

ON *GAMMARUS ZADDACHI OCEANICUS* SEGERSTRÅLE

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(Text-figs. 1-3)

In a survey of the British species of *Gammarus* inhabiting estuarine waters (Spooner, 1947), it was found necessary to divide *G. zaddachi* Sexton into two well-marked morphological forms, with different salinity optima, which in fact behave as distinct species. They were, however, on account of their similarity in important structural features, retained as a single species and named *G. z. zaddachi* and *G. z. salinus* respectively. At the time little could be said about a third subspecies, essentially marine in its distribution (but ranging into brackish water), which Segerstråle (1947) independently described as *G. z. oceanicus*.

It is now clear that *G. z. oceanicus* is, geographically, the most widespread and abundant form of the three, occurring generally on shores in shallow coastal waters all over the boreal and subarctic region of the Atlantic area, southward to Britain, Denmark and the Baltic, and eastward along the Siberian coast at least to 140° E. On the American coast it extends southward at least to New York.

G. z. zaddachi and *G. z. salinus* are both temperate forms, and, as far as is known, confined to the brackish waters of Europe. In the Baltic Sea all three subspecies overlap very widely.

In this further contribution on *G. z. oceanicus* various records of occurrence are given which help to fill in the picture already outlined by Segerstråle (1947, 1948), but which in particular establish the existence of this form as dominant along much of the coast of Scotland.

The ecological relations existing between *G. z. oceanicus* and *G. locusta* on the one hand, and between it and *G. z. salinus* on the other, can now be discussed, but important gaps in knowledge still exist.

A fortunate chance of further exploring the *Gammarus* fauna of the more inaccessible parts of the north-western British coasts was provided by Dr Dorothy C. Gibb, who, in 1948 and 1949, collected a long series of samples of the fauna associated with the brown alga *Ascophyllum nodosum* var. *mackaii*. The great bulk of this fauna was found to consist of littoral gammarids. Among these, especially in the more northern stations, *Gammarus zaddachi oceanicus* occurred with some regularity, evidently flourishing in the littoral zone where this weed, amongst others, provides cover. I am much indebted

to Dr Gibb for the opportunity of identifying the gammarids she had collected. The value of her samples is enhanced by the detailed information of the habitats she acquired during her investigations and will publish in due course.

To various zoologists whose help I have gratefully acknowledged in presenting or lending material of *G. zaddachi*, I must now add the following: Mr J. S. Colman, Mr G. R. Forster, Mr N. A. Holme, and Dr Sven Segerstråle. It has been very instructive to compare samples of different forms from the Baltic, sent to me by Dr Segerstråle, with our own.

My special thanks are also due to Dr Isabella Gordon for the facilities afforded to me for examining the material preserved in the British Museum.

THE CHARACTERS OF *GAMMARUS ZADDACHI OCEANICUS*

A description is given by Segerstråle (1947, pp. 226-9, fig. 3, *a-g*). The main *zaddachi* characters are seen in the form of the gnathopods (in each sex), the well-excavated lateral sinus of the head, the moderate depth of the coxal plates, the shallow rounded ventral expansion of coxal plate 4, the moderately produced epimeral plates, and in the somewhat shortened uropod 3 inner ramus. The arrangement of the antennal hair tufts is also really typical of the species, although the relative shortness and sparseness of the hairs renders this feature much less obvious.

The hinder part of the body is relatively glabrous, as in *G. z. salinus*. Younger specimens of the two subspecies resemble each other closely, but can be distinguished at least by reference to the characters of antenna 1. Adults are readily told apart by the setation and structure of antenna 1; by the dorsal profile of the urosome; and, in life, by the body coloration (see below). From *G. z. zaddachi*, it is further distinguished by the lack of those features in which this relatively hairy form differs from *G. z. salinus* (see Spooner, 1947, pp. 20-1). *G. z. oceanicus* also reaches considerably larger sizes than either of the other two forms, even near the southern limit of its geographical range.

Antenna 1 (Fig. 1). The peduncle of this limb provides the most critical diagnostic feature of *oceanicus*, approaching, as it does, that of *G. locusta*. The hair tufts on the ventral surface are sparse: on segment 1 there are two thin tufts (excluding the apical tuft), rarely a small third, composed of very few shortish hairs, as contrasted with at least four tufts in *G. z. salinus*, and one tuft (sometimes a second slight one) in *G. locusta*; on segment 2 there are normally three tufts, as compared with at least four in *G. z. salinus* and one or two in *G. locusta*; on segment 3 there is one strong tuft, which is often entirely lacking in *G. locusta*, and represented by at least two tufts in other *G. zaddachi*. The relative lengths of the segments approximate to ratio of 10:7.4:3.4, that is to say segments 2+3 are together a little longer than segment 1 (much longer in other *zaddachi*, and just shorter in *locusta*).

