

## Growth, reproduction and feeding of the tropical squid *Ornithoteuthis antillarum* (Cephalopoda, Ommastrephidae) from the central-east Atlantic\*

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**SUMMARY:** Length composition, age, growth, reproductive biology, feeding and parasites were studied using 432 individuals of the squid *Ornithoteuthis antillarum* (1.8-138 mm ML) collected in the open waters of the tropical central-east Atlantic. In the region studied, only a small-sized and early-maturing population of *O. antillarum* occur. Statolith shape, development and microstructure have several peculiar features setting *O. antillarum* apart of other ommastrephids. Assuming growth increments within statoliths to be daily, maximum age of squids does not exceed 182 days. Growth rates of juveniles and immature squids are high and similar to another fast-growing ommastrephid *Sthenoteuthis pteropus*, but they decrease considerably with the onset of maturation. Potential fecundity varies from 50,000 to 220,000 oocytes. It is suggested that the squid is a multiple spawner with frequent releases of small-sized (<1,500 eggs) egg masses. *O. antillarum* can be characterized as a browsing predator, feeding on all available relatively small prey (mainly amphipods as well as larvae and fries of carnivorous fish) in the thermocline and below. *O. antillarum* is infected mainly by didymozoid trematodes, the intensity of infection being 10-50 times less than in the same-sized *S. pteropus*. The life cycle of *O. antillarum* is discussed.

*Key words:* squid, *Ornithoteuthis antillarum*, growth, reproduction, parasites.

### INTRODUCTION

*Ornithoteuthis antillarum* Adam, 1957 is a common nektonic squid inhabiting epipelagic and mesopelagic waters of the tropical Atlantic from the Caribbean Sea to the continental slope of Angola (Nesis, 1987). Another species of the genus, Indo-Pacific *Ornithoteuthis volatilis* (Sasaki, 1915), penetrates with waters of the Agulhas Current to the Southeast Atlantic off southern Namibia, but never achieves tropical Atlantic (Villanueva and Sánchez,

1993). Unlike a majority of other ommastrephid squids which attain large sizes (usually > 300-400 mm of mantle length, ML), this squid is a small-sized animal. Maximum sizes of *O. antillarum* in the tropical Atlantic do not exceed 125 mm ML, whereas in the periphery of the species range (Bermudas and South-west Atlantic) squids attain 190-210 mm ML (Nesis and Nigmatullin, 1979; Roper, 1977; our data).

Some aspects of *Ornithoteuthis antillarum* biology are rather well-studied. It is supposed that mature specimens live both near the continental slope and underwater mountains and spawn there. Paralarvae and juveniles are epipelagic animals distributed by oceanic currents over great depths within the species

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range (Nesis and Nigmatullin, 1977). In the open area of the Gulf of Guinea, paralarvae and juveniles are most abundant in the depth range from 30 to 80 m, *i.e.* at the horizons of the first thermocline and below it (Arkhipkin *et al.*, 1988; Arkhipkin and Schetinnikov, 1989). In the tropical Atlantic, it has been found that *O. antillarum* start maturing at small sizes (40-60 mm ML), all squids > 80-90 mm ML are mature with a sexual ratio of approximately 1:1 (Nesis and Nigmatullin, 1979). *O. antillarum* feed mainly on fry of mesopelagic and bathypelagic carnivorous fishes, amphipods of the family Hyperidae, squid paralarvae and juveniles, and chaetognaths. Its main consumers are tunas and lanternfishes (Nesis and Nigmatullin, 1979).

Very little is known about age, growth and longevity of *Ornithoteuthis antillarum*. The main purposes of the paper are to estimate these parameters using statolith ageing techniques and to analyse peculiarities of the reproductive biology, feeding and parasites of *O. antillarum* in order to construct an “ecological portrait” of the species in open waters of Guinean Gulf and adjacent waters. This is necessary for a better understanding of the role of *O. antillarum* in epipelagic and mesopelagic ecosystems as well as its competition with, and divergence from, another abundant co-inhabitant *Sthenoteuthis pteropus* (Ommastrephidae) in the tropical Atlantic.

## MATERIAL AND METHODS

### Collection of squids

A total of 432 individuals of *Ornithoteuthis antillarum* (1.8-138 mm ML) were collected as bycatch during research surveys for the potentially commercial oceanic orange-back squid, *Sthenoteuthis pteropus* in the central-east Atlantic. These surveys were conducted aboard various research vessels working under the research programmes elaborated in the Atlantic Research Institute of Marine Fisheries and Oceanography (AtlantNIRO) between 1969 and 1988 (Fig. 1).

*Ornithoteuthis antillarum* were taken using two types of fishing gear. Paralarvae and small juveniles (2.2 to 20 mm ML) were caught by a ‘Big Bongo’ plankton sampler (opening diameter 0.6 m; mesh size 0.7 mm) at depths ranging from 0 to 100 m both at night and in the daytime. The duration of each haul was 15 min with an average speed of 3 to 3.4 km/h. Large juveniles and adults (20 to 138 mm ML) were captured by RMT trawls (horizontal openings of 13.6-24 m, vertical openings of 6-8 m with 6 mm mesh) at depths ranging from 0 to 250 m at night. Trawl duration was 30 min with an average speed of 5.6 km/h. Squids were identified using the key by Nesis (1987). The biological analysis of each

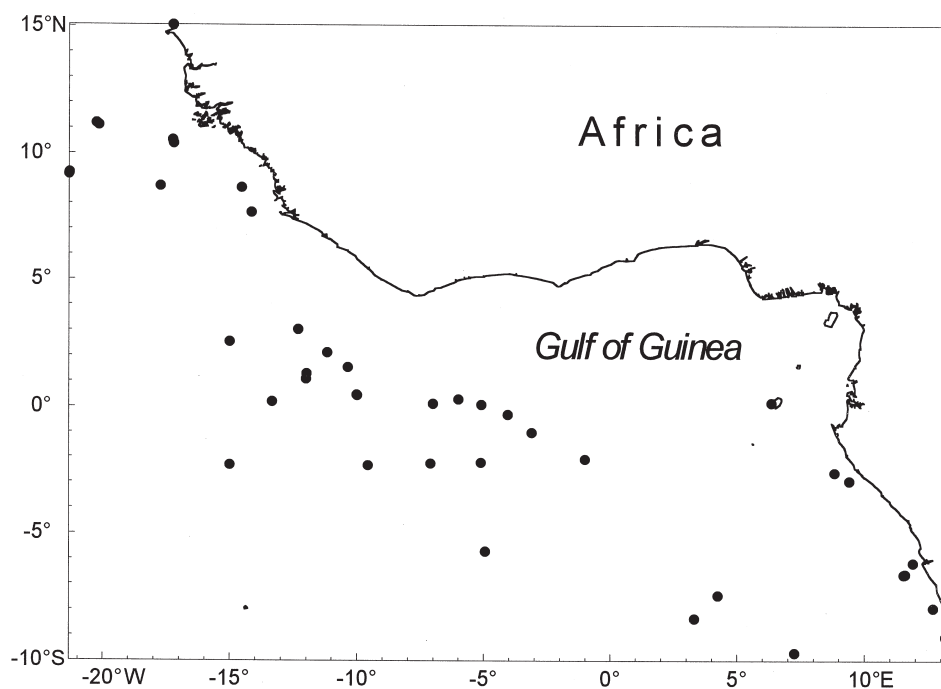


FIG. 1. – Sampling locations of *Ornithoteuthis antillarum* in the central-east Atlantic.

squid included measurements of the dorsal mantle length (ML, to the nearest mm) and total body weight (BW, to the nearest 1 g), an identification of sex and maturity stage (after Zuev *et al.* 1985).

Size distribution of *O. antillarum* was studied using a total of 421 squids (19-138 mm ML) caught by zoological trawls.

