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## Lunar rhythms of vertical migrations coded in otolith microstructure of North Atlantic lanternfishes, genus *Hygophum* (Myctophidae)

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**Abstract** Otoliths of five *Hygophum* species were examined by means of light and scanning electron microscopy. In otoliths of four species (*H. benoiti*, *H. macrochir*, *H. reinhardtii* and *H. taaningi*) a strong cyclic pattern of the incremental structure was observed. In the fifth species (*H. hygomii*) such a pattern did not exist. An analysis of archival data on mesopelagic collections suggested three types of *Hygophum* spp. migratory behavior in relation to the lunar cycle which corresponded with the otolith microstructure. In *H. hygomii* only limited influence of moon phase on the uppermost range of night-vertical migration toward the surface was observed. The abundant nighttime occurrence of this species moved from the 0 to 50 m into the 50 to 100 m depth strata at full moon. In *H. benoiti*, a great part of the population, mainly juveniles, showed a tendency toward cessation of the vertical migrations during the first and fourth quarters of the lunar cycle. *H. macrochir* and *H. taaningi* had the strongest correlation of behavior with the lunar cycle. Both species showed arrested vertical migrations at the new moon phase, staying at day depths during the night, i. e., below 400 m. Thus, sequences of clear growth increments in otoliths represented a fast-growth period associated with the night migration to the warm surface layers, while bands without easily distinguishable incremental structure were interpreted as a period of slow growth in deep, cold waters due to limitation of the upward migration range occurring approximately at new moon.

### Introduction

The lanternfish genus *Hygophum* (Bolin, 1939) includes nine currently recognized species. Five of them, *H. benoiti*,

*H. hygomii*, *H. macrochir*, *H. reinhardtii* and *H. taaningi*, occur in the North Atlantic (Nafpaktitis et al. 1977). Maximum sizes of these species generally do not exceed 60 mm SL, except for *H. hygomii* which may attain 68 mm (Hulley 1981). A characteristic feature of myctophid behavior is the habit of diel vertical migrations practiced by most species over a wide range of depths. The range of *Hygophum* spp. migrations covers almost the entire uppermost 1000 m part of the water column, although there are geographic, seasonal, inter-specific and ontogenetic variations (Badcock and Merrett 1976; Nafpaktitis et al. 1977; Karnella 1987; Brooks and Saenger 1991). The maximum abundance of Atlantic *Hygophum* species was found in the uppermost 100 m layer during the night and below 500 m during the day (Nafpaktitis et al. 1977; Karnella 1987).

Fish otoliths contain significant biological, life history and environmental information coded in their microstructure (Radtke 1987). Since daily growth increments were first recorded by Pannella (1971) these structures have found wide application in age and growth studies of larvae, juvenile and fast-growing fishes (Campana and Neilson 1985; Jones 1986). Substantial differences in vertical distribution and vertical migratory behavior of myctophids, especially in the larvae and early juveniles of most species (Clarke 1973; Badcock and Merrett 1976; Loeb 1979; Karnella 1987), are manifested in the unique microstructure of their otoliths (Gjösæter 1987; Gartner 1991; Linkowski 1991). Recently, Gartner (1991) verified the daily nature of growth increments in otoliths of three myctophid species.

During the examination of sagittal otoliths of several *Hygophum* species (Linkowski 1991) the occurrence of a cyclic growth pattern was observed in some of them. The apparent regularity of these incremental patterns suggested a rhythmic character of the phenomenon. The aim of this paper is to verify the nature of the rhythm as well as explain the mechanism of growth disturbances, e. g. which environmental factors and/or

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behavioral habits might be responsible for such specific otolith growth.

## Materials and methods

### Otolith preparation

Many of the otoliths (sagittae) utilized in the present study were those examined earlier (Linkowski 1991: Table 1). Additional material was also used for studying otolith growth patterns and marginal growth increments deposited after the most recent band in relation to the date of capture in the lunar cycle. These otoliths were obtained from the same collections as those used by Linkowski (1991), i. e., those deposited at Woods Hole Oceanographic Institution (WHOI), Museum of Comparative Zoology, Harvard University (MCZ) and Sea Fisheries Institute in Gdynia (SFI). Otoliths examined came from fishes collected over a wide area of the North and Central Atlantic. Additional information on the otolith material is given in Table 1.

The methods of otolith preparation for scanning electron microscopy (SEM) and light microscopy (LM) were given by Linkowski (1991). The research was mainly carried out by LM, while SEM was used to verify LM images and for the final presentation of illustrations. Only sagittal sections were used in this study. The terminology of otolith microstructure was according to the standards adopted by Campana and Neilson (1985). The microincrements that form the incremental growth sequences (IGS) are assumed to be deposited on a daily basis, as these increments are analogous to increments verified as daily by Gartner (1991) in myctophid species from the Gulf of Mexico. Widths of growth increments, IGS and bands were measured by means of compound microscope connected to a PC image analysis system. The measurements were taken along the radius from the central primordium to the antero-dorsal otolith margin in *H. benoiti* and to the antero-ventral otolith margin in *H. macrochir*.

### Vertical migrations

The vertical distribution and migrations of *Hygophum* species could not be defined on the basis of the 1984 and 1987 "Professor Siedlecki" samples as they were collected with a large pelagic krill trawl (Linkowski 1987, 1991). Rather, vertical distribution data were based on the WHOI mesopelagic fish collections (Backus and Craddock 1977; Craddock et al. 1987; J. E. Craddock personal communication). The "Data Report for Atlantic Pelagic Zoogeography" (Backus and Craddock 1977) included the station data for 1022 Isaacs-Kidd Midwater Trawl (IKMT) collections made in the Atlantic Ocean between 1961 and 1974. The fishing strategy applied during this sampling program (Backus and Craddock 1977), described by Backus et al. (1977), was to maximize catch; thus, during the night the uppermost 200 or 500 m layers were most frequently sampled. It was assumed that in relation to the time of the lunar cycle, the sampling was carried out at random. The phase of the new moon was set as the first day of the lunar cycle.

With respect to *Hygophum* spp. occurrence only positive horizontal collections made in narrow depth strata in the uppermost 200 m layer during the night were considered (Table 2). The abundance of *Hygophum* species, expressed by the number of specimens per hour of trawling was calculated for particular days of the lunar cycle in arbitrarily selected 50 m depth strata, i.e. 0 to 50 m, 51 to 100 m, 101 to 150 m and 151 to 200 m. The collections were assigned to one of the four mentioned strata on the basis of the mean sampling depth. Oblique hauls or nets fishing deeper than 200 m were not analyzed. The IKMT collections which did not yield specimens of *Hygophum* spp. were also excluded from the analysis, as they might indicate either a lack of these species in the uppermost 200 m layer at night or

their total absence at the sampling site. Thus, the calculated abundance indices obtained on the basis of positive IKMT collections are overestimated and have a relative value only. The geographic location of the IKMT stations analyzed to investigate *Hygophum* spp. nighttime, vertical distribution was very similar to that presented by Nafpaktitis et al. (1977: Figs. 9, 11, 13, 15 and 17) for the North Atlantic distribution of this group of species.

Additional information on vertical distribution of *Hygophum* species came from the data report on midwater fishes collected during the multidisciplinary Warm-Core Rings Program in 1981 and 1982 (Craddock et al. 1987, 1992) which included a total of 312 collections made with the MOCNESS-20 midwater trawl at 64 stations. For every station, one 0 to 1000 m or 0 to 1250 m oblique collection and three to five collections from different depth strata were sampled (Craddock et al. 1987). To analyze the influence of the lunar cycle on *Hygophum* spp. vertical distribution, only night, stratified collections were considered. Using such a limitation, the presence of *H. benoiti* was recorded in 30 collections made at 20 stations, *H. taaningi* in 25 and 15, and *H. hygomi* in 22 and 14, respectively. The abundance was expressed by number of fish captured per  $10^4 \text{ m}^3$  of filtered water. Again, the stations were arranged in relation to the lunar cycle.

### Species identification

*Hygophum* species collected by R.V. "Professor Siedlecki" were identified by the author. Materials from WHOI and MCZ collections had already been identified, and the original identifications were accepted to study vertical distribution. However, due to difficulties in field identification of two closely related species, *H. macrochir* and *H. taaningi*, collections of the later species may include some *H. macrochir* (J. E. Craddock personal communication). Only specimens used for otolith extraction were reexamined by the author. This was done on the basis of otolith size and shape as *H. macrochir* was characterized by much larger otoliths than *H. taaningi* (Linkowski unpublished data).

