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Taxonomy and zoogeography of *Sagitta planctonis* Steinhaus, 1896 (Chaetognatha) in the Atlantic Ocean

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ABSTRACT

Depth distribution, morphology, meristic, quantitative and qualitative characters of *S. planctonis* and *S. zetesios* are compared. A factor analysis and a discriminant analysis was made. *S. planctonis* is considered a polytypic species consisting of two formae: *S. planctonis* forma *planctonis* and *S. planctonis* forma *zetesios*.

INTRODUCTION

The chaetognath *Sagitta planctonis* Steinhaus, 1896, is described originally from shallow net hauls in the Atlantic South Equatorial Current. Fowler (1905) described the closely related species *S. zetesios* from deep water in the Bay of Biscay. Since then, both species were regarded synonymous by subsequent authors (Ritter-Zahony, 1909, 1911; Michael, 1911; Germain & Joubin, 1916; Burfield & Harvey, 1926; Tokioka, 1939, 1940), most of these authors commented on the variability of *S. planctonis* and the impossibility of dividing it into two different species, because of the overlap in possible discriminating characters as there are: the number of teeth, the position of the anterior margin of the anterior fins and the place of the seminal vesicles.

David (1956) described a new species *S. marri* from the Antarctic Ocean, closely related to *S. planctonis* and concluded that *S. zetesios* also has to be considered a valid species.

David (1956) considered the number of posterior teeth as the main discriminating character of *S. planctonis* and *S. zetesios*. Animals longer than

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TABLE I. Taxonomic differences between *S. planctonis*, *S. zetesios* and *S. marri* (after David, 1956 and Alvariño, 1969)

	S. planctonis	*S. zetesios*	*S. marri*
body length	up to 37 mm	up to 40 mm	up to 28.5 mm
tail length in % of body length	19.2—21.4%	20—23%	20—28%
number of hooks	8 — 11	8 —11	7 —11
number of anterior teeth	6 — 8 (sometimes 9)	8 —10 (sometimes 12)	6 — 7 (sometimes 8)
number of posterior teeth	10—12 (sometimes 14)	15—19 (sometimes 22)	14—15 (sometimes 17)
length of anterior fins	24—32%	20—26%	10—19%
anterior fins	Rayless at the anterior end and inner edge, beginning at the ventral ganglion or halfway of the ventral ganglion.	rayless at anterior end, beginning at or close to the ventral ganglion.	completely rayed, beginning slightly behind the ventral ganglion.
posterior fins	Sharply triangular.	Triangular.	Rounded.
ovaries	Completely filling body cavity when fully mature, ova in 4 or 5 rows.	Maximally reaching halfway between head and ventral ganglion, ova in 3 rows.	Reaching up to ventral ganglion.
seminal vesicles	Elongate in contact with posterior fins, simple.	Probably as in *S. planctonis*.	Conical, very close to tail fin.
distribution	Bermuda, S.E. Africa, Tasman Sea off N.E. New Zealand and parts of N. Atlantic. Surface living form breeding at a moderate depth 750—1000 m (David, 1956). Subantarctic, mesoplanctonic (Alvariño, 1969).	A deep living form found in most deep oceans absent from the Antartic (David, 1956). Cosmopolitic in temperate and warm oceanic regions, mesoplanctonic (Alvariño, 1969)	Probably a purely Antarctic form, extending from the surface down to about 1000 m, commonest between 750—250 m, breeding in deep water (David, 1956). Circumpolar, antarctic, mesoplanctonic (Alvariño, 1969).

15 mm should have less than 15 posterior teeth in *S. planctonis* and more than 15 in *S. zetesios*.

Alvariño (1964) considered the position of the anterior end of the anterior fins as the key character to distinguish *S. planctonis* and *S. zetesios*.

The differences between *S. planctonis, S. zetesios* and *S. marri* as given by David (1956) and Alvariño (1964, 1969) are compiled in table 1. The occurrence of *S. planctonis* above 200 m was said to be due to upwelling watermasses.

Tokioka (1940) considered *S. planctonis* and *S. zetesios* synonymous; however, in his 1965 paper he considered the three species (sensu David, 1956) as valid.

S. planctonis and *S. zetesios* are sometimes difficult to distinguish in samples from the tropical and temperate Atlantic. They may occur together in the same samples with their intermediates. As the percentage of intermediates in the samples and the occurrence of either the one species or the other, varies with latitude (Pierrot-Bults, 1969, 1970), it was concluded that *S. planctonis* and *S. zetesios* were synonymous, forming a polymorphic species.

Aurich (1971) working with North-Atlantic samples taken between 35°N and 65°N found 5 to 6% intermediates among specimens varying in length from 16 to 25 mm. Specimens longer than 25 mm all belonged to *S. zetesios*. In the samples taken between 35°N and 45°N, *S. planctonis* was the dominant species, more northern samples showed a successive disappearance of *S. planctonis* and the intermediate forms, till about 55°N. Further north *S. zetesios* was the exclusive representative of the group, even in layers above 500 m.

This confirms the theory already developed by Fowler (1905) that *S. zetesios* is mesoplanctonic in the warmer regions, but more epiplanctonic in temperate regions. Ritter-Zahony (1909) reported this phenomenon for the southern hemisphere, and Aurich (1971) proved it to be true for the northern hemisphere as well.

Studying samples from the Dana Expeditions taken off the south-west African coast and samples from the Ocean Acre program*) collected near Bermuda, more information became available on the vertical distribution of the species.

Material studied

In the list of material the following abbreviations are used: h - hour; m.w. - meters wire out; m - real depth of sample in meters; spec. - specimens; ZMUC - Zoologisk Museum Copenhagen; USNM - United States National Museum; ZMA - Zoological Museum Amsterdam.

*) This material was collected by the Ocean Acre Program of the USNM, supported by funds from the U.S. Navy.

ZMUC Dana Expedition

sta.3978 III	30°15′S	13°15′E	13-2-1930	300 m w	02.30 h	14 spec.
sta.3978 VI	do		do	5000 m w	08.45 h	7 spec.
sta.3978 VII	do		do	4000 m w	08.45 h	67 spec.
sta.3978 XI	do		do	1000 m w	08.45 h	10 spec.
sta.3980 IX	23°26′S	03°56′E	17-2-1930	3000 m w	09.10 h	115 spec.

USNM Ocean Acre-all stations bounded by 31°30′—32°30′N and 63°30′—64°30′W.

sta.10— 4A	2-6-1970	800 m	14.55—15.55 h	10 spec.
sta.10— 4B	2-6-1970	800 m	15.55—16.55 h	15 spec.
sta.10—20A	6-6-1970	490 m	16.00—17.00 h	1 spec.
sta,10—23B	7-6-1970	630 m	14.22—15.22 h	8 spec.
sta.10—23C	7-6-1970	630 m	15.22—16.22 h	20 spec.
sta.10—37N	10-6-1970	0— 480 m	15.00—16.00 h	1 spec.
sta.11— 9C	14-1-1971	860— 875 m	22.45—23.45 h	10 spec.
sta.11— 9M	14-1-1971	0— 860 m	23.34—00.45 h	6 spec.
sta.11—13C	15-1-1971	650— 675 m	16.51—17.51 h	1 spec.
sta.12— 4M	27-8-1971	0— 630 m	16.24—17.15 h	10 spec.
sta.12— 5B	27-8-1971	975—1000 m	20.23—21.22 h	12 spec.
sta.12— 7C	28-8-1971	1000—1050 m	09.40—10.40 h	11 spec.
sta.12— 9B	28-8-1971	705— 760 m	20.45—21.45 h	5 spec.
sta.12—16A	30-8-1971	903— 951 m	07.20—08.20 h	1 spec.
sta.12—16M	30-8-1971	0— 930 m	10.20—11.20 h	7 spec.
sta.12—23A	2-9-1971	775— 855 m	06.28—07.20 h	1 spec.
sta.12—27C	3-9-1971	894— 925 m	22.10—23.10 h	4 spec.
sta.12—28B	4-9-1971	109— 113 m	01.20—02.20 h	1 spec.
sta.13—12C	24-2-1972	1051—1068 m	15.50—16.40 h	4 spec.
sta.14— 6A	6-6-1972	761— 842 m	07.00—08.00 h	10 spec.
sta.14— 6B	6-6-1972	760— 800 m	08.00—10.00 h	70 spec.
sta.14—10B	7-6-1972	580— 622 m	07.45—08.45 h	8 spec.
sta.14—10C	7-6-1972	578— 600 m	08.45—09.45 h	13 spec.
sta.14—10M	7-6-1972	0— 578 m	09.45—10.12 h	2 spec.
sta.14—11M	7-6-1972	0—1250 m	17.45—19.45 h	7 spec.
sta.14—12A	7-6-1972	741— 870 m	20.50—21.35 h	16 spec.
sta.14—12B	7-6-1972	741— 795 m	21.35—22.25 h	8 spec.
sta.14—12C	7-6-1972	751— 800 m	22.25—23.10 h	27 spec.
sta.14—12M	7-6-1972	0— 799 m	23.10—23.43 h	23 spec.
sta.14—16P	8-6-1972	0—1038 m	20.55—21.35 h	6 spec.
sta.14—22M	10-6-1972	0—1530 m	09.45—10.45 h	6 spec.
sta.14—23A	10-6-1972	660— 723 m	11.45—12.45 h	7 spec.
sta.14—23B	10-6-1972	654— 674 m	12.45—13.45 h	7 spec.
sta.14—23C	10-6-1972	662— 694 m	13.45—14.45 h	11 spec.
sta.14—24B	10-6-1972	979—1015 m	22.00—23.00 h	6 spec.
sta.14—24C	10-6-1972	980—1025 m	23.00—24.00 h	2 spec.

