Journal of the Marine Biological Association of the United Kingdom Vol 31 No 3 1953

DIURNAL VARIATIONS IN THE GRAZING OF PLANKTONIC COPEPODS

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(Text-figs. 1–3)

Wimpenny (1938) has shown that the percentage of copepods taken in the sea with food in the gut tends to be higher at night than by day. Most planktonic animals perform diurnal vertical migrations, of greater or less extent. Wimpenny's observations may well be a consequence of such migrations.

On the other hand, during investigations into grazing rate of planktonic copepods (Fuller, 1937; Gauld, 1951) some of the measurements have suggested that there is a diurnal variation in the rate at which the copepods collect their food, even under laboratory conditions when migration is impossible, and that they filter the water more quickly at night than by day. The variation in the percentage of copepods containing food may be caused simply by changes in the rate of feeding, this being controlled either by the amount of light in their environment or by some internal rhythm affecting their behaviour.

An investigation of diurnal variations in the feeding behaviour of *Calanus finmarchicus* (Gunn.) was undertaken to investigate (i) its behaviour in nature, and (ii) the possible existence of alternations of feeding and resting periods under laboratory conditions. This species was chosen because it is the dominant copepod species in the Clyde sea area, is readily obtainable in reasonable numbers at all times of the year, and has already been the subject of investigation of feeding rate.

Field Observations

Methods

Calanus were obtained from 10-min. hauls of 50-cm. coarse tow-nets (26 meshes to the inch) taken at 4-hourly intervals through 24 hr. Three nets were fished at once, 25 fathoms apart on a trawl warp, to the end of which was attached a cable depressor (Barnes, 1951). Rigged in this way, the uppermost net fished 2–3 m., the second 35–40 m. and the lowest *c.* 75–80 m. from the surface. There was no means of closing the nets before hauling, but the percentage of the fishing time spent by the lower nets in the upper strata was small and unlikely to have interfered greatly with the results. The hauls were taken at a station just outside Tarbert, Loch Fyne. At this station deep water

(170 m.) was available only half a mile from the harbour where the research vessel could be tied up in harbour, and examination of the animals begun within 20 min. of their capture.

As Wimpenny (1937) has pointed out, the gut contents of *Calanus* are usually very easily observed, and in these investigations were estimated on the living animals as soon as possible after capture. Thirty to forty *Calanus* were transferred from the catch to a Petri dish and most of the water withdrawn so that the animals were compelled to lie on their sides and for the most part motionless. They were then examined under a low-power microscope and the amount of food in the gut recorded. This method of examination was adopted because it was found that in fixed catches, a variable and sometimes important fraction of the animals defaecated when formalin was added to the catch, and it was thought desirable to reduce as much as possible the interval between capture and examination. The number of animals examined varied from haul to haul, but an attempt was made to examine at least fifty, and, if time and numbers permitted, 100 of both Stage V and adult female *Calanus*. Occasionally Stage IV was sufficiently numerous for significant numbers to be counted in addition to the larger stages. After this had been done the catches were fixed with formalin and brought back to the laboratory. In some of the hauls the total numbers of *Calanus* or the numbers of one or other stage were too small for counts to be made quickly on board ship and supplementary counts of fixed material were made in the laboratory.

I am indebted to Skipper R. E. Souter and the crew of M.F.V. *Calanus* for their willing co-operation in taking the 24-hr. stations which comprise the field observations to be recorded here.

Results

Before anything is said about the gut contents of the catches, some remarks must be made about the vertical distribution of the animals. Since closing nets were not used the catches of the bottom net may have been made partly in the upper waters, but the differences in distribution to which attention are to be drawn are too marked to be attributed entirely to this cause, and in any case concern primarily the top net. The tables do not give the total numbers of animals caught (which were never estimated), but on any one occasion the catches of the top net were either of more or less the same size throughout the 24 hr. or else there was a marked difference between catches made in daylight and darkness so that the general picture of diurnal changes in distribution given Tables I and II is a true one.

It can be seen from the tables that only on seven of the thirteen occasions on which hauls were taken, were the catches of the top net distinctly greater in darkness than in daylight, while on 17 April and 11 September 1950, large catches of *Calanus* were taken at the surface throughout the 24 hr. On the four remaining occasions the catches varied rather irregularly and cannot be

looked on as clear evidence for or against vertical movements. It is remarkable that clear evidence of migration was obtained only on two occasions in 1950 (10 July and 21 November), and even on 10 July the vertical movements were not so clear cut as those of 1951, while in 1951 surface hauls in daylight were always blank except in April and May. The presence of adult and Stage V *Calanus* in the surface water during daylight in spring and early summer has already been recorded for the Clyde (Brook, 1886; Marshall & Orr, 1927; Nicholls, 1933; Marshall, Nicholls and Orr, 1934), but it seems that a much larger percentage of the population than usual was present in the surface waters in daylight on 10 April, and also on 11 September 1950, when exceptionally large catches were taken in daylight, although the day was not unusually dull.

