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THE FOOD OF *MEGANYCTIPHANES NORVEGICA* (M. SARS), WITH AN ASSESSMENT OF THE CONTRIBUTIONS OF ITS COMPONENTS TO THE VITAMIN A RESERVES OF THE ANIMAL

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(Text-figs. 1–10)

The importance of *Meganyctiphanes norvegica* (M. Sars) as a source of vitamin A for its predators has been demonstrated by Fisher, Kon & Thompson (1955). Basing their conclusions on the observations of Macdonald (1927) on the feeding of *M. norvegica* in Loch Fyne, Fisher, Kon & Thompson (1954) and Kon (1954) suggested a possible scheme of accumulation of vitamin A in the animal. They also made cursory examinations of the stomach contents from animals caught in the same area and their findings appeared to agree fairly well with those of Macdonald, except that from his results he concluded that phytoplankton was a major item in the diet. This conclusion has been disputed by Einarsson (1945) who called for more detailed investigation of fresh material in order to obtain a clearer picture of the feeding of north Atlantic euphausiids. Such information would be of great value in the study of the vitamin A chain in the plankton. We have, therefore, examined the stomach contents of *M. norvegica* over nearly two years to try to detect every type of food that might be eaten. In addition to our own survey, Dr J. Mauchline (1959) of the Marine Station, Millport, made a more intensive study of the food in relation to the diurnal migrations in July and November.

Earlier work on the food of *M. norvegica* in different areas records the species feeding on copepods, schizopod and decapod larvae, diatoms, dinoflagellates and detritus (Holt & Tattersall, 1905; Paulsen, 1909; Hickling, 1923–5). Macdonald (1927) concluded that larger specimens feed mainly on copepods, small specimens on diatoms and 'wet dust' or flocculent detritus, and intermediate sizes on vegetable detritus. Einarsson (1945) regarded the chief items in the diet to be detritus and crustacean fragments. He also mentioned the occurrence of a reddish-brown substance in the anterior part of the stomach. The nature of this substance has been suggested by Ponomareva (1955), who found in the stomachs of four species of Pacific euphausiids the

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crystalline cones of compound eyes and also remains of the eyes themselves; she considered the dark reddish-brown mass to be the pigmented part of the eyes. The pigment rapidly disappeared on passage through the gut. Ponomareva examined different size-groups from the cyrtopia to the adult stages and found that the groups differed little in the composition of their food; even small euphausiids fed on copepods. She agreed with Einarsson that phytoplankton is not a basic food of euphausiids.

The local environment might account for the presence of vegetable tissues from terrigenous deposits in the Loch Fyne specimens of *M. norvegica* (Macdonald, 1927) and different material might be found in those living farther offshore. In stomachs of *Euphausia krohnii*, caught in the Bay of Biscay, we found contents similar to those of *Meganyctiphanes norvegica*, but none of the terrestrial material present in the stomachs of *M. norvegica* from Loch Fyne. Nevertheless, although *M. norvegica* may be considered as living under specialized conditions in this loch, such sea areas with deep water in close proximity to the land may be important fishing grounds. *M. norvegica* is often a component of the plankton in such areas, not only in Loch Fyne but also in, for example, the Skagerak (Poulsen, 1926), the fjords of the coast of Möre (Ruud, 1926) or the Gulf of Maine (Bigelow, 1914).

MATERIAL AND METHODS

Samples of *Meganyctiphanes norvegica* were collected with 1 m or 2 m stramin nets on one or two consecutive days during each month from September 1956, to April 1958, and in June 1958. The samples for November and December 1957 were kindly collected for us by Dr Mauchline. The area fished in Loch Fyne extended from just north of Arran in a north-westerly direction to the deep water north-east of Tarbert. Apart from one haul taken at about midnight in October 1956, all the specimens examined in 1956 and 1957 were caught during the hours of daylight between 8 a.m. and 6 p.m. A haul was taken at midnight in each monthly series during the period January to April 1958, and in June 1958.

The animals were size-grouped from the length of the carapace at 1 mm. intervals to the nearest half millimetre. Mauchline (1959) discusses the relationship of this measurement to those used by earlier workers, including ourselves. The sexes were not examined separately. Size relationships of the specimens studied are given in Table 1.

Detritus, plant material and copepods were often found in the 'basket' formed by the thoracic legs, but it seems likely that at least some of these, especially whole copepods, such as *Pareuchaeta norvegica*, became adventitiously entangled when the animals were in the net, and so we have assumed that only material that had actually entered the stomach should be considered as food.

In collaboration with Dr Mauchline, we took, with a Jenkin's mud sampler (Mortimer, 1942), kindly lent by the Freshwater Biological Association, mud samples from Loch Fyne, in the area where most of the *Meganyctiphanes norvegica* were caught. The cores, of about 3 in. diameter, were taken on 7 March 1957, at a depth of 175 m. They were cut into sections about 2½ in. long, except the surface layer which was about ½ in. thick and included the

TABLE 1. SIZE DISTRIBUTION OF SPECIMENS OF *MEGANYCTIPHANES NORVEGICA* EXAMINED

		Number of specimens of carapace length (mm)											
Date of hauls	Time	2	3	4	5	6	7	8	9	10	11	12	Total
19–20. ix. 56	D	28	22	24	17	2	0	11	22	6	9	1	142
25–26. x. 56	D	2	6	28	89	35	21	14	13	12	9	1	230
25–26. x. 56	N	0	0	0	1	14	10	0	2	3	0	1	31
22–23. xi. 56	D	0	1	9	37	21	1	35	19	4	0	0	127
19–20. xii. 56	D	0	0	4	28	8	0	32	18	6	0	0	96
9–10. i. 57	D	0	0	3	40	24	3	51	8	2	0	0	131
7–8. ii. 57	D	0	0	2	27	12	3	20	3	0	0	0	67
7–8. iii. 57	D	0	0	7	28	5	1	9	1	0	0	0	51
4–5. iv. 57	D	0	0	0	10	19	7	37	14	3	0	0	90
24. iv. 57	D	0	0	0	0	6	5	7	9	1	0	0	28
22–23. v. 57	D	0	0	0	1	6	34	27	2	2	0	0	72
19–20. vi. 57	D	0	1	1	0	6	65	48	6	1	0	0	128
10–11. vii. 57	D	0	3	42	41	3	15	15	0	0	0	0	119
14–15. viii. 57	D	0	0	2	48	86	38	116	3	2	0	0	295
11–12. ix. 57	D	0	0	0	4	16	36	97	11	0	0	0	164
9–10. x. 57	D	0	0	1	3	12	64	176	26	0	0	0	282
19. xi. 57	D	0	0	0	1	3	45	72	5	0	0	0	126
17. xii. 57	D	0	0	0	0	1	31	81	2	0	0	0	115
15–16. i. 58	D	0	0	0	0	4	42	150	9	0	0	0	205
15–16. i. 58	N	0	0	0	0	2	27	80	5	0	0	0	114
19–20. ii. 58	D	0	0	0	0	10	57	118	2	0	0	0	187
19–20. ii. 58	N	0	0	0	0	7	41	119	3	1	0	0	171
27–28. iii. 58	D	0	0	0	4	9	58	128	2	0	0	0	201
27–28. iii. 58	N	0	0	0	0	3	21	87	1	0	0	0	112
15–16. iv. 58	D	0	0	0	17	13	51	94	2	0	0	0	177
15–16. iv. 58	N	0	0	0	5	7	57	102	1	0	0	0	172
25–26. vi. 58	D	0	0	0	0	0	10	62	10	0	0	0	82
25–26. vi. 58	N	0	0	0	0	0	0	36	13	1	0	0	50
Total		30	33	123	401	334	743	1824	212	44	18	3	3765