sta.14—29C	11-6-1972	1205—1249 m	22.55—23.55 h	3 spec.
sta.14—29M	11-6-1972	0—1179 m	23.55—00.47 h	3 spec.
ZMA Tridens Cruise, 1972				
sta. 7	39°15'N 21°25'W	± 0—700 m	1-6-1972	2 spec.

METHODS

Mathematical methods were applied to attain a justification of some of the findings. Nine parameters, obtained from the "Ocean Acre" material, were considered, viz.: total body length, tail length, anterior fin length, number of anterior teeth, number of posterior teeth, sexual stage, depth at which, month of the year in which, and time of the day at which the sample was taken.

From the "Dana" samples six parameters were considered, viz.: total body length, tail length, position of anterior fin, number of anterior teeth, number of posterior teeth and sexual stage.

The samples from the Dana Expeditions and Tridens Cruise, for which the anterior fin length was not considered, were integrally studied; the "Ocean Acre" chaetognath samples are, however, randomly sorted from the unsorted plankton sample by Dr. S. van der Spoel. This means that the total number of specimens may not be the total number collected, but the variation range seems well covered.

Principal factor analysis with iterative estimated communalities was executed using SPSS (Nie et al., 1970).

Multiple discriminant analysis was performed using the SPSS subprogram DISCRIM based on Cooley & Lohnes (1971).

VERTICAL DISTRIBUTION AND MIGRATION

The most useful discrimination characters proved to be (a) the position of the anterior fins (reaching to the posterior margin of the ventral ganglion in *S. zetesios*; reaching anteriad to the posterior end of the ventral ganglion in *S. planctonis*); (b) the number of posterior teeth (from 15 up to 22 in *S. zetesios*; from 8 up to 14 in *S. planctonis*); and (c) the number of anterior teeth (from 8 up to 12 in *S. zetesios*; from 4 up to 8 in *S. planctonis*).

For the Dana samples from Sta.3978 (32°S 03°E) and Sta.3980 (23°S 03°E) the distribution among the specimens of these discriminating characters gave more or less the same picture as in North-Atlantic samples, published previously (Pierrot-Bults, 1970).

For Sta.3980 22% of the specimens showed all three *S. planctonis* characters, 62.5% showed *S. zetesios* characters and 15.5% were intermediates. For Sta.3978 8.6% of the individuals showed *S. planctonis* characters, while 51.7% showed *S. zetesios* characters and 39.7% were intermediate in character.

Vertical distribution of the two forms was very difficult to trace, as the Dana Expeditions only used open nets and the depth was inaccurately calculated using wire angle and wire length. Still the different samples taken at Sta.3978 are illustrative. At Sta.3978 III (300 m wire out) only *S. planctonis* was present, at Sta.3978 VI (5000 m wire out) only *S. zetesios* and intermediates were present, at Sta.3978 VII (3050 m wire out) both *S. planctonis* and *S. zetesios* as well as intermediates were present At Sta.3980 IX (4025 m wire out) both *S. planctonis* and *S. zetesios* as well as intermediates were present.

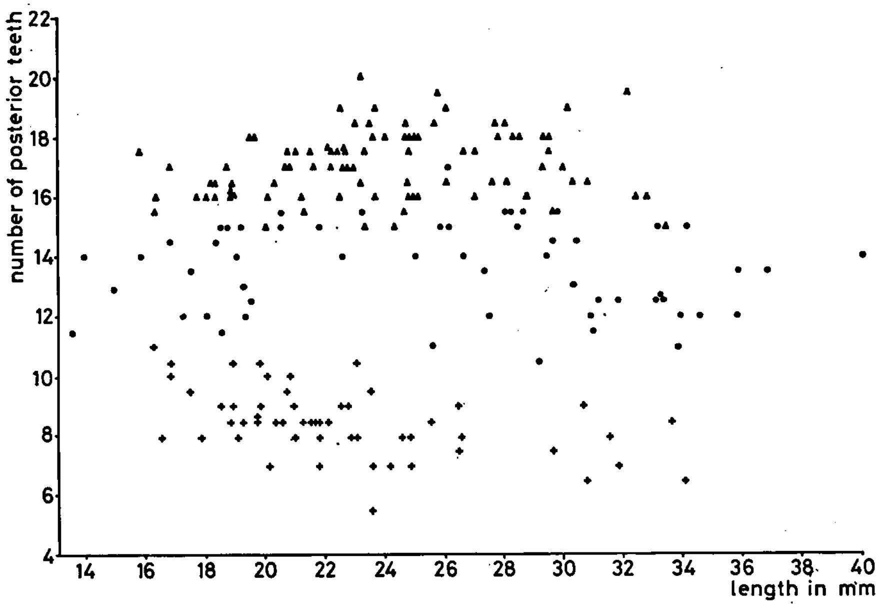


FIG. 1. Diagram of number of posterior teeth (y-axis) in relation to total body length (x-axis) for *S. planctonis* collected by the Dana Expeditions. Triangles - "zetesios"; dots - intermediates; crosses - "planctonis".

Figure 1 shows the number of posterior teeth in relation to total body length for these Dana samples and figure 2 shows this relation for the Ocean Acre samples.

A more accurate estimation of the vertical distribution is possible with the Ocean Acre samples, all taken within the one degree square south-east of Bermuda. These samples showed only *S. zetesios* to be present between 650 and 1068 m depth in February 1971 (Acre 12) and in February 1972 (Acre 13). In June 1970 (Acre 10), June 1972 (Acre 14) and in August and September 1971 (Acre 11). *S. planctonis* was found between 400 and 1200 m, intermediates between 800 and 1000 m, and *S. zetesios* was then found between 900 and 1250 m. *S. planctonis* was absent from the January and February samples, although the samples covered the depth between the surface and 1068 m. In this period *S. zetesios* occurred less deep (650—1068 m) than in June and August (980—1250 m).

