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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)*

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ABSTRACT

The Sternoptychidae caught during a spring expedition in the Mid North Atlantic in 1980 are studied. Distribution patterns and data on abundance are recorded. It is proposed that *Argyropelecus aculeatus* and *A. olfersi* are two formae belonging to one species, the existing phenotypical differences being the result of adaptations to hydrographical circumstances. The intergrading zone of these formae is found at the surface at approximately 45°N and shifts to deeper water layers at lower latitudes.

INTRODUCTION

This paper deals with the marine silver hatchetfishes (Sternoptychidae) collected during the Amsterdam Mid North Atlantic Plankton Expedition 1980. The expedition took place in the period April 11-May 2, 1980 on board the research vessel H.M.S. Tydeman. Discrete depth hauls were made between 30 m and 1200 m depth, in the Atlantic Ocean between 56°N and 24°N at approximately 30°W. For extensive information on the stations, hauls and environmental conditions one 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.

Two of the three genera in the family Sternoptychidae were present in the material: representatives of the tropical coast-bound genus Polyipnus were not found, which is in accordance with the survey paper by Baird (1971). Of the genus Argyropelecus, which was most abundant, three species were found: A. hemigymnus Cocco, 1829, A. aculeatus Valenciennes, 1849 and A. olfersi (Cuvier, 1829). Of the genus Sternoptyx two species were collected: S. diaphana Hermann, 1781 and S. pseudobscura Baird, 1971. For these five species the north-south and vertical distributions and the abundance data are given. The taxonomic differences between A. aculeatus and A. olfersi are discussed. This results in some remarks on the characters given in the literature as diagnostic for these two species.

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MATERIAL AND METHODS

All material was collected with the Rectangular Midwater Trawl (RMT1+8), which is a combined opening and closing net composed of a large net, effective mouth area 8 m², and a smaller one, effective mouth area 0.8 m². For full description of construction and behaviour of the nets one is referred to Baker et al. (1973) and Roe et al. (1980). Accurate measurements of the depth of the net, of temperature and flow were registered with a net monitor system. These records and additional XBT data form the basis of the depth and temperature profile (Van der Spoel, 1981), referred to below.

Along a north-south line at about 30° W, seventeen stations were made between 56° N and 24° N. In general the following layers were sampled at each station: 50-100 m, 100-200 m, 200-300 m, 300-400 m, 400-500 m and 500-1000 m depth.

The material was roughly sorted aboard ship. Almost all fish samples were fixed with formalin 4% with sea-water and preserved in alcohol 70%. The actual numbers of specimens caught are converted into standard numbers related to a fixed amount ($24 000 \text{ m}^3$) of water filtered. The abundance given as standard numbers for the different trawls can be compared also when fishing took place with different gear and with different duration. The special effects of the net size on net avoidance are then, however, neglected. The formula for calculating standard numbers for RMT8 samples is ($3 \times$ number of specimens) / (distance sampled), for the RMTI samples it is $(10 \times 3 \times \text{number of specimens}) / (\text{distance sampled})$. The distance sampled is calculated from direct flow measurements. The factor three was introduced as the distance sampled averaged three kilometres, so the standard numbers for the RMT8 are as close to the actual numbers as possible. Flow through the nets, depth of the nets and shipspeed were such that the mean angle of the mouth of the net, calculated for each trawl, hardly influenced the amount of water filtered, and no special corrections seem necessary (cf. Roe et al., 1980).

SYSTEMATICS

Table I gives the total numbers and average sizes of the species collected. For a full taxonomic description of the species one is referred to Schultz (1964), Baird (1971), and Badcock & Baird (1980).

Argyropelecus Cocco, 1829

A. hemigymnus is characterised by its body-shape (long and narrow trunk), its pigmentation (white bars on trunk) and the form of its postabdominal and preopercular spines (Bauer, 1906; Schultz, 1964; Baird, 1971). A. hemigymnus is the dominant species in the North Atlantic (Jespersen, 1915), which agrees with our findings. In the area sampled more than eight hundred specimens were collected. More than eighty juveniles could not be identified to species level as a consequence of their

Table I. Numbers and standard length of Argyropelecus and Sternoptyx.