D = Caught in daylight. N = Caught at night.

thin layer of water lying above it. All the cores were preserved by shaking with about twice their volume of absolute alcohol. Fat-soluble material extracted from the mud was analysed by our usual method (Fisher, Kon & Thompson, 1952).

RESULTS

In considering intensity of feeding and types of food eaten we have first combined results for animals of all sizes in each monthly group. We then discuss the possible relationship between size and the kind of food eaten. So that the results should be comparable throughout the period of sampling, only day hauls are considered. Finally, the results for night and day hauls are compared.

Intensity of feeding

The intensity of feeding was determined by calculating the percentage of animals with food in the stomach in each monthly haul. However, some stomachs contained only a little detritus or other food, contrasting with others from animals that had obviously been feeding more intensively. From November 1956, a note was, therefore, made of the degree of fullness of the stomach.

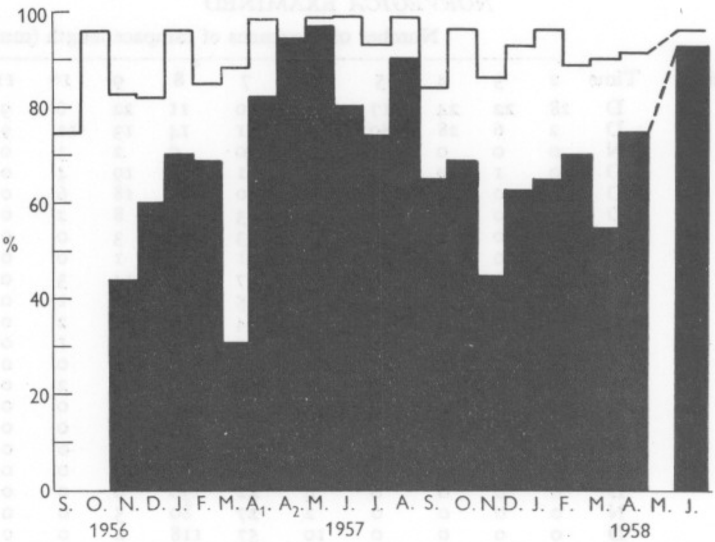

Fig. 1. Seasonal variation in percentage of *Meganyctiphanes norvegica* with stomachs containing food. Shaded portion: percentage with stomachs more than half-full.

Feeding intensity reached its peak during the spring plankton outburst in late April and May (Fig. 1). The high intensity of feeding in August was associated with the presence of numerous young euphausiids and dinoflagellates in the plankton. There was also evidence of a smaller increase corresponding to the autumn plankton surge in October 1956 and 1957. The high percentage of animals with nearly full stomachs in January and February of each year was unexpected. In January 1957, it was at first thought to be associated with an abundance of the copepod *Pareuchaeta norvegica*. In 1958, however, the species was not particularly numerous in these months. We now consider it more likely that increased feeding at this time of year is due to the greater activity associated with spermatophore transference (Mauchline, 1959).

Types of food

The main components of the diet of *Meganyctiphanes norvegica* from Loch Fyne were organic debris, mud particles and other inorganic detritus, Crustacea, dinoflagellates, fern sporangia, dipteran egg membranes, diatoms, algae, and occasionally other items of terrestrial or marine origin.

Organic debris and inorganic detritus were present in many stomachs, as would be expected during daylight when these diurnally migrating animals lie on or near the bottom. Fig. 2 shows the seasonal fluctuations of these two components. The large amounts usually found indicated that this material probably forms the bulk of the diet, except possibly during the spring feeding period.

There was a marked seasonal variation in the occurrence of crustacean fragments in the stomachs (Fig. 3A). Owing to lack of time no attempt was made to identify parts of copepods separately, and all crustacean remains are considered together, save for the easily identified compound eye parts. The presence of these eyes indicates feeding on eucaridan Crustacea and their absence, when the incidence of crustacean fragments remains high, indicates that copepods were the Crustacea eaten, as during the spring increase in April and May.

In Fig. 3B the percentage of stomachs containing crustacean remains including compound eye parts is shown, and the two periods, June–November 1957 and January–April 1958, are those with the highest frequencies. From June onwards late larvae and adolescents of euphausiids are numerous in the plankton and many of the eyes in the stomachs were identified as belonging to euphausiids. The higher incidence of crustacean fragments and eyes in the early months of 1958 than in the same period in 1957 is difficult to explain, but may have been associated with the absence of sufficient alternative food in the water. It is possible that cannibalism occurs when the proportion of euphausiids to other organisms in the plankton is high either because of an abundance of euphausiids, as in the late summer, or because of a scarcity of other plankton organisms, as in the winter. On the other hand, the average size of the *M. norvegica* forming the population sampled was higher in January 1958 (carapace 8·0 mm long) than a year earlier (6·7 mm) and larger animals eat more crustaceans (see p. 299). However, in the smallest size-group (6 mm carapace) for which we have adequate values for both years there were many more animals with stomachs containing crustacean fragments in January 1958 (75%) than in January 1957 (46%), which suggests that the composition of the plankton is the determining factor.