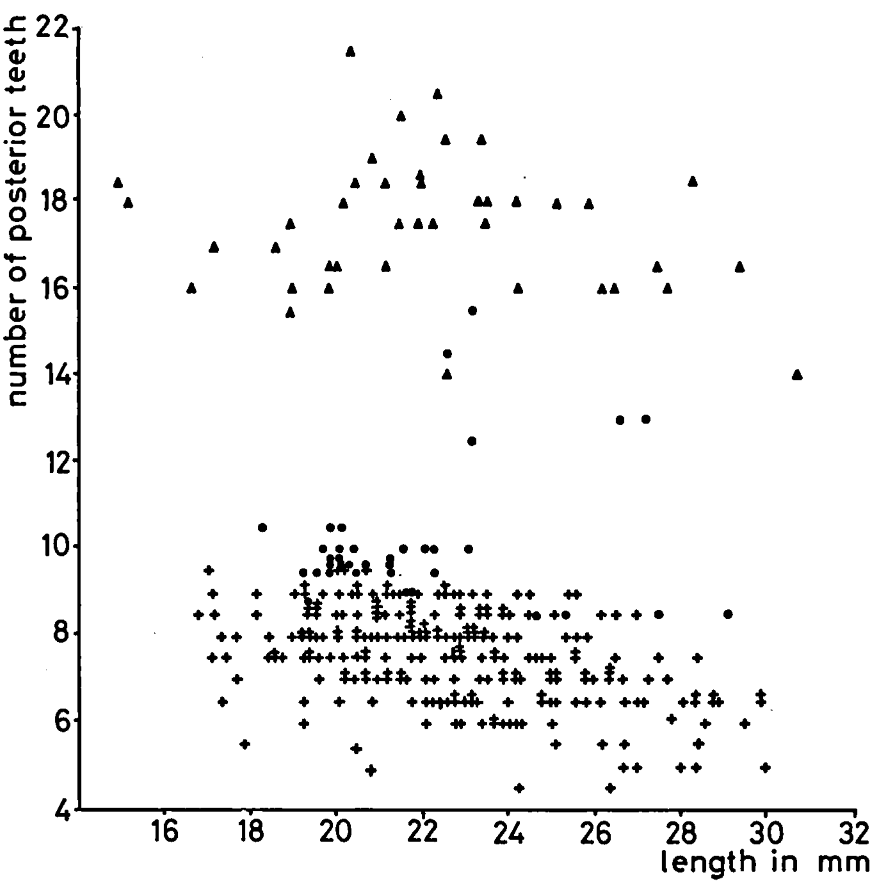


FIG. 2. Diagram of number of posterior teeth (y-axis) in relation to total body length (x-axis) for *S. planctonis* collected by the Ocean Acre cruises. Triangles - "zetesios"; dots - intermediates; crosses - "planctonis".

The time of the day at which the samples were taken did not seem to affect the general vertical distribution considerably.

The vertical distribution for the different months is shown in figure 3.

The absence of *S. planctonis* in the winter season may be due to the seasonal changes in the northern extension of the distribution. The area off Bermuda 32°N near the subtropical convergence is a transitional area of warm central forms and temperate forms. Discontinuities in clinal variation are also reported at these latitudes. In the tunicate *Salpa fusiformis* Cuvier, 1804, showing latitudinal clinal variation in morphological characters (Van Soest, 1972), a discontinuity in the cline is found between 25° and 35°N.

The cold water pteropod *Clio pyramidata* forma *pyramidata* Linnaeus, 1767, is only present in the "Ocean Acre" samples during autumn, while the warm water form *Clio pyramidata* forma *lanceolata* (Lesueur, 1813) is present, above 1500 m throughout the year (Van der Spoel, 1973).

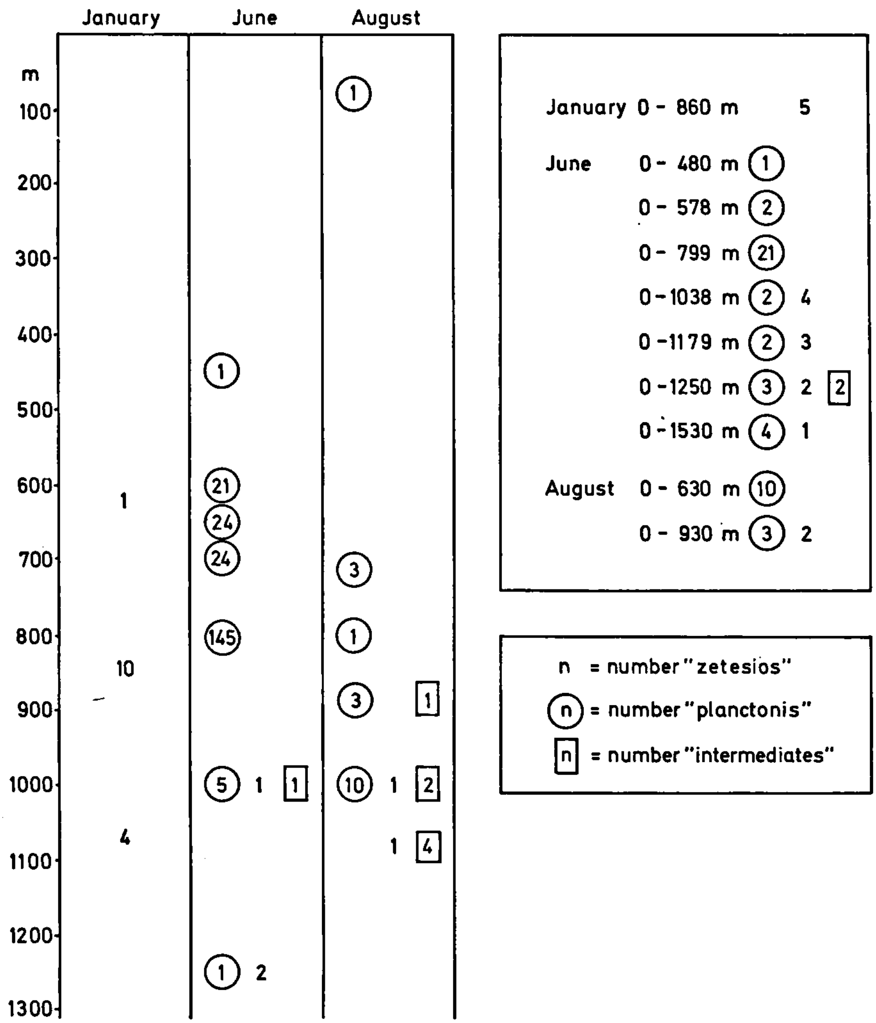


FIG. 3. Vertical distribution of *S. planctonis* in the Bermuda area in the different months of the years 1970—1972.

The occurrence of *S. zetesios* closer to the surface in colder seasons and at higher latitudes seems to resemble the vertical distribution of *Eukrohnia hamata* (Möbius, 1875), (Fowler, 1906; Alvariño, 1964), which changes depth with latitudes. *E. hamata* occurs at greater depths in warmer regions than in cold water areas.

Aurich (1971) found in the Atlantic from 38°N to 48°N *S. planctonis, S. zetesios* and intermediates in samples taken between the surface and 1000 m.

Between 48°N and 56°N *S. planctonis* disappeared, only *S. zetesios* and intermediates being present. North of 56°N no intermediates were found and *S. zetesios* remained the only representative, between depths of 100 and 1500 m.

Kramp (1939) reported *S. planctonis* from 57°N to 64°N between about 400 and 1300 m depth. This record refers in my opinion to *S. zetesios* and intermediates.

Alvariño (1964) found an ontogenetic vertical distribution for *S. planctonis* and *S. zetesios* as it was also recorded for *S. elegans* Verrill, 1873 by Bigelow (1926) and for *Eukrohnia hamata* by Fowler (1905).

The vertical distribution of *S. planctonis* and *S. zetesios* with regard to size, season and sexual stage, is given in figure 5 and table 2. There is no clear indication for ontogenetic vertical stratification. However, if this stratification does exist, it will be very difficult to detect, since the diurnal vertical migration of the specimens masks the possible vertical stratification of the developmental stages.

That, in Chaetognatha, the stage of maturity affects the vertical distribution has already been pointed out by Russell (1933a, b), who in the Plymouth region found that adults of *S. elegans* and *S. setosa* Müller, 1847, are more sensitive to light than juveniles.

David (1955) suggested seasonal migrations in *S. gazellae* Ritter-Zahony, 1909, in the Subantarctic and Arctic waters to be related to temperature, to breeding or to both. Larger animals were found to migrate to deeper levels.

Michael (1911) suggested that *S. bipunctata* Quoy & Gaimard, 1827, lives at an optimum light intensity and changes depth to follow this light intensity. He considered light of more importance than salinity and temperature with regard to vertical migration. Pearre (1973) performed laboratory ex-

TABLE II. Vertical distribution of *S. planctonis* from the Bermuda area in relation with sexual stage and body length.

planctonis	June	stage II	480— 842 m	17.1—29.2 mm
		stage III	580— 892 m	17.9—27.5 mm
		stage IV	751— 842 m	19.3—30.0 mm
	August	stage II	1000—1050 m	26.2 mm
		stage III	630—1050 m	19.3—29.9 mm
		stage IV	113—1050 m	23.1—33.3 mm
zetesios	January	stage I	860 m	17.2—22.0 mm
		stage II	650— 875 m	19.9—28.8 mm
	June	stage I	0—1038—1249 m	15.2—24.2 mm
		stage II	0—1530 m	19.0—27.7 mm
		stage III		
		stage IV	980—1025 m	25.9 mm
	August	stage I	0—931—1250 m	15.0—24.3 mm
		stage II		
		stage III	1050 m	29.4 mm
		stage IV	894—1050 m	26.7—30.7 mm

