

THE LARGER CRUSTACEA ASSOCIATED WITH HOLDFASTS OF KELP (*LAMINARIA HYPERBOREA*) IN NORTH-EAST BRITAIN

by

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Résumé

Les Crustacés Malacostracés associés aux crampons des Laminaires (*Laminaria hyperborea*) au N.-E. de la Grande-Bretagne.

L'auteur décrit la composition de la faune des Crustacés Malacostracés habitant dans les crampons des Laminaires, au N.-E. de la Grande-Bretagne. Des observations sont présentées sur l'histoire naturelle de chaque espèce. Les Amphipodes en sont le groupe dominant, suivi par les Isopodes et les Tanaïdés. Les Mysidacés et les Eucarides vagiles sont imparfaitement récoltés par les méthodes de capture employées. La dominance des Amphipodes est largement assurée par la famille des Ischyroceridae, suivie des Corophiidae, Amphilochidae, Calliopidae, Dexaminidae, Aoridae, Atylidae et Stenothoidae. La plupart des Amphipodes sont tubicoles; les non-tubicoles nagent vigoureusement et se nichent parmi les Algues. Le mode de nourriture et la distribution des Amphipodes, autour de la Grande-Bretagne, sont décrits. Le rôle des facteurs biogéographiques et de l'action dynamique des vagues est mis en évidence et discuté. Une comparaison entre la faune des crampons récoltés en Grande-Bretagne et en Californie est établie en rapport avec des différences distinctives entre les deux habitats.

Introduction

This paper results from the author's investigations of the biology of the fauna inhabiting holdfasts of kelp *Laminaria hyperborea* (Gunn.) Fosl., with special reference to pollution effects along the North East coast of Britain. Accounts of the Nematoda and Bryozoa have already appeared (Moore, 1971 and in press).

For the North East coast, ecological data are available on the arthropod fauna of sandy beaches (Colman & Segrove, 1955 a) and on the interaction between planktonic and benthic populations, both in the surf zone (Colman & Segrove, 1955 b) and offshore (Bossanyi, 1957). Relevant faunistic works, often with ecological remarks, include Scott (1888) on the Firth of Forth, Norman (1867) and Meek (1900 a, b, 1901, 1902) on Northumberland, Norman and Brady (1909) on Northumberland and Durham and Hamond (1967) on Norfolk shores.

Because of the great arthropod diversity supported by kelp holdfasts it is proposed to deal with the Crustacea Malacostraca separately from a subsequent treatment of the smaller Arthropoda (Branchiopoda, Ostracoda, Copepoda and Halacarida). Moore (in press) has described the Cirripedia.

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Methods

Quantitative data presented here pertain to material collected during a widescale kelp survey of the North East coast carried out in July 1969. Seventy-two mature holdfasts were collected from fifteen approximately equidistant sites between St. Abb's, Berwickshire and Flamborough Head, Yorkshire. Practical details are described by Moore (1971). Essentially, single holdfasts were collected in individual polythene bags secured underwater. Hagerman (1966) used this method for sampling the fauna of *Fucus serratus* L. but felt that highly mobile fishes were under-represented. Haage and Jansson (1970) have recently described a fixed cage method for sampling bushy algae which improves the capture of these animals. It is therefore probable that vagile Crustacea such as mysids and eucarids are under-represented in the present report. Consistent diver sampling of holdfasts is only possible on these exposed coasts during the summer period when the generally adverse conditions of turbulence and turbidity ameliorate. Field sampling errors must thus be regarded as minimum for the survey period and any remaining sub-optimal characteristics regarded as uncontrollable but constant.

The following account also includes records of species taken outside the main East coast survey, and from limited samples taken on the West coast of Scotland (sites around Oban, Argyll). Sampling technique was standard throughout.

CLASS MALACOSTRACA

SUB-CLASS PERACARIDA

Order Mysidacea

Records of East coast mysids are given by Norman (1867), Scott, (1888), Meek (1900 a), Norman and Brady (1909), Bossanyi (1957) and Colman and Segrove (1955 a, b). These vagile forms should perhaps not be considered as an integral part of the holdfast fauna, existing as they do in the surrounding water mass. Their agility also prevents their effective sampling by the above technique.

Only one species has been sporadically recorded:

Praunus inermis (Rathke).

This species is characteristic of the shallow sublittoral *Laminaria* zone (Tattersall and Tattersall, 1951) and is known to be common on the North East coast (Meek, 1900 a; Norman and Brady, 1909).

Order Cumacea

Norman (1867), Scott (1888), Meek (1900 b), Norman and Brady (1909), Bossanyi (1957) and Colman and Segrove (1955 a, b) give East coast records of Cumacea. They are typically sand dwelling and only a single individual has been recorded from holdfasts.

Bodotria scorpioides Montagu

The species has previously been recognised in the surf plankton on this coast (Colman and Segrove, 1955 b). Hagerman (1966) found it in association with *Fucus serratus* L. in Sweden.

Order Tanaidacea

Early records are given by Scott (1888) and by Norman and Brady (1909). Only one species has been presently encountered.

Paratanais batei G. O. Sars

Occurred commonly in holdfasts, which represent its typical habitat (Sars, 1899). A preference for areas of strong water movement was suggested from its distribution in the Scottish samples.

The other main species recorded by Colman (1940) and Scarratt, i.e. *Heterotanais orstedii* (Kröyer) was absent locally. Dahl (1948, p. 85) considered that it is a typical brackish water species.

Order Isopoda

The Isopoda and Tanaidacea comprise equivalent components of the malacostracan fauna of local holdfasts. However in comparison with the dominating Amphipoda, little is known of the biology of the species involved (see Colman, 1940; Dahl, 1948; Naylor, 1955 a, b, 1972; Sloane *et al.*, 1961; Hagerman, 1966).

East coast records are given by Scott (1888), Brady (1902), Norman (1904), Norman and Brady (1909), Colman and Segrove (1955 b) and Thompson *et al.* (1966).

The following species have been recorded:

Idotea baltica (Pallas)

Two specimens taken from a holdfast. The species is highly polychromatic (Tinturier-Hamelin, 1963). The specimens collected represented the typical *albafusca* and *flavafusca* types (Tinturier-Hamelin, 1963, Figs. 15 and 16). According to Naylor (1972) *I. baltica* is generally on offshore form although not infrequently found among attached algae on the shore in Britain. Recorded locally by Colman and Segrove (1955 b).

Idotea pelagica Leach

Occurred infrequently in holdfasts. Naylor (1955 b) found it "typically on shores exposed to wave action". Colour was as described by Naylor (1955 b). Recorded by Scott (1888, as *I. marina* L.) in the Firth of Forth and by Thompson *et al.* (1966) from Inner Farne.

Idotea chelipes (Pallas)

Thompson *et al.* (1966) recorded a single individual of this species in a *Laminaria* holdfast from the Inner Farne. It is generally regarded as a brackish water species characteristic of the high littoral in sheltered estuaries and pools (Naylor, 1972).

