

Vertical distribution and population structure of the necrophagous amphipod *Eurythenes gryllus* in the West European Basin*

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ABSTRACT: During 3 cruises to the West European Basin benthopelagic nekton was captured by use of an acoustically released vertical array of 8 to 10 baited traps. The traps were exposed from 5 to 1000 m above the bottom. Nearly all of the 1692 amphipods trapped in total during 18 deployments were identified as the lysianassid amphipod *Eurythenes gryllus* Lichtenstein. Most individuals were recovered from traps deployed 15 m above the sea floor. Above 30 m, catch rates decreased significantly. However, the vertical distribution differed by age and sex: indeterminate juveniles and adult females were only trapped up to 50 m above the bottom. Catch rates of juvenile males and females decreased with increasing distance from the bottom, whereas adult males showed a bimodal distribution with maxima at 15 and at 300 m above the sea floor. Males were prevalent in all but 2 deployments. The characteristic vertical distribution and the population structure at the depths sampled imply an ontogenetic vertical migration of *E. gryllus*: females release their brood near the bottom. The youngest stages stay within a few meters above the sea floor, whereas older stages, especially adult males, migrate into higher water layers.

INTRODUCTION

Necrophagous amphipods of the family Lysianassidae are important members of the deep-sea benthic and benthopelagic community. The lysianassid amphipod *Eurythenes gryllus* Lichtenstein is a highly motile, cosmopolitan scavenger which has been reported to occur directly on the sea floor as well as in midwater up to 1800 m above the bottom (Baldwin & Smith 1987). The majority of studies on the vertical distribution and population structure of this species have been carried out in the North Pacific (Smith et al. 1979, Ingram & Hessler 1983, 1987, Smith & Baldwin 1984, Baldwin & Smith 1987, Bucklin et al. 1987). Reports from the Atlantic have so far been restricted to the near-bottom water layer up to 200 m above the sea floor (Thurston 1979, Wickins 1983, Charmasson & Calmet 1987).

This paper presents results from a sampling programme which was part of the German multidisciplinary research project BIOTRANS. This project studies

the BIOlogical vertical TRANSPORT of organic matter and energetics in the benthic boundary layer of the deep-sea up to 500 m above the sea bottom (Thiel 1986). Scavenging amphipods were caught in sets of baited traps exposed at various distances from the sea floor to a maximum of 1000 m. The population structure of *Eurythenes gryllus* at different depths was analysed to investigate the role of this large amphipod in the vertical transport of organic matter. Although we have no final answer to this question, the alteration in population structure of *E. gryllus* with increasing distance from the sea bed allows some conclusions on the biology and on ontogenetic migrations of this species.

STUDY SITE

The site of investigation was the BIOTRANS-research area (Fig. 1) in the West European Basin, NE Atlantic, within the coordinates 47° to 47°30' N, 19° to 20° W. Sea beam mapping of the area and its surroundings (Heinrich 1986) revealed a variable bottom topography. It is structured by a system of ridges and furrows

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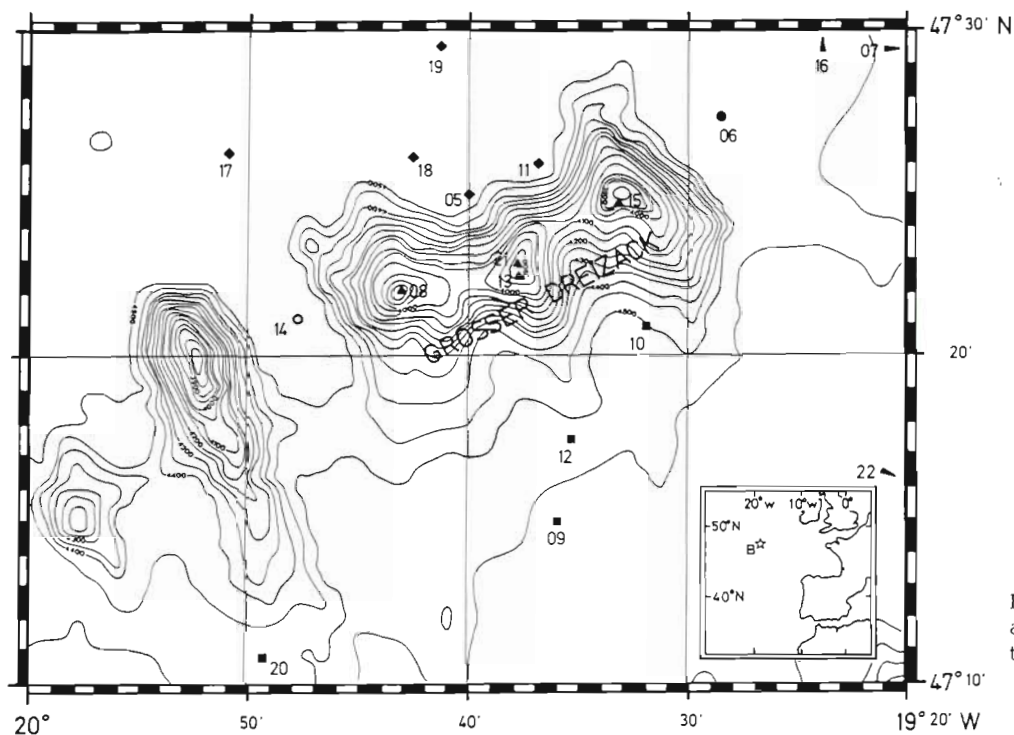


Fig. 1. BIOTRANS research area with the positions of trap deployments indicated by their numbers

stretching more or less parallel to the Mid-Atlantic Ridge (NNE to SSW). At the BIOTRANS site a seamount characterized by 3 peaks named 'Grosser Dreizack' stands apart from the NNE to SSW lying ridges. The Grosser Dreizack is surrounded on 3 sides by broad valleys of about 15 n miles width. To the west it is separated from a neighbouring ridge by a narrower valley of 4 n miles width. Water depth in the valleys ranges between 4500 and 4560 m. The peaks of the Grosser Dreizack rise to about 700 m above the valleys or 3800 m below the sea surface.

