3 Biology and ecology of cephalopod species commercially exploited in Europe

3.1 Species accounts

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3.1.1 Introduction to the main groups of fished cephalopods in Europe

In nearly all commercial situations throughout Europe, there is no species determination in catches of cephalopods. This has been underlined in WGCEPH reports over the years because it is reflected in the official statistics made available to the scientific community. In addition, cephalopods are landed by both commercial and artisanal fleets, and landings from the latter have been relatively poorly documented in the past. As a result of these problems, the utility of cephalopod landings data for assessment of stock status has been called into question (ICES, 2008, 2009). The new métier-based data-collection system introduced in 2009 may help overcome these issues, in that all species caught in sampled métiers should be identified and, indeed, all important métiers should be sampled (see Section 5).

Official cephalopod landing statistics in Europe generally refer to four groups of species that are analogous from country to country, varying only to the extent that their composition reflects species distribution: (i) long-finned squid, (ii) short-finned squid, (iii) cuttlefish, and (iv) octopus. In some countries (e.g. Sweden), the two squid groups are lumped together.

Although there has been little or no official species determination, the identity of the species comprising each of the groups is, largely, known from current or previous scientific sampling. In some cases, the proportions of the main species in each of the groups have been determined, usually within the scope of short-term projects. Proportions of the different species are found to vary seasonally and annually and may also differ according to the gear used (see Bruno, 2008, in relation to landings of *Illex coindetii* and *Todaropsis eblanae* in Galicia, Spain).

In this section, short accounts of each of the main species that occur in commercial catches within European waters are presented, and the countries where species are landed are identified. Each of these species is briefly described, and their main biological and ecological characters are highlighted. Information is drawn from mainstream scientific publications, "grey" literature, and unpublished sources, including original research conducted by the authors. Full descriptions of the main species will be presented in a separate report.

3.1.1.1 Long-finned squid

This group is composed exclusively of species belonging to the family Loliginidae. All of the species exploited in Europe occur in relatively shallow water and are mostly caught by demersal gear. They are among the most valued squid species and generally command higher prices in the market than short-finned squid.

Four species are caught and landed in Europe, of which two are relatively large and two are very small. Adults of the two larger species are similar in size and appearance but can normally be distinguished from each other, whereas the two

smaller species are difficult to distinguish from each other and from the juveniles of the two larger species. They can occur sympatrically, and their identification, therefore, poses problems.

Post-recruit specimens of *Loligo forbesii* can be superficially distinguished from *L. vulgaris* principally by the larger size of the medial suckers on the tentacular club in *L. vulgaris*, whereas in *L. forbesii*, all the suckers are subequal in size (Roper *et al*., 1984). In addition, the papillae present on the terminal portion of the hectocotylus of mature male *L. forbesii* are not found in mature males of *L. vulgaris. Loligo forbesii* has prominent longitudinal stripes of dark chromatophores on the anterior and ventro-lateral surfaces of the mantle. Even though large specimens of *L. vulgaris* can sometimes display similar stripes, these are smaller than in *L. forbesii*, less numerous and different in appearance (Jereb and Ragonese 1986); those of *L. forbesii* are very characteristically "flame-like": each stripe is surrounded by white tissue (devoid of chromatophores) after which a line or border of slightly darker chromatophores is visible to delimit the area surrounding the stripe. In life, *L. forbesii* is usually coloured with more orange tones and *L. vulgaris* with more purple tones.

Alloteuthis spp. can be separated from other members of the family Loliginidae on the basis of their small size as adults and the fact that the mantle length (ML) is 6–15 times greater than its width, i.e. it has a narrower body than all other species. Adult male *A. subulata* and *A. media* possess tentacular club suckers similar to those found in *L. vulgaris*, but the fins do not extend beyond 50% of the total ML, except possibly in male *A. subulata*. Until recently, relative tail length was the characteristic most commonly used to distinguish *A. media* and *A. subulata*. However, molecular data from *Alloteuthis* specimens across the geographic range of the species have demonstrated this characteristic to be unreliable (Anderson *et al*., 2008). As this raises doubts about the reliability of previous identifications, we treat these two species under *Alloteuthis* spp. in this section, although we continue to refer to previous studies using the species name as determined by the author(s) of those studies.

3.1.1.2 Short-finned squid

This group comprises species mainly belonging to the family Ommastrephidae. Occasionally very abundant and very important in catches, landings, and exports from Europe, short-finned squid are less valuable in the market than long-finned squid and more prone to extreme variations in abundance. They all have pelagic distributions and, although sometimes caught demersally, are mainly taken from the water column by trawling and from high-rising gill- and trammelnets.

Three species are most commonly landed in Europe. *Illex coindetii* and *Todaropsis eblanae* mainly occur in the south, but both are occasionally frequent in the north. *Todarodes sagittatus* is more abundant in the north. Particularly in the northern extremes, *Gonatus fabricii* Lichtenstein, 1818, a short-finned squid of the family Gonatidae, is taken. We have not included an account for this species, or for other less frequent or occasional species, but the fact that other species may be landed means that specimens that do not appear to fit the descriptions of the most common species require careful identification.

3.1.1.3 Octopus

Landings in this category consist exclusively of species belonging to the family Octopodidae. Catches and landings are dominated in weight and number by a single

species, *Octopus vulgaris*, which is taken in greater numbers in the southern part of the ICES Area and farther south. Landings of the two *Eledone* species in the area are increasing. The genus *Octopus* is easy to distinguish from the genus *Eledone*, primarily by the presence of a double row of suckers on the arms of the former vs. a single row on the arms of the latter. However, the two *Eledone* species may be difficult to distinguish from each other if specimens are preserved or have been dead for some time. Several other European octopus species may be landed as catch from commercial vessels, but their low abundance makes it hard to determine the extent to which they are representative of regular catches.

3.1.1.4 Cuttlefish

Of the cephalopod categories landed in Western Europe, cuttlefish landings are the highest, mostly from catches concentrated over the continental shelf in the region of the southern Celtic Sea, the approaches to the English Channel, and the northeastern Bay of Biscay. Most landings are composed of catches of a single species, *Sepia officinalis*, but landings of at least two other species are also common in some European countries. Catches are made demersally by means of trawling and artisanal trapping.

The distinction between species can pose difficulties, particularly in juveniles, and more acutely in some geographical areas than in others, because the external appearance of *S. officinalis* varies across its distributional range.

Formerly, *S. officinalis* included two subspecies, *S. o. officinalis* and *S. o. hierredda*, the first distributed in the ICES Area and the second just outside, to the south. Although they are very similar in general appearance, morphological and genetic analysis has demonstrated that *S. officinalis* Linnaeus, 1758 and *S. hierredda* Rang, 1837, are clearly different species of the same genus (Guerra *et al*., 2001). As *S. hierredda* may also be found within the ICES Area, it is useful to know how to tell them apart. The mantle of *S. hierredda* is narrower than in *S. officinalis*, and the unmodified arms and the hectocotylized arm are shorter. The number of transverse rows of reduced suckers on the hectocotylus is generally larger (8 or 9 to 14) in *S. hierredda* than in *S. officinalis* (4 or 5 to 8 or 9). The striated zone of the cuttlebone of *S. officinalis* is somewhat smaller (41% of the ML) than in *S. hierredda* (47%). The cuttlebone of *S. officinalis* is slightly wider and thicker (38% and 13% of the ML, respectively) than that of *S. hierredda* (35% and 12%, respectively). The phragmocone and the outer cone of *S. officinalis* are wider than in *S. hierredda*. The cuttlebone of *S. officinalis* is slightly acuminate at the anterior end, whereas it is very acuminate in *S. hierredda*. The spine of the cuttlebone in *S. officinalis* is usually covered by chitin, especially in adults, whereas that of *S. hierredda* is never covered by chitin. As *S. hierreda* has only recently been recognized as a separate species, few landings data have been attributed to this species. A species account is therefore not included.

Sepia elegans and *S. orbignyana* are also sometimes confused with each other and with *S. officinalis* (particularly younger individuals). *Sepia elegans*, however, is the narrowest of the three, whereas *S. orbignyana* has a more pronounced spine at the terminal end of the cuttlebone than either of the other two.

3.1.2 *Loligo vulgaris* Lamarck, 1798

Common names. European squid (English); encornet (French); Europäischer Langflossenkalmar (German); calamary (Καλαμάρι; Greek); calamaro comune[1] (Italian); lula-vulgar (Portuguese); calamar común (Spanish).

