THE AMPHIPODA OF NORFOLK.

Ьу

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Résumé

L'article contient un inventaire de toutes les espèces d'Amphipodes présentes dans le Norfolk et les mers avoisinantes. Pour chacune, la distribution est brièvement indiquée. L'auteur étudie l'allométrie chez *Metopa borealis*, les caractères intermédiaires de *Parapleustes* sp., la distribution remaniée de *Gammarus zaddachi* et *G. locusta* dans l'aire de Blakeney Harbour, ainsi que les distinctions morphologiques entre *Aora typica* et *Microdeutopus gryllotalpa*. Il fournit des renseignements sur les variations de couleur, la taxinomie, l'existence d'espèces propres à quelques habitats spéciaux et certaines relations existant dans certaines espèces entre la taille, la morphologie et l'habitat préférentiel.

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INTRODUCTION

The scope of this paper is similar to that of previous papers dealing with the marine Hydrozoa (Hamond, 1957, 1963 b) and Polychaeta (Hamond, 1962, 1966), while the Scolt Head area has been described independently (Serventy, 1934; Pantin & al., 1960). In the present survey the amphipods found offshore were taken mostly by dredging, an important minority being captured in the plankton

CAHIERS DE BIOLOGIE MARINE Tome VIII - 1967 - pp. 113-152 (especially in the plankton just above the sea-bed, Hamond, 1965 b) or in the rubbish from whelkpots (Hamond, 1961); intertidally they were collected among algae, among sessile organisms under rocks, or burrowing in sand (cf. Jones, 1948). For the sake of completeness the terrestrial and freshwater species are included, of which the present author has had but limited experience in the field, the material of such species examined by him being mostly preserved. Details of taxonomic, morphological and ecological interest are dealt with under the species concerned, as are all intertidal records; the latter are mentioned individually unless very numerous, when they are summarised. All records from offshore benthonic stations are summarised in tables at the end; the symbols and abbreviations used are as in the survey of the Norfolk Polychaeta (Hamond, 1966).

Previous records

Amphipods have been recorded from the Norfolk area by Anon. (see Apherusa clevei), Metzger (1875), Harmer (1899), Gurney (1904, 1907), Hart (1930), Serventy (1934), Crawford (1935), Ellis (1942), Gilson & al. (1944), Reid (1948), Spooner (1947, 1951), Hazelton (1960), Pantin & al. (1960), and Ingle (1963), as well as in the unpublished notes of the late Arthur Henry Patterson and in private communications to me from Miss R.M. Barnes (Mrs. Race), Brigadier E.A. Glennie, and Messrs. G.I. Crawford, E.A. Ellis, J. Fisher and G.M. Spooner; unpublished records from these sources are referred to in the text by the initials of the contributor concerned.

Between them, the published and unpublished records cover 47 species from marine, brackish, freshwater and terrestrial habitats; of these I have found 35 (all aquatic or marine) as well as another 59 species, all marine, which are here recorded from Norfolk waters for the first time. The total number of species for the area under consideration (the county of Norfolk, and the adjacent sea within 30 miles of the Norfolk coast) is thus 106 species, belonging to 66 genera and 25 families. These counts exclude references to amphipods in my previous papers (Hamond, 1961, 1963 a & b, 1965 a), in which the amphipods were mentioned from other points of view and not (as here) as records intended to increase our knowledge of their geographical and ecological distribution.

Of the previous workers' material the only specimens extant are some in the Castle Museum, Norwich, collected by several workers, and some at Cambridge from collections made at Scolt Head in 1959 (Pantin & al., 1960). Gurney's specimens in the Castle Museum are of the same species (with a few exceptions) and from the same collecting-grounds as are those mentioned in his papers, but are all of much later date, having been collected between 1920 and 1935. Patterson's preserved material of marine animals (principally crustacea), collected by him in the Yarmouth area from 1889 onwards and placed in the Tollhouse Museum in Yarmouth after his death in 1935, was destroyed by bombing during an air-raid in 1940. The amphipods from Sheringham and elsewhere, listed in Table 2, are now in the British Museum of Natural History, as is the dissected

holotype of *Melita reidi* Hamond (1965 a), whose registration number is BM (NH) 1965.128.1. A representative collection of all the species taken by me, including the remaining specimens of M. *reidi* (the only undescribed species found in the present survey), is housed in my own museum.

The limits for the area are by no means natural, and certain species found just outside them may well be caught within them at some future date; for this reason I have included some of Reibisch's records (Table 1) as well as the species found by me at Burgh Castle on 31.8.1963. Most of the species mentioned in Table 1 have in fact been found here, while Burgh Castle, though in Suffolk, is separated from Norfolk by less than 200 metres (the width of Breydon, the estuary of the Yare, at this point).

Systematic list

The order in which the species are listed follows closely that of Chevreux & Fage (1925); identifications are based mainly on this work, also on Sars (1895), Stephensen (1929), and Schellenberg (1942). Papers dealing with individual genera or species are quoted where appropriate; the naming of species is mostly as in Barnard (1958). The account of each species is based in my own observations, except where otherwise indicated by the initials of the observer, and is preceded by a synonymic list of the previous local records (if any) of that species. Comments placed between inverted commas are quotations from my notes, unless credited to someone else.

SUB-ORDER GAMMARIDEA

Family LYSIANASSIDAE

Acidostoma obesum (Bate).

One in bottom plankton just outside Blakeney Bar, 20.7.1963. In captivity it had a strong tendency to curl up tightly and lie still; the colour was pale yellow, with a vaguely defined transverse band of pink spots on each segment of the mesosome. A second specimen (at D. 45) was about half the size of the first, and of a uniform pale cream colour.

Orchomene humilis (A. Costa).

Found only in dredgings; at D.18 the body colour was pale pearly grey, with indistinct orange spots below the surface of the mesosome, and with dark brown eyes. In formalin the orange spots disappear and the eyes go black. An extremely active and fast-swimming species. Tryphosa sarsi (Bonnier).

Fairly frequent in dredgings. I can find no reliable difference between my own material, the *T. nana* of Sars (1895), and the *T. grandimana* of Chevreux & Fage (1925), and take them to be synonymous: Barnard (1962) has come to the same conclusion independently.

Orchomenella nana (Krøyer).

Both in habits and appearance this very much resembles T. sarsi, but is apparently less common locally. At W.33 a small Orchomenella, from among washings of crushed whelkshells (Buccinum undatum) which had contained hermit-crabs (Pagurus bernhardus), was clearly this species, and not O. commensalis which Chevreux & Fage (1925) found in this habitat on the north coast of France.

Family AMPELISCIDAE

Ampelisca tenuicornis, Lilljeborg.

A. tenuicornis Metzger (1875); Hamond (1963 a); A. spinipes Hart (1930), in part; Ampelisca Hamond (1961).

Very common offshore, especially on the siltiest grounds, whether or not they have plenty of shells and stones as well (Hamond, 1963 a). The usual body colour is a bright pink or yellowish pink, with magenta patches on the lower side of the first coxal plate (cf. Schellenberg, 1942, p. 150) and of the third epimeral plate, while very large individuale have magenta along all the coxal and epimeral plates and on the bases of pereiopods 5, 6 and 7; at S.4, however, the body colour was a pale dull grey, without any magenta but with a suffusion of red all over the head.

At D.17 and at D.47 masses of collapsible matted muddy tubes were found, of a tough and somewhat parchment-like texture, which apparently were made by the individuals of this species that came At other out of them in swarms while the haul was being sorted. stations there were no such tubes, so that the animals must have lived singly in shelters of a more or less temporary nature ensconced between the shells and stones which invariably dominated the haul. It is possible that the formation of masses (up to 20 cm in diameter, even when broken) of muddy tubes, resembling a collapsible honeycomb, is a response to the demands made by a soft substratum in which the animals would probably be smothered if they attempted to live there singly; by cementing their tubes together into a sort of turf they are able to spread across the surface of the substratum without sinking into it. Both at D.17 and at D.47 the masses of tubes came from slight pits in the seafloor, in which silt tended to accumulate in large quantities over a substratum of stones and shells.

Ampelisca spinipes, Boeck.

A. spinipes Hart (1930), in part.

Dredged twice only, in both cases with the preceding species. Although Hart mentions only *spinipes*, this is so much the rarer locally that I suspect that some at least of his specimens were really *tenuicornis*.

Family ARGISSIDAE

Argissa hamatipes (Norman).

In bottom plankton over the sandy grounds about a kilometre north-north-east of Blakeney Bar, a single female on each of three occasions; they were all clearly of this species and not of *A. stebbingi* (Bonnier), on the basis of the distinctions given by Gurjanova (1951).

Family HAUSTORIIDAE

The species of *Bathyporeia* were identified according to Watkin (1938).

Bathyporeia pilosa, Lindstrom.

B. pilosa Crawford (Table 2).

Not seen here since (perhaps *B. sarsi?*); with it Mr. Crawford records a *"Bathyporeia* sp.", not *pilosa* nor *pelagica*, but without further comment.

Bathyporeia pelagica (Bate).

B. robertsoni Hart (1930), in part; *B. pelagica* Gilson & al. (1944); Crawford (Table 2).

Common at West Runton above mid-tide level, in little pools in the chalk marl whose floors are covered with sand a few centimetre's thick; here it is often heavily infested with the parasitic copepod *Sphaeronella paradoxa*, which in the Blakeney Harbour area attacks only *B. sarsi*. In this latter area *B. pelagica* is quite common in clean sand outside the Point and off Stiffkey, but is much scarcer inside the Harbour except in the sandbank a few metres northeast of Morston Creek, thus apparently preferring a higher average salinity and less shelter than *B. sarsi*.

