Food and Habits of *Meganyctiphanes norvegica.*

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With 2 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE herring fisheries in the Clyde Sea Area, and in Loch Fyne in particular, have always been considered among the most important of the herring fisheries in Scotland. The factors which cause the herring to occur in this district in large numbers at certain times of the year have so far not been determined. Sir John Murray, who had considerable experience of the lochs in the West of Scotland, during summer and winter, over a period of many years, was of the opinion that not only are some lochs richer in different animal species, but also that others have species peculiar to themselves. For example, the Copepod *Euchæta norvegica* is more abundant in Upper Loch Fyne than any other loch in the West of Scotland. It has never been found in Loch Aber, Loch Sunart, or Loch Carron. *Meganyctiphanes norvegica* and *Thysanoessa raschii* have never been found in Loch Etive or Loch Aber, whereas they are plentiful in Upper Loch Fyne. The hauls I have made with the tow-net in Upper Loch Fyne confirm the presence in abundance in that locality of the above-mentioned Euphausids and the Copepods *Euchæta norvegica* and *Calanus finmarchicus*. *M. norvegica* and *T. raschii* attain their maximum in winter, November to February, and are seldom found during summer. *C. finmarchicus* reaches its maximum numbers in summer, although during winter it is present in large numbers in the deep waters (50–60 fms.). *E. norvegica* is very abundant for the greater part of the year, although scarce in the tow-nets during summer.

That *M. norvegica* forms an important item in the diet of some of our edible fish, more especially the herring, has been proved by many investigators. Hardy (1924) states that Nyctiphanes and Meganyctiphanes form 5·65 per cent of the total food on the east coast. Brook and Calderwood (1885) and T. Scott (1887) have shown that towards the end of the feeding period on both the east and west coasts of Scotland the herring feed extensively on Euphausids. Moore (1896) describes *M. norvegica* as the most important food of the herring on the Atlantic coast of America. Lissner (1919–23) finds that the chief food of the Skager-Rack herring consists of *M. norvegica* particularly during their "restitution" period. Continuing, he says: "It is doubtful that hydrographic conditions induce the herring to go into the Skager-Rack. Rather is one inclined to believe that this migration is at least in part a true food-seeking migration which leads the lean, exhausted and 'spent' herring to a well-spread table." Ehrenbaum (1919–23) remarks that it is noteworthy that the Skager-Rack herring feed chiefly on comparatively large animals, namely, for the most part, *M. norvegica*, 30–35 mm. long, whereas the herring of the west North Sea feed on Copepods and small Euphausids, 10–12 mm. long. Further, he says that we cannot maintain with certainty that *M. norvegica* is present only in the deepest water layers, although it is found there during both day and night. It may well be that the herring is found in the deeper water layers, because of the fact that its food occurs there. Lebour (1924) and Holt and Tattersall (1902–3) have also found Euphausids important in the diet of the herring.

The hake is apparently scarce in Upper Loch Fyne, but three specimens caught in January, 1925, and measuring 10 inches in length were all found to be feeding exclusively on *M. norvegica*. Hickling (1925) found that the small hake seem to select *M. norvegica* in preference to other crustacea or small fish, and suggests that when *M. norvegica* leaves the bottom the small hake follow it in its vertical migration towards the surface.

On many occasions I have found the stomachs of *Gadus virens* well filled with specimens of *M. norvegica* and *T. raschii*.

Owing to the importance of *M. norvegica* in the economy of the sea, especially as food of edible fish (more particularly the herring), the following investigations with regard to food and feeding habits of *M. norvegica* were carried out from October, 1924, to May, 1926. Loch Fyne, for reasons indicated below, is very well suited for such investigation. Unfortunately, the station which we found most valuable, viz. Poll, is situated a day's journey from the Marine Station, Millport, and because of this and for other reasons the visits were not as frequent or prolonged as one would have desired. Visits were made at least once a month and sometimes more often.

Description of Meganyctiphanes norvegica M. Sars.

Synonyms.—*Thysanopoda norvegica* M. Sars; *Thysanopoda nana* M. Sars; *Nyctiphanes norvegica* G. O. Sars; *Euphausia intermedio* Reggio; *Euphausia lanei* Holt and Tattersall; *Meganyctiphanes norvegica* Holt and Tattersall, 1905.

M. norvegica conforms in structure to that of a typical Euphausid (Sars). It is one of the largest known Euphausids in the waters of the Northern Hemisphere, attaining a length (from tip of rostrum to tip of telson) of 44 mm. The eyes are intensely black and very large, 2 mm. in diameter in the fully grown adult. The west-coast fishermen in Scotland call the animal " Súil dhu," i.e. black eye. The body is transparent, but for the region of the stomach which is translucent in the young adult and opaque later, the reason for this opacity being the elaboration of the hepatic cæca during development and the increased pigmentation of the outer surface of the stomach and alimentary tract. The hepatopancreas is well developed in *M. norvegica*, and forms in the larger specimens a conspicuous yellowish mass underneath the carapace.

The pigmentation in *M. norvegica* is characteristic. The mouth parts are vermilion to purple in colour. The thoracic appendages are closely set with scarlet chromatophores. So also is the outer surface of the stomach. Red chromatophores are scattered over the surface of the cephalothorax, abdomen and pleopods. A diffuse orange-coloured band may run down one or both sides of the basal segments of the pleopods. A similarly coloured band may sometimes be seen at the lower lateral edge of the abdominal segments and in the telson. The exuviæ are pigmented, the pigmented parts being the mouth parts, which are remarkably densely coloured, and the regions where the diffuse pale orange colour occurred before ecdysis. The younger adults are not so richly pigmented as those fully grown.

The characteristic luminescent organs of Euphausids are prominent in *M. norvegica*. There are ten in all, as follows: two on the upper surface of the ocular peduncles; two pairs on the coxopodites of the second and seventh thoracic appendages respectively ; an unpaired series on the sternal surface of the abdomen between the bases of each of the first four pairs of pleopods.

General Distribution.

This species has a very wide distribution, being found off the coast of N. Siberia, Spitzbergen, round Iceland, Jan Mayen, and at a few places in the east of Greenland as far north as Lat. 24° N., coast of Norway, Faroe Channel, Orkney, E. and W. Scotland, North of North Sea, Skager-Rack, Cattegat, W. Ireland. It also occurs along the Atlantic coasts of France, off the coast of Portugal, and is known throughout the Mediterranean. Specimens have been found in the Ægean and the Marmora. We meet with it again on the Atlantic coast of N. America, occurring at several places from the Gulf of St. Lawrence southwards, including the Gulf of Maine, being found as far south as Lat. 40° N. The species has not been found on the west coast of Greenland. Though going far to sea and penetrating to depths of hundreds of fathoms, it is not truly oceanic. It seems unable to exist below a depth of 500 fathoms, while it thrives at depths less than 100 fathoms (Holt and Tattersall, 1902–3). Holt and Beaumont (1900) found a number in the stomach of the ground-feeding dog-fish, *Pristiurus melanostoma*, at 154 fathoms. On May 10, 1925, Fleming (1925) examined the stomachs of over a hundred specimens of *Etmopterus spinax*, all of which had been caught in deep water S.W. of Ireland, and found the stomachs of several of the adult fish to contain remains of small squids and *M. norvegica*. Usually they were consumed along with mud. With regard to stomach contents of *E. spinax*, Fleming says: "Stomachs were crammed with mud which was of a greenish colour, and consisted of quartz sand grains and perfect skeletons of various Foraminifera. There were no remains such as setæ of worms, etc., to suggest that the mud had been obtained from the alimentary canals and the quantity of mud suggests that it had actually been eaten by the fish." This is interesting, as it is possible that *M. norvegica* was actually on the bottom when caught by the fish. Herdman (1898) obtained specimens at the surface by means of the pumps of an Atlantic liner, and it is noteworthy that the species was only met with off the coasts of the European and American continents, and not in the central part of the Atlantic. The only occurrence known from the central part of the North Atlantic is that in the Irminger Sea (Stephensen, 1912). Dr. A. G. Huntsman tells me in a letter that *M. norvegica* is a characteristic form of the slope waters, and is carried thence into coastal waters such as the Bay of Fundy. Usually it is found only in the depths, but in the Western Archipelago of the Bay of Fundy the strong tidal currents bring it to the surface, where frequently it may be dipped in large quantities.

Localised Distribution.

