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Cephalopod biology and fisheries in
Europe:
II. Species Accounts.

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Cephalopod biology and fisheries in Europe: II. Species Accounts

Editors

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Contents

1   Executive summary

This report summarizes current knowledge on the identification, geographical distribution, nomenclature, taxonomy, life history, ecology, and exploitation of cephalopod species of interest to fisheries in European waters. The 17 species range from those currently of significant fishery importance and targeted in at least part of their range (*Octopus vulgaris, Sepia officinalis, Loligo vulgaris, Loligo forbesii*), through those regularly landed as bycatch (*Todaropsis eblanae, Illex coindetii, Eledone cirrhosa, Eledone moschata, Todarodes sagittatus*), to those of minor and/or local importance (*Alloteuthis subulata, Alloteuthis media, Sepia orbignyana, Sepia elegans, Sepietta oweniana, Sepiola atlantica, Ommastrephes bartramii, Gonatus fabricii*). The species reviews aim to provide a concise yet comprehensive account of each, while remaining distinctive from previous and recent accounts.

For most of these species, taxonomic status is well resolved, exceptions being the *Alloteuthis* species. There is less clarity about the existence of discrete stocks, although unsurprisingly this relates to the extent of mobility seen in each species. In addition, the superficial morphological similarities of several species make it difficult for a lay person to distinguish them, and indeed create presently unresolved issues for fishery sampling.

The species include benthic, demersal, and pelagic forms, although the existence of horizontal and vertical migrations sometimes tests the limits of such terminology. Most species have a planktonic paralarval phase, although some have hatchlings that immediately adopt a benthic lifestyle. Almost all have annual life cycles, although with a seasonality that varies between both species and regions, and show rapid growth. Most have significant ecological roles as prey and predator, and the high production-to-biomass ratio likely means that their importance is greater than might be indicated from standing stock sizes. However, difficulties with identifying cephalopod remains (identification of their chitnous mandibles is a specialized skill) limit the quality of data on predation. Some information is available on habitat requirements, contaminant burdens, and parasites of these species.

Despite the importance of several species for European fisheries, there is limited management of the fisheries and no routine assessment; data collection is often either not part of routine fishery data collection or the data are inadequate for assessment. Increasingly, however, cephalopods are seen as alternative target species to replace overexploited finfish stocks, and the growing fishing effort means that management will almost certainly be needed within the next few years. Also on the horizon is the development of commercial aquaculture, especially for *Octopus vulgaris.*

2   General introduction

Graham J. Pierce, A. Louise Allcock, and Patrizia Jereb

2.1   Origins and acknowledgements

This is the second *ICES Cooperative Research Report* on cephalopods, the first having been published in 2010 (Pierce *et al.*, 2010). Like the first report, it is based on material originally assembled during the CEPHSTOCK project (Cephalopod Stocks in European Waters: Review, Analysis, Assessment and Sustainable Management, Q5CA-2002-00962, 2002–2005). That, in turn, arose from a series of European collaborative research and fishery-data-collection projects over the preceding decade, notably three large-scale projects coordinated by the late Peter Boyle. For the present report, we started with a set of species reviews originally prepared for Workpackage 5 of the CEPHSTOCK project on the life cycle, ecology, and migrations of the main cephalopod species of commercial importance in European waters. These have been expanded, updated, and extensively reworked.

Both the original and the revised species accounts are multi-authored works and represent the combined input of many colleagues. Editorial work on the 2005 accounts was coordinated by Uwe Piatkowski and Karsten Zumholz, with contributions from many members of the project team. It was always the intent to publish the reviews, but since CEPHSTOCK ended, such work has been unfunded and their completion has been a protracted process. Responsibility for updating and publishing the reviews passed to the ICES Working Group on Cephalopod Fisheries and Life History, being formally incorporated into its terms of reference in 2008 and leading to a Council Resolution to deliver the work as an *ICES Cooperative Research Report*. A plan for completion was drawn up, new lead authors were assigned to each chapter, and significant revisions were undertaken. However, by 2010, it was evident that the accounts were already somewhat out of date and work was needed to harmonize chapter format, so a new round of revisions was instigated. The then core editorial team (Patrizia Jereb, Graham Pierce, Louise Allcock, and Evgenia Lefkaditou) met at the Institute for Environmental Protection and Research in Rome in August 2012 to finish drafting the chapters. This was followed by further exchanges with authors, refereeing, and subsequent revisions. A final editorial meeting (with Patrizia Jereb, Louise Allcock, and Graham Pierce) was held at the National University of Ireland, Galway, in December 2013.

The final list of authors for the report is as follows: Cleopatra Alidromiti, A. Louise Allcock, Eduardo Balguerias, Paola Belcari, Teresa Borges, Manuel Garcia Tasende, Angel F. González, Angel Guerra, Lee C. Hastie, José Iglesias, Patrizia Jereb, Oleg Katugin, Noussithé Koueta, Drosos Koutsoubas, Evgenia Lefkaditou, Ana Moreno, Daniel Oesterwind, João Pereira, Uwe Piatkowski, Graham J. Pierce, Jean-Paul Robin, Pilar Sánchez, M. Begoña Santos, Paolo Sartor, Sonia Seixas, Jennifer M. Smith, Ignacio Sobrino, Antonio Sykes, Tooraj Valinassab, Roger Villanueva, Sansanee Wangvoralak, and Karsten Zumholz.

This report covers not only the main cephalopod species of commercial interest in European waters (*Sepia officinalis*, *Octopus vulgaris*, *Loligo vulgaris*, and *Loligo forbesii*), but also those species of lesser value that are landed routinely, at least in some parts of Europe (*Todaropsis eblanae*, *Illex coindetii*, *Eledone cirrhosa*, and *Eledone moschata*), species of previous fishery importance and present local interest (*Todarodes sagittatus*), and those that are sometimes landed with other species and may occasionally or in specific areas be marketed separately (*Alloteuthis subulata*, *Alloteuthis media*, *Ommastrephes bar-*

trami, Sepia elegans, Sepia orbignyana, Sepietta oweniana, Sepiola atlantica). Finally, we include *Gonatus fabricii*, a species exploited locally for bait, but also identified as having potential commercial fishery value and of high ecological importance as prey of many top predators in the Northeast Atlantic.

The biology and ecology of several of the species covered here were previously reviewed in Boyle (1983a). Updated, but brief, descriptions of these and several other European cephalopod species were included in a review paper by Hastie *et al.* (2009a), and short accounts also appeared within the previous *CRR* (Pierce *et al.*, 2010). In addition, the FAO has published the first thee volumes of the updated version of "Cephalopods of the World" (see Roper *et al.*, 1984; Jereb and Roper, 2005, 2010; Jereb *et al.*, 2014), reviewing the biology, ecology, and fisheries information on living cephalopod species. Finally, two new volumes of species reviews for important squid species around the world (Rosa *et al.*, 2013a, b) were proposed and completed during the process of compiling the present work. Some squid species accounts from the original CEPHSTOCK report and earlier drafts of the present report chapters were used as source material for the more discursive accounts that appeared in Rosa *et al.* (2013a, b), and as far as possible, this shared provenance has been made explicit (see e.g. Pierce *et al.*, 2013); however, we wish to state that any unacknowledged overlap arises from the use of material from earlier versions of the present work as source material.

2.2 Topics covered by the reviews

The accounts included in the present volume follow a series of standard headings, as described below, illustrated with relevant drawings and photographs, and are designed to be easy to follow. They provide more detail than was possible in the FAO volume**s**, with specific focus on European species of interest to fisheries. As noted above, detailed information on distribution has been assembled. In addition, although not representing exhaustive literature reviews, the content aims to provide a concise, structured, and reasonably comprehensive summary of our current understanding of the biology and ecology of these species. These new reviews also specifically address the status of exploitation of these cephalopod species by capture fisheries and, in some cases, aquaculture.

We adopted a common format for the reviews, but allowing flexibility in relation to additional subheadings within the longer species accounts. The topics covered are summarized below.

Common names and synonyms

In the main text, we give common names (if any) in use in those European countries with the most important cephalopod fisheries (France, Greece, Italy, Portugal, Spain, and the UK). Where the name given by the FAO differs from the generally accepted common name, we usually provide both. Common names used in other European countries, including names in national and important regional languages, are listed in Annex 1.

Generally speaking, the various junior synonyms have fallen out of regular use; the exception is *Loligo forbesi* for *Loligo forbesii.* Most authors for this species, from Joubin (1895) to the present day, have used "*forbesi*". However, Steenstrup (1856) clearly states that he named the species after Professor Edward Forbes and consistently used "*forbesii*" in his manuscript. Here, we follow a recent review by Allcock (2010) and also the FAO catalogue (Jereb and Roper, 2010) in accepting Steenstrup's original name.

Geographic distribution

The original starting point for these descriptions of the species' ranges was the relevant entry in the FAO "Cephalopods of the World", augmented with additional relevant information for European waters. However, information on the geographical distribution of these species was re-evaluated for the recently published FAO guides (Jereb and Roper, 2005, 2010), and has been further reviewed and updated for inclusion in the present volume, providing the most comprehensive summaries of distribution available to date. New maps are provided. As some of the detailed information available is ambiguous or contradictory in relation to species range, however, the maps should be treated as a general guide, with details being provided in the text.

It became evident during the review process that many past accounts of distribution are contradictory, sometimes reflecting errors in published sources or in citations thereof, and on other occasions indicating temporary or permanent shifts in species distribution. In addition, there is clearly an issue of what constitutes the "usual" range and which records, therefore, represent occasional excursions beyond the normal range. Our approach here has been to present maps representing the usual distribution, but providing clarification and detailing issues and exceptions within the report text.

Within the text, we generally use local spellings, including accented characters, because knowing the correct local spelling makes it easier to search digital resources for additional information for that area.

Mediterranean Sea

The present report concerns cephalopod species of both the Northeast Atlantic and the Mediterranean Sea. We have assumed that readers are familiar with the geography of the Northeast Atlantic. However, because the Mediterranean lies outside the ICES Area, we provide a description here.

The Mediterranean Sea is a body of water almost completely enclosed by land, a characteristic from which its name derives (from the Latin *mediterraneus*, meaning "in the middle of the land"). It extends from the Strait of Gibraltar in the west to the Dardanelli entrance and the Suez Canal in the north and southeast, respectively, covering an area of ca. 2.5 million km^2. It connects to the Atlantic Ocean in the west through the Strait

of Gibraltar, a threshold only 14 km wide, to the Sea of Marmara in the northeast, and through this to the Black Sea by means of the Strait of Bosphorus. The Suez Canal now connects the Mediterranean to the Indian Ocean. Following the International Hydrographic Organization (IHO, 1953), it is divided into two deep basins, western and eastern, separated by an ideal line connecting Cape Lilibeo (western Sicily) to Cape Bon (Tunisia), and subdivided into a number of smaller waterbodies, each with its own designation. Accordingly, from west to east, the following areas are recognized: the Strait of Gibraltar, the Alboran Sea (between Spain and Morocco), the Balearic Sea (between mainland Spain and its Balearic islands), the Ligurian Sea (between Corsica and Liguria, northern Italy), the Tyrrhenian Sea (enclosed by Sardinia, the Italian peninsula, and Sicily), the Ionian Sea (between Italy, Albania, and Greece), the Adriatic Sea (between Italy, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, and Albania), and the Aegean Sea (between Greece and Turkey).

In addition, there are some other areas of the Mediterranean whose names have been in common use since ancient times and that remain in use today. Among these, the following are worth mentioning, given their association with fisheries-related issues: the Sea of Sardinia, as a part of the Balearic Sea (between Sardinia and the Balearic Islands); the Sea of Sicily (between Sicily and Tunisia), also known as the Strait of Sicily (Cleveland, 1989); the Libyan Sea (between Libya and Crete); the Thracian Sea and the Sea of Crete in the Aegean Sea; and the Levantine Sea, the easternmost area of the Mediterranean.

A further subdivision has been considered in recent years as a practical working approach (GFCM, 2007): western Mediterranean (Algeria, France, Morocco, and Spain); central Mediterranean (Albania, Croatia, Italy, Libya, Malta, Montenegro – reported as Serbia and Montenegro before 2008, and Tunisia); and eastern Mediterranean [Cyprus, Egypt, Gaza Strip, and West Bank (Palestine), Greece, Israel, Lebanon, and Syria]. This working subdivision has been taken into account in reporting FAO fisheries statistics.

Taxonomy

The taxonomy of some groups of Cephalopoda (e.g. Loliginidae) has undergone extensive revision in recent years, whereas that of other groups has remained reasonably stable. We have attempted to use correct nomenclature throughout, based on the most recent taxonomic revisions. Detailed information on taxonomy and nomenclature was given for some of the species included herein in Allcock (2010). For those species, we continue to use the same nomenclature, which is still considered correct, although we have omitted subgeneric classifications for the sepiids. The species are as follows:

1. *Octopus vulgaris* Cuvier, 1797
2. *Eledone cirrhosa* (Lamarck, 1798)
3. *Eledone moschata* (Lamarck, 1798)
4. *Sepia officinalis* Linnaeus, 1758
5. *Sepia elegans* Blainville, 1827
6. *Sepia orbignyana* Férussac in d'Orbigny, 1826
7. *Loligo vulgaris* Lamarck, 1798
8. *Loligo forbesii* Steenstrup, 1856
9. *Alloteuthis subulata* (Lamarck, 1798)
10. *Alloteuthis media* (Linnaeus, 1758)
11. *Illex coindetii* (Verany, 1839)

12.   *Todarodes sagittatus* (Lamarck, 1798)

13.   *Todaropsis eblanae* (Ball, 1841)

With the exception of the species of *Alloteuthis*, these taxa are well defined and rela-tively easy to identify. *Alloteuthis* is problematic, although the validity of the genus has recently been confirmed (Vecchione *et al.,* 2005). However, molecular data from three loci (two mitochondrial and one nuclear) sequenced in samples sourced from across the geographic range of *Alloteuthis* show that relative tail length, which is commonly used to identify European species, does not separate the species (Anderson *et al.*, 2008). The sequence data confirm the presence of two distinct European species nonetheless. However, the type specimens of *A. subulata* and *A. media* cannot be found by the insti-tutes thought to house them, which makes progress difficult in delimiting the species. Redescriptions and neotype designations (if the original types cannot be located) are essential. More recently, morphological characters have been described that appear to effectively delimit the species. The arm length as a fraction of anterior mantle length (measured from the fin's upper edge to the mantle opening) ranges between 81 and 167% in one species (purportedly *A. media*) and between 25 and 52% in the other (pur-portedly *A. subulata*) (Lefkaditou *et al.,* 2012). Further detailed morphological work coupled with molecular genetics is required to confirm the extent of both species. Alt-hough we treat the species separately herein, it is very difficult to know which species (*A. media*, *A. subulata*, or a mixture of the two) was actually being studied in older pa-pers, and much basic work will need to be repeated in future studies to understand how the biology of the two species differs. Further details of the taxonomic issues are considered in each of the species accounts.

In addition to those listed above, the other four species included are:

14.   *Sepietta oweniana* (d'Orbigny, 1841)

15.   *Sepiola atlantica* d'Orbigny, 1842

16.   *Ommastrephes bartramii* (Lesueur, 1821)

17.   *Gonatus fabricii* (Lichtenstein, 1818)

The oegopsids *O. bartramii* and *G. fabricii* are well defined. Most nomenclatural issues revolve around the use of a single *–i* or double *–ii* at the end of the specific epithets. This depends on how the original authority constructed the name, and in both cases here, *-ii* is the correct ending, as used by Lesueur (1821) and Lichtenstein (1818) in their original descriptions.

Sepietta oweniana (d'Orbigny, 1841) is also well defined, although there has been some confusion surrounding the junior synonyms of the species. This was clarified by Bello (2011), and we follow Bello (2011) by including *Sepiola petersii* (Steenstrup, 1887) and *Sepiola scandica* Steenstrup, 1887 as junior synonyms of *Sepietta oweniana.* The nomen-clature of *Sepiola atlantica* is straightforward. The date of the taxon authority was de-termined from dates of publication of text and plates for Férussac and d'Orbigny's 1834–1848 monograph (Tillier and Boucher-Rodoni, 1993).

Within each species account, we indicate the full classification (systematic) of the spe-cies and report the type locality and repository. Remarks on previous misidentifica-tions as well as recent revisions of systematics and relevant results of genetic studies are covered in the following section. We follow the higher taxonomy provided on the Tree of Life (tolweb.org), because this is considered to be the most accurate up-to-date intepretation of cephalopod phylogenetic relationships. Therefore, we do not include "Teuthida", but treat Myopsida and Oegopsida as separate orders without assuming a sister-taxon relationship between them.

Diagnosis

We describe how eggs, hatchlings, juveniles, and adults can be identified, providing photographs where appropriate and, where relevant, providing details on differences between similar species. Note that an identification guide to paralarvae of Mediterranean cephalopod species has recently been as a *Cooperative Research Report* (Zaragoza *et al.*, 2015). Here, we also deal with issues of species status. This is particularly relevant in the case of the two *Alloteuthis* species, for which recent molecular and morphometric studies have done little to clarify the true taxonomic identity of the two familiar European morphotypes. For a glossary of technical terms used, see the cephalopod pages on the Tree of Life website (http://www.tolweb.org/notes/?note_id=587). Unless otherwise stated, lengths given are dorsal mantle length (ML). Total length (TL) is sometimes reported in the literature, e.g. for hatchlings, and is also indicated herein when relevant. For early life stages and species with small adults, measurements are normally given in millimetres, otherwise in centimetres. Weight data normally refer to total body weight. We have not standardized units throughout, but rather use them as given in original papers.

Note that fin length is measured along the anterior–posterior axis, i.e. parallel to the body, and fin width refers to the maximum distance between the distal edges of both fins, measured laterally (perpendicular to the main body axis). In relation to suckers on arms and tentacle clubs, we follow the convention employed by the Tree of Life website in using "series" to refer to longitudinal rows of suckers and "rows" to indicate transverse rows of suckers.

Remarks

For some species, there remain issues or doubts, e.g. in relation to the taxonomic status of the species, the reliability of diagnostic features, or our knowledge of distribution. These issues are discussed in the Remarks section.

Life history

This section gives an account of the life cycle. Egg, paralarva, juvenile, and adult stages are described, considering the growth and maturation processes, spawning and fecundity, and the seasonality of these processes and events. Where relevant, we discuss evidence of how environmental conditions or environmental variation affect growth and maturation. For most species, length–weight relationships and length-at-maturity are available.

Egg and juvenile development

This section summarizes knowledge of early life stages.

Growth and lifespan

Determination of age is essential to allow determination of lifespan and the time-scale of maturation, and to calculate growth rates. We use age data as reported. However, it should be noted that some caution is needed when interpreting apparent geographic differences in lifespan and growth rates obtained by different authors. For example, there are indications that differences in increment interpretation by different readers may have contributed to the different results reported by Arkhipkin (1995) and Raya *et al.* (1999) for *Loligo vulgaris* on the West Saharan shelf. Issues of accuracy and precision are common for age readings based on hard structures in marine animals and are generally addressed through practical workshops and exchange programmes, as for otolith reading in fish species subject to stock assessment. There is a need for regular intercalibration exercises as part of quality assurance for statolith readings (e.g. Jereb *et al.*, 1991).

Cephalopod growth is generally described as continuous and non-asymptotic (Jackson and Moltschaniwskyj, 2002)**,** although the growth of several ommastrephid squid species has been modelled using Gompertz or logistic models (which are both asymptotic models), e.g. Arkhipkin *et al.* (2000), Hendrickson (2004), and Markaida *et al.* (2004). As pointed out by Forsythe and Van Heukelem (1987), cephalopod growth typically has two phases: an initial rapid growth phase often described as "exponential", and a second phase of slower growth sometimes called "logarithmic". During exponential growth, the specific (instantaneous) growth rate is by definition constant. In practice, measured instantaneous growth rates often seem to decline continuously from hatching to maturity (in other words, even if there are two growth phases, the first one is not strictly exponential, and the apparent dichotomy may be more arbitrary than real). Consequently, for growth-rate data to be meaningful, it is essential to report the size (and, if known, the age) of the animals in which it was measured.

Growth rates are reported in several different ways in the literature. In some cases, equations are fitted to data on length or weight vs. age. More commonly, growth is reported either as an absolute rate (mm d^{-1} or g d^{-1}) or as the percentage increase in mantle length or body weight per day (otherwise known as the specific or instantaneous growth rate).

Length–weight relationships

For all species, we present length–weight relationships within the life history section, and, where possible, provide separate equations for both sexes in each region. Generally, length–weight relationships were originally calculated using simple least-squares regression; although, if some other technique was used, we note this fact. It became apparent in compiling and plotting the curves that the equations presented in many source papers (including several written by authors and editors of this report) contain errors. Having established how the errors arose (e.g. wrong specification of units, misplaced decimal points), we corrected those equations.

The use of different units of measurement makes comparisons difficult. Therefore, we present all our data on length–weight relationships as $W = a\text{ML}^b$, where W is body mass (g) and ML is dorsal mantle length (cm). We do not give the equation *per se*, but rather present the values for the parameters a and b. Standardizing all relationships to weight in grammes and length in centimetres and presenting them in a consistent format allows comparisons to be made easily between sexes and locations. This required some recalculation of parameter values, explained below.

Annex 2 contains regression equations used to estimate cephalopod sizes (ML and W) based on measurements of beaks for the 17 species described in this volume.

Using ML in cm is logical, because the parameter a falls in a range that is easily presentable (usually between 0.1 and 1, although it varies by location and species). Use of ML (mm) would lead to greater scope for error, especially in species where the parameter a tends to be small, e.g. in *Todarodes sagittatus*. Off Norway, that species was found to have a relationship between mantle length (cm) and weight (g) defined by the equation $W = aML^b$, where $a = 0.0091$ and $b = 3.23$. This may also be written as $W(g) = 0.0091 ML(cm)^{3.23}$. Of course, it is more common to measure mantle length in mm than in cm. However, if this same relationship is expressed in terms of mm, the parameter a becomes 0.000005342 or 5.342×10^{-6} (the parameter b remains unchanged). Hence, we could also write $W(g) = 0.000005342 ML(mm)^{3.23}$ or $W(g) = 5.342 \times 10^{-6} ML(mm)^{3.23}$. All the equations in this paragraph represent an identical length–weight relationship derived from a single dataset. We argue that, expressed in mm, the value of parameter a is more prone to errors (simple mistyping of the number of zeros) and is more difficult to compare (for example, most people find it intuitively difficult to compare a number $\times 10^{-6}$ with one that is $\times 10^{-3}$).

A length–weight relationship calculated using ML in mm can be converted to one based on ML in cm as follows. As an example, we use the relationship for *T. sagittatus* cited in the above paragraph:

$$W(g) = aML(mm)^b$$

where $a = 0.000005342$ and $b = 3.23$, i.e.:

$$W(g) = 0.000005342\ ML(mm)^{3.23}$$

We can rewrite this as:

$$W(g) = 0.000005342\ ML(cm \times 10)^{3.23}$$

Note that the only thing changed so far is that mm has been rewritten as (cm × 10). All we now do is rearrange the equation to remove the "10" from within the brackets:

$$W(g) = 0.000005342\ ML(cm)^{3.23} \times (10)^{3.23}$$
$$W(g) = (0.000005342) x (10)^{3.23}\ ML(cm)^{3.23}$$
$$W(g) = 0.0091\ ML(cm)^{3.23}$$

In other words, one can simply multiply the value of a, taken from a relationship expressed in mm, by 10^b to obtain the value of a for a relationship expressed in cm. Clearly then, to convert from a relationship expressed in cm to a relationship expressed in mm, one simply divides by 10^b.

In recalculating equations, we have not been able to go back to the original data and rely on simple rearrangement of equations. While this would have facilitated comparison across studies, it is not, strictly speaking, statistically robust. It should be noted that the estimated best fit will have been contingent on the transformation applied to the data (and hence, implicitly, the statistical distribution of weight-at-length) as well as the fitting procedure.

Most studies applied simple linear regression to log-transformed data (implying a log-normal distribution of weight at length and increasing variance in weight at higher length values) despite the fact that this will introduce bias for at least two reasons. First, given that neither length nor weight measurements are error-free, use of orthogonal regression is more appropriate. Second, the mean of a set of log-normally distributed Y values is not the same as the expected Y derived from the straight line fitted to log-

transformed values. This bias in expected Y is usually ignored, but, as noted by Beauchamp and Olson (1973) and Hammond and Rothery (1996), can be corrected by multiplying each weight estimate by $e^{v/2}$ [or $10^{v/2.\log_e(10)}$ if using base-10 logarithms]—where v is the variance about the relevant regression line (see Pierce *et al.*, 2007).

We deliberately avoid using the term "allometry" in relation to the slope coefficient (normally represented as "*b*") of the length–weight relationship. Weight is not a linear measurement, so we argue that length–weight relationships do not express allometry or isometry in the usually intended sense of different body parts growing at different or similar rates. The slope coefficient departs from 3.0 to the extent that cephalopods are not spherical, which is to say usually to a considerable degree (excluding the possibility that average tissue density changes directionally as the animal grows in size).

Maturation and reproduction

We give length-, weight-, and/or age-at-50% maturity values ($ML_{m50\%}$, $BW_{m50\%}$, age $m_{50\%}$) where available, basing our notation on that used by Silva *et al.* (2004). These values are usually given separately for males and females and are obtained by fitting a logistic regression to maturity and size or age data. However, some authors also quote the size at which (say) 75% of animals are mature or the size at which all animals are mature. Additional related terms include "size at first maturity", presumably in the sense of the smallest size at which an animal can mature (ML_{mmin}) or, in practical terms, the smallest mature animal identified. Finally, some authors refer to "mean size at maturity". This sounds as though it should refer to the average of the sizes at which individuals reach maturity, but such information is unlikely to be available, and the term is presumably normally used to indicate the mean size of mature animals. A few references give comprehensive information on the smallest size at maturity, size at 50% maturity, and the size at which all animals are mature.

Another possible source of confusion relates to the maturity scale used and the stage which is regarded as mature. Stage IV is normally used as an indication of maturity, and stage V represents animals in the process of spawning or releasing spermatophores (although in the case of males, the difference between stages IV and V may be an artefact of handling, with post-mortem mechanical pressure forcing spermatophores into the penis). Most cephalopod maturity scales are ultimately based on Lipiński (1979), but the concept has recently been revisited in an ICES-sponsored workshop (ICES, 2010).

In loliginids, the existence of at least two growth forms (presumed to be associated with different reproductive strategies) in males results in (at least) two size modes at maturity and, consequently, $ML_{m50\%}$ values are meaningful only if these modes can be separated in the analysis. The different growth forms may be evident as different size modes in length-frequency distributions. Where these size modes can be followed through time, and especially where they can be linked to distinct hatching periods, it is usual to speak of the existence of two or more "microcohorts". Use of the unmodified term "cohort" is misleading because it normally refers to animals hatched/born in the same year; under this definition, different cohorts of squid probably coexist only for a very short period (if at all), although two cohorts can be present in cuttlefish. As the different hatching periods are usually within the same year and/or separated by only a few months at most, the term "microcohort" is more appropriate.

Because the terminology is now widely used, we follow Rocha *et al.* (2001) in describing spawning strategies (e.g. intermittent terminal spawner, multiple spawner). Part of the

rationale for the development of this terminology was the original definition of itero-parous organisms (Cole, 1954) as those with more than one reproductive event in their lifetime, whereas semelparous organisms reproduce only once, a definition under which it is difficult to decide whether most coleoid cephalopods should be called sem-elparous or iteroparous. However, iteroparity is more commonly understood to imply the occurrence of resting phases, during which gonads become inactive, between spawning events. Under this definition, it is clear that most if not all coleioid reproduc-tive strategies represent variants of semelparity. Neverthless, the categories of Rocha et al. (2001) offer a useful way of classifying these strategies.

Natural mortality

We include a brief section on natural mortality where this information is available. Be-cause of the widely differing life histories (particularly with respect to early life stages), the temporal distribution of natural mortality events can vary greatly between species.

Biological distribution

The environmental characteristics of the species' ranges are described, including the usual ranges of bathymetry, temperature [e.g. sea surface temperature (SST)], salinity, substratum. We generally give salinity without units, although in cases where it would be otherwise unclear, we use the notation "psu" (practical salinity unit). Where infor-mation is available, habitat requirements at particular life stages or for particular activi-ties (e.g. spawning) are described, as are the effects of variation in environmental con-ditions on distribution and abundance. Such inferences are usually drawn from empir-ical statistical modelling or experiments in captivity. Finally, this section describes hor-izontal and vertical migrations.

Trophic ecology

Our knowledge of prey and predators for each species is summarized, and tables are provided with lists of prey and predator species. In the tables, we excluded predation on paralarvae and eggs, not least because it is poorly documented, and we also exclude cannibalism, although its occurrence is covered in the text. Topics such as ontogenetic, seasonal, and environmental variation in diet composition are also discussed.