## Results

### Otolith microstructure

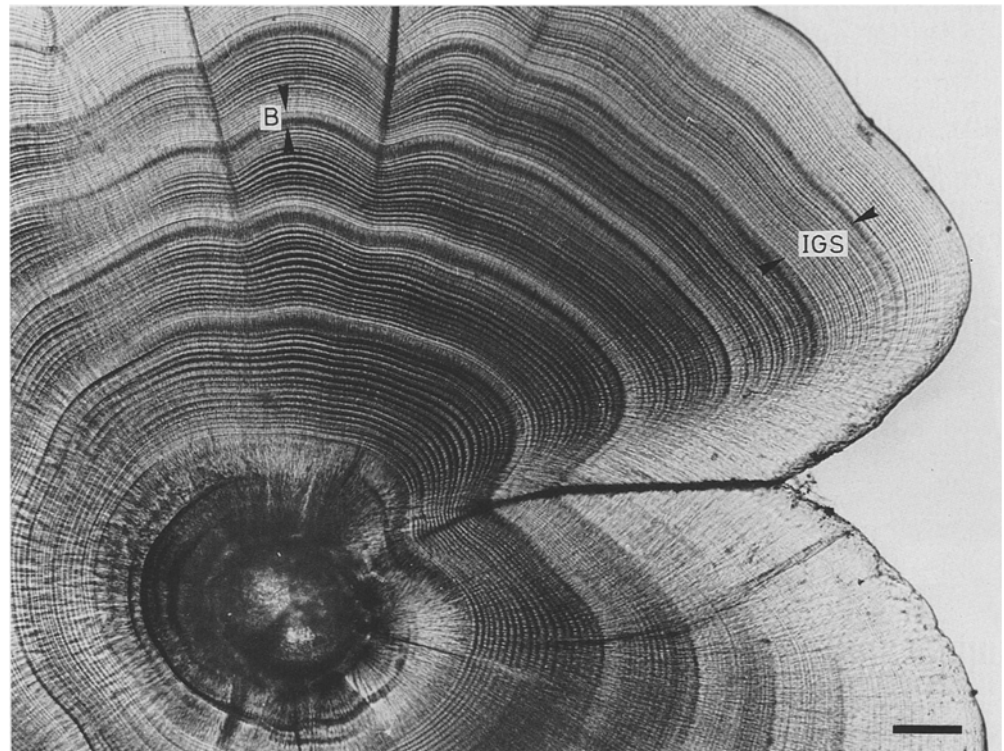
Strong cyclic patterns of otolith growth were observed in three *Hygophum* species. Regular sequences of distinct growth increments, believed to represent an area of fast growth, which I refer to as incremental growth sequence (IGS), were separated by bands without easily distinguishable incremental structure, representing an abrupt slowdown of growth, in most of the post-larval growth portions of the sagitta of the three species (*H. macrochir*, *H. reinhardtii* and *H. taaningi*) over the size ranges examined. This apparent microstructure was visible using both LM (Fig. 1) and SEM images (Fig. 2A–C). However, defining of the incremental structure of bands, which were more deeply etched than IGS, was not possible by means of SEM. Faint and narrow growth increments within the bands were only hardly visible in few specimens under LM (Fig. 3A and B). Cyclic growth patterns were also present in otoliths of juveniles of *H. benoiti*, up to approximately 30 mm SL (Fig. 2D). In larger individuals of this species, the cyclic otolith pattern was limited to a few (3 to 4, rarely 5)

**Table 1** *Hygophum* spp. Otolith materials utilized in present study. The number of otoliths showing cyclic (c) vs non-cyclic (n-c) growth patterns. All collections on the "Oceanus" taken by MOCNESS-10 trawls

Species Vessel	Cruise	Station	Date	Fish size (SL, mm)	No. of otoliths	
					c	n-c
<i>H. benoiti</i>						
Oceanus	49	118,2	13.08.78	18.0	1	
Oceanus	49	121,2	14-15.08.78	13.3-19.4		2
Oceanus	55	128,0	11.02.79	27.8	1	
Prof. Siedlecki	84	19,10	29.07.84	42-46	1	3
Prof. Siedlecki	84	31,15	01.08.84	46		1
Prof. Siedlecki	84	56/25	07.08.84	48	1	
Prof. Siedlecki	84	103/45	18.08.84	24-38	5	3
Prof. Siedlecki	84	134/58	25.08.84	16.0-27.5	20	
Prof. Siedlecki	84	183/79	13.08.84	19-31	6	
Prof. Siedlecki	84	186/81	14.09.84	18-30	6	
Prof. Siedlecki	84	190/83	15.09.84	24	1	
Prof. Siedlecki	84	208/90	19.09.84	21-32	8	
Prof. Siedlecki	84	229/99	24.09.84	28-37	2	
<i>H. hygomii</i>						
Oceanus	49	119,2	14.08.78	35-50		2
Oceanus	49	123,0	15.08.78	38.5		1
Oceanus	49	123,2	15.08.78	13.7-18.0		5
Oceanus	49	124,5	15.08.78	38.5		1
Oceanus	55	125,0	10.08.78	15.4		1
Oceanus	55	127,2	11.02.79	12.2-50.5		10
Oceanus	55	143,1	17.02.79	16.3-19.0		5
Oceanus	55	143,2	17.02.79	14.7-19.6		6
Prof. Siedlecki	84	19/10	29.07.84	35-55		12
Prof. Siedlecki	84	56/25	07.08.84	41-61		17
Prof. Siedlecki	84	60/27	08.08.84	38		1
Prof. Siedlecki	84	139/61	04.08.84	38-39		4
<i>H. macrochir</i>						
Atlantis II	59	RHB 2059	14.11.70	13.3-27.5		5
Atlantis II	59	RHB 2068	20.11.70	15.5-18.3	5	
Atlantis II	59	RHB 2063	15.11.70	14.5-15.6		3
Atlantis II	59	RHB 2071	22.11.70	9.7-25.8	11	5
Atlantis II	59	RHB 2075	24.11.70	30.5-38.6	6	
Atlantis II	60	RHB 2282	4-5.06.73	27.2-41.4	4	
Atlantis II	78	RHB 2924	15-16.08.73	35.0-48.5	2	
Atlantis II	79	RHB 3054	10.12.73	38.2-42.8	4	
Oceanus <sup>a</sup>	49	107,2	09.08.78	11.2-16.7	5	2
Oceanus <sup>a</sup>	49	111,1	11.08.78	-	2	
Oceanus <sup>a</sup>	49	111,2	11.08.78	10.9-35.0	5	1
Oceanus <sup>a</sup>	49	112,0	12.08.78	24.2-24.4	2	
Oceanus <sup>a</sup>	55	147,2-5	19.02.79	11.2-41.8	34	3
Prof. Siedlecki	87	001	27.11.87	42-57	15	
Prof. Siedlecki	87	003	30.11.87	52-59	4	
<i>H. reinhardtii</i>						
Oceanus	55	126	10-11.02.79	18.5	1	
Oceanus	55	127	11.02.79	28.5-34.4	3	
Oceanus	55	128	11.02.79	30.0	1	
Oceanus	55	136,1	14.02.79	23.0	1	
Oceanus	55	136,5	14.02.79	25.4	1	
Oceanus	55	137,2	14.02.79	42.5		1
Oceanus	55	138,3	15.02.79	16.9-19.0		4
Prof. Siedlecki	84	60/27	08.08.84	45-53	2	
Prof. Siedlecki	84	95/42	16.08.84	32-38	3	
Prof. Siedlecki	84	132/57	25.08.84	39-43	3	
Prof. Siedlecki	84	134/58	25.08.84	28	1	
<i>H. taaningi</i>						
Prof. Siedlecki	84	135/59	02.09.84	34-41	3	

<sup>a</sup> Identified previously as *H. taaningi*

**Fig. 1** *Hygophum macrochir*. Photomicrograph of a sagittal section of otolith (SL 43.5 mm) showing cyclic growth pattern consisting of six incremental growth sequences (IGS), separated by bands (B). Scale bar: 100  $\mu$ m



**Table 2** *Hygophum* spp. Night-time Isaacs–Kidd Midwater Trawl collections in the uppermost 200 m. Data from Backus and Craddock (1977) and Craddock (personal communication)

Species	No. of specimens	No. of collections	Total time of trawling (h)
<i>H. benoiti</i>	1716	107	245
<i>H. hygomii</i>	994	137	320
<i>H. macrochir</i>	985	64	163
<i>H. reinhardtii</i>	240	93	204
<i>H. taaningi</i>	491	78	206

IGS, separated by bands outside the otolith center, followed toward the margin by an area of irregular and differentiated but non-cyclic otolith growth. The fifth examined species, *H. hygomii*, did not show any rhythmic changes in otolith growth (Fig. 4A). Among the *Hygophum* species characterized by cyclic otolith growth, examples of non-cyclic growth also occurred (Fig. 4B). The number of examined individuals showing cyclic or non-cyclic growth patterns is given in Table 1. The youngest specimens which did not deposit a band outside of their first, most internal IGS, were designated “non-cyclic” as the character of their growth could not be determined.

