Notes on Euphausiids.

By

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With Figures 1 and 2 in the Text.

(a) Vertical Migration.

THE material for this paper was obtained in two voyages on the Milford steam trawler *Macaw,* and I owe all thanks to Capt. Rumble, and to the crew, not only for much practical help, but for a pleasant time. Capt. Rumble's knowledge of the area worked, based on 30 years' experience, can only be compared with a farmer's knowledge of his own acres, and he has been responsible for determining the position of each haul.

To my Milford host, Mr. Frank B. Rees, I have pleasure in acknowledging my thanks for arranging my voyages, and for many other kindnesses.

Finally, I wish to thank Dr. Allen, F.R.S., for suggesting the work, and for continual advice and encouragement ; and the naturalists at the Laboratory, who have given me so much help in my first effort. The work has been carried out with the help of a grant from the Department of Scientific and Industrial Research.

OBJECT AND METHOD.

This note seeks to demonstrate a vertical migration in certain Euphausiids, by showing that these crustacea are present on, or absent from, the sea-bottom at rhythmically recurring periods.

The hauls were made with the net described below. It was attached to the bosom of the headline of the commercial trawl, and was hauled for a period of between 4½ and 5 hours, in the ordinary fishing operations of the ship. The hauls are, therefore, strictly comparable, and yield ample evidence of the definite nature of the vertical migrations.

Holt and Tattersall (1902–3), in their work on Schizopods, used " nets and bags of fine material fastened to the back of the beam-trawl " ; the net used here is carried, on the headline, at least 4 feet above the ground, and well in advance of the foot-rope, or any other part of the gear which might disturb the soil. The forms taken in the net may be regarded as truly pelagic at the depth and time of haul, and not stirred up from the soil by the passage of the net.

AREA WORKED.

The bulk of the fishing was done on the Smalls grounds, on an area roughly crescentic about the Smalls Light between the bearings S.W. by S., and N.W. ½ N. At the first named limit the light was 36 or more miles distant, at the latter just showing at 18 miles. Fishing was done in depths ranging from 46 to 62 fathoms, 5 hauls in the 24 hours being the rule; and the first voyage was from the 10th to the 16th October, the second from the 18th to the 27th October, 1924.

During the second cruise, a trial trip was made to the Cockburn bank, 80 miles W.N.W. of the Scillies, where a 24-hour series of hauls was made. The fishing was so poor, however, that the ship soon returned to the Smalls.

THE NET USED.

The net is constructed of stramin.* It is 3 feet long, cylindrical in shape, with a diameter of 6 inches: the mouth is supported by a brass ring, to which the net is firmly sewn with the help of a band of duck, or sail canvas. The last 9 inches taper from 6 inches to a diameter of 4 inches, and contain an inner sleeve of medium bolting silk (IV, 50″), which is

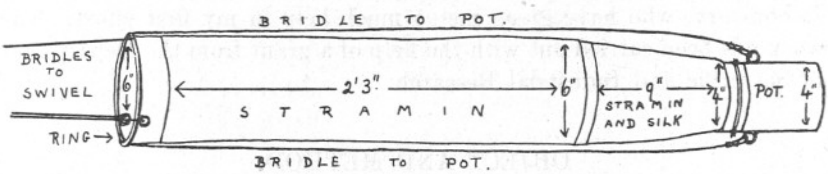

Fig. 1. Small townet of "stramin" and bolting silk, which was attached to the headline of a commercial otter trawl.

attached at the front end to the stramin, but ends freely behind, and is tied, with the outer sheath, over the pot. The last named is preferably independently slung from the ring at the mouth of the net, in order to take the heavy dragging strain off the net itself. Finally, the net is furnished with three legs (bridles) of trawl-twine, which are laid together and secured with a whipping, and spliced to a swivel, which is attached to the headline by a further length of manila.

* "Stramin is a coarse canvas made of hemp, having about 20 threads to 3 cms." Jespersen (1923).

NOTES ON THE CONSTRUCTION OF THE GRAPH.

