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VARIATION IN *DIACRIA TRISPINOSA* (DE BLAINVILLE, 1821) AND *CLIO PYRAMIDATA* LINNAEUS, 1767 (PTEROPODA, MOLLUSCA) OF THE AMSTERDAM MID NORTH ATLANTIC PLANKTON EXPEDITION 1980*

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ABSTRACT

Two thecosomatous pteropods, *Diacria trispinosa* and *Clio pyramidata*, caught during an expedition in the Mid North Atlantic Ocean in 1980 have been studied. The morphological variation of the northern and southern formae of both species is reported. The distributions of the formae are given, transitional zones are described and their abundance throughout the area is estimated. Variation in both species shows a rather smooth cline while the transition of northern into southern formae starts between 40° and 45°N which coincides with the transition of temperate into subtropical waters. The presence of very broad specimens of *Clio pyramidata* forma *lanceolata* between 40° and 45°N suggests the inflow of West Atlantic tropical water populations at these latitudes, carried in by the Gulfstream and the North Atlantic Current.

INTRODUCTION

The material collected during a spring expedition in the Mid North Atlantic Ocean along approximately 30°W longitude proved to be excellently suited to study infraspecific variation in planktonic groups and to trace faunal boundaries which are supposed to exist for a number of taxa in the Mid and East Atlantic between 40°-45°N (Angel, 1979). In the present paper the clinal north-south variation within the two thecosomatous pteropod species *Diacria trispinosa* (De Blainville, 1821) and *Clio pyramidata* Linnaeus, 1767, is discussed. Both species are known to be polytypical and transitions of northern formae into southern

formae are expected to occur in the area concerned (Dupont, 1979; Van der Spoel, 1967). The third thecosomatous species with clinal variation in the North Atlantic is *Limacina retroversa* (Fleming, 1823). The transitional zone of the northern forma *Limacina retroversa* forma *balea* Möller, 1814, into the southern forma *Limacina retroversa* forma *retroversa* (Fleming, 1823) however, is situated north of the area sampled (25°-55°N), viz. approximately between 55°N and 70°N (Van der Spoel, 1967) and therefore this species had to be excluded from the present investigations.

For *Clio pyramidata* a phenomenon unique among molluscs, has been described by Van der

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Spoel (1963, 1967, 1973a) as strobilation of adult specimens, resembling the asexual reproduction in Coelenterata (Pafort & Van der Spoel, 1978; Van der Spoel, 1979). The exact nature of the direct inducement to strobilation in this pteropod is not yet clear, it possibly occurs in areas rich in nutrients or at the boundaries of the distribution area, where environmental conditions become less favourable. Seen in this light the occurrence of strobilating specimens may give an extra dimension to the research into variation in this species.

Although the two thecosomatous pteropods studied were known to show infraspecific north-south variation, the actual cline has never been described in detail. The present material, collected at small geographic intervals along a distinct longitude and within a short period, provided the possibility for a study of morphological clinal variation in *Diacria trispinosa* and *Clio pyramidata*. As several thecosomatous taxa of infraspecific level are considered to be biological indicators of water masses (Furnestin, 1979), some conclusions are possible about water masses and their boundaries in the Mid North Atlantic.

MATERIAL AND METHODS

The material studied has been collected during the Amsterdam Mid North Atlantic Plankton Expedition 1980 in the period April 11-May 2 on board the research vessel of the Royal Dutch Navy H.M.S. 'Tydeman'. Along a line at about 30°W seventeen stations were made between 24°N and 55°N. Most of the material has been sampled with the combined opening and closing Rectangular Midwater Trawl, RMT1+8, developed by the Institute of Oceanographic Sciences (Godalming, Great Britain). For a full description of construction and behaviour of the net the reader is referred to Baker et al. (1973) and Roe et al. (1980). In principle the following layers were sampled at each station with the RMT1+8 net: 50-100, 100-200, 200-300, 300-400, 400-500 and 500-1000 m depth. In addition to these hauls, open net hauls were made with a Rectangular Midwater Trawl (with an opening of 1 m²) in the upper 150 metres and with a Ringnet in the

upper 50 metres. The majority of the pteropod samples have been fixed and preserved with a fixative for calcareous organisms consisting of propylene phenoxetol, propylene glycol and formaldehyde (cf. Heyman, 1981), the other pteropods have been fixed with alcohol 70%. For extensive information on the stations, hauls and environmental conditions the reader is referred to Van der Spoel (1981). The complete data are on permanent file at the Zoological Museum of the University of Amsterdam, where also the material is deposited.

As the layers sampled varied considerably in thickness (50 m to 500 m) it was not possible nor justifiable to estimate the concentrations of specimens in the upper 1000 m. The actual numbers of specimens caught in one specific depth stratum, however, can be converted into standard numbers related to a fixed amount (24000 m³) of water filtered. The abundances given as standard numbers for the different hauls in one depth stratum can be compared with each other, also when different sampling times are involved. To exclude the special effects of mesh size and net size on filtering and net avoidance, only the standard numbers of the RMT8 samples have been used for the abundance data. The formula for calculating standard numbers is $(3 \times \text{number of specimens}) / (\text{distance sampled})$. The factor three is introduced as the distance sampled averaged three kilometres, so the standard numbers are as close to the actual numbers as possible; the distance sampled is 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, considered per haul, hardly influenced the amount of water filtered and no special corrections seemed necessary (cf. Roe et al., 1980).

Of *Diacria trispinosa* the sizes important to discriminate the two formae (cf. Dupont, 1979) have been measured. These are the length of the telonch, measured from the anterior dorsal end to the membrane between protoconch and telonch, and the distance between the tips of the two lateral spines (fig. 1a). To discriminate the two formae, colour pattern and colour intensity have been studied for all the specimens. Three

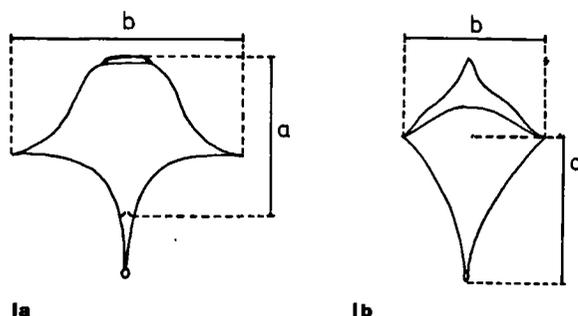


Figure 1. Measurements taken from the shells of *Diacria trispinosa* and *Clio pyramidata*. a — length teloconch, b — width shell, c — length incl. protoconch.

categories could be distinguished, viz. shells with a dark reddish-brown colour, shells with a brown colour restricted to the rims of the shell and shells with an intermediate colour pattern and intensity (fig. 2). In some cases the influence of the two different fixatives used made an accurate identification difficult because the calcareous shells remain transparent when fixed and preserved in alcohol, whereas shells treated with the calcium-fixative lose their transparency and become whitish.

As the width/length ratio for the two formae of *Clio pyramidata* is characteristic, these sizes have been measured. The width of the shell is formulated as the distance between the ends of the lateral sides, the length of the shell runs from the middle of the imaginary width-axis to the tip of the protoconch (fig. 1b). To discriminate the two formae all the specimens have also been studied in respect of the shape of their lateral sides. Two categories could be distinguished, *Clio pyramidata* forma *pyramidata* with completely straight, diverging lateral sides, and *Clio pyramidata* forma *lanceolata* with a more or less outward curving of the diverging lateral sides (fig. 3).

Of both species all the shells have been measured from station samples containing less than 50 specimens. When there were more than 50 specimens, as a rule a minimum of 50 shells have been measured, at random distributed over the hauls. Measurements have been carried out with a micrometer eyepiece (accuracy up to 0.15 mm).

RESULTS

Diacria trispinosa (De Blainville, 1821) forma ***atlantica*** Dupont, 1979 and forma ***trispinosa*** (De Blainville, 1821)

Variation in *Diacria* has been discussed by various authors, recently by Van der Spoel (1967, 1970), Panhorst & Van der Spoel (1974), Rampal (1975), Dupont (1979) and Casanova (1980). *Diacria major* (Boas, 1886) and *Diacria rampali* (Dupont, 1979) are two species closely related to *Diacria trispinosa* (De Blainville, 1821), and they also occur in the North Atlantic Ocean. Since 1886 *D. major* had been described as a subspecies or a forma of *D. trispinosa* until it was Panhorst & Van der Spoel (1974) who first spoke of the species *D. major*. Casanova (1980), however, provisionally prefers to consider it a subspecies of *D. trispinosa*. In the present material *D. major* is sympatric with *D. trispinosa* and forms a clearly distinguishable group. Therefore *D. major* and *D. trispinosa* have been considered in this paper to be two different species. The difference between the two taxa will be discussed in a following paper. No distinct specimens of *D. rampali* have been found.

