Aspects of female reproductive biology of the orange-back squid, *Sthenoteuthis pteropus* (Steenstup) (Oegopsina: Ommastrephidae) in the eastern tropical Atlantic*

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SUMMARY: Orange-back squid females, *Sthenoteuthis pteropus,* were found to mature at two different sizes: 230-270 mm and 380-450 mm mantle length (ML). The systematic status of these groups remains unknown. The ML of mature females varied from 155 to 558 mm (body weight 150-5900 g, respectively). Protoplasmic oocytes of 0.1 mm predominated in the ovaries during the entire life cycle providing a resource for further yolk accumulation. The number of yolk oocytes present at any one time represented only a small part of the Potential Fecundity (PF). Ripe eggs were 0.73-0.87 mm, and egg weight was 0.19-0.26 mg. The PF was 0.6 million to 15.8 million in mature animals and 1.2 million to 17.9 million in immature and maturing females, respectively. In mature females, the total number of yolk oocytes was 20 000 to 1.9 million, including 10 000 to 1 million ripe eggs. Spawning was intermittent. Large females presumably released at least 30-50% of the total oocyte stock. Results indicate that *S. pteropus* is a typical representative of the epipelagic oceanic cephalopod reproductive strategy characterised by small eggs, high fecundity, long intermittent spawning, active feeding, and somatic growth during spawning.

Keywords: *Sthenoteuthis*, squid, fecundity, spawning, egg.

RESUMEN: ASPECTOS DE LA BIOLOGÍA REPRODUCTORA DE LA HEMBRA DE LA POTA NARANJA, *STHENOTEUTHIS PTEROPUS* (STEENSTUP) (OEGOPSINA: OMMASTREPHIDAE) EN EL ATLÁNTICO TROPICAL ORIENTAL. – Se encontraron hembras maduras de la pota naranja, *Sthenoteuthis pteropus* a dos tallas diferentes: 230-270 mm y 380-450 mm de longitud del manto (ML). El status sistemático de estos grupos no se conoce. El ML de hembras maduras varió entre 155 y 558 mm (peso del cuerpo 150-5900 g respectivamente). Los oocitos protoplasmáticos de 0.1 mm predominan en los ovarios durante todo el ciclo de vida suministrando un recurso para la posterior acumulación de vitelo. El número de oocitos presentes al mismo tiempo representaron solo una pequeña parte del potencial de fecundidad (PF). Los huevos maduros midieron 0.73-0.87 mm, y pesaron 0.19-0.26 mg. El PF fue de 0.6 millones a 15.8 millones en animales maduros y 1.2 millones en hembras inmaduras y 17.9 millones en hembras madurando. En hembras maduras, el número total de oocitos es de 20,000 a 1.9 millones, incluyendo de 10,000 a 1 millón de huevos maduros. La puesta fue intermitente. Las hembras grandes presumiblemente liberan por lo menos el 30-50% del total de stock de oocitos. Los resultados indican que *S. pteropus* es un tipito representante la estrategia reproductiva de los cefalópodos epipelágicos oceánicos caracterizada por huevos pequeños, alta fecundidad, puesta larga e intermitente, sin interrupción de la alimentación y crecimiento somático durante la puesta.

Palabras clave: *Sthenoteuthis,* pota, fecundidad, puesta, huevo.

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INTRODUCTION

The orange-back squid *Sthenoteuthis pteropus* (Steenstrup) belongs to the nectonic squid family Ommastrephidae. This species is widely distributed in the tropical and subtropical Atlantic and inhabits epi- (night) and meso- (day) pelagic waters of the high seas, mostly between 20ºN and 20ºS. The oceanographic situation in the region is determined by an interaction between branches of the westward running southern and northern equatorial surface currents and branches of the eastward moving, mostly subsurface, southern and northern equatorial counter currents. This interaction results in the presence of numerous zones of upwelling and sinking as well as in highly dynamic and variable meso-scale eddies that foster water productivity (Khanaychenko, 1974).