Bathyporeia elegans, Watkin.

Found outside the Point with *B. pelagica*, but much less common; not so far taken inside the Harbour except for one in sand at the Freshes and three in plankton hauls in the Pit on separate occasions. It is also found, though seldom, in sand at extreme low water of spring tides, at Holkham, Stiffkey and West Runton.

Bathyporeia guilliamsoniana (Bate).

One in clean sand at extreme low water at West Runton, 24.10. 1960, and one in the same situation at Brancaster on 10.8.1961.

Bathyporeia sarsi, Watkin.

B. robertsoni Hart (1930), in part; Serventy (1934).

The dominant burrowing amphipod in all the sandy grounds in Blakeney Harbour, but scarcer in the outside of the Point; at West Runton it is about as numerous as *B. pelagica*, and is found with it.

Haustorius arenarius, Slabber.

H. arenarius Hart (1930); Serventy (1934); Hamond (1963 a); Crawford (Table 2).

Very common in clean sand off Stiffkey and on the outside of the Point, less so within the Harbour, so that its distribution is rather like that of *B. pelagica*. It is rare at Sheringham (G.I.C.) and has been found only once at West Runton.

Urothöe pulchella (A. Costa).

U. pulchella Gilson & al. (1944).

Not seen here since; probably U. brevicornis.

Urothöe grimaldii, Chevreux, var. poseidonis (Reibisch).

Urothöe grimaldii Hamond (1963 a).

Rare at extreme low water on sandy shores, once in the Harbour and twice at Brancaster; also taken in plankton near the surface, once in the mouth of Morston Creek and twice off the end of the Point.

Urothöe brevicornis, Bate.

U. brevicornis Hamond (1963 a).

Very common in sand between tidemarks in Blakeney Harbour, also outside the Point and at Wells; rare in plankton in the Pit.

Urothöe elegans, Bate.

Found only offshore; in dredgings it is confined to the siltier grounds, where it probably lives interstitially. It has also been taken thrice in bottom plankton outside the Point (see *Argissa*).

Family PHOXOCEPHALIDAE

Phoxocephalus holbølli (Krøyer).

One in bottom plankton close to the Blakeney Overfalls Buoy, 29.3.1965, and a smaller one about half a kilometre from the Buoy,

in a dredge haul (D.40) on the same day. Not previously recorded so far south on the east coast of England.

Metaphoxus fultoni (T. Scott).

One, about 3.5 mm long, at S.4.

Harpinia pectinata, G.O. Sars.

Scarce in dredgings, with a marked preference for silty grounds; once in bottom plankton near the Blakeney Overfalls Buoy, 1.9.1962.

Family AMPHILOCHIDAE

Amphilochus manudens, Bate.

Mainly on the siltier grounds, where it is very common.

Amphilochus spence-batei (Stebbing).

A. spence-batei Hamond (1965 a).

This usually occurs with *manudens*, but is less abundant and on the whole prefers harder and more shelly ground; one was found just below low-water mark among *Eudendrium ramosum* on the Scaup at Hunstanton on 1.11.1963, and five have been taken in bottom plankton outside the Point (see *Argissa*) of which two were morphologically very close to *A. neapolitanus*.

Gitana sarsi, Boeck.

This is the only intertidal amphilochid in Norfolk waters, having occured at West Runton once among *Corallina* in pools and five times among sponges, hydroids and tunicates under rocks; the offshore records are all from hard grounds with plenty of silt except for a single specimen at Q.2, one in bottom plankton outside the Point on 16.11.1961, and one in surface plankton at dusk in the Pit on the same day.

Family LEUCOTHOIDAE

Leucothöe incisa, Robertson.

One in a vertical plankton haul in six fathoms outside the Point (see Argissa) on 1.11.1961. When alive the body was brilliant orange, with a nebulous blood-red spot on the upper edge of the fifth coxal plate.

Family STENOTHOIDAE

I follow Schellenberg (1942) and Barnard (1958) in uniting the Stenothoidae with the Metopidae; Chevreux & Fage (1925) keep them apart.

Metopa pusilla, G.O. Sars.

Very common among hydroids; the greatest number in a single haul was between 100 and 150 at D.20, but it usually occurs singly or in small numbers. It is often cast ashore and may survive there for a time, since one was found, among *Laomedea gelatinosa* which was growing in the lowest reach of Morston Creek, on 18.2.1960.

Metopa borealis, G.O. Sars.

Common inside the "Hjördis" among sessile organisms, especially *Tubularia larynx;* on four occasions single specimens have been taken in bottom plankton (see *Argissa*). All these records were made during September 1962, except for an ovigerous female among mixed hydroids in a trawl, from two to four kilometres west of the Blakeney Overfalls Buoy, on 12.7.1965.

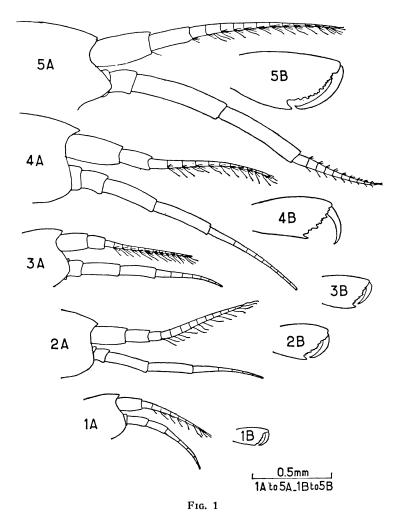
Allometry in Metopa borealis

The above material includes specimens of all sizes, and certain allometric trends were noticed in the peduncular joints of the second antennae (Figs. 1A to 5A), in the size of the propus of the second pair of gnathopods relative to the size of the body (Figs. 1B to 5B), and in the development of the corner tooth of the propus of the second gnathopod, between the palm and the rear margin (Figs. 1C to 5C). It will be noticed, with regard to this latter feature, that the two flanking spines stick out well beyond the corner tooth in young specimens, but are left behind as the corner tooth advances during growth. In the smallest specimens the palm is minutely jagged all the way along, and the corner tooth is hardly apparent, but with growth the corner tooth and the sinus above it both become more distinct, so that the toothed portion of the palm becomes shorter in proportion to the entire length of the palm, and also becomes more curved. The dactyl, also, from being as long as the palm in the smallest examples, falls behind during growth so that in the adult it is only about nine-tenths as long as the palm; this falling behind takes place with relative suddenness at an advanced stage, since the dactyl is almost as long as the palm in Figs. 1C to 4C inclusive, while it is slightly shorter in Fig. 5C.

In the second antennae the last two joints of the peduncle elongate very rapidly with age, while their breadth remains roughly constant in proportion to the size of the animal; these joints are thus very slim in the adult (Fig. 5A) and extend to the tip of the first antenna in the adult, whereas in all younger stages they do not reach quite as far, and are stouter in proportion to their length.

In the literature, the proportions of the joints of both pairs of antennae and the precise form of the second gnathopod are considered some of the most useful and stable specific characters in this otherwise remarkably homogeneous family. In *M. borealis* these characters are certainly not stable, and their usefulness must be accepted with

caution; if growth studies show this kind of variability in other species in the Stenothoidae, the selection of valid taxonomic characters will have to be reconsidered most carefully, not only as regards supposed new species but also with respect to those already known; the very large number of known species (Barnard, 1958) will no doubt be significantly reduced. Quite apart from this, the evolution of different



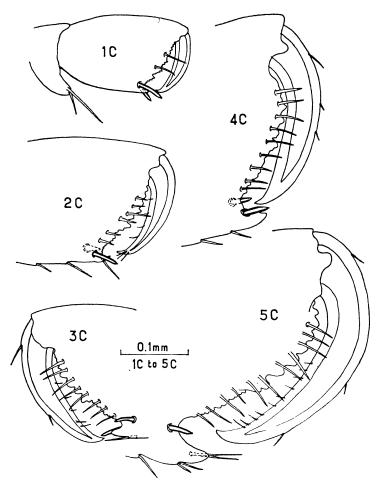
1A to 5A: heads and antennae of the five specimens of *Metopa borealis* mentioned in the text.

1B to 5B: the second gnathopods of the same five specimens.

allometric rates, with different times of starting and stopping (since allometry is by non means necessarily continuous throughout life), could have been an important factor in speciation within the Stenothoidae; it is not too much to say that, if the life of M. borealis could be prolonged to twice its normal span, during the whole of which time the trends described above would be assumed to continue, the oldest

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individuals thus produced would be almost indistinguishable from M. alderi (Figs. 6A, 6B, and 6C). In fact, the evolutionary relationship (if any) is more likely to have been the other way round; it may be supposed that from normal M. alderi there arose a stock, showing precocious maturity (neoteny) at about half the normal adult size,



F1G. 2

1C to 5C: palms of the gnathopods shown in 1B to 5B, magnified to show details of growth changes.

from which the present-day M. borealis is derived. Such a step might be correlated with the change in food from a medusa (*Tima bairdi*) which lives for about seven months of the year, including most of the winter (Russell, 1953), to a hydroid (*Tubularia larynx*) in which the colonies die down completely in winter and in which the individual polyps last for only a few days, being continually renewed during the summer season.

Metopa alderi (Bate).