The hydrography of the area was described by Mittelstaedt (1986) and Klein (1987). Only slight gradients of temperature and salinity occur below 2000 m water depth. Salinity of the bottom water is about 34.9, in situ temperature ranges from 2.54 to 2.63°C, and oxygen content amounts to 5.5 to 5.7 ml O₂ l⁻¹. While the gradients of the physical parameters decrease with decreasing distance from the bottom the particle concentration increases. The thickness of the benthic nepheloid layer (BNL) was determined by Nyffeler & Godet (1986) to be 800 to 1000 m. The particle concentration reaches a maximum at about 80 to 100 m above the sea floor. Bottom topography has a strong influence on the extent of the BNL. Current velocities in the layer up to 1500 m above bottom lie in the range 1 to 4 cm s⁻¹. Near-bottom current velocity are frequently 1 to 2 cm s⁻¹ greater. 'Deep-sea storms' with maximum current velocities of 27 cm s⁻¹ can occur for several days or even weeks (Klein 1987).

MATERIALS AND METHODS

Scavenging amphipods were caught on 3 cruises in 1985 ('Meteor (I)' 70 and 'Polarstern' 8) and in 1986 ('Meteor (II)' 3) with an acoustically released vertical array of 8 to 10 baited traps. The array construction is shown in Fig. 2 together with the heights of the traps above bottom. Deployments were made in 5 subareas of the BIOTRANS site (Fig. 1): (1) valley north of Grosser Dreizack; (2) valley south of Grosser Dreizack; (3) peaks of Grosser Dreizack; (4) channel east of Grosser Dreizack; (5) channel west of Grosser Dreizack.

The traps were made of PVC tube with a length of 80 cm and a diameter of 40 cm. An inverted entrance cone, made from gauze netting (mesh width 1 mm), was attached at each end with an entrance of 4.5 cm diameter, allowing the largest known *Eurythenes gryllus* to enter the trap (Ingram & Hessler 1983). The design of the mooring used during 'Polarstern' Cruise 8 (1985) is shown in Fig. 2. During 'Meteor (I)' Cruise 70 (1985), no traps were employed at 400 and 500 m. During 'Meteor (II)' Cruise 3 (1986), the set was modified by adding traps at 10 and 5 m. On this cruise, deployments were also made with a single trap in the array moored at 1000 m above bottom.

Exposure time was 15 to 44 h for the trap sets and 62 to 74 h for the single traps. Station data are listed in Table 1.

The traps were baited with sliced fish or fish heads (herring, cod) which were placed directly into the traps.

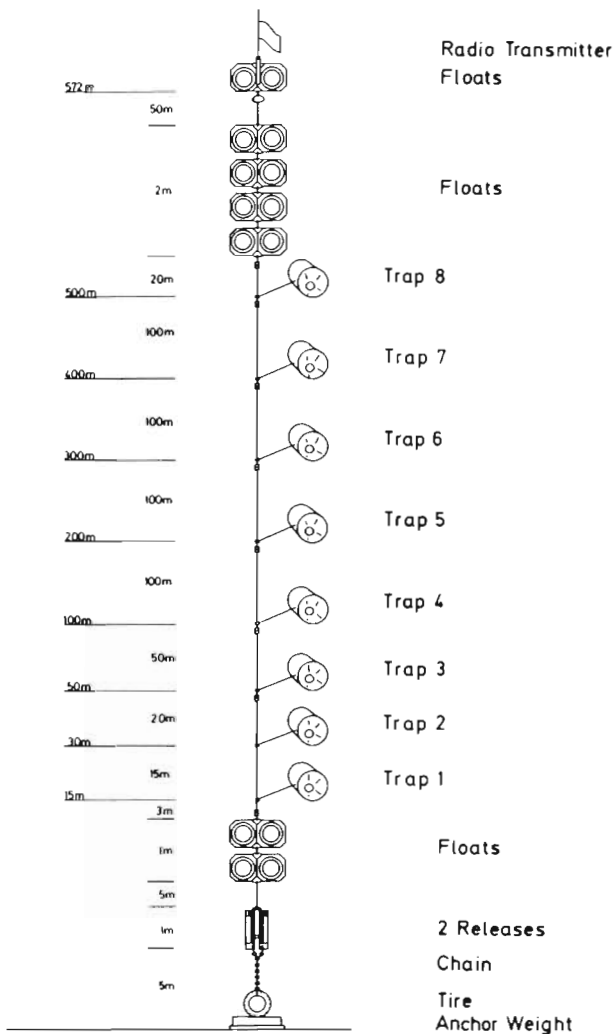


Fig. 2. IHF trap set

For deployment RK 21 the bait was enclosed in perforated containers which prevented the amphipods from feeding on it.

Trapped amphipods were fixed in 4% buffered formaldehyde and later transferred to 70% ethanol. Specimens of *Eurythenes gryllus* were sorted into 5 categories: (1) sexually indeterminate juveniles (no oostegites or genital papillae recognizable); (2) immature males (showing genital papillae); (3) mature males (with calceoli on the antennae); (4) immature females (with oostegites); (5) mature females (oostegites with long interlocking setae).

Determinations of body length were made by straightening the specimen gently on a scale and measuring the distance from the front edge of the head to the tip of the telson to the nearest 0.5 cm. Mean lengths are expressed as geometric means, because the distributions appeared to be positively skewed.

Catch rates were calculated by dividing catch num-

bers by exposure time (in days). For tests on vertical differences of abundance a 2-way ANOVA without replication (mixed model) was applied (Sokal & Rohlf 1969). To achieve homoscedasticity, catch rates were transformed by $y = \ln(x + 1)$. Homogeneity of ratios between the 5 categories was tested by a Chi square contingency table (Sachs 1978).

