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II. Species Accounts.

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Editors

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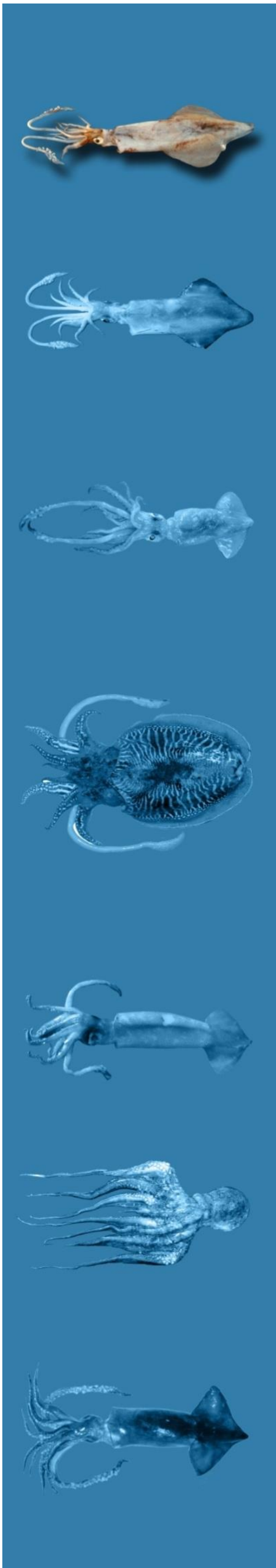

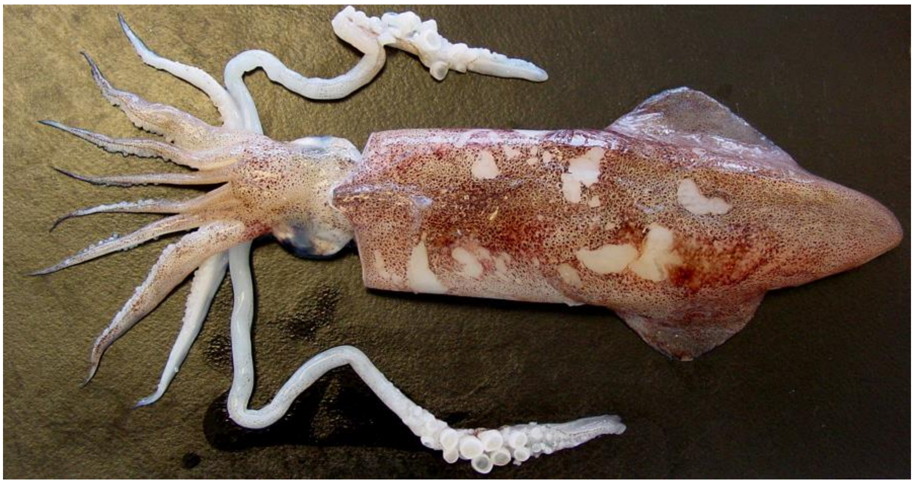

Loligo vulgaris

European squid

11 *Loligo vulgaris* Lamarck, 1798

Ana Moreno, Evgenia Lefkaditou, Jean-Paul Robin, João Pereira, Angel F. González, Sonia Seixas, Roger Villanueva, Graham J. Pierce, A. Louise Allcock, and Patrizia Jereb

Common names

Encornet (France), Καλαμάρι [calamary] (Greece), calamaro mediterraneo (Italy), lula vulgar (Portugal), calamar común (Spain), European squid (UK) (Figure 11.1).

Synonyms

There are no synonyms for *Loligo vulgaris.*

11.1 Geographic distribution

The European squid, *Loligo vulgaris* Lamarck, 1798, is found in the Northeast Atlantic from ca. 55°N to ca. 20°S and throughout the Mediterranean (Jereb *et al.*, 2010). It is one of the most common squids in the coastal waters of the Northeast Atlantic and the Mediterranean (Worms, 1983a). In the North Sea, its distribution extends from the northwest coast of Scotland, where it is occasionally reported (P. R. Boyle and G. J. Pierce, pers. comm.), to the Skagerrak and Kattegat, and a few old records from the western Baltic Sea (Grimpe, 1925; Tinbergen and Verwey, 1945) are supported by more recent information (Muus, 1959 in Hornbörg, 2005). A record of one specimen labelled Bergen (Norway; 60°23′N) is described in Grieg (1933).

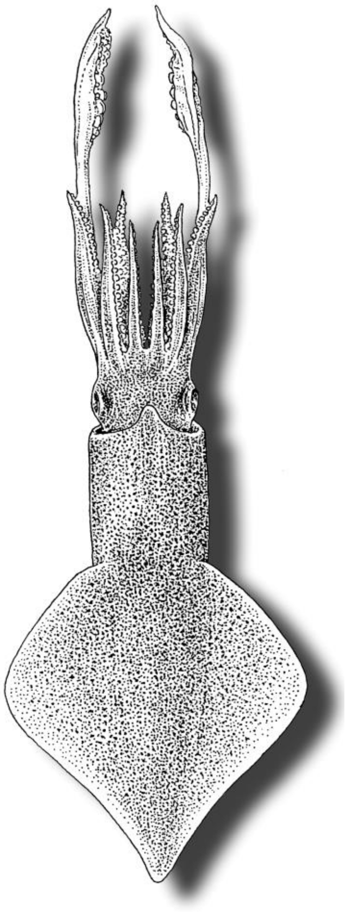

Figure 11.1. *Loligo vulgaris*. Dorsal view. From Muus (1959).

Loligo vulgaris was not included by Massy (1928) in her list of the Cephalopoda of the Irish coast, and an early record of occurrence in the waters of the Isle of Man (Irish Sea; Moore, 1937, in Stephen, 1944) is doubtful. However, it is present in the central and southern North Sea (De Heij and Baayen, 2005; Oesterwind *et al.*, 2010), where it appears mainly in late spring and summer. It is widely distributed in the English Channel, where, according to Royer *et al.* (2002), it is the second most abundant squid species (with slightly fewer recruits than *Loligo forbesii*), and it is occasionally caught in the Celtic Sea (Lordan *et al.*, 2001a). Its distribution extends south along the west coasts of France, Spain, and Portugal (Guerra, 1992; Coelho *et al.*, 1994; Moreno *et al.*, 1994; Cunha *et al.*, 1995). In the Bay of Biscay, trawl surveys in autumn showed that *L. vulgaris* is more abundant than *L. forbesii* in inshore and southern parts of the Bay (with catch rates of up to 150 specimens h^{-1}; Denis, 2000). Along the west coast of Portugal, abundance decreases to the south (Cunha *et al.*, 1995). Farther south along the west coast of Africa, it is found off Senegal and Angola (Baia dos Tigres; Adam, 1962), but, according to Augustyn and Grant (1988), it is never found south of 20°S. *Loligo vulgaris* is widely distributed throughout the Mediterranean Sea (Mangold and Boletzky, 1987;

Bello, 2004; Salman, 2009), including western and central Mediterranean waters (Mangold-Wirz, 1963a**;** Sánchez, 1986a; Belcari and Sartor, 1993; Sánchez and Martin, 1993; Jereb and Ragonese, 1994; Giordano and Carbonara, 1999**;** Relini *et al.*, 2002; Cuccu *et al.*, 2003a), the whole 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). The species has been recorded in the Sea of Marmara (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

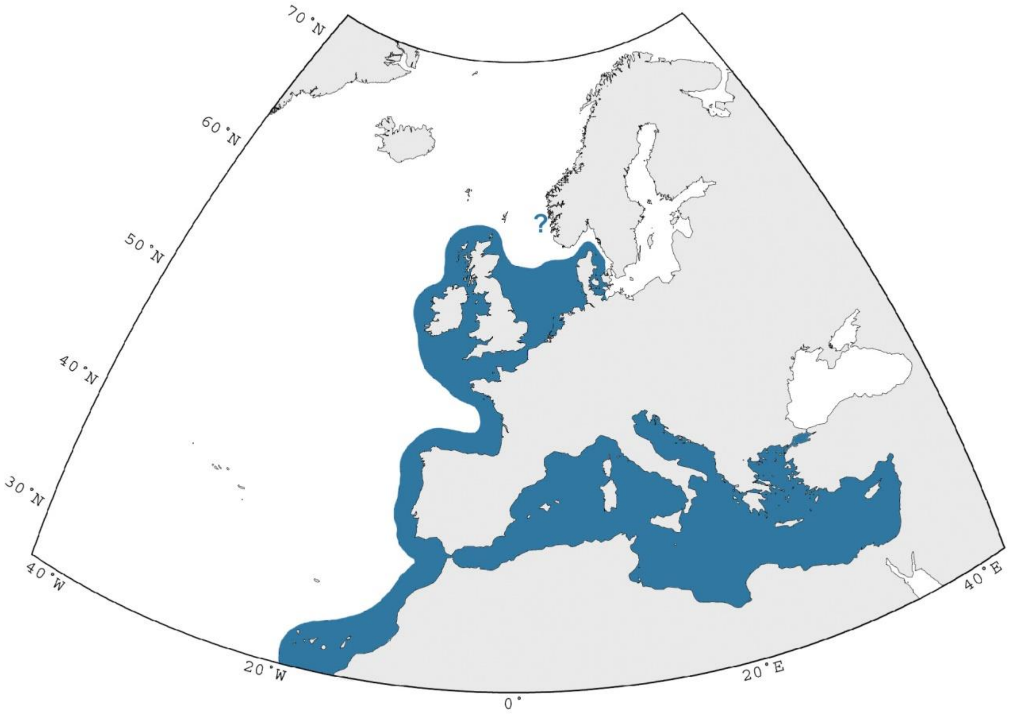

Figure 11.2. *Loligo vulgaris.* Geographic distribution in the Northeast Atlantic and Mediterranean Sea.