A large female with 96 young in her broodpouch was cast up in Morston Creek on 11.3.1955, clinging to the medusa *Tima bairdi* (Hamond, 1957); the young ones were nearly as large as full-grown *M. pusilla*. In the adult the whole of the first antenna was shorter than the very long and heavily built peduncle of the second antenna, whose

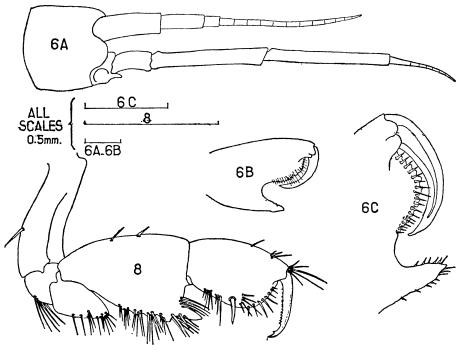


FIG. 3

6: Metopa alderi female. A: head and antennae; B: second gnathopod; C: detail of palm of second gnathopod. 8: Microdeutopus gryllotalpa. Second gnathopod of adult male.

fourth and fifth joints were each about as long as the height of the second coxal plate; the palmar sinus of the second gnathopod was equal to about half the total length of the palm (Figs. 6A, B & C). In all these features the female agreed with M. spectabilis G.O. Sars, which is probably no more than a very marked variety of M. alderi.

Stenothoe monoculoides (Montagu).

Four in bottom plankton outside the Point (as for Argissa), and one among Bugula plumosa inside the "Hjördis", all during September 1962. Stenothoe marina (Bate).

One among Laurencia in the outflow from the Strond Pool Dam, 9.12.1962; on several occasions inside the "Hjördis" during September 1962; 7 ovigerous females and 8 other individuals among Eudendrium rameum and Halecium halecinum growing just below extreme low water on Hunstanton Scaup, 31.7.1961; and several times offshore, where it prefers rough ground with quite a lot of silt and many hydroids. In plankton hauls it has been taken, once at the surface in the Pit (evening of 13.9.1962), and several times outside the Point and in Blakeney Deeps, always near the bottom.

Family CRESSIDAE

Cressa dubia (Bate).

C. dubia Hamond (1963a).

One among Salmacina at West Runton, 3.8.1958, and two among Bugula plumosa inside the "Hjördis", 14.9.1962; very common in dredgings with a strong preference for the same sort of grounds as Stenothöe marina. It lives to all appearances either among hydroids or interstitially in the substratum. The colour is a peculiar reddish brown like varnished mahogany, with the rear edges of all the body segments picked out in a deeper brown.

Family ACANTHONOTOZOMATIDAE

Panoploea minuta (G.O. Sars).

Prefers "earthy" rather than shelly substrata, with a fair amount of silt; also found (one specimen) in bottom plankton outside the Point (as for *Argissa*) on 1.11.1961. All the specimens are certainly this species, and not the extremely similar *Iphimedia obesa* (Rathke).

Family OEDICEROTIDAE

Perioculodes longimanus (Bate & Westwood).

One ovigerous female and 11 other specimens in bottom plankton over sand at 53°03'30"N. 01°00'E., 1.9.1962; one in bottom plankton at 53°00'20"N. 00°59'30"E. on 15.8.1963.

Pontocrates arenarius (Bate).

At extreme low water in clean sand outside the Point, and occasionally in plankton in the Pit.

Pontocrates altamarinus (Bate & Westwood).

One at extreme low water in sand, Holkham Bay, 16.9.1962; otherwise from time to time in Pit plankton, but much rarer than *P. arenarius*.

In naming the two species of *Pontocrates* I follow Schellenberg (1942, ubi syn.) and Barnard (1958); Norman & Scott (1906) refer to *altamarinus* as *arenarius*, and to the true *arenarius* as *norvegicus*, being followed in this nomenclature by Chevreux & Fage (1925). All these authorities agree that there are only these two species of *Pontocrates* in shallow water between France and Scandinavia, and the Plymouth Marine Fauna (1957) is thus clearly mistaken in listing *altamarinus, arenarius, and norvegicus* as three separate species. The true identity of the "*P. arenarius*" recorded by Gilson & al. (1944) and by Crawford (Table 3) cannot, therefore, be stated for certain, nor is it known if they were dealing with one and the same species.

Family CALLIOPIIDAE

Apherusa bispinosa (Bate).

Common on the lower half of the shore at West Runton among *Corallina*, other algae, and sponges; also taken in dredgings (one ovigerous female at D.22), at Q.2, and in bottom plankton outside the Point (as for *Argissa*; one small one on 1.11.1961).

Apherusa jurinei (Milne-Edwards).

Even more abundant at West Runton than is A. bispinosa, mainly among Corallina (whose crimson colour matches its own) but sometimes among other algae; also taken at Q.2.

Apherusa ovalipes, Norman & Scott.

One in surface plankton in Morston Creek at high tide, 6.1.1963.

Apherusa clevei, G.O. Sars.

A. clevei, Bulletin des résultats acquis pendant les courses périodiques.

Very rare at Station H.7 $(53^{\circ}07'N, 01^{\circ}10'E.)$ in May 1907, according to the Bulletin cited here; the un-named author may have been P.J. van Breemen, who at that period was largely responsible for identifying the North Sea plankton taken by the Dutch survey vessels. I took a single specimen in bottom plankton, close to the Blakeney Overfalls Buoy, on 13.9.1965.

Calliopius laeviusculus (Krøyer).

C. laeviusculus Hart (1930); C. rathkei Serventy (1934); Gilson & al. (1944); Crawford (Table 3).

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Very common in and around the "Hjördis" and at West Runton, less so in Morston Creek (only in the lowest reach), the Strond Pool, Wells Rocks and Hunstanton Scaup. It has a strong preference for algae.

Family PLEUSTIDAE

Parapleustes assimilis (G.O. Sars).

An adult female and two smaller specimens among hydroids growing inside the "Hjördis", 21.6.1955.

Parapleustes, sp.

Paramphithöe bicuspis Metzger (1875): Parapleustes sp. Hamond (1965a).

This has been found in small numbers on most of the harder grounds, especially among hydroids, and once in bottom plankton in Blakeney Deeps. As I have shown (Hamond, 1965a), the present specimens all agree among themselves in combining the characters of *P. bicuspis* (Krøyer) and of *P. monocuspis* (G.O. Sars), as described in Sars (1895); the following table lists their salient differences as given by Sars, and the asterisks indicate features shared by the Norfolk animals.

Character	P. bicuspis	P. monocuspis					
Antenna 1, joint 1	*As long as, or longer than, joints 2 and 3 combined.	Shorter than joints 2 and 3 combined.					
Shape of eyelobes	*Rounded	Pointed					
Propus of gnathopod, ratio of length to breadth.	3 or 4: 1 (Norfolk 2.5 or 3: 1)	2 or 2.5:1.					
Pereiopods 5, 6 and 7	*All about the same length.	Rapid progressive increase in length.					
Metasome	Segments 1 and 2 each with keeltooth.	* Segment 1 alone with keeltooth.					
Third epimeral plate, lower rear corner.	*A well-marked tooth with a sinus above it.	A very small tooth, no distinct sinus above it.					
Uropod 3, ratio (length) of outer branch: inner branch.		*2: 3					

It may be seen that, although the Norfolk species has only one keeltooth (and is thus, strictly speaking, "monocusped"), in most of the differential characters it agrees with *P. bicuspis*, and in the proportions of the gnathopod propus it is almost exactly intermediate. The male shown by Chevreux & Fage (1925, fig. 191) resembles those from Norfolk except for slightly heavier gnathopods, a keeltooth on the first metasome segment (thus "bi-cusped"), and a smaller tooth on the third epimeral plate.

Walker (1895) collected *Parapleustes* on the north coast of Wales and, according to Jones (1948), he "observed that only the largest

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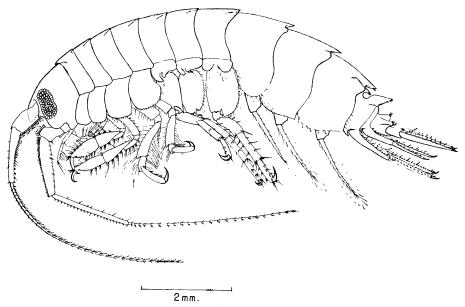
specimens had a dorsal tooth on the first pleon segment, and this varied in length in proportion to the size of the specimen. It seems clear, however, from the descriptions of Sars (1895) that the two species are really distinct". I am much indebted to Dr. N.S. Jones for lending me some of his material (labelled by him "Parapleustes monocuspis (G.O. Sars). Port Erin. 21 miles south-east of Kitterland, 19 fathoms. Stones and gravel with Nemertesia. 20.8.1946"), which appears to be identical with that from Norfolk, in which the curved free rear edge of the first pleon-segment may easily be mistaken for a keeltooth in side view. This feature is hardly noticeable in small or medium sized specimens (Hamond, 1965a, fig. 2) but is more obvious in the larger specimens both from Norfolk and from the Isle of Man. It seems that the specimens from these two places all belong to a species which may be found, on further investigation, to intergrade with either P. monocuspis or P. bicuspis as described by Sars, although at present it appears to be distinct from either; because of this possibility I have deliberately refrained from giving it a specific name.

Family ATYLIDAE

I follow Barnard (1956, 1958) in treating Nototropis as a synonym of Atylus.

Atylus swammerdami (Milne-Edwards).

