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Fecundity of the common cuttlefish, *Sepia officinalis* L. (Cephalopoda, Sepiidae): a new look at an old problem*

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SUMMARY: The potential fecundity (PF) of advanced maturing and mature pre-spawning cuttlefish *S. officinalis* in the Aegean Sea varies from 3,700 to 8,000 (mean 5,871) oocytes, whereas the number of large yolk oocytes increases with mantle length from 130 to 839. Small oocytes predominate at all maturity stages. Spawning animals have a PF of some 1,000-3,000 eggs below that of pre-spawning females. This shows that intermittent spawning, which occurs in captivity, is a normal process in natural habitats. Empty follicular sheaths are resorbed very rapidly, and their number does not represent the number of eggs laid by the female prior to sampling. Regulative oocyte resorption was observed at early maturation in some cuttlefishes.

Key words: fecundity, cuttlefish, *Sepia*, Cephalopoda.

RESUMEN: FECUNDIDAD DE LA SEPIA, *SEPIA OFFICINALIS* L. (CEPHALOPODA, SEPIIDAE): UNA NUEVA VISIÓN DE UN VIEJO PROBLEMA. – La fecundidad potencial (FP) de sepia *S. officinalis* en estado de maduración avanzada y pre puesta en el mar Egeo varia entre 3.700 y 8.000 (media 5.871) oocitos, mientras que el número de oocitos grandes aumenta con la longitud del manto entre 130 y 839. Los ovocitos pequeños predominan en todos los estadios de madurez. Los animales en puesta tienen una FP de 1.000-3.000 huevos menos que las hembras en pre puesta. Esto demuestra que una puesta intermitente, como ocurre en cautividad, es un proceso normal en el habitat natural. Las fundas foliculares vacías son absorbidas muy rápidamente y su número no representa el número de huevos puestos por una hembra antes de su captura. En algunas sepias se observó la reabsorción de oocitos en primeros estadios de la maduración.

Palabras clave: fecundidad, *Sepia*, Cephalopoda.

INTRODUCTION

The common cuttlefish, *Sepia officinalis* L. is distributed in the eastern Atlantic from the North Sea to northwestern Africa (Khromov *et al.*, 1998). Maximum mantle length (ML) is 300 mm for males and 250 mm for females (Mangold-Wirz, 1963; Nesis, 1987). This species was one of the first cephalopods in which reproduction was investigated (Aristotle, 1996), and it remains one of the best known to date.

Egg size of this species varies from 6 x 5 to 9 x 7 mm, and larger females produce larger eggs (Mangold-Wirz, 1963; Boletzky, 1983). The mean total number of ripe and advanced maturing eggs in the ovary increases from 99 to 543 eggs in animals of

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80-190 mm ML (Najai, 1983; Ezzeddine-Najai, 1985). However, it has been shown that this species is (at least sometimes) an intermittent spawner, in which egg production may last as long as 1/3 of the life cycle (Boletzky, 1983, 1987, 1988, 1990). Total fecundity may exceed the ovarian coelom capacity by a factor of 5-10. In captivity, female cuttlefish could spawn as many as 3,000 eggs, with a mean of 2,000 (Hanley *et al.*, 1998), and even 3,000 (Forsythe *et al.*, 1994). However, some females spawn only once and then die, showing a high flexibility in their reproductive strategy (Boletzky, 1986). Fecundity depends on the length of the spawning period, which is highly variable, as well as on the duration of the life span, which varies from 8 months to 2 years (Boletzky, 1987; Le Goff and Daguzan, 1991; Forsythe *et al.*, 1994; Hanley *et al.*, 1998). It is generally admitted that “the fact that the physiology of the animal allows long-continued spawning does not prove that this capacity is always fully exploited under natural conditions; it only proves that the possibility of such protracted spawning really exists, and it suggests that this possibility becomes important under certain environmental conditions to counterbalance high mortality rates” (Boletzky, 1988).

