

Reproductive Biology of *Sepiola intermedia* (Sepiolidae: Cephalopoda) in the Aegean Sea, Eastern Mediterranean

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Abstract

A total of 111 *Sepiola intermedia* specimens were collected from the Aegean Sea at seasonally between 2007 and 2008. The maturity stages of both sexes and the gonadosomatic index values were estimated. It was observed that the ovulation pattern of *S. intermedia* is asynchronous and spawning occurs continuously. Potential fecundity ranges for females and males were determined to be between 148-406 eggs (mean 271) and 54-383 spermatophores (mean 197), respectively. The females with mantle lengths ML between 14-22 mm obtained 68 to 161 spermantangia (mean 96) ranging from 0.3-0.9 mm in length throughout the season inside their bursa copulatrix. The mantle lengths of mature females varied from 15 to 22 mm ML, those of mature males – between 15 and 23 mm ML. This study provides new records on the reproductive biology of *S. intermedia*.

Keywords: Sepiola intermedia, reproductive biology, histology, Aegean Sea, Mediterranean.

Sepiola intermedia (Sepiolidae: Cephalopoda)'nın Ege Denizi'nde (Doğu Akdeniz) Üreme Biyolojisi

Özet

Bu çalışmada 2007-2008 yılları arasında Ege Denizi'nden mevsimsel olarak *Sepiola intermedia*'ya ait 111 adet birey örneklenmiştir. Bu çalışmada gözlenen olgun dişi bireyler 15–22 mm manto boyunda (ML), erkek bireyler ise 15–23 mm ML olarak tespit edilmiştir. Örneklenen bireyler içinden her iki cinsiyete ait gonadosomatik indeks değerleri incelenmiştir. Gonadlardaki yumurtaların olgunluk durumlarına göre gonadın gelişimi asenkronik gonad tipinde olup yumurtlamanın her seferinde az miktarlarda ve uzun bir periyot içinde gerçekleştiği düşünülmektedir.

Üreme potansiyeli dişi bireylerde 148-406 yumurta (ortalama 271), erkek bireylerde ise 54-383 spermatofor (ortalama 197) olarak tespit edilmiştir. 14-22 mm manto boyu arasındaki dişi bireylerin bursa kopulatrikslerinde 68–161 (ortalama 96) arasında spermatangiaya rastlanmıştır. Tespit edilen bu spermatangiaların boyları 0.3–0.9 mm arasında olup, tüm mevsimlerde gözlenmiştir. Bu çalışma *S. intermedia*'nın üreme biyolojisi için yeni katkılar içermektedir.

Anahtar Kelimeler: Sepiola intermedia, üreme biyolojisi, histoloji, Ege Denizi, Akdeniz.

Introduction

Sepiola intermedia Naef 1912, belonging to the subfamily of Sepiolinae, is a small bottom-living species that has a short life span and a maximum ML of 28 mm. It is found in the Aegean Sea as well as in other areas of the Mediterranean Sea and Northeastern Atlantic (Reid and Jereb, 2005). Although being captured in many Mediterranean areas, the species has no commercial value and there is no separate fisheries statistics available for it (Reid and Jereb, 2005).

According to Relini and Bertuletti (1989) S. *intermedia* is one of the Mediterranean's patchy distributed sepiolid species, which has been reported

from studies carried out in different parts of the Mediterranean. The species is the most abundant species among the genus *Sepiola* which have a vertical distribution between 8-200 m (Belcari *et al.*, 1989; Relini and Bertuletti 1989; Sartor and Belcari 1995; Volpi *et al.*, 1995; Würtz *et al.*, 1995). Female Sepiolidae store spermatangia ejaculated spermatophores, either in a specialized seminal receptacle (Heteroteuthis) or on the bursa copulatrix (Sepiola, Sepietta) (Nesis, 1995; Hoving *et al.*, 2008).

The shape of bursa copulatrix in the mantle cavity is used in the identification of the female species (Bello, 1995). Even though studies on *S. intermedia*'s spawning, fecundity and spermatophore

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numbers and length have been conducted (Gabel-Deickert, 1995; Salman and Önsoy, 2004), the reproductive biology of this species remains poorly known.

The present study contributes to our understanding of the biology of the species by providing new data on maturity, size, oocyte growth and ovary development and other reproductive parameters of both sexes.

