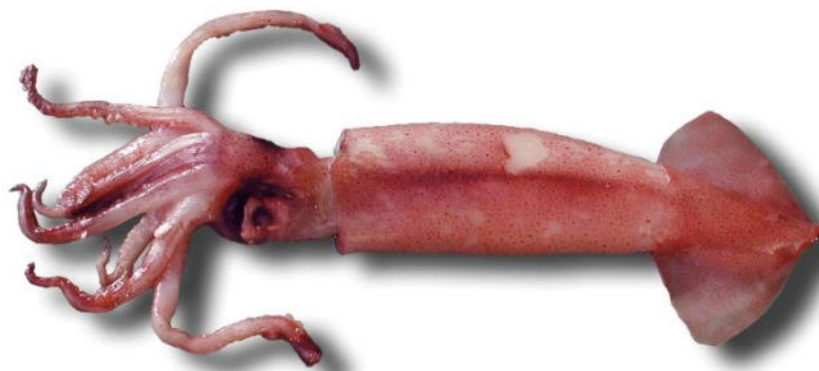# Cephalopod biology and fisheries in European waters: species accounts

Illex coindetii

Broadtail shortfin squid

15   *Illex coindetii* (Vérany, 1839)

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Common names

Faux encornet (France), θράψαλο [thrapsalo] (Greece), Totano (Italy), pota-voadora (Portugal), volador (Spain), broadtail short-fin squid (UK) (Figure 15.1).

Synonyms

Loligo brongniartii Blainville, 1823, *Loligo coindetii* Vérany, 1839, *Loligo pillae* Vérany, 1851, *Loligo sagittata*: Vérany (1851), *Illex illecebrosus coindeti*: Pfeffer (1912).

15.1   Geographic distribution

The broadtail shortfin squid, *Illex coindetii* (Vérany, 1839), is found on both sides of the Atlantic and throughout the Mediterranean Sea (Roper *et al.*, 1998) (Figure 15.2). In the Northwest Atlantic, it is found from off the northeast coast of the United States (i.e. 37°N, Roper *et al.*, 1998) south to ca. 3°N (Roper *et al.*, 1998). In the Northeast Atlantic, it has been reported from as far north as Oslo Fjord, Norway (59°N; Lu, 1973) and the Firth of Forth, east Scotland (Norman, 1890), down to Namibia, between Hollam's Bird Island

Figure 15.1. *Illex coindetii*. **Dorsal view. From Guerra (1992).**

(24°S), and Cape Frio (18°S) (Roeleveld, 1998). It is found in the North Sea, though rarely (e.g. Grimpe, 1925; Oesterwind *et al.*, 2010), but it is not mentioned among the species listed in Swedish waters by Hornbörg (2005). Its extends south and west through the English Channel (Norman, 1890; Marine Biological Association of the United Kingdom, 1931) to the Bristol Channel (Roper *et al.*, 1998), and records exist of it in the Irish Sea (Isle of Man; Moore, 1937, in Stephen, 1944). Although not listed among cephalopod species of the Irish coast by Massy (1928), it is commonly caught by commercial trawl west of Ireland (Lordan *et al.*, 1998b, 2001a), and it is also very common in southwestern Irish waters and in the Celtic Sea (Lordan *et al.*, 2001a). *Illex coindetii* is widely distributed and abundant along the French and Iberian coasts (see references in Adam, 1952; Guerra *et al.*, 1994; Arvanitidis *et al.*, 2002) and throughout the Mediterranean Sea (Mangold and Boletzky, 1987; Bello 2004; Salman, 2009)**,** including western and central Mediterranean parts (Mangold-Wirz, 1963a; Sánchez, 1986a; Belcari and Sartor, 1993; Jereb and Ragonese, 1994; Giordano and Carbonara, 1999; Relini *et al.*, 2002; Cuccu *et al.*, 2003a), the Adriatic Sea (Soro and Paolini, 1994; 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). It has been recorded in the Sea of Marmara (Katağan *et al.,* 1993).

Figure 15.2. *Illex coindetii.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

15.2 Taxonomy

15.2.1 Systematics

Coleoidea – Decapodiformes – Oegopsida – Ommastrephidae – Illicinae – *Illex.*

15.2.2 Type locality

Off Nice, France, western Mediterranean Sea.

15.2.3 Type repository

National Museum of Natural History, Smithsonian Institution, PO Box 37012, MRC 153Washington, DC 20013-7012, USA. Neotype 727457 [fide Roper *et al.* (1998)].

15.3 Diagnosis

15.3.1 Paralarvae

Ommastrephid squids, including *Illex* species, produce some of the smallest cephalopod eggs, which yield unique "rhynchoteuthion" hatchlings, less than 2 mm total length (e.g. O'Dor *et al.,* 1985). They have only two pairs of arms and a proboscis, which later divides to form the tentacles in the adults. The proboscis is ca. 50–75% of the length of the mantle. Division of the proboscis begins at ca. 4 mm ML and is completed by 10 mm ML. Common features at this paralarval stage are the absence of ocular or visceral photophores and the presence of nearly equal-sized suckers on the proboscis tip. According to Sweeney *et al.* (1992), these youngest forms of *Illex coindetii*, *I. argentinus*, *I. illecebrosus*, and *I. oxygonius* cannot be distinguished from each other. However,

research focused on distinguishing features of the early life stages of *I. coindetii* from the Mediterranean Sea is currently underway using *in vitro* fertilization techniques (see Villanueva *et al.*, 2011).

