THE ECOLOGICAL DISTRIBUTION OF BRITISH SPECIES OF *IDOTEA* (ISOPODA)

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(With 4 Figures in the Text)

INTRODUCTION

Descriptions of the ecology of *Idotea* are often generalized, and there appears to be no comprehensive work on the habits of individual species. The present account of the ecology of *Idotea* in the Isle of Man, together with a discussion of relevant literature, includes extended observations on the commoner species, and illustrates that each species has a fairly characteristic range of habitat.

Collections were made on various types of rocky shore, and in some localities quantitative sampling was attempted with the aid of a wire frame enclosing an area of 0·1 m^2. Rock pools were examined, as were regions of the shore subject to the influence of freshwater streams. Surf plankton was collected by dragging a D-net along the edge of the sea on various sandy beaches, and the faunas of surface drift weed and buoys were sampled from a small boat. Dredgings were made off the south coast of the Isle of Man in depths down to about 10 fathoms. Both a naturalist's dredge and a D-net were used, the latter serving mainly to skim accumulations of algae, with accompanying *Idotea*, from a sandy bottom.

Seven species of *Idotea* were found in the Isle of Man—*I. emarginata* (Fabricius), *I. neglecta* G. O. Sars, *I. baltica* (Pallas), *I. linearis* (Pennant), *I. granulosa* Rathke, *I. pelagica* Leach and *I. viridis* (Slabber). Collinge (1917) records two other species from Britain: *I. metallica* Bosc. and *I. sarsi* Collinge. The first of these does not seem to be a British resident, the few specimens which have been recorded being chiefly found amongst *Lepas* on floating wood (Tattersall 1911), whilst the second, *I. sarsi*, is synonymous with *I. baltica*. I have examined the type specimens of *I. sarsi* in the British Museum, and they cannot be distinguished from *I. baltica* (Naylor 1955*c*).

SUBLITTORAL SPECIES

(*a*) Idotea emarginata

Bate & Westwood (1868) record *I. emarginata* from trawl refuse, and they state that the species 'is common all round the coasts of Europe'. Sars (1899) found it in abundance amongst decaying algae down to 20 fathoms, and Tattersall (1906, 1911) found it most commonly on *Laminaria* and floating algae. The *Plymouth Marine Fauna* (Marine Biological Association 1931) records *I. emarginata* as abundant in pools uncovered at half tide in Bovisand Bay, but Moore (1937) states that the species was most commonly trawled and only occasionally found on the shore.

In this investigation specimens of *I. emarginata* have been dredged from beds of algae in and around Port Erin Bay (Fig. 1), and in particular from an accumulation of broken algae on a sandy bottom on the inner side of the ruined breakwater (Fig. 3). In addition, specimens were taken in surf hauls and on buoys in Port Erin Bay, and single specimens were collected on the shore.

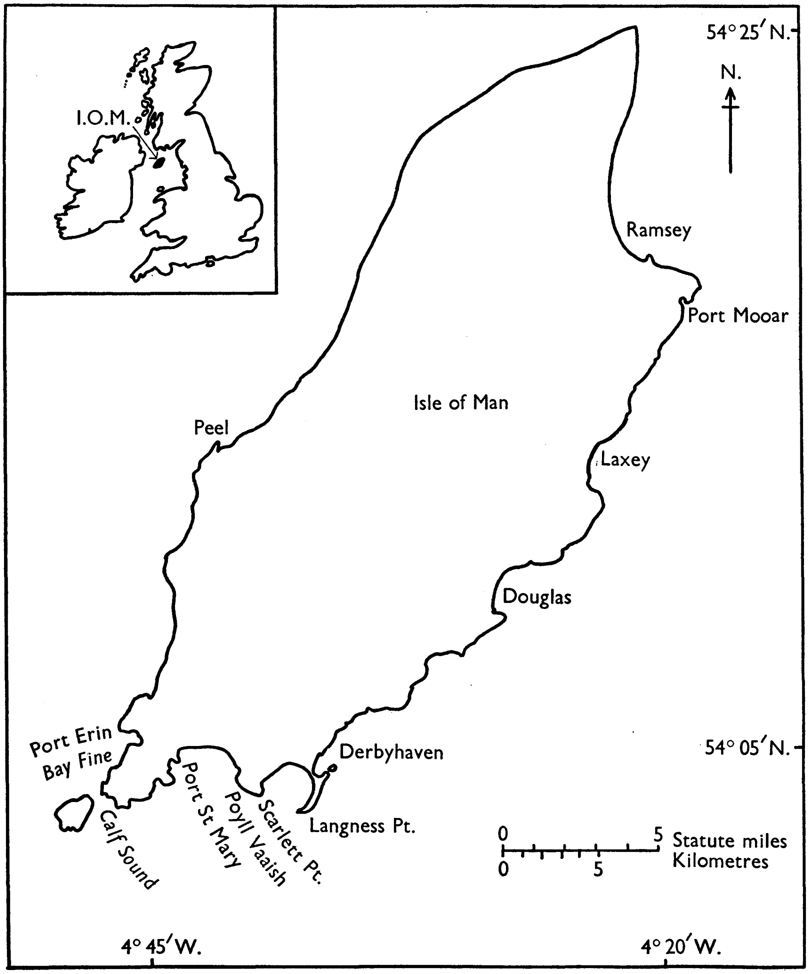

Fig. 1. The Isle of Man, showing localities where *Idotea* were collected.

