

Seasonal variations in length, dry weight, carbon and nitrogen of *Calanus helgolandicus* from the Celtic Sea

H. H. Bottrell and D. B. Robins

Natural Environment Research Council, Institute for Marine Environmental Research, Prospect Place, The Hoe, Plymouth, Devon, PL1 3DH, United Kingdom

ABSTRACT: Seasonal fluctuations in mean dry weight of the copepod *Calanus helgolandicus* were large and contrasted markedly with the small seasonal fluctuations of cephalothorax length. Dry weight was related linearly to cephalothorax length on logarithmic axes by a series of regression equations which were significantly different for each of 8 cruises. Carbon and nitrogen were likewise linearly related to dry weight on logarithmic axes and followed the seasonal fluctuations in dry weight. Dry weight and cephalothorax length showed little or no correlation with food concentration, ingestion rate, population numbers, population biomass or temperature. However, seasonal changes in dry weight could be explained in terms of Vidal's (1980a, b: Mar. Biol. 56: 111–134; 135–146) laboratory studies which relate growth rate and development time to body size, food concentration and temperature.

INTRODUCTION

There is an obvious need for reliable data on seasonal changes in dry weight, in order to minimize errors in calculating zooplankton biomass and production. Despite this, many of the published data for dry weights of marine copepods, including over 50 species, refer to temporally isolated samples (e.g. Orr, 1934; Nakai, 1955; Omori, 1969; Ikedan, 1974; Durbin and Durbin, 1978). Studies of the dry weight over an annual cycle have been made only for *Calanus finmarchicus sensu lato* (Bagorov, 1934; Marshall et al., 1934; Orr, 1934; Comita et al., 1966), *Euchaeta norvegica* (Båmstedt and Matthews, 1975; Bratellid and Matthews, 1978), *Chiridius armatus* (Båmstedt, 1978; Bakke and Alvarez Valderhaug, 1978), and *Centropages typicus* and *Temora stylifera* (Razouls, 1973). Since the taxonomic separation of *Calanus finmarchicus s.l.* (e.g. Rees, 1949; Jaschnov, 1955; Brodsky, 1959; Matthews, 1967) there has been only one seasonal survey of body size of *Calanus helgolandicus* (Claus) (Gatten et al., 1979); this dealt primarily with total lipid and lipid classes, and reported equations relating dry weight, carbon and nitrogen to total lipid for copepodite stage

V, male and female *C. helgolandicus* from the English Channel, but did not report seasonal changes in dry weight.

The studies made on *Calanus finmarchicus s.l.* provided evidence that temperature and food are the main factors affecting body size but, as with studies on the other copepods, did not propose a mechanism to explain the seasonal fluctuations. Vidal (1980a, b) gave details of laboratory investigations of the body size, growth rates and development times in relation to food concentration and temperature for the closely related species *C. pacificus* Brodsky. Vidal's studies will be used here to propose a possible mechanism to explain seasonal variations in body size of *C. helgolandicus* from the Celtic Sea.

In this paper *Calanus* is referred to by the species name used by the author cited in order to avoid confusion arising from taxonomic changes. In particular, it is probable that the species investigated by Bogorov (1934) off Plymouth was *C. helgolandicus* (Claus), and that the species referred to as *C. helgolandicus* (authority unspecified) by Mullin and Brooks (1970) and Paffenhöfer (1971, 1976) and as *C. pacificus* Brodsky by Frost (1972) and Vidal (1980a, b) are the

same species (i.e. *C. pacificus*). *C. helgolandicus* (Claus) and *C. pacificus* Brodsky are considered independent but closely related species (Brodsky, 1975).

MATERIALS AND METHODS

Zooplankton was collected from around a central station (51° 30' N 5° 30' W) situated within a 14.8 × 18.5 km sampling grid in the Celtic Sea on 8 cruises during February, March, May, June, August and October 1978, and January and March 1979. Samples were taken using a half-metre net of 280 µm mesh, fitted with a detachable 500 ml cod-end, deployed between a depth of 100 m and the surface. Immediately after collection the contents of the cod-end were distributed on to pieces of nylon mesh. After removal of the gelatinous zooplankton, the organisms remaining on the gauze were rinsed in deionised water, covered with a thin polythene film and placed in a freezer.

On return to the laboratory the samples were defrosted and copepods carefully removed from the gauze. Only undamaged *Calanus helgolandicus* (Claus) were identified to developmental stage and subsequently used for analysis. Cephalothorax length (distance from tip of rostrum to posterior edge of cephalothorax) was measured to within 25 µm using an eye-piece graticule, after which each *Calanus* was transferred to a numbered aluminium planchet and dried to constant weight in an oven at 60 °C. The dried copepods were stored in desiccators until cool and then weighed individually on a Cahn 25 Electrobalance readable to 0.1 µg. Carbon and nitrogen determinations were made using a Carlo-Erba CHN analyser with cyclohexanone 2, 4-dinitrophenylhydrazine (carbon 51.79 %, nitrogen 20.14 %) as the standard. Carbon and nitrogen measurements were made on individual *Calanus* in most cases but mean values were determined for copepodite stages II and III, using between 2 and 10 individuals per sample. Individual values, rather than means, were used whenever possible for fitting regression lines.

Size distribution (PSD) and total volume (TPV) of the suspended particulate matter, as well as feeding rates of *Calanus*, were measured using a Coulter Counter TA II with Population Accessory. Measurements were made on particles between 1.59 and 128.0 µm equivalent spherical diameter.

Zooplankton population data were obtained from oblique hauls with a Longhurst-Hardy Plankton Recorder (Longhurst and Williams, 1976). Details of these samples are given in Williams and Conway (1982). Biomass for each cruise was calculated by summation of the products of mean numbers of each stage and mean dry weight for each stage.

RESULTS

Between-cruise variability is shown in Fig. 1. Mean cephalothorax length was relatively constant within each copepodite stage during the 14 mo of the study. In contrast, seasonal fluctuations of mean dry weight were not the same for each copepodite stage. The early stages showed little between-cruise variation whereas stage V and adults showed very large fluctuations in mean dry weight.