Other aspects of ecology

Where available, this may include information on parasites, contaminant bioaccumu-lation, and other topics that do not obviously fall under the heading of distributional and trophic ecology. Other topics covered include aspects of population dynamics and abundance fluctuations.

Fisheries and aquaculture

The fisheries section includes information on recruitment, because it is the life cycle process that most directly influences fishery catches. It also describes the nature and current status of the fisheries. Updating information published in the previous *CRR* (Pierce *et al.,* 2010), it briefly reviews which countries catch what species, the fleets and gears involved, the importance of the capture fisheries in terms of landings and effort, and any trends in landings.

We also briefly mention what is known of population structuring in these species and, specifically, how many stocks or management units exist. Where they exist, we de-scribe any current stock assessment and fishery management.

Throughout this section, we assume familiarity with the FAO term "nei", an abbreviation for "not elsewhere included" and used as a recording category in fisheries statistics for groups of species that are not listed individually.

Where relevant, the current status of aquaculture development is described.

Future research needs, bibliography, and illustrations

We wanted to identify gaps that should be addressed in future research, especially relative to future fishery exploitation, assessment, and management.

The bibliography is in two parts: literature cited in the review, which is subsumed within the general bibliography; and additional relevant publications for each species.

Each account is accompanied by photographs, line drawings, and graphic presentations of data. These usually include a photograph and a line drawing of the species at the beginning of each account.

Cephalopod biology and fisheries in European waters: species accounts
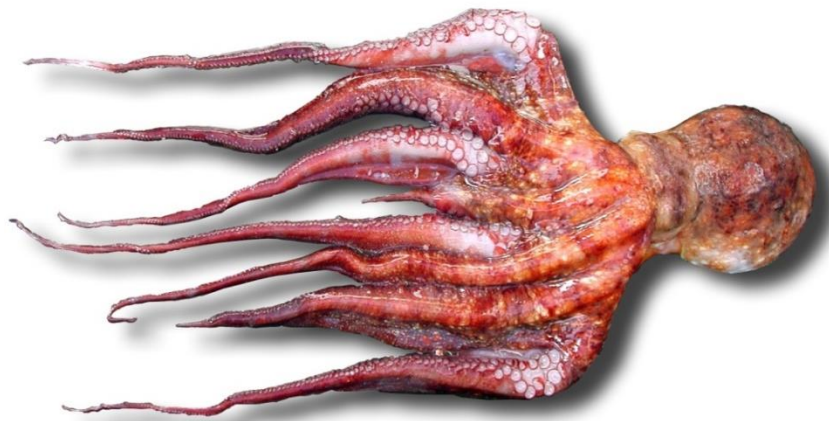
Octopus vulgaris

Common octopus

3 *Octopus vulgaris* Cuvier, 1797

Pilar Sánchez, Roger Villanueva, Patrizia Jereb, Ángel Guerra, Angel F. González, Ignacio Sobrino, Eduardo Balguerias, João Pereira, Ana Moreno, A. Louise Allcock, Evgenia Lefkaditou, Graham J. Pierce, José Iglesias, and Uwe Piatkowski

Common names

Pieuvre, poulpe (France) ; Χταπόδι [chtapodi] (Greece) ; polpo (Italy) ; polvo (Portugal) ; pulpo común (Spain) ; common octopus (UK) (Figure 3.1).

Synonyms

(Following Norman and Hochberg, 2005).
Octopus albus Rafinesque, 1814: 29, *Octopus heteropus* Rafinesque, 1814: 28, *Octopus maculatus* Rafinesque, 1814: 29, *Octopus moscha-*

Figure 3.1. *Octopus vulgaris.* **Dorsal view. From Guerra (1992).**

tus Rafinesque, 1814: 28, *Octopus niger* Rafinesque, 1814: 28, *Octopus ruber* Rafinesque, 1814: 28, *Octopus brevitentaculatus* Blainville, 1826: 187, *Octopus tetradynamus* Rafinesque, 1814: 28, *Octopus pilosus* Risso, 1826: 4, *Octopus cassiopeia* Gray, 1849: 9, *Octopus bitentaculatus* Risso, 1854: 61, *Octopus rabassin* Risso, 1854: 67, *Octopus tritentaculatus* Risso, 1854: 63, *Octopus troscheli* Targioni-Tozzetti, 1869: 156, *Octopus octopodia* Tryon, 1879: 113, *Octopus coerulescentes* Arbanisch (Fra Piero), 1895: 267.

3.1 Geographic distribution

The common octopus, *Octopus vulgaris* Cuvier, 1797, is found in the Northeast Atlantic and the Mediterranean (Figure 3.2), and its presence is also reported in the western Atlantic (Caribbean Sea and northern South America), South Africa, India, and East Asia (Norman *et al.*, 2014; see **Remarks** section below). In the Northeast Atlantic, it extends from Dublin and Liverpool Bay (Massy, 1928), along the southern British coasts (Rees, 1950), occasionally as far as the southern North Sea (Grimpe, 1925; Adam, 1933; Jaeckel, 1958). Common along the French, Spanish, and Portuguese coasts (Magaz, 1934; Bouxin and Legendre, 1936; Sousa Reis, 1985), it is especially abundant on the Sahara Bank, off West Africa between 26 and 19°N (Bas, 1975; Bravo de Laguna, 1989), extending farther south and west to the Cape Verde Islands (Adam, 1962), and as far as the equator (Adam, 1983). Very abundant in the Azores region (e.g. Gonçalves, 1991), it is recorded from Madeira (Rees and Maul, 1956) and the Canary Islands (Hernández-García *et al.*, 1998a, 2002). It is widely distributed and abundant throughout the Mediterranean Sea (Mangold and Boletzky, 1987; Bello 2004; Salman, 2009**),** including the western and central Mediterranean (Mangold-Wirz, 1963a**;** Sánchez, 1986a; Belcari and Sartor, 1993; Jereb and Ragonese, 1994; Cuccu *et al.*, 2003a), the Adriatic Sea (Casali *et al.*, 1998; Krstulović Šifner *et al.*, 2005; Piccinetti *et al.*, 2012**),** the Ionian Sea (Lefkaditou *et al.*, 2003a), and the Aegean Sea and the Levant Basin (D'Onghia *et al.*, 1992; Salman *et al.*, 1997, 1998; Lefkaditou *et al.*, 2003b; Duysak *et al.*, 2008). Old records of the

species in the Sea of Marmara exist (e.g. Demir, 1952, in Ünsal *et al.*, 1999), but *Octopus vulgaris* has not been recorded by more recent research carried out in those waters (Katagan *et al.*, 1993; Ünsal *et al.*, 1999).

Figure 3.2. *Octopus vulgaris.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

3.2 Taxonomy

3.2.1 Systematics

Coleoidea – Octopodiformes – Octopoda – Octopodidae – *Octopus.*

3.2.2 Type locality

Not stated in the original description of Cuvier (1797) but presumed to be western Mediterranean Sea.

3.2.3 Type repository

No type is believed to exist (see Lu *et al.*, 1995).

3.3 Diagnosis

3.3.1 Paralarvae

At hatching, paralarvae have an elongate, conical mantle. They are 2–3 mm long (total length). The arms are subequal in length, with three suckers on each arm and two chromatophores in one row on each arm. Hatchlings from the Northwest Pacific have 3–4 suckers per arm (Villanueva and Norman, 2008). See Hochberg *et al.* (1992) for a description of the full chromatophore pattern (but see also Figure 3.3 below).
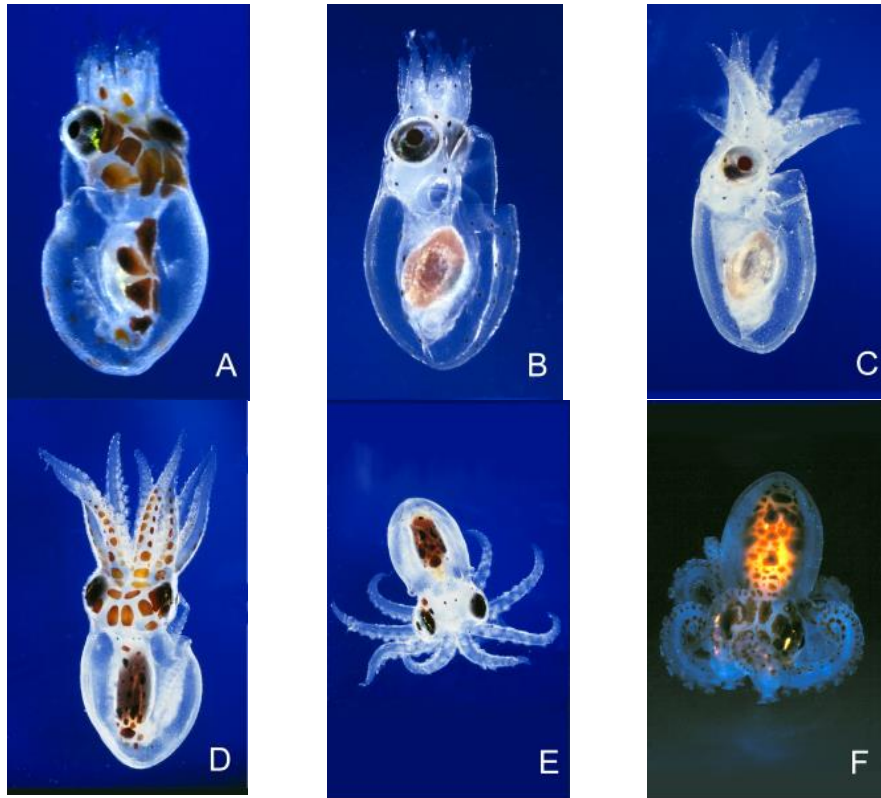
Figure 3.3. *Octopus vulgaris*. **Individuals from hatching to settlement obtained from rearing experiments described in Villanueva (1995a). Images not to scale. Age (d) and mantle length (ML) of the individuals measured fresh are: (A) 0 d, 2.0 mm ML; (B) 20 d, 3.0 mm ML; (C) 30 d, 4.3 mm ML; (D) 42 d, 5.9 mm ML; (E) 50 d, 6.6 mm ML; and (F) 60 d, 8.5 mm ML. Octopuses from this experiment settled between 47 and 54 d. Individuals were photographed under anaesthesia (2% ethanol) potentially causing chromatophore contraction in some cases. Photos: Jean Lecomte, modified from Villanueva *et al*. (1995).**

3.3.2 Juveniles and adults

Adults reach 40 cm ML and 140 cm total length. They have a muscular sac-shaped mantle with a wide pallial aperture that extends beyond its lateral edges. The arms are robust at the base: the lateral arms are longest, and the dorsal ones shortest. The arms have two series (i.e. longitudinal rows) of suckers. Suckers 15–17 of arms 2 and 3 are enlarged in adults, especially in males. The third right arm of mature males is hectocotylized. The ligula is short and spoon-shaped. There are 7–11 lamellae on the outer side of the gill, including terminal lamellae. There are four papillae in the dorsal part of the mantle (one situated in the anterior part, another posterior, and two laterals). The species has reticulated skin, with four whitish spots: two between the eyes and two below the first dorsal papilla. The lower mandible (beak) is illustrated in Figure 3.4 (see also Nixon, 1969, and Clarke, 1986).
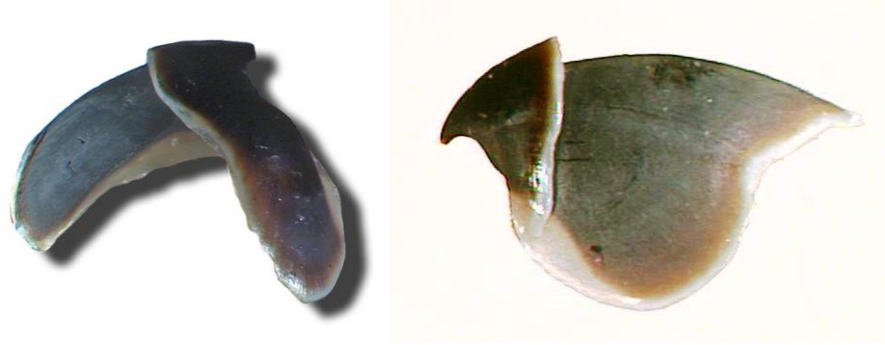
Figure 3.4. *Octopus vulgaris*. **Lower beak (left) and upper beak (right), lateral views. Photo: Evgenia Lefkaditou.**

3.4   Remarks

Octopus vulgaris was traditionally believed to be a cosmopolitan species with a world-wide distribution (Roper *et al.*, 1984). Mangold and Hochberg (1991) and Mangold (1998) redefined its boundaries, suggesting that its distribution was restricted to the Mediterranean and the eastern Atlantic. Subsequent molecular work using the mitochondrial markers 16S rRNA and COIII showed, however, that the distribution of *O. vulgaris* in the Atlantic apparently extends to southern Brazil (Söller *et al.*, 2000) in the west, to Lanzarote and Senegal in the east, and as far south as Tristan de Cunha and False Bay, South Africa (Oosthuizen *et al.*, 2004; Warnke *et al.*, 2004; Teske *et al.*, 2007), and that it is also in the Indian Ocean (Guerra *et al.*, 2010a). Samples from Japan and Taiwan in the Pacific also appear to be conspecific with *O. vulgaris*. Nonetheless, those studies also showed that, throughout this distribution, there are octopuses that have been previously attributed to *O. vulgaris* that are, in fact, distinct species, e.g. *Octopus insularis* recently described from Brazil (Leite *et al.*, 2008). Substantial differences between the chromatophore patterns of paralarvae from the eastern and western Atlantic have been observed, which could provide evidence for the existence of distinct populations or even cryptic *O. vulgaris*-like species along the southern Brazilian coast (Vidal *et al.*, 2010). See Fioroni (1970), Packard (1974), and Messenger (2001), among others, for accounts of chromatophores in *O. vulgaris*.

According to Norman *et al.* (2014), the name *Octopus vulgaris* is currently applied to at least five morphologically similar, but unresolved, taxa with disjunct distributions across subtropical and temperate waters worldwide:

Octopus vulgaris sensu stricto	Mediterranean Sea, Central and Northeast Atlantic
Octopus "vulgaris" type I	Tropical western Central Atlantic
Octopus "vulgaris" type II	Subtropical Southwest Atlantic: Brazil
Octopus "vulgaris" type III	Temperate South Africa and southern Indian Ocean
Octopus "vulgaris" type IV	Subtropical/temperate East Asia

All are of high profile and have high fisheries value. All forms produce small eggs with planktonic hatchlings capable of wide dispersal across the open ocean, potentially supporting gene flow between the disjunct distributions of at least some forms. The species complex is in urgent need of revision and is highly likely to contain cryptic species (Norman *et al.*, 2014). Clearly, the true range of *O. vulgaris* has not yet been elucidated; however, its distribution throughout the Mediterranean and eastern Atlantic is undisputed.

3.5 Life history

The life history of the species is annual, with spawning year-round but with peaks in spring and autumn.

3.5.1 Egg and juvenile development

The early part of the life cycle of this species is reviewed by Mangold and Nixon (1996). The duration of the egg stage depends on incubation temperature, ranging from 20–30 d at 25°C to 100–120 d at 13°C (Mangold, 1983a). Under laboratory conditions, the duration of the planktonic phase seems to be inversely related to rearing temperature, ranging from 33 d at 25°C to nearly 2 months at 21°C. Recently, benthic juveniles of 8–10 mm ML have been found with 23–25 suckers per arm and weighing 100–125 mg fresh weight. Subadults reach 0.5–0.6 kg by 6 months after hatching in the laboratory (Itami *et al.*, 1963; Imamura, 1990; Villanueva, 1995a; Iglesias *et al.*, 2004; Okumura *et al.*, 2005; Carrasco *et al.*, 2006).

Moreno *et al.* (2009) found octopus paralarvae in plankton samples from Portuguese coastal waters (from 57 surveys during the period 1986–2004) mainly in the second half of the year, with peaks in July and November, probably related to two seasonal spawning peaks in Portuguese waters. Those authors also report a relationship between paralarva abundance and favourable upwelling conditions. In Galicia, seasonal upwelling is in late summer and early winter, and the (single) peak in hatchling abundance coincides with maximum zooplankton abundance (Otero *et al.*, 2007).

3.5.2 Growth and lifespan

The life cycle (embryonic and post-hatching life) has been completed under laboratory conditions, resulting in a lifespan of 356 and 339 d for a female and a male of 1.8 and 1.6 kg at death, respectively, reared with food in excess and in temperatures of 17–23°C (Iglesias *et al.*, 2004).

Sánchez and Obarti (1993) reported a maximum age of 15 months in the Mediterranean. Katsanevakis and Verriopoulos (2006) estimated a lifespan of 12–15 months in the eastern Mediterranean using a time-variant, stage-classified, matrix population model based on monthly density measurements of four size stages (1, <50g; 2, 50–200 g; 3, 200–500 g; and 4, >500 g) recorded during scuba diving. Perales Raya (2001) estimated the maximum age of *O. vulgaris* to be 12 months in Sahara Bank populations based on beak growth increment counts, and Hernández-López *et al.* (2001) estimated the maximum ages of males and females to be 12.3 and 13.3 months, respectively, in Canary Island populations. Smale and Buchan (1981) reported a maximum age of 12 months for females and 15 months for males under culture conditions off the east coast of South Africa, whereas Domain *et al.* (2000) reported lifespans of 14–17 months for females and 18–20 months for males in Senegalese waters. Daily increment deposition in *O. vulgaris* stylets has been validated in individuals maintained in aquaria and ranging in size from 248 to 1470 g (Hermosilla *et al.*, 2010).

Octopus vulgaris is characterized by rapid non-asymptotic growth (Alford and Jackson, 1993), with great individual variability in increases in length or weight. This variability has been found both in culture (Iglesias *et al.*, 2004) and in the wild (Domain *et al.*, 2000). Growth rate is influenced mainly by diet (Forsythe and van Heukelem, 1987; García García and Cerezo Valverde, 2006; Cerezo Valverde *et al.*, 2008) and temperature (Aguado Giménez and García García, 2002), although several authors have noted extreme variation in growth, even among individuals reared at the same temperature

and fed the same food (Forsythe and van Heukelem, 1987; Villanueva, 1995a; Semmens *et al.*, 2004).

As in most if not all cephalopods, instantaneous relative growth rates (i.e. % increase in BW d^{-1}, or, sometimes % increase in ML d^{-1}) decrease in older animals, values ranging from 6.14 (%BW d^{-1}) in the smallest individuals to 0.94 in the largest (Forsythe and van Heukelem, 1987). Villanueva (1995a) measured daily growth rates of 2.49% ML d^{-1} and 8.19% BW d^{-1} during the first 2 months of life.

Growth rates, usually for large animals, have been measured in captivity by a number of authors. Mangold and Boletzky (1973) recorded growth rates at temperatures between 10 and 20°C. Although they noted great variation between individuals, daily growth rate was generally faster at higher temperatures. At 20°C, daily growth ranged from 1.68 to 4.14% of BW, although it reached 5% over short periods. This compares with 1.50–1.91% (2.74%) at 15°C and 0.78–1.01% (1.57%) at 10°C. Pham and Isidro (2009) obtained growth rates of 0.67–1.47% of BW d^{-1}. Estefanell *et al.* (2013) recorded growth rates of 1.6–1.8% of BW d^{-1} in captivity. Captive and wild growth rates were measured by Domain *et al.* (2000), the former based on tagging animals off Senegal, in waters of >20°C. Growth was slower in males than in females. The growth rate was ca. 1.36% of BW d^{-1} (both sexes combined) in captivity and between 0.85 (males in 1997) and 1.51% (females in 1998) in the wild, with slower growth at temperatures >25°C.

Length–weight relationships are summarized in Table 3.1.

Table 3.1. *Octopus vulgaris.* **Length–weight relationships in different geographic areas for females (F), males (M), and sexes combined (All). Original equations are converted to W = *a*ML^b, where W is body mass (g) and ML is dorsal mantle length (cm).**

Region	*a*	*b*	Sex	Reference
Galicia	0.442	2.918	F	Guerra (1981)
	0.296	3.029	M	
	0.365	2.961	All	
	2.9	2.17	All	Otero *et al.* (2007)
Gulf of Cádiz	3.277	2.267	F	Silva *et al.* (2002)
	2.489	2.369	M	
	2.895	2.313	All	
South Africa	0.587	2.83	F	Smale and Buchan (1981)
	0.758	2.74	M	
	0.626	2.8	All	
Northwestern Mediterranean Sea	0.542	2.804	F	Guerra and Manriquez (1980)
	0.350	2.988	M	
	0.420	2.917	All	
Balearic Islands	0.413	2.916	F	Quetglas *et al.* (1998a)
	0.442	2.882	M	
	0.437	2.889	All	
Catalan Sea	1.654	2.576	F	Sánchez and Obarti (1993)
	3.306	2.323	M	
Gulf of Alicante	0.51	2.87	All	González *et al.* (2011)
Tunisia	0.371	2.8335	F	Jabeur *et al.* (2012)
	0.485	2.834	M	

	0.399	2.915	All	
Aegean Sea	0.138	2.60	All	Lefkaditou *et al.* (2007)
Northeastern Levant Sea	0.031	3.841	F	Duysak *et al.* (2008)
	0.1685	3.1219	M	
	0.1399	3.2001	All	

3.5.3 Maturation and reproduction

In Galicia, the sex ratio is ca. 1:1 most of the year, although females dominate samples collected in May (1:0.73) and September (1:0.58) (Otero *et al.*, 2007). Quetglas *et al.* (1998a) recorded the sex ratio in the Balearic Sea (Mediterranean) for each season and found no significant differences from 1:1. In the Gulf of Cádiz, the annual sex ratio was estimated as 1.06:1 (male:female) (Silva *et al.*, 2002). However, Smale and Buchan (1981) reported that, off South Africa, male numbers dominated during the months March–September and females during October–February (with the greatest departure from 1:1 in November when the sex ratio was ca. 3:1 in favour of females).

Females mature larger than males (Lourenço *et al.*, 2011a, b). In Galicia, weight at 50% maturity (BWm$_{50\%}$) was 1788 g for females and 903 g for males. The smallest mature females were 12 cm ML and 394 g BW, and the smallest mature males were 10 cm ML and 323 g BW (Otero *et al.*, 2007). In the Gulf of Cádiz, lengths (ML) and weights (BW) of the smallest mature specimens sampled by Silva *et al.* (2002) were 9.4 cm and 250 g in males, and 12 cm and 580 g in females.

Length at maturity (MLm$_{50\%}$) was 10.4 cm ML in males and 17.6 cm ML in females, and BWm$_{50\%}$ was estimated at 671 g in males and 2023 g in females. In the western Mediterranean, mantle length at first maturity is ca. 9.5 cm in males and 13.5 cm in females (Mangold-Wirz, 1963a). Cuccu *et al.* (2013) reported that the smallest mature specimens sampled in Sardinian waters (central western Mediterranean Sea) were 45 mm ML and 190 g BW in males, and 90 mm ML and 310 g BW in females. The MLm$_{50\%}$ was 70 mm for males and 120 mm for females, and BWm$_{50\%}$ was 320 g and 520 g for males and females, respectively. Males matured at 170–470 d, younger than females (210–390 d).

The spawning season extends throughout the year, with two peaks: one in spring and one in autumn in Northeast Atlantic populations. The main spawning season in the Mediterranean is June–July (Mangold, 1997). Rees and Lumby (1954) refer to spawning beginning in May in the English Channel, the precise timing varying with location and, possibly, temperature. In Galician waters, maturity and reproductive indices indicated spring to be the most important spawning season, although mature females are present during the months December–August, with a peak in May that is related to seasonal upwelling (Otero *et al.*, 2007). In northwestern Portugal, the species spawns during the period March–July, again coinciding with the northwest coast upwelling season, whereas on the south coast of Portugal, the species spawns mainly in summer between August and September, although there is sometimes a minor spawning peak in early spring along the south coast (Lourenço *et al.*, 2011a). In the Gulf of Cádiz, the breeding season extends from February to October, with spawning peaks in April–May and August (Silva *et al.*, 2002). In the Gulf of Alicante, the gonadosomatic index peaks between April and July for males and in July for females (González *et al.*, 2011).

The potential fecundity of mature females ranges from 70 000 to 634 445 oocytes (Mangold-Wirz, 1963a; Silva *et al.*, 2002; Otero *et al.*, 2007). Females attach small oval eggs of ca. 2.5 × 1 mm (Mangold-Wirz, 1963a) to hard substrata, mainly rocks, and care for the eggs until hatching.

The maximum number of spermatophores observed in the Needham's sac is 633 (Otero *et al.*, 2007), and the number and length of spermatophores tends to increase with size of male. In Galician waters (northwestern Spain), mean (± s.d.) potential fecundity was estimated at 221 447 ± 116 031 oocytes and mean oocyte length at 3.0 ± 0.8 mm. The mean number of fully developed spermatophores was 182 ± 88, with a mean length of 48.8 ± 10.6 mm (Otero *et al.*, 2007).

3.5.4   Natural mortality

The natural mortality of cephalopods during paralarva and settlement stages is high and is strongly related to environmental factors, which ultimately control the abundance of food for the paralarvae (zooplankton). The link between upwelling episodes and subsequent fishery catch rates for octopuses in Galicia is consistent with environmental factors having a major impact during the pelagic stage of the life cycle (Otero *et al.*, 2008). In the eastern Mediterranean, more than 50% of just-settled individuals die within three months, and the mortality rate falls thereafter up to ca. 6 months after settlement (Katsanevakis and Verriopoulos, 2006).

3.6   Biological distribution

3.6.1   Habitat

Octopus vulgaris is a merobenthic species inhabiting temperate, tropical, and subtropical waters. It is found from the coast out to the outer edge of the continental shelf (200 m) in temperatures of 6–33°C. Rees and Lumby (1954) note that the species tolerates temperatures as low as 6°C in the English Channel. It is a stenohaline species, tolerating salinity ranging from 29 (Delgado *et al.*, 2011) to 40 (Mangold, 1983a).

Local density of *O. vulgaris*, as has been documented for other species of octopuses, is affected by the availability of solid material (rocks, stones, shells, anthropogenic litter, etc) to be utilized for den construction (Katsanevakis and Verriopoulos, 2004).

3.6.2   Migrations

This species undertakes limited seasonal migrations. According to Rees and Lumby (1954), octopuses appear to move away from inshore waters in late summer and spend winter in deeper, offshore waters. No segregation between sexes has been observed (Mangold, 1983a).

3.7   Trophic ecology

3.7.1   Prey

The diet of *O. vulgaris* consists of crustaceans, fish, molluscs, and polychaetes (Table 3.2). No significant variation in diet has been reported for subadults and adults. Anraku *et al.* (2005) showed that prey selection under experimental conditions depended on chemical stimuli detected by chemoreceptors in the arms and lip (see Graziadei, 1971, for a description of the nervous system of the arms). Octopuses drill holes in the shells of shelled molluscs, allowing them to inject cephalotoxin, secreted by the posterior salivary glands, to paralyse the prey (e.g. Ghiretti, 1959, 1960; Cariello and Zanetti, 1977; Nixon, 1979; Nixon *et al.*, 1980).