The distribution and seasonal changes in the population of *I. emarginata* inside the ruined breakwater in Port Erin Bay are described elsewhere (Naylor 1955*b*). The bottom in that locality consists of sand and gravel, with scattered blocks of concrete from the breakwater itself, at a depth of 3–5 fathoms. Algae taken in the D-net hauls, kindly identified by Dr S. M. Lodge, included: *Laminaria digitata* (Huds.) Lamour, *L. saccharina* (L.) Lamour, *Saccorhiza polyschides* (Lightf.) Batt., *Desmarestia viridis* (Müll) Lamour, *Delesseria sanguinea* (Huds.) Lamour, *Ceramium* sp., *Plocamnium coccineum* (Huds.) Lyngb., *Myriocladia tomentosa* Crn., and *Odonthalia dentata* (L.) Lyngb.; some were living, but the bulk of the weed consisted of broken brown algae.

The *Idotea* were associated with the broken algae, and not with the living *Laminaria* as was suggested by Liao (1951). No *Idotea* were found on the *Laminaria* exposed at extreme low water spring tides.

I. emarginata seems to be essentially a sublittoral species, often associated with decaying algae, but it is to be expected that the species will often be washed ashore with such broken algae.

(*b*) Idotea neglecta

Sars (1899), Wahrberg (1930) and Elmhirst (1946) all found this species with decaying algae down to a depth of about 20 fathoms, and Sars associates the species with *I. emarginata*. Kjennerud (1950) in Bergen, found *I. neglecta* in large numbers at a depth of two to three fathoms where wood shavings and fish waste accumulated. Records of this species from the shore are given in the *Plymouth Marine Fauna*, Moore (1937) and Colman (1940).

In Port Erin Bay, during this investigation, *I. neglecta* was found with *I. emarginata* from inside the ruined breakwater. Specimens were found on *Laminaria* beds in Port Erin Bay and in Derbyhaven (Fig. 1), and they have also been taken in townettings in the Irish Sea (Mr A. B. Bowers). I have not found the species on rocky shores, but I have collected it in surf hauls over Port Erin beach and from buoys. Specimens collected on the shore have been sent to me from Dublin (Dr C. F. Humphries) and Belfast (Mr C. Edwards).

I. neglecta, like *I. emarginata*, is predominantly sublittoral, amongst decaying algae; it does not seem to be a resident shore species.

(*c*) Idotea baltica

Sars (1899), Tattersall (1906, 1911) and Nierstrasz & Steckhoven (1930) restrict *I. baltica* to 'shallow' or 'coastal' waters, often amongst floating algae. Specimens were trawled at Salcombe and collected with *I. emarginata* and *I. neglecta* in decaying algae washed ashore in the River Yealm estuary (Marine Biological Association 1931). Small specimens of *Idotea*, taken in hauls of surf plankton at Robin Hood's Bay, were chiefly *I. baltica* (Colman & Segrove 1955). In the Isle of Man Moore (1937) records the species as commonly trawled in Port Erin Bay and Bay Fine (Fig. 1), and he states that occasional specimens were found on the shore.

In this investigation a number of *I. baltica* were taken in dredgings in Port Erin Bay, both inside the breakwater and along the north side of the bay. The species was also taken in dredgings in Derbyhaven, and also on *Halidrys* at LWS in that region. Drift weed in hauls with a shore seine net at Peel yielded many specimens of *I. baltica*, as did surface drift weed at Port Erin. Small specimens are often taken in surf hauls, and I have taken single specimens on rocky shores at Scarlett Pt. and at Ramsey.

In some cases this species is associated with *I. neglecta* and *I. emarginata*, but it is more abundant on surface drift weed than those species. In this respect it is interesting to note that Dahl (1948) found few specimens of *I. baltica* in dredgings off the Swedish west coasts, and he took this as confirmation of his view that the species is associated with surface drift weed. Segerstråle (1944), however, associates the species with attached *Fucus vesiculosus* in the Gulf of Finland (see p. 267).

(*d*) Idotea linearis

Bate & Westwood (1868) found this species in dredgings and on the shore, in many British localities. Collinge (1917) also observed *I. linearis* on the shore, but Tattersall (1906, 1911) found it to be common in some Irish harbours, and often on floating weeds or timber. The *Plymouth Marine Fauna* records the species as common amongst *Zostera* on Drake's Island. I have regularly collected single specimens from dredgings in and around Port Erin Bay (see also Moore 1937), and some specimens have been taken in townettings in Morecambe Bay (Mr A. B. Bowers). I have found only one specimen in the intertidal zone, on the Queen's Pier at Ramsey. Records of *I. linearis* are few, and very few specimens were found in the investigation, but it seems that *I. linearis* is chiefly sublittoral, and is not a common shore species in the Isle of Man.

