

Restriction of body size spectra within species of deep-sea plankton

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ABSTRACT: Studies of the population structure of deep-sea species of micronekton, especially crustaceans and fish, and of abyssal echinoderms and molluscs, suggest that modes in length/frequency histograms are often restricted to narrower ranges of body length than would be expected from population analyses of shelf or coastal congeners. This possible restriction is examined here by using the adult Stage VI copepodid of calanoid copepods of the genus *Euchaeta*. This stage represents the asymptotic body size of the species and is directly comparable between species. The depth range of the 10 most common *Euchaeta* species present in the Rockall Trough (NE Atlantic) was determined. Seasonal changes in the mean body size (prosoma length) were significant in all species except *E. sarsi*. Mean annual prosoma length and its standard deviation was determined for each species. In comparing species, the standard deviation, expressed as a percentage of the mean, decreased with increasing depth of the species. This reflected the decreasing prominence of a seasonal change in prosoma length with increasing depth. Populations of shelf and coastal species of copepods generally showed much larger variations from their mean sizes than oceanic and deep-sea species. This decrease in variability in deep-sea species reflects the much less variable environment in which they live.

INTRODUCTION

Patterns of body growth in deep-sea organisms, both pelagic and benthic, have been of major interest in recent years (Gage & Tyler 1991, Mauchline 1991). Rates of growth have been determined in a variety of species through analyses of length/frequency distributions in diverse organisms such as pelagic decapod, mysid and euphausiid crustaceans, fish, and epibenthic echinoderms and molluscs. The size structure of the populations often exhibits very distinct modes (Aizawa 1974, Mauchline 1986, 1991, Miya & Nemoto 1986a, b, 1987, Gage & Tyler 1991), sometimes even reflecting individual instars within the moulting sequence of crustaceans (Childress & Price 1978, Bishop 1982). The modes often appear to have a narrower range of body length than in shallower- or shelf-living congeners. One possible explanation is narrower time intervals for hatching of the eggs giving rise to less variation in the resulting body lengths of the juveniles. A second explanation, reinforcing the first, is that the deep-sea environment is more homogeneous, not only in its physical characteristics but also in its biotic ones.

This implies that the size cohorts within populations of endemic species are expected to be narrower than those resulting in coastal or shelf environments.

The latter hypothesis is difficult to test using shrimp-like crustaceans, fish, or echinoderms because of the difficulty of identifying comparable entities within their life histories. Calanoid copepods, however, are a suitable tool. They develop from the fertilized egg through a series of naupliar stages followed by copepodid stages. The terminal stage, Stage VI, is the sexually mature adult and represents the asymptotic body size. It is an integration of environmental effects on development and growth, constrained by a genetic component.

The body size of the adult copepod varies seasonally, with depth, and geographically (e.g. Adler & Jespersen 1920, Ussing 1938, Sewell 1948, Marshall 1949, Wiborg 1954, Deevey 1960, 1964, El-Maghraby 1964, Gaudy 1972, Strømgren 1974, Moraitou-Apostolopoulou 1975, Bottrell & Robins 1984). Sewell (1948) equated variation of adult size in a species with environmental temperature, and Sander & Moore (1983) reviewed studies of this inverse relationship. These data, how-

ever, are contradictory and the emphasis has changed to an examination of the primary importance of food and its effects on growth (Deevey 1960, 1966, Sander & Moore 1983, Klein Breteler et al. 1990). Again the results are not entirely conclusive but suggest that regularly fluctuating environmental parameters, especially temperature and food, result in seasonal fluctuations in body size.

Seasonal fluctuations of environmental temperature are virtually absent at depths below about 800 to 1000 m in the Rockall Trough, northeastern Atlantic (Mauchline 1991). Food availability at these depths is seasonally enhanced through deposition of aggregated phyto-detritus (Lampitt 1985, Rice et al. 1986, Zeitzschel 1986, Thiel et al. 1988, Tyler et al. 1992, Billett et al. 1983). The rate of deposition is rapid (Lampitt 1985) and no data are available on its residence time in the deep water column. Tyler et al. (1992) have demonstrated a direct link between the residence time of phyto-detritus on the abyssal sea bed, along with the co-occurrence of fish carcasses, and seasonality in the reproductive biology of the seastar *Plutonaster bifrons*. There may be a dampening of the impact of this seasonal input to the food of pelagic organisms owing to it having a relatively short residence time in the water column.

The genus *Euchaeta* is represented by some 14 species resident in the water column. Size variation within species is examined here relative to their depth of occurrence and compared with that of coastal species of other genera.