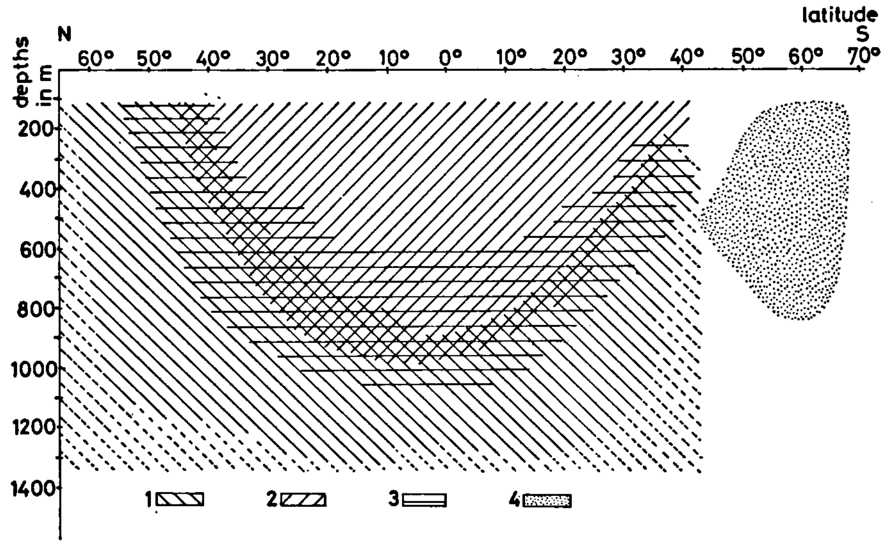


Fig. 4. Latitudinal difference in vertical dispersal of the members of the "*S. planctonis*"-group in the Atlantic Ocean. 1 = "zetesios", 2 = "planctonis", 3 = "intermediates", and 4 = "marri".

periments with *S. elegans*. He concluded that the vertical migration of the natural population is mainly effected by light and food supply. Furthermore the migration is effected by the water temperature and stage of maturity. There is a rapid turnover of large sagitta's in surface waters, but not a large standing crop.

According to Pearre vertical migration is perhaps influenced by the state of satiation of the individuals, which is the mechanism controlling depth.

The picture of ontogenetic vertical distribution is thus greatly blurred by a continuous and individual movement to the surface by the animals to feed and by their sinking when satiated. Diurnal vertical migration of the whole population, probably due to light, causes an upward migration at night-time and the up- an downward migration of the individuals during that time is affected by the food supply and the state of satiation of the animals.

In *S. zetesios* seasonal vertical migration is found, which causes the occurrence in higher levels of this taxon in January and February.

The diurnal migration and the vertical distribution indicate that an intense contact between the individuals of *S. planctonis* and *S. zetesios* populations will exist.

The vertical distributions in the Bermuda area in June and August and off South-Africa in February is thus characterized by an upper layer from 400 m down to about 1050 m in which *S. planctonis* lives, a deeper layer from 900 m to 1250 m in which *S. zetesios* is found and a layer from 600 to 1050 m in which both *S. planctonis* and *S. zetesios* are present as well as intermediates.

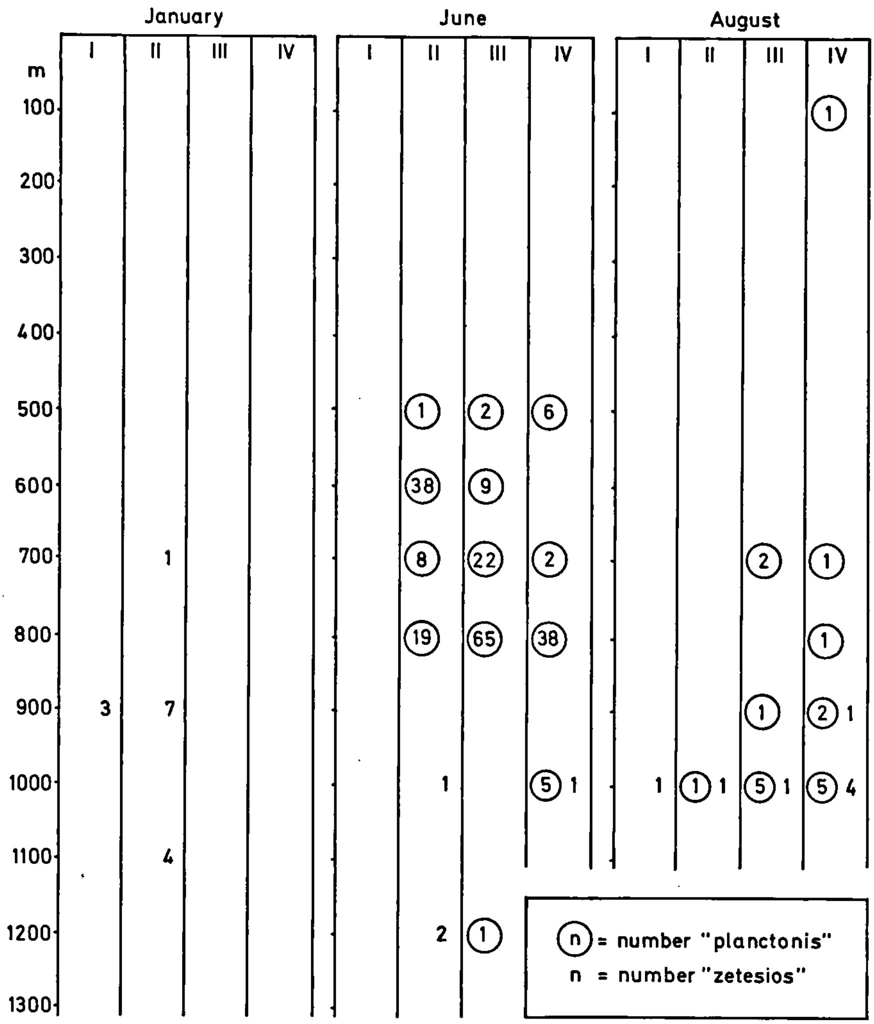


FIG. 5. Vertical distribution (y-axis) in relation to sexual stage (I, II, III and IV) and month (x-axis) of *S. planctonis* from the Bermuda area.

Information on horizontal and vertical distribution for different latitudes is shown in figure 4 (cf. Steinhaus, 1896; Thiel, 1938; Kramp, 1939; David, 1956, 1958; Furnestin, 1966; Ducret, 1968; Pierrot-Bults, 1970; Aurich, 1971, and the present study).

Sexual development

Maturity stages were by lack of histological data divided into four groups, as follows: I juvenile, II testis developing, ovaries hardly seen, III testis mature, tail cavity full with sperm and testis tissue, IV tail empty, ovaries large, eggs mature (see also table II).

Most specimens of *S. zetesios* at a depth from 860—1250 m were in stage II. This may indicate that the majority of mature specimens is living at depths greater than 1250 m, which were not sampled. On the other hand it might be that *S. zetesios* does not reach maturity till late summer or early autumn as the only mature specimens were found in August and September. Unfortunately samples taken in autumn were not available. In the Dana samples taken in February (southern hemisphere) relatively more mature specimens of *S. zetesios* were present.

At Sta.12—7C and 12—27C (August/September 1970) of the Ocean Acre, a few *S. zetesios* specimens were found with large ovaries, between 900—1050 m depth, together with mature specimens from *S. planctonis*. However, the phase in the sexual cycle at which mating is executed, is most probably stage III in which sperm is produced. After mating, but before the eggs are mature, sperm is stored in the seminal receptaculae attached to the ovaries.