3.1.2.1 Adult diagnostic features

Cornea present. Fins rhomboidal, their length up to ca. 66% of dorsal ML. Arms with two rows of suckers; sucker rings with 20 teeth, the distal ones large and pointed and the proximal ones minute or absent. Tentacular clubs with four longitudinal rows of suckers in the "manus", the suckers in the central rows being larger than the marginal ones. Buccal membrane with 15 tiny suckers on the extremity, each with chitinous rings. Left ventral arm (IV) of male hectocotylized. Simple funnel-locking cartilage (Roper *et al*., 1984).

3.1.2.2 Distribution and habitat

Loligo vulgaris occurs along the eastern Atlantic from the British Isles (55°N) to the Gulf of Guinea (20°S; Roper *et al*., 1984), extending out to Madeira (Clarke and Lu, 1995), and throughout the Mediterranean Sea (Belcari, 1999a). Adults are occasionally reported off the northwest coast of Scotland at 57°N (Pierce *et al*., 1994a; Hastie *et al*., 2009a), the North Sea (De Heij and Baayen, 2005), and the Kattegat and western Baltic Sea (Jaeckel, 1937; Muus, 1959; Hornborg, 2005). Paralarvae are absent north of the English Channel (Yau, 1994; Collins *et al*., 2002). *L. vulgaris* is a nectobenthic species that lives in the circumlittoral and upper bathyal zones (Worms, 1983).

3.1.2.3 Life history

Loligo vulgaris demonstrates high geographic variability of reproductive and growth parameters, and temperature is one of the main factors inducing such variability (Moreno *et al*., 2002). Males attain greater lengths (640 mm ML) than females (540 mm ML), with the maximum values recorded on the Saharan Bank (Raya, 2001). The life cycle may be completed within approximately one year, with maximum lifespans of 15 months recorded in western Iberia (Moreno *et al*., 1996; Rocha and Guerra, 1999).

Loligo vulgaris is a terminal spawner, but oocyte maturation and egg-laying occur in separate batches during the spawning period (Rocha and Guerra, 1996; Rocha *et al*., 2001). Fecundity has been estimated at between 10 150 and 42 000 eggs (Baddyr, 1988; Coelho *et al*., 1994; Guerra and Rocha, 1994; Laptikhovski, 2000). Mean spawning age is ten months, and mean age-at-maturity is nine months. Hatching time significantly influences mean age-at-maturity, which is higher in winter cohorts than in summer cohorts (Moreno *et al*., 2005).

The spawning season is shorter in the northern part of the distribution (Moreno *et al*., 2002; Sifner and Vrgoc, 2004). Elsewhere, spawning occurs throughout the year, with two main peaks between November and June, although these occur earlier in more southern latitudes and earlier in the Atlantic than in the Mediterranean (Baddyr, 1988; Coelho *et al*., 1994; Guerra and Rocha, 1994; Moreno *et al*., 1994, 2002; Rocha, 1994; Bettencourt *et al*., 1996; Villa *et al*., 1997; Raya *et al*., 1999; Belcari, 1999a). Spawning areas are poorly known, but egg-mass recoveries indicate that spawning occurs at depths of 2–120 m (Baddyr, 1988; Villa *et al*., 1997; Pereira *et al*., 1998).

[1] All Italian common names are taken from Bello and Borri (1990).

3.1.2.4 Trophic ecology

Predators. Various cetaceans, seals, large pelagic fish, and some demersal fish have been reported to prey on *L. vulgaris* (e.g. González *et al*., 1994a; Orsi-Relini, 1994; Morte *et al*., 1997; Börjesson *et al*., 2003; Salman, 2004; Peristeraki *et al*., 2005).

Prey. Paralarvae feed mainly on crustacean larvae, small mysids, and fish larvae (Boletzky, 1979a). Vertical migrations of paralarvae and juveniles are linked to feeding, and juveniles consume more planktonic prey than bentho-pelagic prey (Nigmatullin, 1975; Worms, 1983; Turk *et al*., 1986). Fish species increase in importance with increasing squid size and are the most frequent prey for adults (Rocha *et al*., 1994; Coelho *et al*., 1997; Lefkaditou, 2006).

3.1.2.5 Fisheries

In the Atlantic and Mediterranean, *L. vulgaris* is mainly a bycatch in the multispecies bottom and pelagic trawl fisheries. In the English Channel and French waters, landings of *Loligo* are normally a mixture of *L. vulgaris* and *L. forbesii* (the species are normally not separated in the official statistics). Farther south (e.g. off Spain and Portugal), *L. vulgaris* is the dominant long-finned squid in the landings (see Chen *et al*., 2006). It is a secondary target species in the Saharan Bank cephalopod trawl fishery (Raya *et al*., 1999) and in the western Portuguese coastal demersal trawl fishery (Fonseca *et al*., 2008). There are also small-scale, hand-jig artisanal coastal fisheries at depths of 20–350 m, especially in Spain and Portugal (Guerra *et al*., 1994). Near the coasts, where the species concentrates during autumn and winter for spawning, small-scale professional and sport fishers usually target the species using hand-jigs.

On the Greek, Portuguese, and northwest Spanish coasts, spawning aggregations are also occasionally targeted by a limited number of fishing vessels using beach-seine (a gear that catches higher quantities than hand-jigs and other artisanal gears), gillnets, and trammelnets. In Galicia (northwest Spain), a seasonal (mainly July–September) fishery targeting juvenile *L. vulgaris* takes place inside the Rías Bajas in waters of 3–40 m depth using seinenets with a bag ("boliche"; Guerra *et al*., 1994; Tasende *et al*., 2005). Juveniles generally recruit to the fishery at approximately 5 months of age (Moreno *et al*., 2007). Nevertheless, the age and size at recruitment to the fishery obviously depends on the fishing gear used. There is no regular assessment and management for *L. vulgaris* fisheries, but landing size restrictions are imposed in Portugal (and in Spain).

The species has been identified in commercial landings in the UK, France, Portugal, Spain, Italy, and Greece.

3.1.3 *Loligo forbesii* Steenstrup, 1856

Common names. Veined squid (English); encornet veiné (French); Langflossenkalmar (German); calamary (Καλαμάρι; Greek); calamaro venato, occhione (Italian); calamar veteado (Spanish); lula-riscada (Portuguese).

3.1.3.1 Adult diagnostic features

Cornea present. Rhomboidal fins of length ca. 75% of dorsal ML, posterior borders slightly concave. Arms with two rows of suckers. Suckers on the manus of the tentacular club are subequal in size; sucker rings with 13–18 sharp conical teeth. Unlike *L. vulgaris*, it lacks enlarged medial suckers on the tentacular club (suckers in all four rows are fairly similar in size). In males, the left ventral arm (IV) is hectocotylized in its distal third by modification of suckers into long papillae that

gradually decrease in size distally. Simple funnel-locking cartilage. Diagnosis adapted from Roper *et al.* (1984).

3.1.3.2 Distribution and habitat

Loligo forbesii is a neritic and largely demersal species occurring in coastal waters and the continental shelf from the Faroe Islands to 20°N in the eastern Atlantic, including the North Sea, extending into the Mediterranean and out to Madeira, the Canary Islands, and the Azores. The species is relatively rare south of the Bay of Biscay and is absent from the Baltic Sea (Roper *et al.*, 1984).

3.1.3.3 Life history

Loligo forbesii is commonly assumed to have an annual life cycle, with pulses of recruitment in April and August–November (Lum-Kong *et al.*, 1992; Pierce *et al.*, 1994a; Collins *et al.*, 1995, 1997; Belcari, 1999b), although some individuals may reach an age of ca. 18 months (Rocha and Guerra, 1999). As in other loliginid squid, the growth pattern comprises an early rapid "exponential" phase followed by a slower "logarithmic" phase (Forsythe and van Heukelem, 1987; Forsythe and Hanlon, 1989). Males can reach sizes larger (610 mm ML on the continental shelf; 940 mm in Azores) than females (420 mm and 460 mm), although some males mature at much smaller sizes (from ca. 120 mm; Boyle *et al.*, 1995), apparently representing alternative growth and maturation strategies, and leading to the presence of (at least) two microcohorts in the fished population (Collins *et al.*, 1999).

Loligo forbesii is semelparous, displaying "intermittent, terminal spawning", in which the females lay eggs in batches and die shortly after spawning (Rocha *et al.*, 2001). Many studies describe an extended spawning season, although it is unclear how long an individual continues to spawn (Guerra and Rocha, 1994; Moreno *et al.*, 1994; Collins *et al.*, 1995). Female *L. forbesii* produce only a few thousand (up to 23 000) eggs in their lifetime, with larger females producing more eggs.