### Statolith analysis and growth rate estimation

Statoliths were extracted from 108 *Ornithoteuthis antillarum* (2.2 to 130 mm ML) aboard ship and stored in 96% ethyl alcohol between June 1985 and September 1988. In respect of monthly sampling, the maximum number of statoliths were collected in September, and none were sampled in October-December and May (Fig. 2). Statoliths were processed and read in the Laboratory of Commercial Invertebrates of AtlantNIRO using the statolith ageing techniques (Arkhipkin, 1991). Terminology and measurement of statoliths followed Clarke (1978) and Lipinski *et al.* (1991). Statoliths of paralarvae (ML < 10 mm) were embedded in Canada balsam without grinding. Statoliths of larger squid (> 10 mm ML) were attached to microscopic slides with a *Pro-texx* mounting medium and ground either on one side (statoliths of juveniles < 20 mm ML) or on both sides (squids > 20 mm ML) using wet waterproof sandpaper (1000 grit). After subsequent polishing (sandpaper of 1500 grit), statolith sections were embedded in Canada balsam, covered with cover glasses and placed in an oven at 80-90°C for 1 hr to dry the balsam.

Statolith microstructure was examined using a 'BIOLAM R-14' light microscope (x400) under transmitted light. Growth increments were counted from the nucleus to the edge of the lateral dome by two observers using an eye-piece micrometer (Dawe and Natsukari, 1991). The total number of growth increments for each specimen was obtained as an average of count numbers if the deviation between the average and counts was less than 5%. If the deviation was more than 5%, the statolith was re-counted. In case of considerable disagreement between the counts for the second time, that statolith was rejected from further analysis. If an increment definition was poor, or the statolith was overground, the other statolith from the same individual was examined.

Unfortunately, periodicity of growth increment deposition within *Ornithoteuthis antillarum* sta-

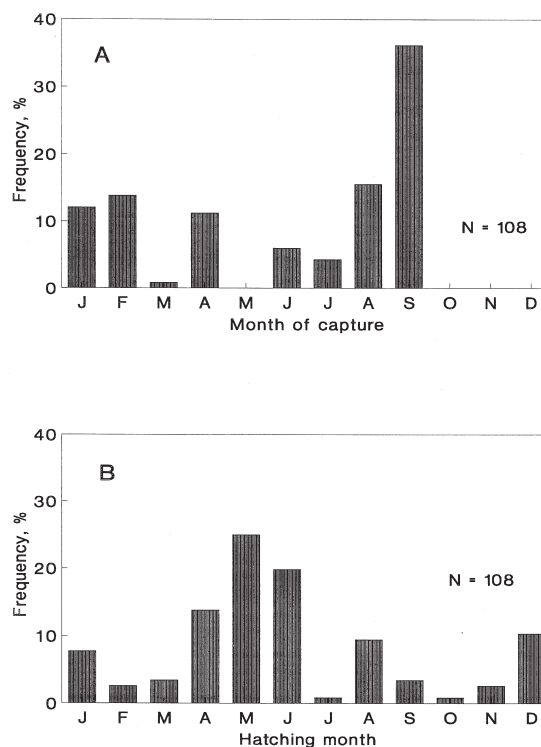


Fig. 2. – Months of capture (A) and hatching dates (B) of *Ornithoteuthis antillarum* in the central-east Atlantic.

toliths is still unknown. However, daily periodicity in formation of statolith growth increments have been validated in two other ommastrephid squids, *Illex illecebrosus* (Dawe *et al.*, 1985) and *Todarodes pacificus* (Nakamura and Sakurai, 1991). Hence, increments in *O. antillarum* statoliths were considered to be daily in the present paper. Therefore, the total number of increments represents squid age in days.

Growth curves were constructed using the method of iterative non-linear least squares (FISH-PARM statistical package, Saila *et al.*, 1988). The formula of the best fitted curve was determined by both the least coefficients of variance of the estimated parameters and highest r-squares. To estimate daily growth rates (DGRs, mm or g per day) and instantaneous rate of growth (G), values of both ML and BW were calculated for each 20-day interval using the formula of the best fitted curve. DGRs and G were calculated after Ricker (1958) as:

$$\text{DGRs} = (W_2 - W_1) / T$$

$$G = (\ln W_2 - \ln W_1) / T$$

where W1 and W2 are calculated ML or BW values at the beginning and end of time interval (T = 20 d).

## Analysis of the reproductive system

Reproductive systems were analysed in seven maturing and mature females of *Ornithoteuthis antillarum* (ML 75-118 mm). Due to the effect of preservation, the eggs when measured were not always perfectly symmetrical. To obviate any selection of the longest or shortest diameter, the micrometer was placed in a horizontal position in the eyepiece, and the egg diameter parallel to the graduation on the micrometer was measured (Clark, 1934). In each female, average egg diameter was estimated in a sub-sample of 50 ripe eggs taken from oviducts. In some oocytes with a regular ovoid form, both longest and shortest diameters were measured. To estimate oocyte number in the ovary, three 15-30 mg sub-samples were taken from the ovary surface, ovary core and intermediate layer. It was possible to count all oocytes in the sub-samples, because oocytes <0.05 mm in diameter were absent in all animals investigated. Total number of oocytes occurring in the reproductive system of prespawning females was considered to be a total oocyte production during ontogeny.

Potential fecundity (PF) was calculated as a sum of the total oocyte number in the gonad and egg number in oviducts. Relative fecundity (RF) was estimated as a ratio PF/ BW. An index of potential reproductive investment (PRI) was calculated as the product of RF and the weight of an individual ripe egg (Nigmatullin and Laptikhovskiy, 1990; Laptikhovskiy and Nigmatullin, 1993).

## Analysis of stomach contents and parasites

Degree of stomachs fullness (DSF) was studied in 272 individuals of 19-130 mm ML. It was identified by the 6-degree scale (Zuev *et al.*, 1985): 0 - empty stomach; 1 - traces of food remains, fullness less than 20% of the stomach volume; 2 - < 50% of stomach is filled with food remains; 3 - food occupied more than 50% of stomach cavity, but not more than 80%; 4 - food occupied the whole stomach cavity, but the stomach wall not extended; and 5 - stomach full with extended walls.

Food items were studied in 85 stomachs with food remains (squids of 21-101 mm ML). Taxonomy of food items were identified by a presence of characteristic parts of prey, i.e. legs (especially the sizes of gnatopods and pereopods in amphipods) and mandibles of crustaceans; beaks, sucker rings, hooks, remnants of gladii and lens of squids; chaets

(teeth) of chaetognats; vertebrae (especially specific form of fish larvae vertebrae), jaws and peculiarities of its dentition, bones and scales of bony fishes etc. (Zuev *et al.*, 1985). The relative lengths of prey items were calculated as a ratio between length of prey and absolute length of squid-consumer in percentage (AL - length of squid from the posterior mantle end to the end of longest arms).

Besides the real food items transit (secondary) food items were also identified. These are food of the squid's prey and get into the squid when ingested with the prey (Nigmatullin and Toporova, 1982).

The role of each food group was estimated using a frequency of occurrence (FO - percentage of stomachs containing food) and proportion in stomach contents (PVV - percentage of virtual volume each food group in stomach contents). FO was calculated for all stomachs with food, PVV only for stomachs with fullness 3-5 degrees (Zuev *et al.*, 1985).

Parasites were analysed in 68 squids of 21-101 mm ML. The mantle cavity, buccal cone, inner organs and especially the digestive system were examined under "MBS-10" dissecting microscope. Additionally, a thorough analysis of stomach walls was performed during food spectrum studies. Therefore, rectum walls were not examined. It is known however, that larvae of tetraphyllidean cestods *Scolex* sp. often infect the rectum walls (Hochberg, 1990). Thus, infection of *O. antillarum* by *Scolex* sp. remains unclear. Incidence (the percentage of infected squids-hosts by given parasites) and intensity of infection (number of specimens of a given parasite in one host) is calculated (after Zuev *et al.*, 1985).

