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VITAMIN A AND CAROTENOIDS IN CERTAIN INVERTEBRATES

III. EUPHAUSIACEA

By L. R. Fisher, S. K. Kon and S. Y. Thompson
National Institute for Research in Dairying, University of Reading

(Text-figs. 1 and 2)

Introduction

Our published work has shown that the northern euphausiids, *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T. inermis*, contain much higher concentrations of vitamin A than we have found in any other marine Crustacea (Kon & Thompson, 1949*a*; Batham, Fisher, Henry, Kon & Thompson, 1951; Fisher, Kon & Thompson, 1952, 1953, 1954). In the antarctic species, *Euphausia superba*, the concentration of vitamin A in samples taken from the alimentary canals of baleen whales (Thompson, Ganguly & Kon, 1949; Kon & Thompson, 1949*b*) was similar to that found in *Meganyctiphanes norvegica* from the gut of arctic baleen whales (Fisher *et al.*, 1952), but both were very much lower than in free-swimming *M. norvegica*. No corresponding free-swimming specimens of *Euphausia superba* had been analysed.

This evidence indicated that the Euphausiacea, as a group, might be richer in vitamin A than other Crustacea. We have, therefore, attempted to obtain as many other euphausiid species as possible for a comparative study, and in fact have now information about eight further euphausiids. Unfortunately, we found no other environment as favourable as Loch Fyne or Monaco for catching easily large numbers of these animals. The numbers of specimens analysed of these species were, therefore, relatively small, but, in most instances, valid results were obtained.

We have now studied samples of *Meganyctiphanes norvegica* from several localities, and the analytical results will be compared to illustrate any geographical variations in the vitamin A and carotenoid concentrations in this species.

During our study of *M. norvegica* (Fisher *et al.*, 1953) we noted certain discrepancies in vitamin A concentrations from different groups, and these we attributed to possible impurities in the preservatives used. We discovered, however, similar differences in the vitamin A content of various groups of *Euphausia pacifica* (see p. 83) where the quality of the preservative was not in doubt and performed therefore some experiments on *Meganyctiphanes*

norvegica and *Thysanoessa raschii* collected from Loch Fyne to elucidate the problem. The results are given in a separate section immediately following those of the systematic studies.

Material Collected

In all, eleven species of euphausiids were collected, some by ourselves and others by marine biologists on various research cruises or whaling expeditions.

Meganyctiphanes norvegica (M. Sars) was the most widely obtained species. Apart from our own collections from Loch Fyne (Fisher *et al.*, 1952, 1954) and from Monaco (Fisher *et al.*, 1953), several groups of this species were collected for us by Dr J. H. Fraser during a cruise of the Scottish Home Department's Fisheries Research ship *Scotia* in August 1951. During his researches on whale-marking at the Norwegian whaling station at Steinshamn in July 1953, Mr Robert Clarke collected samples of this species from the stomach of a 55 ft. ♂ Fin Whale.

Thysanoessa raschii (M. Sars) is a fjord-dwelling species (Einarsson, 1945) and we have obtained specimens only from Loch Fyne.

T. inermis Kröyer lives in more open waters but, apart from the groups that showed an apparent relationship between vitamin A concentration and depth, taken near the Faeroes (Fisher *et al.*, 1952) we have analysed no other free-swimming specimens. A sample of this species was, however, taken from the throat of a 72 ft. ♂ Blue Whale by Mr Clarke at Steinshamn.

Several samples of the antarctic species, *Euphausia superba* Dana, have been analysed. Specimens were collected for us during the cruise of the R.R.S. *Discovery II* in 1950–51, others were taken by tow-net from the whaling factory ship *Balaena* during her 1951–52 expedition, by Mr S. Brown and Mr R. M. Brachi, and another group of specimens was collected during the 1952–53 expedition of this ship by Mr Brachi and Mr H. W. Symons. Some of this last group were collected from the engine-room inlets of the *Balaena* and others by net from a meat-carrying ship.

During a cruise of R.R.S. *Discovery II* in the North Atlantic in August and September 1952, Mr Foxton obtained for us specimens of *Stylocheiron elongatum* G. O. Sars and *Thysanopoda acutifrons* Holt & Tattersall.

While visiting the United States in 1953, one of us (S. K. K.) spent 2 weeks at the Scripps Institution of Oceanography at La Jolla, California, and took part in a 3-day cruise (25–27 May) of the research vessel *Horizon* in waters some 150 miles west from San Diego, during which five species of Pacific euphausiids were collected with a 1 m closing net at depths from 400 m to the surface. These were *Stylocheiron maximum* Hansen, *Euphausia pacifica* Hansen, *Nematoscelis difficilis* Hansen, *Thysanoessa gregaria* G. O. Sars and *T. spinifera* Holmes.

Methods of Preservation

The euphausiids collected from Loch Fyne and Monaco were preserved by boiling in sea water, as previously described (Fisher *et al.*, 1952, 1953), and by keeping the specimens in deep-freeze during the journey to this laboratory. The Monaco specimens were brought, frozen, by air and so were only a few hours out of deep-freeze. Eyes and bodies were separated at Shinfield and the parts were placed in absolute alcohol and stored in the deep-freeze.

The Pacific specimens were preserved by boiling and storage in the ship's refrigerator until the return to La Jolla. With the exception of two of the three groups of *Euphausia pacifica* collected, eyes and bodies were then separated in the laboratory and preserved in absolute alcohol. The two groups of *E. pacifica* were preserved whole in absolute alcohol. All this material was kept in cold storage until despatched to Shinfield. It was at atmospheric temperature for the 6 weeks during which it was in transit.

The specimens collected by Mr Clarke at Steinshamn were preserved in absolute alcohol, and those of Dr Fraser on the *Scotia* by boiling and refrigeration. Both groups were sent to us by post. On arrival here, the alcohol specimens were immediately deep-frozen, and the boiled specimens, which appeared to be in good condition after 2 days in postal transit from Aberdeen, were dissected into eyes and bodies for separate preservation in alcohol in the deep-freeze. Specimens were sorted into size-groups.

