THE MARINE AND BRACKISH-WATER COPEPODS OF NORFOLK: CALANOIDA, MISOPHRIOIDA, CYCLOPOIDA, MONSTRILLOIDA, NOTODELPHYOIDA AND *INCERTAE SEDIS*

by

R. Hamond

Scaldbeck, Morston, Holt, Norfolk

Résumé

L'auteur inventorie, en y joignant quelques données biologiques, les espèces de Copépodes du Norfolk des groupes indiqués ci-dessus. Parmi ces 86 espèces, quatre sont douteuses ; pour les autres, cinq étaient nouvelles à l'époque de leur récolte, une (représentée par un néotype) était perdue depuis longtemps et sept sont nouvelles pour la faune britannique ; toutes les espèces non douteuses se comptent parmi les associés d'Invertébrés benthiques et ont été trouvées ovigères. Par contre, les espèces planctoniques, presque toutes banales, se reproduisent rarement dans nos parages.

Il est montré qu'un biotope favorable, même s'il est transitoire, peut servir, une fois établi dans les eaux du Norfolk, pour l'accumulation rapide d'une faunule riche et variée ; par contre, les conditions inconstantes peuvent rendre la vie extrêmement difficile pour toutes les espèces, sauf les mieux adaptées.

Introduction

This paper presents some of the results of a survey of the copepods of the North Norfolk coast, together with all previous records of the groups in question from within the Norfolk marine area (defined by Hamond, 1969b). Methods of collecting marine samples, and of extracting and examining the copepods from them, have already been described (Hamond, 1965, 1966a, 1967b, 1969d), as have the copepods parasitic on fishes (Hamond, 1969c; Walkey, Lewis & Dartnall, 1970) and some of the harpacticoids (Hamond, 1968b, 1969a, 1970, and unpublished); the present paper deals with all the remaining groups, of which some of the most noteworthy have already been dealt with (Hamond, 1968a).

The modern view is that many fish-parasites and all the Notodelphyoida should perhaps be merged with the Cyclopoida; however, since no entirely satisfactory revised classification has yet been formulated, I have retained the traditional grouping for convenience. Previous authors, including Bourne (1890), Gurney (1904, 1907, 1929, 1931-1933), Möbius (1875), Rae & Rees (1947), Redeke & van Breemen (1904), Serventy (1934), and Watson (in Scott, 1905), as well as Anon.

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(1902-1911) (covering the Durch plankton stations worked in our area by the "Wodan" before the First World War; see Hamond, 1969b), found a total of 21 species of the groups named in the title, of which twelve (in square brackets in the systematic list) are not included in the 74 species found by me, making a total of 86 species.

SYSTEMATIC LIST CALANOIDA

Identified according to Rose (1933). Female calanoids, even of the most common species, are so seldom seen carrying their eggs in Norfolk waters that all my records of ovigerous females are quoted below under the species concerned.

Calanus finmarchicus (Gunnerus).

One stage V copepodite, rather doubtfully of this species, in Morston Creek plankton on 2.6.1962.

Calanus helgolandicus Claus. *C. finmarchicus* Redeke & van Breemen (1904).

Never very numerous but occurring regularly in winter and spring plankton; since it is the absolutely dominant *Calanus* here, I have referred Redeke & van Breemen's record to this, rather than to the preceding species.

Paracalanus parvus (Claus). Redeke & van Breemen (1904); Gurney (1929).

Offshore (Redeke & van Breemen); in the River Bure at Stokesby (Gurney).

Pseudocalanus elongatus (Boeck). Redeke & van Breemen (1904).

This is occasional, and sometimes numerous, in the Blakeney Harbour area, in which the only ovigerous females seen were one on 2.6.1962 and one on 8.4.1963.

Temora longicornis (O.F. Müller). Möbius (1875); Gurney (1904); Redeke & van Breemen (1904).

Although this is by far the most abundant calanoid in North Norfolk waters, where it is often extremely numerous, the only ovigerous female I have seen was in Blakeney Harbour on 6.9.1965. The stomach of a locally caught mackerel (*Scomber scombrus*) that I examined in August 1967 was distended with copepods, all of this species.

Eurytemora americana Williams.

Abundant, including ovigerous females, in the Half Moon Pond at Cley on 8.3.1965, but not found there since in spite of repeated

search; the key by Harding & Smith (1960, p. 13) requires correction in that the furcal rami were covered dorsally with spinules in the females, but not in the males.

Eurytemora hirundo Giesbrecht.

One in whelkpot rubbish at W.32 (see Hamond, 1969b, for station list). This is such an unusual record that I suspect contamination from the plankton. It is possible that this species and the next are synonymous.

Eurytemora affinis (Poppe). Gurney (1904, 1929); *E. affinis* + *E. hirundoides* + *E. hirundo* Gurney (1931).

Common in Breydon (Gurney; own observations); occasionally in winter plankton in Blakeney Harbour.

Eurytemora velox (Lilljeborg). Gurney (1929, 1931); *E. lacinulata* Gurney (1904).

Common in the Broads (Gurney); numerous in brackish ditches at Cley (particularly in Arnold's Marsh) and at Morston (east of the Quay, behind the seawall). In the last-named locality on 17.3.1965, an immature female was found with rounded posterior corners to the fifth pediger, so that she could be identified only by the form of P5.

Ecologically this species and *E. affinis* appear to be mutually exclusive (Gurney; own observations), the latter preferring more saline water.

Metridia lucens Boeck.

One non-ovigerous female in plankton in Morston Creek, 18.3.1962.

Centropages hamatus (Lilljeborg). Möbius (1875); Gurney (1904); Redeke & van Breemen (1904).

Common offshore (Möbius, Redeke & van Breemen) and in the East Norfolk estuaries such as Breydon (Gurney); in North Norfolk it is usually second to *Temora* in abundance, but only one ovigerous female has been seen there, in Morston Creek on 21.5.1966.

Centropages typicus Kryer. Möbius (1875); Gurney (1904); Redeke & van Breemen (1904).

A single non-ovigerous female in bottom plankton about a kilometre north of Blakeney Point, on 1.11.1961.

Isias clavipes Boeck. Redeke & van Breemen (1904).

From July to November, in variable (usually small) numbers. Rakusa-Suszczewski (1969) states that this species is constantly associated with *Sagitta setosa*-plankton, and *Metridia lucens* with *S. elegans*-plankton; however, my records show that *Isias* is much more

frequent than *S. setosa,* and that there were no *S. elegans* in the haul in which *M. lucens* was caught (see above) even though *S. elegans* is far more common in the Blakeney Harbour area than *S. setosa* (cf. Hamond, 1963b, p. 699). It seems as if the Blakeney Harbour area is so unfavourable to all four species that the grouping in pairs mentioned by Rakusa-Suszczewski breaks down, and that each of the four species is able to penetrate the area only as and when conditions are suitable for it.

[*Candacia armata* Boeck. Rae & Rees (1947).

Off the Norfolk coast in December 1938 (Rae & Rees).]

Anomalocera patersoni Templeton. Möbius (1875).

In small numbers only, mostly offshore, from June to October.

Labidocera wollastoni (Lubbock). Redeke & van Breemen (1904).