11.2 Taxonomy

11.2.1 Systematics

Coleoidea – Decapodiformes – Myopsida – Loliginidae – Loligininae – *Loligo*.

11.2.2 Type locality

Mediterranean Sea (exact position not known).

11.2.3 Type repository

Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France. *Loligo vulgaris* (Lamarck, 1798, Bulletin des Sciences, par la Société Philomatique, Paris, 2 (17): 130.

11.3 Diagnosis

11.3.1 Paralarvae

The fins are paddle-shaped, broad, with short bases, each fin much wider than long. The mantle is broad, with a few large dorsal chromatophores and numerous ventral chromatophores. The head is squarish with a few chromatophores on the dorsal surface and 12 chromatophores on the ventral surface. Ten of these are arranged into two "cheek patches" of 5 chromatophores each, posterior to each eye; the remaining pair is located between the eyes. The ventral arms have 2 aboral chromatophores. There is a strong linear relationship between mantle length and eye diameter, which is, therefore, a useful parameter to estimate the size of damaged paralarvae in samples (González *et al.*, 2010). The tentacles have 4 aboral chromatophores. The tentacular clubs are broad and much wider than the tentacular stalks. In the laboratory, size at hatching ranges between 2.92 and 3.85 mm ML (Turk *et al.*, 1986), and individuals hatched in summer are slightly smaller than those hatched in winter (Villanueva, 2000a). The smallest hatchlings collected in the wild by González *et al.* (2010) measured 1.26 mm ML.

11.3.2 Juveniles and adults

The mantle is muscular, cylindrical, moderately slender, and elongated posteriorly. Red chromatophores form abundant wide spots on the mantle, and a green/blue iridescence is apparent in the posterior part of the mantle in live or fresh specimens. The fins are rhomboid, their length exceeding 50% of the mantle length. There are 15 tiny suckers on the buccal membrane, each with a chitinous ring. The left ventral arm of males becomes hectocotylized, with suckers replaced by papillae along 15–33% of the whole arm length. The arms have two series of suckers. The sucker rings on the arms have ca. 20 teeth; on distal suckers, they are large and pointed and on proximal ones minute or even absent.

The tentacles are not retractile. The tentacular clubs have four series of suckers in the "manus"; those in the central two series are markedly larger than the marginal ones. Sucker rings are illustrated in Figure 11.3. There are simple locking cartilages. The eyes have a cornea (Nesis, 1982/87; Guerra, 1992; Jereb and Roper, 2010).

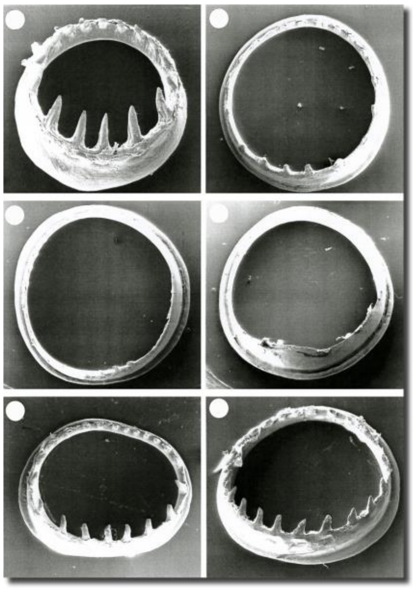

Figure 11.3. ***Loligo vulgaris*****. Various tentacle sucker rings. Photos: Harry Palm and Uwe Piatkowski.**

11.4 Remarks

Mature males and females can be distinguished by means of external characteristics. In mature males of *L. vulgaris*, as in *L. forbesii*, the white testis can be seen through the mantle in the dorsal region between the fins, and there may be evident hectocotylization. Mature females can be easily recognized by the colourful accessory nidamental glands seen in the mid-region of the ventral side of the mantle cavity. Females are also distinguished by the presence of the seminal receptacle, on the ventral buccal membrane, which appears as a small white spot when filled with sperm

(Ngoile, 1987). A detailed description of the reproductive system of *L. vulgaris* can be found in van Oordt (1938).

11.5 Life history

Loligo vulgaris is an annual species with a maximum lifespan of ca. 15 months. Spawning is usually in winter in the northern and eastern portions of its geographic range and year-round with seasonal peaks elsewhere, although there is high spatiotemporal variability in reproductive and growth parameters. Paralarvae are planktonic for 2–3 months.

11.5.1 Egg and juvenile development

Eggs are smaller than those of *L. forbesii*, slightly larger than those of *Alloteuthis subulata* (Mangold-Wirz, 1963a; Boletzky, 2003), and usually measure ca. 2.2 mm in length and 1.6 mm in width, although the size is variable, e.g. 1.82–2.66 mm × 1.51–1.99 mm in Portugal. In the Mediterranean, mature oocytes in the oviduct measure ca. 2.0 × 1.5 mm, and eggs in the egg mass, in stages I and II, measure 2.3 –2.7 mm long by 1.8–2.2 mm wide (Mangold-Wirz, 1963a).

The eggs are generally deposited on a fixed support in relatively shallow water (20–50 m depth; Figure 11.4), and sometimes attached to floating objects in coastal waters (Worms, 1983a). Egg masses comprise multiple strings 60–160 mm long (Mangold-Wirz, 1963a), each string containing an average of 90 ovate eggs embedded in a thick gelatinous coat. Females tend to lay egg strings (30–60 eggs) over existing egg masses of the same species, so one egg mass can contain up to 40 000 eggs, although each female lays only from 3000 (small females) to 6000 (large females) eggs in total.

Figure 11.4. *Loligo vulgaris*. Egg mass attached to the gorgonian *Paramuricea clavata*, 40 m depth, Columbretes Islands, Mediterranean Sea. Photo: Jordi Chias.

Egg deposition apparently occurs throughout the distribution range. For example, egg masses are reported from waters of 15–65 m in northern France and northwestern Spain and at 31–80 m off western and southern Portugal (Pereira *et al.*, 1998). Villa *et al.* (1997) found eggs masses at depths as shallow as 2 m on the south coast of Portugal, although egg deposition in depths <15 m appeared to be restricted to the peak summer months of June–August, and most records were from depths of ≥20 m. The abundance of these egg masses peaked around the end of spring and beginning of summer, similar to the pattern of seasonal abundance of zooplankton. In the Adriatic, egg masses are regularly observed in early spring (March–April) at depths of 12–25 m

(L. Ceriola, pers. comm.). In Morocco, egg masses are found throughout the year attached to hard substrata or branched sessile organisms, on sandy and rocky bottoms, usually at depths of 6–120 m (Baddyr, 1988).

The duration of embryonic development is highly dependent on environmental conditions, e.g. temperature and oxygenation (Worms, 1983a). The final stages of development are characterized by a rapid increase in size, especially in length, while the outer yolk sac is rapidly reduced – partially by utilization of the nutritive material and partially by active transfer of the yolk mass to the inner yolk organ (Naef, 1928). Hatching occurs ca. 125 d after spawning at 13°C, 40–45 d at 12–14°C, 30 d at 17°C, and 26–27 d at 22°C (Mangold-Wirz, 1963a; Boletzky, 1979b). Rosa *et al.* (2012) showed that even a relatively small increase in temperature (2°C), consistent with projected ocean warming, promoted metabolic suppression, premature hatching, and a greater incidence of malformations in "newborn" hatchlings. However, hatchlings also showed some ability to compensate for adverse effects of elevated temperature. The authors state that "heat shock proteins (HSP70/HSC70) and antioxidant enzyme activities constituted an integrated stress response to ocean warming in hatchlings".

Inferences from the embryonic increment widths in statoliths of wild squid suggest that embryonic development typically takes place at temperatures of 12–17°C (Villanueva *et al.*, 2003). Eggs of *L. vulgaris* spawned off the northwestern Iberian Peninsula were estimated to remain at sea, on average, one week longer than those deposited in the Mediterranean, reflecting the slightly higher water temperatures in the Mediterranean Sea. A longer incubation time for egg masses attached to the sea bottom probably increases the mortality risk. Conversely, slower development at lower temperature may improve yolk conversion, leading to larger hatchlings, and increased hatchling survival.