Dinoflagellates were most frequently found in late summer and autumn with minor increases in April and January (Fig. 4). When dinoflagellates were abundant in the plankton they formed an important part of the diet of *M. norvegica*, occurring in the stomachs in enormous numbers. The species most frequently found belonged to the genera *Ceratium*, *Dinophysis*, *Phalacroma*, *Prorocentrum* and *Peridinium* (Fig. 5). *Ceratium* occurred commonly in autumn, 1956, but in the corresponding period in 1957 it was replaced by *Dinophysis* and *Prorocentrum*. A few stomachs contained *Goniaulax*, mostly in

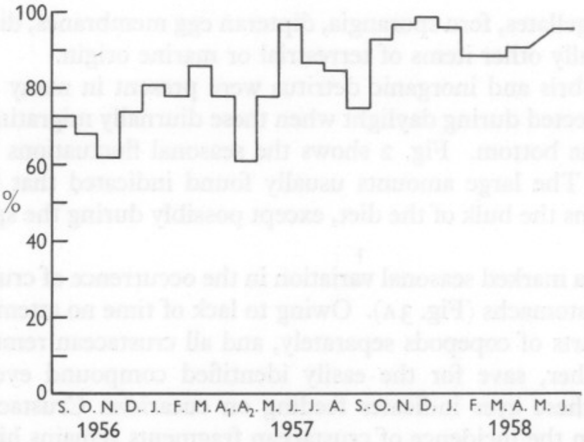

Fig. 2. Seasonal variation in percentage of *Meganyctiphanes norvegica* with stomachs containing organic debris and inorganic detritus.

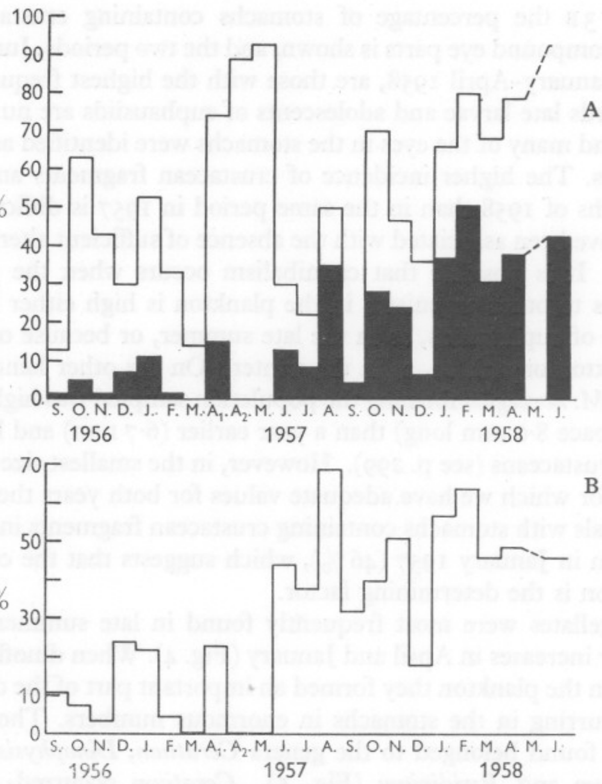

Fig. 3. A, Seasonal variation in percentage of *Meganyctiphanes norvegica* with stomachs containing crustacean fragments. Shaded portion: percentage with stomachs containing compound eyes; B, Seasonal variation in percentage of those *M. norvegica* with stomachs containing crustacean fragments in which compound eyes were also present.

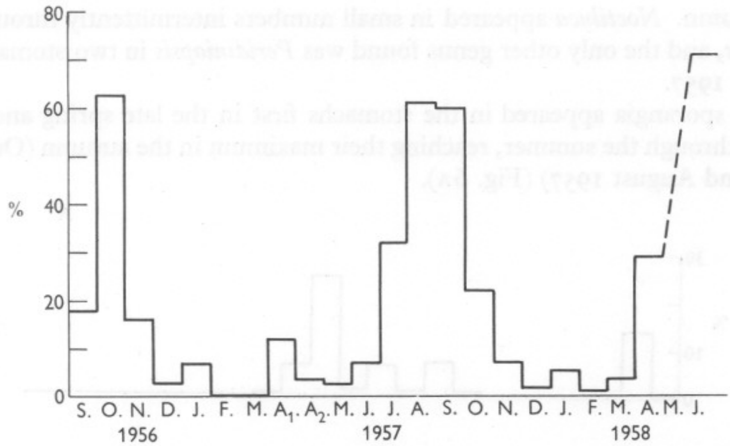

Fig. 4. Seasonal variation in percentage of *Meganyctiphanes norvegica* with stomachs containing dinoflagellates.

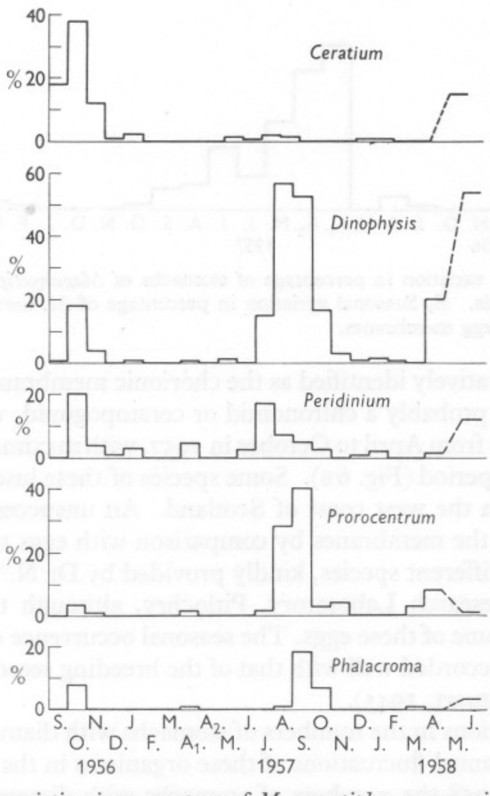

Fig. 5. Seasonal variation in percentage of *Meganyctiphanes norvegica* with stomachs containing different genera of dinoflagellates.

the autumn. *Noctiluca* appeared in small numbers intermittently throughout the year, and the only other genus found was *Peridiniopsis* in two stomachs in August 1957.

Fern sporangia appeared in the stomachs first in the late spring and continued through the summer, reaching their maximum in the autumn (October 1956, and August 1957) (Fig. 6A).