RESIDENT SHORE SPECIES

(*a*) Idotea granulosa

I. granulosa has often been confused with *I. viridis* (see p. 262) and with *I. neglecta* (see Kjennerud 1950). Sars (1899) and Wahrberg (1930) restrict *I. granulosa* to shallow water, King & Russell (1909) record it as the only shore idoteid in their investigations at Millport, and Moore (1937) records the species from crevices and pools on the shore at Port Erin. Packington (1934) working at Robin Hood's Bay, and Colman (1940) at Wembury, each found *I. granulosa* to be the only common shore idoteid, and Elmhirst (1946) observed the species with *Gigartina* on the shore. Kjennerud (1950) found it only on littoral fucoids in Norway. In the Isle of Man I have collected *I. granulosa* from algae on the shore at Port Erin, Port St Mary, Scarlett Pt., Derbyhaven, Laxey, Port Mooar, Ramsey and Peel (Fig. 1). In addition, I have collected and examined specimens from Flamborough and Plymouth, and have examined specimens from Robin Hood's Bay (Dr F. Segrove), Dublin (Dr C. F. Humphries), Belfast (Mr C. Edwards) and Skokholm (Miss E. C. Judges); all came from shore algae. *I. granulosa* occurs on buoys and in surface drift weed, but there is no doubt that it is mainly an intertidal form; it occurred only rarely in dredgings.

Monthly samples of seaweed from known levels on the shore were taken over a period of 15 months, with the object of determining which species of *Idotea* occur on the foreshore, and to study their distribution. (Observations on a wider range of rocky shores are described on p. 261; they compare the distribution of *I. granulosa* and *I. pelagica*.) A selected region of the shore surveyed by Southward (1953) at Port St Mary was used. Southward marked a stretch of limestone rock with a number of cement marks, and traverse *B–B* (see Southward 1953, Fig. 3) of these marks was used in the present investigation; the traverse extends from HWS to LWS. I am grateful to Dr Southward for supplying me with data on the positions of these marks. The shore is of gently shelving strata of limestone and it is exposed to moderate wave action (Southward 1953). The larger algae present were *Fucus spiralis* at HWN, *F. vesiculosus* at MTL, *F. serratus* and *Himanthalia elongata* at LWN, and *Laminaria digitata* at LWS.

A wire frame enclosing 0·1 m^2 was used in taking a representative sample of algae from each station. *Idotea* were removed individually, while the weed in each sample was washed and sorted twice. Five times as many specimens were found in the first sorting as in the second, and it is assumed that most *Idotea* in the weed were removed in the two sortings. The damp weight of the weed in each sample was noted. Whenever possible, samples were taken monthly at HWS, HWN, MTL, LWN and LWS, and no sample was taken more than 5 yd from the traverse. All samples below HWS were of algae on the open shore, but at HWS a 1 lb jar was filled with *Enteromorpha* from pools.

Table 1. *Length-frequencies of* Idotea granulosa *amongst algae at each level sampled in 1953.*

	Tidal levels				
	HWS	HWN	MTL	LWN	LWS
Body length (mm)	*Enteromorpha*	*F. spiralis*	*F. vesiculosus* *Elachistea* sp.	*F. serratus* *H. elongata* *Laurencia* spp. *Cl. rupestris* *Ch. crispus*	*L. digitata* *Rh. palmata* *Cl. rupestris*
1–2	—	—	—	2	37
2–3	—	—	—	8	169
3–4	2	—	7	11	103
4–5	—	—	46	27	57
5–6	—	6	78	54	21
6–7	—	2	69	39	6
7–8	—	6	69	52	3
8–9	—	5	78	56	3
9–10	—	11	68	34	5
10–11	—	6	41	52	1
11–12	—	10	32	27	2
12–13	—	12	15	5	—
13–14	—	6	12	6	2
14–15	—	2	4	7	—
15–16	—	2	7	4	—
16–17	—	1	4	1	—
17–18	—	3	4	—	—
18–19	—	—	1	2	—
19–20	—	—	—	—	—
20–21	—	—	—	1	—
Totals	2	72	535	389	409

At LWS the *Laminaria* fronds were examined but no *Idotea* were found on them; only the holdfasts, with *Cladophora*, and the stipes, with *Rhodymenia*, were retained in the samples. It was not always possible to obtain a sample at LWS, particularly in winter, when low-water spring tides occur in the hours of darkness. *I. granulosa* was the only idoteid found in these samples over the whole 15 months. Specimens were present at each level sampled but they were most abundant at MTL and below.

All specimens collected in 1953 were measured to the nearest whole millimetre below their length, and the length-frequencies of all specimens from each level are given in Table 1. Small specimens were mainly concentrated below LWN, whilst the larger ones were most abundant farther up the shore. Specimens less than 5 mm long were most abundant at LWS on small algae such as *Cladophora* and *Rhodymenia*; those longer than 5 mm were found chiefly on fucoids, particularly *Fucus vesiculosus* at MTL. Hardly any specimens came from the *Laminaria digitata* itself.