Janira maculosa Leach

Occurred sparingly in East coast holdfasts. Sars (1899) found the species (in Norway) "in depths ranging from 30-100 fathoms, on a rocky bottom, overgrown with Hydroida and Polyzoa". Recorded on most British coasts among sponges, ascidians, coelenterates, polyzoans, *Laminaria* holdfasts (Naylor, 1972). Scott (1888) dredged the species "off Bo'ness", and Norman and Brady (1909) found it "not rare" in the coralline zone off the coasts of Northumberland and Durham.

Janiropsis breviremis (G. O. Sars)

Occurred regularly, often in fair numbers. Easily confused with the previous species, especially when no males are present. Immature or damaged specimens are often difficult to specify. Naylor (1972) has summarised the main diagnostic characters. The smoother lateral outline of paraeon somites 1-4 in *Janiropsis* affords probably the best single characteristic. *Janira* also tends to be more heavily pigmented than *Janiropsis* with an unpigmented band between and/or slightly anterior to the eyes. The co-existence of the two species on this coast presents an interesting ecological problem.

Munna kroyeri Goodsir

Frequently taken in kelp holdfasts. Colouration generally brown and cream. Recorded by Scott (1888) from the Firth of Forth, and Brady (1902) from dredge samples off Northumberland and Durham.

Epicarid sp.

Two specimens, provisionally identified as? *Hemioniscus* sp. have been recorded. The material is lodged with Dr. J. Moyse who is currently working on the group.

ASPECTS OF ISOPOD DISTRIBUTION AND BIOLOGY

The distribution of *Janira maculosa* in the Scottish samples suggested an indifference to the water movement characteristics of the site. Dommasnes (1968) found *Janiropsis breviremis* to be apparently exposure-indifferent. He found that *Idotea pelagica* characteristically occurred in exposed localities (as above), whilst *Munna boeckii* Kröyer occurred in shelter. The related species *M. kroyeri*, although posses-

sing similarly delicate appendages, presumably exists on exposed shores by virtue of the increased shelter offered by kelp holdfasts.

A difference between East and West coast holdfasts resides in the absence of *Gnathia* spp. from the East (cf. Colman, 1940). Similarly, no *Jaera albifrons* Leach were found in the course of the East coast investigations although the species is known locally (Wellcome Marine Laboratory, unpublished fauna list) and was recorded by Scarratt (1961) in West coast holdfasts.

The feeding biology of few isopods is known in detail (Naylor, 1972). Probably most *Idotea* species are omnivorous, browsing on algal debris and scavenging animal remains. Feeding differences however depend on habitat and locality (Naylor, 1955 a). Thus in the Baltic, Ravanko (1969) showed *I. baltica* to prefer fragile filamentous algae as food; in their absence however a wide range of other algae were utilised. Jansson (1967) describes how postmarsupial stages of *I. baltica* feed on diatoms epiphytic on *Cladophora*, whilst juvenile isopods utilise *Cladophora* filaments for food.

Order Amphipoda

Probably the most extensive investigations (systematic, ecological and zoogeographical) of rocky shore Amphipoda has been made by Barnard (1969 a) in California (see also Kitching, Macan and Gilson, 1934; Reid, 1941; N. S. Jones, 1948; Barnard, 1958; Truchot, 1963; Vader, 1969; Chardy, 1970; Watling and Maurer, 1972). Other workers have discussed aspects of amphipod biology in relation to algal faunas (Skutch, 1926; Segerstrale, 1928, 1944; Colman, 1940; Dahl, 1948; N. S. Jones, 1948; Ruffo and Wieser, 1952; Wieser, 1952; Ebling *et al.* 1948; Sloane *et al.*, 1961; Cruz, 1965; Zavodnik, 1965; Hagerman, 1966; Dommasnes, 1968; Haage and Jansson, 1970; Mukai, 1971; Norton, 1971). Of these, only Colman (1940), N. S. Jones (1948) and Truchot (1963) present data on *Laminaria* holdfasts. The unpublished work of Scarratt (1961) represents the major previous body of data on the macro-fauna of British *Laminaria* holdfasts. Similar unpublished work of Ghelardi (1960) relates to the fauna of Californian *Macrocystis* holdfasts, though Barnard (1969 a) also included a consideration of this habitat (p. 15).

East coast amphipod records are given by Norman (1867), Scott (1888), Meek (1901), Norman and Brady (1909), Raitt (1937), Colman and Segrove (1955 a, b), Bossanyi (1957), Thompson *et al.* (1966) and Hamond (1967).

Amphipoda (predominantly Gammaridea) represent the most numerous and diverse group of larger Arthropoda inhabiting kelp holdfasts on the North East coast, over 20 species having been recorded. Scarratt (1961) recorded 45 species from West coast holdfasts, whilst Colman (1940), from more limited holdfast samples, listed 16 amphipod species. The group is above all responsive to decreasing wave exposure (see later) which probably contributes to this pattern.

SPECIFIC CONSTITUTION OF THE AMPHIPOD FAUNA INHABITING
KELP HOLDFASTS IN THE NORTH SEA

Table 1 itemises the specific and numerical composition of the amphipods collected during the main East coast survey. Details of species recorded by the author outside this survey are also included in the following account.

TABLE 1.
Relative abundance of Amphipoda collected during the main survey (July 1969)
of the North East coast.

Total number of specimens = 6,353; total number of samples = 72.

Species	Number	Dominance (percentage)
<i>Tryphosa sarsi</i>	6	0.09
<i>Gitana sarsi</i>	114	1.79
<i>Stenothoe monoculoides</i>	52	0.82
<i>Apherusa bispinosa</i>	23	0.36
<i>Apherusa jurinei</i>	229	3.60
<i>Parapleustes</i> sp.	13	0.20
<i>Atylus swammerdami</i>	64	1.01
<i>A. vedlomensis</i>	1	0.02
<i>Gammarellus homari</i>	12	0.19
<i>Tritaeta gibbosa</i>	114	1.79
<i>Dexamine thea</i>	7	0.11
<i>Lembos websteri</i>	94	1.48
<i>Photis reinhardi</i>	23	0.36
<i>Amphithoe rubricata</i>	475	7.48
<i>Jassa falcata</i>	838	13.19
<i>Ischyroceros anquipes</i>	798	12.56
<i>Parajassa pelagica</i>	317	4.99
Jassidae (imm. indet.)	2,039	32.10
<i>Corophium bonelli</i>	1,102	17.35
<i>Caprella linearis</i>	31	0.49
<i>Phthisica marina</i>	1	0.02

SUB-ORDER GAMMARIDEA

Family Lysianassidae

Tryphosa sarsi (Bonnier)

Occurred infrequently in holdfasts. Hamond (1967) notes the species as "fairly frequent in dredgings". Recorded by Meek (1901) from Cullercoats and Beadnell in 1900 (as *Tryphosella*). Sars (1895) states that "it occurs in comparatively shallow water, from 6-20 fathoms, especially where the bottom is sandy".

Family Amphilochidae

Gitana sarsi Boeck

Consistently present in holdfasts although not usually in large numbers. The characteristic dark brown pigmentation easily distinguishes the species. Hamond (1967) considered it to be predominantly intertidal in Norfolk waters with only scattered occurrences from offshore hard ground. According to Sars (1895), it is "sublittoral, occurring not rarely between algae in shallow water". Reid (1941) recorded *G. sarsi* "in *Laminaria* holdfast" at Oldany Harbour, Sutherland.