	total number	standa min.	rd lengt mean	th in mm max.	SL of adults ¹		
A. hemigymnus	851	7	16.8	37	rarely exceeding 35 mm		
A. aculeatus	162	8	16.7	58	often exceeding 70 mm		
A. olfersi	7	16	23.3	32	often exceeding 70 mm		
intermediates A. aculeatus & A. olfersi	5	16	21.4	36			
A. spec. 2	86	_	ca 8	_			
S. diaphana	118	8	14.8	40	rarely exceeding 55 mm		
S. pseudobscura	22	10	21.1	43	often exceeding 55 mm		
S. spec. 2	68		ca 7				

¹ for comparison the standard lengths of adult specimens after Baird (1971) are given

 2 A. spec. and S. spec. stand for unidentified specimens of Argyropelecus and Sternoptyx respectively, smaller than 8-10 mm.

early developmental stage. Because of the abundance of A. hemigymnus a large percentage of the juveniles can be assumed to belong to this species. Six specimens, scattered over the area sampled, had nine instead of the usual eight dorsal fin rays. Other characters showed no more variation than described in literature (Schultz, 1964; Baird, 1971).

A. aculeatus and A. olfersi are known to be very closely related species belonging to the A. lynchus-complex (Baird & Eckardt, 1972). This group is highly specialized and comprises, besides A. aculeatus and A. olfersi, A. lynchus Garman, 1899 and A. sladeni Regan, 1908; the latter two are not present in our material. The most important characters discriminating A. aculeatus and A. olfersi are the shape of the postabdominal and preopercular spines, the depth of the body and the height of the dorsal blade (Norman, 1930; Schultz, 1964; Baird, 1971). The two characters first mentioned are the most practical for discrimination.



Fig. 1. Types of postabdominal spines (pas).

In *A. aculeatus* two postabdominal spines occur: one short and straight spine directed ventrad and a little forwards, and a distinctly larger backwards directed spine which becomes serrated in specimens longer than approximately 25 mm standard length (fig. 1c and d). In *A. olfersi* the two postabdominal spines are short, one is slightly curved



Fig. 2. Types of preopercular spines (pos).

forwards, the other is straight and directed a little backwards (fig. 1a).

Both species possess two preopercular spines. In juveniles of A. aculeatus the lower one is relatively long and straight, pointing ventrad, the upper one is shorter, directed ventrad and slightly laterad or backwards (fig. 2c and d). In adults both preopercular spines are relatively short (fig. 2e and f). In A. olfersi the lower preopercular spine is long and curving forward, the upper one is short (fig. 2a and b).

Both species have a very deep body. In A. aculeatus body depth is usually less than 1.4 into standard length, in A. olfersi it is more than 1.5 (Baird, 1971), but variation of this character in the two species sometimes overlaps. The dorsal blade is high, in A. aculeatus its height almost equals its length, in A. olfersi the height of the blade is approximately one half its length (Baird, 1971), but there is also overlap in this character.

Based on the taxonomic characters described, 162 specimens were identified as A. aculeatus and only 7 specimens as A. olfersi. Within this A. aculeatus — A. olfersi complex, all specimens smaller than 15 mm standard length (86 specimens) were identified as juveniles of A. aculeatus. However, it is doubtful whether the early developmental stage of the body and/or spines of some of these small specimens already allowed of identification. For this reason only specimens with a standard length over 14 mm are considered below.

Table 2. Shape of spines in Argyropelecus olfersi, A. aculeatus and intermediate specimens; for the codes of the shapes see fig. I and 2.

	shape of postabdominal	number of specimens	
A. olfersi	pas-oi	pos-02	
	pas-01	pos-oi	6
intermediate specimens	pas-oA	pos-01	I
	pas-oA	pos-Ao	4
A. aculeatus	pas-A1	pos-Ao	24
	pas-A1	pos-A1	16
	pas-A r	pos-A2	8
	pas-A2	pos-Ao	11
	pas-A2	pos-A1	4
	pas-A2	pos-A2	8
	pas-A2	pos-A3	5









Fig. 4. Variation in height of dorsal blade with standard length.

