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Reproductive mode in the genus *Sepietta* (Cephalopoda: Sepiolidae)

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Abstract
Little is known about the reproductive mode of the sepiolid squids *Sepietta obscura* and *Sepietta neglecta*. An aquarium-kept female of *S. obscura* was observed to spawn five times within 13 days. After death its ovary consisted of oocytes at various stages of maturation, including mature oocytes. The coexistence of oocytes at various stages of maturation was also found in two wild collected females of *S. obscura* and *S. neglecta*. This finding proves that both species are multiple spawners as *Sepietta oweniana*. Although all three species of the genus *Sepietta* share this mode of spawning, there are considerable differences in other respects to reproduction, e.g. egg and adult sizes.

Riassunto
Le informazioni sulle modalità riproduttive dei sepiolidi *Sepietta obscura* e *Sepietta neglecta* sono scarse. Una femmina di *S. obscura* in acquario ha deposto uova cinque volte nel giro di 13 giorni. Alla fine del periodo di riproduzione e dopo la morte spontanea della femmina, nell'ovario erano presenti oociti a diverso stadio di maturazione, inclusi oociti maturi. La coesistenza di oociti a vario stadio di maturazione è stata riscontrata anche in altre due femmine di *S. obscura* e *S. neglecta*. Questi risultati provano che entrambe le specie si riproducono mediante deposizione multipla, come è stato già osservato per *Sepietta oweniana*. Sebbene tutte e tre le specie del genere *Sepietta* condividano una tale modalità riproduttiva, si riscontrano differenze notevoli in altri aspetti riproduttivi, quali la taglia delle uova e degli individui adulti.

Key words
Cephalopoda, Sepiolidae, *Sepietta*, reproductive strategy, fecundity, Mediterranean.

Introduction

Following the influential paper by Boletzky (1987) it has become clear that multiple spawning is a widespread reproductive mode in coleoid cephalopods (see review by Rocha et al., 2001). Multiple spawning may be defined as the co-occurrence of two processes: at least two bouts of egg-laying and the maturation of new oocytes between these bouts (Harman et al., 1989; Maxwell et al., 1998). This mode of reproduction appears to be typical of the Sepiolinae (Gabel-Deickert, 1995), a taxon composed of small size species. Incidentally, the reproductive advantage of multiple spawning is particularly evident in these squids as well as in other small-size cephalopods laying comparatively large eggs (Boletzky, 2002).

The genus *Sepietta*, a member of the Sepiolinae (Sepiolida: Sepiolidae), includes three species, namely *Sepietta oweniana* (d'Orbigny, 1841), *Sepietta neglecta* Naef, 1916 and *Sepietta obscura* Naef, 1916. All of them are distributed in the eastern Atlantic-Mediterranean region (Mangold & Boletzky, 1987). Sepiolinae are considered to have a nectobenthic mode of life (Naef, 1923; Mangold & Boletzky, 1987; Bello & Biagi, 1995).

Sepietta obscura is a littoral species and lives on sandy and muddy bottoms, including *Posidonia oceanica* grass beds. Its reported depth range is 27 to 376 m (Reid & Jereb, 2005), however captures deeper than 150 m are questionable (Bello, pers. comm.); **Tab. 1** reports some collecting data shallower that 27 m. The spawning season in the Mediterranean Sea extends at least from spring to autumn. Its eggs are comparatively large (diameter: 3.7-4.5 mm) (Reid & Jereb, 2005). Note that *Sepietta* sp. in Gabel-Deickert (1995) is indeed *S. obscura*.

Sepietta oweniana is the largest size species in the genus. It occurs within a wide depth range, from 8 to 1,000 m, on soft, muddy bottoms. In the Mediterranean it is most common from 100 to 400 m of depth. In this sea females spawn year around (Reid & Jereb, 2005). This sepioline is a multiple spawner; the mature oocyte size ranges from 2.1 to 2.5 mm (Bello & Deickert, 2003).

The depth range of *S. neglecta* habitat – muddy substrates – is 25 to 475 m. It spawns throughout the year (Reid & Jereb, 2005). The mature oocyte size ranges from 1.4 to 2.8 mm (Lefkatidou & Kaspiris, 1998).

See also **Tab. 1** for a detailed list of papers reporting collecting depth data for the *Sepietta* species.