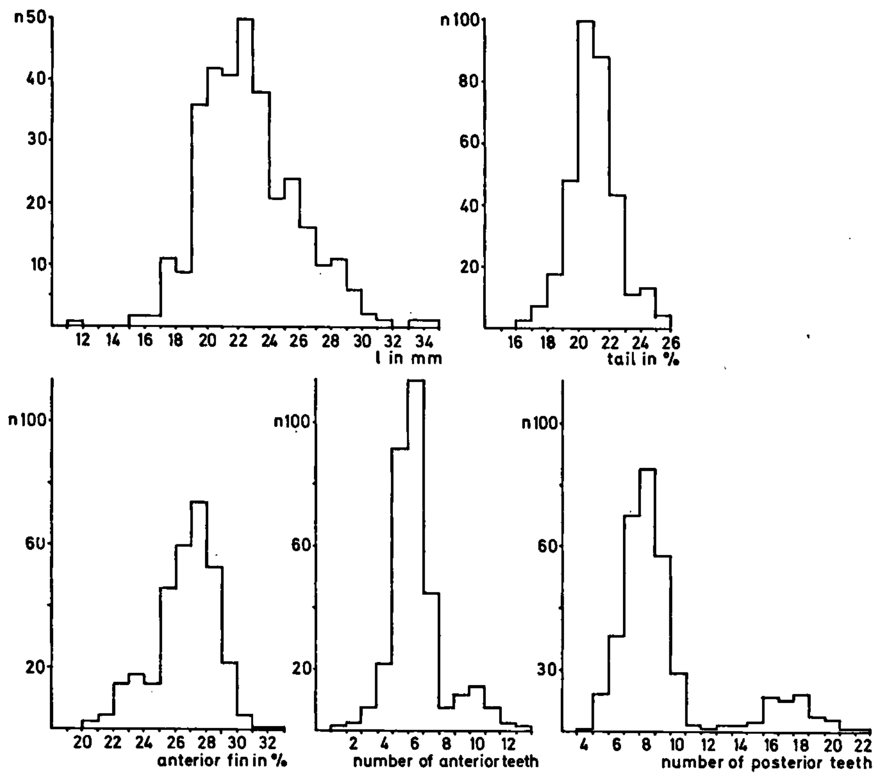


FIG. 6. Histograms for frequency distribution of body length, tail length in % of total body length, anterior fin length in % of total body length, number of anterior teeth and number of posterior teeth of *S. planctonis* from the Bermuda area.

This can be seen in histological slides (Pierrot-Bults, in preparation). To prevent interbreeding not the mature specimens should be reproductively isolated, but the specimens in stage III.

MATHEMATICS

In figure 6 and 7 the frequency distribution of some of the characters used in our mathematical analysis, viz.: total body length, tail length in percentage of total body length, anterior fin length in percentage of total body length, number of anterior teeth, and number of posterior teeth, are given for resp. the Ocean Acre material and the Dana material. The frequency distribution of the number of anterior and posterior teeth and of the length of the anterior fins is double topped.

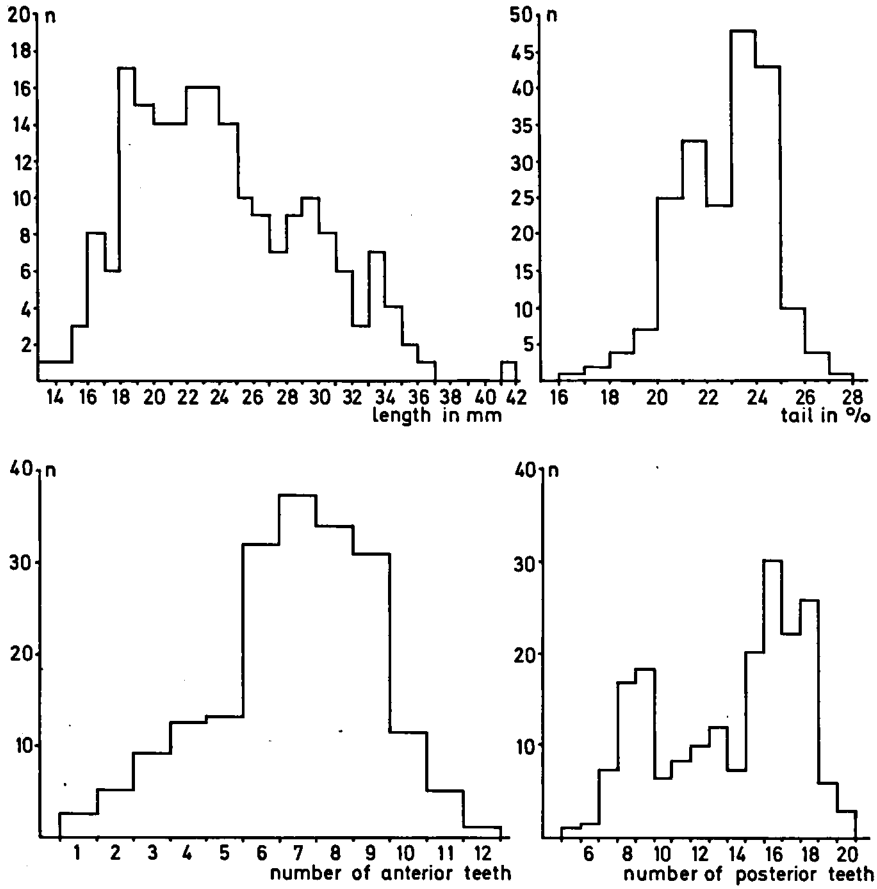


FIG. 7. Histograms for frequency distribution of body length, tail length in % of body length, number of anterior teeth and number of posterior teeth for *S. planctonis* off the South African coast.

Factor analyses were carried out to find the underlying factors explaining a large part of the variation.

In the three factor analyses, using the Acre material, two factors were found in the solution (figs 8a, b and c) explaining 44.5% of the variation in fig. 8a, 41% of the variation in fig. 8b and 62% of the variation in fig. 8c.

In the first factor analysis (fig. 8a) all specimens were used, factor 1 represents body growth with factor loading + 0.49 for body length, + 0.41 for relative anterior fin length, + 0.60 for sexual stage and — 0.80 for relative tail length and also the month of the year is loading on this factor (+ 0.54). Factor 2 represents the number of teeth, anterior teeth loading + 0.73 and posterior teeth + 0.95.

The second factor analysis shown in fig. 8b was carried out for a group with < 15 posterior teeth. Factor 1 represents body length (+ 0.80), relative tail length (— 0.72), month of the year (+ 0.56) and number of posterior teeth (— 0.36). Factor 2 is not very important in this analysis with depth loading + 0.42.

Fig. 8c shows the result of the third factor analysis carried out with specimens with ≥ 15 posterior teeth. Factor 1 represents all aspects of growth,

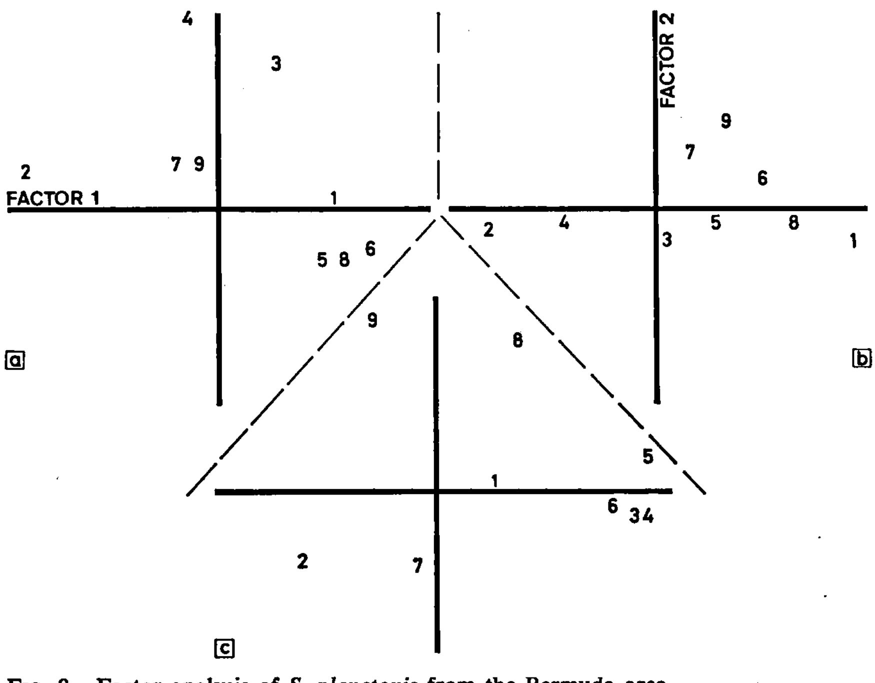


Fig. 8. Factor analysis of *S. planctonis* from the Bermuda area.
A) all specimens, B) specimens with < 15 posterior teeth, C) specimens with ≥ 15 posterior teeth. 1 — body length, 2 — tail length, 3 — anterior teeth, 4 posterior teeth, 5 — anterior fin length, 6 — sexual stage, 7 — daytime, 8 — month, 9 — depth.

length (+ 0.24), relative tail length (— 0.57), relative anterior fin length (+ 0.85), sexual stage (+ 0.74), number of anterior teeth (+ 0.84) and posterior teeth (+ 0.87), whilst factor 2 represents the environmental conditions depth (+ 0.85) and month (+ 0.79).