Adult Females

The details of the observations on adult females are given in Table I, in which the numbers examined from each haul and the percentage of these which contained food is given. If a haul was taken and no *Calanus* seen this is given as $(0)_0$; if a haul was not taken or was lost, it is indicated by a dash. The times are given by the 24-hr. clock and are always Greenwich mean time.

The data of Table I are summarized in Table II, from which it can be seen that the percentage of adult female *Calanus* found to contain food was practically identical in daylight and in darkness. These figures quite clearly furnish no evidence of diurnal rhythm in feeding.

On the other hand, adult female *Calanus* were caught in all twenty-two surface hauls taken in the dark, but only in twenty-seven out of the forty-eight daylight hauls.[1] In consequence, more adult females were found containing food by night (1275) than by day (1041), in spite of the fact that there were more than twice as many daylight hauls as night hauls. These observations then agree with those of Wimpenny (1938) that the feeding of *Calanus* takes place mostly at night, but they also show that the reason for this is that by day *Calanus* is usually absent from the surface water where their food is principally found.

The numbers of female *Calanus* containing food in the deeper nets was nearly always less than in the surface net, the lowest net of the three showing the smallest percentage containing food. Of the adult females taken on all occasions, 68% of those in the middle net and 46·5% of those in the lowest net contained food compared with 86% in the surface net. The percentage of animals containing food varied considerably from one series of hauls to another—the mean for the bottom net from 16% (9. i. 51) to 75% (12. v. 51), that of the mid net from 30% (9. i. 51) to 86% (28. ii. 50)—but in any given series there is no obvious pattern in the occurrence of food in the guts unless

[1] The hauls at 16.00 and 08.00 hr. were always taken in daylight, those at 20.00 and 04.00 hr. in daylight from May to August, and in darkness in the other months.

there is clear evidence of vertical migration, when more of the copepods in the lower nets tended to have food in the gut at midnight and 4 o'clock than they had before midnight.

TABLE I. FEMALES: PERCENTAGE WITH FOOD

(The figures in suffix give the numbers examined.)