Although the reproductive biology of the common cuttlefish appears to be well studied, the total oocyte stock (i.e. potential fecundity) is still unknown. It is not clear what part of this stock is going to be spent. Does the common cuttlefish release most of its eggs during intermittent spawning, or is actual fecundity only a small part of a huge oocyte stock, which remains mostly useless? Moreover, it is not known whether this potential fecundity is related to the animal size. A positive correlation between the number of large yolk oocytes and cuttlefish size is evident, because of the restricted coelom capacity that could not be overcome even by producing smaller eggs in smaller animals. But gonad differentiation in this species occurs at hatching (Montalenti and Vitagliano, 1946; Lemaire and Richard, 1970), and the first oocytes appear in the ovaries a few days later, while it is very difficult to find oogonia even in one-week old cuttlefish (Grasso and di Grande, 1971; Lemaire, 1972). It is almost certain that the formation of the total oocyte stock (potential fecundity) is completed by early juveniles, which can grow at very different rates and attain different sizes at maturity. If this is the case, one should expect an absence of correlation between potential fecundity and animal size. One could even suppose that “big-bang” spawners are large enough to release most of (or all) the oocyte stock simultaneously, whereas intermittent spawners are relatively small females with high potential fecundity, which is extremely large for their coelom capacity. Another question is whether the number of empty follicular sheaths provides any information about the number of oocytes that were ovulated before, as was shown before for large-egged cirromorph octopods (Boyle and Daly, 2000).

This paper aims to shed some light on these problems, the Mediterranean cuttlefish, *S. officinalis* being taken as an example.

MATERIALS AND METHODS

A total of 29 common cuttlefish female of 94-247 mm ML and 100-1,908 g body weight (BW) were examined. Nine of them were collected on 17 January - 2 February 2002 in the Aegean Sea, during the research cruise of R/V “K. Piri Reis” (bottom trawl with vertical opening of 1.6 m and horizontal opening of 10 m, codend mesh size 20 mm, towing speed 2.5 kn, depth range 20-70 m). Bottom depth was monitored by the Scanmar Net Sounder.

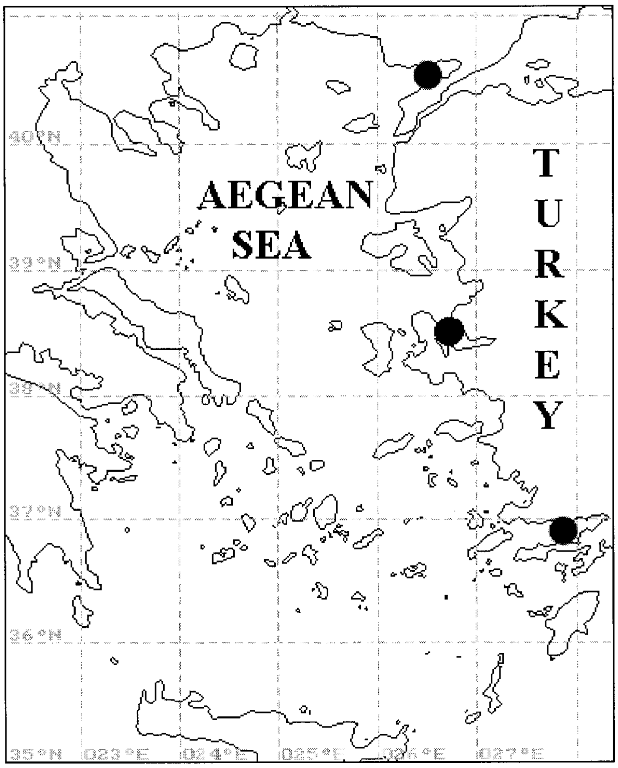

FIG. 1. – Map of the Aegean Sea showing the sampling locations.

Twenty randomly selected females were bought on 9 January and 15 February at Izmir fish market from fishermen, who had caught them in shallow waters of Izmir harbour (Fig. 1).

Cuttlefishes with maximum egg length of up to 2 mm were considered to be "immature" (Mangold-Wirz, 1963). Pre-copulatory (no spermatophores attached to the buccal membrane and no sperm in seminal receptacle) females with larger ovarian eggs but without any ovulated ripe eggs were considered to be "maturing". Pre-copulatory cuttlefishes with some ripe eggs free of the follicular envelope were assigned to be "mature, pre-spawning", whereas mated mature females were supposed to be "mature, spawning". After examination of the samples, two "mature spawning" females were re-assigned as "mature, pre-spawning", because the ripe egg number in their ovarian cavity was similar to the estimated number of relatively "fresh" empty follicles, and fecundity was unusually high for spawning specimens. All mature spawning females were caught in shallow waters by fishermen.