The means and ranges of values of dry weight and cephalothorax length for individuals of each stage for each cruise are given in Tables 1 and 2 respectively. Dry weight showed considerable within-cruise variability, especially during March 1978 in copepodite stages II, III, IV and V. At other times the variability was lower but there was nearly always considerable overlap in the dry weights of successive stages. In

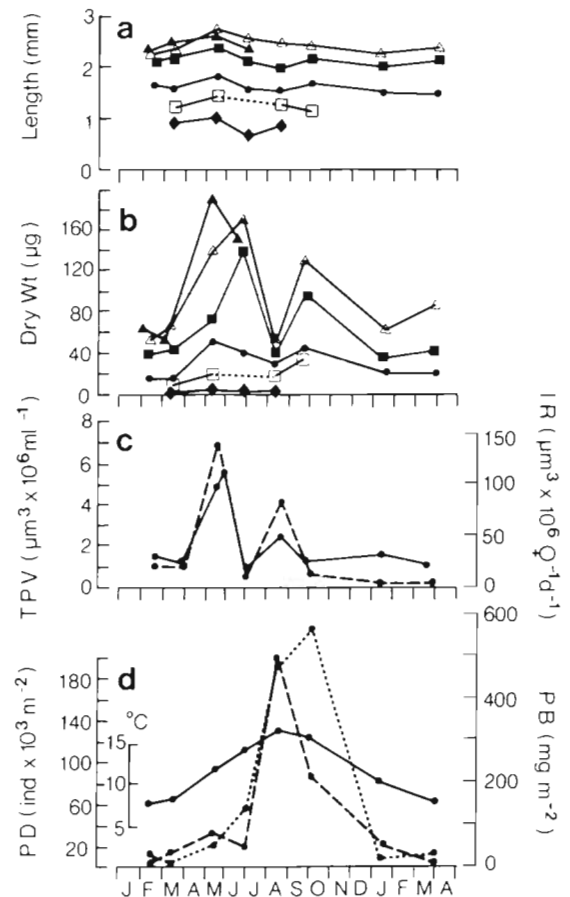


Fig. 1. *Calanus helgolandicus*. Seasonal variability. (a) Mean cephalothorax length for copepodite stages II (◆), III (□), IV (●), V (■), ♀ (△), ♂ (▲); (b) mean dry weight for the same copepods in relation to (c) total particulate volume (TPV, solid line) and ingestion rate of *Calanus* females (IR, dashed line), and (d) temperature (°C, solid line), *Calanus* population density (PD, dashed line) and *Calanus* population biomass (PB, dotted line)

Table 1. *Calanus helgolandicus*. Dry weight: (a) seasonal variations of mean (\pm SE) in μ g; (b) range for each copepodite stage. Number in parentheses is the factor by which the maximum differs from minimum dry weight. Number of observations as in Table 2

Cruise	Copepodite stage					
	CII	CIII	CIV	CV	♀	♂
(a) Mean						
Feb 78	-	-	15.80	39.41 \pm 3.03	57.34 \pm 2.64	61.81 \pm 8.12
Mar 78	2.14 \pm 0.53	4.96 \pm 0.63	12.94 \pm 1.28	46.48 \pm 3.35	68.85 \pm 4.07	52.09 \pm 5.80
May 78	4.96 \pm 0.19	14.78 \pm 0.80	52.77 \pm 2.01	72.75 \pm 2.77	143.17 \pm 5.73	192.29 \pm 25.46
Jun 78	1.99 \pm 0.10	-	40.45 \pm 10.22	144.03 \pm 10.52	172.78 \pm 8.82	150.51 \pm 6.48
Aug 78	2.87 \pm 0.13	10.87 \pm 0.62	30.09 \pm 1.88	41.18 \pm 1.52	53.14 \pm 1.97	-
Oct 78	-	34.71 \pm 2.12	46.11 \pm 1.50	98.89 \pm 4.85	134.29 \pm 5.64	-
Jan 79	-	-	20.31 \pm 2.23	37.72 \pm 1.97	62.48 \pm 4.57	50.25 \pm 3.47
Mar 79	-	-	19.47 \pm 2.38	43.69 \pm 2.06	84.02 \pm 2.27	-
(b) Range						
Feb 78	-	-	-	18.9 - 79.4 (4.2)	34.6 - 85.6 (2.5)	42.4 - 74.2 (1.8)
Mar 78	0.6 - 4.4 (7.3)	0.9 - 14.2 (15.8)	5.6 - 33.5 (6.0)	13.3 - 89.1 (6.7)	34.1 - 124.9 (3.7)	42.4 - 74.4 (1.8)
May 78	4.6 - 5.2 (1.1)	8.2 - 27.8 (3.4)	38.2 - 79.8 (2.1)	43.7 - 107.7 (2.5)	102.4 - 233.9 (2.3)	141.7 - 281.5 (2.0)
Jun 78	1.8 - 2.3 (1.3)	-	24.9 - 57.2 (2.3)	74.2 - 270.1 (3.6)	91.6 - 284.1 (3.1)	92.6 - 227.1 (2.5)
Aug 78	2.6 - 3.4 (1.3)	8.9 - 12.3 (1.4)	23.6 - 39.2 (1.7)	25.8 - 68.3 (2.7)	33.0 - 80.4 (2.5)	-
Oct 78	-	21.9 - 49.0 (2.2)	30.0 - 59.7 (2.0)	60.0 - 167.0 (2.8)	99.0 - 228.5 (2.3)	-
Jan 79	-	-	16.1 - 24.4 (1.5)	21.2 - 68.3 (3.2)	31.3 - 137.8 (4.4)	32.5 - 68.6 (2.1)
Mar 79	-	-	15.6 - 23.8 (1.5)	40.50 - 50.0 (1.2)	52.4 - 98.8 (1.9)	-

Table 2. *Calanus helgolandicus*. Cephalothorax length: (a) seasonal variations of mean (\pm SE) in mm with number of observations in parentheses; (b) range of length for each copepodite stage. Number in parentheses is the factor by which the maximum differs from the minimum length