For five specimens identification was problematic. The shape of their postabdominal spines was intermediate between those of A. aculeatus and A. olfersi (fig. 1b). The shape of the preopercular spines was in one case most like A. olfersi, in the other four specimens they approximated those of A. aculeatus (table 2). The depth of the body and the height of the dorsal blade proved to be of intermediate nature. In fig. 3 the depth of the body is plotted against the standard length for A. aculeatus and A. olfersi and for the five intermediates. Only the area was considered where A. aculeatus, A. olfersi and the intermediates occurred. Of the total of 76 A. aculeatus specimens, 42 were found outside this area, but as their body depth did not significantly differ from that of the 34 specimens plotted, it was not necessary to include their data. The same goes for fig. 4, where the height of the dorsal blade is plotted against the standard length. The height of the dorsal blade is usually given against its length. In the actual material, however, the standard length appeared to be a more distinct size than the length of the dorsal blade at its base, as it is more accurately measured. From the data in table 2 and figs 3 and 4 it can be concluded that the non-identified specimens are intermediates between A. aculeatus and A. olfersi. Fig. 5 shows one of these intermediate specimens.

Sternoptyx Hermann, 1781

The representatives of this genus are recognised by the oblique form of their very deep body. Until recently all specimens from the N.E. Atlantic were assumed to belong to one species: *S. diaphana*. Schultz (1961) even stated that 'nothing could be found that indicated more than a single species for the world'. In 1971, however, Baird introduced a new species called *S. pseudobscura*. The resemblance between *S. diaphana* and *S. pseudobscura* is very strong; the most constant difference is found in the position of the supra-



Fig. 5. Specimen intermediate between A. aculeatus and A. olfersi (20 mm SL, ZMA-117177) a — postabdominal spines; b — preopercular spines.



Fig. 6. Geographic and bathymetric distribution (plots are given at the mean depths of the samples).

anal photophore. In our material S. diaphana turned out to be the dominant species, more than one hundred specimens were collected; of S. *pseudobscura* only twenty-two specimens were caught. The juveniles of the genus Sternoptyx are clearly recognisable by their shape, yolk sac and photophores; when smaller than 8-10 mm distinction of species is usually impossible.

DISTRIBUTION

The vertical and north-south ranges of the species are given in fig. 6. In fig. 7 the standard numbers of A. hemigymnus, A. aculeatus, S. diaphana and S. pseudobscura are plotted against latitudes, to show the latitudinal variation in abundance of the species; the vertical range between 50 m and 1000 m depth has been considered per station. For



Fig. 7. Geographic abundance distribution.

each station the standard numbers for each of the six layers are added up, while for overlapping or repeated hauls the averages were used. The layers differ substantially in thickness, so no calculations of concentrations in the upper 1000 m are permitted. The graphs have to be considered rough indications of the abundance as data from different nets were taken together. *A. olfersi* and the intermediate specimens are left out because their numbers are too small.

A summary of the geographical and bathymetrical data of the present material is given in table 3. When available, corresponding literature data are presented in parentheses.

The horizontal and vertical distributions of the present material correspond with data from Baird (1973), except that *A. aculeatus* and *S. diaphana* are found more to the north than previously known. Approximately one third of the *A. aculeatus* population (56 specimens) and two *S. diaphana* specimens were found north of their formerly assumed northern limits. *S. diaphana* was restricted to water deeper than 400 m although four specimens were caught at night at shallower depths. This incidental occurrence at a shallow depth was also noticed by Badcock (1970).

All Argyropelecus species, the intermediate group included, live deeper at low latitudes than at high latitudes. For the deep-living genus Sternoptyx no such shift to deeper water layers from the north to the south is noticed.

In general A. aculeatus is found in shallower and warmer layers than A. olfersi. The intermediate specimens were caught in an area transitional between that of the A. aculeatus and A. olfersi populations. So, these specimens are not only morphologically intermediate, but also with respect to their geographical distribution they occupy a transitional place.

DISCUSSION

The Sternoptychidae can be added to the various pelagic groups with a faunal boundary in the North Atlantic at about 45° N. In spring, *A. aculeatus, S. diaphana* and *S. pseudobscura* all find their northern distribution border at this latitude (fig. 6).

