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CARBOHYDRATES IN SOME MARINE PLANKTONIC ANIMALS

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There have been few analyses of the fat, protein and carbohydrate fractions in zooplankton, and owing to the difficulty of sorting large numbers of single species, the majority of the earlier determinations were necessarily carried out on mixed zooplankton hauls (Brandt, 1898; Brandt & Raben, 1919; Moberg, 1926; Wimpenny, 1929; Drummond & Gunther, 1934; Vinogradov, 1953). Most of these analyses suggested a relatively high protein and fat content, and this was confirmed by Orr (1934*a*), who investigated the chemical composition of a single species, *Calanus finmarchicus*. Orr's result gave fat, protein and chitin as 20–40, 35–50 and 3 %, respectively of dry weight. Similar high values were also reported by Orr (1934*b*) for *Euchaeta norvegica*. The carbohydrate content was not, however, estimated in either of Orr's investigations since large numbers of animals would have been required. Brandt (1898), after analysing mixed plankton hauls which were predominantly copepods, suggested a carbohydrate content of *ca.* 20 %.

Although many workers have suggested that fat is used as substrate during the respiration of zooplankton, the role of carbohydrate is doubtful, since there is so little information on the glycogen content and on the amount of monosaccharides in plankton animals. Lane, Posner & Greenfield (1952) and Greenfield (1953) reported very high glycogen values in prenatal larvae of *Teredo*, and noted a sharp reduction in the amount in free-swimming larvae. Collyer (1957) found the glycogen reserves in the larvae of *Ostrea edulis* to lie between 13·4 and 15·4 % of the dry organic matter, but found no correlation with size. It therefore appeared highly desirable to investigate the total carbohydrate content (i.e. glycogen and monosaccharides) in certain planktonic animals. It also was of interest to test whether the amount of carbohydrate varied with feeding and activity, since this might indicate whether carbohydrate was normally used as an energy source.

MATERIAL AND METHODS

Experiments were carried out with *Calanus finmarchicus* (Gunnerus)[1] and *Neomysis integer* (J. V. Thompson) at Plymouth, and with *Pleurobrachia pileus* (O. F. Müller) at Southampton. In each case the animals were picked

[1] It is likely that since these specimens were collected in the English Channel they should be referred to the variety *helgolandicus*.

out from diluted plankton hauls. In the experiments with *Calanus*, over 100 animals were used for each carbohydrate determination. For experiments where the animals were first fed, batches of fifty animals were sorted into beakers, each containing a litre of filtered sea water enriched with cultures of diatoms and dinoflagellates. The beakers were placed in a light-tight box in a constant-temperature room at 12° C. For starvation experiments, batches of fifty animals were kept in tall rectangular Perspex vessels (50 × 7·5 × 3·5 cm) containing filtered sea water. These vessels, set up in the constant-temperature room (12° C), were supplied with fluorescent lighting from the top and side. This lighting was used as a stimulus to keep the animals active. The copepods were usually observed to be swimming upwards.

In the experiments with *Neomysis*, the same procedure as described for *Calanus* was followed, except that only twenty to fifty animals were used for each carbohydrate determination. With *Pleurobrachia* three to ten animals, depending on their size, were used. Owing to the high water content, the use of greater numbers of *Pleurobrachia* was of no advantage. A few experiments were attempted using dried *Pleurobrachia*, but as it was likely that the high salt content interfered with the analyses, those experiments were not continued.

The total carbohydrate content was determined by the micro-method of Mendel, Kemp & Myers (1954) and of Kemp and Heijningen (1954). Glycogen in the tissues was first hydrolysed to glucose, the final determination (made by a colorimetric method), including any glucose and fructose originally present as monosaccharides, and also saccharides yielding those sugars. Before each analysis the animals were concentrated by filtering through bolting silk, quickly rinsed with distilled water, and roughly dried on filter-paper. Except in the case of *Calanus*, the wet weight of the whole sample was then obtained. The animals were ground with 5 c.c. of 5% trichloracetic acid containing 0·2% silver sulphate. After boiling for 15 min and then centrifuging, a clear supernatant was obtained. To 1 c.c. of this fluid, 3 c.c. of concentrated H_2SO_4 (May & Baker, 98%, sp.gr. 1·84) was added and the mixture boiled for 6·5 min to develop colour. The intensity of the resulting pink colour was measured in a Unicam spectrophotometer (SP. 600) at 520 mμ. Usually three determinations were made on each sample; the agreement between the subsamples was good. The mean value was then converted into glucose units from a calibration curve, this curve being linear between 50 and 150 μg. glucose. Values below 50 μg. could not, however, be read with accuracy.