Family Stenothoidae

Stenothoe monoculoides (Montagu)

Usually present in holdfasts although not usually in large numbers. Recorded by Colman and Segrove (1955 b) and Hamond (1967) in East coast plankton. The species is usually found associated with littoral or sublittoral algae (Sars, 1895; Hagerman, 1966) and the poverty of such habitats in Norfolk waters may account for the distribution reported by Hamond (1967).

Family Calliopiidae

Apherusa bispinosa (Bate)

Occurred fairly regularly in holdfasts in low numbers. Often deep red in colour although this feature is very variable as noted by Sars (1895). Easily distinguished from *A. jurinei* by smaller size and distinct dorsal spines. Appears to be generally common on lower half of shore along East coast, especially amongst algae (Meek, 1901; Hamond, 1967). Sars (1895) notes the species to be very active "... swimming about with great agility". It has often been recorded in bottom plankton (Watkin, 1941; Colman and Segrove, 1955 b; Hamond, 1967) and offshore benthos (Norman and Brady, 1909).

Apherusa jurinei (Milne-Edwards)

Common in kelp holdfasts although rarely in large numbers. Colour extremely polymorphic, may be completely crimson (as reported by Hamond, 1967), mottled crimson, "tiger-striped" crimson, colourless but with wide mid-dorsal longitudinal stripe of crimson or mottled orange-yellow (as reported by Sars, 1895). Particular colour patterns predominate at different sites, suggesting an ecogenetical polymorphism. Hamond (1967) recorded the crimson form as abundant among *Corallina* in Norfolk. Occurs in deep water offshore (Norman and Brady, 1909).

Family Pleustidae

Parapleustes sp. (Fig. 1)

Infrequent in holdfasts. The specimen illustrated is representative of the material (no females have been taken) and is considered to be a young male on the antennal character noted by Hamond (1965). He described some Norfolk specimens of *Parapleustes* sp. which "... all agree among themselves, but do not fully correspond either to *P. bicuspis* (Kröyer) or to *P. monocuspis* (G. O. Sars), although they are much closer to these two species than to any others hitherto described". The main difference between Hamond's material and the present specimens is the complete absence of dorsal teeth on the pleon segments. In spite of this, the specimens are in general nearer to *bicuspis* than

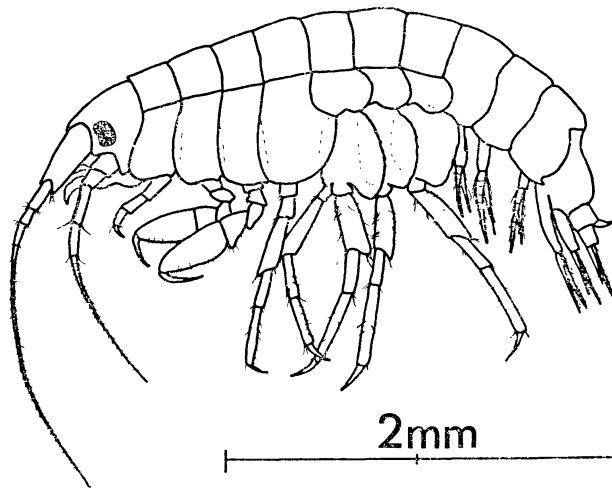


FIG. 1.

Young male *Parapleustes* sp.

monocuspis, as were Hamond's specimens. The present specimens were generally of a creamy yellow colour with large dark brown eyes. The present material reinforces Hamond's conclusion that a re-examination of all European *Parapleustes* would be most desirable.

Family Atylidae

Atylus (= *Nototropis*) *swammerdami* (Milne-Edwards)

Regularly taken from holdfasts, although rarely in large numbers. Being a very fast swimmer, it is often encountered in the plankton (Colman and Segrove, 1955 b; Watkin, 1941; Bossanyi, 1957; Hagerman, 1966; Hamond, 1967). Meek (1901) found it (as *Paratylus*) abundantly amongst weed everywhere along the coast (see also Norman and Brady, 1909). Hamond (1967) suggested that *swammerdami* might intergrade with *A. vedlomensis* in Norfolk waters.

Atylus vedlomensis (Bate and Westwood)

A single large individual referable to this species has been recorded in a holdfast. Similar infrequent records of the species have been made by Meek (1901), Norman and Brady (1909) and Bossanyi (1957) from offshore stations. Hamond (1967) found it most often in the offshore bottom plankton. No specimens intermediate between *vedlomensis* and *swammerdami* were obvious in the present investigation.

Family Gammaridae

Gammarellus homari (Fabricius)

Occasionally taken in holdfasts. Immediately distinguishable by its "strongly carinated and spinous back" (Sars, 1895). The colour of local specimens was generally yellowish variegated with orange/brown. No specimens of the *angulosus* form were encountered. Meek (1901) found the type (as *Amathilla*) to be "fairly common at Cullercoats and elsewhere on the coast" (see also Norman and Brady, 1909). It has been recorded in the bottom plankton (Colman and Segrove, 1955, b; Bossanyi, 1957) and was found by Thompson *et al.* (1966) in low water pools and by Hamond (1967) under rocks at low water.

Family Dexaminidae

Dexamine thea Boeck

Regular feature of the holdfast fauna at certain sites. Colour of local specimens generally yellow blotched with orange/brown. Frequently encountered with sediment particles adhering to its rough body surface. The species was not recorded by Meek (1901) or by Hamond (1967), although it was taken sparingly by Colman and Segrove (1955 b). Norman and Brady (1909) found it among weeds at low water at Sunderland. Its small size and efficient camouflage probably cause it to be overlooked.

Dexamine spinosa (Montagu)

Only a single specimen has been taken from holdfasts. The species is recorded by Scott (1888), Meek (1901), Norman and Brady (1909) and Hamond (1967). Norman and Brady (1909) considered *spinosa* to be rare on the East coast in contrast to other British shores. According to Vader (1969) *D. spinosa* is characteristic rather of sandy bottoms with sparse algal vegetation (in W. Norway).

Tritaeta gibbosa (Bate)

Consistently present in East coast holdfasts. The commensal habit of this species with sponges and tunicates has already been commented upon (see also Norman and Brady, 1909). Local specimens (formalin preserved) were characteristically of a creamy-white

colour with creamy-yellow guts. This colouration together with the inflated appearance of the body and dark eyes provided instant recognition. Sars (1895) however states that *T. gibbosa* is "more or less dark brownish, with a series of pure white patches on each side". It is not clear whether he refers to preserved or live material, but live individuals taken locally have in all cases shown an overall white colouration. Sars states that *Tritaeta* is "by no means very active in its movements". When isolated in a dish of seawater the amphipod immediately turns over on to its back, steadying itself with the third pair of pereopods which are reflexed posteriorly on to the substratum, thus taking up the typical feeding position. The back is arched and pleopod beating conducts food particles to the mouth. The small numbers taken in plankton hauls (Colman and Segrove, 1955 b; Hamond, 1967) probably reflect its sedentary habits.