Groups of *E. superba* collected from the *Balaena* were preserved by boiling and storage in the ship's deep-freeze. Those brought back in May 1952 were sent to us from Liverpool, where the ship docked, by post. The specimens collected in 1953 were kept in deep-freeze on arrival at Liverpool and were transferred in an insulated vehicle to similar storage in London whence they were collected and brought back to Shinfield in an insulated container. Both consignments were separated into eyes and bodies and the 1953 specimens were also size-grouped by length in the way previously described (Fisher *et al.*, 1952, 1954).

Specimens of *E. superba* collected from the *Discovery II* were separated into eyes and bodies immediately after catching and the parts were preserved in absolute alcohol. Unfortunately these specimens were inadvertently stored in a cupboard where the temperature was rather high. The euphausiids collected during the north Atlantic cruise of the *Discovery II* were preserved by boiling and storage in the refrigerator until arrival at Plymouth. They were sent to us by post and arrived in good condition. After dissection into eyes and bodies, which were preserved separately in absolute alcohol, the specimens were stored in the deep-freeze.

In this study we have found that the eyes of *E. pacifica*, when analysed separately from the bodies, had a high concentration of vitamin A, but no vitamin A at all was present in the animals preserved whole. We noted

similar discrepancies in our work on *Meganyctiphanes norvegica* from the Mediterranean (Fisher *et al.*, 1953). To investigate further this loss of vitamin A from whole preserved animals, experiments were now done on *M. norvegica* and *Thysanoessa raschii* collected from Loch Fyne on 21–22 October 1953. The specimens were separated into groups of uniform size, 23–25 mm long for *Meganyctiphanes norvegica* and 11–13 mm long for *Thysanoessa raschii*. These groups were then divided into smaller lots, each of twenty-five specimens of *Meganyctiphanes norvegica* or of twenty specimens of *Thysanoessa raschii*. Of sixteen such lots for each species, eight were boiled and eight left raw. From each group of eight lots four were separated into eyes and bodies and four left whole. All the material was then preserved in absolute alcohol. Two lots of boiled whole animals and corresponding groups of bodies and eyes and one lot of raw whole animals and corresponding bodies and eyes were kept at room temperature and all the rest of the material was stored at -25° C in the deep-freeze. Analyses were done at intervals on successive groups.

Analytical Methods

The same method of analysis for carotenoids and vitamin A was used as reported previously (Fisher *et al.*, 1952). When the samples analysed were sufficient for the purpose, as with *Nematoscelis difficilis*, *Thysanoessa inermis*, *T. raschii*, *Meganyctiphanes norvegica*, *Euphausia pacifica* and some groups of *E. superba*, chromatography on alumina columns was done before saponification in order to separate vitamin A ester from vitamin A alcohol. With species of which we had only a few specimens, only one chromatography was done, after saponification, and vitamin A was estimated all in the alcohol form. The species treated in this way were *Stylocheiron elongatum*, *S. maximum*, *Thysanoessa gregaria*, *T. spinifera*, *Thysanopoda acutifrons*, and the remaining groups of *Euphausia superba*.

Results

Meganyctiphanes norvegica (*M. Sars*)

Specimens from Whales. Two samples of krill, identified as *M. norvegica*, from the stomach of a 55 ft. 5 in. ♂ Fin Whale, were analysed. The results are given in Table I. The concentrations of fat and vitamin A were considerably higher than in previous specimens of this species from whales (Fisher *et al.*, 1952), although the astaxanthin concentrations were similar to those in earlier analyses. The krill had probably been more recently swallowed by the whale than on the previous occasions and less of the vitamin A had been leached out of it.

Specimens from Different Localities. As previously mentioned, we have now information about specimens of *M. norvegica* from several localities. Taking into account the effects of size and season (Fisher *et al.*, 1952, 1954), it is now possible to compare some of the groups. Some of the results shown in Tables

II–IV have been previously reported (Fisher *et al.*, 1953, 1954). In Table II, groups of specimens collected in the Sandy Bank area (61° 54′ N., 05° 45′ W.), near the Faeroes, are compared with groups of similar weights collected in Loch Fyne in November 1950. Fat, vitamin A and astaxanthin were all in similar concentrations in specimens from both areas, apart from two Loch Fyne groups with rather higher concentrations of astaxanthin. In Table III are compared groups of animals collected during August 1951, at a station in the North Atlantic, in the port of Monaco and in Loch Fyne. Whereas the

TABLE I. OIL PER CENT, VITAMIN A PER GRAM AND PER GRAM OIL AND ASTAXANTHIN PER GRAM AND PER GRAM OIL IN EUPHAUSIIDS FROM WHALES AT STEINSHAMN, NORWAY

Species	Weight (g)	Oil (%)	Vitamin A i.u./g	Vitamin A i.u./g oil	Astaxanthin μg/g	Astaxanthin mg/g oil
Specimens from stomach of 55 ft. 5 in. ♂ Fin Whale, collected 17. vii. 53						
Meganyctiphanes norvegica	26	2·2	7·0	310	41	1·8
M. norvegica	22	2·4	9·8	405	62	2·6
Specimens from throat of 71 ft. 8 in. ♂ Blue Whale, collected 16. vii. 53						
Thysanoessa inermis	177	0·9	9·3	1121	32	3·9

No β-carotene was detected in either species.

concentrations of astaxanthin were nearly the same in each set of size-groups from the different localities, the vitamin A reserves of North Atlantic specimens were lower than of those from Loch Fyne or Monaco. The fat concentration in the Monaco specimens was much lower than in those from more northerly waters. Table IV gives the analytical results for groups collected from Loch Fyne and the port of Monaco in January and February 1952. In January the concentrations of vitamin A and astaxanthin were higher and the fat concentrations lower in Mediterranean than in Loch Fyne specimens. In February the astaxanthin concentrations were again higher in the Monaco specimens but the difference between the vitamin A reserves in specimens from the two localities was reduced. The fat concentrations of these two sets of groups were similar.