The abundance of *S. obscura* and *S. neglecta* is low compared to that of *S. oweniana* (e.g. Orsi Relini & Bertuletti, 1989).

Within the genus *Sepietta* it has been shown that *S. oweniana* reproduces by multiple spawning (Bello & Deickert, 2003). Little is known about the reproductive strategy of the other sepioline species, viz. *S. obscura* and *S. neglecta*. The only sources of information are the paper by Boletzky et al. (1971) and the doctoral thesis by Gabel-Deickert (1996).

The aim of this paper is to investigate and compare the

Region	*Sepietta obscura*	*Sepietta oweniana*	*Sepietta neglecta*
	Depth distribution of specimens (m)		
Catalan Sea	2 – 10[a]; 5 – 20[h]	10 – 120[b]; 80 – 700[h]	90 – 120[a]
Northwestern Mediterranean	–	149 – 499[o]	206[o]
Ligurian Sea	0 – 100[j]	50 – 900[j]	30 – 363[j]
Gulf of Naples	3 – 12[i]	80 – 400[i]	–
Northern Tuscany Coast	0 – 50[p]	84 – 584[p]	24[p]
Northern Tyrrhenian Sea	30 – 140[m]	20 – 540[m]	70 – 205[m]
Southern Tyrrhenian Sea	27 – 376[q]	63 – 581[q]	27 – 386[q]
Gulf of Castellammare	75[c]	160 – 610[c]	350[c]
Strait of Sicily	–	51 – 600[g]	86 – 335[g]
Eastern Mediterranean	10[l]	0 – 500[k]	100-500[k]
	Depth distribution of eggs (m)		
Catalan Sea	–	30 – 120[e, f]	–
Atlantic Ocean	–	8[n]; 30 – 130[d]	–

Tab. 1. Ground depth of collection for the three species of *Sepietta* in the Mediterranean Sea (information on egg distribution in the Atlantic from the literature). References: [a] this work; [b] Bello & Deickert, 2003; [c] Bello et al., 1994; [d] Bergström & Summers, 1983; [e] Deickert & Bello, 2005; [f] Gabel-Deickert, 1996; [g] Jereb & Stefano, 1995; [h] Mangold-Wirz, 1963; [i] Naef, 1923; [j] Orsi-Relini & Bertuletti, 1989; [k] Salman et al., 1997; [l] Salman et al., 2002; [m] Sartor & Belcari, 1995; [n] Thorson, 1946; [o] Villanueva, 1995; [p] Volpi et al., 1995; [q] Würtz et al., 1995.

Tab. 1. Batimetria dei fondi dove sono state raccolte le tre specie di *Sepietta* nel Mediterraneo (informazioni sulla distribuzione delle uova in Atlantico dalla letteratura scientifica). Referenze bibliografiche: [a] this work; [b] Bello & Deickert, 2003; [c] Bello et al., 1994; [d] Bergström & Summers, 1983; [e] Deickert & Bello, 2005; [f] Gabel-Deickert, 1996; [g] Jereb & Stefano, 1995; [h] Mangold-Wirz, 1963; [i] Naef, 1923; [j] Orsi-Relini & Bertuletti, 1989; [k] Salman et al., 1997; [l] Salman et al., 2002; [m] Sartor & Belcari, 1995; [n] Thorson, 1946; [o] Villanueva, 1995; [p] Volpi et al., 1995; [q] Würtz et al., 1995.

reproductive mode in respect to the mode of life and the habitat of the three species of *Sepietta*. The study was accomplished through direct observations of the reproductive behaviour of captive females of *S. oweniana* and *S. obscura* and the examination of their ovary condition and those of two wild collected females of *S. obscura* and *S. neglecta*.

Materials and methods

The sampling was carried out on sandy and muddy grounds in the Catalan Sea off Banyuls-sur-Mer (western Mediterranean, 42°29′N 03°08′E). During February to July 1988 and 1989, 28 specimens of *Sepietta obscura* were collected at depths from 2 to 10 m (see also **Fig. 1**). Samples were taken one to three times each week using a small beam trawl (mouth 0.8 m wide, net length 3 m, mesh size 5 mm, cod end with 0.7 mm mesh size). In May 1989 one mature female of *Sepietta neglecta* was caught at a depth of 90 to 120 m with a larger trawl. Species were identified following the descriptions by Naef (1923). The state of maturation was determined according to Mangold (1989).