RESULTS

Taxonomic composition

A total of 1692 amphipods were trapped in 18 deployments. Of these, 1687 belonged to the species *Eurythenes gryllus*, 4 were identified as *Cyphocaris richardi* Chevreux and 1 as *C. anonyx* Boeck. Female *E. gryllus* had 5 pairs of oostegites, in accordance with specimens caught in the North Pacific (Ingram & Hessler 1983) and in the North Atlantic (Charmasson & Calmet 1987). In contrast to these findings, Ingram & Hessler (1983) reported that female *E. gryllus* from the Atlantic had only 4 pairs of oostegites.

Mesoscale variation in catches

The number of amphipods caught in a multi-trap deployment varied from 17 to 309 (Table 2). Normalized for bottom time, catch rates ranged from 17 to 265 ind. deployment⁻¹ d⁻¹. The lowest catch rate was found in Deployment RK 21 with the bait enclosed in perforated containers. This may have affected the effectiveness of the traps, thus the data of this set were excluded from all following calculation.

A regional comparison of mean total catch rates in 1986 revealed that the subareas north and south of the Grosser Dreizack did not differ significantly (Student t-test, log-transformed data). Catches in the other subareas were only represented by single deployments of the array and thus not tested for differences.

Vertical distribution

The vertical distribution of *Eurythenes gryllus* (Fig. 3) was similar in all subareas and in both years. In 1986, nearly 50% of all specimens were caught in the 15 m traps. For individual deployments, the proportion trapped at this height above bottom varied between 7 and 87%. Below and above 15 m the number of amphipods decreased significantly (ANOVA, $p < 0.05$ and $p < 0.01$, respectively). Only 17% of all individuals were caught in water layers higher than 30 m above bottom. However, above 200 m catch rates were significantly higher than between 50 and 200 m ($p < 0.01$).

Table 1. List of stations

Date	Deployment no.	Stn no.	Coordinates		Depth (m)	Bottom time (h)	No. of traps
			North	West			
<u>1985</u>							
20 May	RK 05	117	47°25.0'	19°40.1'	4510	44.2	6
17 Sep	RK 06	170	47°28.0'	19°29.2'	4524	28.0	8
18 Sep	RK 07	177	47°30.1'	19°16.3'	4550	15.0	8
19 Sep	RK 08	183	47°22.4'	19°43.4'	3850	17.5	8
<u>1986</u>							
26 Jul	RK 09	198	47°15.2'	19°36.9'	4554	22.7	10
26 Jul	RK 10	200	47°21.0'	19°32.2'	4436	62.5	1
28 Jul	RK 11	212	47°26.0'	19°37.8'	4532	23.5	10
30 Jul	RK 12	221	47°17.7'	19°35.1'	4526	69.7	1
30 Jul	RK 13	222	47°22.7'	19°37.8'	3882	17.8	10
31 Jul	RK 14	229	47°21.1'	19°47.8'	4518	23.3	9
3 Aug	RK 15	243	47°24.7'	19°33.3'	3849	73.8	1
3 Aug	RK 16	244	47°34.3'	19°24.0'	4577	20.2	9
5 Aug	RK 17	258	47°26.3'	19°50.5'	4540	19.5	9
7 Aug	RK 18	269	47°26.0'	19°43.1'	4531	17.0	9
8 Aug	RK 19	279	47°30.3'	19°41.1'	4546	61.7	1
9 Aug	RK 20	282	47°10.7'	19°49.7'	4475	20.2	9
11 Aug	RK 21	297	47°22.8'	19°37.9'	4053	23.5	9
12 Aug	RK 22	306	47°15.8'	19°15.8'	4551	33.3	10

Table 2. *Eurythenes gryllus*. Total number captured in each trap. Subareas: vs, valley south of Grosse Dreizack; vn, valley north of Grosse Dreizack; p, peaks of Grosse Dreizack; cw, channel west of Grosse Dreizack; ce, channel east of Grosse Dreizack

Trap height (m)	Deployment No.																		Total 1986	
	05	06	07	08	Total 1985	09	10	11	12	13	14	15	16	17	18	19	20	21		22
	vn	ce	ce	p		vs	vs	vn	vs	p	cw	ce	ce	vn	vn	vn	vs	p		vs
< 15	–	–	–	–	–	17	–	67	–	4	1	–	34	8	48	–	6	0	16	201
15	58	220	43	83	404	22	–	24	–	21	123	–	77	125	38	–	63	8	6	507
30	45	62	15	48	170	38	–	3	–	32	0	–	3	3	7	–	6	0	51	143
50	11	4	7	7	29	6	–	1	–	14	0	–	2	1	5	–	2	3	1	35
100	2	2	1	6	11	0	–	2	–	6	1	–	1	2	0	–	1	1	0	14
200	2	1	1	3	7	1	–	0	–	1	1	–	0	0	3	–	1	0	0	7
300	7	8	2	1	18	2	–	3	–	4	9	–	4	9	6	–	10	2	1	50
400	–	5	0	1	6	1	–	2	–	10	5	–	1	2	3	–	3	2	10	39
500	–	7	1	2	10	2	–	0	–	10	1	–	1	3	6	–	0	1	3	27
1000	–	–	–	–	–	–	1	–	4	–	–	0	–	–	–	4	–	–	–	9
Total	125	309	70	151	655	89	1	102	4	102	141	0	123	153	116	4	92	17	88	1032

–: no trap

A similar distribution pattern was found in 1985. The majority of individuals (64%) were caught in the 15 m traps; above 30 m rates decreased significantly ($p < 0.01$). By contrast to 1986, only a slight increase in water layers above 200 m was observed, which was not statistically significant.

A total of 11 amphipods were recovered from the 4 deployments of the single 1000 m traps, with 9 specimens in 3 deployments being *Eurythenes gryllus*. The catch of deployment RK 15, the only one of the single

trap units deployed on the Grosse Dreizack, consisted of 2 *Cyphocaris richardi*.

