

NEW OBSERVATIONS ON THE DISTRIBUTION AND MORPHOLOGY OF THE AMPHIPOD, *GAMMARUS ZADDACHI* SEXTON, WITH NOTES ON RELATED SPECIES

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(Text-figs. 1-7)

Editor's Note. This paper and that by Mr G. M. Spooner (this *Journal*, pp. 1-52), independently bringing forward certain new ideas on the taxonomy of *Gammarus zaddachi* and *G. locusta*, were received for publication simultaneously. As Mr Spooner's paper is a report of work largely carried out before the war, of which summarized results have already been referred to in print (e.g. Report of Council in this *Journal*, Vol. xxiv, pp. 444, 691; Huxley, *The Modern Synthesis*, p. 315), it is given precedence. The authors have since consulted each other over matters in which their contributions overlap, in particular over the taxonomic status of the new forms they distinguish and regarding the names to be applied to them. Dr Segerstråle has kindly consented to adopt the two new names introduced above by Mr Spooner, and to make considerable alterations to his original manuscript.

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INTRODUCTION

As is well known, the species *Gammarus zaddachi*, established by E. W. Sexton in 1912 on material from European brackish and fresh-water localities, has caused great confusion among zoologists, as the characteristics distinguishing it from various related species, particularly *Gammarus locusta*, *G. duebeni* and *G. pulex*, have been very frequently disregarded. This confusion still persists to-day—that is amply shown by the material received for the present investigations from various museums.

In view of the drawbacks brought about by this confusion, not the least on account of the fact that *G. zaddachi* has been accepted as a typical salinity indicator in ecological work while, on the other hand, *G. locusta* is a favourite

object for physiological investigations on osmotic regulation in water animals, zoologists are deeply indebted to Mrs Sexton for a paper, published in this *Journal* in 1942, the aim of which was to clear up the problems that have arisen around *G. zaddachi*. In this paper the author discussed the whole literature on the subject, and was in many cases able to correct previous errors by re-examining the original material. In addition, the author gave a new detailed description of the two forms of the species, the 'saline' and the strikingly hairy 'fresh-water' one, accompanied by numerous excellent figures. Finally, the paper contained a comparison between *G. zaddachi* and the species with which it has most often been confused.

The main differences between *zaddachi* and *locusta* mentioned, and as a rule depicted in Sexton's paper, refer to the setose armature of the peduncle of antenna 1 (in *zaddachi*, numerous clusters of well-developed hairs present; in *locusta*, the peduncle almost glabrous); to the shape of gnathopod 2 (in *locusta*, narrower proportionately, etc.); to the shape of side-plate 4 (in *zaddachi*, inferior margin almost semicircular; in *locusta*, lower portion deep and almost rectangular); to the epimeral plates 2 and 3 (in *zaddachi*, hind-corners subacute; in *locusta*, acutely produced); to the pleon segments 4-6 (in *zaddachi*, dorsal humps only slightly raised; in *locusta*, elevated and prominent); etc.

A characteristic referring to the head sinus should be added to these principal points of difference. In *zaddachi* the sinus is much deeper than in *locusta*. Sexton says that both the species have a slight sinus, but in her figures (1 and 19) the divergence is clearly seen. The deep head sinus in *zaddachi* has been correctly depicted already by Stephensen (1940, fig. 40, I, II, p. 317), in connexion with the description of an atypical form of *locusta*, occurring in his material from northern Norway and adjacent waters; as seen below, it is in reality identical with *G. zaddachi*. To show the difference in shape of the epimeral plates of both species Fig. 1 may be given (cf. also Sexton's text-fig. 1). Fig. 2 illustrates the differences between *zaddachi* and *duebeni*, mentioned in Sexton's paper.

A historical remark may be added here. Oddly enough, it seems probable that the species nowadays regarded as the true *locusta* is not identical with the form found by Linnaeus in 1741 on the seashore at Gothland and named by him (in 1745) *Cancer macrourus coeruleus*, and later on (1761, etc.) *C. locusta*, but rather that he had had to do with *Gammarus zaddachi*. The famous naturalist points out in his description that the last pair of legs had the inner ramus shorter than the outer. As the difference in length is very small in the 'modern' *G. locusta*, but in *G. zaddachi* constitutes one of the most striking characteristics, and, furthermore, as *zaddachi* occurs very commonly together with *locusta* on the shores of Gothland (see below, pp. 236-9), it appears definitely more probable that the amphipod observed by Linnaeus belonged to *zaddachi*. A similar view has already been expressed by the Swedish zoologist Liljeborg. In his account of the Scandinavian species of the genus *Gammarus* (1855) he

emphasized that the species meant by Linnaeus was obviously not *G. locusta* M. Edwards (in which the rami of the last uropods are, as in the *locusta* of the present day [depicted by Sars etc.], 'presque égaux entre eux' [M. Edwards, 1840, p. 45]). He therefore gives this species the name *mutatus* and regards the '*locusta*' found in the Baltic by Zaddach (1844, 1878), i.e. the same which in 1912 was called *G. zaddachi* by Sexton, as Linnaeus's species. In the diagnosis of the two species Liljeborg especially points out the differences in the relative length of the inner ramus of the last uropods, giving for *mutatus* 'rami pedum spuriorum ultimorum circiter aequales' and for *locusta* 'rami

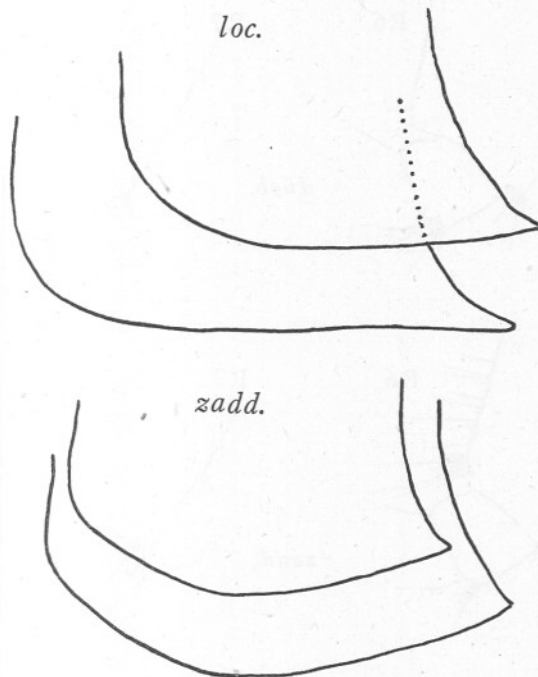


Fig. 1. Second epimeral plates of *Gammarus zaddachi* and *G. locusta* (two of each; males), to show the difference in shape of hind-corner. Setae and spines omitted. Material from the Baltic.

pedum spuriorum ultimorum insigniter inaequales, interior exteriore saltem tertia parte minor'.

The fact that already Liljeborg separated the two forms of *Gammarus* mentioned above into distinct species, may, if only the priority of the nomenclature suggested by him is taken into consideration, motivate changing of the names *locusta* and *zaddachi*, used nowadays, into *mutatus* and *locusta* respectively. But in view of the great new confusion which no doubt would be the consequence of this change, the present author has the decided opinion that

the modern names should be retained as '*nomina conservanda*'. This idea is supported by the fact that Liljeborg erroneously listed the independent species *G. duebeni* as synonymous to *G. locusta*, thus making the value of the diagnosis of this species somewhat doubtful.

In connexion with studies on the *Gammarus* fauna carried out in the Finnish coastal waters since 1941, the present author has obtained results which cast a new light on the distribution and ecological character of the saline form of

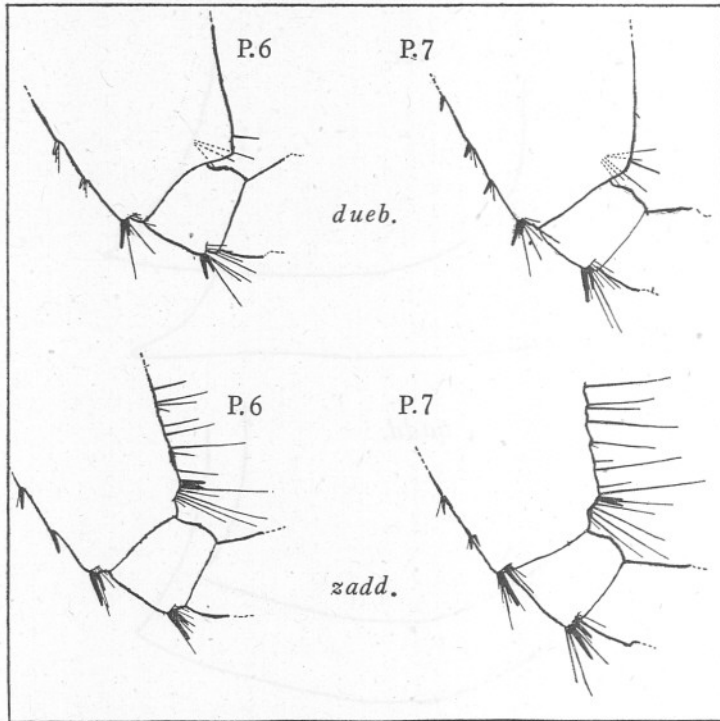


Fig. 2. Segments 2-4 of the peraeopods 6 and 7 of *Gammarus duebeni* and *G. zaddachi* fresh-water form (=ssp. *zaddachi*, according to Spooner; see p. 5), to show the difference between these species in the shape of the postero-distal angle of the basal segment. In the former species this is much more produced (especially in the 6th peraeopod) and lacks the strong spines present in the latter. (From Segerstråle, 1946.)