METHODS

Time series samples of zooplankton were collected at approximately 2 mo intervals between July 1973 and March 1974 and between March 1975 and February 1976 centred on 55° N, 12° 30' W in the Rockall Trough using a combination rectangular midwater trawl of 7 m² and a 1 m² mouth opening. The nets were fished open and these samples were used for studies of seasonal changes in body size. In addition, a multiple rectangular midwater trawl (RMT 8 + 1) (Roe & Shale 1979, Roe et al. 1980) was used to collect a vertical series of samples at 54° 30' N, 13° W in August/September 1979 to define the vertical distribution of the species. Samples were taken at 100 m depth intervals between the surface and 900 m depth by both day and night. Angel et al. (1982) concluded that there was no influence of downwelling daylight on the vertical migration of species at depths greater than 900 m and so hauls were taken at 200 m depth intervals between 900 and 1900 m irrespective of day or night. Full details of the samples taken are given by Hargreaves et al. (1984).

The following species of *Euchaeta* occurred in the samples from the trough:

- E. abbreviata* Park, 1978
- E. acuta* Giesbrecht, 1892
- E. barbata* Brady, 1883
- E. bisinuata* G. O. Sars, 1907
- E. bradyi* With, 1915
- E. gracilis* G. O. Sars, 1905
- E. hansenii* With, 1915
- E. incisa* G. O. Sars, 1905
- E. longissima* Park, 1978
- E. media* Giesbrecht, 1888
- E. norvegica* Boeck, 1872
- E. pseudotonsa* Fontaine, 1967
- E. sarsi* Farran, 1908
- E. scotti* Farran, 1908

Prosomal length was measured from the anterior point of the rostrum to the posterior lateral edge of the last prosomal segment using a micrometer graticule on a binocular microscope. One-way analysis of variance for samples of unequal size (Sokal & Rohlf 1969) was used to test for seasonal variation in prosomal length.

RESULTS

The species were identified in the vertical series of samples and the number per 1000 m³ of water filtered in each depth horizon determined. Four species, *Euchaeta bradyi*, *E. incisa*, *E. longissima* and *E. media*, were either absent or too rare in the samples to determine their vertical position in the water column. The vertical distribution of the adult females in the RMT 1 samples (Fig. 1) show that *E. acuta*, *E. pseudotonsa* and *E. norvegica* perform a diel vertical migration, entering the surface layer at night. Only 2 *E. gracilis* occurred at depths shallower than 500 m and they were in the night samples (Fig. 1); this species was found at night at the surface in other samples from the Trough and so does perform a vertical migration on occasion. The other 6 species do not migrate, none of them being found in the upper 900 m during the night and only a single *E. barbata* being recorded there during the day (Fig. 1). The mean depth of occurrence, during the day, and its standard deviation was calculated for each species and their distributions in the vertical water column are shown in Fig. 2. Although males occurred more rarely than females in the samples, their vertical distribution coincided with that of the females in each species.

The mean prosomal length and its standard deviation was determined in each month for adult females of each species (Fig. 3). There were too few *Euchaeta hansenii* and *E. bradyi* (Table 1) in the seasonal samples to include them. A third species, *E. longissima*, although common throughout the rest of the year

