldi* Bonaparte, frequent the area, and up to 20 have been seen roosting there at night. At times flocks of redpolls, *Carduelis flammea cabaret* (P. L. S. Mueller), and starlings, *Sturnus vulgaris* Linn., feed in this region. Two larks, *Alauda arvensis* Linn had territory in the grassy meadow, and up to a dozen at a time have been seen feeding on the salt meadow.

Rabbits, *Oryctolagus caniculus* (Linn), with burrows further inland, used the salt meadow for feeding and the hummocks for defecating They are, however, not often seen actually on the salt meadow by day, but do frequent it by night Stoats, *Mustela erminea* Linn., are common in the district, and twice were actually seen capturing rabbits on the area. Hedgehogs, *Erinaceus europaeus* Linn. occur on the salt meadow and in the grassy meadow.

Identifications. Identification of the animals caught in any terrestrial study is always a problem to the ecologist, and this is particularly so in New Zealand where there is still so much systematic work to be done on terrestrial invertebrates. Experts in various groups have been most helpful in identifying animals for me, and it is of some interest that already at least 4 new species seem to be present as well as 2 new records for the main islands of New Zealand of species previously known only from the subantarctic islands. This is presumably due to the fact that more intensive collecting has been done on the outlying islands.

Horizontal Distribution of the Fauna

A transect (Fig. 1) 180 metres long was run from the inlet, traversing the *Salicornia,* salt meadow, ecotone and grassy meadow. Levelling showed a rise of only 72 metres (Fig. 2).

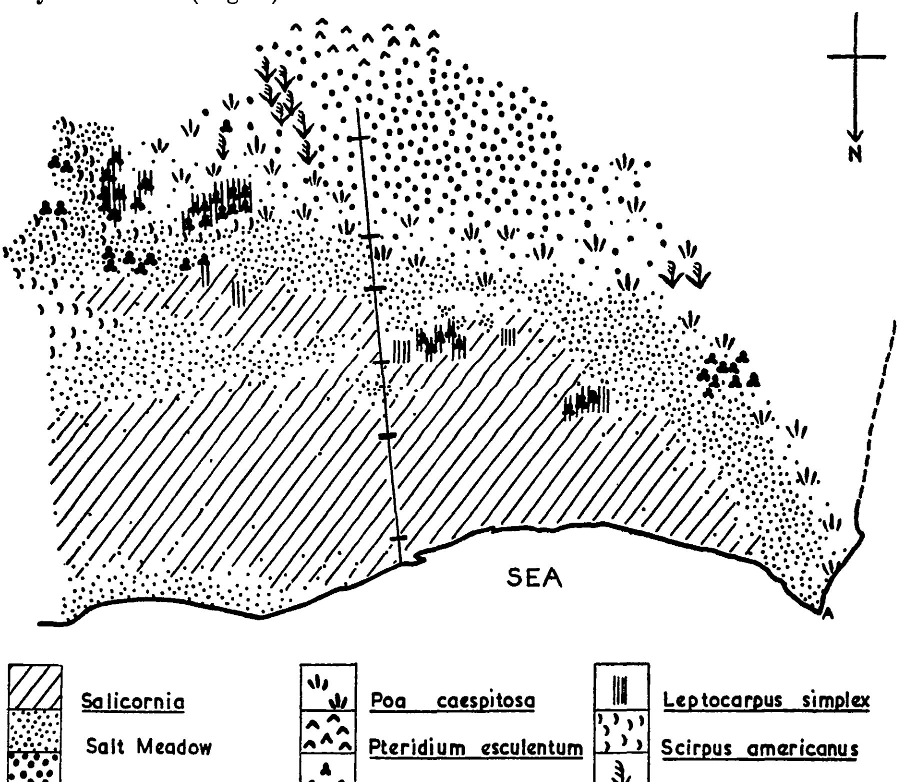
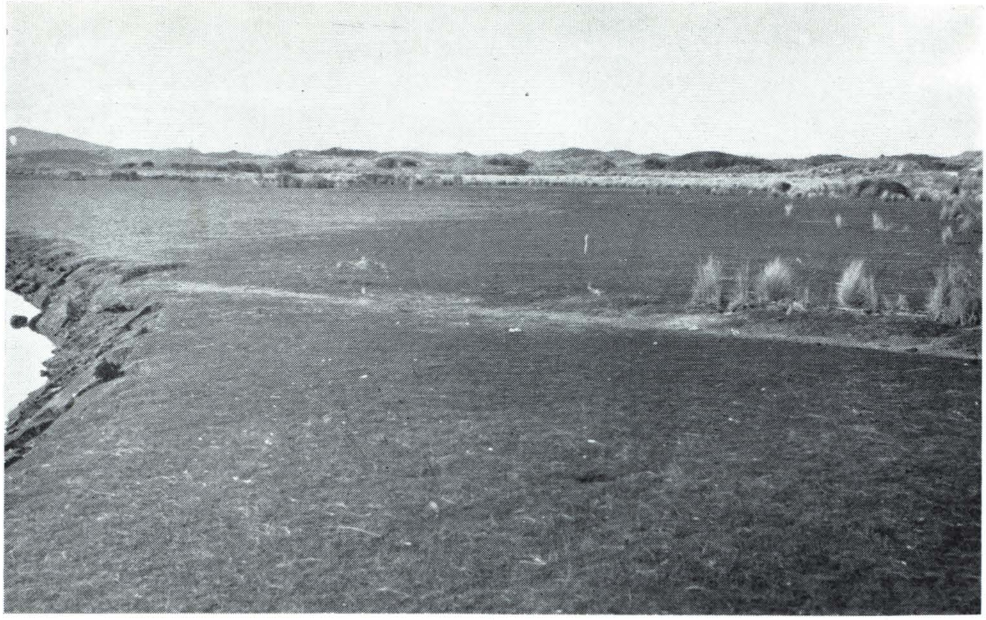
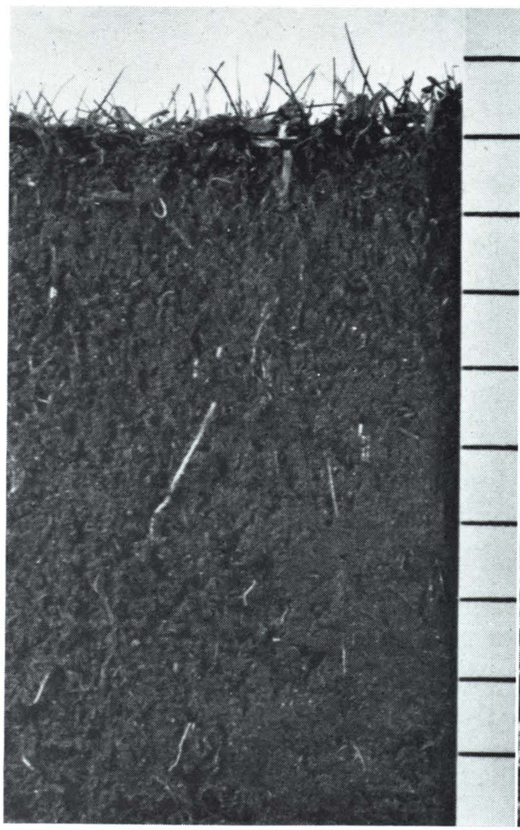


Fig. 1.—Map showing zonation in the salt meadow region. The transect line is shown by the straight solid line crossing the zones. The sampling stations are marked on the transect The photograph (Plate 1a) was taken from the point marked A

Vegetation. In the *Salicornia* zone, there is actually quite a large proportion of saltmeadow plants over which, however, *Salicornia* is dominant In the transect region, *Samolus* is actually the pioneer plant, although in other places *Salicornia* and sometimes even *Leptocarpus* can be seen pioneering Quadrating showed that, in the *Salicornia* zone, *Samolus* is more abundant in the lower regions, and *Selliera* and *Scirpus cernuus* in the intermediate regions, while *Cotula* does not



A



B

C

FIG. a.—View from the point marked A on the map (Fig. 1) looking south-eastwards along the salt meadow (dark turf), showing the paler *Salicornia* zone in the left middle distance and the tussock-ecotone on the right middle distance. In the distance are quite extensive sandhills and behind them (not shown) is the open sea. Hooper's Inlet is shown on the extreme left eroding the *Salicornia* and also the salt meadow where it reaches the water. FIG. b.—Vertical section of salt meadow turf. Each division on the scale = 1 cm. FIG. c.—View from above of salt meadow vegetation. Each division on the scale = 1 cm.

appear until the true salt meadow is reached and *Salicornia* has almost disappeared. *Cotula* appears at 105 m from the water's edge, while *Salicornia* and *Samolus* are last seen at 115 m. The salt meadow, in this part, extends from 100 m to 120 m. *Cotula* prefers the better-drained upper region and also the hummocks. There is an ecotone from approximately 120 m to 140 m in which salt meadow plants give way to grassy meadow plants, and in which *Poa caespitosa* and *Scirpus nodosus* occur. In the grassy meadow, no *Selliera* is seen beyond 140 m, while *Cotula* and *Scirpus* are last seen at 150 m. The vegetation of the grassy meadow consists of the grasses *Holcus lanatus* Linn., *Holcus mollis* Linn., *Anthoxanthum odoratum* Linn. and *Agrostis sp.* with the herbs, *Centaurium umbellatum* Gilib., *Odontites viscosa* Linn., *Leontodon hispidus* Linn., *Acaena sanguisorbae* Valh., *Lagenophora petiolata* Hook., *Trifolium repens* Linn., *Helichrysum filicaule* Hook., *Hydrocotyle novae-zelandiae* D. C. Prodr., *Hydrocotyle sp.*, *Cerastium sp.*, *Gunnera monoica* (Raoul) var. *albocarpa* (T. Kirk), *Gunnera mixta* (T. Kirk).