In moderate numbers (much more frequent that *Anomalocera*), both offshore and in Blakeney Harbour, from June to December.

Parapontella brevicornis (Lubbock). Gurney (1904, 1929).

Sporadically off North Norfolk from June to November, about as numerous as *Isias* or *Anomalocera.*

[*Acartia bifilosa* (Giesbrecht). Anon. (1902-1911); Redeke & van Breemen (1904); Gurney (1929, 1931).

Rare at 53°07'N.01°01'E. (Anon., stn. H.7) in May 1907; in Breydon plankton (Gurney, 1929); East Norfolk (Gurney, 1931).]

Acartia clausi Giesbrecht. Redeke & van Breemen (1904); Gurney (1929, 1931); Serventy (1934).

Off North Norfolk this is usually next in abundance to *T. longicornis* and *C. hamatus,* although rarely it may be more numerous than either.

[*Acartia discaudata* Giesbrecht. Redeke & van Breemen (1904); *A. longiremis* Gurney (1907, 1929).

Offshore (Redeke & van Breemen); in the River Bure near Stokesby on 19.8.1906 (Gurney, 1907) and 4.9.1910 (Gurney, 1929, synonymy), in both cases during a strong influx of seawater up the river.]

Acartia longiremis (Lilljeborg). Anon. (1902-1911); Redeke & van Breemen (1904); *Dias longiremis* Möbius (1875).

Frequent at the Durch plankton stations (Anon.), less common elsewhere offshore (Möbius; Redeke & van Breemen). A very few were found in Blakeney Harbour plankton on 1.8.1959.

MISOPHRIOIDA

Misophria pallida Boeck.

Two females at D.18, without eggs. My previous statements (Hamond, 1968a, 1969d), that this is the only known species of the order Misophrioida, were made in ignorance of the Japanese species (Tanaka, 1965) of *Misophria*, and the comparison of the two known species of *Benthomisophria* by Hulseman & Grice (1964); however, *M. pallida* is still the only species known from shallow waters along the North European coasts, where it is not at all common.

CYCLOPOIDA

Gnathostomata

Oithona helgolandica Claus. *O. similis* Anon. (1902-1911).

Neither frequent nor numerous offshore (Anon.); it appears (Rae & Rees, 1947, p. 112) that Blakeney Harbour is very close to the limit on the east coast of England between this species and *O. nana*. Two non-ovigerous females in surface plankton, one just outside Blakeney Bar on 3.10.1961 and the other in Morston Creek on 2.6.1962.

[*Oithona nana* Giesbrecht. Anon. (1902-1911).

Only in the extreme south-east of the Norfolk area (stn. H.8) in November; common in 1902 but rare in 1903.]

[*Oithona plumifera* Baird. *O. atlantica* Anon. (1902-1911); *O. spinirostris* Rae & Rees (1947, p. 112).

Penetrates as far south as the Dogger Bank; the record from stn. H.5 in November 1906 is only just outside the Norfolk area.]

[*Cyclopinoides littoralis* (Brady). *Cyclopina littoralis* Bourne (1890); Anon. (1902-1911).

Both these authors found it to be not uncommon; Bourne found it in large numbers near the Leman Bank during late February and early March (1889 or 1890; Bourne is not clear on this point). Redeke & van Breemen's *Cyclopina* sp., taken east of Smith's Knoll in August 1901, may also been this species, whose total absence from my own plankton hauls remains inexplicable at present.]

Cyclopina gracilis Claus.

Apparently very eurytopic and euryhaline, but always in small numbers; some of my records are from the open shore (several among *Salmacina* under rocks at West Runton, 3.8.1958 and 14.10. 1962; an ovigerous female among *Pomatoceros* on stones in the Strond Pool near the Dam, 4.5.1964) and the others from algae and submerged angiospers at Cley (Half Moon Pond and Arnold's Marsh), Morston Creek (near the Regatta Winning Post, in marsh pools), and Wells (Abraham's Bosom, the brackish boating lake completely cut off from the sea, whose copepod fauna will be described in a later paper) (Hamond, 1972).

[*Cyclopina norvegica* Boeck.
C. littoralis + *C. gracilis* Gurney (1904);
C. littoralis + *C. gracilis* + *C. elegans* Gurney (1929);
C. norvegica Gurney (1933).

Gurney's records are all from East Norfolk, in estuaries such as Breydon (1904) and in the Bure near Stokesby (1929); in the face of so much name-changing, and lacking either his own material or any further material from the same area, I have entered this species under the last name used by him, which presumably represents his final verdict. It is possibly identical with the preceding species, at least in part.]

Euryte longicauda Philippi. Hamond (1968a).

All my specimens are clearly this and not the very similar *E. minor* (see Sars, 1921; Vervoort, 1964). Intertidally, very rare in the Strond Pool; offshore, in small numbers in faunistically rich dredgings on rough grounds, with plenty of dead shells and hydroids.

Halicyclops incognitus Herbst. Hamond (1963a, p. 14).

Present wherever looked for in the burrows of *Nereis diversicolor* along the North Norfolk coast ; sofar, the burrows of other species of nereid in that area (see Hamond, 1966b) have not been investigated. The way to catch *H. incongnitus* is to turn up, very carefully with a spade, the mud or sandy mud in which *Nereis* is living, so that the burrows are revealed by the breaking-up of the substratum; the walls of the burrows are scraped with the tip of a teaspoon, and the scrapings placed in a screwtopped jar with enough seawater to cover them. In the laboratory the jar is stood on a table with the lid off, but covered by a light-proof box which is suddenly lifted off after about half an hour; the *H. incognitus* will be seen in midwater, or high up on the sides of the jar, as tiny white specks darting swiftly down towards the mud, into which they will escape unless caught with a pipette. This positively geotactic response is released irrespective of the direction of the incident light.

This is a new British record; I am indebted to Prof. J.H. Stock for the information that a species of *Halicyclops* was to be found in the burrows of *N. diversicolor,* and to Dr. H.V. Herbst for con-

firming that the Norfolk material was all of *H. incognitus* (since *H. rotundipes* Kiefer may also be found in the burrows of this polychaete; see Herbst, 1962). Specimens from burrows of *N. diversicolor* in the Salts Hole at Holkham (see Hunt, 1971), a brackish pond isolated from the sea for several centuries, were found to be normal by Dr. Herbst, except that the terminal endopod segment of P4 and the free segment of P5 were both unusually short.

Halicyclops magniceps G.O. Sars. Gurney (1929).

In brackish pools at Salthouse (Gurney), very near the Half Moon Pond where I found it with *Eurytemora americana* (q.v.); one ovigerous female at the mouth of Morston Creek, 6.5.1967, with abundant decaying plant remains in muddy sand; and very abundant in the end of the brackish ditch just east of Morston Church.

Halicyclops neglectus septentrionalis (Kiefer). *Cyclops aequoreus* Gurney (1904); *H. aequoreus propinquus* Gurney (1933).