Table 3.2. Prey composition of *Octopus vulgaris*, as known from studies in the Mediterranean Sea, Northeast Atlantic, and Sahara Bank (compiled from Nigmatullin and Ostapenko, 1976[1]; Guerra, 1978[2]; Ambrose and Nelson, 1983[3]; Nixon and Budelmann, 1984[4]; Sánchez and Obarti 1993[5]; Quetglas *et al.* 1998a[6]; Kallianiotis *et al.*, 2001[7]; Roura *et al.*, 2012[8]; Á. Guerra, pers. comm.[9])

Taxon	Species
Osteichthyes	indet.[6,8]
Blenniidae	*Blennius ocellaris* (butterfly blenny)[6], indet.[9]
Caproidae	*Capros aper* (boarfish)[6]
Carangidae	*Decapterus* spp.[1], *Trachurus* spp.[1]
Carapidae	*Carapus acus* (pearl fish)[6]
Centracanthi-dae	*Centracanthus cirrus* (curled picarel)[6]
Cepolidae	*Cepola macrophthalma* (as *C. rubescens*) (red bandfish)[2,7]
Clupeidae	*Sardinella* spp.[1], indet.[2]
Congridae	*Conger conger* (European conger)[7]
Gobidae	*Gobius niger* (black goby)[7], indet.[9]
Labriidae	indet.[9]
Lotidae	*Gaidropsarus vulgaris* (three-bearded rockling)[6]
Ophichthidae	*Ophichthus rufus* (Rufus snake-eel)[6], *Leptocephalus* spp.[1]
Ophidiidae	*Ophidion barbatum* (snake blenny)[7]
Serranidae	indet.[9]
Soleidae	indet.[1]
Sparidae	*Boops boops* (bogue)[1], *Dentex macrophthalmus* (large-eye dentex)[1], *Dentex gibbosus* (pink dentex)[1], *Dentex* spp.[1], *Pagellus acarne* (auxilliary seabream)[1], *Pagellus erythrinus* (common pandora)[1]
Trachinidae	*Trachinus* spp.[1]
Triglidae	indet.[1,9]
Uranoscopidae	*Uranoscopus* spp.[2]
Chondrichthyes	
Scyliorhinidae	*Scyliorhinus canicula* (lesser spotted dogfish)[7]
Crustacea	
Decapoda	indet.[6]
Dendrobranchi-ata-Penaeiodea	*Melicertus kerathurus*[2], *Solenocera membranacea*[2]
Pleocyemata-Anomura	*Anapagurus laevis*[2], *Anapagurus* spp.[2,5], *Galathea bolivari*[6], *G. intermedia*[6], *G. strigosa*[6], *Galathea* spp.[2,6], *Paguristes eremita*[6], *Pagurus prideaux*[6], Paguridea indet.[6], *Pisidia longicornis*[2], *Pisidia* spp.[5], indet.[8]
Pleocyemata-Brachyura	*Atelecyclus rotundatus*[6], *Atelecyclus* spp.[9], *Calappa granulata*[2], *Cancer pagurus*[9], *Carcinus maenas*[9], *C. aestuarii* (as *C. mediterraneus*)[2], *Dromia personata*[2], *Ebalia granulosa*[6], *E. tuberculosa*[6], *Ebalia* spp.[6], *Eriphia verrucosa*[9], *Ethusa mascarone*[2], *Eurynome spinosa*[6], *Goneplax rhomboides***[2,5,7]**, *Inachus dorsettensis*[6], *Inachus* spp.[2,9], *Liocarcinus corrugatus*[2,6], *L. depurator*[2,5,7], *L. pusillus*[6], *L. vernalis*[5], *Liocarcinus* spp.[2,6,9], *Macropodia* spp.[9], *Maja squinado*[9], *Medorippe lanata*[2], *Necora puber* (as *L. puber*)[9], *Pachygrapsus marmoratus*[9].
	Pachygrapsus spp.[2], Parthenopidae indet.[6], *Pilumnus spinifer*[6], *Pisa armata*[2], *P. nodipes*[2], *Polybius henslowii*[9], *Xantho pilipes*[6,8], indet.[5,6,8]
Pleocyemata-Caridea	*Aegaeon cataphracta* (as *Pontocaris cataphracta*)[2,5], *Alpheus* spp.[2,5], Alpheidae indet.[6], *Crangon crangon*[2], *Eualus cranchii* (as *Thoralus cranchii*)[6], *Palaemon serratus*[5], *Palaemon* spp.[2,9], *Pandalina brevirostris*[2], *Philocheras sculptus*[6], *Philocheras* spp.[2], *Processa* spp.[2], indet.[6,8]

Pleocyemata-Thalassinidea	indet.[8]
Stomatopoda	indet.[1]
Unipeltata-Squilloidea	*Squilla mantis*[2]
Euphausiacea	indet.[8]
Amphipoda	indet.[1,2]
Gammaridea	indet.[6]
Ostracoda	indet.[1]
Peracarida-Isopoda	indet.[1,6]
Cephalopoda	indet.[6]
Myopsida	*Alloteuthis africana*[1], *A. media*[6], *Loligo vulgaris*[1,2,6]
Octopoda	*Eledone moschata*[7], *Octopus vulgaris*[5,9], *Octopus* spp.[1,2]
Sepioidea	*Sepia* spp.[1,2,5,9], Sepiolidae indet.[6]
Gastropoda	indet.[5,7]
Cerithioidea	*Cerithium vulgatum*[3], *Turritella communis*[6]
Conoidea	*Raphitoma reticulata*[6]
Haliotidea	*Haliotis tuberculata*[3]
Muricoidea	*Cymbium* spp.[1]
Naticoidea	*Naticarius hebraeus*[6], *N. intricatoides*[6]
Patelloidea	*Patella caerulea*[3], *P. vulgata*[3]
Trochoidea	*Calliostoma granulatum* (granulated top shell)[6] , indet.[6]
Bivalvia	indet.[1,5,7]
Arcoida	*Arca noae*[3], *Barbatia barbata*[3], *Glycymeris glycymeris*[3]
Pectinoida-Anomioidea	*Anomia ephippium*[3]
Limoida	*Limaria tuberculata*[3]
Mytiloida	*Modiolus barbatus*[3], *Mytilus galloprovincialis*[9], *Mytilus* spp.[3]
Euheterodonta-Solenoidea	*Ensis ensis*[9]
Veneroida	*Acanthocardia tuberculata*[3], *Callista chione* (as *Pitaria chione*)[3], *Cardium* spp.[3], *Chamelea gallina*[3], *Donax semistriatus*[3], *Timoclea ovata*[3], *Venerupis geographica*[3], *Venus verrucosa*[3]
Echinodermata	
Ophiuroidea	indet.[1,5]
Polychaeta	*Laetmonice hystrix* (as *Hermione hystrix*)[4], indet.[1,5]
Foraminifera	indet.[1]

3.7.2 Predators

Coastal fish (*Epinephelus marginatus, Serranus* sp., *Atherina presbyter*) attracted to *O. vulgaris* egg masses during hatching periods have been observed preying on paralarvae (Villanueva and Norman, 2008). Further, paralarvae of 6.5–18 mm TL have been recorded in the stomach contents of albacore (*Thunnus alalunga*) (Bouxin and Legendre, 1936).

Predators of subadult and adult *O. vulgaris* include fish, marine mammals, birds, man, and other cephalopod species (Hanlon and Messenger, 1996). *Octopus vulgaris* has been found in the stomachs of bottlenose dolphin (*Tursiops truncatus*) (Blanco *et al.*, 2001), Risso's dolphin (*Grampus griseus*) (Blanco *et al.*, 2006), and Mediterranean monk seal (*Monachus monachus*) (Pierce *et al.*, 2011) in the Mediterranean Sea. Marine mammal predators of *O. vulgaris* in Galician waters include common dolphin (*Delphinus delphis*), long-finned pilot whale (*Globicephala melas*), and sperm whale (*Physeter macrocephalus*) (Table 3.3, see also at González *et al.*, 1994a; López, 2002; Santos *et al.*, 2004a, 2013, 2014).

Table 3.3. Known predators of *Octopus vulgaris* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalopoda	Common cuttlefish (*Sepia officinalis*)	Alves et al. (2006)
	Veined squid (*Loligo forbesii*)	Rocha et al. (1994)
Chondrichthyes	Bull ray (*Pteromylaeus bovinus*)	Capapé (1977)
	Smooth-hound (*Mustelus mustelus*)	Saïdi *et al.* (2009)
Osteichthyes	Dusky grouper (*Epinephelus marginatus*)	Reñones *et al.* (2002)
	Silver-cheeked toadfish (*Lagocephalus sceleratus*)	Kalogirou (2011)
Pinnipedia	Mediterranean monk seal (*Monachus monachus*)	Pierce *et al.* (2011)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	González *et al.* (1994a), Blanco *et al.* (2001), Santos *et al.* (2007)
	Common dolphin (*Delphinus delphis*)	González *et al.* (1994a), Santos *et al.* (2004a, 2013)
	Harbour porpoise (*Phocoena phocoena*)	Santos *et al.* (2004b)
	Long-finned pilot whale (*Globicephala melas*)	González *et al.* (1994a), López (2002), Santos *et al.* (2014)
	Risso's dolphin (*Grampus griseus*)	López (2002), Blanco *et al.* (2006), Bearzi *et al.* (2011)
	Striped dolphin (*Stenella coeruleoalba*)	Sollmann (2011)
	Sperm whale (*Physeter macrocephalus*)	González *et al.* (1994a)

3.8 Other ecological aspects

3.8.1 Parasites

Hochberg (1983) noted that *O. vulgaris* was one of only two species in which parasites had been studied in detail. In the genus *Octopus*, parasites identified included viruses, fungi, sporozoans, ciliates, dicyemids, digeneans, cestodes, hirudineans, and copepods. He noted that two species of the protist *Aggregata* are known in *O. vulgaris*: *Aggregata octopiana*, reported by Schneider (1875), and *A. spinosa*, described by Moroff (1906). Ciliates found in *O. vulgaris* include *Chromidina coronata*.

González *et al.* (2003) recorded a range of parasite species in *O. vulgaris* from Galicia (more than half of which were also found in *Eledone cirrhosa*): *Aggregata octopiana*, which, according to Gestal *et al.* (2007), is a dangerous pathogen in cultured octopus; *Dicyema typus* (a mesozoan); *Lecithochirium* sp. (a digenean trematode); *Phyllobothrium* sp. and *Scolex pleuronectis* (both cestodes); *Pennella* sp. (a copepod); *Octopicola superbus* (Maxillopoda); and two genera of nematode, *Cystidicola* sp. and *Anisakis simplex sensu stricto.*

3.8.2   Contaminants

As *O. vulgaris* is an important fishery resource, the propensity of cephalopods to accumulate certain metals, notably cadmium, is relevant to human health. Seixas *et al.* (2005a) reported mercury levels from octopuses on the Atlantic coast of Portugal. As expected, the greatest concentrations were in the digestive gland. Although mercury concentrations were slightly higher in samples from Cascais (near Lisbon) than in Viana do Castelo, consistent with the higher concentrations recorded in seawater at Cascais, they were within the range of values legally defined as safe for human consumption. However, cadmium concentrations were above the legal limit for human consumption in samples from Viana in 2002, and two animals also had lead concentrations that exceeded legal limits (Seixas *et al.*, 2005b). In another study based in Portugal, Raimundo *et al.* (2004) found that cadmium concentrations were greatest in octopuses from the north of the country. Storelli *et al.* (2012) measured lead, mercury, and cadmium levels in a range of seafood products in Italy (sources from both within and outside Europe), and found the greatest cadmium concentrations in cuttlefish and octopuses, noting that some of the values were close to the legal limits for human consumption. The highest cadmium concentration recorded in *O. vulgaris* was 0.64 mg g^{-1} wet weight.

3.8.3   Environmental effects

Although the biology and ecology of adult *O. vulgaris* are generally well documented, there are only a few studies on the effect of physical oceanography on the life cycle of the species. The first such studies were made in waters off Great Britain involving the influence of sea surface temperatures on the reproduction and abundance of adults and the effects of currents on their distribution (Rees, 1950; Rees and Lumby, 1954). Garstang (1900) had previously speculated that a "plague" of octopuses in the English Channel at the end of the 19th century was related to warm summers and mild winters, but, considering subsequent "plague" years, Rees and Lumby (1954) concluded there was no close association between high abundance and warm summers. In the Gulf of Cádiz (southern Iberian Peninsula), a negative correlation was found between rain and abundance (Sobrino *et al.*, 2002). Off Tunisia, there is a strong association between low sea surface temperature and abundance, and in the hot season, rainfall also has a positive effect on production (Chédia *et al.*, 2010). Strong upwelling conditions, interpreted from satellite images, have been related to strong recruitment of *O. vulgaris* in Mauritanian waters (Faure *et al.*, 2000). In coastal upwelling areas off West Africa, catches of adult *O. vulgaris* during summer are significantly correlated with the upwelling intensity during the previous winter, indicating the influence of oceanographic conditions on octopus paralarvae and juveniles and the subsequent effects on the fished adult populations (Caverivière and Demarcq, 2002). In the same region, exceptional oceanographic conditions favouring the survival of paralarvae and juveniles also seem to be the origin of demographic explosions of *O. vulgaris* (Caverivière, 1990; Diallo *et al.*, 2002). A similar relationship between upwelling intensity and adult catches has been found. On the northwestern Iberian coast (Otero *et al.*, 2008), wind stress structure

(which is related to upwelling) during spring–summer (prior to the hatching peak) and autumn–winter (during the planktonic stage) affected the early life phase of this species, and explained up to 85% of the year-to-year variability of the subsequent adult catch. The dynamics of coastal upwelling areas seem to favour paralarva transport to the open ocean during upwelling episodes and concentration at the coast under upwelling relaxation or downwelling conditions (González *et al.*, 2005; Otero *et al.*, 2008).

3.9 Fisheries

European vessels fish for *O. vulgaris* mainly in three areas: the Northeast Atlantic, the Mediterranean, and the eastern central Atlantic off West Africa, although landings into the EU from the latter area (mainly by Spain) have dwindled dramatically as the fishery has increasingly been exploited mainly by Moroccan vessels. The estimated landings for this species were 72 801 t from the eastern central Atlantic in 2008, mostly from western Saharan and Mauritanian waters (and only a small fraction was landed in Europe). This compares with 21 581 t from the Northeast Atlantic and 17 010 t from the Mediterranean (FAO, 2010a). The most recent data available from FAO (Fishstat database) indicate a sharp drop in eastern central Atlantic octopus catches in 2010 (down to ca. 55 000 t), although landings from the Northeast Atlantic and Mediterranean in 2010 were at levels similar to those in 2008. Note that landings data reported to the FAO for the eastern central Atlantic and, to a lesser extent, the Mediterranean have normally been for octopuses in general (i.e. including an unspecified proportion of *Eledone* spp.).

In the Mediterranean, *O. vulgaris* overtook *Sepia officinalis* as the most important fished cephalopod species in the late 1970s. However, octopus landings in the Mediterranean have declined fairly consistently since the mid-1980s, and indeed *O. vulgaris* was overtaken as the most important landed cephalopod by *S. officinalis* in 2007 (FAO, 2011). The total octopus landings from the Mediterranean in 2010 were 25 300 t, of which 10 300 t were recorded as common octopus and 7000 t as *Eledone* spp. (FAO, 2011). Estimated total landings of octopods from the ICES area of the Northeast Atlantic in 2010 were ca. 16 600 t, mostly by Portugal and Spain (ICES, 2012), comparable with the 18 300 t recorded for the Northeast Atlantic in the FAO dataset. Although reported total landings have fluctuated from year to year (between 9000 and 18 600 t over the preceding decade), total octopod landings in 2000 and 2010 were similar (ICES, 2012).

Octopus vulgaris is taken throughout the year as a target species in bottom trawls and small-scale coastal fisheries using hand-jigs, pots, trammelnets, and traps in depths between 20 and 200 m. Although the majority of landings arise from offshore trawl fisheries, artisanal fisheries have high local economic and social importance in southern Europe (Pereira, 1999).

In the Gulf of Cádiz, *O. vulgaris* is landed by virtually all the artisanal fleets in the region. The main gears used vary from port to port. For example, in Conil, where more than 50% of the artisanal catches of this species are landed, most are taken by a type of hook and line (*chivos*). Elsewhere in the area, trawls, gillnets, traps, pots, and other types of hooks and lines are used (Silva and Sobrino, 2005). The size range of octopuses captured depends on the size and type of pot used (see Sobrino *et al.*, 2011). In Galicia, ca. 80–90% of landings are by octopus traps (*nasas de polbo*), with most of the remainder caught using traps targeted at other species. In 2008, 1458 vessels were licensed to use *nasas de polbo* (Tasende *et al.*, 2009). Otero *et al.* (2005) used interview data to estimate catches of *O. vulgaris* by the artisanal fleet in Galicia and showed that true landings are

approximately double those reported in official statistics. In the Thracian Sea, octopuses are targeted using pots and taken as bycatch in trammelnets (Lefkaditou *et al.*, 2004).

The importance of the species as a resource has led to a requirement for its molecular identification in fishery products (e.g. to detect substitution of *Eledone cirrhosa*). Espiñeira and Vieites (2012) reported a method to identify fresh, frozen, and processed *O. vulgaris* using real-time PCR (polymerase chain reaction).

Octopus vulgaris is the most abundant and ubiquitous cephalopod species on the Saharan Bank (Northwest Africa from 21 to 26°N). In that area, there are probably two stocks: one off Dakhla (26–23°N) and the other off Cap Blanc (21–19°N) (Murphy *et al.*, 2002). Genetic data indicate the presence of multiple stocks in European waters, with distinct differences between the eastern and western Mediterranean, and Northeast Atlantic and Sahara Bank (Boyle, 2000; Maltagliati *et al.*, 2001; Casu *et al.*, 2002; Cabranes *et al.*, 2008; P. R. Boyle *et al.* unpublished FAIR-CT96-1520 project data).

Although there is no routine assessment of *O. vulgaris* stocks in European waters, exploited cephalopod stocks in the Saharan Bank fishery (an essential resource for many years for a sector of the Spanish fleet) have been assessed under the auspices of the Fisheries Committee for the Eastern Central Atlantic (e.g. FAO, 1979, 1982, 1987) using production models. The methodology continues to be updated to take advantage of developments in available techniques (e.g. Ono *et al.*, 2012).

Cephalopod landings in the European Union are not subject to quota limits. As most octopuses are landed by small-scale fisheries, the activity is mainly regulated at the regional level. Hence, the Galician regional government requires all fishing boats to be licensed. Vessels can use a maximum of five gears, although only one per day, and within specified zones. Fishing is permitted only Monday–Friday, and there are also closed seasons. Minimum landing sizes apply (Tasende *et al.*, 2009). In the case of octopus, a closed season may or may not be imposed.

3.10   Aquaculture

Rearing of *O. vulgaris* is limited to ongrowing subadult individuals captured from the wild, using tanks and cages mainly in Spain, but also in other European Mediterranean countries (Rama-Villar *et al.*, 1997; Iglesias *et al.*, 2000; Aguado and García García, 2002; García García and Aguado Giménez, 2002; Chapela *et al.*, 2006; Rodríguez *et al.*, 2006; Mazón *et al.*, 2007; García García *et al.*, 2009; Domingues *et al.*, 2010; García *et al.*, 2011). On the northwestern Spanish coast, commercial viability is enhanced using readily available mussel-culture rafts as platforms from which to suspend cages. Using fish and crustacean fishery discards as feed, wild subadults can be grown from 800 g to 2.5 kg in 4 months. However, sourcing wild animals for ongrowing from the small-scale fishery would represent an undesirable increase in fishing pressure on the resource and is currently permitted only for pilot schemes. The culture of paralarvae of this species is still under development. At scales other than experimental, the culture of paralarvae is still proving a serious bottleneck to production owing to inadequate artificial diets and high mortality (Navarro and Villanueva 2000, 2003; Villanueva *et al.*, 2004; Iglesias *et al.*, 2004, 2006, 2007; Okumura *et al.*, 2005; Seixas *et al.*, 2010). The lack of a standardized culture method and the absence of appropriate live food to meet paralarval requirements have been identified as two possible causes of this mortality (Iglesias *et al.*, 2007).

Iglesias *et al.* (2004) were able to culture *O. vulgaris* experimentally through the complete life cycle, using both *Artemia* and crustacean zoeae as live prey, with 31.5% of

paralarvae surviving after 40–45 d, survivors reaching 9.5 ± 1.9 mg dry weight at this point. The octopuses reached a weight of 0.5–0.6 kg at 6 months of age and a final weight of 1.4–1.8 kg at 8 months, the time at which they reached maturity and began to spawn. Moxica *et al.* (2006) also reared *O. vulgaris* to the adult stage. Using enriched *Artemia* as food, they obtained 67% paralarva survival and a dry weight of 1.89 mg after 1 month of culture. In that case, *Artemia* was cultured with *Isochrysis galbana* and further enriched with *Nannochloropsis* sp. Several other authors have also reported successful results from adding *Nannochloropsis* sp. to the culture tank and as food for *Artemia* (Hamasaki and Takeuchi, 2000; Hamasaki and Morioka, 2002; Fuentes *et al.*, 2011). Seixas (2009) indicated that *Isochrysis galbana* mixed with *Rhodomonas lens* provided the best microalgal combination because of the high level of polyunsaturated fatty acids (PUFAs) (in *Isochrysis galbana*) and very high level of proteins (in *Rhodomonas lens*).

These studies have together shown that a mixed live diet of enriched *Artemia* and crustacean zoeae is the most balanced diet for producing the best growth and survival results in the paralarva phase, achieving dry weights threefold higher than obtained from feeding with *Artemia* enriched with microalgae. Nevertheless, this approach is currently not transferable to a commercial scale owing to the limited availability of live zoeae.

3.11 Future research, needs, and outlook

Important topics for future research include investigations on early life stages and the influence of environmental conditions on wild octopus populations. Further, the development of inert diets to feed the paralarvae or microencapsulated products to produce enriched *Artemia* with a similar nutritional composition to crustacean zoeae is important for solving the paralarva rearing problem.

Cephalopod biology and fisheries in European waters: species accounts
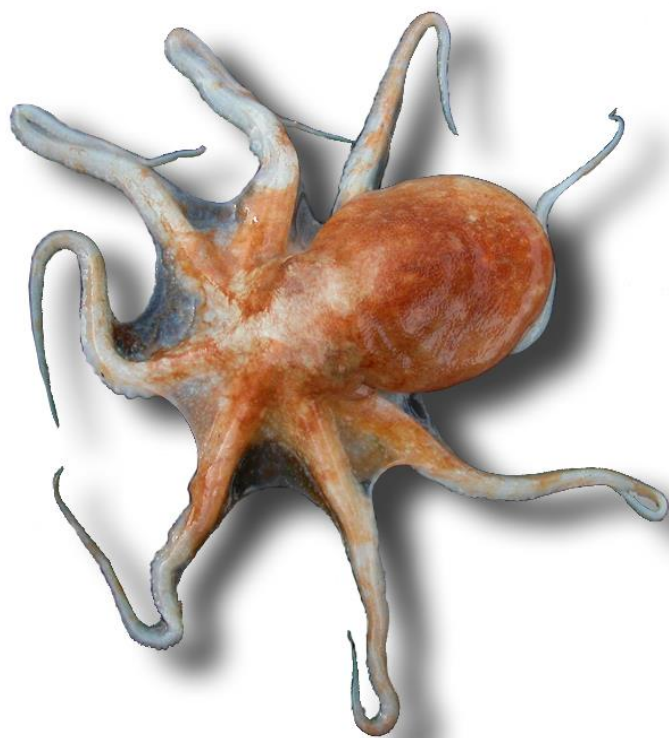
Eledone cirrhosa

Horned octopus
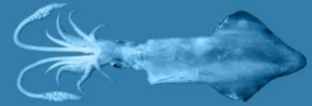
4   *Eledone cirrhosa* (Lamarck, 1798)

Paola Belcari, Paolo Sartor, Patrizia Jereb, Evgenia Lefkaditou, Graham J. Pierce, Uwe Piatkowski, Teresa Borges, and A. Louise Allcock

Common names

Élédone commune, poulpe, poulpe blanc, pieuvre blanche (France); Μοσκιός [moschios] (Greece); moscardino bianco (Italy); polvo do alto, polvo-cabeçudo (Portugal); pulpo blanco (Spain); horned octopus, lesser octopus, curled octopus (UK) (Figure 4.1).

Synonyms

Octopus cirrhosus Lamarck, 1798, *Sepia cirrhosa*: Bosc (1802), *Eledone aldrovandi* Montfort, 1802, *Octopus leucoderma* San Giovanni, 1829, *Eledone genei* Verany, 1839, *Eledone ambrosiana* Risso, 1854, *Eledone halliana* Rochebrune, 1884, *Pallia sepioidea* Rochebrune, 1884, *Moschites cirrosa*: Pfeffer (1908), *Ozaena cirrhosa*: Adam (1934), *Moschites cirrhosa zetlandica* Russell, 1922.

Figure 4.1. *Eledone cirrhosa*. **Dorsolateral view. From Guerra (1992).**

4.1   Geographic distribution

The horned octopus, *Eledone cirrhosa* (Lamarck, 1798), is found in the Northeast Atlantic from ca. 66–67°N south to Moroccan waters and throughout the Mediterranean Sea (Norman *et al.*, 2014) (Figure 4.2). In the northernmost part of its distribution, the species extends to southern Iceland, the Faroe Islands (Bruun, 1945), and the west coast of Norway (Nordgård, 1923; Grieg, 1933), where it seems to reach Ostnesfjord in Lofoten, although it is rarely found north of Trondjemsfjord (Grieg, 1933). Old records in the Skagerrak and Kattegat have been reviewed by Hornbörg (2005). It is a common species in Irish and British waters, abundant along the entire Scottish coast, and common in the Celtic Sea and English Channel (Massy, 1928; Stephen, 1944; Rees, 1956; Boyle, 1983b; Lordan *et al.*, 2001a). It is present in the North Sea (Grimpe, 1925; De Heij and Baayen, 2005; Oesterwind *et al.*, 2010), though more abundant in the northeastern and central eastern areas (De Heij and Baayen, 2005), and extends south along the Atlantic coasts of France, Spain, and Portugal, although the southern limits of its distribution are uncertain (ca. 33°N; Guerra, 1992). *Eledone cirrhosa* is widespread throughout the Mediterranean Sea (Mangold and Boletzky, 1987; Bello, 2004; Salman, 2009), including western and central Mediterranean waters (Mangold-Wirz, 1963a; Sánchez, 1986a; Würtz *et al.* 1992a; Belcari and Sartor, 1993; Jereb and Ragonese, 1994; Giordano and Carbonara, 1999; Relini *et al.*, 2002; Cuccu *et al.*, 2003a), the Adriatic Sea (Casali *et al.*, 1998; Krstulović Šifner *et al.*, 2005, 2011; 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, 2002; Lefkaditou *et al.*, 2003b; Duysak *et al.*, 2008; Mienis *et al.*, 2011). The species has been recorded in the Sea of Marmara (Ünsal *et al.*, 1999).
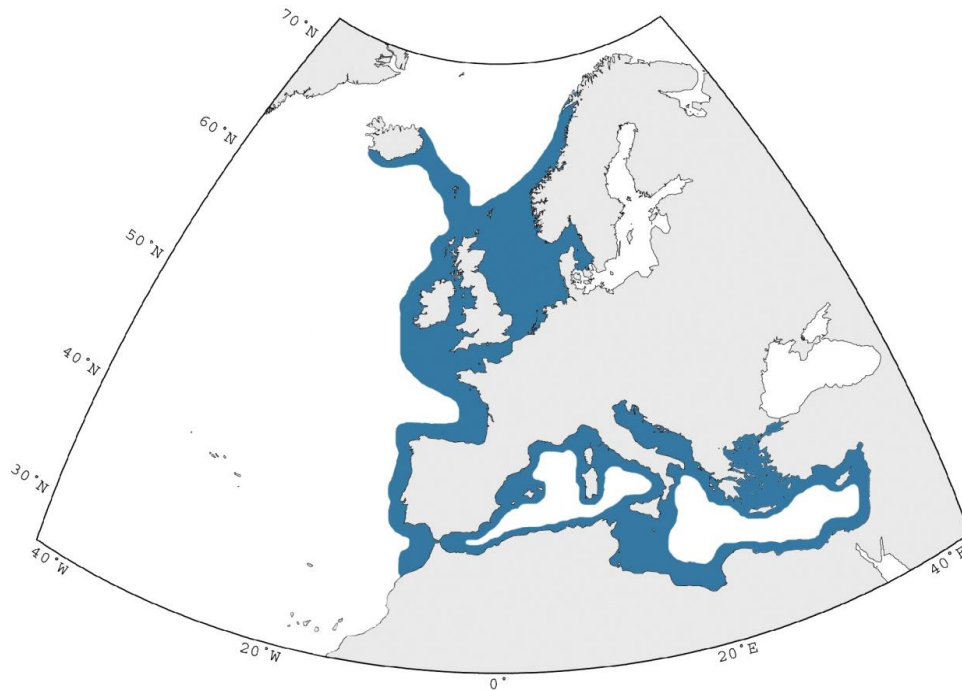
Figure 4.2. *Eledone cirrhosa.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

4.2 Taxonomy

4.2.1 Systematics

Coleoidea – Octopodiformes – Octopoda – Octopodidae – *Eledone.*

4.2.2 Type locality

Not indicated.

4.2.3 Type repository

Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France. Holotype. Specimen not found [fide Lu *et al.* (1995)].

4.3 Diagnosis

4.3.1 Paralarvae

Findings of paralarvae in the Mediterranean and in the Atlantic were reported by Mangold-Wirz (1963a). More recently, paralarvae of *E. cirrhosa* have been collected around the British Isles (Collins *et al.*, 2002) and in the Aegean Sea (Salman *et al.*, 2003).

4.3.2 Juveniles and adults

Figure 4.3. *Eledone cirrhosa*. **Dorsal (left) and ventral (right) views. Photos: Domenico Capua.**

Eledone cirrhosa is a medium-sized species with a maximum body weight <1 kg in the Mediterranean and up to 2 kg in the northern parts of its distribution. Most studies that report body weight do not report mantle length, although Belcari and Sartor (1999a) refer to animals reaching 175 mm ML. The mantle is short and ovoid. The head is narrower than the mantle. Live animals range from orange to yellow, through orange–red to reddish–brown on the dorsal surface, and have greenish iridescence on the ventrum (Figure 4.3). The dorsal surface is covered with numerous warts. A whitish line encircles the lateral periphery of the mantle. There is a cirrhus near each eye. The arms are moderately short, and the suckers are uniserial. The third right arm of males is hectocotylized and is shorter (69–76%) than its opposite left arm. The ligula is very short (3–4% of the length of the hectocotylus), and there is no calamus. The tips of the other arms are modified in males through transverse compression of the suckers (Naef, 1921/1923; Nesis, 1982/1987; Roper *et al.*, 1984; Mangold and Boletzky, 1987; Guerra, 1992). The upper and lower mandibles (beaks) are illustrated in Figure 4.4; see Clarke (1986) for further description.