G. zaddachi and which also complete our knowledge of the morphology of this and the fresh-water form of the species in essential points. These results which, I hope, may considerably facilitate the recognition of *G. zaddachi*, are dealt with in the present paper. In connexion with this subject the relationship between *G. zaddachi* and the closely allied species *G. setosus* and *G. wilkitzkii* will be discussed.

The author feels deeply indebted to Mrs E. W. Sexton (Marine Biological Laboratory, Plymouth) for her most valuable and kind help in sending material and discussing in letters questions concerning the subject. He is also indebted to the late Museumsinspektör K. Stephensen, of the Museum of Copenhagen, for his kindness in repeatedly supplying collections of *Gammarus* from Danish and Arctic waters. The other museums from which material was received for the present investigation, with the names of those to whom the author's thanks are similarly due, are as follows: Bergen Museum, Conservator H. Tambs-Lyche; British Museum, Dr Isabella Gordon; State Museum of Natural History, Stockholm, the late Prof. Dr Sixten Bock; Zoological Museum, Berlin, Prof. Dr Adolf Schellenberg. In addition, Mr D. M. Reid (Harrow) and Cand. phil. Erik Dahl (Lund) have kindly sent samples of various forms of *Gammarus*.

In total the material available embraces collections from the northern Atlantic and the Arctic (Massachusetts, Labrador, Greenland, Iceland, Norway, Spitsbergen, Murman Coast, Novaya Zemlya), the North Sea (Heligoland, coast of Denmark), the Cattegat, the waters around the Danish Isles, and the Baltic.

As mentioned already by Spooner, in his paper in this *Journal*, pp. 1-52 (see Editorial note, p. 219), the results obtained by him and by the present author partly overlap. Thus we have both distinguished Sexton's 'fresh-water form' from two other types of *zaddachi* and have described it. Thanks to the good offices of the Editor we have had the opportunity of going through our papers reciprocally before publication. The name *G. zaddachi* subspecies *zaddachi* given by Spooner to the above-mentioned form will be used also in the present paper. Another form found by both of us and designated subspecies *salinus* by Spooner will also be quoted here under his name. The third form which has been studied mainly by the present author will be described below as subspecies *oceanicus*.

The author wishes to present his thanks to Mr Spooner for most valuable comments and suggestions in letters.

SURVEY OF THE RESULTS CONCERNING THE DISTRIBUTION AND MORPHOLOGY OF *GAMMARUS ZADDACHI*

*The distribution of the saline form.*¹ The saline form of *G. zaddachi* (also formerly called the brackish-water form by Sexton) has hitherto been recorded

¹ As shown by Spooner, Sexton's 'saline form' of *zaddachi* embraces the subspecies *salinus*, erected by him, as well as the subspecies *oceanicus*, described for the first time in this paper. The 'saline form', spoken of here, refers to the latter subspecies.

only from waters with reduced salinity (the southern coast of the Baltic and the estuary of the Elbe, etc.), and has consequently been regarded as a typical brackish-water animal. In reality, this form is, however, mainly marine as, besides being distributed in brackish water, it is also widely found in the northern Atlantic and the Arctic (Fig. 4). In the samples from these waters, labelled *locusta*, the saline form is extremely common, whereas the true *locusta* is almost entirely lacking (besides *zaddachi* the Arctic samples of 'locusta' frequently contain the species *G. setosus* and *G. wilkitzkii*). Structurally the form in question agrees strictly with the saline one living in the Baltic in all essential characteristics, the only difference being its size, which is much larger (body length up to 38 mm.).¹

The northernmost localities from which records of the true *locusta* originate are situated on the north-east coast of Iceland (Bakkafjordur; Cop. Mus.) and northern Norway (Loppa, c. 70½° N.; Stephensen, 1940, p. 318). Thus, the species does not penetrate as far north as does the saline form of *zaddachi*. *Locusta* also does not nearly attain the same size as this form (maximum observed length of *locusta* 29 mm.; Stephensen, 1940, p. 318; a clear difference seen also in the Baltic). The previous literature records of Arctic specimens of *G. locusta* greater than c. 30 mm. might consequently refer to the saline form of *G. zaddachi* (or to the likewise very large allied species *G. setosus* and *G. wilkitzkii* which also hitherto have frequently been determined as *G. locusta*). The saline form of *G. zaddachi* is very euryhaline; in this respect it distinctly surpasses *G. locusta* (for details, see pp. 236-8).

The existence in the northern marine areas of a very *zaddachi*-like form of *G. locusta* has already been realized by Stephensen. In the above-mentioned important paper on the Amphipoda of northern Norway and Spitsbergen with adjacent waters (1940), he points out that the material of *G. locusta* (by him named *G. locusta locusta*) included, besides the typical form, also a deviating one which was much more common in the collections, and which in certain respects agreed with *G. zaddachi*, particularly in the shape of the 4th side-plate. As the collections used for the present investigation contain a number of samples from Stephensen's material, the author has had the opportunity of examining them. The form discussed by Stephensen is a typical *G. zaddachi*, saline form. Stephensen's including it in the species of *locusta* is partly accounted for by the incorrect records of the head sinus in *G. zaddachi* given in previous literature.

The morphology of the saline and the fresh-water form. As is well known, the setose armature of the two forms differs greatly, as it is much more developed in the fresh-water form, especially on the hinder pereopods, the pleon segments 4-6, the telson, and the uropod 3. It is, however, striking that the difference in hairiness between the 1st antennae of both forms,

¹ The author's determination of the Baltic saline form has kindly been confirmed by Mrs Sexton.

although generally quite distinct, has not been observed so far.¹ This may probably be explained by the aim of the descriptions of *zaddachi* mainly having been to point out the characteristics which separate the species from *locusta*; with respect to the 1st antenna, namely, both forms of *zaddachi* clearly differ from this species. But, on the other hand, the comparatively poor hairiness of the antennae in typical saline specimens of *zaddachi* obviously gives it a resemblance to *locusta* great enough to cause confusion with this species. The difficulty of identification has been augmented by the shortness of the peduncle of the 1st antenna in the saline form, a characteristic which has also been overlooked.

The above-mentioned inequality in length of the peduncle of the 1st antenna shows that the view prevailing nowadays of the differences between the saline and the fresh-water form being confined to the strong hairiness of the latter is not correct as the structure of the two forms also differs. In addition, the present investigation has revealed a second structural disparity, viz. in the relative length of the 2nd antenna in the fresh-water form being, in spite of the longer peduncle of the 1st antenna, distinctly greater than in the saline one.

Furthermore, the study of freshly captured animals from Finnish waters has shown that the body colour differs in the two forms of *zaddachi*. The difference is mainly caused by the existence in the fresh-water form of a pattern of transverse and longitudinal bands on the dorsal part of the body; in the saline form there is no pattern. Mrs Sexton's not having observed the divergence is due to the fact that her material consisted only of preserved animals; in alcohol and formol the pattern is completely deleted.²

Finally, the fresh-water form is smaller in size, even in comparison with the Baltic saline form which lives together with the former; if the large Arctic saline form is subjected to the comparison the difference is of course much more marked.

It may be added that the investigation of the comparatively extensive material available to the present author, containing among others the large Arctic specimens, has considerably widened the variation range for certain characteristics (number of spines on pleon segment 4-6, number of spines and setae on the telson, number of joints on the flagella of the antennae).