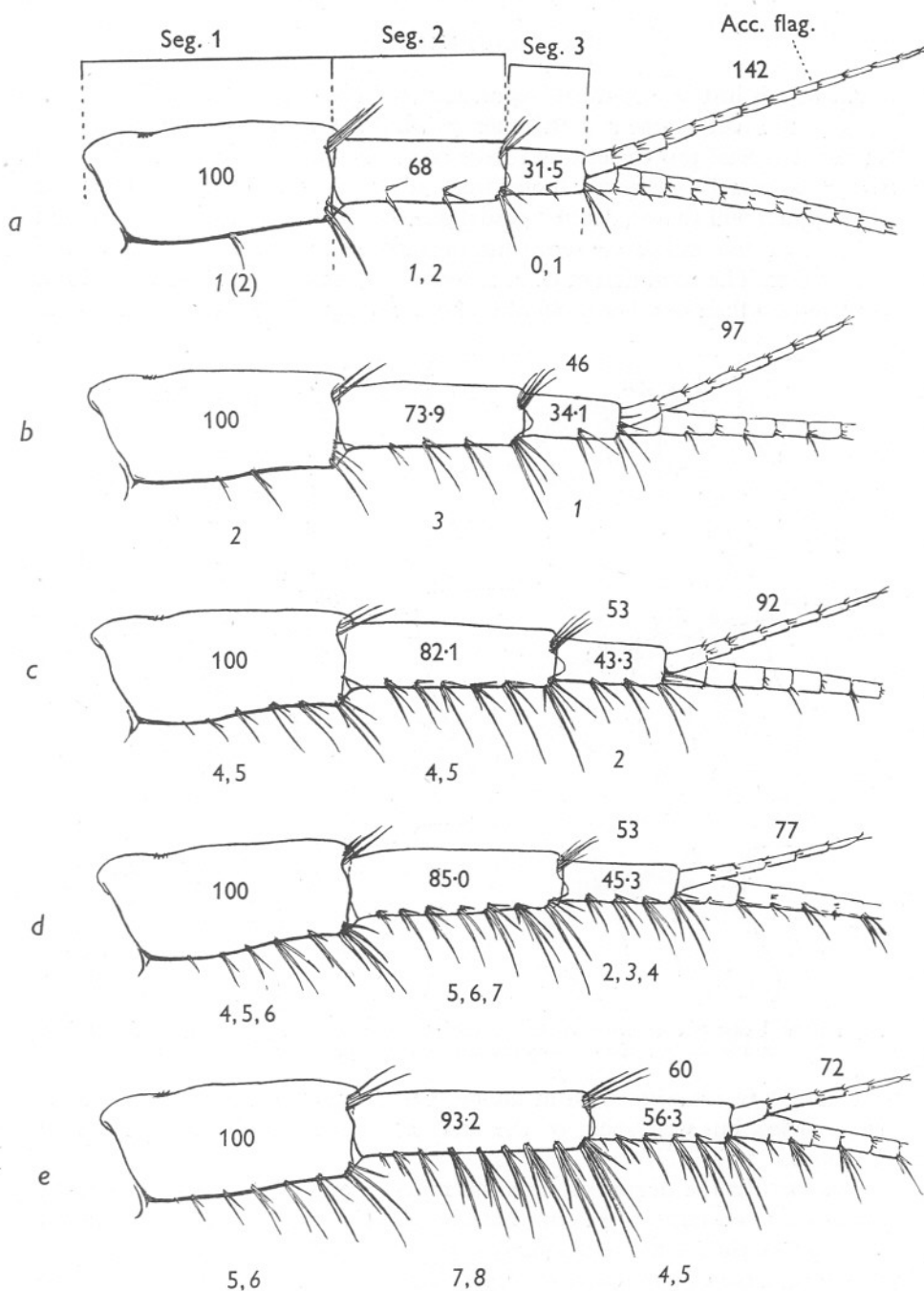


Fig. 1. Antenna and peduncle of an adult male of (a) *G. locusta*, (b) *G. zaddachi oceanicus*, (c) *G. z. salinus*, (d and e) *G. z. zaddachi*; drawn somewhat schematically, viewed from the inner surface. The numbers written on the segments and against the accessory flagellum refer to the mean length relative to the first segment as 100. The end-points of measurements are indicated at the top of the diagram (against the peduncle segments of a). The number written above segment 3 refers to the ratio of this segment to segment 2. The numbers written below the segments represent the typical number of ventral hair tufts present in adults of various ages; those italicized being the most characteristic.

Segment 3 is just less than half segment 2 (as in *locusta*), whereas it is a little longer than half segment 2 in other *zaddachi*. The ratios given in Fig. 1 represent typical proportions and have been calculated from the averages of several accurately measured limbs from adult males. Further reference to this diagram will show a distinct gradation of various metrical characters with *G. locusta* at the end of the series and the most intensely hairy *G. z. zaddachi* at the other. The condition in *G. z. oceanicus* is diagnostic, and is rather closer to *G. locusta* than to other *zaddachi*. The accessory flagellum length is some-

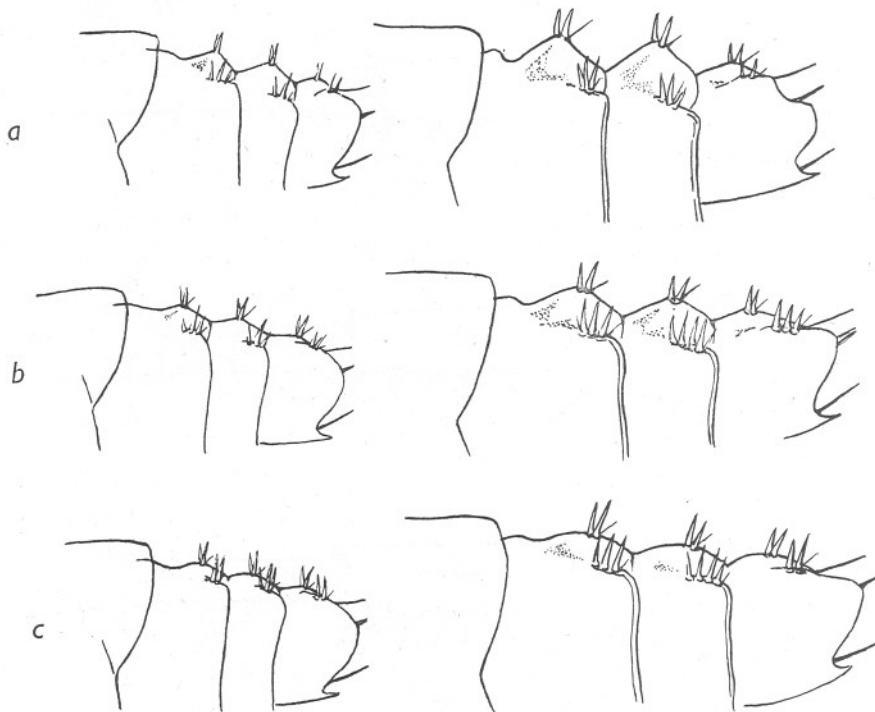


Fig. 2. Dorsal part of urosome viewed laterally, of (a) *G. locusta*, (b) *G. zaddachi oceanicus*, and (c) *G. z. salinus*; immature animal on left, adult male on right.

what longer in *oceanicus* than in *salinus*, possessing 9 or 10 segments in the larger males, but well short of the unusual length of this limb in typical *G. locusta*.

Urosome. In the degree of elevation mid-dorsally of urosome segments 1 and 2, *G. z. oceanicus* is intermediate between *G. locusta* and *G. z. salinus* (Fig. 2). The elevations are distinctly angled, but make an angle of some 135° , whereas in a comparable stage of *G. locusta* they are nearly right-angled. The elevations of *G. z. salinus* are distinctly flattened.

Body colour. This is of a variety of shades of brown (reddish olive to greenish or yellowish), often semi-transparent, without strong banding, at most a

suffused darkening along the margins of the segments. The female is usually darker (as in *G. locusta* and *G. z. salinus*). Lateral orange pigment patches may be present on pleon segments 1-3, but these may be lacking or composed of colourless globules. (In Finland, it seems they are usually lacking or at least colourless.) There are never spots on the mesosome segments laterally, as in *G. locusta*. Where *G. z. oceanicus* and *G. z. salinus* occur together, it is apparently possible to separate the latter by eye owing to its stronger transverse banding.

Size. Adult males normally appear to reach a length of 22-25 mm. (from rostrum to apex of telson) in Scotland, the maximum observed being 27.5 mm. Segerstråle gives maximum of 26 mm. for the Baltic, and Stephensen (1940a,b) one of 38 mm. for the Arctic, and a single exceptional male of 39 mm. from Iceland. The eggs are of similar proportions to those of other *zaddachi*.