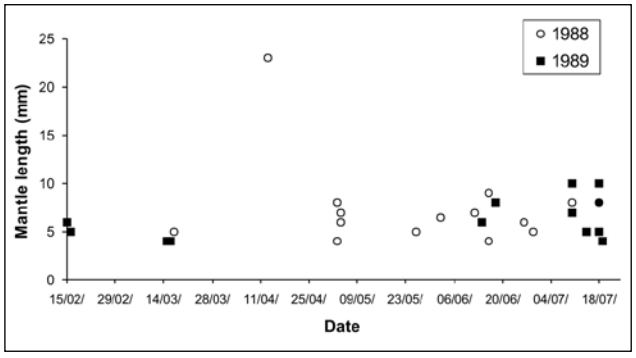

Fig. 1. Sampling dates and mantle length of 28 specimens of *Sepietta obscura*.

Fig. 1. Date di raccolta e lunghezza del mantello di 28 esemplari di *Sepietta obscura*.

Undamaged specimens were sampled in seawater buckets, then transferred to the aquarium soon after capture and kept separately in round 5 litre glass containers (diameter 20 cm). The containers were supplied with running sea water from a depth of about 10 m filtered through a gravel bed. The specimens were fed on live mysids, palaemonid and crangonid shrimps *ad libitum*. Soon after capture the dorsal mantle length (ML) was measured to the nearest 0.5 mm. For the measurement of the mantle length of living specimens the two arms of a tweezers were spread out and held closely to the mantle tip and the mantle margin. Then the distance of the two arms was measured by a ruler. Divergence of the measurement were ±0.5 mm ML in smaller and ±1 mm ML in larger specimens. One of the specimens of *S. obscura* grew to a mature female. When the mantle appeared to enlarge because of oocytes ripening, a male was temporarily transferred for copulation into the container of the mature female. Egg numbers for each clutch, spawning

Water depth (m)	Species	Sex and condition	Number of specimens	Mantle length (mm)
2-10	*Sepietta obscura*	mature female	1	23
	"	immature specimens	27	4-10
	Sepietta oweniana	mature female	1	25
90-120	"	mature females	5	25-34
	"	immature female	1	17
	"	mature males	3	19-30
	Sepietta neglecta	mature female	1	24

Tab. 2. Collecting data for the three species of *Sepietta*.

Tab. 2. Dati di raccolta delle tre specie di *Sepietta*.

duration and total number of eggs until death were recorded daily by routine visits in the morning and in the evening.

After death, the mantle lengths were measured to the nearest 0.1 mm by a dissecting microscope. The specimens were weighed to the nearest 0.1 g after removing the excess of water with paper tissue, the mantle being cut open. In females the ovaries were removed, fixed in Bouin's solution and preserved in 70% ethanol; afterwards they were dissected to count and measure all oocytes larger than 0.1 mm.

The results for *Sepietta oweniana* are reported and discussed in Bello & Deickert (2003).

Results

The sampling data for the three species of the genus *Sepietta* are summarized in **Tab. 2**. In the case of *Sepietta obscura* mainly immature specimens were found, whereas in the other two species mainly mature specimens were collected. **Fig. 2** shows the temperature variations in the aquarium and of sea water at approximately 10 m depth, i.e. where the aquarium water came from. It varied from 9°C in February to 23°C in July.

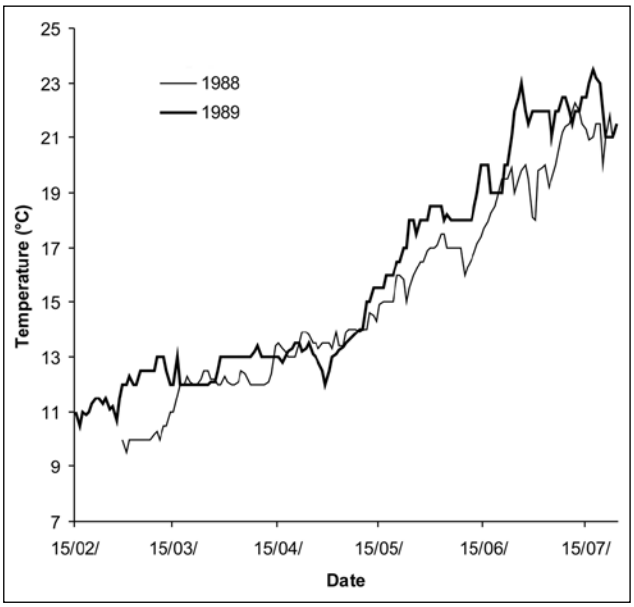

Fig. 2. Temperature variations of the aquarium water (= sea water from 10 m depth).