## RESULTS

### Length composition

Data on length compositions of males and females were pooled over the whole range and period of sampling (Fig. 3). Mantle length of immature males varied from 20 to 80 mm without distinct modes. Length compositions of both maturing and mature males were unimodal (70 and 90 mm ML, respectively). ML range of immature females was similar to that of males, but with two modes (30 and 70 mm ML). Length composition of maturing females was without well-defined modes, whereas that of mature females was with one prominent modal group of 100 mm ML. Mean sizes of mature females (100.39 mm ML, SD = 1.60) were statisti-

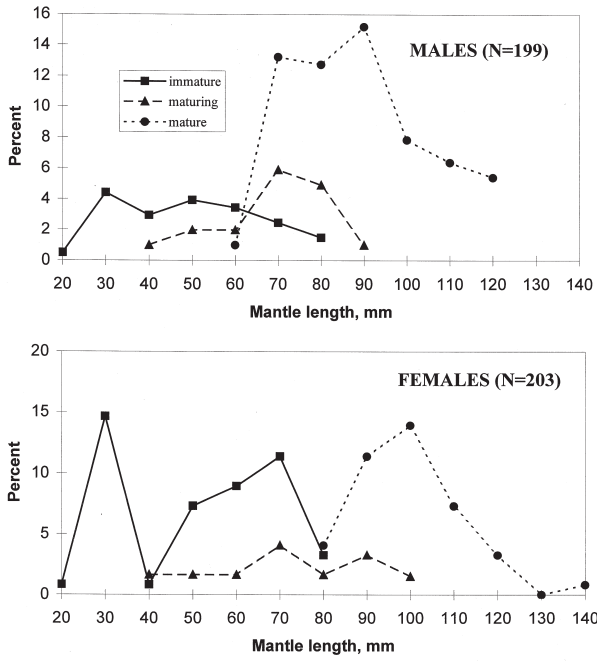


FIG. 3. – Length composition of males and females of *Ornithoteuthis antillarum* in the central-east Atlantic.

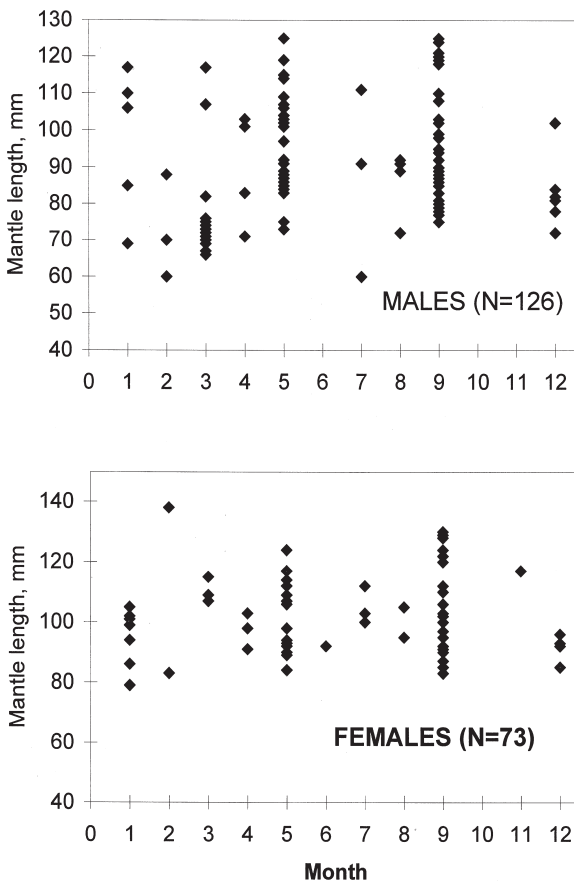


FIG. 4. – Occurrence of different sized males and females of *Ornithoteuthis antillarum* in different months in the central-east Atlantic.

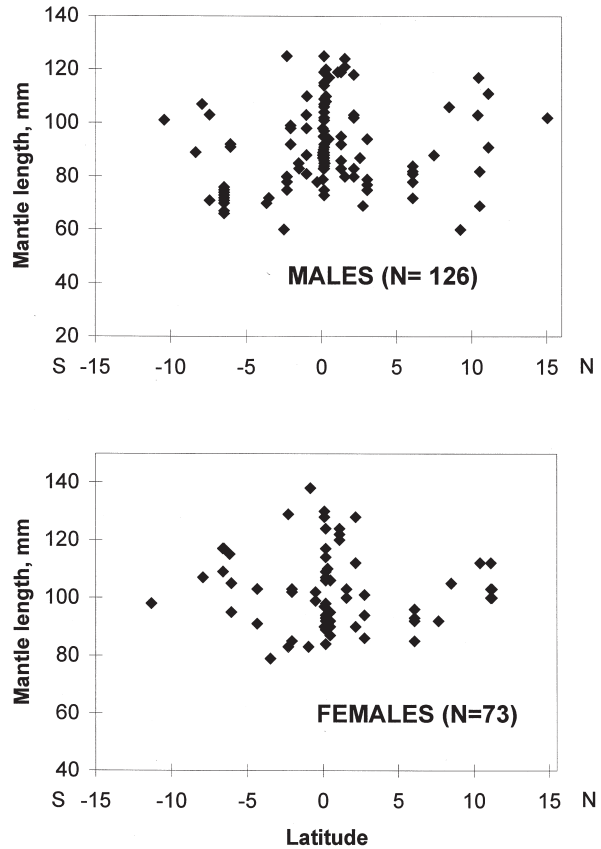


FIG. 5. – Occurrence of different sized males and females of *Ornithoteuthis antillarum* at different latitudes in the central-east Atlantic.

cally larger than those of mature males (88.31 mm ML, SD = 1.73) at  $\alpha = 0.99$  ( $t = 4.749$ ,  $p < 0.001$ ). There were no differences in sizes of mature animals caught at different latitudes and in different seasons (Figs. 4, 5). Sex ratio of all squids was close to 1:1.

### Statolith morphology

Statolith of *Ornithoteuthis antillarum* adults is elongated. The dorsal dome is tongue-shaped, its longitudinal axis is situated almost perpendicular to the rostrum axis. The lateral dome is well-developed and consists of several lobes separated from each other by distinct grooves. The rostrum is long and finger-shaped. The wing is narrow and short, achieving only a midpart of the rostrum (Fig. 6).

### Statolith development and growth

Statolith formation consists of five distinct stages of development, each characterized by specific morphological features (Fig. 6).

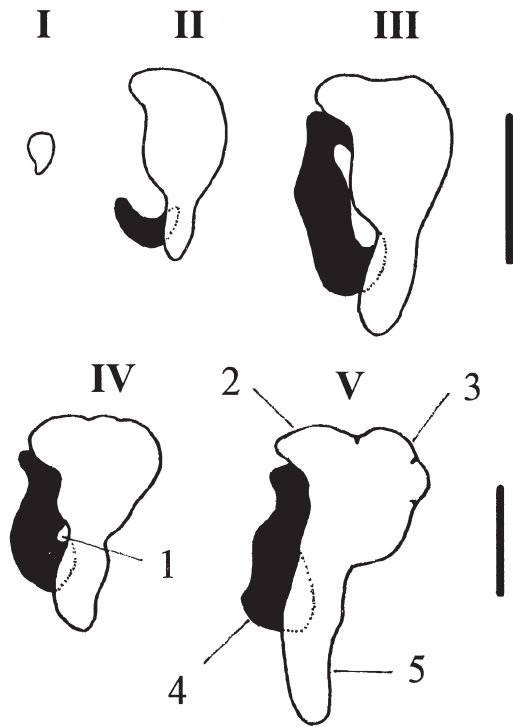


FIG. 6. – Different stages of statolith development (I-V) of *Ornithoteuthis antillarum*. Lower fissure (1); lateral dome(2); dorsal dome (3); wing (4, filled in black); and rostrum (5).

*Stage I* (observed in squids of 0.18-0.95 mm ML, total statolith length, TSL < 0.35 mm). Statolith droplet-shaped, without a wing. At the end of the stage, the rostrum looks like a small cusp on the ventral side of the statolith. *Stage II* (10-14 mm ML, 0.35-0.56 mm TSL). Formation and differen-

tiation of different parts of the statolith, i.e. rostrum, dorsal and lateral domes. A primordium of the wing appears on the inner side of the rostrum. *Stage III* (15-39 mm ML, 0.56-0.91 mm TSL). The wing achieves and attaches the inner part of the dorsal dome, forming a specific dumb-bell shaped fissure. *Stage IV* (28-90 mm ML, 0.8-1.4 mm TSL). Statolith domes and rostrum are finishing their formation and acquire the shape close to the definitive stage. The upper part of the wing accretes with the inner part of the statolith, leaving a small lower fissure near the rostrum. *Stage V* (53-103 mm ML, 1.2-1.86 mm TSL). A definitive stage of the statolith development. The inner part of the wing completely accretes with the statolith domes and rostrum.