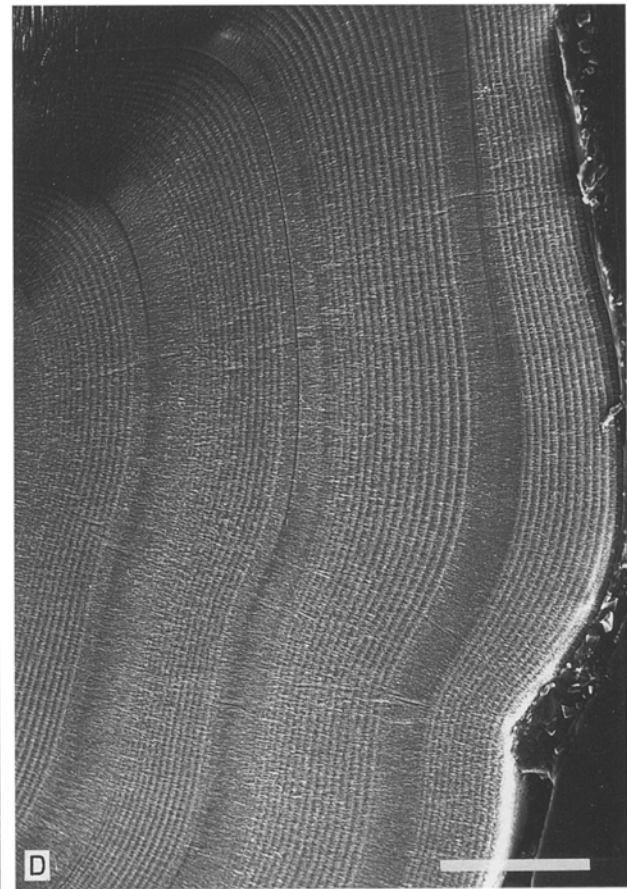
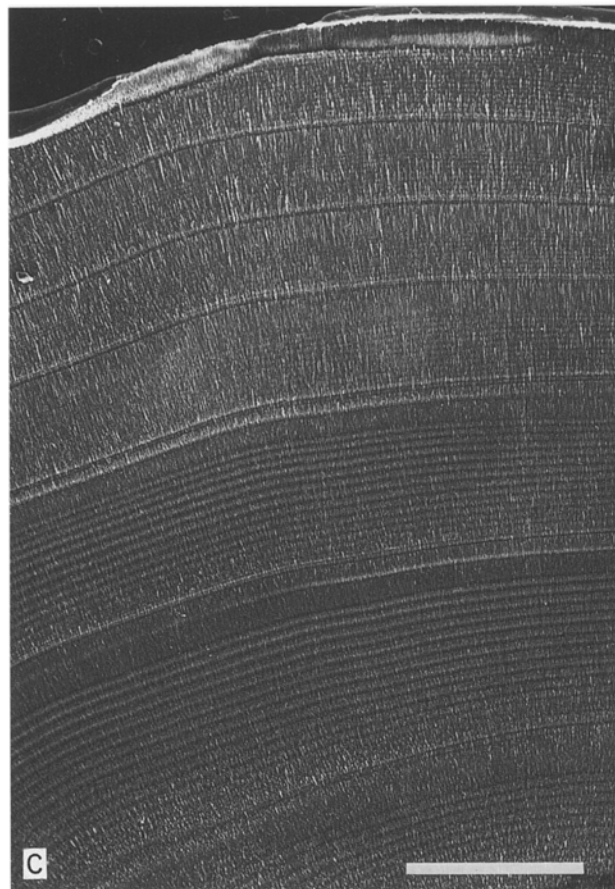
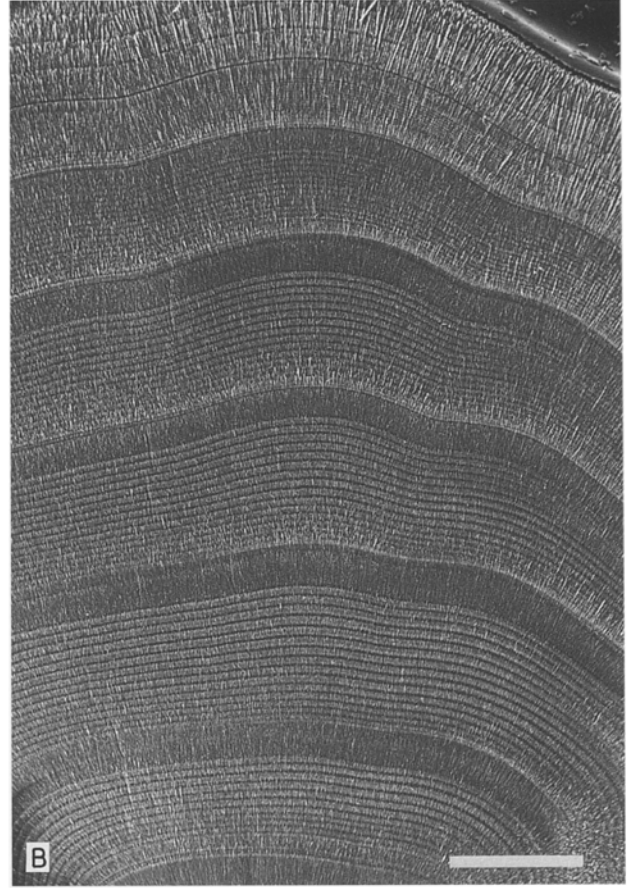
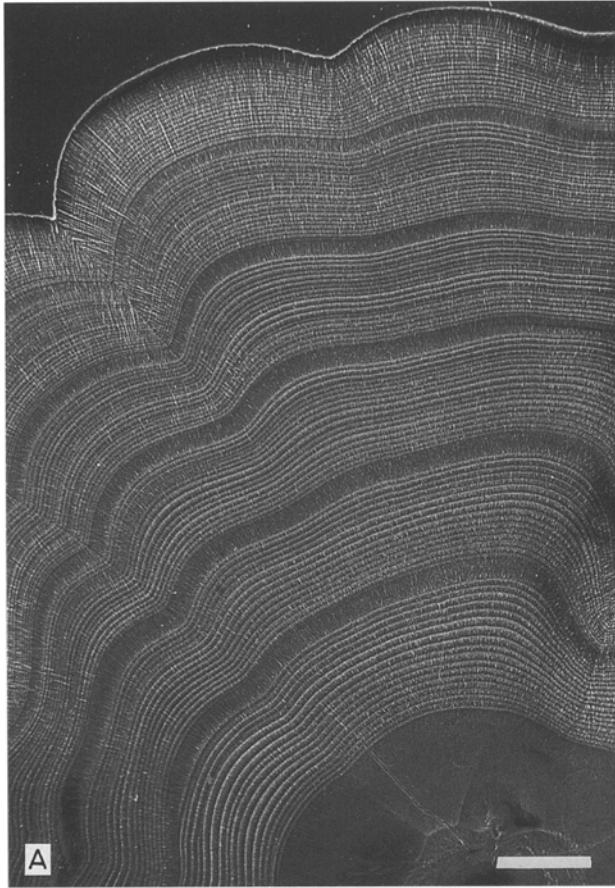
The width of IGS, bands and growth increments varied among the species and also in relation to their position on the otolith radius. In *H. macrochir* a declining tendency of IGS, band and growth increment width was observed toward the otolith margin (Fig. 5). In *H.*

*benoiti* only band width was decreasing, while the opposite trend with regard to IGS width was obvious (Fig. 6). Also a slight but statistically significant ( $F = 38.97$ ;  $df = 4, 756$ ;  $P < 0.00001$ ) increase in growth increment width among the investigated range of IGS was observed in *H. benoiti* otoliths (Fig. 6).

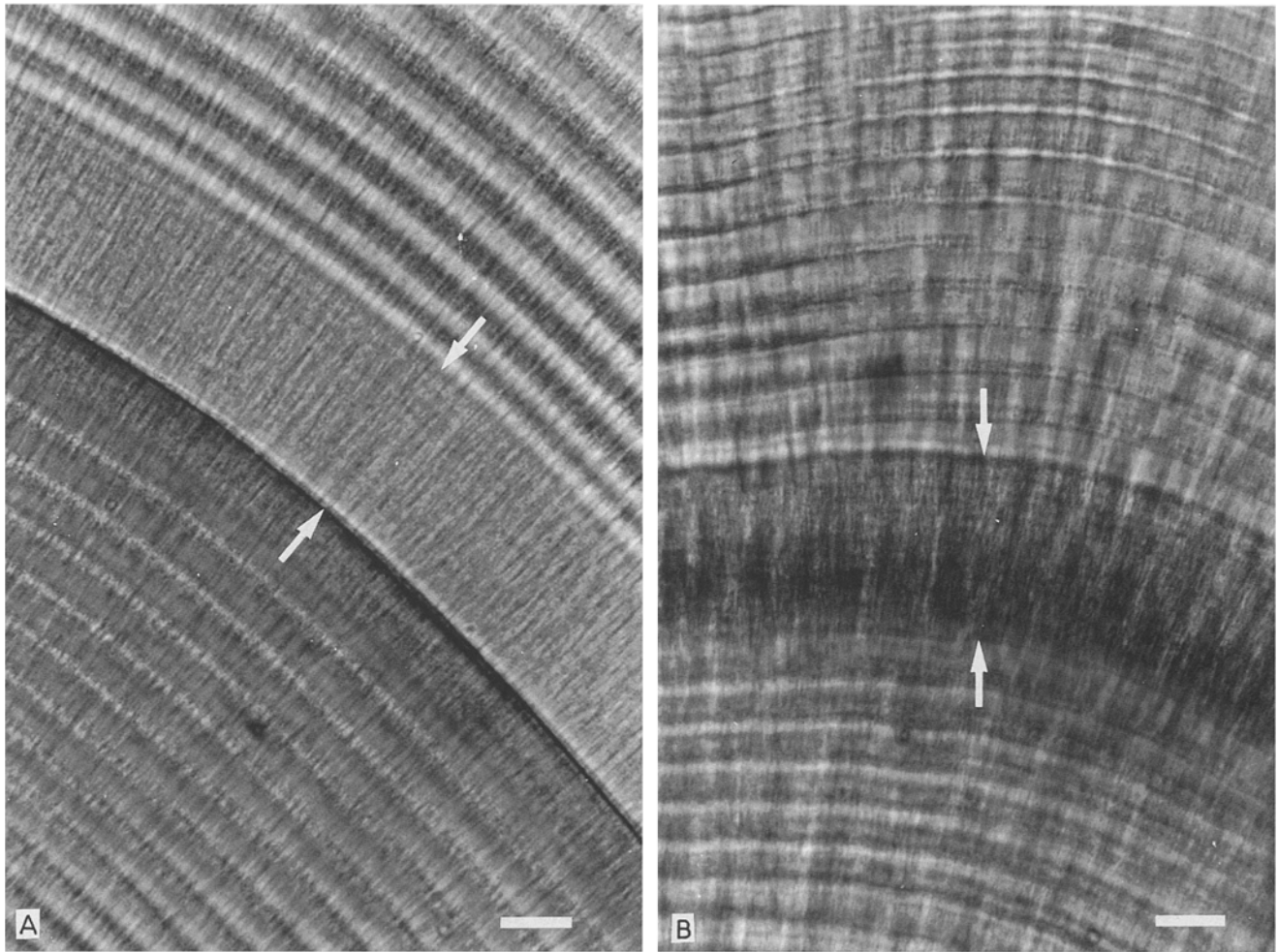
#### Nature of the cyclic pattern in otolith microstructure