15.3.2 Juveniles and adults

The morphology of the species is highly variable, mainly because of the marked sexual dimorphism and the resulting divergence in growth pattern of several body dimensions (mantle, head, arms) during maturation (Mangold *et al.*, 1969; Lleonart *et al.*, 1980; Sánchez, 1983; Hernández-García and Castro, 1998; Lefkaditou, 2006; Petrić *et al.*, 2010). As there are several morphotypes throughout the species' distribution (Roper *et al.*, 1998; Roper and Mangold, 1998), only basic morphological features are reported below.

Figure 15.3. *Illex coindetii*. **Sucker rings of arm (left) and tentacle (right). Photo: Evgenia Lefkaditou.**

The arms bear two longitudinal series of suckers, and the tentacular club dactylus bears 8 longitudinal series of minute, subequal suckers. The largest sucker rings on the manus of the club are notched, forming low, truncate to blunt, rounded crenulations either in the distal half or all around; they are not smooth (Figure 15.3). The tentacle fixing apparatus is weakly developed. Either the left or the right ventral arm of the male is hectocotylized, with the modified portion ranging in length from 15 to 33% of the arm length. The distal trabeculae are modified to form papillary flaps. The length of the suckerless portion at the base of the hectocotylized arm is ca. 13% of the total arm length, and this character is very useful for distinguishing *I. coindetii* from congeneric species. The head–width index is large: 23 (19–26) in mature males and 19 (15–22) in mature females. Lower beaks have long and strong jaw edges, and upper beaks have long and strong hoods. The funnel cartilage has an inverse T-shape. Fins are short and slightly rhomboid, and their width equates to ca. 45–60% of mantle length (ML). Mantle width is 15–25% of ML. The funnel groove lacks both a foveola and lateral pockets (Roper *et al.*, 1998; Roper and Mangold, 1998).

15.4 Remarks

A record of the species at 30°W in the North Atlantic exists (Clarke, 1966, Figure 10[2], p. 120). However, no mention of that finding is reported in Clarke's text, and no other record of specimens found so far from the continental shelf has been reported subsequently, to the best knowledge of the authors of this review.

Presumably, the holotype was deposited in the Museum of Natural History in Nice, but it is neither extant there nor at the Museum National d'Histoire Naturelle, Paris; therefore it is assumed to be lost. Hence, a neotype has been designated: a mature male, 132 mm ML, collected from the Mediterranean Sea (ca. 300 km southwest of Nice), deposited in the National Museum of Natural History, Smithsonian Institution (USNM 727457, Roper *et al.*, 1998).

Recent comprehensive analyses seem to indicate that *I. coindetii* from the Atlantic and Mediterranean belong to a single, widely distributed, highly plastic and variable species (Roper and Mangold, 1998; Martínez *et al.*, 2005a, b; Carlini *et al.*, 2006). However, specimens from different areas sometimes differ strikingly from the "typical" *Illex* from the Catalonian region (Roper and Mangold, 1998). These morphotypes are neither well

defined nor fully understood at present and seem related not only to geographic distribution, but also to local and regional environmental factors; all of these may affect metabolic rates, maturity, growth rates, and morphometric divergence as a consequence of sexual dimorphism (Hernández-García and Castro, 1998). Therefore, a general consensus exists on the need for further studies to investigate this variability.

While statolith morphometric analysis based on landmarks may prove a useful taxonomic tool to distinguish *I. coindetii* from closely related species (Lombarte *et al.*, 2006), hectocotylus, left ventral arm features in females and beak morphometry offer ways to investigate intraspecific variation (Martínez *et al.*, 2002; Petrić *et al.*, 2010).

15.5 Life history

The life cycle of *I. coindetii* is probably annual, even though shorter (6–8 months) and longer (18 months) lifespans have been estimated using different techniques in different areas. Spawning is year-round, with seasonal peaks.

15.5.1 Egg and juvenile development

Eggs are small (0.8–1.3 mm) (Boletzky *et al.*, 1973; Hernández-García, 2002a; Villanueva *et al.*, 2011) and are probably laid on the continental slope in midwater. The egg jelly is completely transparent (Boletzky *et al.*, 1973), and the egg chorion swells markedly during embryonic development. Laboratory observations indicate that chorion expansion is strictly dependent on the presence of oviducal jelly, because fertilized eggs not treated with oviducal jelly show no chorion expansion, which results in 100% embryo mortality (Villanueva *et al.*, 2011). Nidamental gland jelly probably also plays an important role in optimal egg development, even though its function is still poorly understood (see Villanueva *et al.*, 2011, for detail). *Illex coindetii* eggs at hatching are ca. 2 mm long (Boletzky *et al.*, 1973; Villanueva *et al.*, 2011).

The success and duration of embryonic development is related to water temperature. All observations available to date indicate that successful embryonic development for *I. coindetii* takes ca. 10–14 d at 15°C; this temperature corresponds to the median temperature value reported for Mediterranean Sea midwater (Villanueva *et al.*, 2011), where the egg masses are suspected to float.

Even though a thorough morphological description is not yet available, embryos of *I. coindetii* were first observed in the laboratory by Boletzky *et al.* (1973), and paralarvae have been collected off the Spanish Mediterranean coasts (Sánchez and Moli, 1985) and in the eastern Mediterranean (Salman, 2012) more recently. Embryos and newly hatched squids have been photographed by Villanueva *et al.* (2011) and are shown in Figure 15.4. Young individuals are described as active swimmers; they use jet propulsion typical of planktonic cephalopod paralarvae, adopting a head-down, oblique position (Boletzky *et al.*, 1973).

15.5.2 Growth and lifespan

Illex coindetii is a medium-sized squid, commonly reaching 200–250 mm ML throughout its distributional range (Roper *et al.*, 2010a). The maximum mantle lengths recorded for females and males are 379 and 279 mm, respectively (Northeast Atlantic; González *et al.*, 1994b, 1996a). The maximum size of 320 mm ML reported for males in Sánchez *et al.* (1998b), with no specific reference to the record, is probably erroneous. Females are larger than males, and maximum size varies depending on the population examined (see Table 15.1).