In great abundance in the salt-water aquarium tank in Norwich Castle Museum; at that time (about 1961 or 1962) the tank was stocked from an unknown brackish-water locality in East Norfolk, somewhere near Gurney's collecting areas. For this reason I have referred Gurney's records to this species, but some of them may equally well have been *H. magniceps,* or even the true *H. propinquus* (which I have noy yet found here). Dr. Herbst has kindly provided the following table:—

Character	*H. propinquus*	*H. magniceps*	*H. n. septentrionalis*
Furcal ramus	Not longer than broad	Twice as long as broad	Not longer than broad
Dorsal processes on penultimate somite of abdomen.	Absent	Absent	Present

The only Norfolk record of *H. n. septentrionalis* in the wild is of specimens found by me in the *Salicornia*-Marsh on Blakeney Point, where they occurred in small pools among *Pelvetia,* apparently associated with the marsh-snail *Hydrobia ulvae.* When placed soon ofter capture in a dish of seawater with *H. ulvae,* the copepods became very active, scuttling round the snails or over them, whereas in the absence of *H. ulvae* the copepods swam intermittently or lay quietly on the bottom of the dish. Repeat experiments with the same snails and copepods next day did not show this difference in behaviour, nor did the same experiment on later occasions with further material from the same place; moreover, *H. ulvae* occurs in many places where *H. n. septentrionalis* has not been found.

Siphonostomata

Genus *Asterocheres.*

In my 1968a paper, I should have made it clear (cf. Yeatman, 1970, p. 37) that all the Norfolk members of this genus are found intertidally in their largest numbers in sponges (*Halichondria panicea,*

Ciocalypta penicillus), although sometimes found loose among small algae under the rocks where the sponges themselves are also found (under Wells Rocks and at West Runton). No sponges were found at any of the stations in Table 1, except that at D.17 there was a fist-sized lump of unidentified yellow sponge, resembling *H. panicea* but extremely slimy. Tearing this to bits yielded 15 *Tritaeta gibbosa* (often found on sponges; Hamond, 1967a, p. 132), and many other locally common free-living invertebrates; however, the only *Asterocheres* in this haul (a single *A. echinicola*) was found among brittle-stars with *Paranthessius anemoniae* (see below), probably by accident.

TABLE 1
Offshore finds of *Asterocheres* spp.

Station	*A. boecki*	*A. echinicola*	*A. ellisi*
W.27			1
W.30			1
D.17		1	
D.18	2	1	8 ♀, 20, 2 juv.
D.50	1		

The specimens not assigned to either sex were probably females, at least in most cases.

Asterocheres boecki (Brady).

Rare offshore; 5 females in *H. panicea* at West Runton, 2.11.1963.

Asterocheres echinicola (Norman).

Common under Wells Rocks (Hamond, 1963a, as *Ascomyzon* sp.) and Wells Quay, in *H. panicea*; common in this sponge and in *C. penicillus* under rocks at West Runton; rare offshore. A well-known inhabitant of sponges (Stock, 1967).

Asterocheres ellisi Hamond (1968a).

About as plentiful in the above-named sponges as the two preceding species together; less common at Wells, but more common at West Runton, than is *echinicola*. In view of its frequency in Norfolk waters, it is rather curious that it has not yet been recorded elsewhere.

Dermatomyzon nigripes (Brady & Robertson).

Occasionally in dredgings; the Norfolk specimens are clearly all of this species and not of *D. elegans* (Canu, 1892).

Rhynchomyzon purpurocinctum (T. Scott).

Usually with *D. nigripes*, and about as frequent.

Collocheres gracilicauda (Brady).

Definitely this species as redescribed by Stock (1966). On *Ophiothrix fragilis* inside the "Hjördis"; 2 ovigerous females and 44 cope-

podites among 390 hosts on 27.8.1961, and 1 ovigerous female, about 60 adults of both sexes, and about 20 copepodites, among 311 hosts on 13.10.1961.

Scottomyzon gibberum (T. Scott).

1 at D.18, at least 20 at D.20, and 1 at D.45, all of them loose in the dredge. No *Asterias rubens* were recorded in any of these hauls, although they may have been overlooked. The biology of *Scottomyzon* has been excellently surveyed by Röttger (1969, 1971); both he and Barel & Kramers (1970) find that it is confined to *A. rubens*.

Acontiophorus scutatus (Brady & Robertson).

An ovigerous female among *Laurencia* in the Strond Pool on 9.12.1962, and occasional individuals elsewhere between tidemarks (mouth of Morston Creek, under Wells Rocks, and in Wells Quay); otherwise exclusively offshore, where it may be numerous in dredgings and less so in whelkpot rubbish.

Scottocheres elongatus (T. & A. Scott).

Two under Wells Rocks, 20.12.1956, among small algae growing both on the stipes of *Laminaria saccharina* and under the rocks themselves; and a third specimen at S.4.

Bradypontius papillatus (T. Scott).

Occasionally in dredgings, and not uncommon among sponges at West Runton; never found here among small algae (as in Kiel Bay; Remane, 1933, p. 180 and 185).

Artotrogus orbicularis Boeck.

One very fine female specimen, pale golden straw-yellow in colour and minutely punctate all over (Giesbrecht, 1899, plate 10, fig. 34), taken clinging to a flint at Q.2.

Cancerilla tubulata Dalyell.

An ovigerous female (Hamond, 1961, fig. 1) on one out of six *Amphipholis squamata* at W.30; since then I have examined numerous *A. squamata* from between tidemarks without finding any more *Cancerilla*.

Poecilostomata

Poecilostome A.

At D.18 "one very transformed poecilostome, which after dissection proved to be near *Philoconcha*, a Japanese genus parasitic on molluscs. This might represent a new genus and species... I remember collecting similar things near Roscoff, but we have not yet described it" (J.H. Stock, *in litt.*).

Clausia lubbocki Claparède.

A single female at D.18, the first British record (det. J.H. Stock).

Clausia uniseta Bocquet et Stock (1960).

The holotype, and still the only known specimen, at D.18.

Mesnilia cluthae (T. & A. Scott).

3 adult males at D.18, and an adult female at D.53; in both hauls the *Mesnilia* (dead when found) were obtained by breaking up masses of black peat-like material riddled with the tubes of *Polydora ciliata* and with many burrows of small *Zirfaea* and *Hiatella*. This is the first North Sea record of *Mesnilia,* for which Bocquet & Stock (1959a) give the host as *Polydora flava.*

Hemicyclops sp.

A single male in bottom plankton outside Blakeney Bar on 12.12.1961, described by Hamond (1968a). Although very close to *H. aberdonensis* T. & A. Scott (1892), it cannot by named at present, because so many members of this and related genera are still so poorly known (cf. Vervoort & Ramirez, 1966); however, the juveniles found in our area by Bourne (1890, as *Hersiliodes canuensis*) and by me, may possibly belong to this species.

[*Hersiliodes latericia* (Grube). T. Scott (1905).

Found by Arnold Watson at Hunstanton on *Leiochone clypeata,* no data (Scott). This is the first British record; the only other English author to deal with this copepod, Leigh-Sharpe (1939), used a specimen from Roscoff. Scott states that Hunstanton resembles Cherbourg (the type locality for *Hersiliodes*) in having intertidally a submerged forest, which he regarded as a suitable habitat for *Leiochone*; at the present day this submerged horest is best developed a few kilometres east of Hunstanton, near Titchwell and Brancaster (Hamond, 1963a) and has not yielded any further *Leiochone* in spite of frequent collections (Pantin & al., 1960; Hamond, 1966b and unpubl.). Watson's record must be regarded as doubtful, until more specimens are obtained.]