Animals of the Transect. Six sampling stations were chosen. Those at 10 m, 50 m, and 80 m were in the *Salicornia* zone, the ones at 110 m in the salt meadow, 130 m in the ecotone, and 170 m in the grassy meadow.

Sampling at each of these stations was done on 9/4/53 and 15/11/53 (Fig. 2). On the first occasion, five ½ sq dm samples and two 10 cc samples were taken at each of the stations. The soil microfauna was given the usual extraction treatment, while the mesofauna was given only three hours in the funnels as the apparatus could take samples from only three stations at a time However, on the second occasion 5 microfaunal samples as well as 5 mesofaunal samples were taken at each station, because the original kite of the microfauna had shown irregularities that would probably be smoothed out by more extensive sampling. Also on this occasion the ground was very wet, and it was felt advisable to leave the mesofaunal samples for 15 hours in the funnels Thus while the actual numbers of animals extracted on the two occasions are not comparable, their distributions along the transect are.

The crab, *Helice crassa* Dana, runs about on the surface in the *Salicornia* region and digs winding burrows, averaging 30 cm in depth. Its distribution was examined by quadrating methods. On 2/7/53, the numbers of open crab holes were recorded per square metre at every metre along the transect until no more crab holes were found. The last was found at 93 m inland. It was found that the number of open crab holes per square metre varied inversely with the height above sea-level, while the percentage of *Salicornia* per square metre bore only a *general* inverse relationship to the height above sea level.

Caterpillars of the moth, *Scoparia tetracycla* and larvae of the weevil, *Dryopais variabilis* Broun, were not taken in the ordinary samples owing to the depth of their burrows. Their occurrence was studied by means of special samples at every 5 metres between 85 m and 135 m Both caterpillars and weevil larvae occurred right throughout the salt meadow and ecotone, the averages being 45 caterpillars and 14 weevil larvae per sq m No apparent change in numbers with height above sea level was seen, probably because the slope was too slight within the distance sampled. Occasional caterpillar burrows have been found lower down in the *Salicornia* zone. The inhabitants seem to be able to tolerate periodic covering by the tide by having a winding silk-lined burrow in which enough air can be enclosed to last until the burrow is uncovered again The burrow is lined

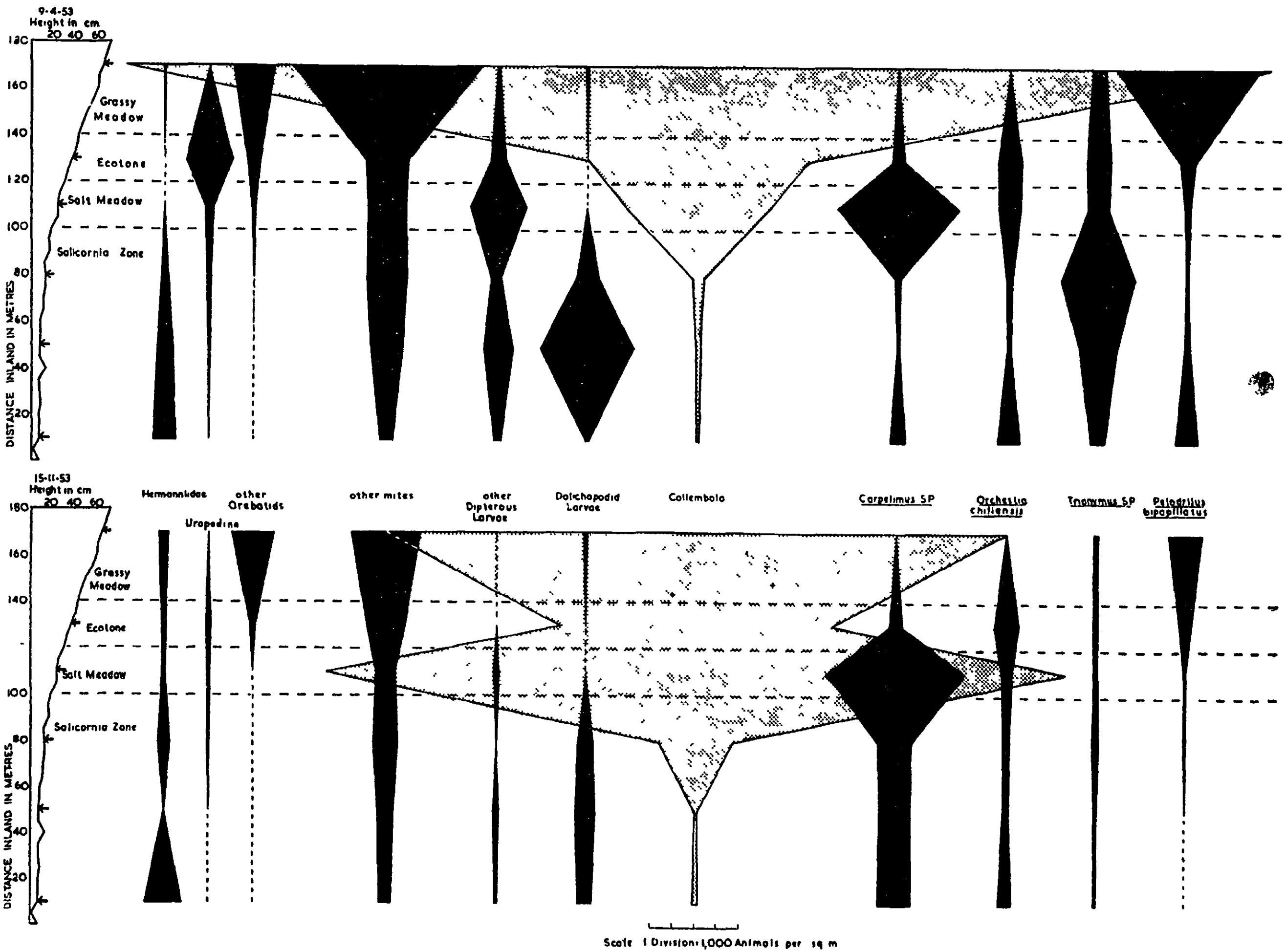


Fig. 2.—Kite diagrams, showing the horizontal distribution of the mesofauna along the transect on 9/4/53 (above) and 15/11/53 (below). The profile of the ground is shown at the left.

with thicker silk when the animal pupates. Weevil larvae also are found well down in the *Salicornia* zone.

The kite diagrams for 9/4/53 and 15/11/53 (Fig. 2) show the area traversed by the transect to be divisible into 5 zones.

1. *Lower Salicornia zone,* which is much the wettest of all zones,, and includes the 10 m and 50 m sampling stations. There is a peak in the population numbers of the Hermanniid mite, and in dolichopodid larvae and crabs. There is also a small peak (composed mostly of adults) in the population of the amphipod, *Orchestia chiliensis* Milne-Edwards. It is particularly interesting that at the 50 m station both the haplotaxid oligochaete, *Pelodrilus bipapillatus* Michaelson and nereid polychaetes were present, burrowing in the soil.

2. *Upper Salicornia zone,* including the 80 m sampling station where *Salicornia* is greatly admixed with *Selliera, Samolus* and *Scirpus cernuus.* The peaks of the coccid, *Trionymus sp.,* and harpacticoid populations occur here. In addition to the mesofauna that was present in the previous zone, there are hymenoptera and Thysanoptera, but field observations show that these are really present right along the transect. The components of the microfauna remain the same. Experiments, with Evans and Guild's (1947) potassium permanganate method of extracting earthworms from the soil, showed that nereids are present here also along with oligochaetes.

3. *Salt Meadow.* Here are the peaks of the staphylinid, *Carpelimus sp.,* the amphipod, *Orchestia chiliensis,* and the more terrestrial dipterous larvae. Most nematodes also seem to prefer this zone. Polychaetes are no longer present. Dolichopodid larvae do occur here commonly and psocoptera occasionally, although Table I does not show this

4. *Tussock-ecotone.* A uropodinad mite has its peak here. In this region aquatic dolichopodid and other brachycerous larvae are no longer present. The soil microfauna is noticeably diminishing and the mesofauna is increasing. The first appearance of truly terrestrial animals is striking—pselaphid beetles, jassid bugs, ants, isopods and the only record of a pseudoscorpion.

5. *Grassy Meadow.* Collemboles (in April), oligochaetes, some of the oribatids and other mites, and also rotifers (mostly *Rotaria macrura* Ehrenberg) reach peaks in their population numbers in this zone. The halophilic staphylinid, *Carpelimus sp,* and the amphipod, *O. chiliensis,* are no longer present. There have been two records from the alcohol pitfall trap of *Talorchestia tumida*

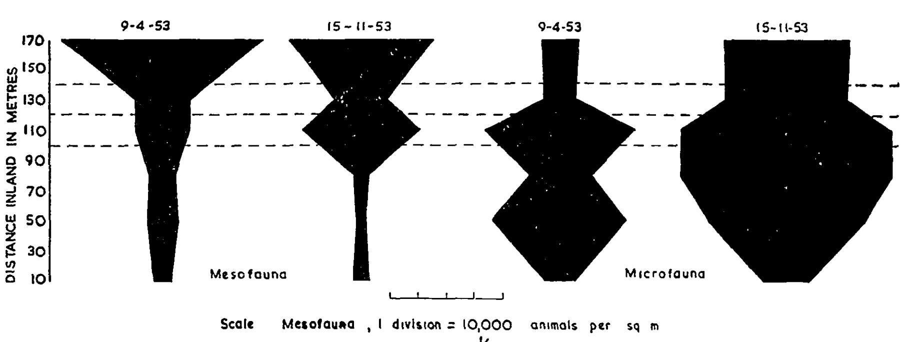


FIG. 3.—Kite diagrams showing the horizontal distribution of the total mesofauna compared with that of the total microfauna on 9/4/53 and 15/11/53.

