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GROWTH AND SEASONAL VARIATIONS IN DISTRIBUTION OF *CHAULIODUS SLOANI* AND *C. DANAE* (PISCES) FROM THE MID NORTH ATLANTIC*

by

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ABSTRACT

In the mid North Atlantic *Chauliodus sloani* is caught mainly between 55° and 29°N, while the majority is caught north of 35°N. The greatest density is found around 40°N. *Chauliodus danae* has the northern limit of its distribution at about 45°N. *C. danae*, in particular the smaller specimens, shows clear vertical migration and has food preference, while *C. sloani* does not show such migration and is most probably a random feeder. In both species there is a significant increase in length from south to north.

From the analysis of growth features in the otoliths it is demonstrated that *C. danae* grows relatively faster than *C. sloani*, though it reaches a smaller maximum length. *C. sloani* attains a greater maximum length and a higher age. Together with some anatomical differences, these are indications that the relation between both species is less close than usually supposed.

RÉSUMÉ

Dans l'Atlantique Nord central *Chauliodus sloani* est capturé surtout entre 55° et 29°N, la majeure partie des exemplaires étant pris au nord de 35°N, et la densité maximum étant enregistrée autour de 40°N. La limite septentrionale de la distribution de *Chauliodus danae* se trouve à peu près à 45°N. *C. danae* (surtout les exemplaires de petite taille) est une espèce effectuant une nette migration verticale et montrant des préférences alimentaires, tandis que *C. sloani* n'effectue pas de migrations verticales et n'a probablement pas de préférences alimentaires. Pour les deux espèces il y a une augmentation significative de la longueur du corps du sud au nord.

L'analyse des particularités de la croissance des otolithes permet de démontrer que la croissance de *C. danae* est relativement plus rapide que celle de *C. sloani*; cependant, *C. danae* atteint une longueur maximum inférieure. *C. sloani* atteint une longueur maximum supérieur et un âge plus avancé. Voici (avec certaines différences anatomiques) autant d'indications que les deux espèces sont moins étroitement apparentées qu'on ne le suppose d'habitude.

INTRODUCTION

Chauliodus sloani Bloch & Schneider, 1801 reaches a far greater maximum length (278 mm) than *C. danae* Regan & Trewavas, 1929 (134 mm) (Regan & Trewavas, 1929; Ege, 1948; Koefoed, 1956; Morrow, 1961, 1964; Marshall, 1979; present study). Marshall (1979: 478-484) developed a theory, mainly on ecological grounds, to explain this difference. The present study of vertical and horizontal distribution to trace specific differences, combined with a growth study proves, however, that the two species are less closely related than supposed by Marshall (1979).

Analysing the Dana material, Ege (1948) found that in the mid Atlantic *C. sloani* is fairly common at 45°N and that all positive records are north of 40°N, while the northernmost catches were at 56°N. He relates the northern border of *C. danae* to the 15°C isotherm (at depths of about 150 m), as most specimens are caught south of it. This means that the northern border for *C. danae* is at about 40°N.

According to Morrow (1964) *C. sloani* is found in the North Atlantic north of the line Bahamas (c. 26°N) — Canary Islands (c. 30°N), while *C. danae* is found up to 48°N with one exception of an animal caught at 51°N.

Haffner (1952: 133) states that the Chauliodontidae in their distribution are restricted "to water masses with narrow

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temperature-salinity relationships and oxygen concentrations". In his opinion, both *C. sloani* and *C. danae* are found together in the North Atlantic, "generally occupying the same water masses, with a slight difference in oxygen preferences".

Reexamining the Dana material, Haffner (1952) concluded that both *C. sloani* and *C. danae* show extensive diurnal vertical migrations. In the North Atlantic Ocean *C. danae* was found at daytime between 500 and 2000 m and at night between 500 m and the surface; *C. sloani* was collected during daytime between 1000 and 1800 m, while at night it was found in the upper 800 m.

Grey (1955) however, could not reach conclusive evidence with respect to the vertical distributions of *C. sloani* and *C. danae*. Morrow (1964) concluded that *C. danae* stays between 500 and 3500 m during daytime and between 500 m and the surface at night, while *C. sloani* stays between 550 and 2500 m during daytime and between 600 m and the surface at night. Clarke (1974) concluded that in the Pacific Ocean *C. sloani* migrates from a daytime depth range of 450-825 m to 45-225 m at night.

Remarks about growth of *C. sloani* and *C. danae* are made by Marshall (1979: 483). He explains the difference in length between the two species by the fact that the longer *C. sloani* lives in the richer peripheral waters of a central gyre in which growth conditions are more favourable, whereas *C. danae* lives in the less trophic central waters.

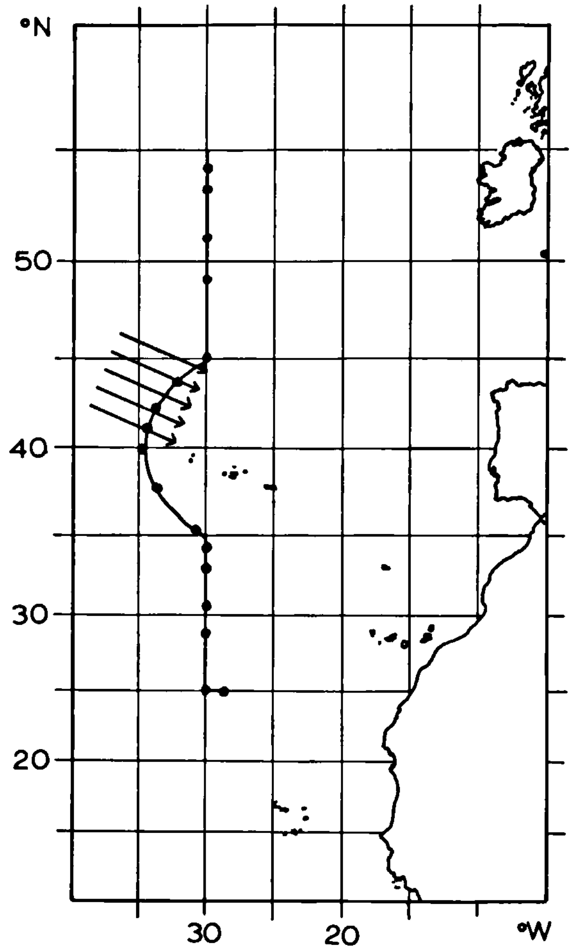

Fig. 1. Transect fished during AMNAPE 1980-1983. Black dots: positions of sampling stations; arrows indicate southern branch of North Atlantic Drift.

MATERIAL AND METHODS

The material for the present study was caught with an acoustically controlled combined Rectangular Midwater Trawl (RMT 1+8) with opening and closing device (Baker et al., 1973). Sampling was done during the Amsterdam Mid North Atlantic Plankton Expeditions between latitudes 55°N to 25°N along approximately 30°W longitude (fig. 1). The successive AMNAPE expeditions, made with the research vessel H.M.S. "Tydeman", were held in 1980 (11 April - 2 May), 1981 (15 September - 6 October), 1982 (1 February - 27 February) and 1983 (27 May - 24 June). In each season the sampling stations were as much as possible at the same positions (fig. 1). This offers the possibility to study the seasonal variations in abundance, distribution and growth of *C. sloani* and *C. danae* in the mid North Atlantic.

Measurements of the depth and speed of the net and water temperature were recorded by a net monitor. For details about positions, hydrographic conditions, etc. see Van der Spoel (1981, 1985) and Van der Spoel & Meerding (1983).

After landing the nets on deck, the cod ends were taken off as soon as possible and their contents carefully transferred into cool boxes filled with filtered seawater of ambient temperature. As soon as time permitted, sorting of the samples started and the fishes were first fixed with 4% formalin for a short time and then preserved in 70% alcohol.

The data concerning the animals are listed in the appendix. All animals are preserved in the collection of the Zoölogisch Museum, University of Amsterdam (ZMA).

The third author analysed in particular the growth features in the otoliths of *C. sloani* and *C. danae* caught in 1981. Through a small incision in the skull, laterally of the brain, one otolith, the sagitta, was taken out, mounted on a glass slide in Canada balsam for microscopic examination and recording of the variations in density, using a densitometer (Van Utrecht, 1971; Van Utrecht & Schenkkan, 1972). Microscopic examination was made in transmitted light at 450 × magnification. The diameter of the otolith was measured, the numbers of growth zones counted and the distance from the centre of the otolith to the first opaque ring was measured, from the first to the second ring, and so on.