Time (hr.)...	12.00	16.00	20.00	24.00	04.00	08.00	12.00
28. ii. 50							
Top	83_{6}	89_{249}	94_{54}	75_{8}	98_{100}	90_{21}	69_{13}
Mid	100_{7}	91_{100}	75_{98}	88_{100}	89_{100}	87_{23}	83_{12}
Bottom	69_{88}	61_{100}	85_{102}	84_{74}	81_{100}	57_{100}	82_{100}
17. iv. 50							
Top	99_{100}	89_{100}	91_{100}	96_{100}	92_{100}	98_{67}	86_{100}
Mid	72_{100}	69_{100}	61_{100}	75_{100}	48_{50}	65_{79}	64_{98}
Bottom	52_{100}	24_{100}	45_{100}	28_{100}	56_{95}	36_{100}	51_{100}
29. v. 50							
Top	100_{5}	100_{2}	100_{4}	100_{4}	100_{1}	100_{3}	$(0)_{0}$
Mid	48_{50}	72_{50}	62_{50}	96_{50}	64_{50}	76_{50}	84_{50}
Bottom	34_{50}	54_{50}	64_{50}	64_{50}	56_{50}	64_{50}	44_{50}
10. vii. 50							
Top	29_{14}	$(0)_{0}$	67_{6}	83_{18}	$(0)_{0}$	50_{2}	0_{2}
Mid	0_{8}	40_{10}	32_{50}	91_{70}	43_{100}	48_{50}	$12{\cdot}5_{8}$
Bottom	39_{100}	40_{83}	69_{100}	84_{51}	79_{100}	26_{100}	20_{20}
11. ix. 50							
Top	78_{100}	91_{100}	78_{100}	88_{100}	73_{100}	74_{100}	92_{100}
Mid	57_{100}	64_{100}	68_{100}	77_{100}	82_{100}	71_{100}	70_{100}
Bottom	21_{100}	24_{100}	40_{100}	36_{100}	29_{100}	—	30_{100}
21. xi. 50	No females seen.						
9. i. 51							
Top	$(0)_{0}$	$(0)_{0}$	84_{19}	68_{19}	55_{9}	100_{1}	$(0)_{0}$
Mid	0_{3}	2_{100}	34_{83}	48_{101}	77_{22}	36_{11}	0_{19}
Bottom	0_{14}	0_{100}	15_{100}	12_{106}	16_{31}	18_{100}	0_{3}
14. ii. 51							
Top	$(0)_{0}$	—	99_{100}	99_{71}	99_{110}	$(0)_{0}$	$(0)_{0}$
Mid	$(0)_{0}$	—	85_{100}	94_{109}	83_{41}	44_{9}	13_{15}
Bottom	17_{17}	—	13_{100}	33_{100}	18_{100}	82_{82}	4_{52}
14. iii. 51							
Top	100_{3}	$(0)_{0}$	80_{5}	100_{5}	82_{43}	100_{1}	100_{3}
Mid	80_{6}	25_{4}	0_{5}	86_{35}	68_{71}	74_{23}	60_{5}
Bottom	63_{94}	47_{100}	36_{44}	50_{44}	33_{100}	0_{3}	40_{20}
5. iv. 51	Very few: top, 78_{18}; mid, 63_{11}; bottom, 72_{82}						
7. v. 51*							
Top	98_{62}	—	90_{41}	85_{100}	—	86_{100}	—
Mid	—	—	—	—	—	—	—
Bottom	76_{100}	—	72_{100}	87_{100}	—	67_{100}	—
4. 7. 51							
Top	$(0)_{0}$	$(0)_{0}$	$(0)_{0}$	100_{60}	$(0)_{0}$	$(0)_{0}$	$(0)_{0}$
Mid	17_{6}	0_{3}	20_{25}	96_{50}	82_{90}	$(0)_{0}$	$(0)_{0}$
Bottom	30_{50}	44_{50}	42_{50}	84_{50}	96_{50}	48_{50}	8_{50}
15. viii. 51							
Top	$(0)_{0}$	$(0)_{0}$	$(0)_{0}$	94_{50}	$(0)_{0}$	$(0)_{0}$	$(0)_{0}$
Mid	40_{35}	62_{50}	62_{50}	100_{50}	76_{60}	76_{50}	94_{50}
Bottom	16_{50}	44_{25}	18_{50}	78_{50}	84_{50}	4_{50}	38_{50}

* The series on 17 May 1951 was taken off L. Ranza and is incomplete: only two nets were used and the times of the hauls were 13.00, 19.00, 22.00 and 07.30 hr.

TABLE II

	No. examined	No. with food	Percentage with food
Daylight	1190	1041	87·5
Darkness	1514	1275	84
Total	2704	2316	86

The decrease in the numbers of *Calanus* with food in the gut in deeper water and its dependence on the stratification of the food organisms was more clearly demonstrated on 11 September 1950 when a more detailed series of hauls was taken at six depths, and water samples taken at roughly corre-