Habitat. Being a marine coastal form, inhabiting the algal zone of shallow waters up to the mid-tide level of the shore, it is apt to occur in company with *G. locusta* in the more southern part of its range (see p. 138). No difference in the general habits of the two forms is yet known. Being also tolerant of some degree of dilution of the sea water and thus penetrating into estuaries, it reaches the zone inhabited by *G. z. salinus*, in so far as the geographical ranges overlap (see p. 137). Apart from these two, it will not normally be accompanied by any other *Gammarus* (s.s.) species in samples from the British Isles. Exceptions to this rule may be found in certain 'mixed' habitats, e.g. at coastal outflows of fresh water which permit the fauna of a stream to mix with that of the shore over which it flows.

DISTRIBUTION OF *GAMMARUS ZADDACHI OCEANICUS* IN BRITAIN

A full list of the British localities from which *G. z. oceanicus* has been recognized is now given. The specimens in question have all been examined by the writer. The following abbreviations are used: G, from the collections of Dr Dorothy Gibb, all from the middle of the intertidal zone amongst *Ascomphyllum*. A.D.H., Prof. A. D. Hobson; B.M., British Museum; coll., collected by; Coll., collection. Localities are classified under vice-counties according to the customary scheme (see, for example, Roebuck, 1921).

Scotland. W. SUTHERLAND. Loch Laxford, N. side, Loch a Chadhfì, G, 22. ix. 48, 5 ♂♂, 6 juv. (apparent inhibited development); Weaver's Bay, G, 21. ix. 48, bays on east and west side, 1 ♂, 3 ♂♂. Badcall Bay, N. side, G, 21. ix. 48, 2 juv. Kylestrome, G, 20. ix. 48, 2 small ♂♂, 1 juv. W. Ross. Gairloch, Badachro Bay, G, 17. v. 48, 1 young ♂. Loch Torridon, Camas Roil, G, 15. v. 48, 5 ♂♂, 5 ♀♀; Ob Mheallaidh, 8. v. 48, 5 ♂♂, 6 ♀♀. Loch Long, Conchra, G, 18. v. 48, 3 ♂♂, 2 ♀♀. Loch Duich, G, in four sites at which samples were taken regularly: site 1, in company with *Gammarus duebeni* (fresh-water seepage over shore), between 18. vi. 48 and 19. i. 49, 21 ♂♂,

8♀♀, 1 juv.; site 2, between 18. vi. 48 and 31. v. 49, 29♂♂, 10♀♀, 3 juv.; site 3, between 18. vi. 48 and 3. iii. 49, 19♂♂, 10♀♀, 7 juv.; site 4, between 18. vi. 48 and 31. v. 49, 41♂♂, 18♀♀, and 4 juv. N. EBUDES. S. Rona, vii and viii. 37, A.D.H. Coll., in stream flowing over shore, well below H.W., ♂ and immature (Beadle & Cragg, 1940, as '*zaddachi* hairless var.'; Spooner, 1947, p. 43). Raasay, vii and viii. 37, A.D.H. Coll., in stream over shore, 6♂♂, 1♀, 11 immature (Spooner, 1947, p. 43). Skye: Loch Dunvegan, G, 2. iv. 48, 2♂♂, 2♀♀; Loch Eishort, G, 6. iv. 48, large ♂ and ♀; Loch Ainort, G, single examples on two occasions (28. x. 48 and 16. xii. 48) at one of four sites regularly sampled between vi. 48 and vi. 49; Strollamus, G, at site 3 (one of three sites regularly sampled), on six dates between 26. iii. 48 and 8. vi. 49, 8♂♂ and 9♀♀. WESTERNESS. Loch Nan Cilltean (stream inflow), G, 8. iv. 48, ♂ and 2♀♀, in company with both *G. z. salinus* and *G. z. zaddachi*. MID EBUDES. Mull: Loch Selve, G, 12. iv. 48, in two samples, 15♂♂, 10♀♀. ARGYLL. Loch Sunart, G, 9. iv. 48, 7♂♂, 4♀♀. Loch Feochan, G, 1. iii. 48, 11♂♂, 7♀♀. Loch Riddon, G, in two of three sites regularly sampled, a few examples only—site 1, 1. ii. 49, 1♂, 1♀; site 3, 11. xi. 48, 1♂, 21. xii. 48, 1♂, 1 intersex, 1♀, 1. ii. 49, 1 large ♂. CLYDE ISLES. Cumbrae, east of Keppel Pier, shore near L.W., 16. ii. 43, 2 large ♂♂ (Spooner, 1947, p. 42 as *salinus*; specimens recently re-examined). No further examples have yet been obtained in the Millport area, where *G. locusta* is undoubtedly the commoner form. KINCARDINE. Muchalls, vii. 49, G. R. Forster, 22 ex. among sample of gammarids collected on the shore, including 8 mature ♂♂, 1 large ♀, and 13 young adults and immatures. FORFAR. Firth of Tay, among the Tees Survey collections (Alexander, Southgate & Bassindale, 1935), in sections IX and X of the estuary (Spooner, 1947, p. 43, as Segerstråle's subspecies = *oceanicus*; p. 52, as '*G. zaddachi* saline form').

England and Wales. DURHAM. Ryhope, Norman Coll. as '*locusta*' (B.M. 1911. 11. 8. 18866-70, part), 2♂♂, 2♀♀ ovig., 1 imm., with 3 *G. locusta*. N.E. YORKS. Robin Hood's Bay, one juvenile, shore between Mill Beck and Stoupe Beck, J. S. Colman and F. Segrove (who inform me that *G. locusta* is the common marine species here, as I was able to see for myself in October 1950).

The distribution map (Fig. 3) gives a fair impression of the extent of the range of *oceanicus* in Britain. There is reasonable negative data for localities south of the areas mentioned, that on the east coast being weakest. Dr Gibb's material includes ten samples from the north and west coasts of Ireland, collected under similar conditions to those from Scotland. *G. z. oceanicus* is lacking in these as well as in such other Irish material as I have seen. The Isle of Man, too, seems to be beyond the southern limit: Mr N. S. Jones (*in litt.*) has kindly confirmed that *oceanicus* has not yet been recognized there. Robin Hood's Bay would seem to be close to the extreme southern limit on the north-east coast, as is Heligoland on the other side of the North Sea.

DISTRIBUTION ABROAD

The essential northern character of the range of *G. zaddachi oceanicus* was shown by Segerstråle (1947, fig. 4). Additional localities in north-east Europe were given by Segerstråle in 1948; and others identified by the present writer, hitherto unpublished, are listed in Appendix I (p. 142).