Figure 4.4. *Eledone cirrhosa*. **Lower beak (left) and upper beak (right). Note that in life, the orientation of the lower beak relative to the upper beak would be rotated vertically by 180° (see diagram for *Octopus vulgaris* in Nixon, 1969). Photo: Evgenia Lefkaditou.**

4.4 Life history

Eledone cirrhosa probably typically lives for 2 years. Breeding is seasonal, with the peak of spawning varying according to region. The paralarva has a short planktonic phase.

4.4.1 Egg and juvenile development

Figure 4.5. *Eledone cirrhosa.* **Mature eggs from oviducts of a spawning female. Photo: Paolo Sartor.**

Fertilization is completely internal; the male spermatangia reach the ovary before the sperm are released. There are few reports of direct observations on eggs in natural environments. Mangold *et al.* (1971) commented that there was only one record of an egg mass found in the sea, near the Shetland Islands, as detailed in Stephen (1944). Fertilized eggs and development to hatching have been observed in aquaria, with almost mature ovarian eggs reaching 7.2 mm in length (Mangold-Wirz, 1963a) (Figure 4.5). Hatching occurs after 3–4 months, usually during April–July, in temperatures of 14–18°C. The newly hatched paralarvae (4.5 mm ML) are truly planktonic (Mangold *et al.*, 1971), but that stage is thought to have a short duration (Collins *et al.*, 2002). Relini and Orsi Relini (1984) collected individuals of 15 mm ML in the Ligurian Sea from the end of January, and Lloret and Lleonart (2002) reported finding the smallest *E. cirrhosa* (30 mm ML) in landings from the northwestern part of the Mediterranean in March.

4.4.2 Growth and lifespan

Eledone cirrhosa is a medium-sized octopus. Most specimens caught are <160 mm mantle length (ML), although, occasionally, individuals of larger size, up to 175 mm ML, are captured, both in the Mediterranean (Belcari and Sartor, 1999a; Cuccu *et al.*, 2003b) and in the Atlantic off Portugal (A. Moreno, pers. comm.). Females attain larger size than males, which generally do not exceed 110–120 mm ML, but occasionally can reach 135 mm ML. On Galician coasts, females can reach 191 mm ML (1150 g) and males 158 mm ML (634 g) (Regueira *et al.*, 2013). In the North Sea off Aberdeen, females may reach 2000 g and males 750 g (Boyle, 1997).

Numerous studies on growth have reported length–weight relationships (Table 4.1). Comprehensive growth studies, defining von Bertalanffy growth parameters, are available for populations in various Italian waters (Agnesi *et al.*, 1998; Cuccu *et al.*, 2003b; Orsi Relini *et al.*, 2006; Giordano *et al.*, 2010). In a recent study on the biology and fishery of *E. cirrhosa* in the Ligurian Sea, Orsi Relini *et al.* (2006) suggested a linear growth model for recruits indicating a maximum age of 300 d, with the function ML (mm) = 0.166 × time (d) + 5.946. During sexual maturation, growth of males does not cease completely, as it does in females (Orsi Relini *et al.*, 2006).

Table 4.1. *Eledone cirrhosa.* **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
Northern Galicia	0.862	2.38	M	Regueira *et al.* (2013)
	0.556	2.60	F	
Western Galicia	0.490	2.61	M	
	0.404	2.76	F	
Western Portugal	0.848	2.30	M	
	0.377	2.73	F	

Western Mediterranean Sea	1.62	2.27	All	P. Sánchez, pers. comm.
Gulf of Lions	0.86	2.61	F	Moriyasu (1983)
	0.91	2.57	M	
Ligurian Sea	0.679	2.47	F	Massi (1993)
	0.768	2.38	M	
	0.726	2.43	All	
	0.159–0.212	2.85–2.9	F	De Rossi (2000)
	0.233–0.247	2.79–2.89	M	
Adriatic Sea	0.394	2.713	All	G. Marano, pers. comm.
	0.336	2.281	All	G. Marano, pers. comm.
Northern Tyrrhenian Sea	0.26–0.47	2.60–2.88	F	Belcari et al. (1990a)
	0.32–0.54	2.52–2.79	M	
Central Tyrrhenian Sea	0.56	2.56	F	Agnesi et al. (1998)
	1.76	1.96	M	
Southern Tyrrhenian Sea	1.46	2.46	F	Giordano et al. (2010)
	0.56	2.15	M	
Thracian Sea	0.841	2.51	F	Lefkaditou et al. (2007)
	0.915	2.43	M	

Forsythe and van Heukelem (1987) reported instantaneous relative growth rates of between 2.8% BW d^{-1} in the smallest individuals and 0.7% BW d^{-1} in the largest. Boyle and Knobloch (1982a) observed that, at 10°C, the species can grow from 10 g to 1 kg in 270 d. In captivity, they recorded growth rates of up to 3.5% BW d^{-1} in individuals of 100 g BW, falling to ca. 1.5% BW d^{-1} at body mass >500 g.

Although *E. cirrhosa* is short-lived and semelparous (Mangold-Wirz, 1963a; Guerra, 1992), it exhibits considerable plasticity in its life cycle throughout its geographic range (Hastie *et al.*, 2009a). In fact, its lifespan has been interpreted in various ways. A combination of a 1- and 2-year cycle was proposed for the North Sea, depending, respectively, on fast-growing, early-maturing animals and slower-growing individuals (Boyle and Knobloch, 1982a; Boyle, 1983b; Boyle *et al.*, 1988). In the Mediterranean, growth studies on young individuals show that sexual maturity can be achieved only in the second year of life (Mangold-Wirz, 1963a). The strictly seasonal reproduction gives one cohort year^{-1} and, after 1 year of growth, juveniles have not reached reproductive size. Given that death follows reproduction, the lifespan of the majority of individuals can be estimated to be ca. 2 years, an interpretation common for *E. cirrhosa* from the Mediterranean (e.g. Moriyasu, 1981; Belcari and Sartor, 1999a; Sánchez *et al.*, 2004; Giordano *et al.*, 2010). However, 2- and 3-year cycles have been proposed for the species based on individual growth and maturation studies and length-frequency analyses of different local stocks. Recent papers, with analyses of length-frequency distributions covering different seasons and/or the complete spatial distribution of *E. cirrhosa* (Lefkaditou and Papacostantinou, 1995; Cuccu *et al.*, 2003b; Orsi Relini *et al.*, 2006), show both the presence of a fraction of adult non-reproducing individuals during the reproductive season and polymodal sizes in spawners. Consequently, a total lifespan of 3 years has been assumed, even though the vast majority of the adult population lives for a maximum of 2 years. The fraction of the population reproducing at age 3 has

been estimated at <10% of adult individuals, but is considered of great biological value in terms of reproductive potential and genetic diversity (Orsi Relini *et al.*, 2006). Recent developments in methods for visualizing potential growth rings in stylets mean that direct age determination of individuals may be possible in future (Barratt and Allcock, 2010).

4.4.3 Maturation and reproduction

In samples collected by Boyle and Knobloch (1982b) in Scottish waters, females were always more numerous than males, the ratio of females to males being 7:1 overall during September 1976 – December 1979. This could be at least partly related to difference in catchability attributable to different body sizes: in 1978, the average female size was 594 g compared with 290 g for males. Regueira *et al.* (2013) also found that the overall sex ratio (ca. 3:1) in their sample from the northwestern Iberian Peninsula was biased towards females. For the Mediterranean, Boyle (1997) noted that the sex ratio was 1:1 in deeper water, but biased towards females in shallow water in spring, which he interpreted as a shoreward migration for breeding.

Males are more precocious than females, attain maturity at a smaller size, and their period of maturation is longer. Fully mature females are rarely found. In the Atlantic off Portugal, 50% of females are mature at 105 mm ML, whereas 50% of males are mature at 80 mm ML (A. Moreno, pers. comm.). Along the Iberian Atlantic coast, animals mature larger at higher latitudes. Size at 50% maturity ($MLm_{50\%}$) for males was 108.9 mm on the north coast of Galicia, 99.25 mm on the west coast of Galicia (i.e. farther south), and 91.4 mm on the west coast of Portugal. The corresponding values for females were 134.5, 121.4, and 100.8 mm, respectively (Regueira *et al.*, 2013). In the Mediterranean, 50% of females are mature at a length of 80–120 mm ML, and 50% of males are mature at 55–90 mm ML (Palumbo and Würtz, 1983–1984; Relini *et al.*, 1994; Tursi *et al.*, 1995; Agnesi *et al.*, 1998; Cuccu *et al.*, 2003b). However, Boyle and Knobloch (1982b) noted that female *E. cirrhosa* become mature at a wide range of body sizes and concluded that maturity was not predictable from body size. Boyle and Thorpe (1984) showed that gonad maturation is linked to an increase in the size of the optic gland. However, as they also noted, the lack of synchrony in individual maturation is an obstacle to the idea that environmental cues might trigger the activity of the optic glands.

Eledone cirrhosa displays seasonal sexual maturity (Belcari *et al.*, 1990b). Across the Mediterranean, regional differences in the timing of spawning have been reported. Generally, sexual maturity occurs earlier in the western basin (spring–summer) than in the eastern basin (summer–autumn) (Belcari and Sartor, 1999a; Lefkaditou *et al.*, 2000; Belcari *et al.*, 2002a; Cuccu *et al.*, 2003b; Orsi Relini *et al.*, 2006; Giordano *et al.*, 2010). In the North Sea, females mature mainly during July–September, and spawning takes place immediately thereafter (Boyle, 1983a; Boyle and Knobloch, 1983), although those authors stress that maturation can occur at any time of year. Indeed, a contemporaneous study on male maturity (Boyle and Knobloch, 1984) found no evidence of seasonality in maturity. In northwestern Iberian waters, the main spawning season is in May and June (Regueira *et al.*, 2013). In Portuguese waters, mature males are found during February–July and mature females during May–August (A. Moreno, pers. comm.).

According to Boyle and Chevis (1992), a significant proportion of eggs fails to develop beyond 2–3 mm long (the size at which vitellogenesis occurs), and those eggs subsequently degenerate. Fecundity estimations vary greatly according to area and maturation stage of ovary and eggs. The mean number of eggs at all stages of maturity was ca. 9000 when estimated for females from the North Sea and 5500 for females from the

Catalan Sea (Boyle *et al.*, 1988). Regueira *et al.* (2013) estimated potential fecundity in the northwestern Iberian Peninsula as 2452.88 ± 36.4 oocytes per ovary, based on a sample of almost 700 females; potential fecundity was positively correlated with both mantle length and body weight. In a study from the northern Tyrrhenian Sea, an average of 2000 eggs in mature ovaries was reported (Rossetti, 1998). According to Regueira *et al.* (2013), mature males have an average of 86.55 ± 1.19 spermatophores, with an average length of 44.97 ± 0.29 mm.

4.4.4 Natural mortality

The main mortality event in the life of *E. cirrhosa* appears to follow reproduction. Records of post-spawning or spent specimens are very rare. Few spent females have been recovered, indicating post-reproductive mortality (Mangold-Wirz, 1963a; Guerra, 1992; Tursi *et al.*, 1995). However, modal progression analysis suggests that a small fraction of adults (5–10%) survive until the following reproductive season in Italian waters (Cuccu *et al.*, 2003b; Orsi Relini *et al.*, 2006).

4.5 Biological distribution

4.5.1 Habitat

Eledone cirrhosa is a typical soft-bottom, eurybathic species. It lives over a wide bathymetric range, generally down to 700 m. It has been reported from 770 m near the Faroe Islands (Massy, 1928), although most catches are made over a smaller depth range, generally from 50 to 300 m (Boyle, 1997; Belcari and Sartor, 1999a; Belcari *et al.*, 2002a; Orsi Relini *et al.*, 2006). Generally, females dominate in water 30–80 m deep, an even sex ratio is reported in the range 100–200 m, and males dominate in deeper water (Mangold-Wirz, 1963a; Palumbo and Würtz, 1983–1984; Tursi *et al.*, 1995; Boyle, 1997; Orsi Relini *et al.*, 2006).

4.5.2 Migrations

Although generally thought of as rather sedentary (Roper *et al.*, 1984), evidence for a pattern of seasonal migration in the Mediterranean is available from analyses of sex ratio and maturity states from a range of depths. The deep-water population (100–200 m) normally has equal numbers of males and females, but trawls in shallower water (60–90 m) in spring catch an increased number of maturing females. This seasonal sex segregation is interpreted as a shoreward (shallower) migration of females for breeding (Boyle, 1997). However, downward vertical migrations linked to spawning have also been proposed. In Italian waters, there are more males than females at depths >300 m (Belcari and Sartor, 1999a). In the Ligurian Sea, Orsi Relini *et al.* (2006), analysing 10 years of biological information, found a similar pattern and suggested that bathyal hard substrata provide suitable seabed for egg laying and attachment.

4.6 Trophic ecology

4.6.1 Prey

Eledone cirrhosa is a carnivorous species and an active predator. Its diet consists mainly of decapod crustaceans (Table 4.2), mostly alpheids and brachyurids, as observed in Scottish waters (Boyle, 1983b, 1986) and different areas of the western Mediterranean Sea (Moriyasu, 1981; Sánchez, 1981; Auteri *et al.*, 1988). Fish, cephalopods, gastropods, and ophiuroids have also been encountered in its gut contents, and cannibalism has been observed (Guerra, 1992).

Table 4.2. Prey composition of *Eledone cirrhosa*, as known from studies in the western Mediterranean Sea and Scottish waters (compiled from Moriyasu, 1981[1]; Sánchez, 1981[2]; Boyle, 1983b[3], 1986[4]; Boyle *et al.*, 1986[5]; Auteri *et al.*, 1988[5]).

Taxon	Species
Osteichthyes	
Gobiidae	*Deltentosteus quadrimaculatus* (four-spotted goby)[2]
Merlucciidae	*Merluccius merluccius* (European hake)[1]
Soleidae	*Solea solea* (common sole)[1]
Crustacea	
Decapoda	indet.[2,6]
Macrura reptantia-Astacidea	*Homarus* spp.(lobster)[3], *Nephrops norvegicus* (Norway lobster)[3,4,5]
Pleocyemata-Anomura	*Galathea intermedia*[1], Paguridae indet.[1,6], *Pisidia longirostris*[1]
Pleocyemata-Brachyura	*Cancer* spp.[3], *Goneplax rhomboides*[1], *Goneplax* spp.[2], Leucosiidae indet.[1,6], *Liocarcinus* spp.[5], Majidae indet.[6], *Monodaeus couchii*[2], Portunidae indet.[6], indet.[2]
Pleocyemata-Caridea	*Alpheus glaber*[1,2], *Alpheus* spp.[6], Crangonidae indet.[5,6]
Pleocyemata-Gebiidea	*Jaxea nocturna*[1]
Cephalopoda	indet.[2,6]
Myopsida	*Alloteuthis media*[1]
Octopoda	*Eledone cirrhosa*[1]
Sepioidea	Sepiolidae spp.[1,4]
Gastropoda	indet.[1]
Bivalvia	indet.[4]
Echinodermata	
Ophiuroidea	*Ophiothrix quinquemaculata*[1], indet.[4,6]
Polychaeta	Aphroditidae indet.[2], indet.[1,6]

4.6.2 Predators

Whales, seals, and fish are considered to be the most important predators of *E. cirrhosa* (e.g. Santos *et al.*, 1999; Brown *et al.*, 2001; Velasco *et al.*, 2001). *Eledone cirrhosa* is an important component of the summer diet of harbour seals (*Phoca vitulina*) in the Moray Firth in some years (Tollit and Thompson, 1996) as well as a prominent component of the diet of some cetaceans (Table 4.3).

Table 4.3. Known predators of *Eledone cirrhosa* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalopoda	Giant squid (*Architeuthis dux*)	Lordan *et al.* (1998a)
	Veined squid (*Loligo forbesii*)	Guerra and Rocha (1994)
Chondrichthyes	Blue shark (*Prionace glauca*)	Clarke and Stevens (1974)
	Cuckoo ray (*Raja naevus*)	Ellis *et al.* (1996)

	Lesser spotted dogfish (*Scyliorhinus canicula*)	Ellis *et al.* (1996)
	Greater spotted dogfish (*Scyliorhinus stellaris*)	Ellis *et al.* (1996)
	Spotted ray (*Raja montagui*)	Ellis *et al.* (1996)
	Spurdog (*Squalus acanthias*)	Ellis *et al.* (1996)
	Thornback ray (*Raja clavata*)	Ellis *et al.* (1996), Farias *et al.* (2006)
	Tope shark (*Galeorhinus galeus*)	Ellis *et al.* (1996)
Osteichthyes	Albacore (*Thunnus alalunga*)	Salman and Karakulak (2009), Romeo *et al.* (2012)
	Atlantic cod (*Gadus morhua*)	Du Buit (1989), Daly *et al.* (2001)
	Haddock (*Melanogrammus aeglefinus*)	Daly *et al.* (2001)
	Ling (*Molva molva*)	Daly *et al.* (2001)
	Monkfish (*Lophius piscatorius*)	Daly *et al.* (2001), Velasco *et al.* (2001), Laurenson and Priede (2005)
	Swordfish (*Xiphias gladius*)	Romeo *et al.* (2009, 2012)
Pinnipedia	Grey seal (*Halichoerus grypus*)	Pierce *et al.* (1991a), Strong (1996)
	Harbour seal (*Phoca vitulina*)	Pierce *et al.* (1991b), Tollit and Thompson (1996), Brown *et al.* (2001), Pierce and Santos (2003), Kavanagh *et al.* (2010)
Pinnipedia	Monk seal (*Monachus monachus*)	Pierce *et al.* (2011)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	González *et al.* (1994a), Santos *et al.* (1997, 2001a, 2005a, 2007)
	Common dolphin (*Delphinus delphis*)	González *et al.* (1994a), Silva (1999a), Santos *et al.* (2004a), De Pierrepont *et al.* (2005)
	Harbour porpoise (*Phocoena phocoena*)	Santos *et al.* (2004b, 2005b)
	Long-finned pilot whale (*Globicephala melas*)	González *et al.* (1994a)
	Northern bottlenose whale (*Hyperoodon ampullatus*)	M. B. Santos, pers. comm.
	Risso's dolphin (*Grampus griseus*)	Clarke and Pascoe (1985), González *et al.* (1994a), Blanco *et al.* (2006), Bearzi *et al.* (2011), MacLeod *et al.* (2014)
	Sperm whale (*Physeter macrocephalus*)	Santos *et al.* (1999)
	White-beaked dolphin (*Lagenorhynchus albirostris*)	Canning *et al.* (2008)

4.7 Other ecological aspects

4.7.1 Parasites

Hochberg (1983, pers. comm.) recorded fungi (*Ulkenia amoeboidea*, *Cladosporium sphaerospermum*), ciliates (*Chromidina coronata*), dicyemids (*Dicyemennea eledones*, *Dicyemennea*

lameerei), helminths including digeneans and cestodes (*Phyllobothrium* sp., *Scolex p. unilocularis*, *Nybelinia lingualis*, *Eutetrarhynchus* sp.), nematodes (unidentified larvae), and copepods (*Pennella "varians"*) in *E. cirrhosa.* Ciliates and dicyemids were found in the kidneys and cestodes in the crop. Polglase (1980) attributed a pathological condition in *E. cirrhosa* to the presence of thraustochytrid and labyrinthulid fungi. These fungi may be found in skin lesions and can present a major problem for maintaining *E. cirrhosa* in aquarium tanks (Hochberg, 1983).

The nematode *Anisakis simplex* has been reported from *E. cirrhosa* in Galician waters (Abollo *et al.*, 1998). Ascaridoids of the genus *Hysterothylacium* have been reported from the digestive tract, and copepods of the genus *Pennella* from the gills of *E. cirrhosa* caught in the northern Tyrrhenian Sea (Gestal *et al.*, 1999). Polglase (1980) refers to the presence of thraustochytrids and labyrinthulids, parasitic protists more usually found in marine algae and seagrasses, in *E. cirrhosa.*

4.7.2   Contaminants

The digestive gland, branchial hearts, and kidney are the main sites of concentration for heavy metals: the digestive gland accumulates most silver, cadmium, cobalt, copper, iron, lead, and zinc; branchial hearts have high concentrations of copper, nickel, and vanadium; and the kidney has high concentrations of manganese, nickel, and lead (Miramand and Bentley, 1992). The species is a strong accumulator of mercury, whose concentration in the muscle tissue was correlated with length in both sexes, but with a reduction in mercury uptake in females near spawning (Rossi *et al.*, 1993). Cadmium concentrations in the mantle decrease over the course of the life cycle, possibly related to a detoxification mechanism involving selenium (Barghigiani *et al.*, 1993).

4.7.3   Environmental effects

Eledone cirrhosa abundance and distribution vary greatly among the various fishing areas of the Mediterranean and North Atlantic and are related to depth and shape of the continental shelf (Lefkaditou *et al.*, 2000; González and Sánchez, 2002). Fluctuations in numbers and biomass indices of *E. cirrhosa* have been linked to climatic factors (e.g. the North Atlantic Oscillation) by a number of authors (e.g. Lloret *et al.*, 2001; Sánchez *et al.*, 2004; Orsi Relini *et al.*, 2006). Sobrino *et al.* (2002) showed that *E. cirrhosa* abundance in the Gulf of Cádiz was highly negatively correlated with rainfall in the previous year, and also negatively correlated with river discharges and sea surface temperature. Sea surface temperature values >20°C in June (before the start of the fishing season) were associated with reduced catches.

4.7.4   Behaviour

"Sand covering", similar to the behaviour seen in *Sepia* spp. and various species of sepiolid, was described for the first time in the lesser octopus by Guerra *et al.* (2006). The animals displayed a burrowing/burying behaviour lasting ca. 50 s. The behaviour continued until the animal was totally covered except for its eyes.

Under aquarium conditions, *E. cirrhosa* is relatively sedentary, spending most of its time in the shelter of dens or rocks or at the edges of the tank space. Time-lapse photography shows that long quiescent periods are interspersed with periods of activity when the animal moves throughout the tank space and often swims. These active spells presumably represent periods of hunting or foraging behaviour (Boyle, 1997).

4.8   Fisheries

The horned octopus is a commercially important species and has great commercial

value in most areas, especially in the western Mediterranean (Mangold and Boletzky, 1987; Sartor *et al.*, 1998a; Relini *et al.*, 1998), although it is routinely discarded by Scottish boats (Pierce *et al.*, 2010) and is among the cephalopod species most commonly discarded by Spanish boats fishing in northern waters (Santos *et al.*, 2012).

In FAO FISHSTAT data for the Northeast Atlantic, *E. cirrhosa* has been recorded separately only since 2000, and the maximum catch recorded (365 t in 2004) is likely to represent only a small fraction of the true landings, most of which are probably subsumed within the "octopuses, etc. nei" (octopus not elsewhere included) category (13 825 t landed in 2004). Landings of octopus reported to ICES are not disaggregated by species. In the Mediterranean, according to FAO data, landings of *Eledone* spp. (combined for *E. cirrhosa* and *E. moschata*) and *Octopus vulgaris* have been recorded separately since 1962. However, the quantity of landings assigned to the category "octopuses, etc. nei" was up to fivefold that assigned to *Eledone* spp. until 2004, after which reported landings in the two categories have been similar, with landings of *Eledone* spp. peaking at almost 9600 t in 2005.

Catches of *E. cirrhosa* are almost entirely taken by bottom trawl. In the Northeast Atlantic, *E. cirrhosa* is present in the landings of Portugal (Fonseca *et al.*, 2008), Spain, and (rarely, given that it is usually discarded) Scotland, but there appears to be little commercial interest in the species (Pierce *et al.*, 2010). In Scottish waters, it can constitute a substantial proportion of the bycatch for trawlers operating close to shore, especially those fishing on soft bottoms for Norway lobster (*Nephrops norvegicus*), although such bycatches are discarded. *Eledone cirrhosa* is the only *Eledone* species present in northern Spanish waters, where it is landed by the bottom-trawl fishery as bycatch, although its commercial value in that region is very low.

Although there are some minor differences by port, almost all *E. cirrhosa* individuals captured in the Mediterranean are landed; the discard percentage is usually <10% (Sartor *et al.*, 1998a).

Because of the biological characteristics of the species, there is seasonal variability in the landings, as reported in studies of the landings of Spanish, Italian, and Greek fleets (Sánchez and Martin, 1993; Belcari and Sartor, 1993; Belcari *et al.*, 1998; Tsangridis *et al.*, 2000; Lloret and Lleonart, 2002). Recruitment of *E. cirrhosa* to the trawl fishery is from January on, mostly in spring and summer, at an estimated age of 5–7 months. Recruits are mainly distributed on the continental shelf, especially where the shelf is wide (Belcari and Sartor, 1999a; Belcari *et al.*, 2002a; Lloret and Lleonart, 2002; Orsi Relini *et al.*, 2006). The highest densities in the Mediterranean have been found in the Gulf of Lions, the Ligurian and northern Tyrrhenian seas, and in the northern Aegean Sea (Belcari *et al.*, 2002a).

In the Mediterranean, *E. cirrhosa* is marketed in two different size categories (Belcari *et al.*, 1998; Belcari and Sartor, 1999a; Orsi Relini *et al.*, 2006; Giordano *et al.*, 2010). Small specimens, generally <50 mm ML, have great economic value and, in some regions, are abundant in the market, being the target of the multispecies trawl fishery in spring and summer that coincides with the recruitment period of the species (Relini and Orsi Relini, 1984; Belcari *et al.*, 1998; Sánchez *et al.*, 2004; Orsi Relini *et al.*, 2006). The fishery for these juvenile *E. cirrhosa* (0 age group, known locally as "popets" in Catalonia and "moscardini" in Tuscany) is an important activity, particularly in three western Mediterranean areas: the Catalan coast, the Ligurian Sea, and the northern Tyrrhenian Sea, where the species is more abundant (Belcari *et al.*, 2002a). Even though there is no minimum legal size applied to *E. cirrhosa* catches, this form of trawling is restricted by the present EC regulations on mesh size.

Tentative stock assessments have been performed for the species in different areas of the western Mediterranean. Local stocks may be underexploited, at equilibrium, or slightly overexploited, depending on the area (Agnesi *et al.*, 1998; Orsi Relini *et al.*, 2006; Giordano *et al.*, 2010). Natural mortality rates estimated on various local stocks with different methods vary from 0.58 to 1.45 (Agnesi *et al.*, 1998; Orsi Relini *et al.*, 2006; Giordano *et al.*, 2010).

4.9   Future research, needs, and outlook

Important topics for future research on the species include investigations on spawning sites, fecundity, description of early life stages, increment reading of beaks and stylets, and genetic studies for stock identification. Further studies on appropriate stock assessment methods are also desirable. Previous taxonomic work (F. G. Hochberg, pers. comm.) suggests that *E. cirrhosa* actually comprises two species: one within the Mediterranean and one in the Northeast Atlantic. This issue could be resolved by raising the subspecies *E. cirrhosa zetlandica* Russell, 1922, which was described from around Scotland, to specific status (F. G. Hochberg, pers. comm.). Further study of parasites in European cephalopods could also help to clarify taxonomy.

Cephalopod biology and fisheries in European waters: species accounts

Eledone moschata

Musky octopus
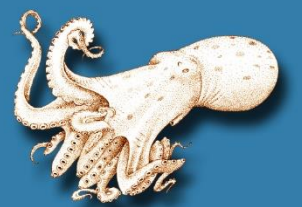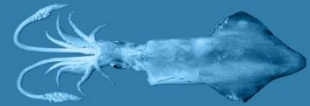
5   *Eledone moschata* (Lamarck, 1798)

Ignacio Sobrino, Ana Moreno, Patrizia Jereb, Eduardo Balguerias, Sonia Seixas, Graham J. Pierce, Evgenia Lefkaditou, and A. Louise Allcock

Common names

Elédone musquée (France); Μοσκιός [moschios] (Greece); moscardino rosso, moscardino muschiato (Italy); polvo cabeçudo, polvomosqueado, polvo-de-cheiro (Portugal); pulpo cabezón, pulpo almizclado (Spain); musky octopus (UK) (Figure 5.1).