If the vertical migrations are a constant habit of these Euphausiids, they should be perceptible in all circumstances of depth and locality. The hauls, on which these results are based, are in all depths from 46 to 62 fathoms and over, on every kind of soil, from fine silt to gravel and stones, and include five hauls from the Cockburn Bank, where physical conditions are probably very different from those about the Smalls.

The results of 31 hauls have been combined in a graph.

The contents of each haul were separated and counted individually, 28,000 specimens of *Nyctiphanes Couchi* (Bell), and 4000 each of *Meganyctiphanes norvegica* (M. Sars) and *Thysanoessa* spp. being dealt with. In the present uncertain state of classification of the genus Thysanoessa, both species are counted together without distinction.

These figures are set out in Table A (p. 738), with the time of capture and depth; similar figures for shrimps (in the broadest sense) and mysids, being also given for comparison.

The mean number of each species caught per hour, during each haul, is obtained by dividing the total number caught, by the duration of the haul in hours, portions of an hour counting as a whole hour.

On the whole series of 31 hauls, for each hour of the day and night, the average number of individuals is obtained by taking the mean of the average number per hour caught during each haul that extends over that hour.

These figures are given in Table B (p. 738), and from them the graph is constructed. In the graph, the numbers for Meganyctiphanes and Thysanoessa are multiplied by ten, in order to make their curves more readily comparable with that of Nyctiphanes.

Less reliance can be placed on the curves for Meganyctiphanes and Thysanoessa than upon that for Nyctiphanes, because the two former species are absent from many hauls, and are in others only present in two's and three's. It will be noticed that the numbers of these two species tend to increase as the water deepens, while their presence on the Cockburn Bank is very marked. This is again a disturbing factor in any effort to show the behaviour of these crustacea with reference to light alone. Meganyctiphanes and Thysanoessa, in fact, seem to be oceanic species where Nyctiphanes is a neritic species. Their recorded distribution favours this, and in the present hauls they occur with other organisms, and especially Pteropods, which point to oceanic conditions. Hence the absence of Meganyctiphanes and Thysanoessa from a given haul may mean, either that they are absent from the locality, or that they are not on the sea-floor at the time of haul, and the results are complicated accordingly.

TABLE A.

SMALLS.

Haul No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Date, Oct.	11	11–12	12	12	13	13	13	13–14	14	14	14–15	15	15	15–16	16	16
Time From	11.50	21.30	07.30	17.30	03.00	08.00	14.00	23.30	09.30	19.30	24.00	05.00	15.00	20.00	01.00	07.30
Time To	16.00	02.30	12.00	22.15	08.00	12.30	18.00	04.30	14.30	24.00	05.00	10.00	20.00	01.00	06.00	12.00
Depth [fms.]	48	48	56	48	48	46	48	56	60	54	51	52	52	50	54	54
	58						52	58	62	54		56	54	62–48		
Nyctiphanes	1967	6	Foul haul.	41	372	47	383	35	742	4	4	682	42	3	13	630
Meganyctiphanes	0	1		0	0	0	118	25	271	2	2	577	213	0	7	55
Thysanoessa	10	2		1	14	7	52	28	476	66	50	280	60	0	13	119
Mysids	0	2		8	31	2	23	9	49	41	35	8	79	4	111	88
Shrimps	0	7		29	11	1	5	9	8	9	3	5	18	8	8	17

	COCKBURN BANK.					SMALLS.									
Haul No.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Date, Oct.	19	19	19–20	20	20	21	21	22	23	23	24	24	25	25	26
Time From	11.30	16.30	22.00	03.00	09.00	08.30	18.00	17.30	04.00	14.00	07.00	18.00	00.00	10.00	00.00
Time To	15.30	21.30	03.00	08.30	14.00	13.00	23.00	22.00	09.00	19.00	11.30	23.00	05.30	14.00	06.00
Depth [fms.]	64	65	65	52	65	55	51	50	51	50	58	54	50	56	56
	66	66								65			54		
Nyctiphanes	576	132	2	8	214	3957	15	14	4455	9000+	1281	17	4	5194	1
Meganyctiphanes	111	32	4	90	30	933	20	1	4	270	98	6	4	255	9
Thysanoessa	175	162	366	32	285	123	240	13	26	58	90	97	81	358	185
Mysids	0	24	75	26	0	2	33	14	66	11	0	35	41	3	48
Shrimps	0	9	33	10	0	0	8	7	13	1	0	4	1	1	4

The numbers of each kind of Crustacean taken at the sea-bottom, together with the depths and times of haul. [Midnight is 2400, midday 1200.]