Chilton, a more terrestrial amphipod. Here the mesofauna is at its maximum and the soil microfauna (apart from the oligochaetes) has decreased considerably.

The most striking thing about this transect is the wide overlap of marine and terrestrial animals. In the lower *Salicornia* zone there are collemboles, coleoptera, cyclorrhaphous larvae, Hemiptera, lepidopterous larvae, mites, spiders and oligochaetes occurring along with amphipods, polychaetes and crabs, while in the ecotone amphipods, *O. chiliensis,* are still present with a more completely terrestrial fauna. All the animals must either be able to adapt themselves to or be widely tolerant of the varying conditions of water and salinity.

Kite diagrams (Fig. 3) show the distribution of the total mesofauna and total microfauna. It is clear that the soil microfauna is greatest in the rich organic upper *Salicornia* and salt meadow regions, and the mesofauna is greatest in the grassy meadow with the tallest vegetation.

Overgaard Nielsen (1949) states that hydrophilous nematodes thrive best in a wet soil, and concerning aerophilous nematodes, "As long as water films are present an increase of the water content will favour the activity of nematodes. However, when the soil becomes permanently waterlogged probably the nutritional conditions are impoverished on account of the reduction of water-air interfaces with a consequent reduction of microbiological activity." It seems likely, therefore, not only that most of the nematodes will on analysis turn out to be hydrophilous, but also that in this highly organic but waterlogged soil, they may feed largely on decaying organic matter. A number of specimens have been observed with brown gut contents. Overgaard (1948b), working on the fauna of moss, however, maintains that "the current opinion that nematodes feed on decaying organic matter cannot be confirmed." He also points out (1949) that arthropods, being typically aerophilous animals, should "have their maximum activities at the time and in places where nematodes are inactive (in the transitional period—I would add, or zone—between moist and dry it is of course possible for both groups to maintain their activities)." This seems to support these results—the arthropods having their maximum abundance in the drier grassy meadow, while the soil microfauna and arthropods are both active in the transitional salt meadow zone.

The only similar transect of which I am aware is that of Weis-Fogh (1947-48), but his was only 12 metres long and was not influenced by the tide. He demonstrated that there was a change in species composition of the fauna from constantly moist to temporarily dry regions.

TABLE I.

Transect–Mesofauna. For each group at each station the first line shows numbers per square metre for 9/4/53, and the second for 15/11/53.

	10m	50m	80m	110m	130m	170m
Isotoma maritima	—	—	80	6,240	—	17,440
	40	—	2,600	32,680	40	15,760
Other Collembola	40	160	440	200	9,880	34,040
	160	40	720	600	12,160	12,240
Thysanoptera	—	—	280	—	—	40
	40	—	80	—	80	320
Orthoptera (Gryllidae)	—	—	—	—	—	—
	—	—	—	—	—	160
Weevils, *Dryopais variabilis*	40	—	—	—	80	—
	—	—	—	—	160	40

	10m	50m	80m	110m	130m	170m
Staphylinids, *Carpelimus sp.*	680	40	240	5,400	520	—
	760	680	600	2,280	320	—
Xantholinus socius	—	—	—	—	—	—
	80	—	—	—	—	—
Staphylinid larvae	—	—	—	80	40	—
	800	760	960	4,040	240	—
Other beetle larvae	—	—	—	—	—	—
	—	—	80	—	—	40
Pselaphidae	—	—	—	—	40	—
	—	—	—	—	—	—
Other beetles	—	—	—	—	—	—
	—	—	—	—	80	—
Coccids, *Trionymus sp.*	720	1,680	3,360	960	1,120	600
	40	80	280	160	200	200
Jassidae	—	—	—	—	40	80
	—	—	—	—	40	40
Other Hemiptera	120	—	—	40	160	1,000
	240	—	320	80	680	600
Lepidoptera, adults	—	—	40	—	—	—
	—	—	—	—	—	—
Lepidoptera, larvae	80	—	40	40	80	360
	—	—	80	—	—	40
Ants	—	—	—	—	40	240
	—	—	—	—	40	120
Other Hymenoptera	—	—	40	—	120	40
	—	—	160	80	120	—
Psocoptera	—	40	—	—	—	—
	—	—	—	—	—	—
Dolichopodid larvae	120	4,240	1,000	—	—	120
	600	840	720	—	—	160
Other brachycerous larvae	40	80	—	—	—	—
	—	120	—	40	—	—
Nematocerous larvae	—	640	—	2,520	480	—
	40	80	—	—	—	—
Cyclorrhaphous larvae	320	560	560	—	120	120
	40	40	—	200	—	—
Dipterous pupae	—	—	—	—	—	—
	—	—	40	—	—	—
Dipterous adults	—	—	80	—	160	—
	40	—	—	—	—	—
Lycosid spiders	—	—	—	—	40	280
	—	—	—	—	—	120
Micryphantid spiders	40	—	240	280	80	120
	40	—	400	—	240	160
Other spiders	—	—	—	—	—	—
	—	—	—	—	—	80
Hermanniidae	1,040	760	360	—	—	80
	1.640	—	520	80	160	400
Other oribatids	—	—	—	160	560	1,840
	—	—	—	—	240	1,880
Uropodina	—	40	200	400	2.040	—
	—	—	40	80	160	—
Other mites	560	1 440	1.800	1,720	1,960	8,520
	480	680	1,120	840	1,720	3,160
Pseudoscorpions	—	—	—	—	40	—
	—	—	—	—	—	—
Amphipods. *O. chiliensis*	1.000	160	240	960	1.080	—
	600	280	280	480	1,160	—
Isopods	—	—	—	—	40	—
	—	—	—	—	40	—

	10m	50m	80m	110m	130m	170m
Oligochaetes	1,000	280	80	240	720	6,400
P. bipapillatus	—	—	40	40	480	15,600
Polychaetes, *Nereis sp.*	—	160	40	—	—	—
	—	40	—	—	—	—
Totals at each level	5,800	10,280	9,120	19,240	19,340	71,320
	5,560	3,640	8,720	41,680	18,440	51,120

Table II.

Transect–Microfauna. For each group at each station the first line shows numbers per square metre for 9/4/53, and the second for 15/11/53.
(Numbers in thousands per square metre)

	10m	50m	80m	110m	130m	170m
Harpacticoids	—	35	50	—	60	—
	4	52	380	122	180	2
Harpacticoid nauplii	—	—	—	—	—	—
	—	24	74	14	6	—
Other copepods	—	—	—	10	—	—
	6	—	—	—	—	—
Nematodes	1,105	4,685	2,235	5,351	1,030	1,105
	1,540	5,412	6,940	7,296	4,012	4,072
Rotifers	—	—	—	—	10	120
Rotaria macrura	12	10	8	8	66	204
Oligochaetes	5	40	—	5	5	5
P. bipapillatus	56	50	38	10	6	120
Totals at each level	1,110	4,760	2,285	5,330	1,105	1,230
	1.618	5,548	7,440	7,450	4,270	4,398

Seasonal Variations

Plants. The flowering period of the salt meadow plants was from October until March, and they continued to grow vegetatively throughout the year. However, *Scirpus americanus* and *Salicornia* both show seasonal aspection.

Animals.—The seasonal changes in the mesofauna and microfauna are shown in Fig. 5, together with the vegetation temperatures throughout the year It will be noticed that the mesofaunal population rises to a peak in February, when the microfauna is low. The microfauna, however, has its peak in August when the mesofauna is at a minimum.

1. *The macrofauna.* A flock of about 90 Banded Dotterel winters on the *Salicornia* and salt meadow zones. Observations (Marples, 1954) over a period of three years show that the dotterel arrive in January and, having maintained a fairly constant winter population here, have left again by August to breed near inland rivers. This migratory rhythm is the most clearly marked seasonal variation in this community The other birds and the mammals only carry out irregular movements.

2. *The mesofauna.* The majority of species in this community are full-time annual residents whose seasonal variation is mainly due to breeding cycles. Where an annual rhythm is visible the peak is in the summer. Brief notes are given on the principal groups Amphipods, *Orchestia chiliensis.* All the amphipods present in October, 1952, were full-grown Females with eggs were caught from September until December. Young were present throughout this period, and by January all those caught were about half-grown. Although they were relatively abundant throughout the year, there is a peak in the amphipod population due

to young animals from November to February, with the highest population, 3,600 per sq m, in mid-January.

Coccids, *Trionymus sp* Large coccids occurred in decreasing numbers until late November, when very small ones appeared. The peak period was from December to March, with a maximum of 9,040 per sq m in early February. Very young coccids were present from late November until January, and by the end of the sampling period the population was a mixture of large and half-grown animals.

Mites show a general increase in numbers from the beginning of October until the end of March Most are present throughout the year, but the active Erythraeid shows clear seasonal variation, having been caught only from mid-October until the end of February. The alcohol pitfall trap results and general field observations bear this out, indicating a maximum in their population in January.