Synonyms

Octopus moschatus Lamarck, 1798, *Eledona moschata*: Risso (1854).
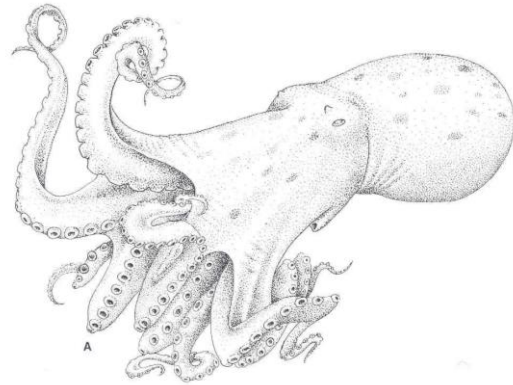
Figure 5.1. *Eledone moschata*. **Dorsolateral view. From Guerra (1992).**

5.1   Geographic distribution

The musky octopus, *Eledone moschata* (Lamarck, 1798), lives in the Northeast Atlantic and in the Mediterranean Sea (Norman *et al.*, 2014; Figure 5.2). In the Northeast Atlantic, it is occasionally found off Portugal as far north as ca. 40°N (Lourenço *et al.*, 2008) and is abundant in Portuguese and Spanish waters of the Gulf of Cádiz (Guerra, 1982, 1992; Reis *et al.*, 1984). It is widespread 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; Jereb and Ragonese, 1994; Giordano and Carbonara, 1999**;** Relini *et al.*, 2002; Cuccu *et al.*, 2003a), the Adriatic Sea (Casali *et al.*, 1998; Krstulović Šifner *et al.*, 2005; Piccinetti *et al.*, 2012)**,** and, though occasionally less abundant, 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). Primarily a Mediterranean species, the southern limits of the Northeast Atlantic distribution of *E. moschata* remain uncertain.

Figure 5.2. *Eledone moschata.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

5.2 Taxonomy

5.2.1 Systematics

Coleoidea – Octopodiformes – Octopoda – Octopodidae – *Eledone.*

5.2.2 Type locality

Not stated in original description.

5.2.3 Type repository

Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France. The type does not appear to be extant (see Lu *et al.*, 1995).

5.3 Diagnosis

5.3.1 Eggs and hatchlings

Eggs are joined by their short stalks in clusters and attached to a substratum. The clusters contain 3–10 eggs, and they have no central stem. The eggs are elongate, measure 12–16 mm long and 4–5 mm wide (Mangold, 1983b). In the Gulf of Cádiz, mature eggs are generally smaller, on average 10.9 mm long (Silva *et al.*, 2004). Hatchlings measure 25–30 mm TL and 10–12 mm ML, ca. 10% of the adult size. At hatching, each arm already bears 30 suckers and is longer than the body (Mangold, 1983b).

5.3.2 Juveniles and adults

The skin is smooth to very finely granulose; there is no ridge around the lateral periphery of the mantle. The arms are subequal in length with uniserial suckers. The web is moderately deep, ca. 30% of arm length. In mature males, the third right arm is hectocotylized (Figure 5.3) and is 85–90% of the length of the third left arm. The ligula is

short (ca. 3% of arm length), and there is no calamus. The distal tips of all other arms of males are modified with two parallel series of flattened laminae or platelets. Internally, the gills have 11–12 filaments per demibranch. Live animals exude a very prominent, musk-like odour, reportedly from glands in the skin. Live animals are greyish-brown with blackish-brown blotches on the dorsum (Mangold and Boletzky, 1987; Relini *et al.*, 1999; Norman *et al.*, 2014). The beaks are illustrated in Figure 5.4.

Figure 5.3. *Eledone moschata.* **Right arm III hectocotylized. Photo: Carlos Farias.**
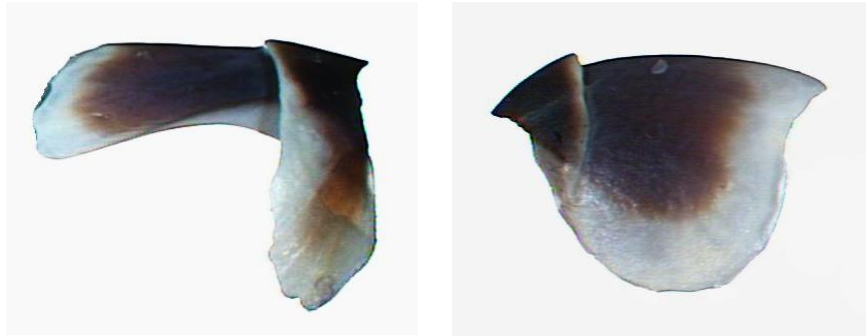
Figure 5.4. *Eledone moschata.* **Lower beak (left) and upper beak (right). Photos: Evgenia Lefkaditou.**

5.4   Remarks

Norman *et al.* (2014) list no synonyms. Norman and Hochberg (2005) listed *Eledonenta microsicya* Rochebrune, 1884 as a synonym of *Eledone moschata*. Robson (1932) suggested that "*Eledonenta microsicya*" should be placed in *Eledone* and that it was more similar to *E. moschata* than to other species of *Eledone*. Nonetheless, he did not synonymize the two species. Silas (1968) treats the species as *Eledonenta microsicya*, but noting Robson's (1932) opinion. The original description (Rochebrune, 1884) is strongly suggestive of *Eledone* (e.g. "*cupules... sur un seul rang*"), but his description of a dirty yellow animal with small black dots and large bluish spots "*jaune sale, finement piquete de tres petits points noirs et orne de larges taches bleuatres*" does not match *E. moschata*. Therefore, the identity of *E. microsicya* remains unsolved, but we do not believe it to be synonymous with *E. moschata*.

5.5   Life history

In contrast to *E. cirrhosa*, hatchlings of *E. moschata* immediately adopt a benthic mode of life. The breeding cycle is seasonal, with one or two peaks in activity, the main one often during the first quarter of the year. There may be alternating long and short life cycles.

5.5.1   Egg and juvenile development

Few records have been published on naturally occurring eggs. Egg masses have been collected in shallow waters in the northern Adriatic Sea. In captivity, embryonic development lasts 4–6 months, depending on temperature (Mangold, 1983b).

After hatching, animals adopt the adult benthic mode of life and immediately begin to feed on live crabs of their own size. A preference for a crustacean diet is clear from the very early stages on (Boletzky, 1975a). Mean growth rate of hatchlings is ca. 6.2% of body weight d^{-1} up to 10 g, 3% d^{-1} between 10 and 100g, and 0.8% d^{-1} thereafter (Mangold, 1983b).

5.5.2   Growth and lifespan

Eledone moschata reaches a maximum size of 150 mm ML and 640 g body weight in the Atlantic (Silva *et al.*, 2004) and 188 mm ML and 1414 g body weight in the Mediterranean Sea (Akyol and Şen, 2007). Boletzky (1975a) reared it, recording a growth rate of 6.6% BW d^{-1} for the first month after hatching and 3.6% BW d^{-1} for the subsequent 3 months. Hatchlings weighed 0.3 g, reaching 2.2 g BW after 1 month and 55 g at 4 months. Forsythe and van Heukelem (1987) give values for instantaneous relative growth rates ranging from 6.94% BW d^{-1} in the smallest animals to 0.99% BW d^{-1} in animals of 50 g BW. Length–weight relationships show some regional variation (Table 5.1).

The proposed life cycle model of this species in the northwestern Mediterranean is based on the alternation of short-lived and long-lived life cycles (Mangold, 1983b; Silva *et al.*, 2004). This model seems to apply in the Gulf of Cádiz. Recruitment is in September and October and presumably originates from the long-living fraction of mature females that spawned at the beginning of the spawning season. Another recruitment pulse is detected in January and February, which is related to the short-lived fraction of the population that spawned at the end of the spawning season. Favourable environmental conditions may lead to faster growth and more rapid sexual development of the short-lived fraction of the population. The smaller spawning peak observed in October in the Gulf of Cádiz could be a consequence of this phenomenon (Mangold, 1983b; Ezzeddine-Najai, 1997; Silva *et al.*, 2004). Lifespan is probably up to 2 years (e.g. Mangold, 1983b).

Table 5.1. *Eledone moschata*. **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
Portugal	1.0048	2.4	F	Lourenço *et al.* (2008)
	0.6325	2.5	M	
	0.8652	2.46	All	
Gulf of Cádiz	0.3573	2.660	F	Silva *et al.* (2004)
	0.2613	2.794	M	
	0.3233	2.702	All	
Thracian Sea (northeastern Aegean Sea)	0.3323	2.814	F	E. Lefkaditou, pers. comm.
	0.2371	2.960	M	
Adriatic Sea	0.6002	2.6644	F	Krstulović Šifner and Vrgoč (2009a)
	0.5246	2.7665	M	

	0.3233	2.702	All	
Montenegro	0.7712	2.4558	M	Ikica *et al.* (2011)
(Adriatic Sea)	1.1185	2.2291	F	
	0.9407	2.33	All	
Izmir Bay (eastern Aegean Sea)	0.3083	2.797	F	Akyol *et al.* (2007)
	0.2548	2.885	M	
	0.2836	2.836	All	
Iskenderun Bay (northeastern Levant Sea)	0.0906	3.324	F	Duysak *et al.* (2008)
	0.2704	2.7902	M	
	0.5645	2.4281	All	

5.5.3 Maturation and reproduction

Sex ratio apparently varies seasonally and with depth, as well as between areas, perhaps indicating geographic variation in the timing of life cycle events, reproductive migrations, and differential survival of the sexes, but also suggesting an incomplete understanding of the life cycle in many areas. Off the Mediterranean French coast and the Gulf of Gabes (Tunisia), males significantly outnumber females, especially during the reproductive season (Mangold-Wirz, 1963a; Ezzeddine-Najai, 1997). In the Adriatic Sea, the overall sex ratio is normally close to 1:1, but males dominate during summer, soon after the spawning season (Krstulović Šifner and Vrgoč, 2009a). Conversely, both commercial and survey trawl data from the Gulf of Cádiz show a clear female dominance in catches throughout the year (Silva *et al.*, 2004). In Portuguese waters, males and females are equally abundant up to 100 m depth, but between 100 and 200 m, females outnumber males (Lourenço *et al.*, 2008). Females outnumber males (1.31:1) at all depths year-round in the eastern Mediterranean (Akyol *et al.*, 2007). Ikica *et al.* (2011) found a sex ratio close to 1:1 in Montenegrin waters.

Weight and size at maturity vary geographically. In the Gulf of Cádiz, the length and weight at maturity (MLm$_{50\%}$ and BWm$_{50\%}$) were estimated to be 12 cm (274 g) in females and 7.8 cm (97 g) in males (Silva *et al.*, 2004). The MLm$_{50\%}$ was estimated to be 11 cm (females) and 9 cm (males) in Tunisian waters (Ezzeddine-Najai, 1997), and 9.5 cm (females) and 8.5 cm (males) in the Adriatic Sea (Krstulović Šifner and Vrgoč, 2009a). Also in the Adriatic Sea, Ikica *et al.* (2011) gives estimates of 7.2 cm and 9.5 cm for MLm$_{50\%}$ in females and males, respectively.

In the Gulf of Cádiz, the spawning season extends throughout most of the year, although there is little or no spawning during summer (Silva *et al.*, 2004). Most spawning is during February–May, but with a secondary peak in September in southern Portuguese waters (Lourenço *et al.* 2008) or in October in the Gulf of Cádiz (Silva *et al.*, 2004). Southwestern and central Mediterranean populations have similar spawning seasons, although slightly time-shifted relative to the Atlantic populations: spawning females are found from November to June–July, peaking between February and May in the Gulf of Gabes (Ezzeddine-Najai, 1997) and between January and April in the Adriatic Sea (Krstulović Šifner and Vrgoč, 2009a). In the eastern Mediterranean, the reproductive season is also extended, with two spawning peaks in the Aegean Sea: one in January and the other in June (Akyol *et al.*, 2007). In contrast, in the northwestern Mediterranean, the reproductive season seems to be restricted to the period January–May (Mangold, 1983b).

As in other cephalopods, various environmental variables, particularly temperature, influence the reproductive biology of this species. Higher temperatures extend the reproductive period and affect the precocity of sexual development (Ezzeddine-Najai, 1997).

Fecundity studies undertaken throughout the distributional range of *E. moschata* indicate substantial variability in the number of oocytes per female and a relationship with the size of the animal. Mean total fecundities were estimated to be 100–500 oocytes in the western Mediterranean (Mangold, 1983b), 210–459 oocytes (mean = 310 ± 60) in the Adriatic Sea (Krstulović Šifner and Vrgoč, 2009a), 273–2896 oocytes (836 ± 193) in the Aegean Sea (Akyol *et al.*, 2007), and 187–944 oocytes (443 ± 154) in the Gulf of Cádiz (Silva *et al.*, 2004). As in other octopus species, there are usually residual oocytes in the ovaries, especially in more mature females. The observed mean number of residual oocytes in females from the Gulf of Cádiz was 295.73 ± 132.079 (6.6% ± 2.91 of the total number of oocytes). There, the average relative fecundity was estimated to be 1.43 ± 0.36 oocytes g^{-1} of female total weight. In the Gulf of Cádiz, the mean size of the largest oocytes was 10.90 ± 1.22 mm, with a maximum size of 14.8 mm. The mean size of all the sampled non-residual oocytes was 10.24 ± 1.07 mm (Silva *et al.*, 2004). In the Adriatic Sea, mean oocyte length and width were 9.39 ± 1.99 mm and 2.57 ± 0.72 mm, respectively (Krstulović Šifner and Vrgoč, 2009a). In the Aegean Sea, Akyol *et al.* (2007) reported an average oocyte length of 6.26 ± 0.10 mm, with a range of 2.6–10.7 mm.

In the Gulf of Cádiz, the mean length of fully developed spermatophores was 13.88 ± 1.60 mm (Silva *et al.*, 2004). The maximum and minimum spermatophore lengths were 17.5 and 10.9 mm, respectively, which were found in two males of 240 (100 mm ML), and 98 g (60 mm ML), respectively. In the Aegean Sea, the average number of spermatophores ranged between 6 and 172 (mean = 52 ± 6), with a mean length of 13.66 ± 0.08 mm (range = 7.3–18.3 mm) (Akyol *et al.*, 2007). In the Adriatic Sea, the number of spermatophores was 45–287 (mean = 120 ± 60), with mean length of 17.71 ± 3.27 mm (range = 9–23 mm) (Krstulović Šifner and Vrgoč, 2009a). In the western Mediterranean, the mean number of spermatophores is ca. 106, with lengths (range = 15–20 mm (Mangold-Wirz, 1963a). The number and size of both oocytes and spermatophores depend mainly on the size of the animal.

Internal insemination has been confirmed by the presence of sperm sacs in the ovaries of some females. However, the number of females found in that state has been small, indicating that the number of spermatophores that reach the ovary is low and that copulation takes place shortly before spawning (Mangold, 1983b).

5.6 Biological distribution

5.6.1 Habitat

Eledone moschata is a coastal species, living on soft sandy and muddy bottoms, occasionally on gravel. It does not seem to live in rocky areas, except possibly when spawning (Gamulin-Brida and Ilijanić, 1972; Mangold, 1983b). It is mainly distributed at depths of 15–200 m in both Mediterranean waters and Iberian waters of the Gulf of Cádiz, where it is most abundant in shallow waters down to 100 m (Gamulin-Brida and Ilijanić, 1972; Salman *et al.*, 1997; Lefkaditou *et al.*, 1998a; Belcari *et al.*, 2002a; Silva *et al.*, 2004). In the northern Adriatic, densities were nearly 700 km^{-2} at 10–50 m, but decreased to <300 km^{-2} at 50–100 m and to ca. 30 km^{-2} at 100–200 m (Krstulović Šifner *et al.*, 2011). In some areas, it is found at greater depths: to 450 m in the Gulf of Cádiz (Silva *et al.*, 2004), 612 m in southern Portuguese waters (Lourenço *et al.*, 2008), and 320

m in the Aegean Sea (Salman *et al.*, 2000). In the western Mediterranean, it is found in water temperatures of 12–23°C and salinities of 36.5–38.5 (Mangold, 1983b).

5.6.2 Migrations

In the Mediterranean Sea, *E. moschata* seems to undergo horizontal migration related to reproduction, moving inshore to spawn (Mangold, 1983b; Mandić and Stjepcević, 1981). According to Mangold (1983b), when not migrating inshore and offshore, *E. moschata* is a truly sedentary species, but it does not seem to be solitary. In the laboratory, the animals seem to be active at night, but quiescent during the day (Mangold, 1983b).

5.7 Trophic ecology

5.7.1 Prey

Eledone moschata preys mainly on crustaceans (Table 5.2). In the Adriatic Sea, there were crustaceans in 65.0% of stomachs that contained food, and fish and cephalopods were present in 37.8 and 21.8% of stomachs, respectively (Krstulović Šifner and Vrgoč, 2009b). That study also showed that the diet of *E. moschata* varies according to body size. Small animals (<80 mm ML) fed mainly on crustaceans (which represented 69% by weight of prey), and larger ones on both fish (37%) and crustaceans (31%). In Izmir Bay (Aegean Sea), prey was dominated by crustaceans, but also included fish, gastropods, bivalves, and urchins. Differences in stomach fullness were observed between morning and midday periods (Şen and Akyol, 2011).

Table 5.2. Prey composition of *Eledone moschata*, as known from studies in the central and eastern Mediterranean (compiled from Krstulović Šifner and Vroč, 2009b[1]; Şen and Akyol, 2011[2]).

Taxon	Species
Osteichthyes	indet.[1,2]
Cepolidae	*Cepola macrophthalma* (as *C. rubescens*) (red bandfish)[1]
Clupeidae	*Sardina pilchardus* (European pilchard)[1]
Engraulidae	*Engraulis encrasicolus* (European anchovy)[1]
Gobiidae	*Gobius* spp.[1], indet.[1]
Merlucciidae	*Merluccius merluccius* (European hake)[1]
Crustacea	indet.[2]
Decapoda	
Dendrobranchiata-Penaeiodea	*Penaeus* spp.[1]
Pleocyemata-Anomura	*Anapagurus laevis*[1], *Munida rugosa*[1], Paguridae indet.[1]
Pleocyemata-Brachyura	*Liocarcinus depurator*[1], *Macropodia longirostris*[1], *Portunus* spp.[1]
Pleocyemata-Caridea	*Alpheus glaber*[1], *Macrobrachium sintangense* (as *Palaemon elegans*)[1], *P. adspersus*[1], Palaemonidae indet.[1]
Amphipoda	indet.[1]
Mysida	indet.[1]
Ostracoda	indet.[1]
Copepoda	*Ctenocalanus vanus*[1], indet.[1]
Cephalopoda	indet.[1]
Myopsida	*Alloteuthis media*[1], *Loligo vulgaris*[1], Loliginidae indet.[1]

Octopoda	*Eledone moschata*[1], indet.[1]
Sepioidea	*Sepietta oweniana*[1], Sepiolidae indet.[1]
Gastropoda	indet.[2]
Bivalvia	indet.[2]
Echinodermata	
Echinoidea	indet.[2]

5.7.2 Predators

Octopod beaks in stomach contents have not always been identified to species level. Clarke (1986) indicated that it was difficult to distinguish lower beaks from the three subfamilies of the Octopodidae, although some species can certainly be separated (e.g. *Octopus vulgaris* from *E. cirrhosa* (M. B. Santos, pers. comm.). Nonetheless, this species is known from cephalopod, fish, seal, turtle, and cetacean stomachs (Table 5.3).

Table 5.3. Known predators of *Eledone moschata* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalop-oda	Common octopus (*Octopus vulgaris*)	Kallianiotis *et al.* (2001)
Chondrich-thyes	Bull ray (*Pteromylaeus bovinus*)	Capapé (1977)
	Smooth-hound (*Mustelus mustelus*)	Saïdi *et al.* (2009)
Osteich-thyes	Common dolphinfish (*Coryphaena hippurus*)	Massutí *et al.* (1998)
	Swordfish (*Xiphias gladius*)	Salman (2004)
Pinnipedia	Monk seal (*Monachus monachus*)	Salman *et al.* (2001), Pierce *et al.* (2011)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	Blanco *et al.* (2001), Poldan (2004)
Turtles	Loggerhead sea turtle (*Caretta caretta*)	Katić (2006)

5.8 Other ecological aspects

5.8.1 Parasites

Hochberg (1983) documents the presence of fungi, ciliates, dicyemids, helminths (including digeneans and cestodes), nematodes, and copepods in *Eledone* spp. Parasites specifically identified in *E. moschata* include the sporozoan *Aggregata "octopiana"*; dicyemids *Dicyema moschatum* and *Dicyemennea eledones*; the helminths *Scolex p. unilocularis*, S. *p. quadrilocularis*, *Acanthobothrium* sp., *Orygmatoscolex pusillum*, *Phyllobothrium pusillus*, and *Nybelinia lingualis*; the nematode *Ascaris moschata*; and the copepod *Pennella varians* (Hochberg, 1983, pers. comm.).

5.9 Fisheries

In the Atlantic (where it is found in the Gulf of Cádiz and along the adjacent Iberian and African coasts), *E. moschata* is taken as bycatch by the Portuguese and Spanish bottom-trawl fleets, although in many cases it is discarded because of its low commercial value. In Portugal, for example, 80–100% of *E. moschata* catches taken by the trawl fleets are usually discarded (Moreno *et al.*, 2010). In recent years (1996–2010), annual landings of musky octopus in the main Spanish ports of the Gulf of Cádiz have averaged ca. 100 t (50–230 t), with a peak between January and April.

Eledone moschata is commercially important throughout the Mediterranean, where it is fished mainly with bottom trawls. Catches obtained with other gear are of lesser importance (Relini *et al.*, 1999). Its economic importance in many Mediterranean countries reflects its great abundance, particularly along the southern and eastern coasts and in the Adriatic Sea (Belcari *et al.*, 2002a). It is especially abundant in the northern Adriatic, where, in early winter, bottom-trawl yields of up to 53 kg h^{-1} may be achieved (Manfrin-Piccinetti and Rizzoli, 1984). However, *E. moschata* is discarded as bycatch by Turkish bottom trawlers because of its poor commercial value (Akyol *et al.*, 2007).

Eledone moschata catches are generally pooled with those of *E. cirrhosa* and *O. vulgaris* in commercial landings and in Mediterranean fishery statistics (Sánchez and Martín, 1993; Belcari *et al.*, 1998). For a summary of recent FAO statistics on octopod catches in the Mediterranean, see the chapters on *E. cirrhosa* and *O. vulgaris*; even when distinguished from landings of *O. vulgaris*, landings for both *Eledone* species are pooled in the FAO database. Although *E. moschata* is a separate category in landings for the Northeast Atlantic, the only record of this species in the FAO database is 1 t landed by Portugal in 2006.

5.10 Future research, needs, and outlook

Important topics for future research on the species include stock separation and investigations of spawning sites. Little is known about its ecology. As is the case for other exploited European cephalopods, separate recording of landings statistics would both enhance our understanding of stock status and help facilitate routine stock assessment. Previous taxonomic work (F. G. Hochberg, pers. comm.) suggests that *E. moschata* is sufficiently different from other *Eledone* species to warrant being placed in a separate genus. This possibility should be pursued with molecular techniques.

Cephalopod biology and fisheries in European waters: species accounts
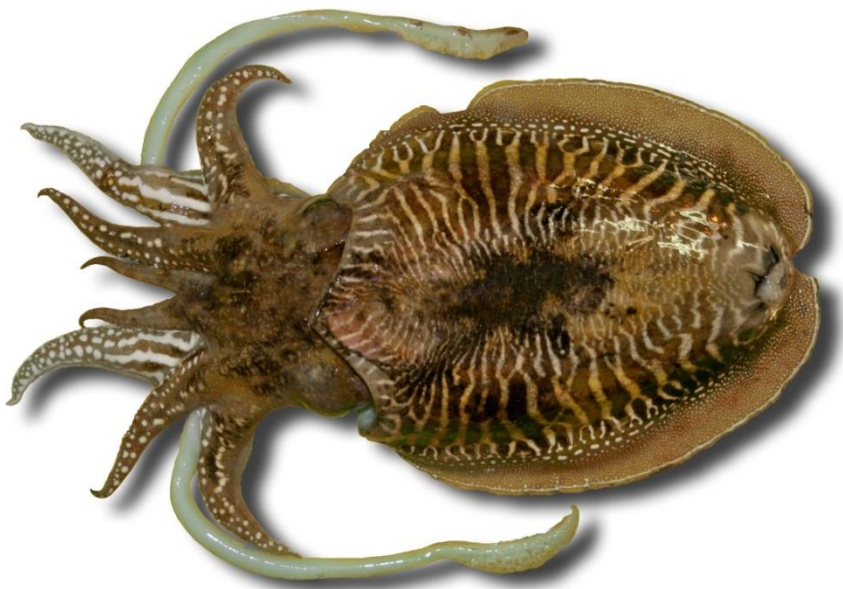
Sepia officinalis

Common cuttlefish
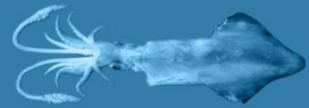
6   *Sepia officinalis* Linnaeus, 1758

Ángel Guerra, Jean-Paul Robin, Antonio Sykes, Drosos Koutsoubas, Patrizia Jereb, Evgenia Lefkaditou, Noussithé Koueta, and A. Louise Allcock

Common names

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

Synonyms

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

6.1   Geographic distribution

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

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

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

It is found in the central and southern North Sea (Figure 6.2), as recent reviews confirm (Gittenberger and Schrieken, 2004; De Heij and Baayen, 2005). It was recorded from all along the Irish coast (Massy, 1928), and records from the east and west Scottish coasts are listed in Stephen (1944), who refers to occasional wanderings of the species in northern areas in years of strong incursions of Atlantic water. It is in the English Channel (e.g. Boletzky, 1983; Lordan *et al.* 2001a) and extends south to Northwest Africa (e.g. Bas, 1975; Bravo de Laguna, 1989) as far south as the border between Mauritania and Senegal (Ikeda, 1972; Hatanaka, 1979a; Guerra *et al.*, 2001). *Sepia officinalis* is abundant and widespread throughout the Mediterranean Sea (Mangold and Boletzky, 1987; Bello 2004; Salman, 2009), including western and central parts (Mangold-Wirz, 1963a; Sánchez, 1986a; Belcari and Sartor, 1993; Jereb and Ragonese, 1994; Giordano and Carbonara, 1999; Relini *et al.*, 2002; Cuccu *et al.*, 2003a), the Adriatic Sea (Casali *et al.*, 1998; Krstulović Šifner *et al.*, 2005; Piccinetti *et al.*, 2012), the Ionian Sea (Tursi and D'Onghia 1992; Lefkaditou *et al.*, 2003a; Krstulović Šifner *et al.*, 2005), the Aegean Sea, and the

Levant Basin (D'Onghia *et al.*, 1992; Salman *et al.*, 1997, 1998; Lefkaditou *et al.*, 2003b; Duysak *et al.*, 2008). Old records of the species in the Sea of Marmara exist (Demir, 1952, in Ünsal *et al.*, 1999), although *S. officinalis* has not been recorded by more recent research carried out in those waters (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

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

6.2 Taxonomy

6.2.1 Systematics

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

6.2.2 Type locality

Simply given as "Oceano".

6.2.3 Type repository

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

6.3 Diagnosis

6.3.1 Paralarvae and hatchlings

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

6.3.2 Juveniles and adults

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

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

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

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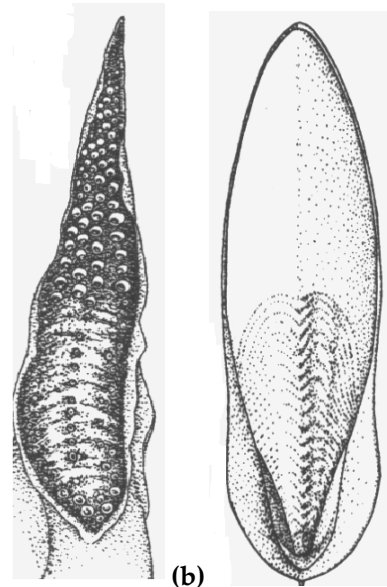
Figure 6.3. *Sepia officinalis*. (a) hectocotylized arm, (b) cuttlebone. From Guerra (1992).

6.4   Remarks

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

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

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

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

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

6.5 Life history

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

6.5.1 Egg and juvenile development

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

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

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

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

6.5.2 Growth and lifespan

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

6.5.3 Maturation and reproduction

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

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

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

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

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

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

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

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

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

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

6.5.4 Natural mortality

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

6.6 Biological distribution

6.6.1 Habitat

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

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

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

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

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

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

6.6.2 Migrations

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

6.7 Trophic ecology

6.7.1 Prey

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

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

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

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

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

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

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

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

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

6.7.2 Predators

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

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

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

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

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

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

6.8   Other ecological aspects

6.8.1   Parasites

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

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

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

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

6.8.2 Contaminants

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

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

6.8.3 Behaviour

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

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

6.9 Fisheries

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

6.10 Aquaculture

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

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

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

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

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

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

6.11   Future research, needs, and outlook

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

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

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

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

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

Cephalopod biology and fisheries in European waters: species accounts

Sepia elegans

Elegant cuttlefish
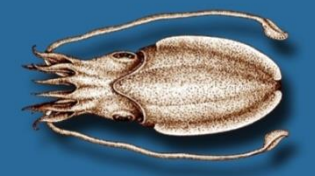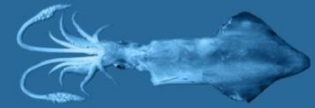
7   *Sepia elegans* Blainville, 1827

Patrizia Jereb, Ignacio Sobrino, A. Louise Allcock, Sonia Seixas, and Evgenia Lefkaditou

Common names

Seiche élégante (France), seppia elegante (Italy), choco-elegante (Portugal), choquito (Spain), elegant cuttlefish (UK) (Figure 7.1).