Family Aoridae

Aora typica Kroyer

Only occasional specimens have been recorded in holdfasts.

Lembos (= *Autonoe*) *websteri* (Bate)

Occurred regularly in holdfasts at certain sites. Males are very characteristic. No males of *L. longipes* (Lilljeborg) have been recorded and so the more numerous female material (many carrying pale green eggs) has arbitrarily been assigned to *websteri*. Work is needed to establish the specific features for diagnosis of *Lembos* females. One difficulty is the fragility of appendages, a perfect specimen being very unusual. Norman and Brady (1909) recorded both species locally. Meek (1901) and Hamond (1967) both recorded *longipes* but not *websteri*. In the latter report, Hamond states that only one complete adult was taken but he does not specify which sex. If the specimen were female, it is possible that this record might also pertain to *websteri*. It is hoped to publish further on this question at a later date.

Family Photidae

Photis reinhardi Kroyer

Occurs regularly in holdfasts although never in large numbers. Stout, rather globular body generally light grey-brown in colour. Hamond (1967) reports it as "exceedingly abundant in certain dredgings, especially on grounds where there is much loose silt as opposed to tenacious clay or peat". Other offshore records are given by Norman and Brady (1909). Sars (1895) records *P. reinhardi* in depths ranging from 20-50 fathoms and describes how its constructs "abodes of mud, which are generally fastened to the stems of Hydroida". The sublittoral occurrence of the species in kelp holdfasts may be related to the provision of the necessary conditions of silting and epiphytic growth.

Family Amphithoidae

Amphithoe rubricata (Montagu)

Common in holdfasts as reported by Meek (1901), also Norman and Brady (1909). Colouration is well described by Sars (1895), and Skutch (1926) has studied the habits of the species. This large and distinctive species was not recorded in Norfolk waters by Hamond (1967), presumably because of the lack of suitable substrata in that predominantly sandy area. The species is generally reckoned to have a cosmopolitan distribution in the northern hemisphere.

Family Ischyroceridae

Jassa falcata (Montagu)

Syn. *J. pulchella* (Leach)

Abundant in East coast holdfasts. I follow the Plymouth Marine Fauna (Marine Biological Association, 1957) in considering *J. dentex*

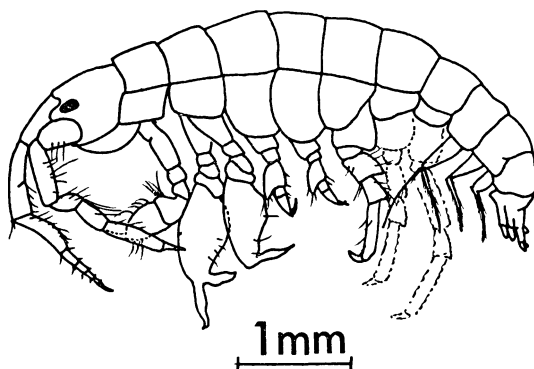


FIG. 2.

Aberrant female *Jassa falcata*

Note antennal and gnathopod deformities.

(Czerniavski) to be merely a variety of the multiform *J. falcata*. The species can be distinguished at all ages from *J. marmorata* Holmes by the absence of a setal fringe on the anterior border of the basal segment of the second gnathopod which characterises *marmorata*. Hamond (1967) records *J. marmorata* in Norfolk but no specimens of this species were encountered locally.

A single female specimen was encountered with various abnormal appendages (Fig. 2). The dactylus of the second right gnathopod was bifurcate, article 6 of the first left gnathopod was inversely inserted and both pairs of antennae were badly contorted basally. Vader (1968) has recorded on abnormal specimen of *Parajassa pelagica* with a bifurcate dactylus on the first gnathopod. He commented upon the paucity of records of such abnormalities in Amphipoda and

noted that *Jassa falcata* which had been examined previously in great numbers by Sexton and Reid (1951) had never been found with limb abnormalities.

Ischyroceros anguipes Kroyer

Abundant in East coast holdfasts. Generally very pale in colour, often suffused with very pale pink but may be nearly colourless, with distinct well-spaced specks all over. The delicate appearance of this species contrasts with the rugged impression of the other Jassidae. The species has been recorded locally by Meek (1901, as *I. minutus*), Norman and Brady (1909) and Hamond (1967).

Parajassa pelagica (Leach)

Locally abundant in holdfasts. Other East coast records are given by Scott (1888, as *Janassa capillata* [Rathke]), Norman (1867, as *Podocerus capillatus* Rathke), Norman and Brady (1909) and Thompson *et al.* (1966), although it is not listed by Meek (1901) or by Hamond (1967). In the latter case this may well again reflect the lack of suitable substrata on Norfolk shores.

Family Corophiidae

Corophium bonelli G.O. Sars

Locally abundant in holdfasts at particular northern sites. No males were discovered in an overall examination of nearly 2,000 individuals, thus conforming with the experience of Sars (1895) and Hamond (1967) in support of the assertion by Crawford (1937, p. 613) that *C. bonelli* is parthenogenetic. Previous East coast records are due to Scott (1888), Meek (1901), Norman and Brady (1909) and Hamond (1967).

SUB-ORDER CAPRELLIDEA

Family Caprellidae

Phthisica marina Slabber

A single specimen has been recorded from East coast holdfasts.

Caprella linearis (L.)

Fairly frequent in holdfasts although never in large numbers. Larger individuals red, smaller ones colourless. The species is abundant amongst offshore hydrozoan growths (Meek, 1901; Hamond, 1967). The relative paucity of hydrozoan colonization of local kelp holdfasts probably contributes to the low density observed.

Caprella septentrionalis Kröyer

A few specimens referable to this species according to the characters given by Harrison (1944) have been taken. The species is highly polymorphic and Stephenson (1929) has commented upon the similarity of certain forms to *C. linearis*. The larger specimens resembled closest *C. s. punctata* Boeck, possessing a bifurcate spine on the dorsum of the head. These specimens were taken from St. Abb's, Berwickshire (Ref. H5/70). Harrison (1944) recorded the species as "found on the East coast of Scotland, St. Andrews and in the Clyde". Hamond (1967), although not listing *septentrionalis*, anticipated its capture from Norfolk carried in the stream of water flowing southwards along the East coast. Stock and Bloklander (1952) have recorded *septentrionalis* washed up on the Dutch coast. However since most authors describing the East coast fauna fail to record the species, and since in the present instance *septentrionalis* has only been taken north of the Scottish border, it seems likely that the species reaches its southern limit in this region. Harrison (1944) points out that the species has not been found on southern coasts.

GENERAL BIOLOGY OF KELP HOLDFAST AMPHIPODA
IN THE NORTH SEA

The family Ischyroceridae dominated the amphipod fauna, followed by the families Corophiidae, Amphithoidea, Calliopiidae, Dexaminidae, Amphilochidae, Aoridae, Atylidae and Stenothoidae (Table 1). Thus the majority of the Amphipoda are tube-dwellers. The adaptive value of this way of life on a wave swept shore is obvious. The holdfast offers protection from physical dislodgement and provides a locus for the accumulation of sediment and detrital material which is utilised by these forms for tube building and food (Skutch, 1926; Enequist, 1949).

