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Cases of niche-partitioning and of habitat-segregation in pelagic marine calanoids of the genus *Euchirella* (Crustacea: Copepoda)

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Two cases of apparent niche-partitioning and one case of alleged habitat-segregation in the calanoid copepod genus *Euchirella* are described. These are examined with regard to their possible implications for making generalizations about the structure of biocoenoses and about mechanisms of speciation in the pelagic marine environment.

Introduction

Within the bathypelagic genus *Euchirella* Giesbrecht, 1888 (Crustacea: Copepoda: Calanoida: Aetideidae), some 23 to 25 species are being accommodated currently (Park, 1978; Bradford & Jillett, 1980; Von Vaupel Klein, 1984; 1989; Razouls, 1995; 1996; Markhaseva, 1996). According to the results of a preliminary phylogenetic analysis (Von Vaupel Klein, 1984; confirmed by Koomen & Von Vaupel Klein, unpubl. data) these can be divided into eight distinct species-groups (fig. 1). Differences between groups are clear-cut and involve a series of characters derived from structural morphology, the more obvious among which are, e.g., general shape of the body, relative length of the urosome, presence or absence of a cephalic crest, and, if relevant, the actual shape of such a crest. Next, numerous distinctive details have been established at the level of the external anatomy of the appendages: in all, 42 out of a total of 72 intragenerically variable characters earlier analyzed, appeared to be discriminative at species-group level (cf. Von Vaupel Klein, 1984: 114-115).

Representatives of *Euchirella* are all fast swimming (cf. Clutter & Anraku, 1968), predominantly predatory species with strongly chitinized, robust bodies, seizing and/or holding their prey with their modified maxillipeds (cf., e.g., Anraku & Omori, 1963; Arashkevich, 1969; Bradford & Jillett, 1980; Greene, 1988; and Von Vaupel Klein & Koomen, 1994, for a review). Their sizes (i.e., total body length, excluding the caudal setae) may vary between 2.0 and 9.0 mm (though more commonly from 3.0 to 8.0 mm, cf. Markhaseva, 1996), which means they represent moderately large organisms among pelagic marine calanoids in general.

The species-groups recognized comprise one to six described species each. Within such groups, differences among members mainly pertain to the structures involved in reproduction, i.e., the genital somite in the female along with the spines on the first basipodal segment of her fourth pair of swimming legs, as well as the fifth pair of legs in the male. On the contrary, the overall body shape of the various species in a group appears to be remarkably uniform.

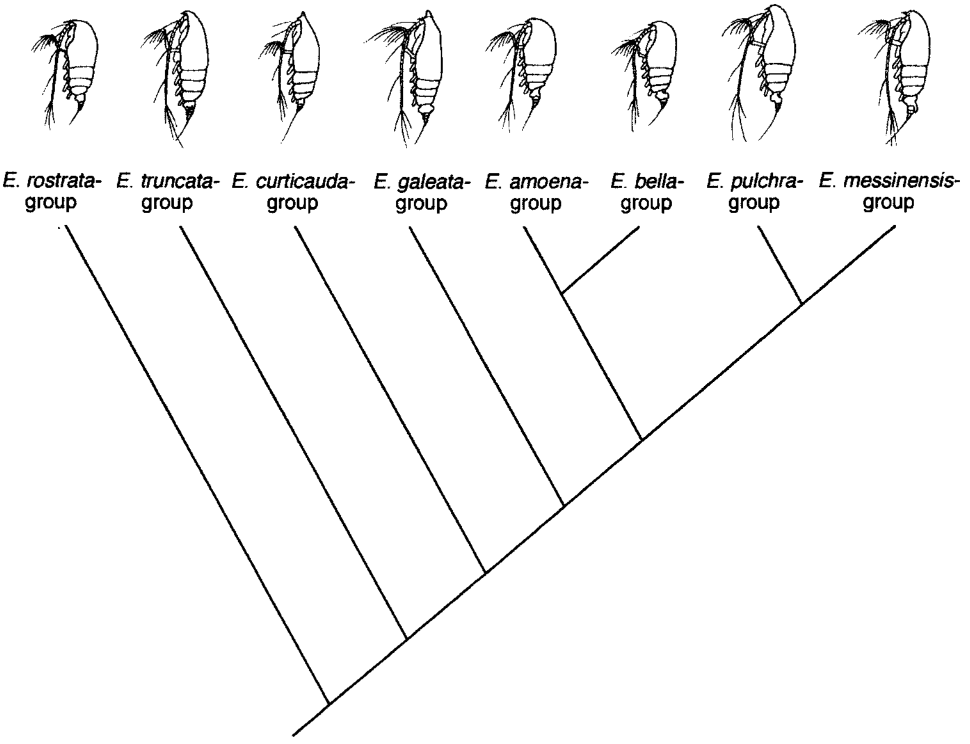


Fig. 1. General body shape of the females and putative phylogenetic relationships among the eight species-groups recognized in *Euchirella* (i.e., the *E. rostrata-*, *E. truncata-*, *E. curticauda-*, *E. galeata-*, *E. amoena-*, *E. bella-*, *E. pulchra-*, and *E. messinensis*-groups). (Modified from Von Vaupel Klein, 1984).

However, in two of the species-groups, i.e., both the *E. curticauda-* and the *E. rostrata*-group, we find cases of species which exhibit overall external appearances that are so similar as to become close to indistinguishable, with the exception only of size. These cases comprise the pair *E. curticauda* Giesbrecht, 1888 versus *E. maxima* Wolfenden, 1905, as well as *E. rostrata* (Claus, 1866) versus the couple *E. latirostris* Farran, 1929 plus *E. rostromagna* Wolfenden, 1911. In another instance, which involves the relationship between *E. latirostris* and *E. rostromagna*, also the body size is virtually equal, but in this case a distinction in the species' respective distributions over the vertical water column may be assumed.