The 'combined' form. Transitional forms between the saline and the fresh-water forms of *G. zaddachi* have previously been found by several authors,

¹ Sexton (1942, p. 597) states: 'In all the animals, saline as well as freshwater, both peduncles and the flagella carry on the under margin dense tufts or clusters of long stiff outstanding setae, some of each cluster extending far beyond the rest.' Strictly, however, the records given (on pp. 597 and 600) of the number of hair clusters on the peduncle of antenna I, as well as of the length of the peduncle, hold good only for the fresh-water form.

I can now add that Spooner, too, has noted differences in setation of the antennae between the fresh-water and those 'saline' animals which are here called *oceanicus*.

² As Sexton mentions (1942, p. 593) that 'the chitinous cuticle varies in the two forms, being thick, strong and opaque in the freshwater, thin and transparent in the brackish water specimens', this difference, according to records kindly given by Mrs Sexton to the present author in a letter, is obviously not real, but due to different preserving methods.

mainly in the Baltic (Sexton, 1912, 1913; Schellenberg, 1934; Höfken, 1937; Dahl, 1944).¹ Specimens of this type are common also in the material from brackish areas available to the present author. Höfken emphasizes that these forms are not properly transitional, but combine characteristics of the saline and the fresh-water form (called by him *G. locusta* and *G. zaddachi*). This agrees with Dahl's statement that the specimens in his material from the Baltic, more or less intermediate between both forms (by him determined *G. locusta* f. *locusta* and f. *zaddachi*), have rather setose antennae (=fresh-water characteristic) but otherwise are very sparsely provided with hairs (=saline characteristic). In the collections from the Baltic examined by the present author this peculiar combined type is abundant. It has proved to be identical with Spooner's subspecies *salinus*.

In the following account details will be given of the morphology and distribution of the different forms of *zaddachi*, as observed in the material studied (distribution records from other areas included).

As will be shown, the combination of the following characteristics is diagnostic of the new subspecies *G. zaddachi oceanicus*: (1) the shortness and sparse setation of the peduncle of antenna 1; (2) the sparse setation of the hinder pereopods, the pleon segments 4-6, and the telson. (In the description a characteristic from the last pereopod and the telson has been chosen as indicator of the hairiness of the hinder parts of the body. With respect to this character, *oceanicus* shows almost complete agreement with *salinus*.)

Unless otherwise stated, the descriptions refer to the *male* (the female has been less thoroughly studied; most characteristics are somewhat less marked in this sex). The records given refer to specimens of at least *c.* 8 mm. in length (in smaller animals the characteristics are mostly not fully developed). All measurements are taken from the tip of the rostrum to the insertion of the telson.

In the list of synonyms an asterisk designates that the author has had the opportunity of examining specimens used for the paper concerned.

***Gammarus zaddachi* Sexton subsp. *oceanicus* subsp. nov.**

SYNONYMS

Sexton, 1912, 1913, 1942; *G. zaddachi*; brackish-water or saline form *in part.*, cf. footnote, p. 223.

*Stephensen, 1917: *G. locusta* var. *Zaddachi*, *in part.*; intermediate form between *G. locusta* and *G. locusta* var. *Zaddachi* (*in part.*). 1940: *G. locusta locusta*, *in part.*

¹ Also the form, found by Poulsen in Danish waters and determined *G. zaddachi* (Poulsen, 1932, p. 6 and fig. 3), seems to belong to the intermediate type. According to Spooner (p. 35), in reality the animals regarded as intermediates by Sexton generally belong to the fresh-water form (=subsp. *zaddachi* Spooner).

- *Hellén, 1919: *G. locusta*, in part.
 *Blegvad, 1922: *G. locusta*, in part.
 *Segerstråle, 1933: *G. locusta* (in part.). 1944: *G. locusta* f. *typica*.
 *Schellenberg, material sent to the author: *G. locusta*.
 *Valovirta, 1935: *G. locusta* f. *typica*.
 Höfken, 1937: *G. locusta*.
 *Suomalainen, 1939: *G. locusta* (in part.).
 *Dahl, 1944: *G. locusta* f. *locusta*.

MORPHOLOGY

Maximum size. Male: Arctic 38 mm. (Stephensen, 1940, pp. 318, 320; north Norway), Baltic 26 mm. (Schellenberg, 1934, p. 11, records a '*G. locusta*', captured near Kiel and measuring 32 mm.; probably a male of *G. zaddachi oceanicus*). Female: Arctic 28 mm. (Stephensen, 1940, p. 319; north Norway), Baltic 22 mm.

Body colour (studied in freshly captured specimens from Finnish waters). Greyish, yellowish, or greenish brown, semi-transparent; usually darker in the female. No dorsal pattern nor, usually, red spots of oil globules on the sides of pleon segments 1-3.

Setose armature of peraeopods, pleon segments 4-6, telson, and uropods. Weak development of the setae, as seen in Sexton's figures (1942, saline form). Peraeopod 7, longest seta in subapical cluster on hind margin of segments 4 and 5 not surpassing tip of spines in the same cluster (Fig. 3g in the present paper).¹ Telson, longest apical seta shorter than distance from its insertion to tip of subbasal spines (Fig. 3e, f).² In marine specimens the telson setae may be comparatively long and partly feathery (Fig. 3f).

Length of antenna 2 in percentages of antenna 1, from 18 males, length 13-20 mm., from the Baltic, Iceland and Labrador; specimens with broken or regenerating flagella excluded: 68-77, average 73%.

Maximum number of segments in the flagella (body length in brackets):

	Male	Female
Antenna 1: primary flagellum	57 (31 mm.)	38 (25 mm.)
accessory flagellum	10 (31 mm.)	11 (25 mm.)
Antenna 2	21 (33 mm.)	22 (25 mm.)

Length of peduncle segments of antenna 1 (Fig. 3a-d; segment 1 measured from tip of the rostrum to distal end of the segment). Ratio of length of segments 2 and 3 combined to that of segment 1, from 1.0:1 to 1.3:1, generally c. 1.1:1. Length of segment 3, 0.4-0.5 of that of segment 2. The end of the

¹ The difference in hair development between *G. zaddachi*, on the one hand, and *G. oceanicus* and *G. salinus*, on the other, is more marked on the posterior than on the anterior margin of the hinder peraeopods.

² This method for measuring the seta concerned has been chosen instead of comparison with the corresponding spines in order to reduce the inaccuracy of results arising from the variability of the spine length.