The non tube-dwelling Amphipoda are in the main characteristically strong swimmers which may nestle amongst algae, for instance species of the families Lysianassidae, Calliopiidae, Atylidae and Gammaridae. Representatives of these families are often present in the night tidal (Watkin, 1941; Colman and Segrove, 1955 b) or offshore bottom plankton (Bossanyi, 1957). Of the remainder, the Caprellidae are capable of maintaining position external to the main protection offered by the holdfast by virtue of their reduced surface area, strongly developed gnathopods and prehensile peraeopods, enabling them to exist amongst growths of hydroids.

The dexaminid *Tritaeta gibbosa* is interesting in its commensal mode of life associated with sponges and tunicates (Fage, 1928; Hamond, 1967). The amphipod excavates a silt-like cavity in the surface of its host and lies with its dorsal surface applied to the base of the cavity in a *Haploops* position. Enequist (1949) considers it

likely that *Tritaeta* feeds on detritus in a similar way to that described for the American species *Polychertia osborni* commensal with the ascidian *Amaroucium* (Skogsberg and Vansell, 1928 cited by Enequist).

Dahl (1948, p. 152) speculated on the relationship between ecology and body shape of algal dwelling Amphipoda. Thus the violent water movement characteristic of exposed shallow-water localities is favourable only to good swimmers or to species with great powers of attachment. Pedestrian amphipods are thus more or less flattened dorso-ventrally (*Corophium*, *Jassa*) with powerful chelae (*Parajassa*, *Jassa* see Dommasnes, 1968), whilst swimming forms (*Gammarus*, *Calliopius*, etc.) are more typically compressed laterally.

Colman (1940) commented (p. 149) upon the great rarity of the genus *Gammarus* in association with intertidal algae, in contrast with the fauna living below stones at the same level. Cruz (1965) however found *G. locusta* commonly in association with *Fucus* (but see Hagerman, 1966), and Gibb (1957) recorded *Marinogammarus* species commonly in association with *Ascophyllum nodosum* (L.) Le Jol. ead *mackaii*, in sheltered Scottish sea lochs.

Hagerman (1966) included many amphipods as detritus feeders, i.e. living on deposited or depositing material, for instance *Apherusa*, *Erichthonius*, *Ischyroceros*, *Amphithoe*, *Microdeutopus*, *Dexamine* and *Calliopius*. He considered others to be scavengers, e.g. *Gammarus* and certain species, e.g. *Amphithoe rubricata* to be direct algal browsers. Generalisations about feeding relationships in Amphipoda have been criticised by Enequist (1949). However, knowledge of specific food requirements is fragmentary. Cruz (1965) using radioactive phosphorus P³² as a tracer showed that *Gammarus* utilises *Fucus* for food as well as shelter. Greze (1968) discovered that *Dexamine spinosa* (Mont.), *Amphithoe vaillanti* Lucas, *Gammarellus carinatus* (Rathke) and *Gammarus locusta* feed selectively upon particular seaweeds. Similarly Ravanko (1969) showed feeding preference for fragile filamentous algae (*Cladophora*, *Ceramium*, *Ectocarpus*) in *Gammarus oceanicus* Sagerstrale (see also Jansson, 1967). In multiple choice laboratory experiments these algae were devoured first in preference to the tougher species of *Chorda*, *Furcellaria* and *Fucus vesiculosus*. The observations of Gibb (1957) have shown that *Marinogammarus marinus* Leach will feed directly on *Ascophyllum* and she recorded fragments of *Ascophyllum* in the guts of preserved *Gammarus oceanicus*. Barnard (1969 b, pp. 28 and 29) was struck however by "the lack of emphasis on herbivorous habits of Gammaridae in the literature... in view of the properly adapted mandibles and the strong infestation of marine plants by amphipods". He concluded on the basis of the lack of visible grazing marks on the macroalgae and of the stomach contents of a few phycophilous species that Gammarids probably graze the microscopic epiflora. However, he saw the maintenance of the basic mandible throughout so many families and genera of amphipods as suggesting that one key to the success of amphipods is their potential omnivorous habit. Hargrave (1970) has recently demonstrated that surface attached microorganisms are selectively assimilated by the deposit feeding amphipod *Hyalella arctica* (Saussure) and that the majority of material ingested may pass

through the gut without contributing directly to the nourishment of the animal. Some of the inquilinous species, e.g. Stenothoidae were presumed by Barnard (1969 b, p. 30) to be "grazing predators, biting off coelenterate polyps or consuming sponge and tunicate tissues", whilst other inquilinous species, e.g. *Polycheria* (and presumably *Tritaeta*) use their mandibles for burrowing into the tests of tunicates (and sponges) for domiciliary purposes rather than feeding (see above).

Direct observations on food selection and specific requirements of phytal amphipods are thus limited. It would seem that organic detritus and algal debris are utilised, particularly by the sedentary tube-dwellers (see Skutch, 1926; Martin, 1966), but overgeneralizations should be avoided in the absence of specific instances. Thus Gauthier (1941, cited by Enequist, 1949, p. 379) recorded the tube-dwelling species *Siphonocetes sabatieri* as feeding on harpacticoid copepods since its intestines contained many such remains. The observation however begs the question: was the amphipod feeding directly upon live benthic copepods or ingesting bottom sediment containing dead harpacticoids and cast exuviae etc.? Enequist (1949) thought the indications were that *S. sabatieri* is a genuine detritus eater.

DISTRIBUTION OF KELP HOLDFAST AMPHIPODA IN BRITAIN

A comparison of the present East coast data with the unpublished records of Scarratt (1961) in particular, allows some assessment to be made of the geographical distribution of holdfast-dwelling Amphipoda around Britain.

For the most part, the East coast fauna is made up of cosmopolitan genera e.g. *Amphithoe*, *Corophium*, *Jassa*, *Lembos*, *Photis* and *Stenothoe*, together with an arctic boreal component represented by *Atylus*, *Gammarellus*, *Ischyroceros* and *Parapleustes*.

Table 2 lists amphipod species which have been recorded from West coast holdfasts and which are known to occur on the East coast although they were not recorded in East coast holdfasts during the present investigation. In the main, the East coast records refer to offshore stations. The only species previously known, and not presently recorded from local holdfasts, is *Hyale pontica*. Hamond (1967) listed *Microprotopus maculatus* as "very common near low water in sheltered places among algae and hydroids, especially among delicate green algae". Its absence from the holdfast survey is possibly attributable to the exposure of the open coast sites examined. The majority of species in Table 2 can be classified as arctic-boreal (*Acidostoma*, *Orchomene*, *Amphilochus*, *Panoploea*, *Iphimedia*, *Cheirocratus*), whilst *Apherusa ovalipes*, *Maera grossimana*, *Microprotopus maculatus*, *Pseudoprotella phasma* and *Caprella acanthifera* are more typically boreal species (Chevreux and Fage, 1925).

Amphipoda recorded from West coast holdfasts with no apparent published East coast record are listed in Table 3. Reference to

Chevreaux and Fage (1925) confirms that these species may all (excepting *Lilljeborgia brevicornis* and *Sympleustes glaber*) be considered as tropico-warm temperate forms. Their presence on the South and West coasts is a reflection of the warmer water carried northwards along the western sea-board of the British Isles by the North Atlantic drift. Extensive documentation exists on the influence of this factor on the macrobiota of rocky shores (see Lewis, 1964 for comprehensive

TABLE 2.

