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Production of the Copepod *Eurytemora affinis* in the Bristol Channel

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ABSTRACT: A shipboard method for determining development rates of copepods under prevailing conditions of food and temperature *in situ* is described. Abundance and development rates of *Eurytemora affinis* were determined at a site towards the seaward edge of its range in the Bristol Channel during 3 seasons of the year. Production of *E. affinis* varied between 0.05 and 0.61 μg dry weight m^{-3} d^{-1} in January and May when the numbers of this copepod were, respectively, 1.42 and 4.83 m^{-3}. Population P/B quotients varied between 0.03 and 0.13 d^{-1} giving an annual P/B of 33 yr^{-1}. For the later developmental stages, the proportion of animals moulting daily varied between 4 % and 33 %, depending on stage and season. The results are discussed in relation to the factors influencing population production at this site in the estuary; it is suggested that food and predation pressures may influence production more than salinity or estuarine flushing. When compared with published rates for this species fed *ad-libitum* on algae in the laboratory, development rates of *E. affinis* in the field were only 10 %–82 %, suggesting that extrapolation of laboratory results to the field to estimated production should only be carried out with care.

INTRODUCTION

During the past half century, many efforts were made to estimate marine productivity (Harvey, 1955; Butler et al., 1979). Such studies have been carried out successfully on phytoplankton (Koblenz-Mishke et al., 1970), macrobenthos (Warwick and Price, 1975), and fish (Gulland, 1971) but far less success has been achieved for zooplankton (Tranter, 1976). Successful studies of phytoplankton production can be attributed to the convenience and precision of the ^{14}C technique (Steeman-Nielsen, 1952). In macrobenthos and fish the comparatively slow turn-over rates allow cohorts to be distinguished and their growth and mortality followed. In contrast, the general ephemerality of most zooplankton, such as copepods, in temperate latitudes results in populations that turn-over many times annually. Together with the effects of water movement, this results in continual mixing which renders the ready identification and sampling of cohorts impossible.

In an attempt to overcome these problems, studies by others have been carried out to determine the growth rates of different species of copepods under controlled conditions using algal food in the laboratory. Many of these laboratory investigations were carried out using unnaturally high algal concentrations, often more than one order of magnitude higher than those which might be expected in the open sea (Harris and Paffenhöfer, 1976a). More recently, copepod growth studies have taken into account the low particulate concentrations that are typical of the open sea; among the species studied have been *Calanus helgolandicus* (Paffenhöfer, 1970), *Pseudocalanus elongatus* (Paffenhöfer and Harris, 1976) and *Temora longicornis* (Harris and Paffenhöfer, 1976b). However, our observations made on the gut contents of copepods from the eastern Bristol Channel have shown that fine particulate material such as silt constitutes their predominant dietary component. The eastern Bristol Channel is a highly turbid estuary with particulate concentrations that are tidally resuspended and may exceed 800 ppm in the study area (Joint and Pomroy, in press). This non-algal material is a major component of the natural particulate regime found in the estuarine environment and yet few studies on copepod growth have taken this important factor into account.

There have been many records of correlations between the abundance of *Eurytemora affinis* and abiotic environmental variables such as salinity and temperature (e.g. Jeffries, 1962; Collins and Williams, unpubl.). More recently, studies of grazing have been carried out by Allan et al. (1977) and by Richman et al.

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(1977). However, apart from the work of Heinle und Flemer (1975), little is known about the production of this species, although McLaren and Corkett (1981) have recently investigated production of *E. herdmani*. In this paper, we describe a technique for determining copepod development rates, based on simple incubation chambers, designed for use on shipboard, which allow the animals to feed on naturally occurring particulate material. We report the seasonal rates of development and production of *E. affinis* using this technique, and discuss what environmental factors may be influencing the production of *E. affinis* in the Bristol Channel (51°18′ N; 03°21′ W).

MATERIALS AND METHODS

Chamber Design and Testing

The criteria for the chamber design were as follows:

(a) The chamber should be suitable for retaining a single copepod without undue restraint, thereby allowing the development of an individual to be followed. It should also allow the free passage of seawater, so that the copepod can grow under the local ambient food and temperature conditions.

(b) The size of the chamber should be suitable for placing under a stereomicroscope for rapid observation of the copepod's developmental stage.

(c) The chamber should be sufficiently robust for use on board ship.

Incubation chambers were made from disposable polystyrene containers (7.1 cm high by 5.0 cm diameter with a nominal capacity of 120 cm^3). To allow seawater to pass through the chamber, holes (2.2 cm diameter) were drilled through opposite sides approximately 1.5 cm from the base and a further hole (0.3 cm diameter) was drilled through the centre of the lid. The holes were covered with nylon mesh of 56 μm aperture, chosen to retain all developmental stages of this species, including the nauplii which averaged 70 μm at their maximum breadth (Katona, 1971).