Patience (1909–10) records large numbers measuring 12–20 mm. taken at the surface with tow-net at midday between Fairlie and Keppel, Cumbrae. The strong tidal current which runs up this channel may account for this unusual occurrence. Throughout the Clyde Sea Area I have found adult *M. norvegica* at the surface, during the day, only at Keppel, and then very rarely and only one individual per haul. Bigelow (1912) found specimens at the surface at several stations in the Gulf of Maine. He says that the distribution of *M. norvegica* over the Gulf of Maine was practically uniform, except that it was found more regularly in the off-shore hauls, being taken in one off-shore station in considerable numbers at 80 fathoms. He also states that the oceanic data of captures indicates that out of six stations all but one show capture at the surface. Bigelow's observations were based only on the occurrence of large adults of unmistakable identity. On the other hand, Holt and Tattersall (1902–3) have only a single record from the surface tow-net worked during daylight. Dr. H. Broch further tells me that it is a well-known phenomenon (among fishermen in the Oslofjord near Dröbak) that *M. norvegica* suddenly appear at the surface and drift ashore in large numbers usually in autumn or early winter. He also says that on one occasion he put them out into the water again, and in a short time they turned and swam ashore. He mentions that the day was cold. He used some of the specimens as bait, and caught a large number of *Gadus virens*. After a few days the fish disappeared, and the beach was lined with a broad brim of dead and decaying Euphausids. On another occasion in the month of October, while fishing for *G. virens*, he observed large shoals of these fish feeding on thousands of *M. norvegica* which suddenly appeared at the surface. We would suggest that the above observations indicate that the appearance of adult *M. norvegica* at the surface is caused partly by the presence of predatory fish and tidal currents.

Measurements of specimens caught are rarely detailed in records of occurrence, but some workers, e.g. Fowler (1903), state that large specimens are only found in deep water, an observation confirmed by Murray, and Vallentin and Cunningham. According to Kramp (1913), in the colder water of the Skager-Rack, *M. norvegica* continually lives from generation to generation having undoubtedly immigrated from the Norwegian Sea, and it may be found in the former water at every season of the year. In the Clyde Sea Area adult *M. norvegica* are most commonly found in the deeper waters (60–80 fms.). They are usually found about 10 fathoms from the bottom. Specimens measuring 35 mm. are very rarely fished less than 60 fathoms, unless during the night. The species is to be found in the deep enclosed waters of Upper Loch Fyne (60–75 fms.) practically throughout the year, although during the summer months they are only present in very small numbers.

With regard to depth as a factor controlling the distribution of *M. norvegica*, the following observation by Bigelow (1912) is interesting: "A phenomenon of some interest is the apparent absence of *M. norvegica* from Massachusetts Bay at all seasons. There seems to be nothing in temperature and salinity to bar it from the waters of the Bay, for in summer, at some depth, the Bay closely reproduces the combination of temperature and salinity in which we found it swarming in Eastport Bay in August (salinity about $37{\cdot}4°/_{\infty}$ to $32{\cdot}6°/_{\infty}$, temp. 52° F.), and in winter the Bay is very little colder than the northern part of the North Sea, where *M. norvegica* is common at that season. Its absence or rarity in the Bay is perhaps analogous to its absence in the southern part of the North Sea, where, as Kramp points out, both salinity and temperature would allow its existence. His explanation is that it is prevented from spreading southwards in the North Sea by the shallow water, *M. norvegica* being, according to his view, chiefly an inhabitant of the deeper water layers. But it can hardly be shallow water which bars it from Massachusetts Bay, because many of our records of the species were from hauls no deeper than the deeper parts of the Bay and because it was found in swarms on the surface at Eastport, in water of almost precisely the same temperature and salinity as the surface water off Cape Ann in November. Food supply, not hydrographic conditions, may be the factor which determines the local occurrence of *M. norvegica* in the Gulf." This last remark is interesting in relation to the present enquiry.

In the Clyde Sea Area specimens were caught in largest numbers in Upper Loch Fyne off Poll, at a depth of from 60–70 fathoms, and at "Cumbrae Deep," midway between the Little Cumbrae Light and Garroch Head Light, at a depth of 50–60 fathoms. In Upper Loch Fyne the numbers caught in each haul were fairly constant, averaging 20 per haul, throughout the months September to May, when *M. norvegica* is most abundant in the Clyde Sea Area. At Cumbrae Deep there was an indication of shoaling. Sometimes the number of specimens in one haul reached two or three hundred. Much more frequently the numbers were not more than 6 per haul, and sometimes no specimens were fished. Other stations visited where specimens were caught were Lower Loch Fyne, Kilbrennan Sound, Cock of Arran, Loch Striven, Loch Long, and Loch Goil. Shoaling was indicated at the Cock of Arran. Very few specimens were found at any time in Loch Long, Loch Goil, or Loch Striven, but of these three lochs most specimens were found at the last mentioned. *M. norvegica* disappeared entirely from these lochs towards the end of November. Young adults were caught in small numbers from October to May. They were found in greater numbers in the winter months of 1924–25 than in the corresponding period, 1925–26. This suggests that spawning may take place at different times of the year, the spawning period varying from year to year. In 1925 eggs did not appear in the tow-nets till May, whereas in 1926 they were found in the first week in March. On both occasions the eggs appeared in fairly large numbers. In every case, except during the occurrence of large shoals already remarked upon, the specimens were caught only within 10 fathoms from the bottom between three hours after sunrise and two hours before sunset. Adults of all sizes tend to disappear from the Clyde Sea Area from May to September. Several hauls were made in May and June in Upper Loch Fyne, where the species is usually most abundant, but no specimens were found during the day, and only a few (not more than 6 in the 1-metre stramin net) during the night. On one occasion, May, 1926, about midday, the surface layers of mud were brought up from the bottom in the 1-metre stramin net, in which were found two specimens of Meganyctiphanes measuring 21 mm. and 27 mm. respectively and one specimen of *T. raschii* measuring 21 mm. Although hauls were made ranging from the bottom to the surface at 10 a.m., 1.30 p.m., and 4.30 p.m. on the same day, no specimens were found. The species, however, was present in tow-nets fishing at midnight at 30 fathoms. It was noted that fair numbers of Meganyctiphanes eggs were present in the tow-nets fishing at 20 fathoms during the day. No eggs were found in the tow-nets fishing at 10 fathoms and the surface.

Adults measuring 29–39 mm. were found in much greater numbers in Upper Loch Fyne than in any other part of the Clyde Sea Area visited, whereas those found in greatest numbers throughout the area measured 21–29 mm. (Fig. 1 and Table I).

Since Loch Fyne is the most important Loch in the Clyde Sea Area, with regard to the occurrence of *M. norvegica*, a description may not be out of place here. "In the Clyde Sea Area Loch Fyne is the largest of the sea lochs, being 41 miles in length from Ardlamont Point to the head and varying in width from 5 miles at Ardlamont Point to $\frac{1}{4}$ mile at Cuill. Loch Gilp terminates the extension of Loch Fyne, which then turns to the N.E. Loch Gair, a mere Bay, and Loch Shira, similar in all but size to Loch Gilp, branch off to the North. The largest streams run parallel to Loch Fyne on both sides with the exceptions of the Aray, the Shira, and the Fyne. Near its head only mountain burns flow into this fjord. Loch Fyne is roughly parallel to the upper part of the Firth of Clyde, and all the lochs branching off the latter run towards Loch Fyne. The upper 6 miles of Upper Loch Fyne are surrounded by hills both high and steep, and this portion is particularly subject to the influence of fresh water, as, in addition to the innumerable torrents that spring into being after every shower, it receives several rivers" (Mill, 1891). We suggest that the inflow of fresh water will carry with it into the loch much vegetable debris which ultimately will be precipitated to the bottom. Upper Loch Fyne is singularly free from strong currents, and there is apparently comparative stillness in the deep trough running from a point midway between Inveraray and St. Catherines to Strachur. According to Gregory (1913) this fjord owes its origin to preglacial earth movements. Murray

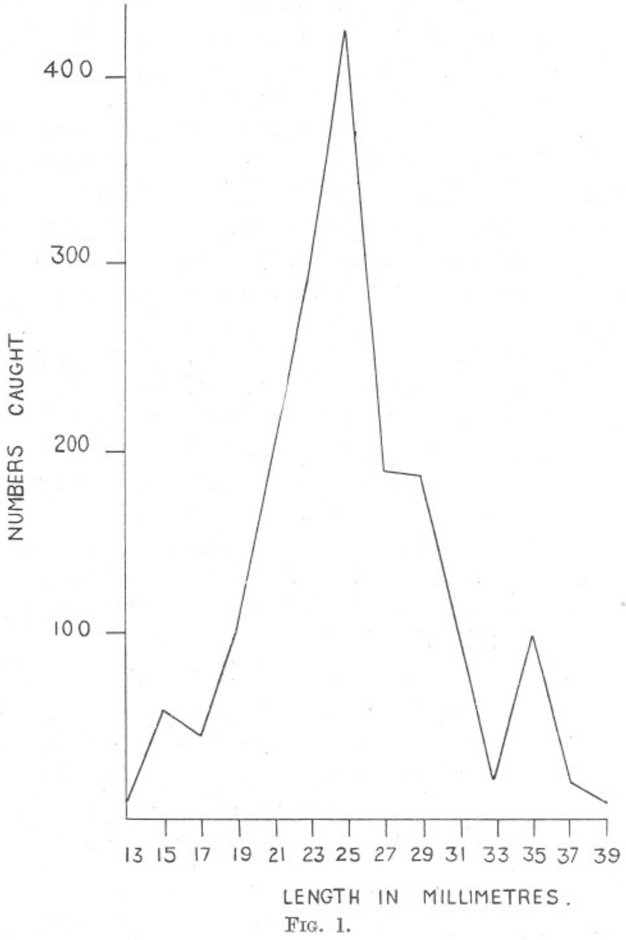

FIG. 1.