Allometric growth of the total statolith length versus mantle length is negative with a high value of the coefficient 'b' (Table 1). Sexual dimorphism in relative sizes of the statoliths was not observed (Fig. 7A). The relationship between TSL and total number of increments within statoliths was best described by logistic curve with rather high value of R<sup>2</sup> (Fig. 7B, Table 1).

### Statolith microstructure

Growth increments were visible in all statoliths studied. They could be grouped into three growth zones which were distinguished by colour and increment width (Fig. 8). Growth increments started radiating from the small and round nucleus (20-24 μm

TABLE 1. – Parameter estimates of different relationships between (TSL) total statolith length in mm, (ML) mantle length in mm, (BW) body weight in g and (NGI) number of growth increments of the power (allometric) function  $Y=aX^b$  and logistic function  $Y(t) = K / \{1 + [(K - Y_0) / Y_0] * \exp(-rt)\}$ .

	Parameter	Estimate	Asymptotic SE	r <sup>2</sup>
Power curves:				
TSL vs ML	a	0.1121	0.009889	0.9513
	b	0.5656	0.01986	
BW vs ML	a	0.0008113	0.0003115	0.9418
	b	2.23		
Logistic curves:				
TSL vs NGI	r	0.05015	0.004061	0.8997
	K	1.573	0.03062	
	Y <sub>0</sub>	0.09	0.02062	
ML vs NGI Females	r	0.0584	0.006746	0.9031
	K	108.3	3.144	
	Y <sub>0</sub>	1.843	0.8457	
ML vs NGI Males	r	0.05995	0.007549	0.8927
	K	97.41	3.073	
	Y <sub>0</sub>	1.81	0.8811	
BW vs NGI	r	0.04918	0.008871	0.7574
	K	34.17	3.171	
	Y <sub>0</sub>	0.25	0.1889	

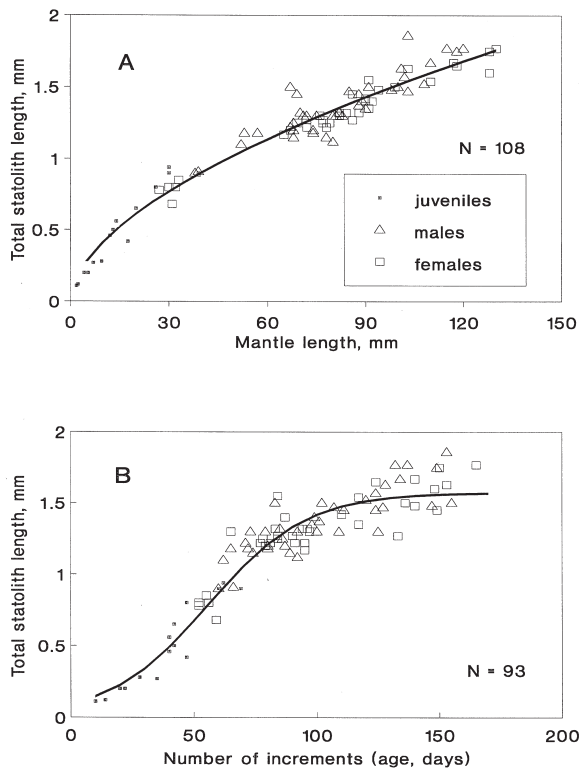


FIG. 7. – Relationships between total statolith length and mantle length (A) and total statolith length and number of increments (B) in *Ornithoteuthis antillarum*.

in diameter). The postnuclear zone was translucent with narrow growth increments (3-6  $\mu\text{m}$  in width). There were from 28 to 34 growth increments within the zone (mean 31.5, SD = 1.19). A prominent check was usually observed on the boundary between the postnuclear and dark zones. The dark zone is brownish in transmitted light and opaque in reflected light of the microscope. In some animals, brown colour of the zone was very intense interfering enumeration of the increments. Growth increments within the dark zone were specific, namely very wide (up to 15-20  $\mu\text{m}$ ) and with a broad discontinuous zone (Fig. 8). The total number of growth increments within the dark zone ranged from 34 to 86 (mean 51.2, SD = 10.6). Often there were numerous inner cracks within the dark zone, which were natural and did not appear during the statolith processing (Fig. 8). The peripheral zone is translucent with growth increments being narrower than those in the dark zone. Their width was gradually decreased from 8-10  $\mu\text{m}$  in the inner part of the zone to 4-5  $\mu\text{m}$  near the statolith edge (Fig. 8). There were no distinct checks in the peripheral zone.

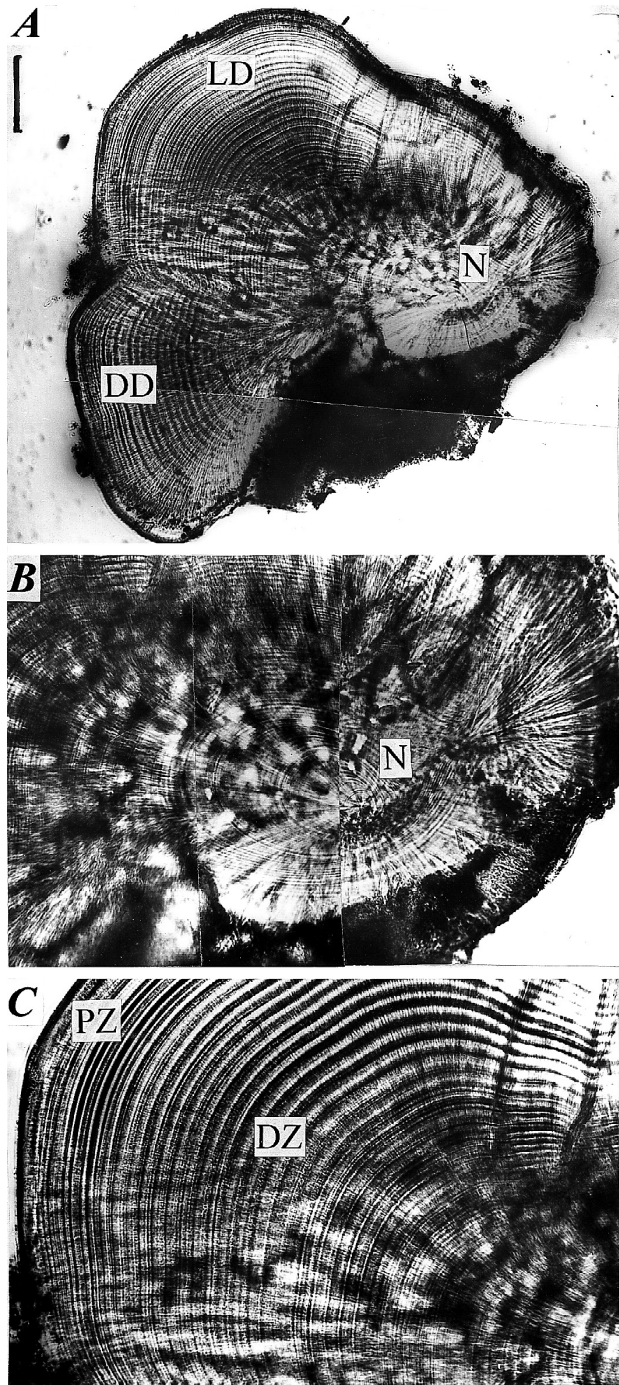


FIG. 8. – Light micrograph of the statolith from a maturing male of *Ornithoteuthis antillarum* (age 92 d, 71 mm ML). Rostrum is removed during grinding. A - general view of the ground statolith: N, nucleus; LD, lateral dome; DD, dorsal dome; B - N, nucleus; PN, postnuclear zone; C - DZ, dark zone; PZ, peripheral zone. Scale bar = 100  $\mu\text{m}$  in A and 50  $\mu\text{m}$  in B and C.