Staphylinids, *Carpelimus sp* (Fig. 4) These animals show an interesting seasonal variation, in that there appear to be two breeding periods, one in spring and one in autumn. There are two peaks of larvae, one October-November and the other February-March, the maximum number being 4280 per sq m in early February The adult population was approximately 2000 per sq m until November, it dropped to approximately 300 per sq m until the end of January and rose to a fairly constant level of approximately 4000 per sq m from February until June, with a peak of 5600 in mid-May. The period in November, December and January, when the numbers of both adults and larvae dropped to such a low level, was in no way peculiar as regards weather conditions, and the numbers

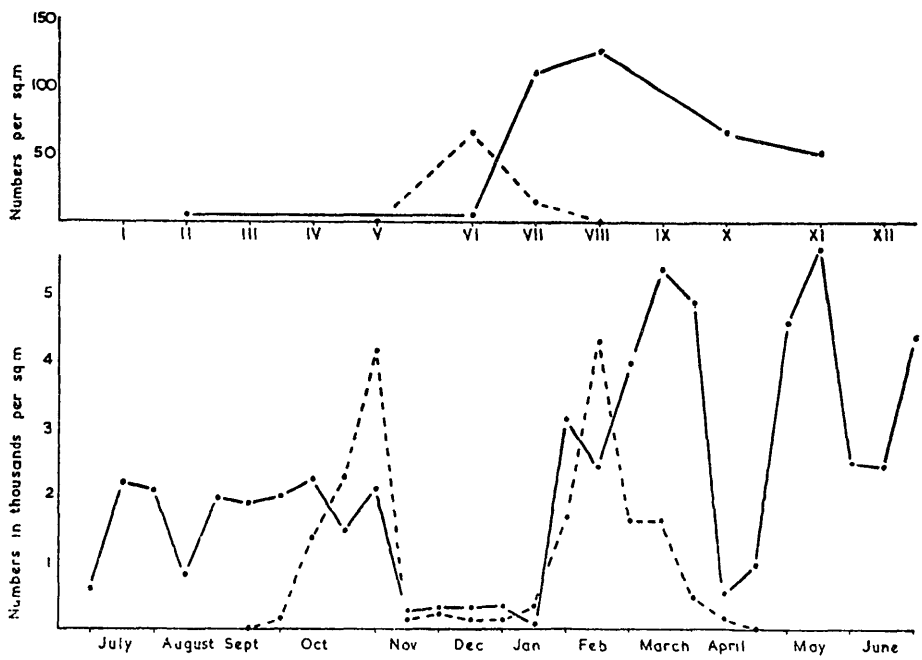


FIG. 4.—Seasonal changes in the population of the staphylinid. *Carpelimus sp*, in the salt meadow (below) compared with those of Bro. Larsen (1949) for *Atheta* and *Tachinus* in a salt marsh in Denmark (above) The solid lines represent adults, and the broken lines larvae.

of other animals did not show a similar drop. This graph was compared with that of Bro. Larsen (1949) for the staphylinids, *Atheta* and *Tachinus,* from dried creeks on the Tipperne Peninsula, Denmark. Her work shows a single peak of larvae and a single peak of adults. It seems likely that this was due to a much more rigorous climate than that of New Zealand. Here, the seasonal change in physical factors, particularly temperatures, was within such a small range that two broods would be possible.

Collembola. This population curve was very erratic indeed, possibly for two reasons. When the tide comes over the meadow a large portion of the springtail population floats and when the water retreats a tidemark of springtails is left. Whether or not this tidemark was happened upon when sampling would produce enormous irregularities. Secondly, Dr. Salmon tells me that another factor to complicate the picture is that on warm summer days, springtails swarm, and eggs are laid and hatch within two or three days. Thus sudden fluctuations in the springtail population occur. and sampling should be done every day for a week or more to detect these changes.

Weevils, *Dryopais variabilis.* These are present in small numbers throughout the year as shown by seasonal and pitfall collections They seem to live in greater numbers on the tops of the hummocks than on the flat, and also occur in the *Salicornia* zone. Too few adults were ever caught for their population to show seasonal fluctuations.

Moths, *Scoparia tetracycla.* Larvae are present in burrows in the soil right throughout the winter. Pupae were not found until November, and adults were emerging in December and January.

Spiders, Micryphantids, though relatively few in number, appear to show a peak period from the beginning of December until the end of April. Lycosids, carrying egg cocoons, have been observed in October, and the pitfall trap in the grassy meadow showed a large population of lycosids with a large proportion of young ones during December and January.

Hymenoptera. The seasonal variations of some of the Hymenoptera was indicated only by the alcohol pitfall trap, which caught the largest numbers in January and February.

It seems that temperature may be the most important physical factor of those measured, which influences breeding in the arthropods. When the graph of the whole arthropod population is compared with that of vegetation temperature (Fig. 5) it is seen that there is a general temperature increase from the beginning of October until the end of April, with a peak period from mid-November until late March. The population curve has an overall increase from early October to the end of March, with a peak period from early January until early March. There are no great extremes of temperature, and no great extremes in population numbers.

It is realised, however, that for any real knowledge of population dynamics insects must be bred in the laboratory so that the lengths of the various stages of the life cycle can be correctly determined, and that each species must be thoroughly examined in each stage of its life cycle, as Borutzky (1939, a and b) has done with *Chironomus plumosus, Tanypus, Corethra* and oligochaetes in Lake Beloie.

3. *The Microfauna.* The graph of the total soil fauna (Fig 5) shows many irregularities, shown also in the separate groups themselves These may be

due either to real population fluctuations or to irregular distribution in space. There does, however, seem to be an overall tendency towards a larger soil population in winter and early spring than in summer and early autumn. The small populations in February, March and April, consist mainly of fully grown animals, many nematodes having eggs and a few harpacticoids with ovisacs, while the large populations in June, July and August consist mainly of larval nematodes although many harpacticoid nauplii are present too. Thus April-May seems to be the most important breeding period of the soil microfauna

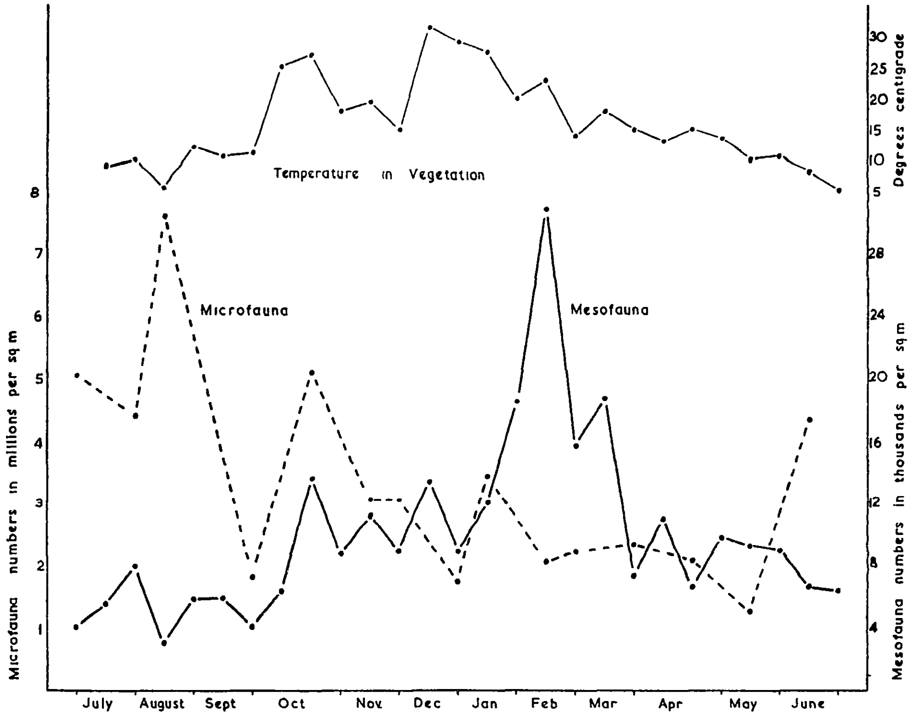


FIG. 5.—Seasonal changes in the numbers of the Mesofauna (excluding the Collembola) compared with those of the Microfauna. The solid line represents the Mesofauna and the broken line the Microfauna. Vegetation temperatures are shown above.

TROPHIC RELATIONSHIPS

A food web (Fig. 6) has been worked out for this community and arranged in trophic levels according to the concept of Lindeman (1942) that "The organisms within an ecosystem may be grouped into a series of more or less discrete trophic levels (Λ_1, Λ_2, Λ_3 . . . . . Λ_n) as producers, primary consumers, secondary consumers, etc., each successively dependent upon the preceding level as a source of energy, with the producers (Λ_1) directly dependent upon the rate of incident solar radiation as a source of energy.

"The more remote an organism is from the initial source of energy (solar radiation), the less probable that it will be dependent solely upon the preceding trophic level as a source of energy."

Allee *et al* (1949) have somewhat modified the use of Λ so that all consumer organisms are included in one trophic level instead of several succeeding ones, but Lindeman's interpretation is used here.

TABLE III.
Seasonal variations of the Mesofauna.