The results of dividing the specimens in two groups before the factor analysis show that in the group with ≥ 15 posterior teeth 62% of the variation is explained by two factors of which factor 1 represents growth and factor 2 the environmental conditions.

The group with less than 15 posterior teeth seems to be less homogenous. The factor analysis explains in this case 41% of the variation (using all specimens 44,5% was explained by two factors).

The best way to assign specimens to groups was investigated on the basis of a number of several variables. This was done with the aid of discriminant analysis.

The discriminant functions found maximally discriminate the members of the different groups and tell us to which group each member probably belongs. In generating the discriminant functions the step-wise selected independent variables were: body length, tail length, anterior fin length, number of anterior teeth and sexual stage.

These variables were used in all four discriminant analyses (figs 9a, b, c and 11) and none of the variables was rejected.

The first discriminant analysis was carried out with group 1 determined by a relative anterior fin length of 24.5% or more and group 3 with a relative anterior fin length of less than 24.5%.

The second discriminant analysis was carried out with group 1 determined by a number of posterior teeth of less than 12 and group 3 by a number of posterior teeth of 12 or more (figure 7).

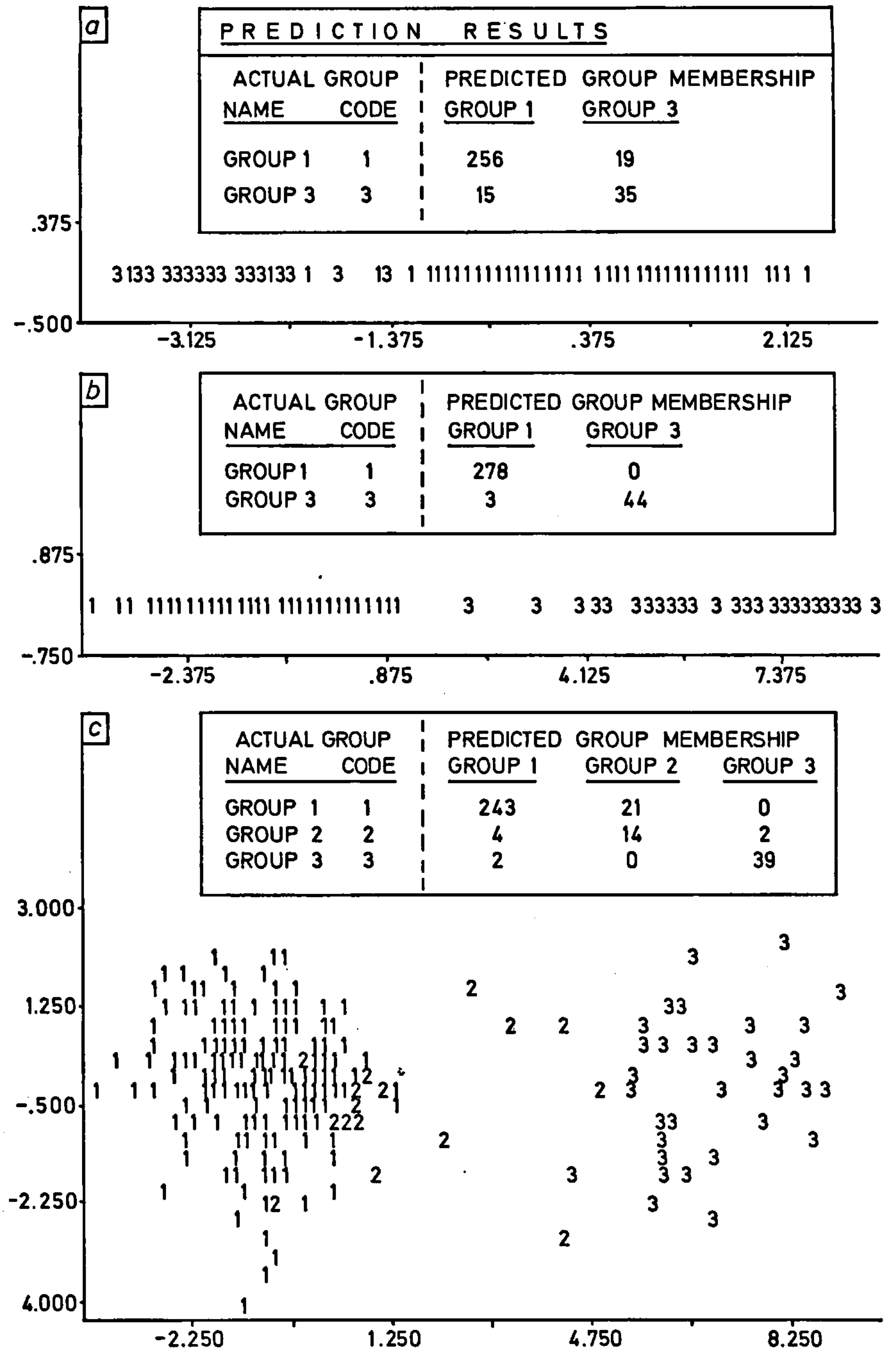
In the third analysis predicted groups were: group 1 determined by ≤ 10 posterior teeth, group 2 with > 10 and < 15 posterior teeth and group 3 determined by ≥ 15 posterior teeth. Group 1 and group 3 are clearly segregated, while group 2 is an in between. According to the computer analysis group 2 is an existing group and comprises about 10% of the total amount of specimens used in this analysis (figure 7).

The results of the discriminant analysis of the material from the Dana Expedition are shown in figure 11. Predicted groups were: group 1 determined by ≤ 10 posterior teeth, group 2 determined by > 10 < 15 posterior teeth and group 3 determined by ≥ 15 posterior teeth.

About 30% of the specimens belonged to group 2 in this analysis.

The results of three analyses with the Ocean Acre material show that 224 specimens belonged to group 1 ("*S. planctonis*") and 32 specimens to group 3 ("*S. zetesios*"). For the remaining 68 specimens the analyses are shown in figure 10. Switching from one group to another shows that the predicted group 1 or group 3 based on number of posterior teeth (group 1 < 15 and group 3 ≥ 15) or relative anterior fin length is not the best division possible.

Comparison of figure 9c and figure 11 shows that in the Ocean Acre material group 2 is closely related to group 1 and in the Dana material group



a) PREDICTION RESULTS

ACTUAL GROUP NAME	CODE	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 3
GROUP 1	1	256	19
GROUP 3	3	15	35

b)

ACTUAL GROUP NAME	CODE	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 3
GROUP 1	1	278	0
GROUP 3	3	3	44

c)

ACTUAL GROUP NAME	CODE	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3
GROUP 1	1	243	21	0
GROUP 2	2	4	14	2
GROUP 3	3	2	0	39

FIG. 9. Discriminant analysis for *S. planctonis* from the Bermuda area.
A) for two groups (1 and 3) predicted by relative anterior fin length; group 1 — anterior fin length > 24.4% of body length; group 3 — anterior fin length ⩽ 24.5% of body length.
B) for two groups (1 and 3) predicted by number of posterior teeth; group 1 posterior teeth < 12; group 3 — posterior teeth ⩾ 12.
C) for three groups (1, 2 and 3) predicted by number of posterior teeth; group 1 — posterior teeth < 11; group 2 — posterior teeth > 10 < 15; group 3 — posterior teeth ≥ 15