The vertical distribution of *Eurythenes gryllus* differed in the 5 age/sex categories. In both years studied, indeterminate juveniles were only trapped up to a distance of 50 m above the bottom. The majority of specimens were found in the 15 m traps (Fig. 4a) with mean catch rates of 27 (1985) and 15 (1986) ind. trap⁻¹ d⁻¹. Above 15 m, catch rates decreased significantly to between 0.9 and 4.6 ind. trap⁻¹ d⁻¹ ($p < 0.01$).

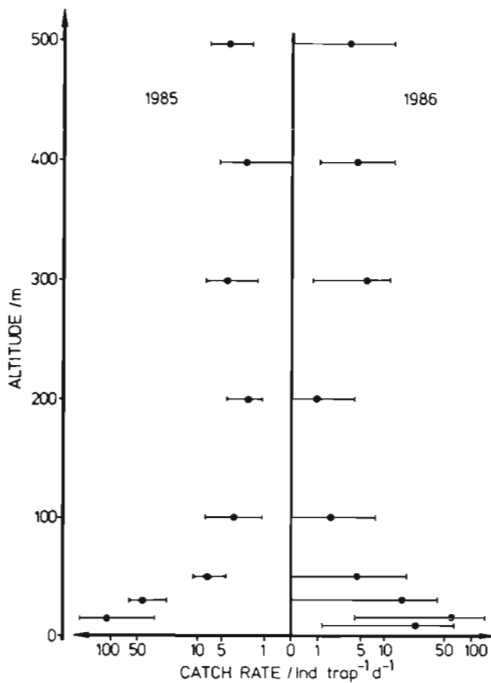


Fig. 3. *Eurythenes gryllus*. Vertical distribution of all categories. Mean catch rates and ranges at each height above bottom sampled

Immature males were found at all heights above the bottom except 1000 m, with maximum average catch rates of 46 and 21 ind. trap⁻¹ d⁻¹ at 15 m (Fig. 4b). Above and below 15 m, their abundance declined significantly ($p < 0.01$). From 50 to 500 m, average catch rates were only 0.2 to 2.1 ind. trap⁻¹ d⁻¹.

The distribution of immature females was similar to that of immature males. Again, the majority were caught in the 15 m traps (Fig. 4c). Average catch rates decreased about an order of magnitude at heights between 15 and 50 m above the bottom from between 19 and 20 ind. trap⁻¹ d⁻¹ to between 0.3 and 3.8 ind. trap⁻¹ d⁻¹.

In both years, mature males showed a bimodal vertical distribution pattern with maxima at 15 and 300 m above the sea floor (Fig. 4d). For the 1986 data, differences between the ranges < 15 m (mean catch rate 1.4 ind. trap⁻¹ d⁻¹), 15 to 30 m (4.8 ind. trap⁻¹ d⁻¹), 50 to 200 m (0.53 ind. trap⁻¹ d⁻¹) and 300 to 500 m (2.8 ind. trap⁻¹ d⁻¹) were significant ($p < 0.01$). The increase of average catch rates above 200 m in 1985 was not significant.

A total of only 16 mature females were trapped in 17 deployments, 10 of them in the 15 m traps. No mature females occurred in traps higher than 50 m above the bottom. Females carrying brood were not captured.

The catches in the 1000 m traps consisted only of large immature females and mature males.

Population structure

The contingency tables (Tables 3 and 4) show that the proportions of the 5 categories selected were not homogeneous within the 1985 and 1986 deployments. The null hypothesis – proportions are equal in all deployments – has to be rejected by the χ^2 test ($\chi^2 = 37.1 > \chi^2_{(12,0.01)} = 26.2$ for 1985 and $\chi^2 = 88.6 > \chi^2_{(32,0.01)} = 53.5$ for 1986). A closer examination of the data reveals that the proportions of immature males, mature males and mature females are very similar in all trap sets, whereas there is a large variability in indeterminate juveniles and immature females. The highly significant negative correlation in deviations from expected values for these 2 groups ($r = -0.957$) indicates that the variability is caused by difficulty in discriminating small females from juveniles and not by real differences between stations. Therefore we assumed that the population of *Eurythenes gryllus* is homogeneous in the area sampled and combined the data from stations of 1985 and 1986, respectively, for analysis of the population structure.

Males were prevalent in all but 2 deployments. The sex ratio ($s = M - F / M + F$) varied from -0.05 to $+0.44$ with an overall ratio of $+0.17$ in 1985 and $+0.16$ in 1986. The larger indeterminate juveniles are probably also females, because males of more than 2.5 cm body length are clearly recognizable by the presence of genital papillae, while it is difficult to recognize the oostegites in small females. Thus, the true total sex ratio of the population is probably not appreciably different from 1:1 (i.e., $s = 0$). There is a trend for increasing male/female ratios with height above bottom (Fig. 5). In both years, the lowest male/female ratio was at 50 m, while the highest ratio occurred 300 m above the bottom. About 25% (1985) and 36% (1986) of all males were mature, but only 3% of females had oostegites with long interlocking setae indicating full maturity, stressing the prevalence of males in the adults, with ratios of $+0.86$ and $+0.89$ for 1985 and 1986 respectively.

The size-frequency distribution of *Eurythenes gryllus* for the combined stations at the heights sampled is shown in Fig. 6 for 1985 and in Fig. 7 for 1986. Large specimens were found at all heights above the sea floor, whereas small specimens with body lengths of less than 4 cm were nearly absent at heights of more than 50 m above the bottom. Mean lengths and length ranges are given in Table 5. The largest individual trapped was a mature female with a body length of 12.9 cm.