Materials and Methods

Samples were collected within the scope of the "Analysis of Effect of Abiotic Environmental Factors on Economic Demersal Fish Population in the Gulf of Izmir" project on board R/V EGESUF. Daytime sampling was carried out seasonally from autumn 2007 to summer 2008 by a commercial bottom trawl (44 mm cod-end mesh size) from sandy and muddy bottoms within a 50-55 m depth of Izmir Bay, Aegean

Sea (Eastern Mediterranean) (Figure 1). The entire catch of the cephalopods was fixed in 10% formalin solution on board. A total of 111 *S. intermedia* specimens (57 males + 54 females) were collected and identified following Reid and Jereb (2005) and Bello (1995). Dorsal mantle length (ML) and total body weight (BW) of the preserved individuals were measured to the nearest 1 mm and 0.01 g, respectively.

To assign maturity status of the studied specimens, Yau and Boyle (1996) and Laptikhovsky *et al.* (2008), sexual maturity criteria were used to create a new maturity scale (Table 1). Sexual maturity stages were assigned as "immature", "maturing", "mature" and "spent".

All oocytes from the ovary and the oviduct were separately counted and measured along the major axis to the nearest 0.1 mm. Gonads (GW) and oviduct were weighed to the nearest 0.0001 g. Gonadosomatic indices (GSI) for females were calculated for each



Figure 1. Sampling area (indicated by full dots)

Table 1. Scale of the *Sepiola intermedia*'s maturity stages, which was modified from Yau and Boyle (1996) and Laptikhovsky *et al.* (2008)

| | Stage | Female | Male |
|----------|-------|---|---|
| Juvenile | (I) | Gonads are microscopic; sexes cannot be distinguished using a s | stereomicroscope. |
| Immature | (II) | Nidamental glands are very small. Ovary is beneath and contains pre-vitellogenic oocytes that are transparent and <0.05 mm in length. | Testis is small and translucent. No spermatophores and no sperm in spermaduct. |
| Maturing | (III) | Nidamental glands are larger. Ovary is beneath the nidamental gland and contains medium size oocytes. No ripe eggs in the oviduct. Bursa copulatrix small and no spermatangia attached. | Testis has enlarged. Usually a few spermatophores in the Needham's sac. |
| | (IV) | Ovary contains all stages oocytes. No ripe eggs in the oviduct. Spermatangia rarely attach to the bursa copulatrix. | |
| Mature | (V) | Ovary similar stage to IV but contains mature oocytes. A few ripe eggs in the oviduct. Spermatangia attach to the bursa copulatrix. | Testis is large, opaque and white in color. Needham's sac contains functional spermatophores. |

sampling period using equation (GSI = (GW (including ovary weight and oviduct weight) / BW) x 100). Males were calculated for each sampling period using (GSI = (GW (gonad weight) / BW) x 100) (except spermatophoric complex) (Gabr et al., 1998). Potential fecundities (PF) of mature females were computed as the sum of the oocytes in the ovary plus the oocytes in the oviduct. Relative fecundity (RF) was calculated as a ratio of potential fecundity (PF) to BW (RF = PF/BW). For mature male specimens, the relative spermatophore length (SpL index = SpL x100/ML) was estimated. The structures of spermatophores were identified acoording to Weil (1927) and Voss (1969). Length at maturity of population (ML₅₀) was defined as the length at which 50% of the population investigated is mature (King, 1996). A log-log function was used to assess the proportion of the mature individuals by size class using nonlinear regression (İlkyaz et al., 1998). The equations;

$$r(l) = \exp(-\exp(-a+bl))$$

and

$$L_{50} = \frac{-\ln(-\ln(0.5)) - a}{b} \cong \frac{0.3665 - a}{b}$$

were applied, where r(l) is the proportion of mature animals in each length class (%), l is the mantle length (mm), Lm is the mean mantle length at sexual maturity (50%, mm), a is intercept, and b is slope.