Not uncommon in plankton in the Pit and among hydroids in and around the "Hjördis", also at Hunstanton and at West Runton; see under *A. vedlomensis*.



F16. 4 Atylus swammerdami, adult male.

Atylus falcatus, Metzger.

Sometimes taken in plankton, more often outside than inside the Point, and usually near the bottom except after dark.

Atylus vedlomensis (Bate & Westwood).

This was habitually mistaken for A. swammerdami until the capture in bottom plankton (as for Argissa) of a large male (Fig. 7) caused a reappraisal of previous identifications. It has been taken at Q.2, once intertidally at West Runton among Corallina, and a few times in Pit plankton, but is most usually found in offshore bottom plankton; only the largest specimens are clearly separable from A. swammerdami, and I suspect that these two species may intergrade in Norfolk waters in the same kind of way as I have shown for several of the local Polychaeta (Hamond, 1966).

Family GAMMARIDAE

Gammarellus homari (J.C. Fabricius).

Amathilla homari Metzger (1875).

The angulosus form is scarce here, and cannot be separated with certainty from the *homari* form which is quite common, especially off Yarmouth where the shrimpers nickname it the "sawback". Found once in Pit plankton, and several times at West Runton, where on 27.3.1963 twenty-five large and brightly coloured examples were found under rocks at low water, all of them being ovigerous females.

Crangonyx pseudogracilis, Bousfield.

C. pseudogracilis Hynes, Macan & Williams (1960).

Very common in Barton Broad, apparently absent from the other Broads (E.A.E.); on 31.8.1963 I found one in a *Lemna*-covered ditch at Thurne Boat Station.

Niphargus kochianus, Bate, var. kochianus, Schellenberg.

N. aquilex Harmer (1899) (fide E.A.G., in litt.); N. k. kochianus Hazelton (1960).

Turns up occasionally in wells; detailed records are given by Hazelton.

Cheirocratus assimilis, Lilljeborg.

One adult male at S.4.

Cheirocratus intermedius, G.O. Sars.

Rare, always offshore. Shortly after death the specimen from D.15 had "general colour yellowish white, with orange blotches on

both pairs of antennae, on the hinder edge of the basis of pereiopod 7, on the propus of pereiopods 6 and 7, and on all the uropods; the top of the head was covered with orange freckles". The specimens obtained during the summer and autumn of 1965 were of a very pale straw-yellow throughout, covered all over with large and small patches of a deep vinous chestnut colour, so that the animal appeared to be of a rich brown; this applied to both sexes and all ages.

Megaluropus agilis, Hoek.

Common in bottom plankton outside the Point (as for Argissa), and found once in the Pit plankton after dark; the colour scheme is a striking pattern of well-defined patches, of lemon-yellow and deep chocolate brown, running irregularly across the body and appendages, while the ommatidia of the eye are pale pink, with a white network running between them.

Melita pellucida, G.O. Sars.

M. pellucida Gurney (1907).

Not uncommon in the brackish ditch behind the seawall to the east of Morston Quay, with Leptocheirus pilosus (q.v.).

Melia palmata (Montagu).

M. palmata Serventy (1934); Hamond (1963a); Crawford (Table 3).

In Blakeney Harbour this is very common on the Freshes Lays, and is found right up Morston Creek as far as the Quay; more rarely is it collected among debris cast up near the "Hjördis", and in plankton in the Pit. It is also common under Wells Rocks, and in East Norfolk has been found several times on Breydon.

Melita obtusata (Montagu).

M. obtusata Metzger (1875).

Not uncommon out to sea, but found only twice intertidally (an ovigerous female cast up near the "Hjördis" on 26.10.1954; a male and a female, both adult, among *Corallina* at West Runton on 24.10.1960) and once in the plankton (as for *Argissa*).

Melita reidi, Hamond.

M. reidi Hamond (1965a).

No more specimens have been found since my original description, to which I have nothing to add.

Maerella tenuimana (Bate).

One female, not ovigerous, at D.18.

Marinogammarus marinus (Leach).

Gammarus marinus Serventy (1934).

One adult and two young males under *Fucus* at high water neaps, about 200 metres southwest of Blakeney Point Lifeboat House, 19.4.1959; one, among *Fucus* covered with *Laomedea*, in the mouth of Morston Creek on 19.12.1962; and many, including several pairs in precopula, in a sandy creek in the marshes at Burnham Overy Staithe on 20.5.1959 (J.F.). As this last record is very close to Scolt Head, it may be assumed that Serventy's record really does refer to this and not to some other species of *Marinogammarus*.

Marinogammarus obtusatus (Dahl).

Very common at West Runton; otherwise found only on the very similar but less well-known adjacent shore of East Runton (23.5.1959, J.F.), and by me under stones west of Cromer Pier on 10.6.1964.

Gammarus pulex (L.).

G. pulex Gurney (1904); Crawford (Table 2).

Apparently common in fresh water, but precise records are very few; in the North Norfolk marshes it occurs from opposite Kelling to as far west as Cley East Bank.

Gammarus duebeni, Lilljeborg.

G. duebeni Gurney (1904, 1907); Crawford (Table 2).

Occurs marginally round Blakeney Harbour (Stiffkey Freshes Sluices, Stiffkey Freshes Backwater Creek, and in the ditch on the east side of Blakeney Bank), possibly through being forced into suboptimal salinities by inability to compete with *G. zaddachi*. *G. duebeni* has also been found on Breydon (Gurney, in Patterson's unpublished notes; A.E. Ellis, per E.A.E.), near Three Mile House on the Bure (W.J. Woolston, per R.M.B.), abundantly behind the seawall at Burgh Castle, and two at Thurne Boat Station (both these finds on 31.8.1963 by me).

Gammarus locusta (L.).

G. locusta Gurney (1904); Hart (1930), in part; Serventy (1934); Gilson & al. (1944); Spooner (1947); Pantin & al. (1960); Hamond (1963a); Crawford (Table 2).

The dominant non-burrowing amphipod on the outside of the Point and on exposed sandy shores to the westward, among freshly cast-up algae and other debris. With *Melita palmata* it is the commonest species under Wells Rocks; it is sometimes numerous on Hunstanton Scaup. In Blakeney Harbour, whereas it formerly extended only as far in as the Threshold in summer, and up to the lowest reach of Morston Creek in the winter, since 1960 or 1961

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it has become common all the year round throughout the Harbour and in the larger creeks, having apparently ousted *G. zaddachi* from the seaward end of the latter's range. *G. locusta* is often taken in Pit plankton. Mr. Spooner has kindly provided me with details of the differences between this species and the "*Gammarus* sp. allied to *locusta*" mentioned in the Plymouth Marine Fauna (1957), from which it is clear that the latter has not yet been found here, all my preserved material being of the true *locusta*.

Gammarus salinus (Spooner).

G. zaddachi salinus Spooner (1951).

Found occasionally in marsh creeks at the landward end of the range of the preceding species; also found on the open shore of the Wash at Snettisham.

Gammarus zaddachi, Sexton.

G. zaddachi Serventy (1934); Spooner (1947); Pantin & al. (1960); Crawford (Table 2); G. zaddachi zaddachi Hamond (1963a); G. locusta Hart (1930), in part.

This was formerly (but see above, under G. locusta) the dominant non-burrowing amphipod all over Blakeney Harbour and among fucoids in the marsh creeks all along the north Norfolk coast, extending behind the seawalls at various places into brackish ditches. In a small pond at Morston, last invaded by the sea in the floods of 1953, this species was found on 6.1.1956 and on 30.3.1957; on both occasions it was numerous, breeding, and accompanied by Cyclops strenuus, Daphnia magna, waterbeetles and toads, none of which can endure more than a fraction of the salinity found just the other side the seawall, in the saltmarshes where G. zaddachi was common at that time. Morphologically the pond specimens and the marsh specimens were indistinguishable; from both these habitats the pairs in precopula were composed of males 15mm long and females 12mm long, whereas the respective lengths of the partners in a pair from brackish water at Haddiscoe (see Corophium multisetosum) were 10mm and 8mm.

Spooner (1947) has shown that G. zaddachi and G. salinus, at that time considered as subspecies of G. zaddachi, are completely intersterile and behave as good species in spite of the trifling extent of the morphological differences between them; they are therefore given full specific rank in the present paper. Mr. Spooner informs me that he now regards G. zaddachi oceanicus, Segerstråle, as equally worthy of specific rank; G. oceanicus has not yet been found here, but is abundant in Scotland and extends (albeit in small numbers) as far south as Robin Hood's Bay in Yorkshire (Spooner, 1951, p. 134).

Pectenogammarus planicrurus, Reid.

P. planicrurus Crawford (Table 2).

A rare species, not seen here since.

Family DEXAMINIDAE

Dexamine spinosa (Montagu).

?Dexamine sp. Crawford (Table 2).

Common among algae and under rocks at low water, and among *Corallina* higher up the shore, at West Runton; otherwise found only inside the "Hjördis" from time to time.

Tritaeta gibbosa (Bate).

Common living freely among algae at West Runton, and among other organisms in dredgings; it is, however, even more abundant at West Runton among sponges and polyclinid tunicates, in whose surface it digs little trenches in which the animals lie singly on their backs with only the uropods and the tips of both pairs of antennae protruding. In a colony of *Botrylloides leachi* from West Runton (11.7.1956) a female was found head downwards, with only her urosome exposed, in an unusually deep flask-shaped cavity which was filled by seven or eight young ones all crowded round the ventral surface of their mother's head and first four segments. Another female, carrying young embryos in her broodpouch, was found in exactly the same posture in a colony of *Archidistoma aggregatum* from W.27. One was taken in bottom plankton (see *Argissa*), and 17 at Q.2 among algae on flints.