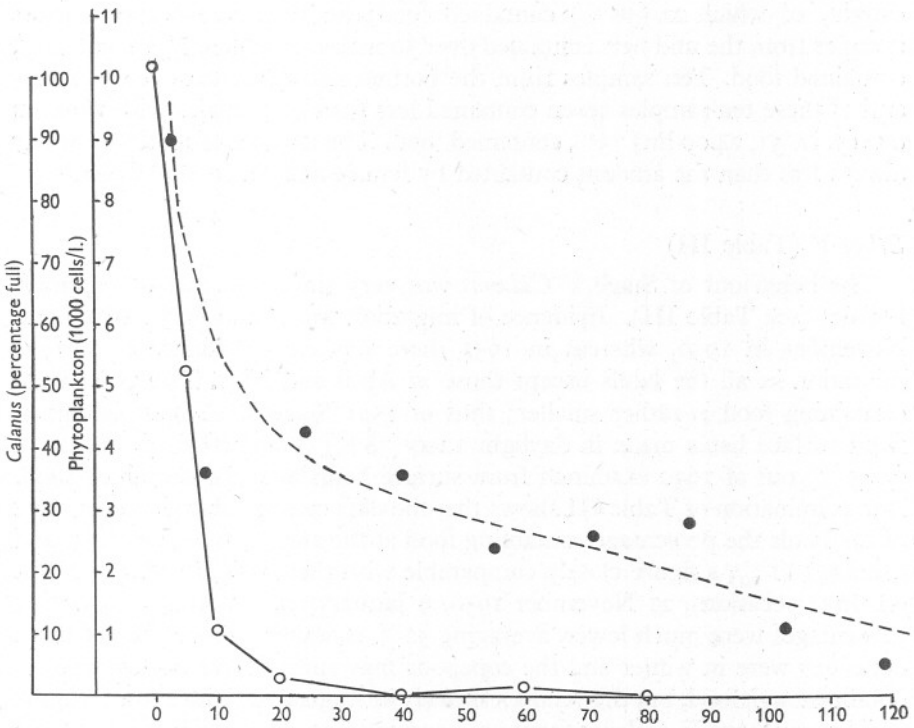

Fig. 1. Percentage of *Calanus* with food and phytoplankton concentration. Symbols: ● and broken line, percentage of *Calanus* with food; ○ and full line, phytoplankton concentration. Horizontal scale: depth in metres (0–120).

sponding depths to show the distribution of the phytoplankton. The results are illustrated in Fig. 1 in which the phytoplankton (1000's of cells/litre) and the percentage of *Calanus* with food are both graphed against depth. It can

be seen that the phytoplankton was concentrated in a narrow stratum about 10 m. deep, in which 90% of the *Calanus* were full; below this stratum the percentage fell from *c.* 40% at 10 m. to 5% at 100 m.

Adult Males

Male *Calanus* were not found in most of the hauls in sufficient numbers to obtain a clear picture of their behaviour. In addition they are relatively opaque and any food they may contain is less easy to see, so possibly small quantities of food, particularly in the anterior part of the gut, were overlooked.

Of the 1555 adult males examined from all the catches 63% were in the lowest net, and 62% of them were empty. On only one occasion were more than twenty-five taken in a surface net (18. iv. 50, 08.00 hr.) when 38 were caught, of which 22 (58%) contained food; on the same occasion three samples from the mid nets contained over 50 males, of which 45, 73 and 44% contained food. Ten samples from the bottom net contained over 50 males and of these ten samples seven contained less than 40% males with food; in one (5. iv. 51, 24.00 hr.) 73% contained food. The amount of food was nearly always less than the amount contained by female and Stage V *Calanus*.

Stage V (Table III)

The behaviour of Stage V *Calanus* was very similar to that of the adult females (see Table III). Evidence of migration was found only in July and November in 1950, whereas in 1951 there was clear evidence of vertical migration in all the hauls except those in April and May. The percentage containing food is rather smaller; thus of 1541 Stage V *Calanus* examined from surface hauls made in daylight 1200 (78%) contained food, and 1181 (72·5%) out of 1630 examined from surface hauls at night contained food. But examination of Table III shows that the data can be subdivided: in most of the hauls the percentage containing food at the surface was over 70% and averaged 81%, a figure closely comparable with that for adult females. But on three occasions, 21 November 1950, 9 January and 15 August 1951, the percentages were much lower, averaging 50% containing food. Two of these occasions were in winter and the copepods may simply have been unable to obtain enough food, but this seems less likely in August, and since from August to January Stage V *Calanus* form an overwintering population it is possible that the small percentage containing food is due to a real change in behaviour.

On 11 September 1950, the percentages containing food were also abnormally low at night, averaging only 31% in agreement with the other observations in autumn. But on this occasion *Calanus* were present at the surface in considerable numbers during the day and of those taken by day at the surface 82% contained food, a percentage comparable to those found in spring and summer catches. The behaviour shown by the *Calanus* here is exactly the

opposite of what would normally be expected because most of them were apparently feeding *by day* and not at night.

TABLE III. STAGE V: PERCENTAGE WITH FOOD

(The figures in suffix give the numbers examined.)