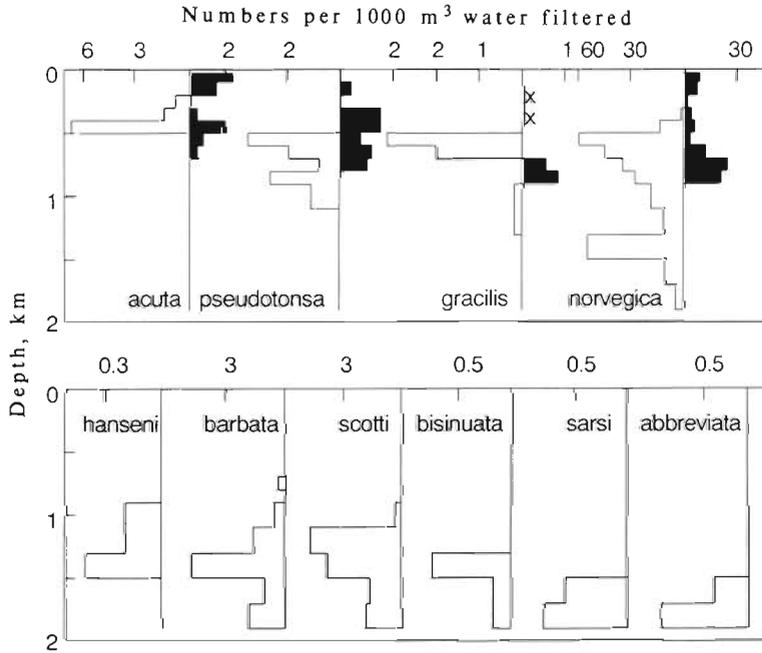


Fig. 1 *Euchaeta* species. Diel vertical distribution of adult females in the Rockall Trough. Black histograms: occurrence at depths shallower than 900 m at night; open histograms: occurrence in the total water column during the day. X: Occurrence in low numbers

(Table 1), did not occur in the July samples and so was also not included. The 1-way analysis of variance shows that there is a significant seasonal change in mean prosome length in all species except *E. sarsi* (Table 2).

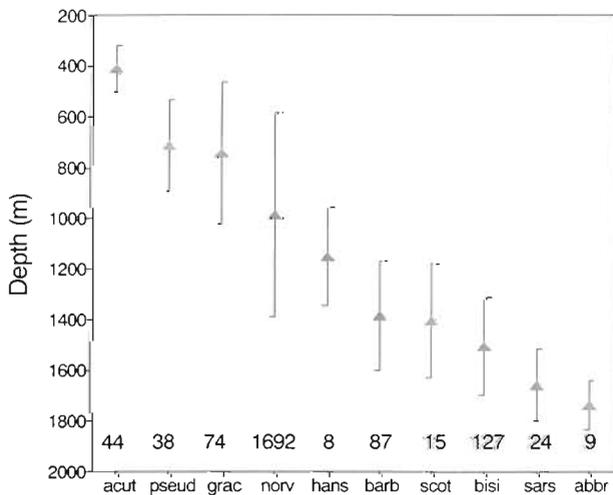


Fig. 2. *Euchaeta* species. Mean depth of occurrence \pm SD for adult females of each species, where sufficient numbers were available. acut = *E. acuta*; pseud = *E. pseudotonsa*; grac = *E. gracilis*; norv = *E. norvegica*; hans = *E. hanseni*; barb = *E. barbata*; scot = *E. scotti*; bisi = *E. bisinuata*; sars = *E. sarsi*; abbr = *E. abbreviata*

All samples of the females of each species were combined to calculate an annual mean prosome length and its standard deviation for each species (Table 1). These are weighted means since they reflect seasonal changes in abundance as well as seasonal changes in prosome length. The standard deviations are plotted as a percentage of mean annual prosome length (Fig. 4), a parameter that is independent of the body size of the species. One species, *Euchaeta norvegica*, is different from the rest; it has the largest vertical range of all the species (Figs. 1 & 2) and also the greatest overall variation in prosome length (Table 1). The other species show an inverse relationship between the amount of variation in prosome length and increasing depth of occurrence.

The prosome lengths of adult female *Euchaeta norvegica* were measured seasonally in a coastal population resident in Loch Etive (west coast of Scotland). The standard deviation as a percentage of the mean was 4.08 as compared with a corresponding value of 4.42 in the Rockall

Trough in the years 1973 to 1975. This implies that the Rockall Trough is a more variable environment for *E. norvegica* than Loch Etive.

Several authors have published raw data on seasonal frequencies of body length of a variety of species of calanoid copepods in coastal regions. Standard deviations expressed as a percentage of the mean sizes have been calculated and are plotted in Fig. 5 and contrasted with the comparable values for the *Euchaeta* species in the Rockall Trough. The Rockall Trough species all show lower values than the coastal species, *E. norvegica* in Loch Etive being an exception.

DISCUSSION

The bathymetric distribution of *Euchaeta* species in the Rockall Trough, although only based on a single vertical series of samples, is supported by previous information on the vertical distribution of individual species (Farran 1926, Østvedt 1955, Roe 1972, 1974, 1984, Deevey & Brooks 1977, Park 1978).

