6 *Sepia officinalis* Linnaeus, 1758

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Common names

Seiche commune (France); Σουπιά [soupia] (Greece); seppia comune (Italy); choco-vulgar, choco (Portugal); sepia común, sepia, choco, jibia (Spain); common cuttlefish (UK) (Figure 6.1).

Synonyms

Sepia filliouxi Lafont, 1869. *Sepia mediterranea* Ninni, 1884.

6.1 Geographic distribution

The common cuttlefish, *Sepia officinalis* Linnaeus, 1758, is found in the Northeast Atlantic and throughout the Mediterranean. In the Northeast Atlantic, there are records from the Faroe Bank and south of the Shetland Islands (Stephen, 1944), and strandings of cuttlebones have been reported along the south and west coasts of Norway as far north as Trondheim (see Nordgård, 1929; Grieg, 1933; Brattegaard

Figure 6.1. *Sepia officinalis*. **Dorsal view. From Guerra (1992).**

and Holthe, 2001). However, these northern records seem related to marked fluctuations in oceanographic conditions that characterize the North Sea, with its occasional important inflows of Atlantic water, causing immigrations of species normally restricted to southern areas. *Sepia officinalis* has also been found in waters off Sweden (Skagerrak, Kattegat areas) since the early 1900s (e.g. Massy 1909, 1928), but it appears not to be present in the Baltic Sea, except for occasional incursions in its westernmost part (Rexfort and Mutterlose, 2009).

It is found in the central and southern North Sea (Figure 6.2), as recent reviews confirm (Gittenberger and Schrieken, 2004; De Heij and Baayen, 2005). It was recorded from all along the Irish coast (Massy, 1928), and records from the east and west Scottish coasts are listed in Stephen (1944), who refers to occasional wanderings of the species in northern areas in years of strong incursions of Atlantic water. It is in the English Channel (e.g. Boletzky, 1983; Lordan *et al.* 2001a) and extends south to Northwest Africa (e.g. Bas, 1975; Bravo de Laguna, 1989) as far south as the border between Mauritania and Senegal (Ikeda, 1972; Hatanaka, 1979a; Guerra *et al.*, 2001). *Sepia officinalis* is abundant and widespread throughout the Mediterranean Sea (Mangold and Boletzky, 1987; Bello 2004; Salman, 2009), including western and central parts (Mangold-Wirz, 1963a; Sánchez, 1986a; Belcari and Sartor, 1993; Jereb and Ragonese, 1994; Giordano and Carbonara, 1999; Relini *et al.*, 2002; Cuccu *et al.*, 2003a), the Adriatic Sea (Casali *et al.*, 1998; Krstulović Šifner *et al.*, 2005; Piccinetti *et al.*, 2012), the Ionian Sea (Tursi and D'Onghia 1992; Lefkaditou *et al.*, 2003a; Krstulović Šifner *et al.*, 2005), the Aegean Sea, and the
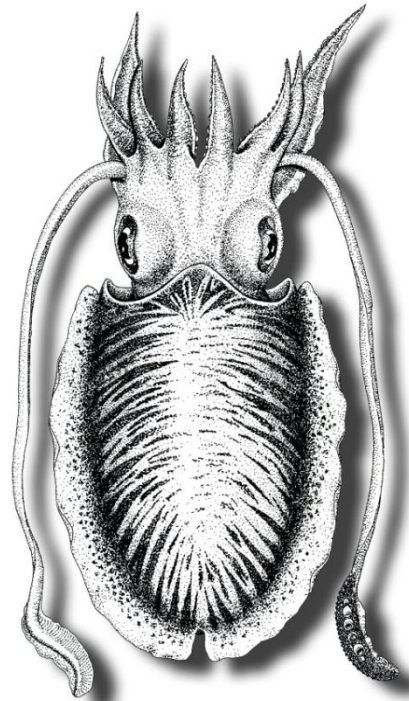
Levant Basin (D'Onghia *et al.*, 1992; Salman *et al.*, 1997, 1998; Lefkaditou *et al.*, 2003b; Duysak *et al.*, 2008). Old records of the species in the Sea of Marmara exist (Demir, 1952, in Ünsal *et al.*, 1999), although *S. officinalis* has not been recorded by more recent research carried out in those waters (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).
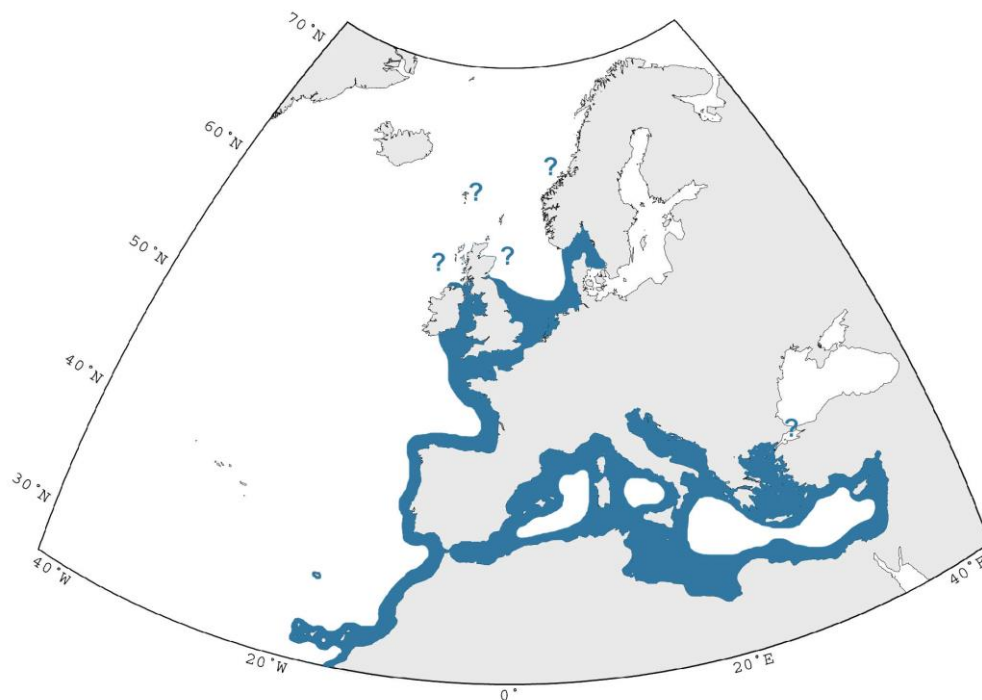

Figure 6.2. *Sepia officinalis.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea**.

6.2 Taxonomy

6.2.1 Systematics

Cephalopoda – Coleoidea – Decapodiformes – Sepiida – Sepiidae – *Sepia.*

6.2.2 Type locality

Simply given as "Oceano".

6.2.3 Type repository

Linnean Society of London, Burlington House, Piccadilly, London W1J 0BF, UK.

6.3 Diagnosis

6.3.1 Paralarvae and hatchlings

The species has no paralarval stage. Hatchlings (6–9 mm ML) are similar to juveniles and adults, except for some body proportions and some behavioural patterns (Boletzky, 1983).

6.3.2 Juveniles and adults

The maximum reliably reported size recorded is probably 45 cm ML (see **Remarks**), but smaller cuttlefish (25–30 cm ML) are more common. *Sepia officinalis* has wide fins,

which extend anteriorly slightly beyond the mantle margin. The arm suckers are tetraserial. A hectocotylus develops on the left ventral arm of maturing males, which has 6 rows of normal size suckers proximally and 4–9 rows of reduced suckers medially (Figure 6.3a). The tentacular clubs have 5–6 suckers in transverse rows, which vary in size, and 5–6 medial suckers are twice the diameter of the others. There is a swimming keel, but this does not extend proximally beyond the base of the club. The cuttlebone (Figure 6.3b) is oblong; anteriorly, it tapers to a point, and posteriorly, it is bluntly rounded. Its spine is short and pointed and surrounded by a chitinous shield. In adults, the spine is embedded in chitin. A shallow, narrow sulcus is present only on the last loculus and is absent from the striate zone. Anterior striae are shaped either like an inverted "U" or a shallow "m". The inner and outer cone limbs are narrow anteriorly, but more broad posteriorly, whereas the lateral limbs are flared ventrolaterally.