Time (hr.)...	12.00	16.00	20.00	24.00	04.00	08.00	12.00
28. ii. 50	Very few: top, 60_5; mid, 38_{63}; bottom, 17_{30}						
17. iv. 50							
Top	93_{100}	78_{100}	74_{100}	90_{100}	87_{100}	91_{80}	81_{100}
Mid	49_{100}	66_{100}	56_{89}	65_{100}	70_{100}	59_{100}	68_{100}
Bottom	41_{100}	25_{100}	26_{100}	49_{100}	48_{100}	33_{100}	34_{100}
29. v. 50							
Top	100_{31}	100_{31}	100_{10}	100_{17}	87_{23}	100_{26}	100_{21}
Mid	24_{50}	32_{50}	46_{50}	58_{50}	50_{50}	48_{50}	66_{50}
Bottom	26_{50}	36_{50}	52_{50}	32_{50}	30_{50}	48_{50}	30_{50}
10. vii. 50							
Top	53_{36}	100_{18}	93_{14}	98_{136}	0_2	81_{26}	89_{62}
Mid	21_{100}	25_{100}	31_{100}	46_{50}	28_{100}	35_{100}	18_{50}
Bottom	27_{100}	43_{97}	17_{100}	18_{50}	37_{100}	14_{100}	8_{50}
11. ix. 50							
Top	99_{100}	92_{100}	20_{100}	36_{100}	38_{100}	49_{100}	88_{100}
Mid	74_{100}	83_{100}	18_{100}	16_{100}	17_{100}	26_{100}	73_{100}
Bottom	10_{100}	13_{100}	9_{100}	6_{150}	19_{100}	—	17_{100}
21. xi. 50							
Top	$(0)_0$	$(0)_0$	18_{100}	47_{58}	52_{100}	0_2	$(0)_0$
Mid	10_{10}	4_{100}	10_{100}	13_{100}	14_{100}	0_{60}	0_7
Bottom	0_{100}	0_{100}	0_{100}	0_{100}	0_{100}	0_{100}	0_{100}
9. i. 51							
Top	$(0)_0$	$(0)_0$	89_{76}	58_{107}	51_{102}	100_1	$(0)_0$
Mid	0_3	2_{100}	36_{83}	48_{101}	77_{22}	36_{11}	0_{19}
Bottom	0_{14}	0_{100}	15_{100}	12_{106}	16_{31}	18_{100}	0_3
14. ii. 51	Very few: top, 100_8; mid, 0_4; bottom, 0_{30}						
14. iii. 51							
Top	75_8	100_1	$87{\cdot}5_{32}$	87_{93}	95_{97}	100_3	84_{50}
Mid	10_{10}	79_{34}	79_{100}	97_{88}	91_{100}	97_{93}	89_{63}
Bottom	80_{90}	20_{100}	14_{100}	52_{100}	36_{88}	20_{15}	68_{89}
5. iv. 51							
Top	60_{10}	78_{53}	$(0)_2$	87_{100}	95_{100}	63_8	100_4
Mid	98_{100}	96_{115}	96_{100}	95_{100}	96_{100}	80_{50}	75_{100}
Bottom	92_{100}	59_{100}	82_{100}	92_{100}	93_{100}	77_{100}	83_{100}
17. v. 51 (see footnote, Table I)							
Top	100_{16}	—	100_{37}	100_{12}	—	100_{59}	—
Mid	—	—	—	—	—	—	—
Bottom	71_{100}	—	64_{100}	51_{100}	—	44_{100}	—
4. vii. 51							
Top	44_9	$(0)_0$	$(0)_0$	100_{50}	$(0)_0$	$(0)_0$	$(0)_0$
Mid	2_{50}	0_{17}	12_{50}	100_{50}	87_{100}	67_6	$(0)_0$
Bottom	8_{50}	8_{100}	22_{50}	36_{50}	43_{50}	13_{50}	3_{50}
15. viii. 51							
Top	$(0)_0$	$(0)_0$	$(0)_0$	38_{50}	$(0)_0$	$(0)_0$	$(0)_0$
Mid	32_{50}	20_{50}	42_{60}	92_{50}	6_{50}	18_{50}	20_{25}
Bottom	12_{50}	8_{50}	20_{50}	22_{50}	16_{50}	0_{50}	12_{50}

The percentage containing food in the lower nets, as with adult females, was less than at the surface, averaging 46% in the middle net and 29% in the lowest net.

Stage IV (Table IV)

On a few occasions, for instance on 29 May 1950, fair numbers of Stage IV were caught. When the numbers were sufficiently large to give significant counts, most of those in the surface water (averaging 91 % for all the samples in Table IV) and a smaller proportion of those from the deeper layers (38 % in the middle net and 23 % in the lowest net from Table IV) contained food, so that the behaviour appears to be closely similar to that of adult female and Stage V *Calanus*.

TABLE IV. STAGE IV: PERCENTAGE WITH FOOD

(The figures in suffix give the numbers examined.)