Seasonal changes in the density of *I. granulosa* on the algae at each level are given in Fig. 2; fairly regular and similar trends are apparent at each level. The large specimens at MTL, and to a less extent at HWN and LWN, showed a marked increase in density during the autumn, falling off in density during the winter and early months of the year. Small specimens at LWS showed a similar trend, and they showed a maximum density in September.

Biological factors such as weed preference, as well as physical factors such as wave action and exposure to the air, affect the distribution of organisms living amongst seaweeds, and it is difficult to separate these factors in the case of *I. granulosa.* Large *Idotea* survive for greater lengths of time in reduced humidities because of their smaller surface:volume ratio, and because of this large specimens should be able to

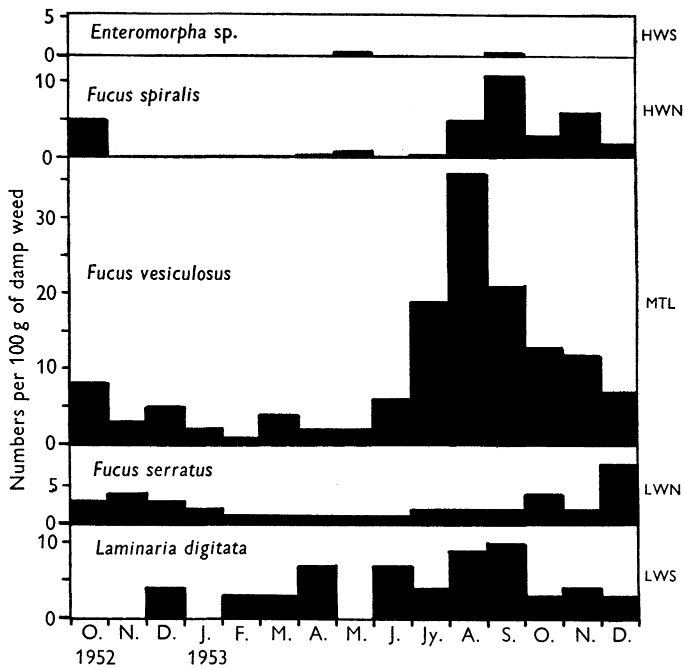

Fig. 2. The number of *I. granulosa* per 100 g of damp weed in monthly samples from five levels on the shore at Port St Mary. Figures for *Laminaria digitata* refer to stipes and holdfasts only. No sample could be taken at LWS in October or November 1952, or in January or May 1953.

extend farther up the shore than small ones, but this does not necessarily imply that small animals are always found below LWN as at Port St Mary. On more sheltered shores, where algal cover is more dense, small *I. granulosa* may extend to between MTL and HWN on *Polysiphonia lanosa*, the small tufted alga on *Ascophyllum* (Colman 1940). The preference for different types of algae by *I. granulosa* of different sizes seems to be at least partly dependent upon a choice of suitable food, and a choice of suitable foothold against tidal water movements. It is noticeable that *I. granulosa* of all sizes prefer shrubby algae; small specimens prefer small tufted algae such as *Cladophora*, whilst large specimens prefer the more branched fucoids, particularly *Fucus vesiculosus*; long, smooth fronded algae such as *Laminaria digitata* appear to be avoided.

(*b*) Idotea pelagica

Dollfus (1895), Elmhirst (1946) and Kjennerud (1950) found *I. pelagica* amongst *Balanus* and *Mytilus* on the shore, and Dollfus goes so far as to say that it is commensal with or parasitic on *Balanus*. Sars (1899) and Tattersall (1906, 1911), on the other hand, state that *I. pelagica* is associated with algae close to the shore. Dahl (1948) collected the species from localities which appear to be exposed to a great deal of wave action. In this investigation *I. pelagica* was found in material scraped from the Port Erin breakwater buoy (Fig. 3), from exposed shores near Port Erin, Peel and Port St Mary, and on the Queen's Pier at Ramsey. In all cases the species was amongst barnacles, *Mytilus* and stunted fucoids (particularly *F. vesiculosus* var. *evesiculosus*), in regions exposed to a good deal of wave action.