A submersible pump (Flygt model 2040.250), mounted on the ship's hull at a depth of one metre supplied sub-surface seawater continuously to trays designed to hold the incubation chambers. Hinged lids allowed the copepods to be held in darkness, and the chambers to be readily removed for observation. The flow of seawater was regulated at a manifold to pass through the trays at an average rate of 3 l min^{-1}. This rate of flow ensured that the water in the trays remained at seawater temperature even in bright sunlight.

The following tests were carried out to check that the incubation chambers met the design requirements.

(1) Food availability: Analysis of the size distribution of particulate matter in seawater was carried out on all cruises using a Coulter Counter, (Model ZB) with 140 μm and 280 μm orifice tubes (Sheldon and Parsons, 1967). The size spectrum did not alter seasonally and consistently showed that the largest particles present were approximately 40 μm in diameter (Fig. 1a). To check whether *Eurytemora affinis* consumed the larger particles which might pass more slowly through the chamber, the gut content of several freshly caught copepods was examined. The fore-gut of these animals was carefully dissected out, the contents separated by sonification (Wotton, 1977) and the particles analysed by Coulter Counter. The results (Fig. 1b, c, d) revealed that the older developmental stages of *E. affinis* were feeding on particles to a maximum size of 45 μm. Heinle and Flemer (1975) have reported that this species can graze on particles within the size range of 2 to 60 μm. These results suggested that the 56 μm mesh was unlikely to influence the quality of the food available for *E. affinis* held in the incubation chamber.

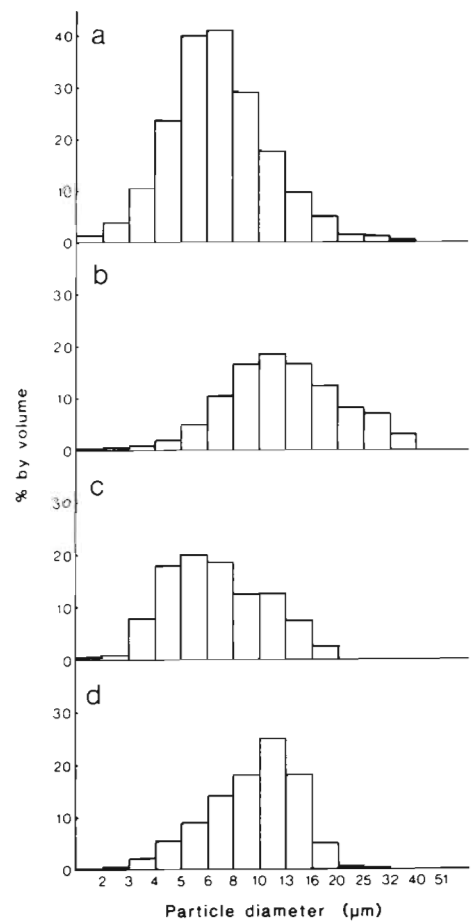

Fig. 1. Size spectrum of natural particulate material found in the water (a), and in the fore-guts of adult female copepods (b), adult male copepods (c), and copepodite Stages IV and V (d)

It was important also to consider the quantitative supply of particulates. The maximum filtering rate of *Eurytemora affinis* grazing on estuarine particulates has been determined by Allan et al. (1977) to be 0.3 cm^3 copepod$^{-1}h^{-1}$. As an arbitrary target, we aimed to ensure that the quantity of particulates in the chamber should not fall (as a result of copepod feeding) by more than 10 % from the ambient concentration. Thus a throughflow not less than 3 cm^3 h^{-1} was required. Experiments were performed to determine the rate at which particulates pass through the chambers, based on the following considerations.

Let the chamber volume be V cm^3 with seawater flowing through at a rate of U cm^3 s^{-1}. The water entering the chamber has a particulate concentration of S_1 cm^{-3}, and at time t the concentration of particulates in the chamber is S cm^{-3}. It is assumed that the contents of the chamber are well-mixed, and S_1 is independent of time.

At time t, the number of particles entering the chamber per second is $U \times S_1$. At the same time, the volume of water leaving the chamber per second $= U$ cm^3.

Since the contents of the chamber are well-mixed, the water contains a particulate concentration S cm^{-3}, so that at time t the number of particles leaving the chamber per second $= U \times S$.

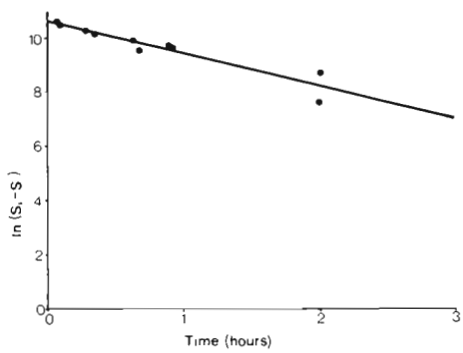

Fig. 2. Parameter determination for water flow rate through incubation chambers

Thus the rate of change of particle concentration at time t,

$$\frac{dS}{dt} = \frac{U(S_1 - S)}{V} \quad (1)$$

If $S = S_0$ at $t = 0$, then $S = S_1 - (S_1 - S_0) \exp(-U/V)$ (2)

Equation 2 gives S at any time t.