Both linear and nonlinear regression analyses of Snedecor and Cochran, (1989) were used. Gonads of 18 females (12 to 21 mm ML) at various maturity stages were used to study oogenesis. Ovaries were removed from the specimens that were fixed in 10% formalin solution on board as before. For preparations of histological sections of the reproductive system, parts were dehydrated and were then embedded in paraffin blocks. Histological sections (5-8 µm thick) were cut and stained using hematoxylin-eosin (HE). The hematoxylin stains the membranes and proteinaceous structures blue and the eosin stains cytoplasmic structures pink. Histological sections were examined using a CX-41 phase contrast microscope and photographed with an Olympus DP-20 digital camera and a stereo binoculer Olympus SZ-61.

Results

Body Size

The observed MLs ranged between 10-23 mm for males (average 17.8 ± 3.1 mm ML), and 12-22 mm for females (average 17.1 ± 2.4 mm ML). The t-test show no difference in the mantle length distributions (P>0.05).

Although mature specimens were observed in all seasons, the smallest individuals were found in spring and autumn. The mean MLs and their standard deviations were 18.1 ± 2.9 , 19.5 ± 1.9 , 16.6 ± 2.5 and 18.1 ± 2.9 for spring, summer, autumn and winter, respectively. Except in summer months, no statistical differences were observed between seasons (P \leq 0.005).

Maturity Stage

The length-at maturity of the population ML_{50} was recorded for both sexes and average MLs at maturation were estimated as 17.4 mm females and as 17.3 mm males (Figure 2). Mean ML of immature female was 13±1.0 mm, maturing 15±1.52 mm and mature females 18±1.87 mm ML. In males, respective values were immature 12±1.70 mm, maturing 17±3.34 mm and mature 19±1.54 mm ML. For females, calculated average GSI values decrease starting from the autumn and reach a minimum in winter. Males had homogeneous GSI values throughout the year, and the maximum value of 2.4% was observed in spring (Figure 3).

Gonad Development, Fecundity and Fertility

In males GSI increase at maturation and maturity was much smaller than those of females (Figure 4).

Oocyte growth occurred asynchronously; small protoplasmic oocytes of 0.5-0.9 mm in diameter predominated during most of the ontogeny. The oocytes sizes varied from 0.1 to 4.2 mm. There were at least 3 groups of oocytes (small/protoplasmic oocyte, 0.1-0.9 mm; medium/vitellogenic large oocyte 1.0-2.7 mm, and large/ripe oocyte 2.8-4.2 mm). The percentage of oocyte size distributions at different gonad stages are given in Figure 5.

The potential female fecundity varied between 148-406 oocytes, with a mean of 271. The number of ripe oocytes in the oviduct was 3-33, and their diameters were 2.6–4.2 mm, which corresponds to 11-26% (mean 17%) of ML (Figure 6A).

A linear relationship between the ML of the 15 mature females and 182 mature eggs from their oviducts shows that there is no correlation in between them (R=0.0031).

The estimated RF for pre-spawning females was 44.8-151.7 (mean 93.9) oocytes/g. The ML of the smallest individual with eggs in the oviduct was 15 mm. Mature male and female specimens were observed every season throughout the year.

Spermatangia attached in bursa copulatrix, which is a distal oviduct wrinkled area, were investigated. In all seasons, the specimens with ML between 14 and 22 mm had 68-161 spermantangia (mean 96) ranging from 0.3 to 0.9 mm inside their bursa copulatrix (Figure 6B).

In a transverse cut of the bursa copulatrix distal



Figure 2. Male and female distribution of the 50% of the population (ML_{50}) at the size-at maturity.



Figure 3. Seasonal gonadosomatic index values of S. intermedia.



Figure 4. Male and female individuals GSI values according to gonad stage.

section, a dense spermatangia group could be seen (Figure 7A).

In the longitudinal section of spermatangia, sperm mass at the aboral part and the cement body at the oral part of the spermatangia can be distinguished easily (Figure 7B). Implanted spermatangia have thin capillary-tubule with oral openings, which extend outwards and this may help spermatozoa transfer from the bursa copulatrix to the eggs to be fertilized (Figure 7B).

The number of spermatophores in the Needham sacs of seventeen mature males between 15 and 21 mm ML ranged between 54 and 383 (mean 195), their lengths varied from 5.0 to 10.0 mm (mean 7.7 mm). The calculated ML/SpL index was 32-52% (mean 40%). The relative size of sperm mass, cement body and the ejaculatory apparatus in respect to the total length of the spermatophore was estimated as 21.4 ± 2.16 , 15.2 ± 1.54 and 63.4 ± 1.05 respectively.