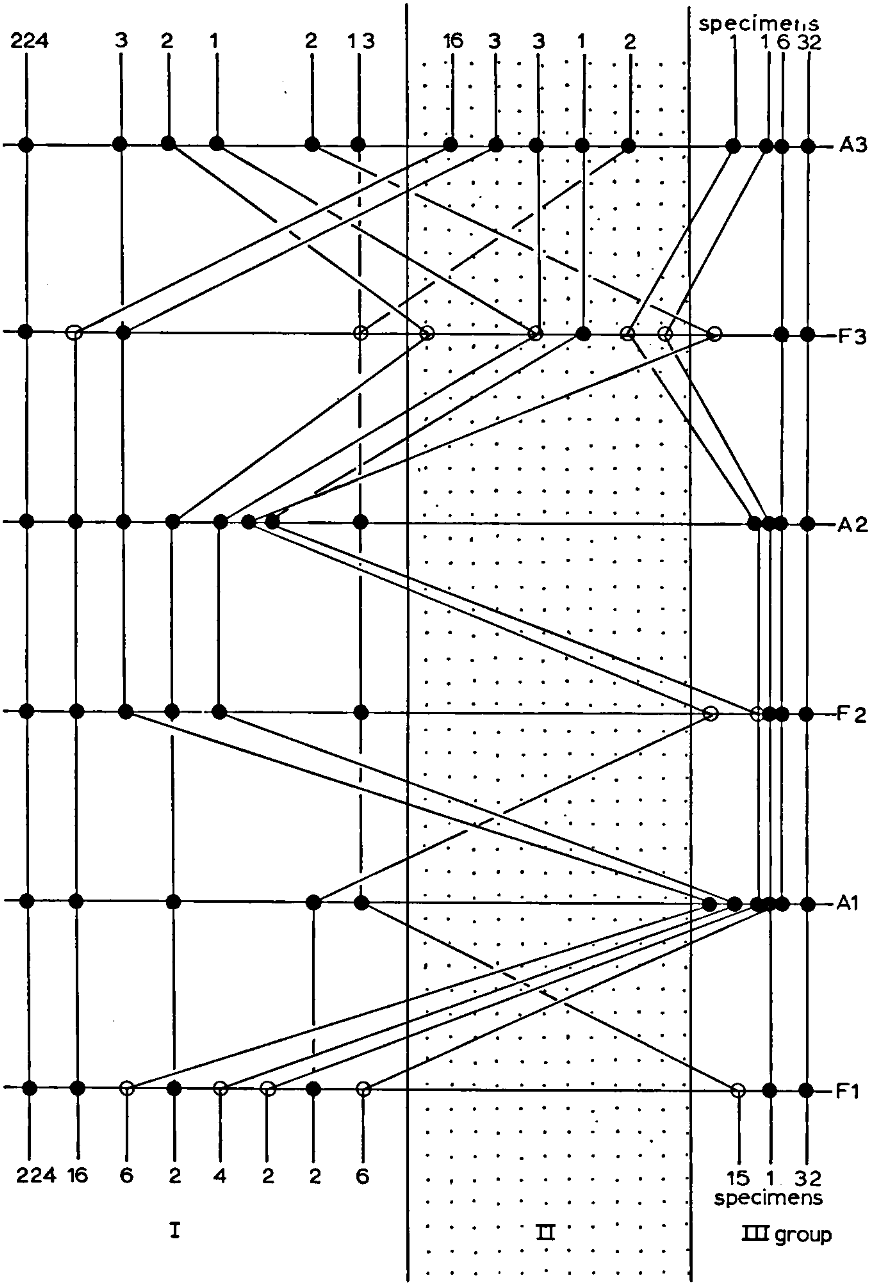
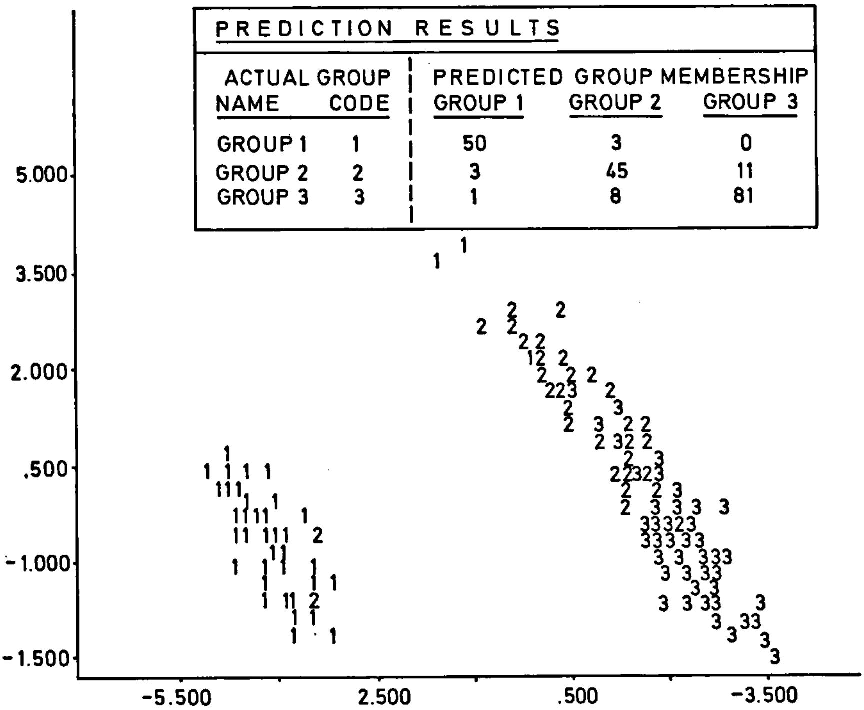


FIG. 10. Diagram for 324 specimens from the Bermuda area in the three discriminant analyses; 68 specimens showed different results in these analyses. F1 — predicted groups in analysis A; A1 — results of analysis A; F2 — predicted groups in analysis B; A2 — results of analysis B; F3 — predicted groups in analysis C; A3 — results of analysis C.



PREDICTION RESULTS

ACTUAL GROUP NAME	CODE	PREDICTED GROUP MEMBERSHIP GROUP 1	GROUP 2	GROUP 3
GROUP 1	1	50	3	0
GROUP 2	2	3	45	11
GROUP 3	3	1	8	81

FIG. 11. Discriminant analysis for *S. planctonis* off the South African coast for three groups predicted by number of posterior teeth; group 1 — posterior teeth < 11; group 2 — posterior teeth > 10—15; group 3 — posterior teeth ⩾ 15.

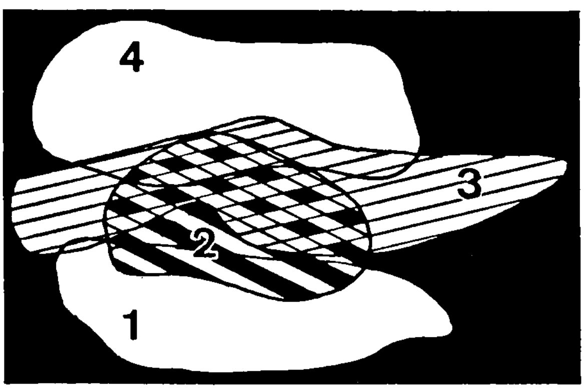


FIG. 12. Relation between body length (x-axis) and number of posterior teeth (y-axis) and the three groups used in the discriminant analyses. 1 = group 1 ("planctonis"); 2 = group 2 Ocean Acre material; 3 = group 2 Dana material; 4 = group 3 ("zetesios").

2 is closely related to group 3. It is possible that this phenomenon is due to the lack of mature specimens of "*S. zetesios*" in the Ocean Acre material.

Figure 12 shows the relation between body length (x-axis) and number of posterior teeth (y-axis) and the division of the three groups used as predicted groups in the discriminant analysis (see also figures 1 and 2).

In the Dana material are juveniles, intermediates and very mature *S. zetesios* specimens. In the Ocean Acre material mature specimens of *S. zetesios* are hardly seen and in this case group 2 consists mainly of intermediates.

Discussion

The vertical distribution (figures 3 and 4) and the existence of morphological intermediates (figures 9 and 11) show that there is neither spatial, nor genetical isolation between the two taxa *S. planctonis* and *S. zetesios*. The distributional pattern in the Atlantic Ocean, with evidence for the presence of intermediates between 04°N and 60°N and 32°S, together with presumed presence of intermediates through the whole South-Atlantic, indicates that differentiation in *S. planctonis* is still on infraspecific level.