The otoliths of *Chauliodus* are more or less flattened circular bodies which are transparent in transmitted light. In the centre is a dark spot or kernel. At a short distance from this is a dark circular ring. This part is considered to be formed in the prelarval period. Then follows a zone with patterns of circular light (translucent) and dark (opaque) rings. At a certain distance from the centre, groups of two or three evidently thicker and darker rings are grouped closely together. Such a group is considered to mark the end of a growth cycle and the start of a next one. The part of an otolith from one border line up to and including the next one is considered to represent a complete growth cycle or growth zone (see also Van Utrecht, 1982 and Van Utrecht & Holleboom, 1985). The otoliths of *C. danae* and *C. sloani* differ slightly in structure but are identical in shape. The regularly interspaced lines are in *C. danae* of a finer structure than they are in *C. sloani*.

For analysis of the horizontal and vertical distribution, the actual numbers of specimens of *C. sloani* and *C. danae* are converted to the "density" or "concentration" per 1000 l of water filtered. This is done so because the numbers of specimens caught actually are relatively small and highly variable. For this purpose the following formula is used (all specimens were caught in the RMT 8 net):

$C_{1000} = \frac{N}{8 \times D}$ (in which C_{1000} = concentration per 1000 l water filtered; N = actual number of specimens; D = distance in km fished. This last figure is multiplied by 8 for the RMT 8 net, which has an effective opening of 8 m^2.)

The figures obtained can readily be compared for the depth layers fished between 0 and 500 m. However, it has to be kept in mind that for the dephts between 500 and 1000 m the situation is completely different. In this case the net was opened at a depth of 500 m, and then each layer of c. 100 m was fished for about 15 minutes until a depth of 1000 m was reached, and the net was closed. So in fact all animals caught between 500 and 1000 m are lumped, and the figures obtained for this depth interval are not comparable to the others. They are only indicative.

RESULTS

Horizontal distribution

When the seasonal variations in density of animals (C_{1000}) are considered (figs. 2 & 3) there is a striking difference between *C. sloani* and *C. danae*. *C. sloani* (fig. 2) in all seasons is almost evenly spread over the area between 35° and 55°N. In spring its density is somewhat greater between 35° and 45°N, in the southern branch of the North Atlantic Drift. From here to the north the numbers of specimens caught diminish. South of 35°N some incidental catches of *C. sloani* occur.

For *C. danae* (fig. 3) the distribution found in the mid North Atlantic is completely different. The northern limit of its area is at about 35°N with some identical catches between 35° and 45°N. Particularly in autumn, *C. danae* reaches its greatest densities in the area between 25° and 35°N. In spring and summer its densities are relatively low. The southern limit of its distribution cannot be determined as no sampling was done south of 25°N.

For both species the data for the winter period are incomplete; only a few stations could be sampled south of 45°N, as this expedition was hampered by bad weather conditions.

It can safely be concluded that there is a relation between the abundance and the seasons in both species. *C. danae* reaches its greatest abundance in autumn. It is also evident that in the mid North Atlantic *C. sloani* reaches higher latitudes than *C. danae*. *C. sloani* is mainly caught between 35° and 55°N, while *C. danae* reaches its northern limit at about 35°N at the Azores Front and is therefore a species belonging to the subtropical fauna, while *C. sloani* tends to belong to the temperate fauna (see also Pafort-Van Iersel, 1985: 22-27). Exceptionally a few specimens of *C. danae* were caught north of 35°N.

The smaller animals (< 50 mm) of *C. sloani* are mainly caught in the southern part of its range, between 35° and 45°N, though also some longer animals are caught here. This is true for all seasons. This species reaches somewhat

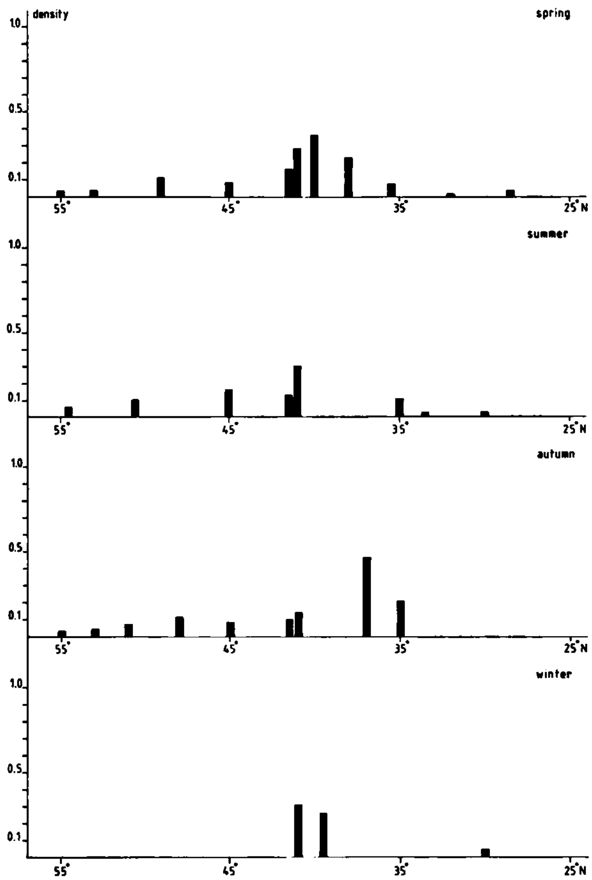

Fig. 2. Horizontal distribution and seasonal variations in density of *C. sloani* along approx. 30°W longitude.

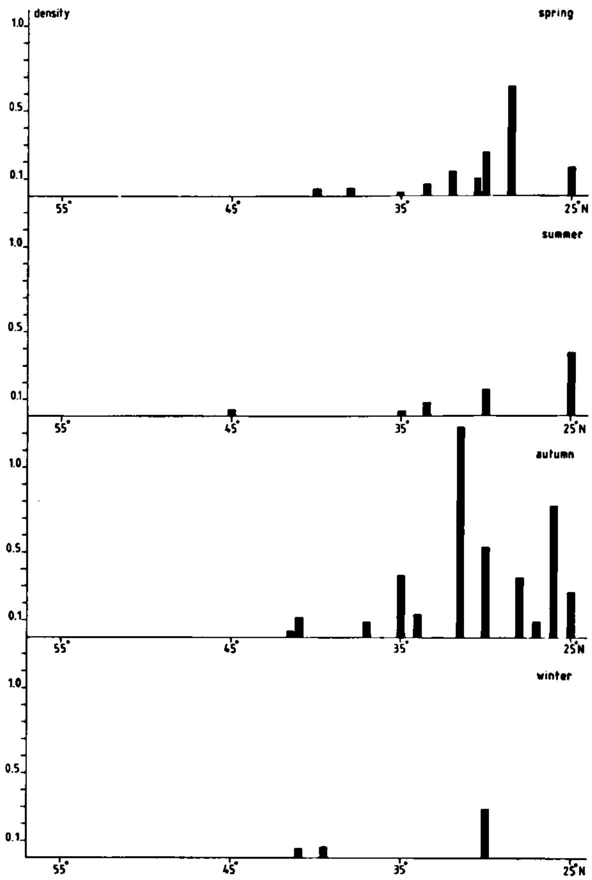

Fig. 3. Horizontal distribution and seasonal variations in density of *C. danae* along approx. 30°W longitude.

greater densities in spring. From the southern part of its range going to 55°N, there is a significant increase in length of the animals (fig. 4).

In *C. danae* there is a decrease in numbers of specimens from 25° to 40°N. Contrary to what is found for *C. sloani* there is no significant increase in length of *C. danae*. In the present samples *C. danae* reaches the greatest densities in autumn between 25° and 35°N, while, moreover, small and larger animals are dispersed at random in the area sampled.

Vertical distribution

The results for the diurnal vertical distribution are shown in fig. 5 for *C. sloani* and in fig. 6 for *C. danae*. In these figures all animals caught during all four expeditions are put together.