Cruise	Copepodite stage					
	CII	CIII	CIV	CV	♀	♂
(a) Mean						
Feb 78	-	-	1.66 - (1)	1.99 \pm 0.03 (30)	2.25 \pm 0.02 (30)	2.26 \pm 0.02 (4)
Mar 78	0.80 \pm 0.02 (13)	1.15 \pm 0.02 (30)	1.59 \pm 0.02 (30)	2.13 \pm 0.01 (30)	2.37 \pm 0.03 (30)	2.46 \pm 0.03 (5)
May 78	0.99 \pm 0.04 (3)	1.35 \pm 0.02 (30)	1.84 \pm 0.02 (30)	2.38 \pm 0.02 (30)	2.80 \pm 0.02 (30)	2.71 \pm 0.03 (5)
Jun 78	0.51 \pm 0 (3)	-	1.50 \pm 0.06 (13)	2.07 \pm 0.03 (19)	2.52 \pm 0.02 (30)	2.36 \pm 0.02 (30)
Aug 78	0.71 \pm 0.02 (5)	1.22 \pm 0.02 (5)	1.48 \pm 0.03 (30)	1.89 \pm 0.02 (30)	2.43 \pm 0.02 (30)	-
Oct 78	-	1.10 \pm 0.03 (15)	1.62 \pm 0.02 (30)	2.11 \pm 0.02 (30)	2.40 \pm 0.02 (30)	-
Jan 79	-	-	1.47 \pm 0.04 (8)	1.97 \pm 0.03 (30)	2.19 \pm 0.03 (30)	2.22 \pm 0.02 (14)
Mar 79	-	-	1.36 \pm 0.05 (3)	2.09 \pm 0.07 (4)	2.33 \pm 0.01 (30)	-
(b) Range						
Feb 78	-	-	-	1.69-2.17 (1.3)	1.97-2.46 (1.3)	2.20-2.29 (1.0)
Mar 78	0.65-0.91 (1.4)	0.81-1.37 (1.7)	1.36-1.78 (1.3)	1.99-2.26 (1.1)	2.16-2.95 (1.4)	2.38-2.56 (1.1)
May 78	0.93-1.03 (1.1)	1.24-1.48 (1.2)	1.68-2.01 (1.2)	2.11-2.68 (1.3)	2.64-3.03 (1.2)	2.62-2.81 (1.1)
Jun 78	0.51- (0)	-	1.38-1.57 (1.2)	1.78-2.40 (1.4)	2.40-2.85 (1.2)	2.16-2.56 (1.2)
Aug 78	0.66-0.76 (1.2)	1.12-1.29 (1.2)	1.37-1.64 (1.2)	1.66-2.10 (1.3)	2.32-2.61 (1.1)	-
Oct 78	-	0.94-1.39 (1.5)	1.50-1.81 (1.2)	1.90-2.32 (1.2)	2.17-2.56 (1.2)	-
Jan 79	-	-	1.37-1.51 (1.1)	1.81-2.26 (1.3)	1.99-2.43 (1.2)	2.11-2.38 (1.1)
Mar 79	-	-	1.29-1.45 (1.1)	1.93-2.26 (1.2)	2.33-2.44 (1.1)	-

contrast, cephalothorax length showed much less within-cruise variability at all times of the year and there was little or no overlap between successive stages.

Although each stage did not attain its maximum dry weight at the same time, the general pattern of seasonal fluctuations in mean dry weight was similar for all stages, that is, high values in spring/early summer and autumn, and low values in August and winter (Fig. 1b). The slight evidence of a seasonal cycle of

cephalothorax length suggested a similar pattern for all stages, the maxima for all stages occurring in May. This coincided with the dry weight maximum for males and for stage IV but preceded the maximum for females and for stage V by over 1 mo (Fig. 1).

The regressions relating the logarithm of dry weight to the logarithm of cephalothorax length for all individuals for each cruise are given in Table 3. There was no evidence for different within-stage relationships for each cruise. A comparison of regressions showed sig-

Table 3. *Calanus helgolandicus*. Linear regressions relating dry weight (DW) to cephalothorax length (CL). Regression equation: $\log_e DW = \log_e a + b \log_e CL$

Cruise	$\log_e a$	$b \pm SE$	df	F	P	R ² (%)
Feb 78	1.8108	2.7383 ± 0.4761	1,63	33	0.001	34.2
Mar 78	1.2741	3.2340 ± 0.1399	1,136	535	0.001	79.7
May 78	1.8274	3.0708 ± 0.0947	1,127	1052	0.001	89.2
Jun 78	2.7346	2.7124 ± 0.1069	1,83	644	0.001	88.6
Aug 78	2.0691	2.2914 ± 0.0994	1,68	532	0.001	88.7
Oct 78	3.1313	1.9231 ± 0.0872	1,103	487	0.001	82.5
Jan 79	1.6934	3.6668 ± 0.4397	1,72	70	0.001	49.1
Mar 79	2.0983	2.7136 ± 0.2125	1,35	163	0.001	82.3

SE = standard error; df = degrees of freedom; F = variance ratio; P = level of significance; R² (%) = % of total variability explained by the regression

nificant differences between the equations for each cruise, i. e. regression equations calculated with a common intercept, a common slope or a common line gave a significant increase in the residual mean square in each case. Since dry weight is a power function of cephalothorax length, it is possible for small fluctuations in length to result in much larger fluctuations in weight. However, the effect of seasonal variations in cephalothorax length on dry weight can be removed by calculating mean dry weights adjusted to a standard length for each stage. A standardized cephalothorax length was calculated for each stage as the mean of all cephalothorax lengths for each stage from all cruises. This value was used in the regression equations in Table 3 to predict the adjusted mean dry weight for each standard length on each cruise (Fig. 2). The pattern of variation remains essentially the same as shown in Fig. 1b and indicates that the large seasonal fluctuations in dry weight of stage V and adults are not explicable by changes in cephalothorax length.