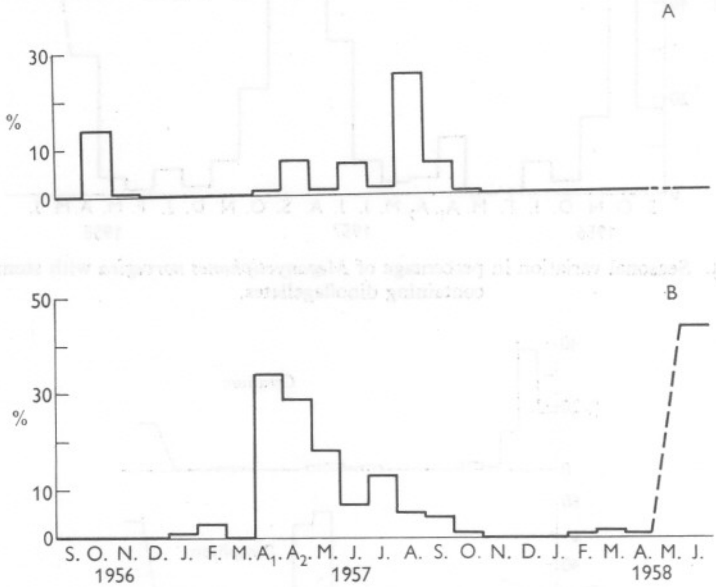

Fig. 6. A, Seasonal variation in percentage of stomachs of *Meganyctiphanes norvegica* containing fern sporangia. B, Seasonal variation in percentage of *M. norvegica* with stomachs containing dipteran egg membranes.

Structures tentatively identified as the chorionic membranes of the eggs of a dipterous insect, probably a chironomid or ceratopogonid, were found in the stomach contents from April to October in 1957, with maximal incidence at the beginning of the period (Fig. 6B). Some species of these insects are present in large numbers on the west coast of Scotland. An unsuccessful attempt was made to identify the membranes by comparison with eggs taken from female chironomids of different species, kindly provided by Dr N. C. Morgan of the Brown Trout Research Laboratory, Pitlochry, although there was a close resemblance to some of these eggs. The seasonal occurrence of the membranes in the stomachs accorded well with that of the breeding season of chironomids in the vicinity (Stuart, 1945).

Seasonal variations in the numbers of stomachs with diatoms (Fig. 7) corresponded to the annual fluctuations of these organisms in the plankton. In the first months of 1958 the numbers of stomachs with diatoms increased from January to April, more closely following the expected cycle of the plankton than in the previous year. Diatoms were never very numerous in the individual stomachs and were not at any time predominant in the contents. The most commonly occurring were species of *Paralia* and *Thalassiosira* and more rarely we found *Coscinodiscus*, *Rhizosolenia*, *Navicula* and *Biddulphia*.

Parts of green, red and brown algae appeared in a small proportion of stomachs throughout the year; the species were not determined. Fern sporangia, insect egg membranes, diatoms, algae and such occasionally occurring items in the stomachs as chrysomonads and radiolarians, sponge spicules, *Sagitta* spp., terrestrial plant material, and various unidentifiable structures were quantitatively unimportant components of the diet.

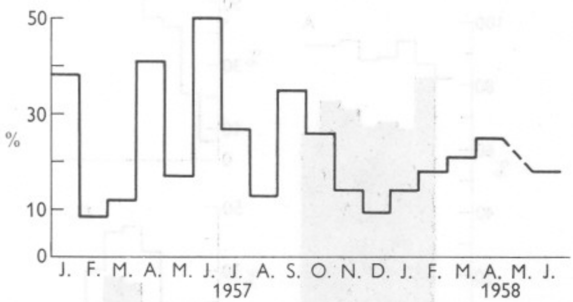

Fig. 7. Seasonal variation in percentage of *Meganyctiphanes norvegica* with stomachs containing diatoms.

Food in relation to size of animal

Stomachs were examined from animals of carapace lengths ranging from 2 to 12 mm. The smallest of these were probably late furcilia stages (Einarsson, 1945); otherwise, all the animals were post-larval. As specimens with carapace lengths of 2, 11 and 12 mm were taken only during September and October 1956, they have been disregarded partly because of their small numbers and partly because of the seasonal bias they would impart. There appeared to be no overall relationship between size and feeding intensity (Fig. 8A).

The percentage of animals with organic debris and inorganic detritus tended to increase with size (Fig. 8B). Since these components are probably mainly derived from the sea floor there is evidence that larger specimens spend a longer time there than smaller ones. By taking net hauls at different depths Mauchline (1959) has demonstrated the vertical layering of size-groups with the largest specimens lowest in the water.

The incidence of crustacean remains in the stomachs increased fairly sharply with size in the smaller animals, reaching a maximum in those of carapace length 8 mm. and then falling slightly (Fig. 8C). Our values were not so high and did not show so simple an increase to the largest size-group as those illustrated by Mauchline (1959), but his results were based on a single set of hauls whereas our histogram is compiled from all our values. The difference may be due to seasonal variation, but no definite indication of it could be derived from an analysis of the monthly values. Compound eyes in stomach contents increased in number with the size of the animals, reaching 28% in the group with carapace length 8 mm. and then falling rather sharply (Fig. 8D). These percentages are higher than those of Mauchline (1959), undoubtedly owing to the much higher values we recorded between October 1957, and June 1958.

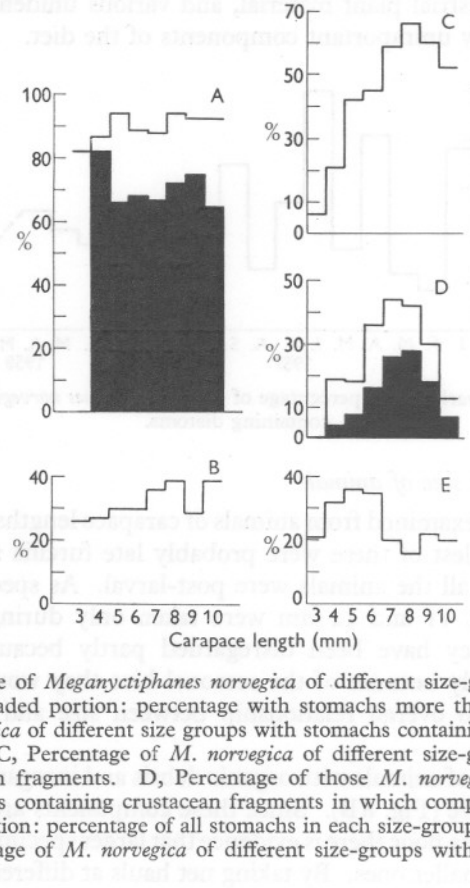

Fig. 8. A, Percentage of *Meganyctiphanes norvegica* of different size-groups with stomachs containing food. Shaded portion: percentage with stomachs more than half-full. B, Percentage of *M. norvegica* of different size groups with stomachs containing organic debris and inorganic detritus. C, Percentage of *M. norvegica* of different size-groups with stomachs containing crustacean fragments. D, Percentage of those *M. norvegica* of different size-groups with stomachs containing crustacean fragments in which compound eyes were also present. Shaded portion: percentage of all stomachs in each size-group with compound eyes present. E, Percentage of *M. norvegica* of different size-groups with stomachs containing dinoflagellates.