The mantle length (ML) of mature females varies from 160 to 650 mm (Zuev *et al.*, 1985). Females become mature at 8-10.5 months, and larger animals mature later (Arkhipkin and Mikheev, 1992). The life cycle of this species is annual, growth rates are very high and the P/B coefficient, which is the ratio between annual population production and population biomass, can be as high as 8-8.5 (Arkhipkin and Mikheev, 1992; Laptikhovsky, 1995). The orange-back squid is characterised by a monocyclic maturation of the reproductive system and intermittent spawning that occurs all year round in epipelagic layers of equatorial waters, mostly at the periphery of meso-scale cyclonic eddies (Burukovsky *et al.*, 1977; Laptikhovsky and Murzov, 1990; Nigmatullin and Laptikhovsky, 1994; Golub *et al.*, 2001). The spawning peak is from late summer to mid-autumn in both hemispheres, with no prominent peak around the equator (Zuev *et al.*, 1985; Zuev *et al.*, 2002). In the 1980s and 1990s, this squid was the focus of the Soviet investigations aimed at developing oceanic cephalopod fisheries on the high seas of the tropical Atlantic and abundant samples were collected (Zuev *et al.*, 2002). Unfortunately most of the findings of this research were never published or were published in "grey literature". Indeed, aside from information on the total number of pre-ovulated yolk oocytes in the ovaries combined with the number of ovulated ripe eggs in the oviducts in mature females, assumed to be "the fecundity" (Zuev *et al.*, 1985), there is no published information on fecundity. This assumption about fecundity was wrong because it did not take into account an intermittent pattern of *Sthenoteuthis* spawning (Harman *et al.*, 1989).

The aim of this investigation is to describe female size at maturation, growth of the reproductive system by weight and egg size and fecundity based on the data obtained by Russian researchers during the last 30 years.

MATERIALS AND METHODS

A total of 24 209 females were collected by different Russian research vessels from 1970 to 1990 (including 574 mature animals) using hand lines and different nets. In all individuals collected, the ML was measured to the nearest 1 mm, the body weight (BW) measured within 1 g, and maturity stage was assigned following the ommastrephid scale (Table 1) developed by Burukovsky *et al.* (1977), and modified by Nigmatullin (1989).

In intermittent spawners like *Sthenoteuthis* spp (Harman *et al.*, 1989; Nigmatullin and Laptikhovsky, 1994), substages V-2 and V-3 do not always occur in sequence. Stage V-3 (when a female is ready to spawn) differs from stage V-2 only by the presence of the maximum fullness in the oviducts. After an egg release the fullness of the oviducts decreases, and the female returns to substage V-2, when she accumulates enough oocytes she enters spawning substage V-3 again.

In 237 females at different maturity stages, the ovary weight, nidamental and oviductal gland

TABLE 1. – A simplified version of the maturity scale of Nigmatullin (1989) used in this study.

Stage	Substage	Most important diagnostic features
I		sex is hardly distinguishable
II		immature animals, sex is obvious
III		early maturation, no yolk oocytes in the ovary
IV		advanced maturation, some yolk oocytes in the ovary, no ripe eggs in oviduct
V	V-1	almost mature, few ripe eggs in oviducts
	V-2	mature, oviducts are full of ripe eggs
	V-3	mature, oviducts with maximum possible fullness
VI		end of spawning, exhaustion process of reproductive system is visible
VII		Senescent spent condition (never found in nature in *S. pteropus*).