	June	July		August		September		October			November		Dece
	26	10	23	7	21	4	18	2	16	30	13	27	11
Isotoma maritime	5,400	680	1,960	10.960	160	2,080	19,200	4,240	5,680	680	27,360	1,400	23,400
Other Collembola	960	80		80		80	120	280	320	240	720	120	960
Thysanoptera			40										80
Weevils, *Dryopais variabilis*							40		40	40	80		
Staphylinids, *Carpelimus* sp.	600	2,160	2,040	800	1.920	1.840	1,960	2,200	1,440	2,080	280	320	320
Staphylinid larvae							160	1,320	2,240	4,120	160	240	160
Coccids, *Trionymus* sp.	720	560	1,520	560	160	200	480	240	80	120	40	120	760
Other Hemiptera	40												
Geometrid larvae	40	40											40
Other Lepidopterous larvae													
Hymenoptera						40	80		1,080				40
Psocoptera	40												
Dolichopodid larvae	120	80			120	80	80	120	280	80	80	280	200
Other Brachycerous larvae	80	120	160	40	440	240	320	200	840	280	280	320	920
Brachycerous adults													
Nematocerous larvae		160	80	80	920	360	200			40	920	1,360	120
Cyclorrhaphous larvae	80	80	80	40	160	120	80	160	480	40	360	1,040	240
Cyclorrhaphous adults													
Lycosid spiders		40	40		40								
Micryphantid spiders		40	40	40	80		80				120		400
Erythraeid mites									80		40		80
Oribatid mites	80	80	360	40	200	80	240	200	440	120	1.200	920	840
Other mites	1.000	2,120	2,520	920	1,440	2,280	520	720	5,880	880	5.240	2,600	8,240
Amphipods, *Orchestia chiliensis*	1,320	80	1,040	400	280	680	640	1,120	760	880	2,360	1,680	1,000
Oligochaetes					40						80		
Totals	10.480	6,320	9,880	13,940	5,960	8.080	24,200	10,800	19.640	9,600	39,320	10,400	37,800

TABLE IV
Seasonal variations of the Microfauna.

	June 26	July 23	Aug. 7	Sept. 18	Oct. 16
Harpacticoid copepods	297.5	225.0	480 0	52.5	585.0
Harpacticoid nauplii	70.0	—	260.0	—	35.0
Oligochaetes, *Pelodrilus bipapillatus*	85.0	25.0	60.0	50.0	37.5
Nematodes, *Oncholaimus* sp.	55.0	37.5	67.5	102.5	155 0
Other Nematodes	4,572.5	4,127.5	6,735.0	1,620.0	4,295 0
Rotifers		—	15.0	—	5.0
Totals	5,080.0	4,415.0	7,617.5	1,825.0	5,112.5

mber	January		February		Maich		April			May		June	
26	8	22	5	19	5	19	1	16	30	14	28	11	25
2,280	400	280	23,560	520	720	14,080	80	40	37,760			480	3,600
240	80	160	200	360	160				1,160	40	80	40	
			80										
			80		40			40					
360	80	3,120	2,400	3,960	5,320	4.840	520	960	4,520	5,600	2,480	2,400	4,320
160	360	1,640	4,280	1,600	1,600	480	160						
2,680	2,160	3,640	9,040	1,200	4,440	2,320	1.240	560	1,000	600	800	1,720	280
40			240	240	520	40					40		
											40		40
			200			80		40	40		40		40
40	240	160	320	40	120	40			120		40		
120	40	280	200	360	200	240	200	360	40	200	160	80	40
120	480	520	280			360	200			80		200	120
40													
480	160	2,280	640	1,680	1,240	40	1,280	1,000	1,280	680	1,560	120	
40	40	400	360	80	160	40	240	120	80	160	160		
												40	
200			40			40		200	120		40		
120	280	440	720	320	560	320	320	40	240	120	80	80	320
120	120	40	120	40									
600	1,000	720	2.960	2,000	1,600	160	560	600	160	400	2,280	80	
2,080	3,400	3.960	7.520	1,840	2,440	1.880	1.160	1,120	1.280	600	320	1,240	440
1,680	3 600	1,480	1,360	2,320	600	560	600	1,440	840	720	880	640	800
		40		40				200			40		
11,400	12,440	17,160	54,600	16,600	19.720	25.520	6,560	6,720	48.540	9.200	7.040	7,120	10.000

November		Dec.	Jan.	Februarv		Mar.	Apiil	May	June
13	27	26	8	5	19	19	16	14	11
220.0	455.0	195.0	340.0	282 5	—	115 0	172.5	5 0	307.5
—	—	35 0	35.0	5.0	—	—	15 0	—	32 5
110 0	42 5	42.5	32 5	17.5	20.0	15.0	37.5	5.0	2 5
240 0	142.5	65.0	72 5	67.5	125 0	50.0	185 0	195 0	80 0
2,500.0	2,432.5	1,395.0	2,967.5	1,670 0	2,095 0	2,185 0	1,667 5	1,075.0	3,947 5
—	5 0	5 0	—	—	—	—	5 0	—	—
3,070.0	3,077 5	1,737.5	3,447.5	2.042 5	2,240.0	2.365 0	2,082 5	1,280.0	4,370.0

In Fig. 6 the solid lines indicate food relationships, actually observed in this community. The broken lines represent assumed relationships based on observations of similar groups in other communities or ones mentioned in the literature. For example, Overgaard (1947) divides nematodes into four dietary groups and Bro. Larsen (1952) found salt-marsh staphylinids eating algae and burrowing in the surface soil. In this study the gut contents of many staphylinids were examined and nothing recognisable was found. Some contained brownish material, and it is assumed that they were eating humus.

Λ_1, the producer organisms, is represented in this community by the four salt meadow plants, as well as by autotrophic bacteria, diatoms and algae.

Of the consumer organisms, which are dependent upon the Λ_1 level, there are several trophic levels:

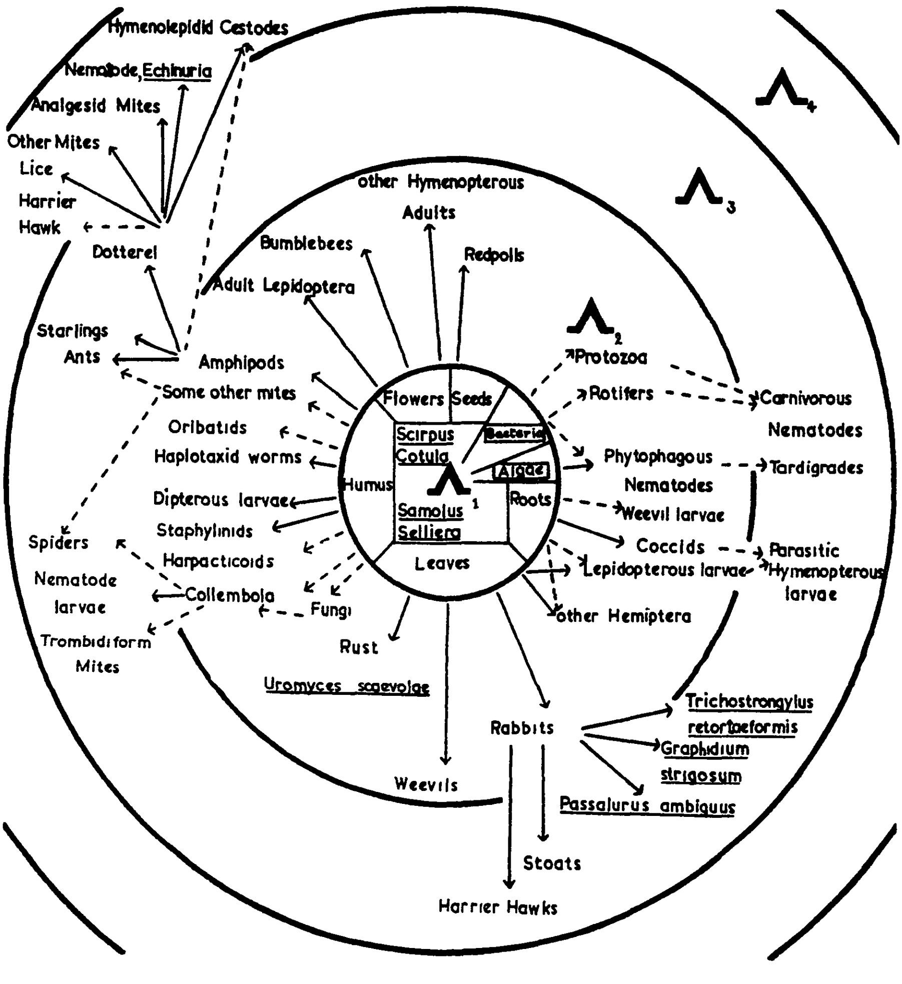


FIG. 6.—Foodweb of the salt meadow community showing trophic levels. The producer organisms are enclosed in boxes. and succeeding trophic levels are enclosed in succeeding concentric circles. Solid lines represent known relationships and broken lines assumed relationships.

$\wedge_2$, the animals feeding directly on the plants. There are several groupings within this level as most of the herbivores of this community appear to feed selectively on a particular part of the plant, for instance, rabbits on leaves and redpolls on seeds. On the other hand, some members of the community appear to feed on more than one part of the plants In their burrows, *Scoparia* caterpillars have been seen with only leaves of all plants. However, the soil is so dense that roots and even stems and humus must have been eaten in making the burrow, as only a pile of sandy earth is found at the mouth of the burrow. Coccids also probably feed on creeping stems as well as on roots. In this trophic level, animals with complex life histories may change, during their life cycle, the part of the plant on which they feed, and may even change from one trophic level to another (see next trophic level, $\wedge_3$). Lepidoptera in their larval stages feed on leaves and probably also on stems and roots, but in their adult stage they feed on the nectar of flowers. In this level, animals that feed on humus mostly live in the thin layer of loose surface soil. On the tops of the hummocks the soil is better drained, and more burrowing and humus feeding animals seem to live there.

$\wedge_3$, the secondary consumers, are the primary carnivores. Besides the animals normally looked upon as carnivores such as stoats, harrier hawks and other birds, spiders and certain mites, this level includes parasites of herbivorous animals such as rabbit nematodes, springtail nematodes and parasitic hymenopterous larvae. However, where one large carnivore feeds upon numbers of smaller prey, numbers of small parasites generally infest one large host.