Due to the limited number of samples available for determination of the nature of the observed cycles in otolith microstructure, statistical analyses of the cyclic pattern were possible only for two species: juvenile *H. benoiti* and *H. macrochir*. A number of growth increments in IGS, i.e. between the two subsequent bands, in the four most internal IGS in *H. benoiti* otoliths showed significant variations ( $F = 18.22$ ;  $df = 3, 100$ ;  $P < 0.00001$ ) and an increasing tendency (Table 3). In *H. macrochir* the number of growth increments in IGS did not differ throughout the examined range of sequences, i.e. IGS<sub>1</sub> to IGS<sub>10</sub> ( $F = 0.741$ ;  $df = 8, 174$ ;  $P = 0.6711$ ) and averaged 18.6 (Table 4). The number of growth increments in the most external

**Fig. 2** *Hygophum* spp. SEM micrographs of sagittal sections of otoliths. Examples of cyclic growth patterns. **A** *H. macrochir* (SL 42.0 mm). **B** *H. reinhardtii* (SL 53.0 mm). **C** *H. taaningi* (SL 34.0 mm). **D** *H. benoiti* (SL 30.1 mm). Scale bars: 100  $\mu$ m







**Fig. 3** *Hygophum* spp. Photomicrographs of sagittal sections of otoliths showing very faint growth increments within the bands (between *arrows*) and clear increments in the incremental growth sequences (outside *arrows*). **A** *H. benoiti*; **B** *H. macrochir*. Scale bars: 10  $\mu\text{m}$

IGS of the largest fish, i.e. IGS<sub>11</sub> and those deposited later, was not studied due to problems with precision of enumeration, as bands deposited outside such external IGS in *H. macrochir* otoliths were reduced to a form of a check, not much wider than a single growth increment of the adjacent IGS (see Fig. 5).

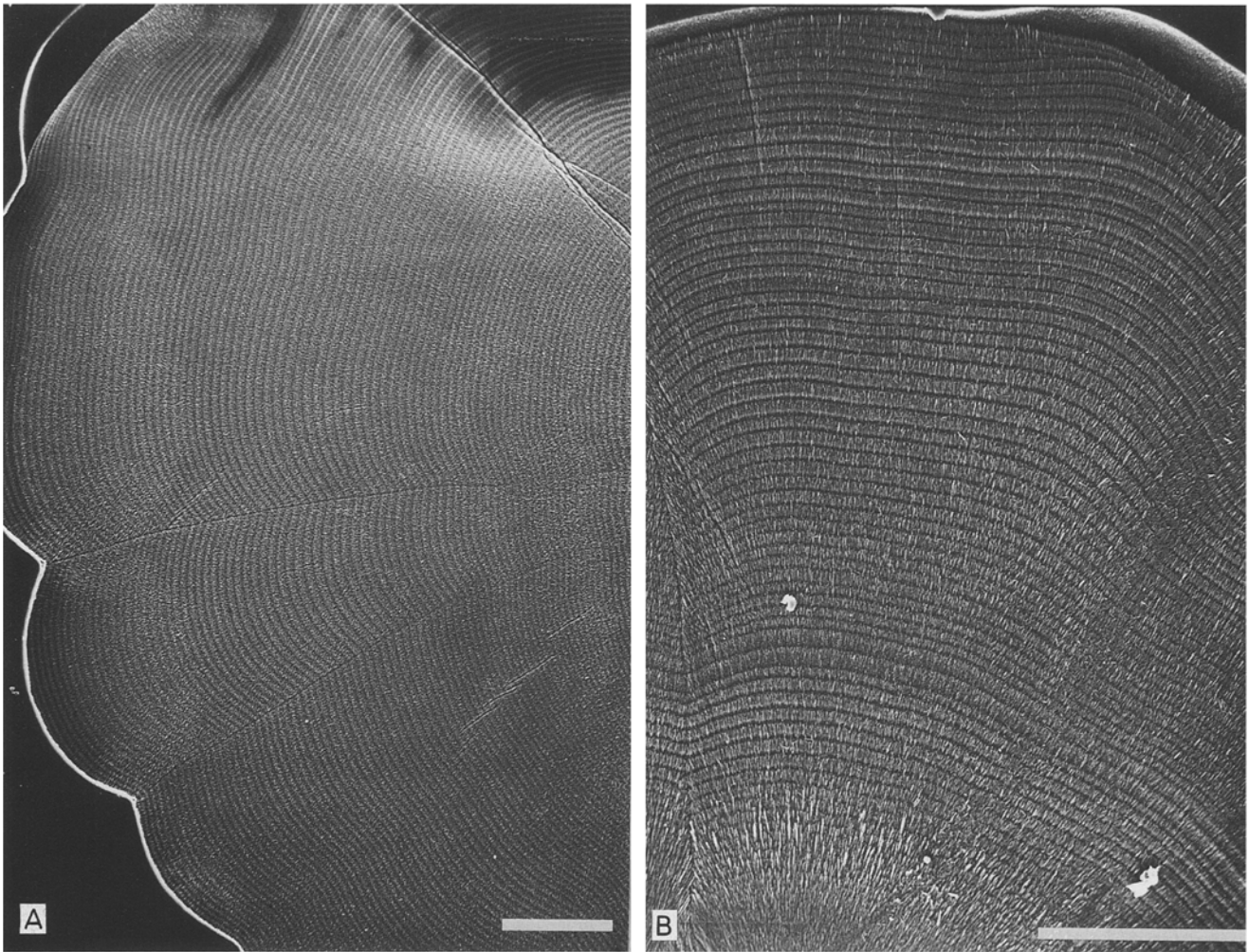
The number of growth increments, which were presumed to be daily, between the most recent band and otolith margin, representing the date of capture, in *H. benoiti* and *H. macrochir* was used to back-calculate the date of the formation of the first increments after the bands (Fig. 7). Moreover, the date of capture in relation to a lunar phase of individuals which had bands deposited at the otolith margin is also indicated on Fig. 7. In otoliths of these two species first increments of a new IGS most often formed between the fourth and the ninth day of the lunar cycle, while the bands at the

otolith margin were observed at the end of the first and beginning of the second quarter of the moon, then at the end of the third and in the fourth quarter.

#### Vertical distribution

To determine if there was any influence of the lunar phase on the uppermost range of *Hygophum* spp. vertical migration during the night, the night-occurrence of these species in the 0 to 200 m layer in relation to the lunar cycle was investigated by plotting night-catches per hour of IKMT trawling by 50 m depth strata in relation to the lunar cycle (Fig. 8). The occurrence of the four most abundant *Hygophum* species present in the IKMT collections (Backus and Craddock 1977; J.E. Craddock personal communication) was studied only, while the less numerous *H. reinhardtii* was excluded from analyses. These data showed also the abundance of the investigated species in the discrete strata of the uppermost 200 m layer.

The strongest correlation of occurrence and abundance to the lunar cycle was exhibited by *H. macrochir*

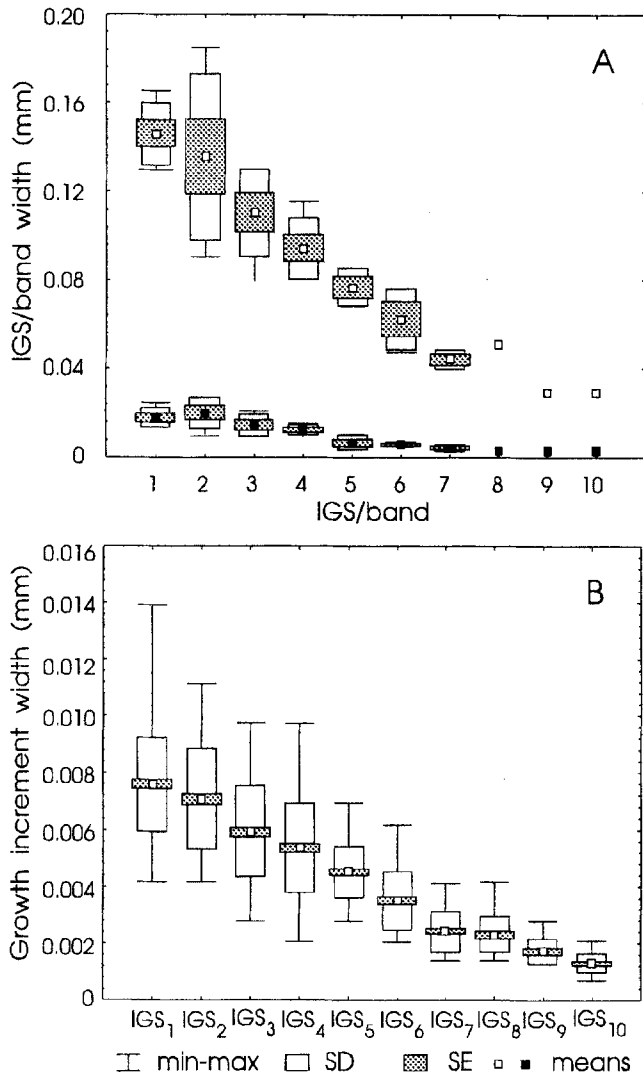


**Fig. 4** *Hygophum hygomii* and *H. reinhardtii*. SEM micrographs of sagittal sections of otoliths. **A** *H. hygomii*. Example of a very uniform otolith microstructure. **B** *H. reinhardtii*. Example of non-cyclic otolith growth. Scale bars: 100  $\mu\text{m}$