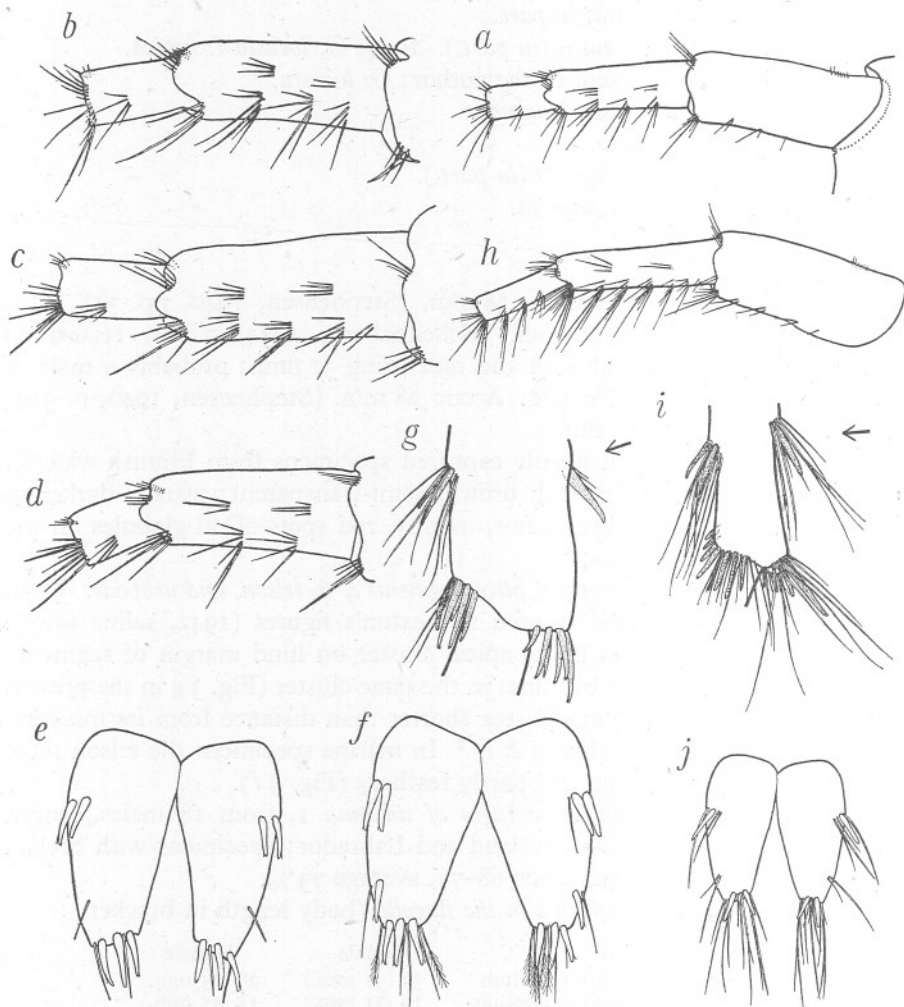


Fig. 3. *Gammarus zaddachi* (male). *a-g*, *z. oceanicus*; *h-j*, *z. zaddachi*. *a-d*, peduncle of 1st antenna (right, from the inner side; in *b-d* only segments 2 and 3 depicted): *a*, south-west Finland (body length 16 mm.); *b*, north Norway (27 mm.); *c*, north Greenland (31 mm.); *d*, north Norway (27 mm.). *e-f*, telson: *e*, north Norway (26 mm.); *f*, Massachusetts (27 mm.). *g*, peraeopod 7, distal part of segment 5 and proximal part of segment 6, west Greenland (27 mm.; the arrow shows the cluster of setae as a characteristic in the diagnosis; the specimen depicted has comparatively long setae on the anterior margin of segment). *h*, peduncle of 1st antenna, south Finland (16 mm.). *i*, peraeopod 7 (for part depicted and arrow, see above), south Finland (19 mm.; the specimen has unusually short setae; for maximum length, see Sexton 1942, fig. 12). *j*, telson, south Finland (18 mm.).

peduncle (when stretched forward, to continue the dorsal line) reaches at least as far as to the end of segment 4 of antenna 2 and at most to somewhat less than half the length of segment 5, generally to about a quarter of this joint.

Number of hair clusters on the under-margin of peduncle segments 2 and 3 of antenna 1 (including apical cluster) (Fig. 3). Segment 2, 3-5, generally 4, clusters; segment 3, 1-2.

Pleon segments 4-6, spine formula:

4th segment	3-6 : 2 : 3-6
5th segment	3-5 : 2 : 3-5
6th segment	2-3 : 2 : 2-3

Telson, number of spines and setae:

	Spines	Setae
Apical	3-4	1-5
Subapical	0-1	0-2
Subbasal	1-3	0-2

Uropod 3 inner ramus, length about three-quarters that of the outer, excepting in large marine specimens in which it may be up to seven-eighths.¹

ADDITIONAL NOTE

The following differences between *z. zaddachi* and *salinus* observed by Spooner, have proved to exist also between the former subspecies and *oceanicus* (material from Finnish waters).

As does *salinus*, *oceanicus* differs from *z. zaddachi* in the following respects: (1) accessory flagellum, number of segments and length somewhat greater; (2) gnathopod 2, a little narrower and hinder margin clearly bulging (in *z. zaddachi* almost straight); (3) epimeral plate 3, posterior distal angle distinctly more acutely produced (epimeral plate 2, difference less pronounced); (4) distal segments of last peraeopod, somewhat more slender; (5) last uropod, inner ramus a little longer. The measurements—certainly few in number—of characteristics 1, 4 and 5 fall within or very near the variation limits given by Spooner for *z. zaddachi* and *salinus*.²

DISTRIBUTION

The form in question is widely spread in the northern Atlantic (material from waters south of the North Sea not available) and in the Arctic, but occurs abundantly also in the brackish water of the Baltic (observed minimum salinity in places of capture *c.* 2.5‰) (see map of the Baltic in Fig. 6; for details see p. 236).³ Depth records: 0-25 m.

¹ It is a common feature in the amphipods that the inner ramus of the last uropods increases with age, as is well known.

² The author has not found calceoli in the (mature) female of *z. zaddachi*. These organs were lacking also in the examined females of *oceanicus* (Spooner mentions that he often found calceoli in the female of *z. salinus* but not of *z. zaddachi*).

³ Spooner has now shown (p. 43) that the subspecies in question occurs also in northern Scotland.

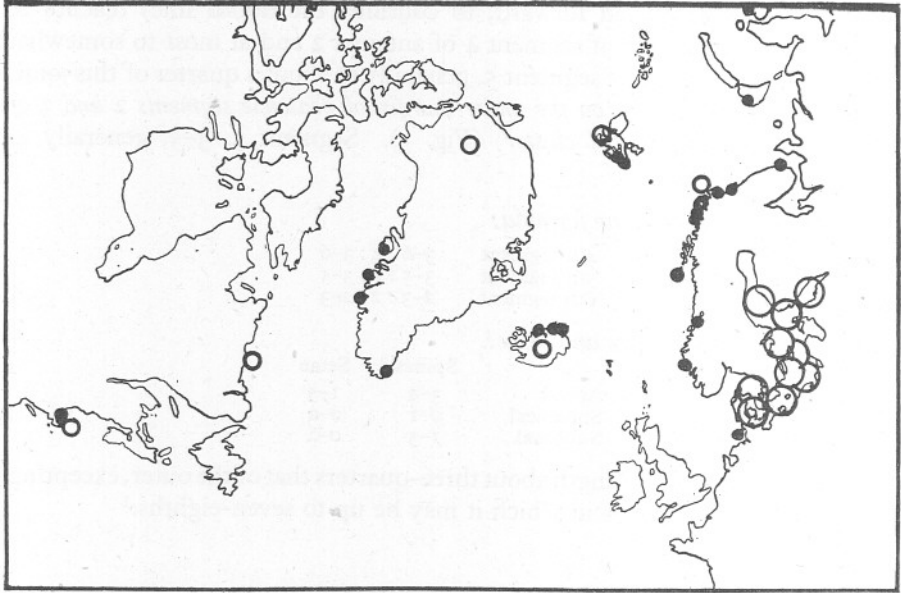


Fig. 4. The distribution of *Gammarus zaddachi oceanicus* according to the material investigated (samples not available from waters south of the southernmost localities seen in the map). Large open rings: more thoroughly studied areas (for details, see p. 236). Small open rings: record of locality not exact or insufficient ('Massachusetts', 'Labrador', 'North Greenland, Norsovak', 'Iceland', 'Spitsbergen, Kobbe Bay', 'Finmarken').

***Gammarus zaddachi* Sexton subsp. *zaddachi* Spooner 1947.**

SYNONYMS

Hoek, 1889: *G. locusta*, var. A.¹

Sexton, 1912, 1913, 1942: *G. zaddachi*, fresh-water form.

Tesch, 1915: *G. locusta*, var.¹

*Stephensen, 1917: *G. locusta* var. *Zaddachi* (*in part.*); intermediate form between this form and *G. locusta* (*in part.*). 1927: *G. duebeni* (at least *in part.*).

*Hellén, 1919: *G. locusta* (*in part.*); *G. duebeni* (*in part.*).

Tesch, 1922: *G. locusta*, Hoek's var. A.

¹ This form, which already Sexton (1942, p. 582) has regarded as belonging obviously to *zaddachi*, seems to be identical with *z. zaddachi*, owing to the presence of long setae on pleon segments 4-6 and telson (Hoek's figs. 11' and 11", pl. X) and of red spots on the pleon; the extremely low salinity in some of the recorded localities is also a favourable indication.

The two specimens, described by Tesch (1915) from the southern part of the North Sea and regarded by him as closely related to Hoek's var. A, might also belong to *z. zaddachi*. Their occurrence in the open sea was due presumably to transport from adjacent coastal waters with reduced salinity.

- Gurjanova, 1930: *G. zaddachi*.¹
 Dementieva, 1931: *G. setosus* f. *baltica*.²
 Schijfsma, 1931: *G. locusta*, Hoek's var. A.
 *Poulsen, 1932: *G. duebeni*. 1933-36: *G. duebeni* (in part.).
 Oldevig, 1933: *G. locusta* (in part.).
 *Segerstråle, 1933: *G. locusta* (in part.). 1944: *G. zaddachi*.
 *Schellenberg: *G. locusta* f. *zaddachi* (determination of samples, Helsinki Mus.).
 Serventy, 1935: *G. zaddachi*.¹
 *Valovirta, 1935: *G. locusta* f. *zaddachi*.
 Lucks, 1937: *G. locusta-zaddachi*.
 Höfken, 1937: *G. zaddachi*.
 *Reid, 1939: *G. sarsi*. 1945: *G. ochlos* nom.nov. (= *G. sarsi*).³
 *Suomalainen, 1939: *G. locusta* (in part.).
 *Dahl, 1944: *G. locusta* f. *zaddachi*, *G. locusta* f. *setosus*.