Fig. 2. Variazioni della temperatura dell'acqua dell'acquario (= acqua del mare a –10 m).

Fig. 3. Female no. 1 (right) and a male of *Sepietta obscura* soon after copulation in the aquarium.

Fig. 3. Femmina n. 1 (a destra) e maschio di *Sepietta obscura* subito dopo la copulazione in acquario.

Sepietta obscura

Fig. 1 gives detailed information on the mantle length at sampling of the 28 specimens of *S. obscura*. Twenty of them died within 5 days after capture. The other eight specimens survived in the aquarium tanks for durations ranging from 23 to 128 days. Five males and one female (no. 1) of these specimens reached maturity. The two smallest specimens were immature females.

The female no. 1 mated with one of the mature males. The copulation lasted only 3 minutes.

Fig. 3 shows both specimens soon after copulation. Ten days later the female started spawning. The observations are summarized in **Tab. 3**. The daily and cumulative distribution of the number of eggs laid by this individual is shown in **Fig. 4**. According to the regression equation of the line fitting the cumulative frequency distribution of eggs laid over time, the average number of eggs laid per day is 9.07 ± 1.51 (= $b \pm s_b$, where b is the regression slope and s_b its standard error). The regres-

Sepietta obscura, female no. 1	
Mantle length	17 mm
Body weight	3.7 g
Survival length in aquarium	81 days
Day of copulation	58th day
First day of spawning	67th day
Spawning duration	13 days
Number of spawning events	5
Batch size range (number of eggs)	10-113
Total number of spawned eggs	233
Average batch size (number of eggs)	46.6

Tab. 3. Spawning duration, batch size and total number of spawned eggs of the aquarium-kept female of *Sepietta obscura*.

Tab. 3. Durata del periodo di deposizione, ampiezza del lotto e numero totale di uova deposte in acquario dalla femmina di *Sepietta obscura*.

sion line intersects the *x*-axis at 12 days before the first spawning event. That is probably the time when the first eggs matured.

The size frequency distribution of the oocytes of female no. 1 and the other female which was already mature at capture (no. 2) is reported in **Fig. 5**. In these two females, oocytes smaller than 0.5 mm made up the bulk of oocytes (**Tab. 4**); their percentages was about 62%. The total number of oocytes plus eggs laid by female no. 1 is here considered to represent the overall oocyte production. Because of its small size at capture it can be excluded that female no. 1 had spawned before capture. However, it is not known whether it would have laid more eggs if it had not been caught.

The present data show that also the sepiolid squid *S. obscura* is a multiple spawner. This is revealed by both the direct observation of multiple spawning of one aquarium-kept female of the species (**Fig. 4**) and the coexistence in the ovary of oocytes at various stages of maturation, including mature oocytes (**Fig. 5**).

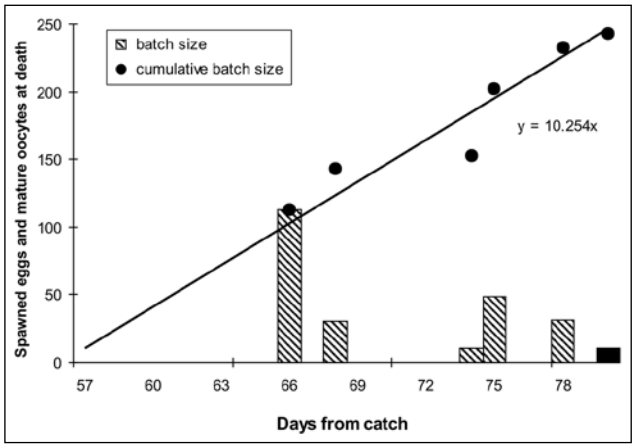

Fig. 4. Daily and cumulative distributions of the number of eggs laid in the aquarium by female no. 1 of *Sepietta obscura*. Line: regression line for cumulative distribution (slope = average number of eggs laid per day). The solid bar at the end of the *x*-axis shows the number of mature oocytes at death.