Dinoflagellates occurred in all size-groups but most frequently in those with carapace lengths from 4 to 6 mm (Fig. 8E). Diatoms were most frequently present (18–20%) in animals of carapace lengths 6–8 mm. Fern sporangia occurred in all size-groups, with the incidence slightly higher in those with carapace lengths from 4 to 6 mm (7–11%). There was no indication that any size of euphausiid was more likely to contain dipteran egg cases, which were found in from 2 to 10% of animals in the size range 3–9 mm inclusive. Algae were absent from the smallest and largest animals and occurred in 6–10% of those animals with carapaces 4–9 mm long.

Seasonal variation of food in relation to size

The intensity of feeding by animals of different size-groups was calculated. Sufficient values were available to construct histograms only for the groups with carapace lengths of 6, 7 and 8 mm. In the 8 mm group (Fig. 9), which contained fairly large numbers of specimens in each month, intensive feeding occurred from December 1956 to February 1957, from April to June 1957,

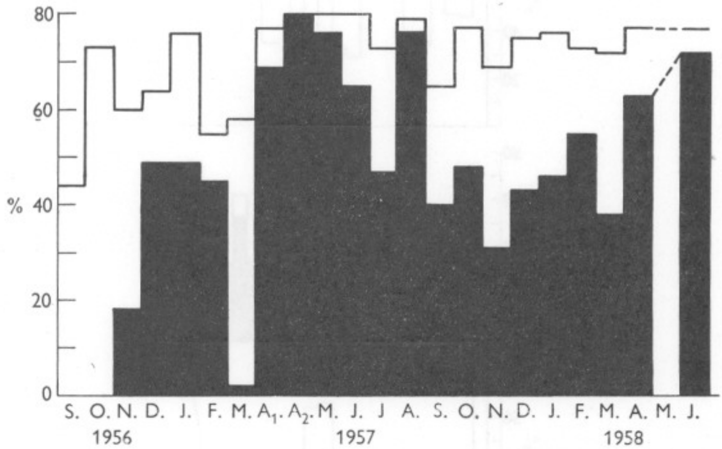

Fig. 9. Seasonal variation in percentage of *Meganyctiphanes norvegica* with a carapace length of 8 mm with stomachs containing food. Shaded portion: percentage of this size-group with stomachs more than half full.

and in August 1957. The winter feeding period occurred again from December 1957 to February 1958. Although there were some small differences, the overall picture presented by the 7 mm group was similar to that for the 8 mm specimens. Animals of this size did not appear in any numbers until January 1957, and feeding activity was at its highest in February–March, late April–June and August–October 1957. Increased spring feeding began again in April and continued through June 1958. Maximal feeding periods for the 6 mm group occurred in December 1956 to February 1957, April–June, August–October 1957, and December 1957 to January 1958. The picture presented by all three size-groups and the fragmentary information for the larger and smaller sizes leaves no doubt that there are three main feeding periods during the year, the most intensive in spring and early summer, and the other two in autumn and in winter.

As in the total population, seasonal incidence of organic debris and inorganic detritus in the various size-groups showed no consistent fluctuations.

The 8 mm group provided the most complete picture of the seasonal variations of crustacean remains in the stomachs and is representative of the other sizes. Fig. 10 A shows that the main peak was, as would be expected, in April and May 1957, although, in 1958, with no information for May, the highest level did not occur until June. January 1957 and February 1958 marked the peaks of the winter feeding periods for this kind of food. August and October

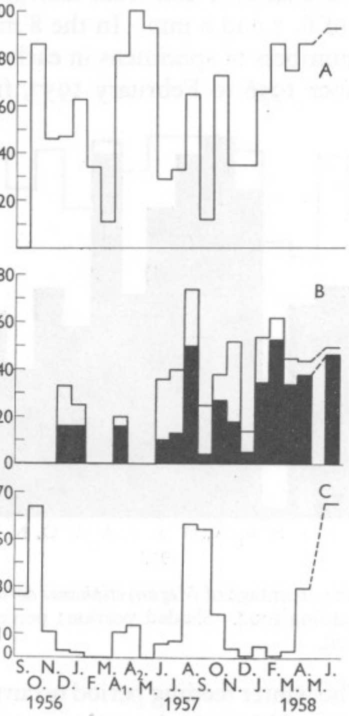

Fig. 10. A, Seasonal variation in percentage of *Meganyctiphanes norvegica* with a carapace length of 8 mm with stomachs containing crustacean fragments. B, Seasonal variation in percentage of those *M. norvegica* with a carapace length of 8 mm with stomachs containing crustacean fragments in which compound eyes were also present. Shaded portion: percentage of all stomachs in 8 mm group with compound eyes present. C, Seasonal variation in percentage of *M. norvegica* with a carapace length of 8 mm with stomachs containing dinoflagellates.

were also months in which Crustacea were present in a high proportion of stomachs, with a marked contrast in September. In the 8 mm size-group there were no animals with such food in September 1956, and those of other sizes showed a low incidence in the same month. The close similarity between the fluctuations in Fig. 10 A and those in Fig. 3 A is remarkable since the 8 mm size-group did not constitute the majority of the population until September 1957.

Our values for the occurrence of compound eyes in the stomachs of animals with 8 mm carapaces are again the most complete and are representative of the other sizes. Incidence of these eyes in the winter and autumn feeding periods was high but they were almost entirely absent from the stomachs of animals caught during the main feeding period in the spring (Fig. 10B). There are probably two reasons for this absence; one is that copepods are far more numerous during the spring increase than at other times and the other is that the euphausiids themselves exhibit much less luminescence at this time of year (Mauchline, 1959). Most of the eyes in the stomachs appear to be those of euphausiids, and their predators, whether of the same or another species, are probably attracted to them by the luminescing of the photophore on the eye-stalk.