### Age and growth of squid

The youngest squid sampled was a paralarva of 1.8 mm ML (10 d). Maximum age was revealed in a mature female of 117 mm ML (182 d) and in a mature male of 83 mm ML (173 d). The largest

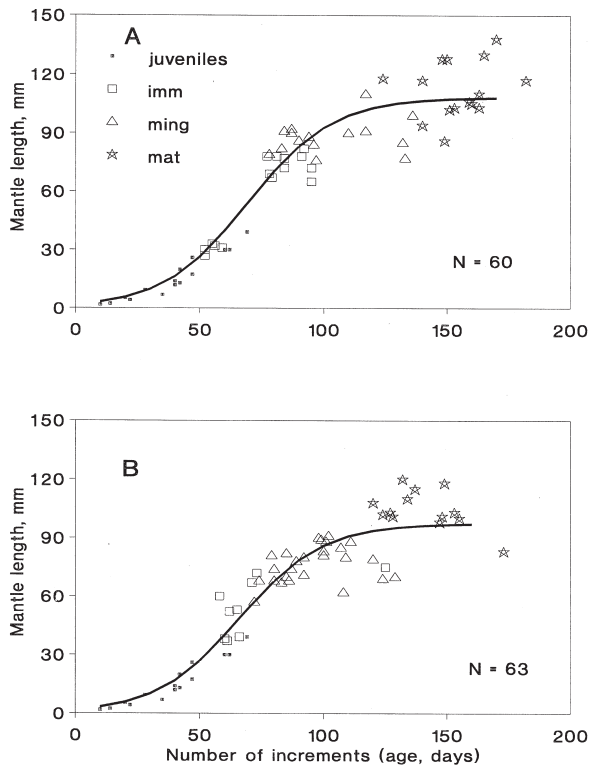


FIG. 9. – Relationships between mantle length and number of increments in statoliths of females (A) and males (B) of *Ornithoteuthis antillarum*. Imm- immature, ming - maturing and mat - mature squids.

squid (mature female of 138 mm ML) was 170 d old (Fig. 9).

Length-at-age data were best described by logistic growth curves (Fig. 9, Table 1). Data on both sexes were treated separately. Sexual dimorphism in growth rates was visible (Fig. 9A,B) on length-at-age plots, but statistical difference was shown only for the parameter 'K' (Table 1). Thus, females attain somewhat larger sizes than males, and the mean ML of mature animals of both sexes differs statistically.

Length-weight relationship was practically the same for both sexes (Fig. 10A), and pooled weight-at age data were best described by the logistic function too (Fig. 10B). However, individual variation in growth in weight was higher than that in length resulting in lower  $R^2$  value of the former relationship (Table 1).

Absolute daily growth rates (DGRs) in length and weight changed similarly in both sexes; they increased, attained a certain maximum and then decreased (Fig. 11A). The age when the maximum DGRs occurred for length was similar for both sexes (60-70 d). Maximum values of DGRs in weight were reached later, at an age of 100 d (Fig. 11A).

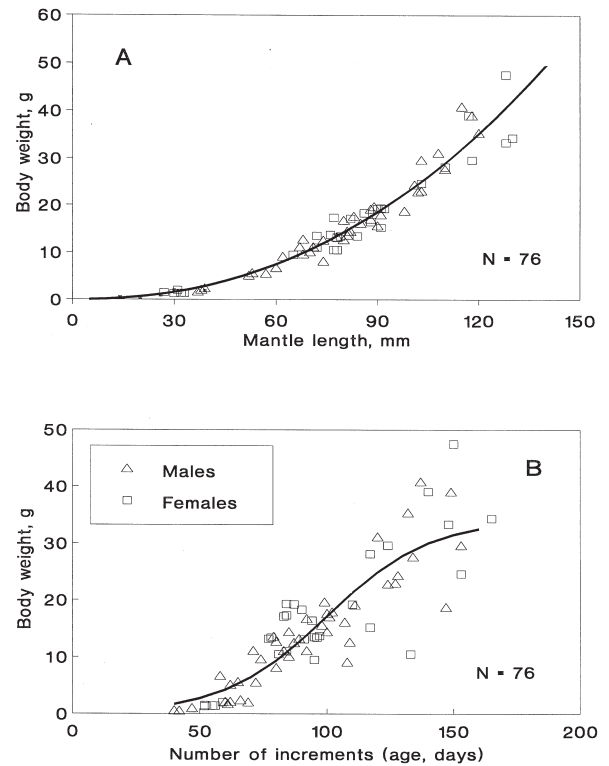


FIG. 10. – Relationships between body weight and mantle length (A) and body weight and number of increments (B) of *Ornithoteuthis antillarum*.

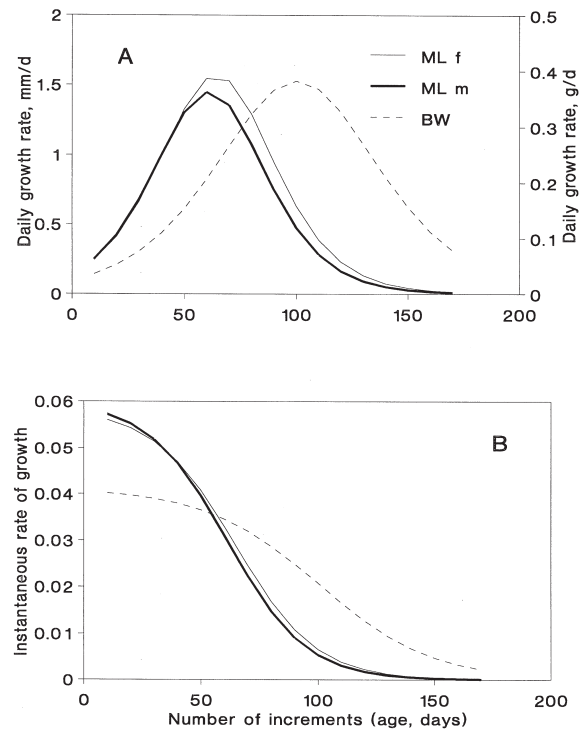


FIG. 11. – Daily growth rates and instantaneous rates of growth in *Ornithoteuthis antillarum*.



Instantaneous rates of growth (G) gradually decreased both in length and weight, those in length more sharply than in weight (Fig. 11B).

### Fecundity

Oocytes of all stages of their development (after Burukovskii *et al.*, 1977) were found in the ovaries of mature females of *Ornithoteuthis antillarum*. However, oogonia were not found (i.e. oocytes < 0.03-0.05 mm in diameter). Protoplasmic oocytes of 0.05-0.15 mm dominated in the mature ovaries.

Maximum diameters of ripe eggs varied from 0.73 to 0.80 mm, and weights from 0.19 to 0.20 mg. There were from 160 to 1,300 ripe eggs in oviducts of mature females. Potential fecundity varied from 50,000 to 220,000 oocytes (Fig. 12A). Relative fecundity ranged from 2,186 to 6,389 oocyte/g (mean 3,341 oocyte/g).

### Age at maturation and hatching dates

Ages at maturation of males and females are shown in Fig. 13. Immature animals (maturity stages 1 and 2) were 50-90 d old with the only exception of an immature male of 72 mm ML (129 d). Age range

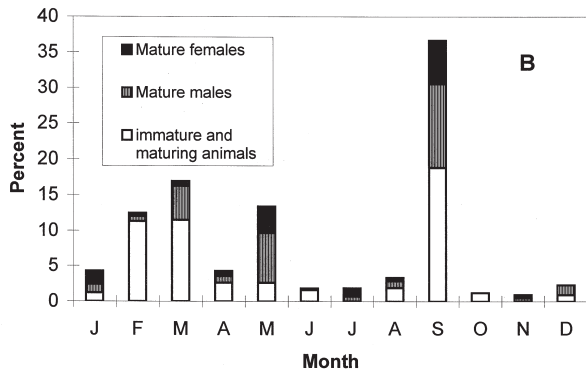
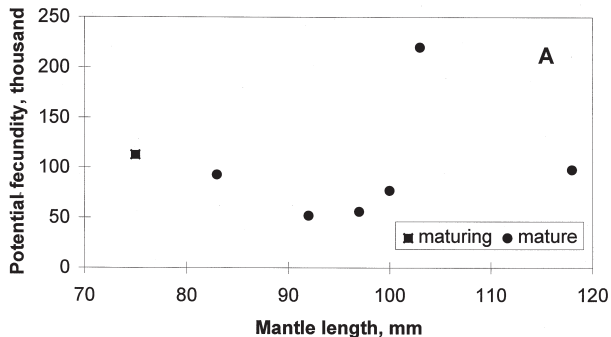


FIG. 12. – Relationship between potential fecundity and mantle length of females (A) and frequency of occurrence of immature, maturing and mature males and females of *Ornithoteuthis antillarum* by month.