The data for both years show a general increase in body length of amphipods with distance from the sea floor (Fig. 8). The small mean sizes in the near-bottom traps were mainly caused by the high proportion of

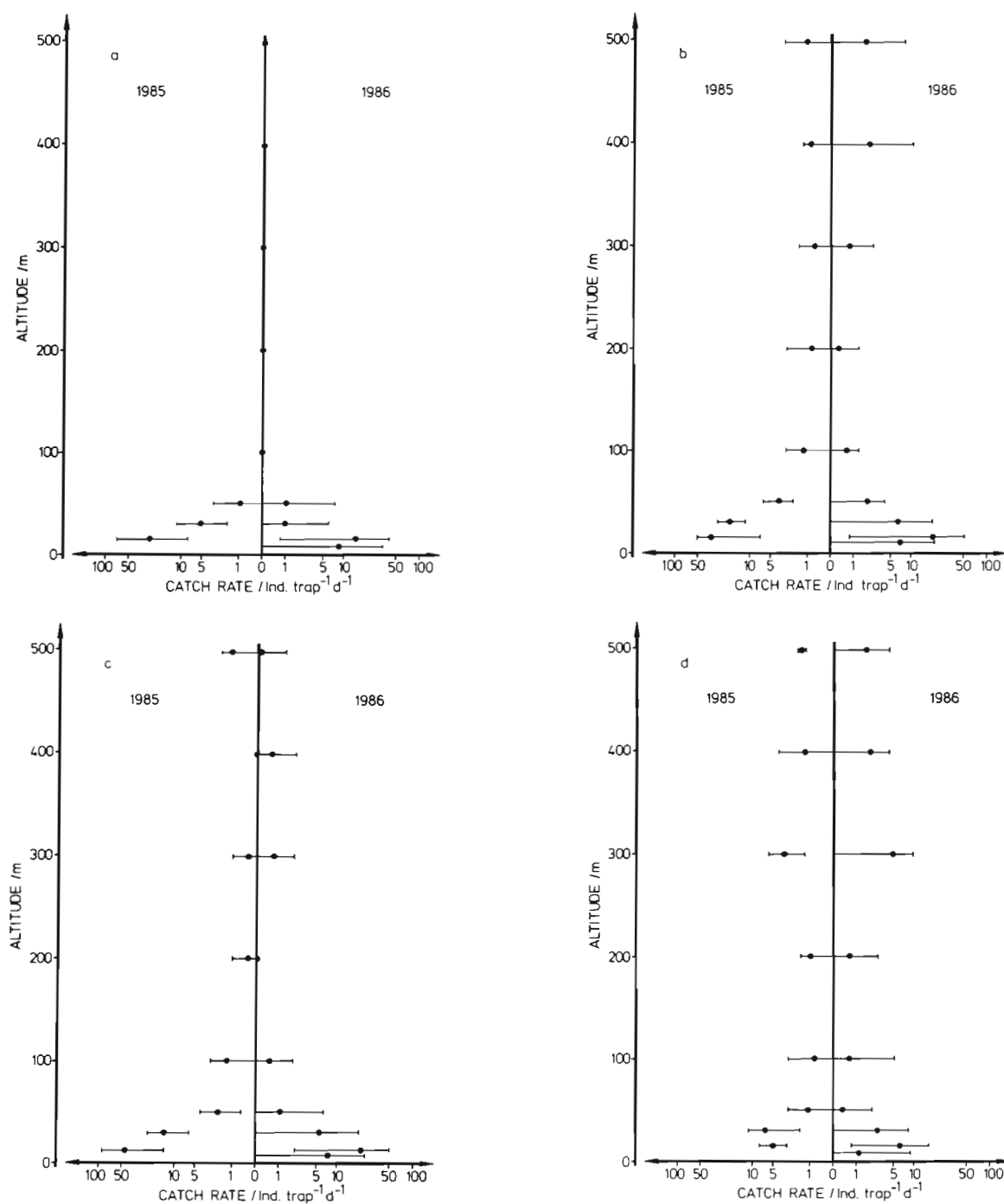


Fig. 4. *Eurythenes gryllus*. Vertical distributions of (a) indeterminate juveniles, (b) immature males, (c) immature females, (d) adult males

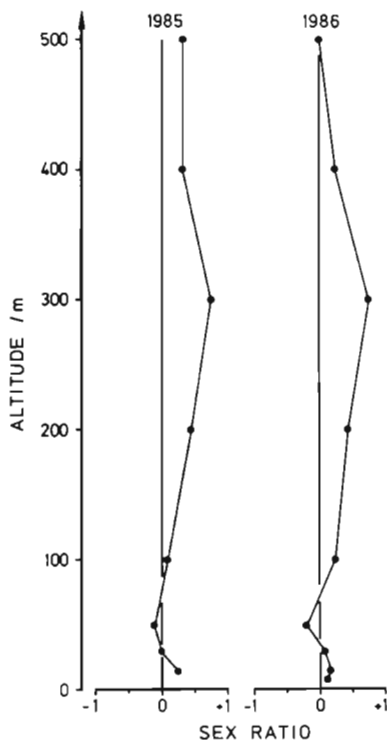
indeterminate juveniles. Above 50 m, where no indeterminate juveniles were trapped, mean body length increased only slightly.

Fig. 9 shows the length-frequency distributions of males and females (all age classes combined) in 1985 and 1986. Several modes can be discriminated, indicating probably non-continuous recruitment. Assuming

that indeterminate juveniles larger than 2.5 cm are females (stippled area in the histograms), the distributions of both sexes in 1985 are quite similar: an increase in numbers was found up to length class 3.75 cm, a second mode occurred in length classes 5.25 cm (males) and 5.75 cm (females), followed by a sharp decrease. In 1986, the highest numbers of females

Table 3. Contingency table for 1985

Group	Deployment no.				Sum	χ^2
	5	6	7	8		
Indet. juv.	18	78	10	16	122	14.4
Imm. males	37	115	19	63	234	4.5
Imm. females	45	82	33	55	215	9.1
Mat. males	24	30	7	17	78	7.1
Mat. females	1	4	1	0	6	2.1
Sum	125	309	70	151	655	
χ^2	8.5	12.9	6.9	8.8		37.1

Fig. 5. *Eurythenes gryllus*. Sex ratio at each height sampled

again were in the small size classes with modes at 2.75, 3.75 and 4.75 cm. A further mode can be observed at length class 6.75 cm. Males showed a tendency of increasing numbers up to length class 6.25 cm. Numbers then decreased rapidly. Females obviously grow larger than males: specimens larger than 9.5 cm were always females.