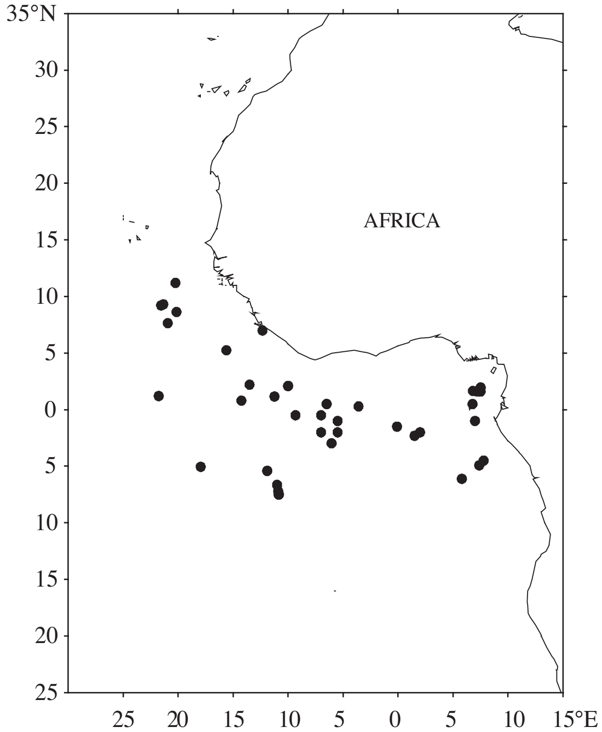

FIG. 1. – Location of stations where fecundity samples were collected.

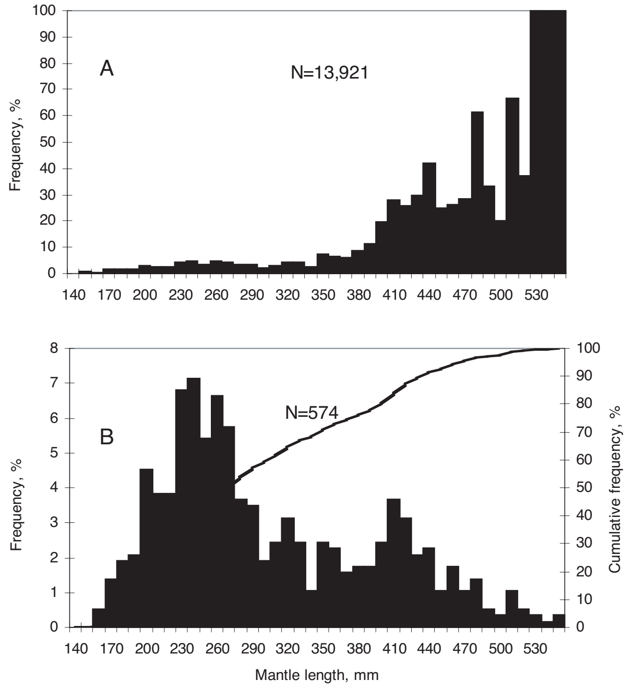

FIG. 2. – Female squid maturation: A, percentage of mature females in the different size groups; B, mature female length frequency (bars, raw data; line, cumulative data).

weight, and stomach weight were measured within 0.1 g. Then the reproductive systems were stored in 6-8% formaldehyde. Fecundity was estimated onshore from 88 females of 141-540 mm ML (120-5200 g body weight (BW), respectively) at different maturity stages collected from January to April in 1986 and 1987, and between September and November 1990 onboard the RV “Saulkrasty” (Fig. 1). As most of the oocytes in the oviducts were misshapen, to make selecting the longest or shortest diameter easier, the micrometer was placed in a horizontal position on the eye-piece, and the diameter parallel to the graduation on the micrometer measured in 50 ripe eggs. To estimate oocyte number and length-frequency in the ovary, three 15-20 mg samples (in immature animals, 3-7 mg) were taken from the ovary surface, the ovary core and an intermediate layer, they were weighed (to 0.1 mg) using electronic balances. All oocytes in these samples were counted under magnification of 40 X because oocytes smaller than 0.05 mm in diameter were absent in all maturing and mature animals. In ovaries of females at stage II, the rare smallest oocytes were 0.03-0.05 mm. These samples were counted in the same way under higher magnification (70 X). Measurements were taken in the same manner as in oviductal eggs. The total number of oocytes in the reproductive system of pre-spawning females was considered to represent the total oocyte production during ontogeny. Potential fecundity (PF) was calculated as the sum of the total oocyte number in the gonad and ripe egg number in the oviducts. Relative fecundity (RF) was estimated as the ratio of PF to BW. An index of potential reproductive investment (PRI) was calculated as the product of RF and the weight of an individual ripe egg (Laptikhovsky and Nigmatullin, 1993; Nigmatullin and Laptikhovsky, 1994).

The degree of stomach fullness was assigned following the 5-degree scale designed by Zuev *et al.* (1985). Statistical analysis was carried out using Graph Pad Prism, Version 3.00.