In all animals the ML was measured within 1 mm and the BW was estimated to the nearest 1 g. Reproductive organs were stored in 4% formaline for 3-10 days before examination. Then the ovary was weighed to the nearest 0.001 g.

In immature animals, a sample of approximately 20-30% of the ovary was taken for examination, all extracted oocytes being counted and measured.

In maturing and mature animals, all medium-sized and large oocytes (> 4 mm) were removed, counted and measured. Their mean weight varied from 27 to 62 mg (mean 46.1 mg), depending on the ovary maturity. Then the rest of the ovary was weighed again, and a sample of some 20-30% of its weight was taken. Empty follicles were also counted. Estimated length frequencies and numbers of small oocytes in the sample were combined with total measurements and counts of large oocytes.

The observed total oocyte stock was assumed to represent potential fecundity (PF). The difference between the estimated number of empty follicular sheaths and the actual number of ripe eggs present was considered to be the minimum number of eggs laid before the female was caught. The number of follicular sheaths together with the PF, minus the number of ovulated ripe eggs was assumed to be the maximum potential fecundity, MPF (Boyle and Daly, 2000).

Oocytes in samples were measured to the nearest 0.1 mm, but measurements were amalgamated into 0.5 mm classes. The egg length along the major axis was measured in 10 randomly sampled ovulated ripe eggs; the mean egg length was then calculated. Mean egg weight was assessed by dividing the weight of ovulated ripe eggs by their number.

RESULTS

Egg length frequencies in ovaries

The smallest oocyte size in immature females was 0.1 mm, whereas in maturing and mature females it was 0.2-0.3 mm. Small oocytes of about 0.5 mm were the most abundant at all the investigated stages of the reproductive cycle (Fig. 2). Their number decreased at maturation, attaining some 40-50% of the total oocyte stock in spawning females.