In seawater with salinity values of 34–42 and at pH values of 7.8–8.4, *L. vulgaris* embryos develop and hatch normally. Beyond those ranges, embryos exhibit severe damage and may die. Concentrations of Ca^{2+}, K^{+}, Mg^{2+}, and SO_4^{2-} ions associated with normal development were: 9–15, 9–15, 46–70, and 15–37 mm, respectively (D'Aniello *et al.*, 1989; Şen, 2005). Paulij *et al.* (1990b) studied the impact of photoperiodicity on hatching of *L. vulgaris* in the laboratory and observed that most embryos hatched soon after the light period ended. Embryos that had developed in constant light showed no such hatching rhythm. If those embryos were exposed to a dark shock, most hatched soon after the onset of darkness. A twilight shock, in which the light was reduced by 50%, did not stimulate hatching.

Effects of photoperiod on embryo development were investigated by Şen (2004a). In natural seawater (37 psu, 20.3°C), a photoperiod of 12 h light and 12 h dark resulted in 100% hatching success, but with 24 h light, hatching success was only 52%. Embryos held under summer photoperiod conditions had slower statolith growth than those held at winter photoperiods, whereas constant light conditions produced significantly slower growth in the embryonic statoliths (Villanueva *et al.*, 2007).

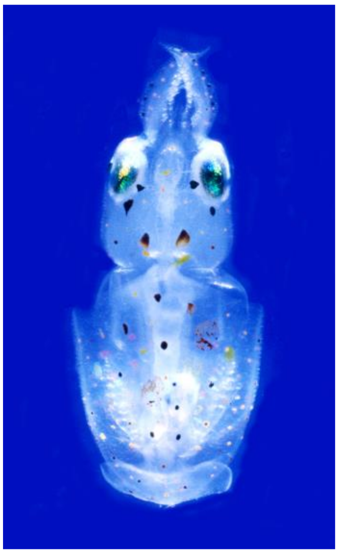

Figure 11.5. *Loligo vulgaris*. Hatchling (under anaesthesia, which may cause chromatophore contraction). Photo: Roger Villanueva.

Total weight, mantle length, and statolith length of newly hatched paralarvae are greater for eggs incubated at lower temperature than for those incubated at higher temperature, as a result of the longer duration of the embryonic development at lower temperatures (Villanueva, 2000a, b).

The paralarvae (Figure 11.5) have a planktonic life style that lasts 2–3 months depending on sea temperature (González *et al.*, 2010; Moreno *et al.*, 2012). Paralarvae are most abundant between the 50 and 125 m isobaths, particularly along the northwestern coast of Portugal (Moreno *et al.*, 2009), where paralarvae up to 9.6 mm ML may be found in plankton samples (Moreno and Pereira, 1998). In Galician waters, paralarval abundance is greatest between May and October (González *et al.*, 2005), later than in Portuguese waters, where paralarvae are found year-round, but abundance is greater in winter and early spring (Sousa Reis, 1989a; Moreno and Pereira, 1998; Moreno *et al.*, 2009).

Little is known about wild *L. vulgaris* paralarvae, mainly because of their similarity to young forms of the co-occurring species *L. forbesii* and *Alloteuthis* spp. (Sweeney *et al.*, 1992). Relevant data from historical collections are compromised because long-preserved specimens lack visible chromatophores, which would otherwise aid species identification (Moreno and Sousa Reis, 1995). Paralarvae appear in low numbers in standard oblique ichthyoplankton and zooplankton hauls, suggesting that some alternative form of directed sampling is needed to study their distribution and seasonality (Moreno and Sousa Reis, 1995; Piatkowski, 1998). Observations in captivity show that, within 20 d of hatching, some squids are able to swim in a horizontal position for several minutes, maintain their position for more than 5 minutes against a current of 2.61 cm s^{-1} and swim several centimetres in pursuit of prey, i.e. in optimal conditions, it is likely that squid start schooling as well as displaying a neritic mode of life within 2 months of hatching (Turk *et al.*, 1986).

11.5.2 Growth and lifespan

Estimates based on length-frequency analysis suggest that *L. vulgaris* can live for up to 4 years (Mangold-Wirz, 1963a). However, counts of daily growth increments in statoliths reveal that lifespan is normally ca. 1 year, although variations have been reported, as detailed hereafter. Slightly longer lifespans (382 and 396 d) have been recorded in males from Galician waters (Rocha and Guerra, 1999) and the West Saharan shelf (Arkhipkin, 1995). Maximum lifespans of 15 months in both sexes were observed in northwestern Portuguese waters by Moreno *et al.* (2007). Note, however, that both Bettencourt *et al.* (1996) and Raya *et al.* (1999) estimated rather shorter lifespans: 9 months in southern Portuguese waters and 10 months on the western Saharan shelf, respectively; it is not clear whether this represents real biological variation or whether methodological issues are partly or wholly responsible.

Male *L. vulgaris* attain greater length and weight than females. In the Northeast Atlantic, maximum mantle length is 546 mm in males (Moreno *et al.*, 2007) and 372 mm in females (A. Moreno, pers. comm.). Larger specimens have been found off the west coast of Africa, males attaining 640 mm and females 485 mm ML (Perales Raya, 2001).

The largest specimens in the Mediterranean Sea (males with an ML of 540 mm and females with 340 mm) were found in the western part (Worms, 1979).

Male and female *L. vulgaris* have different length–weight relationships (Coelho *et al.*, 1994; Guerra and Rocha, 1994; Moreno *et al.*, 2002; Krstulović Šifner and Vrgoc, 2004; Table 11.1), the slope parameter *b* being significantly higher in females (2.38–2.81) than in males (2.20–2.59), corresponding to a greater weight at a given length in females. Comparisons of *b* values across geographic areas suggest a trend of increasing weight at length is (higher *b*) from north to south in the Atlantic and from the Atlantic to the eastern Mediterranean (Moreno *et al.*, 2002).

Growth studies of *L. vulgaris* paralarvae include both laboratory experiments and studies in the wild. Paralarvae have been cultured experimentally by Portman and Bidder (1928), Boletzky (1974, 1979b), Turk *et al.* (1986), and Villanueva (1994, 2000a), and all authors agree that early growth is clearly exponential. As in other squid species, paralarval growth rates are highly variable and strongly related to temperature. Reported average rates of growth in length in the first 75 d post-hatching were 0.05 mm d^{-1} (1.2% ML d^{-1}) under winter temperatures and 0.17 mm d^{-1} (3% ML d^{-1}) under summer conditions (Boletzky, 1979b; Villanueva, 2000b). The increase in weight during this period of life is more pronounced. Villanueva (2000b) measured instantaneous relative growth rates of 3–4% BW d^{-1} at winter temperatures (11°C) and 6–8% BW d^{-1} under summer conditions (19.2°C). As a result, 2 months after hatching, paralarvae reared under summer regimes attain a mean length twice that of winter squid and a mean weight fivefold higher. Nevertheless, there is always a great degree of individual variability in growth rates. In field-based studies using statolith analysis, G (instantaneous relative growth rate) in length (ML) ranged from 1.82 to 2.15% ML d^{-1} (González *et al.*, 2010).

Table 11.1. *Loligo vulgaris.* Length–weight relationships in different geographic areas for females (F), males (M), and sexes combined (All). Original equations converted to $W = aML^b$, where W is body mass (g) and ML is dorsal mantle length (cm).

Region	a	b	Sex	Reference
English Channel	0.192	2.38	F	Moreno *et al.* (2002)
	0.301	2.20	M	
Northwestern Spain	0.104	2.54	F	Guerra and Rocha (1994)
	0.164	2.37	M	
Northwestern Portugal	0.104	2.54	F	Moreno *et al.* (2002)
	0.154	2.41	M	
Southern Portugal	0.135	2.43	F	Coehlo *et al.* (1994)
	0.144	2.38	M	
Sahara Bank	0.109	2.56	F	Moreno *et al.* (2002)
	0.118	2.47	M	
Western Mediterranean Sea	0.187	2.30	F	Sánchez (1986b)
	0.121	2.50	M	
Adriatic Sea	0.197	2.45	F	Krstulović Šifner and Vrgoč (2004)
	0.138	2.44	M	
Greek Seas	0.065	2.81	F	Moreno *et al.* (2002)
	0.078	2.59	M	
Izmir Bay (eastern Aegean)	0.1844	2.3066	All	Akyol and Metin (2001)

Iskenderun Bay (northeastern Levant Sea)	0.0189	3.163	F	Duysak *et al.* (2008)
	0.0182	3.2872	M	
	0.0019	4.0775	All	

Between the ages of 4 and 12 months, males generally grow at 1.2–1.6 mm d^{-1} and females slower at 0.9–1.0 mm d^{-1}. Instantaneous growth rate relative to ML is 0.8–1.0% d^{-1} for males and 0.7–0.9% d^{-1} for females. Differences between male and female growth rates have been observed in most studies that adequately sampled the full size range of animals (Natsukari and Komine, 1992; Arkhipkin, 1995; Bettencourt *et al.*, 1996; Raya *et al.*, 1999; Rocha and Guerra, 1999; Moreno *et al.*, 2007).