Amphipoda recorded from kelp holdfasts on the West coast and known from the East coast of Britain although not presently known to exist in East coast holdfasts.

Species	W. coast record	E. coast record
<i>Acidostoma obesum</i> (Bate)	D.J. Scarratt.	Meek (1901), Norman and Brady (1909), Hamond (1967).
<i>Orchomene humilis</i> (Costa)	N.S. Jones (1948).	Hamond (1967), Norman and Brady (1909).
<i>Amphilochus manudens</i> Bate	D.J. Scarratt, P.G. Moore.	Scott (1888), Norman and Brady (1909), Hamond (1967).
<i>Stenothoe marina</i> (Bate)	D.J. Scarratt.	Meek (1901), Norman and Brady (1909), Hamond (1967).
<i>Panoploea minuta</i> G.O. Sars	D.J. Scarratt, P.G. Moore.	Hamond (1967).
<i>Iphimedia obesa</i> Rathke	D.J. Scarratt.	Meek (1901), Norman and Brady (1909), Scott (1888).
<i>Apherusa ovalipes</i> Norman and Scott	D.J. Scarratt.	Hamond (1967).
<i>Cheirocratus sundevalli</i> (Rathke)	D.J. Scarratt.	Meek (1901), Norman and Brady (1909).
<i>Maera grossimana</i> (Montagu)	D.J. Scarratt.	Scott (1888).
<i>Hyale nilssoni</i> (Rathke)	N.S. Jones (1948), D.J. Scarratt.	Scott (1888), Norman and Brady (1909), Hamond (1967).
<i>H. pontica</i> Rathke	D.J. Scarratt.	*Thompson <i>et al.</i> (1966).
<i>Microprotopus maculatus</i> Norman	D.J. Scarratt.	Hamond (1967).
<i>Eurystheus maculatus</i> (Johnston)	D.J. Scarratt, P.G. Moore, Colman (1940).	Meek (1901), Norman and Brady (1909), Hamond (1967).
<i>Pseudoprotella phasma</i> (Montagu)	D.J. Scarratt.	Scott (1901), Norman and Brady (1909), Hamond (1967).
<i>Caprella acanthifera</i> Leach	D.J. Scarratt, Colman (1940).	Scott (1888).

(*) Holdfast record.

review), but equivalent data on the microbiota are lacking. Goodhart and Harrison (1940) suggested that the occurrence in the littoral zone of certain typically offshore Amphipoda was a feature of shores washed by the North Atlantic drift. They quote the following species as examples, *Ampelisca spinimana* Chevreaux, *Harpinia antennaria* Meinert, *Leucothoe spinicarpa**, *Coremapus versiculatus**, *Phthisica marina* and *Caprella acanthifera**. The inclusion within Tables 2 and 3 of the species above marked with an asterisk (*) would be

further evidence in favour of this hypothesis. Of twenty nine amphipod species recorded from *Laminaria* holdfasts from Roscoff, Truchot (1963) described as most typical *Leucothoe spinicarpa*, *Maera inaequipes*, *Elasmopus rapax*, *Lembos websteri*, *Eurystheus maculatus*, *Jassa falcata* and *Corophium acherusicum*. Thus the dominance of the warm-water element increases (as would be expected) to the South of the British Isles.

TABLE 3

Amphipoda recorded from kelp holdfasts on the West coast but not known from the East coast of Britain.

Species	W. coast record
<i>Perrierella audouiniana</i> (Bate)	D.J. Scarratt.
<i>Nannonyx goesi</i> (Boeck)	N.S. Jones (1948).
<i>Leucothoe spinicarpa</i> (Abildgaard)	N.S. Jones (1948), D.J. Scarratt.
<i>L. incisa</i> Robertson	Colman (1940).
<i>Stenothoe spinimana</i> Chevreux	Colman (1940), D.J. Scarratt.
<i>Colomastix pusilla</i> Grube	D.J. Scarratt.
<i>Lilljeborgia brevicornis</i> (Bruzelius)	N.S. Jones (1948).
<i>Apherusa henneguyi</i> Chevreux and Fage	D.J. Scarratt.
<i>Sympleustes glaber</i> (Boeck)	P.G. Moore.
<i>Maera inaequipes</i> (Costa)	D.J. Scarratt.
<i>Elasmopus rapax</i> Costa	Colman (1940), D.J. Scarratt.
<i>Microdeutopus damnoniensis</i> (Bate)	Colman (1940), D.J. Scarratt.
<i>M. chelifera</i> (Bate)	Colman (1940).
<i>Coremapus versiculatus</i> Norman	P.G. Moore.
<i>Microprotopus longimanus</i> Chevreux	D.J. Scarratt.
<i>Amphithoe vaillanti</i> Lucas	D.J. Scarratt.
<i>Sunamphithoe pelagica</i> (Milne-Edwards)	P.G. Moore.
<i>Pleonexes gammaroides</i> Bate	Duhig (1960), P.G. Moore.
<i>Jassa oca</i> (Bate)	N.S. Jones (1948).
<i>Microjassa cumbrensis</i> (Stebbing and Robertson)	Colman (1940).
<i>Podocerus variegatus</i> Leach	Colman (1940), D.J. Scarratt.
<i>Corophium sextoni</i> Crawford	D.J. Scarratt.
<i>C. acutum</i> Chevreux	D.J. Scarratt.
<i>Caprella acutifrons</i> Latreille	D.J. Scarratt.
<i>C. fretensis</i> Stebbing	D.J. Scarratt.

EFFECT OF WATER MOVEMENT

It can be seen (Tables 2 and 3) that West coast holdfasts harbour a much greater variety of Amphipoda than their East coast counterparts. However, an important consideration, besides the temperature factor, is the effect of exposure to wave action. Certain West coast sites support a rich assemblage of Amphipoda (and other groups) because they are sheltered from wave crash (Lewis, 1964, 1968; Lewis and Powell, 1960; Sloane *et al.*, 1961; P.G. Moore, unpublished). Indirect evidence of this relationship has recently been provided by Gibson (1972), who found that the frequency of occurrence of amphi-

Pods in the stomachs of the fish *Blennius pholis* L., captured on sheltered shores, was significantly greater than in those fish caught on exposed shores. No equivalent sheltered habitats exist on the East coast.

Thus the following species have been found, in a brief field survey (May 1969), to characterise West coast (Scottish) holdfasts (*Laminaria digitata*) in shelter: *Lysianassa ceratina*, *Amphilocheus manudens*, *Eurysteus maculatus*, *Coremapus versiculatus*, *Sunamphithoe pelagica*, *Pleonexes gammaroides*, *Erichthonius brasiliensis*, *Phthisica marina* and *Caprella linearis*.