MORPHOLOGY

Maximum size. Male 22 mm., female 15 mm.

Body colour (studied in freshly captured Finnish specimens). Ground colour distinctly lighter than in *oceanicus*: pale greyish green, sometimes greyish yellow. On the dorsal parts of the body a darker pattern, pale or darker brownish green in colour (Fig. 5). This pattern, the colour intensity and extension of which varies considerably, is composed of a system of transverse and longitudinal bands.⁴ *Transverse bands.* Present on the posterior margin of head and of all body segments, excepting pleon segments 4-6 (the colour effect of these bands is augmented by the partial intervention of each segment into the preceding one; on that account these portions seem especially dark). On account of the bands the body of the animal is distinctly transversely striped. On the anterior margin of head, the first peraeon segment, and all pleon segments, transverse bands also occur. Finally, there are median bands on the peraeon segments (excepting the 1st) and on pleon segments 1-3 (the pleon bands are comparatively strongly developed). The median bands

¹ In view of the very low salinity in the locality, where Gurjanova captured '*zaddachi*' ('almost fresh' water, in the estuary of the Sewernaja Dvina), she very likely had to do with *z. zaddachi*. The same conclusion holds good for the specimens caught by Serventy at the more inland stations in the estuary investigated (River Deben, England).

² The comparatively slight head sinus depicted by Dementieva (fig. 10) is conceivably due to somewhat inaccurate drawing or may refer to a specimen of the true *locusta*; the telson figured is of typical *z. zaddachi* shape.

³ The author has found no essential differences between this very small form (length c. 6 mm.), described on material from the brackish Loch of Stennes, Orkney, and mature specimens of *G. z. zaddachi* of the same size from the Baltic (material kindly sent by Mr Reid).

⁴ Palmer (1933, p. 65) observed brown transverse bands on the body segments and on the appendages of a form of *G. zaddachi*, captured in brackish water on the English coast; it was probably *z. zaddachi* or *z. salinus*.

are frequently more or less reduced, sometimes missing, even on the pleon. *Longitudinal bands*. A median band, more strongly developed on the pleon

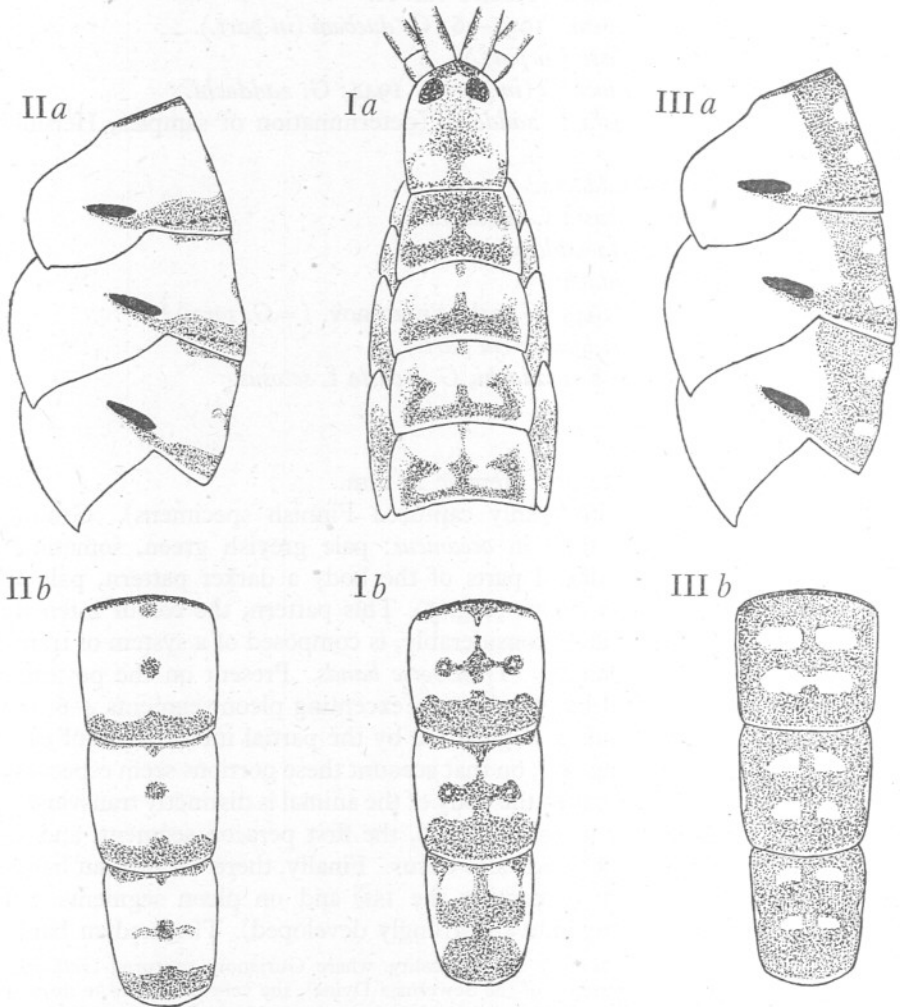


Fig. 5. The pattern in *Gammarus z. zaddachi*. (Material from the south coast of Finland; males.) Three specimens (partly) depicted, to show variation. I a, anterior part of body; I b, pleon segments 1-3 of the same animal. II a and III a, pleon segments 1-3 of two other animals, from the side; II b and III b, the same segments from above. The black oblong patches show the position of the red spots of oil globules.

but sometimes even here strongly reduced (see Fig. 5), runs along the whole length of the body. As a rule it is accompanied on both sides by a band, more developed on the peraeon. The colour pattern is observed also on the antennae (peduncle, flagella), on the peraeopods (especially on segments 1,

3, 5-6), uropods and telson, and, weakly, on the side-plates. A pattern resembling the one just mentioned has been described by Sexton (1939) in *G. tigrinus*.

On the sides of pleon segments 1-3 there are almost invariably red spots of 'red oil globules', known from various other species of the genus *Gammarus* and mentioned in *G. zaddachi* by Sexton (cf. also Palmer, 1933). These are shown in Fig. 5. The pattern and the red spots disappear in preserved animals.

Setose armature of peraeopods, pleon segments 4-6, telson and uropods. Strong development of the setae, as seen in Sexton's figures (1942, fresh-water form). Last peraeopod, longest seta in subapical cluster on hind margin of segment 5 surpassing end of the segment (Fig. 3 *i* in the present paper). Telson, longest apical seta longer than distance from its insertion to insertion of subbasal spines (Fig. 3 *j*). Number of telson setae, see below.

Length of antenna 2 in percentages of antenna 1, from 17 males from the Baltic and the Danish lake Lammefjordssöen, length 13-20 mm.: 78-89, average 84%.

Maximum number of segments in the flagella (body length in brackets):

	Male	Female
Antenna 1: primary flagellum	39 (21 mm.)	31 (15 mm.)
accessory flagellum	8 (20 mm.)	6 (15 mm.)
Antenna 2	19 (20 mm.)	14 (15 mm.)

Length of peduncle segments of antenna 1 (Fig. 3 *h*; for measuring method see p. 227). Ratio of length of segments 2 and 3 combined to that of segment 1, from 1.3:1 to 1.7:1, generally *c.* 1.5:1. Length of segment 3, 0.5-0.7 of that of segment 2. End of peduncle reaching at least to about one-fifth, as a rule to somewhat less than half the length of segment 5 of antenna 2.

Number of hair clusters (including apical cluster) on the under-margin of peduncle segments 2 and 3 in antenna 1 (Fig. 3). Segment 2, 5-9 clusters, generally 6-7; segment 3, 3-5, generally 4.

Pleon segments 4-6, spine formula:

4th segment	2-3 : 2 : 2-3
5th segment	2-3 : 2 : 2-3
6th segment	2-3 : 2 : 2-3

Telson, number of spines and setae:

	Spines	Setae
Apical	1-3	4-17
Subapical	0-1	1-2
Subbasal	1	2-4

Uropod 3 inner ramus, length about three-quarters that of the outer.

DISTRIBUTION¹

Brackish and, locally, fresh water in north and west Europe (highest salinity recorded *c.* 14–18 ‰).² In the Baltic district found practically only in brackish water (the only exception being the record from the Danish Lake Lammefjordssøen, see below).³

Great Britain: see the numerous records given by Spooner. To them may be added Loch of Stennes, Orkney (brackish water, locality for *Gammarus ochlos (sarsi)* = *G. z. zaddachi*; see p. 231).

Ireland: Lakes Lough Nadarragh, Lough Keenaghan, Lough Awaddy, Lough Tullynabour, Lough Erne (Sexton, 1912).