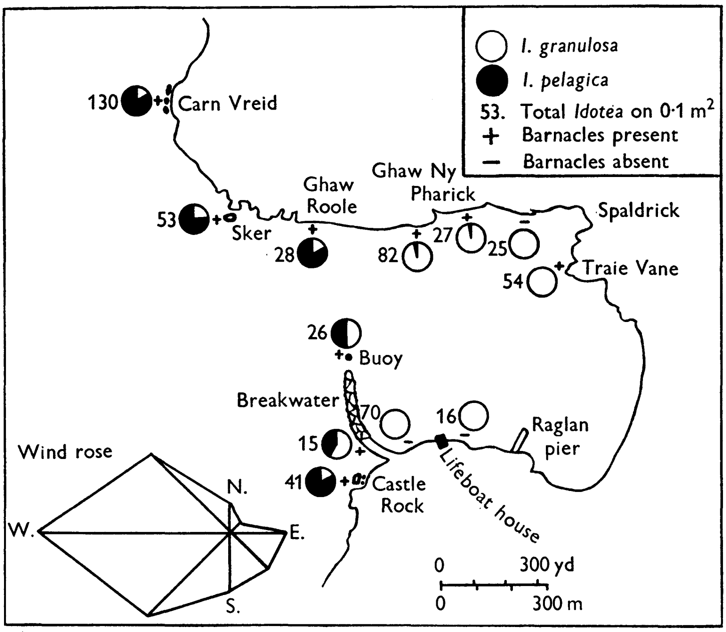

Fig. 3. The distribution of *I. pelagica* and *I. granulosa* in samples of 0·1 m² taken at MTL on shores in and around Port Erin Bay. The wind rose is derived by direct summation of 10-day means of wind speed and direction (June 1951–May 1953), issued by the Service Hydrographique, Charlottenlund, Denmark, and based on wind recordings at Ronaldsway Airport, some five miles east of Port Erin.

During 1952 and 1953 a shore survey was carried out to compare the distribution of *I. granulosa* and *I. pelagica* in and around Port Erin Bay. Some shores were reached on foot, but others were only accessible by rowing boat and on calm days. Samples were taken, as near as could be judged, at MTL, in the *Fucus vesiculosus* (or *Ascophyllum nodosum*) zone. All weeds and barnacles in an area of 0·1 m² were brought back to the laboratory, where all *Idotea* were removed and the dominant organisms noted. At the station on Castle Rock (Fig. 3) similar samples were taken at about HWS, HWN, LWN and LWS in a traverse down the shore. The levels were determined approximately, from the level of predicted low water on a calm day. The prevailing winds are westerly and the outer parts of the area sampled are exposed to a great deal of wave action. The region inside the breakwater receives some shelter, and a decrease in exposure eastwards towards Spaldrick, along the north side of the bay, is apparent from observation. This decrease has been demonstrated qualitatively by Southward (1953).

I. pelagica and *I. granulosa* were the only idoteids found in this shore survey the results of which are shown in Fig. 3. *I. pelagica* was the dominant *Idotea* in the outer parts of the region sampled, where wave action was greatest and where barnacles were largest and most abundant. On more sheltered shores, where algae were dense and barnacles sparse or absent, *I. granulosa* predominated. In the traverse on Castle Rock forty-six out of a total of forty-seven specimens of *I. pelagica* were taken at HWN and MTL, where barnacles were dense. There were fewer *I. granulosa* in the samples (only fourteen in all), but these were found amongst algae as at Port St Mary (see p. 259), mainly at MTL and below.

I. pelagica was mainly found on exposed shores where barnacles were present. Furthermore, most specimens were found inside empty barnacle shells, so that, on less exposed shores, such as at Ghaw ny Pharick, where barnacles were small and flat, few *I. pelagica* were found. But despite its tolerance of wave action and its close relationship with suitable barnacles, *I. pelagica* seems to avoid the most exposed parts of the shore which completely lack algae, even though barnacles may be present. It is probable that regions lacking algae are avoided because they dry out too quickly at low water; the presence of algae retards drying out.

As for the food of *I. pelagica*, cells of fucoids and parts of barnacle appendages have been found in the gut (Naylor 1955*a*). The latter may well have come from damaged or moulted barnacles, but the *Idotea* might be able to bite small pieces from living barnacle cirri. It does seem, however, that *I. pelagica* is an omnivorous scavenger like other members of the genus, seeking shelter amongst the barnacles, rather than being commensal with or parasitic on them.

THE BRACKISH WATER SPECIES

Idotea viridis

I. viridis often appears to have been confused with other species, particularly *I. granulosa*. Accepted texts for identification (Sars 1899, Collinge 1917, Nierstrasz & Steckhoven 1930) give no ecological details, but many workers agree with present observations that *I. viridis* is a brackish water species (Dollfus 1895, Norman 1904, Tattersall 1911, Crawford 1937, Spooner & Moore 1940, Howes 1939*a*, Dahl 1944, 1948, Forsman 1951). In contrast Elmhirst (1946) associates large specimens of the species with *Ascophyllum* and immature ones with *Cladophora*, and Watkin (1941) suggests that the species is seasonally migratory between littoral and sublittoral algae in Kames Bay. These authors appear to have confused *I. viridis* with other species, possibly *I. granulosa* and *I. baltica* respectively. Apart from Manx specimens I have seen *I. viridis* from Holbeach (Lincs.), Langton Herring (Dorset), Tamar Estuary (Devon and Cornwall) and Great Wakering (Essex) sent to me by Mr G. M. Spooner, and from Little Cumbrae Island (Bute) sent to me by Dr R. B. Pike. All these specimens came from brackish water.