Diacria trispinosa is a polytypical species; in the North Atlantic Ocean one finds a northern form, *D. trispinosa* forma *atlantica* Dupont, 1979 and a southern form, *D. trispinosa* forma *trispinosa* (De Blainville, 1821). The present material consists of representatives of both formae while a number of specimens are of an intermediate nature and cannot be classified with either of the two formae. *D. trispinosa* forma *atlantica* is firmly built with a broad aperture and a dark reddish-brown colour especially at the aperture lips and the dorsal ribs. It has a dark ventral spot anterior to the lateral spines; its spines and protoconch are not coloured (fig. 2a). *D. trispinosa* forma *trispinosa* is of slender build with a small aperture, the brown colour is restricted to the rims of the shell and its aperture, sometimes there is a small brown stripe on the middle of the dorsal side of the teloconch posterior to the lateral spines and a light spot on the ventral side anterior to the spines (fig. 2c). The number of specimens not clearly

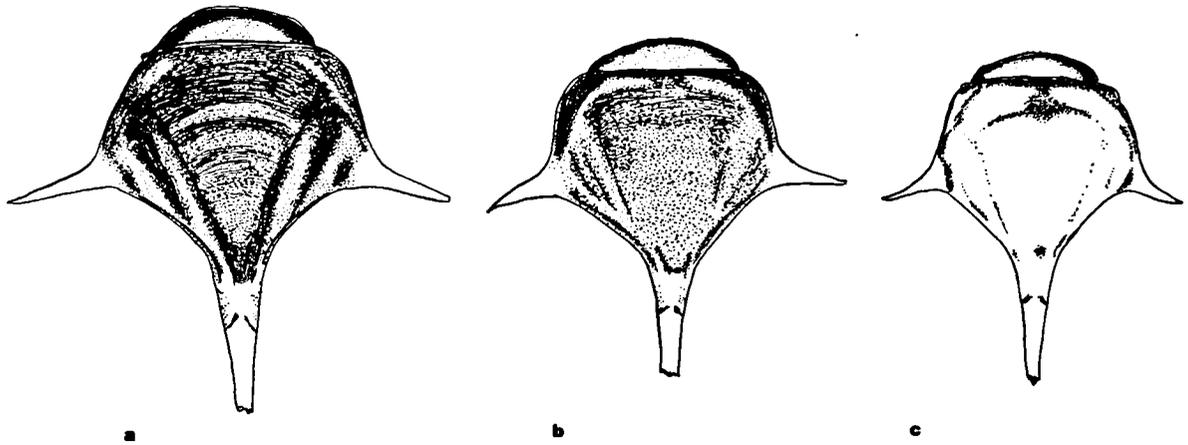


Figure 2. Variation in *Diacria trispinosa* ($\times 11.25$). a — forma *atlantica* (station 14, ZMA 5039), b — transitional form (station 18, ZMA 5241), c — forma *trispinosa* (station 24, ZMA 5266).

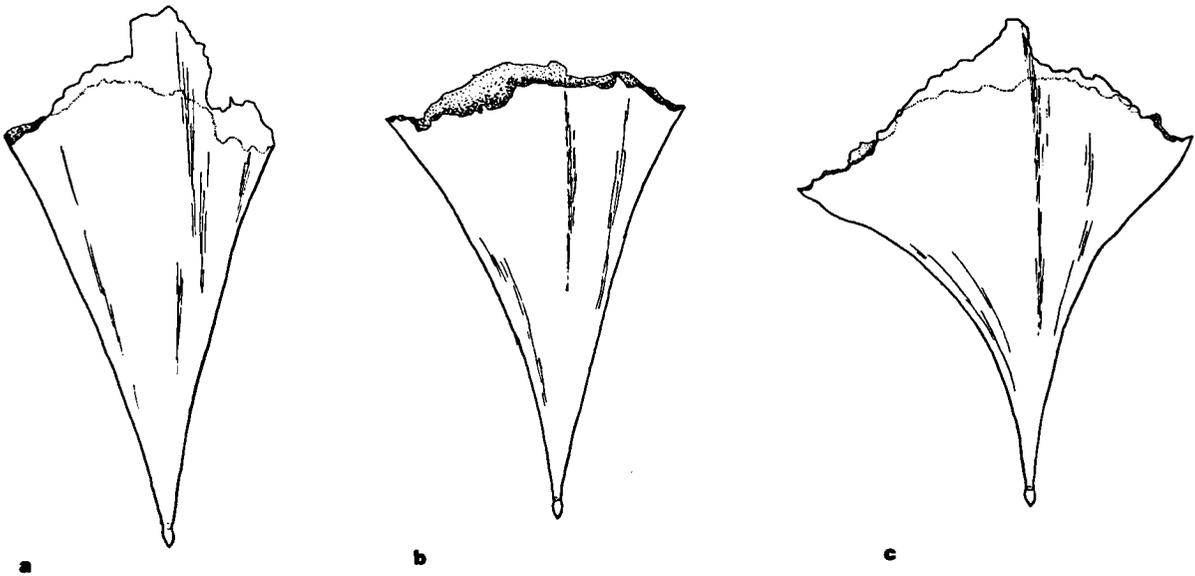


Figure 3. Variation in *Clio pyramidata* ($\times 11.25$). a — forma *pyramidata* (station 14, ZMA 5356), b — forma *lanceolata* (station 18, ZMA 5434), c — forma *lanceolata* (station 18, ZMA 5434).

identifiable as either *D. trispinosa* forma *atlantica* or forma *trispinosa* are of an intermediate shape and colour pattern. Although several colour patterns and colour intensities occur, most of these shells are light-brown with a darker border (fig. 2b).

Table 1 gives the number of specimens of *Diacria trispinosa* sampled during the cruise with some related data. Most specimens have been

caught with the RMT8 net. *D. trispinosa* forma *atlantica* is abundantly present (1547 specimens with a maximum at 41°N of more than 400 specimens in one haul. Of *D. trispinosa* forma *trispinosa* only 21 specimens have been caught, while the intermediate group consists of 90 specimens).

The north-south and vertical distributions of the formae and their intermediates are graphically represented in fig. 4. In this figure catches,

Table 1. Numbers and distribution of *Diacra trispinosa*.
 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

latitude (N)	station-haul no	net type	mean depth net (in m)	period	forma atlantica	transitional forma	forma trispinosa
51°	12-4	RO1	100	D	3	—	—
49°	13-1	RMT8	75	N	25	—	—
		RMT1	75	N	8	—	—
	13-2	RMT8	175	N	3	—	—
	13-4	RMT8	350	N	2	—	—
45°	14-9	RO1	25	N	24	—	—
	14-10	RMT8	75	N	5	—	—
		RMTS	75	N	18	—	—
	14-8	RMT8	150	N	49	—	—
		RMT8	150	N	7	—	—
	14-2	RMT8	250	D	142	—	—
		RMT1	250	D	14	—	—
	14-3	RMT8	350	D	6	—	—
	14-1	RMT8	425	D	3	—	—
42°	16-6	RMT8	75	D-N	132	—	—
	16-1	RMT8	150	D	8	2	—
	16-5	RMT8	250	D	16	—	—
	16-2	RMT8	350	D	138	—	—
		RMT1	350	D	11	—	—
	16-4	RMT8	450	D	94	—	—
		RMT1	450	D	7	—	—
	16-3	RMT1	750	D	1	—	—
41°	17-1	RMT8	75	N	437	8	1
		RMT1	75	N	33	2	1
	17-3	RMT8	250	N-D	3	—	—
	17-2	RMT8	400	N	2	—	—
40°	18-3	RNO	25	N	12	—	—
	18-5	RNO	25	N	2	—	—
	18-6	RMT8	75	N-D	54	21	—
		RMT1	75	N-D	6	—	—
	18-4	RMT8	150	N	2	—	—
	18-8	RMT8	275	D	185	12	—
		RMT1	275	D	2	1	—
	18-2	RMT8	350	N	9	1	—
	18-7	RMT8	400	D	2	—	—
	18-13	RMT8	450	D	—	1	—
38°	19-2	RNO	25	N	2	—	1
	19-13	RMT8	150	D	1	—	—
	19-4	RMT8	350	D	19	—	1
35°	20-12	RMT8	75	N	6	—	—
34°	21-1	RMT8	75	D	1	—	—
	21-9	RMT8	150	N	—	1	—
	21-2	RMT8	250	D-N	32	2	—
		RMT1	250	D-N	2	—	—
32°	22-9	RMT8	75	N	11	22	1
	22-7	RMT8	150	N	—	1	—
30°	24-1	RMT8	75	N	8	12	8
25°	26-11	RMT8	75	D-N	—	2	—
	26-8	RMT8	400	N	—	—	5
	27-23	RMT8	75	D-N	—	1	—
	27-2	RMT8	250	N-D	—	—	1
	27-6	RMT8	350	D	—	—	2
	27-17	RMT8	450	D	—	1	—
total					1547	90	21