The parameters in Equation 2 were determined as follows. Ten incubation chambers of similar known volume were filled with particulate-free seawater. They were placed in trays through which seawater of known particle concentration (S_1) was flowing at 3 l min^{-1}. Pairs of chambers were removed from the tray over a period of 2 h, and their particulate concentration determined by Coulter Counter. From Equation 2, a plot of ln $(S_1 - S)$ against t (Fig. 2) gave a gradient value (equivalent to U/V) of −1.185, from which the mean velocity of particles through the chamber was calculated to be 140 cm^3 h^{-1}. This is some 400 times faster than the maximum filtering rate of *Eurytemora affinis*, according to Allan et al. (1977), and shows that the water flow rate is more than adequate to simulate 'real' conditions.

(2) Post-incubation size: To determine whether the chambers affected the growth of copepods in an unforeseen way, a comparison was made on the January cruise between the cephalothorax lengths of *Eurytemora affinis* that had moulted in the chamber during a 4-d period of incubation (captive individuals) and those of the same developmental stage collected at the same time as the incubated individuals and killed at the start of the incubation (wild individuals). Heinle and Flemer (1975) have shown that *E. affinis* reared in the laboratory are smaller than wild individuals of the same stage. The *t*-test for data with variances not assumed to be equal (Parker, 1973) was used to test the differences of the mean size of captive and wild copepods (Table 1). No significant differences were found between the cephalothorax lengths for any of the pre-adult copepodite stages of the two populations.

Table 1. *Eurytemora affinis*. *t*-test to check the significance between the sizes of copepods after moulting in the incubation chamber (captive) with the wild population

Development stage	Cephalothorax lengths of copepods (mm) Captive mean ± s. d.	Captive range; number	Wild mean ± s. d.	Wild range; number	*t* value	P
CI	0.26 ± 0.02	(0.25 − 0.29; n = 3)	0.28 ± 0.02	(0.25 − 0.29; n = 3)	0.74	0.6 > P > 0.5
CII	0.35 ± 0.05	(0.29 − 0.40; n = 5)	0.36 ± 0.03	(0.33 − 0.40; n = 12)	0.05	P > 0.9
CIII	0.43 ± 0.04	(0.34 − 0.50; n = 16)	0.43 ± 0.02	(0.40 − 0.43; n = 9)	0.32	0.8 > P > 0.7
CIV	0.51 ± 0.03	(0.48 − 0.56; n = 6)	0.50 ± 0.01	(0.48 − 0.52; n = 7)	0.89	0.4 > P > 0.3
CV	0.57 ± 0.01	(0.56 − 0.58; n = 3)	0.56 ± 0.01	(0.54 − 0.58; n = 5)	0.76	0.5 > P > 0.4

Shipboard Production Determination

A series of cruises on board RRS 'John Murray' was carried out in May, August and October 1977 and January 1978, representing each of the 4 seasons. Due to malfunctioning of the pumped water supply, no development experiments were carried out on the August cruise.

Abundance

The abundance of *Eurytemora affinis* was determined by carrying out double-oblique tows through the water column to within 5 m of the bottom, with a Lowestoft 20" (50.8 cm) plankton sampler (Beverton and Tungate, 1967) towed at 6 knots. The frame was fitted with a modified conical nose-cone with a mouth reduced to 8" (20.3 cm), and a net of 280 µm mesh. On the January 1978 cruise, an auxilliary 'pup' sampler with a 56 µm mesh net was used in conjunction with the Lowestoft sampler to provide data on the abundance of the smaller stages. On each cruise, a series of tows (6 in January, 16 in May and 8 in October/November) were made along a north-south transect through Station A (Fig. 3) over a tidal cycle. On the May and October/November cruise, sets of tows were carried out before and after the development experiments.

In the laboratory, a subsample of the material obtained from each tow was analysed to determine the abundance of each developmental stage. The sampler flowmeter readings were corrected for mesh selectivity according to the data of Adams (1976) and Saville (1958) to give estimates of absolute abundance.

Development Experiments

On each of the cruises, experiments were carried out for between 3–5 d while the ship remained at anchor on Station A (Fig. 3). Observations were made daily or twice daily to check the development of copepods retained singly in incubation chambers (38, 21 and 12 copepods were held on the January, May and October/November cruises respectively). Throughout the incubation period, sub-surface salinity and temperature were measured continuously using a Plessey thermosalinograph model 6600T. Water samples were filtered through GF/C glass-fibre filters, stored deep frozen and subsequently extracted with 95 % acetone for photosynthetic pigment analysis as outlined by Strickland and Parsons (1968). Vertical profiles of temperature, salinity and chlorophyll *a* showed that the water column was well mixed.