The *Marine Fauna of the Isle of Man* (Moore 1937) records *I. viridis* several times from Port Erin Bay, but these records are open to some doubt. Two specimens collected in Port Erin Bay and retained in the faunal collection as *I. viridis* are, in fact, *I. granulosa.* Moreover, since the details of habitat accompanying previous records do not agree with what is now known of the ecology of *I. viridis*, it may be suggested that the early records referred to some other species, and that so far as is known the finding of *I. viridis* in this investigation constitutes the first true record of the species in the Isle of Man. Specimens have been found in two brackish pools near Poyll Vaaish, in a similar pool on Langness Pt., and in two connected pools at Scarlett Pt. (Fig. 1). The two pools at Poyll Vaaish and the one at Langness are similar in many ways. All three are quite large (the smallest measures about 10 ft by 5 ft) and all are situated beteeen HWN and HWS on gently shelving, sheltered shores. The pools are permanent, each receiving fresh water, by seepage, as at Poyll Vaaish, or by a definite stream, as at Langness, and each is reached by the sea during the higher tides. Salinity of the pools varies markedly with the state of tide, wind strength and direction, and rainfall. Each pool has a vegetation of large green algae (p. 264).

The pools at Scarlett are situated higher than those already described, but, as will be shown below, they are ecologically similar. They are at the head of a deep gulley in an exposed part of the shore, and the lower pool opens to the gulley by a narrow crevice 5 ft above MHWS. Provided there is sufficient swell the funnelling action of the gulley causes sea water to be forced into the lower pool at all states of tide above about HWN, and during storm conditions the two pools may be merged. Fresh water flows through the pools from a stream farther inland. Salinity in the pools varies widely and irregularly, because of the sporadic effects of both salt and fresh water. The upper pool is only about 6 in. above the lower one, but sea water entering the lower one does not always reach the upper one. Even so the range of salinity is high in the upper pool and it may be correlated with the phase of tide. Samples taken on different visits to the pool, kindly analysed by Mr D. J. Slinn, showed that the lowest value (6·8‰) occurred during neap tides, whilst the highest value (29·5‰) occurred immediately after a high water spring tide. These two values are not necessarily the extreme limits of salinity range in the pool. If neither sea water nor fresh water enters a particular part of the pools for some length of time, evaporation may raise the salinity to a value above that of sea water. On 12 May 1953 sea water entered the lower pool near the gulley, but it had little effect on the salinity of the water at the western end of the pool some 15 ft away; no fresh water entered on that day. The salinity at the western end of the pool, where it was shallow, rose from 36·0 to 38·6‰ in the six hours after high water. Near the gulley, where sea water entered around 1000 h G.M.T., salinity ranged only from 34·3‰ at 1000 h to 34·7‰ at 1600 h. Thus salinity may vary seasonally, daily, and even spatially within the pools.

Temperature ranges in the pools may be great because of the effect of fluctuating air temperature on such small masses of water, but any such ranges are often alleviated by the influx of sea water. On 12 May 1953 temperatures at a depth of 9 in. were noted over a period of six hours from high water. Near the mouth of the gulley, where sea water entered at 1000 h, the temperature rose from 9·1° C (that of sea water) at 1000 h, to 15·5° C at 1600 h. At the western end of the pool sea water had little effect at high water and the temperature rose from 15·5° C at 1000 h to 22·2° C at 1600 h. The day was sunny, but with some breeze; air temperature in the breeze rose from 11·4 to 16·4° C over the six hours.

Oxygen concentrations of samples also taken on 12 May 1953 were lower in the morning than in the evening, presumably in accordance with the photosynthetic and respiratory activities of the algae in the pool (see below). Where the pool was undisturbed by sea water, oxygen concentrations rose sharply from the low value of 2·83 ml/l. at 1100 h to 12·22 ml/l. at 1600 h. Near the mouth of the pool sea water entered at 1000 h and oxygen concentration was 6·5 ml/l. (about that of sea water) at that time; it rose to 10·00 ml/l. in the next six hours.

The biological features of the pools have been studied in some detail, and these may now be described. Three species of algae (all Chlorophyceae) formed three zones around the sides of the pools. *Enteromorpha intestinalis* formed the upper zone, which extended between the pools, *Chaetomorpha aerea* the middle zone, and *Cladophora rupestris* the lowest zone, and the last species was particularly abundant in the deeper parts of the pools. In the crevice between the lower pool and the sea the *Enteromorpha* and the *Chaetomorpha* were absent, but the *Cladophora* was profuse.

Collections of the fauna were made in May 1953 and January 1954. Species taken on both occasions include *Procerodes ulvae* (Oersted), *Littorina saxatilis* (Olivi), *Gammarus duebeni* Lilljeborg, *Jaera nordmanni* (Rathke), *J. albifrons* Leach, *Ligia oceanica* (L.) and *Idotea viridis*. Other species collected during the summer were *Leander serratus* (Pennant), *Carcinus maenus* (Pennant), *Gasterosteus aculeatus* L. and chironomid larvae; whilst additional species in winter included *Gammarus locusta* (L.) and *Melita palmata* (Montagu). At the seaward end of the crevice in May were *Procerodes ulvae*, *Jaera albifrons*, *Gammarus duebeni*, *Hyale prevosti* (Milne-Edwards) and *Littorina saxatilis*, but no *I. viridis* were present.

