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DISTRIBUTION AND VARIATION OF CARINARIIDAE AND PTEROTRACHEIDAE (HETEROPODA, GASTROPODA) OF THE AMSTERDAM MID NORTH ATLANTIC PLANKTON EXPEDITION 1980*

TRUDIE PAFORT-VAN IERSEL

Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam, P.O. Box 20125, 1000 HC Amsterdam, The Netherlands

ABSTRACT

Species of the heteropod families Carinariidae and Pterotracheidae collected in the Mid North Atlantic Ocean in 1980 have been studied. The distribution of the species is given, as well as the morphological variation. It is concluded that two subspecies of *Carinaria lamarcki* actually have to be considered distinctly recognisable and sympatric species, to be called *C. lamarcki* and *C. challengeri*. The vertical distribution of the heteropods studied proves not to be restricted to the photic zone and diurnal vertical migration occurs among the larger species. The horizontal distribution of the two *Carinaria* species and of at least two populations of the *Pterotrachea* species coincides with the southern branch of the North Atlantic Current, while others are restricted to the subtropical waters. Consequently, the present heteropods have to be considered good indicators of water masses and currents.

INTRODUCTION

The present study deals with the systematics and distribution of the heteropod families Carinariidae and Pterotracheidae from the Mid North Atlantic Ocean. During the 'Amsterdam Mid North Atlantic Plankton Expedition' in the spring of 1980 (April 11-May 2) specimens of these families have been collected on board the research vessel H.M.S. 'Tydeman'. The area sampled extends from 55°N to 25°N along approximately 30°W longitude. Most specimens have been collected by discrete depth hauls between approximately 50m and 1000m depth with a combined Rectangular Midwater Trawl (RMT1 + 8). In addition, specimens have been caught in the upper 150m with open nets.

The North Atlantic has been investigated thoroughly for various planktonic taxa, especially in its western and eastern areas. The Mid North Atlantic, however, has been less exhaustively studied and the heteropod families Carinariidae and Pterotracheidae from this region are still fragmentarily known. The other heteropod family, the Atlantidae, has been studied more extensively, although identification to the species level is often difficult, due to small differences between related species (Richter, 1961; Tokioka, 1961; Van der Spoel, 1972; Thiriot-Quiévreux, 1973). For this

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reason, and because of the small numbers of Atlantidae specimens collected, this family has been excluded from the present study. A survey of the Carinariidae and Pterotracheidae is to be found in Van der Spoel's manual (1976). His data are based on the material sampled in the past century by various expeditions, among which some to the Atlantic Ocean. Important contributions have been made by the 'Campagnes des Yachts Hirondelle et Princesse-Alice' 1885-1903 (Vayssière, 1903, 1904, 1913), the 'Michael Sars' North Atlantic Deep-Sea Expedition 1910 (Bonnevie, 1920) and the Dana expeditions (Tesch, 1906). From these collections a number of species have been described rather incompletely, in most cases the descriptions were based on only one, sometimes heavily damaged, specimen. Consequently, there has always been much confusion about the systematics within the heteropods, which has also affected the knowledge on their distribution patterns.

An advantage of the present material is the fact that the samples have all been collected in a similar way, at small geographical intervals, along a distinct north-south stretch and within a short period of time. In this way, the possibility of comparing different samples considerably improved, so that remaining taxonomical problems could be tackled and an accurate distribution picture for this part of the ocean — horizontally as well as vertically — was obtained. This resulted in another interpretation of the taxonomical rank of two taxa of the genus *Carinaria*. Secondly, fishing at different discrete depths at each station provided an image of the vertical distribution of the heteropods which proves to deviate from the general opinion in the literature that the species occupy an epipelagic habitat. Finally, the series of stations along the 30°W longtitude yields information on the north-south distribution and on faunal boundaries between 40°-45°N. Heteropods are active swimmers and solitarily living prey-hunters. This might cause a high degree of gene-flow in the group, which should consequently result in a low speciation rate, while morphological variation within a population will be limited (Van der Spoel, 1972, 1976). In contrast with the heteropods, the passively moving pteropods are represented in the North Atlantic by a great number of species, some of which show morphological variation with northern and southern formae (sensu Van der Spoel, 1971). These species show a clinal north-south variation whereby the transition of the northern forma in to the southern forma coincides with the transition between different water masses (Pafort-van Iersel, 1982). In this paper it is studied whether the heteropods of the present collection, notwithstanding their strong mobility, show morphological variation. Besides, it is attempted to correlate the distribution patterns of the different species and their distinguishable populations with the different water masses characteristic of the 30°W longitude between 55°N and 25°N.

MATERIAL AND METHODS

The material studied has been collected with the combined opening and closing Rectangular Midwater trawl (RMT 1 + 8) developed by the Institute of Oceanographic Sciences (Godalming, Great Britain), an open Rectangular Midwater Trawl (RO1) and an open Ringnet (RNO). For a full description of construction and behaviour of the Rectangular nets the reader is referred to Baker et al. (1973), Roe et al. (1980) and Van der Spoel (1981). The open Ringnet has been designed for this expedition and has a circular mouth opening of 0.78 m^2. For further details on this net the reader is referred to Van der Spoel (1981). In principle, the following layers have been sampled at fifteen stations with the RMT1 + 8 net: 50-100 m, 100-200 m, 200-300 m, 300-400 m, 400-500 m, 500-1000 m depth. In addition to these hauls, open net hauls have been made with the RO1 in the upper 150 metres and with the Ringnet in the upper 50 metres. For information on the stations, hauls and environmental conditions, the reader is referred to Van der Spoel (1981).

The majority of the Carinariidae and Pterotracheidae specimens have been fixed with formalin 2% with sea-water and preserved in propylene-phenocetol — propylene-glycol according to Heyman (1981). Sometimes the preservation was carried out with formalin 2%. Only a few Carinariidae specimens have been fixed and preserved in alcohol 70%, which is a good method for preserving the shells, but causes a strong contraction of the soft bodyparts.

As the layers sampled varied considerably in thickness (50 m-500 m), it is not simple to estimate the concentration of specimens in the upper 1000 m. The actual numbers of each haul, however, have been converted into standard numbers, related to a fixed amount of 24,000 m^3 water filtered. The standard numbers for the different hauls can be compared with each other, also when different sampling times are involved, thus providing an impression of the abundance. For each species standard numbers are given. To exclude special effects of mesh size and net size on filtering and net avoidance, only the standard numbers of the large 8 m^2 net samples have been used for the abundance data. The formula for calculating standard numbers for the RMT8 is (3 × number of specimens)/(distance sampled). The factor three has been introduced as the distance sampled averaged three kilometres, so the standard numbers are as close to the actual ones as possible. The distance sampled has been calculated from direct flow measurements. Flow through the net, depth of the net and ship speed were such that the mean angle of the mouth of the net hardly influenced the amount of water filtered and no special corrections seem necessary (cf. Roe et al., 1980).

In Carinariidae and Pterotracheidae specimens the body is soft and only in Carinariidae is the visceral mass surrounded by a shell. The study of morphological variation of soft-bodied planktonic animals is always difficult. The lack of rigidity restricts the number of characters suitable for such a study. The method of fixation and preservation applied for the present material, prevents strong contraction of the body as much as possible. However, the shells of the Carinariidae specimens had dissolved or fallen apart in most cases and cannot be used for further study. The body of Carinariidae and Pterotracheidae is slightly curved in living specimens, the swimming-fin is directed upwards and the visceral mass points downwards (fig.1). Hence Van der Spoel (1976) considered the position of the fin dorsal and of the visceral mass ventral, whereas other authors considered the position of the fin ventral and of the visceral mass dorsal. There are at least two arguments which support the last supposition. In heteropods, as in all mesogastropods, the pedal ganglia are situated ventrally, innervating the footmuscles and skin (Borradaile, 1963; Bullock, 1965). As in the heteropods these ganglia are found at the base of the swimming-fin, the fin must anatomically be a ventral organ. Secondly, in phylogeny, the swimming-fin has developed from the creeping parts of the gastropod foot, which is also situated ventrally (Tesch, 1907). The dissentient opinion of Van der Spoel created some confusion as the interchange of dorsal and ventral entails the interchange of right and left. For instance, with the treatment of the systematics of *Carinaria* below (Results), some problems arose, due to confusion in the literature about the differences in the length of the right and left tentacles.

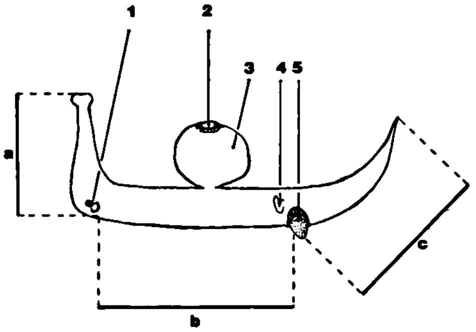

Fig. 1. Diagram of the measurements taken from heteropods: a—snout-length; b - trunk-length; c - tail-length (1 - eye; 2 - fin-sucker; 3 - swimming-fin; 4 - penis; 5 - visceral mass).

The total length of the specimens is hard to measure because of the curved shape of the body. For this reason the length of the body has been measured in three parts (fig.1). The head (a), measured from the tip of the proboscis up to and including the eyes; the trunk (b), measured from the eyes up to the base of the visceral mass; and the tail (c) measured from the base of the visceral mass up to the tip of the tail. These measurements have been taken for all specimens, except for the damaged ones. For the study of morphological variation, the length of the trunk (b) served as a basis for the total length of the animals. In this way, specimens with damaged probosces or tails, of which there were many, do not have to be excluded.

In a number of cases specimens from deep hauls differ in mean length from those in shallow hauls, and sometimes differences in length between the sexes is noticed. To examine whether the differences in dimensions are significant, the data are tested with Student's t-test using a significance-level of 95% ($\alpha = .05$). For convenience, the reader is referred to Sokal & Rohlf (1969) for a description of the test. In all cases, the variances are homogeneous according to their frequency-distribution (F-test), which is a condition for employing the t-test.