From fig. 5 it is clear that *C. sloani* is mainly caught at depths between 200 and 1000 m, during daytime as well as by night. During the night a rather small number of specimens is

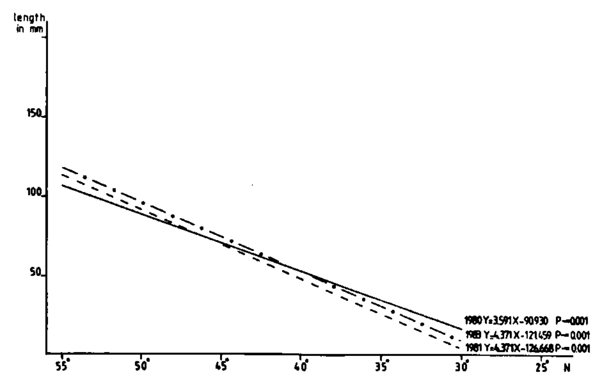

Fig. 4. Regression of body length on latitude of *C. sloani* in successive seasons (—— = 1980; ---- = 1981; -·-·-·- = 1983).

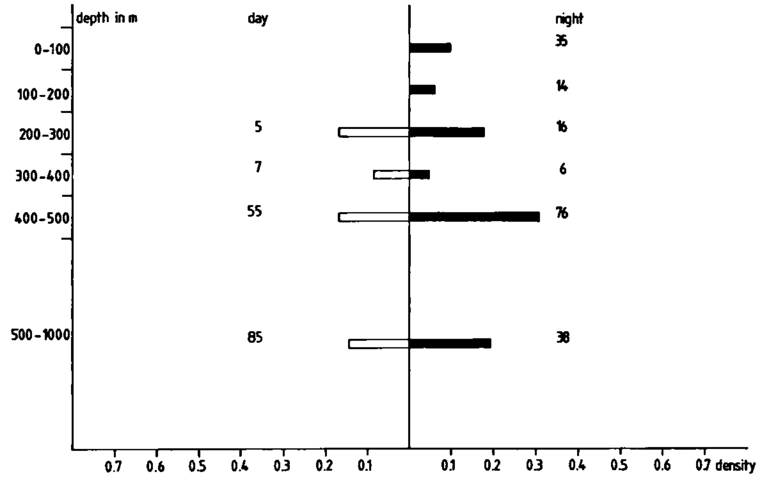

Fig. 5. Vertical distribution of *C. sloani* during day and night. The actual numbers of specimens are also recorded.

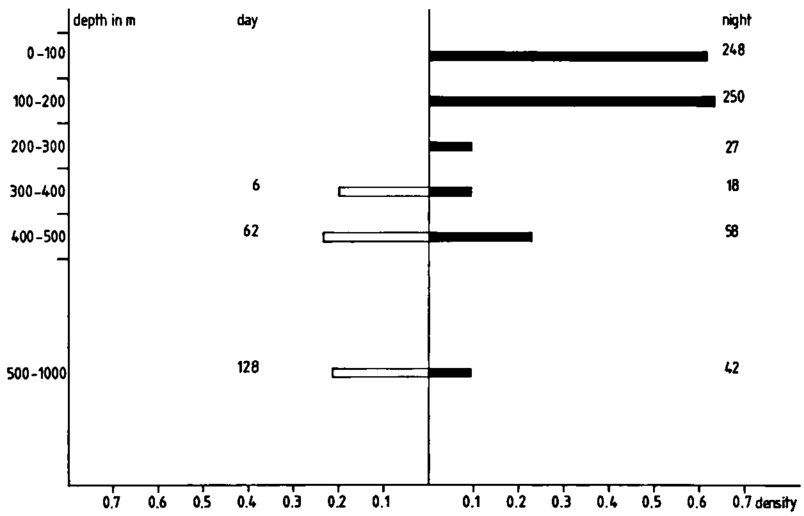

Fig. 6. Vertical distribution of *C. danae* during day and night. The actual numbers of specimens are also recorded.

caught in the upper 200 m, consisting of both animals shorter and larger than 50 mm. This species shows only a slight tendency to diurnal migratory movements.

During daytime *C. danae* is caught at depths between 300 and 1000 m. By night the density of this species at these depths is lower, while the majority of the animals is then caught at depths between 0 and 200 m. So *C. danae* shows more clearly expressed diurnal vertical movements, but also in this species only a part of the population shows vertical migration. In this species only animals up to a length of 50 mm move to the upper 200 m, the longer animals remain at depths below 300 m.

Otoliths

For this study specimens collected during the 1981 expedition were used only. Of *C. sloani* 92 specimens and of *C. danae* 468 specimens were

TABLE I
Measurements of otoliths of *C. sloani*.

Sta.	Length in mm	Ø Otolith min./max. in mm	Width of growth zones in mm						
			1	2	3	4	5	6	7
45	22	0.16/0.17	0.09						
45	23	0.18/0.18	0.10						
47	25	0.13/0.19	0.09	0.01					
45	25	0.20/0.21	0.11	0.01					
45	27	0.19/0.19	0.10	0.01					
45	31	0.20/0.21	0.12	0.02					
47	33	0.13/0.18	0.09						
45	34	0.22/0.23	0.11	0.02					
45	34	0.23/0.25	0.13	0.02					
45	36	0.23/0.24	0.12	0.02					
45	38	0.16/0.19	0.10	0.01					
45	44	0.25/0.26	0.12	0.06					
42	64	0.36/0.41	0.11	0.09	0.05				
42	67	0.35/0.40	0.11	0.08	0.04				
42	73	0.34/0.36	0.11	0.07	0.04				
42	78	0.41/0.47	0.09	0.09	0.07				
39	81	0.37/0.37	0.11	0.08	0.03				
40	88	0.26/0.42	0.11	0.11	0.07				
39	91	0.43/0.45	0.11	0.11	0.04				
42	93	0.46/0.52	0.11	0.10	0.09				
42	114	0.27/0.32	0.09	0.02	0.02	0.02			
36	142	0.43/0.48	0.12	0.07	0.05	0.05			
36	147	0.29/0.36	0.09	0.05	0.05	0.03			
43	158	0.51/0.58	0.11	0.12	0.11				
36	162	0.30/0.50	0.12	0.09	0.09	0.09			
38	163	0.42/0.52	0.11	0.07	0.07	0.08			
45	175	0.82/0.87	0.12	0.15	0.10	0.09	0.05		
37	227	0.88/0.94	0.08	0.05	0.06	0.07	0.08	0.09	0.04

available. From 28 specimens of *C. sloani* and 36 of *C. danae* the otoliths were prepared and used for photometric recording and microscopic examination. The animals were selected at random. Animals with a length below 30 mm do not always have otoliths, due to the fact that fixation with 4% formalin had obviously lasted too long, resulting in dissolution of the otoliths.

Tables I and II list the results of the measurements of the growth zones for *C. sloani* and *C. danae*, respectively. The measurements are in mm and arranged according to the increasing length of the animals. The length of the specimens of *C. sloani* varies from 22 to 227 mm, and of *C. danae* from 31 to 124 mm. From both tables it is clear that the number of growth zones increases with increasing length. In most cases the last growth zone is incomplete as is expressed by the smaller width and greater variation; these are still under formation.

The relation between the number of growth zones and the standard length of the animals is plotted in fig. 7 for *C. sloani* and in fig. 8 for *C. danae*.

Specimens of *C. sloani* with a length of about 22 to 44 mm have all one complete growth zone in their otoliths while the second one is under formation. Animals with a length varying between 64 and 91 mm have two complete growth zones, the third being under formation, and animals of about 93 mm and more have three complete growth zones while the fourth is

TABLE II

Measurements of otoliths of *C. danae*.