Clusters of eggs are normally attached to substrata that include algae, shells, rock crevices, nets, ropes, creels, and other fishing gear that remains submerged and undisturbed. There are few reports of eggs from offshore waters, but this may be because the squid spawn over rocky substratum, making spawning areas largely inaccessible to trawling (Holme, 1974; Lordan and Casey, 1999).

3.1.3.4 Trophic ecology

Predators. Various cetacean species, seals, and large demersal fish have been reported to prey on *L. forbesii* (e.g. Pierce and Santos, 1996; Santos *et al.*, 2004a; De Pierrepont *et al.*, 2005).

Prey. A large number of prey species, including various fish, crustaceans, polychaetes, and molluscs have been identified in *L. forbesii* stomachs. As in most squid, fish are more important in adults, and crustaceans more important in juvenile stages (e.g. Pierce *et al.*, 1994d).

3.1.3.5 Fisheries

Loligo forbesii is the dominant squid species fished north of the English Channel, mainly as bycatch from demersal trawls (Pierce *et al.*, 1994b), although various small directed trawl fisheries exist in coastal waters (e.g. Young *et al.*, 2006a) and are becoming increasingly important. It is the only squid species of economic importance in the Azores, where it is fished by an artisanal fleet equipped with handlines and homemade jigs (Martins, 1982; Porteiro and Martins, 1994). South of the English

Channel, the species is currently less common, but is taken both as a trawl bycatch and by coastal artisanal boats using jigs (Cunha and Moreno, 1994; Guerra *et al*., 1994; Rocha *et al*., 1994). Analysis of morphometric variation and the use of allozyme and microsatellite markers suggest that there is no significant separation of stocks throughout the range of its distribution on mainland coasts. The Azores population probably represents a separate subspecies, and animals from offshore banks (e.g. Rockall) demonstrate some differences from the coastal population (Pierce *et al*., 1994c; Brierley *et al.*, 1995; Shaw *et al*., 1999). It is also consistently present in the eastern Mediterranean trawl catches (Machias *et al*., 2001).

The species has been identified in commercial landings in the UK, France, Portugal, Spain, Italy, and Greece.

3.1.4 *Alloteuthis* spp.

Common names

Alloteuthis subulata Lamarck, 1798. European common squid (English); casseron commun (French); Gepfriemter Langflossenkalmar (German); calamaretto puntuto (Italian); lula-bicuda-comprida (Portuguese); calamarín picudo (Spanish).

Alloteuthis media Linnaeus, 1758. Midsize squid (English); casseron bambou (French); calamaretto comune (Italian); lula-bicuda-curta (Portuguese); calamarín menor (Spanish).

3.1.4.1 Adult diagnostic features

Elongated mantle. Rhomboidal fins attenuate posteriorly into a long, slender tail, which can be more than 50% of the ML in males. Arms with two rows of suckers. Tentacle clubs with four rows of suckers. The central rows of suckers are 3–4 times larger than the marginal suckers (Yau, 1994; Laptikhovsky *et al*., 2002). The left ventral arm (IV) can be hectocotylized in mature males, with 6–8 pairs of normal suckers proximally followed by two longitudinal rows of fine papillae distally (Yau, 1994). Maximum ML of *A. subulata* is 20 cm (Rodhouse *et al*., 1988).

3.1.4.2 Distribution and habitat

Alloteuthis subulata and *A. media* are sympatric throughout much of the range of both species (Roper *et al*. 1984), extending from approximately 60°N to 20°N (Guerra, 1992). They are found in the North Sea and the Mediterranean (Belcari, 1999 c, 1999d). They both occur primarily in shelf waters and are demersal, although *A. media* is reported to migrate offshore in winter (Roper *et al*., 1984) and to make diel vertical migrations (Zuev and Nesis, 1971).

3.1.4.3 Life history

Hatchlings of both species are 2–3 mm long (Zuev and Nesis, 1971; Yau, 1994). In *A. subulata*, sexual maturation can be achieved at 4–5 cm ML in both sexes, although mature males have a wider range of sizes than mature females and reach 50% maturity at a slightly smaller size (7–7.5 cm, compared with 7.5–8 cm in females). *Alloteuthis media* has an ML of up to 12 cm in females and 9 cm in males. Individuals hatching in spring grow 7–8 mm month^{-1} during summer and reach an ML of 7–8 cm the following spring (Zuev and Nesis, 1971). Both species are thought to live for approximately one year (Rodhouse *et al.*, 1988; Mangold-Wirz, 1963; Alidromiti, 2007).

The average estimated potential fecundity of female *A. subulata* is 2200–13 500 eggs per female (mean ~5900 ± 970 s.e.; Hastie *et al*., 2009b). In *A. media*, the potential fecundity has been estimated at 950–1400 eggs for the western Mediterranean and 1500–2500 for the eastern Mediterranean. Oocyte maturation occurs in batches.

Spawning occurs throughout the year, generally with larger numbers of mature squid in spring–summer and smaller numbers in autumn–winter (Rodhouse *et al*., 1988; Nyegaard, 2001; Hastie *et al*., 2009b). A predominance of small squid (<50 mm ML) is observed during autumn (Hastie *et al*., 2009b). Adults of *A. media* migrate to shallow water, spawning at depths of 10–100 m on sand, seagrass meadows, etc. from March to October in the western Mediterranean (Mangold-Wirz, 1963) and year-round in the central and eastern region (Lo Bianco, 1909; Naef, 1923; Laptikhovsky *et al*., 2002; Lefkaditou, 2006). In the North Sea, spawning takes place in June–July (Zuev and Nesis, 1971). Recruits of *A. media* are present practically all year-round in shallower waters of their distribution (Relini and Orsi-Relini, 1984). Seasonal peaks of recruitment are more evident in areas with a wider continental shelf (Mangold-Wirz, 1963; Papaconstantinou *et al*., 1994).

3.1.4.4 Trophic ecology

Predators. *Alloteuthis subulata* has been identified from the stomach contents of several species of marine mammal (Santos *et al*., 2001a, 2001b, 2004a, 2005a, 2005b; González *et al*., 1994a; Meynier, 2004) and from hake (*Merluccius merluccius*; Daly *et al*., 2001), and *Loligo* spp. (Pierce *et al*., 1994d; Rocha *et al*., 1994). *Alloteuthis media* is eaten by various gadid and elasmobranch fish (Zuev and Nesis, 1971; Bello, 1997), and is an important food for demersal fish in the southern Bay of Biscay (Velasco *et al*., 2001).

Prey. The main prey of *A. subulata* in the Irish Sea comprises clupeid fish and crustaceans (Nyegaard, 2001). The diet of *A. media* consists of larvae and juveniles of fish, copepods, and euphausiids (Zuev and Nesis, 1971).

3.1.4.5 Fisheries

Both *A. media* and *A. subulata* can be caught and misidentified as juvenile *Loligo* and can occur among long-finned squid catches throughout their range. In the Gulf of Cadiz, *Alloteuthis* spp. are caught as a bycatch of the multispecies bottom-trawl fleet, and recorded annual landings varied between 55 and 290 t during 1996–2006. Both *Alloteuthis* species are landed, probably in similar amounts (I. Sobrino, pers. comm.). In the Rías Bajas of Galicia (northwest Spain), *Alloteuthis* is a bycatch of the boat-seine fishery directed at *L. vulgaris* (Tasende *et al*., 2005). Studies on bottom-trawl discards have demonstrated that, in the northeastern Mediterranean, *A. media* is totally discarded (Machias *et al*., 2001), whereas in the western Mediterranean, it is normally landed (Sartor *et al*., 1998).

These species have been identified in commercial landings in Spain and are regularly landed in Italy (Belcari, 1999c, 1999d).

3.1.5 *Illex coindetii* Verany, 1839

Common names. Broadtail shortfin squid (English); faux encornet (French); thrapsalo (Θράψαλο; Greek); totano, todaro (Italian); pota voladora (Spanish); pota-voadora (Portuguese).

3.1.5.1 Adult diagnostic features

Mantle width 15–25% of the ML. Rhomboidal fins of width 45–60% of dorsal ML. Arms with two rows of suckers. Tentacular club with eight transverse rows of minute subequal suckers. Left or right ventral arm of male hectocotylized with distal trabeculae modified to papillose flaps. Inverse T-shaped funnel cartilage. Funnel groove with anterior foveola and without side pockets. Diagnosis adapted from Roper *et al*. (1984, 1998) and Roper and Mangold (1998).

3.1.5.2 Distribution and habitat

Illex coindetii is found in the Mediterranean Sea, the eastern Atlantic from 60°N to 17°S and 30°W, and in western Atlantic waters from the Gulf of Mexico to Venezuela (Roper *et al*., 1998; Belcari, 1999e). It is demersal in the middle and lower sublittoral and upper bathyal in temperate latitudes, and it undertakes diel vertical migrations.