Almost all *Euchirella* species described before 1940 have already been shown to exhibit cosmopolitan distributions or nearly so (cf. Razouls, 1995; 1996; also Von Vaupel Klein, 1984: 31), or at least are distributed circumglobally on the Southern Hemisphere. The species pairs or triplets here under consideration are no exception, implying that in each case a substantial overlap in distributional ranges exists. In view of the largely coinciding areas of *E. curticauda* and *E. maxima* on the one hand, and those of *E. rostrata* vis-à-vis *E. latirostris*/*E. rostromagna*, on the other, two cases of niche-partitioning were surmised already during the initial stages of the taxonomic survey of the genus (cf. Von Vaupel Klein, 1982a; 1982b; 1984; 1992). These contentions have next been examined in the light of the work of Hutchinson (1959), who was the first to make an attempt at quantifying the phenomenon of the (presumably) non-overlapping niches of the species that together make up a biocoenosis. His approach involved determining the actual size of primary structures of the feeding apparatus in the various forms at issue, a feature that consequently has been examined in the present study as well. Likewise, the striking similarity in both body shape and size of *E. rostromagna* and *E. latirostris*, geographically co-occurring in the southern ocean, has been probed under a hypothesis of habitat-segregation.

The concept of niche-partitioning, i.e., the splitting of a single ancestral, ecological niche into two new (hence narrower) niches, was introduced into evolutionary biology and systematics by Maynard Smith (1962; 1966) as an essential component of his classical model of sympatric speciation. The principle would adequately explain the absence of competition, hence the conditions for non-interfering coexistence, in two structurally similar forms.

Habitat-segregation is a concept derived from Mayr's (e.g., 1963) scenario alluding to the micro-geographic variant of dichopatric speciation and explains the geographical co-occurrence of closely related species through the effective separation of their factually relevant, respective habitats.

These phenomena of niche-partitioning and habitat-segregation, which are both allegedly instrumental in mechanisms of speciation, and which are both postulated here to be present in *Euchirella*, have next been investigated within the framework of speciation models as currently conceived (cf. Von Vaupel Klein, 1995: 267-269), with an obvious emphasis on the pelagic realm.

Material and methods

For all five species under consideration, the total body length of adult females had been measured and the ratio cephalothorax/urosome had been determined in the course of previous investigations in a standardized way and based on material from the various collections at the author's disposal (cf. Von Vaupel Klein, 1982a; 1982b; 1984: 38, 40-41, 44-46). To these figures, selected literature data have been added in order to widen the scope of the intended comparisons by taking into account data on a much larger number of specimens, obviously also covering more extensive parts of the species' ranges, than the present material would have permitted (cf. Rose, 1933; Brodskii, 1950; Park, 1978; Bradford & Jillett, 1980) (tables 1, 2).

Three representative length measurements of the maxilliped were taken in order to quantify differences in the dimensions of a primary feeding structure of each species. Figure 2 shows how the parameters selected, i.e., lengths of basipodal segments 1 and 2, and length of the longest seta of the endopodite, have been defined. Measurements were taken using permanent slide mounts of the maxillipeds prepared earlier (cf. Von Vaupel Klein, 1982a; 1984; Koomen & Von Vaupel Klein, 1995). Thus, maxillipeds of the following specimens were microscopically examined and their relevant dimensions determined with the aid of the microscope's drawing tube and a ruler:

Euchirella curticauda: 'Dana' Exped. sta. 4771, specimen no 1, 17.xii.1970 and specimen no 1, 9.viii.1982.

Table 1. Dimensions of adult females of *Euchirella curticauda* Giesbrecht, 1888 and *E. maxima* Wolfenden, 1905, allegedly relevant in niche separation.

	E. curticauda	*E. maxima*	Size-factor
Total body length, range (mm) 1)	2.7 - 4.4 2)	6.5 - 7.4 3)	
Do., mean (mm)	3.55	6.95	1.96
CTh/Ur ratio 4)	6.32	6.14	
Mxp Ba1, length (mm)	0.44	0.87	1.98
Mxp Ba2, length (mm)	0.62	1.07	1.73
Mxp longest seta, length (mm)	0.61	1.28	2.10
Average size-factor Mxp-structures			1.94

1) See Material and Methods.
2) Present collections: 3.45-4.15 mm.
3) Present collections: 6.5-8.05 mm.
4) From Von Vaupel Klein (1984: 93).

Table 2. Dimensions of adult females of *Euchirella rostrata* (Claus, 1866), *E. rostromagna* Wolfenden, 1911, and *E. latirostris* Farran, 1929, presumably relevant in the separation of niches.

	E. rostrata	*E. rostromagna*	*E. latirostris*	Size-factors
Total body length, range (mm) 1)	2.0 - 3.95 2)	5.3 - 6.65 3)	5.3 - 6.05 4)	
Do., mean (mm)	2.975	5.975	5.675	1.96 5)/1.05 6)
CTh/Ur ratio 7)	4.74	4.71	5.06	
Mxp Ba1, length (mm)	0.47	0.80	0.71	1.70 / 1.51 8)
Mxp Ba2, length (mm)	0.54	0.97	0.89	1.80 / 1.65 8)
Mxp longest seta, length (mm)	0.63	1.01	1.13	1.60 / 1.79 8)
Average size-factor Mxp-structures				1.70 / 1.65 8)
Do., larger forms only				1.11 6)

1) See Material and methods.
2) Present collections: 2.7-3.85 mm.
3) Present collections: 5.3-6.2 mm.
4) Present collections: 5.4-6.3 mm.
5) Of *E. rostrata* vs the average of the two larger spp.
6) Of *E. rostromagna* vs *E. latirostris*.
7) From Von Vaupel Klein (1984: 93).
8) Of *E. rostrata* vs *E. rostromagna* and of *E. rostrata* vs *E. latirostris*, respectively.