Range of Vitamin A Concentrations. We have now analysed 258 groups of *M. norvegica*, selected by length at 2 mm intervals, in the way previously described (Fisher *et al.*, 1954). The number of specimens per group varied between 1 and 359 and the vitamin A concentrations between 3·1 and 260 i.u./g. The histogram in Fig. 1 shows the number of groups at each concentration and the bulk of these lies between 10 and 20 i.u./g, the average for the whole series, weighted for the numbers of specimens in the groups, being 15 i.u./g. The very high concentrations, namely, those over 100 i.u./g, occurred in only a few groups, all of larvae (see Fisher *et al.*, 1954).

TABLE II. OIL PER CENT AND VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN *MEGANYCTIPHANES NORVEGICA* FROM DIFFERENT LOCALITIES

Specimens collected during November 1950

Locality	Date	No. of specimens	Av. wt. (mg)	Oil (%)	Vitamin A		Astaxanthin	
					i.u./spec.	i.u./g	μg/spec.	μg/g
Sandy Bank, Faeroe	6	91	80	3·9	1·3	16	5·1	65
Sandy Bank, Faeroe	6	225	100	4·1	1·5	16	5·4	55
Loch Fyne	21	93	85	3·2	1·3	15	4·8	56
Loch Fyne	21	92	62	4·6	1·0	17	5·8	93
Loch Fyne	21	238	66	4·0	1·2	18	4·5	68
Loch Fyne	21	174	55	5·1	1·1	20	5·1	93

TABLE III. OIL PER CENT AND VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN *MEGANYCTIPHANES NORVEGICA* FROM DIFFERENT LOCALITIES

Specimens collected during August 1951

Locality	Date	No. of specimens	Av. wt. (mg)	Oil (%)	Vitamin A		Astaxanthin	
					i.u./spec.	i.u./g	μg/spec.	μg/g
63° 18′ N., 18° 39′ W.	29	33	66	2·9	0·5	7·4	3·1	46
Loch Fyne	16	164	55	1·2	0·6	11	2·2	40
Loch Fyne	16	210	80	2·4	0·9	11	2·8	35
63° 18′ N., 18° 39′ W.	29	14	222	2·9	1·7	7·8	9·3	42
Monaco	24	224	224	0·5	6·5	29	14	62
Loch Fyne	16	5	265	5·2	6·5	25	12	46
63° 18′ N., 18° 39′ W.	29	16	297	3·7	3·3	11	22	74
Loch Fyne	16	11	326	6·1	5·2	16	15	47
63° 18′ N., 18° 39′ W.	29	29	360	4·7	3·7	10	17	47
Loch Fyne	16	6	338	4·8	6·0	18	17	50

TABLE IV. OIL PER CENT AND VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN *MEGANYCTIPHANES NORVEGICA* FROM DIFFERENT LOCALITIES

Specimens collected during January and February 1952

Locality	Date	No. of specimens	Av. wt. (mg)	Oil (%)	Vitamin A		Astaxanthin	
					i.u./spec.	i.u./g	μg/spec.	μg/g
Loch Fyne	16. i.	69	96	2·5	0·9	10	5·2	54
Monaco	29. i.	167	83	1·6	1·5	18	5·4	65
Monaco	29. i.	113	80	1·2	1·6	20	5·6	70
Monaco	29. i.	50	95	0·9	1·6	16	5·2	55
Loch Fyne	13. ii.	8	64	2·2	1·1	17	4·2	66
Loch Fyne	13. ii.	13	97	1·5	0·9	10	4·5	48
Loch Fyne	13. ii.	12	125	0·7	3·0	24	6·1	49
Loch Fyne	13. ii.	26	129	1·2	2·0	15	6·3	49
Monaco	12. ii.	150	79	1·5	1·5	20	5·9	74
Monaco	12. ii.	109	69	1·2	1·6	24	5·6	81
Monaco	12. ii.	50	94	2·0	1·7	18	5·8	62
Monaco	19. ii.	87	94	0·8	1·2	13	5·0	54
Monaco	19. ii.	63	101	1·0	1·2	12	5·7	56

Thysanoessa raschii (*M. Sars*)

We have so far analysed 190 groups of measured specimens of *T. raschii* and the range of vitamin A concentrations is shown in Fig. 2. The concentrations were much more widely distributed than in *Meganyctiphanes norvegica* although half the groups had concentrations between 10 and 45 i.u./g., with a weighted average for the whole series of 33 i.u./g. As in *M. norvegica*, very high concentrations were found only in groups of larvae (see Fisher *et al.*, 1954).

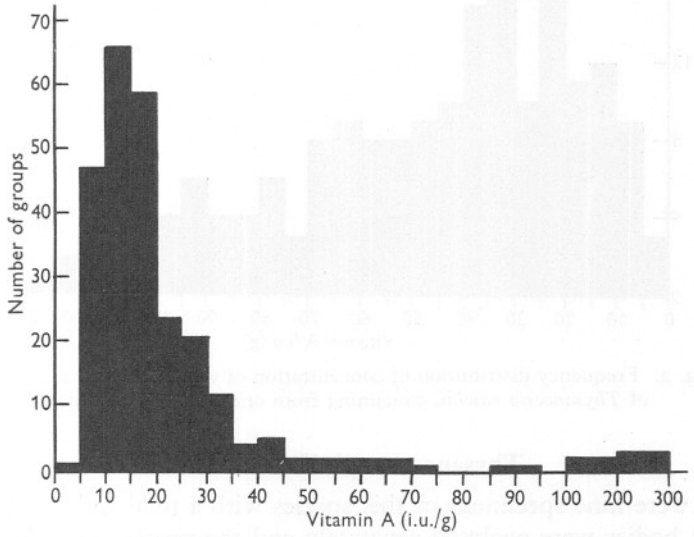

Fig. 1. Frequency distribution of concentration of vitamin A in 258 groups of *Meganyctiphanes norvegica*, containing from one to 359 specimens.

Thysanoessa inermis *Kröyer*

The results obtained from the analysis of specimens taken from the throat of a Blue Whale are given in Table I. The fat concentration was lower than in the samples of *Meganyctiphanes norvegica* collected from a Fin Whale at this station, and also lower than in free-swimming specimens of *Thysanoessa inermis* previously analysed by us (Fisher *et al.*, 1952). The concentrations of vitamin A and astaxanthin were of the same order as found in *Meganyctiphanes norvegica* from the whale and the vitamin A value was similar to that obtained from surface-swimming specimens of *Thysanoessa inermis* (Fisher *et al.*, 1952). The concentration of astaxanthin was only about half that of any of the free-swimming animals.