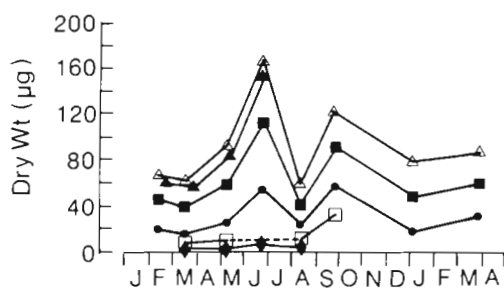


Fig. 2. *Calanus helgolandicus*. Seasonal variability of mean dry weight adjusted to a standardised cephalothorax length for copepodite stages II (◆), III (□), IV (●), V (■), ♀ (△), ♂ (▲). Data are back-transformed from logarithmic values. See text for further details

On logarithmic axes there was a highly significant linear relationship between carbon per copepod and dry weight, and between nitrogen per copepod and dry weight, for all stages and all cruises (Fig. 3a, b). Thus

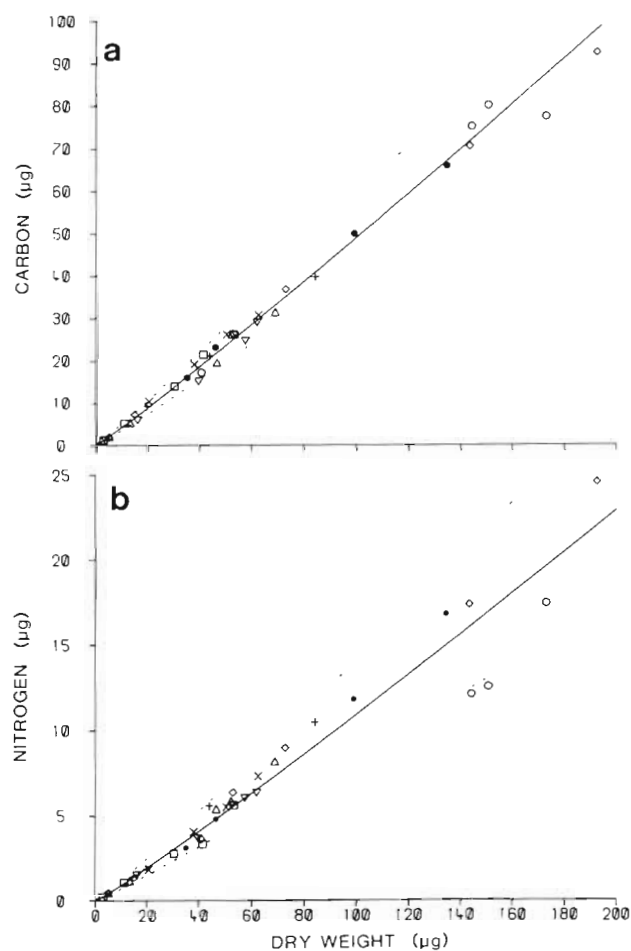


Fig. 3. *Calanus helgolandicus*. Relationship between dry weight and (a) carbon, (b) nitrogen for all copepodite stages on each cruise. Data are back-transformed from logarithmic axes and dotted lines show the 95 % prediction limits on the data. Symbols distinguish cruise: 1978 - February ▽, March △, May ◇, June ○, August □, October ●, 1979 - January ×, March +. Regression equations (±S.E.), with $n = 36$ in both cases, are: $\log_e C = -0.9845(\pm 0.0491) + 1.0593(\pm 0.0130) \log_e DW$ and $\log_e N = -2.5341(\pm 0.0714) + 1.0694(\pm 0.0189) \log_e DW$

Table 4. *Calanus helgolandicus*. Seasonal variations of mean (\pm SE) of (a) nitrogen and (b) carbon as a percentage of dry weight for each copepodite stage

Cruise	Copepodite stage					
	CII	CIII	CIV	CV	♀	♂
(a) Nitrogen						
Feb 78	–	–	9.92	9.52 \pm 0.67	10.60 \pm 0.21	10.34
Mar 78	8.18	7.82	8.41	11.41 \pm 1.54	11.76 \pm 0.56	10.97
May 78	9.68	9.29	12.08 \pm 0.30	12.34 \pm 0.11	12.13 \pm 0.28	12.78
Jun 78	–	–	8.92	8.39 \pm 0.68	10.17 \pm 0.24	8.31 \pm 0.43
Aug 78	8.93	9.94	9.17 \pm 0.33	8.05 \pm 0.96	10.52 \pm 0.58	–
Oct 78	–	8.97	10.49 \pm 0.31	11.95 \pm 0.29	12.50 \pm 0.11	–
Jan 79	–	–	9.06	10.72 \pm 0.54	11.68 \pm 0.23	10.95 \pm 0.39
Mar 79	–	–	9.50	12.71	12.44 \pm 0.11	–
(b) Carbon						
Feb 78	–	–	39.62	38.86 \pm 1.85	43.43 \pm 0.91	47.27
Mar 78	37.01	35.40	38.79 \pm 2.76	41.27 \pm 2.78	45.15 \pm 1.36	49.60
May 78	38.71	49.27	49.90 \pm 0.46	50.60 \pm 0.41	49.38 \pm 0.74	48.23
Jun 78	–	–	42.29	52.29 \pm 1.29	44.93 \pm 2.26	53.32 \pm 1.81
Aug 78	44.23	47.88	46.27 \pm 1.29	51.71 \pm 2.76	49.06 \pm 0.38	–
Oct 78	–	46.10	50.47 \pm 1.00	50.40 \pm 0.41	49.21 \pm 0.23	–
Jan 79	–	–	51.32	50.47 \pm 1.79	48.46 \pm 1.16	51.92 \pm 0.98
Mar 79	–	–	47.67	48.08	47.16 \pm 0.37	–

seasonal fluctuations in carbon and nitrogen are of the same magnitude and follow the same seasonal pattern as the fluctuations in dry weight shown in Fig. 1b. The values of the slope of the regression lines for carbon and for nitrogen are both significantly different from $\beta = 1$ (carbon: $t = 4.57$ and nitrogen: $t = 3.68$, with 34 degrees of freedom $P < 0.001$ in both cases). The slopes are slightly greater than unity (Fig. 3), indicating that carbon or nitrogen expressed as a percentage of dry weight increases only slightly as the dry weight increases. For example, from the regressions a 10 μg copepod is predicted to contain approximately 11 % nitrogen and 50 % carbon. Observed values varied from 8.05 to 12.78 % for nitrogen, and from 35.40 to 53.32 % for carbon (Table 4).