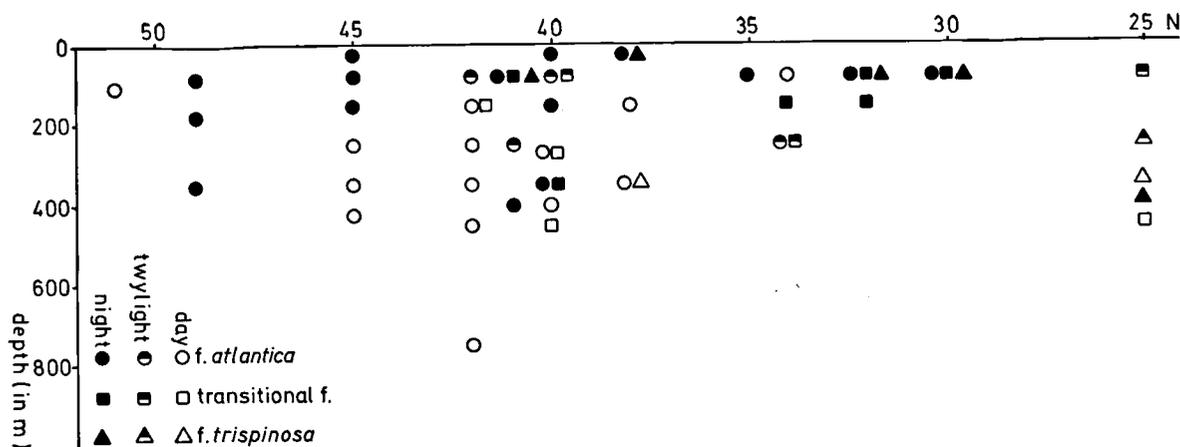


Figure 4. Distribution of *Diacria trispinosa*; all catches with one or more specimens caught with the RMT1+8, open RMT1 or open Ringnet have been plotted at the mean depth of the haul.

divided into day, night and twilight, are plotted at the mean depth of the haul. *D. trispinosa* forma *atlantica* has been caught between 30°N-51°N. It can be expected to occur between 30°N and 60°N in the North East Atlantic (Dupont, 1979), but in the middle of the ocean it probably does not live so far north. The northern distribution boundary is likely to be correlated with the position of a polar front which was situated at approximately 51°N in this spring period (cf. Van der Spoel, 1981). The intermediate specimens occur up to 42°N, the few typical *D. trispinosa* forma *trispinosa* specimens have been observed up to 41°N. Dupont (1979) describes the latter only for latitudes south of 35°N. However, this is not in accordance with the distribution map in the same paper, where specimens have been plotted for the Western North Atlantic Ocean up to 45°N. Consequently, it seems there is no discrepancy between those and the present data.

Within the species, the greatest vertical distribution was found for *D. trispinosa* forma *atlantica*, probably because it is by far the most abundant of the three groups distinguished. *D. trispinosa* forma *atlantica* occurs by day in hauls between 0 and 1000 m depth, with a preference for a depth of about 300 m which is related with a temperature range of 12° to 15° C (cf. temperature profile in Van der Spoel, 1981). At night it

has mainly been found in the upper 200 m with a few specimens in deeper hauls down to 500 m depth. The specimens intermediate between *D. trispinosa* forma *atlantica* and forma *trispinosa* have been caught by day in water between 100 and 500 m deep and show also a preference for a depth of approximately 300 m, which is related with a temperature range of 13° to 15° C. Most of the specimens caught at night occur in hauls of 50 to 100 m depth, a few are present in deeper hauls down to 450 m depth. The few *D. trispinosa* forma *trispinosa* specimens caught by day have been found in hauls between 300 and 500 m depth with a related temperature range of 14°-15° C; when caught at night they all occur in hauls between 50 and 100 m depth. The data above indicate a vertical migration for the whole species and its vertical distribution is in accordance with data Van der Spoel (1973b) gives.

To picture the latitudinal variation in abundance, the standard numbers have been given for the depth stratum of 50 to 100 m, which has been sampled at night or twilight at nearly all the stations, thus providing a comparison of abundances throughout the horizontal range (table 2). For *D. trispinosa* forma *atlantica* the table shows a gradual increase in abundance from north to south down to 41°N. Further to the south its abundance declines simultaneously with the regular increase

Table 2. Abundance of *Diacra trispinosa* specimens caught during night and twilight between 50 and 100 m depth, with the RMT8 net. Abs. nrs. = absolute numbers, stand. nrs. = standard numbers (for explanation see Material and methods).

latitude (N)	station no	forma <i>atlantica</i>		transitional forma		forma	<i>trispinosa</i>
		abs. nrs	stand. nrs	abs. nrs	stand. nrs	abs. nrs	stand. nrs
49°	13	25	15.3	—	—	—	—
45°	14	5	15.	—	—	—	—
42°	16	132	89.2	—	—	—	—
41°	17	437	174.8	8	3.2	1	0.4
40°	18	54	50.7	21	19.7	—	—
35°	20	6	4.6	—	—	—	—
32°	22	11	5.1	22	10.2	1	0.5
30°	24	8	3.6	12	5.4	8	3.6
29°	25	—	—	—	—	—	—
25°	26/27	—	—	3	1.8	—	—

Table 3. Mean length and width of the teloconch of *Diacra trispinosa* caught with the RMT8 net.

latitude (N)	station no	number of specimens	mean length in mm	standard deviation	number of specimens	mean width in mm	standard deviation
51°	12	3	7.43	0.26	3	8.97	0.19
49°	13	11	7.87	0.62	11	8.98	0.52
45°	14	52	7.59	0.32	52	9.62	0.90
42°	16	52	7.10	0.34	51	9.19	0.53
41°	17	51	6.79	0.22	51	9.02	0.62
40°	18	50	6.95	0.38	50	8.64	0.72
38°	19	22	6.69	0.23	20	8.70	0.31
34°	21	34	6.40	0.20	32	8.49	0.49
32°	22	35	6.09	0.21	34	7.64	0.31
30°	24	28	6.10	0.12	24	7.59	0.36
25°	26/27	4	5.81	0.16	3	7.38	0.23

of intermediate specimens. Of the latter a decrease with lower latitudes occurs, as specimens of *D. trispinosa* forma *trispinosa* appear.

To study morphological variation in *Diacra trispinosa*, length and width of the shell, which are characteristic to distinguish the formae, have been measured per station, and are represented in table 3. The data of station 12 are based on the only three specimens caught at this latitude. The numbers of stations 26 and 27 are very small and as these stations are situated at a small distance (30° and 29°W resp.) at the same latitude (25°N), their numbers have been taken together, which, nevertheless, yielded only four specimens suitable for measuring. The latitudinal morphological variation is given in figure 5 and shows the pattern of a smooth cline. In southward direction the dimension of the shell gradually decreases. The mean length at 51°N is 7.43 mm and decreases

to 5.81 mm at 25°N, for the mean width of the shell these sizes are 8.97 and 7.38 mm resp. Between the length of the shell and the geographical latitude, as well as between the width of the shell and the geographical latitude a rather strong linear correlation exists of $r = 0.96$ and $r = 0.86$ resp.

***Clio pyramidata* Linnaeus, 1767 forma *pyramidata* Linnaeus, 1767 and forma *lanceolata* (Lesueur, 1813)**

Variation in *Clio pyramidata* Linnaeus, 1767 has been investigated in detail by Van der Spoel (1967, 1972) who distinguishes at least seven formae within this cosmopolitan species with evident clinal variation. In the North Atlantic Ocean only two formae occur. *Clio pyramidata* forma *pyramidata* Linnaeus, 1767, is found in the northern part and changes into the southern form *Clio pyramidata* forma *lanceolata* (Lesueur, 1813).