Dinoflagellates in the stomachs exhibited the same seasonal trends in all size-groups. Fig. 10C shows these for the 8 mm group, with peaks in October 1956, and August and September 1957. In 1958, a peak as high as those in previous years appeared already in June when the investigation ended. The incidence of the different genera of dinoflagellates exhibited the same seasonal patterns in each size-group as shown by the whole population irrespective of size and illustrated in Fig. 5.

Diatoms, chorionic membranes of dipteran eggs and fern sporangia showed seasonal variations in the size groups similar to those in the whole population (see Figs. 6 and 7).

Diurnal variations in stomach contents

Table 2 shows that there was little difference in the occurrence of food in the stomachs of animals collected during daylight compared with those collected at around midnight, except in October 1956, when the number of stomachs with food was lower at night than in the daytime. This finding is, similar to that of Mauchline (1959) in November for *I*-group animals, that is, those that have taken part in one breeding season. The relationship between the intensity of feeding by day and by night in different size-groups was similar to that obtaining for the whole samples regardless of size.

The incidence of those animals with stomachs more than half full was higher at night in January, March, April and June, and lower in February. The degree of fullness of the stomach was not noted for the October specimens. The occurrence of organic debris and inorganic detritus was very similar in all the day and night hauls irrespective of size of animals examined. When feeding was intensive, especially in spring, the uptake of detritus was lower and no relationship between the size of the animals, their vertical distribution, and the incidence of such material was detected. During periods of less intensive feeding a marked correlation was apparent; with increasing size of animal and, therefore, a lower position in the water, more stomachs contained organic and inorganic particles.

As fern sporangia were present more frequently at night, when the animals normally migrate upwards, we infer that the sporangia occur in the plankton and not resting on the bottom. The incidence of dipteran egg cases did not vary so markedly between day and night, the most appreciable difference being in June when the daytime value was higher. However, since in that month feeding appeared to be at its peak, it seems likely that the egg membranes were in the plankton rather than on the bottom.

TABLE 2. INCIDENCE OF FOOD AND ITS COMPONENTS IN STOMACHS OF *MEGANYCTIPHANES NORVEGICA*

(Figures are percentages of all stomachs examined)

	Time caught	October 1956	January 1958	February 1958	March 1958	April 1958	June 1958
Food present in stomach	D	96	96	89	90	92	96
	N	81	97	85	93	94	98
Stomach more than half full	D	—	65	70	55	75	93
	N	—	70	49	92	92	98
Organic debris and inorganic detritus	D	68	96	89	89	91	96
	N	74	97	82	92	94	98
Crustacean fragments	D	63	66	79	68	79	93
	N	61	80	65	92	74	98
Compound eyes	D	4·8	37	51	31	38	43
	N	0	59	35	21	14	72
Fern sporangia	D	14	0	0	0	0	0
	N	39	0	0·6	1·8	0·6	2·0
Dipteran egg membranes	D	0	0	0·5	1·5	1·1	44
	N	0	0	1·8	1·8	1·1	34
Algal filaments	D	6·9	0·5	0·5	12	2·3	6·1
	N	32	0	0·6	5·4	5·8	4·0

D = Day. N = Night.

When dinoflagellates were abundant, as in October 1956 and June 1958, they were eaten by animals of all sizes by day and by night. In the first four months of 1958, when these organisms were found less often in the stomachs, the incidence of the three commonest genera, *Ceratium*, *Dinophysis* and *Peridinium*, tended to be higher during the day than at night and higher in smaller animals than in larger ones. *Prorocentrum* occurred in appreciable numbers in October and June and *Phalacroma* only in October and, on each occasion, they were more numerous in the animals caught at night. The difference in occurrence of these various genera by day and by night was probably associated with their vertical distribution in the plankton.

Diatoms were relatively unimportant in the diet. Usually *Thalassiosira* was found more frequently in the stomachs of specimens taken at night and *Paralia* in those taken in daylight. There was a tendency for diatoms to occur more often in the smaller animals in January, February and March, but in April and June, when they became more common in the plankton, they were found in about 20 to 30% of nearly all size-groups, with no predominance by day or night.

In October, algal filaments occurred during the day in size-groups up to and including 7 mm, and at night 9 mm, but the incidence was much higher at night than during the day. In the other months of the diurnal study algae occurred much less often and no relationship either to size or time of catching the animals was detectable.

Analysis of mud from bottom of Loch Fyne

Mauchline (1959) has given a brief account of the organisms found on the surface of the mud samples. Living filamentous algae were present, some of littoral origin, but none was attached or growing at that depth. There were also numerous ciliates. Like Mauchline, we found protozoan remains in the stomachs of the euphausiids. Only a few diatoms, mostly *Biddulphia*, were found in the mud. Small polychaetes were present in the deposits and were occasionally also found in the stomachs. The mud contained large numbers of cumaceans and a few isopods. If these were present in the stomachs they were included with the crustacean remains and not identified separately.

TABLE 3. CAROTENOIDS IN MUD FROM THE BOTTOM OF LOCH FYNE

Depth of samples = 175 m.

Sample	Thickness (in. approx.)	Total carotenoids		β-carotene	
		μg	μg/g fat	μg	μg/g fat
A. Surface	½	18	421	Trace	—
A. 2nd layer	2½	55	1070	4·5	87
A. 3rd layer	2½	116	6250	11	574
A. Bottom layer	2½	112	3380	13	397
B. Surface	½	22	3940	Trace	—
C. Surface	½	23	1050	Trace	—

Analysis of extracts from some of the cores for vitamin A and carotenoids (Table 3) shows that vitamin A was not present in measurable amount. The carotenoid content of the organisms just mentioned as living on the surface of the mud would be included in the values given in the table for the surface layers.

DISCUSSION

Although our findings provide new information about the food and feeding habits of *Meganyctiphanes norvegica*, confirming and supplementing that presented by Macdonald (1927) and Mauchline (1959), the picture is obviously very complex. We believe we now have enough information from this study about the qualitative aspects of the diet, although the proportions of its components have been derived from subjective estimates, to try to assess the contributions of the food to the rich reserves of vitamin A present mainly in the eyes. In addition we possess a considerable amount of data, from earlier observations of other workers and ourselves, on the occurrence of vitamin A or its precursors in these components.