Length-Weight Relationship

In January, *Eurytemora affinis* were collected with a hand tow net fitted with a polythene beaker for length-weight determination. Live specimens were carefully washed to remove particulate material and were then collected on glass-fibre pads using vacuum filtration. These were briefly rinsed with distilled water and held frozen. In the laboratory, the cephalothorax lengths of between 10 and 40 specimens of each stage were measured using an ocular micrometer. Care was taken to ensure that limbs did not stick to the planchet surface. The organisms were dried at 60 °C and each copepod weighed using a Cahn Electrobalance.

The length (L) to weight (W) relationship for *Eury-*

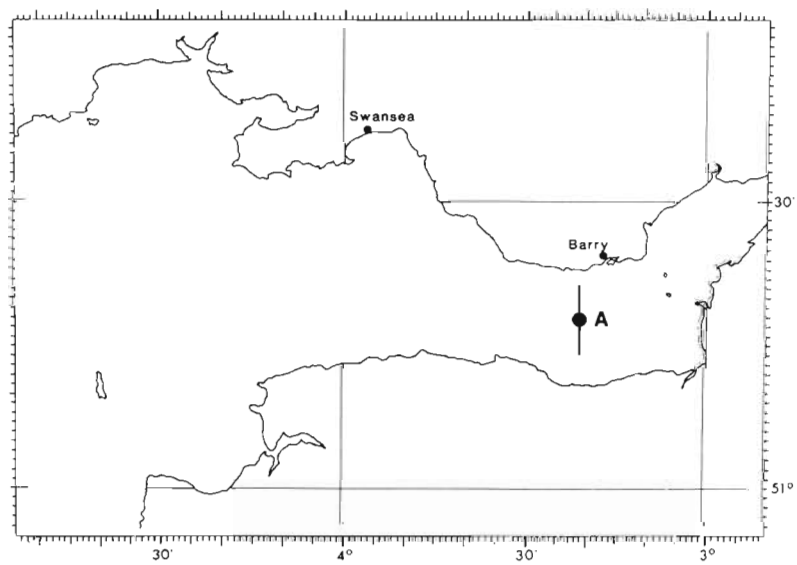

Fig. 3. Chart of Bristol Channel showing plankton tow transect (solid line) and anchor station (A) where incubations were carried out

Table 2. Ambient environmental conditions during development studies

Month	Temperature °C		Salinity ‰		Chlorophyll *a* µg l^{-1}		Phaeopigment µg l^{-1}	
	mean	range	mean	range	mean	range	mean	range
May	9.9	9.7–10.5	29.1	26.5–31.5	1.4	0.5–5.8	1.6	0.4–8.0
Oct.	14.4	14.2–14.9	30.2	28.4–31.8	1.2	0.3–4.8	1.8	0.5–5.9
Jan.	6.5	5.8– 7.2	28.5	25.4–31.1	2.2	0.9–3.8	3.3	2.3–4.2

temora affinis was described by: Log W = a + bL. The equation was solved by the method of least squares. Average dry weights of individual stages were calculated from this equation using the mean length for each stage found for each cruise.

Production Estimation

The daily production of *Eurytemora affinis* was calculated by a method similar to that used by Mann (1969) based on the following equation

$$P_{i \rightarrow i+1} = N_i (W_{i+1} - W_i) PMD_i \quad (3)$$

where $P_{i \rightarrow i+1}$ equals the daily production in dry weight of *Eurytemora affinis* developing from Stage i to Stage $i+1$; N_i and W_i = abundance and dry weight respectively of individuals of Stage i; PMD_i = proportion of the i^{th} developmental stage moulting daily. N_i and PMD_i were determined on each cruise, and W_i estimated using the length to weight relationship in conjunction with length measurements made of copepods obtained on each cruise.

RESULTS

Ambient Conditions

Average values and their ranges for environmental variables during the experimental period of each cruise are shown in Table 2. Although temperature changed seasonally, there was little change in either chlorophyll *a* or salinity between cruises.

Abundance of *Eurytemora affinis*

The mean abundance of *Eurytemora affinis* varied seasonally (Table 3), ranging from 0.24 m^{-3} in November to 4.83 m^{-3} in May. There was considerable variation in abundance between tows, indicating that the copepod is not distributed evenly in the estuary. In January, the population density had risen to 1.41 m^{-3}. It is pertinent that naupliar stages were found in January indicating that the population was reproducing.

Table 3. *Eurytemora affinis*. Population abundance in the eastern Bristol Channel

Date	Abundance (No. m^{-3})	
	average s. e.	range
3/ 5/77	2.62 ± 1.04	0.54 – 7.40
14/ 5/77	4.83 ± 1.62	0.75 – 13.48
25/10/77	0.81 ± 0.37	0.20 – 2.27
2/11/77	0.24 ± 0.02	0.19 – 0.27
24/ 1/78	1.42 ± 0.23	0.91 – 2.26

This contrasts with oceanic species that typically overwinter at late copepodite stages, deferring reproduction until spring.