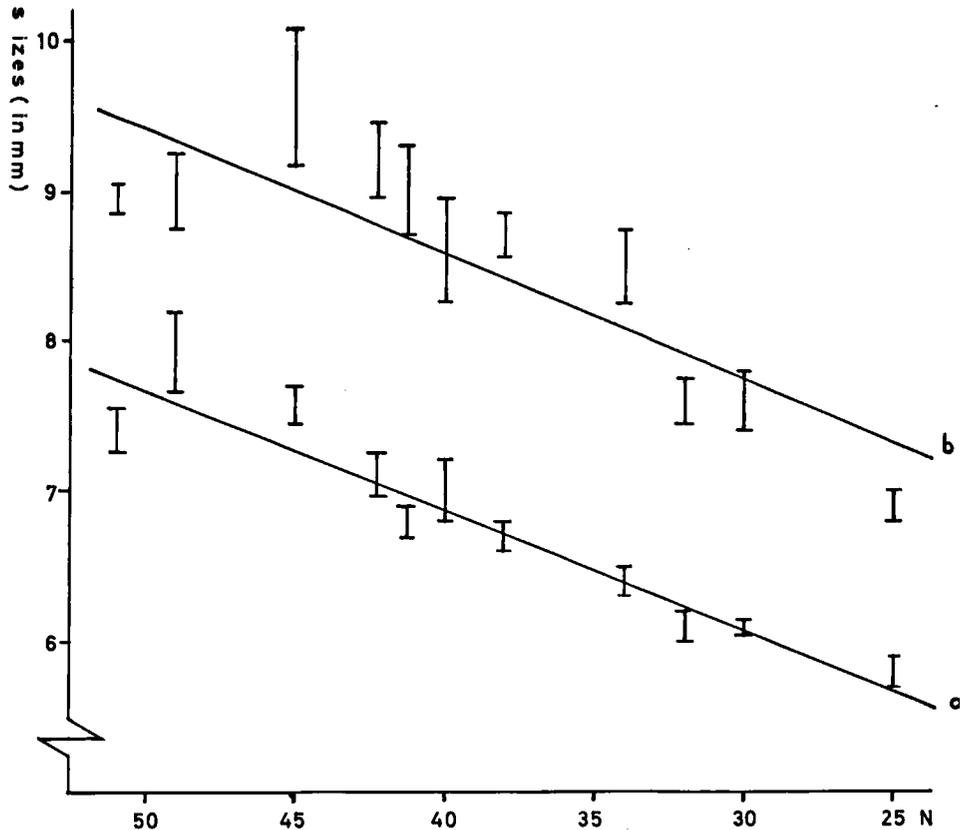


Figure 5. Mean length (a) and width (b) of the shells of *Diacria trispinosa* with corresponding standard deviations, against latitude. Linear regression a — $r = 0.96$, b — $r = 0.86$.

The present material consists of representatives of both formae. The shell of *Clio pyramidata* forma *pyramidata* has straight lateral ribs slightly diverging (fig. 3a), specimens described as *Clio pyramidata* forma *lanceolata* all had more or less curved lateral ribs, a character which can already be recognised in juveniles. In general the lateral ribs of *Clio pyramidata* forma *lanceolata* specimens diverge more strongly than in the forma *pyramidata*, but the extent of this feature does not become clear until a shell length of about 5 mm or more has been reached. There are great differences in the divergence of the lateral ribs and consequently in the width of the shell, illustrated in figures 3b and 3c by two extremes between which all kinds of intermediate forms occur.

Asexual reproduction in *Clio pyramidata* has been described in detail by Van der Spoel (1962,

1967, 1973a, 1979). He described 'aberrant' stages among *Clio pyramidata* forma *antarctica* Dall, 1908 for the first time in 1962. Later on he also reported this phenomenon for the formae *sulcata* (Pfeffer, 1879), *lanceolata* and *pyramidata*, but it remains restricted to the species *Clio pyramidata*. The aberrant stage has to be considered the result of a coelenterate-like strobilation of the body of full-grown male specimens. During strobilation a transverse fission, perpendicular to the body axis, divides the animal into an upper part no longer attached to the shell called 'primary specimen' and a part still attached to the shell called 'aberrant' or 'secondary specimen'. The primary specimen is ontogenetically comparable with the medusa in Coelenterata while the aberrant resembles the polyp stage. The further development of the primary specimen is still puzzling,



Plate I. Aberrant and other specimens of *Clio pyramidata* forma *lanceolata* (station 16, ZMA 5352).

it is supposed to swim out of the shell and either will live on as a pteropod without shell or will form a secondary shell. The soft parts of the aberrant are of a peculiar shape and colour resembling a whitish fingerless glove (Plate 1). Histological investigations have shown that directly after strobilation there is hardly any differentiation in its tissue and that the major part of the top section of the animal is filled with reserve tissue. At a certain moment the aberrant starts to develop into a normal, probably male specimen. The phenomenon of strobilating specimens has been found throughout the distribution range of the species, but it is supposed to occur more often in hydrologically instable areas. In the present material a number of specimens are in an aberrant stage, primary specimens, however, could not be identified.

For the two formae of *Clio pyramidata* table 4 gives, per haul, the total number of specimens as

well as the number of specimens in an aberrant stage. Most specimens have been collected with the RMT8 net. *Clio pyramidata* forma *lanceolata* has been caught most frequently (2607 specimens) with richest hauls at 40°N and 41°N of 470 and 573 specimens respectively. Of *Clio pyramidata* forma *pyramidata* 1878 specimens have been caught with a peak of 783 specimens in one haul at 45°N. Aberrant stages occur chiefly among *Clio pyramidata* forma *lanceolata*. Exceptional, however, is the catch of station 25 haul 9 at 25°N, where eight of the eleven *Clio pyramidata* forma *pyramidata* specimens caught are in aberrant stage. This catch of *Clio pyramidata* forma *pyramidata* specimens is much more to the south than the normal distribution boundary of the forma, so here the high percentage of aberrant stages seems an answer to uncommon environmental circumstances.

Table 4. Numbers and distribution of *Clio pyramidata*.
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

latitude (N)	stationhaul no	net type	mean depth net (in m)	period	forma <i>pyramidata</i> total	forma <i>pyramidata</i> aberrant	forma <i>lanceolata</i> total	forma <i>lanceolata</i> aberrant
55°	10-2	RO1	25	D	2	—	—	—
53°	11-4	RMT8	75	D	6	1	—	—
50°	12-3	RNO	25	D	29	—	—	—
	12-4	RO1	100	D	19	—	—	—
49°	13-10	RO1	25	D	93	—	—	—
	13-1	RMT8	75	N	33	—	—	—
		RMT1	75	N	17	—	—	—
	13-2	RMT8	175	N	35	1	—	—
	13-4	RMT8	350	N	1	—	—	—
	13-9	RMT8	750	N	4	—	—	—
45°	14-4	RNO	25	D	1	—	—	—
	14-9	RO1	25	D	128	—	16	—
	14-10	RMT8	75	N	81	—	1	—
		RMT1	75	N	70	—	57	—
	14-8	RMT8	150	N	783	—	15	—
	14-2	RMT8	250	D	166	—	10	—
		RMT1	250	D	147	—	5	—
	14-3	RMT8	350	D	39	1	7	—
	14-1	RMT8	425	D	57	—	—	—
		RMT1	425	D	—	—	12	—
	14-5	RMT8	700	D-N	4	—	4	—
		RMT1	700	D-N	1	—	—	—
42°	16-6	RMT8	75	D-N	7	—	99	11
	16-1	RMT8	150	D	—	—	1	—
	16-5	RMT8	250	D	4	—	12	—
	16-2	RMT8	350	D	5	—	68	3
		RMT1	350	D	8	—	11	—

(Table 4 Cont.)

latitude (N)	stationhaul no	net type	mean depth net (in m)	period	forma <i>pyramidata</i> total	aberrant	forma <i>lanceolata</i> total	aberrant
41°	16-4	RMT8	450	D	35	2	120	15
		RMT1	450	D	—	—	2	—
	16-3	RMT8	750	D	—	—	5	—
		RMT8	750	D	—	—	4	—
	17-1	RMT8	75	N	30	—	573	16
40°		RMT1	75	N	3	—	79	—
	17-3	RMT8	250	N-D	—	—	197	29
		RMT1	250	N-D	—	—	13	—
	18-3	RNO	25	N	6	—	148	10
	18-5	RNO	25	N	2	—	76	—
	18-6	RMT8	75	N-D	4	—	48	—
	18-4	RMT8	150	N	2	—	13	1
	18-8	RMT8	275	D	6	—	13	—
		RMT1	275	D	—	—	2	—
	18-2	RMT8	350	N	7	—	41	—
38°	18-7	RMT8	400	D	2	—	97	10
		RMT1	400	D	—	—	2	—
	18-13	RMT8	450	D	—	—	193	25
		RMT1	450	D	—	—	10	—
	18-10	RMT8	675	D	22	1	470	20
		RMT1	675	D	1	—	28	1
	19-2	RNO	25	N	—	—	1	—
	19-1	RMT8	250	N	1	—	—	—
	19-4	RMT8	350	D	1	—	—	—
		RMT1	350	D	—	—	4	—
35°	19-22	RMT8	750	D	—	—	32	6
	20-12	RMT8	75	N	—	—	1	—
34°	20-10	RMT8	150	N	—	—	1	—
	21-7	RNO	25	N	—	—	1	—
	21-9	RMT8	150	N	2	—	—	—
32°	21-6	RMT8	750	N	—	—	1	—
	22-9	RMT8	75	N	2	—	2	—
30°	23-2	RMT8	750	D	—	—	5	—
	24-1	RMT8	75	N	—	—	21	—
29°	25-7	RMT8	75	N	—	—	43	—
	25-9	RMT8	150	N	11	8	10	—
	25-4	RMT8	350	N	—	—	6	—
	25-3	RMT8	450	D-N	1	—	2	—
25°	26-11	RMT8	75	D-N	—	—	2	—
	26-4	RMT1	800	D	—	—	22	—
	27-10	RMT8	750	D	—	—	1	—
total					1878	14	2607	147