The spermatophores' spiral coiled sperm mass, cement body and ejaculatory apparatus sections were distinctively recognized even inside the Needham sacs, which had been removed from examined males (Figure 8). The cement body, which is the middle part of a spermatophore connect to the ejaculatory apparatus consist of upper sac, which is connected by



Figure 5. Size distribution of oocytes at different maturity stages of S. intermedia



Figure 6. A: Generel view of the distal oviduct and bursa copulatrix of *Sepiola intermedia*. B: An accurent original drawing of the spermatangium in the bursa copulatrix of *S. intermedia*.

a narrow bridge of the outher membrane to the lower sac (Figure 8).

Discussion

The bursa copulatrix of the subfamily Sepiolinae occur in different shapes and sizes. Spermatangia are implanted in bursa copulatrix, which is located in the genital opening of females, or into the wrinkled area (Jones and Richardson, 2011), which is called seminal receptacle. Implantation area of spermatangia is an enlarged area of distal oviduct (Rodrigues *et al.*, 2012). According to Jones and Richardson (2011) species *Sepiola atlantica* contains 22 sprematangia in its bursa copulatrix, and by Rodrigues *et al.* (2011) it was reported that implanted sprematangia in the bursa copulatrix could survive up to 104 days.

Different numbers of spermatangia can be observed in subfamily Rossinae species, such as *Rossia molleri* 6-21 (Hoving *et al.*, 2009); *Semirossia.patagonica* 2-19 (Önsoy *et al.*, 2008); *Neorossia caroli* 1-30 (Salman, 2011), which do not contain bursa copulatrix.

Yau and Boyle (1996) used egg diameter and bursa copulatrix length to estimate maturity indices in *Sepiola atlantica* but these indices are not applicable to other sepiolidae species because of species-specific length of bursa copulatrix. To determine the accurate sexual maturity stage of *Sepiola intermedia*, a new maturity scale was developed (Table 1).

The GSI values of male individuals, which remain stable throughout the year, indicate that males are equally actively reproduce all year round. Females being to mate while still maturing and mating and spawning continues throughout the year (Table 2). Also the occurrence of small immature individuals (between 10-14 mm ML) throughout the seasons supports this conclusion.

According to the results of this study, the size at maturity of both sexes of *S. intermedia* is 17 mm ML.

Successive cohorts of oocytes in different development stages can be distinguished in the ovaries of maturing and spawning females. These observations suggest that the ovulation pattern of this species is asynchronous which is supported by the classification of gonad developments proposed by Rocha *et al.* (2001).

It has been reported that in general, sepiolids spawn throughout the year whether their lifetime is shorter than a year like the *Sepietta oweniana* or more than a year such as *Neorossia caroli* (Boletzky 1975; Salman, 1998, 2011; Önsoy *et al.*, 2013).

According to Gabel-Deickert (1995), Sepiolidae have low batch fecundity and an extended spawning



Figure 7. A view of the spermatangium in the bursa copulatrix of *S. intermedia* from histological sections A: General view, B: Horizontal section of a sprematangia (Sm: Sperm mass; Cb: Cement body; oo: Oral opening)



Figure 8. General view of the spermatophore, cement body and inner structure in the *S. intermadia* (Sm: Sperm mass; Cb: Cement body; EA: Ejaculatory apparatus).

| ML(mm) | Stage | SptN | SptL (mm) | Season |
|--------|----------|------|-----------|--------|
| 18 | Mature | 68 | 0.3-0.7 | Spring |
| 17 | Mature | 68 | 0.3-0.8 | Summer |
| 19 | Mature | 78 | 0.4-0.9 | Summer |
| 14 | Maturing | 76 | 0.3-0.9 | Autumn |
| 19 | Mature | 111 | 0.5-0.9 | Autumn |
| 16 | Maturing | 146 | 0.3-0.8 | Autumn |
| 20 | Mature | 77 | 0.4-0.7 | Winter |
| 22 | Mature | 161 | 0.4-0.8 | Winter |
| 15 | Mature | 80 | 0.3-0.8 | Winter |

Table 2. Spermatangiums which were found in the Bursa Copulatrix of coupled female individuals of S. intermedia

(SptN: Number of Spermatangia; SptL: Spermatangium length)

period as a result of their short lifespan. From this, Boletzky (1983) reported that species are forced to spawn without any environmental stimuli, as it is also the case for *S. intermedia*. Spawning without any environmental signal and low batch fecundity indicate that this species is a continuous spawner. Similar spawning strategies were reported for subfamily Rossinae (Laptikhovsky *et al.*, 2008), *Heteroteuthis dispar* (Hoving *et al.*, 2008), and *Rondeletiola minor* (Önsoy *et al.*, 2013). In this study, the maximum batch fecundity was estimated to be 33 eggs.