Thysanoessa gregaria *G. O. Sars*

A group of eight specimens, total weight 25 mg, separated into eyes and bodies, was analysed. The results appear in Table V. All the vitamin A was in the eyes, but there were only traces of carotenoid pigment present,

insufficient to be determined, though behaving chromatographically like astaxanthin.

In this small weight of material there was also too little fat for an accurate determination by our technique.

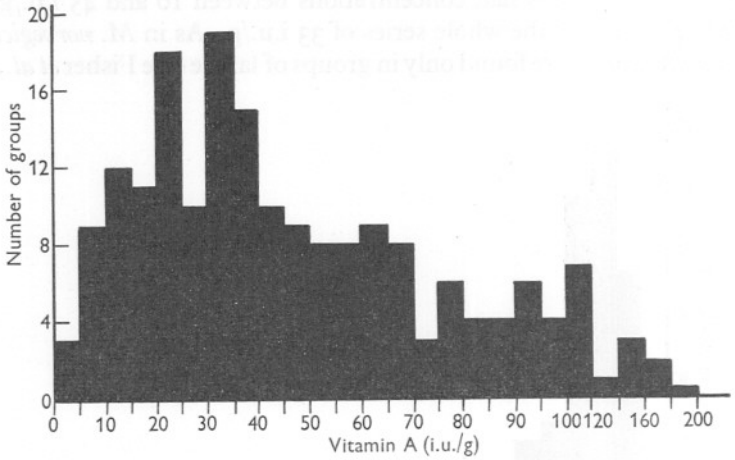

Fig. 2. Frequency distribution of concentration of vitamin A in 190 groups of *Thysanoessa raschii*, containing from one to 479 specimens.

Thysanoessa spinifera *Holmes*

There were nine specimens of this species with a total weight of 127 mg. Eyes and bodies were analysed separately and the results given in Table V show that vitamin A was exclusively in the eyes. The concentrations of fat and astaxanthin, which was the only carotenoid present, were of the order found in free-swimming animals of other species of *Thysanoessa*.

Thysanopoda acutifrons *Holt & Tattersall*

There were five specimens of this euphausiid in the group which weighed 160 mg, and bodies and eyes were analysed separately. The results in Table V show that vitamin A was not found in this species and that the concentrations of fat and astaxanthin were lower than we have found in other euphausiids.

Stylocheiron elongatum *G. O. Sars*

Four specimens of this species were analysed. Their total weight was 127 mg. Results of analyses appear in Table V. Vitamin A was present in a concentration similar to that in other euphausiids except *Thysanopoda acutifrons*. The concentration of fat was rather low compared with that of other species, but that of astaxanthin was much higher than usually found in euphausiids. No other carotenoids were observed.

Stylocheiron maximum *Hansen*

Only two animals of this species, with a total weight of 105 mg, were obtained. These were separated into eyes and bodies for analysis and the results are given in Table V. Vitamin A was again found only in the eyes and the concentration in the whole animals was very similar to that found in *S. elongatum*. Fat concentrations in the two species were also of the same order, but in *S. maximum* astaxanthin was found in lower concentration, resembling that in most other euphausiids.

TABLE V. OIL PER CENT AND VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN SIX SPECIES OF EUPHAUSIIDS

Species	No. of specimens	Av. wt. (mg)	Oil (%)	Vitamin A		Astaxanthin	
				i.u./spec.	i.u./g	μg/spec.	μg/g
Thysanoessa gregaria (P)							
Eyes (pairs)	8	—	—	0·15	—	0	0
Bodies	8	3	—	0	0	0	0
Total	8	3	—	0·15	47	0	0
T. spinifera (P)							
Eyes (pairs)	9	—	—	0·14	—	0·4	—
Bodies	9	14	8·7	0	0	0·5	36
Total	9	14	8·7	0·14	9·4	0·9	63
Thysanopoda acutifrons (A)							
Eyes (pairs)	5	0·3	—	0	0	0	0
Bodies	5	32	0·4	0	0	0·7	21
Total	5	32	0·4	0	0	0·7	21
Stylocheiron elongatum (A)							
Eyes (pairs)	4	2	2·3	0·4	184	2·4	1090
Bodies	4	30	0·8	0	0	1·2	41
Total	4	32	0·9	0·4	13	3·6	113
S. maximum (P)							
Eyes (pairs)	2	7	14	0·7	97	2·6	365
Bodies	2	46	8·4	0	0	0	0
Total	2	53	9·0	0·7	13	2·6	50
Nematoscelis difficilis (P)							
Eyes (pairs)	40	2	5·2	0·3	184	0·5	314
Bodies	40	35	3·3	0·1	3	0·3	10
Total	40	37	3·4	0·4	11	0·8	23

A, specimens collected in North Atlantic on 2 October 1952 from R.R.S. *Discovery II*; P, specimens collected in North Pacific on 25 May 1953 from R.S. *Horizon*.

Nematoscelis difficilis *Hansen*

A group of forty specimens of *N. difficilis*, weighing 1463 mg, was divided into eyes and bodies which were analysed separately as in previous species. The results, given in Table V, show that this species contained vitamin A in a concentration of the usual euphausiid order, but only 75% of it in the eyes, contrasting with 90–100% normally found in other species. The concentration of astaxanthin, or its esters, was lower than in most species examined.

Euphausia superba *Dana*

The results for the various groups examined are shown together in Table VI. The vitamin A concentrations were of the same order in all the groups and all lower than in other euphausiids containing it. Although the conditions of storage of the *Discovery* samples were regarded as unfavourable, the vitamin A concentrations closely resembled those in the corresponding size-group (25–26 mm) of the *Balaena* 1953 samples, which were stored at a much lower temperature. It is suspected that the *Balaena* 1952 samples may have been regurgitated by a whale and, therefore, possibly partially digested. This would account for the rather lower concentration of vitamin A in the eyes and also for the higher concentration of astaxanthin in the bodies than in the free-swimming specimens collected in 1953.