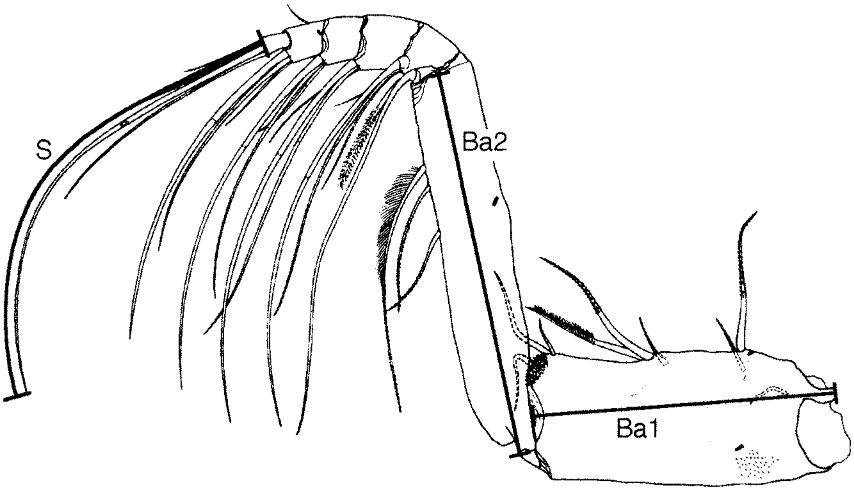


Fig. 2. Measurements taken from maxilliped: Ba1 = length of basipodal segment 1; Ba2 = length of Ba2; S = length of the longest seta of the only ramus, i.e., the endopodite.

E. maxima: 'Dana' Exped. sta. 3683, specimen no 1, 7.i.1971 and specimen no 1, 17.viii.1982.

E. rostrata: 'Dana' Exped. sta. 4771, specimen no 1, 13.i.1971 and specimen no 1, 1.ix.1982; 'Dana' Exped. sta. 4774, specimen no 1, 15.iv.1988, specimen no 1, 18.iv.1988, specimen no 1, 19.iv.1988, specimen no 4, 20.iv.1988, and specimen no 5, 26.iv.1988.

E. latirostris: 'Discovery' Exped. sta. 725, specimen no 1, 17.xi.1972 and specimen no 2, 6.ix.1982; 'Discovery' Exped. [no locality], specimen no 2, 2.ix.1982 and specimen no 1, 3.ix.1982.

E. rostromagna: 'Discovery' Exped. sta. 725, specimen no 1, 6.ix.1982; 'Discovery' Exped. [no locality], specimen no 1, 2.ix.1982, specimen no 1, 3.ix.1982, and specimen no 2, 3.ix.1982 (2 slides).

Geographic ranges have been reconstructed from the work of Razouls (1995; 1996), who has compiled a virtually complete set of literature records of calanoids up to and including 1995/96 from more than 1500 articles.

Data on vertical distribution have primarily been gathered by screening literature reviewing *Euchirella* as a whole or in part (i.e., Vervoort, 1957; 1963; Tanaka & Omori, 1969a; 1969b; Park, 1976; Bradford & Jillett, 1980; Markhaseva, 1996), as far as these reports mention figures of relevance in this respect.

The locality data of the collections at hand (cf. Von Vaupel Klein, 1982a; 1984) have been compared with those published records in order to detect possible discrepancies which were, however, not met with.

Abbreviations used are as follows: C = copepodid; CV = 5th copepodid instar; CVI = 6th copepodid stage = adult; CTh = cephalothorax; Ur = urosome; Gnsom = genital double somite; Mxp = maxilliped; P5 = 5th pair of swimming legs; Ba1, 2 = basipodal segments 1, 2; Ri = endopodite; s = seta.

Results

Fig. 3 shows the habitus of the adult females of *Euchirella curticauda* and *E. maxima*. The general similarity in the shape of the body is obvious: the stout cephalothorax with its strongly depressed cephalic region, the extremely short (hence hardly visible) rostrum, the triangular cephalic crest which comprises a unique, supposedly apomorphic character of the group, and the extraordinarily compressed urosome. The total lengths and the ratios CTh/Ur (cf. Von Vaupel Klein, 1984: 93) are given in table 1: it appears that the CTh/Ur ratio of both species is similar, 6.32 versus 6.14, whereas their total lengths differ by a factor 1.96. Also in table 1, the various measurements taken from the maxillipeds are recorded; these show an average size difference between the two species of a factor 1.94.

The females of *Euchirella rostrata*, *E. rostromagna*, and *E. latirostris* have been depicted in fig. 4. In these species, the cephalothorax is relatively high (and equally wide), looking somewhat inflated, and showing a broadly rounded (i.e., either not at all or only hardly depressed) lateral outline of the cephalic part s.s. A crest is completely absent and the relatively large rostra are quite similar in shape, while the degree of antero-posterior compression of the urosomes is comparable. Total lengths and CTh/Ur ratios (cf. Von Vaupel Klein, 1984: 93) are presented in table 2. The interspecific size discrepancy of *E. rostrata* and the other two forms amounts to a factor 1.96 on the average, that between the two larger species to a factor 1.05. With values of 4.71 to 5.06, the CTh/Ur ratios of this triplet are indeed quite similar and do not deviate appreciably from prevailing conditions in the genus, with its average of 4.23. Comparison of the maxilliped of *E. rostrata* with those of each of the larger species (table 2) reveals differences by a factor 1.65 to 1.70, whereas the distinction between *E. rostromagna* and *E. latirostris* is considerably smaller, measuring a factor 1.11.

Based on the compilations of Razouls (1995; 1996), the geographic distributions of *Euchirella curticauda* and *E. maxima* can be shown to overlap substantially, as is evident from fig. 5. Though less markedly, the same applies to the distribution of *E. rostrata* versus the respective areas occupied by the larger couple from that species-group (fig. 6). These last two forms, then, appear to inhabit grossly sympatric ranges as also recorded in fig. 6, likewise based on data from Razouls (1995, 1996).

The vertical distribution of the five *Euchirella* species, as inferred from the available data, is shown in table 3. In the case of *E. curticauda* and *E. maxima*, actual sympatric occurrence, i.e., sharing of the same bathypelagic habitat between 0 and 3000 m depth with an alleged daytime maximum at 500-1000 m, could in all probability be confirmed. The same applies to the depth range of *E. rostrata* with regard to the two larger species of the *rostrata*-group, which both fall well within the strata usually occupied by the smaller form (i.e., 0-1300 m).