Synonyms

Sepia rupellaria Férussac and d'Orbigny, 1835, *Sepia biserialis* Blainville, 1827, *Sepia italica* Risso, 1854.

7.1   Geographic distribution

The elegant cuttlefish, *Sepia elegans* Blainville, 1827, is found in the Northeast Atlantic, from northwestern Scotland and Ireland (Massy, 1928; Stephen, 1944; Nesis, 1982/87) (Figure 7.2) down to Namibia (Sánchez, 1988; Roeleveld, 1998). It is present in the Celtic Sea (Lordan *et al.*, 2001a) and the English Channel (Marine Biological Association of the United Kingdom, 1931; Roper and Sweeney, 1981) and off the French and Iberian Atlantic coasts (Guerra, 1992). It is caught on the Sahara Bank (e.g. Bravo de La-

Figure 7.1. *Sepia elegans*. **Dorsal view. From Guerra (1992)**

guna, 1989; Balguerias *et al.*, 2000) and extends south to northern Namibian waters (Sánchez, 1988), where it has been recorded at 21°S (Roeleveld, 1998). Records from the Agulhas Bank exist (Filippova *et al.*, 1995), but, as noted by Roeleveld (1998), the geographic position reported by the authors is apparently incorrect. *Sepia elegans* is also widely distributed 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 (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). It has been recorded in the Sea of Marmara (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

Figure 7.2. *Sepia elegans*. **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

7.2 Taxonomy

7.2.1 Systematics

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

7.2.2 Type locality

Sicily, central Mediterranean Sea.

7.2.3 Type repository

Originally Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France**.** Syntypes; specimens not extant [fide Lu *et al.* (1995:315)].

7.3 Diagnosis

7.3.1 Paralarvae

This species does not have paralarvae *sensu* Young and Harman (1988). Hatching size is assumed to be 4 mm ML (Mangold-Wirz, 1963a).

7.3.2 Juveniles and adults

Sepia elegans is a small species, with adult males growing up to 75 mm ML (Ciavaglia and Manfredi, 2009) and females up to 89 mm ML (Adam, 1952). Maximum total weight is ca. 60 g. The mantle is oblong, more than twice as long as wide, with the dorsal anterior margin triangular, acute, and projecting strongly forward. Male and female arms are subequal in length. The left ventral arm is hectocotylized in males (Figure 7.3). It bears 1–2 rows of normal-sized suckers proximally, followed by 9–11

rows of reduced minute suckers medially, followed by normal-sized suckers to the arm tip; suckers are set in two dorsal and two ventral series displaced laterally.

Figure 7.3. S*epia elegans.* **Left arm III hectocotylized. Photo: Carlos Farias.**

Tentacular clubs are short and oval, and the sucker-bearing surface is flattened. There are 6–8 suckers in transverse rows. Suckers differ markedly in size. There are 3–4 greatly enlarged suckers in the middle of the club, and although several dorsal suckers are enlarged, they are never as large as the medial suckers. The cuttlebone is oblong and convex in lateral view. It tapers to a sharp point anteriorly and posteriorly, is recurved ventrally, and its dorsal surface is evenly convex. The last loculus is convex. The anterior striae are an inverted U-shape. The spine is very small, "rather like a small calcareous ridge than a true spine" (Nesis, 1982/1987). Lateral wings are present, but are very small. The animal is reddish brown in life, but paler than *S. orbignyana.* There are a few scattered chromatophores on the head, and the dorsal mantle surface is peppered with scattered purple-black chromatophores, but the fins and the ventral mantle surface are pale (Adam and Rees, 1966; Nesis, 1982/1987; Neige and Boletzky, 1997; Reid *et al.*, 2005). The beaks are illustrated in Figure 7.4.

Figure 7.4. S*epia elegans.* **Lower beak (left) and upper beak (right). Photo: Carlos Farias.**

7.4   Remarks

Floating cuttlebones may enter the eastern side of the North Sea and be found stranded on the Belgian and Dutch coasts (Adam, 1933); however, live *S. elegans* have never been found in the North Sea (e.g. Adam, 1933; Roper and Sweeney, 1981; Nesis, 1982/87). Recent observations confirm this (J. Goud, pers. comm.). The species has been reported from the Agulhas Bank (37°12'S 22°30'E) by Filippova *et al.* (1995), but as noted by Roeleveld (1998), the position given in Filippova's paper is incorrect because it lies south of the Agulhas Bank, in ca. 4000 m depth.

On the basis of morphological features (Khromov, 1987a; Khromov *et al.*, 1998), and, subsequently, genetic divergence (Pérez-Losada *et al.*, 1996; Sanjuan *et al.*, 1996), it has been suggested that *S. elegans* and *S. orbignyana* belong to a different subgenus from the genus *Sepia sensu stricto*, i.e. to the subgenus *Rhombosepion*. Morphometric analysis of both cuttlebone and statoliths, based on landmarks, may prove a useful taxonomic tool for the separation of *S. elegans* from closely related species (Neige and Boletzky, 1997; Lombarte *et al.*, 2006).

7.5   Life history

Although this species spawns year-round, seasonal migrations and seasonal peaks in spawning have been described in some areas. It lives for 12–18 months. There is no paralarval stage.

7.5.1   Egg and juvenile development

The eggs (maximum recorded diameter 5 mm; Guerra, 1984) are attached to available hard substrata, such as alcyonarian (typically *Alcyonium palmatum*) shells, on muddy bottoms, or, less frequently, on coral formations (Mangold-Wirz, 1963a). They closely resemble *S. officinalis* eggs, except for the dimensions (smaller in *S. elegans*) and colour (whitish and translucent in *S. elegans*). The attachment of the eggs to *Alcyonium palmatum* is quite an elaborate and complex procedure, at the end of which the egg resembles a stone on a ring slipped onto the alcyonarian finger-like appendage, as described in detail by Bouligand (1961). After hatching, juveniles immediately adopt a benthic lifestyle.

7.5.2   Growth and lifespan

Growth in mantle length is 2.8 mm month[-1] for males and 3.0 mm for females in the Sicilian Channel (central Mediterranean) (Ragonese and Jereb, 1991), i.e. slightly faster than estimated in the western Mediterranean by Mangold-Wirz (1963a) and in the Ría de Vigo by Guerra (1984) (2–2.5 mm month[-1]). Females attain larger size and are comparatively heavier than males at any given mantle length, and animals become more slender as size increases (Bello, 1988; Guerra and Castro, 1989; Ragonese and Jereb, 1991; Lefkaditou *et al.*, 2007; Ramos *et al.*, 2009; A. Moreno, unpublished data). The largest individuals recorded by Guerra and Castro (1989) were 61 mm ML (males) and 67 mm ML (females). Length–weight relationships are available for several areas (Table 7.1).

Female tentacular clubs are significantly longer than male ones (Bello, 1991a). Bello and Piscitelli (2000) showed that *S. elegans* females ingest more food at any given size and suggested that a cause–effect relationship between sex-related club size and growth rate existed. Subsequent observations on *S. elegans* and *S. orbignyana* demonstrated the existence of a positive correlation between body condition and tentacular club length in males and females of both species (Bello, 2006), and strongly corroborated the hypothesis that there is indeed a cause–effect relationship.

From observations in the field, lifespan is estimated to range between 12 and 18–19 months (Mangold-Wirz, 1963a; Guerra, 1984; Guerra and Castro, 1989), somewhat less than the values obtained by preliminary estimates with length-frequency distribution analysis (i.e. ca. 2 years, Ragonese and Jereb, 1991). However, length-frequency distributions are generally polymodal (see also Guerra and Castro, 1989), making it difficult to identify microcohorts clearly, and growth estimation by means of length-frequency methods is difficult (e.g. Caddy, 1991).

Table 7.1. *Sepia elegans.* **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
Ría de Vigo	0.374	2.272	F	Guerra and Castro (1989)
	0.327	2.311	M	
Portuguese waters	0.289	2.420	F	A. Moreno, pers. comm.
	0.356	2.190	M	
Gulf of Cádiz	0.239	2.476	F	Ramos *et al.* (2009)
	0.227	2.577	M	
Sicilian Channel	0.257	2.506	F	Ragonese and Jereb (1991)
	0.286	2.342	M	
Adriatic Sea	0.196	2.606	F	Bello (1988)
	0.208	2.500	M	
Aegean Sea	0.229	2.515	F	Lefkaditou *et al.* (2007)
	0.248	2.441	M	

7.5.3   Maturation and reproduction

In the Ría de Vigo, males outnumber females in spring and autumn, and the overall sex ratio recorded by Guerra and Castro (1989) was 1.18:1 in favour of males.

The smallest mature males measure 20 mm ML (Volpi *et al.*, 1990), and the smallest mature females 30 mm ML (Guerra and Castro, 1989). In Portuguese waters, ca. 60–70% of males and females are mature at ca. 35 and 45 mm ML, respectively (A. Moreno, pers. comm.), and in the Catalan Sea (western Mediterranean), the equivalent figures are 45 mm ML for males and 65 mm ML for females (Mangold-Wirz, 1963a).

In the Mediterranean and the eastern Atlantic, mature males and females are found throughout the year, which suggests a continuous spawning period (Mangold-Wirz, 1963a; Guerra, 1992; Belcari, 1999a; Reid *et al.*, 2005). As a consequence of this, recruitment is virtually continuous, although alternating peaks and troughs have been observed in the Mediterranean (Bello, 1983–1984; Casali *et al.*, 1988; Volpi *et al.*, 1990; Jereb and Ragonese, 1991a; Würtz *et al.*, 1991; D'Onghia *et al.*, 1992; Ciavaglia and Manfredi, 2009), and two major peaks, one in spring–summer the other in late autumn–mid-winter, have been observed in the Gulf of Cádiz (eastern Atlantic; Ramos *et al.*, 2009).

In the Catalan Sea, spermatophore length ranges between 3.5 and 5.5 mm, depending on male size, and the maximum number of spermatophores found in a mature male has been 95. Mature, smooth eggs measure between 3.7 and 4.2 mm, depending on female size, and mature females carry up to 250 eggs (>1 mm) in their ovaries; however, as is normal for "large" eggs in cephalopods, only a proportion of the eggs reach maturity (Mangold-Wirz, 1963a). It is difficult to establish a correlation between the total

number of smooth eggs in the ovary and the actual total number of smooth eggs produced by a female, because spawning is protracted; when captured, mature females may already have spawned a fraction of their smooth eggs. The maximum number of smooth eggs recorded in a mature female (of 62 mm ML) was 57 (Mangold-Wirz, 1963a). Total fecundity in females from the Gulf of Cádiz varied between 61 and 942 oocytes (in specimens of 34 and 64.2 mm ML, respectively).

7.6 Biological distribution

7.6.1 Habitat

Sepia elegans is a sublittoral species, living on sandy and sand-muddy bottoms. It has been found at various depths, from very shallow (e.g. 2 m in the Ría de Vigo, northwestern Spain, Guerra, 1985a; 6 m in the northern Tyrrhenia Sea, Belcari and Sartor, 1993; 12 m in the southern Tyrrhenian Sea, Bello *et al.*, 1994) down to 494 m (Jereb and Ragonese, 1991a). Records deeper than 450 m are sporadic (e.g. Jereb and Ragonese, 1991a; D'Onghia *et al.*, 1996; Lefkaditou *et al.*, 2003a; A. Moreno, pers. comm.), and most distributional ranges reported for the Mediterranean and the eastern Atlantic indicate maximum depths of <400 m (Adam, 1952; Mangold-Wirz, 1963a; Lumare, 1970; Guerra, 1985a, Sánchez, 1986a; Mannini and Volpi, 1989; Katağan and Kokatas, 1990; Würtz *et al.*, 1991; D'Onghia *et al.*, 1992; Belcari and Sartor, 1993; Bello *et al.*, 1994; González and Sánchez, 2002; Relini *et al.*, 2002; Massutí and Reñones, 2005).

It is the peculiar structure of the cuttlebone, which is small, narrow, with closely packed septa, and modified sutures (Ward, 1991), that allows *S. elegans* to reach these remarkable depths and to be among the deepest living *Sepia* species known. However, depths below the maximum recorded may be lethal for the species (Ward and Boletzky, 1984).

The depth ranges at which maximum concentrations of animals are found vary between areas and seasons (Mangold-Wirz, 1963a; Sánchez, 1986a; Restuccia and Ragonese, 1986; Jereb and Ragonese, 1991a; Würtz *et al.*, 1991; Sánchez *et al.*, 1998a; Belcari, 1999a; Colloca *et al.*, 2003). In addition, migrations can be related to reproduction (see below).

In the Sea of Marmara, the species has been found in brackish waters (salinity between 18 and 25; Ünsal *et al.*, 1999), but in northwestern Spain, it inhabits the outer and central basin of the Ría de Vigo (Guerra 1985a; Guerra and Castro, 1989), indicating a high degree of tolerance to salinity variation, although the species does not enter the internal basin of the Ría de Vigo, where there are marked fluctuations in salinity and temperature (Guerra and Castro, 1989). This indicates that *S. elegans* is a more stenohaline and stenothermic species than *S. officinalis*.

7.6.2 Migrations

A spring–summer migration of the whole population to coastal spawning grounds (40–70 m depth) has been described for the species in the western Mediterranean (Mangold-Wirz, 1963a; Guerra, 1992), and similar displacements have been observed in the Tyrrhenian Sea (off the Tuscany coast; Belcari, 1999a). However, this migratory pattern does not seem to be displayed in other areas, such as the Ría de Vigo (northwestern Spain; Guerra and Castro, 1989) or the Sicilian Channel (Jereb and Ragonese, 1991a), and both presence and absence of migration have been reported for the Adriatic Sea (Casali *et al.*, 1988; Ciavaglia and Manfredi, 2009).

7.7 Trophic ecology

7.7.1 Prey

The species feeds mainly on small crustaceans, fish, and polychaetes (Reid *et al.*, 2005) (Table 7.2). Detailed studies on feeding (e.g. Guerra, 1985b; Castro and Guerra, 1990) suggested that neither diet composition nor prey size varied with body size or maturity. No seasonal changes in diet were observed. However, Bello (1991a, 2006) reported differences in feeding habits between males and females; females eat significantly larger quantities of crabs (Brachyura) and shrimps (Palaemonidae) than males, and the average weight of the stomach contents is greater in females. In the Thermaikos Gulf, Greece, the species feeds mainly on crustaceans and secondarily on fish, and the trophic level is estimated to be 3.53 (Fryganiotis *et al.*, 2007).

Table 7.2. Prey composition of *Sepia elegans*, as known from studies in the Northeast Atlantic and the eastern Mediterranean Sea (compiled from Guerra, 1985b[1]; Castro and Guerra, 1990[2]; Vafidis *et al.*, 2009[3]).

Taxon	Species
Osteichthyes	
Callionymidae	*Callionymus lyra* (dragonet)[2],
Gobiidae	*Aphia minuta* (transparent goby)[1], indet.[2], *Pomatoschistus pictus* (painted goby)[2]
Crustacea	
Decapoda	
Pleocyemata-Anomura	*Galathea intermedia*[2], *Porcellana platycheles*[2], *Pisidia longicornis*[1,2]
Pleocyemata-Brachyura	*Liocarcinus* spp.[1,2], *Polybius henslowii*[1], Portunidae indet.[2], indet.[3]
Pleocyemata-Caridea	*Crangon crangon*[1,2], Hippolytidae indet.[2], Majidae indet.[2], *Palaemon adspersus*[1,2], *P. serratus*[1], *Palaemon* spp.[2], Palaemonidae indet.[2], *Processa edulis*[2], indet.[3]
Euphausiacea	indet.[3]
Mysida	indet.[2]
Ostracoda	indet.[3]
Amphipoda	Caprellidea indet.[2], *Gammarus* spp.[1], Gammaridea indet.[2], indet.[3]
Isopoda	indet.[3]
Cephalopoda	indet.[3]
Polychaeta	indet.[2,3]
Nemertea	indet.[3]
Cnidaria	Hydrozoa indet.[3]
Algae	*Posidonia oceanica*[1], *Zostera marina*[1], indet.[1]

7.7.2 Predators

Sepia elegans has been found in the stomachs of several fish species, including medium-sized hake (*Merluccius merluccius*) (18–44 cm) in the Gulf of Cádiz (Á. Torres, pers. comm.). It is also preyed upon by *S. officinalis* and *Loligo vulgaris* off the south coast of Portugal (Coelho *et al.*, 1997; Alves *et al.*, 2006) and is eaten by the bottlenose dolphin (*Tursiops truncatus)* in Spanish waters of the western Mediterranean Sea (Blanco *et al.*, 2001) (Table 7.3).

Table 7.3. Known predators of *Sepia elegans* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalop-oda	Common cuttlefish (*Sepia officinalis*)	Alves *et al.* (2006)
	European squid (*Loligo vulgaris*)	Coelho *et al.* (1997)
Chondrich-thyes	Lesser spotted dogfish (*Scyliorhinus canicula*)	Kabasakal (2002), Šantić *et al.* (2012)
	Bull ray (*Pteromylaeus bovinus*)	Capapé (1977)
	Marbled electric ray (*Torpedo marmorata*)	Capapé *et al.* (2007)
	Thornback ray (*Raja clavata*)	Kabasakal (2002), Šantić *et al.* (2012)
Osteich-thyes	Common dolphinfish (*Coryphaena hippurus*)	Massutí *et al.* (1998)
	European hake (*Merluccius merluccius*)	Á. Torres, pers. comm.
	Greater amberjack (*Seriola dumerili*)	Matallanas *et al.* (1995)
	John Dory (*Zeus faber*)	Silva (1999b)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	Blanco *et al.* (2001)

7.8 Other ecological aspects

7.8.1 Parasites

Females harbour a dense bacterial community in their accessory nidamental glands, in the lumina of these organs' tubules (Grigioni *et al.*, 2002), as observed in other sepiolids and myopsid squids. Information on the effects of this bacterial community on *S. elegans* physiology is lacking, although studies on bacterial presence in *S. officinalis* revealed correlations between sexual maturity, the colour of the gland, and the total number of bacteria (Van den Branden *et al.*, 1980). Parasites of *S. elegans* include *Aggregata* sp. and *Pennella* sp. (González *et al.*, 2003).

7.8.2 Contaminants

High levels of cadmium have been reported in the elegant cuttlefish (Bustamante *et al.*, 2002b), indicating that efficient detoxification mechanisms have been developed. The high bioavailability of cadmium in the digestive gland cells also indicates a high potential for the trophic transfer of the metal to predators of *S. elegans*. Studies on biochemical composition of tissues distinguished this species from others with a benthic lifestyle and indicated lower lipid and higher protein contents in the gonad (Rosa *et al.*, 2005a).

7.9 Fisheries

Sepia elegans is one of the most abundant cephalopod species in the Catalan Sea, Tyrrhenian Sea, Sicilian Channel, Adriatic Sea, Ionian Sea, and Aegean Sea (Mangold-Wirz, 1963a; Lumare, 1970; Mandić and Stjepcević, 1983; Panetta *et al.*, 1986; Sánchez, 1986a; Jereb and Ragonese, 1991a; Würtz *et al.*, 1991; Belcari and Sartor, 1993; D'Onghia *et al.*, 1996). It is taken mainly as bycatch in the Mediterranean and West African bottom otter-trawl fisheries. Other fishing gears that catch the species include beam trawls (Ünsal *et al.*, 1999) and fish traps (Belluscio and Ardizzone, 1990), and *S. elegans* represents a major fraction of discards in southern Portuguese coastal fisheries (Sendao *et al.*, 2002).

Separate landing statistics are not reported for this species, which, however, represents a significant percentage of the catches in some areas of its distributional range, where it is marketed fresh and frozen (Reid *et al.*, 2005). In the Mediterranean, it is marketed along with *S. orbignyana* and small *S. officinalis* and constitutes a valuable resource locally (Jereb and Ragonese, 1991a). In the Sicilian Channel, research estimated an exploitation rate of 0.73 for the species, which suggests intense fishing pressure on the resource (Ragonese and Jereb, 1991). In the Gulf of Cádiz in the eastern Atlantic, landings ranged between 30 and 110 t year^{-1} in the period 1993–2008 (I. Sobrino, pers. comm.).

7.10 Future research, needs, and outlook

Of the three genera currently recognized within the family Sepiidae (see Khromov *et al.*, 1998, for a recent review), *Sepia* is the most speciose; more than 100 species have been described. However, many species are poorly known, and the systematics of the genus is not yet settled. Among the many questions still unresolved is the validity of the subdivision of the genus into six subgenera or "species complexes" (see Khromov *et al.*, 1998; see also the **Remarks** section). Further research is needed to clarify the systematics of the group and the position of this species within the group.

The species is an important resource in many areas of its distributional range and is subjected to intense fishing pressure in some areas. Detailed studies on its ecology might help preclude potential overexploitation, and separate recording of different cuttlefish species in landings should be encouraged.

Cephalopod biology and fisheries in European waters: species accounts

Sepia orbignyana

Pink cuttlefish
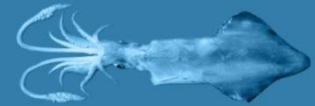
8 *Sepia orbignyana* Férussac *in* d'Orbigny, 1826

Patrizia Jereb, Ignacio Sobrino, A. Louise Allcock, Sonia Seixas, and Evgenia Lefkaditou

Common names

Seiche rosée (France), Κοκκινοσουπιά [kokkinosoupia] (Greece), seppia pizzuta (Italy), choco-de-cauda (Portugal), choquito picudo (Spain), pink cuttlefish (UK) (Figure 8.1).

Synonyms

Acanthosepion orbignyanum Rochebrune, 1884, *Sepia rubens* Philippi, 1844, *Acanthosepion enoplon* Rochebrune, 1884.

8.1 Geographic distribution

The pink cuttlefish, *Sepia orbignyana* Férussac in d'Orbigny, 1826, is found in the Northeast Atlantic and throughout the Mediterranean (Nesis, 1982/1987; Roper *et al.*, 1984; Guerra, 1992; Reid and Jereb, 2005) (Figure 8.2), although the northern limits of its distribution are unclear. It is reported in the Irish Sea and the English Channel (Nesis, 1982/87, Reid and Jereb, 2005), but it is not included among the species listed by Massy (1928) for the Irish coast. In addition, alt-

Figure 8.1. *Sepia orbignyana.* **Dorsal view. From Guerra (1992).**

hough Adam (1952) indicates that its distribution extends to the Arcachon Basin (western France), there is no mention of its presence along the east coast of England in old records (e.g. Grimpe, 1925), and the reference to the English Channel by Norman (1890, p. 484 in Stephen, 1944) apparently is a misquotation. Strandings of cuttlebones of this species are, however, known from North Sea coasts (e.g. the Netherlands; Cadee, 2002). The species can be found south along the French and Spanish coasts (Morales, 1958; Adam and Rees, 1966), in the Bay of Biscay, south to ca. 17°S (southern Angola; Adam, 1962). *Sepia orbignyana* is widely distributed 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, although it is only rarely caught in the northern part (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). The species has been recorded also in the Sea of Marmara (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

Figure. 8.2. *Sepia orbignyana.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

8.2 Taxonomy

8.2.1 Systematics

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

8.2.2 Type locality

La Rochelle, France.

8.2.3 Type repository

Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France. [fide Lu *et al.* (1995: 322)].

8.3 Diagnosis

8.3.1 Paralarvae

This species does not have paralarvae *sensu* Young and Harman (1988). Animals newly hatched in the laboratory measure ca. 6 mm ML (Boletzky, 1988).

8.3.2 Juveniles and adults

Sepia orbignyana is a small species, with adult males up to 96 mm and females up to 120 mm ML (Mangold-Wirz, 1963a). The mantle is oval, with the dorsal anterior margin projecting strongly (Figure 8.3). Male and female arms are subequal in length and rather short. Arm suckers are tetraserial. Medial suckers on the non-hectocotylized arms of males are wider than marginal suckers. The left ventral arm is hectocotylized in males: 1–2 rows of normal size suckers are present proximally, followed by greatly reduced suckers medially, then normal size suckers at the distal end to the arm tip.

Suckers of the hectocotylus are arranged in two dorsal and two ventral series displaced laterally. Clubs are short, oval, and bear 5–6 suckers in transverse rows; suckers vary markedly in size. Three large suckers are present medially with one slightly smaller sucker on each side of them. The cuttlebone is oblong, acute anteriorly, bluntly rounded posteriorly, and strongly recurved ventrally; its dorsal surface is rose-coloured or orange. Shell width is ca. 33% and 33–35% of shell length in males and females, respectively. The spine is long, pointed, and straight, directed slightly upwards, with a ventral keel. The anterior striae are shallow, M-shaped, or wavy. The animal's colour is reddish brown. (Adam and Rees, 1966; Nesis, 1982/1987; Neige and Boletzky, 1997; Reid *et al.*, 2005).

Figure 8.3. *Sepia orbignyana*. Dorsal view. Photo: IAMC-CNR (Mazara del Vallo, Sicily, Mediterranean Sea) research team.

8.4 Remarks

Floating cuttlebones may enter the southeastern North Sea and be found stranded on the Belgian coast (Eneman and Kerckhof, 1983; Nesis, 1982/1987). However, although Muus (1963) mentioned the presence of the species in the southern North Sea, no other records of live *S. orbignyana* from these waters exist (e.g. Adam, 1933; Adam and Rees, 1966; Nesis, 1982/1987), as confirmed also by very recent studies (J. Goud, pers. comm.).

On the basis of the animal's morphology (Khromov, 1987a; Khromov *et al.*, 1998), and, subsequently, results on genetic divergence (Pérez-Losada *et al.*, 1996; Sanjuan *et al.*, 1996), it has been suggested that *S. orbignyana* and *S. elegans* belong to the subgenus *Rhombosepion* within the genus *Sepia*.

Morphometric analysis of cuttlebone and statolith shape based on landmarks may prove a useful taxonomic tool to distinguish *S. orbignyana* from closely related species (Neige and Boletzky, 1997; Lombarte *et al.*, 2006).

8.5 Life history

Lifespan is 12–18 months. Spawning shows a clear summer peak in the Atlantic, but is year-round in the Mediterranean. As with other members of the genus, the hatchlings immediately adopt a benthic life style.

8.5.1 Egg and juvenile development

Eggs are laid in batches of 30–40 and are individually introduced into the tissues of sponges, usually Demospongiae, on muddy bottoms (Boletzky, 1998). The sponge provides protection for the eggs. The eggs are whitish-grey in colour, and their gelatinous envelop is less thick than that of other studied species (features which probably represent an adaptation to the "host organism" used to protect the eggs), although the chorion is very hard (Mangold-Wirz, 1963a). Egg diameter increases with the size of the females; maximum reported egg size is 9 mm (Mangold-Wirz, 1963a).

Information on *S. orbignyana* juveniles comes from rearing experiments (Boletzky, 1988). Newly hatched animals measure ca. 6 mm ML. They immediately settle on the substratum and move only over short distances by active swimming as well as by slowly "walking" along the bottom on their ventral arms. They have not been seen to bury themselves in soft substratum, as typical for *S. officinalis*, but they vigorously raise their dorsal arms and quickly wave them laterally when disturbed. They are able to adhere very efficiently to hard substrata by the ventral skin.

8.5.2 Growth and lifespan

In the Catalan Sea, growth rates of females have been reported to be slightly faster than those of males (Mangold-Wirz, 1963a). Studies of populations in the Sicilian Channel (central Mediterranean) by Ragonese and Jereb (1991) confirmed this finding and reported growth rates of 2.9 mm month^{-1} in males and 3 mm in females. Additional support for these results has subsequently come from studies in the Adriatic Sea (Bello, 1988, 2001), Aegean Sea (Lefkaditou *et al.*, 2007), and Portuguese waters. Bello (2001) used the number of chambers in the cuttlebone as an index of relative age. Females also attain significantly larger size than males and are notably heavier (Bello, 1988; Ragonese and Jereb, 1991). Length–weight relationships are summarized in Table 8.1. All studies reported "b" exponent values <3 in both sexes, showing that animals become more slender as size increases.

Table 8.1. *Sepia orbignyana*. **Length–weight relationships in different geographic areas for females (F) and males (M). 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
Portuguese waters	0.337	2.486	F	A. Moreno, pers. comm.
	0.284	2.340	M	
Catalan Sea	0.6567	2.15	F	Sánchez (1986)
	0.4052	2.35	M	
Sicilian Channel	0.266	2.58	F	Ragonese and Jereb (1991)
	0.272	2.480	M	
Adriatic Sea	0.224	2.560	F	Bello (1988)
	0.208	2.558	M	
Aegean Sea	0.343	2.305	F	Lefkaditou *et al.* (2007)
	0.525	2.441	M	

Female tentacular clubs are significantly longer than male ones (Bello, 1991a). Subsequently, Bello and Piscitelli (2000) showed that *S. orbignyana* females ingest more food at any given size and suggested a cause–effect relationship between sex-related club size and growth rate. Additional observations on *S. orbignyana* and *S. elegans* demonstrated the existence of a positive correlation between body condition and tentacle club

length in males and females of both species (Bello, 2006) and strongly corroborated the hypothesis that there is indeed a cause–effect relationship.