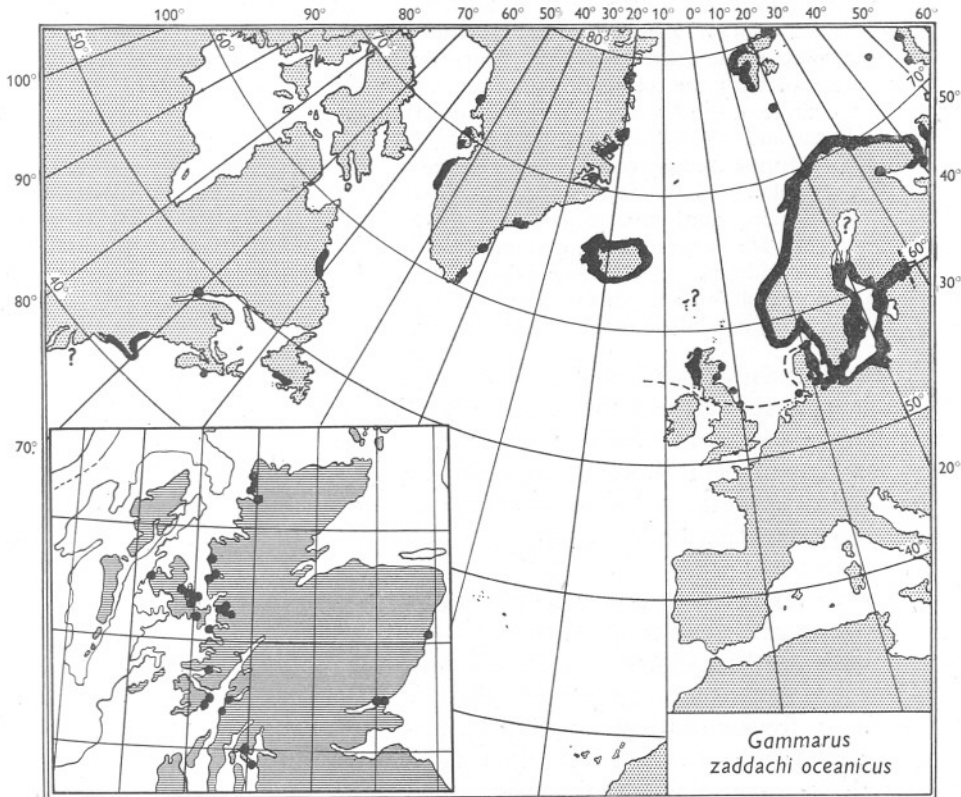


Fig. 3. Distribution of *G. zaddachi oceanicus*, showing regions in which it has so far been identified, except for its eastward extension to 140° E. along the north coast of U.S.S.R. Inset, localities from which *G. z. oceanicus* has been identified in Scotland. Note. The exact locations of Labrador and Newfoundland samples are not known. The absence of records along much of the east coast of Scotland is simply due to lack of investigation.

It is now possible to take account of the records given by Stephensen (1940*a*, *b*, 1944), Holmes (1904), Dementieva (1931), and Gurjanova (1929, 1931, 1932, 1936), records which can, for some good reason or another, be attributed with certainty to *G. zaddachi oceanicus*. These authors have given much information on the status of *Gammarus* in northern waters, and in the light of present knowledge it is often possible to distinguish clearly which of their observations refer respectively to *G. wilkitzkii*, *G. setosus*, or *G. zaddachi oceanicus*. All necessary details are given in Appendix II (pp. 144-7).

The more complete picture now obtained of the geographic range, though still incomplete with regard to its extreme eastern and western limits, may be summarized as follows (Fig. 3).

Coasts bordering the Arctic Ocean southward from the south fringe of Franz Joseph Land (60° E.) and north-east Spitsbergen, both areas lying on the 80th parallel. North coast of Siberia, from at least 140° E. (Brothers Laptev Sea) westward. Novaya Zemlya, at south-western end of the northern island, and west coast of the southern island. Spitsbergen, along the whole western side, where apparently the commonest gammarid. Bear Island. North coast of Russia, on the shore of the Kara Sea and of Chashskaya Bay, westward along the Kanin Peninsula and White Sea coasts. [No published data for coast between 67° and 48° E.] Murmansk coast generally, continuing along whole coast of Norway, southward to Oslo Fjord. Kattegat and all Baltic coasts south of $63^{\circ} 30'$ N. Heligoland. Great Britain, southward to coast of north-east Yorks and Firth of Clyde. (Faeroes?) Iceland, on north, east and west coasts. Greenland coasts to 77° N. on the east side and 73° N. on the west. North American Atlantic coasts including Labrador, Gulf of St Lawrence, Newfoundland, Nova Scotia, Massachusetts, and Connecticut, possibly extending farther south (see p. 140).

It occurs mainly in shallow coastal waters, captures in depths greater than 25 m. being mainly close to the shore, such as in the Norwegian fjords. There are, however, occasional records from deeper water in the open sea. In arctic and subarctic waters it is often accompanied by *G. setosus* Dement. (a species more exclusively restricted to the tidal zone and very shallow water) and sometimes by *G. wilkitzkii* Birula (a species less restricted to the immediate vicinity of the shore).

The extent to which overlapping occurs with the temperate forms *G. locusta* and *G. zaddachi salinus* is discussed below (pp. 137-9).

On many northern shores *G. zaddachi oceanicus* is a dominant littoral animal, and must be of great account bionomically. For example, in Iceland, it is 'one of the most frequent littoral Amphipoda, occurring almost everywhere along the coasts of Iceland... On account of its enormous frequency it is of considerable importance as food for many valuable fishes, as young gadids and plaice, but especially for the charr, when living in saltwater.' (Stephensen, 1940b; as *G. locusta* (L.) s.s., p. 56.)

Its hardiness and adaptability are shown by its persistence in areas such as Cheshskaya Bay, east of the Kanin Peninsula, the restricted fauna of which is discussed by Gurjanova (1929); and more especially, along the north Siberian coast, on the shore of the Nordenskiöld Sea between the meridian 120 and 140° E. The sea here has greatly reduced salinity owing to the discharge of the Lena and other Siberian rivers, and the temperature is always below zero C. The fauna of the littoral is necessarily reduced, with a tidal range of only a few inches; and the adverse effects of ice action and lack of algal cover reduce it further. The only species of littoral animal recorded, indeed, was *G. 'locusta'* (= *zaddachi oceanicus* + *setosus*) (Popov, 1932).

RELATION TO *GAMMARUS ZADDACHI SALINUS*

G. zaddachi salinus does not tolerate normal sea-water salinities, and so, in Great Britain, it is virtually confined to estuaries. It is found, however, in marine habitats when the salinity does not rise above 31 ‰, as in part of the Bristol Channel. In the Baltic Segerstråle (1947) has found it to be widely spread.