Vitamin A concentrations in the 1953 size-groups increase with size up to the group of animals 31–32 mm long, just as we have found (Fisher *et al.*, 1954) in northern euphausiids, but there is an unaccountable drop in the larger groups.

The concentrations of astaxanthin in all the groups are closely similar and about one-third of those we have found in *Meganyctiphanes norvegica*. The proportion of this carotenoid in the eyes of *Euphausia superba* is, however, as high as in *Meganyctiphanes norvegica* (Fisher *et al.*, 1954).

Euphausia pacifica *Hansen*

Three groups of this species were collected; one consisting of 100 specimens, total weight 4·99 g, separated into eyes and bodies, was taken on 25 May 1953; and two groups, of 400 and 1001 specimens, weighing 3·42 and 16·5 g respectively, were taken on 26 May 1953. These two groups were preserved whole, without dissection. Analytical results are given in Table VII. The dissected specimens contained vitamin A, all in the eyes, and the concentration in these animals was as found in most other euphausiids. The whole specimens were smaller but there was a larger bulk of material. Even so, no trace of vitamin A was detected in them. Fat concentrations were the same in the first two groups and lower in the third. Astaxanthin was the only carotenoid present in all three groups in varying concentrations, all rather lower than usually found in, for example, *Meganyctiphanes norvegica*.

Study of Vitamin A Variations in Preserved Euphausiids

It would appear from the results shown in Table VII that vitamin A which might have been present in the eyes of the specimens of *Euphausia pacifica* preserved without previous dissection was destroyed by some substance in the bodies released by preservation. In order to verify this supposition the experiments recorded in Tables VIII and IX were done.

TABLE VI. OIL PER CENT AND VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN *EUPHAUSIA SUPERBA*

Part examined	No. of specimens	Av. wt. (mg)	Oil (%)	Vitamin A i.u./spec.	Vitamin A i.u./g	Astaxanthin μg/spec.	Astaxanthin μg/g
16. vii. 51. *Discovery II* station 2864							
Eyes (pairs)	197	1·4	12	0·6	437	2·3	1690
Bodies	197	195	2·3	0	0	2·1	11
Total	197	196	2·3	0·6	3·2	4·4	22
Early 1952. By net from *Balaena*. Antarctic							
Eyes (pairs)	148	0·7	5·0	0·02	34	0·2	307
Bodies*	—	—	1·4	—	1·3	—	33
Bodies + eyes	—	—	1·5	—	1·8	—	36
Early 1953. Engine room intake of *Balaena*. Antarctic							
Eyes (pairs)	148	3·3	8·4	0·9	263	2·5	753
Bodies	148	828	1·1	0	0	2·5	3·0
Total	148	831	1·2	0·9	1·4	5·0	6·0
Early 1953. By net from meat-carrying ship with *Balaena*. Antarctic							
Whole animals (< 22 mm long)	47	87	4·2	0·3	3·7	0·9	11
Eyes (pairs)	14	1·4	3·2	0·7	508	0·9	653
Bodies	14	124	4·4	0	0	1·1	9·2
Total (23–24 mm long)	14	125	4·1	0·7	5·5	2·0	16
Eyes (pairs)	22	1·4	6·0	0·7	500	2·1	1508
Bodies	22	197	2·9	0	0	0·8	4·2
Total (25–26 mm long)	22	198	2·9	0·7	3·4	2·9	15
Eyes (pairs)	11	1·7	5·8	1·1	653	2·5	1475
Bodies	11	252	3·3	0	0	2·1	8·2
Total (27–28 mm long)	11	254	3·3	1·1	4·4	4·6	18
Eyes (pairs)	22	2·2	1·3	1·3	617	2·8	1288
Bodies	22	264	4·0	0	0	1·4	5·4
Total (29–30 mm long)	22	266	4·0	1·3	5·0	4·2	16
Eyes (pairs)	17	2·9	3·9	2·5	859	4·1	1411
Bodies	17	367	4·2	0	0	2·3	6·3
Total (31–32 mm long)	17	370	4·2	2·5	6·7	6·4	17
Eyes (pairs)	11	2·0	6·8	1·2	591	3·6	1784
Bodies	11	505	2·7	0	0	1·9	3·8
Total (33–34 mm long)	11	507	2·7	1·2	2·3	5·5	11
Eyes (pairs)	23	5·2	6·0	2·0	381	3·5	677
Bodies	23	524	2·2	0	0	5·1	9·7
Total (35–36 mm long)	23	529	2·2	2·0	3·8	8·6	16
Eyes (pairs)	15	3·6	4·5	1·5	425	4·2	1293
Bodies	15	548	2·5	0·5	0·9	3·2	5·9
Total (37–38 mm long)	15	552	2·5	2·0	3·7	7·5	14
Eyes (pairs)	19	3·2	4·3	1·4	453	4·4	1379
Bodies	19	661	1·1	0	0	5·8	8·7
Total (39–40 mm long)	19	664	1·1	1·4	2·2	10	15
Eyes (pairs)	20	3·1	3·5	1·8	584	3·4	1093
Bodies	20	587	1·9	0	0	9·7	17
Total (> 40 mm long)	20	590	1·9	1·8	3·1	13	22

* Somewhat macerated, hence uncountable.

In *Meganyctiphanes* (Table VIII), in all except two instances, the vitamin A content and concentration of the eyes and bodies separately was together greater than that of the corresponding group of whole animals. The two

TABLE VII. OIL PER CENT AND VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN *EUPHAUSIA PACIFICA*

Specimens collected in North Pacific on 25–26 May 1953

Date	Part examined	No. of specimens	Av. wt. (mg)	Oil (%)	Vitamin A		Astaxanthin	
					i.u./spec.	i.u./g	μg/spec.	μg/g
25. v.	Eyes (pairs)	100	1	13	0·5	515	0·7	683
	Bodies	100	49	1·9	0	0	0·4	7·7
	Total	100	50	2·2	0·5	11	1·1	22
26. v.	Whole specimens	400	9	2·2	0	0	0·3	35
26. v.	Whole specimens	1001	17	0·9	0	0	0·2	15

TABLE VIII. VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN GROUPS OF *MEGANYCTIPHANES NORVEGICA* UNDER DIFFERENT CONDITIONS OF STORAGE

Groups of 25 specimens (length 23–25 mm) collected in Loch Fyne on 21–22 October 1953.