TABLE B.

Hour of Day	01	02	03	04	05	06	07	08	09	10	11	12 noon
Mean Number per hour of Nyctiphanes Couchi	1·4	1·4	9·1	101	115	153	213	236	243	285	290	294
Mean Number per hour of Meganyctiphanes norvegica	1·2	1·2	3·3	3·7	16·4	19·1	27·9	49·1	48·5	54	44	49
Mean Number per hour of Thysanoessa spp.	16·6	16·6	15·4	·9	13·5	13·5	15·5	14·7	28	38	33	34

Hour of Day	13	14	15	16	17	18	19	20	21	22	23	24
Mean Number per hour of Nyctiphanes Couchi	373	459	405	386	269	202	192	5·5	4·7	2·0	2·0	1·2
Mean Number per hour of Meganyctiphanes norvegica	56	32	31	27	21·6	16·0	12·9	7·4	1·6	·9	1·3	1·2
Mean Number per hour of Thysanoessa spp.	33	36	13·3	11·7	9·8	15	14	15	14	19	22	19

The mean numbers of each Euphausiid present on the sea bottom for each hour.

THE GRAPH.

It is plain that *Nyctiphanes Couchi* (Bell) has a period of maximum abundance on the sea-floor at 2 p.m., that the numbers fall away very rapidly until 8 p.m., when, shortly after sunset, very few specimens are present. This state of affairs persists until 3 a.m., when a comparatively steady increase in numbers is maintained until the maximum is reached. Dr. Lebour (1924) states that "adults (of Nyctiphanes) and older larvæ all appear to live very near the bottom in the daytime, and come to the surface at night"; the graph bears out the first part of this statement well.

It is widely known that Nyctiphanes approaches the surface at night, and by the courtesy of Miss Lebour and Mr. O. D. Hunt I am allowed to use the following unpublished records of Nyctiphanes taken at the surface at night:—

13.12.23.	11.30 p.m.	Eddystone.	Nyctiphanes cccc.
14.12.23.	3 a.m.	Rame–Eddystone.	Nyctiphanes ccc.
13.11.24.	9 p.m.	30 miles N. of Seven Stones.	"A large haul of Nyctiphanes."

The last record is from almost the same locality and at the same time as many of my hauls.

Finally, some young-fish-trawl hauls have just (22.12.24) been examined, which show the vertical migration well. Taken at L4* just before dawn, at the surface 9 specimens of Nyctiphanes were found, at midwater 685, and at the bottom, 301. Interpreted according to the graph (p. 740) accompanying this paper, this shows that while many specimens of Nyctiphanes are already on the bottom, the bulk of these crustacea are still moving downwards, leaving a few stragglers at the surface.

The curve for *Meganyctiphanes norvegica* again shows a definite period of abundance on the sea-floor by day, and a definite absence at night. It is noticeable, when the hauls are made, that late at night, when Nyctiphanes has become scarce, Meganyctiphanes is still conspicuous, and seems to linger longer on the bottom than Nyctiphanes.

Holt and Tattersall, in their observations on the vertical distribution of *Meganyctiphanes norvegica* from the Biscayan Plankton collected during the cruise of H.M.S. *Research* in 1900, say: "*M. norvegica* . . . was never taken, even at night, in surface nets. It occurs three times in nets towed at 25 fathoms, and thence to the surface, four times in nets towed at 50 fathoms, and only becomes general in nets towed

* Five miles from the shore between Plymouth and the Eddystone Light.