The north-south and vertical distributions of the two formae of *Clio pyramidata* is graphically represented in fig. 6. In this figure catches split into day, night and twilight are plotted at the mean depth of the haul. The zoogeographical data mostly agree with the literature (Van der Spoel, 1967), although the distribution boundaries seem to have shifted somewhat to the south, probably due to the early time of the year. *Clio pyramidata* forma *pyramidata*, for instance, occurs in con-

siderable numbers south of 45°N, whereas it has been described for latitudes between 45°N-65°N, and *Clio pyramidata* forma *lanceolata* has not been found north of 45°N, whereas it could be expected up to 50°N.

The vertical distribution has been studied for the two formae and both have been found in samples ranging from the upper 50 metres down to approximately 1000 m depth, by day as well as at night (table 4, fig. 6). However, there seems

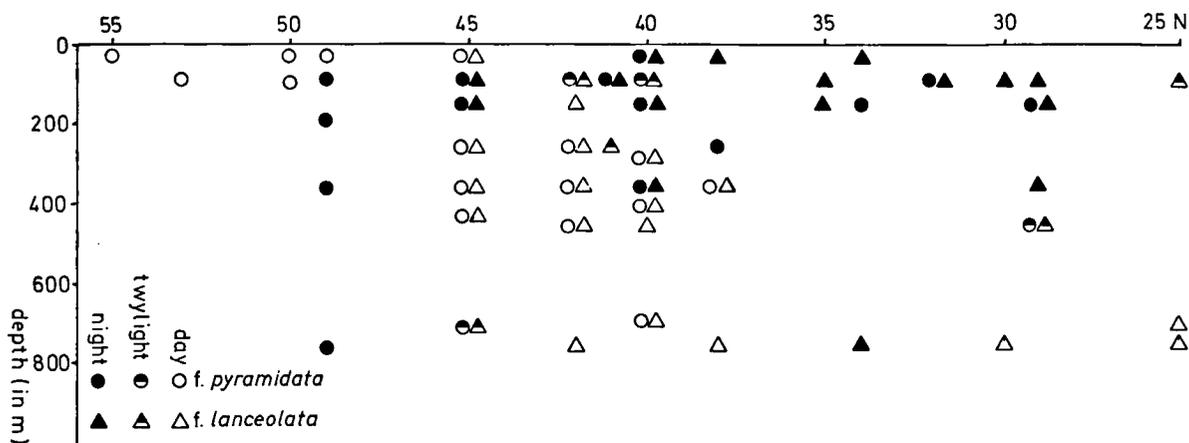


Figure 6. Distribution of *Clio pyramidata*; all catches with one or more specimens caught with the RMT₁+8, open RMT₁ or open Ringnet have been plotted at the mean depth of the haul.

to be a preference, throughout the horizontal area, for the surface zone at night. The most extensive day sample of *Clio pyramidata* forma *pyramidata* specimens has a depth stratum of 205 to 400 m, whereas at night the greatest number has been collected between 85 and 200 m. *Clio pyramidata* forma *lanceolata* was most abundant by day in a sample taken between 440 and 910 m, at night the greatest number was sampled between 45 and 95 m. Van der Spoel (1973b) mentions comparable data for *Clio pyramidata* forma *lanceolata*. He finds a vertical range between 50 and 550 m at night and between 350 and 950 m by day for a population found southeast of Bermuda. Everything considered, the conclusion seems justified that both formae show vertical migration, *Clio pyramidata* forma *lanceolata* living in deeper and colder water than forma *pyramidata*. The temperature range (cf. Van der Spoel, 1981) found by day for *Clio pyramidata* forma *lanceolata* is between ca. 8° and 13° C, for *Clio pyramidata* forma *pyramidata* it is between ca. 11° and 14° C.

To picture the latitudinal variation in abundance the standard numbers for the depth layer of 50 to 100 m with the corresponding latitudes are given in table 5. This depth stratum has also been used for the abundance pattern of *Diacria trispinosa* (table 2). It has been fished either at night or twilight at most of the stations, thus providing an image of the abundance of the formae of *Clio pyramidata* from north to south.

The abundance data for *Clio pyramidata* forma *pyramidata* show a peak at 45°N (station 14) followed by a decline in southern direction. If one assumes that as a consequence of the early spring time the whole population was shifted somewhat to the south, these data are in accordance with earlier ones (Van der Spoel, 1967). The centre of the present population of *Clio pyramidata* forma *pyramidata* is situated at about 45°N and the abundance decreases towards its borders. *Clio pyramidata* forma *lanceolata* shows a gradual decrease in abundance going northwards from 25° up to 35°N. Between 35° and 40°N, however, a rather abrupt rise occurs and between 40° and 42°N (stations 16, 17 and 18) the abundance is very high. Van der Spoel (1967) described the position of the *Clio pyramidata* forma *lanceolata* population in the Atlantic Ocean for latitudes between 40°S and 50°N with the centre of the population south of the area sampled during the present expedition. Therefore, a decrease in abundance with higher northern latitudes towards the border of the population has to be expected. The high abundances found between 40° and 42°N strongly contradict this supposition.

The width variation of *Clio pyramidata*, characteristic of formae, also shows irregularities between 40° and 42°N (table 6). To avoid influences of different developmental stage and mesh sizes of the net only specimens with a length between 6 and 8 mm caught with the RMT8 net

Table 5. Abundance of *Clio pyramidata* specimens caught during night and twilight between 50 and 100 m depth, with the RMT8 net. Abs. nrs = absolute numbers, stand. nrs = standard numbers.

latitude (N)	station no	forma <i>pyramidata</i>		forma <i>lanceolata</i>	
		abs. nrs	stand. nrs	abs. nrs	stand. nrs
49°	13	33	20.2	—	—
45°	14	81	138.5	1	3.0
42°	16	7	4.7	99	66.9
41°	17	30	11.8	573	225.2
40°	18	4	3.7	48	45.1
35°	20	—	—	1	0.8
32°	22	2	0.9	2	0.9
30°	24	—	—	21	9.4
29°	25	—	—	43	34.6
25°	26/27	—	—	3	2.1

Table 6. Mean width of *Clio pyramidata* shells with a length between 6 and 8 mm, caught with the RMT8 net.

latitude (N)	station no	number of specimens	mean width in mm	standard deviation
53°	11	2	4.77	0.31
49°	13	17	4.53	0.58
45°	14	52	4.45	0.78
42°	16	50	7.59	1.16
41°	17	56	7.79	1.27
40°	18	73	7.87	1.35
38°	19	8	5.76	0.75
30°	23/24	20	5.62	0.72
29°	25	24	4.93	0.65

have been used to picture width variation of the shells. This length-category contains a high number of specimens which have reached an adult stage with full-grown gonads and differentiation in the shape of the shells. Damage to the rather vulnerable shells limits the possibility of measuring shells of all the stations. Of stations 20, 21, 22, 26 and 27 no undamaged shells are available, the numbers from stations 23 and 24, situated close to each other at approximately 30°N, have been taken together. The numbers from stations 11 and 19 are restricted to 2 and 8 specimens respectively. Table 6 shows that the mean width of the shells at stations 16, 17 and 18 is far greater than at the adjoining stations. This is in sharp contrast with the hypothesis of a gradual increase in width from north to south (Van der Spoel, 1967). Besides, at the stations mentioned the standard deviation is distinctively higher than at other stations.