(Murray and Hjort, p. 13) has found evidence of an arctic fauna in Upper Loch Fyne. The bottom consists of fine mud, which is believed to be the result of deposition going on since the Glacial period.

A detailed description of the other stations where specimens were caught is unnecessary, as these stations in contradistinction to Upper Loch Fyne do not appear to provide suitable conditions as a permanent habitat for *M. norvegica.*

TABLE I.

TOTAL NUMBERS CAUGHT AT DIFFERENT STATIONS.

October, 1925, to May, 1926.

	Station.	13 mm.		15 mm.		17 mm.		19 mm.		21 mm.		23 mm.		25 mm.		27 mm.		29 mm.		31 mm.		33 mm.		35 mm.		37 mm.		39 mm.	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
October	Loch Fyne	–	–	–	–	–	–	–	–	15	14	14	14	–	–	–	–	2	–	1	1	–	–	–	–	–	–	–	–
	Loch Goil	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
	Loch Striven	–	–	–	3	–	3	1	5	1	5	–	3	1	3	1	–	–	–	–	2	–	–	–	–	1	–	–	–
November	Cumbrae Deep	–	3	–	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	C. of Arran	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
	Loch Striven	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	L. Loch Fyne	–	1	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
	U. Loch Fyne	–	–	–	–	–	–	–	–	3	5	13	7	25	29	2	3	–	4	2	–	–	–	1	3	–	3	–	–
	Kilbrennan S.	–	–	1	–	–	–	–	1	–	–	1	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
December	C. of Arran	–	–	–	1	–	–	–	1	2	1	1	3	3	2	1	2	3	10	9	4	2	–	–	–	–	–	–	–
	U. Loch Fyne	–	–	–	–	–	–	–	5	1	–	2	3	–	–	1	2	1	4	–	–	–	–	–	–	–	–	1	–
January	Cumbrae	–	–	1	1	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	C. of Arran	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	2	–	–	1	–	–	–	–	–	–	–
	Keppel	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	U. Loch Fyne	–	–	–	–	–	–	1	2	4	7	16	30	93	52	10	7	4	1	6	7	1	–	21	8	1	–	4	–
February	Cumbrae	–	5	20	24	23	18	38	39	56	68	54	78	44	36	10	9	15	18	34	14	–	3	–	–	–	–	–	–
	C. of Arran	–	1	–	1	–	–	–	–	1	–	1	–	–	–	–	–	–	–	1	8	–	–	–	–	–	–	–	2
	U. Loch Fyne	–	–	–	–	–	–	3	–	10	4	15	16	59	37	18	14	1	1	1	–	1	–	5	1	2	1	2	–
March	U. Loch Fyne	–	–	–	–	–	–	–	–	1	–	4	–	8	1	9	–	4	–	1	–	7	1	33	6	7	–	1	–
April	U. Loch Fyne	–	–	–	–	–	–	–	–	1	–	1	–	12	14	55	31	55	30	8	5	6	–	13	3	6	2	2	–
	Cumbrae	–	–	–	1	–	–	1	–	1	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
	Loch Long	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
May	U. Loch Fyne	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	1	17	9	–	–	–	–	6	–	–	–	–	–
	Cumbrae	–	–	–	–	–	–	–	–	1	–	–	–	2	–	3	1	4	2	–	–	–	–	–	–	–	–	–	–
	C. of Arran	–	–	–	–	–	–	–	–	–	–	4	1	3	2	–	–	–	–	6	–	2	–	–	–	–	–	–	–

Methods.

From the end of September, 1924, till the end of May, 1926, as far as possible, weekly visits were made to "Cumbrae Deep," and also once a month to Upper Loch Fyne. Tow-nettings were taken fairly regularly at Keppel. The net found most useful for the work had 30 meshes to the inch. A larger net (1-metre stramin net) was tried from April, 1925, onwards. There was no evidence to show that it was relatively more efficient than the smaller net. The rope used was 2-inch tarred hemp. This was found most convenient for handling, as no mechanical power was available for hauling in the nets. The duration of the hauls was from $\frac{1}{2}$ hour to 1 hour. When the weather was calm and there was accordingly very little "drift" the engine was run very slowly. The specimens were as far as possible examined fresh, although the greater majority were examined in 5% formalin into which they were placed shortly after being caught.

Measurements of specimens were taken from tip of rostrum to base of telson.

The carapace was removed and the stomach and gut were then drawn out from the body. Microscopic powers ranging up to oil immersion lens $\frac{1}{12}$ n.a. 1·28 were used.

The Food of Meganyctiphanes norvegica.

Some workers have remarked on the occurrence of much debris in the stomachs of Euphausids. Observations on the stomach contents of Nyctiphanes fished in the Channel have shown that they "nearly always contained some dark substance in their stomachs, but in those from the bottom there was much more debris than fresh organisms, which occurred in numbers in those from the surface." . . . In a sample of 25 examined "from near the bottom, 8 only contained diatoms (*Paralia*) and these singly, whilst the remainder contained sand and debris alone" (Lebour, 1924). With regard to Meganyctiphanes, Thysanoessa, and Nyctiphanes, Hickling (1925) says: "All three species had, in my samples, been feeding on detritus, and not only their leg-baskets, but their mouth-parts and stomachs were often full of it. . . . This detritus consists largely of very flocculent, dust fine, olive-green particles, with fragments of crustacean remains, diatoms, particularly Paralia and Coscinodiscus spp., and inorganic grit. The schizopods had been feeding extensively on it; but it is possible that an alternation of fresh diatom food may be of advantage to Nyctiphanes, at least."

During the first week in February, 1926, there was evidence of a congregation in large numbers on the part of *M. norvegica* and *Thysanoessa raschii* in the "Cumbrae Deep." Several hundreds of both species were fished in one half-hour haul. Ten days later only two or three specimens were fished in a half-hour haul at the same place. It was noticed that during the time these Euphausids were abundant much detritus was present in the nets fished at various depths from 10 fathoms above bottom to 20 fathoms from the surface (Cumbrae Deep is 60 fathoms deep). All the specimens examined of both species were found to be feeding extensively on the detritus which consisted chiefly of decayed vegetable tissues. It was noted later, when very small numbers of Euphausids were fished, that the catches were remarkably free from detritus. The presence of such large quantities of detritus in the tow-nets may possibly be caused by the "dumping" of Clyde river dredgings, which takes place regularly two miles west of the "Cumbrae Deep." The reasons for the sudden appearance and disappearance of this detritus are not apparent, as the "dumpings" take place daily. Water movements have, no doubt, something to do with the distribution of such suspended material. No occurrence of such quantities of detritus in the catches have taken place in any other part of the Clyde Sea at which I have worked.

On another occasion (May, 1925) *M. norvegica* was found in large numbers in the "Cumbrae Deep." This time *C. finmarchicus* was found in great abundance in the tow-nets. On examination the great majority of *M. norvegica* were found to be feeding extensively on this Copepod. About a week later *M. norvegica* was absent from the hauls, *C. finmarchicus* and other Copepods being found in very small numbers.

It is interesting to note that Bigelow (1912) observed a somewhat similar occurrence of large numbers of *M. norvegica* in Eastport Bay, Gulf of Maine, U.S.A., and he suggested that this was probably due to the large amount of detritus and sardine factory refuse present in the water, on which *M. norvegica* was apparently feeding. With regard to the occurrence of large numbers in "Cumbrae Deep" just described, we would not suggest that either the vegetable detritus on the one hand or *C. finmarchicus* on the other attracted *M. norvegica* to this particular locality; but that, finding itself in the presence of an abundance of suitable food brought about by causes probably mechanical (tidal currents, etc.), it fed on vegetable detritus or *C. finmarchicus* voraciously.