For two species (*P. scutata* and *P. coronata*) the latitudinal variation in trunk length led to the theory that the horizontal area has to be divided into two areas each with its own population. To examine this hypothesis, analyses of variance have been carried out. In principle, with these analyses the hypothesis is tested whether two or more sample-means could have been obtained from populations with the same parametric mean with respect to a given variable (e.g. trunk-length), or that the means differ from each other to such an extent that it has to be assumed they have been sampled from different populations. The fact that the two supposed groups are composed of several sub-groups (stations) with unequal numbers, complicates the statistical computations, consequently an analysis of variance of the type 'two-level nested anova with unequal sample-size' has to be applied. There are two important conditions that have to be fulfilled before one can carry out any analysis of variance. Firstly, the data per subgroup have to be normally distributed. A graphical method is sufficient to test for normality (e.g. Rankits). Secondly, the variances per subgroup have to be homogeneous. This condition is tested with Bartlett's test for homogeneity of variances.

For a copious description of the above mentioned methods the reader is referred to Sokal & Rohlf (1969).

If the conditions are not fully met, an analysis of variance is still possible. Glaser (1978) suggests that in such cases the F-statistic should be compared with a F-value belonging to a higher significance-level, in order that the real significance-level remain approximately 95% (real $\alpha \leq .05$).

RESULTS

A short description is given for the species collected, for a full taxonomic treatment of the species the reader is referred to Van der Spoel (1976), Tesch (1949) and Bonnevie (1920). Details are discussed when the present data constituted a deviation of or an amplification on existing ideas. The vertical and latitudinal distribution patterns are described for each species and compared with corresponding data given by Van der Spoel (1976). Finally, attention is paid to morphological variation in relation to vertical and horizontal distributions and sex.

FAMILY CARINARIIDAE

Carinaria lamarcki Peron & Lesueur, 1810 forma **lamarcki** Peron & Lesueur, 1810 and forma **challengeri** Bonnevie, 1920 (fig. 2a and 2b).

Among the *Carinaria lamarcki* specimens two formae (sensu Van der Spoel, 1971) have been distinguished: forma *lamarcki* and forma *challengeri*. In the present material *C. lamarcki* forma *lamarcki* reaches a maximum total body length of 115mm. The mean dimensions of head, trunk and tail are given in table 1. They are firmly built animals with broad pyramidally

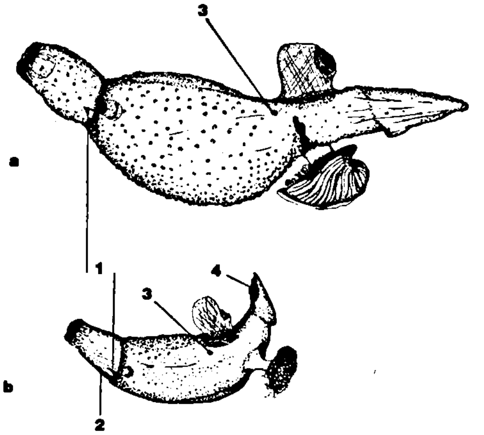

Fig. 2. *Carinaria lamarcki* a - forma *lamarcki* (♂, Station 16, ZMA no 5496, × 1); b - forma *challengeri* (♀, Station 18, ZMA no 6004, × 1) 1 - right tentacle; 2 - left tentacle; 3 -pedal ganglia; 4 - clasper.

shaped keeled shells covering the visceral mass. The trunk is surrounded by a thick cutis beset with numerous tubercles all over its surface. In young specimens the cutis is thinner and the tubercles are less strongly developed, which provides them with a more delicate appearance. The eyes are hard to study as they are hidden by the edge of the cutis at the transition of trunk and proboscis. In the dorsally keeled tail several ramifying muscle bundles are present. The ventral swimming-fin has a distinct muscle pattern of fibres running in two directions obliquely from the base to its border. The fin possesses a sucker in both sexes, in front of the fin-base the pedal ganglia are found. In males the penis is firmly built and recognisable even in the smallest specimens. In most animals two cephalic tentacles are present of which the left one is the largest. Only in a few cases could the right tentacle not be detected (fig. 2a). This agrees with descriptions by authors such as Tesch (1949) and Okutani (1961). According to Van der Spoel (1976), however, the right tentacle is the largest, but in his concept of a dorsal swimming-fin we have to read right for left and vice versa.

The second forma *C. lamarcki* forma *challengeri*, attains in the present material a maximum total body length of only 35 mm. This material also contains mature specimens. In table 1 the mean dimensions are shown. Apart from its smaller dimensions, *C. lamarcki* forma *challengeri* differs from *C. lamarcki* forma *lamarcki* in the possession of a black pigmented clasper on the ventral side of the tail, a darker pigmented visceral mass mounted on a small stalk and a darker pigmented retinal base in the eyes. Furthermore, compared with the nominal forma, the cutis is thin and beset with more, smaller tubercles and the tentacles are stronger developed (fig. 2b). The left one is also distinctively larger than the right one and Van der Spoel's (1976) remark that in this forma the right tentacle is absent suggests that he has left here his concept of a dorsal swimming-fin. Besides, most specimens in the present material do possess a right tentacle, although small and in some cases hard to trace.

The differences between the two formae are obvious and the question arises whether to consider them to be related at an infraspecific or at a specific level (cf. p. 89).

Table 1. Mean dimensions (mm) of *Carinaria* (for measurements see fig. 1).

	C. lamarcki					
	forma *lamarcki* (n = 39)			forma *challengeri* (n = 7)		
	mean	stand. dev.	% of total	mean	stand. dev.	% of total
total length	51	24	100	24	7	100
head	12	5	24	7	2	29
trunk	20	10	39	9	3	38
tail	19	9	37	8	3	33

Distribution

The distribution and abundance of *Carinaria* specimens are given in table 2, together with some related sampling data. Most specimens of *C. lamarcki* forma *lamarcki* and all the specimens of *C. lamarcki* forma *challengeri* have been collected with the RMT8 net. Of *C. lamarcki* forma *lamarcki* 45 specimens have been caught, while the *challengeri* group consists of only 8 specimens. The vertical and north-south distributions are diagrammatically represented in figure 3, where catches are plotted at the mean depths of the hauls.

In contrast with the general opinion, *Carinaria* specimens are not restricted to the upper 200 m and in the day-time they seem to inhabit deeper water (> 200 m) than at night (fig. 3). Below, these statements have been elaborated in a more quantitative way. The catches of *C. lamarcki* forma *lamarcki* have been classified in four groups, viz. those collected by day in the upper 200 m, by day in water deeper than 200 m, at night in the upper 200 m and at night in water deeper than 200 m (table 3). All four categories have been fished in the range where *Carinaria* occurs, although not equally intensively. In table 3 only catches from the RMT8 have been used to exclude special effects of different net types on the catching-rate. For the four categories the numbers have been converted into percentages, corrected for the different amounts of water filtered (cf. Van der Spoel, 1981, table 1). A large part of the population seems to live deeper than 200 m, all specimens caught by day occur in water between 200 m and at least 500 m depth, whereas at night most of them populate the upper 200 m. Although the present figures based on such small numbers have to be considered rough indications, they clearly point to a vertical diurnal migration pattern. The numbers of

Table 2. Numbers, abundance and distribution of *Carinaria lamarcki*.
net type: RMT8—closing RMT8, RMT1—closing RMT1, RO1—open RMT1, RNO—open Ringnet
period: d - day, n - night, d-n - dusk, n-d - dawn
For explanation of actual and standard numbers see Material and Methods.

latitude (N)	station/ haul no	net type	period	mean depth net (in m)	forma *lamarcki* actual nrs.	forma *lamarcki* stand. nrs.	forma *challengeri* actual nrs.	forma *challengeri* stand. nrs.
49°	13/10	RO1	d	25	1		-	
	13/1	RMT8	n	75	1	0.6	-	-
	13/6	RMT8	n-d	450	1	0.7	-	-
45°	14/4	RNO	d	25	4		-	
	14/10	RMT8	n	75	4	3.0	2	2.4
	14/8	RMT8	n	150	-	-	3	2.7
	14/2	RMT8	d	250	2	1.3	-	-
42°	16/6	RMT8	d-n	75	12	8.1	1	0.7
	16/5	RMT8	d	250	4	3.2	-	-
	16/2	RMT8	d	350	4	3.1	-	-
	16/4	RMT8	d	450	1	0.8	-	-
41°	17/1	RMT8	n	75	-	-	1	0.4
40°	18/3	RNO	n	25	2		-	
	18/6	RMT8	n-d	75	1	0.9	1	0.9
	18/4	RMT8	n	150	1	0.9	-	-
	18/8	RMT8	d	250	3	3.0	-	
	18/2	RMT8	n	350	1	0.6	-	-
	18/7	RMT8	d	400	1	0.9	-	-
	18/10	RMT8	d	675	1	0.4	-	-
32°	22/7	RMT8	n	150	1	0.4	-	-
total					45		8	

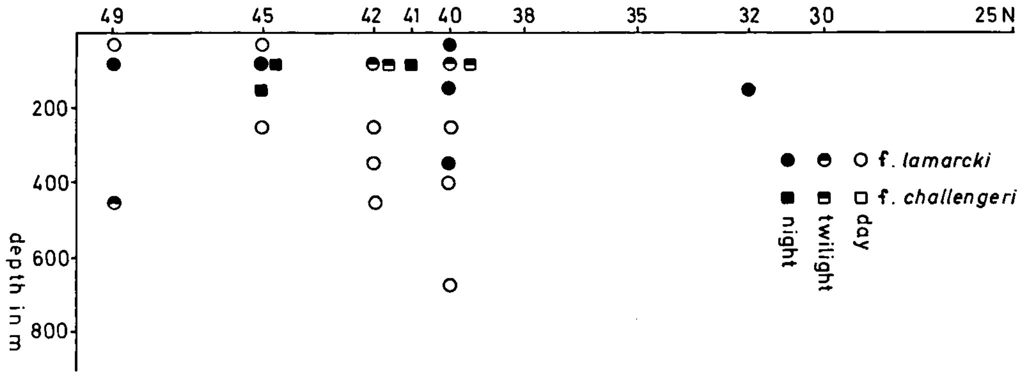

Fig. 3. Distribution of *C. lamarcki*, all catches with one or more specimens caught with the RMT1 + 8, open RMT1 or open Ringnet have been plotted at the mean depth of the haul.