Time (hr.)...	12.00	16.00	20.00	24.00	04.00	08.00	12.00
29. v. 50							
Top	95_{102}	98_{112}	97_{110}	99_{104}	98_{109}	100_{100}	100_{100}
Mid	69_{62}	47_{90}	54_{50}	29_{50}	26_{50}	17_{50}	34_{50}
Bottom	12_{50}	13_{50}	28_{50}	13_{50}	16_{50}	25_{50}	28_{25}
11. vii. 50							
Top	91_{100}	98_{100}	84_{50}	93_{100}	100_{12}	98_{100}	76_{100}
Mid	22_{100}	18_{100}	19_{100}	26_{50}	21_{100}	23_{100}	20_{50}
Bottom	24_{100}	8_{100}	27_{100}	20_{50}	22_{100}	7_{100}	16_{50}
17. v. 51 (see footnote, Table I)							
Top	100_{14}	—	100_{34}	100_{9}	—	100_{24}	—
Mid	—	—	—	—	—	—	—
Bottom	75_{8}	—	100_{9}	9_{21}	—	63_{8}	—
4. vii. 51							
Top	(0)	(0)	(0)	100_{10}	(0)	(0)	(0)
Mid	11_{36}	12_{17}	12_{25}	90_{10}	91_{100}	15_{20}	(0)
Bottom	6_{50}	0_{30}	15_{20}	75_{20}	30_{23}	40_{20}	0_{9}
15. viii. 51							
Top	18_{50}	(0)	(0)	33_{15}	(0)	(0)	(0)
Mid	42_{7}	24_{25}	30_{10}	46_{50}	72_{40}	30_{50}	0_{9}
Bottom	12_{25}	16_{50}	16_{25}	6_{34}	6_{50}	15_{20}	21_{34}

Amount of Food

The amount of food in the gut varied from small quantities to a mass completely filling the mid-gut. An attempt was made to record the different amounts of food which the copepods contained. For example a *Calanus* with food throughout the length of its mid-gut was recorded as 'full', but a 'full' *Calanus* in April when diatoms were abundant obviously contained more food than a 'full' *Calanus* in winter, when phytoplankton was scarce; similarly, a 'full' adult female contained more food than a 'full' Stage V. These and other difficulties in maintaining a constant standard in a subjective estimate of this kind made the value of the estimates rather doubtful. The following general statements, however, are probably a fair summary of the observations.

The amount of food contained in the guts of the copepods with food was greatest in spring (April, May) when nearly all would be packed with food. During the summer the *Calanus* were not quite so well filled, but in winter

the quantity was distinctly less, and small even in many animals at the surface. The amount of food in individuals captured in the lowest net was nearly always less than that found at the surface: for instance copepods with packed guts were rarely seen in the deepest catches. The *Calanus* in the middle net were in an intermediate condition; when food was abundant, most would contain a large amount of food, but at other times the amount might be distinctly less than at the surface. As would be expected from their sizes, females contained in general rather more than Stage V and these distinctly more than Stage IV; males contained much less for their size than any of the other stages and in general contained distinctly less than Stage V.

Calanus finmarchicus *and* C. helgolandicus

Rees (1949) has drawn attention to the existence of two possible subspecies of *C. finmarchicus* and has suggested that they differ in temperature tolerance. Marshall & Orr (1952) have recorded the presence of *C. helgolandicus* in the Clyde, occasionally in fair numbers, and have shown that the two forms differ in the time of spawning. It would be interesting to see whether its feeding behaviour is also different. The catches were accordingly examined to see if any *C. helgolandicus* were present, but, except on one occasion, 11 September 1950, this form was absent altogether or made up an extremely small fraction of the catch. So far as could be seen from these small numbers the feeding behaviour of the two forms was identical. It has already been seen that the conditions in September 1950 were unusual and the presence of *C. helgolandicus* might explain the abnormality, but the numbers of *C. helgolandicus* do not vary very much from one haul to another, and since they did not rise above 32 % of any catch, they are too few in number to account for the large changes in feeding behaviour observed. Further, the percentage of *C. helgolandicus* containing food did not differ significantly from that of *C. finmarchicus*.

Laboratory Observations

Methods

In the laboratory the existence of a possible periodicity in grazing rate was investigated, as in the field observations by direct examination of the gut contents. The copepods were kept in a suspension of a food organism, usually a species of *Chlamydomonas* (cf. Gauld, 1951), and examined from time to time, usually at intervals of 4 hr., and the amount of food recorded.

Results

Preliminary Investigations

Before the other experiments and any field observations were started, a number of experiments were made to see how long a copepod would take to fill its gut when it began to feed and how long it would remain full after it had ceased feeding. The former were done by keeping copepods in sterile sea

water for some hours, usually overnight, to make sure they were empty. They were then put into suspensions of *Chlamydomonas* and examined at intervals of 10–15 min. to see how full they were. It proved very difficult to get any satisfactory observations. The transference of the copepods from a beaker to a watch-glass for examination disturbed them, and when they were returned to the beakers some time might elapse before they settled down, during which they darted about the beaker rapidly and normal feeding would not take place. The time taken to settle down varied quite erratically. However, in a moderately thick suspension of *Chlamydomonas*, comparable to those used in the experiments, *Calanus* can fill its gut in 10–15 min. at most and in thicker suspensions in a very few minutes indeed. It is unlikely that the natural phytoplankton on which the *Calanus* examined in the field were feeding would ever be as rich as that used in the experiments except possibly at the height of the spring maximum, but even in suspensions comparable in density to natural phytoplankton *Calanus* can fill its gut in less than 30 min.