Mauchline (1992) infers that there is a seasonal trend in body size of *Euchaeta barbata* s. str. and *E. barbata* f. *farrani*. Analysis of variance validates this seasonality, as it does also for the other species except *E. sarsi*. Larger samples of *E. sarsi* might show a significant trend. The pronounced seasonality in prosome length

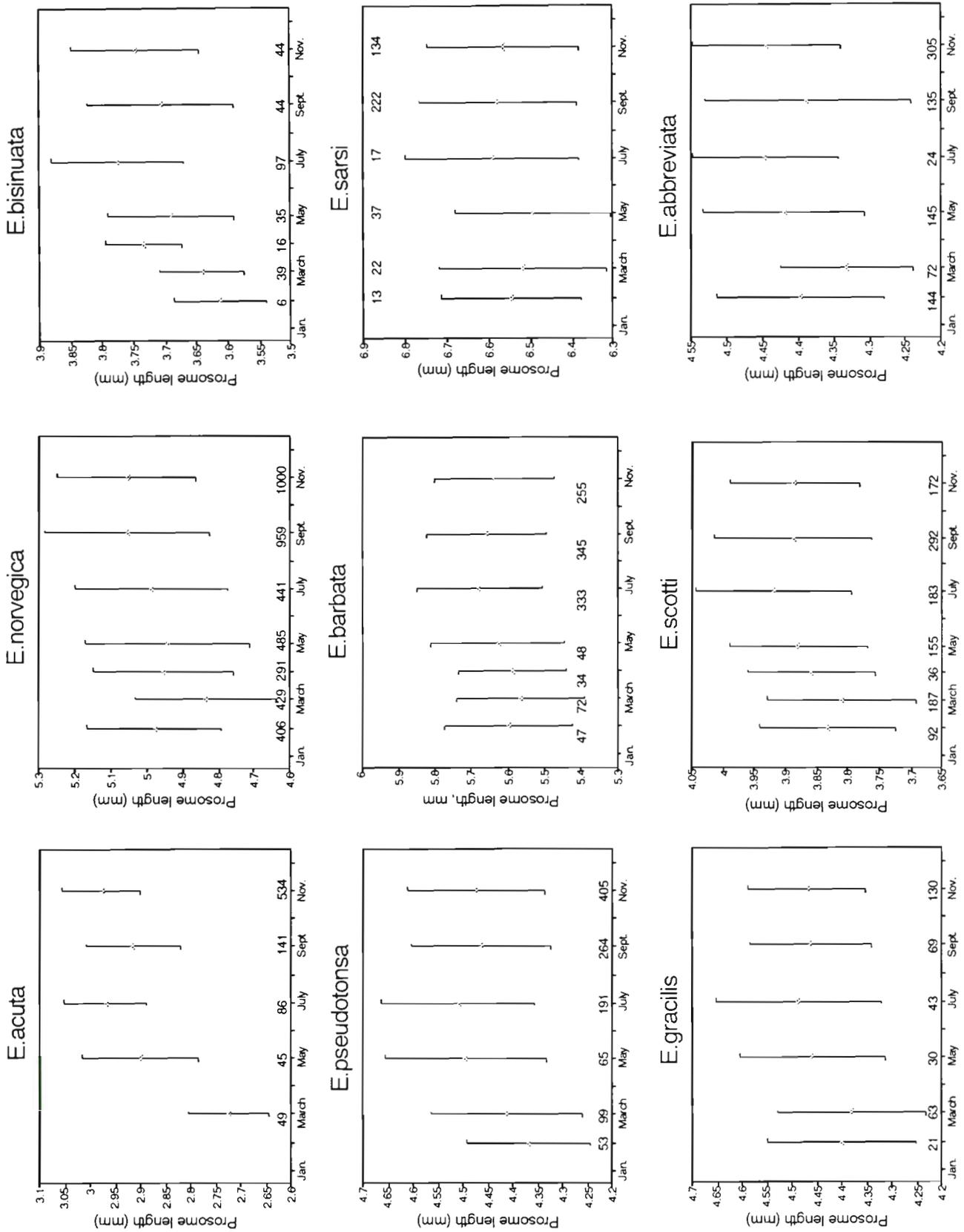


Fig. 3. *Euchaeta* species. Seasonal changes in mean prosome length \pm SD for adult females

Table 1. Adult female *Euchaeta* species. Mean prosome length, its range, and the number (n) of individuals examined from the Rockall Trough

Species	Prosome length in mm		n
	Mean	Range	
<i>E. acuta</i>	2.948	2.578 – 3.292	869
<i>E. pseudotonsa</i>	4.470	3.975 – 4.907	1088
<i>E. gracilis</i>	4.451	3.975 – 4.845	358
<i>E. norvegica</i>	4.997	4.348 – 5.839	4011
<i>E. hanseni</i>	6.337	5.652 – 6.832	99
<i>E. barbata</i>	5.647	4.845 – 6.087	1136
<i>E. scotti</i>	3.874	3.478 – 4.224	1117
<i>E. bisinuata</i>	3.726	3.478 – 4.099	279
<i>E. sarsi</i>	6.564	5.963 – 7.019	447
<i>E. abbreviata</i>	4.413	4.037 – 4.845	825
<i>E. longissima</i>	4.171	3.851 – 4.472	679
<i>E. bradyi</i>	6.189	5.714 – 6.894	25