Sta.	Length in mm	Ø Otolith min./max. in mm	Width of growth zones in mm 1	2	3	4
49	31	0.19/0.20	0.11	0.03		
49	31	0.16/0.22	0.09	0.04		
49	33	0.18/0.24	0.09	0.02		
49	33	0.23/0.25	0.12	0.05		
49	34	? / ?	0.10	0.05		
49	34	0.22/0.22	0.11	0.02		
49	36	0.15/0.21	0.11	0.02		
49	40	0.17/0.22	0.10	0.06		
49	41	0.23/0.27	0.11	0.06		
49	41	0.25/0.30	0.12	0.08		
47	42	0.16/0.20	0.09	0.03		
55	52	0.27/0.31	0.11	0.09		
50	56	? / ?	0.11	0.08		
51	64	0.34/0.41	0.11	0.10	0.02	
51	65	0.22/0.26	0.12	0.03		
55	66	0.25/0.34	0.11	0.11	0.02	
51	69	0.33/0.37	0.11	0.08	0.03	
47	78	0.39/0.47	0.11	0.12	0.10	
50	79	0.22/0.29	0.10	0.08		
55	79	0.43/0.51	0.12	0.11	0.07	
49	82	0.36/0.45	0.11	0.09	0.04	
49	83	0.39/0.50	0.11	0.08	0.06	
50	87	0.36/0.40	0.11	0.09	0.07	
45	88	0.38/0.47	0.11	0.09	0.09	
45	89	0.33/0.42	0.11	0.07	0.02	
49	89	0.56/0.60	0.11	0.10	0.06	
51	91	0.43/0.46	0.11	0.11	0.05	
50	93	0.40/0.45	0.10	0.09	0.08	
48	95	0.36/0.39	0.11	0.09	0.06	
42	97	0.41/0.53	0.11	0.09	0.07	
50	101	0.38/0.46	0.11	0.11	0.03	
52	102	0.60/0.68	0.10	0.10	0.11	0.03
49	104	0.44/0.51	0.12	0.10	0.09	0.03
52	108	0.53/0.60	0.13	0.12	0.11	0.02
55	118	0.45/0.48	0.11	0.11	0.09	0.02
51	124	0.48/0.61	0.09	0.11	0.11	0.08

still incomplete. In the otolith of an animal of 227 mm, six complete growth zones are present and a seventh still incomplete.

In *C. danae* the animals with a length between 30 and 56 mm have one complete growth zone and the second one developing. Animals with a length of about 64 to 101 mm have two complete growth zones while the third one is still incomplete. Animals with a length varying between 104 and 124 mm have three complete growth zones and a fourth one is under formation.

The actual width of the first zone in the otolith of *C. sloani* varies between 0.08 and 0.125 mm ($\bar{x} = 0.108$ mm), the width of the second zone varies between 0.02 and 0.15 mm ($\bar{x} = 0.084$ mm) and the third one varies between 0.02 and 0.11 mm ($\bar{x} = 0.069$) (fig. 9). From these figures it can be concluded that the increment per growth zone decreases with the increase of the number of growth zones. The same conclusion can be drawn when the data are cumulated. The distances from the centre of the otolith to the consecutive dark (opaque) lines are illustrated in fig. 11.

For *C. danae* (fig. 10) it can be concluded that the mean width of the growth zones is fairly constant. The actual width of the first growth zone varies between 0.09 and 0.125 mm ($\bar{x} = 0.106$ mm), the width of the second zone varies between 0.07 and 0.12 mm ($\bar{x} = 0.990$ mm), that of the third between 0.086 and 0.112 mm ($\bar{x} = 0.101$ mm). The distances from the centre of the otolith to the consecutive dark (opaque) lines in *C. danae* are plotted in fig. 12, showing a regular increase in diameter of the otolith of about 0.11 mm per growth cycle. The greater width of the first two growth zones in the otoliths of *C. sloani* may be an indication of a greater growth rate in this species, compared with *C. danae*, resulting in a greater total length.

Figs. 13 and 14 show a selection of the recordings of the variations in density of the otoliths; these are arranged according to the increase in length of the animals. From these figures it is evident that the length of the recorded track increases with increasing length of the specimens (see also tables I and II). When comparing the recordings, it is clear that a pattern of two groups of peaks and hollows is present in each growth zone. The border line is mostly a deep sharp hollow between two such groups. The hollows mark the dark line, which can be seen in transmitted light and have a far greater density than the preceding and following adjacent lines. The pattern found in both species stays fairly constant in the first three

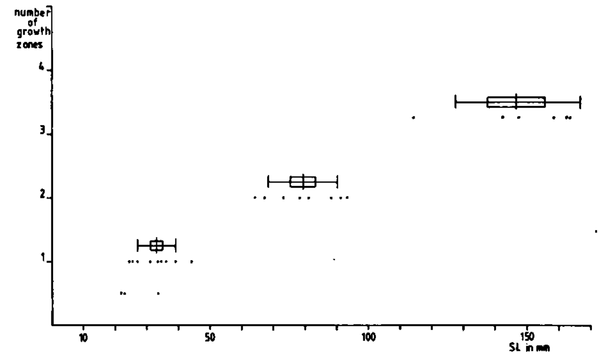

Fig. 7. *C. sloani:* relation of length and number of growth zones in the otoliths. The vertical line represents the arithmetic mean, the horizontal line the range. The box represents the standard error.

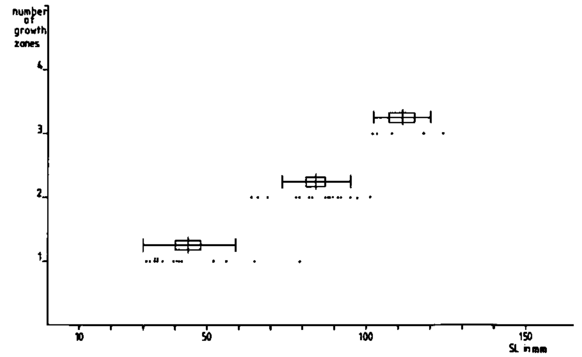

Fig. 8. *C. danae:* relation of length and number of growth zones in the otoliths. For explanation see fig. 7.

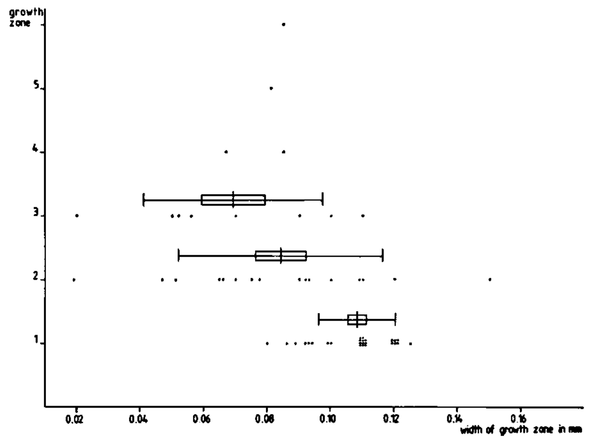

Fig. 9. *C. sloani:* width of successive growth zones in the otoliths. For explanation see fig. 7.

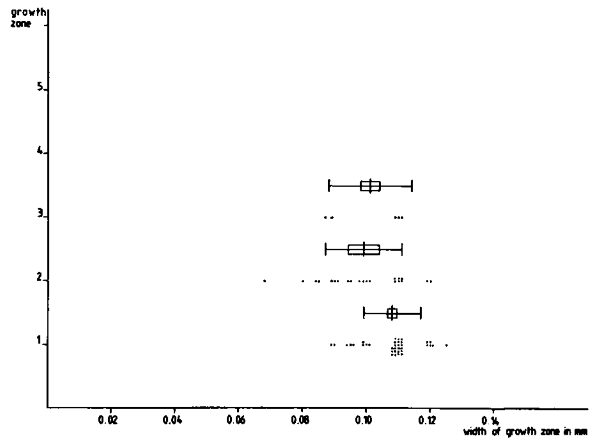

Fig. 10. *C. danae:* width of successive growth zones in the otoliths. For explanation see fig. 7.

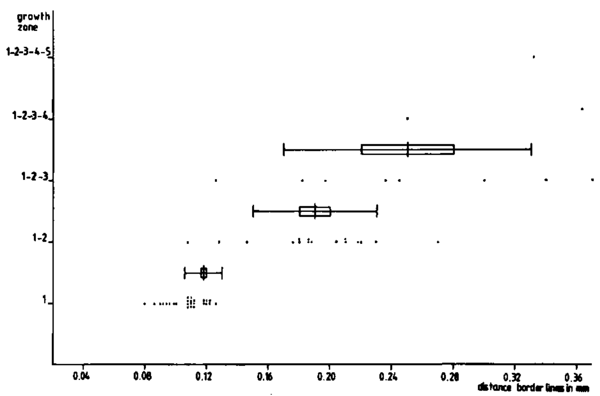

Fig. 11. *C. sloani:* radius of the otolith. For explanation see fig. 7.