DISCUSSION

The vertical distribution of *Eurythenes gryllus* in the BIOTRANS area appears to follow a clear pattern, with highest numbers in the near-bottom layer and decreasing abundance above 30 m off the sea floor. Above 200 m, a slight increase in relative abundance could be observed.

This pattern applies for the plains as well as for the peaks of the seamounts, rising up to 700 m above the plains. Thus the occurrence of *Eurythenes gryllus* seems to be determined by distance from the sea floor, regardless of absolute water depth. Seamounts therefore have a kind of 'lift effect' for these benthopelagic animals. The similarity of the vertical distribution pattern and homogeneity of the population structure in peak and basin subareas implies a common population of *E. gryllus* in the area. However, the comparison is limited by the low number of samples per subarea and the high variation in catch rates. Contrary to our findings, Bucklin et al. (1987) reported a genetic isolation of an *E. gryllus* population living on the crest of a seamount in the North Pacific from populations living in the basins. They suggested that dispersion took place horizontally, separating midwater and crest populations from basin populations. However, the vertical distance between basin and crest was much larger than in the BIOTRANS area.

Analyses of the vertical distribution of scavenger populations derived by means of baited traps have to be interpreted with some caution. The results depend to a large extent on the assumption that the traps

Table 4. Contingency table for 1986

Group	Deployment no.									Sum	χ^2
	9	11	13	14	16	17	18	20	22		
Indet. juv.	25	37	19	44	15	27	29	6	9	211	41.1
Imm. males	21	31	32	52	30	49	33	23	25	296	6.0
Imm. females	25	22	36	27	54	51	29	43	37	324	27.7
Mat. males	17	10	14	18	22	26	23	18	17	165	6.7
Mat. females	1	2	1	0	2	0	2	2	0	10	7.2
Sum	89	102	102	141	123	153	116	92	88	1006	
χ^2	4.1	18.7	1.2	19.7	11.5	2.8	4.3	17.7	8.9		88.6

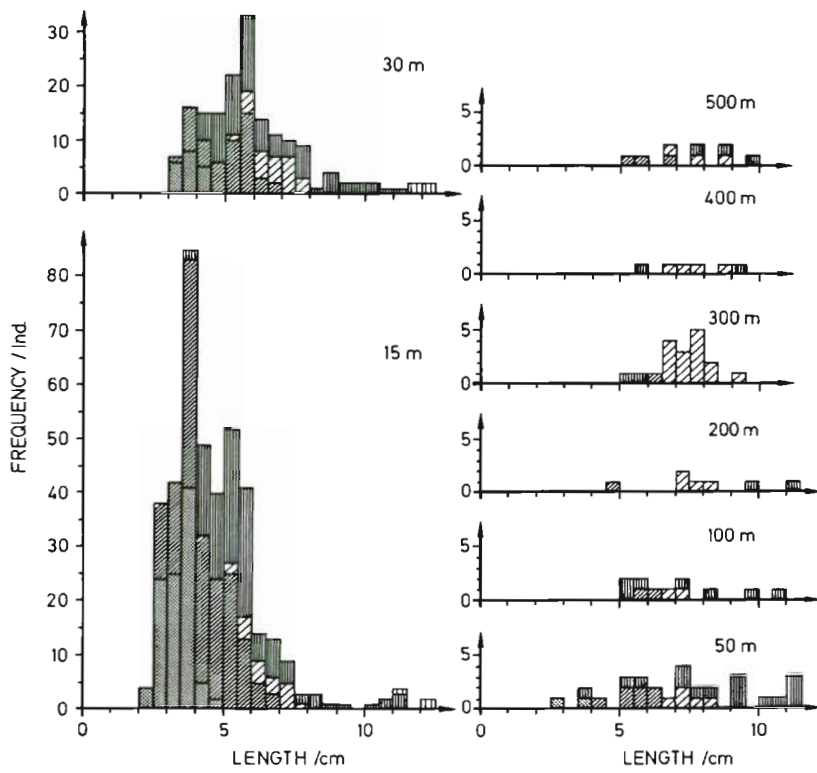


Fig. 6. *Eurythenes gryllus*. Length-frequency distributions at each height sampled, 1985