Conchyliurus cardii Gooding, sub-sp. *tapetis* Bocquet & Stock (1958a).

This subspecies is new to the British Isles; during August 1961 it was very common in *Scrobicularia plana* from Blakeney Harbour, Brancaster, and Thornham, and less so in *Petricola pholadiformis* and *Barnae candida* from the submerged forest at Brancaster. These bivalves are new hosts for the sub-species *tapetis.*

If kept apart from its host in a small dish of seawater, *C. c. tapetis* is very apt to crawl above the waterline and die of dessication, as noted by Humes & Cressey (1958) for *C. torosus*; because of this I was unable to study thoroughly an epizoic suctorian (?*Thecacineta* sp.).

Lichomolgus agilis (Leydig).

Widely distributed in North Norfolk waters on a variety of nudibranchs (*Archidoris pseudoargus, Onchidoris fusca, Acanthodoris pilosa,* and *Aeolidia papillosa*); at D.17 a single male was found loose in the dredge, in which the only nudibranchs were two *Tritonia hombergi.*

Modiolicola insignis Aurivillius.

Not infrequent in *Modiolus modiolus* taken offshore.

Sabelliphilus elongatus M. Sars. Hamond (1966b).

Occasionally on *Sabella pavonina* under Wells Rocks; habits exactly as described by Gotto (1960).

Macrocheiron fucicolum Brady.

One female in Harbour plankton on 1.8.1959, and one specimen among hydroids (*Kirchenpaueria pinnata*) in the Strond Pool on 17.8.1962; seven specimens in a tube of miscellaneous material from Scolt Head (locality p of Pantin & al., 1960) by courtesy of Dr. K.A. Joysey. The Norfolk specimens are all clearly of this species and not of *M. mutatum* Stock (Vervoort, 1964, p. 47).

Pseudanthessius gracilis Claus.

One among *Laminaria*-holdfasts in the Threshold, 8.7.1959; a pure white ovigerous female among *Sidnyum turbinatum* at West Runton on 29.7.1961, and a specimen (?copepodite) at extreme low water there on 3.8.1958.

Pseudanthessius sauvagei Canu.

Six, among 7 *Echinocardium cordatum* at extreme low water, Holkham Bay, 16.9.1962.

Pseudanthessius liber (Brady & Robertson).

Frequent on *Psammechinus,* and also taken loose in the dredge on several occasions, whether or not there were any *Psammechinus* in the same haul; invariably offshore.

Paranthessius anemoniae Claus.

One female, adult but not ovigerous (det. J.H. Stock) among about 20 brittle-stars (*Ophiothrix fragilis*) at D.17. This is the first British record of *P. anemoniae* (redescribed by Bocquet et Stock, 1959c), and the first record of it from a host other than the sea-anemone *Anemonia sulcata,* which is unknown in Norfolk waters.

Hermannella rostrata (Canu).

The generic name *Herrmannella* is used for this and the following species on the advice of Professor A.G. Humes (*in litt.*), instead of *Paranthessius* as formerly. *H. rostrata* is very common here in *Cardium edule* (but not in any other species of *Cardium*), less

frequent in *Venerupis pullastra,* and occasional in *Scrobicularia plana* and *Ensis siliqua*; *S. plana* is a new host for this species, the others being in the list of hosts given by Bocquet et Stock (1959b, as *Paranthessius*).

Hermannella barneae (Pelseneer).

In moderate numbers in *Barnea candida* from the submerged forest at Brancaster and Titchwell (cf. Hamond, 1963a); the specimens, the first for the British Isles, agree closely with the redescription by Bocquet et Stock (1958c). The *Petricola pholadiformis,* living in the same peat, cheek by jowl with *B. candida,* were nevertheless uninfected by *H. barneae,* and specimens of the latter experimentally introduced into either of the siphons of *Petricola* were always forcibly ejected at once; on the other hand, both species of bivalve were infected by *Conchyliurus cardii tapetis.* An ovigerous female and a copepodite of *H. barneae* (det R.V. Gotto) were found among seven *Zirfaea crispata* (new host) in thick clay at extreme low water at Gore Point, Holme, on 9.8.1967.

Heteranthessius sp.

One loose in the dredge at D.18, too young for specific determination (J.H. Stock *in litt.;* see Bocquet, Stock et Bénard, 1959).

Anthessius teissieri Bocquet et Stock (1958b).

An adult male in plankton with *Hemicyclops* sp. (q.v.), clearly this and not *A. arenicolus* Brady. Otherwise confined to the body surface of *Buccinum undatum,* where it appears to be scarce, and not yet found on the very few *Neptunea antiqua* or *Colus gracilis* examined.

Anthessius leptostylis G.O. Sars.

Of this species, new to the British Isles, a single specimen was found when sorting the catch (as in Hamond, 1966a) at D.57. In this haul there were also 46 *Buccinum undatum* of all sizes, which were washed with seawater during sorting, kept thereafter in a separate container, and on reaching the laboratory were poured with their water into a larger vessel to which tapwater with magnesium sulphate had been added. The whelks remained in this mixture overnight, after which it was filtered; no animals whatever were found in the filtrate, which is surprising considering how successful this method had been when applied to whelks from W. 34. Bresciani & Lützen (1962) also found *A. leptostylis* on *Buccinum* in Swedish waters. The present specimen must therefore either (a) have deserted its host in the dredge or during the initial washing, or (b) must have been captured when on the way from one host to another.

The known geographical distributions of *A. leptostylis* (see Bresciani & Lützen, 1962) and *A. teissieri* (see Bocquet et Stock, 1958b), although probably very incomplete, suggest that the latter is found from Norway to France and therefore probably all round the British Isles, whereas the former seems to be a northern species for which

Norfolk is the most southerly habitat known; it is also the only place apart from Norway where these two species have been found together. The present specimen shows certain differences from that described by Sars (1918, plate CIII, as *Pseudomolgus leptostylis*) in the form of the first maxillipede (Fig. I, 4), in the third endopod segment of P4 (only three spines, instead of four spines and a seta; Fig. I, 1),