Table 2. Presence of seasonal differences in mean prosome length within species of *Euchaeta* shown in Fig. 3 tested by ANOVA. The seasonal differences are significant in all species except *E. sarsi*

	df	SS	F
<i>E. acuta</i>			
Between months	4	3.232	114.7***
Within months	850	5.991	
<i>E. pseudotonsa</i>			
Between months	5	1.229	11.9***
Within months	1071	22.099	
<i>E. gracilis</i>			
Between months	5	0.480	5.3***
Within months	350	6.389	
<i>E. norvegica</i>			
Between months	6	20.090	76.3***
Within months	4004	175.887	
<i>E. barbata</i>			
Between months	6	1.136	6.8***
Within months	1125	31.480	
<i>E. scotti</i>			
Between months	6	1.366	16.7***
Within months	1110	15.158	
<i>E. bisinuata</i>			
Between months	6	0.667	11.4***
Within months	274	2.678	
<i>E. sarsia</i>			
Between months	5	0.300	1.7
Within months	439	15.506	
<i>E. abbreviata</i>			
Between months	5	0.918	14.1***
Within months	819	10.699	

***p < 0.001

of *E. acuta* is reduced in the other species with depth. The reduction in the proportions of the standard deviations relative to the means found with depth is a func-

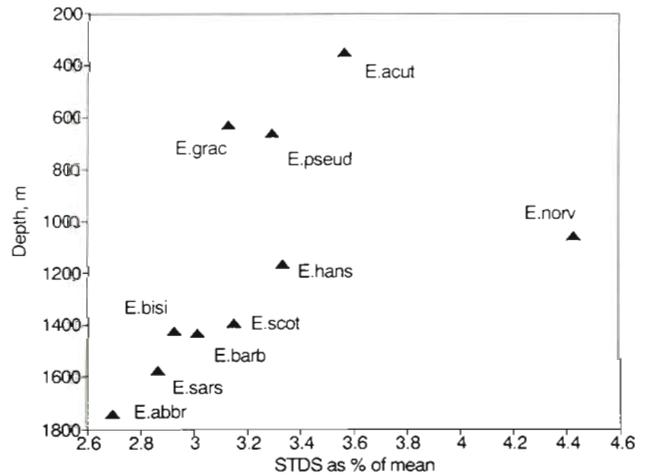


Fig. 4. *Euchaeta* species. Standard deviation of annual mean prosome length of adult females expressed as a percentage of the annual mean prosome length for each species and plotted relative to the mean depth of occurrence of each species as defined in Fig. 2

tion of this restriction of seasonal variability in prosome length. Coastal species such as *Temora longicornis* and *Centropages hamatus* exhibit very marked seasonal changes in mean prosome length within populations, reflected in their standard deviations. Seasonal changes in body size are caused by a complex of

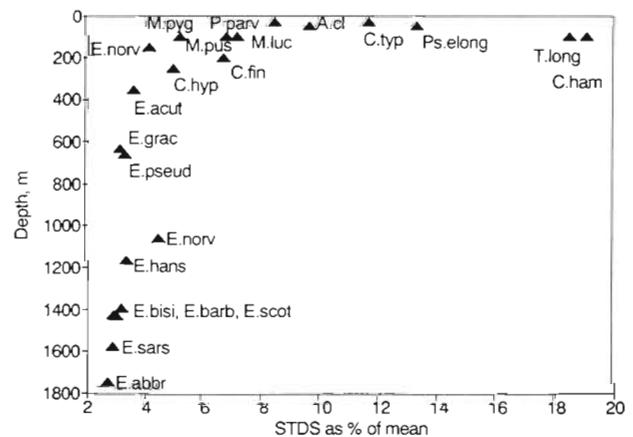


Fig. 5. Calanoid copepods. The data on the *Euchaeta* species in Fig. 4 are replotted along with comparable data derived from total body length measurements of coastal copepods supplied by various authors. A.cl = *Acartia clausi* (Marshall 1949); C.fin = *Calanus finmarchicus* (Adler & Jespersen 1920, Wiborg 1954); C.hyp = *C. hyperboreus* (Wiborg 1954); C.ham = *Centropages hamatus* (Marshall 1949); C.typ = *C. typicus* (Digby 1950); M.luc = *Metridia lucens* (Wiborg 1954); M.pus = *Microcalanus pusillus* (Wiborg 1954); M.pyg = *M. pygmaeus* (Marshall 1949); P.parv = *Paracalanus parvus* (Marshall 1949); Ps.elong = *Pseudocalanus elongatus* (Marshall 1949, Wiborg 1954); T.long = *Temora longicornis* (Adler & Jespersen 1920, Marshall 1949)