Table 3. Vertical distribution of *C. lamarcki* forma *lamarcki* during day and night (for explanation see text).

	night-catches		day-catches	
	act. nrs.	%	act. nrs.	%
0-200 m	7	27	0	0
>200 m	1	3	16	70

C. lamarcki forma *challengeri* are too small (8 spec.) to elaborate in the same way, besides, none of them have been collected in the daytime.

C. lamarcki forma *lamarcki* has been caught between 49°N and 32°N. In table 2 the abundance of the species has been given as standard numbers and show the highest abundance for *C. lamarcki* forma *lamarcki* at 42°N. The northernmost occurrence of *C. lamarcki* forma *lamarcki* in the present material coincides with the northern boundary known from the literature. To the south, it is known to occur down to the tropical South Atlantic, whereas in the present material it has not been found south of 32°N latitude. The horizontal distribution ranges of the two formae overlap, *C. lamarcki* forma *challengeri* occurring between 45°N and 40°N, a smaller range than that of the former forma, which may be due to its lower abundance. *C. lamarcki* forma *challengeri* seems to be most abundant at 45°N (table 2), which is slightly more to the north than *C. lamarcki* forma *lamarcki*. However, literature data only refer to an occurrence south of 40°N.

Variation

Variation in the dimensions of the specimens has been studied in relation with their distribution and sex. *C. lamarcki* forma *challengeri* is so rare that a biometrical study of horizontal variation is impossible. Besides, all eight specimens have been caught in the upper 200 m and six of them are females, hence the study of vertical or sexual variation is also excluded.

For *C. lamarcki* forma *lamarcki* (table 4) the mean length of the trunks is studied at different latitudes, at shallow and deep levels and of males and females. Table 4 shows that the present material does not point to variation from north to south, but this does not mean such a variation does not exist as the numbers per

Table 4. Variation in trunk-length of *C. lamarcki* forma *lamarcki* specimens caught with the RMT8.

	trunk-length in mm				
	min.	mean	max.	stand. dev.	n
total	7	19	44	10	38
49°N (St. 13)	19	31	42	12	2
45°N (St. 14)	7	18	36	11	6
42°N (St. 16)	8	16	34	6	21
40°N (St. 18)	9	25	44	13	8
32°N (St. 22)	12	12	12	-	1
0-200 m depth	7	17	44	10	20
>200 m depth	9	22	44	10	18
males	7	21	44	11	19
females	8	18	42	9	19

latitude are very small. In water deeper than 200 m the mean length is considerably larger than in the upper 200 m (17 and 22 mm resp.), but this difference is not significant (α = .05). The histograms of figure 4 shows that the shallow samples are mostly composed of very small specimens, whereas in the deeper samples more large specimens occur. Probably this is related with the occurrence of a vertical migration pattern in adults, as will be discussed below (cf. p. 92). Males also appear to reach a larger mean length than females (21 and 18 mm resp.); here the difference is not significant either (α = .05).

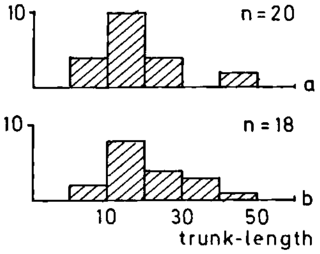

Fig. 4. Histograms of trunk-length of *C. lamarcki* forma *lamarcki* for 0-200 m depth (a) and for water deeper than 200 m (b).

Family Pterotracheidae
Genus *Pterotrachea* Niebuhr (MS. Forskål), 1775
The species of this family do not possess a shell. In the genus *Pterotrachea* cephalic tentacles are absent.

Pterotrachea scutata Gegenbaur, 1855 (fig. 5)
Pterotrachea scutata is distinctively recognisable by its gelatinous dorsoventral flattened disc formed by a thickening of the cutis between the eyes and the swimming-fin. As the specimen becomes larger this disc develops more strongly than the rest of the body; like the rest of the trunk and tail, it is covered with tubercles. The proboscis is rather short and can be bent backwards into a groove of the gelatinous disc. The body is transparent and in the present material reaches a maximum total length of 106 mm. The visceral mass is pear-shaped, which is characteristic of the species. The cylindrical eyes are longer than the diameter of the retinal base, the lense is amber-coloured. The swimming-fin, only in males with a sucker, is rather vulnerable. The cutis surrounding the fin-base is beset with warts, especially in larger specimens. The pedal ganglia are found at the edge of the fin-base or slightly in front of it. The mean dimensions of head, trunk and tail in *P. scutata* are given in table 5.

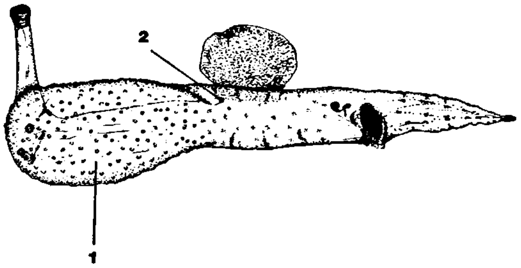

Fig. 5. *Pterotrachea scutata* (♂, Station 19, ZMA no 6031, × 1) 1 - dorso-ventral flattened cutis disc; 2 - pedal ganglia.

Table 5. Mean dimensions (mm) of *Pterotrachea* specimens (for measurepoints see fig. 1).

	mean	stand. dev.	% of total length
P. scutata (n = 66)			
total length	58	25	100
head	13	6	22
trunk	31	14	53
tail	14	7	24
P. coronata (n = 91)			
total length	84	42	100
head	23	10	27
trunk	42	24	50
tail	19	8	23
P. hippocampus (n = 22)			
total length	41	18	100
head	9	4	22
trunk	22	11	54
tail	10	4	24
P. minuta (n = 18)			
total length	19	6	100
head	4	1	23
trunk	11	4	57
tail	4	1	20

Table 6. Numbers, abundance and distribution of Pterotracheidae specimens.
net type: RMT8 - closing RMT8, RMT1 - closing RMT1, RO1 - open RMT1, RNO - open Ringnet
period: d - day, n - night, d-n - dusk, n-d - dawn
act. - actual numbers, st. - standard numbers (for explanation see Material and Methods).

latitude (N)	station/ haul no	net type	period	mean depth in m	*P. scutata*		*P. coronata*		*P. hippocampus*		*P. minuta*		*F. desmaresti*	
					act.	st.	act.	st.	act.	st.	act.	st.	act.	st.
45°	14-8	RMT1	n	150	-		-		1		-		-	
		RMT8	n	150	1	0.5	1	0.5	-	-	-	-	-	-
	14-2	RMT8	d	250	-	-	1	0.7	-	-	-	-	-	-
42°	16-9	RNO	d	25	-		1		-		-		-	
	16-1	RMT8	d	150	-	-	1	0.7	-	-	-	-	-	-
	16-2	RMT1	d	350	1		-		-		-		-	
		RMT8	d	350	5	3.9	1	0.8	-	-	-	-	-	-
41°	17-1	RMT8	n	75	-	-	2	0.8	-	-	-	-	-	-
	17-3	RMT8	n-d	250	5	4.7	3	2.8	-	-	-	-	-	-
	17-2	RMT8	n	425	-	-	-	-	1	0.4	-	-	-	-
40°	18-3	RNO	n	25	-		1		-		-		-	
	18-6	RMT1	n-d	75	-		1		-		-		-	
		RMT8	n-d	75	-	-	2	1.9	-	-	-	-	-	-
	18-4	RMT8	n	150	2	1.7	3	2.5	-	-	-	-	-	-
	18-8	RMT1	d	250	-		1		-		-		-	
		RMT8	d	250	-	-	12	11.9	-	-	-	-	-	-
	18-2	RMT1	n	350	1		-		-		-		-	
		RMT8	n	350	2	1.3	-	-	-	-	-	-	-	-
	18-1	RMT8	n	800	1	0.5	-	-	-	-	-	-	-	-
38°	19-19	RMT1	d	75	-		1		-		-		-	
		RMT8	d	75	3	2.4	3	2.4	1	0.8	-	-	4	3.2
	19-13	RMT8	d	150	-	-	2	1.5	6	4.4	-	-	-	-
	19-1	RMT1	n	250	-		1		-		-		-	
		RMT8	n	250	7	5.8	9	7.4	-	-	-	-	-	-
	19-4	RMT8	d	350	1	0.8	2	1.5	-	-	-	-	-	-
	19-6	RMT8	d	450	1	0.7	-	-	-	-	-	-	-	-
35°	20-13	RNO	n	25	-		-		2		-		-	
	20-10	RMT8	n	150	5	4.5	14	12.5	-	-	3	2.7	-	-
	20-8	RMT1	n	250	1				-		-		-	
		RMT8	n	250	10	8.0	2	1.6	-	-	-	-	-	-
	20-1	RMT8	d	700	-	-	-	-	-	-	-	-	3	1.8
34°	21-9	RMT8	n	150	-	-	-	-	1	0.9	1	0.9	-	-
	21-2	RMT1	d-n	250	-		2		-		-		-	
		RMT8	d-n	250	3	1.2	11	4.3	-	-	-	-	-	-
	21-10	RMT8	n-d	350	-	-	3	2.5	-	-	-	-	-	-
	21-3	RMT8	n	450	2	1.5	-	-	-	-	-	-	-	-
32°	22-8	RNO	n	25	-		-		1		-		-	
	22-7	RMT1	n	150	1		1		-		-		-	
		RMT8	n	150	2	0.8	7	2.8	5	2.0	-	-	-	-
	22-1	RMT8	d	750	2	0.8	-	-	-	-	-	-	-	-
31°	23-3	RMT8	d	450	1	0.6	-	-	1	0.6	-	-	-	-
	23-2	RMT8	d	750	-	-	-	-	1	0.5	-	-	-	-
30°	24-4	RNO	n	25	-		-		1		2		-	
	24-2	RMT1	n	150	-		-		-		3		-	
		RMT8	n	150	4	4.1	23	23.6	-	-	16	16.4	-	-
	24-3	RMT8	n-d	250	-	-	2	0.8	-	-	-	-	-	-
28°	25-9	RMT1	n	150	1		-		-		-		-	
		RMT8	n	150	4	2.9	3	2.2	-	-	6	4.4	-	-