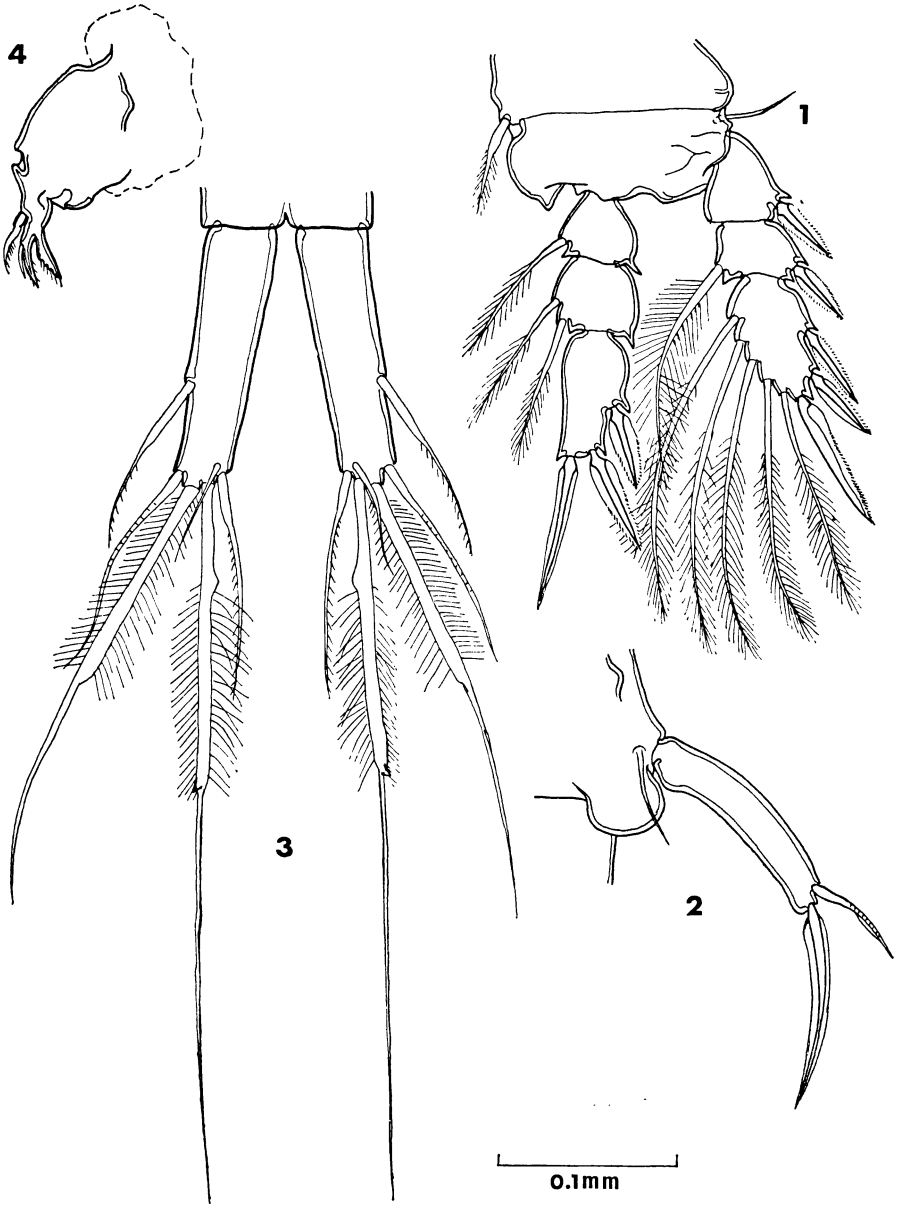

FIG. I
Anthessius leptostylis G.O. Sars.
1 : P4; 2 : P5; 3 : furca with setae; 4 : first maxillipede.

in the curved form of P5 which bears only two spines (Fig. I, 2) instead of being almost straight and bearing three spines and a seta, and in the furcal setae not being evenly tapered but having a thicker basal portion sharply separated from a thinner distal portion (Fig. I, 3), very much as in *A. teissieri* (the Norfolk material of which shows this last character very clearly). Since this last character is confined to the two species which both infest *Buccinum,* it may be an adaptation to life on the surface of the whelk, convergently assumed by these two species; it is rather curious that Sars, who saw them both (in 1921, plate LXXIV, he shows *A. teissieri* under the name of *Pseudomolgus arenicola*), never noticed it in either of them, although his drawing of the furca of *A. teissieri* has an almost imperceptible suggestion of it in the largest seta of the left furcal ramus. The present specimen is almost certainly immature, which would explain the differences between it and those seen by Sars; sofar, no author has given details of juveniles of this species.

Anthessius sp. Hamond (1968a).

A single specimen among mixed benthonic material from S.4; as previously stated, it is impossible to say whether it belongs to *A. solecurti* or to *A. minor,* which are in any case very closely related.

Corycaeus anglicus Lubbock. Anon. (1902-1911); Redeke & van Breemen (1904).

Never common, mostly in August but also in November (above records); a single adult female, not ovigerous, in surface plankton off the end of Blakeney Point at dusk on the evening of 26.9.1961. In the North Sea *Corycaeus* is characteristic of the southern half, very much as *Sagitta setosa* (cf. Rae & Rees, 1947), *Margelopsis haeckeli* and *Mitrocomella brownei* (see Hamond, 1963b), and North Norfolk is close to the northwestern limit for all these species except *S. setosa,* of which small patches may occur in coastal waters as far north as the Tyne (information from Dr. J.B. Buchanan) and perhaps further north.

[*Oncaea* sp. Anon. (1902-1911).

Extremely rare in 1906, at H.5 in May and at H.8 in November; no details are given by which the species could be recognised.]

MONSTRILLOIDA

Monstrilla grandis Giesbrecht.

Present every year in the plankton (very common during 1965) from July to October inclusive; most abundant in August and September. Both sexes agree well with the account in Rose (1933). Sofar I have taken 19 males and 44 females; most of the latter had no eggs at all, but one had eggs still filling the body cavity and seven bore eggs on the ovigerous setae.

Thaumaleus rigidus (Thompson).

At the same season as *M. grandis,* but much rarer. Two spent females in plankton in Blakeney Harbour, 17.9.1958; one spent female in bottom plankton about a mile north of Blakeney Bar, 6.7.1955; and a female with the body cavity still full of eggs, in Blakeney Harbour plankton, 6.9.1965.

The capture of a single female of each species of monstrillid with eggs still inside it (presumably, therefore, before it had found a mate at the start of its planktonic phase) implies that the hosts of both species live nearby; however, I have never seen a monstrillid larva in any invertebrate in North Norfolk waters.

NOTODELPHYOIDA

Notodelphys allmani Thorell.

Infests between 2 and 10 percent of *Ascidiella scabra* in dredgings, and a lower percentage of *Microcosmus claudicans*; these hosts were common off North Norfolk in the late nineteen-fifties, but by the time I left for Australia in 1968 they had become very scarce. Also in the late nineteen-fifties, *Perophora listeri* was sometimes found in dredgings, and often contained a small bright red *Notodelphys* which was always immature. Dr. R.V. Gotto thinks that these may have been young *N. allmani* which had entered the *Perophora,* either by mistake (and were therefore fated never to attain maturity), or as a temporary host from which they would later migrate to *Ascidiella* or *Microcosmus* in which they would grow to full size; the latter possibility receives some support from the finding, that specimens from these latter hosts were always larger than those from *Perophora,* but I was unable to keep either the *Notodelphys* or its hosts alive in order to test this experimentally.

Notodelphys elegans Thorell. Möbius (1875).

Infests a small percentage of *Ciona intestinalis,* either in dredgings or cast ashore; confined to this host, in which *N. allmani* is never found here. In contrast to the preceding species, *N. elegans* was apparently more plentiful at the time I left Norfolk than it had been a few years earlier, since *Ciona* had become more abundant in dredgings as the hosts of *allmani* became less so.

Doropygus pulex Thorell.