Very large specimens of ≥300 mm ML are occasionally captured on both sides of the Atlantic and in the Mediterranean (e.g. González *et al.*, 1996a; Roper *et al.*, 1998; Ceriola *et al.*, 2006; Perdichizzi *et al.*, 2011). However, these represent extremes in the populations and may be late-hatching members of the previous year class or individuals that, for some reason, do not reach maturity, do not spawn, and continue to grow, a phenomenon that has been suggested for other squid species (e.g. Verrill, 1881, in Roper and Mangold, 1998; Cuccu *et al.*, 2005).
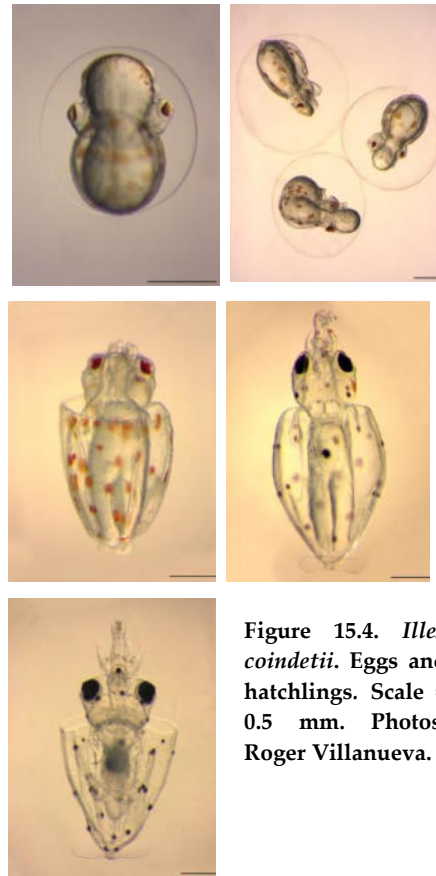

Figure 15.4. *Illex coindetii.* **Eggs and hatchlings. Scale = 0.5 mm. Photos: Roger Villanueva.**

Table 15.1. *Illex coindetii.* **Maximum mantle length (mm) for females (F) and males (M) in different geographic areas of the Northeast Atlantic and Mediterranean Sea.**

Region	ML (mm)		Reference
	F	M	
Northeast Atlantic	379	279	González *et al.* (1994b)
Portuguese Atlantic	286	217	Arvanitidis *et al.* (2002)
Northwest African coast	300	230	Arkhipkin (1996)
Spanish Mediterranean	170	140	Sánchez (1984)
French Mediterranean	263	200	Mangold-Wirz (1963a)
Northern Tyrrhenian Sea	245	175	Belcari *et al.* (1989b)
Central Tyrrhenian Sea	200		Gentiloni *et al.* (2001)
Southern Tyrrhenian Sea	300	210	Perdichizzi *et al.* (2011)
Sicilian Channel	230	180	Jereb and Ragonese (1995)
Southwestern Adriatic Sea	220 (300*)	200	Ceriola *et al.* (2006)
Western Adriatic Sea	280	183	Soro and Paolini (1994)
Eastern Adriatic Sea	216	187	Petrić *et al.* (2010)
Northern Aegean Sea	240	182	Lefkaditou (2006)
Levantine Basin (Cyprus)	180	145	Salman *et al.* (1998)

* Only one specimen, not considered in calculations.

Based on length frequency analyses, the maximum lifespan of *I. coindetii* from different

geographic areas has been estimated to be 12–18 months, whereas direct age determination by statolith reading has indicated lifespans as short as 6 months (Table 15.2).

Length frequency distributions for cephalopod species of interest to fisheries are generally polymodal, but it is difficult to identify microcohorts, and growth estimates by means of length frequency methods are difficult to make (Sánchez, 1984; Caddy, 1991; Jereb and Ragonese, 1995; Arvanitidis *et al.*, 2002). Therefore, direct age determination methods are applied more frequently. Despite the acknowledged validity of the methodology (Jereb *et al.*, 1991; Jackson, 1994; Ceriola and Milone, 2007), several authors have advised caution in interpreting age values from statolith readings (e.g. Lipiński and Durholtz, 1994; González *et al.*, 2000; Bettencourt and Guerra, 2001).

Growth rate (see Table 15.2) is high, faster in females than in males, and often two or more groups are identifiable in the population, each with different growth rhythms, depending on the hatching period (Jereb and Ragonese, 1995; Sánchez, 1995; Belcari, 1996; González *et al.*, 1996a; Arkhipkin *et al.*, 2000; Ragonese *et al.*, 2002). Spring–summer hatched squids grow faster than autumn–winter hatchings. González *et al.* (1996a) measured instantaneous relative growth rate as well as absolute growth rate. Although there was considerable variation, the fastest relative growth rate was recorded in 6-month-old individuals of both sexes (1.33% ML d^{-1} and 4.49% BW d^{-1} in males; 1.73% ML d^{-1} and 5.06% BW d^{-1} in females) and the slowest growth in 13-month-old males (0.10% ML d^{-1} and 0.03% BW d^{-1}) and 14-month-old females (0.18% ML d^{-1} and 0.81% BW d^{-1}).