Guernea coalita (Norman).

Males have not yet been found here, but the females are not uncommon on hard grounds with plenty of silt, where they probably live interstitially.

Family TALITRIDAE

Talitrus saltator (Montagu).

T. saltator Serventy (1934); Pantin & al. (1960); Crawford (Table 3); T. locusta Gurney (1907).

Frequent among drifted material on the terminal spit of Blakeney Point; it was also abundant under driftwood on Horsey Beach on 14.7.1961, although none could be found there 12 months previously (R.M.B.).

Talitroides alluaudi (Chevreux).

Talitrus alluaudi Ellis (1942).

In a fern house of Messrs. Daniels Bros., Norwich, collected by A.E. Ellis and determined by D.M. Reid; not seen here since. It lives

terrestrially among plants in the Seychelles, Java and Madagascar, whence it is often imported into Europe without managing to become acclimatised (Schellenberg, 1942).

Talorchestia deshayesi (Audouin).

T. deshayesi Serventy (1934).

Found on the Point with *Talitrus*, but scarcer; one, taken on the outside of the Point at high-water mark on 15.4.1957, had hanging on one of its gills a deutonymph of the mite *Phaulodynichus minor* (Halbert).

Orchestia mediterranea, A. Costa.

O. mediterranea Gilson & al. (1944).

An adult male among *Pelvetia* in the *Salicornia*-marsh on Blakeney Point, 21.8.1961, and a non-ovigerous female in plankton in the mouth of Morston Creek, 8.6.1966.

Orchestia gammarella (Pallas).

O. littorea Gurney (1907); Hart (1930); A.H.P.; O. gammarella Serventy (1934); Pantin & al. (1960).

Common among the remains of *Spartina* at high-water mark, all along the marshes on the south side of Blakeney Harbour; found in a similar habitat on the north shore of Breydon (6.9.1942, E.A.E.). I found a single female submerged among red algae, at half-tide level (exceptionally low down the shore for this species), in Backwater Creek (a tributary of Morston Creek) on 19.12.1962.

Orchestia cavimana (Heller).

O. bottae Reid (1947, 1948).

It is by no means certain that O. cavimana and O. bottae (Milne-Edwards) are synonyms (Schellenberg, 1942; den Hartog, 1963). In Norfolk O. cavimana is restricted to almost fresh water south-east of Norwich (Rockland Broad, and the reedy swamps near Surlingham and Brundall) where Mr. E.A. Ellis states that it has been fairly common for at least thirty years; the Castle Museum possesses an adult male and three adult females collected by him in Rockland Broad in July 1928.

Family HYALIDAE

Hyale nilssoni (Rathke).

H. nilssoni Serventy (1934); Crawford (Table 2).

Occasionally on the Strond, and on the flats opposite the Strond (between the Pit and the Lifeboat House); also on Wells Rocks, on the deck of the "Hjördis", and once in Pit plankton (12.4.1963).

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All the specimens that I have seen were bright green, and had eyes that were black or very dark brown. My own findings agree with those of Reid (1947, p. 23) and of den Hartog (1963, p. 47), that the character used in the key by Chevreux & Fage (1925) seems to have no taxonomic value; the rear margin of the propus in pereiopods 6 and 7 can have a variable number of spines or setae, sometimes different on the two sides of the same specimen.

Family AORIDAE

Aora typica, Krøyer.

A. gracilis Metzger (1875); A. typica Pantin & al. (1960).

In small numbers among algae, hydroids and polyzoa, near lowwater mark on all sheltered shores (also occasionally in the Strond Pool) and on moderately rough ground out to sea. In general appearance this species very much resembles the next. I find that the following characters, none of them mentioned in the literature, permit reliable separation of both sexes and all ages, from half-grown upwards, of the living animals; the characters of the first and second antennae are often visible even when the animals have retired into their tubes.

Character	A. typica	M. gryllotalpa					
Body colour		Very pale greenish yel- low, but so thickly covered with larger black dots as to appear almost black.					
Colour of both pairs of antennae	thickly covered with small brown speckles; each fla-	Varying from bright golden to faint horny brown, no pink rings round flagella and no surface speckling.					

When these two species are seen side by side these differences permit of instant separation; they may persist for a limited time if preserved in weak formalin in the dark. The differences are based entirely on Norfolk specimens, and their reliability when applied to other populations remains to be investigated.

Microdeutopus gryllotalpa, A. Costa.

M. gryllotalpa Serventy (1934).

Found intertidally at Wells and in Blakeney Harbour with Aora, but much more abundant, especially among algae in the creeks; never taken offshore. The first gnathopod of the male is not normally more massive or elaborately toothed than that shown in fig. 8; but a large male, taken in Morston Creek during June 1966, had gnathopods very much as shown by Chevreux & Fage (1925) and by Schellenberg (1942).

Microdeutopus anomalus (Rathke).

M. anomalus Metzger (1875).

Not seen here since; the possibility that this record really applies to M. gryllotalpa seems remote, not only because of the differences in the first gnathopods of the males but because Metzger's material was taken several miles from land. Andersson (1953) has found differences in the third uropods which reliably distinguish both sexes of this species from those of M. gryllotalpa.

Lembos longipes (Lilljeborg).

This species seems to prefer hydroids; one complete adult (and several others whose identity was not quite certain owing to injury) was taken at D.20.

Family PHOTIDAE

Microprotopus maculatus, Norman.

M. maculatus Serventy (1934).

Very common near low water in sheltered places among algae and hydroids, especially among delicate green algae growing naturally; scarce in the plankton, where it is apparently carried about on algal fragments rather than by its own powers of swimming. A single specimen was found on 29.3.1956 in the sandbank south of Wells Lifeboat House (cf. Schellenberg, 1942, pp. 203, 204).

Photis reinhardi, Krøyer.

P. reinhardi Hamond (1963a).

Intertidally the only records here are of

(a) a non-ovigerous female on 31.7.1961 among hydroids, and

(b) four among *Eudendrium ramosum*, and six among a *Ceramium*-like red alga, on 1.11.1963.

These were all at or slightly below extreme low-water mark on the Scaup at Hunstanton, a habitat better described as the upper limit of the sub-tidal (Hamond, 1963). *Photis reinhardi* is scarce in plankton, but exceedingly abundant in certain dredgings, especially on grounds where there is much loose silt as opposed to tenacious clay or peat.

Eurystheus maculatus (Johnston).

Scarce offshore; intertidally only on Hunstanton Scaup (15.7.1957) where the single specimen found was "slender, very active, with a pinkish-brown body and bright red eyes". All my specimens are definitely *E. maculatus* and not *E. melanops* (G.O. Sars).

Podoceropsis nitida (Stimpson).

Noenia excavata (female) and N. rimapalmata (female), Metzger (1875).

Rare at low-water mark and common offshore, especially in whelkshells tenanted by *Pagurus bernhardus*; also dredged among dead shells with hydroids.

Megamphopus cornutus, Norman.

Not uncommon in dredgings (with a preference for rough ground with plenty of silt) but are in bottom plankton outside the Point (as for *Argissa*). A female from D.18 had in her broodpouch the neotype of the parasitic copepod *Sphaeronella valida* (see Green, 1958).

Leptocheirus pilosus, Zaddach.

Microdeudopus [sic] gryllotalpa Gurney (1904); Microdeudopus [sic] versiculatus + Coremapus versiculatus + Leptocheirus sp. Gurney (1907); Leptocheirus pilosus Crawford (Table 2).

In ditches behind the seawall east of Morston Quay, with Melita pellucida, Gammarus zaddachi, Corophium volutator, Sphaeroma rugicauda and Nereis diversicolor, in February 1965. Gurney's 1904 record may possibly refer in part to the true M. gryllotalpa, but only in the most saline waters; his other records, coming as they do from a brackish habitat, are undoubtedly all of L. pilosus.

Leptocheirus pectinatus (Norman).

L. pectinatus Hamond (1963a).

In dredgings, confined to rough and silty grounds, where it may be extremely abundant.

Family ISCHYROCERIDAE

Jassa falcata (Montagu).

J. falcata Hamond (1963a).

Extremely abundant in the "Hjördis" and among algae, hydroids and polyzoa cast up near her; sometimes found at West Runton, and one at D.4. The animals build their muddy nests in such numbers among red algae (mostly *Ceramium*) on the deck of the "Hjördis" that the algae themselves are almost invisible.

Jassa marmorata, Holmes.

In spite of careful search none were seen here until 23.9.1965, when I found two adults, together with 3 *J. falcata*, in plankton near the Blakeney Overfalls Buoy, and 3 adult males and about 30 adult females in a sample of weed growing on the Buoy itself. The alga

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had no other animals in it whatsoever. An examination of the "Hjördis" four days later disclosed no *J. marmorata*, although *J. falcata* was as numerous as usual; it seems, therefore, that *J. marmorata* is a recent arrival in Norfolk waters, perhaps on the bottom of a ship. This is made even more likely by the fact that the Blakeney Overfalls Buoy lies close to the main shipping lane between, on the one hand, ports from the Wash northwards, and, on the other hand, ports on the coasts of the southern North Sea and the English Channel. Collections in the "Hjördis" on 8.3. and 20.6.1966 revealed only *J. falcata*.

Jassa pusilla (G.O. Sars).