latitude (N)	station/ haul no	net type	period	mean depth in m	*P. scutata* act.	st.	*P. coronata* act.	st.	*P. hippocampus* act.	st.	*P. minuta* act.	st.	*F. desmaresti* act.	st.
	25-6	RMT8	n	250	1	0.9	-	-	-	-	-	-	-	-
	25-4	RMT8	n	350	2	1.9	-	-	1	1.0	-	-	-	-
25°	26-7	RNO	d	0	-		-		1		-		-	
	26-9	RNO	d	25	-		-		1		-		-	
	26-10	RMT8	d	150	-	-	1	0.8	-	-	3	2.4	-	-
	26-1	RMT8	n-d	350	1	0.5	-	-	3	1.6	-	-	-	-
	26-8	RMT8	d	400	1	0.2	10	2.1	-	-	-	-	-	-
	27-3	RNO	n-d	25	-		-		3		-		-	
	27-7	RNO	d	25	-		-		1		-		-	
	27-23	RMT8	d-n	75	-	-	1	0.4	-	-	-	-	-	-
	27-20	RMT8	d	150	-	-	-	-	4	2.9	-	-	-	-
	27-2	RMT8	n-d	250	-	-	18	12.7	2	1.4	1	0.7	-	-
	27-6	RMT8	d	350	3	1.2	-	-	-	-	-	-	-	-
total					74		146		37		35		7	

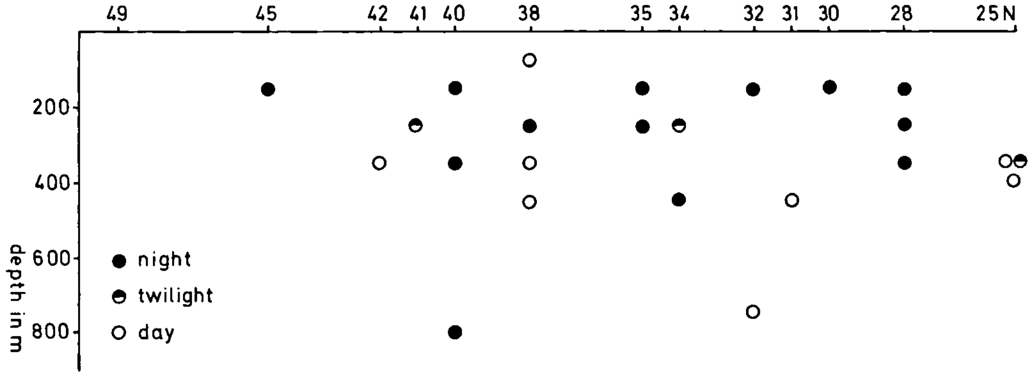

Fig. 6. Distribution of *P. scutata*, all catches with one or more specimens caught with the RMT1 + 8, open RMT1 or open Ringnet have been plotted at the mean depth of the haul.

Distribution

The distribution and abundance of *P. scutata* are given in table 6. Most of the 74 specimens collected have been caught with the RMT8 net, only 5 specimens have been acquired from the small RMT1 net of the combined RMT1 + 8 net. The vertical and north-south distributions are diagrammatically presented in figure 6.

The vertical distribution of *P. scutata* (table 6 and figure 6) is comparable with that of *Carinaria*. The depth distribution is by no means restricted to the upper 200m. Day-catches proceed from deeper water than night-catches and specimens have been obtained from water of at least 520 m depth. The boundary between the main day and night habitats seems to be even deeper than for *Carinaria*, viz. at 300 m approximately. In table 7 the specimens have been divided into four categories and converted into percentages in the same way as for table 3, Nearly 50% of the population lived deeper than 300 m. Relatively, at night more specimens have been caught in the upper 300 m than in deeper water, while in the day-time the reverse was found. As for *Carinaria lamarcki*, the above data point to a vertical diurnal migration pattern as well.

P. scutata has been caught between 45°N and 25°N. The species is less abundant (table 6)

Table 7. Vertical distribution of *P. scutata* during day and night (for explanation see text).

	night-catches		day-catches	
	act. nrs.	%	act. nrs.	%
0-300 m	39	45	3	9
>300 m	8	35	14	12

south of 35°N. *P. scutata* is known to have a very wide north-south range of a neritic type. Real Mid North Atlantic records are available from 45°-35°N, the present data confirm this, and at the same time indicate a more extensive southern distribution in the open North Atlantic Ocean.

Variation

The latitudinal variation in trunk-length (table 8) shows that the mean length in the northern part of the area exceeds that of the southern part, while between 38°-40°N a more or less sharp transition occurs between large and small trunk-lengths. The histogram of the trunk-lengths (fig. 7a) appears to be two-topped, one top formed by specimens with a trunk-length between 10 and 20 mm, the other formed by specimens of 40-50 mm trunk-length. When the histogram is split up for the latitudes between 40°-45°N and those south of 40°N, the southern area turns out to be mainly populated by very small specimens, whereas in the northern part these small specimens are absent,

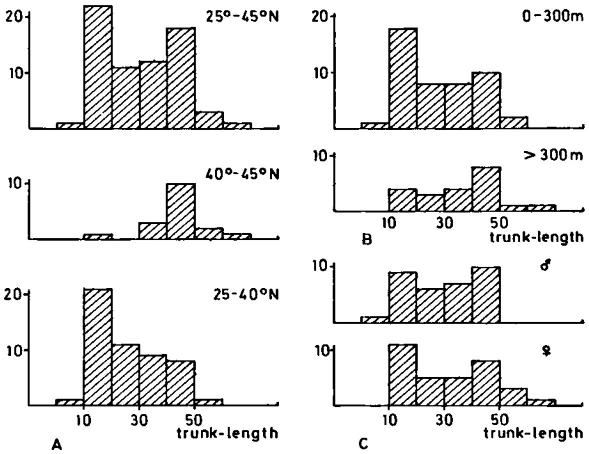

Fig. 7. Histograms of the trunk-length of *P. scutata* for different latitudes (A), depths (B) and sexes (C).

Table 8. Variation in trunk-length (in mm) of *P. scutata* and *P. coronata* specimens caught with the RMT8.

	P. scutata					*P. coronata*				
	min.	mean	max.	st.dev.	n	min.	mean	max.	st.dev.	n
total	9	31	62	14	66	8	41	101	25	101
45°N (St.14)	43	43	43	-	1	69	84	99	15	2
42°N (St.16)	40	49	62	7	6	90	94	98	4	2
41°N (St.17)	38	47	53	5	5	35	68	95	22	5
40°N (St.18)	19	37	46	10	5	10	66	101	20	16
38°N (St.19)	11	27	48	14	11	17	52	85	25	10
35°N (St.20)	9	20	35	8	15	8	25	42	10	14
34°N (St.21)	18	33	48	11	5	10	27	56	14	12
32°N (St.22)	17	33	44	12	3	18	29	48	13	6
30°N (St.24)	11	22	31	8	5	8	33	68	15	22
28°N (St.25)	14	25	51	12	7	17	23	32	6	3
25°N (St.26/27)	19	34	47	10	5	15	28	48	10	9
0-300 m	9	28	53	13	47					
>300 m	11	36	62	13	21					
0-200 m						8	40	101	24	60
>200 m						8	43	99	25	41
males	9	30	49	13	33	17	46	101	26	37
females	11	32	62	14	33	8	46	99	23	47

except for one exception. The distinct difference in length between the northern and southern areas may be caused by the presence of two distinct populations in the corresponding areas, or by latitudinal differences in developmental stages. For testing the hypothesis that two different groups are present, an analysis of variance has been employed. The conditions for such an analysis of a normal distribution of length per station and a homogeneity of variances per station prove to be approximately satisfied. The analysis of variance carried out shows that there exists no significant difference between stations within the same group ($F_s = 1.83$, $F_{\alpha = .025(df_1 = 8,\ df_2 = 60)} = 2.41$, $\alpha_{real} \leq .05$), but there is a significant difference between the two groups. ($F_s = 20.41$, $F_{\alpha = .005(df_1 = 1.df_2 = 8)} = 14.7$, $\alpha_{real} \leq .01$) The conclusion to be drawn from these tests is that *P. scutata* specimens collected between 40°-45°N belong to a population with a different mean trunk-length than those gathered south of 40°N.

The mean trunk-length of specimens caught in the upper 300 m and of specimens caught deeper than 300 m depth is 28 and 36 mm resp.; this difference proves to be significant ($\alpha = .05$). With respect to the sexes, females reach a larger mean length than males (30 and 32 mm resp.), but the difference between the sexes is not significant ($\alpha = .05$). The histogram of fig. 7c shows that among both sexes many small specimens have been found, while females ultimately reach a larger body length.