3.1.5.3 Life history

Illex coindetii is a medium-sized squid (Sánchez, P., *et al*., 1998). The maximum ML is generally larger in females than males. The largest sizes are found in Northeast Atlantic populations, with males growing to 370 mm and females to 320 mm (González *et al*., 1996; Sánchez, P., *et al*., 1998). The life cycle is probably annual, although lifespan estimates vary from six months (based on statolith increments; Arkhipkin *et al*., 1998) to 24 months (length frequency analyses; Mangold-Wirz, 1963).

The age at which *I. coindetii* matures is variable: 100–271 days in males and 140–285 days in females (González and Guerra, 1996; González *et al*., 1996; Arkhipkin *et al*., 2000). The number of mature eggs in the ovary and oviducts ranges from 50 000 to 200 000. It is an "intermittent spawner", with females spawning several times during a prolonged spawning period lasting from a few days to a few weeks (González and Guerra, 1996). Spawning may occur year-round, but seasonal peaks exist and vary widely through the geographic range (e.g. Sánchez, 1984; Tursi and D'Onghia, 1992; Sánchez and Martin, 1993; Jereb and Ragonese, 1995; Belcari, 1996; Arvanitidis *et al*., 2002; Hernández-Garcia, 2002; Ceriola *et al*., 2006).

3.1.5.4 Trophic ecology

Predators. *Illex coindetii* has been found in the stomachs of various marine mammals, including Risso's dolphin (*Grampus griseus*), bottlenose dolphin *(Tursiops truncatus*) (Santos, M. B., *et al*., 1997, 2007), long-finned pilot whale (*Globicephala melas*), and common dolphin *(Delphinus delphis*) (González *et al*., 1994a; Silva, 1999). It has also been recorded from swordfish (*Xiphias gladius*; Bello, 1985), greater forkbeard (*Phycis blennoides*; Morte *et al*., 2002), and the sharpnose sevengill shark (*Heptranchias perlo*; Henderson and Williams, 2001).

Prey. The diet of *I. coindetii* is composed of fish, crustaceans, and cephalopods; it is also cannibalistic. It is mainly a neritic, nekto-benthic predator with a wide spectrum of prey, but adults perform significant vertical migration and also take pelagic prey (Sánchez, P., *et al*., 1998).

3.1.5.5 Fisheries

Illex coindetii is taken throughout the year as bycatch in bottom and pelagic trawls, and, to a lesser extent, in gill- and trammelnets, at depths of 100–400 m in the Mediterranean, off West Africa, and in the Northeast Atlantic. Its fishery value is increasing. Although separate statistics are generally not reported, the annual catch

for the last decade probably ranged from 5000 t to 12 000 t. There is thought to be a single stock throughout the region.

The species has been identified in commercial landings in Ireland, the UK, France, Spain, and Portugal (in the Northeast Atlantic), and Spain, Italy, and Greece (in the Mediterranean).

3.1.6 *Todarodes sagittatus* Lamarck, 1798

Common names. European flying squid (English); toutenon commun (French); Pfeilkalmar (German); katamachi (Καταμάχι; Greek); beitusmokkur (Icelandic); totano viola (Italian); akkar (Norwegian); pota-europeia (Portuguese); pota europea (Spanish).

3.1.6.1 Adult diagnostic features

Tentacle club suckers on dactylus are arranged in four rows, suckers on elongate carpus in 10–12 pairs; entire club relatively long, extending along stalk. Arm suckers with enlarged central tooth, 7–9 regular teeth, and virtually no small alternating teeth. Funnel groove with anterior foveola and without side pockets. Reference: Roper *et al*. (1984).

3.1.6.2 Distribution and habitat

Todarodes sagittatus is found throughout the eastern Atlantic to ca. 40°W, and from the Arctic Ocean to ca. 13°S. The range includes the North Sea and the Mediterranean (Clarke, 1966; Zuev *et al*., 1976; Roper *et al.*, 1984). They occur in both the open ocean and coastal waters, and from the surface to near-bottom at depths up to 2500 m. They migrate vertically between the surface at night and near-bottom waters during the day (Mangold-Wirz, 1963; Korzun *et al*., 1979; Nesis, 1987).

3.1.6.3 Life history

The largest reported male from northern Europe had an ML of 640 mm, and the largest unsexed specimens an ML of 750 mm (in Clarke, 1966). More recent records indicate that females reach a maximum ML of 520 mm (males 426 mm) off northern Europe (Lordan *et al.*, 2001a) and 600 mm (males 385 mm) in the Mediterranean (Cuccu *et al.*, 2005). However, the records given by Cuccu *et al.* (2005) represent quite unusual findings for Mediterranean populations (e.g. Quetglas *et al.*, 1999) and for Italian waters (e.g. Jereb and Ragonese, 1990; Belcari, 1999f). It was hypothesized that such large sizes may result from unusually old animals. Age-at-maturity has been estimated at 15 months, although Nesis (1987) suggested that individuals larger than 50 cm are at least 2 years old, a hypothesis also proposed by Lordan *et al.* (2001a). Generally speaking, however, individuals in the Mediterranean and the southern part of the distributional range mature at much smaller body sizes than those in the North Atlantic (Hernández-García *et al.*, 1998a; Piatkowski *et al.*, 1998; Arkhipkin *et al.*, 1999). Females produce 12 000–18 000 eggs (Laptikhovsky and Nigmatullin, 1999).

Spawning probably takes place on the continental slope in late winter or early spring off northern Europe, in March and April off France, and between September and November in the western Mediterranean (Piatkowski *et al.*, 1998; Quetglas *et al.*, 1998a; Arkhipkin *et al.*, 1999; Lordan *et al*., 2001a). Females always outnumber males. Ripe males seem to be present throughout the year, whereas mature females are present exclusively during the spawning period.

3.1.6.4 Trophic ecology

Predators. *Todarodes sagittatus* has been found in the stomachs of various cetaceans (González *et al.*, 1994a; Clarke and Pascoe, 1997; Santos, M. B., *et al.*, 2001b, 2007; Öztürk *et al*., 2007) and large fish, such as swordfish (*Xiphias gladius*; Bello, 1985, 1991, 1993; Guerra *et al*., 1993; Salman, 2004; Peristeraki *et al*., 2005).

Prey. The diet of *T. sagittatus* is composed of fish, crustaceans, and cephalopods; the presence of cannibalism has also been noted. In northern waters, *T. sagittatus* feeds primarily on small herring (*Clupea harengus*) and cod (*Gadus morhua*; Hernández-García, 1992; Piatkowski *et al*., 1998; Quetglas *et al*., 1999).

3.1.6.5 Fisheries

A directed fishery off Norway has taken 10 000 t in some years (e.g. Wiborg, 1972, 1978, 1979b, 1987; Besteiro, 1985; Sundet, 1985; Bjørke and Gjøsæter, 2004). In the Mediterranean, the main fishery is operated by Italian bottom-trawl vessels, with annual catches (mainly bycatches) of ca. 3000 t. In other parts of its distributional range, it is taken as bycatch in trawl fisheries (e.g. Joy, 1990; Jónsson, 1998; Lordan *et al*., 2001b; González and Sánchez, 2002; Lefkaditou *et al*., 2003a). The fishery is concentrated from August to December in ICES Division IIa. Common fishing methods include jigging off Norway (Sundet, 1985) and in the Mediterranean (Ragonese and Bianchini, 1990) and purse-seines around the Canary Islands (Clarke, 1966). No landings data for this species alone are reported; it is grouped with other short-finned squid. It is probable that two separate stocks exist, one in the northern and another in the southwestern part of the range.

The species has been identified in commercial landings in Norway, Ireland, Spain, Portugal, Italy, and Greece.

3.1.7 *Todaropsis eblanae* Ball, 1841

Common names. Lesser flying squid (English); toutenon souffleur (French); thrapsalo (Θράψαλο; Greek); totano tozzo (Italian); pota-costeira (Portuguese); pota costera (Spanish).

3.1.7.1 Adult diagnostic features

Mantle width larger than 33% of the total ML. Rhomboidal fins of length less than 50% of dorsal ML, width 75–90% of dorsal ML. Arms with two rows of suckers. Dactylus of tentacular club with four longitudinal rows of small suckers. Manus of club with six transverse rows of four suckers, each with median pairs up to fourfold larger in diameter than lateral suckers. Left and right ventral arms (IV) of mature males are hectocotylized. Inverse T-shaped funnel-locking cartilage. Funnel groove without anterior foveola and without side pockets. Reference: Roper *et al*. (1984).