J. pusilla Hamond (1963a).

Twice at West Runton, and moderately common offshore among sponges. At W.31 nearly a hundred, of both sexes and all ages, crept out of masses of sponge on the carapaces of six or seven *Hyas araneus*.

Ischyrocerus anguipes, Krøyer.

One female (releasing young) at D.40, and a second specimen in bottom plankton close to the Blakeney Overfalls Buoy on the same day (29.3.1965); two at D.42 and one at D.49. All these localities are close to the Buoy, and all are of females (none ovigerous except the first) whose identifications is not altogether certain.

Family COROPHIIDAE

Unciola crenatipalma (Bate).

Dryope crenatipalma Metzger (1875).

Not common; appears to prefer the rougher grounds, with plenty of pebbles and *Flustra foliacea*.

Siphonoecetes dellavallei, Stebbing.

S. dellavallei Hamond (1965).

The species is possibly less rare than the records suggest, since it appears to prefer clean and apparently barren sand, containing a few dead shells and almost no other animals at all.

Corophium volutator (Pallas).

C. grossipes Gurney (1907), in part; C. volutator Hart (1930), in part; Serventy (1934), in part; Gilson & al. (1944), in part; Pantin & al. (1960); Ingle (1963); Crawford (Table 2).

The ecology of this species is only poorly known locally owing to confusion with the next two species; now that Stock (1952, 1960) and Ingle (1963) have clarified the specific characters of these three species, it is to be hoped that their ecology will be re-investigated ab initio. At present, all that can be said is that C. volutator seems to prefer the muddier creeks in the salt-marshes, and to flourish at a slightly higher tidal level and a slightly lower average salinity than does C. arenarium. Hart (1930) collected both in the Freshes and over on the Point (in Yankee Creek), and states (in a marginal note to the reprint which he sent me) that all his specimens were determined by Mr. Spooner as volutator; this is curious, as all the Corophium that I have found on the Point, whether in Yankee Creek or elsewhere, were arenarium.

C. volutator has also been found on the open shore at Snettisham (14.6.1962, coll. S. & M. Hornsey) and abundantly in the mud of Breydon by the seawall near Burgh Castle, on 31.8.1963.

Corophium arenarium, Crawford.

C. volutator Hart (1930), in part; Serventy (1934), in part; Gilson & al. (1944), in part; C. sp. (?arenarium) Pantin & al. (1960); C. arenarium Ingle (1963).

Along the North Norfolk coast this species seems to replace *volutator* in the lowest reaches of the creeks, and on the upper part of the shore nearby where the substratum is of muddy sand; these localities are regularly covered by tides of almost full North Sea salinity, so that there is seldom any question of *arenarium* being exposed to prolonged outflows of almost fresh water or of being landlocked in a marsh pool. *C. arenarium* has once or twice been taken in Pit plankton, and on 16.9.1962 was found in enormous numbers all over the flat upper part of the shore at Holkham.

Corophium multisetosum, Stock.

C. grossipes Gurney (1904, 1907), in part; C. multisetosum Ingle (1963).

Apparently common in the Bure, since Gurney found it frequently among *Cordylophora* and in the muddy river bed, at any rate between 1900 and 1935; I have not looked for it there myself, but on 18.5.1966 I found a large male and a juvenile specimen among *Cordylophora* on a piece of waterlogged wood from the bottom of the Cut at Haddiscoe, just under the bridge. *C. multisetosum* prefers much lower salinities than either *C. volutator* or *C. arenarium*, and in Norfolk seems to be confined to the East Norfolk river system (including the Norfolk Broads), where it has a distribution similar to that of *C. lacustre* (cf. Stock, 1952, p. 6).

Corophium bonelli, G.O. Sars.

C. bonelli Hamond (1963a).

Not uncommon in dredgings, especially at D.17 and at D.47, where hundreds were found apparently sharing the tubes of *Ampelisca tenuicornis* with the owners themselves. Of the very large sample of *C. bonelli* at D.17 about 30 per cent were ovigerous females; these were all the largest specimens above a certain size, and from them there

was an even gradation in size down to the very smallest young ones. At D.47 most of the specimens were full-grown or nearly so. Neither in these hauls nor anywhere else have I seen any sign of a male; this appears to support Crawford's conclusion (1937, p. 613) that *C. bonelli* is parthenogenetic. I also follow Crawford in ascribing the specific name to Sars instead of to Milne-Edwards (but see Barnard, 1958).

Apart from dredgings it may sometimes be not uncommon inside the "Hjördis", and very small ones have occasionally been found under rocks at West Runton and among holdfasts of *Laminaria* saccharina in the Treshold; in offshore bottom plankton (as for *Argissa*) it is very rare.

Corophium lacustre, Vanhöffen.

C. crassicorne Gurney (1904); C. lacustre Crawford (1935).

Common among Cordylophora, especially around Potter Heigham, Ludham, and Haddiscoe; at the latter place 18 specimens (including 2 adult males and 3 ovigerous females) were taken with C. multisetosum (q.v.).

"Hauling up a bit of bark-like rubbish from the bottom of the Waveney at St.Olaves, I discovered a small Corophium which I have no doubt was Corophium bonelli. It answered in every way to this species as given in Bate & Westwood's Crustacea, vol. 1." (A.H.P., 10.8.1928). Patterson's material is now lost, but the above-mentioned sample from Haddiscoe Cut (part of the Waveney, and only a few hundred yards from St.Olaves) was taken with the express purpose of repeating his capture of Corophium; it yielded only C. lacustre and C. multisetosum. There is no evidence that the salinity, on which the distribution of species of *Corophium* is strongly dependent, has substantially altered at St.Olaves during the last century, so that Patterson also very probably caught one or other of these two species. I assume that in fact he had *lacustre* before him, since he would certainly not have distinguished C. multisetosum from the "C. longicorne" (probably C. volutator) which was so abundant in the mud round his houseboat in the seaward end of Breydon. On the other hand, C. lacustre bears a general resemblance to the alleged C. bonelli of Bate & Westwood, whose figures and descriptions are not altogether adequate by modern standards; both these species are small and stumpy, in contrast to the large and long-legged members of the volutator-group mentioned above.

Family CHELURIDAE

Chelura terebrans, Philippi.

Chelura Hamond (1963a); C. terebrans Hamond (1963b).

Common in the mast-stump of the "Hjördis"; so far found nowhere else.

Family PODOCERIDAE

Dulichia monacantha, Metzger.

Twelve (including two ovigerous females) were caught in the plankton, both inside and outside the Point, between the middle of March and the end of April, 1963. Near the Blakeney Overfalls Buoy, in bottom plankton, eight specimens (of which three were ovigerous) were taken on 29.3.1965, and a single ovigerous female on 18.7.1965.

Dulichia sp. indet.

Dulichia sp. Metzger (1875).

The only distinctive character in Metzger's description of this un-named species (immediately preceding his original description of D. monacantha) is the shape of the female second gnathopod, which is far more like that of D. porrecta, Bate, than of any other North European species.

SUB-ORDER HYPERIIDEA

Family HYPERIIDAE

Hyperia medusarum (O.F. Müller).

H. medusarum G.M.S.

"Found in a dead Aurelia at low tide on Blakeney Point in 1949 by Mr. N.E. Hickin. This was a year in which Aurelia was said to be very uncommon there, so this specimen may have been carried some distance" (G.M.S., in litt., 22.4.1954). Not seen here since, in spite of frequent examination of Aurelia and other medusae.

Hyperoche medusarum (Krøyer).

Common, swimming freely in the plankton, especially offshore, during the whole of July and August 1965, but not before nor since; *Aurelia* and large *Beröe* were also unusually abundant at that time, while *Chrysaora* and *Cyanea* were present in average numbers, but none of them harboured any amphipods.

Parathemisto gracilipes, Norman.

Taken in the plankton from July to April, being most common in the winter plankton between November and March, rare at other times; only two ovigerous females have been seen, one in December and the other in March.

SUB-ORDER CAPRELLIDEA

Family CAPRELLIDAE

Phthisica marina, Slabber.

One ovigerous female and 15 other specimens at D.22; one ovigerous female and 12 other specimens at D.23. Breeding in August.

Pseudoprotella phasma (Montagu).

Two ovigerous females and two smaller individuals at D.18.

Pariambus typicus (Krøyer).

Common on the sun-star, Solaster papposus, and found several times among dredgings and whelkpot rubbish; rare in plankton, while great numbers (including many ovigerous females) were found all over a *Rhizostoma* taken in a shrimptrawl off Caister-on-Sea on 23.7.1959 (R.M.B.).

Caprella linearis (L.).

C. linearis Hamond (1963a).

Very common among hydroids, both out to sea and cast ashore, but not usually exceeding 15 mm. in length; inside the "Hjördis", however, it grows to a length of 20 or even 25 mm. and, in appearance, attitude and markings, closely resembles *C. aequilibria* Say, especially as shown in the photograph by Wilson (1947, pl. 41). According to the characters given by Harrison (1944) these large specimens are, however, clearly *C. linearis.*

Caprella septentrionalis, Krøyer.

Not yet found on the Norfolk coast, but it forms part of the material of presumed northern origin washed ashore on the Dutch island of Terschelling (Stock & Bloklander, 1952); these authors quote Carruthers (1925) to the effect that part of the branch of the Gulf Stream, running round the north of Scotland, comes southwards down the east coast of England until deflected by Norfolk (which bulges out) so that the current is made to turn east and go across to Holland and Germany. This caprellid, therefore, must have passed our coast on the way to Terschelling, and will probably be found in Norfolk waters at some future date.