The most commonly occurring food substances were inorganic detritus and organic debris, particularly in the stomachs of animals caught during the day when they were on or near the sea bottom and filter-feeding in the manner described by Mauchline (1959). Fox (1950) discussed the value of such material in the nutrition of marine animals and stressed its importance as a source of carotenoids. Marine muds have been shown to be particularly rich in carotenes (Fox, Updegraff & Novelli, 1944). Our own results (Table 3) indicate that, although β-carotene is present in the mud, a euphausiid that consumed the mud occupying a circular area of 3 in. diameter and ½ in. thickness would not obtain enough to be measured by our technique (i.e. probably less than 1 μg). Certainly it would take in a greater amount of other carotenoids, but these would mostly be xanthophylls which, so far as we know, would not be vitamin A precursors. With allowance for greater thickness of the deeper mud samples there was some indication of an increase in carotenoid concentration and in the proportion of β-carotene with depth. Fox & Anderson (1941) found a similar increase in the ratio of carotenes to xanthophylls with the depth and, therefore, age of the mud. Our observations of living *Meganyctiphanes norvegica* in aquaria show that the animals do not penetrate far below the mud surface and so they would be unlikely to reach the layer richer in carotene.

Many stomachs contained what Mauchline (1959) has described as a 'green mush' of small particle size which he believes to be synonymous with Macdonald's (1927) 'flocculent detritus'. We do not know whether this material was derived from the bottom or from suspended matter in the sea water itself. Fox (1937) attempted to assess the importance of suspended matter and microplankton as a source of carotenoids by filtering 4000 l. of sea water. He extracted from the deposit 0·1 mg of xanthophylls and 0·02 mg of carotenes. Fox, Isaacs & Corcoran (1952) estimated that, in the sea off the Californian coast, the colloidal or otherwise finely particulate matter, which they called leptopel, included only 1·5–4% of living cells. Loch Fyne is less than 3 miles wide in the area where most of the euphausiids were caught, and the heavy rainfall (Barnes & Goodley, 1958), washes down a considerable quantity of detritus from the land, evidence of which has been provided by the occurrence of fern sporangia and dipteran egg cases in the stomachs of *Meganyctiphanes norvegica*. It is probable, therefore, that these waters contain more suspended material than those examined by Fox and his colleagues and are consequently a richer source of carotenoids than their data would suggest.

Crustacea become increasingly important in the food of *M. norvegica* as it grows. During the spring increase, copepods predominate but at other times of the year the presence of compound eyes indicated that eucaridan species are more commonly eaten. Many of these eyes were undoubtedly of euphausiid origin. In bulk of material the most important copepods in the planktonic community inhabited by *M. norvegica* are *Calanus finmarchicus* and *Pareuchaeta norvegica*. We have found occasionally small amounts of vitamin A in *P. norvegica* (Fisher *et al.* 1952) but none at all in *Calanus finmarchicus* (Fisher *et al.* 1952; cf. Euler, Hellström & Klussmann, 1934, and Lederer, 1938). We have now analysed twenty-two other species of copepod and found the vitamin in only two species of *Gaetanus* from the Bay of Biscay (Fisher & Kon, 1959). All these results refer only to the ester and alcohol forms of vitamin A. The recent finding of vitamin A aldehyde in fish eggs (Plack, Thompson & Kon, 1958) indicated that this form might be present in other marine organisms but not detected by our normal analytical technique. Using the gradient elution method of Plack, Kon & Thompson (1959) we have found no vitamin A aldehyde in *Calanus finmarchicus*. All our evidence indicates that copepods are not a source of preformed vitamin A for euphausiids feeding on them. Earlier results show that the main carotenoid in copepods is astaxanthin possibly with small quantities of β-carotene. In the recent chromatographic analysis of extracts from *C. finmarchicus*, however, using the gradient elution method, we obtained a pigment, or pigments, which exhibited a complex absorption spectrum with three peaks all below 400 mμ. This pigment will be the subject of further study and its possible significance as a provitamin A will be investigated. Previously we demonstrated that the most striking increase in both the absolute amount and the concentration of vitamin A in *Meganyctiphanes norvegica* occurred during the spring period (Fisher *et al.*, 1954) just at the time when, as we have now confirmed, they feed mainly on copepods which contain no obvious provitamin or vitamin A, rather than at other times of year when they are eating the eyes of eucaridan Crustacea which we know to be rich in the vitamin. In laying stress on the absence of compound eyes from the stomachs during the spring feeding period (see Figs. 3 and 4), we realize that our 1958 results did not show this absence. In 1957, however, compound eyes were absent from the stomachs only in the second April and the May hauls, which were taken during the period of 74 days between the first April and the June hauls. In 1958 no hauls were taken over the 78 days that elapsed between the hauls in April and in June. Thus we may well have missed the period corresponding to that in 1957 when no compound eyes were found in the stomachs and the euphausiids were feeding on copepods. Moreover, *Calanus finmarchicus* was not caught in large numbers in the area until 13 May in 1958, which is much later for its appearance than is normal; in 1957, it became abundant between the first and second collecting trips in April.

We have suggested astaxanthin derived from copepods as a possible precursor for vitamin A in the euphausiids (Fisher *et al.*, 1954; Kon, 1954) but this pigment is present not only in copepods but in all crustaceans, especially in their eyes (Fisher *et al.*, 1952). If astaxanthin is indeed the precursor euphausiids obtain from copepods it must be in them in a more available form than in other crustaceans to account for the more rapid increase in the vitamin A reserves of euphausiids when they feed almost exclusively on copepods. In any event, the vitamin A they derive from eating other Eucarida is unlikely to account for all the reserves built up in *Meganyctiphanes norvegica*. Some additional source must exist.

After detritus and Crustacea, dinoflagellates appear to us to be the next most important component of the diet of *M. norvegica*, particularly in the younger adults. In the late summer and early autumn dinoflagellates reach their maximum incidence in the stomachs, which may be packed full of them. The only information we have about provitamins and vitamin A in dinoflagellates is for the marine species *Prorocentrum micans* (Scheer, 1940) and two species of *Peridinium*, the freshwater *P. cinctum* (Strain, Manning & Hardin, 1944) and the marine *P. trochoideum*[1]. There is no information about the vitamin itself in *Prorocentrum micans* or *Peridinium cinctum*; it was absent from *P. trochoideum*. In all three species the carotenoids included both carotenes and xanthophylls. In *Prorocentrum micans* about 10% of the carotenoids were carotenes and the rest presumably xanthophylls. The carotenes were almost entirely β-carotene in *Peridinium cinctum* and *P. trochoideum* in quantities greater than in diatoms. As in *Prorocentrum micans* most of the carotenoids in *Peridinium* were xanthophylls at a concentration higher than in most diatoms (Strain *et al.*, 1944). The three main xanthophylls separated from extracts of *P. cinctum* were peridinin (first detected in *Peridinium* spp. by Kylin (1927)), dinoxanthin and diadinoxanthin, of which the first was the most abundant (Strain *et al.*, 1944). The chemical properties of these xanthophylls are still unknown, but they are unlikely to be provitamins A. β-carotene from dinoflagellates is, however, undoubtedly an important seasonal precursor of the vitamin for *Meganyctiphanes norvegica*.