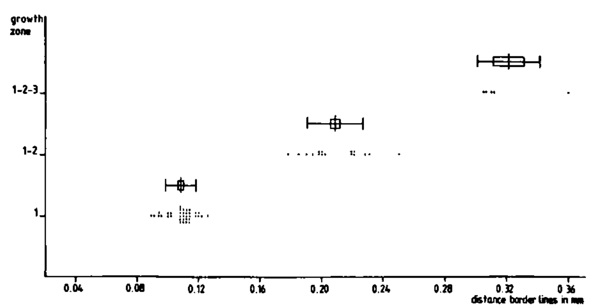

Fig. 12. *C. danae:* radius of the otolith. For explanation see fig. 7.

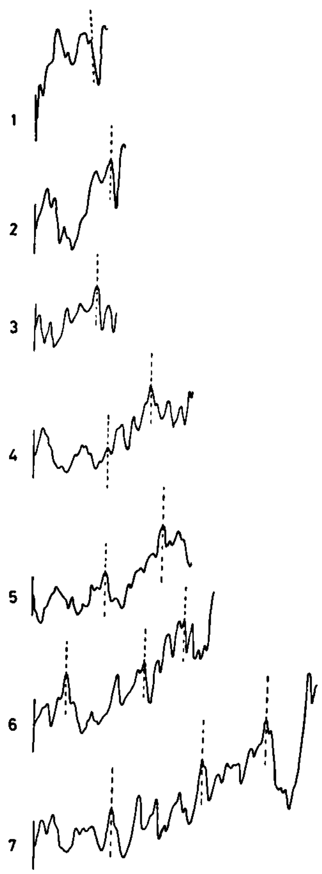

Fig. 13. *C. sloani:* recordings of variations in density in the otoliths of animals with a length of 25 mm (1), 31 mm (2), 36 mm (3), 64 mm (4), 91 mm (5), 93 mm (6) and 158 mm (7). The solid vertical line left in each recording indicates the centre of the otolith, dashed lines indicate dark rings, marking margins of respective growth zones.

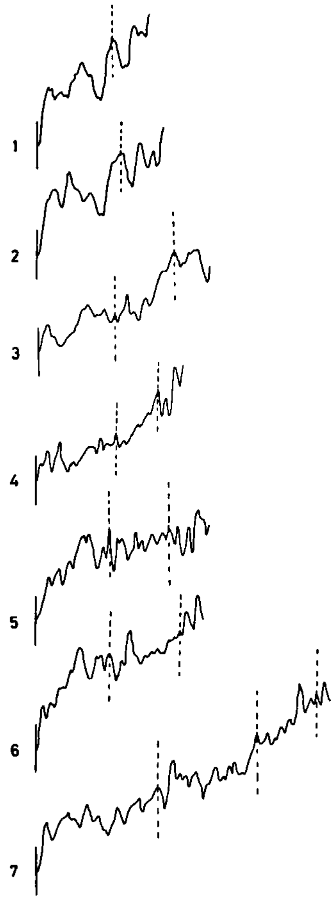

Fig. 14. *C. danae:* recordings of variations in density in the otoliths of animals with a length of 33 mm (1), 41 mm (2), 69 mm (3), 82 mm (4), 83 mm (5), 95 mm (6) and 108 mm (7). For explanation see fig. 13.

growth zones formed. The uniformity of this pattern in the recordings, in these zones, can be explained from the fact that specimens of *C. sloani* and of *C. danae* then live under the same conditions. What happens after formation of the third growth zone is not known. No specimens of *C. danae* with more than three growth zones, and only very few specimens of *C. sloani* with more than three completed growth zones were caught during the 1981 expedition.

When the curves for both species are compared it is striking that the line for *C. sloani* starts at a higher level than it does for *C. danae*. However, the slope of the line for *C. sloani* is smaller. So it can be concluded that the growth rate in *C. danae* is relatively higher than in *C. sloani*.

The relation between the minimum and maximum diameter of the otolith and the standard length of the animals is shown in figs. 15 (*C. sloani*) and 16 (*C. danae*). This relation gives an impression of the growth of the animal and of their otoliths. In the figures regression lines are drawn. The correlation coefficient and the value for *P* are rather high for both species. There is a significant increase of the otolith diameter with increasing length. From this it

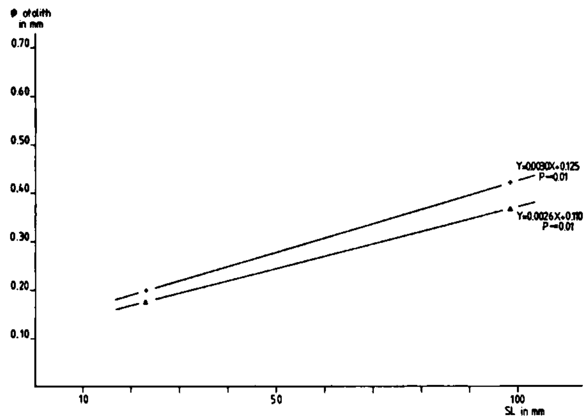

Fig. 15. *C. sloani.* Growth of the otolith measured along the smallest (▲—▲) and greatest (+—+) diameter.

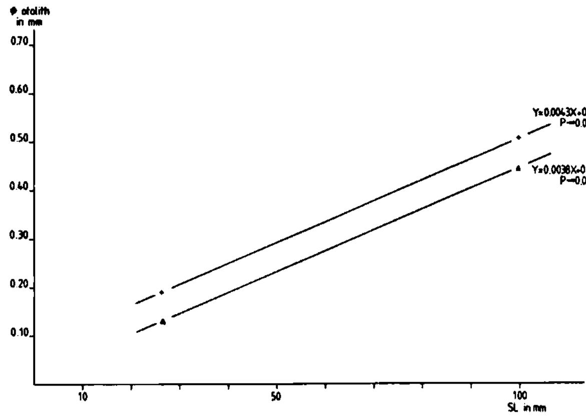

Fig. 16. *C. danae.* Growth of the otolith measured along the smallest (▲—▲) and greatest (+—+) diameter.

can be concluded that there is a direct relation between the growth of the otolith and the growth of the animal.

In figs. 17 (*C. sloani*) and 18 (*C. danae*) the development of the successive growth zones is shown. The regression lines in both figures are based on the measured distance from the last-formed opaque ring towards the rim of the otolith. The only exception is the line representing the development of all growth zones together. This line is based on measurements of the radius (distance from the centre towards the rim) of the otolith.

No results about the development of the first growth zones are reproduced here, because the otoliths of these animals, which are mostly smaller than about 30 mm, were in many cases dissolved.

From fig. 17 (*C. sloani*) it can be seen that the line representing the development of the third growth zone has a smaller slope compared with the other regression lines. The reason for this is not clear. Perhaps in this period the physiological activity of the animals differs from the activity in other periods.

The regression lines representing the development of all growth zones together show a high correlation coefficient and a high value for *P* for both species. The correlation coefficient and value for *P* for the lines representing the development of the second growth zone are reasonable. The two other regression lines show low correlation coefficients and low values for *P*. The low correlation coefficient and low value for *P* for the fourth growth zone is based on the fact that the development of this zone is not yet completed. The reason for the poor results for the line representing the development of the third growth zone is not known.

DISCUSSION

The greatest length of *C. sloani* in the present samples is 243 mm and of *C. danae* 134 mm, so *C. sloani* reaches a considerably greater length. This was also demonstrated by Regan & Trewavas (1929), Ege (1948), Koefoed (1956), Morrow (1961, 1964) and Marshall (1979).