R. HAMOND

ECOLOGY OF THE NORFOLK AMPHIPODS

Habitat preferences

The following list gives the species most likely to be found in a given habitat. The term "interstitial" is used here in its original sense (see 9, b), as applied to moderately small organisms able to live between the fragments of their preferred substratum. However, a specialised meaning has become attached to it during the past forty years as a result of work on the fauna of certain sands and shell-gravels; this "interstitial fauna" consists of many peculiar forms not usually found elsewhere. Unfortunately I have not yet come across this assemblage in Norfolk (where the substratum appears to be unsuitable), but it is possible that *Melita reidi* is a member of it (Hamond, 1965a).

- 1. Terrestrial, at least in part:-
 - (a) Fully terrestrial; Talitroides alluaudi.
 - (b) Terrestrial/fresh water; Orchestia cavimana.
 - (c) Terrestrial/salt water; Talitrus saltator, Talorchestia spp., Orchestia ssp. (except O. cavimana).
- 2. Fresh water:-
 - (a) Subterranean; Niphargus kochianus kochianus.
 - (b) Standing water; Crangonyx pseudogracilis, Gammarus pulex, Corophium lacustre.
 - (c) Gently flowing water; those listed under 2 (b), and Corophium multisetosum.
 - (d) Moderately fast-flowing water; G. pulex.
- 3. Brackish water:-
 - (a) Fresh/brackish; Gammarus duebeni, Melita pellucida, Leptocheirus pilosus, Corophium lacustre, C. multisetosum.
 - (b) Brackish/salt; Gammarus zaddachi, G. salinus, Melita palmata, Corophium volutator.
- 4. Upper shore, among algae:-
 - (a) Over sand and mud; Hyale nilssoni.
 - (b) Under rocks; Calliopius (and Pectenogammarus, according to Reid, 1940).
- 5. Middle and lower shore, among algae:-
 - (a) Over sand and mud; Gammarus locusta, Marinogammarus marinus, Microprotopus maculatus, Microdeutopus gryllotalpa.
 - (b) Among Corallina and other algae, on hard chalk; Apherusa jurinei, A. bispinosa, Dexamine spinosa, Atylus swammerdami.
 - (c) Under rocks, with few algae or none; Marinogammarus obtusatus.
- 6. Algae loose on sand; as for 5 (a), with Aora typica.
- 7. Burrowing in sand:-
 - (a) Intertidally; Pontocrates spp., all Haustoriidae except Urothoe elegans.
 - (b) Offshore; Megaluropus agilis, Pontocrates spp., Siphonoecetes dellavallei, and possibly Atylus falcatus, A. vedlomensis, Argissa hamatipes, Acidostoma obesum and Perioculodes longimanus.

- 8. "Hjördis" (wreck at extreme low water); Jassa falcata, large Caprella linearis, and many other species from time to time.
- 9. Dredgings:-
 - (a) With an apparent preference for silt among shells and stones; Orchomene humilis, Tryphosa sarsi, Orchomenella nana, Ampelisca spp., Urothöe elegans, Harpinia pectinata, Amphilochus spp., Gitana sarsi, Panoploea minuta, Cheirocratus spp., Melita reidi, Guernea coalita, Photis reinhardi, Leptocheirus pectinatus, Corophium bonelli and Pariambus typicus.
 - (b) Interstitial or semi-interstitial, not clearly separable from 9 (a); Urothöe elegans, Metaphoxus fultoni, Harpinia pectinata, Cressa dubia, Gitana sarsi, Melita reidi, Guernea coalita and Pholis reinhardi.
 - (c) Among hydroids; Metopa pusilla, Stenothoe marina, Cressa dubia, Parapleustes sp. aff. bicuspis, Melila obtusata, Maerella tenuimana, Lembos longipes, Eurystheus maculatus, Megamphopus cornulus, Dulichia sp. aff. porrecta, Caprella spp., Phthisica marina, Pseudoprotella phasma, and possibly Atylus swammerdami, A. vedlomensis, Aora typica and Cheirocratus spp. Metopa borealis is especially fond of Tubularia larynx.
- 10. Boring in wood; Chelura terebrans.
- 11. Sharing gastropod shells with pagurids; *Podoceropsis nitida*, and possibly *Orchomenella nana*.
- 12. Associated with echinoderms; *Pariambus typicus*. I have not found *Urothöe marina* in the burrows of *Echinocardium cordatum* as stated by Mortensen (1927, p. 334).
- 13. Associated with medusae; Metopa alderi, Hyperia medusarum, and sometimes Pariambus typicus.
- 14. Free, in plankton; Dulichia monacantha, Parathemisto gracilipes, Hyperoche medusarum. Many intertidal species come out for a swim when covered by the tide in order to feed or to mate, and regain their accustomed habitat among algae or in the sand as the tide ebbs. Offshore, many species occur in bottom plankton, though rarely in large numbers; these are, like the intertidal species, basically benthonic forms.

Some trends in the ecology of the marine species

Analysis of the distribution of the Norfolk marine amphipods from high-water mark downwards shows that:—

(1). Species found on several shores are more exclusively intertidal than are species found on only one shore (see Table 4; the five shores analysed are Hunstanton, the Scolt Head area, Wells, Blakeney Harbour, and West Runton); however, *Aora typica*, the only species recorded from all five shores, is also fairly common subtidally.

(2). Species found only offshore have a much greater abundance, both of species and of individuals, on the C_2 and F_4 grounds (see Hamond, 1963a) than do those found intertidally as well, while those found on two shores are more widespread among the minor categories of substratum than are those found only on one shore. All species found on E_2 or F_3 grounds also occur intertidally.

(3). The proportion of species presumably associated with hydroids in highest among the offshore-only group (Table 4) and falls

sharply with each group as the number of shores inhabited by the group increases. Conversely, species making nests among algae are all intertidal, and the few instances hitherto of such species occurring offshore (*Microprotopus maculatus* from W.24, and from a shrimp-trawl at 53°02'N. 00°30'E., on 19.7.1962; Jassa falcata at D.4, and in plankton near the Blakeney Overfalls Buoy) appear to be exceptional; on the other hand, the occurrence of Jassa marmorata on the Buoy is in line with its distribution elsewhere, such as in Plymouth Sound (Plymouth Marine Fauna, 1957).

(4). Burrowers are well represented in all habitats but, whereas the intertidal burrowers are all fairly large compared to the grains of sand or particles of mud among which they burrow, this is not so true of the offshore burrowers, many of whom may be as small as, or even smaller than, the harder particles of the substratum in which they live. There is no clear functional distinction at present between burrowers, interstitial dwellers, and species (including most offshore species) which prefer plenty of silt for some unknown reason; nevertheless, these types appear to have arisen by convergent evolution at the family level, the Haustoriidae being dominant between tidemarks and other families replacing them out to sea.

(5). A few species are characteristic of certain shores; thus, West Runton has five very common species which are unknown (Apherusa jurinei, Marinogammarus obtusatus) or rare (A. bispinosa, Dexamine spinosa, Tritaeta gibbosa) on other shores; this is not invalidated by the fact that Tritaeta is sometimes common offshore. Jassa falcata is abundant in the "Hjördis" but is very rare elsewhere. From Blakeney Harbour westwards Gammarus locusta, G. salinus, G. zaddachi, Corophium volutator and C. arenarium dominate the marshes and creeks, while in the clean sand near the open sea the two species of Pontocrates and all the intertidal haustoriids are found burrowing, and Gammarus locusta predominates among algae lying loose on the surface of the sand.

(6). Sexual dimorphism in amphipods usually concerns the antennae (of which either pair may be longer in the male than in the female, or may bear calceoli in the male but not in the female) or the gnathopods (which are often more heavily built in the male, especially the second pair); in *Argissa* the urosome shows dimorphism. As regards the size and shape of the gnathopods the semi-terrestrial Talitridae are the most strongly dimorphic; somewhat less so are most of the nest-building species and the dwellers among hydroids offshore, while the interstitial, planktonic, and burrowing forms are moderately or not at all dimorphic. It is impossible to say, of a group of closely allied species or genera, that those living intertidally will be more or less dimorphic in any respect than those living offshore, or that the larger species exhibit stronger dimorphism than the smaller ones; this latter finding is of interest when contrasted with the fact that, in most species, the sexual distinctions become increasingly marked with size and age. In many species living in or on sand, both intertidally and offshore, the second antennae bear calceoli in the male but not in the female; similar dimorphism for the first

antennae is found here only in *Apherusa*, of which the two common species live among algae on a rocky shore (West Runton), while the other two are found on are occasions in the offshore plankton.

Acknowledgements

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Summary

All species of amphipods found in Norfolk and nearby are listed, with details of their occurrences and ecological preferences. Allometry in *Metopa borealis*, the intermediate characters of *Parapleustes* sp., the altered distributions of *Gammarus zaddachi* and *G. locusta*, and the distinctions between *Aora typica* and *Microdeutopus gryllotalpa*, are commented on; details are given of colour patterns and features of taxonomic interest in various species, as well as of the characteristic species found in various habitats and of some correlations between size, morphology and preferred habitat.