Table 15.2. *Illex coindetii.* **Growth rates (absolute values) and lifespan of populations from the Northeast Atlantic and Mediterranean Sea.**

Method	Growth rate (mm d^{-1})		Lifespan (months)		Region	Reference
	F	M	F	M		
DA	1.11	-	12	12	Northeast Atlantic	Sánchez *et al.* (1998b)
DA	0.72	0.84	13	15	Galician waters	González *et al.* (1996a)
DA	-	-	8	6	Sierra Leone	Arkhipkin (1996)
DA	-	-	10	8	West Sahara	Arkhipkin (1996)
DA	0.44	-	18	18	Western Mediterranean	Sánchez *et al.* (1998b)
DA	1.55	1.78	6–7	6–7	Sicilian Channel	Arkhipkin *et al.* (2000)
DA	0.06–1.17	0.06–1.09	13.5	14.5	Northern Aegean	Lefkaditou *et al.* (2007)
CM	0.39–0.43	0.33–0.34	24	12–20	Western Mediterranean	Mangold-Wirz (1963a)
CM	0.47	0.38	17.7	16.6	Catalan Sea	Sánchez (1984)
MPA	0.67	0.73	18	11	Southern Celtic Sea – Bay of Biscay	Arvanitidis *et al.* (2002)
MPA	0.50–0.86	0.30–0.83	15	15	Galician waters	González (1994)

MPA	0.92	-	13	-	Portuguese waters	Arvanitidis *et al.* (2002)
MPA	0.32–0.45	0.32–0.45	14–16	14–16	Sicilian Channel	Jereb and Ragonese (1995)
MPA	0.82	0.84	15	10	Greek Seas	Arvanitidis *et al.* (2002)

DA = direct ageing using statoliths; CM = cohort monitoring, MPA = modal progression analysis. F=female. M=male.

Sexual differences in the length–weight relationship exist (Table 15.3). Values of the coefficient *b* are always lower in females, reflecting morphometric sexual dimorphism of adult animals, whereby males exhibit a marked increase in head and arm robustness and become heavier than females at same length (e.g. Belcari, 1996; Ceriola *et al.*, 2006).

Table 15.3. *Illex coindetii*. Length–weight relationships in different geographic areas for females (F) and males (M). Original equations converted to W = *a*ML^b, where W is body mass (g) and ML is dorsal mantle length (cm).

Region	a	b	Sex	Reference
Southern Celtic Sea – Bay of Biscay	0.058	2.76	F	Arvanitidis *et al.* (2002)
	0.296	3.17	M	
Northwestern Spanish waters	0.033	2.91	F	González *et al.* (1996a)
	0.022	3.16	M	
	0.016–0.017	3.09–3.12	F	Sánchez *et al.* (1998b)
	0.006–0.007	3.57–3.58	M	
Portuguese waters	0.046	2.76	F	Arvanitidis *et al.* (2002)
	0.016	3.30	M	
Catalan Sea	0.027–0.041	2.89–3	F	Sánchez *et al.* (1998b)
	0.017–0.040	3.02–3.24	M	
Northern Tyrrhenian Sea	0.022	3.04	F	Belcari (1996)
	0.011	3.39	M	
Sicilian Channel	0.043–0.046	2.79–2.83	F	Ragonese and Jereb (1992)
	0.021–0.022	3.19–3.21	M	
Central eastern Adriatic Sea	0.002	3.02	F	Petrić *et al.* (2010)
	0.016	3.45	M	
Southwestern Adriatic Sea	0.030	3.00	F	Ceriola *et al.* (2006)
	0.011	3.58	M	
Greek Seas	0.047	2.83	F	Arvanitidis *et al.* (2002)
	0.018	3.25	M	
Iskenderun Bay (northeastern Levant Sea)	0.019	3.16	F	Duysak *et al.* (2008)
	0.018	3.29	M	

15.5.3 Maturation and reproduction

Sex ratios close to 1:1 have been recorded in most of the populations studied (e.g. Jereb

and Ragonese, 1995; Sánchez *et al.*, 1998b; Arvanitidis *et al.*, 2002; Ceriola *et al.*, 2006); significant deviations have been recorded only in Galician waters (González and Guerra, 1996) and in the Ionian Sea (Tursi and D'Onghia, 1992).

Age at maturation varies between 120 and 271 d in males and between 120 and 285 d in females, depending on the geographic area and season considered (González *et al.*, 1996a; Arkhipkin *et al.*, 1998). Individuals of this species mature at a wide range of sizes. Although size at maturity shows some degree of geographic variation in both sexes (e.g. Arvanitidis *et al.*, 2002; Hernández-García, 2002a), males mature at a lower minimum size than females. Also, a west–east gradient of decreasing mantle length values at maturity has been found in populations from the Atlantic to the eastern Mediterranean (Table 15.4).

Table 15.4. *Illex coindetii.* Size at 50% maturity (MLm$_{50\%}$) in populations from different geographical areas of the eastern Atlantic and Mediterranean Sea.

Region	MLm$_{50\%}$ (mm)		Reference
	Females	Males	
Southern Celtic Sea – Bay of Biscay	248	153	Arvanitidis *et al.* (2002)
Galician waters	184	128	González and Guerra (1996)
Portuguese waters	191	129	Arvanitidis *et al.* (2002)
Eastern Atlantic	172–218	127–166	Hernández-García (2002a)
Western Mediterranean	150	120	Sánchez *et al.* (1998b)
Central Tyrrhenian Sea	120	105	Gentiloni *et al.* (2001)
Southern Tyrrhenian Sea	150	105	Perdichizzi *et al.* (2011)
Sicilian Channel	150	120	Jereb and Ragonese (1995)
Adriatic Sea	146	137	Ceriola *et al.* (2006)
Eastern Ionian Sea	140–187	120–152	Lefkaditou *et al.* (2008)
Aegean Sea	146–181	113–138	Lefkaditou *et al.* (2007)

Illex coindetii females spawn several times during the spawning period, which may last for several weeks (González and Guerra, 1996). Spawning is year-round, but seasonal peaks exist and vary with area throughout the Mediterranean and Atlantic (e.g. González and Guerra, 1996; Sánchez *et al.*, 1998b; Belcari, 1999c; Ceriola *et al.*, 2006; Lefkaditou *et al.*, 2007). This variability is thought to be related to differences in water temperature (Arvanitidis *et al.*, 2002; Hernández-García, 2002a).