factors, both physical and biotic. These act, in the case of coastal species of the genera *Acartia*, *Centropages* and *Temora*, on successive generations of these species within one breeding season (e.g. Gaudy 1972, Daro & Gijsegem 1984). Species such as *Calanus finmarchicus* have fewer generations within a year than these small species but seasonal variation in size is still prominent.

The comparison of populations of *Euchaeta norvegica* between the Rockall Trough and Loch Etive showed that the latter was less variable. Loch Etive has an inner basin of maximum depth of 150 m, *E. norvegica* being primarily confined to the deep water in this basin. Renewal of this deep water is aperiodic with a mean residence time of 1.3 yr (Edwards & Edelsten 1977). Consequently, it lives in an environment with relatively stable physical conditions although biotic factors exhibit the normal seasonal fluctuations. Its vertical range in the Rockall Trough is from the surface to 1900 m (Fig. 1), with a small proportion of the population probably occurring even deeper. The vertical distribution is bimodal (Fig. 1) and there is a clear increase in mean prosome length of individuals with increasing depth (Table 3). This extreme vertical range, from the surface at night, to more than 2000 m depth is probably the source of this greater variation.

The 3 shallowest-living species, *Euchaeta acuta*, *E. gracilis* and *E. pseudotonsa*, perform a diel vertical migration. Their variation in prosome length (Figs. 4 & 5) is compatible with their bathymetric ranges and does not have a component ascribable to their diel vertical migrations.

These relatively large standard deviations in coastal species were expected. What was not foreseen is the regular decrease in the standard deviations with modal

depth of occurrence exhibited by the deep-living, non-migrating *Euchaeta* species (Fig. 4). Vertical migrators and non-migrators among the micronektonic shrimps and fish have different patterns of annual growth in body size (Mauchline 1991). Such a sharp distinction does not exist among the calanoid copepods (Figs. 4 & 5). *E. norvegica* is exceptionally eurybathic, and this factor may, in itself, account for its larger than average standard deviation (Fig. 4), which is placed in a more general context in Fig. 5.

The regular decrease in the size spectra of species with depth may reflect a decreasing impact of the seasonal deposition of aggregated phytodetritus and other surface-derived detritus. Tyler et al. (1992) link this seasonal input with the seasonality in the reproductive patterns of the seastar *Plutonaster bifrons*. The detritus is deposited and accumulated on the abyssal floor and is available in utilizable concentrations to the seastars for some 4 to 8 wk (Gage & Tyler 1991). Its impact in the water column probably decreases with increasing depth owing (1) to consumption on its passage downwards and (2) to shorter residence times in the depth horizons at utilizable concentrations. Further, *Euchaeta* species have the feeding appendages of carnivores rather than detritivores and so may not use this food source to any great extent, even if available.

The next step will be to examine the differing life history strategies of these *Euchaeta* species relative to their modal depth of occurrence. They might be expected to show a progression from complex responses in shelf and coastal environments, resulting in polymorphic populations, to a relatively simple population structure in the deep sea. These data beg the question as to whether a population parameter such as the standard deviation of the mean might act as a bioassay tool to relate variation in one environment or habitat with that in another.

Table 3. *Euchaeta norvegica*. Mean prosome length \pm SD of individuals in the different depth horizons of the vertical series of samples taken during the day; the numbers (n) in the sample are given

Depth horizon (m)	Mean	SD	n
0 – 100	–	–	–
100 – 200	–	–	–
200 – 300	–	–	–
300 – 400	4.969	–	2
400 – 500	4.881	0.183	78
500 – 600	4.889	0.194	252
600 – 700	4.828	0.207	152
700 – 800	4.930	0.226	84
800 – 900	5.022	0.216	85
900 – 1100	5.006	0.205	105
1100 – 1300	5.000	0.217	100
1300 – 1500	5.107	0.216	287
1500 – 1700	5.069	0.253	116
1700 – 1900	5.199	0.320	27

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