Pterotrachea coronata Niebuhr (MS. Forskål), 1775 (fig. 8)

P. coronata (fig. 8) is the heteropod species which can reach the largest dimensions. From the Indian and Pacific Oceans specimens are known of a length of up to 260 mm. In the present collection the largest specimen attains a total length of 188 mm. *P. coronata* is the most abundant species. The long and slender body is transparent and has a thin smooth and vulnerable cutis. The swimming-fin, proboscis, penis and visceral mass are also vulnerable and easily get lost. The cilindrical eyes are long as in *P. scutata*, the diameter of the lens exceeds that of the retinal base. The shape of the visceral mass is slender, rod-like and is characteristic of the species. In large animals two or more spines develop on the cutis between the eyes. The fin bears a sucker in males only, the cutis surrounding the fin-base is beset with warts. The pedal ganglia are found just in front of the fin-base. The mean dimensions *P. coronata* are presented in table 5.

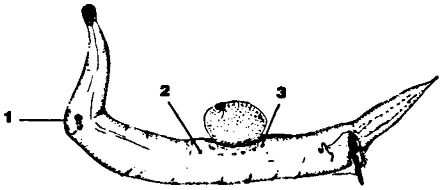

Fig. 8. *Pterotrachea coronata* (♂, Station 18, ZMA no 6009, × 1/2) 1 - spines between eyes; 2 - pedal ganglia; 3 - warts around swimming-fin.

Distribution

Most of the 146 specimens collected have been caught with the RMT8 net, 7 specimens occurred in the closing RMT1 net and 2 in hauls made with the Ringnet.

Table 6 and figure 9 show that *P. coronata* is not restricted to the upper 200 m, while, like in *Carinaria lamarcki* and *P. scutata*, a vertical migration pattern appears to exist. In table 9 the numbers of specimens for the four categories (cf. table 3) have been converted for equal amounts of water. These figures then show that 39% of the population occurs in water deeper than 200 m. In the day-time 24% of the specimens have been sampled, only 7% in the upper 200 m against 17% in water deeper than 200 m. At night, 77% of the specimens have been collected, 55% inhabits the upper 200 m.

P. coronata is present between 49°N and 25°N, with reduced abundance north of 41°N. According to Van der Spoel (1976), *P. coronata* is the only species of the genus occurring in the

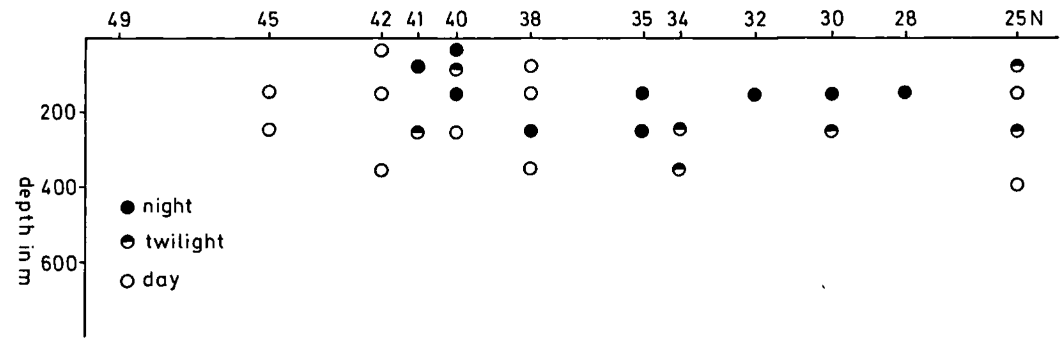

Fig. 9. Distribution of *P. coronata*, all catches with one or more specimens caught with the RMT1 + 8, open RMT1 or open Ringnet have been plotted at the mean depth of the haul.

Table 9. Vertical distribution of *P. coronata* during day and night (for explanation see text).

	night-catches		day-catches	
	act. nrs.	%	act. nrs.	%
0-200 m	53	55	7	7
>200 m	11	22	26	17

centre of the Atlantic. It is found between 30°S and 40°N. Our data show a distribution extending up to 49°N, although the abundance between 40°-49°N is low.

Variation

Variation in trunk-length in *P. coronata* has been studied in respect with latitude, depth and sex (table 8). The mean trunk-length at the stations between 38° and 45°N is much larger than the mean length south of 38°N; between these two areas a rather abrupt transition takes place of large specimens into small ones. As in *P. scutata*, the possibility of the presence of two different populations, a northern and a southern one, can be investigated by carrying out an analysis of variance. The hypothesis tested concerns the existence of two different groups situated at 38°-45°N and 25°-35°N respectively. The present data appear to fulfil approximately the conditions of normality and homogeneity. The analysis of variance yielded that the stations are comparable—there is no added variance component among stations ($F_s = 1.89$, $F_{\alpha=0.25,(df_1=9,\, df_2=90)} = 2.28$, $\alpha_{real} \leq .05$)—while among the two groups a significant difference in trunk-length occurs. ($F_s = 44.87$, $F_{\alpha=.001(df_1=1,\, df_2=6)} = 25.5$, $\alpha_{real} \leq .002$) Consequently, the specimens collected between 38°-45°N belong to a different population with respect to their mean trunk-length than those collected south of 38°N.

The difference in mean trunk-length between specimens collected in the upper 200 m and specimens caught in water of more than 200 m depth is distinct (40 and 43 mm resp.) though not as evident as in *P. scutata* and not significant ($\alpha = .05$). The present material does not show differences in trunk-length between males and females.

Pterotrachea hippocampus Philippi, 1836 (fig. 10a) and **Pterotrachea minuta** Bonnevie, 1920 (fig. 10b)

Pterotrachea hippocampus and *P. minuta* show a strong resemblance, in a number of cases they are hard to separate. Both species are described

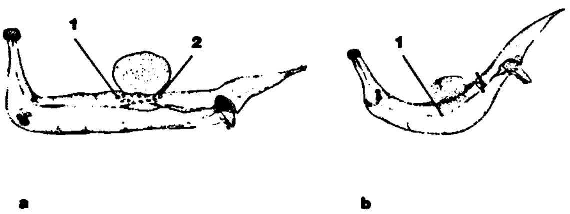

Fig. 10. a. *Petreotrachea hippocampus* (♀, Station 21, ZMA no 6058, × 1) b. *Pterotrachea minuta* (♂, Station 24, ZMA no 6054, × 2) 1 - pedal ganglia; 2 - warts around swimming-fin.

together in favour of a clear treatment of their distinctive characters.

P. hippocampus reaches a total length of 80 mm according to literature data, in our material the largest specimen measured 84 mm. Characteristic of the species are the triangular eyes with a broad and darkly pigmented retina, which is so strongly curved that one top reaches the lens (fig. 11a). Another characteristic feature is the shape of the visceral mass, which resembles that of *P. scutata* and is approximately 2.5 times as long as it is broad. The lowest half of the visceral mass, where the gonads are found, is darkly coloured, especially in males.

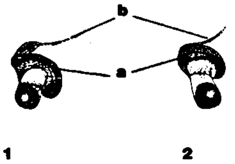

Fig. 11. Right eye of 1. *P. hippocampus* (Station 21, ZMA no 6058, × 7.5) and 2. *P. minuta* (Station 24, ZMA no 6054, × 7.5) a - retinal base; b - optic nerve.

The pedal ganglia are found slightly in front of the insertion of the swimming-fin. In large specimens the cutis surrounding the fin-base is beset with small warts. Between the eyes sometimes protrusions of the cutis, so-called spines, are present.

P. minuta is a small species with a maximal total length of 50 mm reported in the literature; in the present material the largest specimen measures 36 mm. *P. minuta* is considered a valid species intermediate between *P. coronata* and *P. hippocampus* (Tesch, 1949, Van der Spoel, 1976). The shape of the eyes resembles that of *P. hippocampus*, but is not as triangular as in the latter. The retina, too, is broad and curved at one side in the direction of the lens, but does not reach it (fig. 11b). The visceral mass is slender as in *P. coronata*, 3 times as long as it is broad. The swimming-fin bears a small sucker in males, the pedal ganglia are found just in front of the insertion of the fin as in *P. hippocampus*. Warts are supposed to occur at the trunk around the fin, but they have not beeen found. Spines between the eyes are absent.

As mentioned before, in a number of cases it is hard to decide whether a specimen belongs to *P. hippocampus* or to *P. minuta*. The most distinctive character proves to be the shape of the retinal base in the eyes. Ultimately, it has been possible to divide the specimens into two groups, *P. hippocampus* with a curved retina reaching the lens, and *P. minuta* with a not so broad and curved retina (figs 11a and 11b resp.). The other discriminating feature is found in the shape of the visceral mass. In table 10 the length/width ratio of the visceral mass is given, figure 12 shows this length/width ratio against the trunk-length of *P. hippocampus* and *P. minuta*. Up to 10 mm length, which corresponds with a total length of approximately 18 mm, there is an overlap of the length/width ratios in the two species. The majority of the specimens, however, can be identified on the shape of their visceral mass.

Table 10. Length/width ratio of visceral mass in *P. hippocampus* (n = 24) and *P. minuta* (n = 25).

	min. l/w ratio	mean l/w ratio	max. l/w ratio	stand. dev.
P. hippocampus	1.9	2.3	3.0	0.3
P. minuta	2.2	3.1	4.5	0.6

Distribution

Of *P. hippocampus* 37 specimens have been collected, of *P. minuta* 35 (table 6). Most specimens have been caught with the RMT8 net, the closing RMT1 net yielded 1 *P. hippocampus* and 3 *P. minuta* specimens, the open Ringnet produced 10 *P. hippocampus* and 2 *P. minuta* specimens. The vertical and north-south distributions of the species are diagrammatically presented in figure 13.