It is clear that purely marine organisms will often be washed into the pools even though they may not survive; *I. viridis* was the only idoteid found in the pools.

As has been stated, several writers describe *I. viridis* as a brackish water form, and these observations agree. However, as Forsman (1951) points out for *Gammarus duebeni*, it only applies in so far as *I. viridis* is found in marine habitats more or less influenced by fresh water. It is not true to say that *I. viridis* (or *G. duebeni*) is physiologically dependent upon brackish water (as will be demonstrated later, on p. 265), nor is it necessarily found in water which is permanently brackish. The common features of the Manx localities where *I. viridis* occurs appear to be: a sheltered, permanent pool with a sporadic supply of both salt and fresh water, and a vegetation of the larger green algae. These features conform with the habitat of *I. viridis* on Little Cumbrae Island (Dr R. B. Pike, personal communication), though the habitat described by Howes (1939*a*, *b*) seems to be subject to rather less salinity changes than those described for the pools at Scarlett. In the river Tamar (Crawford 1937, Spooner & Moore 1940) salinity changes do occur, and the association of *I. viridis* with green algae or *Zostera* is noted by Spooner & Moore.

ECOLOGICAL ADAPTATION AMONGST *IDOTEA* SPECIES

Some experiments have been carried out to determine how different *Idotea* species react to conditions designed to simulate various environmental factors.

(*a*) *Resistance to changes in salinity*

Ranges of salinity tolerance have been worked out for *I. viridis*, *I. granulosa*, *I. pelagica* and *I. emarginata*. Solutions were made up from filtered sea water diluted with distilled water or concentrated with Tidman's Sea Salt. 2000 ml of each of the following solutions were made up: 0, 12·5, 25, 50, 75, 100, 112·5, 125, 150, 175 and 200 % sea water; salinity therefore ranged from 0 to 70‰. Fresh solutions were made up at intervals. All *Idotea* were kept in sea water and were used as soon as possible after capture. Five specimens of one species were placed in each solution, and the condition of the specimens was noted every few hours. The specimens were removed

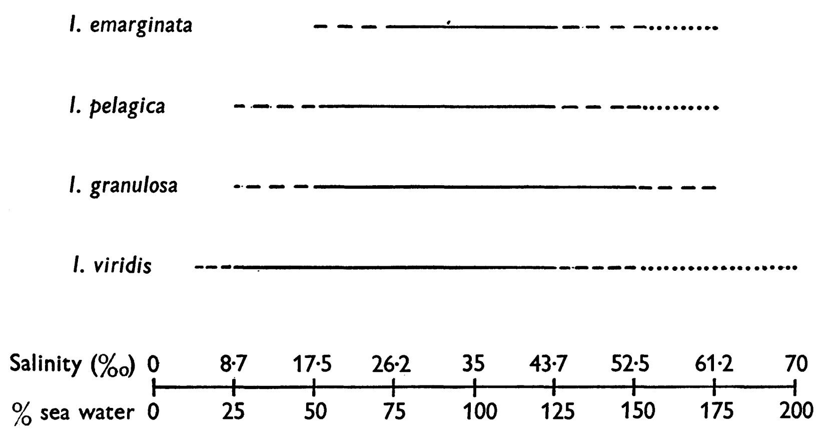

Fig. 4. Ranges of salinity toleration of four species of *Idotea*, after 48 h under experimental conditions (——, over 80 % healthy survival; - - - -, less than 80 % healthy survival; . . . ., a few surviving, but comatose).

when their condition had been constant for some hours (usually after about 48 h), and the experiment was repeated with each species in turn. All four series of experiments were carried out a second time with other specimens of each species, and there were no major discrepancies between the two sets of experiments. Temperatures ranged from 10–14° C, depending on when the experiment was carried out, but the temperature during any one experiment never varied by more than one degree Centigrade altogether.

I. viridis survived longer in reduced salinities than the other three species (Fig. 4), and the lowest salinity tolerated by *I. viridis* in these experiments agrees closely with that described for Swedish specimens, namely 4–6‰ (Dahl 1944). The shore species *I. pelagica* and *I. granulosa* will be subject to the influence of rainfall on the shore, and it is significant that they have a lower limit of toleration than the sublittoral species *I. emarginata*. The position is less clear-cut in the higher salinities, but certainly some *I. viridis*, and no other species, were alive, though comatose, after 48 h in 200 % sea water. Indeed, some *I. viridis* were alive, though torpid, after four weeks in open dishes (with food), from which water had been allowed to evaporate and the salinity raised to more than twice that of sea water; this was not tried for other species. *I. viridis* is clearly a markedly euryhaline species; it tolerates lower salinities than other species, and no others survived for any length of time in 200 % sea water.