Marshall (1979) developed a theory to explain this difference in maximum length. This theory is based on the tendency for resident mesopelagic fishes in central waters to be smaller than their relatives in peripheral waters with a higher productivity. Marshall (1979: 478-484) supposes that both species of *Chauliodus* are migrators, and that *C. danae* is a species living in less productive central waters and therefore remains shorter than *C. sloani* which lives in richer peripheral waters. The present results do not agree with this theory, because, in spite of the supposed lower produc-

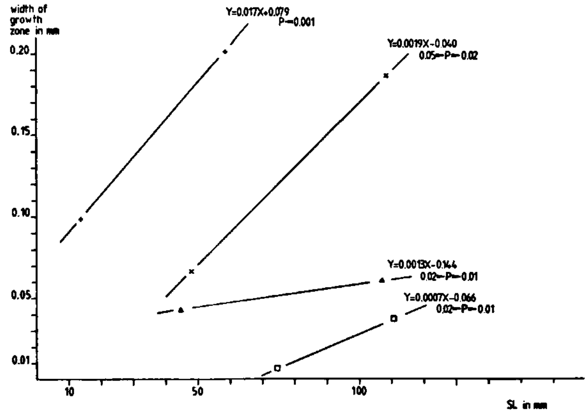

Fig. 17. *C. sloani*. Growth of the zones in the otoliths. In line 1 (+—+) all growth zones are taken together, line 2 (×—×) represents the growth of the second zone, line 3 (▲—▲) that of the third, and line 4 (□—□) that of the fourth zone.

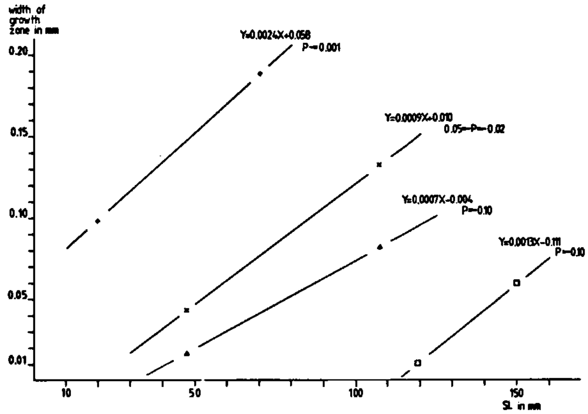

Fig. 18. *C. danae*. Growth of the zones in the otoliths. For explanation see fig. 17.

tivity of the water, *C. danae* grows faster than *C. sloani*.

The otoliths of *C. sloani* and *C. danae* have some features in common. Each growth zone consists of a wide translucent zone and two narrow opaque rings. In the translucent zone regularly interspaced, slightly darker lines are present. In the otoliths of *C. danae* the dark lines are, however, of a finer structure than in *C. sloani*. Measurements of the width of the successive growth zones show that the increase in diameter of the otolith of *C. danae* is regular, while in *C. sloani* the width diminishes with increasing number of growth zones (cf. figs. 17 & 18).

The differences between the two species in otolith data, in horizontal and vertical distribution, and in maximum length are probably related to differences in their way of living. From the present results it can be concluded that *C. danae*, in particular the smaller animals, undertakes diurnal vertical migrations in permanently stratified waters, while *C. sloani* does not show this clearly, in contrast to Haffner's (1952) conclusions. Moreover, analysis of stomach contents (Grey, 1955) reveals that *C. danae* mainly feeds on small crustaceans, while *C. sloani* feeds on fish, algae and eggs. So it can be concluded that the nonmigratory *C. sloani* feeds at random while *C. danae* is a vertical migrator with food preferences. These differences in feeding habits have a great influence on their energy-use. For *C. danae*, living in warm water, it means that the energy-use is high, resulting in a fast development (Grey, 1955) and a small length. Low energy-use is reflected in a slow development (Clarke, 1974) and a greater length, as e.g. in *C. sloani*, living in cold water. It also means that *C. sloani* can reach a higher age than *C. danae*. This is demonstrated by the difference in the maximal number of growth zones in the otoliths of both species; in *C. sloani* six complete zones and the seventh under formation, in *C. danae* three complete zones and the fourth under formation.

There are, moreover, some anatomical differences in specimens of the two species, having the same length (fig. 19). The tendons of the dorsal muscles, which throw the head backward, are in *C. sloani* relatively broad and long and have a more lateral insertion on both sides of the head. In *C. danae* these tendons are shorter and more slender, while they have their insertion closer to the midline and more at the dorsal surface of the head.

Summarizing, *C. sloani* and *C. danae* differ in a number of aspects: *C. sloani* is a species mainly occurring north of 40°N with its

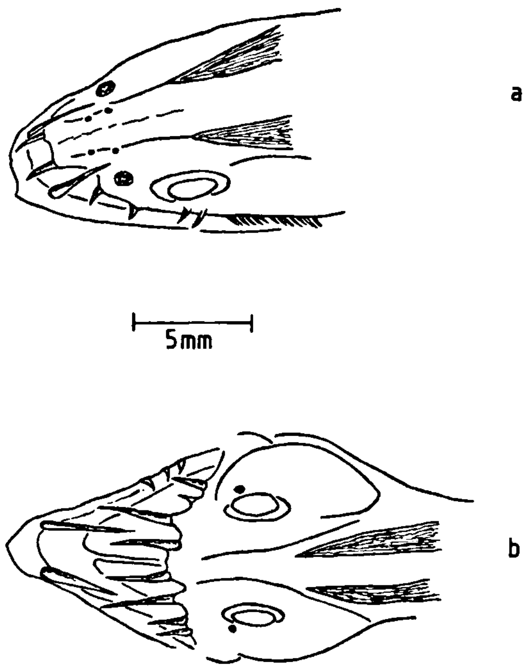

Fig. 19. Insertion of the tendons of the dorsal muscles on the head: a, *C. sloani*; b, *C. danae*.

greatest abundance in spring, while *C. danae* mainly occurs south of 40°N with its greatest abundance in autumn. *C. sloani* hardly undertakes vertical migrations, grows relatively slowly, reaches a higher age and greater maximum length, while *C. danae* grows relatively fast, reaches a lower age and a smaller maximum length.

All these points may indicate that both species are far more apart than expected at first sight.

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APPENDIX

Geographic, bathymetric, and morphometric data for the two *Chauliodus* species studied. Animals marked * are not measured due to damage.

Sta.	Haul	Position	Date	D(ay) N(ight)	Depth in m	*C. sloani* Number of specimens	*C. sloani* Length in mm	*C. danae* Number of specimens	*C. danae* Length in mm
10	3	54°54.0′N 30°32.3′W	14-IV-'80	D	480-1010	1	155		
11	1	53°00.8′N 29°58.1′W	15-IV-'80	D	290- 995	2	148, 183		
13	1	48°58.9′N 30°01.3′W	16-IV-'80	N	40- 100	5	68-107		
13	2	49°01.1′N 30°00.6′W	17-IV-'80	N	130- 220	4	51-101		
13	3	40°00.9′N 29°42.7′W	17-IV-'80	N	215- 310	2	102, 103		
13	4	48°59.8′N 29°35.1′W	17-IV-'80	N	310- 400	1	111		
13	6	49°00.7′N 29°31.0′W	17-IV-'80	N/D	375- 500	10	30-142		
13	9	49°00.8′N 29°18.5′W	17-IV-'80	D	480-1005	4	26-167		
14	1	45°02.8′N 29°59.3′W	18-IV-'80	D	375- 500	6	49-105		
14	3	45°10.2′N 29°50.5′W	18-IV-'80	D	280- 410	2	113, 126		
14	5	45°15.0′N 29°50.0′W	18-IV-'80	N	430-1000	7	34-210		
14	8	45°21.8′N 29°46.4′W	19-IV-'80	N	85- 200	1	110		
16	3	41°47.8′N 35°02.8′W	20-IV-'80	D	490-1000	17, 1*	37-53		
16	4	41°39.1′N 34°59.1′W	20-IV-'80	D	365- 495	2	47, 48		
16	6	41°31.6′N 34°55.9′W	20-IV-'80	N	45- 100	2	53, 68		
17	1	41°01.4′N 35°31.3′W	21-IV-'80	N	45- 95	7	57-118		
17	2	41°10.6′N 35°30.9′W	21-IV-'80	N	330- 505	19	30-61		
18	1	39°58.5′N 36°24.9′W	22-IV-'80	N	520-1130			1	119
18	2	39°52.2′N 36°18.1′W	22-IV-'80	N	265- 430	2	47, 53	1	40
18	4	39°47.2′N 36°16.6′W	22-IV-'80	N	110- 205	2	93, 110		
18	7	39°47.8′N 36°07.9′W	22-IV-'80	D	360- 470	23, 1*	39-71	3	32-57
18	10	39°53.9′N 35°58.9′W	22-IV-'80	D	440- 910	12	33-70		
18	13	39°59.8′N 35°47.2′W	22-IV-'80	D/N	420- 510	26	31-58	1	33
19	6	38°05.1′N 35°44.9′W	23-IV-'80	D	370- 495	1	48		