P. hippocampus is not restricted to, but occurs mainly in the upper 200 m (table 6 and figure 13). The deepest caught specimen came from a haul ranging from 505-960 m depth. The figures from table 11 (cf. table 3) show that approximately three quarters of the population can be found in the upper 200 m; they do not

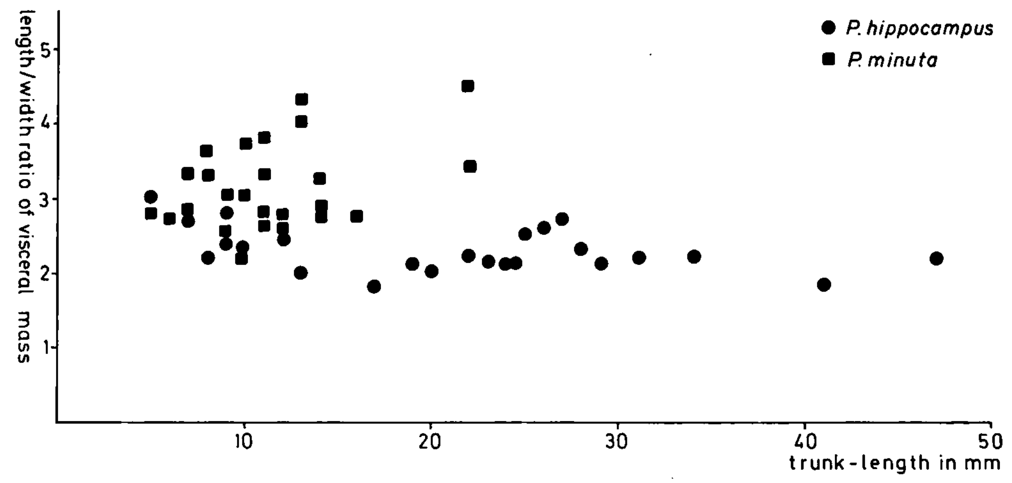

Fig. 12. Length/width ratio of visceral mass against trunk-length of *P. hippocampus* and *P. minuta*.

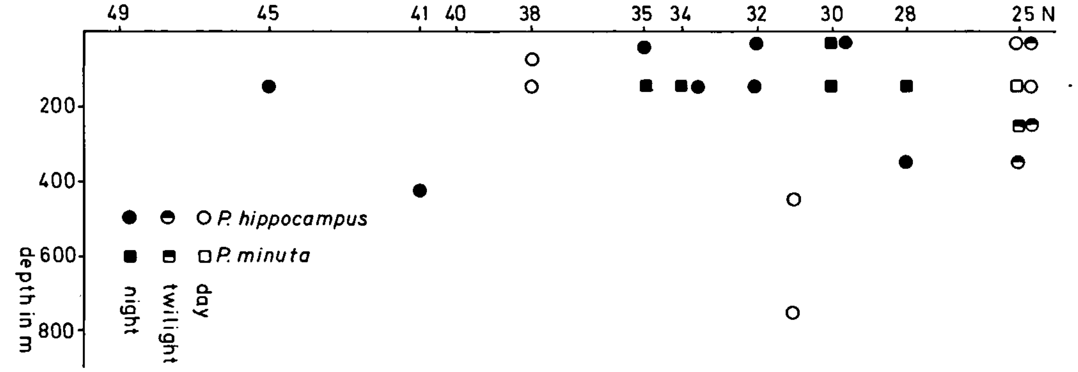

Fig. 13. Distribution of *P. hippocampus* and *P. minuta*, all catches with one or more specimens caught with the RMT1 + 8, open RMT1 or open Ringnet have been plotted at the mean depth of the haul.

Table 11. Vertical distribution of *P. hippocampus* during day and night (for explanation see text).

	night-catches		day-catches	
	act. nrs.	%	act. nrs.	%
0-200 m	6	27	11	50
>200 m	2	13	2	11

suggest a vertical migration pattern because the few specimens found deeper than 200 m have been caught by day as well as at night. *P. minuta* shows a vertical distribution chiefly restricted to the upper 200 m, only one specimen has been caught in a haul from 180-300 m depth.

P. hippocampus has been found at stations up to 45 °N, *P. minuta* at stations up to 35 °N. Little can be said with respect to the abundance of the populations as the numbers collected are small. *P. hippocampus* seems to be rare between 40°-45°N, for *P. minuta* no increase or decrease from north to south is found. The present distribution data form a deviation or at least a complementation of literature data. According to Van der Spoel (1976), *P. hippocampus* is a coast-bound neritic species, while *P. minuta* may be also considered a neritic species, although its distribution is far less known. During the present expedition, however, *P. hippocampus* and *P.*

minuta have both been collected in the open ocean at a great number of different latitudes.

Variation

The study of morphological variation in both species has been hampered because the numbers of specimens available for meristics had been reduced by various kinds of damage. Especially in the small and vulnerable species *P. minuta* many specimens are incomplete.

Variation in body size has been studied, based on the length of the trunk. Table 12 gives the mean trunk-lengths for both species at different latitudes, for the upper 200 m and deeper waters, and for males and females. With respect to the latitudinal variation in *P. hippocampus* it turns out that the specimens caught between 25°-40°N are considerably smaller than the specimens from 40°-45°N. The numbers are so small that no statistical analyses are possible, but it seems clear that there is a disjunction at approximately 40°N. The question arises whether this latitude forms a separation between two different populations or a growth discontinuity within one population. For *P. minuta* the data are insufficient for conclusions about latitudinal variation. For *P. hippocampus* no differences in length have been observed for shallow and deep water, of *P. minuta* only one specimen occurred deeper than 200 m, moreover, the trunk of this specimen could not be measured due to damage. In *P. hippocampus* females become considerably larger than males (mean trunk-length 27 and 21 mm, resp.), in *P. minuta* the reverse occurs, males are slightly larger than females (mean trunk-lengths 12 and 10 mm, resp.), in both cases the differences are not significant ($\alpha = .05$).

Genus *Firoloida* Lesueur, 1817

Firoloida desmaresti Lesueur, 1817 (fig. 14)

Firoloida desmaresti, of the monotypical genus *Firoloida*, is a small species with a body-length of up to 40 mm. In the present material the largest specimen measured 19 mm. The transparent body bears a centrally situated swimming-fin with a sucker in males only. In males, a tentacle beside each eye, a voluminous penis and a rudimentary tail which ends in a filamentous thread are found (fig. 14). Females lack a tail, an egg string is present behind the visceral mass.

Table 12. Variation in trunk-length (in mm) of *P. hippocampus* and *P. minuta* specimens caught with the RMT8.

	P. hippocampus					*P. minuta*				
	min.	mean	max.	st. dev.	n	min.	mean	max.	st. dev.	n
total	5	20	47	10	29	5	11	22	4	23
45°N (St.14)	41	41	41	-	1					
41°N (St.17)	47	47	47	-	1					
38°N (St.19)	19	24	29	4	6					
35°N (St.20)	23	24	25	1	2	12	13	14	1	2
34°N (St.21)	27	27	27	-	1	16	16	16	-	1
32°N (St.22)	5	10	19	5	4					
30°30′N (St.23/24)	24	26	28	2	3	5	10	22	4	20
28°N (St.25)	11	11	11	-	1					
25°N (St.26/27)	8	18	34	8	10					
0-200 m	5	21	41	9	21					
>200 m	10	21	47	12	9					
males	10	21	34	7	13	5	12	22	5	10
females	16	27	47	9	11	7	10	23	2	9

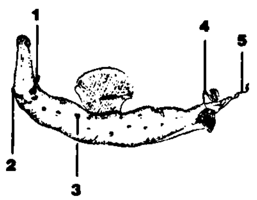

Fig. 14. *Firoloida desmaresti* (♂, Station 19, ZMA no 6036, × 2) 1 - right tentacle; 2 - left tentacle; 3 - pedal ganglia; 4 -penis; 5 - rudimental tail.

Distribution

Only 7 specimens have been collected in two hauls with the RMT8 net at two different latitudes, viz. 38°N (station 19) and 35°N (station 20) (table 6). Both hauls have been made by day. The catch at 38°N proceeds from shallow water (50-110 m depth), whereas the haul at 35°N has been made from 505-870 m depth. The occurrence at the stations 19 and 20 only, seems to indicate a relation with the subtropical waters of the Azores. According to literature data (Van der Spoel, 1976) *F. desmaresti* should be common in the whole Atlantic between 40°N and 40°S.

Variation

The small number of *F. desmaresti* specimens prevents investigation of morphological variation within the species. The dimension of head and trunk are given in table 13.

Table 13. Dimensions of *Firoloida desmaresti* in mm (for measurepoints see fig. 1).

latitude (N)	length of head	length of trunk	sex
38°	3	9	♀
	4	13	♀
	3	12	♂
	4	-	♂
35°	4	8	♂
	4	11	♂
	4	15	♂
mean	3.7	11.3	

CONCLUSIONS

TAXONOMY

In the present material only two representatives of the Carinariidae have been found: *Carinaria lamarcki* forma *lamarcki* and *C. lamarcki* forma *challengeri*. No other *Carinaria* species could be expected to occur in the North Atlantic. The monotypical genus *Pterosoma* Lesson, 1827 is not expected to be found in the N. Atlantic, because it is considered to be restricted to the Indo-Pacific waters. Of *Cardiapoda* d'Orbigny 1836, however, both species occur in the North Atlantic. *Cardiapoda placenta* (Lesson, 1830) is a coast-bound neritic species of subtropical waters. Its neritical distribution accounts for its absence in the present material. *Cardiapoda richardi* Vayssière, 1903 has been collected from oceanic localities in the North Atlantic Ocean e.g. by the 'Michael Sars' North Atlantic Deep Sea Expedition in 1910 (Bonnevie, 1920). Tesch (1949) describes *C. richardi* as a common species in the area off the Azores and in the Sargasso Sea. *C. richardi* has not been caught, however, during the present expedition; maybe its abundance was too low during the early spring of 1980.