It is evident from the above results that organic detritus forms an important item in the diet of *M. norvegica.* It is very difficult to estimate the actual amount of detritus in the gut, and in the meantime no attempt has been made to do so. Of the substantial pieces of vegetable tissues some pieces found in the stomach were as large as 1 sq. mm. Strands of vegetable tissue frequently attained a length of 5 mm. Among the coloured pieces of vegetable detritus of land origin which appeared in the stomach, pieces of leaves of *Blechnum spicant*, *Sphagnum*, and herbaceous bark, were most common; while the most common pieces of decayed vegetable tissue which occurred in the gut were pieces of Gymnosperm and cellular parenchyma. From Tables 2 and 3, giving the food analysis, it is concluded that: (1) organic detritus is eaten most abundantly during the first months of the year; (2) Meganyctiphanes, ranging from 21–29 mm., feed more extensively on vegetable detritus than do larger or smaller specimens (it should be noted that this size was by far the most abundant in the Clyde Sea Area (see Fig. 1)); (3) Copepods are eaten most extensively by the larger specimens, viz. 31–39 mm., and (4) the smaller specimens, 13–19 mm., feed most extensively on diatoms and "wet dust." The stomach contents in all cases show that, when substantial pieces of organic detritus are abundant, sand grains are present in comparatively small quantities, or altogether absent, whereas, when flocculent detritus is abundant and substantial pieces of organic detritus less abundant, sand grains are more numerous. Of the microplankton food organisms diatoms are the most important. *Paralia sulcata* and the naviculoid forms are typical of deep water. *P. sulcata* is most frequently found singly, and is present from May to October in the large majority of specimens indicated in column 1 of Tables II and III. *Thalassiosira nordenskioldi*, *T. gravida*, and *Coscinodiscus* spp., are eaten frequently, and occur in greater abundance than any other diatom in each individual stomach. *Fragillaria*, *Navicula* spp., *Pleurosigma*, and *Nitzschia*, are eaten occasionally. *Skeletonema* does not appear in the gut until February, and then not in such large quantities as *Thalassiosira*, although the latter is not so abundant in the tow-nettings as *Skeletonema*.

Among Dinoflagellates, *Peridinium pellucidum* and *P. depressum* are eaten most abundantly in November and March. *Phalocroma rotundata* is found in the gut in greatest abundance during December and January. *Dinophysis* and *Prorocentrum* appear occasionally from November to April. *Ceratium tripos* was found in small numbers in the stomach of a large specimen in October, 1924, and again in May, 1925; both specimens were caught in Upper Loch Fyne. *Heterocapsa triquetra* is eaten frequently and sometimes in large numbers in January and February.

Silicoflagellates are eaten in very small quantities. *Distephanus speculum* and *Dictyocha fibula* occur from October to March; the former is more common.

Crustacean remains are very frequently found in most guts throughout the "Period" (October to May). *Calanus finmarchicus* is the most abundantly eaten Copepod. *Pseudocalanus elongatus* is of second importance in the smaller adults, whereas *Euchæta norvegica* occurs most frequently in the gut of the largest specimens. *Oithona helgolandica* and *Acartia clausi* are present most frequently in December and January, but appear to be of less importance as food than the other Copepods mentioned.

TABLE II.

Length, 13–19 mm. October, 1924, to May, 1925.

Date.	Number examined. Column 1	Percentage of Specimens in whose Alimentary Tract food as specified is present. Diatoms % Column 2	Dino-flagellates % Column 3	Silico-flagellates % Column 4	Crust. remains % Column 5	Detritus C.V.T. % Column 6	Detritus D.V.T. % Column 7	Detritus F.D. % Column 8	Silic. parts., etc. Column 9	Analysis of food indicating percentage of specimens in whose gut specified food is most abundant. Diats. & F.D. % Column 10	Crust. remains % Column 11	C.V.T. & D.V.T. % Column 12
Sept. 23rd – November	149	100	74	6	100	8	12	100	83	48	36	10
December – January	250	92	54	18	100	43	50	90	74	33	52	15
February – March	94	74	23	–	92	44	68	82	82	46	44	10
April – May	246	100	5	–	67	40	85	100	90	60	5	23
UPPER LOCH FYNE. Length, 31–39 mm.												
January – February	24	25	–	8	100	66	42	50	12	–	50	25
April – May	45	58	26	–	100	100	29	43	17	–	23	50
Length, 21–29 mm.												
February	26	100	58	–	100	100	4	69	38	19	31	46
CUMBRAE DEEP. Size, 31–39 mm.												
May	5	100	100	—	100	–	–	50	–	–	100	–
Length, 21–29 mm.												
. . . .	234	87	—	—	100	18	27	37	10	–	74	–

C.V.T. (Coloured Vegetable Tissues), consist of Blechnum, Sphagnum, herbaceous bark, leaves of Phanerogams and Gramineæ, Filamentous Algæ, e.g. *Cladophora* and *Ectocarpus*, etc.; Thalloid Algæ, e.g. *Ulva*, *Laminaria*, etc. Thalloid Algæ occurred much less commonly than Filamentous Algæ.

D.V.T. (Decayed Vegetable Tissues). These were pieces of cellular parenchyma, Gymnosperms (woody tissue). Strands of algal tissues, possibly *Laminaria*, which occurred most abundantly.

F.D. (Flocculent Detritus). This has been termed "Wet Dust." It consists of a mass of greenish brown unidentifiable particles, amongst which may be found the shells of diatoms and peridinians, spores of algæ, and what would appear to be argillaceous particles. In the qualitative analysis of food (Column 10) we have combined Diatoms and Dinoflagellates with flocculent detritus, as, owing to the fine state of division of the latter, it was impossible to say how much of it could be attributed to disintegrated microplankton.

Some observations have been made on the food of the larvæ of *M. norvegica* with the following results. The nauplius has no mouth. Although an open mouth is present in the Metanauplius it was not found to feed. From the Calyptopis stage to the late Cyrtopia stage filamentous algæ and pieces of coloured vegetable debris seem to be increasingly substituted for diatoms. The remains of small Copepods also appeared in the stomachs of the late larvæ, e.g. Cyrtopia. It is interesting to note that the great majority of larvæ, like the adults, had recognisable food in the gut. There was no marked difference in character of food between those caught during the night and those caught during the day. In the adult specimens the "food basket" (formed by the endopodites of the thoracic appendages) was frequently filled with food. This food was, as a rule, entangled by viscid strands. At the General Meeting of the Linnean Society of London on 17th December, 1925, Dr. H. Graham Cannon gave an account of the Feeding Mechanism of the fresh-water Ostracod, *Pionocypris vidua,* and suggested that, like many other animals which feed on detritus, these Ostracods make use of a viscid secretion for capturing food particles. Holt and Tattersall (1902–3) and Lebour (1924) have remarked on the "food basket" in Meganyctiphanes and Nyctiphanes being well filled with food material. We have so far not been able to determine whether this viscid matter is secreted by *M. norvegica.* Viscid material was also found in the stomach. The "food basket" was found to be filled with food, chiefly organic detritus, most frequently in the first three months of the year. Those specimens caught nearest the bottom were generally found to have their food baskets well filled with food, chiefly organic detritus. It would appear then that when the adult *M. norvegica* seeks the bottom layers, in depths of 60–80 fathoms, it feeds on matter in suspension, the material eaten being microplankton, organic detritus, and to a lesser extent silicious particles. Accordingly, *M. norvegica* may be classed as a "Suspension feeder" (see Hunt, 1925). The larvæ are found near the surface, where they feed chiefly on diatoms, and to a certain extent on coastal filamentous algæ and coloured vegetable detritus.

As already pointed out (Holt and Tattersall, 1902–3), *M. norvegica* appears to be most commonly met with inside the 100-fathom line. This depth, according to Murray, is the average depth in the open ocean at which mud commences to be laid down, and may be taken with regard to our western seaboard to be the limit of wave action where the organic particles from the continents and shallow waters slowly come to rest on the bottom, and supply food to a wealth of Crustacean forms which are captured in such situations. Murray terms this region the "mud line," and believes it to be the great feeding ground of the ocean (Murray and Renard, 1891 ; Murray, 1895). The question now arises, how far is the

TABLE III.

Length, 13–19 mm. October, 1925, to May, 1926.