Growth rate estimates in *L. vulgaris* reveal great individual variability in size-at-age, particularly, in males. Growth rates depend on hatching season and in particular on environmental conditions close to hatching, as proposed by Forsythe (1993). *Loligo vulgaris* hatched at warm temperatures have higher ML-at-age than specimens hatched at low temperatures (Rocha and Guerra, 1999; Moreno *et al.*, 2007).

Researchers agree that squid growth (in terms of length-at-age) does not conform to the generalized von Bertalanffy model (von Bertalanffy, 1938), often adopted to describe fish growth (Jackson, 1994). For juvenile and adult *L. vulgaris*, power, exponential or double exponential models generally provide the best fit to length-at-age data, depending on sex, hatching season, and geographic area (Natsukari and Komine, 1992; Arkhipkin, 1995; Bettencourt *et al.*, 1996; Raya *et al.*, 1999; Rocha and Guerra, 1999; Moreno *et al.*, 2007). However, a logistic model best describes growth of females hatched in the warm season on the northwestern Portuguese shelf, with an inflection seen close to age at 50% maturity (agem$_{50\%}$) (Moreno *et al.*, 2007). Perales Raya (2001) also observed such an inflection in female growth. Average growth curves calculated using equations presented in the above-mentioned studies are plotted in Figure 11.6.

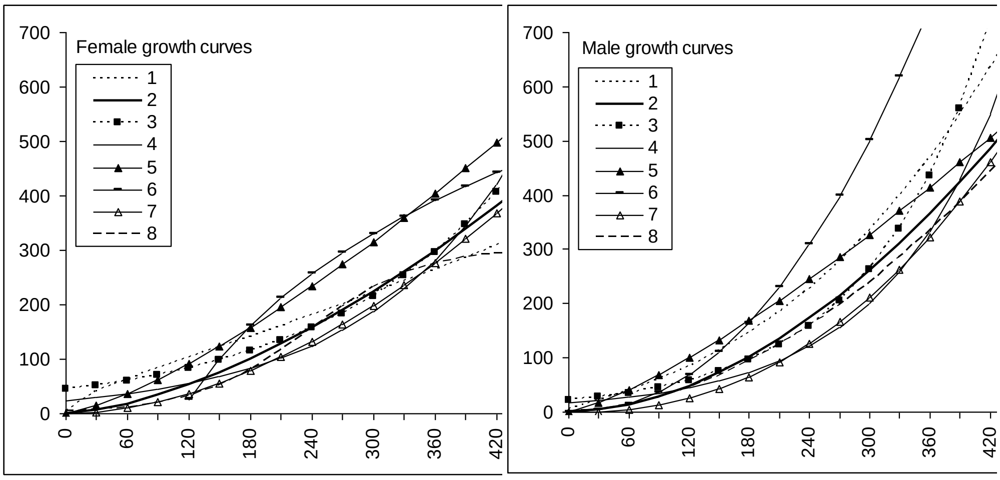

Figure 11.6. ***Loligo vulgaris*****. Growth curves (length in mm vs. age in d), according to 1, Natsukari and Komine (1992); 2, Arkhipkin (1995); 3, Rocha and Guerra (1999); 4, Rocha and Guerra (1999) autumn-winter hatchers; 5, Bettencourt *****et al.***** (1996), spring-summer hatchers; 6, Raya *****et al.***** (1999); and 7,8, Moreno *****et al.***** (2007) cold and warm season hatchers.**

11.5.3 Maturation and reproduction

The sex ratio is generally ca. 1:1 across the distribution range, although seasonal shifts in sex ratio have also been reported (Baddyr, 1988; Guerra and Rocha, 1994; Raya *et al.*, 1999; Moreno *et al.*, 2002; Krstulović Šifner and Vrgoč, 2004) as well as differences in sex ratio between size classes. Raya *et al.* (1999) found that the proportion of males was greatest in the smallest size classes, which is consistent with findings for *L. forbesii*.

A wide range is observed in body size of mature animals of both sexes: 80–640 mm in males and 120–360 mm in females. Across its geographic distribution, *L. vulgaris* males mature at both a lower minimum size and a large maximum size than females. In the northwestern Mediterranean, there is a positive relationship between ovary weight and size at ML >14 cm, the size at which sexual maturation starts in females (Sánchez and Demestre, 2010).

Based on examination of animals sampled at several sites in the Atlantic and Mediterranean, Moreno *et al.* (2002) calculated the size at which 50% of individuals are mature ($MLm_{50\%}$) as 168 mm in males and 188 mm in females. However, the fit for males is misleading, because two modes in size at maturity were detected in males from most areas in the Northeast Atlantic, the first at ca. 180 mm, and the second at 300–330 mm, at which size all males are mature (Coelho *et al.*, 1994, Guerra and Rocha 1994, Moreno *et al.* 1994). Morphometric analysis of small and large mature males revealed no significant differences except in relation to size, suggesting that the two groups of males belong to the same population (Moreno *et al.*, 1994). Two modes in size at maturity are not found in females. Given that two size-dependent reproductive strategies are known in males (guarding by large males and sneaking in by small males, see Hanlon and Messenger, 1996), it seems likely that natural selection favours the existence of two growth and maturation strategies, intermediate-sized animals being at a disadvantage.

Size at maturity shows some degree of geographic variation in both sexes (Moreno *et al.*, 2002; Smith *et al.*, 2011). Size at maturity ($MLm_{50\%}$) of females appears to be higher in the southern part of the Northeast Atlantic (220–230 mm; Bettencourt, 1994; Raya *et al.*, 1999) than in the north (176–195 mm; Guerra and Rocha, 1994; Moreno *et al.*, 2005), and lower in the western and central Mediterranean (160–165 mm; Mangold-Wirz, 1963a; Krstulović Šifner and Vrgoč, 2004) relative to the Atlantic. Comparisons are more difficult for males, but there are no clear geographic trends in minimum size at maturity, which is ca. 120 mm in the English Channel (Moreno *et al.*, 2002) and Galician waters (Guerra and Rocha, 1994), ca. 90–110 mm in southern Portuguese waters (Bettencourt, 1994), on the Saharan Bank (Raya *et al.*, 1999), and in the Mediterranean (Mangold-Wirz, 1963a; Moreno *et al.*, 2002; Krstulović Šifner and Vrgoč, 2004), but somewhat lower (80 mm) in northwestern Portuguese waters (Moreno *et al.*, 2002).

There is also seasonal variation in size at maturity across the distributional range (Moreno *et al.*, 2002). Differences in size at maturity have also been observed between squid that had hatched at different times of the year (Boavida-Portugal *et al.*, 2010). In northwestern Portuguese waters, females that hatched during the warm season were smaller at maturity ($MLm_{50\%}$ = 156 mm) than those that hatched during the cold season ($MLm_{50\%}$ = 191 mm). In males, two modes in size-at-maturity were present within both seasonal cohorts, indicating that the existence of two size modes is not due to the existence of different cohorts (Moreno *et al.*, 2005).

Age studies confirm that males mature ca. 1 month earlier than females (Rocha, 1994; Arkhipkin, 1995; Bettencourt *et al.*, 1996; Moreno *et al.*, 2005). In Portugal, males mature at a mean age of 9 months, and spawning takes place at a mean age of 10 months. A high percentage of the population is mature before 1 year (Moreno *et al.*, 2005). Farther south, on the Saharan Bank, minimum age at full maturity is 250 d in males (ca. 8 months) and 285 d in females (ca. 9.5 months) (Arkhipkin, 1995).

Most studies suggest that small mature *L. vulgaris* are usually younger than large mature ones (Rocha, 1994; Arkhipkin, 1995; Bettencourt *et al.*, 1996; Moreno *et al.*, 2005), but some studies show that small and large mature animals can have similar ages (Perales Raya, 2001).

Age at maturity is related to time of hatching; females hatched during the warm season have faster growth rates earlier in life and reach maturity at younger ages than those hatched in the cold season. Growth rates of the warm-water cohort animals decline after maturation, possibly related to less favourable environmental conditions. In contrast, females hatched during the cold season have slower initial growth rates, but their late maturation and the favourable environmental conditions they encounter later result in increased growth rates towards the end of their life cycle (Moreno *et al.*, 2005, 2007). The influence of hatching time on age at maturity is more pronounced than its influence on size at maturity (Moreno *et al.*, 2005).