Length-Weight Relationship

Cephalothorax length showed a regular increase as the copepod developed (Fig. 4) and the variability of size generally increased with age. There were no significant differences between the sizes found on different cruises.

The length-weight relationship (Fig. 5) is described by

$$\mathrm{Log}_{10} W = 2.088\ (\pm 0.119)\ L - 0.859\ (\pm 0.083) \quad (4)$$

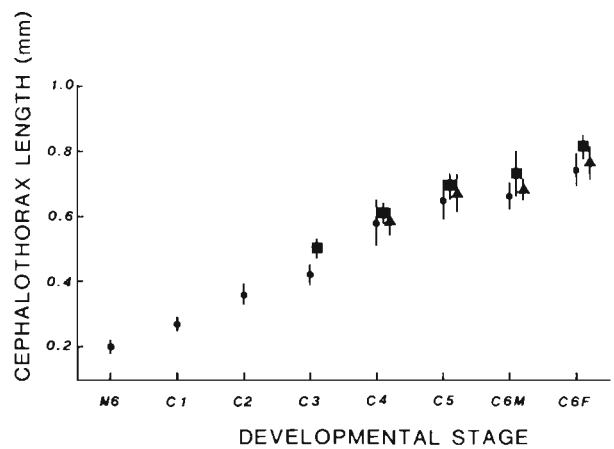

Fig. 4. *Eurytemora affinis*. Size of different developmental stages during January (●), May (■) and October (▲). Vertical bars: standard deviations

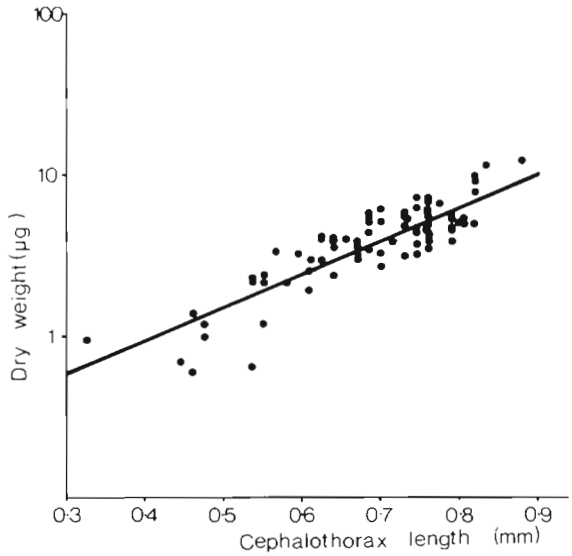

Fig. 5. *Eurytemora affinis*. Length to weight relationship of different developmental stages

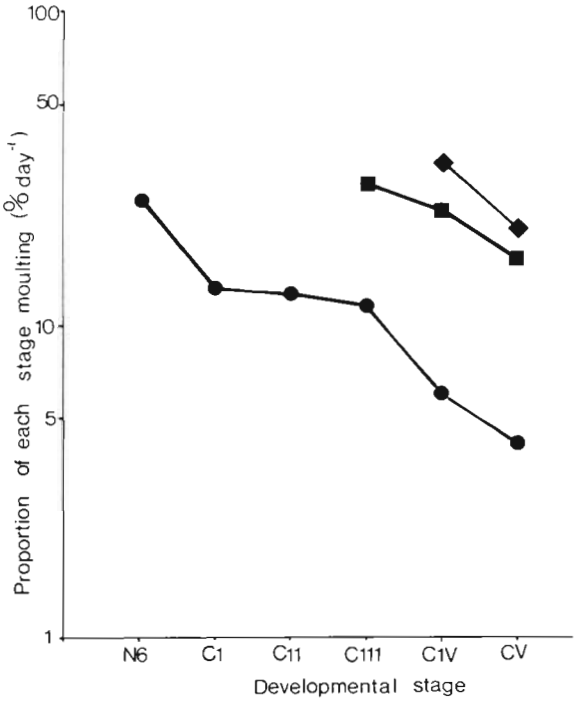

Fig. 6. *Eurytemora affinis*. Variation in the proportion of the population moulting daily during January (circles), May (squares), and October (diamonds)

where W = dry weight in µg; L = cephalothorax length in mm; figures in parentheses = standard deviations for parameter values. With 86 data points, the correlation coefficient was 0.885. Although copepod length/weight relationships are commonly expressed in log/log form, in this case the log/linear equation gave a statistically better fit, as was found for adult female *Eurytemora affinis* (Heinle and Flemer, 1975) and for *Acartia tonsa* (Heinle, 1966).