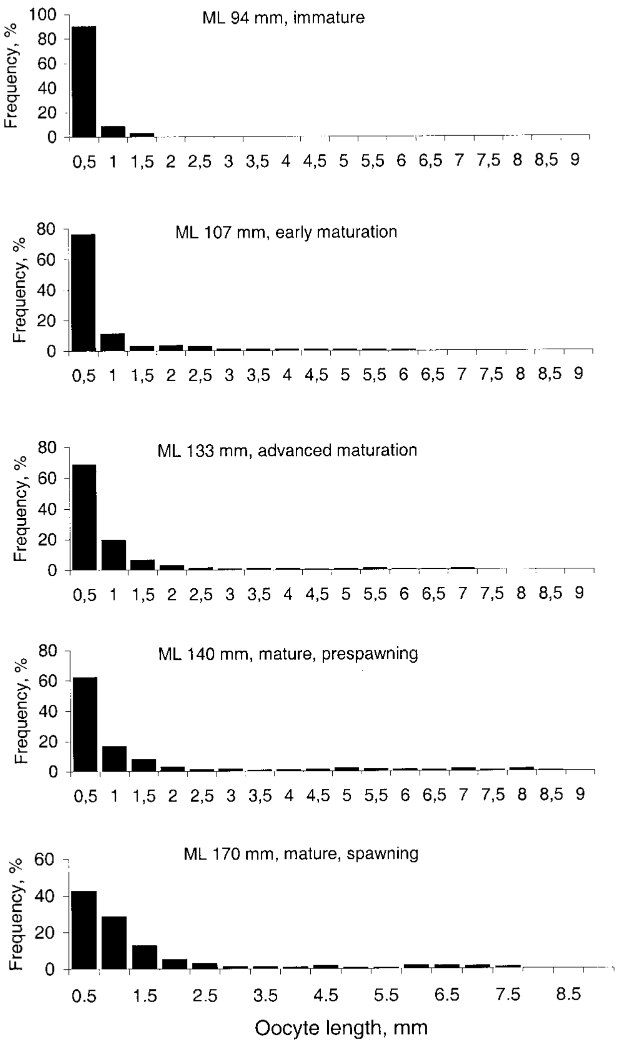

FIG. 2. – Oocyte size distribution in the common cuttlefish, *S. officinalis*

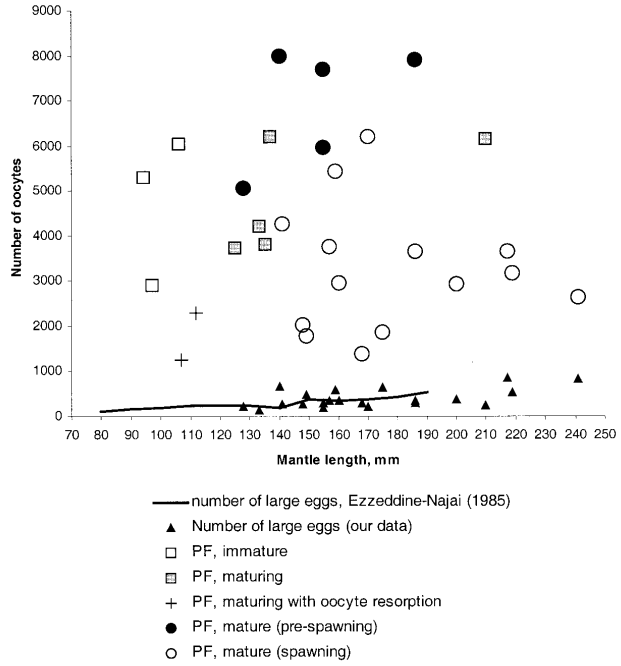

FIG. 3. – Fecundity of the common cuttlefish, *S. officinalis*.

In maturing and mature females some batches of developing eggs were seen. In animals of 140-170 mm ML such a batch contained some 200-300 eggs.

Ripe egg length varied from 6.45 to 7.53 mm, egg weight from 109.9 to 167.5 mg, larger eggs being generally heavier (r=0.58, *p*=0.06). Egg weight was positively correlated with female weight (r=0.64, *p*=0.03), whereas the correlation between egg length and mantle length was not significant (r=0.22, *p*=0.19), probably because of the variations in egg shape.

Oocyte resorption at maturation and maturity

Oocyte resorption was observed in two (of six) maturing females of 107 and 112 mm ML respectively, which were at the early maturation stage and had an unusually low PF (Fig. 3). Resorbing oocytes were at the early yolk stage and represented 4.8 and 3.5% of oocyte stock respectively. Because of the low fecundity, one could assume that more than 50% of the initial oocyte stock was resorbed in these animals.

In one mature pre-spawning female (ML 128 mm) one resorbing oocyte was found in some 30% of the rest of ovary, which remained after all the large oocytes had been taken away. No oocyte atresia was found in the other mature pre-spawning and spawning animals.

Fecundity

The number of large eggs (both mature and ovulated) in the ovary increased with BW from 130 to 839, larger females having more eggs (r=0.70, *p*=0.01). The potential fecundity of maturing and mature pre-spawning animals was much higher. It varied from 3,700 to 8,000 (mean 5,871). Heavier females had higher PF (r=0.67, *p*=0.05). The coefficient of correlation between the ML and PF was lower (r=0.50, *p*=0.08).

In mature spawning females the PF was 1,380-6,200 (mean 3,265), and the MPF varied from 2,040 to 6,400 (mean 3,785) (Fig. 4). There were no significant correlations between the PF of the spawning females and either BW (r=-0.18) or ML (r=-0.06). Differences in fecundity between pre-spawning and spawning animals could not be explained by differences in female sizes: in our sample mature spawning females were even larger (141-241, mean 179 mm ML; 442-1908, mean 844.5 g BW) than maturing and mature pre-spawning animals (125-210, mean 150 mm ML; 148-874, mean 448 g BW).

Empty follicular sheaths were found in ovaries of all cuttlefishes with ovulated ripe eggs in the ovarian cavity. In spawning females their numbers exceeded that of ripe eggs (Fig. 4), showing that some eggs had been laid before the female was caught. These follicles showed all stages of gradual resorption, before presumably total disappearance. The latter idea is corroborated by the fact that MPF in spawning animals is lower than PF of prespawning females.