Individual maturity in sampled animals is often described using a five-point scale, modified from Lipiński (1979) by Boyle and Ngoile (1993a). Sex has been identified macroscopically in squid from 4 months of age (Arkhipkin, 1995; Moreno *et al.*, 2005), and the beginning of gonad maturation (maturity stage 2) has been observed from ca. 5 months in males and 6 months in females (Moreno *et al.*, 2005). The process of maturation is fast. In Portuguese waters, from the beginning of visible maturation, specimens of both sexes can become fully mature in less than 1 month (Moreno *et al.*, 2005).

Variability in the rate of maturation is high, with standard deviations of 1–1.5 months from the mean age at each maturity stage. Large immature males frequently appear in samples, suggesting that growth and maturation can become uncoupled.

There is considerably greater reproductive investment in terms of gonads, genital tract, and glands in females than in males. The gonadosomatic index (GSI) in males is between 1.6 and 3.8% compared with up to 30% in females (Worms, 1983a). Gonad weight is better correlated with size than with age in both sexes (Moreno *et al.*, 2005; Sánchez and Demestre, 2010).

Geographic and seasonal variation is found in GSI. GSI is lowest in the Western Sahara, where *L. vulgaris* attain the largest sizes (Moreno *et al.*, 2002). Females hatched under warmer temperatures that achieve earlier maturation also have a higher GSI (i.e. they invest a greater proportion of their total mass in reproduction) than females hatched during the cold season, which mature later in life. There are marked differences in GSI between 7-month-old individuals of these two hatching groups (Moreno *et al.*, 2005).

Males seize females by the head during copulation. Spermatophores are passed to the female through the penis with the aid of the hectocotylized arm (Ngoile, 1987) and placed in the female's buccal membrane and into a spermatheca while in a head-to-head position (Mangold-Wirz, 1963a). Mating may take place prior to arrival as well as at the spawning grounds.

Eggs are fertilized by sperm from the spermatheca. The nidamental and oviducal glands secrete a mucus that coats eggs and forms egg strings 60–160 mm long (Worms, 1983a). Females lay egg strings close to other egg masses, visual and/or chemical stimuli probably being involved (Mangold-Wirz, 1963a).

Loligo vulgaris is clearly semelparous because the ovaries show no evidence of regression and regrowth between spawning bouts (Mangold, 1987). However, the process of oogenesis involves "partial ovulation" (Rocha and Guerra, 1996), i.e. the development of oocytes is asynchronous, and mature ovaries have polymodal distributions of oocytes (3–5 modal groups), suggesting that egg-laying takes place in several batches during the spawning period. Rocha and Guerra (1996) applied the term "intermittent terminal spawning" to describe this strategy (see also Rocha *et al.*, 2001). When fully mature, the oviduct of the female is filled with ripe eggs. Spawning has rarely been seen in the laboratory (Mladineo *et al.*, 2003).

Small protoplasmic oocytes, <0.4 mm in diameter, dominate throughout the reproductive cycle (Rocha and Guerra, 1996; Laptikhovsky, 2000), as in other loliginid species (Sauer and Lipiński, 1990; Collins *et al.*, 1995a). As there is continuous oocyte maturation, several types of oocyte are found in the mature ovary at various stages of development and differing in appearance and size. The smallest, completely immature oocytes, measure 0.17–0.68 mm in diameter. Larger, but still immature, oocytes measure 0.86–1.65 mm, and maturing oocytes with a characteristic reticulated surface measure 1.55–2.45 mm. The largest, fully mature oocytes have a smooth surface. These large eggs show some geographic variation in size, with greater mean size recorded in Galician waters and in the western and central Mediterranean (2.3–2.8 mm; Mangold-Wirz, 1963a; Guerra and Rocha, 1994; Krstulović Šifner and Vrgoc, 2004), intermediate size in southern Portuguese waters (2.2 mm; Coelho *et al.*, 1994), and low mean size along the northwest coast of Africa (1.9 mm; Laptikhovsky, 2000) and northwestern Portugal (1.1–1.2 mm; Boavida-Portugal *et al.*, 2010).

Worms (1983a) estimated maximum fecundity as 7000 eggs, but this value was based on counting only ripe eggs in the oviduct. Other studies that consider the yolk oocyte stock in the ovary and oviduct have estimated maximum fecundity to be between 10 150 and 42 000 eggs (Baddyr, 1988; Coelho *et al.*, 1994; Guerra and Rocha, 1994; Lopes *et al.*, 1997; Laptikhovsky, 2000). This may still be an underestimate if the protoplasmic oocytes also contribute to the total fecundity of an individual. On that basis, Laptikhovsky (2000) estimated a potential fecundity of 28 500–74 200 eggs, with higher values generally in larger squid (fitted regression: potential fecundity = $136.84\ ML^{1.11}$**)**. However, the correlation between the number of oocytes and the ML is generally weak, and other studies show that small mature females may have more oocytes than females that mature at a larger size (Guerra and Rocha, 1994; Krstulović Šifner and Vrgoč, 2004).

Spermatophore formation in mature males appears to be continuous. The maximum number of spermatophores is slightly over 1000, and their length varies between 7.5 and 20 mm. Larger animals have larger spermatophores, although the number of spermatophores is not related to mantle length (Mangold-Wirz, 1963a; Guerra and Rocha, 1994; Krstulović Šifner and Vrgoč, 2004).

Loligo vulgaris has an extended seasonal spawning season in most regions, although geographic variation is also evident. The spawning period is seasonally restricted in the North Sea (Tinbergen and Verwey, 1945), in the English Channel (Moreno *et al.*, 2002), and in the central (Krstulović Šifner and Vrgoč, 2004) and eastern Mediterranean (Moreno *et al.*, 2002). Spawning throughout the year has been reported farther south in the Atlantic, from the northwestern Spanish coast to Western Sahara (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; Vila *et al.*, 2010), and in the western Mediterranean (Worms, 1983a). In some areas where spawning is year-round, two peaks are observed.

The timing of peak spawning also shows geographic variation and is earlier south than north in Atlantic waters and earlier in all Atlantic areas than in the Mediterranean.

Spawning takes place between November and April (peaking in February) in the English Channel, mostly during the same period along the northwestern Spanish coast, and throughout the year, with peaks in late autumn/early winter and late spring, in Portuguese waters and the Saharan Bank. In the Adriatic Sea, spawning is mainly between January and May (peaking in April–May), and in Greek seas, between November and May (peaking in April).

11.6 Biological distribution

11.6.1 Habitat

Loligo vulgaris paralarvae are reported in plankton samples from off Galicia and Portugal (Moreno and Pereira, 1998; Piatkowski, 1998; González *et al.*, 2005) and as far south as 21°N along the northwestern African coast (Guerra *et al.*, 1985). *Loligo* sp. paralarvae (some possibly of *L. vulgaris*) are recorded in plankton samples from the English Channel (Collins *et al.*, 2002). *Loligo vulgaris* paralarvae were absent from plankton samples collected in neritic waters around Scotland, the northwestern North Sea, and the Rockall Trough area (Yau, 1994), but they have been reported from the eastern Mediterranean (Salman, 2012). In Portuguese waters, paralarvae are most abundant over depths of 80–90 m (Moreno *et al.*, 2009). In winter, their distribution extends offshore, but in summer and autumn, they concentrate closer inshore (Moreno and Sousa Reis, 1995; Moreno *et al.*, 2009). Paralarvae are transported to the inner parts of the rías during upwelling events, which favours their coastal retention (González *et al.*, 2005). The distribution of paralarvae is limited to areas with surface water temperatures of 13–20°C (Moreno and Sousa Reis, 1995; Moreno *et al.*, 2009), and abundance is greater near the cold limit of the range, at 13–14°C (Rocha *et al.*, 1999; Moreno *et al.*, 2009).

Loligo vulgaris is neither pelagic nor fully benthic; it is more or less restricted to the sea bottom during the spawning season, but displays pelagic behaviour at other times, e.g. when hunting (Worms, 1983a). It can be described as nektobenthic and neritic; it is usually more abundant in water shallower than 100 m (Sánchez and Guerra, 1994; Salman *et al.*, 1997; Sánchez *et al.*, 1998a; Tserpes *et al.*, 1999), but is found from the coast to the limits of the upper slope (200–550 m). Where the shelf is narrow, the range at which *L. vulgaris* is caught extends into deeper water, as in Algerian waters (Mangold-Wirz, 1963a), and the Ionian Sea (Lefkaditou *et al.*, 2001).

Off the Portuguese coast, *L. vulgaris* can be found from the coast to water 100 m deep (Cunha *et al.*, 1995), with spawning females concentrating where the depth is 80–100 m (Moreno, 1998). In the Gulf of Cádiz, it is mainly distributed between depths of 15 and 100 m (Vila *et al.*, 2010). In the Mediterranean, it lives in the circumlittoral area and shelf, mainly at depths of 10–150 m, although off the Algerian shelf, it has been captured as deep as 550 m; it is most common at 50–60 m (Mangold-Wirz, 1963a; Worms, 1983a).