RESULTS

Calanus

The results of a few experiments with *Calanus*, mostly Stages V and VI ♀♀, suggested a rather low concentration of carbohydrates in the body (Table 1). Most of the determinations were made on copepods which had been kept in the laboratory and were either fed or starved, but in Expt. nos. 9 and 10 analyses of freshly caught *Calanus* were made and gave values of 1·7 and 1·4 μg sugar as glucose per copepod (Table 1). Copepods which were fed on phytoplankton in the laboratory gave rather variable carbohydrate contents (viz. 2·24–0·63 μg per copepod), and the same was true of those *Calanus* which were starved, though the values then tended to be lower (1·76 to < 0·25 μg

TABLE 1. CARBOHYDRATE CONTENT OF *CALANUS FINMARCHICUS*

Expt. no.	No. of animals used	Carbohydrate per copepod (μg)	% carbohydrate per wet weight	Remarks
1	125	2·24	0·18	Fed
2	125	1·76	0·14	Unfed
3	200	0·41	0·03	Unfed
4	200	1·15	0·09	Unfed
5	150	1·10	0·09	Fed
6	250	0·72	0·06	Fed
7	130	0·63	0·05	Fed
8	200	< 0·25	< 0·02	Unfed
9	140	1·70	0·13	Fresh animals
10	200	1·40	0·11	Fresh animals

per copepod). There is thus the suggestion that starvation (with continued activity of the copepods) tended to reduce carbohydrate, whereas feeding appeared to build up a small carbohydrate reserve. It is probable that the rise in body sugar with feeding would have been clearer, and the results less variable, had feeding been really active. Many workers, notably Marshall & Orr (1955), have commented on the variability of feeding activity seen in *Calanus* kept in the laboratory. In our experiments it appeared from a qualitative examination of the faecal pellet production that the *Calanus* were not feeding actively.

In these preliminary experiments the *Calanus*, though counted, were generally not weighed. In Expt. no. 9, however, with freshly caught animals, the *Calanus* were weighed after roughly drying on filter-paper, and gave a mean of 1·26 mg per copepod (wet weight). This value (1·26 mg) has been used as a first approximation to convert the weight of carbohydrate per copepod to carbohydrate per body weight (Table 1). It then appears that in freshly caught *Calanus* carbohydrates amount to 0·11–0·13 % of the body (wet) weight. According to Marshall & Orr (1955) the water content of female *Calanus* is 78 % and that of Stage V 65 %. On the assumption of 70 % water content for a mixture of females and Stage V copepodites, the carbohydrate content of freshly caught *Calanus* expressed as percentage dry weight would be

$$0{\cdot}12 \times \frac{100}{30} = 0{\cdot}4\,\%.$$

In starved copepods the maximum carbohydrate (wet weight) was 0·14% and the minimum as low as < 0·02%. For fed copepods the values were slightly higher: range 0·18–0·05% of the body (wet) weight (Table 1).

Neomysis integer

It was possible to carry out rather more experiments on *Neomysis* and in all determinations the wet weight of the animals was first obtained. The results of experiments on animals which had been fed in the laboratory gave values of 0·42–0·20% sugar as glucose of the body (wet) weight. There was again the difficulty that although *Neomysis* fed on phytoplankton cultures, the intensity of feeding, as judged from faecal pellet production, appeared to be variable. Different periods of feeding were tried, but the intensity still varied considerably. It is of interest that the highest carbohydrate content (0·42%) was obtained in Expt. no. 13 (Table 2) where particularly marked feeding was noted.

TABLE 2. CARBOHYDRATE CONTENT OF *NEOMYSIS INTEGER*
(Fed Animals.)