Reproductive outputs in males and females vary with body size. Approximately 800 000 oocytes were recorded in a 250 mm ML female (Laptikhovsky and Nigmatullin, 1993), and 1555 spermatophores were counted in a mature male of 245 mm ML (González and Guerra, 1996). Spermatophore length varied between 14 and 38 mm.

15.6 Biological distribution

15.6.1 Habitat

Illex coindetii has been recorded from surface waters to >1000 m, but concentrations peak between 100 and 400–600 m, depending on the geographic area considered (Roper *et al.*, 2010a). It lives close to muddy, sandy, and debris-rich bottoms, which are often covered by *Funiculina* spp. in the middle and lower sublittoral and upper bathyal domains (Roper *et al.*, 2010a). It has been found associated with decapod crustaceans, such as the deep-water rose shrimp (*Parapenaeus longirostris)*, and, more significantly, with

fish such as the European hake (*Merluccius merluccius*) and the blue whiting (*Micromesistius poutassou*) (Jereb and Ragonese, 1991b; Rasero *et al.*, 1996; Dawe and Brodziak, 1998), often along with the lesser flying squid (*Todaropsis eblanae*) (Mangold-Wirz, 1963a; Lumare, 1970; Rasero *et al.*, 1996; Dawe and Brodziak, 1998; Ciavaglia and Manfredi, 2009; Silva *et al.*, 2011), but also with the horned octopus (*Eledone cirrhosa*) and the midsize squid (*Alloteuthis media*) (Krstulović Šifner *et al.*, 2005, 2011; Silva *et al.*, 2011).

Juveniles and adults share the same depth range in some areas of the Mediterranean (Sánchez *et al.*, 1998b; Ceriola *et al.*, 2006), even though a major concentration of small specimens is observed in shallower waters (<200 m). Large and mature squids were found throughout the whole depth range (Sánchez *et al.*, 1998b). The presence of upwelling of cold waters rich in nutrients and contributing to high productivity in the area near Gibraltar is considered to influence positively the presence and abundance of *I. coindetii* on the slope and upper shelf of the Gulf of Cádiz (Silva *et al.*, 2011). However, mature animals, especially females, have been reported to concentrate in regions with lower upwelling activity in Greek waters (Lefkaditou *et al.*, 2008); it has been suggested that concentrations in relatively more protected areas may be related to "spatial protection" of paralarvae, assuming that hatching areas are close to the spawning areas.

15.6.2 Migrations

Adults, at least, undergo vertical migrations from the bottom to the upper layers at night, even though they remain below the thermocline (Sánchez *et al.*, 1998b). Seasonal migrations have been observed in the French Mediterranean and the Catalan Sea (Mangold-Wirz, 1963a; Sánchez *et al.*, 1998b), with the bulk of the population seeking shallow waters (70–150 m) in spring, where they remain all summer. In autumn and winter, the population spreads over a wide bathymetric range.

15.7 Trophic ecology

15.7.1 Prey

Like most muscular, fast-swimming ommastrephids, *I. coindetii* is an opportunistic predator (e.g. Rasero *et al.*, 1996; Sánchez *et al.*, 1998b; Lordan *et al.*, 1998b; Lelli *et al.*, 2005). The diet is composed of fish, crustaceans, and cephalopods, in decreasing order of importance (Sánchez, 1982; Rasero *et al.*, 1996; Lordan *et al.*, 1998b; Sánchez *et al.*, 1998b; Lelli *et al.*, 2005) (Table 15.5). Usually, one of these main groups is dominant, depending on prey availability and size of squid. Food composition changes with growth (Lordan *et al.*, 1998b) and are related to important changes in squid mouth structures (Castro and Hernández-García, 1995), foraging behaviour, and prey availability in the water column, as well as to increasing body size. As the squid grow, fish and squid become increasingly important prey, and cannibalism may occur, although it is probably of minor importance, except in conditions of very high squid abundance or scarcity of other prey (Dawe and Brodziak, 1998).

There are no significant differences in the diets of males and females, although significantly more mature females than mature males have prey remains in their stomachs (Rasero *et al.*, 1996; Lordan *et al.*, 1998b), which has been interpreted as implying that the increasing energetic demands of gonad development is fulfilled by feeding (Rosa *et al.*, 2005b).

Throughout its life cycle, *I. coindetii* is likely to compete actively for prey with other cephalopods and fish. However, although all cephalopod hatchlings begin to feed immediately as predators (Boletzky and Hanlon, 1983), attempts to feed rhynchoteuthions have not been successful (Balch *et al.*, 1985). A peculiar "suspension feeding mechanism" has been suggested for these early life stages (O'Dor *et al.*, 1985).

Table 15.5. List of the main identified prey from *Illex coindetii* stomach contents (compiled from Hernández-García, 1992[1], Castro and Hernández García, 1995[2], Rasero *et al.*, 1996[3], Lordan *et al.*, 1998b[4], Sánchez *et al.*, 1998b [5], Stowasser, 2004[6], Lelli *et al.*, 2005[7]; Lefkaditou 2006[8]; Vafidis *et al.*, 2008[9]; Petrić *et al.*, 2011[10]).