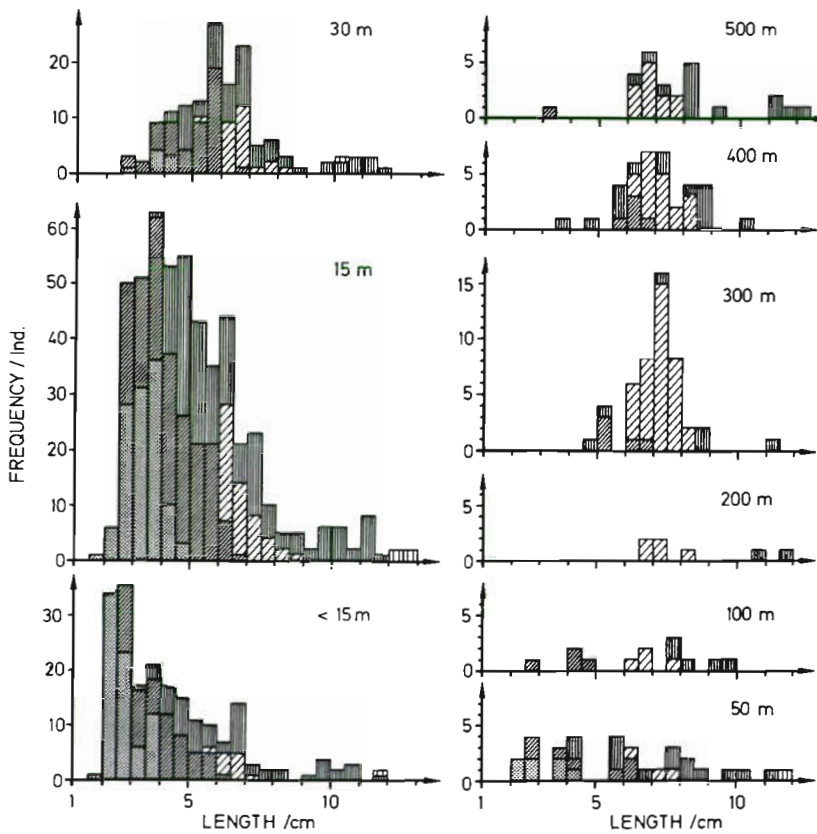


Fig. 7. *Eurythenes gryllus*. Length-frequency distributions at each height sampled, 1986

Table 5. *Eurythenes gryllus*. Mean lengths (geometric means) and length ranges

Group	Mean 1985 (cm)	Mean 1986 (cm)	Range (cm)
Juv.	3.38	3.03	1.5– 5.0
Imm. males	4.46	4.29	2.5– 7.0
Mat. males	6.96	6.88	5.0– 9.0
Imm. females	6.13	6.53	3.0–12.5
Mat. females	12.00	11.75	10.0–13.0

exposed at different heights represent the same area of attraction, i.e. the odour plumes generated by the bait are of equal size. Horizontal distribution of odour is mainly caused by advection, thus different current velocities in the depth layers sampled will generate varying sizes of the odour plumes.

The intermediate minimum of amphipods trapped in the layer 100 to 200 m may for instance be related to a minimum in current velocities, as observed by Mittelstaedt (1986) and Klein (1987).

Because scent is dispersed not only horizontally but also vertically (Sainte-Marie & Hargrave 1987), it is certain that animals are also attracted from layers below or above a trap. This may explain the varying proportions of amphipods caught between the traps 5 to 30 m above the bottom, where the vertical distance between traps was relatively short and thus the possibility of interference greater than between upper traps.

Additionally, social behaviour, as discussed by

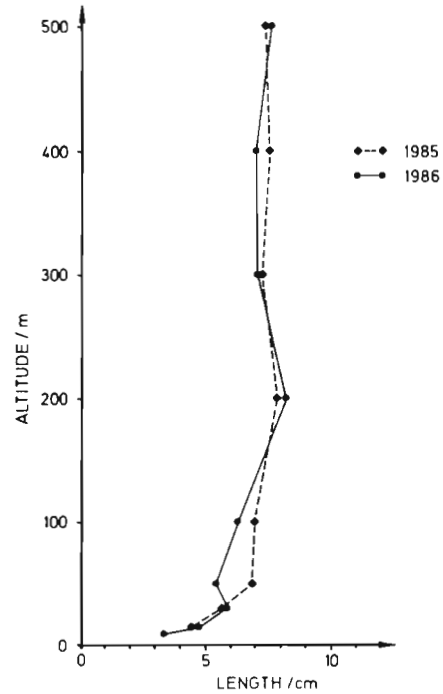


Fig. 8. *Eurythenes gryllus*. Mean body length versus height above bottom

Ingram & Hessler (1983), and an additional attraction by means other than olfaction, e.g. noise generated by chewing mouthparts (Smith & Baldwin 1984), could also bias the results on vertical distribution.

Despite the restrictions of the methodology, the

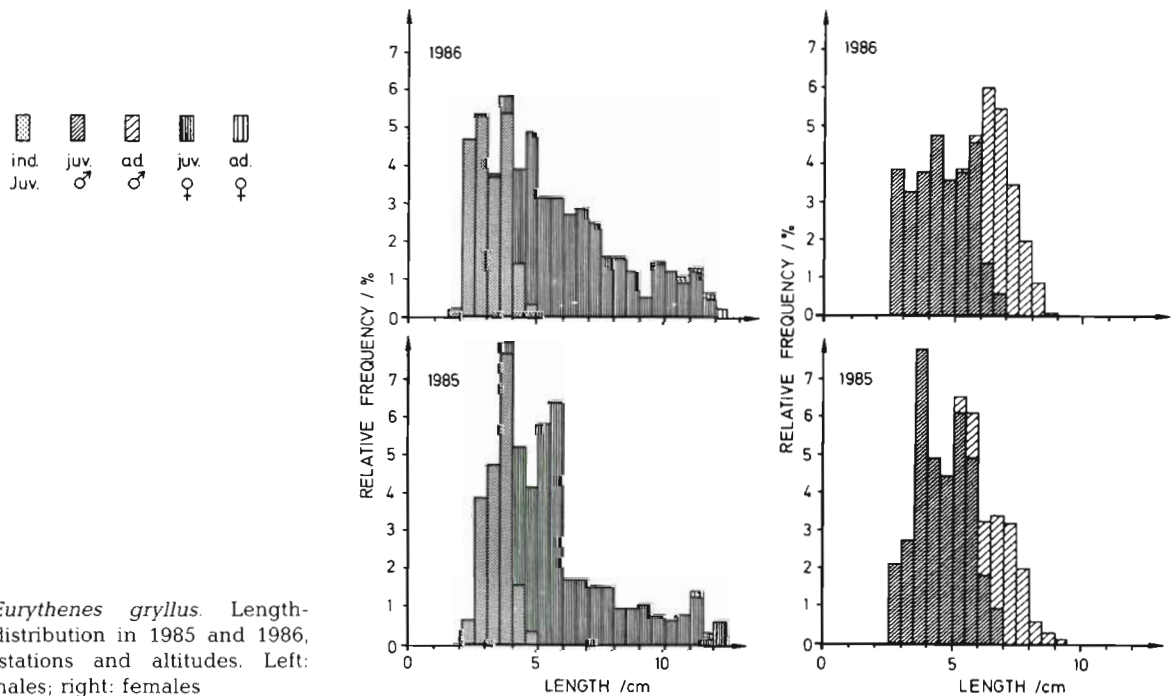


Fig. 9. *Eurythenes gryllus*. Length-frequency distribution in 1985 and 1986, combined stations and altitudes. Left: males; right: females