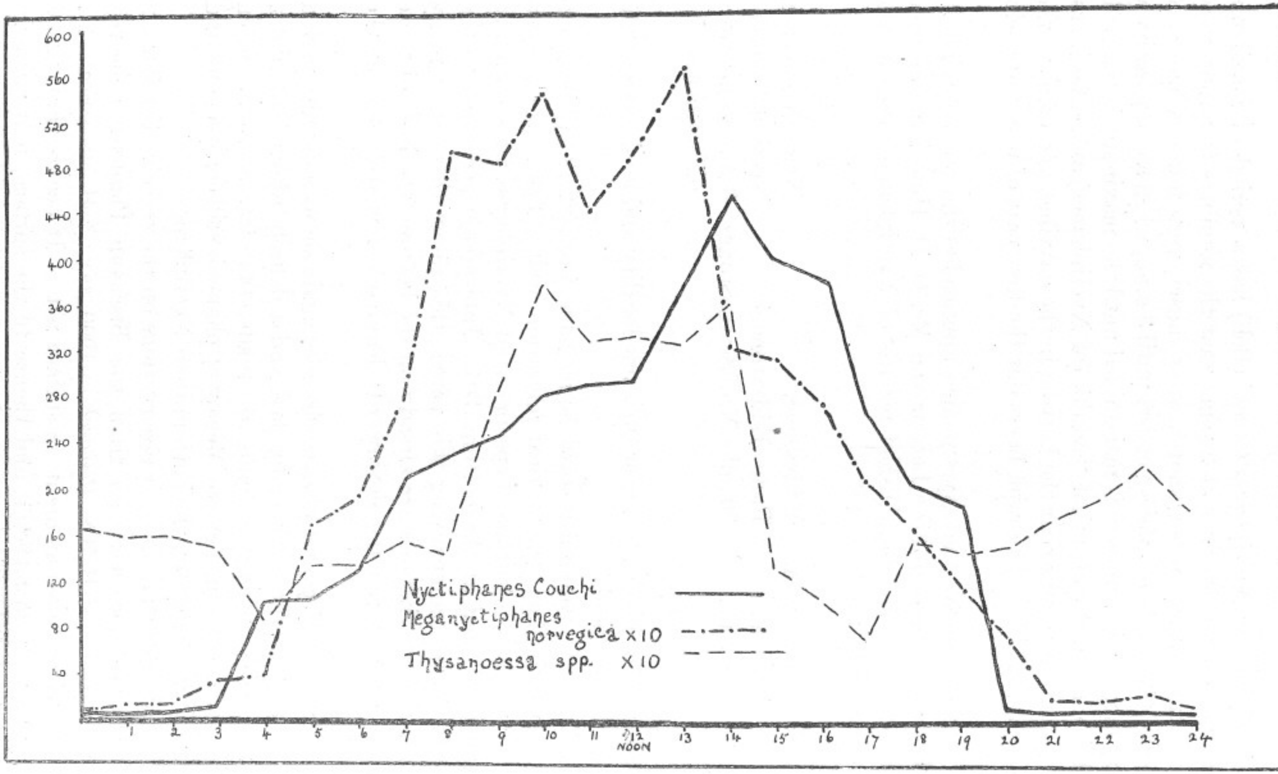

FIG. 2. Graph showing the average number of individuals captured per hour during each hour of the day and night. The figures for Meganyctiphanes and Thysanoessa are multiplied by ten.

at 100 fathoms." "We suppose that the species is subject to no marked diurnal movement, but is . . . an inhabitant of the upper 100 fathoms." Finally the authors add "The species certainly occurs at the surface, or quite near it, at night off the west coast of Ireland."

Thysanoessa differs in that it exhibits a double crest, one at midnight, and a second, much greater one, at 10 a.m. The corresponding periods of scarcity are at 4 a.m. and 5 p.m.; but the amplitude of the waves is much smaller than in the first two species, and in favourable conditions Thysanoessa seems to be present in quantity, at all hours, on the sea-floor.

DISCUSSION.

The graph suggests that light is a factor of prime importance in governing vertical migration. Helland-Hensen, in Murray and Hjort (1912 a.) states that a sensitive plate is blackened in 80 minutes at 1000 metres; while Shelford and Gail (1922) show that in the waters of Puget Sound the light intensity at 120 metres was 14-foot candles, where that at the surface was 6550. But the roughness of the surface, and freedom from silt, are of vital importance to light penetration.