Lifespan is estimated to be 12–18 months (Mangold-Wirz, 1963a), although preliminary estimates from analysis of length-frequency distributions suggested a longer life, i.e. ca. 3 years (Ragonese and Jereb, 1991). As in many cephalopods, length-frequency distributions generally are polymodal, although it is difficult to identify microcohorts, and growth estimation by means of length-frequency methods is generally unreliable for cephalopods (e.g. Caddy, 1991).

8.5.3 Maturation and reproduction

A predominance of females in June–July is reported for the species in Portuguese waters (A. Moreno, pers. comm.).

In the Mediterranean, the smallest recorded mature male measured 35 mm ML (Belcari and Sartor, 1993), and the smallest mature female, a recent record from the Adriatic Sea, measured 40 mm ML (Ciavaglia and Manfredi, 2009). In Portuguese waters, slightly smaller sizes at first maturity have been observed, i.e. 29 mm ML for males and 32 mm ML for females (A. Moreno, pers. comm.). In the Catalan Sea, ca. 60% of males and females are mature at 50 mm and 80 mm ML, respectively (Mangold-Wirz, 1963a). Equivalent figures for Portuguese waters are 47 mm ML for males and 65 mm ML for females (A. Moreno, pers. comm.).

In Mediterranean waters, spawning is probably year-round (Mangold-Wirz, 1963a; Jereb and Ragonese, 1991a; Belcari and Sartor, 1993; Ciavaglia and Manfredi, 2009), with peaks of activity from spring to autumn. Recruitment also appears to be continuous throughout the year, with peaks in spring and autumn (Jereb and Ragonese, 1991a; Würtz et al., 1991).

Spermatophore length ranges between 5 and 11 mm, and mature males can carry up to 100–150 spermatophores. Mature, smooth, eggs measure 7–9 mm, depending on female size, and mature females may carry up to 400 eggs (>1 mm) in their ovaries; however, as is usually the case for "large" eggs in cephalopods, probably only a fraction reaches maturity (Mangold-Wirz,1963a). It is possible that mature females have already spawned a proportion of their smooth eggs when examined, so the number of smooth eggs in the ovary is not representative of the total number of smooth eggs produced by the female. The maximum number of smooth eggs recorded in a mature female of 91 mm ML was 113 (Mangold-Wirz, 1963a).

8.6 Biological distribution

8.6.1 Habitat

The depth range reported for *S. orbignyana* extends from very shallow (15–20 m; Belcari and Sartor, 1993; Bello *et al.*, 1994; Casali *et al.*, 1998; Ciavaglia and Manfredi, 2009; I. Sobrino, pers. comm.) down to maximum recorded depths of 565 m in the Mediterranean Sea (Cuccu *et al.*, 2003a) and 580 m in the eastern Atlantic (Gulf of Cádiz, I. Sobrino, pers. comm.). However, the species is most abundant between 50 and 250 m throughout the Mediterranean Sea, as confirmed by numerous studies (Mangold-Wirz, 1963a; Adam, 1952; Lumare, 1970; Restuccia and Ragonese, 1986; Sánchez, 1986a; Auteri *et al.*, 1988; Mannini and Volpi; 1989; Soro and Piccinetti-Manfrin, 1989; Katağan and Kocatas, 1990; Repetto *et al.*, 1990; Jereb and Ragonese, 1991a; Würtz *et al.*, 1991; D'Onghia *et al.*, 1992; Belcari and Sartor, 1993; Katağan *et al.*, 1993; Salman *et al.*, 1997; Quetglas *et al.*, 2000; González and Sánchez, 2002; Ciavaglia and Manfredi, 2009). There

is also a major concentration of the species between 340 and 360 m in the Gulf of Cádiz (eastern Atlantic, I. Sobrino, pers. comm.). As in *S. elegans*, it is the peculiar structure of the cuttlebone, which is small, narrow, and with closely packed septa and modified sutures (Ward, 1991), that allows this species to reach these remarkable depths and to be among the deepest living *Sepia* species known. Records from below 450 m are scarce (e.g. Lefkaditou *et al.*, 2003a), and captures below 550 m extremely so, because that is the depth below which the shell starts to implode (Ward and Boletzky, 1984).

The pink cuttlefish is a demersal species that lives mainly on sandy and sandy-muddy bottoms. It is frequently sympatric (and confused) with *S. elegans (*e.g. Jereb and Ragonese, 1991a), and has been found associated with the horned octopus (*Eledone cirrhosa)* in some areas (Lumare, 1970). In the Sea of Marmara, the species can live in brackish waters (Ünsal *et al.*, 1999), and in Portuguese waters, it prefers water temperatures >12°C (A. Moreno, pers. comm.).

Studies on the demersal assemblages in the Moroccan southern Atlantic zone (Serghini *et al.*, 2008) indicate that the distribution of *S. orbignyana* is characterized by marked spatial and temporal variability.

8.6.2   Migrations

In the Mediterranean, males and females are usually found together throughout the year, and no onshore spawning migrations have been reported (Mangold-Wirz, 1963a; Jereb and Ragonese, 1991a; D'Onghia *et al.*, 1992; Ciavaglia and Manfredi, 2009).

8.7   Trophic ecology

8.7.1   Prey

Sepia orbignyana feeds mainly on crustaceans, but small fish, cephalopods, and other invertebrates can also form part of the diet (Table 8.2). In captivity, it will feed on small prawns and mysids (Boletzky, 1988).

Table 8.2. Prey composition of *Sepia orbignyana*, as known from studies in the eastern Atlantic and the Mediterranean Sea (compiled from Allué *et al.* 1977[1]; Auteri *et al.*, 1988[2]; Vafidis *et al.*, 2009[3]).

Taxon	Order / Species
Osteich-thyes	indet.[1,2,3]
Crustacea	Decapoda-Natantia indet.[3], Decapoda-Brachyura indet.[3], Mysida indet.[3], Amphipoda indet.[3], Tanaidacea indet.[3], indet.[1,2]
Mollusca	Cephalopoda indet.[1,2,3], indet.[1]
Poly-chaeta	indet.[3]
Echino-dermata	
Crinoi-dea	*Leptometra phalangium*[2]
Ophiu-roidea	*Ophiothrix quinquemaculata*[2]

8.7.2 Predators

Very little information is available as to which species prey on *S. orbignyana*, but it has been found in the stomachs of at least three fish species (Table 8.3). In some cases, however, its presence in the stomach contents of scavenger species, such as the lesser spotted dogfish (*Scyliorhinus canicula*) (Olaso *et al.*, 2002) or seabirds, such as Audouin's gull (*Larus audouinii*) (Oro *et al.*, 2008), is most probably attributable to its being discarded by fisheries. Scars found on cuttlebones have been interpreted as toothmarks (Bello and Paparella, 2003).

Table 8.3. Known predators of *Sepia orbignyana* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Chondrich-thyes	Lesser spotted dogfish (*Scyliorhinus canicula*)	I. Sobrino, pers. comm.
	Thornback ray (*Raja clavata*)	Kabasakal (2002)
Osteichthyes	Black-bellied anglerfish (*Lophius budegassa*)	I. Sobrino, pers. comm.
Aves	Audouin's gull (*Larus audouinii*)	Oro *et al.* (2008)

8.8 Other ecological aspects

8.8.1 Contaminants

High levels of cadmium have been reported in the pink cuttlefish (Bustamante *et al.*, 2002b), indicating that it has efficient detoxification mechanisms. The high bioavailability of cadmium in the digestive gland cells also indicates a high potential for the trophic transfer of this metal to its predators.

8.8.2 Biochemistry

Studies on the biochemical composition of tissues indicate a lower lipid content and higher protein content in the gonad than in other cephalopod species with a benthic lifestyle (Rosa *et al.*, 2005a).

8.9 Fisheries

Sepia orbignyana is one of the most abundant cephalopod species in some areas of the Mediterranean, i.e. Catalan Sea, Tyrrhenian Sea, Sicilian Channel, southern Adriatic Sea, and Aegean Sea (Mangold-Wirz, 1963a; Lumare, 1970; Mandić and Stjepcević, 1983; Sánchez, 1986a; Jereb and Ragonese, 1991a; Würtz *et al.*, 1991; D'Onghia *et al.*, 1992, 1996; Belcari and Sartor, 1993). It is taken mainly as bycatch, both in the Mediterranean and in West African otter-trawl fisheries. Separate landing statistics are not reported, but *S. orbignyana* represents a significant percentage of the catches in some areas. In the Mediterranean Sea, it is marketed fresh and frozen, along with *S. elegans* and small *S. officinalis*, and constitutes a valuable resource locally.

In the Sicilian Channel, research studies have shown an exploitation rate of 0.60 for this species, which suggests intense fishing pressure (Ragonese and Jereb, 1991). More recent studies on the selectivity of diamond, hexagonal, and square-mesh codends (Tosunoğlu *et al.*, 2009) confirmed that the current legal minimum mesh size and codend configurations for demersal trawling are not suitable for regulating fishing on this species, or indeed on other cephalopod species.

8.10 Future research, needs, and outlook

Sepia is the most speciose genus of the Sepiidae, but many species are poorly known, and the systematics of the genus are not clearly resolved (see Khromov *et al.*, 1998, and Reid *et al.*, 2005, for recent reviews). Khromov *et al.* (1998) proposed subdivision of the genus into six "species complexes", but genetic data are still required to test this idea. Further research is needed to clarify the systematics of the group and the position of this species within the group.

Considering the relative importance of the resource in many areas of its distributional range and the intense fishing pressure detected in some of these areas, detailed studies on ecological aspects would be welcome to avoid potential overexploitation. It is essential that separate statistics are collected for landings of individual *Sepia* species.

Cephalopod biology and fisheries in European waters: species accounts

Sepietta oweniana

Common bobtail
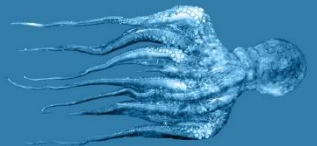
9   *Sepietta oweniana* (d'Orbigny, 1841)

Paola Belcari, Uwe Piatkowski, Paolo Sartor, Evgenia Lefkaditou, Graham J. Pierce, A. Louise Allcock, and Patrizia Jereb

Common names

Sépiole commune (France), Είδος σεπιέττας [eidos sepiettas] (Greece), seppiola comune (Italy), chopo-anão (Portugal), sepieta comùn (Spain), common bobtail squid (UK) (Figure 9.1).

Synonyms

Sepiola petersii Steenstrup, 1887, *Sepiola scandica* Steenstrup, 1887, *Sepiola oweniana* d'Orbigny, 1841.

9.1   Geographic distribution

The common bobtail squid, *Sepietta oweniana* (d'Orbigny, 1841), lives in the Northeast Atlantic from Norway south to Mauritania and throughout the Mediterranean to the Sea of Marmara (Reid and Jereb, 2005) (Figure 9.2). In the Northeast Atlantic, it extends from the west coast of Norway as far north as off Alesund (62°45′N; Grieg, 1933), and is regularly encountered in the Skagerrak and Kattegat (Hornbörg, 2005). It is recorded off the Faroe Islands (Nielsen, 1930) and is widely distributed along the coast of Scotland and in Irish waters (Massy, 1928; Stephen, 1944), the Porcupine Seabight (southwestern Ireland; Collins *et al.*, 2001), and the Celtic Sea (Lordan *et al.*, 2001a). It is

Figure 9.1. *Sepietta oweniana*. **Dorsal view. From Muus (1963).**

recorded in the North Sea (De Heij and Baayen, 2005; Oesterwind *et al.*, 2010) and extends south along the French and Spanish coasts to Morocco and south to 14°N (Guerra, 1992). *Sepietta oweniana* is widely distributed 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 (Guescini and Manfrin, 1986a; Krstulović Šifner *et al.*, 2005), 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). The species has been recorded also in the Sea of Marmara (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

Figure 9.2. *Sepietta oweniana.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

9.2   Taxonomy

9.2.1   Systematics

Coleoidea – Decapodiformes — Sepiolidae – Sepiolinae – *Sepietta.*

9.2.2   Type locality

Not designated : "…nous ignorons entièrement d'où ils viennent…" [d'Orbigny, in Férussac and d'Orbigny, 1834–1948 (1841): 230].

9.2.3   Type repository

Originally Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France; specimen not extant [fide Lu *et al.*, (1995: 322)].

9.3   Diagnosis

9.3.1   Paralarvae

This species does not have paralarvae *sensu* Young and Harman (1988). Hatching size varies between 2.5 and 5 mm ML (Naef, 1921/1923; Mangold-Wirz, 1963a; Bergström and Summers, 1983; Cuccu *et al.*, 2010). Although measurements taken on live specimens may give larger values than measurements taken on fixed specimens (e.g. 3–5 mm ML; Bergström and Summers, 1983, vs. 2.5 mm ML; Naef, 1921/1923), this is unlikely to account for all the above-mentioned variability.

9.3.2 Juveniles and adults:
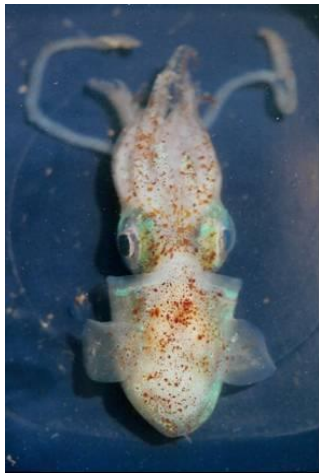
Figure 9.3. *Sepietta oweniana*. Dorsal view. Photo: Evgenia Lefkaditou.

Sepietta oweniana (Figure 9.3) is a small species. A maximum ML of 45 mm for females (Ciavaglia and Manfredi, 2009) and 35 mm for males (e.g. Mangold-Wirz, 1963a; Salman, 1998; Sartor *et al.*, 1998b) was reported for the Mediterranean Sea. However, a larger size of 50 mm is reported for an unsexed specimen from the North Sea (Bergström and Summers, 1983), and a record of 52 mm exists for an unsexed specimen from the northeastern Ionian Sea (Lefkaditou *et al.*, 2003a). The mantle is dome-shaped, more rounded in females, posteriorly. Fins are wide, rounded, and semi-circular, with pronounced anterior lobes, or "earlets"; they do not extend beyond the mantle either anteriorly or posteriorly. Arm suckers are biserial.
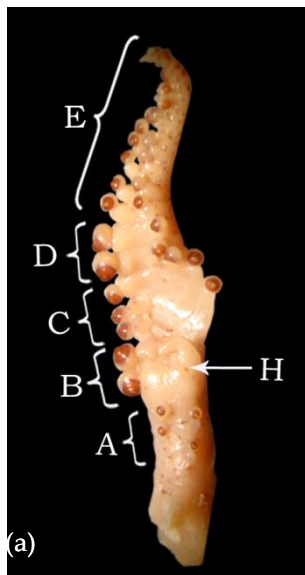
Figure 9.4. *Sepietta oweniana*. (a) typical hectocotylus: A, four basal suckers; H, copulatory apparatus; B, first couple of enlarged suckers; C, two – four smaller suckers; D, second couple of enlarged suckers; E, distal smaller suckers. From Cuccu *et al.*, (2009a). (b) bursa copulatrix. Photo: Evgenia Lefkaditou.

In males, the proximal ends of arms I are fused; the first left dorsal arm is hectocotylized with a modification affecting the basal portion of the arm and the dorsal series of suckers. At the base of that arm, there are normally 4 basal suckers, followed by a typical fleshy hook, the copulatory apparatus. In the dorsal series of suckers on this modified arm, two conspicuously enlarged suckers are followed distally by 2–4 smaller suckers, then another 2 larger suckers; the remaining suckers decrease in size towards the distal tip of the arm (Figure 9.4). The ventral series bears moderately enlarged suckers, and the oral surface of the modified region is broadly concave. The copulatory apparatus consists of a fleshy transverse swelling with a long, hook-like, inwardly curved horn, and a deep cleft medially over a flask-like rugose bulb, swelling at the dorsal edge. The female bursa copulatrix (Figure 9.4) is very large and extends posteriorly beyond the gill insertion.

Figure 9.5. *Sepietta oweniana*. **Tentacular club. Photo: Evgenia Lefkaditou.**

The tentacular clubs (Figure 9.5) are long and well-developed, with 16–32 suckers in transverse rows; all the suckers are of similar (minute) size, giving the club surface a velvety appearance. Light organs are absent. The animal's colouration is reddish brown, with many iridescent gradations, especially on the dorsal side (Naef, 1921/1923; Guerra, 1992; Reid and Jereb, 2005).

9.4 Remarks

Six specimens were reported from Visakhapatam waters (Bay of Bengal, Indian Ocean) by Mohan and Rao (1978). However, no other records of the species in the Indian Ocean exist. Intraspecific variability in the number of suckers at the base of the hectocotylus has been reported for the populations of the Ligurian Sea (Orsi Relini and Bertuletti, 1989), Sardinian waters (Cuccu *et al.,* 2009a), and the Sicilian Channel (Jereb and Di Stefano, 1995; Jereb *et al.*, 1997a). A variation from the usual number of 4 basal suckers was observed in one specimen off Mola di Bari (southern Adriatic Sea; Bello, 1995a); however, in that case, the hectocotylus appeared to have been truncated and then regenerated.

Also, anomalous hectocotyli, differing from the typical structure, have been observed in Sicilian and Sardinian populations (Jereb *et al.*, 1997a; Cuccu *et al.*, 2009a), and a double hectocotylization has been reported for a specimen of the Sicilian population (Jereb *et al.*, 1997a). To date, it is not clear whether these anomalous hectocotyli are functional, something which would be particularly interesting to ascertain, because of the supposed morphological correlation between the hectocotylus and the bursa copulatrix. The high percentage of variants observed within mature animals would indicate that sexual maturity is not affected by such malformations. Observations from the Sardinian populations indicate that the phenomenon is not limited to mature animals, but that it also occurs in immature specimens (Cuccu *et al.,* 2009a). Similar variability has been described for *Sepiola atlantica* (Guerra, 1986), in which it has been attributed to high genetic plasticity.

In his recent review of the nomenclature in the genus *Sepietta,* Bello (2011) demonstrated that both binomina *Sepiola petersii* Steenstrup, 1887 and *Sepiola scandica* Steenstrup, 1887 are junior synonyms of *Sepietta oweniana* (d'Orbigny, 1841).

It has recently been clarified that the first "written" description of *S. oweniana* and the first "illustrated" description appear in different sections of the major work produced by Férussac and d'Orbigny (1834-1848) (Groenenberg *et al.*, 2009; Bello, 2011). It has been noted that the text of Férussac and d'Orbigny was issued in 10 "livraisons" (Tillier and Boucher-Rodoni, 1993, p. 100) and that each provide the date of publication of each book. Based on this evidence, the correct date of publication of the species is 1841, the written description (published in 1841) having priority over the illustrated one (published in 1842) (Art. 21.6 of the International Commission on Zoological Nomenclature, 1999) (Bello, 2011).

Sepietta oweniana and *S. neglecta* females are similar in external appearance, and the character currently used to discriminate sepiolid females, i.e. the bursa copulatrix, is also identical in these two species (Bello, 1995b), making it very difficult to distinguish between them at small size (*S. oweniana* is larger). According to Naef (1921/1923) and others (e.g. Guerra, 1992; Bello, 1995b; Lefkaditou and Kaspiris 1996; Reid and Jereb, 2005), the only difference between the two species is in the tentacular clubs, which are smaller, more delicate, and bear fewer suckers in *S. neglecta*. According to Lefkaditou and Kaspiris (1996), club-length indices can be used to discriminate the two species.

9.5 Life history

Lifespan appears to be 6–12 months. Hatchlings apparently initially adopt a planktonic-necktobenthic mode of life. Animals mature at 4–5 months of age, and spawning takes place year–round, but with regionally varying seasonal peaks.

9.5.1 Egg and juvenile development

The eggs are spherical to lemon-shaped and greyish-white in colour (Figure 9.6). The average egg size at laying varies between 2.4 and 3 mm (larger diameter; Mangold-Wirz, 1963a; Bello and Deickert, 2003; Cuccu *et al.*, 2010), but the eggs swell during embryonic development to ca. 5.0–5.7 mm (Mangold-Wirz, 1963a; Cuccu *et al.*, 2010). Eggs are released during several spawning events onto various solid substrata, both living and dead, with a preference for ascidians (*Microcosmus* spp) in the Catalan Sea (Mangold-Wirz, 1963a; Deickert and B**e**llo, 2005). The egg envelope was described as "thin and elastic" by Mangold-Wirz (1963a), although hard egg envelopes have subsequently been observed in egg clutches from the Catalan Sea (A. Deickert, pers. comm.). Similarly, eggs in a clutch found 544 m deep by Cuccu *et al.* (2010) were covered by a hard shell, as is typical for other sepiolids that spawn at depths of 500–600 m (e.g. *Rossia macrosoma*; Mangold-Wirz, 1963a).

Figure 9.6. *Sepietta oweniana***. Egg clutch. From Cuccu** *et al.* **(2010).**

The number of eggs in wild-collected egg clutches available from the literature is reported in Table 9.1. The overall number of eggs lies within the range of eggs spawned in aquarium studies, i.e. between 2 and 176 (see Bergström and Summers, 1983; Bello and Deickert, 2003), with median values between 30 and 50. It has been suggested that unusually large clutches from the field may result from more than one spawning event by the same female or from several females spawning on the same piece of substratum (Mangold-Wirz, 1963a; Deickert and B**e**llo, 2005).

Table 9.1. *Sepietta oweniana.* **Number of clutches (Nc), number of eggs (or range) (Ne), and clutch size (CS, mean number of eggs) as observed in egg clutches collected from the sea (modified from Deickert and Bello, 2005).**

Region	Nc	Nc	CS	Reference
Northeast Atlantic				
Kattegat	1	130	-	Thorson (1946)
Skagerrak	4	32–103	53.25	Bergström and Summers (1983)
Mediterranean Sea				
Catalan Sea	-	30–60	-	Mangold-Wirz (1963a)
	89	3–62	23.91	Bello and Deickert (2003)

The duration of egg development is highly dependent on water temperature. Data from the literature indicate incubation times of 25 d at 23°C (Jecklin, 1934, in Mangold-Wirz, 1963a), 30 d at 20°C (Mangold-Wirz, 1963a), 2–3 months at ≥10°C, and 6 months at 6.8°C (Bergström and Summers, 1983). Embryo and hatchling are illustrated in Figure 9.7.
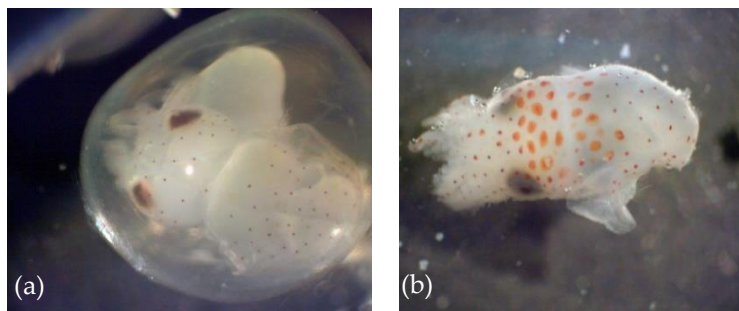
Figure 9.7. *Sepietta oweniana.* **(a) embryo, (b) newly hatched animal. From: Cuccu *et al.* (2010).**

The only information available on *S. oweniana* juvenile behaviour comes from aquarium- based observations by Bergström and Summers (1983). Newly hatched individuals take shelter on the bottom and do not start feeding until they are ca. 1 day old. They then actively search for food day and night, swim freely to catch their prey, and spend short periods on the bottom. This planktonic-nektobenthic life strategy gradually changes with age, and they eventually spend more time on the bottom or buried in the sand. At ca. 10 weeks of age, they settle into a diurnal activity pattern, spending daylight buried in the sand and emerging to feed at night (Bergström and Summers, 1983). In rearing experiments, food was given once a day consisting mainly of juvenile shallow-water crustaceans. Juvenile *S. oweniana* preferred mysids of ca. 0.5–0.67 of their own body length, but were occasionally seen capturing prey their own size.

Because the spawning period extends year-round and the growth rate is fast, recruitment is nearly continuous, and several cohorts succeed one another. Consequently, it is difficult to identify different cohorts (D'Onghia *et al.*, 1995; Sartor *et al.*, 1998b).

9.5.2 Growth and lifespan

Growth after hatching seems relatively independent of water temperature and is quite rapid. Studies in the laboratory report an average growth rate of 4–8 mm month[-1], with slightly faster growth rates in females (5.3 mm month[-1] on average vs. 4.2 mm month[-1] in males; Bergström and Summers, 1983). However, recent observations by Giordano *et al.* (2009) on samples from the southern Tyrrhenian Sea indicated no significant difference in growth rate between males and females. Putative age estimates based on

statolith reading suggest an age of ca. 4.5–6 months for mature and spent females and 5–5.5 months for mature males from southern Portuguese coasts (Czudaj *et al.*, 2012). Based on this information, animals grow and mature within 6–7 months of hatching. The whole life cycle, therefore, would be completed between 6 months and one year, depending mainly on the duration of embryonic development (Boletzky, 1975b; Mangold and Froesch, 1977; Bergström and Summers, 1983). Length–weight relationships are summarized in Table 9.2 below.

Table 9.2. *Sepietta oweniana.* **Length–weight relationships in different geographic areas for females (F) and males (M). Original equations were 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 Tyrrhenian Sea	0.225	1.61	F	Giordano *et al.* (2009)
	0.344	1.29	M	
Northern Aegean Sea	1.0019	1.97	F	Lefkaditou *et al.* (2007)
	0.905	2.12	M	

9.5.3 Maturation and reproduction

Sex ratios have been observed to differ from 1:1 in some areas, both in the Atlantic and in the Mediterranean. A slight predominance of females over males was reported in the Catalan Sea (Mangold-Wirz, 1963a), whereas a slight predominance of males over females has been reported for the Skagerrak (Bergström and Summers, 1983), the northern Tyrrhenian Sea (Sartor *et al.*, 1998b), Sardinian waters (Cuccu *et al.*, 2010), and the Strait of Sicily (Jereb *et al.*, 1997b).

Males mature smaller than females, although size at first maturity and size at 50% maturity are variable in both sexes, throughout the distributional range (Table 9.3). Size at 50% maturity shows a similar degree of variability in both sexes and is comparable among the different Mediterranean populations, except for the Catalan Sea, where it appears that mature females are larger. Again, with the exception of the Catalan Sea, females in the Atlantic mature at a slightly larger size than females in the Mediterranean. However, as noted by Cuccu *et al.* (2010), it is possible that females from the Catalan Sea carrying "large" oocytes had already spawned their "smooth" oocytes before being captured and examined. If this is the case, size at maturity of females from the Catalan Sea would probably be comparable with data from other Mediterranean areas.

Mature animals are found throughout the year both in the Northeast Atlantic and in the Mediterranean, suggesting almost continuous spawning for this species (e.g. Mangold-Wirz, 1963a; Bergstom and Summers, 1983; Belcari and Sartor, 1999b; Reid and Jereb, 2005; Czudaj *et al.*, 2012). Peaks in reproductive activity, however, are reported in both areas for females. In the Northeast Atlantic, peaks have been documented in March and August–November for Gullmar Fjord (Skagerrak, Northeast Atlantic; Bergström and Summers, 1983), and in early summer and autumn–winter (maximum in February) for Portuguese waters (Czudaj *et al.*, 2012).

Table 9.3. *Sepietta oweniana*. **Data on sexual maturity for females (F) and males (M) and potential fecundity (PF) in females, as available from the literature; MLm$_{min}$, mantle length of the smallest mature specimens; MLm$_{50}$, mantle length at 50% sexual maturity. Modified from Cuccu *et al.* (2010).**

Region	Sex	ML	MLm$_{min}$	MLm$_{50}$	PF	Reference
Northeast Atlantic						
Gullmar Fjord	F	-	-	33	130	Bergström and Summers (1983)
	M	-	-	23	-	
Portuguese waters	F	14.0–36.0	20.1	24.4	18–616	Czudaj *et al.* (2012)
	M	14.0–28.0	13.4	20.8		
Mediterranean Sea						
Catalan Sea	F	20.0–40.0	30	>35	150–200	Mangold-Wirz (1963a)
	M	20.0–35.0		*	-	
"	F	16.5–38.5	24.5	-	643–1185	Bello and Deickert (2003)
Ligurian Sea	F	10.0–35.0	20	-	-	Orsi Relini and Bertuletti (1989)
	M	14.0–30.0	18	-	-	
Northern Tyrrhenian Sea	M	13.0–40.0 14.0–35.0	19 15	26 21	- -	Sartor *et al.* (1998b)
Southern Tyrrhenian Sea	F M	18.0–34.0 15.0–29.0	24 18	24 18	60–106 -	Giordano *et al.* (2009)
Sardinian seas	F	12.9–30.8	18.5	24	45–263	Cuccu *et al.* (2010)
	M	13.4–29.1	14.3	20		
Strait of Sicily	F	14.5–36.8	18	-	-	Jereb *et al.* (1997b)
	M	14.0–34.0	14	-	-	
Adriatic Sea	F	-	24	-	-	Guescini and Manfrin (1986a)
	M	-	17	-	-	
Aegean Sea	F	14.0–36.0	22	28	58–236	Salman (1998)
	M	18.0–35.0	21	24	-	

* 75% of male specimens were mature at 20 cm ML.