observed vertical distribution pattern of *Eurythenes gryllus* appears to be a common feature of this species in different parts of the world's oceans, regardless of environmental differences. In the North Pacific, a similar pattern, but without an intermediate minimum, was found by Ingram & Hessler (1983), Smith & Baldwin (1984) and Baldwin & Smith (1987). In the Atlantic southeast of the BIOTRANS area, Charmasson & Calmet (1987) also reported a rapid decrease of catch rates above 10 to 20 m from the bottom.

Some information on the population dynamics of *Eurythenes gryllus* can be derived from the size-frequency distributions. However, discrete size groups representing instars are not clearly recognizable, although there is some indication for polymodality in the histograms. Probably the class intervals of 0.5 cm are too large and obscure sharp delineations, as found by Thurston (1979), Baldwin & Smith (1987) and Ingram & Hessler (1987), using size intervals of 1 or 0.5 mm. Relatively low numbers in the smallest size groups, which prefer the near-bottom layers, are probably an artifact because the lowest traps were at least 5 m above the sediment, in 1985 even 15 m.

Generally, the size-frequency diagrams show a trend for decreasing numbers with increasing length. The number of males declines rapidly beyond a length of 7 cm, indicating high mortality in these size groups. However, mortality seems low for females larger than 6 cm: in both years, numbers of successive length classes show only a slight decrease.

The high prevalence of males in the adults is caused by their earlier maturity. They reach maturity at Instar VIII (Ingram & Hessler 1983) at a length of 5 to 7 cm. The smallest mature females trapped had a body length of 10 cm. While growing to this length they still suffer mortality.

The occurrence of modes in different size classes may be an indication for non-continuous recruitment. Comparison of the successive years reveals a shift of modes which might indicate the growth of cohorts between the sampling dates. In 1985, the peaks of abundance for males are in length classes 3.75 and 5.25 cm. The corresponding modes in 1986 in length classes 4.25 and 6.25 cm point to an annual growth of about 0.5 to 1.0 cm. For females, the modes are shifted from 3.75 and 5.75 cm in 1985 to 4.75 and 6.75 cm in 1986, also implying an annual growth of about 1 cm. This is less than rates calculated from data of Ingram & Hessler (1987) for the Pacific. These authors reported a shift in peak abundance from Instar III to Instar V in successive years. The mean length in Instar III was 3.2 cm, in Instar V 4.8 cm (males) and 5.0 cm (females), giving an annual growth of nearly 2 cm.

The comparison of modes between males and females shows that in both years peak abundances of

males are in lower length classes than that of females. If the modes in both sexes represent the same year classes, this would indicate a higher growth rate for females than for males.

Very small juveniles of 1.5 to 2.5 cm were only found up to 15 m above the sea floor, with the exception of 2 individuals trapped at 50 m. The proportion of this group decreases from 18% of all juveniles in traps at 10 m above bottom to 3% at 15 m. These observations fit well with the findings of Thurston (1979) in the North Atlantic: only juvenile *Eurythenes gryllus* were caught in a trap deployed directly on the sediment, nearly 85% of them from 15 to 25 mm length.

The fact that small juveniles and mature females were only found within 50 m above the sediment leads to the conclusion that reproduction takes place near the bottom. The bimodal distribution of adult males with a second peak of abundance at 300 m above the sediment is somewhat contradictory to this hypothesis. Although there was still a large proportion of adult males near the bottom it is not clear why nearly half of the adult males occurred higher than 200 m. One explanation may be that large females trapped in higher layers without long setae on their oostegites are adult too, but in a preparatory stage before a brood. Multiple brooding with a reduction of marginal setae on the oostegites between broods is common in shallow-water amphipods (Steele & Steele 1975). Little is known about the mating behaviour of deep-sea lysianassids. Other gammaridean males seize the females before the parturial moult, i.e. before the oostegites are fully developed, and wait for copulation until the moult takes place. This points to the possibility that mating also occurs in higher layers.

Thus the development of *Eurythenes gryllus* might be as follows: females release their brood near the sediment. The youngest stages stay within a few meters of the bottom, probably feeding on small detrital particles rather than on larger food items. For larger specimens feeding on large particles it might be advantageous to keep a certain distance from the sea floor to have a 'larger chemosensory view of the sediment' (Ingram & Hessler 1983). The zone of maximum abundance lies within the benthic boundary layer where maximum turbulent diffusion occurs, reaching 20 to 80 m above bottom in the BIOTRANS area (Mittelstaedt 1986). It is also possible that older stages are capable of predation with some degree of independence from descending food. Some indication for predatory behaviour in *E. gryllus* was found by Templeman (1967). Mating probably occurs in all water layers. Females with brood then descend to the near-bottom layer. The reason that ovigerous females have never been trapped may be that they do not feed at all, or that they are extremely rare.

The vertical separation of developmental stages in the water column implies that *Eurythenes gryllus* migrates vertically, at least on an ontogenetic scale. *E. gryllus* is thus responsible for a bidirectional vertical transport of organic matter in and above the benthic boundary layer of the deep-sea. For an estimation of the amount of organic matter transported it would be necessary to obtain quantitative data on the abundance and on population parameters, as growth and mortality, of these scavenging amphipods.

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