As regards the vertical ranges of *E. rostromagna* and *E. latirostris*, putatively set at 0-500 and 500-1000 m, respectively, actually relevant records are limited by only few authors having made the correct distinction between these closely similar forms. In reality, apart from the original descriptions, of course (cf. Wolfenden, 1911; Farran, 1929), only Vervoort (1957), Bradford & Jillett (1980), and Von Vaupel Klein (1984) seem to have grasped the true identity of these two species. Hence, no previous records can be qualified as reliable in this respect, whereas the recent accounts of Razouls (1994; 1995; 1996), in which the proper distinction is made, give no data on

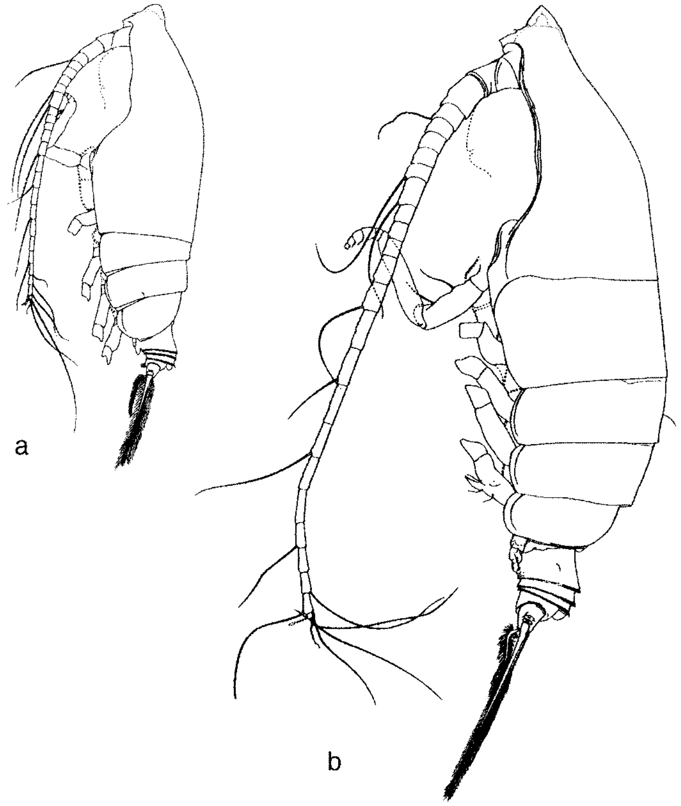


Fig. 3. Left lateral view of adult females of *Euchirella curticauda* Giesbrecht, 1888 (a) and *E. maxima* Wolfenden, 1905 (b), depicted at the same magnification to show similarity in general body shape and proportions as opposed to the obvious difference in size. (The antenna, the mouthparts, the distal segments of the swimming legs, the smaller setae of the antennule, and the setae of the maxilliped have been omitted).

vertical occurrence. Markhaseva (1996: 145) simply excluded this couple from her review of *Euchirella*, stating that they "may be identical".

This obviously means that the scanty records available have as yet to be qualified as insufficient to firmly establish the effective distinctness of the vertical ranges of *E. rostromagna* and *E. latirostris*.

Discussion

Copepods of the genus *Euchirella* have been shown to live on a mixed diet with a prevailing raptorial component (for references, see Introduction). They allegedly prey chiefly on the notably sluggish, herbivorous species of calanoids with which they share the pelagic zone. The choice of the adult female to investigate structures used in feeding is obvious, considering that this sex (CVI♀) and the (undifferentiated) fifth copepodid instar together constitute the main feeding stages, the adult males (CVI♂)

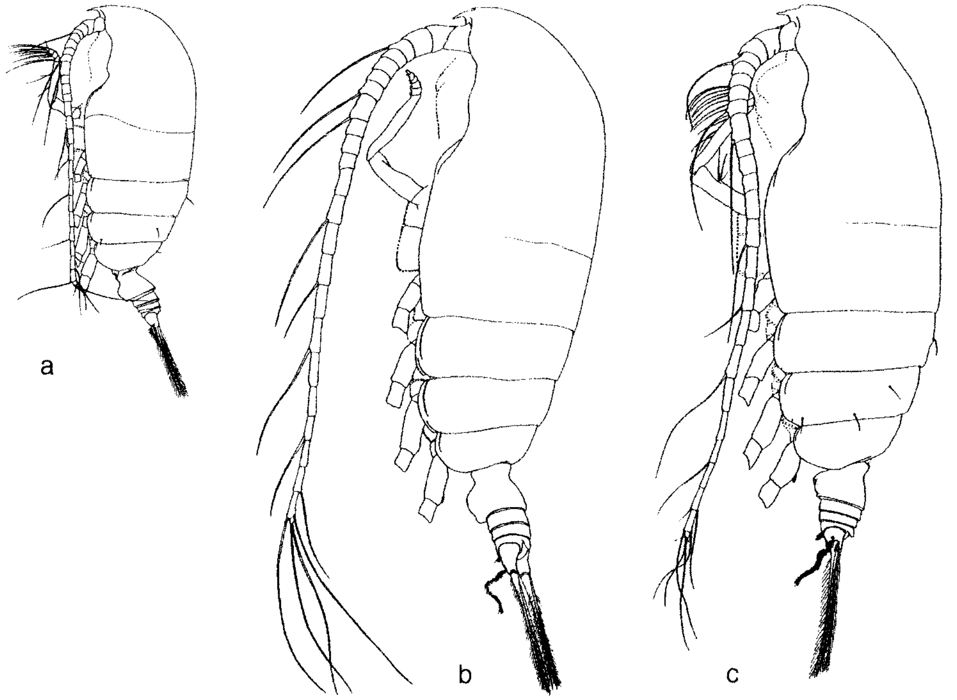


Fig. 4. Left lateral view of adult females of *Euchirella rostrata* (Claus, 1866) (a), *E. rostromagna* Wolfenden, 1911 (b), and *E. latirostris* Farran, 1929 (c). All specimens depicted at the same magnification, which clearly emphasizes the similarity in body shape and proportions versus the difference in size between *E. rostrata* and the other two species. (The antenna, the mouthparts, the distal segments of the swimming legs, and the smaller setae of the antennule have been omitted, just as, in the middle figure, the setae of the maxilliped; though in the other two species the more obvious maxillipedal setae are shown, this has no specific purpose in the present context).

having no functional mouthparts any longer. As in the majority of calanoids, the morphology of the CV is as yet hardly documented, whereas adequate descriptions of the females exist.