Fig. 4. Distribuzioni giornaliera e cumulativa del numero di uova deposte in acquario dalla femmina n. 1 di *Sepietta obscura*. Linea: linea di regressione della distribuzione cumulativa (pendenza = numero medio di uova deposte al giorno). La colonna nera alla fine dell'asse delle ascisse indica il numero di oociti maturi dopo la morte.

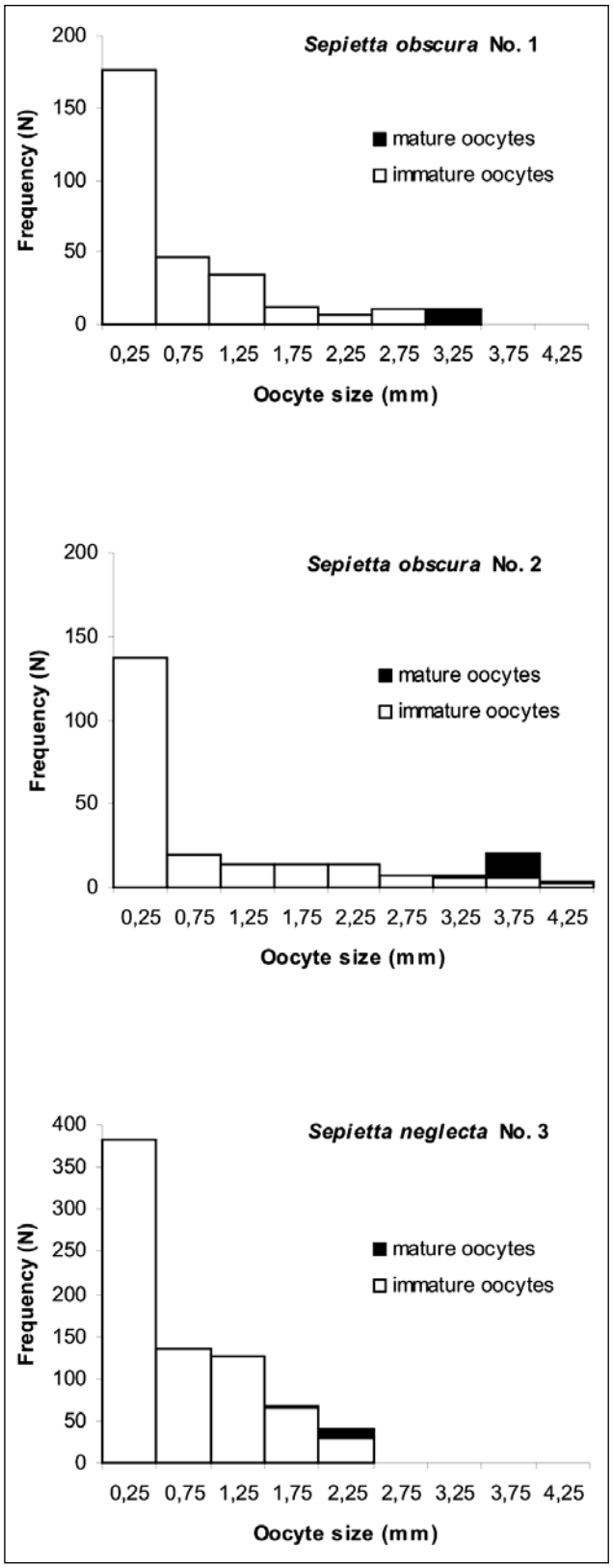

Fig. 5. Size frequency distributions of oocytes of the two females of *Sepietta obscura* and one female of *Sepietta neglecta*. *X*-axis: length of oocytes and mature ovarian eggs (mm); *Y*-axis: oocyte frequency.

Fig. 5. Distribuzione di taglia degli oociti delle due femmine di *Sepietta obscura* e di una femmina di *Sepietta neglecta*. In ascissa: lunghezza degli oociti e delle uova ovariche mature (mm); in ordinata: frequenza degli oociti.