France: Nantes and Belle-Île-en-Loire (Sexton, 1942, p. 583).

Belgium: see Spooner.

Netherlands: mouth of the Rhine and the Waal, Zuiderzee (Hoek, 1889; Tesch, 1922; and Schijfsma, 1931: *G. locusta* var. A).

Germany: see Spooner.

Denmark: Lake Lammefjordssøen (north-west Sealand; Copenh. Mus.); for marine localities see below. Spooner also gives several records from Danish waters.

Norway: Bolstadfjorden (near to Bergen; Bergen Mus.).

Baltic: all over the area, throughout the Gulf of Bothnia and the Gulf of Finland, to the Danish waters (for details see pp. 236–8).

? White Sea, mouth of the Sewernaja Dvina (see p. 231, footnote 1).

***Gammarus zaddachi* Sexton subsp. *salinus* Spooner 1947**

As mentioned previously, in the *Gammarus* material studied by the author from the Baltic, a form of *zaddachi* was often found to which a peculiar combination of characteristics of the forms now named *z. zaddachi* and *z. oceanicus* is typical. The peduncle of antenna 1 is about as setose and elongate as in the former subspecies, whereas the hinder peraeopods, the pleon segments 4–6, and the telson are almost glabrous, as in the latter.

The opportunity given to the author of reading Spooner's manuscript and our reciprocal examination of British and Finnish material respectively has made it clear that the 'combined' Baltic form is identical with Spooner's subspecies *salinus*.

As this 'combined' type was captured only in waters where also *z. zaddachi* and *oceanicus* occurred, it seemed possible to the author at the first sight that it represented a curious result of crossbreeding between these two forms. Now,

¹ In order to make the list more useful it has been completed by references to Spooner.

² Tesch, 1922, Zuiderzee (Hock's var. A).

³ Compare *Gammarus duebeni*, which, in this area, is confined to brackish water, though in western Europe, etc. it is found also in fresh-water localities (cf. Segerstråle, 1946).

however, Spooner's interesting statement of *salinus* and *z. zaddachi* being incapable of producing fertile eggs with one another has given evidence of the genetical independence of the former type, and thus has motivated the establishing of it as an independent subspecies.

As already indicated the separation of *salinus* from *zaddachi* is easy, whereas the limit between the former subspecies and *oceanicus* may sometimes appear to be vague, owing to the partial overlapping of the main distinguishing characteristics, viz. the length and setation of the peduncle of antenna 1. As to the latter characteristic which is more useful in practice, it is typical that *salinus* has at least six tufts on the under-margin of peduncle segment 2, against four tufts in typical *oceanicus*. But the range of variation of both subspecies also includes the tuft number of five, and this number seems to be comparatively common in *salinus*. As pointed out previously, the number of tufts on the last peduncle segment might, in such instances, be a reliable distinctive characteristic. In *oceanicus*, from purely marine localities, where the brackish *salinus* is not to be expected, more than two tufts have practically never been found by the author, whereas *salinus* ♂ typically has at least three.¹ Specimens with five tufts on the second peduncle segment and three on the third might consequently belong to *salinus*, not to *oceanicus*. In freshly captured animals also the colour will, presumably, prove to be a good distinctive characteristic. The examination of a number of such specimens of typical *salinus* from Finnish waters showed that they all had the pattern which is found in *z. zaddachi* (p. 231), though it was generally much less distinct than in that form (the red spots were also present in many specimens). Further observations on more extensive material are necessary, but the foregoing statements seem at any rate to make it very likely that the colour will prove an additional characteristic which reliably distinguishes *salinus* from *oceanicus*.

In the material from the Baltic specimens have also been observed in which the setation of the last pereopods, or of the telson (the two characteristics chosen as indicator of the hairiness of the hinder parts of the animal), or of both, is somewhat more strongly developed than in typical *oceanicus*. The setose armature of antenna 1 in these specimens is never as sparse as in typical *oceanicus*. The author is inclined to suppose that these varieties belong to *salinus*.

Details of the distribution of *salinus* in the Baltic, as well as in Danish waters, are given in the following section. Regarding the occurrence of the subspecies outside this district, see Spooner (pp. 41-3).

¹ The only exception refers to a couple of specimens observed in the material from Heligoland. They bear three hair clusters on the segment in question, and the length of the last peduncle segment compared with the length of the second segment is 0.6, against at most two and 0.5 respectively in the typical marine form. It does not seem quite impossible that these specimens have been transported to Heligoland from adjacent brackish waters on the continental coast (cf. the assumed transport in another case, p. 230, note 1).

THE DISTRIBUTION OF *GAMMARUS ZADDACHI* AND *G. LOCUSTA* IN
CERTAIN WATERS

The Baltic and Denmark (excluding Randers Fjord and Ringkøbing Fjord)

Material. Number of samples investigated (abbreviations of Museum names: Cop. = Copenhagen, Hels. = Helsinki-Helsingfors, St. = Stockholm): Finnish waters, c. 230 (Hels., and the author's collections); the archipelago from Stockholm to Kalmar, 12 (St.); coast of Blekinge, 4 (St.); Gothland, 20 (St.); Bornholm, 5 (St., Cop.); Danzig, 1 (St.); east of Rügen, 2 (Cop.); Rügen-Danish Isles, 12 (Cop.); The Sound, 3 (Cop., St.); Falster-Sealand, 6 (Cop.); Great Belt, 6 (Cop.); Little Belt and adjacent southern waters, 3 (Cop.); Ise Fjord, 2 (Cop.); Cattegat, 10 (Cop.); west coast of Denmark, 5 (Cop.).

Regarding the literature records, the surveys by Stephensen (1928, 1929), Oldevig (1933) and Schellenberg (1942) could not be used, as the differences between *G. locusta* and *zaddachi* are here not recognized. But the data published by Poulsen (1932) and Dahl (1944), though not correct in the species determinations, can be reinterpreted in the light of the samples of these authors' material available to the writer. From the south coast of the Baltic *G. zaddachi oceanicus* has been recorded (as saline form) by Sexton (1912, 1913) who also records, and figures, *locusta* from these waters.

Gammarus zaddachi oceanicus. This form is the main *Gammarus* in the Baltic and around the Danish Isles. It is lacking only in the 'innermost' parts of the Gulf of Bothnia and of the Gulf of Finland (Fig. 6; in the Gulf of Bothnia, which has been studied less thoroughly, the northernmost record of *oceanicus* is c. 63° 30' N.) and other strongly diluted localities. In the Gulf of Finland the 'innermost' records (Virolahti: Kiuskeri and Pien Kalastaja) lie at the isohaline of c. 2.5‰ salinity (surface, year average). On the south coast of Finland, from which area a great quantity of material has been investigated, the form in question greatly outnumbered *z. zaddachi* in the outer parts of the archipelago, at least as far eastward as in Pellinge, and even in a sample from the island Peninsaari (near Lavansaari, at 28° 2' E.) *oceanicus* is clearly predominating (115 *oceanicus* against 4 *z. zaddachi*). On the Finnish coast *oceanicus* is especially common in the *Fucus* vegetation (cf. Segerstråle, 1944; *oceanicus* here called *G. locusta* f. *typica*). The bulk of the material of *oceanicus* originates from a depth of a few metres, but there are also a number of samples from the open sea between Rügen and the Danish Isles with depths of c. 20 m.

In the samples from the Cattegat *oceanicus* is sparsely represented and entirely lacking in the material from the Danish west coast.