In the Scottish records previously given (Spooner, 1947, p. 42), that for Cumbrae should be transferred to *oceanicus*, but the Fairlie Sands and Clachan Strand records apply to typical specimens of *salinus*. Additional British localities for *G. z. salinus* are given below, which establish its occurrence in Cumberland, in the west and north of Ireland, and well up on the west and east coasts of Scotland. (As before, G refers to Dr Gibb's material.)

England and Wales. S. DEVON. R. Yealm estuary, present in both Coflete and Newton Creeks (in 1948), but confined in them to a stretch of a few hundred yards. R. Exe estuary, present in small sample of gammarids taken near Starcross, 23. vi. 47. GLAMORGAN. Cardiff, Bristol Channel off Flatholme, coll. R. D. Purchon, 12. ix. 47, 4 ♂♂; in trawl 29. ix. 47, ♂, 4 ♀♀ (conforming with occurrence on the opposite Somerset coast). CUMBERLAND. R. Esk estuary, at Eskmeals, 31. v. 50, plentiful in river channel, upstream from the railway bridge, in company with *G. z. zaddachi*. E. NORFOLK: Breydon, coll. R. Gurney, viii.-21, 1 ♂ (B.M. 1949.11.30.9.)

Scotland. ARGYLL. Loch Riddon, G, at two of three sites regularly sampled over a year: site 2, 11. viii. 48, 1 ♂ and 1 ♀; site 3, 30. ix. 48, 1 ♂, 2 ♀♀, 1 juv., 11. xi. 48, 3 ♂♂, 1. ii. 49, 1 ♂ (in site 3 accompanying *G. z. oceanicus*). WESTERNNESS. Loch Nan Cilltean, G, 8. iv. 48, 3 (2 ♂♂ and 1 ♀ with eggs) in a sample containing also 3 *G. z. oceanicus*, 5 *G. z. zaddachi*, 7 *Marinogammarus marinus*, and 1 *M. stoerensis*, showing clear mingling of faunas of stream and shore. S. ABERDEEN. Aberdeen, coll. G. R. Forster, 1949, 2 ♂♂. N. ABERDEEN. Newburgh, estuary of R. Ythan, coll. G. R. Forster, vii. 49, 3 ♂♂, 1 ♀, 2 juv.

Ireland. W. DONEGAL. Mullroy Bay, G, area 1 (head of estuary), 8 ♂♂, 7 ♀♀ (breeding), in company with about equal number of *Gammarus z. zaddachi*. N. GALWAY. Ballynakill Bay, G, north-east corner, 4 juv. with 1 ♀ *G. z. zaddachi*.

There is therefore a region of considerable extent along the west coast of Scotland (at least from the Firth of Clyde to the border of West Ross (probably farther); as well as the greater part of the north-east coast of England and east coast of Scotland, where *oceanicus* and *salinus* may come in contact. The Tay estuary samples contain only *oceanicus* in the region where *salinus* would be expected, but the number of specimens is small, and no significance can be attached to the absence of the latter. More detailed investigation in this region would be of interest. That *oceanicus* and *salinus* can overlap, in the way that

locusta and *salinus* overlap, is shown by the samples from Loch Riddon and Loch Nan Cilltean. In the last, unique so far for Britain, all three subspecies of *G. zaddachi* occur together, as frequently may happen in collections from parts of the Baltic.

There is no evidence at all of intergrading between *salinus* and *oceanicus*, and it may be inferred that, as has been proved between the typical form of *zaddachi* and *salinus*, they cannot interbreed. For all practical purposes, therefore, the three forms can be treated as distinct species.

OVERLAP WITH *GAMMARUS LOCUSTA*

Speaking broadly the marine 'niche' occupied by *G. zaddachi oceanicus* in the north is occupied by *G. locusta* (L.) in south Britain and the Low Countries southward. There is therefore special interest attached to the question of the ecological relations of the two forms in those areas in which overlap occurs. So far an adequate detailed investigation has not been made, but would certainly be valuable.

In Europe the overlap zone begins in Denmark. *G. locusta* is still the dominant form on the west coast, where indeed the existence of *G. z. oceanicus* has still to be proved. On the Baltic shores both forms are numerous, and *oceanicus* becomes dominant passing eastwards into the low salinities of the Baltic Sea. As Segerstråle (1947) shows, *locusta* reaches Finland but has a lower limit of some 5.5‰ , while *oceanicus* persists to about the 2.5‰ isohaline. Along the whole coast of Norway *oceanicus* is clearly dominant, *locusta* occurring sparingly from Oslo fjord to $70\frac{1}{2}^{\circ}$ N. (Appendix II, p. 146). In Iceland the occurrence of *locusta* has recently been proved (Segerstråle, 1950), but it is clearly overwhelmingly outnumbered by *oceanicus*. There is nothing in the data associated with these continental records to suggest any important difference in habitat, except only that *oceanicus* is rather more tolerant of reduction in salinity.

In Britain, passing northwards, all that can be said so far is that *locusta* is still the dominant form at the known southern limit of *oceanicus* (Clyde Sea Area and north-west Yorkshire), but in no great distance *oceanicus* becomes at least as frequent as *locusta*. At least this is so in the sheltered lochs of the west coast, where *oceanicus* perhaps adapts itself more readily to the variously lowered salinities. Among Dr Gibb's samples of the *Ascophyllum mackayi* fauna there were very few *locusta* at all. On the other hand, only *locusta* have so far been seen in samples from Muck (Inner Hebrides) and Barra (Outer Hebrides). There is a distinct tendency for samples to contain only one or other of the two forms, and some real segregation by habitat is suggested. It is this aspect, in particular, which requires further study.

THE BREEDING PERIOD OF *GAMMARUS ZADDACHI OCEANICUS*

In Britain most species of *Gammarus* breed in all months of the year, including *G. zaddachi zaddachi* and *G. z. salinus*. Segerstråle (1950) finds that these two forms also breed throughout the year in Finland, but points out that *G. z. oceanicus* has a resting period from the end of July to mid-November, and that during August, September and October no females could be found with broods in their pouches.

Evidence from British samples also points to a non-breeding season in the autumn for *oceanicus*. Females which are not breeding have their brood-plates reduced to an immature condition (smaller in size and lacking the fringe of finger-like processes): they are therefore at once recognized from females which are potentially capable of breeding, even if the contents of the brood pouch have been discharged or accidentally lost after preservation.