Date.	Number examined. Column 1	Number of Specimens in whose Alimentary Tract recognisable food is present. Diatoms % Column 2	Dino-flagellates % Column 3	Silico-flagellates % Column 4	Crust. remains % Column 5	Detritus C.V.T. % Column 6	D.V.T. % Column 7	F.D. % Column 8	Silic. parts., incl. Sponge spicules % Column 9	Analysis of food indicating percentage of specimens in whose gut specified food was most abundant. Diats. & Dinoflag. F.D. % Column 10	Crust. remains % Column 11	C.V.T. & D.V.T. % Column 12
October . November .	21	100	76	52	62	25	25	100	90	45	30	20
December . January .	16	75	63	31	100	68	75	100	62	25	50	5
February . March . .	172	92	18	2	70	97	91	100	66	42	35	25
April . . May . .	5	100	100	–	100	–	–	100	100	100	–	–
					Length, 21–29 mm.							
October . November .	162	81	86	14	98	86	46	100	78	5	60	30
December . January .	180	53	68	17	93	90	75	100	61	3	50	42
February . March . .	150	69	33	1	90	93	71	100	56	20	25	40
April . . May . .	160	62	50	–	100	75	44	100	57	66	12	–
					Length, 31–39 mm.							
October . November .	16	–	–	–	100	25	26	25	12	–	25	70
December . January .	65	15	–	–	100	60	80	26	15	–	30	60
February . March . .	130	7	–	–	100	98	92	12	35	–	45	50
April . . May . .	59	50	42	–	100	76	63	16	–	–	73	–

abundant life peculiar to boreal waters due to supplies of nutriment from the shore? To answer this important question satisfactorily would require much more intensive work on the Atlantic Slope waters, as at present we know little or nothing of the food and feeding habits of the deep living macroplankton, which, according to Jespersen (1924), is particularly abundant on the eastern Atlantic Slope. Although an intensive study has been made of the food of *C. finmarchicus* by Marshall (1925), the material being for the most part obtained in comparatively shallow waters off Keppel Pier, Millport, no systematic investigation of the food of Copepoda, including *C. finmarchicus*, which inhabit the deeper water layers, viz. 50–100 fathoms, has so far been carried out. This enquiry we believe is of particular importance with regard to deep sea fishing, and would be fruitful in producing valuable information. With regard to Upper Loch Fyne, where *M. norvegica* is apparently a permanent inhabitant, it may be useful to consider the conditions prevailing in this region which might account for its constant occurrence there. In the first place, if we consider the depth distribution of *M. norvegica* throughout the world, we find that the depth (60–80 fms.) in Upper Loch Fyne is favourable, it being necessary, apparently, for this species to seek these depths periodically. Two comparatively large streams enter the loch about one mile distant from the deep trough in which *M. norvegica* is found. It is a well-known fact that the detrital matter which is carried into the sea by rivers is rapidly deposited on meeting salt water. There will therefore be a fairly constant deposition in the deeps of detrital material carried in by the above-mentioned rivers. This will at least provide some suitable food in the form of land vegetable detritus. Again the entrance of cold fresh water to the lochs will reduce the temperature of the surface salt water of the latter; the warmer lower layers rising to the surface will bring about mixing. Accordingly, detrital matter will be kept longer in suspension, and therefore more will be available as food for *M. norvegica*, which is a "suspension feeder." Marshall and Orr, at present engaged on a biochemical survey of the Clyde Sea Area, believe that mixing of waters in lochs is an essential factor in causing the repeated sudden increase of diatoms which is characteristic of sea lochs. (See also Nathanson's work in Mediterranean, 1909.) Such diatom increases, which may occur several times in the year, especially in spring and autumn, again form a source of food supply for *M. norvegica*. It is also to be remembered that large supplies of *E. norvegica* and *C. finmarchicus*, which form another source of food, are always to be had in the deeps. It is interesting to note that not only in Upper Loch Fyne, but in other widely separated parts of the world, e.g. the shores of Norway, Gulf of Maine in North America, etc., *M. norvegica*, *E. norvegica*, and *C. finmarchicus* are found together abundantly in deep waters (60–80 fms.).

It may be that there are some conditions which are equally favourable to all three organisms.

An examination of the stomachs of *E. norvegica* and *C. finmarchicus* taken from 60 fathoms in Upper Loch Fyne revealed very little recognisable food. In common with Euphausids, masses of brownish green flocculent detritus containing a few shells of diatoms and peridinians were found in the stomachs of both species. It was noted that during the winter months there was no appreciable difference in the percentage feeding during the day and night. This does not agree with Marshall (1924). It is to be noted, however, that the specimens examined by that author were for the most part taken from surface waters.

With regard to the feeding of *E. norvegica* (Sars, 1903) the mature males have so far never been found with any food remains in their digestive tracts, whereas the immature males and mature and immature females were commonly found to feed, and the body cavity to contain much yellow oil. The mature male is very slender, and the mandibles and other mouth parts are degenerate. The immature male resembles the female in structure much more closely than when mature, and was erroneously believed by Lubbock (Claus, 1863) to be a different species. Dana, also, was deceived by this striking resemblance, and described the immature male as a female with five pairs of legs. The mature males occur much less frequently than do the mature females. It is interesting to note that the functional males apparently do not feed, and possibly die off after mating.

Finally, we wish to draw attention to the importance, brought about by the above investigations, of the debris of plants of land and coastal origin as a source of food for Euphausids. It is a surprising conclusion that the herring, which is essentially a planktonic feeding fish, should be dependent, even though indirectly, on the abundance of terrigenous vegetable detritus. How much the deeper living Copepods, which are, no doubt, eaten by the herring, utilise such detritus is left for future investigations. The importance of detritus as food of bottom animals has been shown by Petersen and others, and Murray suggested a correlation between the bottom deposits and the distribution of animal life. It may well be that the nature of the bottom deposits, together with the presence or absence of bottom-currents, are important factors in the distribution of *M. norvegica*.

Vertical Diurnal Migrations of Macroplankton in Upper Loch Fyne.

During the early part of the year, when the macroplankton is very rich in Upper Loch Fyne, an attempt was made to determine if there was any evidence of vertical diurnal migration on the part of *Meganyctiphanes norvegica*, *Thysanoessa raschii*, *Calanus finmarchicus*, and *Euchæta* *norvegica*, the members of the macroplankton which are present in greatest abundance in these waters.

The first series of hauls was made on 19th–20th January, 1926. The hauls were made every four hours in the deep trough that runs parallel to the shore off Poll. Each haul lasted half an hour. Fortunately, a hard up-loch wind blew continuously over the 24 hours, so that the boat drifted about one mile during each haul. At 4 a.m., however, the wind blew somewhat harder, and it was estimated that during this haul the boat travelled about $1\frac{1}{2}$ miles. Lights were placed at convenient vantage points on the shore so that bearings could be taken, the moon being in her first quarter and the sky cloudy. Rain and hail showers were common throughout the 24 hours. Two tarred hemp 2-inch ropes were used. On one a 1-metre stramin net was attached to fish at 65 fathoms, and ordinary coarse tow-nets, 30 meshes to the inch, were attached to fish at 50 fathoms and 40 fathoms respectively. On the other rope a 1-metre stramin net was attached to fish at 30 fathoms, and ordinary coarse tow-nets as above were attached to fish at 20 fathoms, 10 fathoms, and surface respectively. The nets were open-nets, therefore they were liable to catch anything in the water between the depths to which they were sunk and the surface. The length of time that the nets were fishing at the stated depths was, however, much longer than at the intermediate depths passed through while shooting and hauling. Accordingly, although the results are not as accurate as would be obtained with closing nets, they are not without relative value. According to Russell (1925) the variation in depth at which a net may be fishing is very great on account of currents, etc. In the enclosed waters of Upper Loch Fyne it is believed that any currents present are chiefly surface currents, accordingly one can judge approximately by the angle at which the rope enters the water how deep the nets are fishing. We suggest that in Upper Loch Fyne variation in depth at which nets may be fishing as a result of action of bottom currents is apparently at a minimum. In comparing the numbers in the catches at the various depths account has to be taken of the much greater fishing capacity of the nets used at 30 fathoms and 65 fathoms. To make the numbers comparable we have divided the numbers caught by the 1-metre stramin nets by four.

The second series of hauls was made on 24th–25th February. The hauls were made at longer intervals than the first series. The moon was almost full, but the sky was overcast. The wind was blowing from the south-west.

The results shown in Tables IV–VIII indicate that there is a vertical diurnal migration on the part of *M. norvegica*, *T. raschii*, *C. finmarchicus*, and to a lesser extent of *E. norvegica*. All sizes of *Meganyctiphanes* migrate towards the surface. Even the largest specimens (39 mm.) are found

Table IV.