(*b*) *Resistance to desiccation*

The shore idoteids *I. granulosa* and *I. pelagica*, unlike the sublittoral and brackish water species, are periodically exposed to the air, and it is of interest to study this as a factor limiting the distribution of the various species.

When placed in constant humidity chambers, in which humidity was controlled by the use of sulphuric acid solutions (Williamson 1951), it is found that the shore species show no appreciably higher resistance to desiccation than a sublittoral species, *I. emarginata*, or the brackish water species, *I. viridis*. Field observations tend to bear this out since *I. granulosa* shelters in wet weed when the tide is out and *I. pelagica*, though inhabiting barnacle shells on exposed coasts, seems to prefer the presence of some algae (see p. 262), presumably for the moisture which the latter retain. It seems, therefore, that exposure to the air is an absolute limiting factor for all species, and that it is some factor other than tolerance of exposure to the air which allows the shore species to inhabit the intertidal zone which the other species seem unable to colonize.

(*c*) *Possible structural adaptations*

The relation between ecology and body form of organisms in seaweeds has been discussed by several authors (see Dahl 1948), and there may be some relation between wave action and the morphology of *Idotea*. Those species which are tolerant of wave action, *I. pelagica* and, to a less extent, *I. granulosa*, are more robust and have stout appendages, which are less liable to be broken and which enable the *Idotea* to cling on more strongly. *I. pelagica* is subject to greatest wave action and it has the shortest antennal flagellum of any species studied (Naylor 1955 *c*), besides having the largest claws. Perhaps it is inability to tolerate wave action which precludes sublittoral species from inhabiting the intertidal zone.

DISCUSSION

Idotea occur mostly amongst algae and, since shore algae may be washed away from the intertidal zone and sublittoral algae may be washed ashore, some mixing of sublittoral and littoral *Idotea* must take place. Wherever possible, therefore, extended observations must be made on resident breeding populations, if specific environments are to be determined.

Distinct environments are attributable to the following species: *I. viridis*, in brackish water; *I. granulosa*, amongst algae in the littoral zone, in moderate shelter; and *I. pelagica*, on exposed coasts amongst barnacles. Laboratory observations show that *I. viridis* is better able to tolerate reduced salinities than other species, and it does seem that the shore species are better adapted, structurally, to withstand the mechanical effects of wave action.

The distribution of the sublittoral species is less clear, but present observations on *I. emarginata* and *I. neglecta*, and those on *I. neglecta* in Norway (Kjennerud 1950) agree in suggesting that these two species are associated with decaying organic matter (see also Sars 1899, Elmhirst 1946). Kjennerud found *I. neglecta* on decaying animal matter, whereas *I. emarginata* was found amongst broken algae at Port Erin, but no valid generalization may be made from these observations; *I. neglecta*, for example, is often found together with *I. emarginata* on decaying algae (p. 257). No published work can be found on breeding populations of the two other sublittoral species, *I. baltica* and *I. linearis*, and further work is necessary, particularly with regard to the suggestion that *I. baltica* is associated with surface drift weed.

It may be that all species are potentially capable of survival in the sub-littoral zone, where conditions are fairly uniform. But, as Forsman (1951) points out when dealing with *Gammarus duebeni*, 'a very variable and therefore difficult and hazardous environment can only be mastered by especially hardy species', and the restriction of a species to a particular region, with exclusion from other habitats which it could tolerate, is possibly due to biological factors such as competition (see also Beadle & Cragg 1940, Jones 1948). Such factors may restrict *I. pelagica* and *I. viridis* to their respective rigorous environments.

These conclusions apply to Manx, and probably to other British specimens as well, but to what extent they apply to other regions is not clear. On the west coast of Sweden, where conditions are almost fully marine, *I. viridis* is a brackish pool species (Forsman 1951), and *I. baltica* seems to be associated with drift weed (Dahl 1944). In the Gulf of Finland, however, *I. viridis* is an open water form and it extends, with *I. granulosa* and *I. baltica*, into regions where salinity is permanently below 10‰; *I. baltica* is there associated with attached *Fucus vesiculosus* (Segerstråle 1944). Not only is salinity low in that region, but tidal influence is negligible, and several organisms appear to have different habitats from specimens of the same species in fully marine conditions.

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SUMMARY

1. Manx *Idotea* are divided into three groups on an ecological basis: (*a*) *I. emarginata*, *I. neglecta*, *I. baltica* and *I. linearis* are predominantly sublittoral, down to about 10 fathoms, amongst decaying and living algae; (*b*) *I. granulosa* and *I. pelagica* are shore species, the former amongst *Ascophyllum* and *Fucus*, and the latter on exposed shores, where it shelters in empty barnacle shells; and (*c*) *I. viridis* inhabits brackish pools at HWN and above. The horizontal and vertical distribution of the last three species are discussed in some detail.

2. Experiments were carried out to test the adaptation of the various species to environmental factors such as salinity and humidity, and ecological adaptation amongst the species is discussed.

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