and *H. taaningi*. They did not occur in the uppermost 200 m layer at the beginning of the first and at the end of the fourth moon quarter, while only very few records were noted at the end of the first and at the beginning of the fourth quarter. The highest IKMT catch rates of *H. macrochir* were distributed in 0 to 50 and 51 to 100 m strata. The other species whose occurrence was strongly influenced by a moon phase, *H. taaningi*, seemed to be distributed in slightly deeper waters, i.e. at 101 to 150, 51 to 100 and 151 to 200 m depth strata. The night-vertical distribution of *H. benoiti* showed a less conspicuous relation to the lunar cycle. All size groups of postlarval *H. benoiti* were present in the investigated depth strata at night with only several catches showing very high abundance in the uppermost 50 m layer, and high abundance in 51 to 100 m strata during a few days of the second, third and the beginning of the fourth

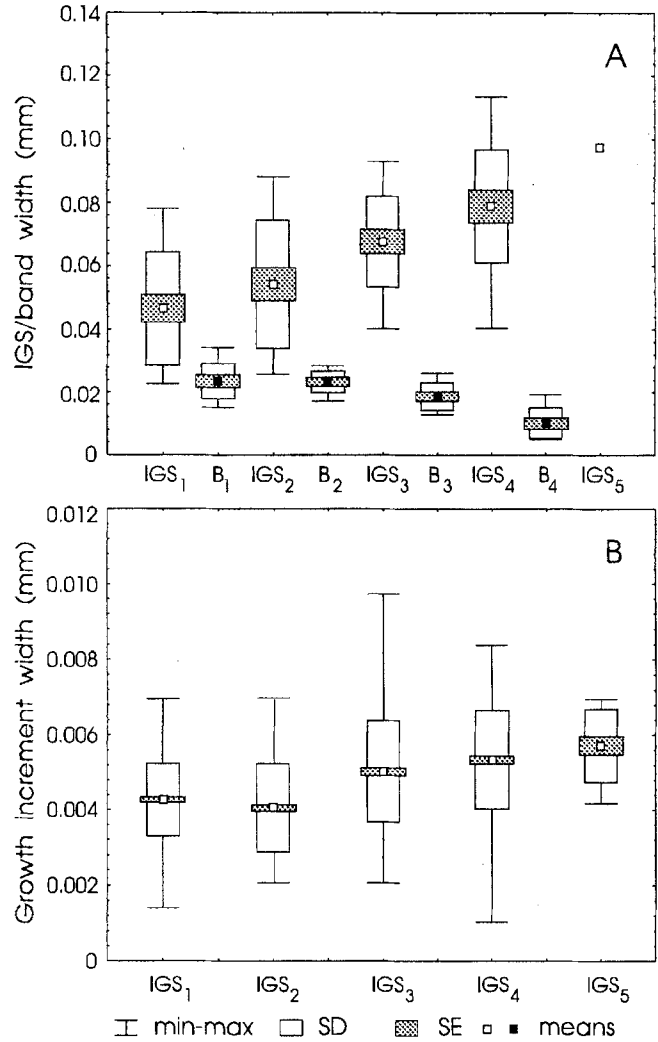
quarter of the lunar cycle. When larger individuals over 30 mm SL were excluded from the analysis, it was apparent that few *H. benoiti* juveniles were collected in the 200 m depth strata during the first and fourth quarter of the moon. The occurrence of *H. hygomii* in the uppermost 200 m layer did not seem to be related to the lunar cycle in the same way as in the previous three *Hygophum* species. The highest catches of this species occurred in the uppermost depth strata, i.e. 0 to 50 m, throughout the greater part of the lunar cycle except the period in the middle of the cycle, close to the full moon phase, when the peak of catches shifted toward the next depth strata (51 to 100 m) and no catch was recorded in the shallowest depths.

The data on *Hygophum* spp. vertical distribution (Craddock et al. 1987), although containing a limited number of collections of only three species (*H. benoiti*, *H. hygomii* and *H. taaningi*) gave the possibility of monitoring their occurrence down to the depth of 1000 m (Fig. 9). Unfortunately, *H. hygomii* specimens were collected only at the beginning and at the end of the lunar cycle, because of a chronological/geographic



**Fig. 5** *Hygophum macrochir*. Morphometrics of microstructural features in otoliths. **A** Incremental growth sequence (IGS) widths (open rectangles) and band widths (filled rectangles). **B** Growth increment widths in the incremental growth sequences (IGS<sub>1</sub>–IGS<sub>10</sub>)

gap in sampling of this species in the middle of a cycle, i.e. *H. hygomii* did not occur in the area sampled at full moon (Craddock et al. 1987). However, the available data indicated that the new moon phase did not limit the night-vertical migration of *H. hygomii* to the surface, although a significant part of the population did not perform such movements, staying at depths of several hundred meters. Conversely, the vertical distributions of *H. benoiti* and *H. taaningi* were highly correlated with the lunar cycle. At the beginning and the end of the lunar cycle these species did not migrate to the surface layers, and almost the entire populations of both species stayed at depths below 400 m, while in the middle of the cycle, close to the full moon phase, a great part of *H. benoiti* and *H. taaningi* populations occurred in the uppermost layers, while only a small fraction remained at greater depths.



**Fig. 6** *Hygophum benoiti*. Morphometrics of microstructural features in otoliths. **A** Incremental growth sequence (IGS<sub>1-5</sub>) widths (open rectangles) and band (B<sub>1-4</sub>) widths (filled rectangles). **B** Growth increment widths in the incremental growth sequences (IGS<sub>1</sub>–IGS<sub>5</sub>)

**Table 3** *Hygophum benoiti*. Number of growth increments in the internal first four incremental growth sequences (IGS) in *H. benoiti* otoliths. (N number of IGS examined)

IGS no.	N	Range	Mean	95% Confidence interv. for mean
1	46	6–16	11.85	11.19–12.51
2	34	10–19	14.38	13.61–15.15
3	18	12–18	15.11	14.05–16.17
4	6	17–18	17.17	15.34–19.00
Total	104			

**Discussion**

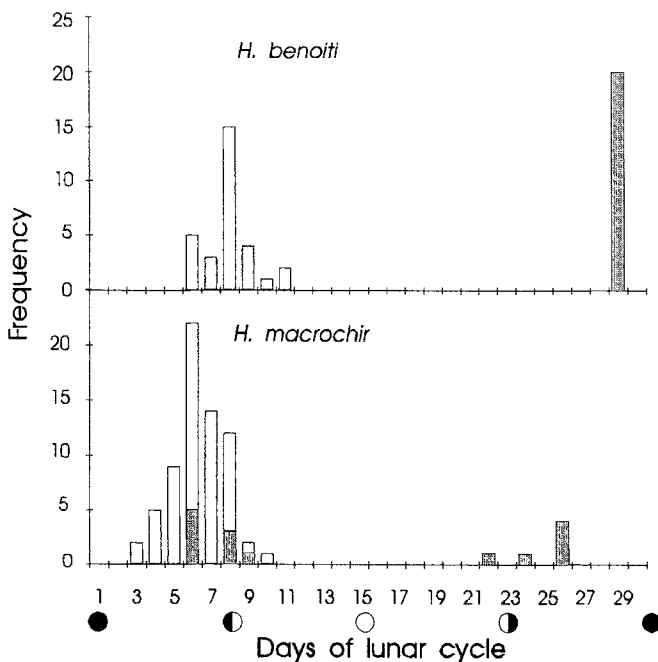
Otolith microstructure

Groupings of increments in regularly repeated clusters have often been found in otoliths of fishes that were



**Table 4** *Hygophum macrochir*. Number of growth increments in incremental growth sequences (IGS) in *H. macrochir* otoliths. (*N* number of IGS examined)

IGS no.	<i>N</i>	Range	Mean	95% Confidence interv. for mean
1	33	12–25	18.58	17.75–19.40
2	26	14–24	19.31	18.37–20.24
3	23	15–24	18.39	17.40–19.30
4	21	15–23	18.00	16.97–19.03
5	18	15–24	18.72	17.61–19.83
6	17	13–23	17.82	16.67–18.97
7	16	17–22	19.13	17.94–20.31
8	14	15–21	18.57	17.31–19.83
9	10	15–22	18.90	17.40–20.40
10	6	15–22	19.00	17.07–20.93
Total	184		18.61	18.27–18.96