Date tested	Preserved	Dissected	Vitamin A		Astaxanthin	
			i.u./spec.	i.u./g.	μg/spec.	μg/g
30. x.	AF	W	3·1	15	10	48
30. x.	AF	E+B	2·7	13	8·4	39
23. xi.	AR	W	0·9	4·7	8·2	45
23. xi.	AR	E+B	2·4	10	14	57
27. xi.	AF	W	1·4	6·2	11	48
27. xi.	AF	E+B	2·3	10	14	60
27. xi.	AF	W	2·6	11	13	52
27. xi.	AF	E+B	2·3	10	8·9	40
9. xi.	BR	W	1·7	6·8	10	42
9. xi.	BR	E+B	3·1	14	6·4	29
23. xi.	BR	W	2·0	9·1	6·8	30
23. xi.	BR	E+B	2·6	12	6·3	30
27. xi.	BF	W	1·6	4·5	13	54
27. xi.	BF	E+B	2·8	13	13	59
27. xi.	BF	W	1·6	6·6	14	57
27. xi.	BF	E+B	4·0	18	13	61

A, raw specimens preserved in alcohol; B, boiled specimens preserved in alcohol; R, room temperature; F, deep-freeze; W, whole specimens; E+B, eyes and bodies analysed separately and results combined.

exceptions were the alcohol-preserved group of raw specimens which had been placed at a low temperature immediately after dissection and preservation on the ship, and might, therefore, be regarded as a control group and one of the alcohol-preserved groups of raw specimens stored for nearly 5 weeks in the deep-freeze. The content and concentration of astaxanthin were not consistently altered by the various methods of preservation or by the separation of eyes from bodies.

Although differences were found between dissected and whole animals in the vitamin A content and concentration of *Thysanoessa* (Table IX), they were

not so marked as in *Meganyctiphanes*. The week-old alcohol-preserved raw specimens kept at a low temperature had a higher vitamin A content and concentration in whole than in dissected specimens. In the other groups the vitamin A concentrations were always higher in dissected than in whole animals. In all except one group the astaxanthin content and concentration were markedly higher in the dissected than in the whole specimens, in contrast to the results for *Meganyctiphanes* (Table VIII).

TABLE IX. VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN GROUPS OF *THYSANOESSA RASCHII* UNDER DIFFERENT CONDITIONS OF STORAGE

Groups of 20 specimens (length 11–13 mm) collected in Loch Fyne on 21–22 October 1953.

			Vitamin A		Astaxanthin	
Date tested	Preserved	Dissected	i.u./spec.	i.u./g	μg/spec.	μg/g
30. x.	AF	W	0·7	37	0·9	47
30. x.	AF	E+B	0·5	25	1·1	56
25. xi.	AR	W	0·5	27	0·6	33
25. xi.	AR	E+B	1·0	59	1·5	89
27. xi.	AF	W	1·4	68	0·7	33
27. xi.	AF	E+B	1·5	75	1·0	51
27. xi.	AF	W	0·6	28	1·1	51
27. xi.	AF	E+B	0·9	58	1·4	90
9. xi.	BR	W	1·1	61	1·1	64
9. xi.	BR	E+B	1·6	69	1·6	66
25. xi.	BR	W	0·9	38	0·7	33
25. xi.	BR	E+B	1·0	42	0·5	20
27. xi.	BF	W	0·6	28	0·9	40
27. xi.	BF	E+B	0·8	38	1·2	57
27. xi.	BF	W	0·4	15	1·0	38
27. xi.	BF	E+B	0·4	22	1·1	54

A, raw specimens preserved in alcohol; B, boiled specimens preserved in alcohol; R, room temperature; F, deep-freeze; W, whole specimens; E+B, eyes and bodies analysed separately and results combined.

DISCUSSION

Comparison of the concentrations of vitamin A, astaxanthin and oil in *M. norvegica* collected from three different localities in August 1951 (Table III) shows that the specimens taken from the open sea were poorer in vitamin A but not in astaxanthin than those from more enclosed waters. Fat concentrations were similar in the two more northerly groups but much lower in the Mediterranean animals. We have previously pointed out (Fisher *et al.*, 1953) that the low fat content might be associated with the relative poverty in plankton of the Mediterranean (Bernard, 1938), but if that were so it is surprising that the reserves of vitamin A and astaxanthin accumulated by the euphausiids were not similarly reduced. A further comparison of the Loch Fyne and Monaco specimens collected in February 1952 (Table IV) supports the earlier evidence of little difference between them in vitamin A concentration, although in January the Monaco samples were richer than the only

comparable Loch Fyne sample. Astaxanthin concentrations were again very similar in samples from both localities taken in both months. Fat concentrations in the January samples from Monaco were lower than in the Loch Fyne sample. The February samples from both places had similar fat concentrations. Samples of *M. norvegica* from Loch Fyne and The Faeroes area, two places relatively close together, differed little in their reserves of fat, vitamin A or astaxanthin (Table II).

According to Sheard (1953) some eighty-six species of the order Euphausiacea are recognized. In our studies of the vitamin A and carotenoid contents of animals of this order we have so far analysed eleven species, in nine of which vitamin A was found in high concentrations. The vitamin was absent from *Thysanopoda acutifrons*, but the amount of material analysed was small, although smaller weights of other species have been found to contain vitamin A. The eyes of *T. acutifrons* are, however, noticeably smaller than those of the other euphausiids we have examined and, since nearly all the vitamin A of euphausiids is found in the eyes, the two facts may be in some way associated, although Chun (1893) in his paper on euphausiid eyes makes no mention of any peculiarities in the genus *Thysanopoda*. Further investigation of the species with a larger amount of material is clearly indicated. The concentration of vitamin A in the samples of *Euphausia superba* we have examined was lower than in the other species of Euphausiacea containing it, but it is possible that some destruction of the vitamin A may have occurred during the passage of these specimens from the Antarctic through the tropics to this country. Even so, the concentration of vitamin A in this species is still higher than in any of the decapod Crustacea we have examined, the richest example of these being *Acanthephyra purpurea* Milne-Edwards. The average values for vitamin A concentrations of the euphausiids we have studied are compared in Table X, which shows clearly how much richer in vitamin A they all, with one exception, are than other Eucarida so far examined by us.