As already noted, animals may, during their life cycle, change from one trophic level to another, as do the parasitic Hymenoptera. These have been found in adult form feeding upon flowers. It has only been assumed that their larvae are parasitic. It has been assumed that the possible hosts are coccids and caterpillars. Thus these animals would belong to the $\wedge_3$ level as larvae and to the $\wedge_2$ level as adults.

A $\wedge_4$ level of secondary carnivores and parasites of primary carnivores has been found. The harrier hawk acts as a secondary carnivore when it eats dotterel, and probably as a tertiary carnivore if it eats the skink, *Lygosoma smithii* Gray, which eats spiders, but the skink has so far been found only on the grassy meadow and so has not been included in this food web.

Parasites of a primary carnivore have been found in the form of the ecto- and endoparasites of the banded dotterel. An interesting problem is found here the dotterel appears to feed exclusively upon amphipods, while wintering in the inlet. It has a Hymenolepidid cestode parasitic in its intestine in fairly large numbers. If this cestode passes its larval stage in the amphipod, there is another instance of an animal which passes from one trophic level to another during its life history, but both stages this time are parasitic, that is, its larval stage belongs to $\wedge_3$ and its adult stage to $\wedge_4$.

The dead plants and animals will pass back to form humus so that most of the organic matter goes back into the ecosystem again. This is due to the activity of heterotrophic bacteria, which are present at every level from $\wedge_2$ to $\wedge_{n+1}$.

However, some material from this community will not pass back into the cycle again as it has been removed by such animals as the harrier hawk, rabbit or stoat, which have wide ranges and may put material removed from one such small community back into another. Also, animals which feed in other communities bring material to this one. For instance, gulls make castings of fish bones or mollusc shells upon the salt meadow, and the tide brings in drifted materials.

Numbers and Biomasses

The pyramid of numbers (Fig. 7 horizontal axes) was worked out for 5/2/53 as this represented the peak in numbers of the arthropod population. The average lengths of the animals were determined by drawing 10 animals of each species with the aid of a camera lucida, and measuring their lengths with a map measurer and micrometer slide. Nematodes were sorted into three groups, large, medium and small. The average size for each species or group was worked out. The vertebrates, being only transient members of this community, are omitted from this estimation of numbers and biomass per square metre.

The pyramid shows that the smallest animals of the community are most abundant, and the largest animals are least abundant. The very largest animals of the community—rabbit, harrier hawk, stoat, banded dotterel, starling and redpoll are too few in comparison with the rest of the fauna to show at all in

TABLE V.

Numbers of animals and zoomasses for 5/2/53, the date of the maximum mesofaunal numbers, for 7/8/53 when the Microfauna was most abundant, and the average numbers and zoomasses for 27 fortnightly samples

Numbers per Square Metre.

	5/2/53. Date of Maximum Mesofauna.	7/8/53. Date of Maximum Microfana.	Average for 27 fortnights.
Collembola	23,760	11,040	7,140
Thysanoptera	80	—	7
Weevils, *Dryopais variabilis*	80	—	13
Staphylinids, *Carpelimus sp.*	2,400	800	2,384
Staphylinid larvae	4,280	—	693
Coccids, *Trionymus sp.*	9,040	560	1,380
Other Hemiptera	240	—	49
Lepidopterous larvae	200	—	27
Hymenoptera	320	—	88
Psocoptera	—	—	1
Dolichopodid larvae	200	—	138
Other Brachycerous larvae	280	40	266
Nematocerous larvae	640	80	618
Cyclorrhaphous larvae	360	40	165
Lycosid spiders	40	—	28
Micryphantid spiders	720	40	176
Erythraeid mites	120	—	24
Other mites	10,480	960	2,990
Amphipods, *O. chiliensis*	1,360	400	1,250
Total Mesofana	54,600	13,960	17,437
Harpacticoid copepods	282,500	480,000	248,833
Harpacticoid nauplii	5,000	260,000	32,500
Oligochaetes, *P. bipapillatus*	17,500	60,000	38,833
Nematodes, 0–1 mm.	782,500		
1–2 mm	630,000	6,802,500	2,995,000
2–3 mm	325,000		
Rotifers	—	15,000	2,333
Total Microfana	2,042,500	7,617,500	3,317,499
Total Fauna	2,097,100	7,631,460	3,334,936

TABLE V.
Zoomasses per square metre in milligrams.

	5/2/53.	7/8/53.	Average for 27 fortnights.
Collembola	669.3	311.4	201.4
Thysanoptera	2.1	—	.2
Weevils, Dryopais variabilis	448.0	—	72.8
Staphylinds, *Carpelimus sp.*	586.3	195.4	572.4
Staphylinid larvae	147.0	—	23.8
Coccids, *Trionymus sp.*	2,724.1	161.9	399.9
Other Hemiptera	268.7	—	54.9
Lepidopterous larvae	2,300.0	—	310.5
Hymenoptera	42.7	—	11.7
Psocoptera	—	—	.02
Dolichopodid larvae	704.9	—	486.5
Other Brachycerous larvae	189.3	27.0	179.8
Nematocerous larvae	201.2	25.2	194.3
Cyclorrhaphous larvae	512.6	57.0	235.0
Lycosid spiders	722.2	—	505.5
Micryphantid spiders	160.6	8.9	39.3
Erythraeid mites	31.0	—	5.4
Other mites	579.5	56.7	176.7
Amphipods, *O. chiliensis*	9,193.6	2,704.0	8,456.0
Total Mesofauna	19,483.1	3,547.5	11.926.3
Harpacticoid copepods	1,041.9	1,770.2	917.7
Harpacticoid nauplii	2.8	145.3	18.2
Oligochaetes, *P. bipapillatus*	1,774.5	6,084.0	3,937.7
Nematodes. 0–1 mm	41.0		
1–2 mm	1,641.1	20,880.7	8.188.5
2–3 mm	1.459.5		
Rotifers	—	8.4	1.3
Total Microfauna	5,960.8	28,888.6	13,063.4
Total Fauna	25,443.9	32,436.1	24,989.7

this pyramid, which has been constructed for the fauna of 1 sq m However, the largest animals shown on the pyramid, from 3 to 9 mm in length, are all large herbivores or debris eaters, except for the lycosid spiders.

It is also clear that there is a group of small carnivores in each of the three smaller size ranges: certain mites in the 0–1 mm Erythraeid mites and micryphantid spiders in 1–2 mm, and *Oncholaimus* in 2–3 mm group. Thus it does not seem to be true for this community that carnivores are predominantly at the apex of the pyramid, and herbivores at the base. Each size range seems to have its own large number of herbivores and smaller number of carnivores, although carnivores probably feed on herbivores in adjacent size ranges as well.

"Biomass" or weight of a species population per unit area has been used by authors dealing with animals only. In this paper, the terms "zoomass" and "phytomass" are used because both kingdoms are being considered, and the term "biomass" is reserved for the total weight of living material per unit area in the community

The separate species zoomasses were determined for the mesofauna by direct weighing of a counted number of animals. The wet weight was obtained by weighing the animals after gently drying their outsides between blotting paper. Most workers give dry weight of animals, but wet weight has here been used because the weight of the soil microfauna could be calculated only as wet weight. Weights of nematodes were estimated by the Overgaard Nielsen (1949) method. Several nematodes of each group, mounted in lactophenol, were measured for length, using a camera lucida and micrometer slide, and also the diameter of the nematode halfway down the oesophagus. After measurement the volume was calculated and the weight using his estimation of the specific gravity of a nematode = 1. This method was also used for oligochaetes and harpacticoids. Their specific gravity was assumed to be approximately the same as that of nematodes. Rotifers and harpacticoid nauplii were too few for any direct calculations to be done. Their average weights were therefore assumed to be the same as that of Group 2 nematodes. The weight of a bacterium is assumed to be ·000, 000, 001 mg. From average wet weights of one animal of each species or group and the records of numbers per square metre, the species zoomasses were calculated.

In Fig. 7, by means of a three dimensional histogram, the pyramid of numbers, plotted on the horizontal axes, is compared with the zoomasses of the corresponding size groups, plotted on the vertical axis. The date selected was 5/2/53, when the mesofauna reached its maximum It seems to indicate that somewhat of a