The total length ranges as derived from the larger review works consulted herein comprise less extreme values than are sometimes reported in the primary literature. This takes its origin from the fact that use has been made of the mean value of length ranges given in review works. These, viz., are based on large numbers of specimens from wide geographic ranges and may be supposed to take into account all previous primary literature. Hence, those data were considered fairly representative as a proxy for an actual, calculated average from direct observations, contrary to just taking the mean of the very extremes from individual accounts on specific collections of limited scope. Thus, the 'average' length values mentioned here are considered to give an adequate estimate of the actual differences in body size of the species under consideration.

The general observation that interspecific size-differences are instrumental in con-

Table 3. Inferred depth ranges of the *Euchirella* species under consideration, based on literature data [1]).

	Vertical range (m depth)
E. curticauda Giesbrecht, 1888	0-3000 (with a maximum density at 500-1000) [2])
E. maxima Wolfenden, 1905	0-3000 [3])
E. rostrata (Claus, 1866)	0-1300 [4])
E. rostromagna Wolfenden, 1911	0-500 [5])
E. latirostris Farran, 1929	500-1000 [6])

[1]) Since literature records are not consistently informative with regard to the time of day of collecting, the data compiled have tentatively been interpreted as daytime values unless stated otherwise. Most probably, though, the upper 100 or 200 m should be excluded from the range of occurrence during the day, while most if not all species are known to ascend to the surface layer (i.e., 0-100 or 0-200 m depth) at night.

[2]) Compiled from Tanaka & Omori, 1969a; Park, 1976; Bradford & Jillett, 1980; Markhaseva, 1996.

[3]) Compiled from Vervoort, 1963; Tanaka & Omori, 1969a; 1969b; Park, 1976; Bradford & Jillett, 1980.

[4]) Compiled from Vervoort, 1957; Tanaka & Omori, 1969a; Park, 1976; Bradford & Jillett, 1980; Markhaseva, 1996.

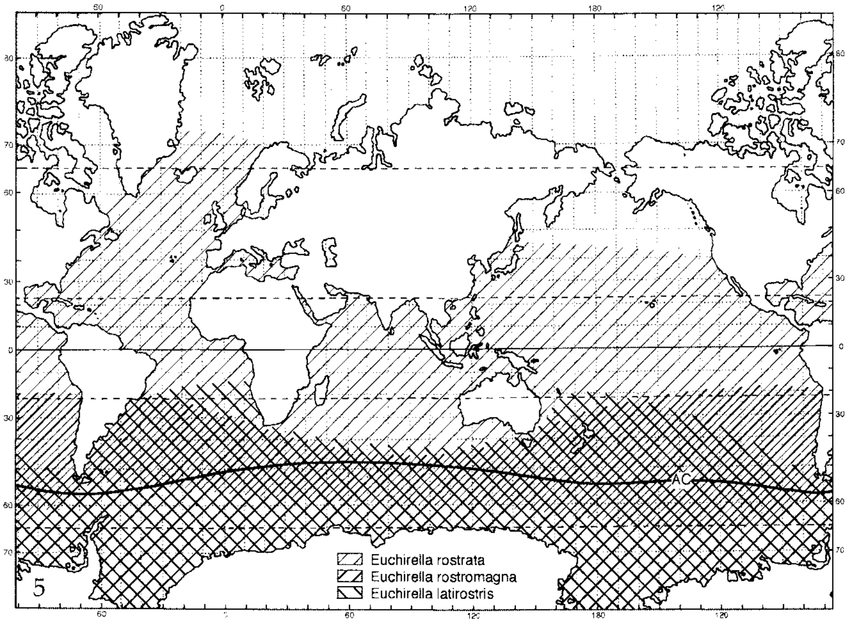
[5]) Compiled from Vervoort, 1957; Bradford & Jillett, 1980 [records by Wolfenden (1911: 235-236) and Farran (1929: 236-237) are not in contradiction].

[6]) Compiled from Vervoort, 1957; Bradford & Jillett, 1980 [though described by Farran (1929: 234-236) from a horizontal haul at 80m depth, time of day or night not stated].

solidating (arrays of) niches in a biocoenosis has since long been made for aquatic communities, even with an emphasis on small crustaceans, and notably on copepods (cf. Hutchinson, 1951). The same principle has recently been recognized in various terrestrial invertebrate assemblages as well (cf., e.g., Minelli & Foddai, 1997). The fact that also intraspecific variation in body dimensions is found in, i.a., neritic marine copepods occurring in (temporal or spatial sequences of) more finely structured habitats, underlines the importance of an adequate body size for properly performing a given role in a biotic community (cf. Steuer, 1923; Myers & Runge, 1987; Runge & Myers, 1987; Pessotti et al., 1987).

To consider the size of food gathering or -processing attributes in determining possible distinctness of niches has been based on the work of Hutchinson (1959), who studied species of higher vertebrates, i.e., birds and mammals. According to his survey, differences at the specific level between the trophic structures of adult organisms can be described by a factor 1.1 to 1.4, with an average of 1.28. This applies if (a) the species at issue are closely related, i.e., congeneric, (b) have a similar morphology, and (c) are occurring sympatrically. In other words: if they would be (i.e., at least in our opinion) potential competitors for (food) resources within the same biocoenosis.