Females	Body weight (g)	ML (mm)	Number (and %) of oocytes		Total number of oocytes	Number of mature oocytes (size, mm)	Number of laid down eggs (size, mm)	Overall number of produced oocytes
			small 0.1-0.5 mm	large > 0.5 mm				
S. obscura no. 1	3.7	17	176 (61.5%)	110 (38.5%)	286	10 (3.2)	233 (3.3)	529
S. obscura no. 2	7.2	23	137 (62.3%)	83 (37.7%)	220	17 (3.8)	0	237
S. neglecta no. 3	5.4	24	382 (51.6%)	358 (48.4%)	740	14 (2.0)	0	754

Tab. 4. Number of oocytes and eggs of two mature females of *Sepietta obscura* (no. 1, no. 2) and one mature female of *Sepietta neglecta* (no. 3).

Tab. 4. Numero di oociti e uova di due femmine mature di *Sepietta obscura* (n. 1 e n. 2) e di una femmina matura di *Sepietta neglecta* (n. 3).

Sepietta neglecta

In the female of *S. neglecta* (no. 3), which was found in deeper water (**Tab. 2**), the ovary showed also a wide variety of oocyte sizes (**Fig. 5**). Oocytes smaller than 0.5 mm made up about the half of the total amount of oocytes (52%) (**Tab. 4**).
Sepietta neglecta too is likely to be a multiple spawner. This is supported by the coexistence in the ovary of oocytes at various stages of maturation (**Fig. 5**).

As for the closely related *S. oweniana*, Bello & Deickert (2003) proved that it also reproduces by multiple spawning.

Discussion

Although all three species of the genus *Sepietta* are multiple spawners, there are considerable differences in their reproductive mode and features of their life cycle (**Tab. 5**).
In *Sepietta obscura* the adult body size is smaller and the egg size is larger than in *Sepietta oweniana*. Smaller adult body size and larger eggs suggest a lower individual fecundity for *S. obscura* compared to *S. oweniana.* According to the direct observations in the aquarium, *S. obscura* laid on the average about half the number of eggs per day than *S. oweniana* (**Tab. 5**). Such figures, of course, cannot be highly representative for the species since the behaviour of captive animals may greatly differ from that of wild animals. However, the total number of oocytes which is only about one third in *S. obscura* with respect to *S. oweniana* strongly corroborates the hypothesis that the individual fecundity of *S. obscura* is indeed lower.
It is assumed that the advantages of large eggs and small adult body size in *S. obscura* are the relatively large hatchlings, which have a higher survival rate in their habitat (Boletzky, 2002), and a shorter generation time, which somehow balances the lower individual fecundity. To discuss this hypothesis, results of this paper and literature data on the mode of reproduction and features of the life cycle of the three species of the genus *Sepietta* are summarized in **Tab. 5**.

Sepietta obscura is a littoral species, whereas *S. oweniana* lives mainly in deeper water (**Tab. 1**). The littoral environment is more unpredictable with considerable temperature variations during the year (**Fig. 2**) (for Banyuls-sur-Mer see Bhaud et al., 1967), swell action, and turbidity. The large hatchlings of *S. obscura* adopt the nectobenthic mode of life of the adults after leaving the egg capsule. They cover themselves with sand at daytime and start foraging at dawn (Boletzky & Boletzky, 1970). On the contrary, the smaller hatchlings of *S. oweniana* are planktonic-nectobenthic (Bergström & Summers, 1983). After hatching they search actively for food throughout the day and night, swim freely to catch prey, and spend only short periods of time on the bottom. The behaviour gradually changes up to an age of 10 weeks, when the juveniles adopt the typical nectobenthic mode of life of adult sepiolids. The planktonic-nectobenthic hatchlings risk being preyed upon by both benthic and pelagic predators virtually 24 hours a day, therefore the survival rate is likely to be considerably lower than that of the larger hatchlings of *S. obscura*. An advantage of the planktonic early life stage is the higher chance of dispersal for *S. oweniana*; this species has, in fact, the widest geographical distribution within the genus *Sepietta*.
The generation time is determined by the length of the embryonic development and the growth rate from hatching to maturity. The embryonic development at temperatures from 16°C to 17°C is 45 days long for *S. obscura* and 40 days for *S. oweniana*. The embryonic development is strongly affected by temperature with a faster development at higher temperatures (Boletzky, 1975; Bergström & Summers, 1983). The *Posidonia oceanica* grass beds, which are thought to be the spawning ground of *S. obscura* (Mangold-Wirz, 1963), are situated at the same depth as the nearby sampling area of this species. In these areas temperatures of 22°C are reached in summer (**Fig. 2**) (Bhaud et al., 1967), which probably accelerates the embryonic development to about 1 month, whereas lower temperatures, down to 10°C in winter, slow it down. The spawning season of *S. obscura* extends at least from spring to autumn, whereas the females of *S. oweniana* definitely spawn year around (Reid & Jereb, 2005). A major spawning location for *S. oweniana* in the Catalan Sea is between 90 to 120 m depth (Deickert & Bello, 2005).