TABLE I. BREEDING IN *GAMMARUS ZADDACHI OCEANICUS*

Period	Adult females		Approx. percentage breeding
	Developed	Undeveloped	
1 Jan.-6 Feb.	8	5	60
7 Feb.-14 Mar.	18	1	95
15 Mar.-20 Apr.	23	0	100
21 Apr.-26 May	13	0	
27 May-2 July	4	0	
3 July-7 Aug.	3	2	60
8 Aug.-13 Sept.	1	3	25
14 Sept.-19 Oct.	—	—	—
20 Oct.-25 Nov.	0	3	0
26 Nov.-31 Dec.	3	14	20

Table I shows the results of analysing Dr Gibb's west-Scottish material. The year is divided into ten periods. In the first column is given the number of reproductively active females observed, and in the second that of females clearly large enough to be mature, but with reduced brood plates. The latest animal with a brood was taken on 11 September, and the earliest on 4 December. But there is evidently considerable variation among individuals, and the rest period for any single individual could easily be 5 months. The data, as far as they go, indicate a non-breeding season from early September to mid-December, with its peak at the end of October. There is maximum breeding in March, April, May and June.

The onset of the non-breeding season appears to be later than in Finland by perhaps a month or 6 weeks, and renewal of reproduction also to be later by about a month.

GAMMARUS ZADDACHI OCEANICUS IN AMERICA

A few years ago, through the kindness of Mrs Sexton, I was able to examine some so-called *G. locusta* from eastern North America (lent by Dr C. R. Shoemaker). From sketches and measurements made at the time it was

subsequently noted that the specimens belonged not to *locusta* s.s., but to *zaddachi oceanicus*. The data attached to the specimens were 'Newfoundland, 1885'.

The same belated conclusion is also true of a sample of 6 ♂♂ (largest 31 mm.) from 'Lac Tadoussac: July 1938: V.D.V.', lent to me in 1939 by Mr G. I. Crawford. This locality is on the Gulf of St Lawrence.

Segerstråle (1947, p. 230) has indeed drawn attention to the occurrence of *G. zaddachi oceanicus* on the Atlantic coast of North America, having identified one sample from Labrador and two from Massachusetts. These would previously have been regarded as '*locusta*'.

More recently four additional samples of N. American '*locusta*', from Nova Scotia, and the New England states (see Appendix, p. 144, for details), have been critically examined and found to be *G. zaddachi oceanicus*. These are in the British Museum Collection. All date from about 1880, and had originally been determined as *G. ornatus* Edw. on S. I. Smith's authority.

The question arises whether the true *G. locusta*, as we now understand that species (Sexton, 1942; Spooner, 1947), occurs on the western side of the Atlantic at all. A search for clues amongst the American literature has provided a fairly certain answer: the common species which for long has passed under the name of *locusta*, and earlier on of *ornatus*, is in fact *G. zaddachi oceanicus*.

In his work on the Amphipoda of southern New England, Holmes (1904, pp. 500-1; pl. X, no. 3) gives a description, some illustrations, and a photograph of the *Gammarus* '*locusta*' of that region (syn. *G. ornatus* Edw.), describing it as 'the species of amphipod decidedly most often met with in the collections from New England'. This cannot possibly be the true *G. locusta*, as is at once apparent from the photograph on his plate X (no. 3). In this the relative depth of the coxal plates, the shape of coxal plate 4, the depth of the lateral head sinus, the relative length of antenna 1 peduncle segment 2 and of the accessory flagellum, etc., are characteristic of *G. zaddachi oceanicus* as opposed to *G. locusta*. Furthermore, the drawings of the male gnathopod 3 and uropod 3 (figure on p. 501) show diagnostic features which exclude *G. locusta* and conform to *G. z. oceanicus*. Other points in the written description again agree with the latter against the former (accessory flagellum of 8 segments; the spination of male gnathopod 2 hand; no orange pigments on mesosome); and there is no hint that a mixed population is being described.

There is thus as yet no evidence that *G. locusta* (L.) occurs on the American side of the Atlantic, and until positive evidence is forthcoming it can only be assumed that all references to *G. 'locusta'* on the Atlantic seaboard refer to *G. zaddachi oceanicus*. The validity of the name '*ornatus*' will have to be seriously considered.¹

¹ Milne-Edward's (1830) description referred to specimens from Boston, Mass. It is sufficiently detailed to exclude all species except *G. zaddachi oceanicus* and *G. locusta* s.s., hence might be held to define the former by elimination.

(N.B. Statements referring to the occurrence of *G. 'locusta'* on the Pacific coast of America should be heavily queried. South of the Behring Sea it is furthermore very doubtful whether records apply even to a related species.)

The extent to which *G. zaddachi oceanicus* ranges southward along the Atlantic shore of the U.S.A. is not known. As it is so plentiful on the Connecticut coast, it might well extend beyond New Jersey; but if its southern limit is reached as comparatively abruptly as in Britain, it may not exceed the 40th parallel of latitude.

Segerstråle (1947, fig. 3f) figures the telson of a specimen from Massachusetts, showing that two of the apical setae are delicately plumose. The first American male which I examined in detail also showed precisely the same feature but several others do not. Otherwise the possession of plumose setae (excepting the pleopods and uropod 3 rami) is a diagnostic feature of *G. setosus* Dement., in which all, or nearly all, the hairs on the urosome dorsally and on the telson are of this type.

SUMMARY

A number of records of *Gammarus zaddachi oceanicus* from northern Britain are given, which indicate that this form extends down the respective coasts to the Clyde Sea Area and Yorkshire.

It is an important subarctic and boreal littoral crustacean which formerly was confused with *G. locusta*. Some additional localities are quoted and some re-identifications are made from literature, when illustrations or biometric data enable this to be done.

The ecological relations between *G. z. oceanicus*, on the one hand, and *G. z. salinus* and *G. locusta*, on the other, are discussed.

It is emphasized that the animal which has all along been known in eastern America as *G. locusta* (formerly *G. ornatus*) is really *G. z. oceanicus*.

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APPENDIX I

LIST OF SPECIMENS OF *GAMMARUS ZADDACHI OCEANICUS* EXAMINED
(OTHER THAN BRITISH). NEW, OR REVISED, IDENTIFICATIONS

(G.I.C., G. I. Crawford. B.M., British Museum.
Cop.Mus., Copenhagen Museum)

Baltic & Kattegat

POMERANIA. Strela-Sund, near Stahlbrode, E. of Stralsund, Dr E. Schwarz, as *G. locusta*, 16 ♂♂, 3 ♀♀ (ovig.), with 2 *G. z. salinus* (B.M. 1933.

11. 1. 2-10, part). S.W. SWEDEN. Bohuslän, as *G. locusta*, 2 imm., with 2 adult *G. locusta* (B.M. 97.6.1.33, part).