Although Hutchinson's (1959) conslusions have been rebutted by Simberloff & Boecklen (1981), their critique mainly regarded the statistical aspect of his methods as well as the simple, single factor that author presented as his result. On their turn, however, those conclusions have been shown to be unwarranted by Losos et al. (1989), who pointed out that with a more sophisticated mathematical approach many Hutchinsonian ratios as reported in the literature match the raw data very well, and significantly so. Hutchinson's (1959) methods thus have subsequently been followed



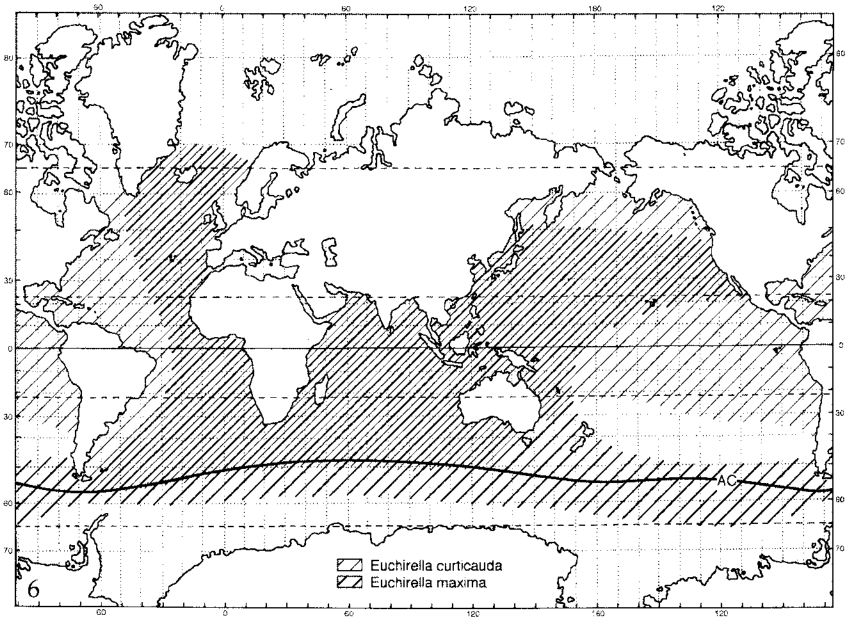


Fig. 5. Map showing the distributional areas of *Euchirella curticauda* Giesbrecht, 1888 and *E. maxima* Wolfenden, 1905, respectively; note the large overlap in ranges; AC = Antarctic Convergence (composed after data from Razouls, 1995; 1996).

Fig. 6. Map showing the distributional areas of *Euchirella rostrata* (Claus, 1866), *E. rostromagna* Wolfenden, 1911, and *E. latirostris* Farran, 1929, respectively; note the considerable overlap in range of *E. rostrata* and the other two species which, in their turn, are virtually coinciding in a strictly geographic sense; AC = Antarctic Convergence (composed after data from Razouls, 1995; 1996).

(and successfully applied) by a wide range of ecologists within an equally wide range of specific conditions involving grossly different taxa of vertebrates (for references see Simberloff & Boecklen, 1981; Losos et al., 1989). Furthermore, according to general ecological principles that are widely adhered to (cf., e.g., Odum, 1959), there can be no doubt that every species has its own niche (i.e., at least one, cf. Von Vaupel Klein, 1984: 156- 157; in fact every semaphoront is due to fill its own niche in the ecosystem it forms part of). Also, the observation that the acquisition, handling, and ingestion of food makes up an important aspect of a species' niche can hardly be surprising: next to shelter and breeding sites (or, more generally, the opportunity to successfully reproduce), food prominently figures among the chief requirements for any organism to maintain a viable population within an ecological community. Then, if two species share the same area and habitat, in other words, are components of the same biocoenosis, *and* show hardly different shapes but differ decidedly in size, the conclusion that their apparently unhampered coexistence must be based on differences in the size of their nourishment, of which the dimensions of their feeding structures would bear witness, seems fully justified. As regards the size factor determined by Hutchinson (1959), the actual value of it might not be completely universal, but the fact that such a factor (a) does constitute a real feature of ecological relationships among congeners, and (b) has a fairly constant value among comparable organisms in comparable communities, may firmly be rooted in the competitive exclusion principle of Hardin (1960). Hence, this supposition has found wide recognition and has thus been generally adopted, both within ecology (cf., e.g., Owen-Smith, 1985, for various groups of African ungulates) as well as beyond, i.e., in evolutionary biology (cf., e.g., Stanley, 1975: 57).

So far, this aspect of congeneric coexistence has not been investigated in marine invertebrates, but on the analogy of having been established in the terrestrial vertebrate communities investigated, its existence in the pelagic marine environment may well be expected. Besides, if we do not try to determine its value, the existence of the factor as such in the pelagic marine realm will never be discovered. Thus, the present observations are meant to provide the first data in the quest for (the value of) a niche-discriminating size factor in the pelagic environment. The size-factors found, ranging between 1.60 and 2.10 (with average values of 1.65-1.96, tables 1-2) are well above the 1.28 established by Hutchinson (1959), which may be surmised to constitute an intrinsic characteristic of the biocoenosis here under consideration.

To represent the actual size of the feeding structures of the organisms at issue, that of the maxillipeds may be considered a relevant dimension since aetideid (and also euchaetid) copepods use their maxillipeds, which are remarkably modified as compared to those in other families of calanoids, for seizing and/or holding prey (cf. Von Vaupel Klein, 1982b; Von Vaupel Klein & Koomen, 1994, and references cited therein). This implies that these appendages can provide appropriate parameters for detecting differences in performance of catching food items of different size ranges, hence for defining the nutritional aspect of a species' niche.