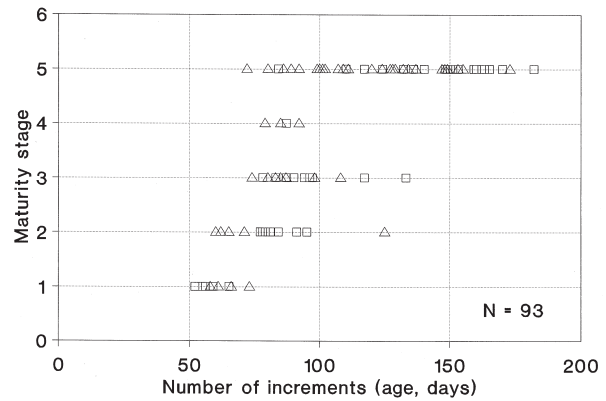


FIG. 13. – Maturation of *Ornithoteuthis antillarum*. Symbols are the same as in Fig. 10.

of maturing squids at the maturity stage 3 was wide (from 65 to 134 d), whereas that at the maturity stage 4 was narrow and left-shifted. Probably, this shift appeared due to a small number of squids captured at maturity stage 4 (only 4) and was therefore an artifact. Age range of mature animals was wide both in males and females. The youngest mature male studied was 69 d old, the youngest female was 80 d old. All squids > 134 d were mature.

Proportions of mature squids varied seasonally (Fig. 12B). The highest occurrences of mature males and females were observed in January, May and September. Mature squids were absent in catches in September and were caught in very low quantities in February and June.

Taking into account backcalculated hatching dates, *Ornithoteuthis antillarum* hatched throughout the year (Fig. 2B).

### Qualitative aspects of feeding

Qualitative aspects of *Ornithoteuthis antillarum* feeding at night were analyzed separately for both sexes at different maturity stages (Table 2). The degree of stomach fullness (DSF) was minimum in juveniles and maximum in medium-sized maturing males and females. Mature squids had medium values of the DSF confirming the suggestion of their active feeding.

### Feeding spectrum

The feeding spectrum of *Ornithoteuthis antillarum* included epi- and mesopelagic species of meso- and macroplanktonic and micronektonic crustaceans, nemertines, chaetognaths, heteropod

TABLE 2. – The degree stomach fullness (DSF) in males and females of *Ornithoteuthis antillarum* at different stages of maturity

	Immature	MALES		FEMALES		
		Maturing	Mature-copulating	Immature	Maturing	Mature-spawning
Number of spec. studied	16	25	113	49	28	41
ML, mm	30-83	<b>52-98</b>	60-125	18-88	<b>49-96</b>	79-138
Proportion of squid with empty stomachs	62.5	16.7	29.8	24.3	14.3	41.0
Proportion of squids with full stomachs (4-5)	6.3	29.2	9.5	12.2	42.9	17.9
Mean DSF	0.8	2.2	1.5	1.3	2.3	1.7

TABLE 3. – Food spectrum of *Ornithoteuthis antillarum* in open waters of the Central-East Atlantic. Frequency of occurrence (FO, %) for stomachs with DSF from 1 to 5, and proportion of virtual volume in stomachs with DSF ranging from 3 to 5

Prey category	21 - 40		Mantle length (mm)		61 - 101	
	FO	PVV	FO	PVV	FO	PVV
<b>CRUSTACEA</b>	<b>69.0</b>	<b>61.8</b>	<b>81.5</b>	<b>46.8</b>	<b>84.6</b>	<b>25.0</b>
Copepoda						
<i>Candacia</i> sp.	14.3	26.3	3.7	+	<b>15.4</b>	+
Eupausiacea			7.4	+	7.7	+
Mysidacea			3.7	+		
Amphipoda	50.0	35.4	48.1	28.7	53.8	18.0
Hyperiididae	7.1	+				
<i>Phronima</i> sp.	11.9	2.7				
<i>Phrosina semilunata</i>	31.0	32.7	48.1	28.7	53.8	18.0
Decapoda						
caridean shrimps	4.7	+	11.1	8.7	15.4	1.0
Oplophoridae					7.7	+
crabs larvae	7.1	+	14.8	9.4	15.4	4.6
<b>NEMERTINA</b>	<b>2.4</b>	<b>+</b>				
<b>CHAETOGNATA</b>	<b>40.5</b>	<b>9.5</b>	<b>37.0</b>	<b>5.0</b>	<b>53.8</b>	<b>5.8</b>
<b>HETEROPODA</b>	<b>4.7</b>	<b>+</b>	<b>3.7</b>	<b>+</b>		
<b>TEUTHIDA</b>	<b>23.9</b>	<b>7.3</b>	<b>33.3</b>	<b>25.0</b>	<b>15.4</b>	<b>13.0</b>
<i>Abraliopsis</i> sp.			7.4	-	7.7	-
<i>Enoploteuthis</i> sp.					7.7	-
<i>Onychoteuthis banksi</i>			3.7	-	7.7	-
<i>Thysanoteuthis rhombus</i>	2.4	-				
<i>Octopoteuthis</i> sp.	2.4	-				
<i>Liocranchia</i> sp.	2.4	-				
<b>PISCES</b>	<b>47.6</b>	<b>30.0</b>	<b>62.9</b>	<b>23.1</b>	<b>84.6</b>	<b>56.5</b>
fishes larvae	23.9	4.5	11.1	5.6	7.7	0.5
plankton-eater fishes fry	7.1	6.1	7.4	+	23.0	18.0
Myctophidae					23.0	18.0
Gonostomatidae					7.7	-
Exocoetidae	7.1	-				
carnivorous fishes fry	16.6	19.1	29.6	16.8	53.8	38.0
Paralepididae			7.4	6.2	15.4	-
<i>Alepisaurus</i> sp.					7.7	-
Stomiidae	4.7	-			7.7	
Sternoptychidae			3.7	+		
<b>TRANSIT FOOD ITEM</b>	<b>9.5</b>	<b>-</b>	<b>22.0</b>	<b>-</b>	<b>53.8</b>	<b>-</b>
Copepoda	4.7	-	22.2	-	53.8	-
Isopoda	2.4	-				
Hyperiididae	2.4	-	3.7	-		
Thecosomata	2.4	-				
<b>Number of stomachs studied</b>	<b>42</b>	<b>11</b>	<b>27</b>	<b>16</b>	<b>13</b>	<b>10</b>

molluscs, squid and teleost fishes (Table 3). The main food items were the carnivorous amphipod *Phrosina semilunata*, chaetognaths and fish larvae and fry. The secondary food items were juvenile squids, shrimps, crab larvae and large copepods belonging to the genus *Candacia* (mainly *Candacia pachydactyla*). Other food items were occasional food prey. Low proportions of chaetognaths in the virtual volume of stomach contents (PVV) were due to the fast digestion of their delicate body tissues.

Preliminary analysis did not reveal a sexual dimorphism in the food spectrae of the same-sized males and females. Pooled data for both sexes were analyzed separately for three different size groups in order to reveal any ontogenetic changes in the food spectrum. Size variability in the feeding spectrum of *Ornithoteuthis antillarum* is low in the ML range studied. New food items did not appear after the juvenile phase of ontogenesis. Main and secondary food items also did not change after this phase with the exception of fish food items (Table 3). Proportion of fish food items increased with ML, especially for fry of planktophagous and carnivorous fishes. Simultaneously, a proportion of fish larvae decreased (Table 3).