Norway

W. NORWAY. Bergen (near), Molde, 19. vi. 39, G.I.C., 1 ♂, 11 yng ♂♂ and imm. (B.M. 1942.8.5.73-77). N. NORWAY. Tromsø, 30. vi. 39, half-tide, G.I.C., 15 advanced imm. (B.M.). Lofoten Is., Svolvær, 26. vi. 39, mid-tide, G.I.C., 1 imm. Skaervoy, S. of Hammerfest, 2. vii. 39, half-tide, G.I.C., 10 ♂♂, 6 ♀♀, 10 imm. (B.M., 1942.8.5.51-55). Malangen, Nordbotten, vii. 1881, Cop.Mus., ♂ and ♀ (with *G. setosus*). Porsangerfjord, Honningsvåg, 5. vii. 39, mid-tide, G.I.C., 2 ♂♂, 2 imm. (with *G. duebeni* and *Marinogammarus finmarchicus*) (B.M.). Porsangerfjord, Rimabukt, 10. vii. 39, L.W. to half-tide, G.I.C., large ♂. Porsangerfjord, Suogalma, 6. vii. 39, L.W. to half-tide, G.I.C., 6 ♂♂, 8 ♀♀ (7 ovig.), c. 65 imm. and yng adults (B.M. 1942.8.5.44-50). Lang Fjord, Finmark, as *G. locusta*, Norman Coll., 1 imm. (B.M. 1911.11.8.18852).

Iceland

E. ICELAND. Berufjörður, 0-3 m., 14. vii. 1900, Cop.Mus., 2 ♂♂ and 1 ♀ (with other spp.), shore, below 'ordinary high water'. Loðmundarfjörður, 9. v. 1898, Cop.Mus., 7 ♂♂, 6 ♀♀, 2 imm. 'midtfjords i bunden, 13 m. St. 7'. S.E. ICELAND. Hornafjörður shore, 29. viii. 36, Cop.Mus., 6 ♂♂, 1 ♀, 19 imm. W. ICELAND. Hvammsfjörður shore, 19. vii. 1886, Cop.Mus., 6 ♂♂, 6 ♀♀, many imm.

Spitzbergen

As *G. locusta* var. *zaddachi*, A. Schellenberg det., 2 large ♂♂ of 34 and 35 mm., 6 imm., with *G. setosus* (B.M. 1934.9.1.21-24, part).

Greenland

E. GREENLAND. Angmagssalik, 4 m., 10. viii. 33, Cop.Mus., 1 ♂, 1 ♀ (with *G. setosus* and *G. wilkitzkii*). Angmagssalik, Tasiusak, Cop.Mus., large ♀ [nec *setosus*]. 'GREENLAND'. 7 ♂♂, 1 ♀, ex coll. Cop.Mus. S.E. GREENLAND. Lindenowsfjord, 50-75 m., 28. vii. 35, Cop.Mus., 2 ♂♂, 3 ♀♀ (not breeding) (with *G. setosus*). W. GREENLAND. Holsteinsborg, ex coll. Cop.Mus., 5 ♂♂, 6 ♀♀, 9 imm., (breeding actively) (with *G. setosus*). Holsteinsborg, N. Strömfjord, 1911, Cop.Mus., 6 ♂♂, 3 ♀♀ (with *G. setosus*). Waigat, Sakkrak, 1892, 5 ♂♂, 2 ♀♀, Cop.Mus. Upernavik, 12. vi. 36, Cop.Mus., ♂. Davis Strait, 63° 27' N, 54° 12' W., E. Whymper, (B.M. 79.26 as '*locusta*'), 1 ♀, not breeding, with several juvenile *G. wilkitzkii*.

N. America

CANADA, QUEBEC. Lac Tadoussac, July 1938 (V.D.V.), per G.I.C., 6 large ♂♂, largest 31 mm. NEWFOUNDLAND, 1885, per E. W. Sexton, adult ♂♂. NOVA

SCOTIA. Off Halifax, loc. 74, 1881, U.S. Fish. Comm., '*G. ornatus* Edw.', Norman Coll. as '*locusta*' (B.M. 1911.11.8.18929-932), 3 ♂♂, 1 ♀.
 MASSACHUSETTS. Gloucester Harbour, U.S. Fish. Comm., '*G. ornatus* Edw.', Smithsonian Inst., (B.M. 80.26 as *locusta*), 1 ♂ (c. 34 mm.), 1 ♀ with brood.
 CONNECTICUT. New Haven, '*G. ornatus* Edw.', S. I. Smith, Norman Coll. as '*locusta*' (B.M. 1911.11.8.18919-928), 4 ♂♂, 11 ♀♀, (most ovig.). 'N.E. AMERICA'. '*G. ornatus* Edw.', S. I. Smith, Norman Coll. as *locusta* (B.M. 1911.8.18933-937), 2 ♂♂, 4 ♀♀ (not breeding).

APPENDIX II

Re-identifications from the Literature

DEMENTIEVA (1931)

At the time this paper was written all northern marine *Gammarus* were still referred to *G. locusta*, but it was realized that much variation existed. Dementieva's biometric data aimed at expressing the differences between certain selected populations in a more precise form. Her results enable these populations to be identified. She rightly concluded, incidentally, that her 'typical forms' (*zaddachi oceanicus*) and 'brackish-water forms' (*setosus*) were distinct species.

Population	Dementieva's name	Data or illustrations	Re-identification
Kola Gulf (Murmansk)	<i>G. locusta</i> 'typical forms'	Tables 5, 7; figs. 7a, 8a, 12a-c	<i>G. zaddachi oceanicus</i> Seg.
Baltic Sea	<i>G. locusta</i> 'typical form'	Table 7; table on p. 77 (left col.)	<i>G. zaddachi oceanicus</i> Seg.
Belouchia Bay (Novaya Zemlya)	<i>G. locusta</i> 'brackish-water form'	Tables 5, 6; figs. 7b, 8b, 12a-c	<i>G. setosus</i> Dement.
Zabloula Bay (Novaya Zemlya)	<i>G. locusta</i> 'brackish-water form'	Figs. 7c, 8c; table 6	<i>G. setosus</i> Dement.
Barents Sea	<i>G. locusta</i> 'deviating form'	Table on p. 76; fig. 9	<i>G. wilkitzkii</i> Birula
Baltic Sea	<i>G. locusta</i> 'deviating form'	Fig. 10; table on p. 77 (right col.)	<i>G. zaddachi zaddachi</i> Spooner
Kola Bay, etc.	<i>G. duebenii</i>	Figs. 11, 12a, b and e	<i>G. duebeni</i> Lillj.

G. zaddachi oceanicus is the 'typical' form characteristic of the Kola Gulf shore, where it is not normally mixed with *G. setosus*. When it extends into shallow arms of the sea diluted with river water or land drainage it may overlap the range of *G. duebeni*. In Novaya Zemlya, *G. z. oceanicus* is reported from the seaward end of the bays visited, in which it tends to be replaced by *G. setosus* in shallower and fresher parts. In Mituschikha Bay both occurred together at the same depth. In the north Baltic, *G. zaddachi oceanicus* and

G. zaddachi zaddachi occur together, as is now well known from Segerstråle's investigations. *G. z. oceanicus* of the Baltic are smaller than those of such typical habitats as the shore of Kola Bay, and their limbs are a little stouter.