The background colour of live animals is light brown. There are scattered white spots on the head and dark pigment around the eyes. There are no dorsal eye spots. Arms I–III have a broad, longitudinal brownish band medially, which extends onto the head. There are bold transverse zebra stripes on the dorsal mantle during the breeding season. The fins have a narrow white band along the outer margin and small white spots that are larger towards the junction of the mantle and fins. The fourth arms of mature males have black and white zebra stripes and white arm spots. (Guerra, 1992; Reid *et al.,* 2005).
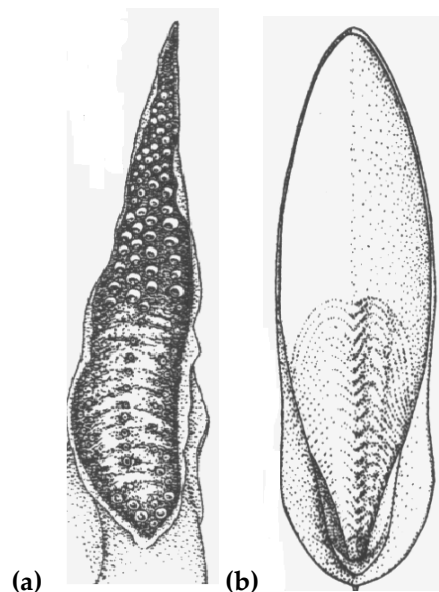

(a)   (b)

Figure 6.3. *Sepia officinalis.* (a) hectocotylized arm, (b) cuttlebone. From Guerra (1992).

6.4   Remarks

Morphological and genetic analyses have shown that *S. officinalis* Linnaeus, 1758 and *S. hierredda* Rang, 1837 are different species of the same genus (Guerra *et al.*, 2001). The mantle of *S. hierredda* is narrower, and both the unmodified arms and the hectocotylized arm are shorter than those of *S. officinalis.* The number of transverse rows of reduced suckers on the hectocotylus is higher (8–14) in *S. hierredda* than in *S. officinalis* (4–9). The striated zone of the cuttlebone of *S. officinalis* is smaller (41% of ML) than in *S. hierredda* (47%). The cuttlebone of *S. officinalis* is slightly acuminate at the anterior end, but very acuminate in *S. hierredda.* The spine of *S. officinalis* is usually covered by chitin, especially in adults, whereas the spine of the cuttlebone of *S. hierredda* is never covered by chitin. Additionally, 13 diagnostic allozyme loci distinguish these species (Guerra *et al.*, 2001).

The genus *Sepia* Linnaeus, 1758 comprises ca. 100 species. Khromov *et al.* (1998) proposed a subdivision of the genus into six species complexes, although this suggestion has not been widely adopted. Allozyme electrophoresis (Pérez-Losada *et al.*, 1999) of 32 presumptive loci indicated that *S. officinalis* (assigned to the genus *Sepia sensu stricto*) was not closely related to its European congeners *Sepia elegans* and *Sepia orbignyana,* both placed in *Sepia (Rhombosepion)* by Khromov (1998).

Young *S. officinalis* can be distinguished from *S. orbignyana* and *S. elegans* by their brown, rather than red, skin colour, the shape of the cuttlebone, and the club sucker

arrangement (Guerra, 1992). Comprehensive genetic work on microsatellite DNA variation shows that extensive population subdivisions exist in *S. officinalis* (e.g. Sanjuan *et al.*, 1996; Shaw and Pérez-Losada, 2000; Pérez-Losada *et al.*, 2002).

Off the Northwest African coast, the distribution ranges of *S. officinalis* and *S. hierredda* overlap. Recent data and information seem to agree on the southern limit of *S. officinalis* (16–17°N) and the northern limit of *S. hierredda* (Cap Blanc, 21°N), thus framing the area of overlap (16–21°N; e.g. Guerra *et al.*, 2001; Reid *et al.*, 2005). However, broader areas of overlap were reported earlier (see Ikeda, 1972 and Delgado de Molina Acevedo *et al.*, 1993 for additional details). This resulted in confusion about the maximum size for the species, because of disagreement about the identity of the (at the time) subspecies examined. According to recently given range distribution limits, the maximum size ever recorded for *S. officinalis* would be 45 cm ML (Delgado de Molina Acevedo *et al.*, 1993; African waters between 21 and 26°N off Sahara), although a maximum size of 49 cm ML was reported for *S. officinalis* by Ineji (1990), who studied specimens from Mauritanian waters, i.e. the area of overlap. The maximum size ever recorded for *S. hierredda* is 50 cm (Bakhayokho, 1983; African waters off Senegal). However, maximum sizes recorded for *S. officinalis* farther north off Portuguese and French coasts are smaller, reported as 36 and 38 cm ML, respectively (J. Pereira and J-P. Robin, pers. comm.).

6.5 Life history

Sepia officinalis has a short (1-year) or long (2-year) life cycle, and these two life-cycle modes may arise alternately or simultaneously. Breeding shows one or two seasonal peaks. Hatchlings immediately assume a nektobenthic lifestyle.

6.5.1 Egg and juvenile development

Sepia officinalis generally lay eggs in depths less than 30–40 m, attached in clusters to various plants, sessile animals such as tubeworms, or dead structures such as drowned trees, cables, or nets. No parental care has been reported in the species.

Egg diameters are 12–14 mm (Boletzky, 1983). The length of embryonic development varies with temperature and ranges from 40–45 d at 20°C to 80–90 d at 15°C (Naef, 1921/1923; Richard, 1971; Boletzky, 1983). Higher temperatures also result in greater rates of oxygen consumption during embryogenesis. Pimentel *et al.* (2012) recorded an 11-fold difference between oxygen consumption rates of eggs incubated at 13 and 19°C.

Hatchling size varies from 6 to 9 mm ML. Hatchlings immediately adopt a nektobenthic lifestyle; they are similar to adults both in morphology and basic behaviour, although the behaviour patterns of adults become more diverse through learnt behaviours (Hanlon and Messenger, 1996). Hatchlings are sufficiently advanced to feed actively within hours of hatching and seem to show innate preferences for shrimp-like prey (Darmaillacq *et al.,* 2004). However, food imprinting has been demonstrated in cuttlefish hatchlings: visual exposure to crabs for 5 h after hatching changes prey preference from shrimp to crabs (Darmaillacq *et al.*, 2006). Such visual learning has also been demonstrated in late embryos just prior to hatching (Darmaillacq *et al.*, 2008).

Young cuttlefish can adapt to very low food intake and remain alive with growth rates much lower than normal, allowing animals to survive under unfavourable conditions (Boletzky, 1983).

6.5.2 Growth and lifespan

This species lives ca. 2 years (Dunn, 1999a). In the English Channel, all animals appear to overwinter twice before spawning (Boucaud-Camou and Boismery, 1991; Boucaud-Camou et al., 1991). In the Bay of Biscay, early-season hatchlings may develop to maturity after a single winter, spawning late in the season, whereas other individuals may spawn early in the season, having overwintered twice (Le Goff and Daguzan, 1991a).

Growth is linear in the early part of the life cycle (Domingues et al., 2002), but growth in laboratory culture slows as size increases (Richard, 1971; Pascual, 1978; Forsythe and van Heukelem, 1987; Forsythe et al., 1994; Koueta and Boucaud-Camou, 1999, 2003; Domingues et al., 2001a, 2002, 2003a). Growth patterns differ between the sexes (Boletzky, 1983). Approaching maturation, female cuttlefish growth rate slows much faster than male growth rate (Domingues et al., 2002, 2003a) because they invest more energy in reproduction.

Table 6.1. *Sepia officinalis*. **Maximum mantle length (ML) (mm) for females (F) and males (M) in different geographic areas of the Northeast Atlantic and the Mediterranean Sea.**

Region	F	M	Reference
Bay of Biscay	290	350	Le Goff and Daguzan (1991a)
Ría de Vigo	235	205	Guerra and Castro (1988)
Biscay Gulf	280		Santurtún et al. (2003)
Catalan Sea	250	300	Mangold-Wirz (1963a)
Tyrrhenian Sea	230		Belcari et al. (2002b)
Thracian Sea	264	320	Lefkaditou et al. (2007)
Izmir Bay (eastern Aegean Sea)	241	324	Onsoy and Salman (2005)
Iskenderun Bay (Levant Sea)	200		Duysak et al. (2008)

Temperature plays a major role in determining both the growth rate and life span of *S. officinalis* (Richard, 1971; Pascual, 1978; Forsythe et al., 1991, 1994; Domingues et al., 2001a, 2001b, 2002, 2004). *Sepia officinalis* can be cultured at a wide range of temperatures, and it still grows at temperatures as low as 9.5°C (Richard, 1971). Generally, growth rate increases with increasing temperature, although it appears that growth slows as the upper physiological tolerance limit is approached. For example, Pascual (1978) reported slower growth at 30°C, which is at the upper tolerance limit for the species (Richard, 1971; Domingues, 1999), than at 22°C. Water temperature at hatching (e.g. Bouchaud and Daguzan, 1989, 1990) likely contributes to the variation in growth rate in *S. officinalis*, (Le Goff and Daguzan, 1991a).