Although we agree with Einarsson (1945) and Ponomareva (1955) that diatoms do not form an important component of the diet of *M. norvegica*, those diatoms eaten will contribute to the carotenoids taken up by the euphausiid. Vitamin A itself does not occur in those species in which it has been sought, namely *Coscinodiscus concinnis*, *Skeletonema costatum* and *Thalassiosira gravida*[1]. The main carotene was β-carotene which formed up to about 5% of the total carotenoids. It was the principal carotene in several other species studied by Strain *et al.* (1944). These workers also characterized the xanthophylls. The most abundant was fucoxanthin and of the others the most important were diadinoxanthin and diatoxanthin. Goodwin (1952) has suggested that these two pigments may be *cis*-isomers of lutein and zeaxanthin respectively. If so, neither of them is a provitamin A. Zeaxanthin has the same molecular structure as β-carotene with the addition of an hydroxyl group to each of its β-ionone rings and could be an intermediate between β-carotene and astaxanthin, which has the structure of zeaxanthin with a ketone group in each β-ionone ring. It is possible, therefore, that diatoxanthin may be a connecting link between the important plant carotenoid, β-carotene, in the phytoplankton and the equally important animal carotenoid, astaxanthin, in the crustaceans feeding on it.

Filamentous algae were a constant, if only minor, constituent of the food of

[1] Fisher, L. R., London Univ. Ph.D. thesis, 1953.

Meganyctiphanes norvegica. Most of those eaten were probably green algae with carotenoids similar to those of land plants, possessing β-carotene as their principal vitamin A precursor.

Young *M. norvegica* have in their food several sources of β-carotene, namely dinoflagellates, vegetable detritus of terrestrial origin, algae and diatoms. It is probable that they convert β-carotene into vitamin A like higher animals. As they grow larger they become increasingly carnivorous, feeding more and more on Crustacea, although still taking dinoflagellates when these are abundant. The Crustacea provide them with preformed vitamin A when eucaridan species are eaten, but in the spring copepods are eaten almost exclusively and their principal carotenoid is astaxanthin. It is possible that this carotenoid may be converted into vitamin A just as it is said to be by poeciliid fish (Grangaud & Massonet, 1955). Evidence of the rapid accumulation of the vitamin at a time when the euphausiids are feeding on copepods supports this hypothesis (Fisher *et al.*, 1954).

The fern sporangia found in small numbers in the stomachs of *M. norvegica*, indicate that there may be an inkling of truth in the long-held belief that the bracken-clad hills bordering the loch nourish the Loch Fyne herring, one of the predators of *M. norvegica*, and impart to them and the kippers made from them their renowned high quality (Kerr, 1928, 1949; McCallien, 1938). Macdonald (1927) also discussed the dependence of the herring, through *M. norvegica*, on the abundance of terrigenous vegetable detritus. Essentially the reasoning is correct but we now know that the food chain is longer and more complex, involving both organic and inorganic nutrients from the land. The phytoplankton flourishes on the former and the zooplankton feeds, in turn, on it as well as on the land-derived vegetable material with its carotenoids, especially β-carotene. Such a diet produces specimens of *M. norvegica* in Loch Fyne larger than any we have seen from other waters, including the North Sea, the north Atlantic and the Mediterranean; these large animals are much richer in vitamin A than those we have analysed from the other localities mentioned (Fisher *et al.*, 1955).

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SUMMARY

Feeding intensity in *Meganyctiphanes norvegica* in Loch Fyne reached its peak during the spring plankton outburst, falling slightly during the summer, to be renewed in the early autumn and decreasing to a minimum in November.

There was a well-defined period of increased feeding from December to February, followed by another decrease in March.

The main food items in decreasing order of importance were organic debris and inorganic detritus, Crustacea, dinoflagellates, diatoms, algae, fern sporangia and dipteran egg membranes. Organic and inorganic material was taken at all seasons, although possibly in smaller amounts during the spring feeding period, when the euphausiids spend more time actively swimming.

Crustacean material occurred most commonly in the stomachs in the spring, when the absence of compound eyes indicated that it was probably all of copepod origin. These eyes, mostly euphausiid, occurred frequently in the stomachs from June onwards and during the late winter.

Dinoflagellates predominated in later summer when some stomachs were packed with them. Diatoms were most numerous during the spring but were never eaten to the same extent as the dinoflagellates. Fern sporangia and dipteran egg capsules appeared in the stomachs in the spring and summer months. Algae were eaten by a few animals at all seasons.

Size of the animal and feeding intensity showed no apparent relationship. The percentage of stomachs containing organic and inorganic particles increased with the size of the animal. Crustacean remains also occurred more frequently in larger animals, but less commonly in the largest specimens of all. Dinoflagellates were eaten by all sizes, with the highest incidence in those of intermediate size.

No consistent differences were observed between the intensities of feeding by day and at midnight. When feeding was intensive, especially in the spring, the relative uptake of organic and inorganic material was lower than during periods when feeding was on a reduced scale.

When the dinoflagellates were abundant in the plankton they occurred in large numbers at all times, but, when they were scarcer, the numbers of *Ceratium*, *Dinophysis* and *Peridinium* tended to be higher in stomachs by day than by night and those of *Prorocentrum* and *Phalacroma* by night.

Samples of mud taken at a depth of 175 m from the bottom of Loch Fyne contained no measurable vitamin A. The amount of carotenoid pigments and of β-carotene increased with the distance below the surface.

Preformed vitamin A is present in compound eyes and its precursor, β-carotene, in dinoflagellates, diatoms, algae and fern sporangia, all of which are eaten by *Meganyctiphanes norvegica*, and so contribute to its high vitamin A reserves. In the spring, however, when the food consists almost entirely of copepods with astaxanthin as their main, if not only, carotenoid, vitamin A concentrations increase most rapidly. It is possible that astaxanthin is a vitamin A precursor in euphausiids.

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