Taxon	Species
Osteichthyes	
Acropomatidae	*Synagrops microlepis* (thinlip splitfish)[1,5]
Ammodytidae	*Gymnammodytes semisquamatus* (smooth sandeel)[3], indet.[6]
Argentinidae	*Argentina sphyraena* (argentine)[3,4], *Argentina* spp.[4], *Glossanodon leioglossus* (small-toothed argentine)[4]
Carangidae	*Trachurus trachurus* (Atlantic horse mackerel)[3,4,10]
Cepolidae	*Cepola macrophthalma* (red bandfish)[3]
Centracanthidae	indet.[7]
Chlorophthalmidae	*Chlorophthalmus atlanticus* (Atlantic greeneye)[5]
Clupeidae	*Sardina pilchardus* (European pilchard)[5,7], *Alosa alosa* (allis shad)[7], *Sprattus sprattus* (European sprat)[3], indet.[7]
Congridae	indet.[6]
Engraulidae	*Engraulis encrasicolus* (European anchovy)[5,7]
Epigonidae	*Epigonus telescopus* (black cardinal fish) [2,5]
Gadidae	*Gadiculus argenteus* (silvery pout)[3,4,5,7,8,10], *Micromesistius poutassou* (blue whiting)[3,4,5,7], *Phycis blennoides* (greater forkbeard)[10], *Trisopterus minutus* (poor cod)[10], indet.[6,7]
Gobiidae	*Aphia minuta* (transparent goby)[3,4], *Gobiusculus flavescens* (two-spotted goby)[3], indet.[3,4,6,7]
Lotidae	*Gaidropsarus biscayensis* (Mediterranean bigeye rockling)[5], *G. macrophthalmus* (big-eyed rockling)[3], *G. vulgaris* (three-bearded rockling)[3], *Gaidropsarus* spp.[8], indet. larvae[4]
Macrouridae	indet.[7]
Merlucciidae	*Merluccius merluccius* (European hake)[3,4,7]
Myctophidae	*Ceratoscopelus maderensis* (Madeira lanternfish)[5,8], *Diaphus dumerelii*[1,2], *Diaphus* spp.[1,4,8], *Hygophum benoiti* (Benoit's lanternfish)[8], *Lampanyctus crocodilus* (jewel lanternfish)[5], *Myctophum punctatum* (spotted lanternfish)[5], *Notoscopelus elongatus* (elongated lanternfish)[5,8], indet.[7]
Paralepididae	*Sudis hyalina* (baracundina)[5]
Pleuronectiformes	indet.[3]
Scombridae	*Scomber colias* (Atlantic chub mackerel)[5], *Scomber scombrus* (Atlantic mackerel)[4]
Scorpaenidae	indet.[7]
Soleidae	*Microchirus boscanion* (Lusitanian sole)[2], *Solea* spp.[2]

Sparidae	*Dentex* spp.[2], *Diplodus* spp.[2,3]
Sternoptychidae	*Argyropelecus hemigymnus* (half-naked hatchetfish)[4], *Maurolicus muelleri* (pearlside)[2,3,4,5,7,8,10]
Triglidae	indet.[7]
Zeidae	*Zeus faber* (John dory)[3]
Crustacea	
Decapoda	indet.[6]
Dendrobranchiata-Penaeiodea	*Parapenaeus longirostris*[5], Penaeidae indet.[1]
Macrura reptantia	indet.[7]
Pleocyemata-Brachyura	*Polybius henslowii*[3], indet.[7]
Pleocyemata-Caridea	*Alpheus glaber*[5], Crangonidae indet.[7], *Dichelopandalus bonnieri*[4], Pandalidae indet.[2], *Pasiphaea sivado*[1,2,5, 7], *P. multidentata*[5], *Pasiphaea* spp.[3,4,5,7], *Plesionika heterocarpus*[1,5], *Plesionika martia*[3], *Plesionika* spp.[2,5,7], *Sergia robusta* (as *Sergestes robustus*)[3], Sergestidae indet.[7]
Stomatopoda	indet.[6]
Euphausiacea	*Euphasia* spp.[5], *Meganyctiphanes norvegica*[3,4,5], *Nyctiphanes couchii*[5], *Thysanopoda* spp.[2], indet.[4,6,9]
Mysida	indet.[5,6,7,9]
Amphipoda	Gammaridea indet.[3], *Vibilia armata*[5], indet.[2,5,7,9]
Copepoda	*Oncaea* spp.[5], Calanoida indet.[7], indet.[5,6]
Cephalopoda	
Myopsida	*Alloteuthis subulata*[3], *Alloteuthis* spp.[2,4], *Loligo forbesii*[4], *Loligo* spp.[2,3,5], Loliginidae indet.[6]
Oegopsida	*Abralia veranyi*[2], Enoploteuthidae indet.[1], Histioteuthidae indet.[7], *Illex coindetii*[2,3,4,5,7,10], Ommastrephidae indet.[1,6,7], Onychoteuthidae indet.[1], *Onychoteuthis banksii*[7], *Todarodes sagittatus*[4], *Todaropsis eblanae*[2,3,4,5,7,10]
Octopoda	*Octopus* spp.[2], indet.[7]
Sepioidea	*Rossia macrosoma*[4,7], *Sepia bertheloti*[2], *S. orbignyana*[1], *Sepia* spp.[1,2], *Sepietta oweniana*[4,7], Sepiolidae indet.[4,5,6,7], indet.[7]
Gastropoda	*Heliconoides inflatus*[7], *Limacina retroversa* (retrovert pteropod)[4], indet.[7]
Bivalvia	indet.[7]
Tunicata	indet.[5,9]
Chaetognatha	indet.[5]

15.7.2 Predators

No information on predators of larval and small juveniles of *Illex* is available at present (Dawe and Brodziak, 1998). Adults are found in the stomachs of various cetaceans, bony fish, and sharks, as well as being eaten by other squid species (Table 15.6).