Quantity of consumed prey items varied from 4 to 25 (average 8-12) specimens /stomach. As a rule, there were 3-9 *Phrosina* and 4-12 fish larvae and fry in such stomachs. No more than 2-3 specimens of chaetognaths, crab larvae and squid juveniles were observed in one stomach.

Sizes of consumed food items varied from 2 to 50 mm (usually 10-30 mm in length). Copepoda *Candacia* were the smallest (2.5-4 mm, i.e. 3-6% AL), whereas chaetognaths and fry of deepwater carnivorous fishes were the longest (25-28% AL).

There were observed transit (secondary) food items in the stomachs of *O. antillarum*, namely hyperiid, isopod and copepod crustaceans and thecosomats (Table 3). In most cases they were absolutely intact. Quantity of the transit food items (mainly copepods *Oncea* spp., *Rhinocalanus* spp., *Corycella* spp.) varied from 1 to 24 spec/stomach, their length ranged from 0.3 to 2 mm (0.3-1.7% AL).

### Parasites

Generally, squids of the ML range studied (21-101 mm) were 92.6% infected with helminths. All squids > 40 mm ML were infected. Three groups of helminths were present: cestodes, nematodes and trematodes. Two pleurocercoids of the cestod *Nybe-*

TABLE 4. – Size related changes in trematods metacercaria Didymozoidae infection of *Ornithoteuthis antillarum* in open waters of Central-East Atlantic. I - incidence, %; II - mean and III - range of intensity, spec./host; N: number of squids studied

ML, mm	I	II	III	N
21-30	77.0	7.1	1-16	13
31-40	90.5	11.3	2-51	21
41-50	100	16.5	3-45	10
51-60	100	27.3	2-120	13
61-101	100	27.0	5-104	11

*linia lingualis* (2 mm in length) were found in the outer coverings of the stomach of an immature female (63 mm ML). A single nematode larva *Porrocaecum* sp. was found in stomach cavity of an immature male (38 mm ML).

Didymozoid trematodes were the most abundant parasites in *O. antillarum*. They already appeared in small numbers in squids of 21-25 mm ML. During ontogenesis, the intensity of infection of didymozoids sharply increased, and all squids > 40 mm ML were infected with these trematodes (Table 4).

Didymozoid metacercariae were encysted one by one under the outer coverings of the stomach. Once metacercariae were found in the cavity of a blood vessel, and twice in the stomach cavity among food remnants. In one case of massive infection, they were concentrated mainly on the dorsal side of the stomach near the main blood vessel. Their sizes varied from 0.25 to 0.5 mm. Metacercariae were found mainly alive, but some of them were died with degeneration of the body. These dead metacercariae were found only in large maturing and mature squids.

## DISCUSSION

### Length composition

Our data on length composition of *Ornithoteuthis antillarum* in the central-east Atlantic confirm previous assumptions by Nesis and Nigmatullin (1979) on rather small sizes of mature animals in this region. In the open waters of the tropical Atlantic, mature squids do not exceed 140 mm ML, whereas squids near the continental slope and at higher latitudes (north of 20°N in the Northwest Atlantic and south of 20°S in the Southwest Atlantic) have been found to be still immature at these sizes (Nesis and Nigmatullin, 1979, our data).

Thus, only a small-sized population inhabiting open waters of the tropical Atlantic was studied in the present paper.

### Statoliths

Statolith shape of *Ornithoteuthis antillarum* is specific and different from other ommastrephid squids (Arkhipkin and Murzov, 1986a, Clarke, 1978). The most specific character is a large finger-shaped rostrum and well-developed lateral dome, separated from the dorsal dome by distinct groove. In all other ommastrephids studied, the rostrum is smaller and the lateral dome is not well-distinguished from the dorsal dome as in *O. antillarum*.

Statolith development also has some peculiar features. In *O. antillarum*, the upper part of the developing wing attaches firstly to the dorsal dome and only then to the medium part of the statolith (like in onychoteuthid *Onychoteuthis banksi*, Arkhipkin and Nigmatullin, 1997), whereas in most ommastrephids the upper part of the developing wing attaches with its inner surface to the medium part of the statolith, leaving free the proximal part of the wing (i.e. in *Sthenoteuthis pteropus*, Arkhipkin and Mikheev, 1992).

Generally, the statolith microstructure is similar to that of other ommastrephids studied. The nucleus has a shape and size close to those of other oceanic ommastrephids (Arkhipkin, 1989). As in ommastrephids *Illex illecebrosus* (Morris and Aldrich, 1984) and *Dosidicus gigas* (Arkhipkin and Murzov, 1986b), growth increments can be grouped into three main growth zones. The total number of increments within the postnuclear (=paralarval) zone of *O. antillarum* is very close to that of another tropical ommastrephid *S. pteropus* (33 increments, Arkhipkin and Mikheev, 1992), reflecting possible similarity in the duration of paralarval ontogenetic phase in the two ommastrephid squids. The most peculiar feature within the statolith microstructure of *O. antillarum* is the hypertrophically developed discontinuous zone of the growth increments in the dark zone. This is a unique character among ommastrephid squids. However, reasons for its strong development remain unclear. The peripheral zone resembles those of other ommastrephid squids.

Negative allometric growth of statoliths (TSL vs ML) seems to be characteristic for all ommastrephids (Arkhipkin, 1989). However, rates of the relative growth of the statolith range between species. High values of the coefficient 'b' of the

allometric growth curve shows that *O. antillarum* has maximum rates of statolith growth among ommastrephids studied (Arkhipkin and Murzov, 1986a; Arkhipkin, 1989), possibly due to fast development of the enlarged rostrum of the statolith.

### Age and growth

The maximum age of mature *Ornithoteuthis antillarum* studied did not exceed 182 d, suggesting a 6-month life cycle for this species in the tropical Atlantic. Its ommastrephid co-inhabitant *S. pteropus* has been shown to have a 1-yr life span, but it achieves much larger sizes (up to 650 mm ML, Zuev *et al.*, 1985; Arkhipkin and Mikheev, 1992) than *O. antillarum*. A 6-month life span has also been described for fast-maturing tropical populations of another ommastrephid, *Illex coindetii*, inhabiting shelf and slope waters of Sierra-Leone (Arkhipkin, 1996). Unlike *S. pteropus*, sexual dimorphism in maximum ages of *O. antillarum* is not observed.

Maximum absolute daily growth rates (DGRs) in length coincide with the development of the dark zone of the statolith (average age range from 32 to 82 d). A slight difference in male and female DGRs (DGRs of females were somewhat higher at ages > 60 d) causes somewhat larger maximum sizes of mature females. The DGRs in length of *O. antillarum* are similar to those of fast-growing *S. pteropus* at ages < 60 d. As a result, squids of both species have quite similar ML at these ages (Arkhipkin and Mikheev, 1992). However, *O. antillarum* starts maturing at ages > 60 d and considerably decreased its DGRs in length, whereas *S. pteropus* remains immature and quickly over-grows the former species. Moreover, both DGRs and instantaneous daily growth rates (G) in weight of immature and maturing *O. antillarum* are considerably less than those of immature *S. pteropus*. This results in different body proportions of both species; namely a slender arrow-shaped body of *O. antillarum* and a powerful spindle-shaped body *S. pteropus*.

In maturing *O. antillarum*, DGRs in length decrease whereas DGRs in weight increase and remain at the highest level until an age of 100 d. This is due to continuing body growth, but re-distribution of the energy from somatic (reflected as DGRs in length) to generative (reflected as DGRs in weight) growth. Mature squids almost stop their growth in length, though still growing with low DGR in weight. Insignificant sexual dimorphism in growth rates of *O. antillarum* is a rare feature among

ommastrephids which have usually pronounced sexually dimorphic growth resulted in different body dimensions of mature males and females (Arkhipkin, 1989; Arkhipkin and Mikheev, 1992). Probably, poorly pronounced sexual dimorphism in *O. antillarum* is caused by similarity in ages of maturation of both sexes and peculiar reproductive strategy of females, which is discussed below.