APPENDIX (continuation)

Sta.	Haul	Position	Date	D(ay) N(ight)	Depth in m	*C. sloani* Number of specimens	*C. sloani* Length in mm	*C. danae* Number of specimens	*C. danae* Length in mm
19	22	37°48.5'N 35°17.4'W	24-IV-'80	D	500-1000	17	28-58	2	24, 33
20	1	35°27.2'N 31°51.6'W	25-IV-'80	D	505- 870	3	46-100		
20	8	35°14.0'N 31°32.5'W	26-IV-'80	N	205- 305			1	48
21	6	33°40.5'N 30°40.6'W	27-IV-'80	N	510-1000			2	36, 66
21	9	33°30.7'N 30°39.3'W	27-IV-'80	N	105- 200			5	20-48
21	10	33°26.1'N 30°38.1'W	27-IV-'80	N/D	300- 400			1	76
22	1	32°19.0'N 30°03.1'W	27-IV-'80	D	500-1000	1	40	3	50-128
22	5	32°07.3'N 29°54.5'W	27-IV-'80	N	295- 405			2	32, 61
22	6	32°04.1'N 29°54.0'W	27-IV-'80	N	195- 300			6	67-100
22	7	31°58.2'N 29°54.0'W	28-IV-'80	N	90- 200			25, 2*	17-83
22	9	31°55.9'N 29°52.2'W	28-IV-'80	N	45- 100			1	21
23	2	30°39.9'N 29°59.5'W	28-IV-'80	D	505- 960			4	20-39
23	3	30°32.4'N 30°00.6'W	28-IV-'80	D	385- 500			5	17-22
24	2	29°48.1'N 29°57.5'W	29-IV-'80	N	110- 205			8	17-40
24	3	29°44.0'N 29°57.7'W	29-IV-'80	N/D	200- 300			14	46-92
25	1	28°42.0'N 29°59.1'W	29-IV-'80	D	490-1000	1	36	22, 1*	17-134
25	3	28°34.7'N 29°58.1'W	29-IV-'80	N	390- 500	2	36, 39	12	19-61
25	4	28°30.6'N 29°57.2'W	29-IV-'80	N	290- 405			3	49-90
25	6	28°27.2'N 29°56.5'W	29-IV-'80	N	195- 300			5	51-89
25	7	28°23.5'N 29°55.9'W	30-IV-'80	N	40- 100			2	18, 19
25	9	28°20.0'N 29°55.8'W	30-IV-'80	N	100- 200			84	14-44
26	1	24°57.9'N 29°59.1'W	1- V-'80	D	200- 450			5	18-46
26	4	24°52.0'N 29°59.5'W	1- V-'80	D	510-1090			16, 1*	17-68
26	8	24°44.9'N 30°00.6'W	1- V-'80	D	300- 500			1	18
26	11	24°47.9'N 30°07.6'W	1- V-'80	N	55- 100			1	19
27	2	24°48.7'N 28°35.3'W	2- V-'80	N/D	180- 300			10, 1*	17-61

APPENDIX (continuation)

Sta.	Haul	Position	Date	D(ay) N(ight)	Depth in m	C. sloani		C. danae	
						Number of specimens	Length in mm	Number of specimens	Length in mm
27	10	24°48.6'N 28°47.2'W	2- V-'80	D	475-1000			17, 1*	16-102
27	17	24°51.7'N 28°40.4'W	2- V-'80	D	400- 500			13	18-23
27	23	24°56.3'N 28°37.6'W	2- V-'80	N	45- 100			10, 1*	19-25
36	8	55°07.0'N 30°10.3'W	8- X-'81	D	0-1000	2	142, 162		
36	12	55°07.4'N 30°05.4'W	8- X-'81	D/N	0-1140	1	147		
37	9	52°58.5'N 29°47.4'W	7- X-'81	D/N	400-1000	1	227		
38	1	50°59.8'N 29°58.2'W	6- X-'81	D	0- 415	1	46		
38	8	50°57.8'N 29°50.0'W	6- X-'81	D	0-1005	2	163, 175		
38	12	50°50.4'N 29°38.6'W	6- X-'81	N	0- 205	5	42-192		
38	14	50°48.4'N 29°35.3'W	6- X-'81	N	0- 315	4	50-75		
39	2	47°56.3'N 30°38.3'W	5- X-'81	N	55- 100	1	53		
39	9	47°46.5'N 30°23.5'W	5- X-'81	D	310- 390	3	41-91		
39	10	47°43.4'N 30°18.8'W	5- X-'81	D	405- 500	7	26-74		
39	14	47°39.1'N 30°13.8'W	5- X-'81	D	500-1020	2	35, 36		
40	1	45°09.4'N 29°57.1'W	2- X-'81	D	385- 570	3	26-88		
42	1	41°37.8'N 34°32.2'W	30-IX-'81	D	200- 315	5	64-114		
42	5	41°42.5'N 34°23.4'W	30-IX-'81	D	405- 500	1	93	1	97
42	6	41°44.4'N 34°20.5'W	30-IX-'81	D	460- 870	3	32-44	1	27
43	1	41°05.6'N 35°40.4'W	29-IX-'81	D	385- 565	7	25-158		
43	5	41°10.3'N 35°42.4'W	29-IX-'81	D	500- 995	6, 1*	23-39	7, 3*	25-34
45	10	37°08.8'N 35°01.0'W	27-IX-'81	D/N	505-1010	25, 1*	20-175	5, 1*	24-28
45	11	37°05.7'N 35°06.5'W	27-IX-'81	N	385- 530	3	27-34	2	20, 88
45	13	37°03.8'N 35°09.4'W	27-IX-'81	N	195- 380			1	89
47	2	35°07.3'N 31°34.4'W	23-IX-'81	N	180- 300			3	22-42
47	3	35°07.7'N 31°29.0'W	23-IX-'81	N	425- 855	11	25-41	4	19-34
47	6	35°07.6'N 31°22.7'W	23-IX-'81	N	50- 105	1	43	28, 5*	17-46

APPENDIX (continuation)

Sta.	Haul	Position	Date	D(ay) N(ight)	Depth in m	*C. sloani* Number of specimens	*C. sloani* Length in mm	*C. danae* Number of specimens	*C. danae* Length in mm
47	7	35°07.1'N 31°19.5'W	24-IX-'81	N	95- 190			3	41-78
47	9	35°06.7'N 31°16.4'W	24-IX-'81	N	360- 520	4	23-31		
48	2	34°09.0'N 31°20.8'W	22-IX-'81	N	210- 300			2	80, 95
48	5	34°11.9'N 31°16.2'W	23-IX-'81	N	110- 200			3	57-79
48	7	34°12.4'N 31°05.6'W	23-IX-'81	N/D	290- 440			2	22, 89
48	8	34°12.9'N 31°11.9'W	23-IX-'81	N	500-1150			3, 1*	18, 71
48	11	34°12.7'N 31°05.8'W	23-IX-'81	D	390- 495			7	21-27
49	1	31°40.4'N 29°49.4'W	21-IX-'81	D/N	410- 490			29, 1*	19-34
49	3	31°43.1'N 29°42.6'W	21-IX-'81	N	515-1000			10, 1*	27-104
49	6	31°44.5'N 29°35.3'W	21-IX-'81	N	45- 107			132, 6*	19-41
49	8	31°45.6'N 29°32.9'W	22-IX-'81	N	105- 230			27, 3*	18-89
49	9	31°47.4'N 29°30.0'W	22-IX-'81	N	200- 325			1	82
50	2	30°05.3'N 29°46.7'W	20-IX-'81	N	730-1200			2	76, 101
50	5	29°58.4'N 29°48.2'W	20-IX-'81	D	490- 745			36	16-96
50	7	30°09.1'N 29°42.3'W	20-IX-'81	N	385- 508			1	25
50	9	30°12.0'N 29°40.0'W	21-IX-'81	N	260- 410			3	19-79
50	12	30°14.5'N 29°39.8'W	21-IX-'81	N	210- 305			1	27
50	13	30°18.5'N 29°39.3'W	21-IX-'81	N	110- 195			53, 4*	18-87
51	7	28°03.3'N 29°51.9'W	19-IX-'81	N	395- 500			25	21-124
51	12	28°07.0'N 29°52.8'W	19-IX-'81	N	500-1050			6	18-64
51	14	28°17.2'N 29°53.4'W	20-IX-'81	N	190- 300			3	64-69
52	1	24°49.8'N 30°00.3'W	18-IX-'81	N	30- 90			17, 1*	17-25
52	5	24°57.5'N 30°01.2'W	18-IX-'81	D	490-1005			9, 1*	19-98
52	14	25°04.1'N 29°55.1'W	18-IX-'81	N	400- 510			7, 2*	17-108
53	10	25°09.4'N 28°34.3'W	17-IX-'81	N	170- 300			3	58-92
54	11	26°08.2'N 24°31.0'W	16-IX-'81	N	30- 92			22	20-27