As emphasized by Gabel-Deickert, (1995) to know the reproductive biology of members of a subfamily Sepiolinae is better by investigating and comparing with other sepiolid members, which gives knowledge on the reproductive characteristics of the species separated from each other under taxonomic differences in the evolutionary process.

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References

- Belcari, P., Biagi, F. and Sartor, P. 1989. Sepiolinae (Mollusca: Cephalopoda) del mar Tirreno settentrionale. Atti Della Societa Toscana Di Scienze Naturali, 96: 207-218.
- Bello, G. 1995. A key for the identification of the Mediterranean Sepiolids (Mollusca: Cephalopoda). Bulletin de l'Institute Oceanographique Monaco n 16 spécial, 41-55.
- Boletzky, S.V. 1975. The reproductive cycle of Sepiolidae (Mollusca:Cephalopoda). Pubblicazioni della Stazione Zoologica di Napoli, 39: 84-95.
- Boletzky, S.V. 1983. Sepiola robusta In: P.R. Boyle (Ed.), Cephalopoda life cycles, Vol I. Academic Press London: 53-68.
- Gabel-Deickert, A. 1995. Reproductive patterns in Sepiola affinis and other Sepiolidae (Mollusca, Cephalopoda). Bulletin de l'Institute Oceanographique Monaco n°16 spécial, 73-83.
- Gabr, H.R., Hanlon, R.T., Hanafy, M.H. and El-Etreby, S.G. 1998. Maturation, fecundity, and seasonality of reproduction of two commercially valuable cuttlefish, *Sepia pharaonis* and *S.dollfusi*, in the Suez Canal.

Fisheries Research, 36:99-115.

- Hoving, H.J.T., Laptikhovsky, V., Piatkovski, U. and Önsoy, B. 2008. Reproduction in *Heteroteuthis dispar* (Rüppell, 1844) (Mollusca:Cephalopoda): a sepiolid reproductive adaptation to an oceanic lifestile. Marine Biology, 154:219-230. doi: 10.1007/s00227-008-0916-0
- Hoving, H.J.T., Nauwelaerts, S., Genne, B.V., Stamhuis, E.J. and Zumholz, K. 2009. Spermatophore implantation in *Rossia molleri* Steenstrup, 1856 (Sepiolidae; Cephalopoda). Journal of Experimental Marine Biology and Ecology, 372:75-81. doi:10.1016/j.jembe.2009.02.008
- İlkyaz, A.T., Metin, C. and Kınacıgil, H.T. 1998. A computer program about the calculation of the selectivity parameters in towed fishing gear illustrated with cover cod-end method (L50 Version: 1.0.0). Journal of Fisheries and Aquatic Science, 15: 305-314.
- Jones, N.J.E. and Richardson, C.A. 2011. Distribution and reproductive biology of the little cuttlefish *Sepiola atlantica* (Cephalopoda: Sepiolidae) around Anglesey, North Wales. Helgoland Marine Research, 66: 233-242. doi: 10.1007/s10152-011-0265-0
- King, M. 1996. Fisheries Biology Assessment and Management. Fishing News Books, England.
- Laptikhovsky, V.V., Nigmatullin, C., Hoving. H.J.T., Önsoy, B., Salman, A., Zumholz, K. and Shevtsov, G.A. 2008. Reproductive strategies in female polar deep-sea bobtail squid genera *Rossia* and *Neorossia* (Cephalopoda: Sepiolidae). Polar Biology, 31: 1499-1507. Doi:10.1007/s00300-008-0490-4
- Nesis, K.N. 1995. Mating, spawning and death in oceanic cephalopod: a review. Ruthenica, 6: 23-64.
- Önsoy, B., Ceylan, B. and Salman, A. 2013. Reproductive biology of the bobtail squid, *Rondeletiola minor* (Cephalopoda: Sepiolidae) from the eastern Mediterranean. Journal of the Marine Biological Association of the United Kingdom, 93: 851-854. doi: 10.1017/S0025315411002153
- Önsoy, B., Laptikhovsky, V. and Salman, A. 2008. Reproductive biology of the Patagonian bobtail squid, *Semirossia patagonica* (Sepiolidae: Rossinae) in the south-west Atlantic. Journal of the Marine Biological Association of the United Kingdom, 88: 1019-1022. doi:10.1017/S0025315408001355
- Reid, A. and Jereb, P. 2005. Family Sepiolidae Leach, 1817. In: P. Jereb, C.F.E. Roper (Eds.), Cephalopods of the world. An annotated and illustrated catalogue of cephalopod spacies known to date. Vol I Chambered Nautiluses and Sepiolids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and