RESULTS

Female size at maturation

The first ripe eggs were found in the oviducts of females as small as 140 mm ML, whereas the largest maturing female that did not have any ovulated eggs was 450 mm ML. The ML of fully mature females (substage V-2 and V-3) varied from 155 to 558 mm (body weight 150-5900 g). Length frequencies of these adults, as well as the percentage of mature squid among the total sample, suggested the presence of two waves of maturation (Fig. 2 A, B). Most females

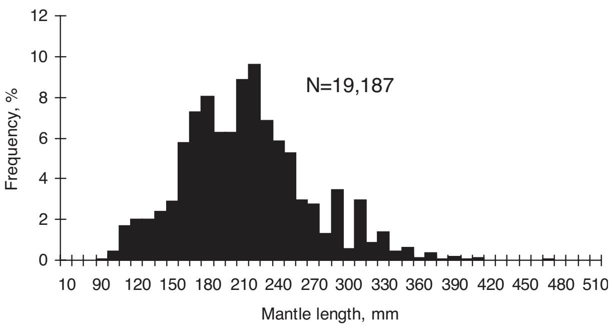

FIG. 3. – Immature female length frequency

were mature at 230-270 mm ML, whereas some matured at 380-450 mm ML. Length frequencies of immature squid also demonstrate bimodal distribution with peaks at 170-180 and 210-220 mm (Fig. 3).

Maturation of the reproductive system

Changes in the weight of the components of the reproductive system at maturation and spawning are shown in Table 2. During early maturation (stage III-IV), the growth in weight of the reproductive system was mostly due to an increase in both ovary and nidamental gland volume. A further increase in weight in mature females was due to the ripe eggs accumulating in the oviducts and the simultaneous accumulation of secretions in both nidamental and oviductal glands. An increase of the relative ovary weight (% BW) also occurred during maturity due to an almost three-fold increase in the percentage of yolk oocytes (Table 3) from stage IV to maturity. The mature reproductive system can attain up to 20% BW.

Oocyte size distribution was unimodal at all stages of maturation (except V-3) with oocytes of 0.1 mm predominating. Oocytes of 0.2-0.3 mm were also abundant in mature squid at substages V-2 and V-3 (Fig. 4). No oocytes smaller than 0.05 mm were

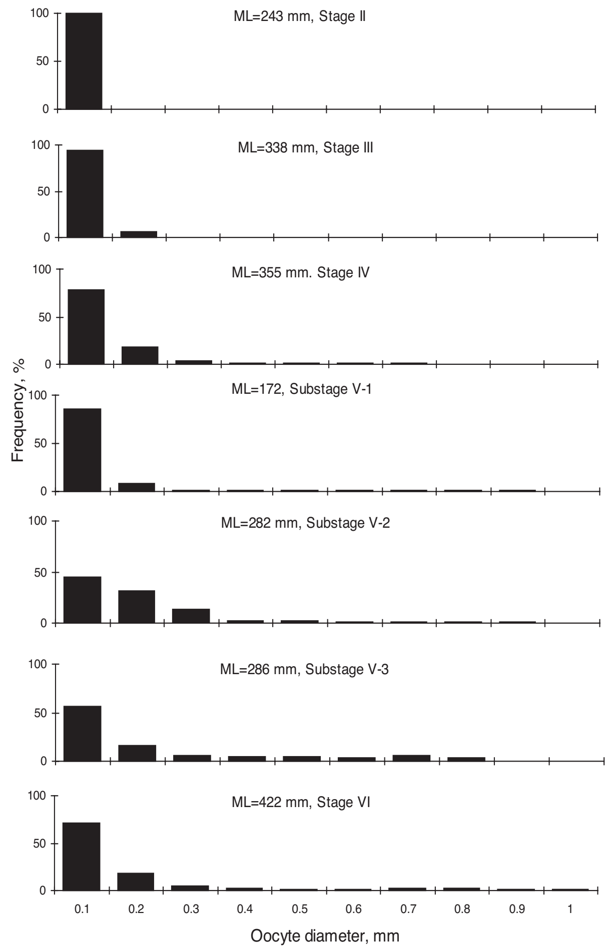

FIG. 4. – Changes in oocyte size distribution in individual maturation

found in maturing and mature animals, and no oogonia were observed at any maturity stage including juveniles. Oocyte atresion was not found. In ovaries of immature females (stage II, ML> 150 mm), the smallest oocytes were 0.03-0.05 mm. This suggests that the total number of oocytes in the reproductive system of immature, maturing and prespawning mature females represents the total oocyte production during ontogeny.