The present data together with the deviatingly high abundances (table 5) at these very latitudes, give rise to the assumption that here two different types of populations are present. One population with the transitional species of *Clio pyramidata* forma *pyramidata* into forma *lanceolata*, and, between 40° and 42°N, of another extensive population of more typical and wider *Clio pyramidata* forma *lanceolata* specimens. This supposition is confirmed when the correlation between the width of the shell and the latitude is studied (fig. 7). When data of all the stations are considered, no linear correlation exists ($r = 0.17$). However, when the supposed inflow of the more typical *Clio pyramidata* forma *lanceolata* population is excluded from the calculations by leaving out the data of stations 16, 17 and 18, the linear regression becomes rather high ($r = 0.61$) with a slight clinal increase in width with lower latitudes.

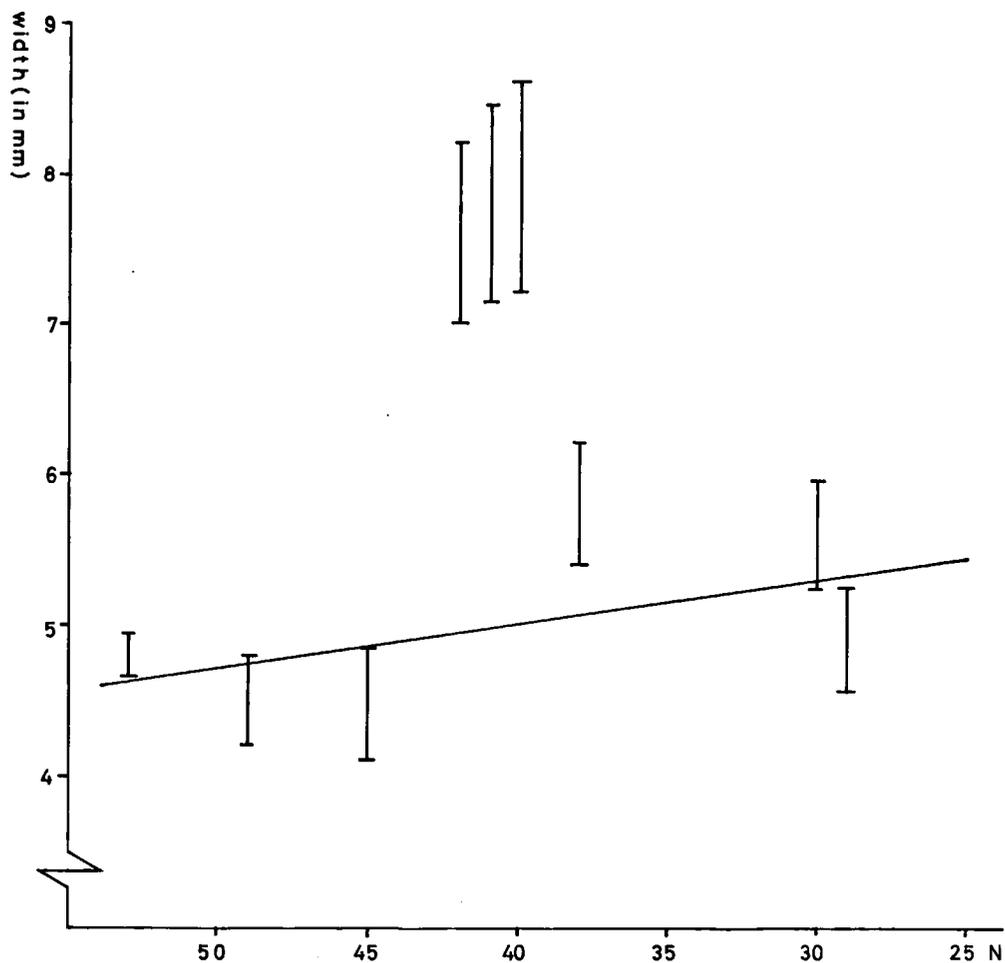


Figure 7. Mean width of the shells of *Clio pyramidata* with corresponding standard deviations (shell length between 6 and 8 mm). Linear regression: $r = 0.61$ (stations 16, 17 and 18 excluded).

Moreover, histograms of the width of the shells at the different stations based on the data used for table 6 turn out to be double-peaked for the stations 16, 17 and 18, while for station 14 it is clearly single-peaked (fig. 8). This, too, suggests that at the three former stations two different patterns in the width of the shell coexist. In contrast, the population of station 14 is built up uniformly and the same is suggested by the histograms of the remaining stations (except perhaps station 23/24), but their numbers are too small to justify any conclusions. Although the phenomena described above point to the presence of two separate types of populations it proves to be impossible to classify individual specimens

with either of the two groups on the basis of external characteristics of body-shape or shell structure. Nor is it possible to distinguish the populations on account of their vertical distribution. They do not live above one another as wide and less wide specimens occur in the same hauls in day as well as in night samples.

DISCUSSION

Several planktonic groups show a faunal boundary in the Mid and East Atlantic Ocean between 40° and 45°N. McIntyre & Bé (1967) describe in detail the geographic distribution in the Atlantic of Coccolithophores; they distinguish four basic

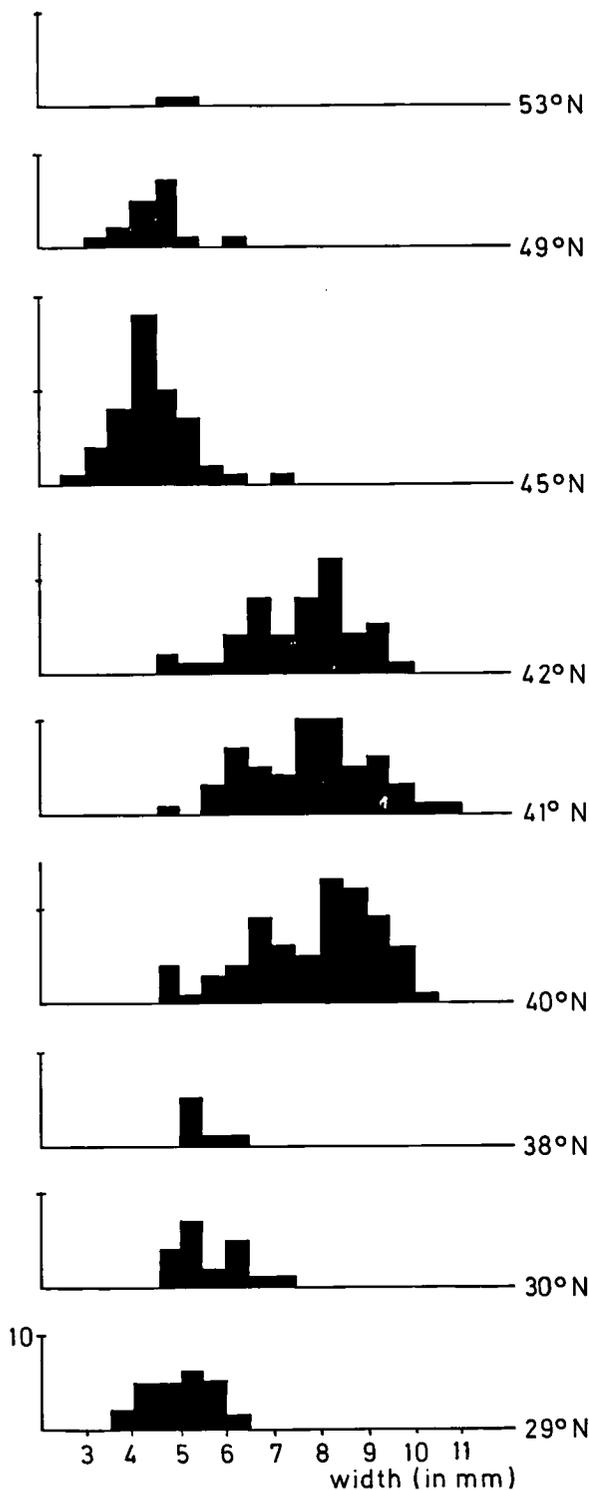


Figure 8. Histograms of the width of the shells of *Clio pyramidata* at different latitudes (shell length between 6 and 8 mm).

zones: the tropical zone up to 20°N, the subtropical zone, the northern border of which corresponds with the Subtropical Convergence at about 40°N, the transitional zone bounded by this convergence in the south and the Polar Front in the north and the subpolar zone north of it. A variety of zooplankton groups seem to follow the same overall pattern. Angel (1979) mentions, for example, euphausiid, ostracod and mesopelagic fish communities with boundaries between the subtropical and transitional zones. However, he suggests that these boundaries lie somewhat more northwards, in the region of 44°N, at least at the north-west corner of the Iberian Peninsula. For some polytypic species the transition of formae (sensu Van der Spoel, 1971) has been described at these latitudes, e.g. for pteropods (Van der Spoel, 1967), tunicates (Van Soest, 1972) and chaetognaths (Pierrot-Bults, 1975). Data of the present expedition add to these the variation pattern of *Argyropelecus olfersi* (Cuvier, 1829), belonging to the silver hatchetfishes (Sternoptychidae) (Pafort-van Iersel, 1981). The intergrading zone of the northern forma *Argyropelecus olfersi* forma *olfersi* (Cuvier, 1829) into the southern forma *Argyropelecus olfersi* forma *aculeatus* Valenciennes, 1849 has been found at the surface between approximately 45° and 50°N and shifts to deeper water layers at lower latitudes.