Expt. no.	Wet weight (mg)	% carbohydrate per wet weight	% carbohydrate per dry weight
11	160·0	0·31	1·55
12	142·0	0·20	1·00
13	180·4	0·42	2·10
14	353·4	0·22	1·10
15	243·6	0·24	1·20
16	228·0	0·28	1·40
17	251·0	0·23	1·15
18	208·0	0·22	1·10
19	310·0	0·25	1·25
20	276·7	0·20	1·00
21	318·8	0·22	1·10
22	980·0	0·22	1·10
23	389·2	0·29	1·45
24	403·0	0·26	1·30
25	333·3	0·23	1·18
26	278·0	0·39	1·95

The percentage of carbohydrate found in unfed *Neomysis* tended to be somewhat lower than in fed animals, though the range was considerable, viz. 0·28–0·15% glucose per body (wet) weight (Table 3). This suggests that carbohydrate is utilized to some extent with activity, and is stored during feeding. A somewhat closer comparison is possible for fed and unfed *Neomysis*, however. In some ten experiments the starved and fed cultures were set up simultaneously as paired experiments (Table 4). Only in one experiment (Expt. no. 28) was a greater percentage of glucose found in starved than in fed animals. In several of the pairs of determinations the reduction in carbohydrate with starvation was considerable (e.g. Expt. nos. 11 and 27, *ca.* 50%; Expt. nos. 13 and 29, *ca.* 40%), but in other experiments there was little or no change. In one of these experiments showing little change

(Expt. no. 33) duplicated unfed *Neomysis* cultures gave 0·21 and 0·24% carbohydrate against 0·23% for the fed animals (Expt. no. 17). But in the two unfed cultures, of a total of 300 mysids originally sorted, only 212 were recovered after 48 h starvation, although only a single intact dead mysid was seen. On closer examination several *Neomysis* were observed to be feeding on fragments of other mysids, suggesting that extensive cannibalism had occurred.

TABLE 3. CARBOHYDRATE CONTENT OF *NEOMYSIS INTEGER*

(Unfed animals.)

Expt. no.	Wet weight (mg)	% carbohydrate per wet weight	% carbohydrate per dry weight
27	190·0	0·15	0·75
28	161·6	0·28	1·40
29	444·2	0·16	0·80
30	389·2	0·20	1·00
31	258·7	0·20	1·00
32	251·0	0·25	1·25
33*a*	334·2	0·21	1·05
33*b*	305·5	0·24	1·20
34	392·0	0·17	0·85
35	398·4	0·27	1·35
36	455·5	0·20	1·00

TABLE 4. A COMPARISON OF THE CARBOHYDRATE CONTENT OF FED AND UNFED *NEOMYSIS INTEGER*

(The pairs of experiments cited were set up simultaneously.)

Fed		Unfed	
Expt. no.	% carbohydrate per wet weight	Expt. no.	% carbohydrate per wet weight
11	0·31	27	0·15
12	0·20	28	0·28
13	0·42	29	0·16
14	0·22	30	0·20
15	0·24	31	0·20
16	0·28	32	0·25
17	0·23	*33*a*	0·21
		*33*b*	0·24
18	0·22	34	0·17
19	0·25	35	0·27
20	0·20	36	0·20

* Expt. 33 was run in duplicate.

A certain amount of cannibalism had been suspected in some of the earlier pairs of fed and unfed experiments, but only Expt. no. 33 gave clear proof. Lucas (1936) found *Hemimysis* carrying dead mysids and amphipods, and he observed that the prey was being masticated. Tattersall & Tattersall (1951) also claimed that mysids were partly carnivorous.

It may be suggested that in those experiments listed in Table 4, where the unfed mysids showed very little or no reduction in carbohydrate as compared with fed animals, the reserves of carbohydrate were maintained to some extent by some of the so-called unfed *Neomysis* feeding on their less active fellows.

Attempts were made to limit cannibalism by reducing the starvation period (e.g. Expt. nos. 34–36: 4–5 h starvation), but this in turn raised difficulties in that the period was then likely to be insufficient to reduce carbohydrate reserves markedly. The short-term starvation results, in fact, fell well within the range for the whole unfed series—0·27 and 0·20 %—and were by no means the lowest values obtained. While, therefore, it is difficult to ensure complete starvation conditions experimentally for *Neomysis*, there is little doubt that where marked reduction in feeding occurred, carbohydrate content was lowered.