TABLE 2. – Weight of the reproductive system at different maturity stages expressed as percent of the BW (OV, ovary; OVD, oviducts; OVG, oviductal glands; NG, nidamental glands; RS, total reproductive system) and index of nidamental gland length (NGL) in % of ML; Mean values in brackets.

Stage	I	II	III	IV	V-1	V-2	V-3	VI
Numbers	16	53	26	12	19	98	11	2
ML, mm	125-172	207-266	333-420	141-452	169-399	170-540	250-513	422-513
BW, g	57-172	285-710	1292-2610	118-3600	195-2305	170-5203	490-3808	2735-5360
OV, %	0.6-1.1 (0.8)	0.3-1.2 (0.9)	0.1-4.4 (1.3)	0.2-2.6 (1.4)	2.1-4.5 (3.3)	1.1-8.4 (4.3)	0.6-7.4 (3.5)	2.5-3.7
OVD, %			<0.1 (0.07)	0.1-0.2 (0.1)	0.2-0.4 (0.3)	1.0-8.6 (3.9)	1.8-8.3 (5.0)	0.4-0.6
OVG, %					0.1-0.3 (0.2)	0.1-1.1 (0.3)	0.1-2.9 (0.4)	0.2
NG, %			0.1-1.0 (0.5)	0.8-1.0 (0.9)	0.4-3.3 (1.7)	0.1-8.8 (3.0)	1.8-9.7 (4.4)	2.1-3.2
RS, %			0.2-6.6 (1.6)	3.4-3.7 (3.6)	3.8-6.9 (5.3)	2.7-14 (8.7)	6.3-18 (12.9)	5.2-6.3

* - data from one female only

TABLE 3. – Yolk oocyte percentage (relative to the total oocyte stock in the ovary) at different maturity stages (YO, %), the mean value in brackets, standard deviation (italicised) and values of *t*-criteria. Values of *t*-criteria higher than or corresponding to p=0.05 (differences are significant) are in bold.

	Stage III	Stage IV	Stage V-1	Substages V-2 and V-3
YO. min-max. (Mean),	0-0.8 (0.13)	0.7-6.1 (2.9)	1.2-4.0 (2.8)	0.9-16.9 (7.04)
S.D.	*0.23*	*2.24*	*1.21*	*3.84*
Stage III		**4.367**	**8.380**	**6.675**
Stage IV			0.247	**3.092**
Substage V-1				**2.795**
Substages V-2 and V-3				