The indication is, therefore, that sufficient light may be present, in this case, to affect organisms taken at the greatest depths worked (62 fathoms), and the possible part played by light in these movements will be discussed later.

The search for food may play its part. 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. On the other hand, Dr. Lebour (1924) states that *Nyctiphanes Couchi* taken at night in the upper waters had been feeding on diatoms, with Sagitta and crustacea; while Holt and Tattersall (1902–3) say, of Meganyctiphanes, that it had its leg-baskets "more or less stuffed with prey, including copepods, schizopod and decapod larvæ, fragments of Spirialis, and other matter."

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.

Esterly (1911) demonstrates a vertical migration in *Calanus finmarchicus* for the San Diego waters. He shows that at sunset an immediate upward movement commences, that the majority of the specimens are collected between 5 and 10 fathoms from the surface at midnight, and that after this they begin to leave the surface, collecting in greatest quantity at 100 fathoms by 6.35 a.m. His conclusion is that light acts by altering the geotropism of these animals in such a way that the sense of the tropism is reversed.

This suggestion may be employed to explain the analagous vertical migration exhibited by these Euphausiids. When the light grows stronger, they become positively geotropic, and swim downwards, where they remain just above the sea-floor until the light begins to fail. Their positive geotropism is then either reversed or overcome, and they quit the bottom.

Against this, is the fact that Meganyctiphanes, at least, is recorded from well over 1000 metres, where the light must be exceedingly feeble ; and that in January, 1924, at midday, I found great numbers of Meganyctiphanes at the surface, and captured one in a bucket, between Cape St. Vincent and the Morocco coast.

Finally, Esterly (1917) noted a "physiological rhythm" in "two species of Acartia, and, to some extent, in Calanus." It is easily noted that Caridea and Mysids, Amphipods and Cumacea, become much more lively at night ; they appear much more frequently in my net. *Nephrops norvegicus* (the "Dublin Prawn") and Portunus are much scarcer in the trawl at night, as compared with the huge bags full which are often swept up by day. Fishermen say that the same applies to the "Queen" (*Pecten opercularis*). A physiological rhythm, resulting in a greater activity at night, may be an important factor in the vertical movements of Euphausiids.

As important consequences of vertical movements in these schizopods, one might mention, firstly, that the species are brought within the reach of pelagic fish, and especially herring and mackerel ; and, secondly, that there is introduced the possibility of extensive migrations on the tidal streams. The tides run very strongly in the Smalls area, and with a favourable combination of tidal conditions with the hours of darkness, a specimen which comes within the full force of the tidal stream, aided perhaps, by a surface drift due to wind, might return to the bottom 18 miles distant from its starting point. It is assumed that the stream is greatly diminished in intensity, owing to friction, in the lowest fathom or two of water, where these Euphausiids apparently congregate during the day.* With this assumption, it is worth suggesting that they use the tidal streams to effect the sudden appearances and disappearances which they often exhibit, their own powers of locomotion being relatively slight.

* Mr. D. J. Matthews, in a letter, has kindly informed me that "the tide streams on the bottom are strong, often nearly as strong as at the surface, but not always in quite the same direction."

(b) Euphausiids and Hake.

The importance of Euphausiids to the Fisheries may be seen from the following records of their presence in the stomachs of food-fish :—

Mackerel (Bell, 1865); Herring (Brook and Calderwood, 1885); Mackerel, Herring, and Sea-trout (Holt and Tattersall, 1902–03); Mackerel, Pilchard, Sprat, and Herring (Dr. Lebour, 1924); while Hardy (1924) shows that *Nyctiphanes Couchi* forms 5·6 per cent of the total annual food of herrings taken in drift-nets.

To this important list I would add hake, and suggest that Euphausiids are of importance directly to small hake, and indirectly to the larger hake. By "small hake," I do not refer to the "small hake" of the market, which have a minimum length of about 18 inches, but to the little hake of 8 or 10 inches upwards, which are often taken in vast quantities, and are commercially valueless.