Spirulidae). FAO, Rome:153-203.

- Relini, O.L. and Bertuletti, M. 1989. Sepiolinae (Mollusca, Cephalopoda) from the Ligurian Sea. Vie et Milieu, 39:183-190.
- Rocha, F., Guerra, A. and Gonzales, A.F. 2001. A review of reproductive strategies in cephalopods. Biological Review, 76:291-304.
- Rodrigues, M., Garci, M.E., Troncoso, J.S. and Guerra, A. 2011 Seasonal abundance of the Atlantic bobtail squid *Sepiola atlantica* in Galician waters Marine Biology Research, 7:812-819. doi: 10.1080/17451000.2011.578649
- Rodrigues, M., Guerra, A. and Troncoso, J.S. 2012. Reproduction of the Atlantic bobtail squid *Sepiola atlantica* (Cephalopoda:Sepiolidae) in the northwest Spain. Invertebrate Biology, 131:30-39. doi: 10.1111/j.1744-7410.2011.00253.x
- Salman, A. 1998. Reproductive biology of *Sepietta* oweniana (Pfeffer, 1908) (Sepiolidae: Cephalopoda) in the Aegean Sea. Scientia Marina, 62:379-383.
- Salman, A. 2011. Reproductive biology of *Neorossia caroli* (Cephalopoda: Sepiolidae) in the Aegean Sea. Scientia Marina, 75:9-15. doi: 10.3989/scimar. 2011.75n1009
- Salman, A. and Önsoy, B., 2004. Analysis of fecundity of some bobtail squids of the genus Sepiola (Cephalopoda:Sepiolida) in the Aegean Sea (Eastern Mediterranean). Journal of the Marine Biological Association of the United Kingdom, 84:781-782.
- Sartor, P. and Belcari, P. 1995. Sepiolidae (Mollusca:Cephalopoda) of the Northern Tyrrhenian Sea. Bulletin de l'Institute Oceanographique Monaco n°16 spécial, 15-17.
- Snedecor, G.W. and Cochran W.G. 1989. Statistical methods, 8th Edition. Iowa. 503 pp.
- Würtz, M., Matricardi, G. and Repetto, N. 1995. Sepiolidae

(Mollusca:Cephalopoda) from the lower Tyrrhenian Sea. Central Mediterranean. Bulletin de l'Institute Oceanographique Monaco n°16 spécial, 35-39.

- Volpi, C., Borri, M. and Zucci, A. 1995. Notes on the family Sepiolidae (Mollusca, Cephalopoda) off the Northern Tuscany coast. Bulletin de l'Institute Oceanographique Monaco n°16 spécial, 27-34.
- Voss, N.A. 1969. A monograph of the Cephalopoda of the North Atlantic. The Family Histioteuthidae. Bulletin of Marine Science, 19:713-867.
- Weill R. 1927. Recherches sur la structure, la valeur systématique et le fonctionnement du spermatophore de *Sepiola atlantica* d'Orb. Bulletin biologique de la France et de la Belgique, 61:59–92.
- Yau, C. and Boyle, P.R. 1996. Ecology of *Sepiola atlantica* (Mollusca:Cephalopoda) in the shallow sublittoral zone. Journal of the Marine Biological Association of the United Kingdom, 76:733-748.