One ovigerous female in the branchial sac of *Molgula occulta* at D.22.

Pachypygus gibber Thorell.

Off North Norfolk an ovigerous female was found in *Polycarpa gracilis* at W.33, and non-ovigerous females in two out of 14 *Molgula*

socialis at D.33. Off East Norfolk (in the Yarmouth shrimptrawls) it was found in one out of four *M. socialis* off Corton, 27.7.1960, and in 3 out of 8 *M. socialis* from off Caister, 23.7.1959. Only a single parasite was found in each host.

Ascidicola rosea Thorell.

Of 46 *Microcosmus claudicans* at D.18, three each contained a single female of this species.

Botryllophilus ruber Hesse.

Not uncommon at West Runton in *Morchellium argus* and *Sidnyum turbinatum*; occasionally inside the "Hjördis", most often in *S. turbinatum* but sometimes in *S. elegans*; and offshore, rather rarely in *Botrylloides leachi.* I have used the familiar name *ruber,* pending a proposed revision of this genus (see Stock, 1970, p. 16).

Enterocola fulgens P.J. van Beneden.

Exclusively in *Polyclinum aurantium* at West Runton; when the corms of this ascidian are sliced longitudinally, the enterocolids show up as brilliant red spots near the periphery, against the dull yellowish brown of the colony. The rate of infection varies widely, some colonies having none and others containing up to 40 *E. fulgens* each; the males are usually much scarcer than the females.

Mycophilus roseus Hesse.

Not uncommon in *Botrylloides leachi,* mostly in August, including males and clumps of eggs as described by Lang (1948).

Haplostoma brevicauda (Canu).

The creamy-white females are found exclusively in the peduncles of the corms of *Sidnyum turbinatum,* in which they are not uncommon at West Runton; I also found a single male there on 1.8.1957 among *Corallina,* and a male (probably of this species) among each of two large collections of *Ophiothrix* inside the "Hjördis" (see above, *Collocheres*). On both occasions the inside walls of the "Hjördis" had plenty of *S. turbinatum* growing on them, over which the *Ophiothrix* was creeping in a layer three or four individuals deep.

Haplostome A.

One ovigerous female, bearing a marked general resemblance to *Doropygus pulex,* in *Sidnyum turbinatum* at West Runton on 1.8.1957. According to Dr. Gotto (*in litt.*), this is much more primitive than most haplostomes and might represent a new genus and species; the specimen was incomplete, but a brief description is given below in case it is found again.

Body more or less *Doropygus*-like (Fig. II, 5), flabby and poorly muscled; the outline of the tenuous egg-sac (dotted line, OS) is inserted from memory. Furca (lost during dissection) provided with short setae (number and arrangement not recorded), but not with

hooks. Antennule (Fig. II, 6) with a swollen basal segment and three much smaller free segments. Antenna (Fig. II, 7) two-segmented, the terminal segment with four sawlike teeth. No mandibles, maxillules, or maxillae. Maxillipede (Fig. III, 9) two-

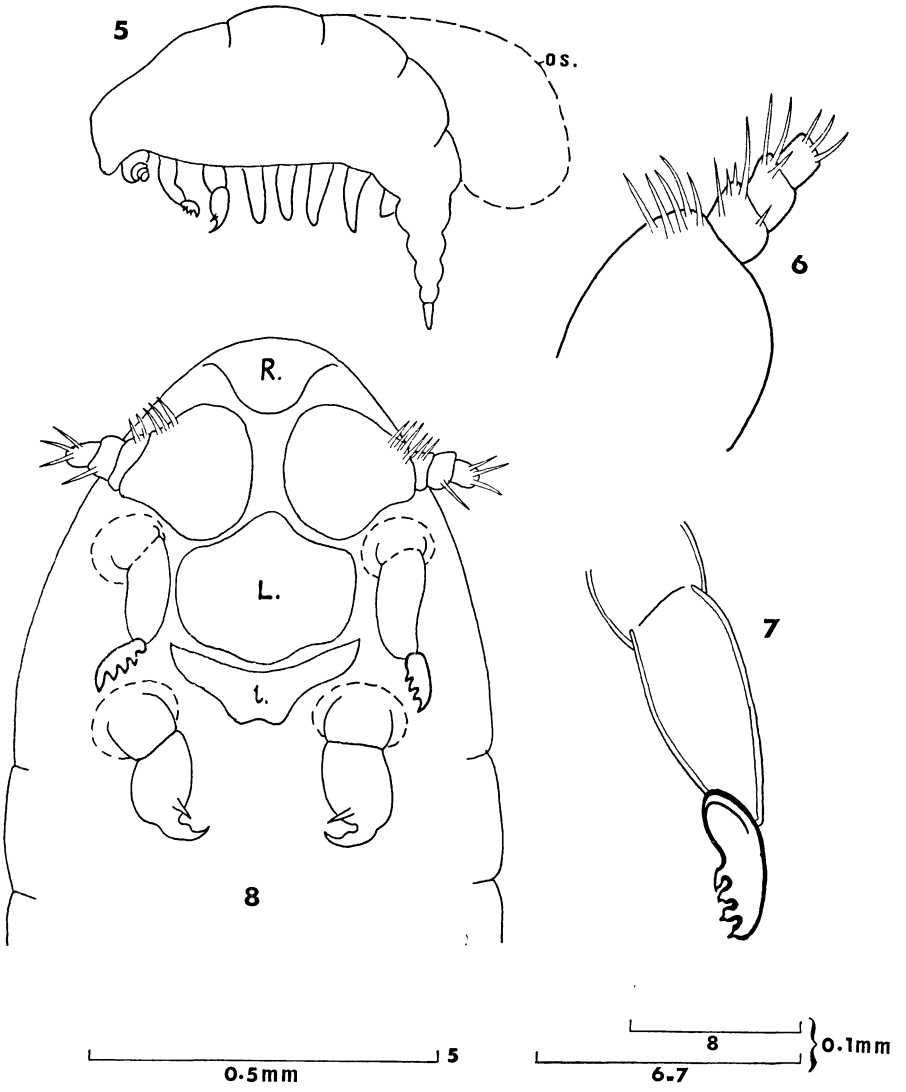

FIG. II
Haplostome A
5 : outline in side view; 6 : A1; 7 : A2; 8 : oral area in ventral view. OS : egg-sac.

segmented, with a terminal claw and a small ancillary spine. Both rami of P1 to P4 inclusive (Fig. III, 10 to 13) are one-segmented; it is uncertain whether P4 has an endopod. P5 not observed in detail. Number of abdominal somites uncertain (apparently 3 or 4). Colour in life pale grey, the viscera deep green, with the eggs in the eggsac

a transparent refractive amber colour, like globules of oil. Total length about 0.9 mm. The resemblances to the haplostomes is clearly shown by the layout of the oral area (Fig. II, 8), apart from which a hypothetical reduction of the swimming legs to the limits indicated by