3.1.7.2 Distribution and habitat

The geographical distribution is discontinuous. The species is known from the Mediterranean Sea, the eastern Atlantic from 61°N to 40°S, the southwestern Pacific, and the southwestern Indian Ocean off Australia. It is demersal and associated with sandy and muddy bottoms, mainly in the lower sublittoral and upper bathyal over the continental shelf, inhabiting depths of 20–780 m (Adam, 1952; Belcari, 1999g).

3.1.7.3 Life history

Eggs of mature females are 0.8–2.5 mm in length (Mangold-Wirz, 1963; Hastie *et al*., 1994; Laptikhovsky and Nigmatullin, 1999). The hatching season extends from

October to March in British waters (Hastie *et al*., 1994; Collins *et al*., 2002) and from March to July, with a peak in May, in northwestern African waters (Laptikhovsky and Nigmatullin, 1999). Growth rates vary with the season of hatching and are higher in later-hatched individuals. French fishery data suggest monthly growth rates of 0.76 cm (males) and 1.22 cm (females; Robin *et al*., 2002). Maximum ML is 290 mm and 220 mm for females and males, respectively (Robin *et al*., 2002). Lifespan is approximately 1–2 years for both males and females.

Size-at-maturity varies with geographic location (González *et al*., 1994b; Hastie *et al*., 1994; Belcari *et al*., 1999; Zumholz and Piatkowski, 2005), with an ML of 120–130 mm in males and 140–200 mm ML in females. Total fecundity in mature females varies from 4500 to 28 000 eggs in Scottish waters (Hastie *et al*., 1994) and from 43 000 to 275 000 eggs off West Africa (Laptikhovsky and Nigmatullin, 1999). *Todaropsis eblanae* is an intermittent terminal spawner. The spawning season varies geographically.

3.1.7.4 Trophic ecology

Predators. The main predators of *T. eblanae* are toothed whales and dolphins (Clarke and Pascoe, 1985; Pascoe, 1986; Blanco *et al*., 2001; Santos, M. B., *et al*., 2001a, 2001b, 2007), sharks (Clarke and Stevens, 1974), and several teleost fish species (Meyer and Smale, 1991; Lipinski *et al*., 1992).

Prey. The diet is composed of fish, crustaceans, and cephalopods (Rasero *et al*., 1996; Lordan *et al*., 1998; Zumholz, 2000; Form and Oelschlägel, 2004).

3.1.7.5 Fisheries

Juveniles recruit to the fishery at ca. 3 months of age. *Todaropsis eblanae* is taken throughout the year as bycatch in otter-trawl fisheries and, to a lesser extent, with gill- and trammelnets, longlines, and jigging at depths of 100–400 m in the Mediterranean, off West Africa, and in the Northeast Atlantic (Robin *et al*., 2002). Most catches are made at a depth of ca. 200 m. As for other ommastrephids, in general, no separate landings data are available for this species; landings are pooled with those of other ommastrephid squid species. *Todaropsis eblanae* is less important than *I. coindetii* in French short-finned squid landings (Robin *et al*., 2002) and more important than *I. coindetii* in Spanish and Portuguese short-finned squid landings, although seasonal variation occurs (Bruno, 2008).

The species has been identified in commercial landings in Ireland, UK, France, Spain, and Portugal (in the North Atlantic), and Spain, Italy, and Greece (in the Mediterranean).

3.1.8 *Eledone moschata* Lamarck, 1798

Common names. Musky octopus (English); elédone musquée (French); Moschuskrake (German); moshios (Μοσχιός; Greek), moscardino muschiato (Italian); polvo-mosqueado (Portuguese); pulpo cabezón (Spanish).

3.1.8.1 Adult diagnostic features

Arms uniserial. Living animal exudes a very prominent, musk-like odour, reportedly from glands in the skin. Live colour greyish-brown, with blackish-brown blotches on dorsum. Skin smooth to very finely granulose. No ridge occurs around the lateral periphery of the mantle. Web moderately deep – 30% of arm length. Right arm III hectocotylized, length only 60–70% of left arm III. Ligula short (3% of arm length); calamus absent. Distal tips of all other arms of males modified by subdivision of

universal suckers into two parallel rows of flattened laminae or platelets. Gill demibranch with 11–12 lamellae. Reference: Roper *et al.* (1984).

3.1.8.2 Distribution and habitat

This species is distributed at depths of 15–200 m in Mediterranean and Iberian waters, with the greatest abundance down to 100 m (Lefkaditou *et al.*, 1998a; Belcari and Sbrana, 1999; Belcari *et al.*, 2002a; Silva *et al.*, 2004). It is relatively abundant on the southern Portuguese coast and in the Gulf of Cadiz, where it extends to 450 m (Guerra, 1984; Reis *et al.*, 1984).

3.1.8.3 Life history

Hatchlings of *Eledone moschata* are 25–30 mm long (ML 10–12 mm), eventually reaching a maximum length of 150 mm in the Gulf of Cadiz and along the Portuguese coast and 190 mm in the Mediterranean (Mangold, 1983; Silva *et al.*, 2004; E. Lefkaditou, pers. comm.; S. Lourenço, pers. comm.). Females reach maturity at an ML of 12 cm in the Gulf of Cadiz and 11 cm in Tunisian waters (Ezzeddine-Najai, 1997; Silva *et al.*, 2004). Males mature at slightly smaller sizes. Estimates of fecundity (oocytes per female) include ca. 450 ± 150 for the Gulf of Cadiz (Silva *et al.*, 2004) and 100–500 for the northwestern Mediterranean populations, where egg length ranged between 12 and 16 mm (Mangold, 1983).

In the Gulf of Cadiz, the spawning season extends from October to July (Silva *et al.*, 2004). Peak spawning occurs from February to May, with a secondary peak in October. The southern Mediterranean populations spawn from November to July (Ezzeddine-Najai, 1997). In the northwestern Mediterranean waters, the reproductive season is shorter, from January to May–June (Mangold, 1983; Belcari *et al.*, 2002a).

The life-cycle model of this species in the northwestern Mediterranean is based on the alternation of short-lived and long-lived life cycles (Mangold, 1983; Silva *et al.*, 2004), whereby populations hatched at different times vary in growth rate and rate of sexual development according to prevailing environmental conditions.

3.1.8.4 Trophic ecology

Hatchlings are able to feed on live crabs of their own size. Their preference for crustaceans is clear from the very early stages onward (Boletzky, 1975). Captive studies confirm a preference for crustaceans over molluscs and fish (Şen, 2007).

3.1.8.5 Fisheries

This species is caught mainly as bycatch of bottom-trawl fisheries; in the Gulf of Cadiz it is often discarded by the Spanish fleet because of its low commercial value. In the main ports of this region, annual landings of *E. moschata* averaged ca. 100 t during 1996–2004, with a maximum from January to April. In the Mediterranean, this species is of considerable economic importance, especially on the south and east coasts and in the Adriatic Sea (Belcari and Sbrana, 1999; Belcari *et al.*, 2002a).

The species has been identified in commercial landings in Spain, Italy, and Greece.

3.1.9 *Eledone cirrhosa* Lamarck, 1798

Common names. Horned octopus, lesser octopus (English); élédone commune, poulpe, poulpe blanc (French); moshios (Μοσχιός; Greek); moscardino bianco (Italian); polvo-do-alto (Portuguese); pulpo blanco (Spanish).

3.1.9.1 Adult diagnostic features

Suckers uniserial. Orange-red and reddish-brown dorsally; greenish iridescence ventrally. Dorsal side covered with numerous warts. A whitish line encircles the lateral periphery of the mantle. A cirrus is present near each eye. Right arm III of males is hectocotylized, shorter (69–76%) than its opposite, with a very short ligula (3–4% of the length of the hectocotylus), calamus absent; terminal suckers of the other arms of males modified and transversely compressed. Diagnosis adapted from Roper *et al.* (1984).

3.1.9.2 Distribution and habitat

Eledone cirrhosa is a common species in the Northeast Atlantic, extending from 67°N to the northwest African coasts (Guerra, 1992) and throughout the Mediterranean Sea. It appears occasionally in the Kattegat (west of Sweden; Hornborg, 2005) and in the Marmara Sea (Unsal *et al*., 1999). It is a typical soft-bottom eurybathic species that lives to a depth of 770 m (Massy, 1928), although it is mainly distributed between 50 and 300 m (Belcari and Sartor, 1999a; Belcari *et al*., 2002a).