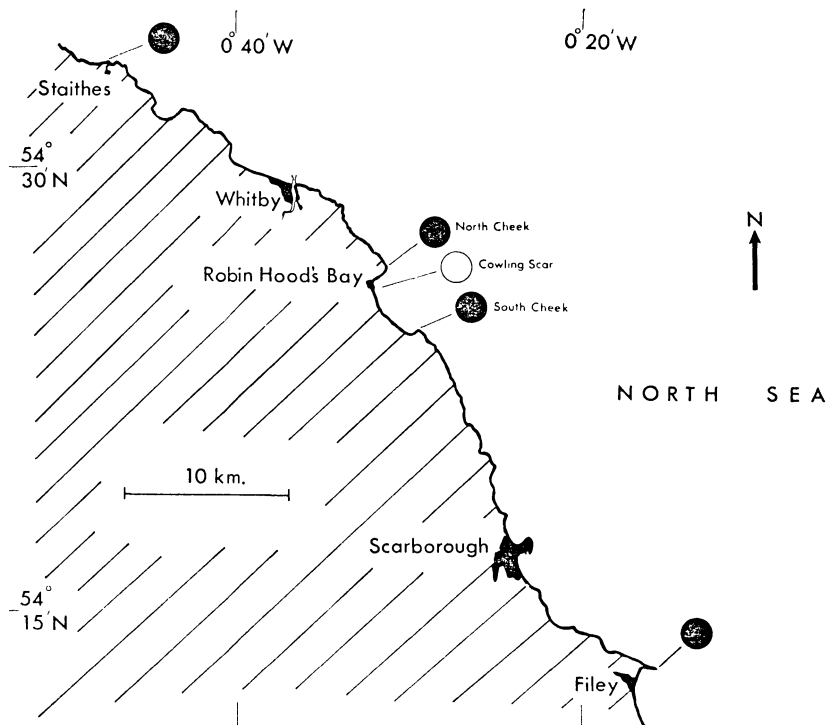


FIG. 3.

Map showing local distributional records for the amphipod *Parajassa pelagica*. Full circles: positive records; open circles: negative records.

Exposed West coast samples were characterised, as on the East coast, by *Jassa falcata*, *Lembos websteri*, *Tritaeta gibbosa* and *Gitana sarsi*. *Corophium bonelli*, *Stenothoe monoculoides* and *Amphithoe rubricata* also apparently tolerate strong water turbulence.

The preference shown by *Jassa falcata* for areas of strong water movement is well documented (Milne, 1940; Ebling *et al.*, 1948; Duhig, 1960; Sloane *et al.*, 1961; Daro, 1970; Norton, 1971; Watling and Maurer, 1972). Dommasnes (1968), working on *Corallina* fauna, found *Parajassa pelagica* to be particularly characteristic of exposed conditions. According to him, *Stenothoe monoculoides* and *Apherusa jurinei* are indifferent to the water movement regime, whilst *Amphi-*

thoe rubricata, *Apherusa bispinosa*, *Dexamine thea* and *Corophium bonelli* prefer more sheltered conditions. Sloane *et al.* (1961) found that *Dexamine thea*, *Erichthonius brasiliensis* and *Corophium bonelli* preferred quiet water stations in Lough Ine.

Thus the occurrence in exposed coast holdfasts (both East and West) of *Dexamine thea*, *Amphithoe rubricata*, *Apherusa bispinosa* and *Corophium bonelli* is probably a reflection of the more sheltered microclimate within the holdfast interstices.

Parajassa pelagica is particularly characteristic of exposed sites (Dommasnes, 1971; Vader, 1969). It has been recorded locally (Yorkshire) from Staithes, Filey Brigg and Robin Hood's Bay (North and South Cheeks) but never from the most consistently sampled site in Robin Hood's Bay, beyond Cowling Scar (Fig. 3). The latter is certainly less exposed than the former sites, although not greatly so, and thus suggests that *Parajassa pelagica* may have a much narrower exposure requirement than was previously suspected.

Consequent upon variations in water movement will follow variations in the "sediment factor" (Moore, 1972) with its associated effects on the holdfast fauna (Moore, 1971, 1972 and in press). Observations on this factor in relation to amphipods are provided by Dahl (1948), Enequist (1949), Barnard (1958), Truchot (1963) and Bellan-Santini (1972). Obviously tube-dwelling species are reliant upon a ready source of building material. The ramifying interstices of kelp holdfasts accumulate particulate material which could be easily utilised. The mobility of sediment within and around holdfasts on exposed coasts is thought to be of great significance in determining overall faunal composition (Moore, 1971, 1972 and in press). Thus respiratory and feeding requirements of tubicolous forms are liable to modification caused by changes in suspended matter. Field and laboratory evidence however is conflicting (Dahl, 1948; Enequist, 1959; Barnard, 1958; P. G. Moore, unpublished).

KELP HOLDFAST AMPHIPODA IN BRITAIN AND CALIFORNIA

The works of Barnard (1969 a) and Ghelardi (1960) both include data on the amphipod fauna Californian kelp holdfasts. Barnard collected both intertidal (*Macrocystis*, *Egregia* and *Laminaria*) and subtidal (*Macrocystis*) holdfasts, whilst Ghelardi confined his attention to these latter.

Intertidal holdfasts in California were dominated by *Hyale rubra frequens* (Stout) followed by *Aorides columbiae* Walker with twenty-one other species as abundant secondary dominants (Barnard, 1969 a, p. 16). The most important of these were *Parapleustes pugettensis* (Dana), *Eurystheus thompsoni* (Walker), *Erichthonius brasiliensis* (Dana), *Elasmopus rapax mutatus* Barnard, *Photis conchicola* Alderman, *Elasmopus holgurus* Barnard, *Oligochinus lighti* Barnard and *Najna? consiliorum* Darzhavin. In two subtidal *Macrocystis* holdfasts, Barnard found the dominant Amphipoda in one to be *Photis bifurcata*

Barnard, *P. brevipes* Shoemaker, *Microdeutopus schmitti* Shoemaker, *Maera simile* Stout, *Eurystheus thompsoni* and *Heterophlias seclusus escabrosa* Barnard and, in the second, *Ceradocus spinicaudus* (Holmes), *Cymadusa uncinata* (Stout), *Maera simile*, *Microdeutopus schmitti* and *Eurystheus mamolus* (Barnard). There is thus a considerable contrast between littoral and sublittoral holdfast Amphipoda in California, few of the latter species occurring in the intertidal zone (Barnard, 1969 a).

In Britain, littoral holdfast bearing kelps (*Laminaria digitata* Lamour, *L. saccharina* Lamour) are restricted to the lower shore. No contrast, equivalent to the American situation, between the amphipodan fauna of littoral and sublittoral holdfasts (*L. hyperborea*) is thus apparent. Colman (1940), working near Plymouth on intertidal algae, reported the following species from littoral *L. digitata* holdfasts, *Leucothoe incisa*, *Stenothoe monoculoides*, *Apherusa jurinei*, *Elasmopus rapax*, *Microdeutopus damnoniensis*, *M. chelifera*, *Lembos websteri*, *Eurystheus maculatus*, *Amphithoe rubricata*, *Jassa falcata*, *Microjassa cumbrensis*, *Podocerus variegatus*, *Caprella acanthifera* and *C. linearis*. Differences between this littoral fauna (see also N. S. Jones, 1948, p. 425) and that reported above from sublittoral North Sea holdfasts are attributable to the warm water element in the Plymouth fauna rather than to elevation on the shore.