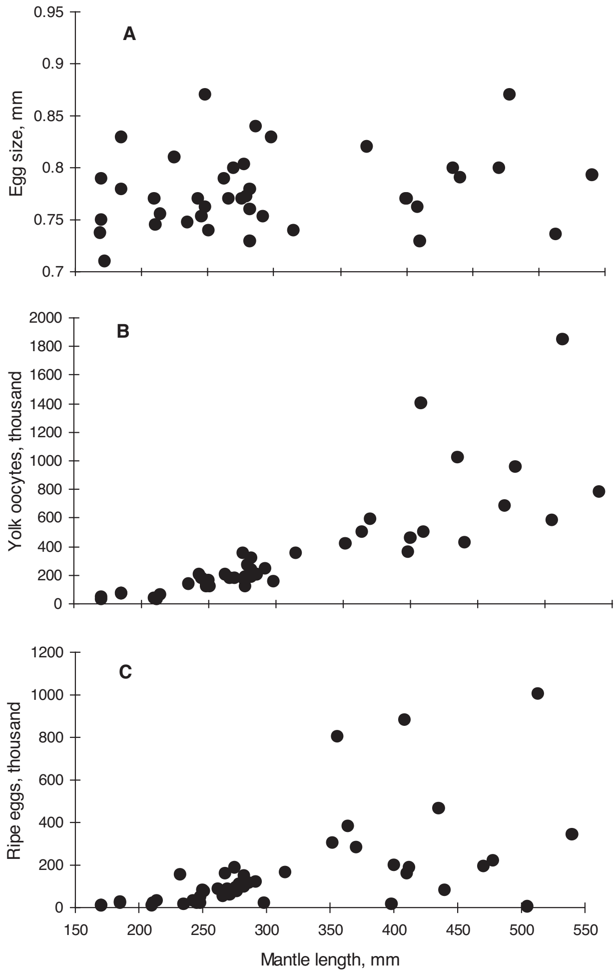

FIG. 5. – Ripe egg size (A), total number of yolk oocytes in the reproductive system (B) and ripe egg number in oviducts (C) in mature females at stages V-2 and V-3 combined.

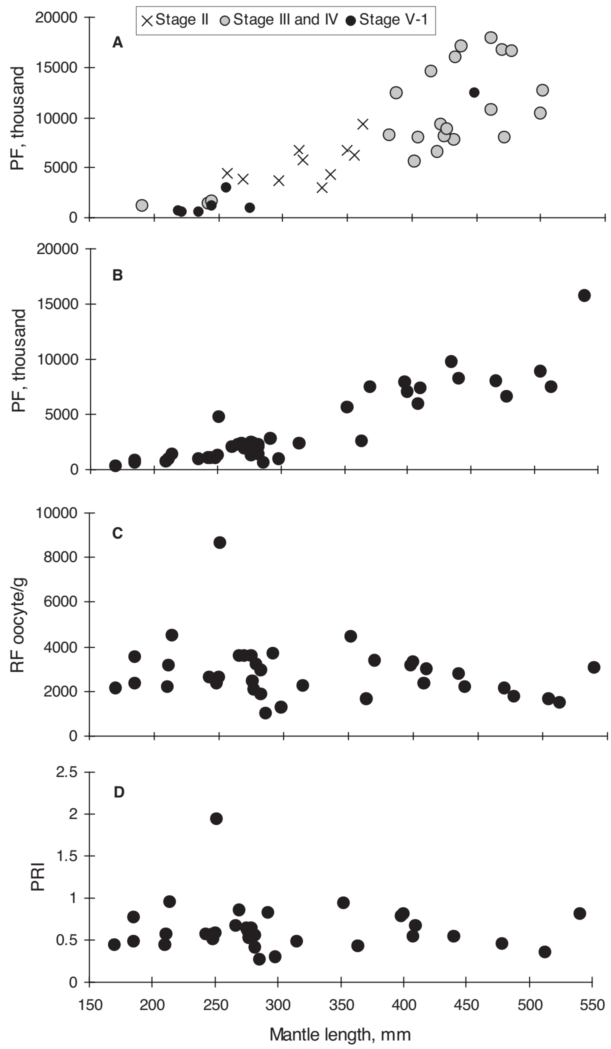

FIG. 6. – Potential fecundity in premature (A) and mature females (B), relative fecundity (C) and Index of Potential Reproductive Investment (D).

Fecundity

The size of ripe eggs (ES) was 0.73-0.87 mm, and egg weight (EW) was 0.19-0.26 mg. Egg size was similar among females, regardless of ML (Fig. 5A). However, larger females had heavier eggs. Spearman's correlation between ML and ES was r=0.24 (P=0.13), and between ML and EW it was r=0.58 (P<0.0001). There was no significant correlation between egg size and egg weight (r=-0.12, P=0.394).

Female *S. pteropus* accumulated from 10 000 to 1 million ripe eggs in their oviducts, depending on ML (Fig. 5C). When the numbers of ripe eggs in the oviducts and yolk oocytes in ovaries were com-

TABLE 4. – Variation of the potential fecundity (PF, millions) between maturing and mature orange-back squid.

Maturity	Minimum PF	Maximum PF	Mean PF	Standard error
Maturing (ML 355-452 mm, mean 398 mm, N=17)	6.555	17.910	11.890	0.948
Mature (ML 400-540 mm, mean 456 mm, N=11)	5.800	15.810	8.292	0.829

bined, the total number of yolk oocytes in the reproductive system doubled to approximately 20 000 –1.9 million (Fig. 6B).