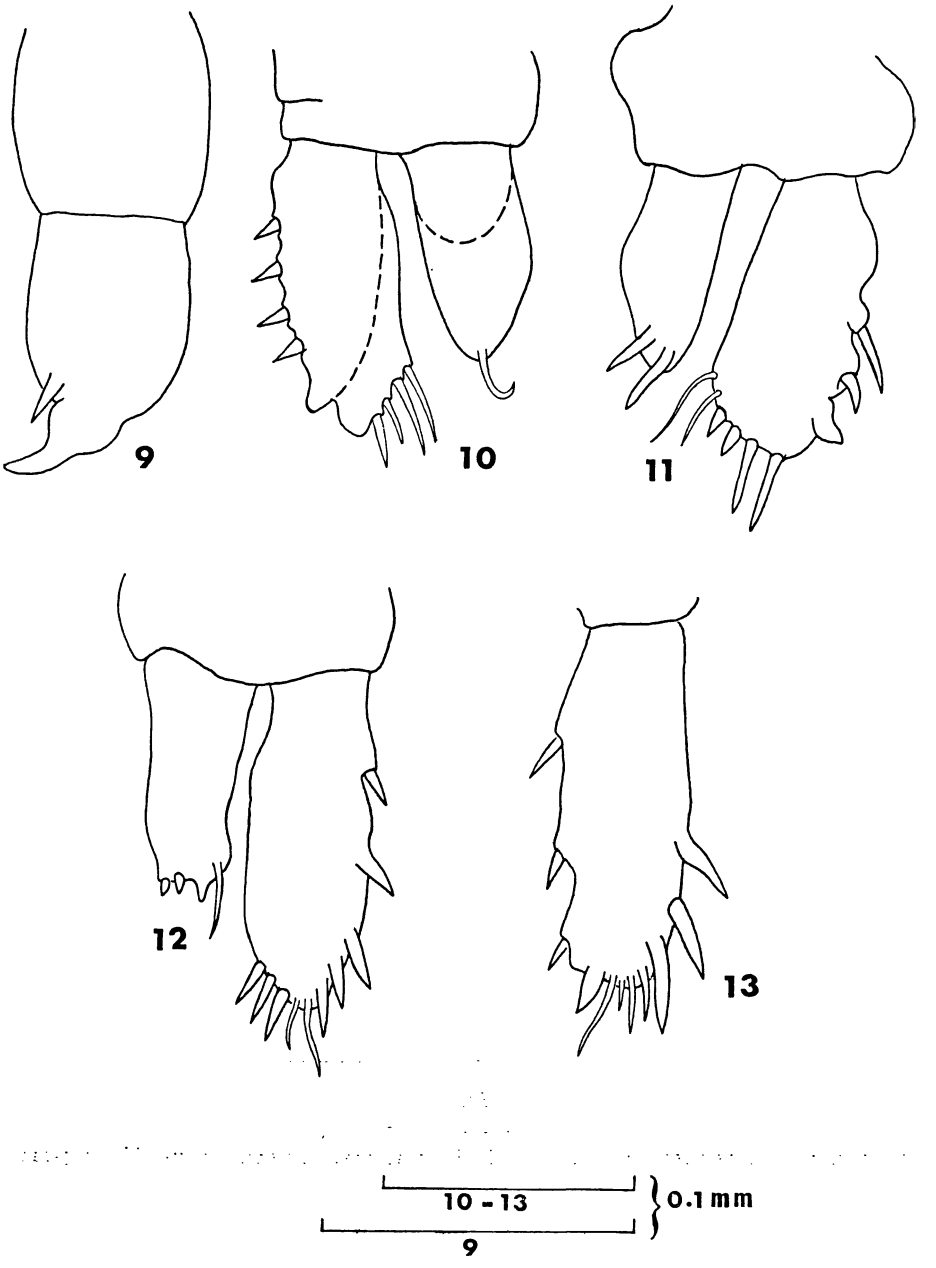

FIG. III
Haplostome A
9 : Mxp; 10 : P1; 11 : P2; 12 : P3; 13 : P4.

dotted lines in Fig. II, 10 would result in feet indistinguishable from the stumplike limbs of haplostomes. Unfortunately the specimen no longer exists, but the above account was compiled from notes and sketches kindly sent by Dr. Gotto, who thinks that this species is either an indirect ancestor of the "normal" haplostomes, or (much less likely, though not impossible) the hitherto unknown female of *Agnathaner.*

Agnathaner freemani Hamond (1968a).

The holotype male, and the still the only known specimen, at D.53; no female is yet known in this genus, of which the males are very rare (see Canu, 1892, for both the previously known species).

Incertae sedis

Under this heading are grouped certain species whose affinities with other copepods are still obscure .

[*Herpyllobius polynoes* (Kröyer). *Sylenium* [sic] *crassirostris* Möbius (1875).

A single female with eggsacs on the head of *Harmothoe imbricata* from P.105, in the copepod section of Möbius's paper; on a later page, in the section dealing with polychaetes, he refers to it as *Herpyllobius arcticus* on the head of *Polynoe cirrata.* According to the careful revision by Lützen (1964), this is the only European record of this otherwise exclusively Arctic copepod; I have examined hundreds of apparently suitable polynoids in North Norfolk waters (Hamond, 1966b) without finding any herpyllobiids.]

Splanchnotrophus gracilis (Hancock & Norman).

One male loose in the dredge at D.20 (det. J.H. Stock); a female in a large pure white *Acanthodoris pilosa* under a rock at about low water level of neap tides at West Runton, 9.3.1961; a solitary female in the larger, and a female with six attendant males in the smaller, of two *Eubranchus pallidus* which were crawling on *Halecium halecinum,* the latter growing naturally just below extreme low water mark on Hunstanton Scaup on 31.7.1961.

[*Nicothoe astaci* Audouin & Milne-Edwards.

Van Oorde-de Lint & Schuurmans Stekhoven (1936, p. 8) record this species from Norfolk, without further details; during the last few years before I left Norfolk the lobster was so scarce and expensive that I have not been able to examine any. Lemercier (1966) has shown that this species is a relatively unmodified choniostomatid; the biology is well described by Mason (1959).]

Choniosphaera maenadis (Bloch & Gallien, 1933).

Ovigerous females were common on the spawn of a female *Carcinus maenas* taken in the Threshold on 8.7.1959, clinging to the crab's eggs exactly as shown by Gallien & Bloch (1936, pl. 1, fig. 1);

the male is unknown, according to the very thorough work of Fischer (1956). Several other ovigerous female *Carcinus* from North Norfolk have been examined, without finding any more *C. maenadis,* of which the only other British record is from Whitstable, also on *Carcinus*-eggs (Needham, 1933, as "an unknown choniostomatid").

Choniosphaera cancrorum Connolly (1929) is so like *Lecithomyzon maenadis* Bloch & Gallien (1933), that they are almost certainly congeneric (as also assumed by Lemercier, 1963), although I consider it advisable to keep the two alleged species apart until they have been directly compared with one another. On the east coast of the United States the hosts are *Cancer amoenus* Herbst, *C. irroratus* Say, and *C. borealis Stimpson* (all in Connolly, 1929), and more recently *Carcinus maenas* (in Johnson, 1957); I have examined ovigerous females of several common Norfolk crabs (see Hamond, 1971) without finding either this or any other associated copepod; however, a few harpacticoids were found, all of them belonging to common and widespread species.