According to Bonnevie (1920) the differences between the two varieties of *Carinaria lamarcki* are the possession of a dark-pigmented ventral clasper on the tail and a smaller maximum length of the body in the variety *challengeri*. Tesch (1949) makes no differentiation in formae or varieties, he states 'the only point of difference is that "*C. lamarcki* var. *challengeri*" is much smaller than "*C. lamarcki* var. *lamarcki*".' The small dimension of *C. lamarcki* forma *challengeri* should be due to the fact that *challengeri* only occurs in the Atlantic and not in the Mediterranean while specimens of *C. lamarcki* forma *lamarcki* from the Atlantic also attain a smaller body size than the truly Mediterranean *C. lamarcki* forma *lamarcki* specimens. The latter may attain a size of 220 mm and Tesch ascribes the larger dimensions to the warmer conditions of the Mediterranean. However, the development of animals in warmer waters may be faster and sexual maturity may be attained at an earlier stage; in general, the mean size of a warm-water variety is smaller than that of a cold-water variety (Sverdrup et al., 1942). The higher viscosity of cold water enables a species to achieve larger sizes without losing buoyancy. Besides, in colder water a longer period is needed to reach full sexual maturity in which period a specimen often keeps on growing. In general, both phenomena lead to larger specimens in colder waters. Probably the large dimensions which *C. lamarcki* forma *lamarcki* specimens can attain in the Mediterranean is due to the exceptionally high salinity in this inland sea, resulting in an exceptionally high buoyancy. Even at a depth of 1000 m the salinity of the Mediterranean amounts to more than 38‰ (Sverdrup et al., 1942), whereas in the area of the present expedition the salinity even at the surface never exceeds 37‰. Furthermore, Tesch ignored the other distinct difference between the two formae mentioned by Bonnevie, viz. the black clasper at the ventral side of the tail. Van der Spoel (1976), too, considered the differences between *C. lamarcki* forma *lamarcki* and *forma challengeri* to be marginal. He describes *C. lamarcki* forma *lamarcki* with a small tail clasper although unpigmented. In the present material, however, no such clasper has been distinguished. Moreover, according to Van der Spoel *C. lamarcki* forma *lamarcki* should possess a right cephalic tentacle larger than the left one, whereas in *C. lamarcki* forma *challengeri* the reverse should occur. Probably the confusion about right and left has caused the mentioning of this point as a difference between these formae. In fact, both taxa possess a left tentacle stronger developed than the right one. Tesch (1949) was the first who mentioned the unequal development of the tentacles in *Carinaria*, the left one always being longer than the right one. According to Okutani (1961) in *C. lamarcki* forma *challengeri* the right tentacle should even be missing altogether.

In the present collection in all cases both taxa possess a well-developed left tentacle, whereas the right tentacle is smaller and in a few specimens could not be found. In *C. lamarcki* forma *challengeri* both tentacles are stronger developed than in *C. lamarcki* forma *lamarcki*. Furthermore, *C. lamarcki* forma *challengeri* is smaller than *C. lamarcki* forma *lamarcki*, its maximum length being 32 mm against 114 mm in the forma *lamarcki*. In addition to these differences, *C. lamarcki* forma *challengeri* has the black pigmented clasper on the tail, its visceral mass is darker pigmented than in the other forma and there are more, though smaller, tubercles on the cutis of the trunk. In all cases identification could be made without problems and therefore the question arises whether these taxa have to be considered belonging to one species. If they form two subspecies sensu Van der Spoel (1971), the distribution areas of the subspecies would have to be allopatric. This is not the case, *C. lamarcki* forma *challengeri* occurs at latitudes and depths where *C. lamarcki* forma *lamarcki* is also abundantly present. The concept 'forma' sensu Van der Spoel (1971) does not fit either because between two formae of a species no sharp taxonomic separation should exist: in the centre of its distribution area a forma clearly differs from another, but in the periphery of their distribution areas, at the place where the two distribution areas overlap, specimens occur with the same gene composition (intermediates) as a result of gene flow. In the present material no such intermediate specimens have been found, while the distribution areas of the two taxa overlap to a great extent. Consequently, the distinct differences, the sympatric occurrence and the lack of intermediate specimens unequivocally lead to the conclusion that *C. lamarcki* forma *lamarcki* and *C. lamarcki* forma *challengeri* are in fact two different species to be called *Carinaria lamarcki* Péron & Lesueur, 1810 and *Carinaria challengeri* Bonnevie, 1920. Although in 1904 Vayssière described for the first time a probably representative of *C. challengeri* as *Carinaria pseudorugosa* it was in 1920 Bonnevie who described the taxon in full detail. After that, *C. challengeri* has been known as *C. lamarcki* var./forma *challengeri*. Vayssière's description depended on one badly fixed specimen with a dark-pigmented clasper on the dorsal side of the tail. It is now assumed that this *C. pseudorugosa* is identical with *C. challengeri*, the dorsal position of the clasper being due to a twisting of the body of Vayssière's damaged specimen. If he has been the first author to describe the species, his nomenclature has not been used for at least fifty years and the name is to be considered a 'nomen oblitum'. According to the rules of the Zoological Nomenclature the valid name of the species is proposed to be *C. challengeri* Bonnevie, 1920.

Bonnevie always had considered *C. challengeri* specimens juveniles of *C. lamarcki* because they were smaller and very similar and in her material the black clasper seemed to be more clearly present in the smaller specimens than in larger ones; she believed it to be a juvenile character, disappearing with growth. When she perceived that *C. challengeri* specimens with a length of 30-40 mm had already attained sexual ripeness she considered it henceforth a small variety of *C. lamarcki* without discussing the possibility of a position at species level.

The maximum length of *C. lamarcki* in the present material is considerably smaller than the maximum length of specimens known from the Mediterranean (114 and 220 mm resp.). Tesch (1949) also mentioned the smaller sizes in the Atlantic Ocean and to my opinion (see above) these differences are determined by the great differences in salinity. The lack of a noticeably clinal length variation from north to south in the present collection indicates that the slight increase of the sea-water salinity in this section* is too small to be expressed in a distinct clinal length variation in the present species. Moreover, the slight increase in salinity is coupled with an increase in temperature* and both phenomena are supposed to work antagonistically with respect to body sizes (Sverdrup et al., 1942).

Of the Pterotracheidae all the species are represented in our samples, even *Pterotrachea hippocampus* and *P. minuta*, which are supposed to be neritic, only to be found in the Mediterranean Sea and along the coasts of the Atlantic and Indo-Pacific Oceans (Van der Spoel, 1976). *P. coronata*, *P. scutata* and *Firoloida desmaresti* are clearly recognisable species; it is more difficult to discriminate between *P. hippocampus* and *P. minuta*, two closely related species. Tesch (1949) and Van der Spoel (1976) consider *P. minuta* an intermediate species between *P. coronata* and *P. hippocampus* which is expressed in the intermediate structure of the eyes and the shape of the visceral mass. With respect to the morphology *P. minuta* resembles *P. hippocampus* more strongly than *P. coronata*. Differences between small specimens of *P. hippocampus* and specimens of *P. minuta* are often slight but a close examination of the eyes leads to a decisive identification in all cases, where the shape of the visceral mass does not (fig. 11). In spite of the small differences, the absence of intermediate specimens between the sympatric *P. hippocampus* and *P. minuta* confirms that it is justified to consider them two valid species and not formae or subspecies of one species.

A remark should be made about the reported occurrence of a fin sucker sometimes noticed in females of *P. coronata* (Tesch, 1949). In the present material this phenomenon has not been observed, and to my opinion it seems probable that these 'females' have in fact been males of which the penis got lost. The penis in *P. coronata* is a very slender organ in comparison with that of the other heteropod species studied, its loss hardly leaves any noticeable traces. Consequently, such specimens can very easily be mistaken for females.

VERTICAL DISTRIBUTION

Several authors emphasize that the habitat of heteropod species is situated in the upper photic layers of the sea (Bonnevie, 1920; Tesch, 1949; Van der Spoel, 1976). When found in samples from meso- or bathypelagic waters, the correctness of the observations is usually doubted, such specimens are supposed to have entered the net on its way up to the surface. An example of this is the interpretation Bonnevie (1920)

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* mean surface water salinity and temperature at 49°N: 35.39‰ and 10.9°C; at 32°N: 35.55‰ and 19.3°C (cf. Van der Spoel, 1981).

gives of the catch of three *P. coronata* specimens in three different hauls down to 1700 m depth at three different stations during the 'Michael Sars' expedition of 1910. Diurnal vertical movements, too, are usually not supposed to occur among heteropods. Okutani (1961) was the first author who tentatively suggested that among *Carinaria* species possibly diurnal vertical movement occurs to some extent, while Richter (1974) puts forward that *P. coronata* and *P. scutata* live in waters deeper than 200 m and that all heteropods move to the surface waters at night.

The present data neither point to an occurrence restricted to the upper 200 m nor to the absence of a vertical migration pattern. Fifty per cent of the *C. lamarcki* specimens, converted for equal amounts of water filtered, proceed from depths of more than 200 m. The deepest caught specimen has been found in a haul from 440-910 m made by day. Of *P. coronata* 49% occurs deeper than 200 m, while of *P. scutata* 45% even occurs deeper than 300 m. The deepest caught specimens of these two species have been found in hauls from 300-500 m and 520-1130 m respectively. *P. hippocampus* has been collected in hauls down to 960 m depth but chiefly occurs in the upper 200 m (77%). *C. challengeri* and *P. minuta* have been found in shallow hauls down to 200 m and 300 m resp., but these concern, with one exception, only hauls made at night or twilight. Consequently, with the present data it is not possible to ascertain whether these two species occur deeper by day. *F. desmaresti* seems to have an extensive vertical distribution, by day specimens have been collected from shallow waters (50-110 m) as well as from deep waters (505-870 m). Bonnevie (1920: 9) also mentions a specimen of *F. desmaresti* caught at 1000 m depth, but she expresses her doubts about this observation by putting a question-mark behind the record.