The area discussed in this paper was minutely described for coccolithophores (Protozoa) (Angel, 1979), resulting in a division of a subtropical faunal zone and a transitional zone. The subtropical and the transitional zones shade off into one another at approximately 40°N. The boundaries of foraminiferan, euphausiid and mesopelagic fish communities show a close resemblance to the coccolithophore pattern, although recent 'Discovery' investigations indicate that the comparable zoogeographical boundary for ostracods is more to the north, at approximately 45°N (Angel, 1979). At this latitude there also exists a transi-

geographical distribution between 25°N-55°N		depth dist between 50	temperature			
range	highest conc.	day	night	range		
25°-55°N (25°-55°N)	_	N : 300-400 S : ≥400	200-300	13°-14°C		
(200-700)						
S of 49°N (S of 35°N)	25°-42°N	N : 200-400 S : 300-500	100-300	14°-16°C		
		(350-550)	(100-200)			
34°-53°N (35°-65°N)	_	200-600 (400-600)	 (200-300)	11°-13°C		
35°N-53°N	_	300-500		13°-14°C		
C of roll						
$S \text{ of } 53^{\circ}\text{N}$	25°-45°N	300-500 — ≥400		9°-12°C		
$(25^{\circ}-45^{\circ}N)$ $31^{\circ}-42^{\circ}N$	35°N	(700-900) ⊘≥500		8°- 11°C		
(20°-40°N) S of 41°N	_	(800-: ≥4	1500) 100	9°-12°C		
	geographica between 2 range 25°-55°N (25°-55°N) S of 49°N (S of 35°N) 34°-53°N (35°-65°N) 35°N-53°N S of 53°N S of 53°N (25°-45°N) 31°-42°N (20°-40°N) S of 41°N	geographical distribution between 25°N-55°N range highest conc. 25°-55°N (25°-55°N) S of 49°N 25°-42°N (S of 35°N) 34°-53°N (35°-65°N) 35°N-53°N S of 53°N 25°-45°N (25°-45°N) 31°-42°N 35°N (20°-40°N) S of 41°N	geographical distribution between 25°N-55°N range $(25^{\circ}-55^{\circ}N)$ depth dist between 50 day $25^{\circ}-55^{\circ}N$ $-$ N: 300-400 (25°-55°N) $(25^{\circ}-55^{\circ}N)$ $S: \geqslant 400$ (200- (200- (S of 49°N) $25^{\circ}-42^{\circ}N$ (S of 35°N) $S of 49^{\circ}N$ $25^{\circ}-42^{\circ}N$ ($35^{\circ}-55^{\circ}N)$ N: 200-400 (S of 35°N) $34^{\circ}-53^{\circ}N$ $ 200-600$ ($35^{\circ}-65^{\circ}N)$ ($400-600$) $35^{\circ}N-53^{\circ}N$ S of 53^{\circ}N $ 300-500$ S of 53^{\circ}N $ 300-500$ S of 53^{\circ}N $25^{\circ}-45^{\circ}N$ ($700-31^{\circ}-42^{\circ}N)$ S of $41^{\circ}N$ $-$ S of 41^{\circ}N $ \geq 4$	geographical distribution between 25°N-55°N rangedepth distribution between 50 m-1200 m day $25^{\circ}-55^{\circ}N$ - $25^{\circ}-55^{\circ}N$ - $(25^{\circ}-55^{\circ}N)$ N: 300-400 (200-700) $(25^{\circ}-55^{\circ}N)$ S: ≥ 400 (200-700) $(25^{\circ}-55^{\circ}N)$ S: $\geq 300-500$ (350-550) $(56 f 35^{\circ}N)$ S: $300-500$ (350-550) $34^{\circ}-53^{\circ}N$ - $(35^{\circ}-65^{\circ}N)$ ($35^{\circ}-65^{\circ}N)$ (400-600) (200-300) $35^{\circ}N-53^{\circ}N$ - $300-500$ -S of $53^{\circ}N$ 25^{\circ}-45^{\circ}N (25^{\circ}-45^{\circ}N) $(25^{\circ}-45^{\circ}N)$ (700-900) (200-900) $31^{\circ}-42^{\circ}N$ $35^{\circ}N$ ≥ 500 (20^{\circ}-40^{\circ}N)(800-1500) ≥ 400		

Table 3. Geographical and bathymetrical data for Argyropelecus and Sternoptyx. Data in parentheses according to Baird (1971).

* A. spec. and S. spec. stand for unidentified specimens of Argyropelecus and Sternoptyx respectively, smaller than 8-10 mm.

tional area where chaetognath (Pierrot-Bults, 1975) and pteropod (Van der Spoel, 1967) formae change into other formae of the same species.