Zusammenfassung

Alle Arten von Amphipoden, die im Norfolk und im den angrenzenden Meeresteilen gefunden wurden, sind katalogisiert. Es gibt auch Daten über Taxonomie, Ökologie, Fundorte, Farbe, die Beziehungen zwischen Grösse, Morphologie und bevorzugtem Biotop, und die beherrschenden Arten in einingen Biotopen, sowie Allometrie in Metopa borealis, die intermediären Besonderheiten von Parapleustes sp., die veränderte geographische Verbreitung von Gammarus locusta und G. zaddachi, und der Unterschiede zwischen Aora typica und Microdeutopus gryllotalpa.

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TABLE 1.

Species recorded by Reibisch (1906) from stations north-east of the Norfolk coast. The name used by him, if different from that used in this paper, is given in brackets; the synonymy is according to Schellenberg (1942). Most of these species are recorded from Norfolk in the present paper, and the others may be found there.

STATION 70. 54°10' N. 02°09' E., 39 metres, fine sand between patches of hard ground.

Hippomedon denticulatus, Bathyporeia pelagica, B. tenuipes (as B. gracilis), Urothöe elegans, U. marina, Stenothöe marina, Parapleustes sp. (as Paramphithöe bicuspis), Megamphopus cornutus, Podoceropsis nitida (as P. excavata), Ischyrocerus anguipes (as Jassa minuta).

STATION 71. 54°10' N. 02°17' E., 39 metres, fine and coarse sand.
H. denticulatus, Tryphosites longipes, Bathyporeia pelagica, B. tenuipes (as B. gracilis), B. guilliamsoniana (as B. norvegica), U. elegans, Apherusa clevei, Melita obtusata, Megaluropus agilis, P. nitida (as P. excavata).

STATION 72. 52°41' N. 03°22' E., 37 metres, fine and coarse sand with shell fragments.

B. tenuipes (as B. gracilis), U. elegans, Ampelisca brevicornis, A. spinipes, Amphilochus neapolitanus (perhaps the same as my A. spence-batei, see Hamond, 1965a), S. marina, Perioculodes longimanus, M. obtusata, Cheirocratus sundevalli, P. nitida (as P. excavata), Phthisica marina (as P. acaudata).

TABLE 2.

Amphipods collected on Sheringham beach (G.I. Crawford, personal communication).

	1948	1949	1952
Calliopius laeviusculus	\boldsymbol{x}	\boldsymbol{x}	\boldsymbol{x}
Apherusa sp.		\boldsymbol{x}	\boldsymbol{x}
Dexamine sp.	x	\boldsymbol{x}	\boldsymbol{x}
Pontocrates ⁻ arenarius			\boldsymbol{x}
Oedicerotid sp.			\boldsymbol{x}
Hyale nilssoni	\boldsymbol{x}		
Gammarus locusta	\boldsymbol{x}	\boldsymbol{x}	\boldsymbol{x}
G. duebeni	\boldsymbol{x}		
Melita palmata	\boldsymbol{x}		?
Pectenogammarus planicrurus	x	\boldsymbol{x}	
Bathyporeia pilosa			\boldsymbol{x}
Bathyporeia sp.	\boldsymbol{x}		\boldsymbol{x}
B. pelagica			\boldsymbol{x}
Haustorius arenarius			\boldsymbol{x}

Mr. Crawford also found the following:- Gammarus pulex in fresh water at Mr. Grawford also found the following:— Gammarus pulex in fresh water at Sheringham and Beeston, G. duebeni and Corophium volutator at Salthouse, Talitrus at West Runton (these all in 1949), and G. zaddachi, Leptocheirus pilosus, Palae-monetes varians and Neomysis integer all in a pool just east of Blakeney Bank in 1952. The four species in the table, for which no specific names are given, are excluded from the counts of families, genera, and species, in the section on Previous Records.

TABLE 3.

Number of shores on which species is found	Number of species in group	Number (and percentage) confined to intertidal zone	Number (and percentage) associated with hydroids offshore
4	5	5(100)	0(0)
3	7	6(84)	ŎŎŎ
2	23	13(55)	3(13)
1	12	5(42)	4(33)
0	22		9(41)

From this it is seen that 7 species are found on any 3 of the shores mentioned on p. ; of the 7,6 are found only between tidemarks and none are associated with hydroids out to sea. The number of shores on which a group of species is found varies directly as to the percentage of species found only intertidally and inversely as to the number of species found among hydroids offshore,

					1100	corus	or an	ipmpo	us 11	un u	cuge	ana			ations		mond	nogica	ar oru	er).											
	D. 1	D. 4	D. 5	D. 6	D. 8	D. 9	D. 10	D. 11	D. 14	D. 15	D. 16	D. 17	D. 18	<u>s.</u>	D. 20	D. 22	D. 23	D. 26	D. 32	D. 34	D. 35	D. 40	D. 42	D. 44	D. 45	D. 47	D. 48	D. 49	D. 50	D. 51	. <u> _</u> ⊺∘
cidostoma obesum													10 15 0												1						
chomene humilis yphosa sarsi													40/50 14	1	1 11	17	9 2							3	1	1					5
chomenella nana									-						1	•	-					_			-	-					
pelisca tenuicornis pelisca spinipes	8			1					cabl) ca20	1	8	20/30	ca	40	5 10	61	1			1	5	10	ca35	ca50	8		ca50		8	
othöe elegans									Ŭ						3	2	17								ca20	16		55	few	43	1 :
xocephalus holbølli																						1									
aphoxus fultoni pinia pectinata												3	1		1		1														
philochus manudens												2	38	1	62	39	10												1		
philochus spence-batei													9	1	18	1	1											2			
ına sarsi opa pusilla		1										2	12	>	0/150	3	4		1				7	8	ca20	2		9	3	3	200
nothöe marina		-		_						_			1	-	1	2	î		-					U		-		· ·	ĭ		
ssa dubia				3						7	2	>50	ca200	>	>200	$>52\\23$	49 3						2	1	4	2	1		1	8	
oploea minuta erusa bispinosa													10		2	23	3														
apleustes sp.			1	1	1					4		1	4		2	ŝ							1		2						
lus swammerdami nmarellus homari			1																	1		2									1
irocratus assimilis			1																			4									
irocratus intermedius										1		1												5	12			3	2	6	
aluropus agilis ita obtusata												1			12													1			
ita reidi												1	2		14		4														
erella tenuimana										•			1																		
taeta gibbosa ernea coalita			1							2		ca15	18		9	14															
a typica												6	8		5	2								4			3	3		2	
nbos longipes															ca6													_			
roprotopus maculatus otis reinhardi												30/4	0 4	3	œ	2	93	1	10				9	17	ca100			2 ca50	1		
ystheus maculatus													27	U		ĩ	00	•	10					••	Carot	·		Cabu	1		
oceropsis nitida		1									2		6		19	1						1			1			-			
amphopus cornutus tocheirus pectinatus			1							3			8 16		13 16	~ ~	54									10		5		4	
sa falcata		1	•							Ŭ					10	~~~~	•											1			
sa pusilla													2			1							2								
yrocerus anguipes iola crenatipalma			1				6			4			20/30			2						1	2					1			
honoecetes dellavallei			-				0			•						-				1											
ophium bonelli												8	23		6	9 16	$15 \\ 13$							4	ca100) >150	1	5	few	8	
hisica marina udoprotella phasma													4			10	19														
iambus typicus									1				-		:a20		6											2			
prella linearis			2			fev	V	few		21			8			>25												2		8	
Fotal 47 spp.			_																												-

TABLE Records of amphipods from dredge and shrimptre ations (in chronological order).

 $\mathbf{25}$

∞ ca

few >50 ca60

few

ø

2 23

8 11

31 ca80 ca310 ∞

Spp./station

œ

5 ca190 <50

	W. 24	W. 25	W. 26	W. 27	W. 28	W. 29	W. 30	W. 31	W. 32	W. 33	W. 35	W. 8	Totals
Tryphosa sarsi			1				2						3
Orchomenella nana						_		2		1			3
Ampelisca tenuicornis				1	6	2	3			6			18
Amphilochus							0						0
manudens							2						2
Gitana sarsi Matang pusilla							T	A					1 0
Metopa pusilla Stenothöe marina						1		4				4	9
Cressa dubia			3			1	9	1				2	8 2 16
Parapleustes sp.			ĭ		5	$\hat{2}$	2	-				-	ĨŎ
Melita obtusata			-		-	-	-			2			2
Tritaeta gibbosa				26		12	11	6					55
Guernea coalita							1						1
Microprotopus													
maculatus	1												1
Eurystheus maculatus	3	£	22		6	10	1			14			ca60
Podoceropsis nitida Jassa pusilla		few	44		0	10		<100		14			< 100
Unciola crenatipalma						1		<100					< 100
Pariambus typicus						1			30/40	8			ŵ
									00/10	ŵ			~
Total 18 spp. Spp/station	1	1	4	2	3	7	9	5	1	1	1	2	
	1		*	-		•			1	. *	1	-	
Individuals/station	1	few	27	27	17	29	32	ca110	30/40	o ∞	1	6	

		TABLE 3	5.	
Records	of	amphipods	from	whelkpots.

Tables 5 and 6 include only those stations at which amphipods were taken; full station lists are given elsewhere (Hamond, 1963a, and in press). If an accurate count was prevented by shortage of time, one of the following abbrevations was used :---

few

stands for an uncounted number, less than 20.
stands for an uncounted number, between 100 and 600, rarely more than 300.
stands for a number greater than x by not more than about ten per cent.
stands for a number, not accurately counted but within ten percent of x either way 8

>x < x < x < ca.x

x either way. stands for a number between x and y.

x/y