C. lamarcki, *P. scutata* and *P. coronata* show also a pattern of vertical diurnal movement. The majority of the specimens of all three species collected at night came from the surface layer, whereas by day most specimens have been collected in waters deeper than 200-300 m (tables 3, 7, 9). The data of *P. hippocampus* do not give a clear indication for the existence of a diurnal vertical migration pattern (table 11), although the deepest collected specimens have been obtained by day (fig. 13). For *C. challengeri*, *P. minuta* and *F. desmaresti* the data are insufficient to draw conclusions in this respect.

Mainly the larger specimens seem to participate in the diurnal migration, of *C. lamarcki*, *P. scutata* and *P. coronata* the mean body lengths of deeply caught specimens is larger than that of the shallow ones. It seems plausible that the possibility or neccessity of vertical movement is not present in the earliest life stages. About the feeding habits of young heteropods nothing is known but very likely they feed rather passively on phytoplankton and small zooplankton present in the photic layers. Therefore, in this stage of life a vertical movement pattern is not expected to exist, only in a later phase is the swimming capacity such that active prey hunting is possible. Tesch (1949) also mentions the phenomenon that chiefly among the larger specimens prey hunting occurs. The vertical diurnal movement among the larger, i.e. older specimens of a species seems to be secondary behaviour. The food of large heteropods is known to be very varied (Bonnevie, 1920; Tesch, 1949) and exists for instance of crustaceans, salps, chaetognaths and fishes, the greater part of which show vertical migration. While following prey animals consequently the larger heteropods show the same vertical migration pattern.

In all, the vertical distribution among Carinariidae and Pterotracheidae in the Mid North Atlantic Ocean is broader than has been assumed hitherto. Moreover, all but one of the species of which sufficient data are available, show clear vertical migration. The exception is formed by *P. hippocampus*, a small species. Maybe slight vertical movement exists in *P. hippocampus*, but could not be made visible with the restricted material, on the other hand it seems possible that only the larger species have sufficient swimming capacity for hunting migration prey animals. In that case the other small species are not expected to show vertical migration either. The argument often heard, that heteropods are bound to the upper 200 m because of the amount of light they need to detect their prey, contradicts the facts. Like mesopelagic fishes, heteropods will be able to detect their prey with their well-developed eyes down to great depths by optical stimuli such as (reflection of) very slight amounts of light, shade-forming or bioluminescence.

GEOGRAPHICAL DISTRIBUTION

The distribution of heteropods is not very well known. Most species show a cosmopolitan warm-water distribution, but detailed data are often absent due to much systematical confusion in the past. Many synonyms have been used and changes of names frequently occurred. A short discussion is given of the horizontal distribution and length variation (if present) of the seven species collected and a comparison is made with literature data as given by Van der Spoel (1976).

Carinaria lamarcki. A good 90% of the specimens occurs in the area typified by Van der Spoel (1981) as the southern branch of the North Atlantic Current, viz. from 40°-45°N. North of this area three specimens occur at 49°N and south of it only one specimen has been found, at 32°N. According to literature data *C. lamarcki* is a very common species in the Mediterranean and Caribbean Seas but less abundantly present in the open North Atlantic Ocean up to 60°N. Tesch (1949) mentions large numbers in the Sargasso Sea, but he refers to observations in the western part of it. The above suggests a neritic distribution and a populating of the open Ocean out of the Mediterranean and Caribbean Seas. Dispersion from the Caribbean into the open North Atlantic could have taken place via the Florida Current and the Gulfstream, this would explain the distribution at the 30°W longitude restricted to the water of the North Atlantic Current.

C. challengeri. This species too is restricted to the southern branch of the North Atlantic Current though less abundantly present than *C. lamarcki.* Literature data are very scarce due to its low abundance, moreover the species has been considered in most cases synonymous with *C. lamarcki.* Records are often of neritic areas, specimens have been reported from the west coast of Gibraltar and Central America and from east of Japan, no specimens are known from the Caribbean area. Therefore, it cannot be concluded that the present specimens originate from this area.

Pterotrachea scutata. Specimens of this species have been found up to 45°N. The trunk-length of the northernmost specimens is larger than that of specimens in the south (table 8). An analysis of variance shows that the specimens collected between 40°-45°N belong to a different population than those collected south of 40°N. The northern population consists of adult animals with a mean trunk-length of 45mm, the southern population consists of smaller specimens of 26 mm mean trunk-length. Inspection of the data yielded no suggestion about an increase of trunk-length with higher latitudes. Consequently, the data do not point to an increase of body length related to a decrease of temperature, as often occurs in planktonic groups (Sverdrup, 1942), with a discontinuity, for whatever reasons, at 40°N. Like the *Carinaria* species, the first mentioned population is found in the water of the southern branch of the North Atlantic Current. *P. scutata* is known to have a very wide north-south distribution. It occurs in tropical, subtropical and temperate waters and may even, incidentically, penetrate the cold areas north of Ireland. It is not improbably that here too the Florida Current, the Gulfstream and the North Atlantic Current play an important role in the dispersion of the species. The occurrence of a great number of specimens along the 30°W longitude points at least to a distant-neritic and maybe even oceanic distribution of *P. scutata* which has hitherto been considered neritic.

P. coronata. This species too has been found up to 45°N but seems to have a stronger preference for subtropical waters than *P. scutata.* In the present collection it is found in abundance in the Sargasso Sea area (south of 38°N) while

P. scutata is most abundant north of this area (table 6). *P. coronata* is very common, a fact confirmed by the present data, and it is the only species of the family of which an occurrence in the centres of the oceans was assumed. In the North Atlantic its distribution was supposed to be restricted to latitudes south of 40°N. However, in the present samples it is also found between 40°-45°N. Like for *P. scutata*, the analysis of variance shows that the specimens from the northern stations belong to a different population than the southern specimens. The mean trunk-length of specimens sampled between 38°-45°N is much larger than that of specimens collected between 25°-35°N. (65 and 24 mm resp.). Therefore, along the 30°W longitude two *P. coronata* populations are found, the distribution of the northern one determined by the southern branch of the North Atlantic Current, the southern one present up to 38°N, while at 38°N specimens of both populations occur.

P. hippocampus. Specimens of this species are rather common south of 38°N, only in two cases have they been found more northwards: one specimen at 40°N and one at 45°N. The trunk-lengths of the latter two are 47 and 41 mm resp. while the mean trunk-length of the more southerly caught specimens is 18 mm. Although no statistical analysis is possible with the restricted numbers, it seems obvious that the two specimens collected in the North Atlantic Current water at 40° and 45°N belong to a different population than the specimens collected between 25° and 38°N. The present data point to a distant-neritic or oceanic distribution whereas the species is known as a coast-bound neritic one.

P. minuta. This species too has a restricted north-south distribution and has not been found north of 38°N. Until now it has been considered a neritic species though its distribution is less completely known than the distribution of *P. hippocampus*. However, the occurrence at various stations in the Mid North Atlantic by no means points to a distribution restricted to the coasts of the continents.

Firoloida desmaresti. The distribution pattern of this species is obscure. Some authors describe it as rare, others call it extremely common (Tesch, 1949). Sometimes swarms of specimens are recorded, forming scattering layers. In the North Atlantic it should be met with regularly south of 40°N. In our material, however, it only occurs in two hauls with a total of seven specimens. The only stations where *F. desmaresti* has been collected are situated south-west of Azores, pointing to a more or less coast-bound distribution.

The present study intends to contribute to the investigations of distribution boundaries in the Mid North Atlantic. The question to be solved is whether the distribution areas of plankton groups can be correlated with hydrographical phenomena. Angel (1979) gives a survey of plankton groups with a boundary between subtropical and transitional faunas at approximately 40°-45°N. Material of the present collection adds to these groups species of the mesopelagic silver hatchetfishes (Sternoptychidae) (Pafort-van Iersel, 1981). The horizontal distribution of the heteropods of the present study confirms the existence of north-south boundaries. The distribution ranges of the two *Carinaria* species is limited in the north by the 45°N latitude and in the south by the 40°N latitude. Three *Pterotrachea* species (*P. scutata*, *P. coronata, P. hippocampus*) are likewise restricted to the waters south of 45°N. Moreover, the specimens of *P. scutata* and *P. coronata* and maybe of *P. hippocampus* too, caught between 38°/40°-45°N and specimens of the same species collected more southwards belong to different populations. The distribution of the first-mentioned populations as well as that of the *Carinaria* species coincides with the southern branch of the North Atlantic Current, while the southern populations are restricted to the subtropical waters. The restriction to water of the North Atlantic Current possibly suggests a tropical West Atlantic origin, followed by a dispersion via the Florida Current, Gulfstream and North Atlantic Current. This suggestion is supported by the occurrence in the same expedition material of tropical specimens of *Clio pyramidata* Linnaeus, 1767 forma *lanceolata* (Lesueur, 1813) between 40°-42°N (Pafort-van Iersel, 1982). Winkler (1982) also reports for the same collection a hydromedusa species (*Pandea conica* (Quoy & Gaimard, 1827)) collected around 42°N which could have been transported from the Bermuda area in the West Atlantic eastwards by the southern branch of the North Atlantic Current.

Summarizing, one can point to the remarkable fact that the very mobile and actively swimming heteropods which always show a high degree of gene-flow and a low degree of infra-specific variation, prove to be so clearly restricted in their distribution by water masses and currents. Apparently the differences between the North Atlantic Current and the adjoining waters cause environmental differences to such an extent that they form a boundary between favourable and intolerable conditions for the life and development of a population or of a species. Consequently, like a number of other molluscs (Furnestin, 1979) the heteropods of the present study have to be considered excellent indicators of different water masses in the open ocean.

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Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam,
P.O. Box 20125, 1000 HC Amsterdam, The Netherlands.