Forsythe and van Heukelem (1987) indicate that daily growth in weight declines with increasing size from 5.5% BW d^{-1} to 3.75% BW d^{-1}. Domingues et al. (2001b) recorded growth rates in hatchlings of 12.4 ± 4.5% BW d^{-1}, declining to 7.3 ± 0.7% BW d^{-1} after 40 d. Domingues et al. (2003b) measured growth rates during the first 40 d of hatchling life, obtaining values ranging from 2% BW d^{-1} to 10% BW d^{-1}. Growth rate depended on diet (being faster on a shrimp than on a fish diet) and declined between 25 and 40 d of age in both feeding groups. Baeza-Rojano et al. (2009) found that cuttlefish hatchlings fed with mysids and gammarids grew faster (6.7 ± 0.4 and 5.7 ± 0.9% BW d^{-1}, respectively) than those fed with caprellids (1.6 ± 0.2% BW d^{-1}).

For the English Channel stock, Dunn (1999a) fitted von Bertalanffy growth curves to monthly length-frequency data and showed that a strong seasonal growth pattern overlies almost linear growth in length and weight. Growth was fastest between July

and October in males (32.7 mm ML month⁻¹), and between August and December in females (25 mm ML month⁻¹). There was no growth in males between October and December, or between April and May. Slowest growth in females (<4 mm ML month⁻¹) was between December and May (Dunn, 1999a). The fastest monthly growth rate in (post-recruit) males is equivalent to slightly over 1 mm d⁻¹. As the modal size of males in July was 88 mm ML, specific (daily) growth rate during July–October therefore typically ranged from ca. 1.20% in August to 0.57% in October. Similarly, the female growth rate over the peak growth period ranged from 0.67% ML d⁻¹ to 0.39% ML d⁻¹.

Length–weight relationships have been published for populations from several areas from the eastern Atlantic and the Mediterranean Sea (Table 6.2).

Statolith increments in *S. officinalis* are difficult to visualize, and initially other hard structures such as the cuttlebone were examined for age determination (Ré and Narciso, 1994; Le Goff *et al.*, 1998). Results from recent rearing experiments have both verified the daily periodicity of statolith rings and indicated that increments in other hard structures such as the cuttlebone, eye lens, and beaks cannot be used for age determination (Bettencourt and Guerra, 2000, 2001). However, in cuttlefish older than 240 d, statolith rings are hardly visible (Bettencourt and Guerra, 2001).

Table 6.2. *Sepia officinalis.* **Length–weight relationships in different geographic areas for females (F), males (M), and sexes combined (All). Original equations converted to $W = a\mathrm{ML}^b$, where W is body mass (g) and ML is dorsal mantle length (cm).**

Region	a	b	Sex	Reference
English Channel	0.243	2.78	F	Dunn (1999a)
	0.305	2.64	M	
Spain, Ría de Vigo	0.264	2.70	F	Guerra and Castro (1988)
	0.265	2.70	M	
Portugal, Ria de Aveiro	0.242	2.74	F	Jorge and Sobral (2004)
	0.264	2.66	M	
Portugal, Ria de Sado	0.366	2.60	F	Serrano (1992)
	0.275	2.69	M	
	0.069	3.15	F	Neves *et al.* (2009)
	0.464	2.35	M	
Adriatic Sea	0.220	2.773	All	Manfrin Piccinetti and Giovanardi (1984)
Hellenic Seas	0.0064	2.18	F	Lefkaditou *et al.* (2007)
	0.0025	2.37	M	
Izmir Gulf (eastern Aegean)	0.0867	3.1571	All	Akyol and Metin (2001)
Iskenderun Bay (Levant Sea)	0.1082	2.9226	F	Duysak *et al.* (2008)
	0.1415	2.7832	M	
	0.1159	2.8771	All	

Challier *et al.* (2002) applied statolith-ageing techniques to *S. officinalis* collected in the wild. Age and growth were estimated using statolith increments from juveniles of 5.3–13 cm ML collected between October and December 2000 in the French part of the English Channel and from August to December in the Bay of Seine. The pattern of juvenile growth seen was consistent with previous studies based on length-frequency distributions (Medhioub, 1986; Dunn, 1999a).

Although there is only one spawning season per year (and hence one annual cohort) in the English Channel, Challier *et al.* (2002) identified several microcohorts, each representing animals hatched in a particular month. Juveniles hatched in late summer grew more slowly than those hatched earlier (1.18 mm ML d^{-1} in June, 0.69 mm ML d^{-1} in July, and 0.46 mm ML d^{-1} in August) and, at any given age, were smaller than animals of the same age hatched earlier. Although temperature appears to be the most important environmental factor affecting seasonal growth variation, there is high interindividual variation even within microcohorts.

Back-calculations from statolith ring number indicated that most cuttlefish hatch during summer, but some hatching takes place throughout the year (Challier *et al.*, 2005). Fitted growth models (both exponential and linear) indicated that the growth rate of prerecruit specimens was significantly faster in 2002 (23–29 mm ML month^{-1}) than in 2000 (14–19 mm ML month^{-1}). The latter growth rate is consistent with that estimated by Medhioub (1986). Growth rates also varied spatially. In the Bay of Seine, they were 0.018 mm ML d^{-1} in 2000 and 0.0328 mm ML d^{-1} in 2002, but off the north coast of the English Channel they were 0.0295 mm ML d^{-1} in 2000 and 0.0294 mm ML d^{-1} in 2002. These differences could be due to the influence of low salinity and high turbidity in the Bay of Seine and/or density-dependent effects, because density varies between areas (Challier, 2005). Growth rates were directly correlated with the RNA/DNA ratio in muscle (Clarke *et al.,* 1989; Castro and Lee, 1994; Koueta *et al.*, 2000; Sykes *et al.*, 2004). The RNA content of tissues typically increased with feeding and growth (Melzner *et al.*, 2005).

6.5.3 Maturation and reproduction

Dunn (1999a) found that the overall sex ratio of cuttlefish in commercial trawl catches was not significantly different from 1:1.

Common cuttlefish attain sexual maturity at a wide range of sizes. In the English Channel, 4% of males matured at 8.1–9.1 cm ML in August at an age of ca. 1 year. Of the remaining males, the first matured at 11.4 cm ML, MLm$_{50\%}$ was reached at 14.6 cm ML, and all were mature at 17.0 cm ML. In females, the smallest sexually mature individuals were 14.2 cm ML, MLm$_{50\%}$ was 16.4 cm ML, and all females were mature at 23.0 cm ML (Dunn, 1999a). In the Mediterranean Sea, males mature as small as 6–8 cm ML, although males >10 cm ML may still be immature. Females may become fully mature at sizes of 11–25 cm ML (Mangold-Wirz, 1963a; Boletzky, 1983). Off the coast of Africa, first maturity is between 12 and 14 cm ML in males and at 14 cm in females (Hatanaka, 1979b).

Early gonad growth (before attainment of maturity) is linked to somatic growth and is therefore temperature-dependent. Light and, more particularly, short wavelength light (blue to blue-green), has a decelerating effect on gonad maturation via the hormonal control of optic glands, whereas in mature animals, it stimulates mating and spawning. High temperatures and weak light intensities / short days result in fast growth rates and gonad maturation. In shallow water under summer conditions of high temperature, high light intensity, and long day length, growth accelerates and maturation decelerates. In deeper water under winter conditions, growth is slow because of the low temperature, but maturation is largely unaffected (rather than accelerated) (Richard, 1966, 1971, 1975; Boletzky, 1983).

At maturity, the reproductive organs may represent up to 16% of body weight in females and a maximum of 5% of body weight in males (Boletzky, 1983). Males may carry up to 1400 spermatophores (Mangold-Wirz, 1963a). Estimates of fecundity for

females vary widely, although some of the variation probably relates to how fecundity is measured. According to Mangold-Wirz (1963a), females lay 150–4000 eggs, depending on their size. Laptikhovsky *et al.* (2003) reports that potential fecundity (PF) of advanced maturing and mature prespawning *S. officinalis* in the Aegean Sea varies from 3700 to 8000 (mean 5871) oocytes, whereas the number of large yolky oocytes increases with ML from 130 to 839. Further, spawning females typically have a PF of 1000–3000 fewer eggs than pre-spawning females. This provides evidence that intermittent spawning, which does take place in captivity (Boletzky, 1987a), is a normal process in natural habitats. Female common cuttlefish may release a number of eggs equivalent to ca. 50% of PF during spawning.