Table 15.6. Known predators of *Illex coindetii* in the Northeast Atlantic and Mediterranean Sea.

Taxon	Species	References
Cephalopoda	European squid (*Loligo vulgaris*)	Dawe and Brodziak (1998)
	European flying squid (*Todarodes sagittatus*)	Dawe and Brodziak (1998)
Chondrich-thyes	Black-mouthed dogfish (*Galeus melastomus*)	Valls *et al.* (2011)
	Lesser spotted dogfish (*Scyliorhinus canicula*)	Kabasakal (2002)
	Sharpnose sevengill shark (*Heptranchias perlo*)	Henderson and Williams (2001)
	Shortfin mako (*Isurus oxyrinchus*)	Maia *et al.* (2006)
	Smooth-hound (*Mustelus mustelus*)	Kabasakal (2002)
	Thornback ray (*Raja clavata*)	Kabasakal (2002), Farias *et al.* (2006), Šantić *et al.* (2012)
Osteichthyes	Albacore (*Thunnus alalunga*)	Consoli *et al.* (2008), Romeo *et al.* (2012)
	Atlantic bluefin tuna (*Thunnus thynnus*)	Karakulak *et al.* (2009), Romeo *et al.* (2012), Battaglia *et al.* (2013)
	Blonde ray (*Raja brachyura*)	Farias *et al.* (2006)
	Blue whiting (*Micromesistius poutassou*)	Macpherson (1978)
	Common dolphinfish (*Coryphaena hippurus*)	Massutí *et al.* (1998)
	Conger eel (*Conger conger*)	Lordan *et al.* (1998b)
	Greater forkbeard (*Phycis blennoides*)	Morte *et al.* (2002)
	Mediterranean spearfish (*Tetrapturus belone*)	Castriota *et al.* (2008), Romeo *et al.* (2009, 2012)
	Saithe (*Pollachius virens*)	Lordan *et al.* (1998b)
	Smooth lanternshark (*Etmopterus pusillus*)	Xavier *et al.* (2012)
	Swordfish (*Xiphias gladius*)	Bello (1985), Moreira (1990), Salman (2004), Peristeraki *et al.* (2005), Romeo *et al.* (2009, 2012)
	Yellowfin tuna (*Thunnus albacares*)	Dragovich (1970)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	González *et al.* (1994a), Santos *et al.* (1997)
	Common dolphin (*Delphinus delphis*)	González *et al.* (1994a), Silva (1999a)
	Long-finned pilot whale (*Globiocephala melas*)	González *et al.* (1994a)
	Risso's dolphin (*Grampus griseus*)	Carlini *et al.* (1992), González *et al.* (1994a), Santos *et al.* (1997), Blanco *et al.* (2006), Bearzi *et al.* (2011)
	Striped dolphin (*Stenella coeruleoalba*)	Würtz and Marrale (1993), Alessandri *et al.* (2001)

15.8 Other ecological aspects

15.8.1 Parasites

Illex coindetii is one of the most important cephalopod paratenic hosts in the life cycle of several parasites, such as cestodes of the genus *Phyllobothrium* and nematodes such as *Anisakis simplex* and *A. physeteris* (Pascual *et al.*, 1994, 1995, 1996a, 1999; Abollo *et al.*, 1998; Gestal *et al.*, 1999; Petrić *et al.*, 2011); it also appears to be infested by copepods of the genus *Pennella*, especially in some areas of its distribution (Pascual *et al.*, 2001). It functions as a trophic bridge for parasite flow within the marine ecosystem, because it is the prey of the parasites' final hosts (e.g. cetaceans such as *Delphinus delphis, Tursiops truncatus, Stenella coeruleoalba,* and others). Recent studies have demonstrated for the first time its role as a second, rather than first, paratenic host (Petrić *et al.*, 2011). Additional information on parasites of *I. coindetii* and *T. eblanae* (Pascual *et al.*, 1996b) suggests that these species are sympatric and share similar econiches and that parasites may also be useful as an indirect indicator of the migratory habits of the squid.

15.8.2 Environmental effects

Recent observations show high correlations between the *I. coindetii* life cycle and environmental parameters, such as water temperature, trophic enrichments, current regimes, and other oceanographic features (Jereb *et al.*, 2001; Arvanitidis *et al.*, 2002; Ceriola *et al.*, 2006, 2007; Lefkaditou *et al.*, 2008). These results suggest high levels of environmentally driven flexibility for the species. Based on all information gathered, it is likely that *I. coindetii,* an ommastrephid squid exploited almost exclusively by bottom trawl, can be singled out as a key/indicator species in the context of dynamic environments and high fishing pressure areas, such as some Mediterranean regions (Ceriola *et al.*, 2007). Because of its short life cycle and highly variable abundance levels, it may indicate changes in environmental conditions and fishing pressure, although it may be difficult to disentangle fishing pressure and global warming effects.