Table 4. *Eurytemora affinis*. Standing stocks and daily production for different development stages in the Bristol Channel

Date	Development stage	Abundance (no. m^{-3})	Dry weight (µg)	Standing crop (µg m^{-3})	Weight increase (µg)	Proportion moulting (% d^{-1})	Production (µg m^{-3} d^{-1})
3rd May	C III	0.36	1.53	0.55	1.07	28.3	0.109
	C IV	0.52	2.60	1.35	1.22	22.9	0.145
	C V	0.54	3.82	2.06	1.79	15.6	0.151
	C VI	1.20	5.61	6.73			
14th May	C III	0.36	1.53	0.55	1.07	28.3	0.109
	C IV	0.20	2.60	0.52	1.22	22.9	0.056
	C V	1.60	3.82	6.11	1.79	15.6	0.447
	C VI	2.67	5.61	14.98			
25th Oct.	C IV	0.11	2.25	0.25	1.22	33.3	0.045
	C V	0.07	3.47	0.24	1.39	20.0	0.019
	C VI	0.63	4.85	3.06			
2nd Nov.	C IV	0.11	2.25	0.25	1.22	33.0	0.045
	C V	0.11	3.47	0.38	1.39	20.0	0.031
	C VI	0.02	4.85	0.10			
24th Jan.	N VI	0.06	0.36	0.02	0.14	25.2	0.002
	C I	0.21	0.51	0.11	0.27	12.6	0.007
	C II	0.11	0.78	0.09	0.26	12.6	0.004
	C III	0.09	1.04	0.09	1.21	11.7	0.013
	C IV	0.35	2.25	0.79	0.90	6.0	0.019
	C V	0.16	3.15	0.50	0.86	4.0	0.006
	C VI	0.44	4.01	1.76			

Development Rates

Development rates of *Eurytemora affinis* varied from stage to stage and from cruise to cruise (Fig. 6). During each experimental period, the moulting rates of the different stages were inversely related to their ages. Developmental rates also proceeded faster when water temperatures were warmer.

Standing Stock

Standing stocks of the copepod, estimated from the dry weights of each stage and their abundance, varied between 0.7 μg m^{-3} found on 2nd November and 22.2 μg m^{-3} on 14th May (Table 4). In January, the biomass was 3.4 μg m^{-3}.

Production and P/B

Eurytemora affinis production rates varied seasonally, the lowest rate (0.051 μg m^{-3} d^{-1}) occurring in January (Table 4). In May, values of 0.405 and 0.612 μg m^{-3} d^{-1} were estimated and rates of 0.064 and 0.076 μg m^{-3} d^{-1} were found in October and November respectively. Production of the individual stages varied, depending on their abundance and growth rates. Despite the fact that the younger stages moulted faster than adults, the greater abundance and larger increase in weight per moult of older stages resulted in greater productivity of the CIII to CV stages in January.

The daily P/B values (Table 5) show a clear relationship with stage for each of the 3 cruises. The highest P/B ratio was 0.20 for Copepodite III in May and lowest P/B was 0.01 for Copepodite V in January. Population P/B, obtained by dividing the population production by standing stock varied from 0.03 in January to 0.13 in October.

Table 5. *Eurytemora affinis*. Daily P/B values in the eastern Bristol Channel

Month	Stage	Daily P/B	Population P/B
May	C III	0.20	0.09
	C IV	0.11	
	C V	0.07	
Oct.	C IV	0.18	0.13
	C V	0.08	
Jan.	N VI	0.09	0.03
	C I	0.06	
	C II	0.05	
	C III	0.14	
	C IV	0.02	
	C V	0.01	

DISCUSSION

Analysis of some of the factors likely to influence the rates of development of individuals and the population of *Eurytemora affinis* will be discussed below. Estimates of production of copepods in estuaries and neritic regions are uncommon. The available data for some species are summarised in Table 6 showing that P/B quotients vary between species and contrasting environments. Our estimate for *Eurytemora affinis* (P/B of 33 yr^{-1}) is toward the upper end of the values found in temperate regions. The data of Heinle (1966) and Newbury and Bartholomew (1976) with P/B values of 182 yr^{-1} for *Acartia tonsa* and 285 yr^{-1} for mixed copepod species, were derived in regions with higher summer temperatures.

A school of thought advocated by McLaren and others (McLaren and Corkett, 1981, and papers cited therein) proposes that copepods commonly develop in the field at maximal rates. This significant concept suggests that development may be determined by factors other than food which is deemed to be present in excess. Temperature is the environmental variable which is usually considered to limit development (e.g. McLaren and Corkett, 1981). This idea has the attractive corollary that estimating copepod production in nature is made easier to compute, since laboratory data on development rates made under conditions of excess food may be used. How do our rates compare with such laboratory-derived rates?