The reproductive behaviour of this species is well known (Hanlon and Messenger, 1996). The species has elaborate courtship behaviour, during which spermatophores are transferred to a special pouch under the buccal mass of the female (Boletzky, 1983). A single pair can mate several times in succession, with the female sometimes laying between matings. Under culture conditions, temporary mate guarding by the male has been observed, but when guarding relaxes, other mature males can copulate with the female, providing evidence of promiscuity, at least in the laboratory. Sperm competition may be relevant in this species (Hanlon *et al.*, 1999), and microsatellite DNA markers provide evidence of multiple paternity (Á. Guerra, pers. comm.). Unbalanced sex ratios are seen in mating and egg-laying areas along the west coast of Normandy. Zatylny (2000) proposed that this was linked to sperm storage.

Sepia officinalis is an intermittent terminal spawner *sensu* Rocha *et al.* (2001). This reproductive pattern is characterized by "group synchronous ovulation and monocyclic spawning". Although egg laying is in separate batches and the spawning period tends to be relatively long, somatic growth does not generally take place between spawning events (Rocha *et al.*, 2001).

Sepia officinalis spawns mainly in spring and summer in the western Mediterranean and Gulf of Tunis, but winter spawning has also been observed (Mangold-Wirz, 1963a; Najaï, 1983). Spawning extends from early spring to late summer in southern and central Portugal and the Atlantic and Mediterranean coasts of southern Spain, with a spawning peak in June and July (Villa, 1998; Tirado *et al.*, 2003; Jorge and Sobral, 2004). A similar spawning season is found northwest of the Iberian Peninsula, but winter spawning has also been recorded there (Guerra and Castro, 1988). In the Bay of Biscay and the Gulf of Morbihan, spawning takes place from mid-March to late June (Le Goff and Daguzan, 1991a). Along both the north and the south coasts of the English Channel, the spawning season of *S. officinalis* extends from February to July (Dunn, 1999a; Royer, 2002; Royer *et al.*, 2006; Wang *et al.*, 2003). Environmental factors (much milder winter conditions in some areas) probably account for most of the variation observed in *S. officinalis* spawning times (Boletzky, 1983). Restricted food supply in early life may delay maturation and extend the lifespan in this species (Boletzky, 1979a).

The length of time spent under optimal conditions in the early juvenile phase (inshore spring and summer conditions) determines whether an individual becomes sexually mature during the first winter. The first females to arrive at the spawning grounds in many areas have overwintered twice and are ca. 18 months old (Boletzky, 1983). Later in spring and up to late summer, mature females of smaller size appear in the shallower waters and spawn. These are only 14–16 months old and could be offspring of large animals that spawned early the previous year. This is the basis of a hypothesis of a cycle of alternating shorter and longer generations. One- and two-year-old breeders have been observed in southern Brittany at the same time; the spawning season for

these two groups overlaps, and they most likely interbreed (Le Goff and Daguzan, 1991b).

6.5.4 Natural mortality

Females die shortly after spawning, and mass mortality has been observed on the French and Spanish Atlantic coasts (Richard, 1971; J-P. Robin, pers. comm.; Á. Guerra, pers. comm.), but nothing of comparable intensity has been reported from the Mediterranean (Boletzky, 1983). Other causes of natural mortality include predation and disease.

6.6 Biological distribution

6.6.1 Habitat

Sepia officinalis is a neritic, nektobenthic, or demersal species found on the continental shelf and is particularly common on sandy and muddy substrata covered by algae and marine grasses (*Zostera* and *Posidonia*). Its depth distribution extends from subtidal waters to 200 m. Individuals are most abundant in the upper 100 m, with large animals found at greater depth (Guerra, 1992; Reid *et al.*, 2005). Shell morphology limits its depth range; shells of large animals implode between 150 and 200 m, whereas advanced embryonic specimens and newly hatched animals implode between 50 and 100 m (Ward and Boletzky, 1984).

Sepia officinalis is relatively tolerant of variations in salinity. Animals have been observed in coastal lagoons in the Mediterranean at a salinity of 27 (Mangold-Wirz, 1963a). Observations from the western Mediterranean and the Northeast Atlantic have shown that juveniles and adults can survive for some time at salinities of 18 ± 2 if slowly acclimatized (Boletzky, 1983; Guerra and Castro, 1988). In culture, some embryos of *S. officinalis* from eggs collected off the southwest coast of the Netherlands hatched at a salinity of 26.5, but there was no hatching below 23.9; below 22.4, embryos with morphological malformations were found (Paulij *et al.*, 1990a).

The temperature limits of the species range from 10 to 30°C. At temperatures <10°C, individual cuttlefish do not feed, remain inactive, and die within a couple of days (Richard, 1971; Bettencourt, 2000).

Hatchlings and young *S. officinalis* have been successfully cultured in tanks with an open seawater system in which the temperature reached 30°C (Domingues *et al.*, 2001b); indeed, the species lives in the lagoon system of the Ria Formosa (southern Portugal) where temperatures reach 27 ± 3°C in summer (Domingues *et al.*, 2002). Oxygen affinity in *S. officinalis*, expressed as P_{50} (partial pressure of gas at which the blood remains 50% saturated), increased as a function of temperature from 12 mm Hg at 5°C to near 38 at 17°C. This is an indication that the species does not have the ability to accommodate large temperature ranges in its natural habitat (Brix *et al.*, 1994). Recent findings by Melzner *et al.* (2006, 2007) support the hypothesis that the upper thermal tolerance limit is due to oxygen limitation. Moreover, Johansen *et al.* (1982) concluded that the common cuttlefish is not very tolerant of low oxygen concentrations. This may explain the variations in densities between the Northwest African coast and the northern Benguela, where low oxygen concentrations are common as a consequence of shallow-water eutrophication (Guerra and Sánchez, 1985).

Analysis of a time-series of 18 years of landings per unit effort of cuttlefish in southwestern Spain indicates that the abundance of *S. officinalis* does not correlate with rainfall, river discharge, or sea surface temperature (Sobrino *et al.*, 2002). The species is

apparently able to endure changing environments, not only during its adult phase, but also during the early juvenile stage (Sobrino *et al.*, 2002). However, strong precipitation had a negative influence on cuttlefish abundance in the Ria de Aveiro (central Portugal) and, together, high solar radiation, air temperature, near-bottom salinity, and good water clarity seemed to influence catches of the species positively (Jorge and Sobral, 2004).

6.6.2 Migrations

Seasonal migrations between shallow and deeper water are a well-known ecological feature of *S. officinalis*. In the western Mediterranean, they migrate inshore in spring and summer to mating/spawning grounds and offshore in autumn to to the winter feeding grounds, although not all animals migrate at the same time, size, and age (Mangold, 1966). The migrations are over different distances, from a few dozen to several hundred nautical miles, and represent an important displacement of biomass, something that has also been observed elsewhere (Richard, 1971; Najaï, 1983; Guerra and Castro, 1988; Boucaud-Camou and Boismery, 1991; Coelho and Martins, 1991; Le Goff and Daguzan, 1991b; Jorge and Sobral, 2004). The autumn/winter offshore migration in the English Channel is mainly influenced by cooling of littoral waters (Boucaud-Camou and Boismery, 1991). However, day-length reduction and decreased light intensity, which are other factors influencing maturation and spawning (Boletzky, 1983; Boucaud-Camou *et al.*, 1991), are also involved in this migration. Hence, the relatively deep milder waters at the central axis of the Channel seem to constitute the common hibernation area to all cuttlefish in the English Channel, which they leave at the end of winter. Spring inshore displacements are mainly attributable to an increase in temperature in littoral waters. These displacements were documented by tagging experiments (Boucaud-Camou and Boismery, 1991), but this spatial and temporal pattern is also supported by an analysis of georeferenced data from both sides of the English Channel (Dunn, 1999a; Denis and Robin, 2001; Royer, 2002; Wang *et al.*, 2003; Royer *et al.*, 2006). In the western part of the English Channel and the southern part of the Celtic Sea, local abundance is positively correlated with sea surface temperature, with cuttlefish expanding their distribution farther north in the spawning seasons in warm years. The centre of high abundance in offshore deep water shifts north in warm winters and south in cool winters (Wang *et al.*, 2003).