Meganyctiphanes norvegica.

January 19th–20th, 1926.

	8–8.30 p.m.				12–12.30 a.m.				4–4.30 a.m.				8–8.30 a.m.				12–12.30 p.m.				4–4.30 p.m			
Depth in fms.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.
10	25	–	1	**1**																				
	21	1	1		25	1	1																	
20	25	4	2		35	1	–	**3**																
	27	–	2																					
	35	–	3	**13**																				
30*	21	1	–	**1**	23	14	6		21	–	3													
					27	7	6		23	3	7													
					31	4	2		25	17	12													
					35	3	1	**11**	27	1	–	**13**												
									31	–	1													
									35	3	1													
									39	2	1													
	21	1	–		21	1	–		25	2	1	**3**												
	23	1	1		23	1	–																	
40	25	8	2	**18**	25	7	2	**15**																
	27	1	1		31	2	–																	
	31	1	–		35	1	–																	
	35	2	–		39	1	–																	
	21	–	1		21	1	–		21	1	–		25	–	2									
	23	2	–		23	2	2		23	1	–		29	1	–	**3**								
	25	5	3		25	3	3		25	4	–													
50	27	4	–	**22**	27	1	–	**15**	27	1	–	**10**												
	29	1	1		31	1	–		29	–	1													
	31	1	1		35	2	–		31	–	1													
	35	3	–						39	–	1													
	21	–	4		23	1	–		19	–	1		23	–	1		21	–	1		25	3	2	
	23	4	15		25	2	1		21	1	–		25	2	2		23	1	3		27	1	–	**2**
	25	21	11		31	1	–		23	2	–		39	1	–	**2**	25	3	2	**3**				
65*	27	4	4	**18**	35	2	3	**2**	25	18	9	**12**					27	1	–					
	29	2	–						31	2	4													
	31	–	1						35	9	2													
	33	–	1																					
	39	–	4																					

* The hauls at 30 and 65 fms. were made with the metre net: the numbers in the "total" columns are, therefore, the total divided by four.

Table V.

Thysanoessa raschii.

January 19th–20th, 1926.

Depth in fms.	8–8.30 p.m. Length in mm.	♂	♀	Total.	12–12.30 a.m. Length in mm	♂	♀	Total.	4–4.30 a.m. Length in mm.	♂	♀	Total.	8–8.30 a.m. Length in mm.	♂	♀	Total.	12–12.30 p.m. Length in mm.	♂	♀	Total.	4–4.30 p.m. Length in mm.	♂	♀	Total.
	15	2	–		*15*	4	5		*17*	3	1													
10	*17*	3	–	**7**	*17*	7	5	**24**	*21*	2	2	**8**												
	21	1	1		*21*	1	2																	
	15	9	8		*15*	7	11		*15*	4	3													
20	*17*	12	9	**50**	*17*	23	18	**77**	*17*	12	10	**46**												
	21	4	8		*19*	4	4		*21*	10	7													
					21	7	3																	
30*	*17*	–	1	**1**	*15*	15	17		*15*	48	76		*15*	3	4									
					17	29	35	**33**	*17*	162	111	**161**	*17*	9	7	**12**								
					19	11	15		*19*	51	36		*19*	3	1									
					21	21	19		*21*	69	93		*21*	12	9									
	15	2	3		*15*	17	14		*15*	7	4		*17*	2	3	**5**								
40	*17*	4	4	**17**	*17*	15	18	**108**	*17*	6	12	**44**												
	19	1	3		*19*	5	8		*19*	4	7													
					21	12	19		*21*	2	3													
	15	–	2		*15*	3	2		*17*	18	5		*17*	2	2									
50	*17*	1	1	**5**	*17*	11	8	**27**	*19*	3	4	**86**	*21*	2	1	**7**								
	19	–	1		*19*	–	1		*21*	27	29													
					21	1	1																	
	15	–	2		*15*	4	5		*15*	19	27		*17*	9	13									
65*	*17*	1	1	**1**	*17*	1	1	**9**	*17*	44	59	**63**	*21*	7	8	**9**					*17*	2	–	**1**
	19	–	1		*19*	13	6		*19*	23	27													
					21	2	4		*21*	35	20													

* The hauls at 30 and 65 fms. were made with the metre net: the numbers in the "total" columns, therefore, are the total divided by four.

TABLE VI.

VERTICAL DIURNAL MIGRATIONS.

February 24th–25th.

Meganyctiphanes norvegica.

Depth in fms.	6.15–6.45 p.m. Length in mm.	♂	♀	Total.	1.30–2 a.m. Length in mm.	♂	♀	Total.	10–10.30 a.m. Length in mm.	♂	♀	Total.	1–1.30 p.m. Length in mm.	♂	♀	Total.
Surface.																
10	*29*	1	–	**1**												
	23	2	1													
	25	2	1	**9**												
20	*27*	–	2													
	35	–	1													
	21	1	–		*23*	1	–		*25*	3	2					
30*	*25*	3	4		*25*	2	1	**1**	*27*	1	2	**3**				
	29	–	1	**2**					*35*	2	–					
	23	1	1		*25*	1	–	**1**	*25*	2	–					
	25	3	–						*27*	1	–	**3**				
40	*27*	1	–	**8**												
	37	–	1													
	39	1	–													
	25	3	1		*31*	1	–		*25*	2	–					
50	*27*	2	–	**7**	*29*	1	–	**2**	*39*	1	–	**3**				
	35	1	–													
	19	2	–		*25*	2	1		*23*	2	–		*17*	1	–	
	21	3	–		*27*	4	2	3	*25*	3	–		*19*	1	–	
	23	2	3		*35*	1	–		*37*	–	1	**2**	*21*	6	4	
	25	20	8						*39*	–	1		*23*	14	10	
65*	*27*	8	3	**13**									*25*	18	20	**25**
	29	1	–										*27*	6	5	
	33	1	–										*29*	7	3	
	39	1	–										*31*	–	1	
													35	1	–	
													37	2	–	

Thysanoessa raschii.

Depth in fms.	6.15–6.45 p.m. Length in mm.	♂	♀	Total.	1.30–2 a.m. Length in mm.	♂	♀	Total.	10.–10.30 a.m. Length in mm.	♂	♀	Total.	1–1.30 p.m. Length in mm.	♂	♀	Total.
Surface.																
10	*15*	3	–	**3**												
	15	2	1													
	21	3	–	**6**					*19*	1	–	**1**				
20																
	15	6	12		*15*	2	3		*17*	2	4					
30*	*17*	2	6		*19*	2	4	**3**	*19*	3	1	**4**				
	19	3	2	**10**					*21*	4	3					
	21	1	4													
	23	1	3													
	17	1	–		*15*	2	1		*15*	2	1					
	15	1	1	**5**	*17*	1	1	**6**	*21*	1	–	**6**				
40	*19*	1	1		*19*	1	–		*23*	2	–					
	15	2	2		*17*	2	1		*15*	1	–					
50	*21*	2	1	**7**	*19*	2	–	**5**	*17*	3	4	**9**				
									19	1	–					
	15	16	7		*15*	2	8		*17*	1	2		*17*	3	1	
	17	4	10		*17*	1	9		*21*	3	2	**2**	*19*	2	3	**3**
	19	6	3	**15**	*19*	4	3	**8**					*21*	1	2	
	21	–	12		*21*	2	4									
65*	*23*	1	–													

* The hauls at 30 and 65 fms. were made with the metre net: the numbers in the "total" columns are, therefore, the total divided by four.

at 30 fathoms below the surface. These organisms are to be found in the bottom layers at all times of the day and night. It appears that at midday the greatest numbers are to be had immediately above the sea bottom. At that time *M. norvegica* and *T. raschii* seem to be on the sea

TABLE VII.

VERTICAL DIURNAL MIGRATIONS OF CALANUS FINMARCHICUS AND EUCHÆTA NORVEGICA. January 19th–20th, 1926.

Numbers per 20 c.c.*

Depth in fms.	8–8.30 p.m. Euchæta.	Calanus.	12–12.30 a.m. E.	C.	4–4.30 a.m. E.	C.	8–8.30 a.m. E.	C.	12–12.30 p.m. E.	C.	4–4.30 p.m. E.	C.
Surface.	–	8	–	3	–	1	–	–	–	–	–	–
10	–	25	–	20	–	10	–	–	–	1	–	–
20	–	50	4	28	–	14	–	15	–	12	–	14
30	–	1	2	45	–	36	–	70	–	13	–	13
40	9	120	7	140	1	115	4	200	1	210	1	12
50	6	130	4	200	3	123	5	180	3	150	8	230
65	33	63	40	100	10	100	40	150	90	140	50	120

TABLE VIII.