It follows from the above results that seasonal variations in dry weight, carbon and nitrogen of *Calanus helgolandicus* from the Celtic Sea cannot be explained by variations in cephalothorax length.

Field measurements of total particulate volume, particle size distribution, temperature, ingestion rate of female *Calanus*, and the numerical abundance and biomass of the *Calanus* population were made on each cruise. The percentage of variability in cephalothorax length and in dry weight of copepodite stages IV and V and females explained by changes in some of these variables is given in Table 5.

Total particulate volume (TPV) taken as a measure of food concentration, varied both spatially and temporally. There was no obvious relationship between copepod dry weight and TPV; the maximum of TPV

Table 5. *Calanus helgolandicus*. Percentage of variability ($\% R^2$) of cephalothorax length (CL, mm), dry weight (DW, μg) and female ingestion rate (IR , $\mu\text{m}^3 \times 10^6 \text{d}^{-1}$) explained by total particulate volume (TPV, $\mu\text{m}^3 \times 10^6 \text{ml}^{-1}$), *Calanus* numerical abundance (numbers, ind m^{-2}), *Calanus* biomass (mg m^{-2}) and temperature ($^{\circ}\text{C}$). Probability levels are given for the significant relationships only

Variables	Stage		
	IV	V	♀
CL v. TPV	46	37	60*
CL v. Numbers	8	16	< 1
CL v. Biomass	3	4	3
CL v. Temperature	< 1	2	13
DW v. TPV	33	< 1	4
DW v. TPV (lagged)	10	84**	55*
DW v. Numbers	6	< 1	3
DW v. Biomass	13	8	19
DW v. Temperature	47	28	17
♀ IR v. TPV	–	–	89***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

occurred in May when dry weights of stage V and females were increasing to their June maxima which coincided with the minimum mean TPV (Fig. 1b, c). Likewise, the August low in dry weights coincided with the dinoflagellate bloom, and the September peaks of dry weight occurred when TPV had dropped to $1.2 \mu\text{m}^3 \times 10^6 \text{ml}^{-1}$ (= ppm). The possibility of a lag effect between food concentration and dry weight was investigated. Lagging TPV by the sampling interval

gave a significant correlation with dry weight of stage V and females but not for stage IV

The ingestion rate of females followed closely the food concentration curve (Fig. 1c); there was a highly significant correlation ($P < 0.001$) between TPV and female ingestion rate (Table 5). Therefore, changes in ingestion rate do not provide a better explanation than TPV for seasonal changes in mean dry weight.

Calanus helgolandicus females in the Celtic Sea respond to seasonal changes in particle size distribution (PSD) by having a filtering rate curve (filtering efficiency) which varies to suit the PSD of the natural particulates on which they are feeding (unpubl.). It seems unlikely that seasonal changes in PSD would have a significant effect on seasonal changes in dry weight or cephalothorax length.

Seasonal fluctuations in temperature showed the sinusoidal curve typical of temperate latitudes with a maximum in August and low winter temperatures (Fig. 1d). There were no significant correlations between temperature and either dry weight or cephalothorax length (Table 5).

Seasonal fluctuations in numerical abundance and biomass of the *Calanus* population were similar except that biomass reached a maximum in October when numerical abundance was declining (Fig. 1d). This was due primarily to the marked increase in the dry weight of stage V copepodites and females in October (Fig. 1b). No significant correlations were found between either cephalothorax length or dry weight and both measures of population size (Table 5).

DISCUSSION

In the present study between-stage variability in dry weight was explicable in terms of differences in cephalothorax length, using linear regressions whose parameters were significantly different for each cruise. The highly significant linear relationship between dry weight and carbon or nitrogen implies that for each cruise the between-stage changes in carbon and nitrogen are also explicable by differences in cephalothorax length. In contrast, between-cruise fluctuations in mean dry weight, carbon and nitrogen of each copepodite stage were not explicable in terms of any of the directly measured variables, i.e. cephalothorax length, food concentration, ingestion rate, temperature and *Calanus* population size. Although introducing a lag effect gave a significant correlation between food concentration (TPV) and dry weight of copepodite stage V and of females, published development times for *Calanus* do not support this as a convincing explanation. Development times for the closely related species *C. finmarchicus* and *C. pacificus* (Marshall and

Orr, 1955; Vidal, 1980b) suggest that *C. helgolandicus* will develop from copepodite stage V to adult in approximately 4 to 14 d under the food and temperature conditions found in the Celtic Sea between June and September 1978. Therefore, it is most unlikely that *Calanus* would remain in the same copepodite stage over the 5 to 12 wk interval between cruises.

No attempt will be made to compare absolute values of dry weights and cephalothorax lengths from the present study with the earlier studies on *Calanus finmarchicus s. l.* (Marshall, 1933; Bogorov, 1934; Orr, 1934; Marshall et al., 1934; Comita et al., 1966). The methodology employed was often different, e.g. drying at 110 °C and weighing groups of 100 *Calanus* in the earlier studies as against drying at 60 °C and weighing individuals in the present study. The relatively recent taxonomic separation of *Calanus finmarchicus s. l.* further compounds the problems of comparison. However, it is possible to compare seasonal patterns of change and their relationship to environmental factors.

Comita et al., (1966) have summarized the earlier studies on seasonal changes in dry weight of *Calanus finmarchicus s. l.* (see their Fig. 4). They noted that dry weights were usually lowest in February or March and that each study showed a sudden large increase in dry weight during March and April in Scottish waters (Marshall et al., 1934; Orr, 1934; Comita et al., 1966), or during April and May in the English Channel (Bogorov, 1934). This coincided with the spring diatom increase. The spring maximum of dry weight was usually attained in April or May, but in some years continued into June. After the maximum, which did not always coincide for all the stages, there was a rapid decrease in dry weight followed by a seasonal pattern which differed greatly from one study to another. In the English Channel the post-spring decrease was not large and there was a rise to secondary maximum in August followed by a decrease to minimum dry weights in October and December (Bogorov, 1934). In Loch Striven there was a continuous fall from June to September or October when observations ceased. On this fall was superimposed a series of fluctuations related to the production of each brood (Marshall et al., 1934). In Loch Fyne the dry weight of copepodite stage V *C. finmarchicus* continued to rise slightly from April to August and fell little until October (Orr, 1934). In the Bute Channel, dry weights decreased from the spring maximum to an August minimum but increased again during September and October to reach a maximum in December and January when dry weights were similar to those of the spring maximum (Comita et al., 1966).