GURJANOVA, E., SACHS, S. & USCHAKOW, P. (1929)

The *G. 'locusta'* from Kola Bay, referred to in this paper may be taken to refer to *G. z. oceanicus*. *G. setosus*, as we now know, is quite scarce in this area, and *G. locusta* (s.s.) scarcely reaches it and is at best very rare.

GURJANOVA, E. (1929)

G. 'locusta' is reported as 'everywhere in large numbers, littoral'. In this area, Cheshskaya Bay, conditions are rigorous and only euryhaline and eurythermal species survive. This must be chiefly *G. zaddachi oceanicus*, if not entirely. At most a minority may be *G. setosus*.

GURJANOVA, E. (1931)

Amongst the amphipod fauna of the east Murmansk coast (Portschnicha Bay) *G. 'locusta'* is described as a characteristic littoral species. (*G. wilkitzkii* is now clearly distinguished.) Since *G. setosus* proves to be quite scarce on this coast, the remarks can be taken as referring to *G. zaddachi oceanicus*.

GURJANOVA, E. (1932)

By the time of publication of this paper (and perhaps earlier) Gurjanova already distinguished *G. setosus* as separate from *G. 'locusta'*, and refers to it as *G. locusta* var. *mutata*.

In an account of the fauna of that obscure and peculiar region off the Siberian coast known as Nordenskjöld's Sea (or the Sea of the Brothers Laptev), records are given of two of the three arctic *Gammarus*.

Gurjanova's name	Re-identification	Occurrence
<i>G. locusta</i>	<i>G. zaddachi oceanicus</i>	73° 05' N., 140° 45' E., 16.5 m., 0.42° C., 2 ex 73° 20' N., 139° 08' E., 16 m., 0.45° C., 1 ex 'also previously from ten other stations in the region of the New Siberian Islands'
<i>G. wilkitzkii</i>	<i>G. wilkitzkii</i>	72° 9' N., 135° 45' E., 20 m., 0.3° C.

Note that Popov (1932), in describing the conditions of life in the Brothers Laptev Sea, refers to '*G. locusta*' being spread all along the littoral of the Siberian coast, and indeed as being the only littoral marine animal! There is virtually no tide here (a few inches at best); the temperature is always minus, and the water has greatly reduced salinity owing to the inflow of several large

rivers, including the Lena. Presumably this must be taken to cover *G. zaddachi oceanicus* and *G. setosus*, since the latter was eventually reported from the Laptev Sea, and would be chiefly coastal.

GURJANOVA, E. (1936)

Further records are given of *Gammarus* from the Nordenskjöld Sea and from the Kara Sea. *G. setosus* is now distinguished specifically. References to *G. 'locusta'* now refer solely to *G. zaddachi oceanicus*. It is recorded from a station 69° 25' N., 67° 15' E. (shore of the Kara Sea).

G. setosus is reported from the Laptev Sea for the first time (74° 50' N., 112° 50' E.).

STEPHENSEN (1940a)

This is the first occasion on which it is recognized that differences exist between the *G. locusta* of temperate and south Europe, and the form which still passed under the name of *locusta* from the north. The full extent of difference is, however, not appreciated, and the name *locusta* is still retained for both. In so far as the records here quoted are Stephensen's own determination it is possible to distinguish between true *G. locusta* and *G. zaddachi oceanicus* (= Stephensen's northern form of *locusta*).

It is made clear that *G. locusta* (s.s.) ranges into Denmark, but is usually not found farther to the north. In Norway it occurs, but is scarce, and records are given for Oslo fjord; Evenskjaer; Vannøy; and Loppa (c. 70½° N.) (p. 318). In fig. 40, II and III apply to *G. locusta*.

The remaining records (unless simply quotations from literature) refer to *G. zaddachi oceanicus*, as does fig. 40 I. The records may be summarized as follows: south and west Norway, several samples from Oslo fjord to Trondheim fjord; north Norway, numerous samples all along the coasts of mainland and islands, to the frontier; Bear Island, in one sample; west Spitsbergen, in Grieg's material; north-east Spitsbergen, at 80° 40' N.

It is clear that all along the Norway coast *G. zaddachi oceanicus* is far more numerous than *G. locusta*.

G. setosus is treated separately, under the name of *G. locusta setosus*. There are three records from the Norway coast, on which it is clearly very scarce; and others from west Spitsbergen; north-east Spitsbergen; Greenland and Arctic America.

G. wilkitzkii is recognized as a distinct species, but Stephensen holds that it is possibly synonymous with *G. zaddachi* [= *G. z. zaddachi*] of which it would be a large-sized Arctic representative. A discussion on this topic (pp. 334-6) points out the difficulties in finding qualitative differences 'which cannot be explained as being due to the ordinarily very great difference in size'. Stephensen, however, minimizes the real differences in the antennal setation, the significance of the relative elongation of several limb segments, and of

the long uropod 3 inner ramus. Moreover, he entirely ignores the diagnostic propod of female gnathopod 2, which is quite unlike that of *G. zaddachi*. There is no question that *G. wilkitzkii* is separate from *G. zaddachi*.

STEPHENSEN (1940b, 1944)

In these excellent accounts of the amphipod faunas of Iceland and east Greenland, all *G. locusta* s.s. refer to *G. zaddachi oceanicus*, and *G. locusta setosus* to *G. setosus*.

In Iceland, *G. z. oceanicus* is the form which attains an 'enormous frequency' and is recorded all round the coast. Recently the true *G. locusta* has been found to occur (Segerstråle, 1950); but evidently it was not seen by Stephensen, and must be very scarce, being at the extreme northern limit of its range. *G. setosus* occurs fairly freely round the Iceland coast, more freely than in Norway, but is clearly outnumbered by *G. z. oceanicus* (see 1940b, pp. 56-8 and fig. 7).

In Greenland the occurrence of *G. z. oceanicus* is proved on the east coast northward to Hvalrosodden (77° N.). Other information exists to show it occurs on the west coast to at least 73° N. (material identified by Dr Segerstråle or myself). Judging, however, from the numbers and sizes of specimens recorded, it may be concluded that *G. z. oceanicus* flourishes less in Greenland than in Iceland or Norway, and is considerably outnumbered by *G. setosus*. It is *G. setosus* now which attracts attention from its numbers, e.g. at Angmagssalik it 'occurs everywhere on the coast, both on rock facies and on sediment shares found at river mouths'. A difference in the bathymetric range of the two forms is noted, confirming Dementieva's (1931) records from Novaya Zemlya, namely that *G. setosus* in east Greenland is 'a character form of the tidal zone, only exceptionally at depths of more than a few metres', while *G. z. oceanicus* was taken mostly in shallow water from low-water mark downwards to about 20 m., rarely still deeper (50-75 m.) (see 1944, pp. 108-12; fig. 8).