6.7 Trophic ecology

6.7.1 Prey

Sepia officinalis is a trophic opportunist: its diet includes crustaceans, bony fish, molluscs, polychaetes, and nemertean worms (Nixon, 1987; Castro and Guerra, 1990; Pinczon du Sel *et al.*, 2000). The main crustacean prey items are mysids, shrimps, prawns, and crabs, but *S. officinalis* also feeds on amphipods, isopods, and ostracods. It feeds on gobies, sandeels, whiting, and wrasses, but can also prey on some flatfish. The most common cephalopod prey are various sepiolid and sepiid species (Table 6.3). Large cuttlefish are also cannibalistic, capturing and eating smaller individuals. Amphipods, mysids, caridean shrimps, and other small crustaceans, which commonly swarm in large schools just above the bottom, are important in the diet of juvenile cuttlefish (Nixon and Mangold, 1998; Blanc *et al.*, 1998). Cannibalism begins during the juvenile stage (ML < 3.0 cm) (Henry and Boucaud-Camou, 1991). Other small-sized items found in the stomach of cuttlefish, such as bryozoans, foraminiferans, bivalve molluscs, insects, and algae, should be regarded with caution, because they could be the prey of prey, or accidentally ingested (Castro and Guerra, 1990).

Table 6.3. Prey composition of *Sepia officinalis*, **as known from studies in the Mediterranean Sea and the Northeast Atlantic (compiled from Najaï and Ktari, 1979[1]; Castro and Guerra, 1989[2]; Le Mao, 1985[3]; Castro and Guerra, 1990[4]; Henry and Boucaud-Camou, 1991[5] Pinczon du Sel and Daguzan, 1997[6]; Blanc** *et al.*, **1998[7]; Nixon and Mangold, 1998[8]; Pinczon du Sel** *et al.*, **2000[9]; Vafidis** *et al.*, **2009[10]).**

Taxon	Species
Osteichthyes	
Ammodytidae	*Ammodytes tobianus* (small sandeel)[4], indet.[4,8]
Anguillidae	*Anguilla anguilla* (European eel)[6,8]
Atherinidae	*Atherina presbyter* (sand smelt)[3,8]
Belonidae	*Belone belone* (garfish)[3]
Bothidae	*Arnoglossus laterna* (Mediterranean scaldfish)[2], *Arnoglossus* spp.[2]
Callionymidae	*Callionymus lyra* (dragonet)[3,4], indet.[8]
Carangidae	*Trachurus trachurus* (Atlantic horse mackerel)[8]
Clupeidae	indet.[3]
Gadidae	*Trisopterus luscus* (pouting)[2], *Trisopterus* spp.[4,6], indet.[3]
Gobiidae	*Aphia minuta* (transparent goby)[4], *Deltentosteus quadrimaculatus* (four-spotted goby)[4], *Gobius niger* (black goby)[4], *G. paganellus* (rock goby)[4], *Gobius* spp.[2,4,7], *Lesueurigobius friesii* (Fries's goby)[2,4], *Pomatoschistus minutus* (sand goby)[4], *P. pictus* (painted goby)[4], *Pomatoschistus* spp.[3,4], indet.[3,6,8]
Gobiesocidae	*Lepadogaster* spp.[4]
Labridae	*Symphodus* spp.[4], indet.[3,4,6,8]
Moronidae	*Dicentrarchus labrax* (European seabass)[3]
Mullidae	*Mullus surmuletus* (striped red mullet)[8]
Pleuronectidae	indet.[3]
Soleidae	*Buglossidium luteum* (solenette)[4], indet.[8]
Sparidae	*Spondyliosoma cantharus* (black seabream)[3]
Syngnathidae	*Syngnathus acus*[3], *S. typhle* (broadnosed pipefish)[4], *Sygnathus* spp.[3,4,6,7], indet.[4]
Trachinidae	*Echiichthys vipera* (as *Trachinus vipera*) (lesser weaver)[4]
Crustacea	
Decapoda	
Dendrobranchiata-Penaeiodea	*Penaeus* spp.[1]
Macrura reptantia-Astacidea	*Nephrops* spp.[8]
Pleocyemata-Anomura	Galatheidae indet.[4], *Pagurus bernhardus*[3], Paguridae indet.[4], *Pisidia longicornis*[2,3,4], *Porcelana platycheles*[2,4], Porcellanidae indet.[2]
Pleocyemata-Axiidea	indet.[7]
Pleocyemata-Brachyura	*Asthenognathus atlanticus*[4], *Atelecyclus undecimdentatus*[2,4], *Carcinus maenas*[3,4,6,7,8], *Ebalia* spp.[8], *Galathea* spp.[8], *Inachus* spp.[3,4], *Liocarcinus corrugatus*[2], *L. depurator*[2,3,4,6,8], *L. marmoreus*[4], *L. navigator*[7], *Liocarcinus* spp.[3,4], *Necora puber* (as *L. puber*)[3,6,8], *Pilumnus spinifer*[4], *Macropodia rostrata*[3], *Macropodia* spp.[3,8], *Maja squinado*[3,8], Majidae indet.[3,4], *Polybius henslowii*[2], Portunidae indet.[2,3,4], indet.[2,6,7,8,9,10]

Pleocyemata-Caridea	*Crangon crangon*[2,3,4,6], (as *C. vulgaris*)[5,8], Crangonidae indet.[4], *Palaemon adspersus*[2,4,7], *P. serratus*[2], *Palaemon* spp.[4,6,7], Palaemonidae indet.[4], *Philocheras fasciatus* (as *C. fasciatus*)[5,8], *Processa edulis*[4], indet.[2]
Mysida	indet.[3,8,9,10]
Ostracoda	indet.[1]
Amphipoda	*Ampelisca brevicornis*[7], *A. spinipes*[3], *Ampelisca* spp.[3], Caprelloidea indet.[3,4], *Dexamine spinosa*[7], *Echinogammarus marinus*[7], *Ericthonius* spp.[3], Gammaridea indet.[3,4], *Phtisica marina*[7], indet.[1,3,4,7,9,10]
Isopoda	*Sphaeroma* spp.[1], indet.[7]
Copepoda	indet.[1]
Cephalopoda	
Sepioidea	*Sepia elegans*[4], *S. officinalis*[2,3,4,6,8], *Sepia* spp.[4], *Sepiola* spp.[2], indet.[1]
Gastropoda	Thecosomata indet.[1]
Bivalvia	Lamellibranchiata indet.[1], *Mytilus edulis*[3], *Polititapes virgineus*[3]
Polychaeta	*Marphysa* spp.[3], Nereidae indet.[3], indet.[1,9,10]
Nemertea	indet.[1]
Algae	*Cymodocea* spp.[1], *Posidonia oceanica*[2], *Zostera marina*[2], indet.[1,8]

Significant ontogenetic changes in the diet of this species have been found, with the progressive replacement of crustaceans by fish (Castro and Guerra, 1990). The natural diet of young cuttlefish (<8.5 cm ML) captured from the wild was mainly crustaceans (89%), with fish constituting only 4.6% (Blanc *et al.*, 1998). Ontogenetic changes in the size of prey taken have also been well documented (Blanc *et al.*, 1999; Blanc and Daguzan, 2000). Small specimens (ML <6.5 cm) of *S. officinalis* and adult *S. elegans* (ML 4.5–6.5 cm) consume similar prey, although in different proportions, suggesting there may be trophic competition between the two species at that size range (Castro and Guerra, 1990). Prey remains found in cephalopod stomachs tend to be difficult to identify visually because they are chopped into small pieces by the beaks during ingestion. Molecular prey identification currently looks to be the most promising solution (Roura *et al.*, 2012). Previous work used antisera raised to prey proteins, and a study by Kear and Boyle (1992) used *S. officinalis* as an experimental animal, showing that, when fed on *Euphausia superba*, prey antigenicity in the digestive tract persisted for up to 8 h.

Despite the small size of the mouth, cuttlefish can seize relatively large prey with their prehensile arms and tentacles. This, together with voracity, versatile feeding habit, and highly evolved visual and sensory systems, allows them to occupy a broad trophic niche. Further, migrations enable *S. officinalis* populations to exploit the temporal and spatial variability of productive systems and fluctuating populations of prey (Rodhouse and Nigmatullin, 1996).

The tentacles of *S. officinalis* can reach prey in less than 15 ms. Prey handling is rapid, and neurotoxins secreted by the posterior salivary glands paralyse the prey within 10 s of capture (Hanlon and Messenger, 1996). External digestion does not appear to take place, and (when feeding on crustaceans) many pieces of exoskeleton are ingested (Guerra *et al.*, 1988).

Several studies have investigated the diel pattern of feeding, showing that most feeding is during darkness (Castro and Guerra, 1989; Pinczon du Sel *et al.*, 2000; Quintela and Andrade, 2002). Hence, prey detection in *S. officinalis* may involve light emitted from their light organs or may even be facilitated by dinoflagellate luminescence (Fleisher and Case, 1995).