PF was much higher than both these values. It varied from 1.2 to 17.9 million in immature and maturing females and from 0.56 to 15.8 million in mature animals (Fig. 6A, B respectively). Oocyte resorption was not found in any maturity stage, suggesting that the decrease in oocyte numbers in adult animals was caused by egg release at spawning.

PF was higher in larger females. Its relation to ML and BW may be described by the following equations:

$$PF = 0.0002\ ML^{2.8499},\ r=0.82$$
$$PF = 4.248\ BW^{0.9585},\ r=0.80$$

Relative fecundity (RF) and the index of potential reproductive investment (PRI) were similar among mature animals of different sizes (Fig. 6C, D) and did not correlate with the ML (Spearman r=-0.23 and r=-0.07, P=0.171 and P=0.710 respectively).

As no spent animals have ever been collected in the genus *Sthenoteuthis*, even in the spawning grounds that extend over most of the tropical Atlantic (Zuev *et al.*, 1985), we tried to estimate the actual fecundity using data on maturing and spawning females. Our data shows that in a random sample of large maturing squid, the mean PF of maturing females was 30% higher than that of mature animals (Mann-Whitney U-test, P=0.0074) (Table 4). In addition, two large females at stage VI of the late-maturing group (ML of 422 mm and 505 mm) had very low PFs of 5.8 and 8.9 million (Fig. 6B). This difference could be explained by a gradual egg release by mature females at spawning. However, these two females were not fully spent, as they still had a further 0.5 million (ML 422 mm) and 2 million (ML 505 mm) yolk oocytes, respectively. With this residual fund taken into account, the actual fecundity of the large females may be as high as 4.0-5.5 million, which is approximately 35-50% of the PF.

The number of ripe eggs in the oviducts increased with size, with the largest mature females having up to 1 million eggs, which is 4-6 times less than the actual fecundity. This suggests an intermittent spawning pattern.

Feeding intensity at maturity

The mean degree of stomach fullness for immature, maturing and mature squid ranged between 2.2 and 2.6 (Fig. 7) with a statistically significant decrease with increasing maturity (Kruskal-Wallis ANOVA test, P<0.0001). Females with full stomachs were found in high numbers at each maturity stage, indicating that squid continue feeding during the spawning period. A relatively minor decrease in feeding intensity happens only at stage V-3, shortly before egg release.

DISCUSSION

The hypothesis that there are two different size groups of mature *S. pteropus* females was first formulated earlier based on the small sample size available (Zuev *et al.*, 1985). They suggested that while most females have a one-year life cycle, some could live for two years and mature during their second year of life. However, it has since been determined that all female orange-back squid have a one year life cycle (Arkhipkin and Mikheev, 1992). Thus, the existence of the two size groups of mature females remains unexplained (Zuev *et al.*, 2002). Our data show that these groups exist and their existence is probably the result of either a cryptic speciation, or

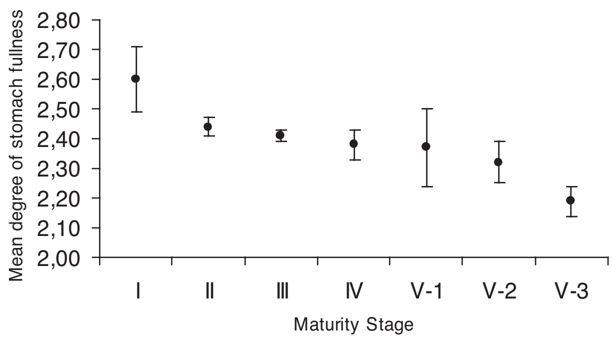

FIG. 7. – Mean degree of stomach fullness at different maturity stages (with 0.05 Confidence level error bars).

alternative life cycle strategies in different populations. The first hypothesis is more likely because small early-maturing squid are only distributed in equatorial Atlantic, where their range overlaps completely with that of the large, late-maturing squid, which occur over the entire species range (Zuev *et al*., 2002).