This boundary, shared by a number of zoological taxa, is probably partly caused by instable conditions north of 42°N, due to the disturbance of the vertically stratified structure of the water column in winter (Pierrot-Bults & Van der Spoel, 1979). Although the hydrographical surface pattern is still reflected in the distribution of mesopelagic organisms, other than surface water influences become important for this distribution (Angel, 1979). Ostracods and fishes, for example, show faunal borders within one water mass, probably due to minor physical differences (Pierrot-Bults & Van der Spoel, 1979).

The Sternoptychidae are widely distributed and represented by characteristic species assemblages in several zoogeographical regions (Baird, 1971). The Mid North Atlantic Ocean comprises two different species assemblages: the subarctic assemblage of A. hemigymnus, A. olfersi, A. gigas Norman, 1936, S. diaphana and S. pseudobscura, and the central assemblage of A. hemigymnus, A. aculeatus, S. diaphana, S. pseudobscura and probably A. gigas. The boundary between these two assemblages is supposed to be situated at approximately

35°N. This is not in accordance with the present material, A. aculeatus has been caught in considerable numbers north of 35°N up to the above described faunal border at 45°N, which results in horizontal overlap with A. olfersi. Besides, A. gigas, a rare species quite restriced locally, was lacking in our samples, which is not surprising. Summarising, the present data indicate, unlike Baird (1971) notes, the existence of a wide-spread upper mesopelagic species (A. hemigymnus), a central water upper mesopelagic species (A. acu*leatus*). In colder water in between these two and two deep mesopelagic species (S. diaphana and S. pseudobscura) lives the species A. olfersi. Consequently, the present data do not allow of a grouping into assemblages within this family.



Fig. 8. Distribution of the formae *A. olfersi aculeatus* and *A. olfersi olfersi* and their intergrading zone (hatched).

The depth ranges of the Argyropelecus species gradually shift to deeper layers from north to south, which points to an adaptation to a distinct temperature range and not primarily to fixed depth layers. This penetration into lower latitudes associated with submergence, was also noticed for other groups such as mesopelagic fishes, chaetognaths and ostracods (Angel, 1979). For Sternoptyx no such shifting to deeper layers at lower latitudes is found. Sternoptyx, however, lives in water layers deeper than 500-600 m, where no marked temperature variation from the north to the south exists, as can be concluded from temperature profiles (Van der Spoel, 1981).

The boundary between the A. aculeatus and A. olfersi populations coincides with the vertical faunal border at about 45°N, and changes into a more or less horizontal border formed by the 13°-14°C isotherms (fig. 8). As morphologically intermediate specimens occur in this transitional zone, A. aculeatus and A. olfersi may form one polytypic species. A comparable situation in the same area was described for chaetognaths by Pierrot-Bults (1975). She found that the taxa Sagitta planctonis Steinhaus, 1896 and S. zetesios Fowler, 1905 had to be considered one polytypic species: S. planctonis. S. planctonis planctonis is adapted to warmer water, S. p. zetesios to colder water and the intermediates show an intermediate preference. The transitional zone with intermediate specimens is also found between 40°-45°N at the surface layers in the Northern Atlantic, shifting to deeper layers at lower latitudes. The fact that this border separates formae of a polytypic species for at least two different groups, is remarkable and makes investigations of other groups worthwhile.

The differences between the two taxa of chaetognaths and hatchetfishes seem to be in both cases the result of selective pressures, probably correlated with temperature. It is not clear, at present, if other parameters are involved. Temperature is known to be an important factor for growth. Animals of the same planktonic species living at lower temperatures become larger than animals living at higher temperatures (cf. Pierrot-Bults, 1975). This explains the larger standard length often noticed for *olfersi*, which is adapted to lower temperatures than *aculeatus*.

The occurrence of a number of intermediate specimens indicates that there is no genetical barrier between aculeatus and olfersi. The differences between the two populations, however, show that the transitional zone does restrict gene flow to a certain extent. Because there are no strong limitations to gene flow and there is no sharp taxonomic separation between aculeatus and olfersi, it seems reasonable to use here the concept forma (sensu Van der Spoel, 1971) instead of the concept subspecies. According to Van der Spoel (1971) a forma is the result of differences in selective pressure in the various parts of the distribution of a species. The central area of formae show clear taxonomic differences but there are intergrading zones between them, as in the present case. Consequently, the taxa olfersi and aculeatus are formae of a polytypic species, for which the names Argyropelecus olfersi fo. olfersi (Cuvier, 1829) and Argyropelecus olfersi fo. aculcatus Valenciennes, 1849 are available.

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