Studies on demersal species assemblages, based on trawl surveys, have shown that in areas with extended continental shelves, such as the northern Tyrrhenian Sea, *L. vulgaris* is more abundant at depths <50 m, associated with other coastal species such as *Sepia officinalis* and *Octopus vulgaris* (Sánchez *et al.*, 1998a). In other areas, it is associated with species with a wider bathymetric distribution on the continental shelf, such as *Eledone moschata, Alloteuthis* spp., *Diplodus annularis, Pagellus erythrinus, Dentex* spp., *Seranus cabrila, Spicara flexuosa, Spicara smaris, Boops boops, Citharus linguatula, Mullus barbatus, Trachinus* spp., and *Pagrus pagrus*. Depth influences the composition of assemblages associated with *L. vulgaris* more than any other factor (Pereira *et al.*, 1997).

Generally, *L. vulgaris* inhabits temperate waters, with juveniles and adults in water with temperatures ranging from 12.5 to 20°C. Abundance is, however, greatest in water with sea surface temperatures between 13 and 15°C. The animals require a relatively high temperature for reproduction, and their migration to the spawning grounds is later in years when coastal waters take longer to warm or warm later (Mangold-Wirz, 1963a).

In Portuguese waters, the distribution of the species is clearly associated with bottom water temperature (Pereira *et al.*, 1998). It tends to concentrate in the north in autumn, closer to the offshore limits of its distribution, and in the south in summer, close inshore, where summer bottom temperatures are warmer.

Juveniles and adults can live in waters with rather low salinities, although they do not usually enter estuaries or lagoons (Mangold-Wirz, 1963a). Indeed, the species is found in very shallow water only when the salinity rises above 30, suggesting a tolerance range of 30–36 in the North Atlantic (Tinbergen and Verwey, 1945), with a slightly higher upper limit in the Mediterranean (37.7–38.15) (Salat *et al.*, 1978). However, in the Sea of Marmara, Ünsal *et al.* (1999) recorded *L. vulgaris* in waters where the salinity was always >25. Laboratory experiments have shown that eggs die very early below a salinity of 24 (Şen, 2004b).

The suitability of substratum for egg-string attachment seems to be the main reason for association of *L. vulgaris* with particular bottom types, although some prey species, e.g. sandeels, may also be associated with particular substrata. In the Atlantic, *L. vulgaris* is most abundant over coarse sand bottoms and scarce over silt bottoms. In Portuguese waters, its bathymetric distribution seems to be related to the offshore limit of occurrence of sandy bottoms (Pereira *et al.*, 1995). However, in the Mediterranean, it is reported over all bottom sediment types, although mainly over coastal silt in spring and summer and over offshore sandy bottoms in autumn and winter (Mangold-Wirz, 1963a; Worms, 1983a). In the Adriatic, it may also be found over bottoms covered by sea grasses (*Zostera* and *Posidonia* beds), especially in autumn (Gamulin-Brida and Ilijanić, 1972).

Recruitment and spawning are known throughout the geographic range of the species. Investigations on spawning grounds along the south coast of Portugal have shown that the greatest number of egg-mass records coincides with the highest values of zooplankton abundance (Villa *et al.*, 1997). Sexual segregation has not been observed in the Northeast Atlantic population (Guerra, 1992), although Worms (1983a) found that landings by boat in the western Mediterranean indicate an interesting segregation by sex (80–90% of one sex), suggesting that males and females gather in different schools.

11.6.2 Migrations

Horizontal migratory movements by *L. vulgaris* are mainly related to sexual maturation and spawning (Worms, 1983b). Onshore and offshore migrations, related to reproduction, are well-described for Mediterranean populations. Large (maturing or mature) animals move towards shallow coastal waters for mating and spawning; some squid mate during this migration. Some immature animals also perform this offshore/onshore migration, but some time after the mature individuals. These crossed migrations result in a complex population structure. Males arrive at the spawning grounds some days before females. Large mature animals spawn first and then leave littoral waters. This results in a progressive decrease in the mean size of squid in fishery catches over the spawning season (Mangold-Wirz, 1963a). Irrespective of size, a large proportion of the individuals (mainly females) die a few days or weeks after spawning (Worms, 1983a). Small squids hatched near the coast migrate towards deep water, mostly in autumn and winter (Sánchez and Guerra, 1994).

In the Atlantic, *L. vulgaris* migrates long distances (south–north and north–south), possibly up to 500 km. According to Tinbergen and Verwey (1945), it actively migrates north in spring, probably entering the North Sea from the English Channel and migrating along the Belgian, Dutch, northwestern German, and Danish coasts, where it is found in late summer. Seasonal variation in fishery catches also suggests the existence of seasonal migrations in the Iberian Peninsula and Bay of Biscay (Moreno *et al.*, 2002). In Portuguese waters, an indication of horizontal migration is the occurrence of late winter/early spring recruitment peaks locally unmatched by previous spawning peaks. A late summer spawning peak on the south coast of Portugal, reported by Bettencourt *et al.* (1996), could result in a recruitment peak along the northwest coast after juvenile migration (Moreno *et al.*, 2002).

In some areas, such as in the coastal waters of the Thracian Sea, inshore–offshore movements appear to be temperature-driven, with temperature significantly affecting beach-seine catches of *L. vulgaris* (Lefkaditou *et al.,* 1998b).

Feeding is the main reason for daily vertical migration to the surface at night. *Loligo vulgaris* paralarvae perform diel vertical migrations, arriving near the surface some time after sunset and remaining in the surface layers at least until midnight (Sousa Reis, 1989b). Differences in catches between day and night suggest that post-recruit *L. vulgaris* live close to the seabed by day and disperse vertically into the water column at night (Roper and Young, 1975), where they can be seen near the surface. Juveniles also undertake diel vertical migration, although mature adults tend to remain close to the bottom (Mangold-Wirz, 1963a). Feeding at night is supported by recent tagging experiments on *L. vulgaris*; tagged squid moved within a small area during the day, but covered a larger area from sunset to sunrise (Cabanellas-Reboredo *et al.*, 2012a).

11.7 Trophic ecology

11.7.1 Prey

Loligo vulgaris is an active cephalopod characterized by a fast growth rate and digestion (Bidder, 1950), suggesting that prey abundance could be a decisive factor influencing species distribution. However, the wide spectrum of its prey composition does not limit it to a specific biotope, except in the early stages, when a more restricted range of pelagic prey of small size is needed.

Hatchlings can feed exclusively on the inner yolk sac, but the digestive tract is fully functional even before the complete reabsorption of yolk (Worms, 1983a). Juvenile and adult *L. vulgaris* are carnivorous predators, attacking, seizing, and eating relatively large active prey. Prey sizes estimated from stomach content remains are smaller than squid sizes (Rocha *et al.,* 1994).

Juvenile squid consume more planktonic than benthopelagic prey, particularly planktonic crustaceans such as copepods, mysids, and euphausids, but also fish larvae (Nigmatullin, 1975; Boletzky, 1979b; Worms, 1983a), indicating an ontogenetic shift in the species' diet. Laboratory rearing revealed that decapod crab zoeae and mysids were the easiest food for young squids to capture (Boletzky, 1979b; Villanueva, 1994). *Palaemonetes* larvae (shrimp) were easily captured and appeared to be the preferred food species of paralarvae, whereas fish larvae were the preferred food of juveniles (Turk *et al.*, 1986). Observations in captivity also suggest that, although paralarvae will attack conspecifics, they never display cannibalism (Boletzky, 1979b).

Fish are the most common prey of adult *L. vulgaris*, their incidence increasing in the diet with increasing squid size (Rocha *et al.*, 1994; E. Lefkaditou, pers. comm.). Cephalopods and crustaceans are of lesser importance in the diet, although there is evidence of regional differences (Guerra and Rocha, 1994; Hasan *et al.*, 1994; Pierce *et al.*, 1994a). Remains of polychaetes have also been found in the stomach contents of *L. vulgaris* from the Iberian Atlantic coast.

Despite the difficulties associated with identification of squid prey to species level, which (to date) has generally been possible only when otoliths, beaks, or other hard parts are found among food remains, a broad spectrum of species has been recorded in the diet of *L. vulgaris* in several regions (Table 11.2; see also Pierce *et al.*, 1994a; Rocha *et al.*, 1994; Coelho *et al.*1997).

Diet and food intake varies with season, most probably related to a combination of seasonal changes in prey abundance, in fishing grounds, and hence in sample source (Pierce *et al.*, 1994a; Rocha *et al.*, 1994). In northwestern Spain during late spring, summer, and early autumn when *L. vulgaris* are fished inshore by jigging, the frequency of cephalopods, crustaceans, and polychaetes in the diet increases relative to the rest of the year, when the squid are caught offshore by trawling.

Cannibalism does not seem to play an important role in the species' trophic ecology, because remains of *L. vulgaris* have been rarely reported in stomach contents. No differences in feeding habit have been observed between sexes, and females do not decrease food intake during maturation (Worms, 1983a; Rocha *et al.*, 1994).