The trophic position of *S. officinalis* in an estuarine community (a *Zostera* meadow in San Simón Inlet, Ría de Vigo) was investigated using ¹³C and ¹⁵N stable isotope signatures from muscle tissue of *S. officinalis* and sympatric organisms (Filgueira and Castro, 2002). Surprisingly, small cuttlefish appeared to be at a higher trophic level. This may be explained by the complex migrations and life cycle of the species. The smallest mature animals used in this study (60 mm ML for males and 80 mm ML for females) might never have left San Simón Inlet, their isotopic composition representing the local foodweb. The largest animals were probably coming back from deeper water and had an isotopic composition that did not result from the local foodweb. As the metabolic rate of large animals is slower than that of smaller ones, isotopic signals from deeper water will also persist longer in their tissues. Using more tissues with different nitrogen and carbon turnover rates can, therefore, be useful (e.g. Hobson and Cherel, 2006).

6.7.2 Predators

The first evidence of predation on eggs of *S. officinalis* came from the Ría de Vigo (northwestern Spain) at a depth of 10 m in late April 2010. A tompot blenny (*Parablennius gattorugine*) attacked a black ink-stained cuttlefish egg mass in a late stage of development that had been laid on pod weed (*Halydris siliquosa*) (Guerra and González, 2011). Recently, various crab species have also been recorded as preying upon *S. officinalis* eggs (Á. Guerra, pers. comm.).

Juvenile and adult *S. officinalis* are preyed upon by a wide range of fish species, and adult *S. officinalis* are taken by several species of marine mammal (Table 6.4). Hatchling and juvenile common cuttlefish are taken by *Serranus cabrilla* in *Posidonia* grass areas of the Mediterranean (Hanlon and Messenger, 1988). Pollack (*Pollachius pollachius*) exert great predatory pressure on young cuttlefish in French waters of northern Brittany (Le Mao, 1985). In the Bay of Biscay, Velasco *et al.* (2001) found *S. officinalis* in the stomach contents of *Pagellus acarne*, *Aspitrigla cuculus*, *A. obscura*, *Lophius piscatorius*, *L. budegassa*, *Trisopterus luscus*, *Lepidorhombus whiffiagonis*, and *L. boscii*. In Morbihan Bay, young cuttlefish have been found in the stomach contents of *Dicentrarchus labrax*, *Labrus bergylta*, *Spondyliosoma cantharus*, and *Conger conger* (Blanc and Daguzan, 1999). Elsewhere, *S. officinalis* has been recorded from the stomachs of numerous teleosts and cartilaginous fish species (Table 6.4).

Two pinnipeds (Atlantic grey and monk seals) and three dolphin species (bottlenose, Risso's, and oceanic striped) are known to feed on *S. officinalis* (Table 6.4). Additionally, some remains identified as *Sepia* spp. or simply Sepiidae have been observed in the harbour porpoise and in bottlenose, common, and oceanic striped dolphins (Santos, 1998).

Table 6.4. Known predators of *Sepia officinalis* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Chondrich-thyes	Black-mouthed dogfish (*Galeus melastomus*)	Velasco *et al.* (2001)
	Blainville's dogfish (*Squalus blainville*)	Martinho *et al.* (2012)
	Bluespotted seabream (*Pagrus caeruleostictus*)	Hamida *et al.* (2010)
	Blue shark (*Prionace glauca*)	Clarke and Stevens (1974)
	Bull ray (*Pteromylaeus bovineus*)	Capapé (1977)
	Lesser spotted dogfish (*Scyliorhinus canicula*)	Morte *et al.* (1997), Kabasakal (2002), Martinho *et al.* (2012)
	Pelagic stingray (*Pteroplatytrygon violacae*)	Lipej *et al.* (2013)
	Smooth-hound (*Mustelus mustelus*)	Morte *et al.* (1997), Saïdi *et al.* (2009)
Osteichthyes	Ballan wrasse (*Labrus bergylta*)	Blanc and Daguzan (1999)
	Bib (*Trisopterus luscus*)	Velasco *et al.* (2001)
	Black seabream (*Spondyliosoma cantharus*)	Blanc and Daguzan (1999)
	Black-bellied angler (*Lophius budegassa*)	Velasco *et al.* (2001)
	Brill (*Scophthalmus rhombus*)	Vinagre *et al.* (2011)
	Comber (*Serranus cabrilla*)	Hanlon and Messenger (1988)
	Common pandora (*Pagellus erythrinus*)	Rosecchi (1983)
	Conger eel (*Conger conger*)	Blanc and Daguzan (1999)
	Dusky grouper (*Epinephelus marginatus*)	Reñones *et al.* (2002)
	European barracuda (*Sphyraena sphyraena*)	Kalogirou *et al.* (2012)
	European hake (*Merluccius merluccius*)	Larrañeta (1970), Velasco *et al.* (2001)
	European seabass (*Dicentrarchus labrax*)	Blanc and Daguzan (1999)
	Fourspot megrim (*Lepidorhombus boscii*)	Velasco *et al.* (2001), Teixeira *et al.* (2010)
	Greater amberjack (*Seriola dumerili*)	Matallanas *et al.* (1995)
	Longfin gurnard (*Aspitrigla obscurus*)	Velasco *et al.* (2001)
	Megrim (*Lepidorhombus whiffiagonis*)	Velasco *et al.* (2001)
	Monkfish (*Lophius piscatorius*)	Daly *et al.* (2001), Velasco *et al.* (2001)
	Pollack (*Pollachius pollachius*)	Le Mao (1985)
	Red gurnard (*Aspitrigla cuculus*)	Velasco *et al.* (2001)
	Silver-cheeked toadfish (*Lagocephalus sceleratus*)	Kalogirou (2011)

	Spanish bream (*Pagellus acarne*)	Velasco *et al.* (2001), Fehri-Bedoui *et al.* (2009)
	Spotted flounder (*Citharus linguatula*)	Teixeira *et al.* (2010)
	Swordfish (*Xiphias gladius*)	Hernández-García (1995), Salman (2004)
	Turbot (*Scophthalmus maximus*)	Vinagre *et al.* (2011)
	Twaite shad (*Alosa fallax*)	Assis *et al.* (1992)
	Yellow-mouth barracuda (*Sphyraena viridensis*)	Kalogirou *et al.* (2012)
	Yellow-stripe barracuda (*Sphyraena chrysotaenia*)	Kalogirou *et al.* (2012)
Pinnipedia	Atlantic grey seal (*Halichoerus grypus*)	Ridoux *et al.* (2007)
	Monk seal (*Monachus monachus*)	Salman *et al.* (2001)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	Cockcroft and Ross (1990), Poldan (2004), Dos Santos *et al.* (2007)
	Risso's dolphin (*Grampus griseus*)	Clarke and Pascoe (1985), Blanco *et al.* (2006), Bearzi *et al.* (2011)
	Oceanic striped dolphin (*Stenella coeruleoalba*)	Spitz *et al.* (2006)

6.8 Other ecological aspects

6.8.1 Parasites

Various parasites, including protistans and metazoans, such as fungi, coccidians, microsporidians, ciliates, dicyemids, diageneans, cestodes, nematodes, brachyurans, copepods, and isopods, are known in juvenile and adult *S. officinalis*, but most of them do not appear to be very important as mortality factors at pre-reproductive stages. For example, the copepod *Metaxymolgus longicaudata* is sometimes associated with this cuttlefish, but its effects have not been elucidated (Ho, 1983). Massive digestive tract infections with *Aggregata eberthi* might result in a decrease or malfunction of absorption enzymes (Gestal *et al.*, 2002a, b). Sexual stages of the coccidian *Aggregata eberthi* are found in the digestive tract of *S. officinalis*, and asexual stages infect the digestive tract of crustaceans. Transmission is likely via consumption.

The virus-like particles found in the stomach epithelium of wild *S. officinalis* have a structure similar to vertebrate "retroviruses" (Hanlon and Forsythe, 1990). Cultured in the laboratory, this species showed susceptibility to a highly virulent systemic infection by bacteria (*Pseudomonas* and *Vibrio*), which does not appear to be related to external injury (Hanlon and Forsythe, 1990).

To date, few interspecific associations (excluding parasitism) have been reported for this species. Bacterial populations associated with *S. officinalis* have been localized, mainly in the accessory nidamental glands, the renal appendages, and the shell epithelium. The accessory nidamental glands are coloured intense orange-red in mature females, and this colour is due to carotenoid pigments, which are found in symbiotic bacteria (Van den Branden *et al.*, 1980). Five symbiotic bacterial taxa (*Agrobacterium*, *Roseobacter*, *Rhodobium-Xanthobacter*, *Sporichthya*, and *Clostridium*) were identified in the tubules of the accessory nidamental glands, and three taxa of Pseudomonodaceae were located in the renal appendages and the shell epithelium. All these bacteria, except

Gram-positive ones, were also present in embryos, suggesting vertical transmission, i.e. maternal transmission at egg stage (Grigioni and Boucher-Rodoni, 2002).