Comparison of our data with laboratory rates is not straightforward because of the different ways in which experiments were carried out and results recorded. Assuming that the development times of *Eurytemora affinis* recorded by Heinle and Flemer (1975) are equivalent to the reciprocal of PMD and that for our data, the relative development rates of different stages remain as found in January, comparisons are possible. Table 7 suggests that development times are faster with individuals fed on algae *Isochrysis galbana*, *Chlamydomonas reinhardti* and *Chaetoceros* sp. by Heinle and Flemer (1975) than was found by our *in-situ* technique. Assuming this is not a methodological problem, this suggests that *E. affinis* is living in a nutritionally sub-optimal environment. Moreover, the degree of sub-optimality alters seasonally, since the discrepancies in the development times are larger in winter (90 % difference) than in summer (36 %) or autumn (18 %). The discrepancies cannot be related simply to algal concentrations *in-situ* since chlorophyll *a* concentrations were similar in winter and summer (Table 2). In this environment, the seston comprises principally detrital silt and other tidally resuspended material with a high inorganic content. Although *E. affinis* ingests this material (Fig. 1 and pers. obs.), it is

Table 6. P/B quotients of some copepods in neritic regions

Species	Region	Temperature (°C)	Daily P/B (d^{-1})	Annual P/B (y^{-1})	Source
Pseudocalanus elongatus	Gdansk Bay	3–7	.01–.05	12	Ciszewski and Witek (1977)
Copepod ssp.[a]	Kungsbacka Fjord	7–14	.02–.06	15	Olsson and Olundh (1974)
Acartia clausi	Black Sea		.04	16	Zaika (1968)
Oithona similis	Nearshore Black Sea		.04	16	Zaika (1968)
Acartia bifilosa	Gdansk Bay	7–18	.03–.12	17	Ciszewski and Witek (1977)
Paracalanus parvus	Nearshore Black Sea		.07	25	Greze et al. (1968)
Oithona minuta	Nearshore Black Sea		.08	31	Greze et al. (1968)
Acartia clausi	Nearshore Black Sea		.09	32	Greze et al. (1968)
Eurytemora affinis	East. Bristol Channel	6–14	.03–.13	33	This study
Acartia clausi	Coastal lagoon Washington	8–20	.12–.23	57[c]	Landry (1978)
Pseudocalanus elongatus	Nearshore Black Sea		.16	58	Greze et al. (1968)
Eurytemora herdmani	Halifax	8–18	ca. .16–.17[c]	–	McLaren and Corkett (1981)
Acartia tonsa	Patuxent River Chesapeake Bay	0–32	.50	182[c]	Heinle (1966)
Copepod spp[b]	Hawaii lagoon	27–29	.78	285[c]	Newbury and Bartholomew (1976)

a: *Acartia* spp. *Paracalanus parvus, Pseudocalanus minutus* – b: Paracalanidae – c: Calculated from authors data

Table 7. *Eurytemora affinis*. Comparison of development times of the copepod under simulated *in-situ* conditions and fed on algae (After Heinle and Flemer, 1975)

Temperature (°C)	Development time from CI to CVI (d) This study[a]	Algal fed[c]
5.5 – 6.5	66	35
9.9 – 10	19[b]	14
14.2 – 15	13[b]	11

a: Obtained by summing reciprocals of PMD values for each size
b: Assuming same proportion of duration between stages as January
c: From Heinle and Flemer (1975)

likely to be assimilated less readily than algae and thus may 'dilute-out' the algal food. Although seston data were not recorded during development experiments, it is known from other work in the region that particulate levels during winter can be 3 to 6 times the values found in summer (IMER, unpubl.). In this case, the phytoplankton-to-seston levels would be lower in winter than summer. We thus put forward the hypothesis that development of *E. affinis* in this environment may be related to a 'phytoplankton-to-seston' ratio which may act as an index of food availability.

A further factor that may influence the development performance of *Eurytemora affinis* is salinity. It is known that the centre of abundance of this species is typically found at salinities less than 15–20 ‰ S (e.g. Cronin et al., 1962; Jeffries, 1962). In the Severn Estuary the abundance of *E. affinis*, some 30 km upstream has been found, on occasion, to be 2 or 3 orders of magnitude higher than was found in this study (Burkill, unpubl.). Thus, the copepods found in the Bristol Channel form a component of the population that may be 'washed-out' by the net water movement down the estuary. Outside its apparent salinity optimum, the species' capacity to grow may be impaired. However, since salinity altered little from cruise to cruise (Table 2), the seasonal variation in the discrepancies in development times, discussed earlier, cannot be explained simply by salinity effects. Moreover, we have frequently observed adults mating and females carrying spermatophores and egg-sacs in this region and this, together with the results of this research, suggest the population is capable of reproducing at 30 ‰ S, which is much higher than the salinity at its centre of abundance. Our findings tend to confirm Katona (1970) who recorded that *E. affinis* reproduced at 33 ‰ S with generation times not significantly different from those found at 5 ‰ or 20 ‰ S. In fact, Bradley (1975) in a study of the physiological tolerance of *E. affinis* to temperature and salinity, concluded that there was no cause-effect relationship between salinity and the distribution of this copepod, and suggested that other factors had to be considered to explain the observed distribution. Among the factors that might affect the distribution and population development of *E. affinis* are passive transport by water movement and predation.