Recruitment in particular is likely to be affected by environmental conditions (Jereb *et al.*, 2001; Ceriola *et al.*, 2007; Lefkaditou *et al.*, 2008; Cuccu *et al.*, 2009b), because of egg-mass properties. Egg masses have never been recorded in nature for *Illex* species. However, observations in captivity (Durward *et al.*, 1980; O'Dor *et al.*, 1985) showed that *Illex* species can produce gelatinous egg masses while swimming in open water. Other observations indicate that the gel functions as a buoyancy mechanism that prevents eggs from sinking, and that complete density equilibration requires many days under most conditions (O'Dor *et al.*, 1985). Such a mechanism would retain pelagically spawned eggs of *Illex* in zones where temperatures are most favourable for embryonic development. In addition, favourable environmental conditions are likely to have a positive effect on the survival of hatchlings and early juveniles. Despite consistency in the location of spawning areas, interannual variability has been observed in the location of main recruitment areas, which could be related to mechanisms such as association with mesoscale eddies, affecting post-hatching dispersal (e.g. Lefkaditou *et al.*, 2008). An increase in the density of recruits in the populations of the southern Adriatic and the eastern Ionian Sea in the mid-2000s may have resulted from a combination of increased temperature in the entire water column of the central Mediterranean, the decline of many *I. coindetii* predators, and the increased presence of some potential prey in the area investigated (Ceriola *et al.*, 2007; Lefkaditou *et al.*, 2008). Distribution, recruitment, and abundance are closely related to ocean climate variability for the most broadly distributed and most highly migratory congener, *Illex illecebrosus* (Dawe and Brodziak, 1998). Although such relationships may not hold as strongly for the less migratory *I coindetii,* only additional time-series of reliable data could help clarify these

issues.

15.9 Fisheries

Illex coindetii is taken throughout the year in the Mediterranean, off West Africa, and in the Northeast Atlantic as bycatch in bottom and pelagic trawls, and, to a lesser extent, with gill- and trammelnets, in depths of 100–400 m (Mangold and Boletzky, 1987; Jereb and Ragonese, 1995; González *et al.*, 1994b, 1996b; Ceriola *et al.*, 2008; Hastie *et al.*, 2009a; Tosunoğlu *et al*, 2009). It is of increasing fisheries value and represents a valuable resource in some areas of its distribution range because of the size of the catches (Jereb and Ragonese, 1995).

The high interannual variation in ommastrephid landings throughout the Mediterranean and the eastern Atlantic is one of the characteristics of ommastrephid fisheries (Stergiou, 1989; González *et al.*, 1996b; Sánchez *et al.*, 1998b). Also, there is marked seasonality in trawl landings, which varies depending on the area: peaks may arise in summer (e.g. northern Tyrrhenian Sea; Belcari *et al.*, 1998) or winter and spring (e.g. southern Celtic Sea and Bay of Biscay; Arvanitidis *et al.*, 2002). An increasing trend in abundance has been observed in the Ionian Sea in recent decades (Lefkaditou *et al.*, 2008; Maiorano *et al.*, 2010). However, a significant inverse correlation with fishing effort has also been shown (Maiorano *et al.*, 2010), and gear selectivity studies confirm that current legal minimum mesh size and codend configurations for demersal trawling do not favour sustainable fishing for this or other cephalopod species (Tosunoğlu *et al.*, 2009).

FAO fishery data (FAO, 2011) for the Mediterranean for the decade beginning in 2000 indicate that landings of *I. coindetii* have varied from 1800 t in 2003 to >5150 t in 2005; no clear trend is evident. This represents between 3.9 and 7.7% annually of Mediterranean landings of cephalopods. However, it is not clear that the identification to species is reliable.

The different ommastrephid species are separated in Spanish landings from ICES Subdivisions VIIIcW and IXaN, based on market sampling. *Illex coindetii* typically made up ca. 60–80% of monthly ommastrephid landings during the years 1998–2003, the rest being mainly *Todaropsis eblanae*, although considerable month-to-month fluctuation was evident in both areas, and the proportion was typically much lower (as low as 0%) during several months within the period October–March (Bruno *et al.*, 2009).

Although the broadtail shortfin squid is recognized as a separate category in fishery landings by FAO, it is not routinely distinguished from other ommastrephids in most parts of the Northeast Atlantic. During the decade since 2000, up to 450 t of this species have been recorded for the Northeast Atlantic, a small fraction of the 6000–16 000 t of "Various squids nei" landed, a proportion of which could have been *I. coindetii*. In ICES data, catches of this species are subsumed under the shortfin squid category. Since 2000, annual landings of this category in the European ICES area varied from ca. 5 500 t to as low as 970 t in 2007; the overall trend seems to have been downwards (ICES, 2012).

The high interannual variation in ommastrephid landings in the Mediterranean and Northeast Atlantic is typical of ommastrephid fisheries (Stergiou, 1989; González *et al.*, 1996b; Sánchez *et al.*, 1998b). A marked seasonality in trawl landings is also evident, but it varies depending on the area; peaks in summer in the northern Tyrrhenian Sea (Belcari *et al.*, 1998) contrast with peaks in winter and spring in the southern Celtic Sea and Bay of Biscay (Arvanitidis *et al.*, 2002).

The analysis of seven populations of *I. coindetii* from the eastern Atlantic and eastern Mediterranean showed no significant overall genetic differences among samples (Martínez *et al.*, 2005b). Additional comparisons of individuals from the northern Tyrrhenian Sea (western Mediterranean) and Atlantic Iberian waters revealed the presence of a homogeneous population structure, the summer Italian and the spring Atlantic samples being the most divergent (Martínez *et al.*, 2005a).

15.10 Future research, needs, and outlook

Like other ommastrephids, *I. coindetii* plays an essential role in the oceanic system, acting as an "*ecosystem accelerator*". As animals with high food intake and fast conversion rates, these squids function as energy transformers and accumulate high quality proteins, making them available to higher consumers. In addition, the species has a significant commercial value, one that has increased over the past decade, in many parts of Europe.

The existence of different morphotypes, neither well-defined nor fully understood at present, related not only to geographic distribution, but also to local and regional environmental factors, should be investigated further. Even though *I. coindetii* has been a target for research in the past few decades, and rather extensive literature provides sufficient basic information, further detailed studies are required to elucidate its important role as a potential recorder of environmental and ecological change as well as an indicator of possible overexploitation. This will help towards sustainable management of the resource throughout European seas.