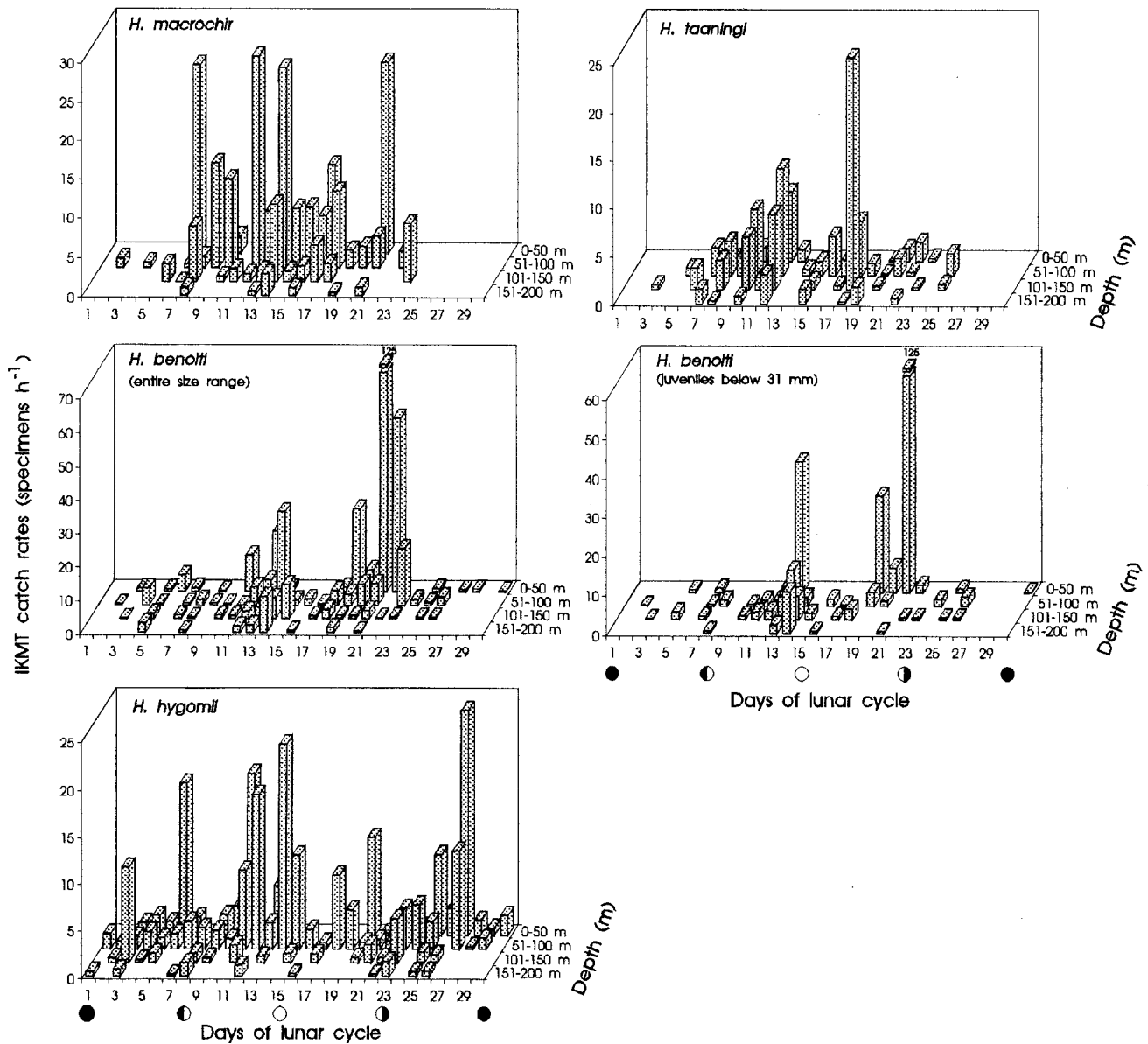


**Fig. 7** *Hygophum benoiti* and *H. macrochir*. Time (lunar day) of capture of individuals with bands deposited at the otolith margin (filled bars) and back-calculated time of formation of the first growth increment in the most external incremental growth sequence (open bars) in relation to lunar cycle

known to synchronize their activities with tides (Pannella 1980). Periodic patterns of 7, 14 or 28 to 30 growth increments were reported in many fish species and a priori referred to as lunar or tidal patterns (Pannella 1971, 1974, 1980; Brothers et al. 1976; Rosenberg 1982). The first evidence of lunar patterns in the otoliths of marine fish correlated with a tidal modulation of the environment was given by Campana (1984). On the basis of his studies on juvenile starry flounder, Campana (1984) concluded that the observed lunar patterns in otolith growth were a consequence of the temperature regime induced by a biweekly tidal cycle. Similar

changes of environmental factors may be responsible for the formation of biweekly growth patterns in otoliths of many fish species of intertidal and sublittoral environments. The existence of such growth patterns, including a monthly lunar rhythm recorded in otoliths of deep-sea fishes, such as those found in *Hygophum* species, cannot be explained by changes analogous to those introduced by tides in the sublittoral environment. Most probably cyclic growth patterns in otoliths of deep-sea fishes are introduced by behavioral rhythms rather than environmental changes. However, the direct influence of the moon, including illumination during the night, gravitation, atmospheric pressure, and magnetic field on the behavior of deep-sea fishes cannot be excluded. The known examples of endogenous control of lunar rhythms in terrestrial animals, coastal and freshwater fishes (Boetius 1967 in Gibson 1978; Grau et al. 1981; Neumann 1981; Kavaliers 1982; Farbridge and Leatherland 1987; Neilson and Perry 1990) suggest the existence of a similar endogenous lunar rhythm also in some *Hygophum* species. Bands similar to those separating IGS in *Hygophum* spp. otoliths have not yet been reported in otoliths of any other fish species showing lunar periodicity of growth. Closer examination of bands in *Hygophum* spp. otoliths confirmed the incremental structure of these features. However, a poor definition of the growth increments deposited within bands did not allow for their precise enumeration and width measurements. If one assumes that sagittal growth increments are deposited daily, the prominent width of the bands, observed in juveniles and/or subadults of *Hygophum* species suggests that the deposition of a band may take place over several days. Such a conclusion may be supported by the observed occurrence of bands at otolith margins and the time of formation of the first IGS growth increments in relation to the lunar phase. The otoliths terminated by a band at their margins were recorded over an extended period of time, i.e. at least between the end of the third and the beginning of the second quarter of the moon, while the back-calculated time of formation of the first growth increments in IGS was restricted to a much shorter fraction of the lunar cycle. Thus, it is expected that bands represent a period of on average, 10 to 15 d which together with a time of deposition of adjacent IGS may fit the duration of a lunar cycle.

Bands in *Hygophum* spp. otoliths were characterized by poor transparency when compared to the neighboring IGS. Brothers (1985 in Volk et al. 1990) suggested that optically dense otolith bands or zones which resulted from greater deposition of organic matrix were formed during periods of falling water temperatures. Moreover, the positive relationship existed between the width of optically dense zones in *Oncorhynchus keta* alevin otoliths, and the number of temperature units accumulated during exposure to cold water (Volk et al. 1990). Visual effects obtained by Volk et al. (1990) in otoliths of embryonic and juvenile chum salmon, i.e.,



**Fig. 8** *Hygophum* spp. Night-distribution in the uppermost 200 m layer on the basis of Isaacs-Kidd Midwater Trawl catches. Data from Backus and Craddock (1977) and J.E. Craddock (personal communication)

optically dense bands produced by sudden drops in water temperature, closely resembled the microstructure of bands in *Hygophum* spp. otoliths. Also, the temporary exposure of a juvenile walleye pollock to a low water temperature produced a widely etched broad groove in a SEM viewed sagittal section of the otolith (Nishimura and Yamada 1984: Fig. 4), similar to bands in SEM images of *Hygophum* spp. otoliths. The bands separating IGS in *Hygophum* spp. otoliths appeared concave when etched with 1% HCl, which suggested increased organic matrix contents according to observations of Pannella (1980) and Mugiya et al.

(1981). On the basis of the above mentioned examples there is little doubt that the main environmental factor responsible for the bands' formation is temperature, i.e., prolonged effect of a low, stable temperature vs abrupt temperature changes in a diel cycle, enforcing formation of the clear incremental structure of IGS. Moreover, the bands observed in otoliths of some *Hygophum* species resemble structures already reported in otoliths of several myctophids and referred to as "bands" by Gartner (1991) but deposited in the so-called "perinuclear zone = middle zone = postlarval zone = transitional zone" (Gjøsaeter 1987; Ozawa and Penaflo 1990; Gartner 1991; Linkowski et al. 1993). Recent interpretations of this zone, i.e. as a record of habitat shift in the form of downward migration of larval myctophids from warmer surface waters to cold deep water (Gartner 1991), enhanced by a temporarily