The data from the Celtic Sea conform to this pattern of similarities between the winter and spring periods

and dissimilarities for the rest of the year. There was a marked increase in dry weight during April and May, which did not coincide for all copepodite stages. The rest of the seasonal pattern consisted of a large decrease in August followed by a secondary maximum in September which declined to low winter levels. This latter part of the seasonal pattern is similar to that described for *Calanus* from the English Channel (Bogorov, 1934), differing only in the size of the decrease in June and August.

Orr (1934) offers no explanation for the seasonal fluctuations of dry weight in Loch Fyne while in the other studies only qualitative explanations are offered. In the English Channel and Loch Striven it is suggested that low temperatures produce large copepods and that high temperatures produce small ones (Bogorov, 1934; Marshall et al., 1934). It is suggested also that the minor summer fluctuations in Loch Striven are related to diatom increases (Marshall et al., 1934). In the Bute Channel the weight changes were thought to be related to food fluctuations. Attempts to derive both qualitative explanations and quantitative relationships for the seasonal changes in the Celtic Sea data were likewise unsuccessful.

A seasonal survey of body size of *Calanus helgolandicus* (Gatten et al., 1979) showed dry weight to be correlated with total lipid and nitrogen for copepodite stage V and males, but only with nitrogen for females. The seasonal fluctuations of total lipid exhibited the same seasonal pattern as fluctuations in dry weight of *Calanus* from the English Channel (Bogorov, 1934) and from the Celtic Sea (Fig. 1b). Gatten et al. (1979) concluded that fluctuations in phytoplankton lipid did not explain the seasonal fluctuations of lipid in *C. helgolandicus*.

Deevey (1960, 1964) investigated the relative effects of temperature and phytoplankton concentration on the seasonal variations of cephalothorax length of marine copepods from various geographical areas. She found that in areas with an annual mean temperature range of 14 °C or more there was a significant negative correlation between cephalothorax length and temperature at the time of sampling. In areas with an annual mean temperature range of 14 °C or less there were significant positive correlations between cephalothorax length and mean phytoplankton concentration of the previous month. This implies that the phytoplankton is not limiting the cephalothorax length of marine copepods in areas of high annual temperature fluctuation. McLaren (1963) and Corkett and McLaren (1978) concluded, primarily from their work on *Pseudocalanus*, that food concentration has no effect on the final cephalothorax length of marine copepods. It is unfortunate that cephalothorax length was used as the dependent variable in these studies. The present

study (Fig. 1a, b) and data from others (Bogorov, 1934; Marshall et al., 1934; Comita et al., 1966) have shown cephalothorax length, although a good indicator of developmental stage, to be a less sensitive measure of seasonal changes in body size than dry weight. Also the relationship between cephalothorax length and dry weight did not remain constant for *Calanus* from the Celtic Sea (Table 3).

Laboratory studies on *Calanus helgolandicus* (Mullin and Brooks, 1970; Paffenhöfer, 1971, 1976), *C. pacificus* (Frost, 1974), *C. cristatus* (Omori, 1970), and *Temora longicornis* (Harris and Paffenhöfer, 1976) have shown food concentration to affect body size measured as dry weight. However, none of these studies has defined the relationship. In a series of laboratory experiments Vidal (1980a, b) showed that food concentration, temperature and body size (dry weight) were fundamental in determining the growth rate and development times of *Calanus pacificus*.

The relationships defined by Vidal are summarized below and in Fig. 4a-f. He found that weight-specific growth rate (Fig. 4a, d) increased for all body weights with increasing food concentration up to a maximum level above which food concentration had no further effect, and that maximum growth rate decreased with increasing body weight. The critical food level at which maximum growth rate was attained increased with increasing temperature and body weight. In small copepodites the maximum growth rate decreased rapidly as temperature decreased (Fig. 4a) but became gradually less temperature dependent with increasing body size such that in copepodite stages V and VI maximum growth rate was virtually independent of temperature (Fig. 4d). He found also that development times (Fig. 4b, e) decreased to a minimum value with increasing food concentration and that the critical food concentration at which minimum development times were attained increased with increasing temperature and stage of development (and therefore body weight). Above the critical food level development times increased as temperature decreased. The development time-temperature relationship was such that low temperature retarded the development rate of early copepodites proportionally more than that of later copepodites. Development time increased with stage of development (and therefore body weight) at all temperatures and food concentrations.

The outcome of the complex of relationships and differential effects defined by Vidal (1980a, b) was that the early (small) copepodite stages, which develop faster than the later (large) copepodite stages, showed little variation in dry weight. The dry weight of stage II copepodites was found to be relatively unaffected by either food concentration or temperature (Fig. 4c). In contrast, the later copepodite stages showed much

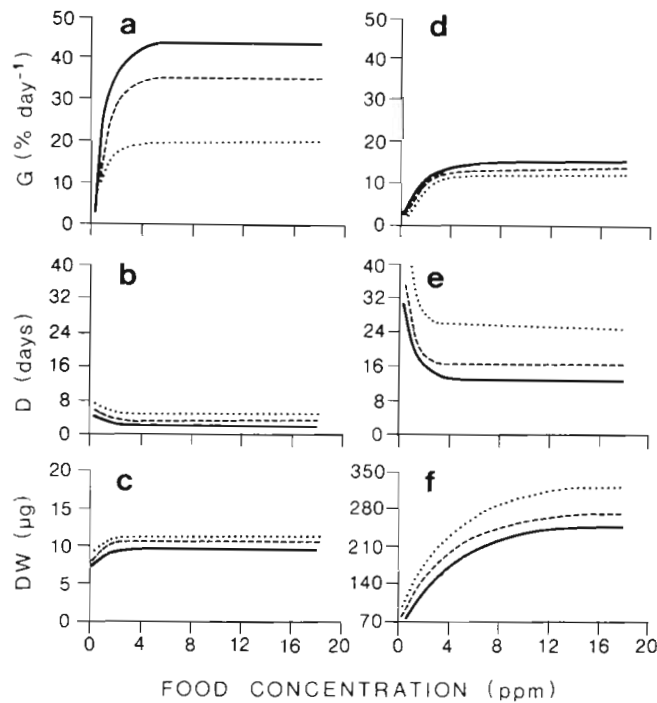


Fig. 4. *Calanus pacificus*. Relationships between food concentration and weight-specific growth rate (G), development time (D) and dry weight (DW) for copepodite stage II (a), (b), (c), and stage VI (d), (e), (f), cultured at 15.5 °C (solid line), 12 °C (dashed line) and 8 °C (dotted line). (Redrawn from Vidal 1980a, b)