The two pteropod species studied in this paper both show a faunal boundary in the North Atlantic. The transition of the northern forma *Diacria trispinosa* forma *atlantica* into the southern forma *trispinosa* starts at 42°N, being the northernmost position from where transitional specimens have been identified. Gradually the number of these specimens increases together with a decrease of the typical *Diacria trispinosa* forma *atlantica* specimens. *Diacria trispinosa* forma *trispinosa* specimens were scarcely found between 25° and 41°N, probably the centre of this population is situated south of the area sampled. This would agree with Dupont (1979) who describes the Atlantic population of typical *Diacria trispinosa* forma *trispinosa* specimens between 35°S and 35°N. The difference between the formae so far considered are restricted to the shape of the

shells. Measurements show that the length and width of the shells decrease from northern to southern latitudes. At the transitional zone at 42° or 41°N no sharp decline in size has been traced; on the contrary, in the area sampled, a strong linear relation between size and latitude exists (fig. 5). The conclusion to be drawn from these data is that the *Diacria trispinosa* population in the North Atlantic shows a smooth cline with smaller specimens at lower latitudes. With respect to the vertical distribution *Diacria trispinosa* shows a vertical migration in accordance with data from Van der Spoel (1973b). At night the specimens mainly occur in the upper 100-200 metres, in the daytime the specimens prefer a depth of about 300 m, correlated with a temperature range of 12° to 15° C. The southern *Diacria trispinosa* forma *trispinosa* seems to inhabit deeper water by day than its northern counterpart, the numbers, however, are so small that a conclusion would be premature.

Clio pyramidata, as expected (Van der Spoel, 1967), has been caught throughout the area. *Clio pyramidata* forma *lanceolata* is present up to 45°N, *Clio pyramidata* forma *pyramidata* frequently occurred north of 40°N whereas only a few specimens of this forma were caught south of 40°N. Consequently, in the present material the transition of *Clio pyramidata* forma *pyramidata* into forma *lanceolata* takes place between 40° and 45°N. As has been illustrated in table 6, figures 7 and 8, the present data concerning the width of the shells suggest the presence of two different types of populations. One type, to be called 'local', is present in the whole range sampled, with typical *Clio pyramidata* forma *pyramidata* specimens in the north, changing into *Clio pyramidata* forma *lanceolata* going southwards. The large number of very wide typical *Clio pyramidata* forma *lanceolata* specimens between 40° and 42°N belong to the second type of *Clio pyramidata* population. At these latitudes, the local populations show the transitional stage of *Clio pyramidata* forma *pyramidata* into forma *lanceolata* and consequently display a small shell width, whereas the second type of populations consists of very wide specimens, which points to an origin in regions at lower latitudes. The mean width of

the second type found between 40° and 42°N is even distinctively larger than that of the local type at the southernmost stations sampled. Consequently, the whole area sampled south of 40°N consists of representatives of the local populations which are transitional between typical *Clio pyramidata* forma *pyramidata* and typical forma *lanceolata* specimens. The centre of the latter must be located south of 25°N, at least in this early time of the year, which is in accordance with Van der Spoel (1967), who describes the Atlantic *Clio pyramidata* forma *lanceolata* population between 40°S and 50°N. Latitudinal variation in *Clio pyramidata* is expressed by changes in the width of the shell. When the measurements of the stations between 40° and 42°N (16, 17 and 18) are excluded to avoid mixing of data of two different population types, the width of the shell proves to increase with lower latitudes. In the local population the transition of *Clio pyramidata* forma *pyramidata* into forma *lanceolata* starts between 40° and 45°N. Because of the low number of local specimens from stations 16, 17 and 18 a possible sharp increase in the width of their shells may be obscured by the high number of wide specimens. The data of the remaining stations, however, show a rather strong linear relation between the width of the shell and the latitude (fig. 7), so the conclusion is justified that in the North Atlantic variation in the local *Clio pyramidata* population forms a smooth cline.

Clio pyramidata shows vertical migration in accordance with Van der Spoel's (1973b) data for *Clio pyramidata* forma *lanceolata*. At night most specimens are collected in the upper 200 m, in the daytime *Clio pyramidata* forma *pyramidata* is most abundant in the depth stratum of 200 to 300 m whereas the most extensive samples of *Clio pyramidata* forma *lanceolata* have been taken between 400 and 900 m. Both formae occur in shallower water in the northern part of their distribution area (fig. 5). The southern forma, *Clio pyramidata* forma *lanceolata*, seems to prefer deeper water than its northern counterpart. Data of *Diacria trispinosa*, discussed above, point in the same direction, although less clearly. There are many other examples of northern temperate species penetrating into lower latitudes by sub-

mergence and undoubtedly adaptations to a distinct temperature range play an important role here. Angel (1979) mentions, for instance, planktonic ostracods and mesopelagic fishes with such a distribution pattern. Of the present expedition material the Scyphomedusa *Periphylla periphylla* (Péron & Lesueur, 1809) (Linnenbank, intern. rep.) and the silver hatchetfish *Argyropelecus olfersi* (Cuvier, 1829) (Pafort-van Iersel, 1981) show the same phenomenon: between 45° and 50°N they have been caught in surface waters, whereas at lower latitudes they live in deeper waters. The chaetognath *Sagitta planctonis* Steinhilber, 1896, also submerges with lower latitudes (Pierrot-Bults, 1975). The situation within this species, however, is not quite comparable with that of *Clio pyramidata*. Specimens of the northern form *Sagitta planctonis* forma *zetesios* live deeper than specimens of the southern form *Sagitta planctonis* forma *planctonis* of the same latitudes, whereas the reverse occurs in *Clio pyramidata*.

The abundance of *Clio pyramidata* forma *lanceolata* between 40° and 42°N is very high (table 5), the same applies to *Diacria trispinosa* forma *atlantica* (table 2). Also in some other groups high abundances have been found. Winkler (1982) recorded at these latitudes the highest abundance of the Hydromedusa *Pandea conica*, from material of the same expedition. Moreover, the density of the deep-scattering-layer (DSL) between 400 and 600 m depth had its maximum around 40°N, and the numbers of scattering groups measured at noon showed a distinct peak in this area (Schalk, intern. rep.). All these observations point to an overall increase in biomass in this region. South of 38°-40°N the abundances of *Clio pyramidata*, *Diacria trispinosa*, Hydromedusae (Winkler, 1982) and of scattering groups is very low and the density of the DSL has become a factor ten lower than at 40°N (Schalk, intern. rep.), which all points to the oligotrophic Sargasso Sea water. The occurrence in this area of young Apoda, for instance leptocephali of *Serrivomer parabeani* Bertin, 1940 (Van Utrecht, pers. comm.) whose mating dominion is supposed to be in the Sargasso Sea, confirms this supposition.

Altogether, the situation between 40° and 42°N is remarkable. It suggests that in this part of the ocean influences of different water masses are active which accounts for changes in the ecological circumstances. In their turn, these are responsible for the number of planktonic groups with a faunal boundary in this area, to which the present material adds two groups with an infra-specific transition of northern into southern formae (viz. *Diacria trispinosa* and *Clio pyramidata*). Moreover, there is a high abundance of several planktonic groups, the peak in the density of the DSL, the high numbers of scattering groups, and the high diversity, e.g. in the number of Hydromedusa species (Winkler, 1982). A rise in production can be the result of mixing of water masses each with its own limitation to reproduction and growth, due to restriction of physical and chemical conditions. After mixing there are no longer restrictions, which consequently causes a revival of biological activity. Fraser (1961) has suggested the same for crustaceous plankton around the British Isles. High production will also have been intensified by spring conditions probably present at that very moment at these latitudes. Finally, in the stations of this region, in contrast with the other stations, many *Clio pyramidata* specimens were found to be in an aberrant stage (table 4). The occurrence of many aberrants suggests instable hydrological conditions (Van der Spoel, 1979) which hamper normal reproduction, thereby causing its replacement by a form of vegetative reproduction. The aberrant specimens may be considered a stage of inactivity as an answer to less favourable conditions as in the case of the very high percentage of aberrants among the few *Clio pyramidata* forma *pyramidata* specimens found far south of their environment proper (Table 4), probably brought there by the Canary Current. In its turn the population of very wide *Clio pyramidata* forma *lanceolata* specimens at 40° to 42°N seems out of place and in unsuitable circumstances, which would account for its high percentage of aberrant specimens. The high percentage of vegetatively reproducing specimens may also be caused by the mentioned nutritional enrichment at places where different water masses meet, which causes biological activity to

become concentrated on nourishment and not on sexual reproduction.