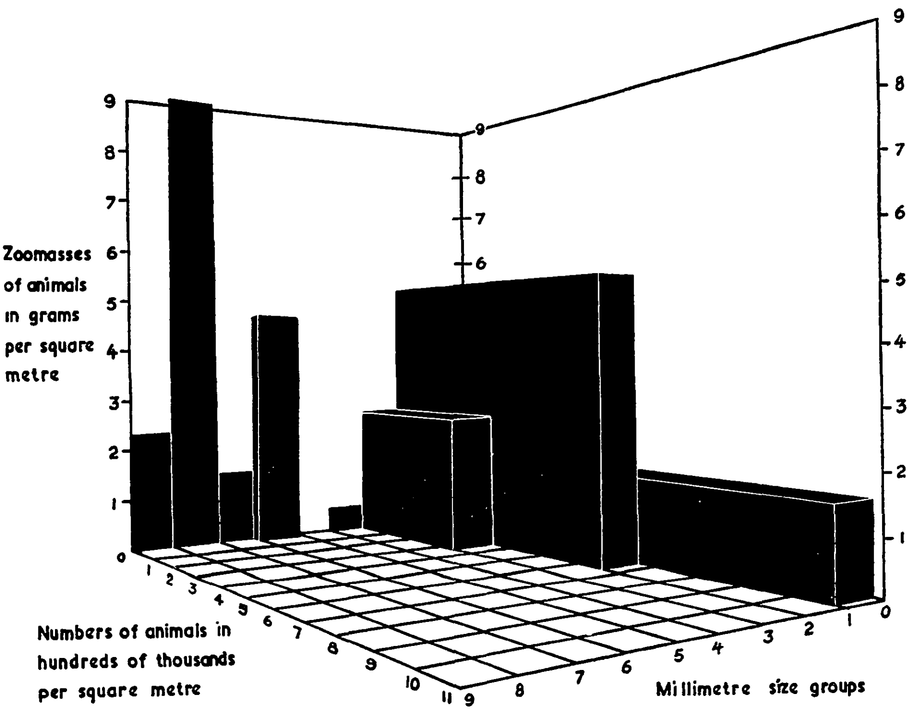


FIG. 7.—Three-dimensional diagram showing the relationship of size group zoomasses to the Pyramid of Numbers on 5/2/53. The horizontal axes show the size groups and the numbers of animals in each—i.e., the Pyramid of Numbers, while the vertical axis shows the zoomasses of the animals in each size group. The animals in the size group are: 0–1 mm, harpacticoids and their nauplii, nematodes, other mites; 1–2 mm, Collembola, Thysanoptera, Hymenoptera, Coccids, Micryphantids, Erythraeid mites, nematodes; 2–3 mm, Staphylinids and their larvae, nematocerous larvae, other Hemiptera, *Oncholaimus* and other nematodes; 3–4 mm, cyclorrhaphous larvae, 4–5 mm, none; 5–6 mm, weevils, oligochaetes, other brachycerous larvae; 6–7 mm, dolichopodid larvae, lycosids; 7–8 mm, amphipods; 8–9 mm, lepidopterous larvae.

pyramid of zoomasses exists. There appears to be an approximately inverse relationship between the lengths of the animals and their numbers. Also the species population zoomass may be determined either by size or by numbers. This explains why the amphipods which are few in numbers but large in size (7–8 mm size group) have a large species zoomass, while there is also a fairly large zoomass for the 1–2 mm size group, which is due to the coccids, small but present in large numbers.

Table V shows some interesting facts about seasonal numbers and zoomasses. The maximum number of animals per sq m occurring in the year was 7,631,460 in August, with a maximum zoomass of 32,436·1 mg when the soil microfauna was most abundant.

This zoomass and that for the year's average are slightly too high because the nematodes were all treated as being average sized individuals, whereas many small ones were actually present In February, when the mesofauna was most abundant, the total zoomass was 25,363 9 mg when there were only 2,097,100 animals per sq m. Average figures for the year were 3,334,936 animals per sq m, weighing 24,989 7 mg These numbers should be compared with those in Table VI. It can be seen that the numbers of animals per square metre is infinitely greater in work where automatic extraction methods have been used, and greater still in work where several methods have been used in order to deal with different groups of animals.

Macfadyen (1952, p. 105, Table 5) gives a table comparing the numbers of mites and collemboles per square metre in his work with the results of several recent authors. The results for the salt meadow are for comparison:

	Mites.	Collemboles.
1953 Salt Meadow (mean for 27 fortnights)	3,000 per sq m	7,100 per sq m

Overgaard Nielsen (1949) refers to a table given by Stöckli (1946). He gives the biomasses in Kg per hectare. These have here been converted to gm per sq metre for comparison with the average biomasses of the salt meadow fauna.

Stockli (1946)		Salt Meadow (1953)	
Microflora	2021.9 g		
Protozoa	37.9		
Nematodes	5.0	Nematodes	8 2 g
Enchytraeids	1.5	Haplotaxidae	3.9
Earthworms	400.0	Mites	.2
Mites }		Collembola	.2
Collembola }	1.1		—
Protura }			—
Diplura		Amphipods	8.4
Other invertebrates	79 7	Other invertebrates	4.1

Overgaard Nielsen also gives "an extract from a table in Bornebusch (1930) with the corrections suggested by Trägardh and Forsslund on the assumption that Bornebusch's technique of extraction was not selective and that his average weights of a single mite and collembole can be maintained."

ZOOMASSES IN GRAMS PER SQUARE METRE.

Bornebusch (1930) in Forest Soil.		Salt Meadow (1953).
Oligochaeta	1.596	3.938
Myriapoda	1.755	—
Araneina	.067	.557
Acarina	4.490	.182
Collembola	6,850	.201

Diptera	1.034		(larvae) 1.095
Coleoptera	3.797		.669
Other Insects	.987		.777
To this Overgaard adds:		Amphipods	8.456
Nematoda	4.500		8.189

Overgaard concludes from a comparison of these results with others he obtained from his own work and that of Weis-Fogh that "microarthropods (mites and collemboles) constitute a larger weight than nematodes in raw humus and probably most organic soils, while in mineral soil the opposite is found." However, although the salt meadow soil is highly organic it is peculiar in being peaty, and thus too dense to support a larger weight of microarthropods than nematodes. Thus my results directly oppose his.

TABLE VI.

History of quantitative work in terrestrial ecology. For comparative purposes all records have been converted to numbers per square metre. Automatic extraction methods began in earnest with Ladell (1936).

(Numbers all converted to number per square metre)

Year.	Author	Country and Place	Type of area.	Part of Population studied.	No. of Animals per sq. metre.
1907	McAtee		Wood	Total population	301
			Meadow	Total population	3,374
1916	Beebe	Para, Brazil	Forest debris	Total population	2,691
		New York, Zoological Park, U.S.A	Uncleared wood	Total population	700
		Labrador	Tundra, reindeer moss	Total population	32
1918	Wolcott		City lots	Total population	910
1922	Sanders, Shelford	Lake Michigan. U S.A.	Pine hollow	Total population	1,260
			in dunes, subterranean ground, herbs, shrubs, trees	Subterranean	25
1924	Weese	Illinois, U S A.	Elm-maple forest	Supposed to be	
			soil	total pop. (but	145
			leaves.	no mites or	786
			herbs and shrubs	apterygotes)	375
1926	Blake	Illinois. U S A	Coniferous forest	Total population	413
			Deciduous forest	Total population	1,012
1930	Smith-Davidson	Illinois, U.S.A.	Tree-layer society of maple oak climax forest 0-18 m in 11 trees	Total population	3,351
1930	Bird	Canada	Aspen Parkland		
			Prairie		815
			Salix petiolaris	Total population	1,583
			Salix longifolia	Total population	1,045
			Aspen	Total population	1,320
1916	Cameron	Cheshire. Eng.	Meadow	Insects	205
			Alluvial pasture	Insects	378
1920	Morris	Cheshire, Eng.	Arable land, manured plot	Insects and other Invertebrates	3.713
			control plot		1 218

Year.	Author	Country and Place.	Type of area.	Part of Population studied.	No. of Animals per sq metre.
1924	Thompson	Aberystwyth, Wales	Pasture field	Total population	1,963
			Ungrazed grassland	Total population	94,744
			Ungrazed grassland	Total population	98,511
1927	Edwards	Aberystwyth, Wales	Light drift pasture	Inserts and other	129,167
			Alluvial	Invertebrates	63,206
1936	Ladell		Fallow land	Arthropods	11,778
			New grass	Arthropods	23,507
1937	Ford	Oxford, Eng.	*Bromus* tussock meadow in soil and vegetation	Arthropods	67,022
1939	Baweja	Rothamsted, Eng.	Sterilization of plots, soil only maximum population, unenclosed sterilized plot,	Total population	27,491
			unenclosed control plot		16,622
1945	Strickland	Trinidad	Soil and litter of a cacao estate	Arthropods	37,375
1947	Strickland	Trinidad	Cacao plot	Arthropods	50,131
		Trinidad	Savannah plot	Arthropods	18,995
		Trinidad	Savannah sub-plot		28,062
1948	Salt *et al.*	Cambridge, Eng.	Grass field	Arthropods	263,581
1953	Present paper	Dunedin, N.Z.	Salt meadow	Arthropods maximum	54,600
				Total fauna maximum	7,631,460

Unfortunately van der Drift (1950) gives his results in a diagram from which numbers cannot be deduced readily, and he calculated the species volumes, not zoomasses. Thus his results are not comparable.

Total Biomass.—An approximate total biomass has been worked out for the salt meadow. It is not a complete biomass because no figures have been obtained for the algae, diatoms or fungi. There are indications that the numbers of these are small, and that the error brought about due to neglecting them will be well within the range of approximation already accepted. For reasons already given the figures for bacteria and protozoa could hardly be more approximate.

Total zoomass (maximum)		32,436.1 mg
Phytomass	bacteria	9.9 mg
	higher plants	1,680,000.0 mg
		1,712,446.0 mg

Therefore, approximate total biomass = 1,712 g per sq m.

Weight of Organic Matter per Square Metre. For an approximate idea of the weight of organic matter in animals, the organic content of amphipods was determined, from the loss of weight on incineration of the air-dried animals. Thus 78 83% dry weight of amphipods is organic matter. It has been assumed that this percentage of organic matter is constant for invertebrates, so that the weight of animal organic matter has been calculated from this

Live plants and their roots were sorted from the soil, and by incineration, the weight of live plant organic matter was found. The remainder of the soil was incinerated, giving an estimate of dead organic matter + animal organic matter. The animal organic matter, estimated by the method described above, was subtracted from that obtained when the soil was incinerated, the new result being the weight of dead organic matter in the soil.