Simulation in captivity of injuries caused by jigging (loss of one or both tentacles) showed that squid missing tentacles are less able to catch fast-swimming prey (e.g. fish), but can compensate by changing their diet and predation behaviour (Cabanellas-Reboredo *et al.*, 2011).

Table 11.2. Prey composition of *Loligo vulgaris*, as known from studies in different regions of the Northeast Atlantic, Saharan Bank, and northern Aegean Sea (compiled from Guerra and Rocha, 1994[1]; Pierce *et al.*, 1994a[2]; Coelho *et al.*, 1997[3]; Lefkaditou, 2006[4]).

Taxon	Species
Osteichthyes	
Ammodytidae	*Ammodytes tobianus* (small sandeel)[1], *Gymnammodytes semisquamatus* (smooth sandeel)[1], *Hyperoplus lanceolatus* (greater sandeel)[1], indet.[1,2]
Argentinidae	*Argentina sphyraena* (Argentine)[1], *Argentina* spp.[4]
Atherinidae	*Atherina presbyter* (sand smelt)[1,2], *Atherina* spp.[1,3]
Blenniidae	*Blennius ocellaris* (butterfly blenny)[1], *Blennius* spp.[1]
Callionymidae	*Callionymus reticulatus* (reticulated dragonet)[1], *Callionymus* spp.[1,2], indet.[3]
Carangidae	*Trachurus trachurus* (Atlantic horse mackerel)[1,3], *Trachurus* spp.[2], indet.[3]
Cepolidae	*Cepola macrophthalma* (red bandfish)[1]
Clupeidae	*Clupea harengus* (Atlantic herring)[2], *Sardina pilchardus* (European pilchard)[3], *Sprattus sprattus* (European sprat)[1], indet.[1,2]
Engraulidae	*Engraulis encrasicolus* (European anchovy)[3]
Gadidae	*Gadiculus argenteus* (silvery pout)[1,2,4], *Micromesistius poutassou* (blue whiting)[1,2], indet.[1,2]

Gobiidae	*Aphia minuta* (transparent goby)[1], *Gobiusculus flavescens* (two-spotted goby)[1], indet.[1,2,3,4]
Hemiramphidae	indet.[3]
Lotidae	*Gaidropsarus* spp.[4]
Myctophidae	*Diaphus dumerilii*[3], indet.[3]
Percidae	*Gymnocephalus cernuus* (ruffe)[3]
Pleuronectidae	indet.[3]
Scombridae	*Scomber scombrus* (Atlantic mackerel)[3]
Sebastidae	*Helicolenus dactylopterus* (blackbelly rosefish)[2]
Soleidae	*Microchirus boscanion* (Lusitanian sole)[3], *Microchirus* spp.[3]
Sparidae	indet.[2,3,4]
Sternoptychidae	*Maurolicus muelleri* (pearlside)[2],
Triglidae	*Chelidonichthys* spp.[3]
Crustacea	indet.[1,2]
Decapoda	indet.[3]
Dendrobranchiata-Penaeiodea	indet.[1]
Pleocyemata-Brachyura	Portunidae indet.[1]
Euphausiacea	indet.[3]
Mysida	indet.[1]
Amphipoda	Gammaridae indet.[3]
Isopoda	indet.[3]
Cephalopoda	
Myopsida	*Alloteuthis media*[4], *A. subulata*[2], *Loligo forbesii*[2], *L. vulgaris*[3], Loliginidae indet.[3]
Oegopsida	Cranchiidae indet.[3]
Sepioidea	*Rondeletiola minor*[1], *Sepia elegans*[3], *Sepia* spp.[3], *Sepietta* spp.[1], Sepiolidae[4], indet.[2]
Octopoda	*Octopus* spp.[3]
Gastropoda	*Turitella* spp.[1]
Bivalvia	indet.[1]
Polychaeta	indet.[1,2,3]
Phyllodocida	*Hediste diversicolor* (as *Nereis diversicolor*)[1], *Nephtys* spp.[3], *Nereis* spp.[3], *Perinereis* spp.[3]

11.7.2 Predators

Identification of long-finned squids in the stomach contents of numerous predator species in European seas remains at the level of the family Loliginidae (although it should be possible to distinguish beaks of *Alloteuthis* spp. from beaks of *Loligo* spp.). Nonetheless, *L. vulgaris* has been identified in the stomach contents of several large pelagic and demersal fish as well as marine mammals (Table 11.3).

Table 11.3. Known predators of *Loligo vulgaris* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References

Cephalopoda	Common octopus (*Octopus vulgaris*)	Quetglas *et al.* (1998a)
Chondrichthyes	Blainville's dogfish (*Squalus blainville*)	Martinho *et al.* (2012)
	Blackspotted smooth-hound (*Mustelus punctulatus*)	Jardas *et al.* (2007)
	Blonde ray (*Raja brachyura*)	Farias *et al.* (2006)
	Bull ray (*Pteromylaeus bovinus*)	Capapé (1977)
	Eagle ray (*Myliobatis aquila*)	Jardas *et al.* (2004)
	Lesser spotted dogfish (*Scyliorhinus canicula*)	Martinho *et al.* (2012)
	Marbled electric ray (*Torpedo marmorata*)	Capapé *et al.* (2007)
	Pelagic stingray (*Pteroplatytrygon violacea*)	Lipej *et al.* (2013)
	Smooth-hound (*Mustelus mustelus*)	Morte *et al.* (1997), Kabasakal (2002)
	Thornback ray (*Raja clavata*)	Kabasakal (2002), Farias *et al.* (2006)
	Torpedo ray (*Torpedo* spp.)	Abdel-Aziz (1994)
Osteichthyes	Atlantic bluefin tuna (*Thunnus thynnus*)	Battaglia *et al.* (2013)
	Atlantic stargazer (*Uranoscopus scaber*)	Sanz (1985)
	Common two-banded seabream (*Diplodus vulgaris*)	Rosecchi (1987)
	Greater amberjack (*Seriola dumerili*)	Matallanas *et al.* (1995)
	Lesser weever (*Echiichthys vipera*)	Creutzberg and Duinevald (1986)
	Spotted flounder (*Citharus linguatula*)	Teixeira *et al.* (2010)
	Swordfish (*Xiphias gladius*)	Hernández-García (1995), Salman (2004), Peristeraki *et al.* (2005)
Pinnipedia	Mediterranean monk seal (*Monachus monachus*)	Guclusoy (2008)
Cetacea	Harbour porpoise (*Phocoena phocoena*)	Börjesson *et al.* (2003)
	Bottlenose dolphin (*Tursiops truncatus*)	San Miguel (1977), Orsi Relini *et al.* (1994), Blanco *et al.* (2001), Santos *et al.* (2007)
	Common dolphin (*Delphinus delphis*)	González *et al.* (1994a), Santos *et al.* (2013)
	Long-finned pilot whale (*Globicephalus melas*)	González *et al.* (1994a), Santos *et al.* (2014]
	Risso's dolphin (*Grampus griseus*)	González *et al.* (1994a), Bearzi *et al.* (2011)

11.8 Other ecological aspects

11.8.1 Parasites

The copepod *Pennella varians* has been found on the gills, and various species of helminths in the stomach, intestine, and digestive tube of *L. vulgaris* (Dollfus, 1958; González *et al.*, 2003). Zuev and Nesis (1971) recorded a range of parasites in *L. vulgaris*: the cestodes *Scyphophyllidium pruvoti* and *Phyllobothrium loliginis*, the trematode *Isancistrum loliginis*, and the nematode *Filaria loliginis.* The polychaete *Capitella hermaphrodita* lives in the external envelopes of the egg capsules, eating them, but not attacking the eggs.

11.8.2 Contaminants

Heavy metal accumulation from seawater in the embryos of *L. vulgaris* seems to be lower than recorded in *Octopus*, probably because of the presence of a mucilaginous envelope in the squid egg mass, but seems to be higher than in cuttlefish, because of the good protection provided by the *Sepia* egg shell (Lacoue-Labarthe *et al.*, 2011a). Increasing seawater $p\mathrm{CO}_2$ (ocean acidification) enhanced the uptake of both silver and zinc, and led to reduced uptake of cadmium and mangansese in *L. vulgaris* embryos (Lacoue-Labarthe *et al.*, 2011b).

A recent study indicated that methyl mercury levels in *L. vulgaris* from Portuguese waters have had no adverse implications for human health, although maximum consumption levels were suggested for octopuses and cuttlefish, and the authors expressed concern that other metals accumulated by cephalopods, e.g. cadmium, may pose a greater threat to consumers (Cardoso *et al.*, 2012).

11.9 Fisheries

The main recruitment areas along Atlantic coasts are located in the south, from Galician through Portuguese waters, where recruits are found throughout the year (Pereira *et al.*, 1998). In the remaining areas of the distribution range to the north, recruits are present in high proportions only in the main recruitment seasons.