3.1.9.3 Life history

Females reach a maximum size of 190 mm ML compared with 135 mm ML in males. They attain maturity at smaller sizes in the Mediterranean than in the Atlantic, and males mature at smaller sizes than females (Belcari and Sartor, 1999a; Belcari *et al.* 2002a; A. Moreno, pers. comm.).

A combination of a 1- and 2-year life cycle (fast-growing, early-maturing animals vs. slower-growing, late-maturing animals) is proposed for the North Sea (Boyle and Knobloch, 1982; Boyle, 1983; Boyle *et al*., 1988). In the Mediterranean, the lifespan of most individuals is estimated to be approximately 2 years (e.g. Moriyasu, 1981, 1983; Belcari *et al.*, 1990, 2002a; Sánchez *et al*., 2004), with less than 10% reaching maturity at ca. 3 years old (Lefkaditou and Papaconstantinou, 1995; Cuccu *et al*., 2003; Orsi-Relini *et al.*, 2006). Note, however, that these conclusions are based on length frequency analysis, the validity of which has been called into question (E. Lefkaditou, pers. comm.)

Fecundity estimates vary widely: ~9000 eggs in the North Sea, ~5500 eggs in the Catalan Sea (Boyle *et al*., 1988), and ~2000 eggs in the Tyrrhenian Sea (Rossetti, 1998). *E. cirrhosa* spawns in summer–autumn in the North Sea (Boyle, 1983; Boyle and Knobloch, 1983) and in spring–summer farther south (A. Moreno, pers. comm.). In the Mediterranean, the spawning season is earlier in the western basin (spring–summer) than in the eastern basin (summer–autumn; Belcari and Sartor, 1999a; Lefkaditou *et al*., 2000).

3.1.9.4 Trophic ecology

Predators. Whales, seals, and fish are considered to be the most important predators of *E. cirrhosa* (e.g. Pierce *et al*., 1991; Tollit and Thompson, 1996; Santos *et al*., 1999; Brown *et al*., 2001; Daly *et al*., 2001; Velasco *et al*., 2001).

Prey. *Eledone cirrhosa* is a carnivorous species and active predator. The diet is mainly composed of decapod crustaceans, mostly alpheids and brachyurids (Boyle and Knobloch, 1981; Sánchez, 1981; Auteri *et al*., 1988). The species also feeds on molluscs and cephalopod eggs, and cannibalism has been observed (Moriyasu, 1981; Guerra, 1992).

3.1.9.5 Fisheries

Eledone cirrhosa has great commercial value in the western Mediterranean and usually less than 10% of catches is discarded (Mangold and Boletzky, 1987; Sartor *et al*., 1998; Relini *et al*., 1998). Across Europe, landings come almost entirely from bottom-trawl fisheries, and *E. cirrhosa* appears together with *E. moschata* and *Octopus vulgaris* in the catch statistics. It is marketed in two distinct commercial categories in the Mediterranean, where small specimens (<50 mm ML) have higher economic value (Belcari *et al*., 1998; Belcari and Sartor, 1999). In some regions, these small octopus are a target of the multispecies trawl fishery in spring and summer that coincides with the recruitment period of the species (Relini and Orsi-Relini, 1984; Belcari *et al*., 1998, 2002a; Belcari and Sartor, 1999; Sánchez *et al*., 2004). Recently, this fishery was banned in the Catalan Sea (P. Sánchez, pers. comm.). *Eledone cirrhosa* is the only *Eledone* species present in northern Spanish waters, where it is landed by the bottom-trawl fishery (ca. 700 t year^{-1} on average, 1998–2006) as bycatch, although its commercial value is very low. It is occasionally landed in small quantities in Scotland, but there appears to be little commercial interest in the species (G. Pierce, pers. comm.).

The species has been identified in commercial landings in Portugal, Spain, Italy, and Greece.

3.1.10 *Octopus vulgaris* Cuvier, 1797

Common names. Common octopus (English); pieuvre, poulpe (French); chtapodi (χταπόδι; Greek); Gemeiner Krake (German); polpo comune (Italian); pulpo común (Spanish); olagarro (Spanish, Basque); pop roquer (Spanish, Catalan); polbo (Spanish, Galician); polvo-vulgar (Portuguese).

3.1.10.1 Adult diagnostic features

Suckers biserial. ML to 40 cm; total length to 140 cm. Arms robust at base, lateral arms longest, dorsal arms shortest. Suckers 15–17 of arms II and III enlarged in adults, especially males. Right arm III of mature males hectocotylized; ligula short and spoon-shaped. Gill demibranch with 7–11 lamellae, including terminal lamellae. Four papillae in the dorsal part of the mantle (one situated in the anterior part, another posterior and two laterals). Reticulated skin with four whitish spots, two between the eyes and two below the first dorsal papilla. Diagnosis adapted from Guerra (1992).

3.1.10.2 Distribution and habitat

Octopus vulgaris is especially abundant in the Mediterranean Sea and the eastern Atlantic (Belcari and Sartor, 1999b). Molecular genetic work has demonstrated that the distribution of *O. vulgaris* in the Atlantic extends to southern Brazil (Söller *et al.*, 2000) in the west, to Lanzarote and Senegal in the east, and as far south as Tristan de Cunha and False Bay, South Africa (Warnke *et al.*, 2004). Samples from Japan and Taiwan in the Pacific also appear to be conspecific with *O. vulgaris.* A benthic species, *O. vulgaris* inhabits the coastline to the outer edge of the continental shelf (200 m). It undertakes limited seasonal migrations.

3.1.10.3 Life history

Octopus vulgaris has a life cycle of 12–14 months (Domain *et al.*, 2002; Iglesias *et al.*, 2004) and terminal spawning with egg care by the female. The incubation period of the eggs is 22–25 days at 25°C (Mangold, 1997), but longer at lower temperatures (36 days at 23°C, 60 days at 21°C, 80 days at 17°C, and 120 days at 13°C; Mangold and Boletzky, 1973; Caverivière *et al.*, 1999; Martins, 2003). Paralarvae are planktonic

for 1–3 months, depending on the effect of temperature on growth rate, and adopt the benthic life mode of the adults at ca. 7.5 mm ML (Villanueva, 1995). The mortality on the paralarvae phase is thought to be very high and dependent on environmental conditions, with highly variable recruitment success (Faure, 2002).

Growth is very rapid, and large individual variation in growth rates has been observed both in culture experiments (Iglesias *et al*., 2004) and in wild populations (Domain *et al*., 2000). Juveniles can reach 0.5–0.6 kg within six months of hatching, and 1.4–1.8 kg within eight months, at a mean temperature of 18°C (Iglesias *et al*., 2004). Maximum size is 400 mm ML.

The potential fecundity of mature females ranges from 100 000 to 500 000 oocytes. The eggs are small, approximately 2.5 mm long (Mangold, 1997). The spawning season extends throughout the year, with two peaks in Atlantic populations within the main upwelling regions: winter and summer in western Portuguese waters (Moreno, 2008), and spring and autumn in Moroccan waters (Faraj and Bez, 2007) and the Canary Islands (Hernández-García *et al*., 2002). A single spawning peak occurs in late winter/spring in northwest Spain (Fernández-Rueda and García-Flórez, 2007; Otero e*t al*., 2007) and in summer in the northern Gulf of Cadiz (Rodríguez-Rúa *et al*., 2005; Moreno, 2008) and the Mediterranean (Sánchez and Obarti, 1993; Mangold, 1997; Belcari *et al*., 2002b).

3.1.10.4 Trophic ecology

Predators. Fish, marine mammals, birds, and other cephalopods prey on *O. vulgaris* (Hanlon and Messenger, 1998). Marine mammals include common dolphin (*Delphinus delphis*; López, 2002; Santos *et al*., 2004b), bottlenose dolphin (*Tursiops truncatus*; Blanco *et al*., 2001*),* Risso's dolphin *(Grampus griseus*), long-finned pilot whale *(Globicephala melas*; López, 2002), and Mediterranean monk seal (*Monachus monachus*). Fish predators of adults and juveniles include conger eel (*Conger conger)* and Mediterranean moray eel *(Muraena helena*), whereas Mediterranean dusky grouper (*Epinephelus marginatus*), serranid fish (*Serranus* sp.) and the sand smelt (*Atherina presbyter*) prey on hatchlings (Villanueva and Norman, 2008).

Prey. Paralarvae feed mainly on decapod crustacean larvae (Villanueva and Norman, 2008). Diet of juveniles and adults may include crustaceans, teleost fish, other cephalopods, and polychaetes. On the Mediterranean coast of Spain in Cataluña, 80% of the diet comprises crustaceans (Guerra, 1978; Sánchez and Obarti, 1993; Quetglas *et al*., 1998b), but in the Algarve (Portugal), a similar proportion comprises bivalves (Rosa *et al*., 2004).