Weight of dead organic matter	17,374.4 g
Weight of organic matter in plants	760.9 g
Weight of organic matter in animals	25.6 g
Total organic matter in 1 sq m soil =	18,160.9 g

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APPENDIX

FAUNAL NOTES

PROTOZOA	
Ciliata	
Loricate Verticellidae *Pachytrocha* sp	Epizootic on 1 species of harpacticoid copepod
2 other ciliates	Free living and present in very small numbers.
Mastigophora—1 species	
PLATYHELMINTHES	
Cestoda	
Hymenolepididae	Present in large numbers in intestine of dotterel.
ANNELIDA	
Polychaeta	
Nereis sp	In the surface soil of the *Salicornia* zone.
Oligochaeta	
Rhododrilus cockayni Benham	Occurs in hummock soil. First record for New Zealand Previously known only from sub Antarctic islands Known to be euryhaline, and usually lives near the sea.
Haplotaxidae *Pelodrilus bipapillatus* Michaelson	Occurs in increasing abundance from the edge of the inlet towards the grassy meadow. Very abundant in grass meadow Only oligochaete present on flat part of salt meadow Commonly found in swamps in the South Island.
NEMATODA	
Dorylaimidae	Free living nematodes. All present in soil of salt meadow.
Dorylaimus sp.	
Plectidae	
Plectus sp.	
Cyatholaimidae	
Paracyatholaimus sp.	
Camacolaimidae	
Leptolaimus—probably n sp	
Oncholaimidae	
Oncholaimus sp	
Trichostrongylidae	
Trichostrongylus retortaeformis (Zeder)	Large numbers present in small intestine of rabbit.
Graphidium strigosum (Dujardin)	In stomach of rabbit
Oxyuridae	
Passalurus ambiguus (Rudolphi)	Large numbers in caecum and colon of rabbit.

Acuariidae	
Echinuria sp.	1 specimen recorded from intestine of banded dotterel.
Thelaziidae	3 ♂ and 1 ♀ from gut of skink.
ROTIFERA	
Lepadella sp.	Present in small numbers on salt meadow.
Rotaria macrura Ehrenberg	Present in small numbers in ecotone. Abundant in grassy meadow.
TARDIGRADA	
Macrobiotus sp.	Only 1 record, from salt meadow.
ARTHROPODA	
Crustacea	
Ostracoda	Only 1 record, from salt meadow.
Copepoda	
Harpacticoida—2 species	Common in salt meadow soil
Other copepods	Appear occasionally on salt meadow, probably after tide has been over it.
Amphipoda	
Orchestia chiliensis Milne-Edwards	Abundant in salt meadow, hummocks, *Salicornia* zone and ecotone.
Orchestia bollonsi Chilton	Occurs on hummocks, under logs on salt meadow and in ecotone.
Talorchestia tumida Chilton	Only 1 record from grassy meadow
Isopoda	Occur in ecotone and grassy meadow.
Brachyura–Grapsidae	
Helice crassa Dana	Burrows occur in *Salicornia* region in decreasing numbers up to salt meadow where none occur.
Arachnida	
Araneina	
Agelenidae—1 species	Probably new species
Micryphantidae—1 species	Most common spider on salt meadow Probably new species.
Linyphiidae—1 species	Under logs on salt meadow and ecotone
Lycosidae—2 species	1 species very common, ubiquitous 1 species much less common.
Salticidae—1 species	Uncommon on salt meadow.
Pseudoscorpiones—1 species	Only 1 record in ecotone
Acarina	
Oribatei	5 families occur. The Hermanniidae are commonest in the *Salicornia* zone, while the rest prefer the higher regions.
Gamasides	3 families occur in the salt meadow region.
Uropodina	1 family which occurs in the salt meadow, but is commonest in the ecotone.
Trombidiform—Erythraeidae	Common on the salt meadow in summer.
Chelytidae	Occurs on the salt meadow.
Insecta	
Collembola	
Ceratophysella armata (Nic)	Grassy meadow and salt meadow.
Entomobrya multifasciata Tulb.	Grassy meadow.
Isotoma maritima Tulb.	Ecotone, grassy meadow, and salt meadow. Most common salt meadow species.
Tullbergia subantarctica Salm.	Ecotone First record of this sub-Antarctic species on New Zealand mainland.
Parafolsomia decemoculata Salm.	Ecotone. First record of this sub-Antarctic species on New Zealand mainland.
Hypogastrura titahiensis Salm.	Salt meadow.
Sminthurinus tunicatus n.sp.	Dr. Salmon is to describe this.

Orthoptera	
Blattidae—1 species	Only one record, from hummocks
Gryllidae—2 species	Grassy meadow
Psocoptera—1 species	Few present in salt meadow and ecotone.
Anoplura	
Mallophaga—1 species	2 specimens recorded from 1 banded dotterel
Thysanoptera—1 species	Few present in salt meadow, ecotone and grassy meadow.
Hemiptera—Heteroptera	
Capsidae—1 species	Occurs regularly though in moderate numbers on salt meadow, grassy meadow and hummocks.
Homoptera	
Cercopidae—at least 1 species	Grassy meadow.
Jassidae—1 species	Grassy meadow, ecotone, hummocks.
Coccidae—3 species, including 2 species of *Trionymus*	Most important bugs on salt meadow and hummocks. Also occur in ecotone and grassy meadow.
Lepidoptera	
Geometridae—1 species	Caterpillars occur on salt meadow
Pyralidae—*Scoparia tetracycla* Meyr.	Caterpillar common, burrowing to a depth of about 8 cm in salt meadow, ecotone and *Salicornia* zone.
Nymphalidae	
Argyrophenga antipodum Doubleday	Adults found in grassy meadow.
	Several other Lepidoptera are known to be present in the grassy meadow.
Coleoptera	
Carabidae—at least 2 species	1 species in ecotone and hummocks. 1 species in grassy meadow.
Staphylinidae	
Carpelimus sp	Small species, most abundant on salt meadow. Also present in ecotone and grassy meadow.
Xantholinus socius Fauvel	Larger species, occurs on hummocks, but not numerous
Pselaphidae—1 species	Present in ecotone and grassy meadow, where ant-nests occur. Probably myrmecophiles.
Curculionidae—	
Dryopais variabilis Broun	Common on salt meadow, hummocks and ecotone.
Melolonthidae—	
Pyronoto festiva Fabricius	Occurs in grassy meadow.
Odontria sp	Occurs in grassy meadow.
	Several other species of beetle are known to be present in the ecotone and grassy meadow.
Hymenoptera	
Formicoidea	Occur on salt meadow, but nests are in ecotone and grassy meadow
Apoidea, Bombidae	Bumblebees have occasionally been observed on the salt meadow in summer.
Other hymenoptera—at least 4 species	Occur in *Salicornia* zone, salt meadow, ecotone, and grassy meadow.
Diptera	
A Nematocera	
Tipulidae—2 species	The small species is common on the salt meadow throughout the year. The large species has been observed occasionally in summer on the salt meadow and grassy meadow.
Chironomidae—1 species	Occurs on grassy meadow.
Ceratopogonidae—1 species	Occurs on salt meadow.

B. Brachycera	
Dolichopodidae—2 species at least	Very common in *Salicornia* zone and salt meadow.
Another brachyceran—1 species	Larva present commonly in salt meadow.
C. Cyclorrhapha	
Lonchopteridae—	
Lonchoptera dulcia Curran	Occurs in grassy meadow.
Ephydridae—	
Scatella nelsoni (?) Tonn & Mall.	*Salicornia zone* and salt meadow.
Scatella nitidifrons Tonn & Mall. *Ephydra novae-zelandiae* Tonn & Mall. *Ephydra sp.*	*Salicornia* zone.
Hydrellia n.sp	*Salicornia* zone and salt meadow To be described by Mr. R Harrison.
Muscidae—at least 2 species	Salt meadow.
Calliphoridae—at least 2 species	
Calliphora erythrocephala Meigen	Salt meadow, *Salicornia* zone, grassy meadow
REPTILIA	
Lygosoma smithii Gray	Skink, once found in grassy meadow.
AVES	
Circus approximans gouldi Bonaparte Harrier Hawk	About 6 harriers include the spit in their feeding range Several roost in the salt meadow region
Limosa lapponia baueri Naumann Eastern bar-tailed godwit	Occasionally on the *Salicornia* at high tide.
Charadrius bicinctus Jardine and Selby Banded Dotterel	A flock of about 90 winters on the *Salicornia* and salt meadow zones.
Haematopus ostralegus finchi Martens South Island Pied Oyster-catcher *Himantopus himantopus leucocephalus* Gould Pied stilt	Occasionally feed and roost at high tide in *Salicornia* zone, and salt meadow.
Larus dominicanus Lichtenstein Southern Black-backed Gull *Larus novaehollandiae scopulinus* Forster Red-billed Gull	Roost occasionally in large numbers at high tide on salt meadow.
Alauda arvensis Linn. Skylark	Up to 6 birds at a time have been seen feeding on the salt meadow.
Sturnus vulgaris Linn. Starling *Carduelis flammea cabaret* (P. L. S Mueller) Lesser Redpoll	Flocks feed on *Salicornia* and salt meadow.
MAMMALIA	
Erinaceus europaeus Linn. Hedgehog	Found occasionally on salt meadow and grassy meadow. Probably also in ecotone.
Oryctolagus caniculus Linn. Rabbit	Feeds on salt meadow, ecotone and grassy meadow.
Mustela erminea Linn. Stoat	Common in grassy meadow and ecotone.

MISS K. PAVIOUR-SMITH
Dept. of Zoology
University of Otago
Dunedin