All the fish mentioned in the first paragraph are pelagic. It is a matter of common knowledge that hake are pelagic at night, and leave the sea-floor to hunt in the upper waters. This is so much the case, that trawlers working the distant deep-water grounds will lie hove-to all night rather than waste coal in useless fishing. I suggest an explanation of this fact, though there are certain localities, such as off Rabat in Morocco, and to the west of Scotland, where hake is said to be equally abundant in the hauls by night as by day.

Big hake are omnivorous, but may exhibit marked preferences. Thus, when the shoals of herring and mackerel are present, hake will follow them, and feed on stragglers. They will take almost anything, however, and I have found Nephrops and Loligo in the stomachs of hake.

In this case, the chief food of hake was found to be small hake, bib, horse-mackerel, and smelt, with a strong predominance of small hake.

A series of observations on the stomach contents of these fish was made. Half a bucket full of each kind (about 25 specimens) was dissected and the stomach contents noted.

On small hake 20 such observations were made.

(*a*) Seven batches of hake caught between 8 p.m. and 6 a.m. These hake, which had stayed on the bottom, or returned thither during the night, had either empty stomachs or decomposed remains; in two batches only were a few Meganyctiphanes found, with frequent fragments of shrimps.

(*b*) Seven batches of hake caught between 6 a.m. and 2 p.m. These contained abundant Meganyctiphanes and less Nyctiphanes in every case, except one batch caught at 9 a.m. on October 23rd, in which Meganyctiphanes was rare.

(*c*) Six batches of hake caught between 2 p.m. and 8 p.m. Of these, one batch taken at 4 p.m. on October 26th contained abundant fresh Meganyctiphanes, with Nyctiphanes and various shrimps. In all other cases the stomachs were empty, or contained half-digested remains of Meganyctiphanes, whose eyes were very noticeable, with shrimps.

Thirteen batches of bib (*Gadus minutus*) were similarly dealt with. This fish is present in equal numbers throughout the day and night, and it seems to feed most constantly on shrimps, chiefly Crangon, Pandalus, Nika, and more rarely, Alpheus, with Gonoplax, Portunus, and small Nephrops. Sepiola is occasional, and there is one note of a small fish being present. In 5 out of 6 batches of day-caught bib, Meganyctiphanes, and especially Nyctiphanes, were present in quantity, in addition to the usual diet of other crustacea. In no case are Euphausiids present in night-caught bib.

Three batches of horse-mackerel (*Caranx trachurus*) were examined. This fish is truly pelagic, and makes irregular appearances on the sea-bottom. A batch taken at 11 a.m. had empty stomachs; at 1 p.m. and at 2 p.m. batches were examined which contained abundant Nyctiphanes.

Smelt (*Osmerus eperlanus*) is also a true bottom liver, and is present in equal quantity at all hours. Two batches were examined: one at 1 a.m. contained unidentifiable debris, one at 7.15 p.m. contained abundant Nyctiphanes.

Thysanoessa was only noted once, in a hake, and can only be taken rarely, in comparison with the other two species of Euphausiids.

CONCLUSIONS.

While all these fish are probably omnivorous, they may exhibit distinct selection. Small hake seem to select Meganyctiphanes, and to a less extent, Nyctiphanes, in preference to other crustacea or small fish. It seems fair to suggest that when Meganyctiphanes leaves the bottom, the small hake will follow it in its vertical migration, and thus no longer appear in the trawl.

Big hake are likewise omnivorous, but in the present case show a preference for small hake over bib or smelt. I suggest, therefore, that they follow the small hake into the upper waters, where they may also find other pelagic fish, such as mackerel, horse-mackerel, and occasionally herring.

Bib and smelt are bottom-livers, and take what they can find, chiefly shrimps and other decapods, at all hours, and, in addition, the Euphausiids (especially Nyctiphanes) when these are present on the bottom during the day.

Hjort (1912) repeatedly refers to vertical migrations in many other fishes ; and whether this tentative explanation of the vertical movements of hake will hold for other fishing grounds, can only be seen by much further work in this direction. It is hoped to continue observations throughout the year.

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(*b*) Hjort, J., pp. 95, 96, 664.

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