VERTICAL DIURNAL MIGRATIONS OF CALANUS FINMARCHICUS AND EUCHÆTA NORVEGICA. February 24th–25th, 1926.

Numbers per 20 c.c.†

Depth in fms.	6.15–6.45 p.m. Euchæta.	Calanus.	1.30–2 a.m. E.	C.	10–10.30 a.m. E.	C.	1–1.30 p.m. E.	C.
Surface.	–	8	–	4	–	–	–	–
10	4	10	1	15	–	20	–	6
20	8	40	1	10	2	20	–	12
30	15	40	2	20	1	10	–	25
40	35	90	1	5	1	6	–	22
50	16	70	12	8	10	20	3	40
65	50	60	40	50	30	40	40	50

bottom since they only appear at 65 fathoms (i.e. 5 fathoms above the bottom), and then in very small numbers. At the surface the greatest numbers are to be found before and at midnight. All the species tend to leave the surface long before daylight. Esterly (1912), with reference to Copepods, says: "The animals appear to leave the surface before the

* The catches made at 30 fms. and 65 fms. respectively were placed in a wide mouth glass vessel, and the volume made up to 2800 c.c. The contents were now well mixed, and a dip was taken with a glass capsule capacity 20 c.c. The catches made at the other depths were in each case placed in a wide mouth glass vessel, and the volume made up to 700 c.c. A 20-c.c. sample was dipped, as indicated above.

† See previous table.

light increases at all in intensity. This suggests that decreasing light is not the cause of downward movement." Russell (1925) says, with regard to *C. finmarchicus*, "I have no observation between 12.20 and 4 a.m. at the surface, but at any rate the 12.30 haul in the 3rd series indicates

TABLE IX.

Date.	Hour.	Position.	Depth in fms.	Depth of Sample.	Temp. C°	Salinity.	Diff.	Average.
17.11.86	11.55	Strachur	76	Surface	7·1	25·32		
				Bottom	7·4	31·98	6·66	
	8.35	Inveraray	56	S.	6·5	22·16		8·04
				B.	7·7	31·57	9·41	
29.12.86	17.5	Strachur	71	S.	0·8	31·76		
				B.	0·3	33·36	1·60	
30.12.86	9.0	Inveraray	71	S.	3·3	29·57		2·65
				B.	3·8	33·26	3·69	
4.2.87	15.50	Strachur	72	S.	6·1	27·59		
				B.	6·6	32·95	5·36	
29.3.87	14.0	Strachur	75	S.	11·0	17·78		
				B.	10·3	31·81	14·03	
	13.0	Inveraray	66	S.	10·7	22·82		11·49
				B.	11·0	31·77	8·95	
10.5.87	15.30	Strachur	72	S.	10·7	31·83		
				B.	10·1	33·01	1·18	
	16.30	Inveraray	63	S.	10·1	31·44		
				B.	9·2	33·07	1·63	1·16
	19.20	Strachur	72	S.	14·2	32·66		
				B.	15·5	33·42	·76	
16.6.87	10.50	Inveraray	60	S.	18·4	19·26		
				B.	16·8	33·32	14·06	
8.7.87	12.15	Strachur	72	S.	17·5	32·97		
				B.	17·2	33·45	·48	
	11.20	Inveraray	60	S.	18·3	32·08		·83
				B.	13·8	33·25	1·17	
23.9.87	16.40	Strachur	74	S.	15·7	32·12		
				B.	13·3	33·36	1·24	
	17.30	Inveraray	64	S.	14·0	31·33		1·19
				B.	13·9	32·47	1·14	

that they had already started to leave the surface." Apparently there are a number of specimens of all the species investigated which do not migrate to the surface, but remain at or near 65 fathoms. This suggests that light is not the only factor, if it is a factor, affecting their diurnal vertical movements. Hickling (1925) finds that Meganyctiphanes and Thysanoessa " tend to increase as the water deepens, while their presence on the Cockburn Bank is very marked." He remarks further that this is " a disturbing factor in any effort to show the behaviour of these crustacea with reference to light alone."

Dr. H. Broch has kindly sent me specimens of Meganyctiphanes measuring from 21–29 mm. which were caught at the surface in daylight in the Oslofjord in October. Elmhirst has records of all sizes of *M. norvegica* during the day from October to May in different years either in tow-nets off Keppel, Millport, or being eaten by gulls dipping at the surface. These may have been brought to the surface by mixing brought about by the strong current which runs up Fairlie Channel (Elmhirst, 1922).

An extract has been made of other factors, such as vertical distribution of temperature and salinity, from data brought together by Mill (1891), as follows :—

Poll, the position at which the hauls were made in Upper Loch Fyne, lies approximately midway between Inveraray and Strachur. From Table IX we see that the largest difference in surface and bottom salinity at Strachur is found from November to March. The same also applies to Inveraray, except for the June record. The reason for the low surface salinities recorded at Inveraray is, no doubt, due to the proximity of that position to the influence of river waters from the Shira and Aray (see Fig. 2). The low surface salinity recorded on 16–8–87 is possibly the result of very heavy rainfalls which generally occur intermittently throughout the summer in this district. Assuming that the average of the differences of surface and bottom salinities at the two positions indicate the condition at Poll we find that here again the largest differences occur from November to March. There is no marked variation in differences between surface and bottom temperatures throughout the year. The lower temperatures, however, are found from November to April. As stated earlier in this paper, Euphausids are found most abundantly in Upper Loch Fyne from November to April. Thus we may correlate wide differences of surface and bottom salinity and low temperatures, i.e. averaging 7° C. with maximum abundance of Euphausids in Upper Loch Fyne.

Salinity then, at least within comparatively wide limits, would not appear to be a controlling factor in the vertical diurnal migration of Euphausids found in the Clyde Sea Area. Experiments now in progress in the Laboratory indicate that *T. raschii* can live happily for weeks at a very low salinity, ca. 15 ‰.

That light has a lethal effect on certain macroplanktonic organisms is suggested by our experiments on Meganyctiphanes in captivity and the experiments of Huntsman already cited. There may be an optimum

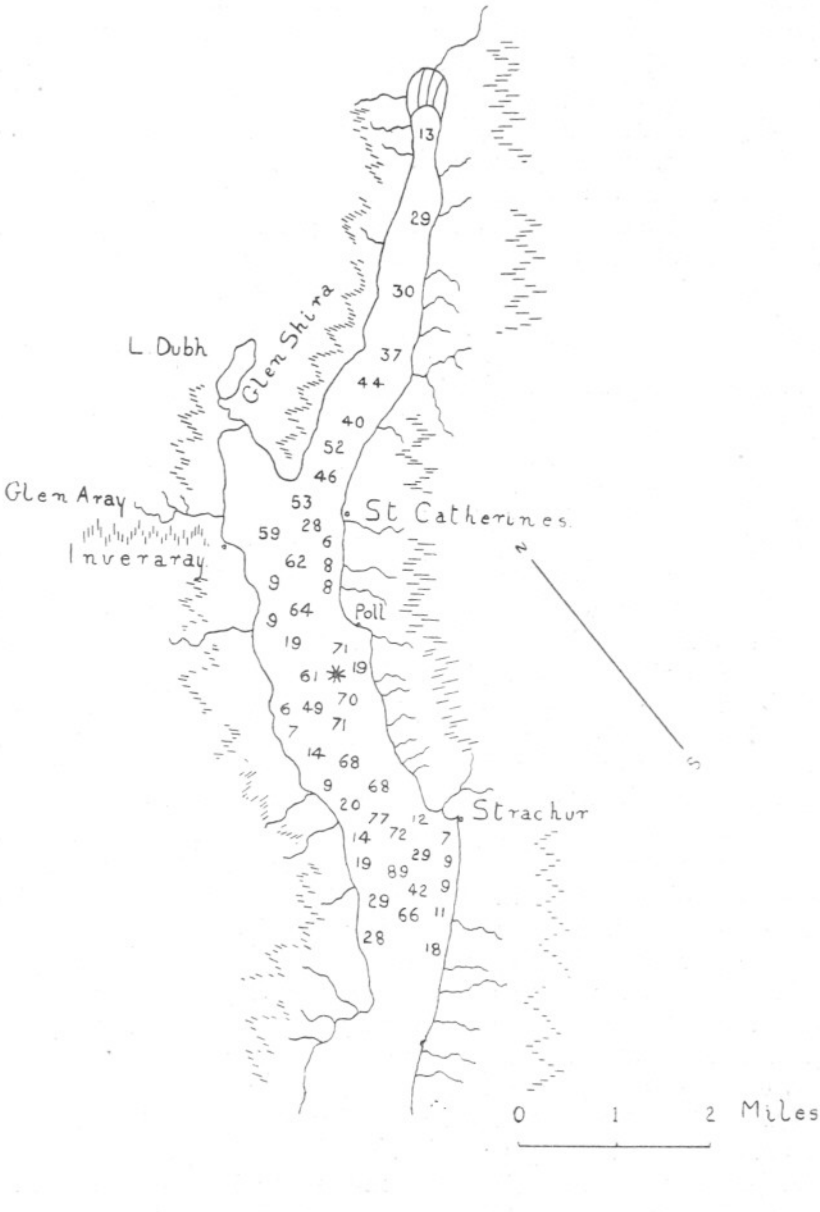

FIG. 2.—Upper Loch Fyne. * Station at which hauls were made.