In the Northeast Atlantic, there are one or more seasonal peaks in recruitment, males usually recruiting earlier to the fishery (Boyle and Pierce, 1994). Along the Portuguese coast and on the Saharan Bank, the recruitment periods can be longer (Moreno *et al.*, 2002). In northwestern Portugal, recruitment to the fisheries starts at ca. 5 months of age and at mantle lengths from 60 mm (Moreno *et al.*, 1996). Recruitment takes place in water 20–50 m deep (Moreno, 1998). On the Saharan Bank, the main recruitment season extends from June to September, but with secondary recruitment peaks in some years in November–December (Raya *et al.*, 1999). In the western Mediterranean, the main recruitment season is in late summer (Lloret and Lleonart, 2002), and in the Catalan Sea, the minimum size at recruitment is ca. 40 mm (Mangold-Wirz, 1963a). In the Thracian Sea, recruits of 5–12 cm ML appear on inshore fishing grounds in May, whereas maturing large individuals migrate inshore in autumn (Anon., 2000).

In the Atlantic and Mediterranean, *L. vulgaris* is mainly a bycatch of the multispecies bottom and pelagic trawl fisheries and is landed throughout the year. It is a secondary target species in the Saharan Bank cephalopod trawl fishery (Raya *et al.*, 1999), and is usually landed mixed with *L. forbesii* (the two species are usually not separated in official statistics). There are also directed small-scale coastal fisheries, based on hand-jigging, beach-seining, and other artisanal gears, as well as gillnets and trammelnets, especially in Spain and Portugal, which target the animals when they enter coastal waters in autumn and winter to spawn (Guerra *et al.*, 1994; Simon *et al.*, 1996; Lefkaditou *et al.*, 1998b).

In the Northeast Atlantic, *L. vulgaris* is probably the main component of long-finned squid landings, which have fluctuated from ca. 7000 to 12 500 t annually over the past decade, peaking in 2003 and being lowest in 2008 (ICES, 2012). (A lower total in 2009 was excluded since France did not report its landings in 2009). The FAO Fishstat database (FAO, 2011) shows landings of "common squids nei" in the Northeast Atlantic varying from 1700 to 5700 t annually in the decade up to 2010. However, it is likely that much of the common squid landed found its way into the "various squids nei" category (which peaked at ca. 13 500 t in 2004). In the Mediterranean, FAO landings statistics for "common squids nei" ranged from ca. 4000 to 6000 t in the decade up to 2010. Although the category "European squid" exists in the FAO database, a maximum of only 22 t (in 2010) was assigned to this species in Mediterranean landings, and no landings from the Northeast Atlantic were assigned to the category.

At a local level, better quality statistics are sometimes available for landings of *L. vulgaris.* In the coastal rías of southern Galicia (northwestern Spain), squid are targeted during the months July–September using a boliche (boat-seine). According to a study carried out during 1999–2003, *L. vulgaris* is the primary target and makes up 46% of catches by weight. More than 90 other species are recorded in the catches, but a substantial proportion (mainly undersized fish) are discarded (Unidad Técnica de Pesca de Bajura; Tasende *et al.*, 2005). The species is also taken using boliche in Malaga (Mediterranean coast of Spain) (Anon., 1981).

Information available on discarding practices has improved since implementation of the EU's Data Collection Framework (ICES, 2012). *Loligo vulgaris* is frequently discarded by the Spanish fisheries in western Irish waters and on Rockall Bank (12–92% of *Loligo* spp. discards), but the percentage of discards from northern Iberian waters and the Gulf of Cádiz is close to zero (Santos *et al.*, 2012). Borges *et al.* (2001) recorded *L. vulgaris* among the species frequently discarded in southern Portugal. However, recent data indicate that the discard rate of *L. vulgaris* by Portuguese trawl fleets in ICES Subarea IXa is very low (0–6%) (Prista *et al.*, 2012). The percentage of discards of *Loligo* spp. by the UK fleets in the English Channel is also very low (0–4%). On the other hand, long-finned squids seem to be 100% discarded by the German and Netherlands trawl fleets (ICES, 2012). No information is officially available for the Mediterranean Sea, where long-finned squids have never been reported as discarded (P. Jereb, pers. comm.). There is no discarding of *L. vulgaris* in the southern Adriatic, where even new recruits are landed for local consumption (L. Ceriola, pers. comm.).

Variation in catches and catch rates in squid is often attributed to environmental factors; to a large extent, such variations can be explained by environmental effects on abundance and on the seasonality of the life cycle. However, there may also be environmental effects on behaviour and activity that affect catch rates. Hence, Cabanellas-Reboredo *et al.* (2012b) observed that catch rates of *L. vulgaris* in the recreational jig fishery in the Balearic Islands were maximized by low sea surface temperature, low wind speed, low atmospheric pressure, and days close to the new moon. Catches were best around sunset, when the sunlight is still sufficient to allow recreational fishing lures to be effective, and the squid have already shifted to a more active pattern of movement characteristic of night-time.

Accounts of fishing for *L. vulgaris* in European waters in the early 1990s are given by Cunha and Moreno (1994), Guerra *et al.* (1994), and Shaw (1994). Balguerias *et al.* (2000) describe the origins of the Saharan Bank cephalopod fishery, of which *L. vulgaris* is a (minor) component; for many years, until termination of Spain's agreement with Mauritania, Spanish vessels took a significant proportion of the cephalopod catches from that region.

Initial molecular genetic studies based on mitochondrial DNA have suggested that *L. vulgaris* is genetically rather homogeneous across the Northeast Atlantic (ICES Area), relative to other cephalopod species such as *Sepia officinalis* and *Octopus vulgaris* (ICES, 2004). This conclusion is consistent with earlier studies based on multivariate analysis of morphometric data and isozyme electrophoresis, which also showed no significant population or subpopulation differences. A study by Garoia *et al.* (2004) using microsatellites suggested a single population within the Adriatic Sea. However, the same study showed that eastern and western Mediterranean samples were consistently different from Atlantic samples, and from each other. The Western Sahara samples were the most different among the Atlantic samples.

As with all European cephalopods, there is no regular stock assessment for *L. vulgaris*, and management is largely limited to landing-size regulations in southern Europe. The applicability of assessment methods for these stocks is limited by inadequate and inaccurate statistical information and because most catches are made as bycatch in finfish fisheries (Boyle and Pierce, 1994). However, a small number of stock assessment exercises have been carried out in Europe. For the English Channel, Royer *et al.* (2002) estimated natural mortality (M) empirically using Caddy's method (Caddy, 1996) assuming an annual life cycle (as in *L. forbesii*) and a mean fecundity of 15 000 eggs. This gave a monthly M rate of 0.2. They then applied depletion methods and monthly cohort analysis, which showed that recruitment was highly variable (range 2.4–14 million in the 1993–1996 year classes). Exploitation diagnostics indicated that juvenile *L. vulgaris* can undergo high fishing mortality when *L. forbesii* recruitment is low. For both species fished in the English Channel, exploitation levels were above the optimum, but *L. vulgaris* was more consistently overexploited. Application of depletion models to catch-per-unit-effort data from trawls and beach-seines in the Thracian Sea (northeastern Mediterranean, Greece) showed no notable effect of the fisheries on squid population size (Tsangridis *et al.*, 1998).

The existence of relationships between recruitment strength and environmental conditions experienced by juveniles or spawners of the previous generation suggests that fishery forecasting is feasible, however. In the northwestern Mediterranean, cooler weather conditions in May are apparently associated with better landings of *L. vulgaris* in autumn (Sánchez *et al.*, 2008).

11.10 Future research, needs, and outlook

Loligo vulgaris is one of the most economically important myopsid squid species, given its commercial value in areas such as the French and Iberian coasts, the Saharan Bank, and the Mediterranean. It has also been a target of research for many years and is therefore one of the best-known European cephalopod species.

Difficulties inherent in describing and understanding temporal and spatial patterns of distribution, abundance, and life-cycle biology, however, reflect the profound influences of varying environmental conditions. The need for further research on these topics increases as humankind faces the challenges of predicting the impacts of climate change and ocean acidification on the species.

The increasing use of molecular methods of prey identification (based on amplifying and sequencing prey DNA) has the potential to provide a step change in our understanding of squid trophic relationships, and indeed such techniques already allow recognition of *L. vulgaris* in commercial food products (Herrero *et al.*, 2012). This is relevant both to studies of *L. vulgaris* diet, the analysis of which currently relies on relatively scarce and difficult-to-identify hard remains, and studies on predators of squids, notably due to the near impossibility of distinguishing beaks of *L. vulgaris* and *L. forbesii.*

It is evident from the great fisheries importance of this species and the poor taxonomic resolution of ICES and FAO fishery statistics that there is an urgent need for adequate recording of the species of squid landed in European fisheries. This is already achieved in some countries at local or regional levels, and Robin and Boucaud-Camou (1995) demonstrated that market sampling could be used to quantify month-to-month changes in the proportions of the two *Loligo* species in landings along the French coast of the English Channel.