The Antarctic Convergence is a boundary and seemed to have acted as a barrier causing the development of a different taxon in the Antarctic waters, viz. *S. marri*. The meristic and quantitative characters of *S. marri* are not included in this study due to lack of specimens. The morphology of the

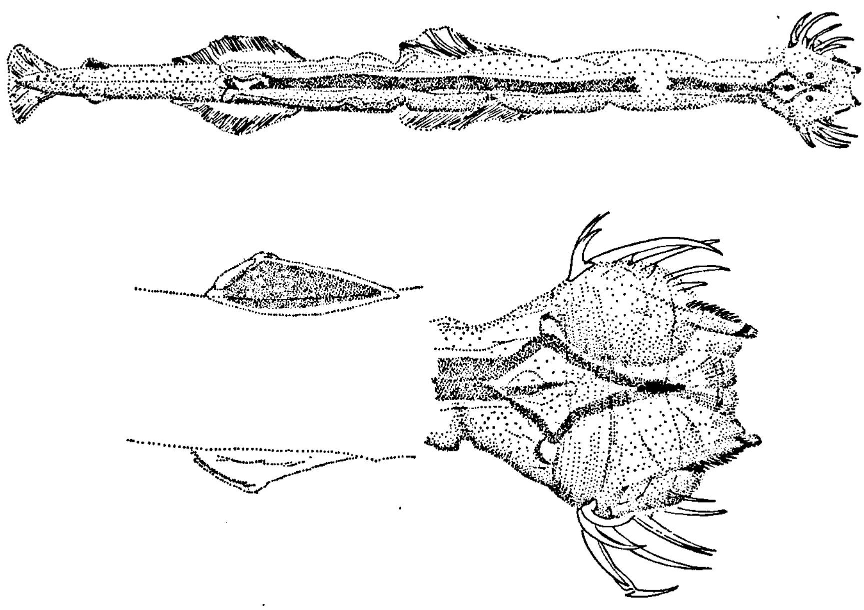


FIG. 13. Type specimens of *S. marri* David, 1956, from ventral.

anterior fins, which are completed rayed and rather short, the absence of a large collarette and the different place of the seminal vesicle seen in the type specimens (figure 13), indicate a level of evolution different from that in *S. planctonis* and *S. zetesios*. Whether or not there is (restricted) geneflow between *S. zetesios* and *S. marri* is not known. The possibility of geneflow cannot be excluded, as the Antarctic Convergence is only a rather sharp discontinuity in temperature in the superficial Subantarctic water. The cold Antarctic surface layers sink below 200 m (Mackintosh, 1946; David, 1963). For species living at a considerable depth as does *S. marri*, contact with *S. zetesios* at the other side of the Antarctic Convergence could be possible since *S. zetesios* is rather tolerant for lower temperatures, as is shown by its occurrence in cold water areas in the northern North Atlantic. However, there is neither proof of sympatric occurrence of *S. marri* and *S. zetesios*, nor proof of the occurrence of intermediates, so *S. marri* is considered a valid species. It may have developed from a peripheral isolate, and lives allopatric from its near relatives *S. planctonis* and *S. zetesios*, which is according to Mayr (1966) an indication that it has reached species level not so long ago.

In a previous paper (Pierrot-Bults, 1970) *S. zetesios* was considered synonymous with *S. planctonis*, the latter being a polymorphic species because of the occurrence of two forms with their intermediates in the same samples.

The more accurate samples from different depths available now, however, show a certain difference in depth distribution of the two forms and a change in depth correlated with latitude. The term "morph" as used by Mayr (1966) is on the infrapopulational level and is not appropriate in this case.

S. zetesios is the form adapted to lower temperatures, and not primarely to greather depths, as is shown by the occurrence in more upper layers during the winter season at 32°N (Ocean Acre area) and throughout the year at higher latitudes (Aurich, 1971). The occurrence of more teeth and greater body length for forms living at lower temperatures is known also for *S. elegans*. *S. elegans elegans* Verrill, 1873, is confined to more temperate regions, whilst *S. elegans arctica* Aurivillius, 1896, is a more arctic-boreal form, showing greater body length and more teeth (Fraser, 1952). It is not known whether these differences are discontinuous.

Comparing the data on the distribution of *S. planctonis*, *S. zetesios* and intermediates based on cruises of "Gauss" and "Anton Dohrn" in Aurich's paper (1971) with the temperature depth sections given by Dietrich (1969) for the same cruises, different temperature preferences for the different forms are seen. Temperatures down to about 10°C are typical for *S. planctonis*, down to about 7°C for the intermediates, and down to above 5°C for *S. zetesios*. The occurrence of *S. zetesios* at 44°N in layers about 500 m coincides with colder upwellings in that area as shown in figure 14. Thus *S. zetesios* is adapted to colder water, *S. planctonis* to warmer water, the intermediates show intermediate preference.

The status of the taxa has to be considered an infraspecific one.

It is difficult to detect strong barriers in the Ocean and isolation in some

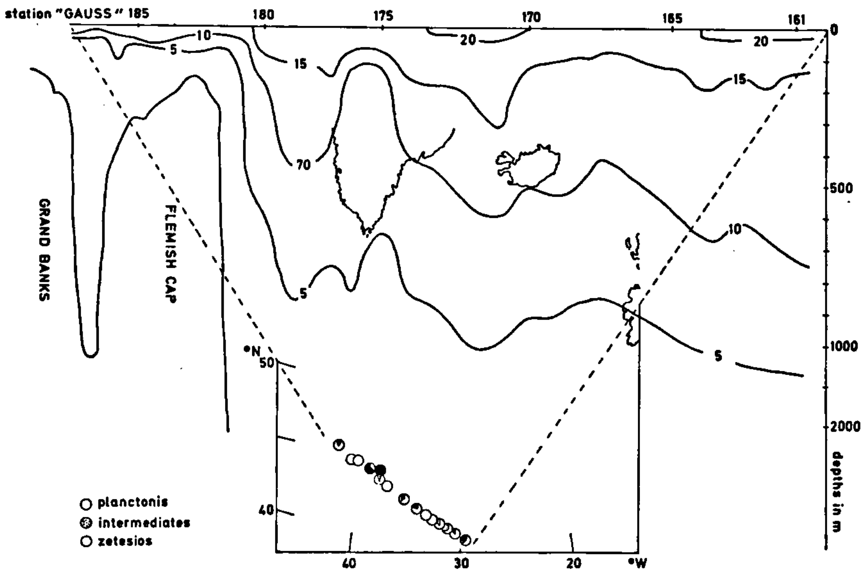


FIG. 14. Distribution of *S. planctonis* in the North Atlantic in relation to temperature after Dietrich, 1969 and Aurich, 1971).

taxa may not have gone as far at to effect a reproductive isolation and consequently it did not result in the occurrence of different species. Still certain differences can be recognized among the representatives of some marine taxa, as a result of different selective pressure at different latitudes or water depths.

Mayr's (1966) discussion about infraspecific variation covers the concepts subspecies, varieties, morphs, ecotypes and ecological races. For taxonomists who want to name different infraspecific forms only the concept subspecies is available with nomenclatorial value. This concept remains rather vague in taxonomic literature.

Mayr (1966) gives a definition, but further on in his book the term subspecies is admitted to be an arbitrary instrument only created purely for taxonomical convenience and including more than one type of infraspecific taxa.

Huxley (1949: 110) distinguishes isolated and non-isolated subspecies and in his other book (1945: 210), he states that subspecies as found in nature, are in reality two distinct types. Independent subspecies are so fully isolated that geneflow is interrupted; the second type, dependent subspecies, interbreed with their neighbours along intergrading zones. Independent subspecies may differentiate into full species and, given sufficient time, will normally do so, whilst dependent subspecies normally will not do the same, but will evolve as part of the whole interbreeding complex. Thus some subspecies are "species in the making": the independent subspecies; and some are not: the dependent subspecies.

In nature, different kinds of limitations to geneflow exist, unlimited geneflow changes over gradually into reproductive isolation. It will be practically impossible to distinguish between all the stages with more or less limited geneflow.

However, when it is sufficiently clear that certain differences between populations are not caused by strong limitations in geneflow, it would be sensible to use a special term for this phenomenon of the dependent subspecies. The concept forma (sensu Van der Spoel, 1971) seems to be synonymous with the concept dependent subspecies (Huxley, 1949). This leaves the term subspecies (Mayr, 1966) for an independent subspecies, evidently caused by strong limitations in geneflow.

The forma is caused by selective pressure on the gene pool, resulting in different phenotypes and genotypes under different environmental conditions, without barriers restricting the geneflow from one forma to another. The formae are thus always characterized by discontinuous variation. This phenomenon must not be confused with sympatric speciation, because reproductive isolation does not occur and the differentiation will not reach a specific level. There is no reason to believe that a barrier exists throughout the Atlantic Ocean preventing or restricting geneflow between *S. planctonis* and *S. zetesios*. The differences between these two forms seem to be the result of selective pressure, probably correlated with temperature. Temperature is an important factor for growth, development, length of the life cycle and reproductive potential. According to Sameoto (1971) the lower the mean temperature during the life cycle is, the larger the mature animal will be and the longer it takes to mature.

Differences in temperature are thus highly affecting the life cycle of planktonic invertebrates. Animals of the same species, living at higher temperatures, mature earlier, perhaps having more reproductive cycles a year, whilst animals, living at lower temperatures, may reach maturity in a two-year cycle (Dunbar, 1941; Sameoto, 1973).

All this may result in the development of formae of a species. *S planctonis* and *S. zetesios* are considered to be formae (sensu Van der Spoel, 1971): *S. planctonis* forma *planctonis* Steinhaus, 1896, and *S. planctonis* forma *zetesios* Fowler, 1905.

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