In view of their unique richness in vitamin A among the Crustacea it may be profitable to discuss the affinities of the Euphausiacea. In the two most recent accounts of the order (Banner, 1950; Sheard, 1953) it has been placed with the order Decapoda in the series Eucarida, division Eumalacostraca of the subclass Malacostraca. Vitamin A is present in most of the Decapoda we have studied (Kon, 1954), but in much lower concentrations (see Table X) than in the euphausiids. We have learnt from Dr I. Gordon of the British Museum that the taxonomic position of the order Euphausiacea is not yet definitely established. She informs us that her views correspond to those of the late Dr S. W. Kemp who believed, with Calman (1910), that they should be more closely associated with the Penaeidea, themselves a suborder of the Decapoda.

Comparative biochemistry has provided support for morphological evidence used in taxonomy in the work of Baldwin and his colleagues on muscle phos-

phagens in the animal kingdom (see Baldwin, 1937). It is possible that we may have in vitamin A, or the ability to accumulate it, a similar taxonomic indicator related to variations in the enzyme systems of the different groups of Crustacea. We have shown (Fisher *et al.*, 1953) that the Penaeidea have similar concentrations of vitamin A to those of other Decapoda, whereas the Euphausiacea are much richer, so that, on this evidence, the two groups are not so closely related as are the Penaeidea with the Decapoda.

TABLE X. DESCENDING ORDER OF AVERAGE VALUES FOR VITAMIN A CONCENTRATIONS IN EUPHAUSIACEA, AND IN DECAPOD RICHEST IN VITAMIN A

	Vitamin A (i.u./g)	Localities	No. of groups
Thysanoessa gregaria	47	P	1
T. raschii	33	A	190
T. inermis	16	A	3
Meganyctiphanes norvegica	15	A, M, N	258
Stylocheiron elongatum	13	A	1
S. maximum	13	P	1
Euphausia pacifica	11	P	1
Nematoscelis difficilis	11	P	1
Thysanoessa spinifera	9·4	P	1
Euphausia superba	3·1	An.	13
Acanthephyra purpurea	2·7	A	1

Average concentrations have been weighted for the numbers of specimens in each group. Values for free-swimming specimens only have been taken. A, Atlantic; An., Antarctic; M, Mediterranean; P, Pacific; N, Norwegian Sea. Vitamin A absent from *Thysanopoda acutifrons*.

The Euphausiacea live in similar habitats to the Mysidacea, with which they were for long classified as the Schizopoda. We have analysed four Mediterranean species of mysids (Fisher *et al.*, 1953) and *Hemimysis lamornae*, obtained from the aquarium tanks of the Plymouth laboratory, and they all lacked vitamin A. More recently we were supplied by Dr Dexter S. Haven of the Virginia Fisheries Laboratory with a large sample of *Neomysis americana* (S. I. Smith), collected from the York River, Virginia, on 9 February 1954, and found in them a vitamin A concentration of 1·9 i.u./g. Nevertheless, the evidence so far indicates that the euphausiids are biochemically very different from other Crustacea, including the Penaeidea, considered to be their nearest relatives, and the Mysidacea which are their nearest neighbours in the sea.

Einarsson (1945), Banner (1950) and Sheard (1953), who have all written at length on the Euphausiacea, are unanimous in stressing the importance of these animals in the economy of the seas. Sheard ascribes to them two general roles: 'the first being that of intercepting organic nutrient material' derived from the breakdown of phytoplankton, for example, the faecal pellets of grazing herbivores, 'and of returning it directly to the carnivore population'; 'the second (together with the pelagic larvae of bottom-living invertebrates) being that of delivering some products of the bottom cycle of organic

production to the pelagic (nutrient) cycle'. The second function would be achieved by the detrital feeders. Sheard further points out that 'this dual buffer and transference role of Euphausiacea', may explain 'the apparent excess of production of carnivores, when measured against primary nutrient values and phytoplankton production in subtropical and tropical seas'.

More detailed information about the role of euphausiids as food organisms for many whales and fishes has been provided by Einarsson (1945). He stated that the Blue Whale (*Balaenoptera sibbaldi*) lives exclusively on euphausiids, *Thysanoessa inermis* and *Meganyctiphanes norvegica* in arctic and *Euphausia superba* in antarctic seas. The Fin Whale (*Balaenoptera physalus*) also feeds largely on these species. We have already (Fisher *et al.*, 1952) drawn attention to the direct passage of the rich vitamin A supplies of these euphausiids to the stores of the whale.

Sperm Whales (*Physeter catodon*) feed on cuttlefishes and squids, in which vitamin A has been found in good concentrations in the liver (Brachi, 1953; Kon, 1954). These cephalopods live mainly on Crustacea and since ten-armed forms, important as whale food, are pelagic in habit they probably feed largely on free-swimming species, among which, by virtue of their enormous numbers and swarming habits, the euphausiids must rank as of considerable importance. Hjort & Ruud (1929) definitely stated that euphausiids form the food of the squid, *Gonatus fabricii*, which is eaten by the Bottle-nose Whales (*Hyperoodon rostratus*). It seems likely, therefore, that euphausiids are directly or indirectly the main source of vitamin A for all species of commercially valuable whales.

Copepods are the most important item in the diet of the herring (*Clupea harengus*), but they contain no more than traces of vitamin A (Fisher *et al.*, 1952). Recent work in this laboratory, so far unpublished, has shown that herring-liver oil may contain vitamin A in concentrations up to 60,000 i.u./g, and that the concentration is also high in the intestine. Einarsson (1945) in a review of the literature points out that, next to copepods, euphausiids are the food animals most favoured by the herring and, in some localities, they may form the bulk of the diet, as for example in the Skagerrak, where Poulsen (1926) reported that in May herring were feeding almost exclusively on *Meganyctiphanes norvegica*. This euphausiid is eaten by herring in the Clyde Sea area to the extent that the stomach becomes distended, the condition being described by fishermen, who reject these fish, as 'gut-poke'. Moore (1898) described *M. norvegica* as the most important food of the herring off the Atlantic coast of America.