Sphaeronella leuckarti Salensky.

All these specimens were kindly identified by Dr. J. Green, as follows:—

(a) at D.47 there were about 150 small, 16 ovigerous females, and four females of full size but with *S. leuckarti,* of *Corophium bonelli*; the infected females had a total of two male *S. leuckarti* between them, as well as one female parasite each. *C. bonelli* is a new host for *S. leuckarti.*

(b) on the upper part of the shore at Holme, just north of the Firs Nature Reserve, a strip of tough clayey black mud was sampled; of 5 *Corophium volutator* in a small sample, one had a pupa, a mature female with two eggsacs, and two males, all of *S. leuckarti,* on 8.8.1967.

(a) the next day a much larger sample of the same mud (about a square foot, dug to a depth of about two inches) yielded 171 *C. volutator* of which 3 were ovigerous females, one had both its own eggs and a female *S. leuckarti,* and no less than 40 each had a female *S. leuckarti* only; there were also a few male *S. leuckarti.* It seems likely that this very high percentage (ca. 22 p. 100) of infection must have seriously hindered the reproductive effort of the *Corophium* population, at least for the time being.

All Norfolk *S. leuckarti* fall within the range of variation described by Green (1958).

Sphaeronella valida Scott.

One ovigerous female (the neotype; Green, 1958) in the brood-pouch of the typical host, *Megamphopus cornutus,* at D.18; no further specimens here since then.

Sphaeronella paradoxa Hansen.

Common in *Bathyporeia sarsi* in the Pit of Blakeney Harbour, and in *B. pelagica* at West Runton, but not in *B. pelagica* from the

outside of Blakeney Point (only a short distance from the Pit), nor in any other Norfolk species of *Bathyporeia* (see Hamond, 1967a). Once only, in plankton off the end of Blakeney Point on 29.7.1963 at about 0100 hours (calm and very dark, no moon), was a female *B. sarsi* taken which had its own eggs and *S. paradoxa* together in the broodpouch; normally the parasite seems to inhibit the host from producing eggs or embryos. In the same haul there were three other adult *B. sarsi* each carrying a female *Sphaeronella,* and 25 half-grown *B. sarsi* which were uninfected when caught; in a dish in the laboratory the newly hatched copepodites of *Sphaeronella* were seen to swim to the halfgrown *B. sarsi* and to cling to their gills. Together with the apparent absence of free stages of *Sphaeronella* in the sand in which infected *B. sarsi* are relatively common, this suggests that infection of new hosts takes place when the amphipods come out of the sand in swarms shortly after the latter has been covered by the rising tide. Such swarms are very frequent in Pit plankton and are a constant feature of plankton hauls in the mouth of Morston Creek; the greatest numbers are taken on calm moonless nights from May to October.

Infected *Bathyporeia* are very easy to pick out, since the amphipods themselves are pure white and their ovaries and embryos brilliant blue, whereas the female *S. paradoxa* is a deep yellow, buff, or pale orange colour; however, the males and copepodites can be seen only under the microscope. *S. leuckarti* was also easy to see, being opaque cream against the dull brown of its *Corophium* host; the colour of *S. valida* was not recorded. *S. paradoxa* is new to the British Isles.

DISCUSSION

Of the 86 species listed above, four are doubtful; it is possible that the record of *Calanus finmarchicus* should be sunk in *C. helgolandicus,* that of *Eurytemora hirundo* in *E. affinis,* and those of *Cyclopina norvegica* in *C. gracilis.* I must regard the records of *Cyclopinoides littoralis* as doubtful until I have seen it in plankton samples from the area concerned; other members of the Cyclopinidae are strictly benthonic in Norfolk waters, and very largely so elsewhere.

Of the 82 remaining species, five (apart from *Anthessius* sp., which at present cannot be named with confidence) were new to science at the time they were found, one (*Sphaeronella valida*) represents the rediscovery of a long-lost species, seven (excluding *Hersiliodes,* q.v.) are new to the British Isles, and four are reported from new species of hosts. Those new to science or new to the British Isles are all known or suspected associates of benthonic hosts; on the other hand, the Norfolk plankton contains hardly any unusual species, consisting of almost exactly the species that would be expected here from the work of previous authors. However, the planktonic forms are very seldom ovigerous here, whereas the ben-

thonic species, whether free-living or associated, are frequently so.

The large number of interesting species found at D.18 clearly shows that the southern North Sea, traditionally regarded as poor in species and individuals, is capable of elaborating faunistically rich biotopes, granted suitable conditions to begin with and for a sufficiently long period. At D.18 the dredge bit deeply into large quantities of black submerged peat on which there was a thick growth of *Nemertesia antennina*; the relatively unworn appearance of many of the dead bivalve shells (mainly *Modiolus modiolus* and *Mya truncata*), and the large quantities of hydroids and polyzoans growing on them, indicated that here was a stable biotope in which this faunal assemblage had had a relatively long time to mature by the ingress and establishment of various species from outside. The empty *Polydora*-burrows and bivalve-tunnels in the peat, as well as the colonial epizoonts and the unworn shells, afforded excellent opportunities for micro-shelter; the extreme richness of this fauna was possibly due also to the absence of *Lanice conchilega* and the scarcity of *Pomatoceros triqueter*, both of which probably destroy either the larvae, or the detrital and microbial food-sources, of a good many other animals (cf. Hamond, 1966b, p. 424). D.18 was only about 400 metres north to northwest of the Blakeney Overfalls Buoy, but repeated hauls using the Buoy as a marker have failed to strike the peat again (although some was found at D.53; see *Mesnilia cluthae*); probably the stormy weather during the winter of 1957-1958 scoured away the projecting part of the peat.

When comparing the numbers, either of species or of individuals, of associated copepods actually found in Norfolk waters with the numbers of potential hosts occurring there (polychaetes, 1966b; amphipods, 1967a; decapods, 1971; molluscs, echinoderms, and tunicates, in preparation), it is very noticeable how all too often a likely-looking host species yields no associates after repeated examination, and not infrequently a host species that harboured numbers of an associate at a certain time or place is found to have few or no associated on a later occasion. These fluctuations are of course familiar to everyone who collects copepods associated with invertebrates, but when they are superimposed on the fluctuations of the host species themselves (which are often very marked in an unstable environment such as Norfolk waters), then the extreme difficulty of attempting to plan experimental work from one year to the next with any but the most common species will be readily understood. In such an environment the only way to approach a true knowledge of the fauna is by continuous sampling over many years, until the level of diminishing returns is reached; even now, it is possible that a few sofar unrecorded species live locally.

Summary

Of the groups mentioned in the title, the species sofar found in Norfolk waters are listed, with notes on their biology. Of 86 species, four are doubtful, five were new to science when found here, one long-lost species has been rediscovered, and seven more are new to the British Isles. New host records are given for four species. Whereas the benthonic species show many features of interest and are often found reproducing here, the planktonic species are almost all what

one would expect to find in this area, and are very seldom seen to reproduce. It is shown that the establishment in the Norfolk area of a suitable biotope for even a limited time can result in the development of a rich, even though localised, fauna; conversely, unstable conditions make life extremely precarious for all save a few resistant species.

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