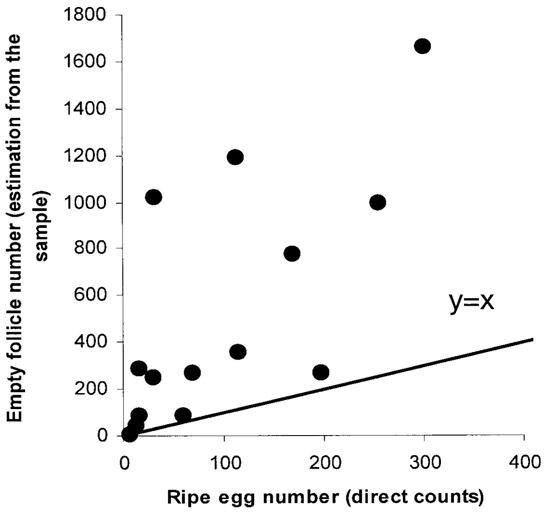

FIG. 4. – Relation between number of ripe eggs and empty follicles in spawning females. The line y=x assumes a situation in which the number of empty oocyte sheaths is equal to the number of ripe eggs.

DISCUSSION

Our estimations of the number of large eggs are consistent (Fig. 3) with the maximum number of ripe eggs observed in *S. officinalis* off Tunisia (Najai, 1983). However, it appears that in our small sample females were generally larger. A probable reason is that our sampling was carried out in the early part of the spawning season, when larger females arrive at the spawning grounds (Boletzky, 1983). On the other hand, despite a huge number (743) of females, which were sampled for fecundity off Tunis, there were no animals larger than 190 mm amongst them (Najai, 1983). Possibly, the animals of the Tunisian population were generally smaller than the cuttlefish in the Aegean Sea and in the western Mediterranean (Mangold-Wirz, 1963).

Ripe egg size in Aegean cuttlefish (6.5-7.5 mm, ML 128-241 mm) was smaller than in both the western Mediterranean (7-9 mm, female ML of 138-232 mm, Mangold-Wirz, 1963) and Tunisian waters (6-10 mm, female ML 80-190 mm, Ezzedine-Najai, 1985). This could be evidence of some shift of the reproductive strategy to the *r*-trend in the Aegean cuttlefishes.

The potential fecundity is much higher than the actual number of large eggs. In maturing and mature prespawning females of 130-210 mm ML, it exceeds the coelom capacity by a factor of 10-20. A comparison between the PF of prespawning females and that of the spawning animals allows one to assume that an "average" spawning female (mean BW 844.5 g) released about 1,000-3,000 eggs before being caught. This is in accordance with the mean fecundity of intermittent-spawning females observed in captivity: about 3,000 eggs in animals of 600-900 g BW (Forsythe *et al.*, 1994). This indicates that intermittent spawning occurs in natural populations of cuttlefish, as was recently assumed (Rocha *et al.*, 2001), and is not a phenomenon occurring mostly in captivity. It suggests that common cuttlefish females release a number of eggs equivalent to about 50% of PF during spawning in a natural habitat. However, because of the high flexibility of life cycles in this species, many individual variants are probably possible.

Higher fecundity in larger pre-spawning cuttlefish could be explained by limited resorption of oocytes at early maturation. In smaller cuttlefish this process is probably more intensive, relating to the restricted coelome capacity. Such "regulative resorption" (Nigmatullin, 2000) has been observed in large-egg squids and octopods (Boyle and Chevis, 1992; Nigmatullin *et al.*, 1996; Laptikhovsky, 1999; 2001). It is very likely that all juvenile cuttlefishes have very high potential fecundity which, depending on their growth through foraging, is "adjusted" to the actual female capacity by resorption of any excess of oocytes.

It is evident that in *S. officinalis* the number of empty follicular sheaths does not provide any information about the number of oocytes that were ovulated (and laid) earlier, although this count would probably be useful in cold water cephalopods with large eggs (Boyle and Daly, 2000). In the subtropical squid *Loligo vulgaris reynaudi*, empty follicles are resorbed in less than one day (Y.C. Melo, SFRI, Cape Town, pers. comm.). In cuttlefish, in which eggs are much larger, it probably takes longer. On the other hand, MPF in spawning females was much lower than PF of pre-spawning females, showing that this resorption occurs very fast. This is the main reason why in cuttlefishes the MPF could not be used to reconstruct the initial oocyte stock.

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