light intensity which is sought by each of the species under discussion, and to obtain this light intensity vertical migrations may be necessary. At the same time in any attempt to explain vertical diurnal migrations, on the part of Euphausids at least, we must take into account factors such as tidal currents, temperatures, food requirements, proximity of ecdysis, sexual maturity, etc., if we are to arrive at trustworthy conclusions. It would appear then that the stimulus which has diurnal vertical migrations as its response is something less apparent than a mere presence or absence of light, but rather a summation of many factors. Further investigations are at present being carried out.

Observations on Meganyctiphanes norvegica in Captivity.

Adult specimens measuring 25–31 mm. have been kept in captivity for nine weeks, January to March, in outside sea-water in tanks fitted with plungers.

Three tanks measuring 12 inches by 18 inches by 12 inches were used. All light was completely shut off from two of the tanks. These tanks had their walls covered with black paper and the top covered in with thick cardboard, in the centre of which was a small hole to permit the entrance of a piece of cord to which the plunger was attached. Thus the contained specimens were practically in darkness. The other tank was freely exposed to diffuse daylight. The water was changed every day during the first week and every second day thereafter. There were from seven to nine specimens in each tank. Those specimens which lived longest, viz. nine weeks, were found in the darkened tanks. The shortest lived specimens in the darkened tanks lived for three weeks. In the undarkened tank none were found alive after fifteen days. It appeared, in some cases at least, that death took place just as the animal was about to moult. A few specimens, however, moulted successfully in all the tanks. Huntsman (1924) found that the unfavourable effect of light depends upon the condition of the individuals as well as upon the strength of light.

In our experiments it was noticed that in the undarkened tank the specimens always sought that part of the tank where the light was least intense. Light then would appear to have some effect on Meganyctiphanes, but as to the nature and extent of that effect we are unable to say without further experiments. One or two comments are made on this matter under Diurnal Migrations.

A ½-inch layer of mud, dredged from Cumbrae Deep at 60 fathoms, was put in the undarkened tank after all the specimens in that tank had died. Fresh specimens were put in, and their movements observed. They would frequently lie perfectly still on their sides on the surface of the mud. Suddenly they would work their pleopods actively, thus stirring up the mud and organic particles from the bottom. Raising themselves slightly above the mud they would, by lateral movements of the thoracic appendages and movements of the pleopods, cause the cloudy water to pass from before backwards through the " food basket." Having caught a quantity of suspended detritus in the " food basket," they would once more settle on the bottom and proceed to devour their catch. Few Copepods were fed to any of the specimens, and at death the stomachs contained organic detritus.

The movements of the animals are sometimes very rapid. The normal position of the telson is slightly flexed downwards, but when a quick movement is necessary the abdomen is straightened, and the uropods quickly brought to the median position. The telson was never seen to be drawn under the abdomen, as is the case with Crangon, Pandalus, and allied Crustaceans. When rising to the surface the movement is frequently gyratory. The animals, as a rule, do not swim to the bottom, but with the pleopods held forward close to the abdomen they fall slowly to the bottom. They may at times swim quickly, occasionally breaking surface. Again they often make complete somersaults, as many as eight in succession, the telson and uropods together proving a very efficient and powerful steering apparatus.

No specimens have been seen to luminesce voluntarily in captivity after being twenty-four hours out of the sea. Immediately on being taken out of the sea the luminescent organs are very active, especially at night. On one occasion six specimens, averaging 27 mm. in length, were placed in a two-litre jar. By means of the light emitted voluntarily (i.e. without mechanical or other disturbance on my part) it was possible to read newspaper print. The light appeared suddenly like a flash, remained three or four seconds, and disappeared more slowly than it had come. The luminescent organs in the ocular peduncle seemed to be most powerful. Sometimes they alone would light up. The thoracic luminescent organs lit up together as also did the abdominal set.

When specimens were placed in 10% formalin immediately on being caught the luminescent organs would invariably light up momentarily. Murray (1912) believed that the luminescent organs are used as a kind of " bull's-eye lantern," and enable Meganyctiphanes to see and pick up the minute particles of organic matter which are settling on the bottom deposits. This seems probable as the amount of light penetrating to 60–80 fathoms is extremely small. That these organs may have other functions is possible, as is suggested by the fact that in *Stylocheiron carinatum* there are only three present, one between the bases of the first pair of pleopods and one on either of the penultimate legs. In the male the latter luminescent organs attain an extraordinary development (Sars).

Apart from the occasions when the luminescent organs are active, Meganyctiphanes must be practically invisible. The greater part of the body is transparent, and those parts which are opaque are thickly covered with red pigment bodies. Owing, however, to the fact that red rays are nearly all absorbed at the above-mentioned depths, the red colour would tend to be as invisible as would black. Accordingly, the invisibility of Meganyctiphanes is doubly secured. This invisibility would appear to decrease the probability of attack by enemies. *M. norvegica*, however, apparently lays itself open to attack when it luminesces. Certain fish may have learned to associate such luminescence with suitable food. For example, there are certain deep living angler-fish which have luminescent lures. Lissner (1919–23) suggests that the fact that the majority of the food organisms of the herring caught in the Skager-Rack and North Sea are luminescent is significant. This assisting and elaboration of the visual sense respectively by means of luminescent organs and relatively large eyes would appear to be a very efficient adaptation to the environment. Should, however, this specialisation tend to bring about the destruction of the species by attracting enemies one would expect to see a reduction of the luminescent organs. It may be that although the luminescent organs are essential in the life of *M. norvegica* they form under certain circumstances a considerable source of danger. The balance, however, would appear to be in the animal's favour. Owing to the limited nature of our knowledge of the environmental relations of Meganyctiphanes and other Euphausids it is impossible at present to make any general conclusions of value.

Parasites.

The following are some parasites found in *Meganyctiphanes norvegica* :—

Ectoparasites.

1. *Staphylocystis racemosus* (Coutière), a dinoflagellate found on the carapace of a specimen caught at "Cumbrae Deep" in March, 1925. The only record of this parasite is that of Kroyer on *Pasiphæa tarda* in N.E. Iceland.

2. A Suctorian often present on the pleopods. Not yet identified.

Endoparasites. A Gregarine appears in the gut from the second Calyptopis stage to the adult of 29 mm. length. This Gregarine appears in spring, and becomes more common during early summer.

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SUMMARY.

1. Vegetable detritus of land and coastal origin is of notable importance as a source of food, especially to those specimens measuring 21–29 mm., which is the most abundant size found in the Clyde Sea Area.

2. Meganyctiphanes in the Clyde Sea Area for the most part lives and feeds between 10 and 20 fathoms above a muddy bottom, usually in waters about 60–80 fathoms deep.

3. Meganyctiphanes feeds by selecting from the surrounding water the suspended micro-organisms and detritus, and would thus come under the category of a "suspension feeder."

4. The larger specimens measuring 29–31 mm. are found chiefly in Upper Loch Fyne. The largest specimens measuring 37 mm. are found exclusively in Upper Loch Fyne.

5. Adult specimens tend to decrease in numbers from May till September. During these months they appear to live during the day immediately above or on the muddy bottom.

6. The association of *Meganyctiphanes norvegica, Thysanoessa raschii, Euchæta norvegica*, and *Calanus finmarchicus*, in large numbers in Upper Loch Fyne would indicate that conditions there are specially favourable to all these species.

7. In Upper Loch Fyne *M. norvegica, T. raschii, E. norvegica*, and *C. finmarchicus*, make partial vertical diurnal migrations, specimens being found a few fathoms from the bottom during both day and night.

8. Under certain circumstances light appears to have a harmful effect on *M. norvegica*.

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