The growth of the reproductive system of orange-back squid is similar to that in other cephalopods. The relative weight of the entire reproductive system of mature females typically varies between 10-20 % but can be as high as 30 % in more advanced squid (Burukovsky *et al*., 1977). This is similar to that in the shelf squid family Loliginidae, in which species accumulate numbers of large eggs in the oviduct before spawning (Fields, 1965; Robaina and Voglar, 1986; Rodhouse *et al*., 1988; Laptikhovsky *et al*., 2002).

A predominance of small protoplasmic oocytes, combined with unimodal oocyte size distribution, is particular to all ommastrephids and serves as a basis for intermittent spawning (Harman *et al*., 1989; Laptikhovsky and Nigmatullin, 1993; Nigmatullin and Laptikhovsky, 1994; Snyder, 1998). However, the proportion of yolk oocytes in orange-back squid ovaries is much lower than in the squid subfamilies Illicinae and Todarodinae (Laptikhovsky and Nigmatullin, 1993; Nigmatullin and Laptikhovsky, 1999).

Apart from *Dosidicus gigas* and *S.oualaniensis* (Nigmatullin *et al*., 1999; Zuev *et al*., 2002), the PF in *S. pteropus* is one of the highest amongst all squid species. Actual fecundity is about half as much, but it is still very high and exceeds the total number of yolk oocytes simultaneously present in the female ovary and oviducts combined. Given this enormous fecundity, it is not surprising to find that the egg size in the orange-back squid is among the smallest known for oceanic cephalopods. The PRI of this species is also much higher than in Illicinae and Todarodinae and is similar to that of *D. gigas* (Laptikhovsky and Nigmatullin, 1993; Nigmatullin *et al*., 1999; Nigmatullin and Laptikhovsky, 1999). The correlation between the egg weight and female size indicates that the species has an extreme r-strategy with the smallest possible egg size. The lack of correlation between the egg size and both female size and egg weight could be explained by the different degree of egg shrinking at preservation making small differences in egg size unrecognisable. However, large females still had heavier eggs.

Using, even partially, this huge number of eggs could only be achieved by an extended intermittent spawning, which has been suggested earlier for *S. oualaniensis* (Harman *et al*., 1989; Snyder, 1998), and for other ommastrephid squid (Laptikhovsky and Nigmatullin, 1993; Nigmatullin and Laptikhovsky, 1994, 1999; Rocha *et al*., 2001). As females become mature at an age of 8-10.5 months and the life span of this species is about one year (Arkhipkin and Mikheev, 1992), spawning in the orange-back squid could last for up to 3-4 months. During these months, the female may release several cohorts of ripe eggs, which have accumulated in the oviducts. A large female can have up to one million ripe eggs in her oviducts, but these would not necessarily be laid in one night as a single egg mass. More likely, the egg stock in the oviducts could be released by a series of small egg masses, such as the one found by Laptikhovsky and Murzov (1990), which contained about nineteen thousand eggs (Laptikhovsky and Murzov, 1990). Such a long reproductive period is possible because of continuous feeding, which only decreases slightly with maturation, but not to the same extent as in the ommastrephid squid genus *Illex*, which stops feeding almost completely during the relatively short spawning period (Laptikhovsky and Nigmatullin, 1993).

Sthenoteuthis spp. is among the most oceanic squid species in the Ommastrephidae, which is "oceanic" itself when compared with the low-fecundity Loliginidae and Sepiolidae that inhabit shelf waters. The main direction of the evolution of this family was from initial slope-shelf habitats to high sea habitats (Nigmatullin, 1979). It is hypothesised that the penetration of *Sthenoteuthis* spp. into offshore pelagic waters of open ocean provoked a drastic increase in mortality because of the dispersal of the early staged squid by the complicated system of superficial currents and counter-currents found in equatorial waters. A strategy of intermittent spawning over a relatively long reproductive period would ensure a higher probability that some egg masses would hatch when conditions were favourable for offspring survival. The necessary increase in fecundity co-evolved with the production of eggs of the smallest size known for cephalopods (Nigmatullin and Laptikhovsky, 1994). This hypothesis is supported by the fact that other cephalopod families reproducing in the oceanic epi-pelagial also have very high fecundity with intermittent spawning of small eggs (Nigmatullin and Arkhipkin, 1998; Laptikhovsky, 1999; Laptikhovsky and Salman, 2003).

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