The water content was determined on two samples of *Neomysis*, and the dry weight was found to be 19·0 and 19·9 %, respectively, of the wet weight. As an approximation, therefore, the dry weight was reckoned as 20 % of the wet weight, and the percentage of carbohydrate to dry body weight has been calculated for all the experiments. For fed animals the values varied from 2·10 to 1·00 % (mean 1·30 %); for unfed mysids, from 1·40 to 0·75 % (mean 1·06 %) (Tables 2 and 3).

Pleurobrachia pileus

The carbohydrate values found in *Pleurobrachia* varied from a maximum of 0·05 % of the body (wet) weight to as little as 0·001 %. In two experiments (Expt. nos. 42 and 50) the value was below 0·001 %, though the precise level was uncertain. The very low values are explainable largely on the high water-content characteristic of ctenophores. The minimal values were barely detectable by the spectrophotometric method used, but the use of greater quantities of *Pleurobrachia* was not advantageous, since this also increased the volume of fluid. Although the figures for the lowest concentrations may be open to some criticism, there is no doubt that they are of the correct order of magnitude, and it therefore appears that there is an unusually wide range in the carbohydrate values obtained. This is in contrast to the results for both *Calanus* and *Neomysis*, where although a range was experienced, this was not nearly so great, unless animals were specifically starved. All the results quoted for *Pleurobrachia* in Table 5 were for fresh animals analysed as soon as possible—certainly the same day as collected. However, some hours elapsed, with the sorting of plankton hauls and preparation of the material, before the analyses, and this was especially true where several sets of determinations were made in one day. It is well known that *Pleurobrachia* is an active swimmer, and also a voracious and destructive carnivore, feeding on zooplankton. It is probable that like many other marine carnivores, the speed of digestion and assimilation is high, and the great variability in the carbohydrate content of freshly caught animals may reflect the variation between those that have fed very recently and those animals which have not eaten for a few hours. Some support for this theory comes from the analyses in Expt. nos. 58–62 (Table 5) which were specifically carried out on *Pleurobrachia* which were caught, sorted and used as rapidly as possible. The results gave carbohydrate contents varying from 0·010–0·007 %, i.e. the range was not so great, and no extraordinarily low values were obtained. By contrast, a few *Pleurobrachia* were left to starve in the laboratory in breffits of filtered sea water for 48 h. They were still healthy and active after starvation, but when analysed gave very much lower sugar values (viz. 0·0015– 0·0010 %).

TABLE 5. CARBOHYDRATE CONTENT OF *PLEUROBRACHIA PILEUS*

Expt. no.	% carbohydrate per wet weight	% carbohydrate per dry weight
37	0·011	0·275
38	0·057	1·425
39	0·002	0·050
40	0·007	0·175
41	0·005	0·125
42	< 0·001	< 0·025
43	0·006	0·150
44	0·001	0·025
45	0·009	0·225
46	0·007	0·175
47	0·001	0·025
48	0·001	0·025
49	0·001	0·025
50	< 0·001	< 0·025
51	0·046	1·150
52	0·003	0·075
53	0·004	0·100
54	0·002	0·050
55	0·003	0·075
56	0·001	0·025
57	0·002	0·050
58	0·007	0·175
59	0·006	0·150
60	0·009	0·225
61	0·008	0·200
62	0·009	0·225

Expt. nos. 58–62 refer to determinations made on animals immediately following capture.

Though the evidence is not strong, these last experiments suggest that carbohydrate is utilized by *Pleurobrachia* fairly rapidly. Some *Pleurobrachia* were fed on zooplankton in the laboratory, but we were unable to feed a sufficient number to obtain a reliable analysis for experimentally fed animals. Analyses made by one of us (S.K.) on *Pleurobrachia* suggested that the dry weight of the body amounted to only 3·75 and 4·62 %, respectively, of the wet weight. This agrees fairly well with the values of 4·6 % (Cooper, 1939), and 4·5 % (Vinogradov, 1953). We have assumed a mean value of 4 % for all our experimental animals and from this we have calculated the percentage of carbohydrate to dry weight of body. The maximum obtained is 1·43 %, but values as low as 0·025 % were also found (Table 5).