APPENDIX (continuation)

Sta.	Haul	Position	Date	D(ay) N(ight)	Depth in m	*C. sloani* Number of specimens	*C. sloani* Length in mm	*C. danae* Number of specimens	*C. danae* Length in mm
55	1	27°10.1′N 19°54.6′W	15-IX-'81	N	40- 105			3	18-20
55	4	27°02.5′N 20°17.7′W	15-IX-'81	D	570-1000			7	52-118
55	14	26°57.5′N 20°32.9′W	15-IX-'81	N	400- 500			1	67
55	15	26°55.9′N 20°38.6′W	15-IX-'81	N	290- 395			2	67, 87
62	13	40°53.3′N 35°39.3′W	12-II-'82	N	0-2000			1	26
62	27	40°55.4′N 35°35.1′W	13-II-'82	D	400- 490	2	38, 61	4	24-30
62	39	40°56.3′N 35°33.0′W	14-II-'82	D	505- 980	13, 1*	34-51	4, 1*	26-123
63	24	39°47.7′N 35°50.3′W	16-II-'82	N	295- 410	2	86, 121		
63	27	39°41.9′N 35°46.2′W	17-II-'82	N	385- 500	9	38-48		
63	28	39°36.2′N 35°43.1′W	17-II-'82	N	505-1000	12, 2*	31-51	2	30, 37
65	13	29°59.8′N 29°42.9′W	19-II-'82	N	285- 445			4	51-88
65	18	30°00.0′N 29°37.5′W	19-II-'82	N	400- 525			4	51-117
65	20	29°59.4′N 29°34.8′W	19-II-'82	N	490-1010			5	19-87
66	1	30°00.2′N 29°29.1′W	20-II-'82	N	515- 995	1	39	1	94
66	5	30°00.9′N 29°19.1′W	20-II-'82	D	300- 415			6	22-75
68	1	30°02.4′N 28°10.8′W	21-II-'82	N	400- 505			2	26, 80
68	4	30°02.6′N 28°05.7′W	21-II-'82	N	40- 115			21	18-27
68	5	30°02.6′N 28°03.0′W	21-II-'82	N	80- 190			18, 1*	19-50
74	12	54°22.0′N 29°49.0′W	19-VI-'83	N/D	400- 502	2	42-157		
76	26	50°21.3′N 29°29.7′W	17-VI-'83	D	500- 995	5	151-215		
76	30	50°20.0′N 29°20.7′W	17-VI-'83	D	400- 500	2	68, 92		
78	1	44°58.5′N 30°03.8′W	14-VI-'83	N/D	500-1000	1	191		
78	14	44°59.3′N 29°54.9′W	14-VI-'83	D	300- 400	2	80, 85		
78	36	45°00.8′N 29°57.0′W	14-VI-'83	D/N	400- 503	15	24-100	1	62
78	39	45°02.3′N 30°01.3′W	14-VI-'83	N	500-1000	1	141		

APPENDIX (continuation)

Sta.	Haul	Position	Date	D(ay) N(ight)	Depth in m	*C. sloani*		*C. danae*	
						Number of specimens	Length in mm	Number of specimens	Length in mm
78	42	45°02.6'N 30°06.7'W	14-VI-'83	N	140- 300	12	53-86		
78	53	44°57.0'N 30°01.0'W	15-VI-'83	N	50- 98	6	57-76		
78	54	44°56.8'N 29°56.1'W	15-VI-'83	N	98- 200	4	66-101		
78	55	44°58.3'N 29°52.4'W	15-VI-'83	N	302- 400	1	59		
78	57	45°00.6'N 29°55.9'W	15-VI-'83	N/D	398- 500	9	23-178		
78	60	45°03.3'N 29°59.1'W	15-VI-'83	D	1002-1752	1	81		
80	1	41°34.5'N 34°51.6'W	12-VI-'83	N	198- 340	2	63, 72		
80	18	41°37.6'N 34°50.3'W	12-VI-'83	N	103- 195	1	82		
80	19	41°39.1'N 34°48.2'W	12-VI-'83	N	52- 105	6	57-77		
80	21	41°40.9'N 34°47.1'W	13-VI-'83	N	0- 50	3	53-61		
81	3	40°54.7'N 35°30.8'W	11-VI-'83	N	402- 500	7	25-81		
81	6	40°56.2'N 35°31.6'W	11-VI-'83	N	500-1000	6	29-243		
81	7	41°00.3'N 35°32.1'W	11-VI-'83	N	95- 200	1	86		
81	8	41°02.4'N 35°32.3'W	11-VI-'83	N	35- 100	1	64		
81	16	40°56.6'N 35°24.6'W	12-VI-'83	N	400- 500	24, 2*	22-65		
84	24	35°09.6'N 31°31.8'W	5-VI-'83	D/N	494-1000	3	23-30	1	110
84	31	35°11.1'N 31°27.9'W	5-VI-'83	N	45- 100	2	72, 78		
84	37	35°11.8'N 31°31.4'W	6-VI-'83	N/D	505-1000	8, 1*	20-56		
84	45	35°10.9'N 31°30.4'W	6-VI-'83	D	400- 500	1	72	1	22
84	72	35°09.2'N 31°26.6'W	6-VI-'83	N	405- 495	7, 1*	24-27		
84	75	35°08.6'N 31°23.8'W	7-VI-'83	N	100- 150	1	51	1	33
84	76	35°09.3'N 31°27.4'W	7-VI-'83	N	145- 200			1	86
85	12	33°28.1'N 30°10.3'W	4-VI-'83	N	98- 200			1	56
85	14	33°30.9'N 30°12.0'W	4-VI-'83	N	50- 102	1	55	4	22-37
87	2	30°00.1'N 29°47.0'W	1-VI-'83	N	500-1000			2	72, 90
87	6	29°57.9'N 29°36.8'W	2-VI-'83	N	200- 305			2	71, 87

APPENDIX (continuation)

Sta.	Haul	Position	Date	D(ay) N(ight)	Depth in m	*C. sloani* Number of specimens	*C. sloani* Length in mm	*C. danae* Number of specimens	*C. danae* Length in mm
87	10	29°58.9′N 29°35.7′W	2-VI-'83	N	293- 398			3	81-96
87	14	29°59.1′N 29°30.0′W	2-VI-'83	D	395- 550			3	76-81
87	35	30°00.9′N 29°04.0′W	2-VI-'83	D/N	500-1000	1	36	6	28-82
89	29	24°52.8′N 30°03.5′W	30- V-'83	N	515-1000			4	41-91
89	36	24°47.9′N 30°02.1′W	31- V-'83	N	370- 520			3	89-117
89	39	24°54.5′N 29°58.8′W	31- V-'83	N	90- 202			14, 1*	17-111
89	54	24°50.1′N 30°02.9′W	31- V-'83	D	390- 518			25, 3*	19-27
987	6	29°59.1′N 28°06.6′W	3-VI-'83	N	55- 105			7	20-35
987	7	29°59.1′N 28°04.2′W	3-VI-'83	N	395- 528	1	46	1	103
987	8	29°59.8′N 27°55.3′W	3-VI-'83	N	85- 193			7, 1*	20-72
987	9	29°59.5′N 27°51.9′W	3-VI-'83	N/D	180- 295			8	20-84

Second draft received: 9 December 1986