Gammarus zaddachi zaddachi is represented in the material from the very end of the Gulf of Bothnia and the Gulf of Finland to the Sound (Isle Hven). In the 'innermost' parts of the Gulfs (Fig. 6) and other strongly diluted areas it is the only abundant *Gammarus* (in addition *G. duebeni* occurs here locally; cf. Segerstråle, 1946). The author found the amphipod in great numbers inhabiting the vegetation of *Phragmites* in estuarine localities. The animal is

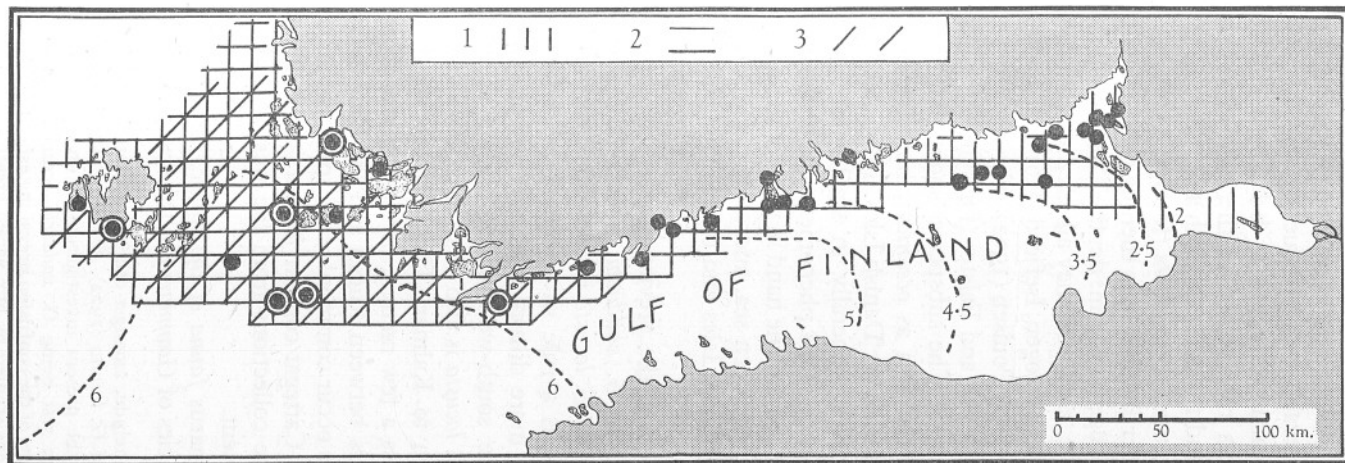


Fig. 6. The occurrence of *Gammarus zaddachi zaddachi* (1), *G. zaddachi oceanicus* (2), and *G. locusta* (3) along the north coast of the Gulf of Finland and in the south-west Finnish waters. The black dots show the origin of the material investigated. Localities for *G. locusta* indicated by rings. As seen, there are three *Gammarus* zones: (a) in the innermost part of the Gulf only *G. z. zaddachi* occurs, (b) westward from here to near the mouth of the Gulf *oceanicus* also is found, (c) the south-west waters are inhabited, in addition, by *G. locusta*. In addition, *G. z. salinus* occurs in the area, having about the same distribution as does *oceanicus*. Broken lines represent isohalines (‰).

common also in the Finnish archipelago, but, as mentioned above, less numerous than *oceanicus* in the *Fucus* vegetation of the outer zone. However, it generally occurs considerably more frequently than does *oceanicus* in very shallow water (with a maximum depth of half a metre or so) in this zone. From the Swedish waters represented in the material, i.e. the coast from Stockholm to Blekinge, and the coast of Gothland, there are numerous finds; also Dahl frequently captured *z. zaddachi* (for synonymy, see p. 231) in the latter waters. From deeper Baltic waters there is only one sample containing *z. zaddachi* taken east of Rügen, in 21 m. depth. The Danish material includes some samples containing *z. zaddachi*; they all refer to a depth of at most a few metres (Ore Strand: Sliphavnskrogen, Isefjord: Hovvig). But from this district there are also records given by Poulsen (1932), who captured the form in the waters between Sealand, Möen and Falster (for synonymy, see p. 231).

Gammarus zaddachi salinus. The subspecies shows, on the whole, the same limits of distribution in the area as *oceanicus*, but it is not present in the material from localities outside the Danish Isles. The type in question is found in most *Gammarus* samples, generally in small numbers, but locally it occurs in striking abundance. This phenomenon is observed in localities of quite different natures, viz. on the one hand in parts of the Finnish archipelago, which are not exposed to the open sea, and on the other in the open waters between Rügen and the Danish Isles and on the coast of the Great Belt (at Nyborg).

Gammarus locusta. Most of the previous records of this species from the Baltic area actually refer to *G. zaddachi*, mainly to subsp. *oceanicus* (for synonymy, see p. 227).¹ But *G. locusta* is also widely distributed in the Baltic district, though it is not as a rule so abundant as *zaddachi* and does not penetrate as far into the more diluted waters. Thus *locusta* on the Finnish coasts is confined to the south-west waters with a minimum salinity of c. 5-6‰ (see Fig. 6). *G. locusta* is also missing in the Swedish samples from the waters off Stockholm to Kalmar. The depth in the places of capture generally does not surpass a few metres; in the material from the open and comparatively deep waters between Rügen and the Danish Isles, where *zaddachi oceanicus* and *salinus* occur commonly, the species is practically missing.

The samples from the Cattegat contain *locusta* in much greater numbers than *zaddachi*, and in the collections from the west coast of Denmark only the former species is present.

Summary of the Gammarus fauna of the Baltic. The forms treated above are the only common species of *Gammarus* of this area. Besides them the area

¹ The Danish collections include, amongst other, the material used by Blegvad for his investigation on the biology of *G. locusta* (1922). Of c. 210 specimens from this collection, examined in connexion with the present investigation, c. one-third (70 specimens) proved to belong to this species, the rest being *G. zaddachi oceanicus*, and *salinus*. This result is by no means surprising in view of the confusion prevailing especially in earlier years. Blegvad also observed that the specimens studied by him varied greatly.

seems to harbour only *G. duebeni*, which is confined to very shallow water and to special localities (it occurs mainly in brackish rockpools and similar small basins on the shore of islands, exposed to the sea; see Segerstråle, 1946). There is no evidence for the occurrence of *G. setosus* Dement. Dementieva's *G. setosus* f. *baltica* and Dahl's *G. locusta* f. *setosus* from Baltic localities are attributed to *G. z. zaddachi* (see synonyms, p. 231).

Randers Fjord

A comparatively large collection of *Gammarus*, made by Johansen and Ussing during their investigations of the invertebrate fauna of this water, situated on the north-east coast of Jutland in Denmark and interesting because of the decreasing salinity from the mouth to the more inland parts, is discussed in Stephensen's paper of 1917. He records the following species and forms from the area: *G. locusta*, *G. locusta* var. *Zaddachi*, an intermediate form between *G. locusta* and this form, as well as *G. duebeni* and *G. pulex*. Later on, in 1927, Stephensen identifies some of the intermediates between *G. locusta* and *G. locusta* var. *Zaddachi* as *G. duebeni*. The material concerned was deposited in the Museum of Copenhagen, and all of it, excepting that of *G. pulex* and *G. duebeni*, was kindly sent by Mr Stephensen to the author, who has thus had the opportunity of going through it.

The results are as follows. Most specimens labelled *G. locusta* are correctly determined (one being an intermediate between the subsp. *oceanicus* and *zaddachi* of *G. zaddachi*). The form called *G. locusta* var. *Zaddachi* is mainly *G. z. zaddachi*, whereas the 'intermediate form between *G. locusta* and *G. locusta* var. *Zaddachi*' includes all three subspecies of *G. zaddachi*; in addition, there are some *G. locusta* and one *G. duebeni* (this species captured at St. 9, depth 0 m.). In a number of samples of *G. zaddachi*, the subspecies could not be determined, on account of the very small size of the animals. The study of the material has given the following ranges of distribution:

<i>G. zaddachi zaddachi</i> :	St. 2 (salinity from 1-2 to 12°/‰)
<i>oceanicus</i> :	St. 8-10 (salinity from 5 to at least 24°/‰)
<i>G. locusta</i> :	St. 10 (salinity from c. 17 to at least 24°/‰).

As seen from the above records the subspecies of *zaddachi*, as well as *locusta*, follow one another in the same order as in the Baltic area. The salinities at the most inland localities for *z. oceanicus* and for *locusta*, are higher in Randers Fjord than in the Baltic, but this phenomenon is obviously due to the comparatively scanty material from the Fjord.

Ringkøbing Fjord

This water, located on the west coast of Jutland, is connected with the North Sea through only a narrow opening. The water is consequently brackish, the (surface) salinity averaging in the main part of the area c. 4-8°/‰. The

Gammarus fauna has been treated by Poulsen (1933-6). He records the following species: *G. locusta*, occurring only in the very opening of the Fjord; *G. duebeni*, common everywhere, excepting in the saltiest part, and observed also in the lowermost course of the river Vondaa; *G. zaddachi*, found only in a small basin, which is separated both from the Fjord and from the North Sea.

Fortunately, the collection received for the present investigation from the Copenhagen Museum includes about forty samples of the Ringkøbing Fjord material (the determination, however, is not given on the labels), thus enabling the author to check the records which were given by Poulsen and of which some appeared doubtful.