Thus, the mere fact that such differences are found between two phylogenetically closely related species sharing the same biocoenosis, may well be interpreted as strong evidence in favour of a case of niche-partitioning. This becomes the more convincing if one realizes that the plankton communities under consideration are known to comprise close to a hundred species of calanoids alone, which, each with 12 distinct feeding stages, will thus account for an odd 1200 niches already (cf. also Von Vaupel Klein, 1984: 155-157). Among them are invariably at least 20-30 species of *Euchirella* and *Pseudochirella*, and/or *Euchaeta* or *Paraeuchaeta* present, which organisms represent a trophic level of larger, predatory forms. This inevitably evokes the assumption that apparently the subdivision of prey organisms, hence also the specialization among predators, must be extremely finely graded in an ecological sense (cf. also Mullin, 1967). Then, taking into account the differences measured between *E. curticauda* and *E. maxima* on the one hand, and those between *E. rostrata* and *E. rostromagna*/*E. latirostris* on the other (cf. tables 1-2), it seems justified to interpret both relationships as comprising the results of processes of niche-partitioning. With the emergence of two new species from a single ancestral form, the original niche of that ancestor has apparently been split up among the two daughter species, through their difference in size, warranting a minimum of competition between the two new forms which thus presumably hunt for similar organisms that fall, however, into distinctive size categories.

The assumption that food items for the larger and the smaller species in a pairwise comparison would be similar but differ in size, is further supported by comparing the lengths of the various structures of the maxillipeds in a relative sense. In *E. curticauda*, Ba1 : Ba2 : largest seta as 26 + 37 + 37 = 100, while in *E. maxima* as 27 + 33 + 40 = 100. Likewise, in *E. rostrata* these values were determined at 29 + 33 + 38 = 100, as compared to 29 + 35 + 36 = 100 in *E. rostromagna* and 26 + 33 + 41 = 100 in *E. latirostris*. In each case, there appears to be no basis to suppose, within one group, any large discrepancies in the qualitative features of the prey involved. Comparison between species-groups seems unwarranted, given the distinctness in shape of the body as outlined above. Admittedly, the data here presented are interpreted under the premise that the behaviour of the members of a group is not fundamentally different, for the availability of any particular attribute may be of importance as such, its effective functioning depends on the manner in which it is used by the organism (cf., e.g., Marcotte, 1984). However, behavioural aspects of the ecology of *Euchirella* spp. are as yet largely unknown and even, at present, virtually inaccessible in view of the species' bathypelagic way of life.

As regards the situation observed in *E. rostromagna* and *E. latirostris*, which despite their closely similar morphology and size occur largely sympatrically, the partitioning of niches does not seem probable. Although subtle anatomical differences exist, the most conspicuous one involving the density of the setules on the large setae of the antenna (cf. Von Vaupel Klein, 1984: 45-46, pl. 1a, b), the small differences in feeding structures are not indicative of the two species occupying distinct niches. On the other hand, the available data would indicate (cf. table 3) that these species, with practically coinciding horizontal distributions, may well be separated in a vertical sense. Where *E. rostromagna* can be found at depths ranging from 0 to 500 m, *E. latirostris* appears to inhabit the deeper strata between 500 and 1000 m. In this case, then, it would appear that the phenomenon of habitat-segregation is at issue: two closely related species inhabiting the same geographical range but avoiding contact by actually living in separate zones of the water column. As far as the present data allow, this situation may be contrasted to the usually much wider vertical ranges of the other species of the genus, among which *E. curticauda*, *E. maxima*, and *E. rostrata*, which have been found over stretches of well over 1000 m, anywhere between the surface and 3000 metres of depth (cf. table 3). Yet, in view of the still undecisive data, it should be pointed out with some emphasis that an ecological separation between two sibling species, involving a qualitative type of nutritional specialization, is not to be precluded, if the assumption of distinction over the vertical would prove to be false after all.

The actual effectiveness of a spatial separation of species by the simple distinctness of their (daytime) depth ranges as here postulated would not seem improbable. A comparable subtlety in differences between (physical parameters of) the microhabitats of sibling species has been documented by Bergmans & Janssens (1988) for brackish water harpacticoid copepods in neritic biotopes. Likewise, De Meester (1994) demonstrated that inhabiting vertically distinct ranges may constitute an effective means to separate distinct clones of cladocerans (e.g., of *Daphnia* spp.).

With respect to the biological meaning of such a stratification of habitats, however, it should be noted that avoiding contact does not necessarily imply avoiding competition. If the environment is homogeneous in relation to the euphotic zone, the organisms still compete for the same food, as has been pointed out by De Meester (1994). This applies, of course, primarily to herbivorous species, but the effect on carnivores is directly dependent on the resulting (homo- or heterogeneity of) distribution of those primary grazers and detritivores preyed upon.

Euchirella curticauda and *E. maxima* would thus bear testimony of an event of niche-partitioning in the past, as would *E. rostrata* considered opposite the couple *E. rostromagna*/*E. latirostris*. Obviously, detailed data would be required to assess to what extent the mechanism of character displacement (cf. Brown & Wilson, 1956) still influences today's picture, viz., by comparing the dimensions of specimens of each of these species collected in regions of overlap, with material originating from areas in which the species is the sole representative of its (species-)group (i.e., as far as relevant: relatively few zones of exclusive occurrence are known at present, cf. figs 5-6).

As regards the speciation mechanisms involved, to recognize niche-partitioning as such is insufficient to identify with due certainty the mode of speciation that has acted in the past. Out of the six to eight (sub-)modes currently acknowledged (table 4) (cf. also Von Vaupel Klein, 1984; 1994; 1995; in- or excluding microgeographic and alloparapatric speciation as separate models, cf. Mayr, 1963; Endler, 1977; Wiley, 1981: 54-55; Brooks & McLennan, 1991: 100- 102), three require niche-partitioning (i.e., both parapatric models and the classical mode of sympatric speciation), while in stasipatric speciation this would seem favourable. On the contrary, the scenarios of the macro- and the microgeographic modes (subdividing the model of dichopatric speciation) as well as the peripatric model, are allegedly neutral with regard to this aspect, though upon resumed contact following the completion of speciation the new species may well differentiate further through the action of character displacement. Niche-partitioning definitely does not fit within the scenario of Bush's (1975b) submodel of the sympatric mode.