The data discussed above indicate that between 40° and 45°N different waters meet, which is reflected in the composition of the plankton community. Besides the expected transition of subtropical into temperate waters, the biological data indicate the inflow of western waters around 41°N. This is confirmed not only by the presence of the typical *Clio pyramidata* forma *lanceolata* populations, but also by the record (Winkler, 1982) of some tropical Hydromedusae species (e.g. *Pandea conica*) known from the Bay of Bermuda, among other places. It is tempting to introduce here influences of eddies of which it is known that they not only constantly differ from the encircling waters in hydrological features, but also in the composition of their faunas (Sherman et al., 1977). This, however, does not provide a solution to the problem as their mean width in the North Atlantic is about 200 km, which can hardly affect the whole range from 40° to 42°N. Besides, the hydrological data, e.g. temperature and salinity (cf. Van der Spoel, 1981), do not indicate the presence of eddies. The same applies to the recently described Meddies, various small eddies with a supposed origin near the Mediterranean (Kerr, 1981). A more plausible theory is that western water populations have been transported from the tropical West Atlantic as far as the Azores by the Gulfstream and the southern branch of the North Atlantic Current. Typical *Clio pyramidata* forma *lanceolata* populations are known to inhabit the tropical West Atlantic (Van der Spoel, 1967). However, they have never been reported before from 40° to 42°N in the Mid Atlantic, so, whatever the explanation, the transport by the North Atlantic Current in north-eastern direction must have extended over a larger stretch than usual.

Summarised, the above shows that for the two pteropod species studied the transition of northern into southern formae starts between 40° and 45°N, and that the changes in characteristic dimensions form a smooth cline in both cases. The transitional areas coincide with the transition of temperate into subtropical waters. The presence of a tropical population of *Clio pyramidata* forma

lanceolata suggests the inflow of western water via Gulfstream and North Atlantic Current. In that case this study unequivocally supports the statement by Furnestin (1979) that, at an infra-specific level, some thecosomatous pteropods are excellent biological indicators of water masses.

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REFERENCES

- ANGEL, M. V., 1979. Zoogeography of the Atlantic Ocean. In: S. van der Spoel & A. C. Pierrot-Bults (Eds), Zoogeography and diversity of plankton: 168-190. (Bunge, Utrecht).
- BAKER, A. de C., M. R. CLARKE & H. J. HARRIS, 1973. The N.I.O. combination net (RMT1+8) and further developments of rectangular midwater trawls. J. mar. biol. Ass. U.K., **53**: 167-184.
- CASANOVA, J. P., 1980. Campagnes du 'Meteor' dans l'Atlantique N-E. Siphonophores, Méduses et Thécosomes; distribution verticale et comparaisons faunistiques avec la Méditerranée. 'Meteor' Forsch. Ergebnisse, (D), **32**: 15-32. (Berlin, Stuttgart).
- DUPONT, L., 1979. Note on variation in *Diacria* Gray, 1847, with descriptions of a species new to sciences, *Diacria rampali* nov. spec., and a forma new to science, *Diacria trispinosa* forma *atlantica* nov. forma. Malacologia, **18**: 37-52.
- FRASER, J. H., 1961. The oceanic and bathypelagic plankton of the N.E. Atlantic. Mar. Res. Scot., **4**: 1-48.
- FURNESTIN, M. L., 1979. Planktonic molluscs as hydrological and ecological indicators. In: S. van der Spoel, A. C. van Bruggen & J. Lever (Eds), Pathways in Malacology: 175-194. (Bohn, Scheltema & Holkema, Utrecht).
- HEYMAN, R. P., 1981. Narcotisation, fixation and preservation experiments with marine zooplankton. Versl. techn. Geg. ITZ, Univ. Amsterdam, **28**: 1-36 (mimeographed).
- KERR, R. A., 1981. Small eddies proliferating in the Atlantic. Science, **213**: 632-634.
- MCINTYRE, A. & A. W. H. BE, 1967. Modern Coccolithophoridae of the Atlantic Ocean. I. Placoliths and Cyrtholiths. Deep-Sea Res., **14**: 561-597.
- PAFORT-VAN IERSEL, T., 1981. The Sternoptychidae (Pisces, Stomiatoidei) of the Amsterdam Mid North Atlantic Plankton Expedition 1980, with a note on specimens intermediate between *Argyropelecus aculeatus* Valenciennes, 1849 and *A. olfersi* (Cuvier, 1829). Beaufortia, **31** (4): 97-106.

- PAFORT-VAN IERSEL, T. & S. VAN DER SPOEL, 1978. The structure of the columellar muscle system in *Clio pyramidata* and *Cymbulia peroni* (Thecosomata, Gastropoda), with a note on the phylogeny of both species. *Bijdr. Dierk.*, **48** (2): 111-126.
- PANHORST, W. L. & S. VAN DER SPOEL, 1974. Notes on the adult and young stages in *Diacria* (Gastropoda, Pteropoda). *Basteria*, **38**: 19-26.
- PIERROT-BULTS, A. C., 1975. Taxonomy and Zoogeography of *Sagitta planctonis* Steinhaus, 1896 (Chaetognatha) in the Atlantic Ocean. *Beaufortia*, **23** (297): 27-51.
- RAMPAL, J., 1975. Les thécosomes (Mollusques pélagiques). Systématique et évolution. Ecologie et biogéographie Méditerranéennes. Thèse Doct. ès-Sciences nat., Univ. Prov. Marseille: 1-485 (mimeographed).
- ROE, H. S. J., A. DE C. BAKER, R. M. CARSON & R. WILD, 1980. Oceanographic Sciences' rectangular midwater trawls: Theoretical aspects and experimental observations. *Mar. Biol.*, **56**: 247-259.
- SHERMAN, K., D. BUSCH & D. BEARSE, 1977. Deepwater Dumpsite 106: Zooplankton Studies. Base line Report of Environmental Conditions in Deep Water Dumpsite 106. U.S. Dept. of Commerce, Rockville, Md.: i-xx.
- SOEST, R. W. M. VAN, 1972. Latitudinal variation in Atlantic *Salpa fusiformis* Cuvier 1804 (Tunicata, Thaliacea). *Beaufortia*, **20** (262): 59-68.
- VAN DER SPOEL, S., 1962. Aberrant forms of the genus *Clio* Linnaeus, 1767, with a review of the genus *Proclio* Hubendick, 1951 (Gastropoda, Pteropoda). *Beaufortia*, **9** (107): 173-200.
- , 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda): 1-375. (Noorduyn & Zn, Gorinchem).
- , 1970. Morphometric data on Cavoliniidae with notes on a new form of *Cuvierina columnella* (Rang, 1827) (Gastropoda, Pteropoda). *Basteria*, **34**: 103-151.
- , 1971. Some problems in infraspecific classification of holoplanktonic animals. *Z. zool. Syst. EvolForsch.*, **9** (2): 107-138.
- , 1972. Pteropoda Thecosomata. *Cons. Int. Explor. Mer. Zooplankton Sheet* **140-142**: 1-12.
- , 1973a. Strobilation in a Mollusc; the development of aberrant stage in *Clio pyramidata* Linnaeus, 1767 (Gastropoda, Pteropoda). *Bijdr. Dierk.* **43**: 202-215.
- , 1973b. Growth, reproduction and vertical migration in *Clio pyramidata* Linné, 1767 forma *lancoolata* (Lesueur, 1813), with notes on some other Cavoliniidae (Mollusca, Pteropoda). *Beaufortia* **21** (281): 117-134.
- , 1979. Strobilation in a pteropod (Gastropoda, Opisthobranchia). *Malacologia* **18**: 27-30.
- , 1981. List of discrete depth samples and open net hauls of the Amsterdam Mid North Atlantic Plankton Expedition 1980. *Bull. zool. Mus. Univ. Amsterdam* **8** (1): 1-10.
- WINKLER, J., 1982. The Hydromedusae of the Amsterdam Mid North Atlantic Plankton Expedition 1980 (Coelenterata, Hydrozoa). *Beaufortia*, **32** (3): 27-56.

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