To find out how long food could remain in the gut the exact opposite procedure was followed. A number of *Calanus* were kept for some time in a fairly thick suspension of *Chlamydomonas* until they were full. They were then transferred into sterile sea water and examined as before at short intervals. Although a very small quantity of food matter may remain for several hours in the gut of a copepod which is swimming in sterile sea water, the bulk of the food will be digested and the undigestible residue passed out in about 1–2 hr.

Twenty-four-Hour Experiments

Observation of the amount of food in the gut gave no clear evidence of a consistent feeding rhythm, either for adult female or for Stage V *Calanus*. A typical series of observations is illustrated in Fig. 2. Each horizontal line illustrates the behaviour of an individual copepod and the vertical columns correspond to the hour of the observations. The quantity of food in the gut is given in an arbitrary scale—a column blacked to its full height means that the gut was quite full; three-quarters its height means that the anterior part of the gut was full but the posterior half was empty (usually because a faecal pellet had been passed out recently); half the height that the gut was only partly full, and one-quarter that only a small quantity of food was present. A white column means that the gut was empty.

It can be seen from the diagram that most of the adult females were feeding continuously throughout the 24 hr., the few drops in the columns were almost certainly due to the ejection of a faecal pellet just before examination. They were not, of course, perfectly consistent, as numbers 2 and 7 show. Stage V's (Fig. 3) seemed to be much less voracious and were much less predictable in their behaviour. Although feeding was not continuous and long gaps apparently intervened between meals, no consistent rhythm of feeding and resting can be deduced from these data. One point, however, emerges very plainly.

Calanus can spend a long time in a dense suspension of food without feeding —some observations were carried on over several days, and although the

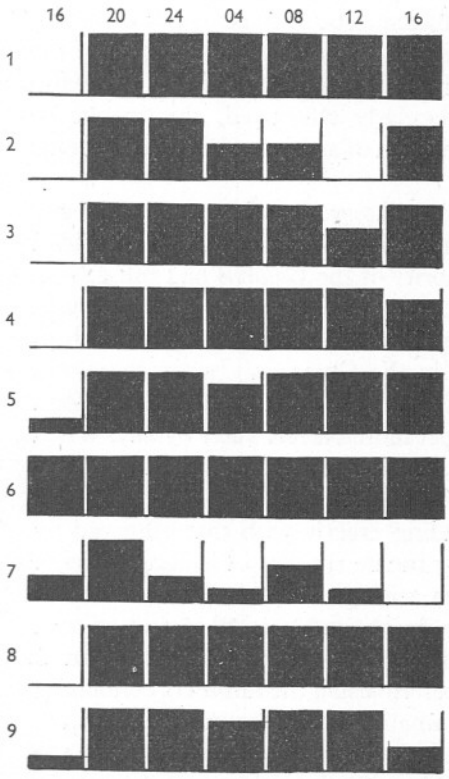

Fig. 2. Feeding of adult female *Calanus*. For explanation see text.

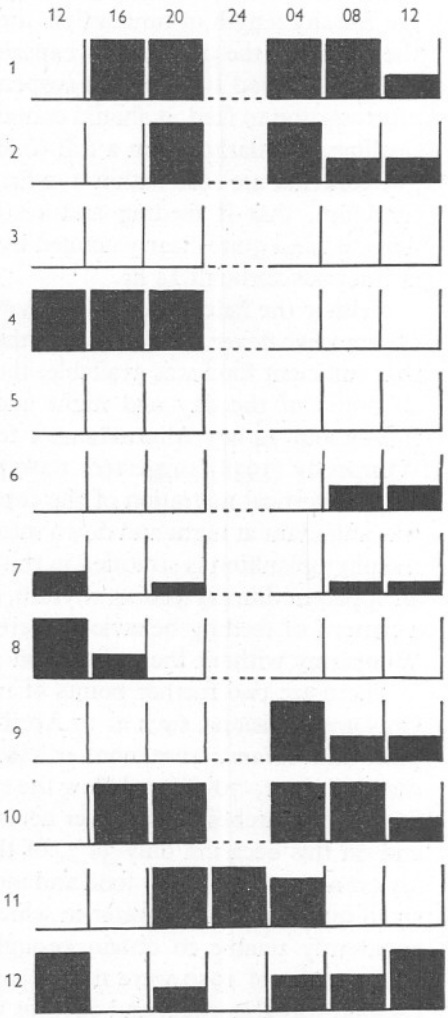

Fig. 3. Feeding of Stage V *Calanus*. For explanation see text. A broken line in 24 hr. column indicates that no observations were made at midnight.

copepod appeared to be perfectly healthy and was seen, at least on some occasions, swimming normally, no food was ever observed in the gut.