A detailed study of the food of the cod (*Gadus callarias*) was made by Brown & Cheng (1946), who concluded that, for cod from the Bear Island and Spitzbergen Bank areas, pelagic Crustacea, especially *Thysanoessa inermis*, are the most important component from February to August, and young herring from November to December. Capelin (*Mallotus villosus*) is the principal food

of the cod off the Murman coast and sand-eels (*Ammodytes* spp.) off Andanes and Iceland. The capelin feeds on *Thysanoessa inermis*, according to Saemundsson (1937). Wiborg (1949) stated that the main food of cod of the O-II-groups from deep water along the coast of northern Norway consisted of euphausiids, especially *T. inermis* and *Meganyctiphanes norvegica*. Thus euphausiid vitamin A also seems to be the source of the rich reserves found in cod-liver oil.

Halibut-liver oil is one of the richest natural sources of vitamin A, and Lovern & Sharp (1933) studied the food of this fish in an attempt to find the source of its reserves. The torsk (*Brosmius brosme*) was the commonest species eaten and torsk-liver oil proved richer in vitamin A than most cod-liver oils. Poulsen (1926) reported that torsk was one of the species to be found feeding on *Meganyctiphanes* in the Skagerrak. McIntyre (1952) more recently reported that halibut around Iceland and the Faeroes feed mainly on *Sebastes marinus*, together with other fish, especially herring, decapod Crustacea, especially *Nephrops norvegicus* and some cephalopods. Lovern, Edisbury & Morton (1933) drew attention to the wide variations between the potencies of individual samples of halibut-liver oil and these variations may be associated directly with the type of food eaten, some fish feeding consistently on food richer in vitamin A than that eaten by others. Euphausiids may, therefore, be the initial source of the vitamin A in halibut liver.

Saemundsson (1926) and Macdonald (1927) reported that the saithe (*Gadus virens*), which is the basis of important fisheries, also feeds on euphausiids. Lovern *et al.* (1933) mentioned that saithe-liver oil is of similar vitamin A potency to that of the cod and hake. The hake itself (*Merluccius vulgaris*) was reported by Hickling (1927) to feed selectively on *Meganyctiphanes*, and this euphausiid has been observed by us in the stomachs of hake caught in Loch Fyne.

An example of a number of fish listed by Lovern *et al.* (1933) as being poorer in vitamin A than the cod is the haddock (*Gadus aeglefinus*). This species has been recorded as feeding occasionally on euphausiids in Icelandic waters (Saemundsson, 1937), around Bear Island (Robertson, 1932) and in the Barents Sea (Zatsepin, 1939). In the Skagerrak, Poulsen (1926) found haddock feeding in May almost exclusively on *Meganyctiphanes norvegica*. Einarsson (1945) considers, however, that euphausiids are not of major importance as food for this fish and they were not found in any of the stomachs of haddock, from Icelandic waters or the Murman coast, examined by Brown & Cheng (1946). Einarsson (1945) names several other economically important species of fish which feed on euphausiids, and the foregoing review emphasizes the importance of this order of Crustacea not only because of the two more general roles mentioned by Sheard (1953) but also in the more specific part they play as a source of the vitamin A stores of marine vertebrates. We have previously (Fisher *et al.*, 1954) discussed, and are still investigating, possible sources of

euphausiid vitamin A, and it may be that the animals of this order possess an enzyme equipment that permits them to break down carotenoids other than those normally regarded as vitamin A precursors and in such a way that vitamin A appears as an end-product in very large amounts which are accumulated in the eyes. These reserves are passed on directly from the euphausiids to their cephalopod and vertebrate predators which store the vitamin in their livers, accumulating it throughout life (Macpherson, 1933), only a small proportion being utilized.

It certainly seems that the euphausiids form a unique reservoir in the sea of vitamin A which they accumulate from an unusual source (see Fisher *et al.*, 1954). The vitamin itself exhibits certain peculiar properties, both in its discrepant physicochemical and biological potencies (Fisher *et al.*, 1952) and in its apparent destruction under certain conditions of storage now reported. We are making an intensive biochemical study of these phenomena and also seeking material to extend our observations on the one hand to other species of Euphausiacea to determine whether high concentrations of vitamin A are a universal feature of the order, and on the other to other Crustacea to search for a species as rich in vitamin A as any of the Euphausiacea.

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Summary

Eleven species of Euphausiacea, namely, *Meganyctiphanes norvegica*, *Thysanoessa raschii*, *T. inermis*, *T. gregaria*, *T. spinifera*, *Thysanopoda acutifrons*, *Euphausia superba*, *E. pacifica*, *Nematoscelis difficilis*, *Stylocheiron maximum* and *S. elongatum* have been analysed for fat, vitamin A and carotenoids. Vitamin A was present in all species except *Thysanopoda acutifrons*, but in *Euphausia superba* the concentrations were of a lower order although still higher than found by us so far in any decapod crustacean.

Astaxanthin, or its esters, was the only carotenoid found in all the species of euphausiids examined.

Groups of *Meganyctiphanes norvegica* from enclosed waters, namely, Loch Fyne and the Mediterranean Sea, had higher reserves of vitamin A than those from Atlantic waters. The fat concentrations of the Mediterranean specimens were lower than those of animals from more northerly waters but the vitamin A or astaxanthin concentrations of the two groups were similar.

In *Euphausia pacifica*, *Meganyctiphanes norvegica* and *Thysanoessa raschii*, the vitamin A content of animals separated into eyes and bodies before preservation and analysis was higher than that of animals left whole. The possible presence in the bodies of a substance causing destruction of vitamin A is being investigated.

The role of euphausiids is discussed as a vital link in the passage of nutrient substances from detritus, phytoplankton and zooplankton to marine vertebrates, with particular reference to the possible conversion by these Crustacea of carotenoids to vitamin A which they accumulate in their eyes.

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