### Reproductive strategy

Egg size and relative fecundity of *O. antillarum* are practically the same as *S. pteropus* (Nigmatullin and Laptikhovskiy, 1994). Differences in absolute values of potential fecundity (up to 20 million in the latter species) are related to the much larger ML and 1-yr life span of *S. pteropus*.

Taking into account age-at-maturation in *O. antillarum* females, it is possible to suggest that the spawning period lasts from 1.5 to 3 months. If a female spawns at least half of fecundity as observed in other ommastrephids (Nigmatullin and Laptikhovskiy, 1990; Laptikhovskiy and Zorikova, 1992; Laptikhovskiy and Nigmatullin, 1993, Nigmatullin and Laptikhovskiy, 1994), daily egg production might be about 500 - 1,500 eggs (0.4-0.9% BW), that is close to the observed egg number in oviducts. This suggests that spawning is intermittent with multiple and small egg masses. Probably, females release one egg mass each night or one time per several nights.

This complex reproductive adaptation in females corresponds to low quantity of spermatophores in the Needham sac of males (<50-60 spermatophores, Sabirov, 1995). Probably, matings are frequent and spermatophores are quickly spent, not accumulating in large quantities in the Needham sac. The same phenomenon was observed in *T. rhombus* (Nigmatullin *et al.*, 1995). Mating is supposed to be in "head-to-head" position; there are up to 40-50 seminal reservoirs on the buccal membrane of female, and up to 10-15 spermatangues in mature females (Usanov G.V., pers. comm. and our data).

A similar kind of spawning was revealed in other oceanic epipelagic cephalopods: *Argonauta* spp., *Tremoctopus violaceus* and *Abralia trigonura* (Nesis, 1977; Young and Mangold, 1994). This is an adaptation to the utilization of relatively large potential fecundity during a rather short spawning period, and to the maximum egg dispersion in epipelagic waters.

Like most of other ommastrephids (Arkhipkin,

1989), *O. antillarum* is characterized by round-the-year spawning. It is confirmed by two independent factors, such as round-the-year occurrence of mature animals of both sexes and hatching dates throughout the year as determined by statolith analysis. Moreover, time of the highest occurrence of mature animals practically coincide with peaks in hatching dates (April-May, August-September and December-January).

Thus, *Ornithoteuthis antillarum* from the open waters of the central-east Atlantic is characterized by a short 6-month life cycle, young age at maturation; prolonged mature phase in males and females (about a half of the whole ontogenesis), similar sizes and growth rates of both sexes; small ripe eggs (close to the minimum known among ommastrephids); high potential fecundity; round the year population spawning; intermittent individual spawning by frequent releasing of small-size egg masses; and frequent mating with transfer of relatively small number of spermatophores (first dozens) by males to females. These ecological features show that populations of *O. antillarum* from the tropical Atlantic are one of the most r-oriented among squids of the family Ommastrephidae and cephalopods as whole.

### Feeding

A majority of food items of *Ornithoteuthis antillarum* belong to carnivorous species of the lower epipelagic complex of organisms, inhabiting depths ranging from 30 to 400 m at night (Vinogradov, 1977; Parin *et al.*, 1977). It has been documented previously that *O. antillarum* is characterized by early shift in feeding of carnivorous invertebrates and fishes (Nesis and Nigmatullin, 1979). It is notable that the food spectrum of all size groups of *O. antillarum* lacks such an abundant group of oceanic macroplankton as euphausiids. It is due to that fact that euphausiids-phytophagues concentrate above the thermocline where they actively feed (Vinogradov, 1977). However, the main feeding habitat of *O. antillarum* at night is situated both in the layer of the thermocline and below it, where squids feed on relatively inactive prey (except squids). *O. antillarum* can be characterized as an active browsing predator feeding on all available relatively small prey (Nesis and Nigmatullin, 1979). Probably, this type of feeding corresponds to a lack of well-defined ontogenetic differences in the food spectrum. Similar patterns of ontogenetic differences in the food spectrum has been revealed in

*Thysanoteuthis rhombus* which possess approximately the same type of feeding (Nigmatullin and Arkhipkin, in press). On the other hand, the food spectrum of *O. antillarum* differs from that of *S. pteropus* which feed mainly on crustacea (main food item is euphausiids) and planktophagous fish larvae and fry and can be characterized therefore as an active attacking predator (Zuev *et al.*, 1985).

Similar to oceanic squids of the families Ommastrephidae (Nigmatullin, Laptikhovskiy, 1994), Thysanoteuthidae (Nigmatullin and Arkhipkin, in press) and Enoploteuthidae (Laptikhovskiy, 1996), mature and spawning males and females of *O. antillarum* continue feeding. Contrary to this, nearshore ommastrephids (Nigmatullin and Laptikhovskiy, 1994) and oceanic *Onychoteuthis banksi* (Arkhipkin and Nigmatullin, 1997) cease feeding during the spawning period.

### Parasites

Intensity of infection of *Ornithoteuthis antillarum* is from 10 to 50 times less than in the same-sized *S. pteropus* from the same region (Gaevskaia and Nigmatullin, 1981). These considerable differences in intensity of infection between the two species probably correspond to differences in their food spectra. *S. pteropus* juveniles (<100 mm ML) feed mainly on crustaceans (FO=90-100% with prevalence of copepods, euphausiids and amphipod-hyperiid) and chaetognaths (main metacercaria carriers to squids) (Zuev *et al.*, 1985). On the contrary, *O. antillarum* feed mainly on fish and squids, the role of crustaceans in its diet being much less than in *S. pteropus*. Moreover, amphipod *Phrosina* prevail among crustacean food items, the role of which in trematod transport is still unknown. Another reason of such a low intensity of infection of *O. antillarum* by didymozoids might be rather low feeding activity of this squid. In both ommastrephids, degrees of stomach fullness (DSF) are similar. However, *O. antillarum* inhabit water layers with lower temperatures that may result in lower metabolism and rates of food digestion than in the same-sized *S. pteropus* juveniles.

### Scheme of the life cycle

Paralarvae (1-10 mm ML, age up to 32 d) are twice less abundant in the tropical Atlantic than those of another ommastrephid *S. pteropus*. They occur mainly in the thermocline water layer and do

not make vertical migrations (Arkhipkin *et al.*, 1988). The postnuclear zone of the statolith corresponds to this ontogenetic stage. Paralarvae grow fast (5-6% ML d<sup>-1</sup>) and probably feed on small zooplankton.

Juveniles and immature squids (10-70 mm ML, age 32-82 d) start their vertical migrations from the thermocline water layer at night to lower epipelagic waters (100-150 m depth) during the daytime (Arkhipkin and Schetinnikov, 1989). The dark zone forms in the statolith. Absolute daily growth rates are maximum in the ontogenesis, but relative daily growth rates constantly decrease (from 5 to 1% ML d<sup>-1</sup>). Juveniles feed mainly on amphipods *Phrosina* sp., squids, fish larvae and fish fry. Squids quickly infect with didymozoid metacercaria.

Maturing and mature adults (60-140 mm ML, age 82-182 d) make well-defined vertical migrations from the thermocline waters at night to upper mesopelagic waters (300-400 m) in the daytime (Nesis and Nigmatullin, 1979). The peripheral zone forms within the statolith. Both absolute and relative daily growth in length decrease up to minimum levels in the ontogenesis by the end of the stage. Squids feed mainly on fishes (carnivorous fish fry) and are totally infected with didymozoids. Owing to frequent occurrence of mature squids of both sexes and mated females, mating and spawning of *O. antillarum* probably takes place in epipelagic waters.

Main ecological features of the *O. antillarum* life cycle (i.e. main habitat of all ontogenetic stages in waters of the thermocline and below it; fast growth rates; short 6-month life span; medium values of fecundity; and early transfer to squid and fish diet) enable the species to diverge the spatial, temporal and trophic aspects of its ecological niche from another abundant ommastrephid (*S. pteropus*) and successfully co-exist with it in the open waters of the tropical Atlantic.

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