Discussion

A copepod cannot be feeding, i.e. filtering water through its maxillae and ingesting the material accumulating on the maxillae, and yet have an empty gut for any length of time unless the water is nearly or absolutely barren. As the results of the preliminary experiments show, the gut fills up quite rapidly when a copepod is put into a suspension of food and, within an hour at most after starting to feed, it should contain sufficient food to make it clear that it is feeding. Similarly, when a full *Calanus* is put into barren water most of the gut contents are lost within 1–2 hr. of the cessation of feeding. It is plain, therefore, that if feeding and resting regularly alternated, this would be detected and quite clearly defined by estimation of amount of the gut contents at intervals through 24 hr.

Neither the field observations nor the laboratory experiments provide any evidence whatever of a diurnal rhythm of this kind. On the contrary, provided that sufficient food was available, the majority of the *Calanus* had full guts at all hours of the day and night and apparently were feeding continuously throughout 24 hr. Alternation of feeding and non-feeding periods, such as Wimpenny (1938) suggested, took place in the Clyde only when there was marked vertical migration of the copepods, into the surface water where food was abundant at night and down into deepet more barren water by day. When the phytoplankton is stratified in this way, diurnal vertical migration produces an apparent diurnal feeding rhythm, as was seen on many occasions in 1951—a pattern of feeding behaviour corresponding exactly with that observed by Wimpenny without the postulation of any innate rhythm in feeding activity.

There are two further points of interest arising out of these observations. On some occasions, such as 17 April 1950, no obvious vertical migration took place and *Calanus* were more or less evenly distributed at least as far down as the lowest net, 70–80 m. below the surface. As usual the numbers containing food in the catches of the lower nets were smaller than those in the upper net, and on this occasion only 39% of the *Calanus* (females and Stage V) in the lowest net contained any food and most of these (29% of the total) only a very small quantity. In the water in which they were caught these copepods were apparently unable to obtain enough food to maintain themselves. If the observations of 1950 were not all made on occasions when the behaviour of *Calanus* was abnormal, and obvious vertical migrations do not take place over long periods, it may yet be possible that although the population was not migrating up to, and down from, the rich surface layers all together as it does when the copepods display normal migratory behaviour, it was in a continuous state of flux, some *Calanus* migrating upwards to feed and others downwards out of the rich water at all times of the day. What stimuli would induce these movements in the individual *Calanus* is difficult to say unless they are hunger and repletion. In the absence of such movement, a considerable

fraction of the population apparently remained in deep water where the copepods in time would starve.

Secondly, on most occasions in 1951 vertical migration was clearly marked and the copepods spent the daylight hours in deep water, below the strata where food is abundant. In previous work (Gauld, 1951) I was able to show that *Calanus* was able to filter about 80 ml. in 24 hr., and the amount of food required by *Calanus* in 24 hr. has been estimated as 0·002–0·013 mg. (dry weight) (Marshall *et al.*, 1935). If the vertical migration is taking place, this amount of food must be collected not in 24 hr., but during the hours of darkness only, i.e. in 8–12 hr., depending on the season, and must be present not in 80 ml. but in 30–40 ml. of sea water.

Summary

Records were made of the presence or absence of food in the guts of *Calanus finmarchicus* caught in three different depths, at intervals of 4 hr. through 24 hr.

It was found that 80–100% of the *Calanus* caught at the surface were full of food at all hours of the day.

The number of *Calanus* containing food in deeper water was distinctly less. This may be correlated with the abundance of its food close to the surface.

Diurnal vertical migrations took place on some occasions when samples were taken, but not on all.

In the absence of vertical migration *Calanus* was abundant at the surface and feeding continuously at all hours of the 24 hr. Where vertical migration took place feeding was mostly at the surface and was restricted to the hours of darkness, i.e. in summer to a period distinctly less than 8 hr. round midnight.

Laboratory observations confirm the absence of any feeding rhythm.

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