Does hydrodynamic flushing have a significant effect on the copepod population? Analysis of the effects of this process in detail is beyond the scope of this paper, although it is possible to compare, in a simple manner, the flushing rate of the estuary with the copepod's growth rate using chemostat theory. This

assumes the copepod behaves as a conservative dissolved constituent of seawater and the population is under steady state conditions. If B is the copepod biomass, G its growth rate and F the estuary's flushing rate (the proportion of the estuarine volume that is exchanged per unit time) then, under steady state,

$$\text{the rate of change of biomass} = Be^{G} - FB \qquad (5)$$

For the copepod to maintain itself in the estuary, its growth rate must equal or exceed the rate at which it is flushed out, i.e. $G \log_e (1+F)$.

Uncles and Radford (1980) have determined the residence times (equal to $^1/F$) of the estuary landward of the experimental site to vary between 60 d and 150 d. These data give values for the right-hand side of the above equation of 0.007 d^{-1} and 0.017 d^{-1}. In contrast, G (equal to P/B quotient) varies between 0.03 d^{-1} and 0.13 d^{-1} suggesting the copepod is well able to maintain itself in this part of the estuary. Upstream where the flushing will be very much higher, it is likely that the copepod will be more greatly affected by this process.

Is predation a factor influencing the *Eurytemora affinis* population? Several carnivorous species were found in the plankton hauls carried out to estimate copepod abundance. There was an inverse relationship between the abundance of *E. affinis* and carnivore abundance (Fig. 7), suggesting that predation influences the abundance of this copepod. In January, the commonest planktonic group capable of taking *E. affinis* are mysids (*Gastrosaccus spinifer, Schistomysis spiritus* and *Schistomysis ornata*). Copepod remains have been recorded in the stomachs of *S. ornata* and *S. spiritus* (Mauchline, 1967, 1970), and evidence of carnivory by *G. spinifer* has been reported by Blegvad (1915). In Chesapeake Bay, the mysid *(Neomysis integer)* was found to consume *E. affinis* and mortality due to predation was the principal cause of the spring decrease in population levels (Heinle and Flemer, 1975). In May, decapods such as *Crangon crangon* and *Pasiphaea sivado* formed the largest component capable of consuming copepods. In the Severn Estuary, the former species is known to take animal material (Lloyd and Yonge, 1947). Although the diet of *P. sivado* is unknown, the related species, *P. multidentata* consumed copepods as a substantial part of their diet (Apollonia, 1969). Chaetognaths (*Sagitta* spp.) dominated the carnivorous component of the plankton in October. In addition to the invertebrate predators, it is known that fish are predators of *E. affinis:* Hardy (1924) found that this species was the most important item in the food of young herring *(Clupea harengus)* in the Thames Estuary. In the Solway Firth, *E. affinis* was found in considerable numbers in the stomachs of herring, cod, dab and plaice (Scott, 1902). Although the numbers of fish in our plankton samples were low, over 40 species of fish have been found in the region and the area has been considered important, both as a route for migratory species and as a nursery area for post-larval and juvenile stages of a number of marine species (Hardisty and Huggins, 1975).

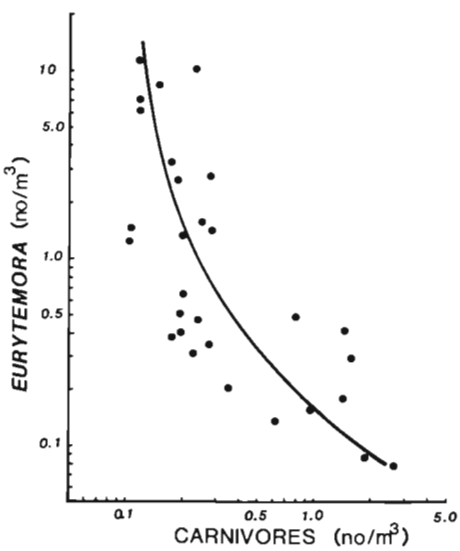

Fig. 7. *Eurytemora affinis*. Abundance as a function of carnivore abundance for separate hauls made in January, May and October. Line is fitted by eye

It seems therefore that in a region with a salinity higher than that at the centre of abundance, the population density and production of *Eurytemora affinis* were low (range 0.2 to 4.8 m^{-3} and 0.05 to 0.61 μg m^{-3} d^{-1}), but the species was capable of growing with a P/B quotient of 33 yr^{-1}, which is higher than many recorded values for copepods. However, the P/B quotient for *E. affinis* is expected to be higher in nutritionally optimal environments since faster development rates were recorded by Heinle and Flemer (1975) than found here. Of the environmental factors considered, apart from nutrition, it is suggested that predation influences the levels of population and that salinity and flushing in this region are not so important. A more definitive analysis of the separate effects of the different environmental factors on *E. affinis* would require further work under controlled conditions. Development rates for individuals feeding on natural particulates were lower (10 %–82 %) than published values for copepods fed artificially on algae suggesting that extrapolation of laboratory results to estimate growth rates in the natural environment should be carried out with care.

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