greater variation in dry weight, and according to Vidal (1980a) were lightest at high temperatures and heaviest at low temperature for a given food concentration (Fig. 4f). The development times of stage V copepodites were longer at low temperatures than at high temperatures but their growth rates were similar at all temperatures. Clearly dry weight is a balance between growth rate and development times, the latter determining the length of time a particular growth rate is experienced. For example, in late copepodites a given growth rate over a long development time results in heavier individuals than the same growth

rate over a shorter development time, whereas different growth rates (i.e. at different food concentrations below the critical level for growth) can produce late copepodites of similar dry weights for different development times. The pattern of little variation in the dry weights of the early copepodite stages and progressively more variation in the later copepodites is an agreement with the degree of variation observed in the copepodite stages in the Celtic Sea (Fig. 1b).

The ability of the two-way relationships defined by Vidal (1980a, b) to predict the seasonal variations in dry weight of female *Calanus helgolandicus* from the Celtic Sea was examined. The data for stage V-VI given in Table 3 of Vidal (1980b) were used to produce a three-dimensional graph with dry weight as the dependent variable and stage duration and food concentration as the independent variables. Stage durations of *C. helgolandicus* were predicted from food and temperature conditions in the Celtic Sea, and their dry weights predicted from stage durations and food concentrations (Table 6). Agreement between the dry weights from the Celtic Sea and predictions based on Vidal's work are reasonably good between May and September 1978. The dramatic change in dry weights observed in August is particularly well accounted for, the temperature and food conditions giving high growth rates and very short development times which result in females of low dry weight. There are 2 possible explanations for the poor agreement between observed and predicted dry weights in the 4 winter months (February, March 1978 and January, March 1979). Firstly, although Vidal (1980a) states that there is always an inverse relationship between body size (dry weight) and temperature, his data (see Table 3 in Vidal, 1980b) do not always support this interpretation. At 8 °C (the lowest experimental temperature used by Vidal, 1980a, b) some of his observations have a dry weight lower than that observed at 12 °C. Vidal (1980a) attributes this to clumping of the cells of *Thalassiosira eccentrica* at 8 °C which resulted in retarded growth of *Calanus pacificus*. The second explanation for the dis-

Table 6. *Calanus helgolandicus*. Summary of seasonal fluctuations in dry weight of females, food concentration and temperature in the Celtic Sea with development times and dry weights predicted from Vidal (1980a, b) for these food concentrations and temperatures

	Feb	Mar	May	Jun	Aug	Sep	Jan	Mar
Food concentration (ppm)	1.4	1.1	5.2	1.0	2.5	1.2	1.6	1.2
Temperature (°C)	8	8	11.5	14	16.5	15.5	10	8
Stage duration (d) b	12	15	6	10	4	7.5	10	14
♀ Dry weight (µg) a	57	69	143	173	53	134	63	84
b	115	120	150	120	55	105	105	120

a = Dry weights observed in Celtic Sea
 b = Dry weights and development times predicted using relationships derived for *Calanus pacificus* (Vidal, 1980a, b)

crepancy between observed and predicted dry weights is provided by the Celtic Sea data. Total particulate volume (TPV) may not always be the best expression of food concentration. The TPV for February/March 1978 and January/March 1979, although similar to the TPV for June and September, have a considerably lower organic content (12 to 18 % as against 21 to 32 %), and hence lower food quality. The percentage organic content during the May and August bloom periods ranged from 26 to 40 % and 20 to 70 %, respectively (unpubl.). If the values for food levels during the winter months are decreased relative to food levels in June and September, then using Vidal's (1980b) lowest food concentration, the predicted dry weights decrease to values between 70 and 85 μg . Since these winter food levels are below the critical concentration for growth, any further decrease in food concentration will further reduce dry weight.

Relationships derived for *Calanus pacificus* in the laboratory using diatom monocultures as food provide an acceptable explanation of the seasonal fluctuations in dry weight observed in the Celtic Sea for *C. helgolandicus* which had fed on natural particulates. The generality of the spring increase in dry weight is a result of overwintering *Calanus* of relatively poor somatic condition, due to low food and temperature, responding to marked spring increases in phytoplankton concentration and temperature. The dissimilarities in the rest of the seasonal pattern are a result of local variation in food and temperature conditions. A knowledge of the interactions between food concentration, temperature and body size and their differential effects on growth rates and development times as defined by Vidal (1980a, b) explains why previous studies were unable to provide convincing explanations for the seasonal fluctuations in dry weight.