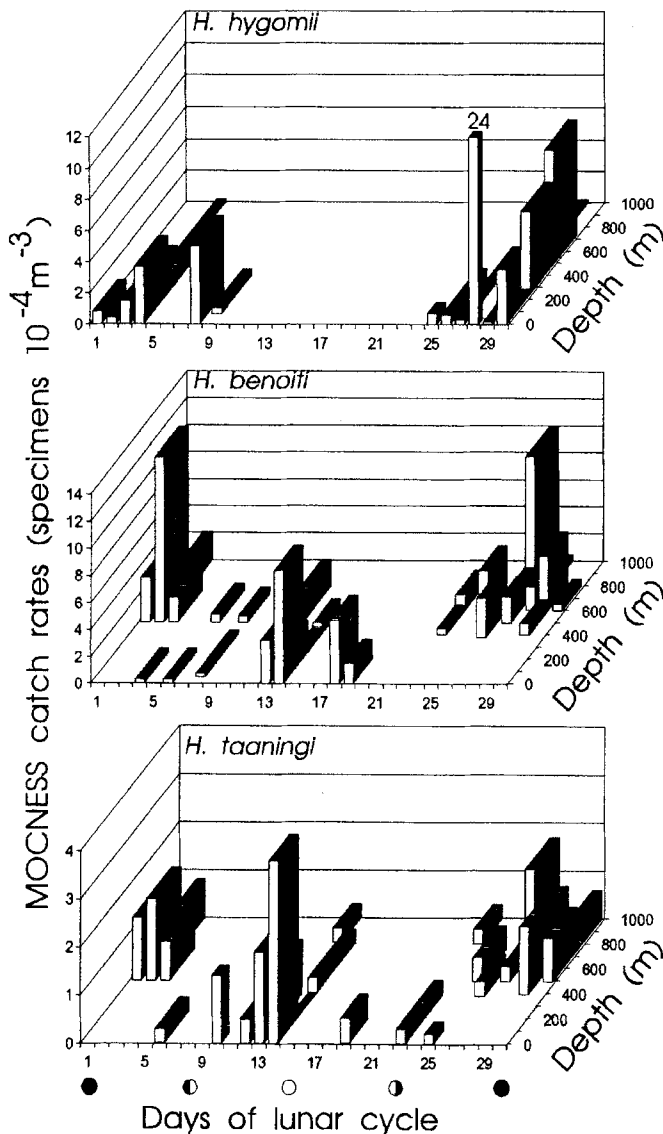


Fig. 9 *Hygophum* spp. Night-time vertical distribution on the basis of MOCNESS-20 collections in relation to lunar cycle. Data from Craddock et al. (1987)

non-migratory behavior of early juveniles of some species (Gartner 1991; Linkowski et al. 1993), do not contradict the interpretation presented here of *Hygophum* spp. otolith microstructure.

The morphometrics of otolith microstructural features suggested a declining tendency of IGS, band and growth increment width in *H. macrochir* toward the otolith margin. As the number of growth increments in IGS in this species did not differ throughout the examined range of sequences, these findings are interpreted as a result of a natural slowdown of the otolith and somatic growth with age. An opposite tendency with regard to IGS width observed in *H. benoiti* otoliths, in which the cyclic pattern was not stable and the number of growth increments in the subsequent IGS increased, might be interpreted as a result of a gradual change of behavior. A slight increase of growth increment width

observed towards the otolith margin among the five IGS studied in the *H. benoiti* otoliths could be explained by a change of otolith growth in juvenile fish, i.e. otolith growth is more pronounced along the antero-dorsal radius due to the formation of postrostrum.

#### Vertical migrations

Among four species of *Hygophum*, three types of migratory behavior in relation to the lunar cycle were observed. The first type, represented by *H. hygomii*, showed no apparent change in the uppermost range of night-migration during any moon phase. A sizable fraction of the *H. hygomii* population always occurred in the 0 to 200 m depth strata at night during the whole lunar cycle. However, the uppermost limit of the abundant nighttime occurrence of this species moved from the 0 to 50 m surface layer to the 50 to 100 m depth strata at full moon. The second type of behavior was characterized by *H. benoiti*, in which a large part of the *H. benoiti* population tended to cease vertical migrations during the first and fourth quarters of the lunar cycle, staying at depths of 400 m and more. This tendency was more clear in juvenile fish than in adults. The third type of *Hygophum* spp. vertical-migratory behavior which had the strongest correlation with the lunar cycle was represented by *H. macrochir* and *H. taaningi*. These species disappeared almost totally from the surface waters (< 100 m) at the beginning and the end of the lunar cycle, i.e. they arrested vertical migrations at new moon phase and, at night, stayed below 400 m.

Clarke (1973), who first investigated changes in night-vertical distribution of myctophids in relation to moon phases, observed that most of lanternfishes occurred 50 to 75 m deeper at full moon than at new moon. Such behavior, particularly in near-surface tropical myctophids, may result in the periodicity of growth in accordance with the phases of the lunar cycle, increasing with a new moon and decreasing with full moon, e.g. as in *Myctophum nitidulum* (Giragosov and Ovcharov 1992). Clarke (1973) noticed that the behavior of the *Hygophum* species appeared to be different from that of the other myctophids. The two *Hygophum* species studied by him (*H. proximum* and *H. reinhardtii*) indicated a shallower nighttime distribution during full moon. Moreover, adults of *H. proximum* and *H. reinhardtii* at night during new moon occurred shallower than the juveniles, which is opposite to the tendency characteristic for the great majority of myctophid species (Clarke 1973). It suggests a similar ontogenetic change of vertical migration pattern in these two species to that observed in *H. benoiti*, i.e. a lunar rhythm of vertical migrations, rather clear in early juveniles which gradually disappears with age.

A universal temperature profile for the whole geographical and vertical range of *Hygophum* spp. distribution does not exist. However, it is well known that in

the Atlantic water masses inhabited by the examined species, the temperature gradient between the near-surface depths of *Hygophum* spp. night occurrence and the average day distribution, i.e. below 500 m, may range from approximately 5 to almost 20 °C, e.g. Brooks and Saenger (1991: Fig. 15), Badcock and Merrett (1976: Fig. 2). Another example illustrating the mentioned temperature gradient were temperatures recorded at MOCNESS-20 stations during the sampling of materials used in the present paper (Craddock et al. 1987). The 0 and 500 m temperatures of the Slope Water had a range of 12.5 to 26.0 and 5.1 to 5.5 °C, respectively (Craddock et al. 1987: Tables 12 and 13). Such or similar temperature gradients influence the fish during its diel vertical migrations enforcing deposition of growth increments and making them very clear, as observed in otoliths of many myctophid species (e.g., Gjösæter 1987; Gartner 1991; Linkowski et al. 1993). Any deviation from this diel rhythm of vertical migrations must be imprinted in otoliths, e.g. the observed temporarily non-migratory behavior in the lunar cycle of *Hygophum* species is imprinted in the form of the prominent bands without a distinct incremental structure.

Light was found to be the main environmental factor responsible for the control of vertical migrations of marine animals (Boden and Kampa 1967; Longhurst 1976). According to Brooks and Saenger (1991) night and day distribution of a bladdered group of midwater fish seemed to be determined by the night distribution of zooplankton biomass and the day midwater light field, respectively, while other environmental variables showed little direct influence. On the basis of vertical abundance distributions for a representative group of species with swimbladder (including *H. hygomii*, *H. benoiti* and *H. taaningi*), fish were found concentrated in the 0 to 150 m euphotic zone at night and in the 400 to 1000 m zone during the day (Brooks and Saenger 1991). According to Roe and Badcock (1984) absolute light levels could not closely control the distributions and migrations of any mesopelagic fish populations studied by them. Clarke (1973) also pointed out the discrepancy between the shift in vertical distribution of the majority of myctophid species, which appeared to occur only 50 to 75 m deeper at full moon, while according to Clarke (1970) the depths of isolumens at full moon are about 200 m greater than at new moon. The lunar cycle influence on some *Hygophum* species' vertical migratory behavior, contrary to that seen in the majority of migratory myctophids or, e. g. eels (Tesch 1989), is counterintuitive with regard to moon light avoidance.

Depth niches of individual bladdered midwater fish species are organized to reduce competition, although the maximum day occurrence of this group in the 400 to 1000 m interval must be due primarily to non-trophic factors (Brooks and Saenger 1991). According to these authors: "During daytime hours, many species

apparently remain inactive in the relatively cold waters of the 400 to 1000 m dimly lit twilight zone to avoid attracting predators while at the same time conserving energy for growth and reproduction" (Brooks and Saenger 1991). The night occurrence at day depths of many vertically migrating mesopelagic fish species has often been recorded (Badcock 1970; Goodyear et al. 1972; Clarke 1973; Badcock and Merrett 1976; Nafpaktitis et al. 1977; Gartner et al. 1987; Karnella 1987; Brooks and Saenger 1991) and interpreted as the effect of local environmental conditions, seasonal effects or ontogenetic changes (Neilson and Perry 1990). Percy et al. (1979) found that a nonmigratory part of the *Stenobranchius leucopsarus* population, fish which stayed at depths of 300 to 500 m at night, probably fed in deep water. However, the adaptive significance of the bimodal nocturnal distribution of this lanternfish was unknown (Percy et al. 1979). Craddock et al. (1992) reported that in warm-core Gulf Stream meander/ring up to 80% of vertical migrators such as *Ceratoscopelus warmingii* or *Lampanyctus pusillus* did not migrate into the upper 200 m at night, remaining deeper than 600 m. Possibly, the nonmigratory part of the population of these species fed also in deep water, as their otoliths did not show any strong cyclic microstructural pattern similar to that in *Hygophum* spp. (Linkowski unpublished). According to Hopkins and Gartner (1992) trophic competition for myctophids is reduced through resource-partitioning although with considerable overlap at niche boundaries. A temporary nonmigratory behavior observed in several myctophid species might be interpreted as an additional mechanism toward reduction of inter- and intraspecific competition for food resources. However, an interpretation of the prolonged time of nonmigratory behavior of several *Hygophum* species, which is correlated with the lunar cycle, poses a more complex question concerning the benefit of this behavior. There is little doubt that the reported cyclic bands in the otoliths represent a drastic slowdown of somatic growth. Thus, even if the *Hygophum* species feed in deep cold waters during the nonmigratory behavior, the obtained energy is not sufficient to support somatic growth or is utilized in a different way. The vertically migrating species are more similar to surface dwellers in terms of respiratory rate than they are to deeper living species (Torres et al. 1979). According to Torres et al. (1979): "The energetic benefit (...) to the vertical migrator is determined by the metabolic cost of the migration itself and the probable increase in daily ration due to the migration into more productive shallower layers". The significance of metabolic enzyme activity and the relation between temperature and available food for diel vertical migrations of mesopelagic species was also stressed by van der Spoel and Schalk (1988). The temporary cessation of diel vertical migrations by the migratory species, i.e., staying at depths of several hundred meters during prolonged periods as observed in several *Hygophum*

species does not contradict energetic advantages of vertical migrations. The apparent slowdown of *Hypogomphus* spp. growth rate during the nonmigratory behavior vs faster growth during regular vertical migrations in diel cycle supports the existence of the energetic benefit to a vertical migrator. However, there might also be advantages to nonmigratory behavior, as suggested by Pearcy et al. (1979), e.g. the energy conserved during such a period may be converted into lipids, which play an important role as buoyancy regulators in mesopelagic fishes.