The British counterpart of the Californian species *Hyale rubra frequens*, described by Barnard (1969 a, p. 19) as being "monotonous" in its intertidal ubiquity, is its cogener *H. nilssoni*. This species similarly has an unusually extensive range for an intertidal animal (Colman, 1940 reported a vertical range of 3.5 m from below mean high-water springs to mean low-water springs), but is rarely recorded in low shore *Laminaria* holdfasts (Jones, 1948 as *H. prevosti*). Instead *H. nilssoni* is characteristically abundant in algae of the littoral fringe and eulittoral zone (Lewis, 1964) e.g. *Pelvetia*, *Fucus spiralis* and *Ascophyllum* (Colman, 1940; Jones, 1948; Wieser, 1952; Lewis, 1964; P. G. Moore, unpublished).

Only a few species are common to Californian and British holdfasts viz., *Amphithoe rubricata*, *Erichthonius brasiliensis*, *Jassa falcata*, *Lilljeborgia brevicornis* and *Tritaeta gibbosa* (c.f. present report and data of Ghelardi). *Amphithoe rubricata*, *Erichthonius brasiliensis* and *Jassa falcata* have an acknowledged cosmopolitan distribution (Chevreux and Fage, 1925; Barnard, 1969 b). *Lilljeborgia brevicornis* has been characterised as bipolar and amphiboreal (Barnard, 1969 b). Ghelardi's record of *Tritaeta gibbosa* from California extends into the Pacific the previously known Eastern Atlantic range of the species (Chevreux and Fage, 1925; Barnard, 1969 a, b).

According to Ghelardi (1960), the principal sublittoral Amphipoda (both in terms of frequency and abundance) in live *Macrocystis* haptera from La Jolla are *Amphithoe rubricata*, *Iphinotus* sp., *Photis californica* Stout and *Podoceros kermadeci*. He found the central core of debris within *Macrocystis* holdfasts to be characterised by *Eurystheus thompsoni*, *Photis californica*, *Acidostoma* sp., *Corophium* sp. and *Maera hirondeilli*.

The discrepancy between the amphipod species lists from Barnard's and Ghelardi's *Macrocystis* holdfasts may be explicable in terms

of their restricted censusing. However, differences in wave exposure, holdfast size and degree of holdfast decomposition will also be important. The characteristic decay of the central core of older *Macrocystis* holdfasts represents a factor without parallel in the British *Laminaria* habitat. Mortality of *Laminaria* plants is typically due to storm damage, more often removing the plant entire, although occasionally only breaking off the stipe (Kitching, 1937). Grazing by *Echinus esculentus* L. and the excavation of cavities under the holdfast by the limpet *Patina pellucida* (L.) also contributes to the instability of the kelp forest, although to what extent seems variable (Kitching, 1937; Kain and Svendsen, 1969).

Isolated North Sea holdfasts left *in situ* after removal of the stipe rot away fairly quickly, so the specialised exploitation of intra-holdfast debris by *Acidostoma* sp. in Californian *Macrocystis* beds (Ghelardi, 1960) is without a British equivalent. So too the occurrence within *Macrocystis* rhizomes of plant burrowers (*Lignophliantis pyrifer* and possibly *Heterophlias seclusus escabrosa*) commented upon by Barnard (1969 a, pp. 15 and 16) represents a further distinction between the niche spectra of Californian and British holdfast-dwelling Amphipoda. It seems unlikely that *Laminaria* tissue *in situ* is of any importance as food for British Amphipoda (see Martin, 1966). Indeed, apart from *Echinus* and *Patina*, direct kelp grazing appears to be a generally unexploited niche throughout the various taxa inhabiting *Laminaria* holdfasts.

Excepting these differences, the sublittoral amphipod fauna of Californian and British kelp holdfasts is similarly dominated by tube-dwelling genera (variously *Amphithoe*, *Aorides*, *Corophium*, *Erichthonius*, *Eurytheus*, *Ischyroceros*, *Jassa*, *Lembos*, *Microdeutopus* and *Photis*) and nestling types (*Elasmopus*, *Hyale*, *Maera*, *Parapleustes*) whose presence within holdfasts is largely a reflection of the protection and shelter that holdfasts offer from otherwise inclement conditions.

SUB-CLASS EUCARIDA

Order Decapoda

Norman (1867), Scott (1888), Meek (1902), Norman and Brady (1909) and Thompson *et al.* (1966) include East coast decapod records. In general sublittoral Decapoda are excluded by their size from all but the largest or most "open" holdfasts. Colman (1940) described how the crab *Pilumnus hirtellus* (L.) would shelter in the pits excavated in holdfasts by the limpet *Patina pellucida* (L.) at Wembury.

Decapoda Natantia

Eualus pusiolus Kröyer

Recorded singly on three occasions. The specimens all showed the normal non-bifurcate rostrum (Greve, 1963). Greve has noted

that the species prefers to reside among *Laminaria* in Norway, and Allen (1966) reported its occurrence near inshore rock outcrops off Northumberland.

Decapoda Reptantia

Galathea squamifera Leach

Single individual recorded. Meek (1902) records the species as "common" and Scott (1888) as "common in the littoral and laminarian zones".

Porcellana longicornis (L.)

Frequent in holdfasts, generally in low numbers (see Norman and Brady, 1909). Occurs in lower shore and offshore (Norman, 1867; Scott, 1888; Meek, 1902; Thompson *et al.*, 1966).

Pirimela denticulata Montagu

Occurred singly in holdfasts on a number of occasions. Recorded from Whitburn (Norman and Brady, 1909). Evans (1921) reported the species in an intertidal rock pool near North Berwick (probably washed there by high seas). Edwards (1966) recorded two specimens in the Clyde and has summarized Scottish records. The species is commoner in France and other more southerly parts of its range (Edwards, 1966) and becomes increasingly rare northwards (Fauchald, 1961; Edwards, 1966).

Cancer pagurus L.

Small individuals recorded occasionally in holdfasts.

Hyas coarctatus Leach

Only two specimens taken from holdfasts. Scott (1888) noted the species as "fairly common, from the laminarian zone outwards". Norman and Brady (1909) found it frequent in deep water off Northumberland and Durham.

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Summary

The composition of the malacostracan crustacean fauna inhabiting kelp holdfasts in North-East Britain is described. Observations on the natural history of each species are presented. The Amphipoda form the dominant group followed by the Isopoda and Tanaidacea. Vagile Mysidacea and Eucarida are possibly under-represented due to sampling technique. Amphipod dominance was largely due to the family Ischyroceridae, followed by the families Corophiidae, Amphilo-chidae, Calliopiidae, Dexaminidae, Aoridae, Atylidae and Stenothoidae. The majority of the Amphipoda are tubicolous; the non tube-dwelling Amphipoda being characteristically strong swimmers which nestle amongst algae. Their feeding habits and distribution around Britain are described as existing data allow. The importance of geographical temperature factors and exposure to wave action is discussed. Comparison is made between the fauna of British and Californian kelp holdfasts and related to the distinctive differences between the two habitats.

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