Features	*Sepietta obscura*	*Sepietta oweniana*	*Sepietta neglecta*
Size			
Mantle length at first maturity (mm), females	15 – 18[k]	18 – 26[k]; 20 – 30[j]	17 (mature)[c]
Mantle length at first maturity (mm), males	11 – 16[k]	16 – 18[k]; 20 – 25[j]	15 – 17[k]; 12; 13 (mature)[n]
Maximum adult size (mm), females	23[k]	34[k]; 40[j]	24[a]
Maximum adult size (mm), males	21[k]	28[k]; 35[j]	22[k]; 26[m]
Body weight of mature females (g)	3.7 – 7.2[a]	8.9 – 11.7[b]	5.4[a]
Egg size (mm)	3.2 – 3.8[a]; 3.7 – 4.5[l]	2.1 – 2.5[b]; 2.4[i]	2.0[a]; 1.4 – 2.8[h]
Hatchling mantle length (mm)	–	2 – 3[g]; 2.5 ± 0.3[d]	–
Life cycle			
Length of embryonic development at 16-17°C (days)	45[f]	40[d]	–
Mantle growth rate (mm / month)	up to 10 mm ML: 2.5[e] from 10 mm ML on: 5[e]	females: 4.2[d] males: 5.3[d]	–
Reproduction			
Total number of oocytes (range or mean ± s)	220; 286[a]	890 ± 190.6[b]	740[a]
Batch size range [mean] (number of eggs)	10 – 113 [46.6][a]	2 – 176 [53.3][b]	–
Average spawned eggs / day (± s)	9.06 ± 22.51[a]	16.74 ± 1.78 [b]	–
Total number of eggs spawned in the aquarium	233[a]	428[b]	–
Estimated individual fecundity	300[a]	1,000[b]	–

Tab. 5. Comparative table on size, reproduction and life cycle features of the three species of the genus *Sepietta*. References: [a] this work; [b] Bello & Deickert, 2003; [c] Bello et al., 1994; [d] Bergström & Summers, 1983; [e] Boletzky et al., 1971; [f] Boletzky, 1975; [g] Gabel-Deickert, 1996; [h] Lefkatidou & Kaspiris, 1998; [i] Naef, 1928; [j] Mangold-Wirz, 1963; [k] Orsi-Relini & Bertuletti, 1989; [l] Reid & Jereb, 2005; [m] Villanueva, 1995; [n] Volpi et al., 1995.

Tab. 5. Tabella comparativa sulle caratteristiche di taglia, riproduzione e ciclo biologico delle tre specie del genere *Sepietta*. Referenze bibliografiche: [a] this work; [b] Bello & Deickert, 2003; [c] Bello et al., 1994; [d] Bergström & Summers, 1983; [e] Boletzky et al., 1971; [f] Boletzky, 1975; [g] Gabel-Deickert, 1996; [h] Lefkatidou & Kaspiris, 1998; [i] Naef, 1928; [j] Mangold-Wirz, 1963; [k] Orsi-Relini & Bertuletti, 1989; [l] Reid & Jereb, 2005; [m] Villanueva, 1995; [n] Volpi et al., 1995.

At 90 m the temperature increases slowly from 11.5°C in January to 14°C in September (Bhaud et al., 1967). In this temperature range embryonic development takes between 50 to 75 days for *S. oweniana* (Bergström & Summers, 1983). Although the eggs of *S. obscura* are larger, the embryonic development in their habitat is shorter than for *S. oweniana* for most of the year.