6.8.2 Contaminants

Studies on the concentration and distribution of heavy metals in tissues of *S. officinalis* have shown high levels of bioaccumulation (Miramand and Bentley, 1992; Bustamante *et al.*, 2004, 2006; Miramand *et al.*, 2006; Lacoue-Labarthe *et al.*, 2008a, b, 2009, 2010). Culture experiments at different stages of the life cycle of *S. officinalis* using zinc and cadmium tracers with seawater, sediments, and food as uptake pathways showed that food is the likely primary route for bioaccumulation, and that the digestive gland plays a major role in the subsequent storage and presumed detoxification of these elements, regardless of the uptake pathway (Bustamante *et al.*, 2002a, b). Bioaccumulation rates of silver and cadmium during early development have been observed to differ (Lacoue-Labarthe *et al.*, 2008a).

Juvenile physiology (digestive, immune and nervous systems) can be disturbed by heavy metals (e.g. silver, cadmium, copper) and some pharmaceutical residuals (Le Bihan *et al.*, 2004), impacting behaviour and negatively affecting embryo growth and hatchling survival (Le Bihan *et al.*, 2004; Lacoue-Labarthe *et al.*, 2010; Di Poi *et al.*, 2013). Ecotoxicological studies using bioassays from isolated digestive gland cells demonstrated that some heavy metals (copper, zinc, and silver) disrupt enzymatic systems (Le Bihan *et al.*, 2004). Malformed common cuttlefish caught in the Bay of Arcachon could be a product of the teratogenic effects of the antifouling compound tributyltin (TBT) (Schipp and Boletzky, 1998).

6.8.3 Behaviour

The seasonal migrations between shallow and deeper waters bring *S. officinalis* into contact with various types of soft and rocky bottoms. The ability of small juveniles to attach themselves to a hard substratum may be important because it allows them to withstand strong water movement without being carried away. These animals are able to bury themselves in soft bottoms, and the behavioural pattern of this sand covering is well established at hatching (Boletzky, 1983). *Sepia officinalis* has a considerable repertoire of defensive strategies involving a large number of chromatic, textural, and postural components (Hanlon and Messenger, 1996).

Sepia officinalis does not form shoals, neither in the wild or in the laboratory (Guerra, 2006). However, in culture, individuals tolerate one another except under extreme food deprivation. This tolerance is higher in young animals than in subadults and adults (Hanlon and Messenger, 1996). A feeding hierarchy first appearing after 4 months, which stabilizes after 5 months, has been found in the species (Warnke, 1994). Captive-rearing experiments indicated that the behaviour of *S. officinalis* is strongly affected by aquarium conditions and suggested that the species is probably semi-solitary under natural conditions (Boal *et al.*, 1999).

6.9 Fisheries

Sepia officinalis is an important species for the commercial fisheries of many countries. In data reported by FAO, most cuttlefish landings for the Northeast Atlantic area are grouped under "Cuttlefish and bobtail squid nei", with only a small proportion distinguished as common cuttlefish. However, both these categories likely consist mainly of *S. officinalis.* Cuttlefish landings from this area increased rapidly after the mid-1980s, rising from a (then) high of 12 000 t to almost 31 000 t in 2004. FAO values for the Mediterranean indicate that common cuttlefish landings have been relatively stable

over the past two decades (typically ca. 10 000 t annually), but again a large proportion (≥50%) of landings of Sepiidae are grouped under "Cuttlefish and bobtail squid nei", so the true figures for *S. officinalis* are uncertain. The mean annual catch of this species in Europe during the years 1993–2003 was ca. 41 000 t, taken more or less equally from the Atlantic and the Mediterranean (Hastie *et al.*, 2009a).

In European waters, French and Italian fisheries make the biggest landings. The main areas of capture of cuttlefish are Italian waters, the English Channel, and the Bay of Biscay. The UK, Greece, Spain, and Portugal are also important European producers, as are Tunisia, Turkey, and Morocco outside of Europe. In northern areas (English Channel and adjacent waters), *S. officinalis* is usually the only cuttlefish species landed, whereas in southern fisheries, official statistics can include other Sepiidae (mainly *S. elegans* and *S. orbignyana* and farther south – Mauritania, Senegal – *S. hierredda*).

Northern fisheries are mainly based on trawling (Dunn, 1999a, b; Denis and Robin, 2001), although trap fishing can be significant during the inshore spawning season. Farther south, cuttlefish are caught by a variety of artisanal gears, including gillnets, trammelnets, traps, and jigs.

Recruitment is defined as the renewal of a stock via young classes that enter the fishery, so it depends on the size selectivity of the fishery and on the life cycle of the exploited population. In *S. officinalis*, both factors vary widely across the distribution range. Trawlers that land the majority of cuttlefish in many regions operate on both inshore and offshore fishing grounds and take both juvenile and adult specimens, whereas traps catch mainly spawning adults in inshore waters.

In the English Channel fishery, the length structure of trawler landings suggest that juveniles enter the fishery in autumn and spring; there are two peaks for each annual cohort, related to the migration cycle (Royer *et al.*, 2006). However, a more detailed analysis of age-at-recruitment (Challier *et al.*, 2005) showed that the second peak was not constant and that age-at-recruitment was similar throughout the year (3–4 months). UK beam trawlers operating offshore probably catch only larger and older cuttlefish, but there is no biological sampling available for that fleet.

Studies have shown considerable genetic structuring throughout the range of *S. officinalis* (e.g. Pérez-Losada *et al.*, 1999, 2002, 2007; Wolfram *et al.*, 2006; Turan and Yaglioglu, 2010). This is generally best explained by a model of isolation by distance, although some contemporary physical barriers to gene flow do exist, including the Almería–Oran front.

High population structuring favours treating local populations, like that exploited by inshore small-scale fisheries in San Simon Inlet, as discrete stocks. Indeed, mtDNA evidence of population structuring in Turkish coastal waters has been further supported by studies on body morphometry and cuttlebone chemistry, revealing four discrete stocks in Antalya and Iskenderun bays, Izmir Bay in the Aegean Sea, and the Sea of Marmara (Turan and Yaglioglu, 2010). However, genetic differences are unclear in northern fisheries (Wolfram *et al.*, 2006). Spatial distribution on wintering grounds suggests that there can be exchanges between the Bay of Biscay and the English Channel (Wang *et al.*, 2003). The rationale for defining the English Channel stock as a management unit relies on the fact that catch per unit effort is lower in adjacent waters (Royer *et al.*, 2006). Also, the life cycle is 2 years there, but can be shorter in the Bay of Biscay.

There is currently no routine stock assessment of this species in Europe. However, several exercises have been carried out to test the feasibility of different methods and to indicate the exploitation status of past cohorts.

In the *S. officinalis* gillnet fishery in San Simón Inlet during 1997–2001, the estimated instantaneous rate of natural mortality (M) over a 6-month period (November–April) was in the range 2.27–3.38, the mean being 2.70 (Outeiral, 2002; F. Rocha, pers. comm.; Á. Guerra, pers. comm.). These values were estimated by different methods based on data for the Galician Rías from Guerra and Castro (1988) and Bettencourt (2000) and are similar to those calculated by Emam (1994) for the exploited population of *Sepia prashadi* in the Gulf of Suez. The mean value of M estimated for *S. officinalis* in San Simón Inlet corresponds to an annual mortality rate (A) of ca. 93% of the total number of individuals of a given population, which is very high, and reflects the known catastrophic post-spawning mortality.

The first model of population abundance and exploitation rate applied to *S. officinalis* was developed in the Bay of Biscay (Gi Jeon, 1982). That exercise used virtual population analysis (VPA), with a monthly time-scale for catches and two age groups (according to the bimodal length structure). Low exploitation rates were obtained, but it is questionable whether the authors had access to sufficiently comprehensive fishery statistics in the years 1978–1979.

In the English Channel, Leslie–De Lury depletion methods were applied by Dunn (1999b) "assuming a UK stock" (French catches were not included even if they were fished in English waters). That approach relies on the existence of homogeneous trends in landings per unit effort, and data from the UK beam trawl fleet were more suitable than data from the French otter-trawl fleet. UK beam trawlers operate offshore, whereas French trawlers move between inshore and offshore areas, with consequent variations in cuttlefish catchability.