The results are as follows. (1) The main *Gammarus* of the Fjord is not *duebeni*, but *zaddachi*. All the specimens of this species, which are large enough to be identified, belong to *z. zaddachi*. *G. duebeni* is certainly present in the material, but occurs only in a few samples, all taken in very shallow water (0-0.5 m.). The localities are: the mouth of the River Vondaa; near the bridge in this river; off Gammelsogns Mølle; on the shore *c.* 200 m. east of the mouth of the River Falen; Gjødøl Canal, near the bridge at Lønne Klit.

(2) *G. z. zaddachi* occurred in different parts of the Fjord, from the shore to open areas with depths of *c.* 3 m. (maximum depth of the area *c.* 6 m.). In addition, one sample has been collected in the mouth of the River Vondaa, near the bridge (3 July 1921).

(3) The true *locusta* was found only in one sample (Søndre Dyb, 3.5 m.). Poulsen records the species from the saltiest parts of the Fjord. These samples are lacking in the material available to the present author, but as the characteristics given for this species by Poulsen are quite correct there is no reason to doubt these determinations.

(4) The '*G. zaddachi*' mentioned in Poulsen's paper seems not to be included in the preserved material, but the illustrations given suggest that the form of the species in question is *oceanicus*.

THE RELATIONSHIP BETWEEN *GAMMARUS ZADDACHI* AND THE SPECIES *G. SETOSUS* AND *G. WILKITZKII*

In the material from the Arctic there are numerous samples containing the large species *G. setosus* and *G. wilkitzkii* (many of the samples are labelled *G. locusta*), thus enabling the author to compare them with *G. zaddachi*.

G. setosus (material: about thirty-five samples from Arctic Canada, Greenland, Iceland, Spitsbergen, east coast of Murman, Novaya Zemlya, Kara Sea, the Arctic Sea off Siberia). This species was separated from *G. locusta* and established as an independent species by Dementieva (1931), mainly on material from Arctic waters (the amphipod regarded by this author as a Baltic form of *setosus* is obviously identical with *G. z. zaddachi*). Stephensen

(1940) records it as *G. locusta* subsp. *setosus*, and gives the first accurate description of the form.

The examination of the specimens in the present material showed that the species is as little allied to the true *locusta* as is *zaddachi*, but there is a close relation between *setosus* and the last-mentioned species, especially subsp. *oceanicus*. As in *zaddachi* the head sinus is deep, the 4th side-plate has the same semicircular lower margin, the pleon epimera show no difference in shape, the last uropods have the inner ramus of the same relative length, and as to the relative length of the peduncle of antenna 1 there is a strict agreement with *zaddachi oceanicus*.

The main differences are as follows. (1) The common occurrence of plumose setae in *setosus*, particularly on peraeopods 5-7 (segments 4-6), pleon segments

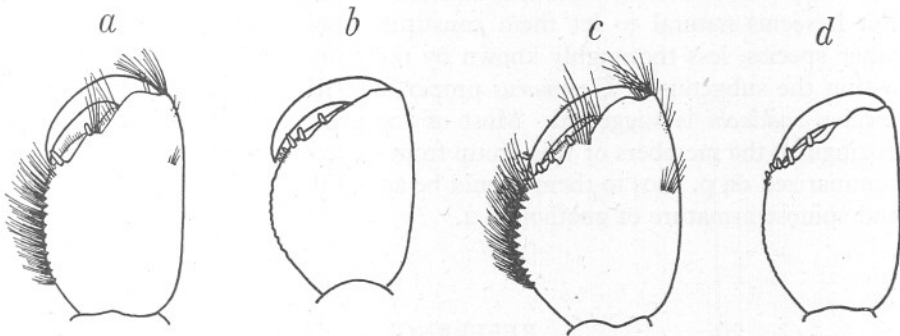


Fig. 7. Second gnathopods of *Gammarus zaddachi oceanicus* (a, b) and *Gammarus setosus* (c, d) (males) to show variation in shape. a, *oceanicus*, typical (Murman Coast, body length 30 mm.). b, *oceanicus*, approaching typical *setosus* (Spitsbergen, 25 mm.). c, *setosus*, typical (east Greenland, 32 mm.). d, *setosus*, approaching typical *oceanicus* (the Arctic Sea off Siberia, 26 mm.). In b and d the setae are omitted.

4-6, and the telson; here practically all the setae are feathery (cf. Stephensen, 1940, fig. 41). In addition the apical hairs on the telson are markedly longer than in *z. oceanicus* (in the male about three times as long as the corresponding spines (or longer), against at most about twice the length in *z. oceanicus*). (2) The 2nd and 3rd peduncle segments of antenna 1 bear hair clusters, on the under side, from 5 to about 7, and 2-3 respectively, whereas *z. oceanicus* has 3-5 and 1-2 respectively. (3) The eyes are generally distinctly smaller in *setosus*. (4) The 2nd gnathopod in this species is as a rule considerably stouter and its hind margin much more bulging; besides, the gap between the mid-palm spine, present in the male, and the palmar-angle spine-row is usually far less pronounced (Fig. 7) (in addition, in the female the latter spine group occupies a greater part of the palma in *setosus* than in *z. oceanicus*).

According to the author's observations only the characteristics mentioned above under (1) always separate *setosus* from *zaddachi oceanicus*, whereas, when comparing the former species with large specimens of *oceanicus*, the other

characteristics may overlap more or less (Fig. 7). Even in the occurrence of feathery setae there may be some transition, *oceanicus* occasionally having single plumose hairs on the last uropods, pleon segments, and telson (Fig. 3f), but the difference is nevertheless very marked.

Besides *G. setosus*, the very large Arctic species *G. wilkitzkii* (length up to 48 mm.; Gurjanova, 1930) is closely allied to *zaddachi*. It has even been reported by some writers, amongst others Stephensen, as possibly being identical with this species. In fact, the differences between *z. zaddachi* and *wilkitzkii* are small.¹ They seem, however, to be great enough to justify retaining the latter as an independent species, as suggested by Sexton (1942). The same conclusion appears to hold good regarding *setosus*. If these two forms were considered subspecies of *zaddachi*, the still closer relation between the subspecies *zaddachi*, *oceanicus*, and *salinus* would not be so clearly seen. But it seems natural to let them constitute—possibly together with some other species, less thoroughly known by the author—an independent group within the subgenus of *Gammarus* proper, and naming this group after the species *zaddachi* is suggested. Most of the principal characteristics which distinguish the members of this group from *G. locusta* are the same as those summarized on p. 220; to them should be added the differences in the shape and spinose armature of gnathopod 2.

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¹ The following divergence observed in material investigated by the author may be added to those listed by Sexton (1942). The peduncle of antenna 1 is still longer than in *z. zaddachi*, viz. as long as the distance from tip of rostrum to hind margin of peraeon segment 2; in *z. zaddachi* the peduncle reaches at the most to the middle of the said segment.

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THE STRUCTURE, TADPOLE AND BUDDING
OF THE ASCIDIAN *PYCNOCLAVELLA*
AURILUCENS GARSTANG

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(Text-figs. 1-3)

Pycnoclavella aurilucens was recorded and briefly described by Garstang in 1891 from a limited locality in the Plymouth area, and has not been found with certainty of identification from any other region. There has been a tendency to subordinate it as a species of *Clavelina*, but the dissimilarities are greater even than the original description implies and this procedure is not justified. The genus is accordingly retained, and a more detailed account of the colony, with the first description of the tadpole larva and process of budding, is presented.

Colonies are usually found growing on gorgonians, large hydroids and calcareous algae at depths of 25-30 m. associated with coarse shell gravel and polyzoa such as *Lepralia*. It is known to occur only in the Plymouth region, unless the form known as *Clavelina nana* reported from Roscoff and Banyuls (Giard, 1873, Lahille, 1890) turns out to be identical with it. The external appearance of the colonies and of the constituent zooids has been well described by Garstang in the second volume of this *Journal*. In brief, the colonies are encrusting, the thoracic parts of the small delicate zooids extending freely from a greenish matrix in which the abdomens are embedded. The endostyle and peripharyngeal bands are picked out in yellow or white pigment and are very striking; the zooids are very contractile.

STRUCTURE OF THE ZOOID

The zooids (Fig. 1) in general structure are much like those of *Clavelina*. They are much smaller and consequently have a less elaborate branchial sac, there being seven rows of gill-slits, rarely eight or nine. The endostyle is comparatively massive, as noted by Garstang, and the siphons independent and without lobes as is in other members of the Clavelinidae. Dorsal languets, corresponding in number to the rows of stigmata, occur along the dorsal line of the branchial sac. The oesophagus is long, the stomach squarish in cross-section as in *Clavelina* and leading into a typical post-stomach, the latter in turn connected with the intestine proper by a vertically aligned mid-intestine. The rectum opens into the atrial cavity level with the most posterior row of