Habitat-segregation, on the contrary, constitutes an indispensable prerequisite for this last-mentioned variant of sympatric speciation (cf. Bush, 1975b) just as well as for the microgeographic model, while, again, also this phenomenon would seem optional (and then favourable) among the processes involved in a stasipatric event. Here, too, various models seem to be indifferent in this respect (i.e., the macrogeographic variant of dichopatric speciation as well as the peripatric mode), whereas habitat-segregation would decidedly not fit the parapatric models nor the classical sympatric submode (table 4).

In most groups of *Euchirella*, speciation seems to be intimately connected with Reproductive Isolating Mechanisms (RIM's, cf. Bush, 1975a; or, for that matter, with Specific Mate Recognition Systems or SMRS's, cf. Paterson, e.g., 1985) involving the (secondary) reproductive organs, i.e., the Gnsom of the female in conjunction with the male's P5 and/or with the coupler of the spermatophore (cf., e.g., Fleminger, 1967; 1975; Fleminger & Hulsemann, 1974; Ferrari, 1978; Von Vaupel Klein, 1982b: 72-84). However, this aspect seems less relevant in the *E. rostrata*-group, in which the females all have smooth, symmetrical genital somites. The situation in the *E. curticauda*-group is almost similar. Here, the asymmetry found in *E. maxima* is only slight compared to that in most other species-groups (cf. Von Vaupel Klein, 1982b; 1984). However, size differences (of almost a factor 2) alone may well account for the existence of an effective RIM already, whence reproductive isolation might at least be assumed to have evolved concurrently with the separation of the niches. Viewed the other way around, a simultaneous progress in both niche-partitioning and (the reproductive aspects of) speciation would even seem imperative given the observation by Paterson (1985: 28) that species, once established, constitute rather stable units, their ecological niches included. This obviously implies that the actual divergence process would provide the best (if not only) opportunity to effectuate such changes, whence a shift in niche(s) and the development of RIM's would have to be closely intertwined by necessity.

Habitat-segregation, as inferred for *E. latirostris* and *E. rostromagna*, obviously has a comparable effect: in the absence of actual encounters, mechanical isolation by differences in secondary reproductive structures will have no selective value, meaning the Gnsom's can 'afford' to be similar. The aforegoing reasoning, of course, entirely departs from a mechanical point of view, thus disregarding possible chemical and/or (subtle) tactile cues which may well be of influence in the actual mating process but on which there are no data available as yet.

In view of the above, though having ruled out various specific modes of speciation to match the three separate cases investigated, multiple possibilities still remain: something which obviously prevents an unequivocal conclusion to be drawn. Evidently, more data will have to be incorporated in order to allow anything of a firm conclusion about the mechanism(s) involved, especially if speciation mechanisms throughout the entire genus are to be considered. Among these are, obviously, detailed data on both recent and past distribution patterns of the species within a framework of palaeogeographic conditions, unambiguous figures on vertical ranges, as well as a precise knowledge of morphology and reproductive isolating mechanisms: all this to be structured within a fully resolved phylogeny.

In view of the alleged uniformity of the pelagic realm, a relatively high incidence of sympatric and stasipatric mechanisms has often been assumed in the past, such in contrast to the conditions in neritic habitats (cf., e.g., Battaglia, 1982). However, the observation that, with the exception of the macrogeographic mode (cf. Von Vaupel

Table 4. Modes of animal speciation recognized herein. [1]

Speciation model	Submodels	Niche-partitioning	Habitat-segregation
Dichopatric [2]	Macrogeographic	o	o
	Microgeographic	o	+
Peripatric [3]		o	o
Parapatric	Parapatric s.s. [4]	+	-
	Alloparapatric [5]	+	-
Sympatric	classical [6]	+	-
	Bush's variant [7]	-	+
Stasipatric [8]		(+)	(+)

+ = involved; - = not involved; (+) = optional; o = not relevant.

[1] cf. Bush (1975a), White (1978), Wiley (1981), Cracraft (1984), Brooks & McLennan (1991), Minelli (1993); also Von Vaupel Klein (1984; 1994; 1995).
[2] cf. Mayr (1963), Cracraft (1984).
[3] cf. Mayr (1954), Cracraft (1984).
[4] cf. Smith (1955; 1965; 1969), Endler (1977).
[5] cf. Key (1968), Endler (1977).
[6] cf. Maynard Smith (1962; 1966).
[7] cf. Bush (1975b).
[8] cf. White (1968; 1978).

Klein, 1984: 155-157), all models would seem suited to account for speciation events in the marine pelagial, decidedly precludes making suppositions involving a quantitative preponderance of any (sub-)mode of speciation at the moment.

Conclusion

Apparently, niche-partitioning in *Euchirella* may be brought about, or at least maintained, by size-differences in the maxillipeds ranging between 1.65 and 1.94. Similarly, it seems probable that effective segregation of habitats may be achieved by dividing a vertical range of 1000+ metres into zones of c. 500 m, the boundary layer between which may provisionally be assessed at c. 50-100 m given the general accuracy of (vertically closing) collecting gear and measurements of actual fishing depth.

In conclusion, what has been shown here is that both the phenomena of niche-partitioning and of habitat-segregation may be considered real, i.e., to adequately describe natural relationships among organisms that exist in the real world, also in the realm of pelagic marine plankters. The closely similar morphology, the differences in size, and the co-occurrence in a geographical sense of one pair and one triplet of species from the genus *Euchirella,* all can be satisfactorily understood with reference to those two evolutionary phenomena. These observations qualify, in other words, among the first and foremost prerequisites necessary in beginning to understand evolution, and in particular speciation, in the pelagic marine environment.

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I take great pleasure in dedicating this study to my mentor in copepodology, Prof. Dr. W. Vervoort, Emeritus Professor of Systematic Zoology at Leiden University and former Curator Coelenterata et al., as well as Director of the Leiden Museum, by that time still known as Rijksmuseum van Natuurlijke Historie, on the occasion of his 80th birthday on the 12th of June, 1997.

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