The whole English Channel cuttlefish stock was assessed using VPA with a monthly time-scale by Royer *et al.* (2006). Recruitment strength varied by a factor of two for cohorts in the years 1996–1999. The exploitation pattern suggested greatest fishing mortality at older ages and showed cohorts fully exploited, but without significant growth-overfishing (when catches are made before the cohort reaches maximal biomass). Interactions between fishing fleets underlined the fact that catches of inshore trapfishing depend on the activity of offshore trawlers (which fish the cohorts at a younger stage in winter). It is worth noting that the consequence of trapfishing for adults on recruitment (i.e. recruitment-overfishing) in the trawl fishery could not be estimated in the absence of a stock–recruitment relationship.

In small-scale fisheries, like those around the Galician coast, the quality of fishery statistics can be improved using interviews and applying the Gomez–Muñoz model (Rocha *et al.*, 2006).

On other fishing grounds, abundance trends have been monitored even if no population model has yet been fitted. Landing-per-unit-effort indices for the Gulf of Cádiz (Sobrino *et al.*, 2002) and for Portuguese waters (Jorge and Sobral, 2004) are useful for analysing fishery and environmental variations.

Sepia officinalis fisheries are probably close to their maximum sustainable production in several areas of the species distribution given that negative trends in captures have been observed in recent years in some heavily fished areas (e.g. the Mediterranean).

In the European Union, *S. officinalis* is not a quota species. Nevertheless, some management measures have been implemented at local scales. Minimum landing size restrictions exist in Galicia (8 cm ML) and also in Portugal (Hastie *et al.*, 2009a). The reduction in catches of recruits in France is sought via the progressive banning of trawlers within 3 miles of the coast.

Existing fishing effort limitations mainly concern métiers specifically targeting cuttle-fish, such as trapfishing. In Normandy (France), the trapfishing fleet is regulated via licences, which also state the number of traps allowed per boat.

Common cuttlefish is usually marketed fresh or frozen and is a highly appreciated food item, particularly in European Mediterranean countries, Spain, Portugal, Japan, China, and the Republic of Korea.

6.10 Aquaculture

Sepia officinalis adapts easily to laboratory culture because of its large eggs, good sur-vival of hatchlings, voraciousness of the hatchlings, sedentary behaviour, tolerance to crowding and handling, acceptance of dead prey, and easy reproduction in captivity (Forsythe *et al.*, 1994). Therefore, laboratory culture has been successful around the world since the early 1960s (Schröder, 1966; Richard, 1966, 1971, 1975; Pascual, 1978; Yim, 1978; Boletzky, 1979a, 1983; Boletzky and Hanlon, 1983; DeRusha *et al.*, 1989; Lee *et al.*, 1991; Forsythe *et al.*, 1994; Domingues, 1999; Bettencourt, 2000; Domingues *et al.*, 2001b, 2002, 2006).

During the first few weeks of their life, cuttlefish have to be fed live prey, usually mysid shrimps (Richard, 1975; Forsythe *et al.*, 1994; Domingues, 1999; Domingues *et al.*, 2001a). Subsequently, they accept dead food such as frozen shrimps, fish, and crabs (De Rusha *et al.*, 1989; Forsythe *et al.*, 1991; Koueta and Boucaud Camou, 1999; Domingues *et al.*, 2001b; Koueta, 2001; Koueta *et al.*, 2002). Some researchers have cul-tured the species using this transition to dead food (Pascual, 1978; Forsythe *et al.*, 1994), whereas others fed live prey throughout the life cycle (Domingues *et al.*, 2001a, b, 2002).

In the past few years, feeding experiments using *S. officinalis* have been conducted with either moist or dry pellets (Castro, 1990; Lee *et al.*, 1991; Castro *et al.*, 1993) or surimi (fish myofibrillar protein concentrate (Castro *et al.*, 1993; Castro and Lee, 1994; Domingues, 1999; Domingues *et al.*, 2005), demonstrating that cuttlefish readily accept prepared diets. Feeding rates on prepared diets have been considerably lower than with a normal laboratory maintenance diet of crustaceans (Richard, 1971, 1975; Pascual, 1978; Boletzky, 1979a; Lee *et al.*, 1991; Castro *et al.*, 1993; Castro and Lee, 1994; Forsythe *et al.*, 1994; Koueta and Boucaud-Camou, 1999, 2001; Koueta *et al.*, 2000; Domingues *et al.*, 2001b, 2002, 2003a, b, 2004), and also considerably lower than rates during transition periods when cuttlefish were fed thawed catfish fillets. During these transition periods, feeding rate varied between 3.5 and 10% BW d^{-1} (Domingues, 1999). Despite the ac-ceptance of the prepared diets, negative growth with artificial diets was common, and the fastest growth rates reported in the literature, close to 0.5% BW d^{-1} (Castro, 1990; Lee *et al.*, 1991; Castro *et al.*, 1993; Castro and Lee, 1994; Domingues, 1999; Domingues *et al.*, 2005) are almost tenfold lower than growth rates recorded during normal labor-atory maintenance of this species (5% BW d^{-1}) (Pascual, 1978; Lee *et al.*, 1991; Forsythe *et al.*, 1994; Domingues *et al.*, 2001b, 2002; Sykes *et al.*, 2003). Also, mortality rates when feeding artificial diets are usually higher than with natural diets (DeRusha *et al.*, 1989; Lee *et al.*, 1991; Castro *et al.*, 1993). Effects of polyunsaturated fatty acids (PUFA) in the diet on survival, acceptance of alternative food, and growth of juvenile cuttlefish have been demonstrated (Koueta *et al.*, 2002, 2006).

Prey density also affects growth of *S. officinalis*; faster growth rates were obtained at higher prey density, and vice versa.

Because of the ease of culture and progress in culturing methods, *S. officinalis* is an ideal laboratory animal for various experimental purposes and a useful research model in

physiology, neuroscience, nutritional biochemistry, ageing, molecular biology, and immunology (Sykes *et al.*, 2006).

6.11 Future research, needs, and outlook

The biology of *S. officinalis* is relatively well known; it is the most extensively studied of all cuttlefish species. Nevertheless, there are still uncertainties concerning the separation of stocks and populations. The effects of climatic change on the distribution and abundance of *S. officinalis* populations does need to be studied. Of particular importance is the threat of increasing ocean acidification, because the cuttlebone and statoliths of *S. officinalis* are calcareous structures, and their development is heavily influenced by pCO$_2$ in seawater. Experimental studies show that during elevated seawater pCO$_2$ conditions, cuttlebone calcification increases (Gutowska *et al.* 2008, 2010a, b), and that morphology and calcification in statoliths of hatchlings are distorted, leading to abnormalities in balance maintenance and prey-capture efficiency (Maneja *et al.,* 2011).

Recent experimental studies demonstrate that diet, temperature, and salinity can affect trace-element composition in the statoliths of *S. officinalis* (Zumholz, 2005; Zumholz *et al.,* 2006, 2007a). Further, investigations on the carbon- and oxygen- isotope composition and ratios (δ^{18}O, δ^{13}C) of the cuttlebone of *S. officinalis* have been shown to be a useful a tool for predicting ecological information and environmental history scenarios (e.g. Bettencourt and Guerra, 1999; Rexfort and Mutterlose, 2006).

Because of the short life cycle and often dramatic changes in popuation abundance, fishery management of the species is difficult, and stocks require regular monitoring. The current low level of routine fishery data collection on European cephalopods, including *S. officinalis*, coupled with the high data demands associated with stock assessments, means that analytical assessment is generally impractical. Therefore, the ICES Working Group on Cephalopod Fisheries and Life History recommended examining trends in relative exploitation rates (i.e. catch/survey biomass) by seasonal cohort. The Group also recommended a comparison of maturity and length composition data by cohort, from research surveys and the fishery, in order to assess trends in recruitment and length at 50% maturity (L$_{50}$) (ICES, 2010). Fundamental to the implementation of any such approach is the collection of reliable species-level landings statistics.

To carry out analytical stock assessments on such short-lived species, it is necessary to monitor biological variables regularly, ideally every week or month. Quarterly sampling is insufficient for any cephalopod species. Even length composition sampling should be carried out on a more regular basis in those métiers in which cephalopods are considered as "G2 species". In order to avoid unnecessary sampling effort, however, sampling should take into account the seasonality of cephalopod landings and discards, with sampling concentrated during times when cephalopod catches are biggest (ICES, 2010).

Effective technologies using statoliths and new methods for age determination in this species are also needed. Age determination is important for understanding the demographic structure of populations and hence to improve the sustainable exploitation of this species. Finally, study of anthropogenic contaminant bioaccumulation would improve knowledge of the effects of these toxins on the recruitment phase and on the quality of mature animals as human food.