3.1.10.5 Fisheries

Octopus vulgaris is taken throughout the year as a target species in bottom and pelagic trawls and via hand-jigs, pots, trammelnets, and traps in small-scale coastal fisheries at depths of 20–200 m in the Mediterranean (Belcari *et al*., 2002b), off West Africa, and in the Northeast Atlantic. Although some countries report landings of this species separately, others group all landings of Octopodidae together. In Galicia (northwest Spain), where annual landings for 1998–2006 were ca. 1500 t, the species is targeted by the artisanal fleet using traps (called "nasa de polbo"), which are fairly specific to octopus (which forms 80–90% of the total catches in this gear); it is also caught in traps set for other species, in trammelnets ("trasmallos" and "miños"), and on hooked lines ("raña"; Bañón *et al*., 2007). In the Gulf of Cadiz, both bottom trawlers and artisanal vessels take this species, and annual landings have fluctuated widely, from 500 t to more than 2000 t in 1994–2006.

The species has been identified in commercial landings in Spain, Portugal, Italy, and Greece.

3.1.11 *Sepia officinalis* Linnaeus, 1758

Common names. Common cuttlefish (English); seiche commune (French); Gemeiner Tintenfisch (German); soupia (Σουπιά; Greek); seppia comune (Italian); sepia común (Spanish); choco-vulgar (Portuguese).

3.1.11.1 Adult diagnostic features

Up to 450 mm ML. Mantle oval. Tentacular club with five or six suckers in each transverse row, the medial one moderately enlarged; swimming keel not extending proximally beyond the base of the club. Hectocotylus on left arm IV of males: after the 5–7 proximal sucker rows, there are from 4–5 to 8–9 (medial) horizontal rows of reduced suckers. Cuttlebone posteriorly rounded with parallel sides. Anterior striae are inverted U-shape, or shallow M-shape. Colour light brown. Head with scattered white spots and with dark pigment around eye orbits. Arms I–III have a broad, longitudinal brownish band medially, extending onto head. Dorsal mantle has bold transverse zebra-stripe pattern during the breeding season; paired dorsal eye spots absent. Fins with narrow white band along outer margin and with small white spots, becoming larger toward junction of mantle and fins. Mature males with arms IV emboldened by white and black zebra bands and white arm spots. Diagnosis adapted from Roper *et al.* (1984), Guerra (1992), and Reid *et al.* (2005).

3.1.11.2 Distribution and habitat

Sepia officinalis extends through the eastern Atlantic and Mediterranean Sea (Belcari, 1999i). In the eastern North Atlantic, it extends from the Shetland Islands and southern Norway (not present in the Baltic Sea, except for occasional incursions with the northeasternmost Atlantic waters), south through the Mediterranean Sea (including Aegean Sea, Sea of Marmara, and Levantine Sea), to northwest Africa, with the southern boundary coinciding approximately with the border between Mauritania and Senegal (16°N; Reid *et al.*, 2005). Seasonal migrations occur from deeper, offshore overwintering grounds to shallower, coastal spawning and nursery grounds.

3.1.11.3 Life history

Hatchling ML ranges from 6 to 9 mm (Boletzky, 1983). Growth rates vary directly with temperature and inversely with size. In the English Channel, statolith analysis indicates that the growth pattern is exponential in hatchlings and early stages, whereas logistic curves are a better fit for larger size classes (7–106 mm ML; Challier *et al.*, 2005a).

Common cuttlefish attain sexual maturity at a wide range of sizes. In the Mediterranean Sea, mature males of 6–8 cm ML were observed. Males over 10 cm ML, however, may still be immature. A similar situation exists in females. Length at first maturity is ca. 13 cm ML in females. Females produce 150–4000 eggs, depending on their size. The main spawning season covers spring and summer, but there is also winter spawning, which is especially pronounced on the Atlantic coast. 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 and, hence, determines the lifespan, which may vary from ca. 14 to 24 months. The species has an intermittent terminal spawning strategy

(Boletzky, 1983; Guerra and Castro, 1988; Boucaud and Daguzan, 1990; Boucaud-Camou *et al.,* 1991; Gauvrit *et al.,* 1997; Belcari, 1999h; Dunn, 1999; Rocha *et al.,* 2001).

3.1.11.4 Trophic ecology

Predators. *Sepia officinalis* has been found in the stomachs of marine mammals, including Risso's dolphin (*Grampus griseus*; Clarke and Pascoe, 1985), the Mediterranean monk seal (*Monachus monachus*; Salman *et al*., 2001), and (in South Africa) fur seals (*Arctocephalus pusillus*; Castley *et al*., 1991). It is also eaten by elasmobranchs, including the blue shark (*Prionace glauca*; Clarke and Stevens, 1974) and smooth hound (*Mustelus mustelus*; Morte *et al*., 1997).

Prey. The diet mainly consists of small crabs, shrimps, demersal fish, cephalopods, and polychaetes. A significant change from crustaceans to fish occurs with growth. Cannibalism is relatively common at all sizes.

3.1.11.5 Fisheries

Sepia officinalis is an important species for the commercial fisheries of many countries. The main producer countries in the last decade were France in the Northeast Atlantic, followed by Italy and Tunisia in the Mediterranean Sea (Belcari *et al.*, 2002c). In northern fisheries (English Channel, Bay of Biscay), cuttlefish are primarily caught by otter and beam trawlers, either as a target species or as bycatch when the target is demersal finfish. In southern fisheries, artisanal gears dominate, and cuttlefish are caught by gillnets, trammelnets, and a great variety of highly selective gears, such as traps, lures, jigs, and spears. Generally, trawlers operate in inshore and offshore fishing grounds, taking both juvenile and adult specimens, whereas artisanal gears (e.g. traps) catch spawning animals mainly inshore. In Galicia, cuttlefish is mainly caught with trammelnets from January to May (during the main reproductive period) on inshore fishing grounds (Arnáiz *et al.*, 2001). In the inner area of the rías, cuttlefish is also caught with fykenets ("butróns") and traps ("nasa de choco"). Management options of interest for this resource include effort regulations (licences are issued in inshore artisanal fisheries) and minimum landing size. Catches of this species are not recorded separately by all countries, often being grouped with other cuttlefish, although FAO records separate catch statistics for this species along the Spanish Atlantic coast, and separate statistics are probably also available for the French Atlantic coast.

The species has been identified in commercial landings in the UK, France, Spain, Portugal, Italy, and Greece. *Sepia elegans* Blainville, 1827

3.1.12 *Sepia elegans* Blainville, 1827

Common names. Elegant cuttlefish (English); seiche elegante (French); seppia elegante (Italian); choco-elegante (Portuguese); choquito sin punta (Spanish).

3.1.12.1 Adult diagnostic features

Up to 89 mm ML (Adam, 1952). Mantle oblong, length more than twice width. Club short, oval; sucker-bearing surface flattened, with 6–8 suckers in transverse rows; suckers differ markedly in size: 3–4 greatly enlarged suckers toward posterior end of club and several dorsal suckers enlarged, but not as large as medial suckers. Hectocotylus present on left ventral arm of males: 1–2 rows of normal size suckers proximally, 9–11 rows of reduced minute suckers medially, then normal size suckers to arm tip; suckers in two dorsal and two ventral series displaced laterally. Cuttlebone outline oblong. Anterior striae are inverted U-shape. Spine absent, but

ridge and small lateral wings present. Dorso-posterior end of cuttlebone with short, rugose, calcareous keel. Colour reddish brown. Dorsal mantle pale, peppered with scattered purple-black chromatophores. Fins and ventral mantle pale. Reference: Reid *et al*. (2005).

3.1.12.2 Distribution and habitat

Sepia elegans extends through the eastern Atlantic from western Scotland in the north to Namibia (21°S) in the south and is present throughout the Mediterranean Sea (Jereb and Roper, 2005). It is a sublittoral species, living on sandy and sandy–muddy bottoms at depths to ca. 450 m (Jereb and Ragonese, 1991). The species is tolerant of fluctuations in salinity and has been found in brackish waters (salinity 18–25) in the Sea of Marmara (Unsal *et al*., 1999) and the estuarine waters of the Ria de Vigo (Guerra, 1984).