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## References

- Backus RH, Craddock JE (1977) Data report for Atlantic pelagic zoogeography. Tech Rep Woods Hole Oceanogr Instrn: 77-4
- Backus RH, Nafpaktitis BG, Craddock JE, Haedrich RL, Robison BH, Karnella C (1977) Family Myctophidae. Mem Sears Fdn mar Res 1(7): 266-297
- Badcock J (1970) The vertical distribution of mesopelagic fishes collected on the SONDR Cruise. J mar biol Ass UK 50: 1001-1044
- Badcock J, Merrett NR (1976) Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog Oceanogr 7: 3-58
- Boden BP, Kampa EM (1967) The influence of natural light on the vertical migrations of an animal community in the sea. Symp zool Soc Lond 19: 15-26
- Brooks AL, Saenger RA (1991) Vertical size-depth distribution properties of midwater fish off Bermuda, with comparative reviews for other open ocean areas. Can J Fish aquat Sciences 48: 694-721
- Brothers EB, Mathews CP, Lasker R (1976) Daily growth increments in otoliths from larval and adult fishes. Fish Bull, US 74: 1-8
- Campana SE (1984) Lunar cycles of otolith growth in the juvenile starry flounder, *Platichthys stellatus*. Mar Biol 80: 239-246
- Campana SE, Neilson JD (1985) Microstructure of fish otoliths. Can J Fish aquat Sciences 42: 1014-1032
- Clarke GL (1970) Light conditions in the sea in relation to the diurnal vertical migration of animals. In: Farquhar GB (ed) Proceedings of an international symposium on biological sound scattering in the ocean. US Government Printing Office, Washington D.C., pp 41-50
- Clarke TA (1973) Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish Bull, US 71: 401-434
- Craddock JE, Backus RH, Daher MA (1987) Midwater fish data report for warm-core Gulf Stream rings cruises 1981-1982. Tech Rep Woods Hole Oceanogr Instrn: 87-42
- Craddock JE, Backus RH, Daher MA (1992) Vertical distribution and species composition of midwater fishes in warm-core Gulf Stream meander/ring 82-H. Deep-Sea Res 39 (Suppl 1): 203-218
- Farbridge KJ, Leatherland JF (1987) Lunar periodicity of growth cycles in rainbow trout, *Salmo gairdneri* Richardson. J interdiscip Cycle Res 18: 169-177
- Gartner JV Jr (1991) Life histories of three species of lanternfishes (Pisces: Myctophidae). I. Morphological and microstructural analysis of sagittal otoliths. Mar Biol 111: 11-20
- Gartner JV Jr, Hopkins TL, Baird RC, Milliken DM (1987) The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. Fish Bull, US 85: 81-98
- Gibson RN (1978) Lunar and tidal rhythms in fish. In: Thorpe JE (ed) Rhythmic activity of fishes. Academic Press, New York, pp 201-213
- Giragosov VYE, Ovcharov OP (1992) Age and growth of the lanternfish, *Myctophum nitidulum* (Myctophidae), from the tropical Atlantic. Vop Ikhtiol 32 (2): 61-68
- Gjøsaeter H (1987) Primary growth increments in otoliths of six tropical myctophid species. Biol Oceanogr (NY) 4: 359-382
- Goodyear RH, Zahuranec BJ, Pugh WL, Gibbs RH Jr (1972) Ecology and vertical distribution of Mediterranean midwater fishes. Mediterr biol Stud final Rep 1(3): 91-229
- Grau EG, Dickhoff WW, Nishioka RS, Bern HA, Folmar LC (1981) Lunar phasing of the thyroxine surge preparatory to seaward migration of salmonid fish. Science, NY 211: 607-609
- Hopkins TL, Gartner JV Jr (1992) Resource-partitioning and predation impact of a low-latitude myctophid community. Mar Biol 114: 185-197
- Hulley PA (1981) Results of the research cruises of F.R.V. "Walter Herwig" to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). Arch Fisch Wiss 31 (Beih 1): 1-300
- Jones C (1986) Determining age of larval fish with the otolith increment technique. Fish Bull, US 84: 91-103
- Karnella C (1987) Family Myctophidae, lanternfishes. In: Gibbs RH, Krueger WH (eds) Biology of midwater fishes of Bermuda Ocean Acre. Smithsonian Contr Zool 452: 51-168
- Kavaliers M (1982) Endogenous lunar rhythm in the behavioural thermoregulation of a teleost fish, the white sucker, *Catostomus commersoni*. J interdiscip Cycle Res 13: 23-27
- Linkowski TB (1987) Age and growth of four species of *Electrona* (Teleostei, Myctophidae). In: Kullander SO, Fernholm B (eds) Proceedings of the 5th Congress of European Ichthyologists. Stockholm, 12-16 August 1985. Swedish Museum of National History, Stockholm, pp 435-442
- Linkowski TB, (1991) Otolith microstructure and growth patterns during the early life history of lanternfishes (family Myctophidae). Can J Zool 69: 1777-1792
- Linkowski TB, Radtke RL, Lenz PH (1993) Otolith microstructure, age and growth of two species of *Ceratoscopelus* (Osteichthyes: Myctophidae) from the eastern North Atlantic. J exp mar Biol Ecol 167: 237-260
- Loeb VJ (1979) Vertical distribution and development of larval fishes in the north Pacific central gyre during summer. Fish Bull, US 77: 777-793
- Longhurst AR (1976) Vertical migration. In: Cushing DH, Walsh JJ (eds) The ecology of the seas. Saunders Company, Philadelphia, pp 116-137
- Mugiya Y, Watabe N, Yamada J, Dean JM, Dunkelberger DG, Shimuzu M (1981) Diurnal rhythm in otolith formation in the goldfish, *Carassius auratus*. Comp Biochem Physiol 68A: 659-662
- Nafpaktitis BG, Backus RH, Craddock JE, Haedrich RL, Robison BH, Karnella C (1977) Family Myctophidae. Mem Sears Fdn mar Res 1(7): 13-265
- Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? Adv mar Biol 26: 115-168



- Neumann D (1981) Tidal and lunar rhythms. In: Aschoff J (ed) Handbook of behavioural neurobiology. Plenum Press, New York, pp 351–380
- Nishimura A, Yamada J (1984) Age and growth of larval and juvenile walleye pollock, *Theragra chalcogramma* (Pallas), as determined by otolith daily growth increments. J exp mar Biol Ecol 82: 191–205
- Ozawa T, Penaflo GC (1990) Otolith microstructure and early ontogeny of a myctophid species *Benthoosema pterotum*. Nippon Suisan Gakk 56: 1987–1995
- Pannella G (1971) Fish otoliths: daily growth layers and periodical patterns. Science, NY 172: 1124–1127
- Pannella G (1974) Otolith growth pattern: an aid in age determination in temperate and tropical fishes. In: Bagenal TB (ed) The proceedings of an international symposium on the ageing of fish. Unwin Brothers, Surrey, England, pp 28–39
- Pannella G (1980) Growth patterns in fish sagittae. In: Rhoads DC, Lutz RA (eds) Skeletal growth of aquatic organisms. Plenum Press, New York, pp 519–560
- Pearcy WG, Lorz HV, Peterson W (1979) Comparison of the feeding habits of migratory and non-migratory *Stenobrachius leucopsarus* (Myctophidae). Mar Biol 51: 1–8
- Radtke RL (1987) Information incorporated in Antarctic fish otoliths. In: Kullander SO, Fernholm B (eds) Proceedings of the 5th Congress of European Ichthyologists. Stockholm, 12–16 August 1985. Swedish Museum of National History, Stockholm, pp 421–425
- Roe HSJ, Badcock J (1984) The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 5. Vertical Migrations and feeding of fish. Prog Oceanogr 13: 389–424
- Rosenberg AA (1982) Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds. Fish Bull, US 80: 245–252
- Spoel S van der, Schalk PH (1988) Unique deviations in depth distribution of the deep-sea fauna. Deep-Sea Res 35: 1185–1193
- Tesch FW (1989) Changes in swimming depth and direction of silver eels (*Anguilla anguilla* L.) from the continental shelf to the deep sea. Aquat living Resour (Nantes) 2: 9–20
- Torres JJ, Belman BW, Childress JJ (1979) Oxygen consumption rates of midwater fishes as a function of depth of occurrence. Deep-Sea Res 26A: 185–197
- Volk EC, Schroder SL, Fresh KL (1990) Inducement of unique otolith banding patterns as a practical means to mass-mark juvenile Pacific salmon. Am Fish Soc Symp 7: 203–215