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LITERATURE CITED

- Bakke, J. L. W., Valderhaug, A. (1978). Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population biology, biomass and calorie content of *Chiridius armatus* (Crustacea, Copepoda). *Sarsia* 63: 247-254
- Båmstedt, U. (1978). Studies on the deep-water pelagic community of Korsfjorden, western Norway. Seasonal variations in weight and biochemical composition of *Chiridius armatus* (Copepoda), *Boreomysis arctica* (Mysidacea), and *Eukrohnia hamata* (Chaetognatha) in relation to their biology. *Sarsia* 63: 145-154
- Båmstedt, U., Matthews, J. B. L. (1975). Studies of the deep-water pelagic community of Korsfjorden, western Norway. The weight and biochemical composition of *Euchaeta norvegica* Boeck in relation to its life cycle. In: Barnes, H. (ed.) Proceedings of 9th European Marine Biology Symposium. University Press, Aberdeen, p. 311-327
- Bogorov, B. G. (1934). Seasonal changes in biomass of *Calanus finmarchicus* in the Plymouth area. *J. mar. biol. Ass. U. K.* 19: 585-611
- Bratellid, T. E., Matthews, J. B. L. (1978). Studies on the deep-water pelagic community of Korsfjorden, western Norway. The dry weight and calorific content of *Euchaeta norvegica* (Copepoda), *Boreomysis arctica* (Mysidacea) and *Meganyctiphanes norvegica* (Euphausiacea). *Sarsia* 63: 203-211
- Brodsky, K. A. (1959). On phylogenetic relations of some *Calanus* (Copepoda) species of the northern and southern hemispheres. *Zool. Zh.* 38: 1537-1553
- Brodsky, K. A. (1975). Phylogeny of the family Calanidae (Copepoda) on the basis of a comparative morphological analysis of its characters. In: Zvereva, Z. A. (ed.) Geographical and seasonal variability of marine plankton. Israel Program for Scientific Translations 1975, Jerusalem, p. 1-127
- Comita, G. W., Marshall, S. M., Orr, A. P. (1966). On the biology of *Calanus finmarchicus*. XIII. Seasonal changes in weight, calorific value and organic matter. *J. mar. biol. Ass. U. K.* 46: 1-17
- Corkett, C. J., McLaren, I. A. (1978). The biology of *Pseudocalanus*. *Adv. mar. Biol.* 15: 1-123
- Deevey, G. B. (1960). Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bull. Bingham oceanogr. Coll.* 17: 55-86
- Deevey, G. B. (1964). Annual variations in length of copepods in the Sargasso Sea off Bermuda. *J. mar. biol. Ass. U. K.* 44: 589-600
- Durbin, E. G., Durbin, A. G. (1978). Length and weight relationships of *Acartia clausi* from Narragansett Bay, R. I. *Limnol. Oceanogr.* 23: 958-969
- Frost, B. W. (1972). Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 17: 805-815
- Frost, B. W. (1974). Feeding processes at lower trophic levels in pelagic communities. In: Miller, C. B. (ed.) The biology of the oceanic Pacific. Oregon State University Press, Corvallis, p. 59-77
- Gatten, R. R., Corner, E. D. S., Kilvington, C. C., Sargent, J. R. (1979). A seasonal survey of the lipids in *Calanus helgolandicus* (Claus) from the English Channel. In: Naylor, E., Hartnoll, R. G. (ed.) Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford, p. 275-284
- Harris, R. P., Paffenhöfer, G.-A. (1976). Feeding, growth and reproduction of the marine planktonic copepod *Temora longicornis* Muller. *J. mar. biol. Ass. U. K.* 56: 675-690
- Ikeda, T. (1974). Nutritional ecology of marine zooplankton. *Mem. Fac. Fish. Hokkaido Univ.* 22: 1-97
- Jaschnov, V. A. (1955). The morphology, distribution and systematics of *Calanus finmarchicus* s. l. *Zool. Zh.* 34: 1210-1223
- Longhurst, A. R., Williams, R. (1976). Improved filtration systems for multiple serial plankton samples. *Deep Sea Res.* 23: 1067-1073

- Marshall, S. M. (1933). On the biology of *Calanus finmarchicus*. II. Seasonal variations in the size of *Calanus finmarchicus* in the Clyde Sea area. J. mar. biol. Ass. U. K. 19: 111-138
- Marshall, S. M., Nicholls, A. G., Orr, A. P. (1934). On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to phytoplankton. J. mar. biol. Ass. U. K. 19: 793-818
- Marshall, S. M., Orr, A. P. (1955). The biology of a marine copepod, *Calanus finmarchicus* (Gunnerus). Oliver and Boyd, Edingburgh
- Matthews, J. B. L. (1967). *Calanus finmarchicus* s. l. in the North Atlantic. The relationships between *Calanus finmarchicus* s. str., *C. glacialis* and *C. helgolandicus*. Bull. mar. Ecol. 6: 159-179
- McLaren, I. A. (1963). Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Bd Can. 20: 685-727
- Mullin, M. M., Brooks, E. R. (1970). The effect of concentration of food on body weight, cumulative ingestion, and rate of growth of the marine copepod *Calanus helgolandicus*. Limnol. Oceanogr. 15: 748-755
- Nakai, Z. (1955). The chemical composition, volume, weight and size of the important marine plankton. Tokai Reg. Fish. Res. Lab., Spec. Publ. 5: 12-24
- Omori, M. (1969). Weight and chemical composition of some important oceanic zooplankton in the North Pacific. Mar. Biol. 3: 4-10
- Omori, M. (1970). Variations of length, weight, respiratory rate and chemical composition of *Calanus cristatus* in relation to its food and feeding. In: Steele, J. H. (ed.) Marine food chains. Edinburgh, Oliver and Boyd, Edinburgh, p. 113-126
- Orr, A. P. (1934). On the biology of *Calanus finmarchicus*. IV. Seasonal changes in weight and chemical composition of *Calanus* from Loch Fyne. J. mar. biol. Ass. U. K. 20: 613-632
- Paffenhöfer, G.-A. (1971). Grazing and ingestion rates of nauplii, copepodites and adults of the marine planktonic copepod *Calanus helgolandicus*. Mar. Biol. 11: 286-298
- Paffenhöfer, G.-A. (1976). Feeding, growth and food conversion of the marine planktonic copepod *Calanus helgolandicus*. Limnol. Oceanogr. 21: 39-50
- Razouls, S. (1977). Analyse pondérale, élémentaire et calorimétrique des stades juvéniles de copépodes pélagiques au cours d'une année. J. exp. mar. Biol. Ecol. 26: 265-273
- Rees, C. B. (1949). Continuous plankton records: The distribution of *Calanus finmarchicus* (Gunn.) and its two forms in the North Sea. Hull Bull. mar. Ecol. 2: 215-275
- Vidal, J. (1980a). Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. 56: 111-134
- Vidal, J. (1980b). Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature and body size on the development and moulting rates of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. 56: 135-146
- Williams, R., Conway, D. V. P. (1982). Population growth and vertical distribution of *Calanus helgolandicus* in the Celtic Sea. Neth. J. Sea Res. 16: 185-194

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