3.1.12.3 Life history

After hatching, juveniles immediately adopt a benthic lifestyle. Growth was calculated at 2.8 mm month^{-1} for males and 3.0 mm month^{-1} for females in the Sicilian Channel (Ragonese and Jereb, 1991), a little faster than that estimated in the western Mediterranean by Mangold-Wirz (1963) and in the Ria de Vigo by Guerra (1984; 2–2.5 mm month^{-1}). Lifespan ranges between 12 and 19 months. The smallest mature males have been reported at 20 mm, and females at 30 mm ML (Guerra and Castro, 1989; Volpi *et al*., 1990). However, most individuals attain maturity at larger sizes (Mangold-Wirz, 1963; Volpi *et al*., 1990; Jereb and Ragonese, 1991), at approximately 1 year of age. Males may carry ca. 95 spermatophores and females ca. 250 eggs.

In the Mediterranean Sea, as well as in the Atlantic, mature males and females are present throughout the year, which suggests a continuous spawning period (e.g. Mangold-Wirz, 1963; Roper *et al*., 1984; Guerra, 1992; Belcari, 1999i). The eggs (maximum diameter 5 mm; Guerra, 1984) are attached to alcyonarians (sea fans), shells, etc., on muddy bottoms or, less frequently, on coral formations (Mangold-Wirz, 1963). Continuous recruitment also occurs, with peaks observed in several Mediterranean areas (Volpi *et al*., 1990; Jereb and Ragonese, 1991; Wurtz *et al*., 1991; D'Onghia *et al*., 1992; Casali *et al*., 1998).

3.1.12.4 Trophic ecology

Predators. *Sepia elegans* has been identified from stomach contents of very few predators, but has been reported from the dolphinfish (*Coryphaena hippurus*; Massuti *et al*., 1998) and the bottlenose dolphin (*Tursiops truncates*; Blanco *et al*., 2001).

Prey. This species feeds mainly on small crustaceans, fish, and polychaetes (Reid *et al*., 2005). Detailed studies on feeding (e.g. Guerra, 1985; Castro and Guerra, 1990) suggest that there is no change in diet with growth and/or maturity and that the variety of prey does not decrease with increasing size.

3.1.12.5 Fisheries

Sepia elegans is taken mainly as a bycatch in Mediterranean and West African trawl fisheries (Roper *et al*., 1984; Belcari, 1999i; Reid *et al*., 2005). Separate statistics are generally not reported for *S. elegans*, which represents a very significant percentage of the catches in some areas of its distributional range (Reid *et al*., 2005). In the Mediterranean Sea, it is marketed along with *S. orbignyana* and small *S. officinalis*, and constitutes a valuable resource locally. In the Sicilian Channel, an exploitation rate of 0.73 was estimated for the species (Ragonese and Jereb, 1991), which suggests very

intensive fishing pressure on this resource. It is separately recorded in landings from the Gulf of Cadiz, where it typically forms ca. 7% of cuttlefish landings (the remainder being *S. officinalis*). This species is marketed fresh and frozen.

The species has been identified in commercial landings in Italy and Spain.

3.1.13 *Sepia orbignyana* Férrusac in Orbigny, 1826

Common names. Pink cuttlefish (English); seiche roseé (French); seppia pizzuta (Italian); choco-de-cauda (Portuguese); choquito con punta (Spanish).

3.1.13.1 Adult diagnostic features

Up to 120 mm ML (Mangold-Wirz, 1963). Mantle oval. Club short, oval, with 5–6 suckers in transverse rows. Suckers differ markedly in size: three large suckers medially with one slightly smaller sucker on each side of these. Hectocotylus present on left ventral arm (IV): 1–2 rows of normal size suckers proximally, greatly reduced suckers medially, then normal size suckers distally to arm tip. Suckers of hectocotylus in two dorsal and two ventral series displaced laterally, with a gap between them. Cuttlebone outline oblong. Anterior striae shallow M-shape, or wavy. Spine long, pointed (prominent), straight, directed dorsally, with ventral keel. Colour reddish brown. Reference: Reid *et al*. (2005).

3.1.13.2 Distribution and habitat

Sepia orbignyana occurs in the eastern Atlantic from the Irish Sea in the north to southern Angola (17°S) and is present throughout the Mediterranean Sea (Jereb and Roper, 2005). It is a demersal species that prefers sandy and sandy–muddy bottoms. Its greatest abundance is at depths of 50–250 m (Mangold-Wirz, 1963; Casali *et al*., 1998). Records from the Sea of Marmara indicate that it can occur in brackish waters (Unsal *et al*., 1999).

3.1.13.3 Life history

Newly hatched animals observed in the laboratory (Boletzky, 1988) measured 6 mm ML. Females attain larger sizes and grow faster than males (Bello, 2001). Growth was calculated at 2.9 mm month^{-1} for males and 3.0 mm month^{-1} for females in the Sicilian Channel (Ragonese and Jereb, 1991). Lifespan is considered to vary between 12 and 18 months (Mangold-Wirz, 1963). Estimates from length frequency analyses, although widely considered to be unreliable for cephalopods, indicate a longer lifespan of 2 years for males and 3 years for females (Ragonese and Jereb, 1991). Males reach maturity from 35 mm ML, and females from 65 mm ML (Belcari and Sartor, 1993). Mature males, aged 6 or 7 months, carry ca. 100 spermatophores; females aged 9 or 10 months carry ca. 400 eggs (Roper *et al*., 1984).

In Mediterranean waters, spawning is probably continuous. The eggs, laid individually, whitish or greyish in colour and slightly more elongate than those of *S. officinalis* (Mangold-Wirz, 1963), are deposited in various sponges to form clusters of 30–40 (Reid *et al*., 2005).

3.1.13.4 Trophic ecology

We found no reports of this species from predator stomach contents. *S. orbignyana* feeds mainly on crustaceans and fish (Auteri *et al*., 1988).

3.1.13.5 Fisheries

Sepia orbignyana is taken mainly as bycatch throughout the Mediterranean and in the West African trawl fisheries, although targeted fisheries also exist (e.g. Roper *et al*., 1984; Mangold and Boletzky, 1987; Belcari, 1999j; Reid *et al*., 2005). Separate statistics are not reported, but *S. orbignyana* represents a very significant percentage of the catches in some areas. In the Mediterranean Sea, it is often marketed along with the congener *S. elegans* and small *S. officinalis* and constitutes a valuable resource locally (Belcari, 1999j). Studies carried out in the Sicilian Channel demonstrated an exploitation rate of 0.60 for this species (Ragonese and Jereb, 1991), which suggests intensive fishing pressure on the resource, as already hypothesized by other authors (e.g. Boletzky, 1983). It is marketed fresh and frozen.

The species has been identified in commercial landings in Italy.

3.2 Application of DNA-based markers in European cephalopod fisheries and biology

Paul Shaw

3.2.1 Introduction

In the past 30 years, DNA-based markers, such as allozymes, mitochondrial DNA (mtDNA), and microsatellites, have made a substantial contribution to many fields of whole organism biology. In particular, population biology (population structuring, individual interactions), phylogenetics, and systematics have benefited from the application of dependable, genetically determined, inherited markers that are not influenced by the environment and individual habits. The value of DNA-based markers has been demonstrated by their widespread use with finfish and their fisheries (see Carvalho and Pitcher, 1995).

Despite the obvious benefits of these markers, their input to cephalopod biology has been limited until the last ten years. Substantial early success was achieved using allozymes to address issues of population structuring (e.g. Brierley *et al.*, 1995), species identification and systematics (e.g. Augustyn and Grant, 1988), and particularly in identifying cryptic species (e.g. Yeatman and Benzie, 1994). The recent development of microsatellite DNA markers for cephalopod species and their application to the study of population structure (e.g. Shaw *et al.*, 1999) and mating strategies (e.g. Shaw and Boyle, 1997) – and the increasing use of DNA sequencing for phylogenetics/systematics purposes (e.g. Strugnell *et al.*, 2005) – has demonstrated the potential for greater contributions to cephalopod biology on a number of levels.

3.2.2 Population genetics of commercially important cephalopods in European waters

3.2.2.1 *Loligo forbesii*

Allozyme (Brierley *et al*., 1995), microsatellite (Shaw *et al*., 1999), and mitochondrial DNA data (Norman *et al*., 1994) all indicate that this species is comprised of a single genetic stock throughout its range along the Atlantic coast of Europe (northwestern Scotland to southern Portugal), but that a significantly differentiated population exists in the Azores archipelago. Shaw *et al*. (1999) also indicated the possibility of genetically differentiated populations on off-shelf banks northwest of Scotland (particularly on Rockall Bank). This genetic pattern of large-scale homogeneity is consistent with what is known of the life-history characteristics of this species, which is highly mobile and migratory as juveniles and adults. The genetic differentiation of