The growth rate, which is temperature independent (Boletzky et al., 1971), is lower after hatching in *S. obscura* than in *S. oweniana*. This may be due to the different feeding behaviour of the hatchlings and subsequent stages of these two species. After three months, the growth rate of *S. obscura* changes to match the higher rate of *S. oweniana*. In *S. obscura* the first mature females occur at 15 mm ML; all females are mature at 19 mm ML. Maturity can therefore be reached after 4 to 5 months. *Sepietta oweniana* takes about 4 to 6 months to reach maturity.

Generation time in *S. obscura* can be as short as 5 to 6 months in summer and about 1 or 1.5 months longer in winter. In *S. oweniana* the generation time is about 6 to 8 months with only half a month difference in the winter (Bergström & Summers, 1983). Due to the high temperature in the habitat of *S. obscura*, the generation time of this littoral species is assumed to be seasonally shorter than in *S. oweniana*.

When females reach maturity, i.e. when the first mature ovarian eggs occur, multiple spawning may start. As for *S. obscura*, female no. 1 reached maturity about two week before the first spawning event (see in **Fig. 4** the intersection of the regression line with the *x*-axis), and then kept on spawning over two weeks. When we consider the size range of mature females, which is 19 to 23 mm ML, and take into account their growth rate, we realize that mature females continue to grow for at least a month. The size range of mature *S. oweniana* in the Catalan Sea is given in Mangold-Wirz (1963) as 30 to 40 mm ML, which means that females of this species keep on growing for at least two more months after the onset of maturity and most probably go on spawning during that time. A spawning duration of two months is quite possible for sepiolids, as shown in the smaller species *Sepiola affinis* where in an aquarium-kept female, multiple spawning lasted 2 months (Gabel-Deickert, 1995). The size range of mature females in *S. affinis* is 16 to 22 mm ML (Gabel-Deickert, 1996) and the growth rate is 2.5 mm ML/month (Boletzky et al., 1971), which leads to a growth phase after maturity of more than two months. It seems that the calculated duration of the mature phase of life gives a good reference to the possible spawning period. Spawning duration multiplied by the daily number of eggs pro-

vides an idea of the individual fecundity of *S. obscura*, which may reach about 300 eggs, whereas in *S. oweniana* it may reach about 1,000 eggs. If these figures are compared to the number of oocytes, it seems that they also give a good indication of the individual fecundity, despite the fact the oocytes are continuously produced (Bello & Deickert, 2003).

The third species of the genus *Sepietta*, namely *Sepietta neglecta*, is thought to be the sister species of *S. oweniana* (Bello, 1998). Data for *S. neglecta* are very limited (**Tab. 5**). The depth distribution of this species is intermediate between those of *S. obscura* and *S. oweniana* (**Tab. 1**). The adult body size of *S. neglecta* is close to that of *S. obscura*, whereas its eggs are even smaller than those of *S. oweniana*. The spawning ground of *S. neglecta* is likely to be the same as in *S. oweniana*, since the mature female of *S. neglecta* in this study was found in the same area (**Tab. 2**). The length of the embryonic development is unknown, but it is probably shorter than in *S. oweniana* because of the smaller egg size. The hatchlings of *S. neglecta* are nectobenthic, they cover themselves with sand at daytime and start feeding at dawn (Boletzky & Boletzky, 1970). The growth rate from hatching to maturity is the same as in *S. obscura*, implying that maturity is reached after 4 to 5 months. Therefore generation time should be no longer than 5.5 to 7.5 months. The only reference to the individual fecundity is the number of oocytes, which is similar to that of *S. oweniana*.

Conclusions

Of the three species of the genus *Sepietta*, *S. oweniana* is the most successful in terms of geographical distribution, range of depth distribution, and density in the Mediterranean Sea. The high individual fecundity results in a large amount of planktonic-nectobenthic hatchlings, which enhance the overall dispersal capability. The high growth rate of the planktonic-nectobenthic hatchlings results in a short generation time. The large adult body size and comparatively small eggs ensure a high fecundity.

Sepietta obscura successfully occupies a shallow water habitat, which does not seem to be favourable to *S. oweniana*. The large hatchlings of *S. obscura* adopt the nectobenthic mode of life of the adults since they leave the egg capsule, which enables them to survive in the unpredictable shallow water environment. However, the larger egg size and the smaller body size of *S. obscura* results in a lower fecundity than in *S. oweniana*.

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