DISCUSSION

The data presented on the carbohydrate reserves of certain planktonic animals, though preliminary, suggest that the amount of sugar in the body is low. For *Calanus* the maximum would appear to be of the order of 0·2% of the wet body weight; for *Neomysis*, where our values are a little more certain, the maximum is approximately 0·4% of the wet body weight. It is of some interest that in a determination made on the copepod *Anomalocera patersoni* the amount of carbohydrate was 0·17% of the wet body weight. This is of the same order as the mean figure for freshly caught *Calanus*. For *Pleurobrachia*, as would be expected from the very high water content, even the maximum percentage (0·057%) is much lower than for the crustaceans, but the difference is less obvious if we calculate carbohydrate as a percentage of dry body weight. Thus, for *Neomysis* the maximum is 2·1%, whereas for *Pleurobrachia* it is 1·4%. These values are very much lower than those suggested by Brandt (1898) and Brandt & Raben (1919) for plankton. For example, for 'copepods', Brandt (1898) gives a summary: protein 59%, fat 7%, carbohydrate 20%, chitin 4·7%, ash 9·3%. Thus his figure for the amount of carbohydrate reckoned on a dry-weight basis is approximately × 10 our suggested values. However, Brandt's values are based on a few analyses of mixed marine plankton hauls (predominantly copepods) and also on some analyses of freshwater copepods, and it is difficult to compare his data with analyses of single species of zooplankton. It may be significant that Brandt & Raben (1919) give an analysis for a named zooplanktonic species (*Sagitta*) and the percentage of carbohydrate is then lower (*ca.* 14%).

Our preliminary data also suggest that there is a rise in carbohydrate in our animals with feeding. This agrees with the findings of previous workers, who showed a rise in blood sugar levels with feeding in crayfish and insects (Hemmingsen, 1924). There also appears to be a fall in the total carbohydrate content in starving planktonic animals, as has been found in the shore form *Carcinus* by Kleinholz & Little (1949), and this fall could be associated with activity, suggesting thus that sugars may be metabolized to some extent. However, as the rate of utilization of sugar is not rapid, it might be inferred that fat is utilized to a greater extent.

A few preliminary analyses of the fat content of *Neomysis integer*, using the method of Kumagawa & Suto (1908), as modified by von Brand, Weinstein, Mehlman & Weinbach (1952), gave fat values varying from 0·2 to 0·8% of the wet body weight. Since the dry weight is only a fifth of the wet weight of the body (p. 244) the amount of fat varies from 1 to 4% of dry body weight. Orr (1934*a*, *b*) quotes values of 20–40% as the fat content in *Calanus* and *Euchaeta*, reckoned on a dry-weight basis. Brandt (1898), however, gave a value of *ca.* 7% for copepods which is more comparable to the present figures.

It is generally known that carbohydrates may be converted into fats by many vertebrates. Whether a similar process is involved in these planktonic animals is uncertain, but it could be responsible for the low carbohydrate, as compared with high fat values, in zooplankton. It is also of interest to recall the suggestion made by Zeuthen (1955), based on respiratory quotient studies in butterflies, that carbohydrates, when they are metabolized, are first converted to fat before combustion in the muscles. Whether a similar process goes on in crustaceans is not known.

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SUMMARY

The carbohydrate content of three species of planktonic animals (*Calanus finmarchicus*, *Neomysis integer*, *Pleurobrachia pileus*) was estimated.

In *Calanus* fed on phytoplankton the carbohydrate content varied from 2·24 to 0·63 μg per copepod or 0·18–0·05 % of the wet body weight. In fed *Neomysis* the carbohydrate content was 0·42–0·20 % of the wet body weight. Analyses of *Pleurobrachia* gave values for carbohydrate of 0·05–0·001 % wet body weight.

In all three species it appeared that starvation tended to lower the carbohydrate content.

The mean percentage of carbohydrate expressed as dry body weight is approximately 0·4 % for *Calanus*, 1·3 % for *Neomysis* and 0·2 % for *Pleurobrachia*.

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