In the Mediterranean, peaks of reproductive activity are recorded in May–September in the Catalan Sea (western Mediterranean; Mangold-Wirz, 1963a), in July in the northern Tyrrhenian Sea (central Mediterranean; Sartor *et al.*, 1998b), in winter (February–March) in the Strait of Sicily (central Mediterranean; Jereb *et al.*, 1997b), and in March–April and November in the Aegean Sea (Salman, 1998; Lefkaditou and Kaspiris, 2005).

Spawning is usually in relatively shallow coastal water, although records exist of egg masses in deeper waters (down to 544 m; Cuccu *et al.*, 2010). Several sequential egg-laying events have been observed in aquaria by Bello and Deickert (2003), who, combining these observations with the examination of ovaries, concluded that *S. oweniana* can be considered a "small-size multiple spawner", which continues to feed and grow during the spawning phase. The same conclusion was reached by Cuccu *et al.* (2010). The main features of this life strategy are the continuous production and ripening of oocytes, and the continuous laying of egg batches over an extended period of time. These results would support the hypothesis that females from the Catalan Sea with "large" eggs, reported by Mangold-Wirz (1963a), may indeed have been mature females that had already spawned their "smooth" eggs.

Recent observations from Portuguese waters (Czudaj *et al.*, 2012) report females with potential fecundity values higher than those recorded in other areas of the species' distribution range. However, the highest potential fecundities for this species are those recorded by Bello and Deickert (2003) for wild-caught females from the Catalan Sea kept in an aquarium (Table 9.3).

Mating takes place head-to-head and is a rather quick and violent event (e.g. Mangold-Wirz, 1963a; Bergström and Summers, 1983). Spermatophores are placed inside the female's mantle cavity, on the bursa copulatrix area, where spermatangia are stored.

9.6 Biological distribution

9.6.1 Habitat

Sepietta oweniana is a demersal species, living within a wide depth range from 20 m down to >1000 m (i.e. 1027 m, R. Villanueva, unpublished data in Guerra, 1992). In the Northeast Atlantic, it is most common between 50 and 300 m (Bergström and Summers, 1983; Collins *et al.*, 2001), but also occurs on the upper slope (between 300 and 500 m) in the Gulf of Cádiz and in southern Portuguese waters (Silva *et al.*, 2011; Czudjac *et al.*, 2012). In the Mediterranean, major concentrations are most frequent between 200 and 400 m, near the shelf break (Lumare, 1970; Bello and Motolese, 1983; Guescini and Manfrin, 1986a; Belcari *et al.*, 1989a; D'Onghia *et al.*, 1995; Villanueva, 1995b; Jereb *et al.*, 1997b; Quetglas *et al.*, 2000; González and Sánchez, 2002; Lefkaditou *et al.*, 2003a; Lefkaditou and Kaspiris, 2005; Ciavaglia and Manfredi, 2009; Giordano *et al.*, 2009; Guijarro *et al.*, 2011). In some areas and seasons (e.g. in the Ligurian Sea and the northern Tyrrhenian Sea), major concentrations have been reported between 400 and 500 m (Orsi Relini and Massi, 1988; Orsi Relini and Bertuletti, 1989; Mannini and Volpi, 1989), but in other areas (e.g. in the Gulf of Naples and the Adriatic Sea), the species has been reported to be more abundant in shallower water (Naef 1921/1923; Mangold-Wirz, 1963a; Soro and Piccinetti Manfrin, 1989; Ciavaglia and Manfredi, 2009).

Sepietta oweniana prefers soft, muddy substrata throughout its range. It is often found on fishing grounds for Norway lobster (*Nephrops norvegicus*) and shrimp and is very frequently associated with *Rondeletiola minor* (e.g. Naef 1921/1923; Mannini and Volpi, 1989; Belcari *et al.*, 1989a; Bello *et al.*, 1994; Villanueva, 1995b; Jereb *et al.*, 1997b; González and Sánchez, 2002; Lefkaditou and Kaspiris, 2005; Ciavaglia and Manfredi, 2009).

Sepietta oweniana is found regularly in the Kattegat and Skagerrak between the eastern North Sea and the brackish western Baltic Sea (Bergström and Summers, 1983; Hornbörg, 2005). However, its tolerance to salinity variations seems to be lower than in other bobtail squid, because it has never been found in brackish waters (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

9.6.2 Migrations

Seasonal movements related to reproduction and vertical movements, mostly linked to trophic relationships, have been reported for this species in several geographic areas, both in the North Atlantic and in the Mediterranean Sea (Mangold-Wirz, 1963a; Bergström and Summers, 1983; Orsi Relini and Bertuletti, 1989; Mannini and Volpi, 1989; Lefkaditou and Kaspiris, 2005). However, no similar movements have been observed in other areas, such as in the northern Aegean Sea and the Strait of Sicily (D'Onghia *et al.*, 1996; Jereb *et al.*, 1997b), possibly because the continental shelf is narrower in those areas.

9.7 Trophic ecology

9.7.1 Prey

The food spectrum of *S. oweniana* is mainly crustaceans, mostly mysids, euphausiids, and decapods, but fish also seem to constitute a conspicuous fraction of the natural diet (Orsi Relini and Massi, 1988). Cannibalism has been observed in aquarium studies, and cephalopod remains (belonging mainly to the Sepiolidae) were found in the stomachs of wild-caught specimens (Orsi Relini and Massi, 1988). Specific preferences for the euphasiid *Meganyctiphanes norvegica* in North Atlantic waters (Bergström, 1985) and the decapod *Pasiphaea sivado* in the Ligurian Sea (Orsi Relini and Massi, 1988) have been observed (Table 9.4), consistent with the existence of trophic migrations in response to prey abundance and distribution.

Sepietta oweniana has been successfully cultured in aquaria (Bergström and Summers, 1983; Bergström, 1985), fed on mysids (*Praunus flexuosus* and *P. inermis*), amphipods (*Ericthonius*), and large copepods. Adults fed on *Praunus flexuosus* and the shrimps *Palaemon elegans*, *Thoralus cranchii*, and *Crangon crangon.*

According to aquarium observations (Bergström, 1985), the prey-attack system and actual prey capture are essentially visual, as observed for *S. officinalis* (Messenger, 1968) and for other species of Sepiolinae (Boletzky *et al.*, 1971; Boletzky, 1975b). Observations of hatchlings and juveniles attacking air bubbles and floating particles suggest that prey capture is initially indiscriminate (Bergström, 1985). Individuals are able to catch prey of considerable size, even animals larger than themselves (Bergström, 1985). Adults feed at very low light intensity (Bergström, 1985); dusk and dawn are probably the main periods of feeding in the natural environment (Boletzky, 1975b).

Table 9.4. Prey composition of *Sepietta oweniana*, as known from studies in the Northeast Atlantic (Bergström, 1985[1]) and the Mediterranean Sea (Orsi Relini and Massi, 1988[2]; Vafidis *et al.*, 2009[3]).

Taxon	Species
Osteichthyes	indet.[2,3]
Crustacea	
Decapoda	
Pleocyemata-Caridea	Pandalidae indet.[1], *Pasiphaea sivado*[2]
Pleocyemata-Brachy-ura	indet.[3]
Amphipoda	indet.[3]
Euphausiacea	*Meganyctiphanes norvegica*[1,2], indet.[2]
Mysida	indet.[2,3]
Peracarida	Isopoda indet.[2], *Natatolana borealis* (as *Cirolana borealis*)[2]
Mollusca	Cephalopoda indet.[2], Solenogastres indet.[3],
Echinodermata	
Crinoidea	*Leptometra* spp.[2]
Cnidaria	Anthozoa indet.[3]
Polychaeta	indet.[3]

9.7.2 Predators

Sepietta oweniana is potentially available to all benthic and demersal predators of the continental shelf and slope, and is eaten mostly by fish of medium and large size, but also by cetaceans and crustaceans (Table 9.5). It seems particularly vulnerable to some species of elasmobranch (Sartor, 1993; Bello, 1997).

Table 9.5. Known predators of *Sepietta oweniana* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Crustacea	Giant red shrimp (*Aristaeomorpha foliacea*)	Bello and Pipitone (2002)
	Deep-water rose shrimp (*Parapenaeus longirostris*)	Sobrino *et al.* (2005)
Cephalopoda	Common cuttlefish (*Sepia officinalis*)	Alves *et al.* (2006)
	Musky octopus (*Eledone moschata*)	Krstulović Šifner and Vrgoč (2009b)
Chondrichthyes	Black-mouthed dogfish (*Galeus melastomus*)	Macpherson (1981), Kabasakal (2002), Fanelli *et al.* (2009)
	Kitefin shark (*Dalatias licha*)	Matallanas (1982)
	Lesser spotted dogfish (*Scyliorhinus canicula*)	Macpherson (1981)
	Rabbit fish (*Chimera monstrosa*)	Bello (1997)
	Smooth lanternshark (*Etmopterus pusillus*)	Xavier *et al.* (2012)
	Thornback ray (*Raja clavata*)	Kabasakal (2002), Šantić *et al.* (2012)
	Velvet belly lanternshark (*Etmopterus spinax*)	Macpherson (1981), Sartor (1993), Neiva *et al.* (2006)

Osteichthyes	Atlantic cod (*Gadus morhua*)	Bergström and Summers (1983)
	Blue-mouth (*Helicolenus dacty-lopterus*)	Neves *et al.* (2011)
	European hake (*Merluccius mer-luccius*)	Carpentieri *et al.* (2000, 2005)
	Haddock (*Melanogrammus ae-glefinus*)	Bergström and Summers (1983)
	Swordfish (*Xiphias gladius*)	Salman (2004)
Cetacea	Common dolphin (*Delphinus del-phis*)	Santos *et al.* (2004a, 2013)
	Harbour porpoise (*Phocoena phocoena*)	Börjesson *et al.* (2003), Santos *et al.* (2005b)
	Harbour seal (*Phoca vitulina*)	Brown *et al.* (2001)
	Striped dolphin (*Stenella coerule-oalba*)	Würtz and Marrale (1993)

9.8 Other ecological aspects

Studies carried out on the demersal community structure of the western Mediterranean (Biagi *et al.*, 2002) reported a species assemblage recurrent off the western central Italian coasts from 200 to 450 m. *Sepietta oweniana* plays an important role in this faunistic assemblage, both in terms of frequency of occurrence and in percentage abundance; there, the species was found associated with Norway lobster (*Nephrops norvegicus*), European hake (*Merluccius merluccius*), and greater forkbeard (*Phycis blennoides*).

9.9 Fisheries

Sepietta oweniana is one of the most abundant bobtail squid throughout its distributional range and one of the most abundant cephalopods caught in some Mediterranean areas (Reid and Jereb, 2005). It represents an important bycatch of many trawl fisheries, both multispecies fisheries and those targeting shrimp. In southern Sicilian waters a targeted fishery exists for sepiolids (Jereb *et al.*, 1997b). Specific statistics are not available, but the species is commonly sold in Mediterranean markets and is valued as a delicacy in areas such as southern Sicily. In the Mediterranean, catches are generally most abundant in summer, and a marked seasonality has been observed in some areas (e.g. the northern Tyrrhenian Sea; Belcari *et al.*, 1998).

9.10 Future research, needs, and outlook

Important topics for future research include the separation of stocks and cohorts. In particular, additional studies on the Catalan population may help in better understanding maturation strategies and clarifying values for size at maturity that look anomalous in comparison with those recorded for other Mediterranean populations. In order to understand the effect of fishing pressure on the species, it is essential that fishery landings are identified to species.

Cephalopod biology and fisheries in European waters: species accounts
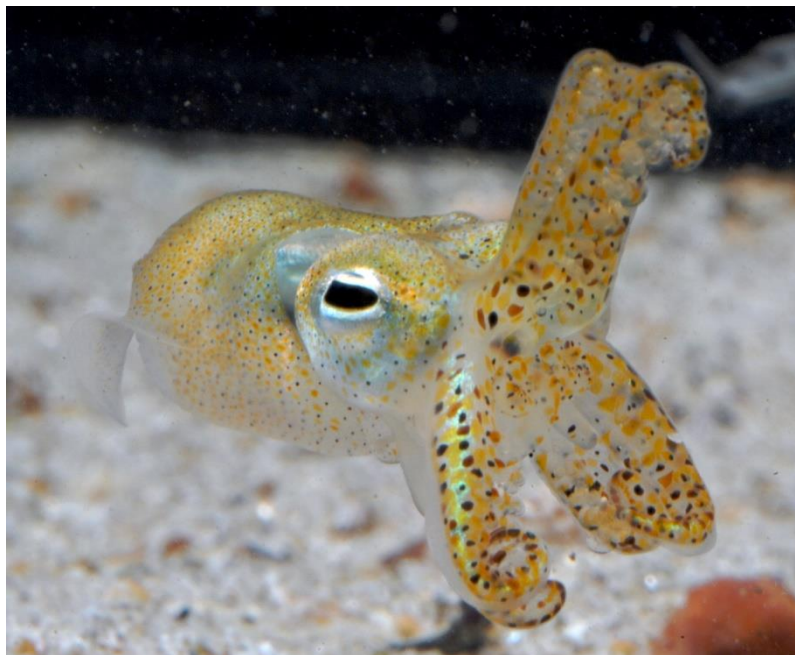
Sepiola atlantica
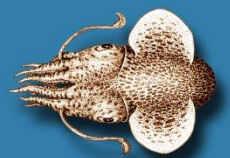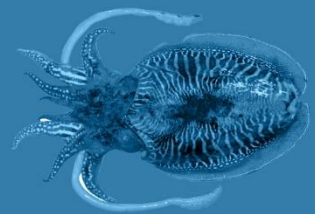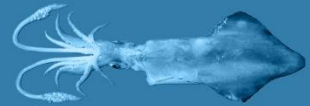
Atlantic bobtail

10 *Sepiola atlantica* d'Orbigny, 1842

Ángel Guerra, Graham J. Pierce, Lee C. Hastie, A. Louise Allcock, Evgenia Lefkaditou, and Patrizia Jereb

Common names

Sépiole grandes oreilles (France), chopo-anão (Portugal), sepiola atlántica (Spain), Atlantic bobtail squid (UK) (Figure 10.1).

Synonyms

None.

10.1 Geographic distribution

The Atlantic bobtail squid, *Sepiola atlantica* d'Orbigny, 1842, is found in the Northeast Atlantic from ca. 65 to 35°N (Reid and Jereb, 2005) (Figure 10.2). Its distribution extends from Iceland (Degner, 1925; Adam, 1939; Bruun, 1945) and the Faroe Islands (Nielsen, 1930) to the Norwegian Sea and the west coast of Norway (Grimpe, 1925; Grieg, 1933; Jaeckel, 1958). Old rec-

Figure 10.1. *Sepiola atlantica*. **Dorsal view. From Guerra (1992).**

ords from the Skagerrak and Kattegat (Grimpe, 1925) are confirmed by recent information (Hornbörg, 2005), and incursions into the western Baltic Sea have been reported (Grimpe, 1925). Widely distributed and very common in the North Sea (Russell, 1922; Grimpe, 1925; Adam, 1933; Gittenberger and Schrieken, 2004; De Heij and Baayen, 2005; Oesterwind *et al.*, 2010), it extends along the north and west coasts of Scotland (Russell, 1922; Stephen, 1944), through Irish and British waters (Massy, 1928; Lordan *et al.*, 2001a), the Porcupine Seabight (southwestern Ireland; Collins *et al.*, 2001), and the Celtic Sea (Lordan *et al.*, 2001a). From the English Channel (Pfeffer, 1908; Grimpe, 1925), it extends south along the west coasts of France and Spain (Guerra, 1992) to Northwest Africa off the Moroccan coast (as far as due west of Casablanca; Robson, 1926). A single record from the Mediterranean Sea has never been confirmed (Würtz *et al.*, 1995).

Figure 10.2. *Sepiola atlantica*. **Geographic distribution in the Northeast Atlantic.**

10.2 Taxonomy

10.2.1 Systematic

Coleoidea – Decapodiformes — Sepiolidae – Sepiolinae –*Sepiola.*

10.2.2 Type locality

Bay of Biscay, France.

10.2.3 Type repository

Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France**;** syntype 2-1-1209 [fide Lu *et al.* (1995)].

10.3 Diagnosis

10.3.1 Paralarvae

The size of individual hatchlings obtained in the laboratory ranges between 1.1 and 1.7 mm (Rodrigues *et al.*, 2011a). In Galician waters (northwestern Spain), they range from 1.5 to 2.0 mm ML and have been collected in midwater both night and day. Paralarvae are similar to adults except for their shorter arms and tentacles in relation to mantle length (Á. Guerra, pers. comm.).

10.3.2 Juveniles and adults

Recent observations on populations around Anglesey (north Wales; Jones and Richardson, 2012) and from the Ría de Vigo (Galicia, northwestern Spain; Rodrigues *et al.*, 2011b) recorded maximum mantle length as 24 mm for females, larger than previously reported for the species (i.e. 21 mm; Yau and Boyle, 1996; Reid and Jereb 2005). Adult males and females are of similar size. Fins are short and do not exceed mantle length anteriorly or posteriorly. Arms IV bear biserial suckers proximally, and 4–8 rows of

minute suckers at the distal tips; the remaining arms bear two series of suckers throughout.

Figure 10.3. *Sepiola atlantica*. Hectocotylized arm. From Guerra (1992).

The dorsal left arm is modified (hectocotylized) in mature males (Figure 10.3) and strongly bent in its distal half; it is characterized by the presence of a fleshy pad formed from enlarged and fused sucker pedicels, and a copulatory apparatus formed by a large swollen horn, with secondary lobes, basally. In the dorsal series of suckers, distal to the copulatory apparatus, there are 3–4 slightly enlarged suckers with swollen pedicels, followed by 3–4 greatly reduced suckers, then by 3–5 greatly enlarged suckers, ca. halfway along the arm. Tentacular clubs bear 8 longitudinal series of suckers, arranged in transverse rows; suckers in the dorsal series are larger than those in the ventral ones.

Mature females do not have a "muscle constrictor" and have a small bursa copulatrix. Paired, kidney-shaped light organs (photophores) are present inside the mantle cavity on each side of the ink sac (Guerra, 1992; Bello, 1995b; Reid and Jereb, 2005). There is a dimorphism in the brachial crown in mature individuals, with males having a muscular nodule at the base of the ventral arms (Rodrigues *et al.*, 2012).

10.4 Remarks

A single record of *S. atlantica* in the Mediterranean Sea exists (Würtz *et al.*, 1995). However, the presence of this species has not otherwise been reported there, either before or since (e.g. Bello 1986, 1992a, 2004; Mangold and Boletzky, 1987; Salman, 2009); therefore, that record is likely a misidentification.

The subfamily Sepiolinae, to which *Sepiola* belongs, can be distinguished from other subfamilies in the Sepiolidae by several features: the anterior edge of the mantle does not cover the funnel ventrally and is fused with the head dorsally by a cutaneous occipital band that occupies from 33 to 50% of the head width. Unlike other genera within the subfamily Sepiolinae, *Sepiola* species have a pair of kidney-shaped light organs (photophores) inside the mantle cavity, over the ink sac. *Sepietta* species do not have photophores, and in *Rondeletiola*, the light organ is large and round, being formed by the fusion of the two organs (Guerra, 1992; Bello, 1995b; Reid and Jereb, 2005).

Recent molecular data (Groenenberg *et al.*, 2009) highlighted the presence of an additional species of sepiolid in the North Sea, now described as *Sepiola tridens* De Heij and Goud, 2010, which is closely related to *S. atlantica*. In their study, Groenenberg *et al.* (2009) found that some one-third of samples they originally identified as *S. atlantica* formed a separate well-supported clade in a phylogenetic tree constructed from Bayesian inference analysis of the mitochondrial gene cytochrome oxidase subunit I (COI: the "barcode of life" gene). The molecular data suggested that members of this clade, now described as *S. tridens,* were more closely related to *S. atlantica* than to any of the other *Sepiola* species in the North Sea, a fact supported by their morphological similarity. However, despite the similarity, De Heij and Goud (2010) identified differences in the tentacular club (length <7 mm in adult *S. tridens* vs. >7 mm in adult *S. atlantica*; 6 club sucker rows in *S. tridens* vs. 8 club sucker rows in *S. atlantica*), in the hectocotylus (5–8 large suckers on the crest before the tip in *S. tridens* vs. 3–4 in *S. atlantica*) and in

body patterning (light pink base colour with a strong honeycomb pattern of chromatophores on the dorsum of *S. tridens* vs. a whitish base colour with a less strong pattern on dorsum in *S. atlantica*). The *S. tridens* used in the molecular study were captured in slightly deeper water (*S. tridens* 43–94 m, *S. atlantica* 19–68 m; Groenenberg *et al.*, 2009). A preliminary analysis of additional trawl data confirmed the difference; the average capture depth for *S. tridens* was 81.8 m vs. 37.4 m in *S. atlantica* (De Heij and Goud, 2010). Subsequent data (De Heij and Goud, 2010) show that *S. tridens* is also present in much deeper water 250 km west of Ireland. De Heij and Goud (2010) report *S. tridens* from the North Sea, the Skaggerak, the English Channel, the Celtic Sea, southwestern Ireland, deep water west of Ireland, and off northwestern Spain. It is possible that some records of *S. atlantica* actually pertain to *S. tridens*, although De Heij and Goud (2010) confirm that the populations in Firemore Bay (Yau and Boyle, 1996) and Ría de Vigo (various authors) likely do pertain to *S. atlantica*. *Sepiola tridens* has been identified genetically in samples collected off the Portuguese shelf at night at bottom depths of 100–148 m. Its presence off the Portuguese coast increases its southern geographic limit to 41°23′N (Roura, 2013).

10.5 Life history

An intermittent terminal spawner, *S. atlantica* spawns year-round with peaks in summer and autumn. Hatchlings resemble adults, but have a brief pelagic phase. Lifespan probably varies between 7 and 10 months.

10.5.1 Egg and juvenile development

Eggs are laid singly, but attached close together in clusters to hard structures on the seabed, including hydroids and bryozoans (e.g. *Cellaria* spp.) (Rees, 1957; Rodrigues *et al.*, 2011c). Eggs are spherical, with a slightly pointed apical tip, resulting in a typically droplet-like shape. In an aquarium-based study, the major axis of egg capsules ranged in length between 1.75 and 4.92 mm (mean 2.75 ± 0.44 mm; Rodrigues *et al.*, 2011c). The duration of embryonic development determined in aquaria is strictly dependent on water temperature, varying from 61.8 (± 3.8) d at 13°C, to 40.1 (± 4.8) d at 16.4°C, and 22.6 (± 1.7) d at 18°C (Rodrigues *et al.*, 2011a). The percentage of eggs that successfully hatch varies from 98.5 to 100%. Newly hatched paralarvae measure 1.1–1.7 mm (1.5 ± 0.3 mm) ML. Total length ranges between 2.6 and 3.6 mm (3.2 ± 0.5 mm), and body weight between 0.077 and 0.098 g (0.081 ± 0.02 g). There are no relationships between hatchling body size and the duration of the embryonic phase, or between hatchling length and weight (Rodrigues *et al.*, 2011a). Similar results were obtained by Jones and Richardson (2010), who recorded embryonic development duration of 33 d at 14.4°C. Newly hatched individuals measured 1.91 mm ML and entered a pelagic paralarval phase lasting 6 d. Some 10–20 days after hatching, the internal yolk sac was exhausted (Jones and Richardson, 2010).

Recruitment occurs year-round, but peaks in spring, early summer, and autumn have been observed in Scottish and Galician waters (Yau, 1994; Yau and Boyle, 1996; Rodrigues *et al.*, 2012).

10.5.2 Growth and lifespan

Little information is available on *S. atlantica* growth. Measured as the increase in dorsal mantle length, growth recorded in aquaria consisted of two distinct phases: relatively slow during the first 120 d (ca. 0.05 mm d^{-1}; 0.043 mm d^{-1} in males and 0.055 mm d^{-1} in females) and increasing slightly thereafter until day 210, when it levelled off (Jones and

Richardson, 2010). Limited data are available on length–weight relationships (Table 10.1).

Table 10.1. *Sepiola atlantica*. **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). Only records from the ICES Area are included.**

Region	a	b	Sex	Reference
West coast of Scotland	0.581	2.46	F	Yau and Boyle (1996)
	0.572	2.75	M	
North Sea	0.557	2.30	All	Robinson *et al.* (2010)

Rodrigues *et al.* (2013) reported regression equations to predict body weight and mantle length from measurements on the beaks of individuals sampled in the Ría de Vigo (both sexes combined):

$\ln(BW) = 1.486 + 2.174 \times \ln(LRL$ and $\ln(ML) = 3.173 + 0.974 \times \ln(LRL)$

$\ln(BW) = 1.590 + 2.734 \times \ln(URL)$ and $\ln(ML) = 1.223 + 3.206 \times \ln(URL)$

where LRL is the lower rostral length (mm) and URL the upper rostral length (mm).

The lifespan of *S. atlantica* likely varies between 7 and 10 months, depending on the duration of embryonic development, which, as noted above, is related to water temperature (Jones and Richardson, 2010).

10.5.3   Maturation and reproduction

Yau and Boyle (1996) reported a sex ratio in animals of >10 mm ML (the sex of smaller animals could not be determined accurately) of ca. 1:1 in Scotland (ratio of males to females 1.4:1.0, $n = 138$). Rodrigues *et al.* (2011b) also reported that the sex ratio did not differ significantly from 1:1 in Galicia.

Observations on the population in Loch Ewe (northwest coast of Scotland; Yau and Boyle, 1996) showed that MLm$_{50\%}$ was ca. 13 mm in males and 16 mm in females. However, the mean body size of mature animals was similar in both sexes (ca. 15 mm). Mature animals were present from March to August, suggesting an extended spawning season, but with a peak in June for both sexes. The number of mature ova in females ranged between 42 and 126. Juvenile occurrence peaked in May, and no juveniles were recorded in March (Yau and Boyle, 1996). Similar results were obtained from studies of the population around Anglesey (north Wales; Jones and Richardson, 2012), where MLm$_{50\%}$ was 13–14 mm in males and 16–17 mm in females. In the Ría de Vigo (northwestern Spain), however, *S. atlantica* matures smaller; the smallest mature males measured 8.05 mm ML, the smallest mature females 6.47 mm (Rodrigues *et al.*, 2012), and MLm$_{50\%}$ was 8.9 and 9.8 mm for males and females, respectively.

Sepiola atlantica is an intermittent terminal spawner, with group-synchronous ovary maturation; it lays multiple eggs and deposits egg clutches in multiple locations (Rodrigues *et al.*, 2011c).

Examination of the ovaries has revealed that immature oocyte size varies between 0.03 and 3.75 mm (maximum diameter; Rodrigues *et al.*, 2011c). Mature oocytes range in size between 1.57 and 5.42 mm (Rodrigues *et al.*, 2012). The largest oocytes have been found in the largest females. The total number of eggs laid by a single female ranges between 31 and 115, and potential fecundity (i.e. the sum of the number of oocytes in

the ovary and the oviducts plus the number of eggs already spawned) from 119 to 304 (Rodrigues *et al.*, 2011c).

The maximum number of spermatophores recorded in males is 1243 (Rodrigues *et al.*, 2012), with a mean value of 369. Spermatophore length ranges from 3.31 to 9.23 mm. No significant relationship was observed between number of spermatophores and mantle length (Rodrigues *et al.*, 2012).

Mating behaviour has been studied in the laboratory (Rodrigues *et al.*, 2009). There was no courtship in any of the mating events observed. The male moved quickly towards the female, holding her around the middle of the ventral mantle region with his arms. Positioned underneath the female, the male then introduced his pair of dorsal arms into the female's mantle cavity (the left dorsal arm is hectocotylized and transfers spermatophores), while grasping her ventral body with the laterodorsal pair of arms, and neck with the lateroventral pair, sometimes introducing these arms into the female's mantle cavity. Male colour remained constant throughout mating, whereas females slowly and continuously changed their chromatic patterns. Mating duration varied between 68 and 80 min (Rodrigues *et al.*, 2009).

10.6   Biological distribution

10.6.1   Habitat

Sepiola atlantica inhabits the continental shelf, its distribution extending to the edge of the slope. It can be considered a neritic species, occurring from the sublittoral zone to depths of 150 m. In Scottish waters, it is most common between 50 and 120 m (Yau, 1994; Yau and Boyle, 1996). In Iberian waters, it is commonly found from 6 to 50 m, as well as inside the Galician Rías (sheltered tectonic valleys), and it prefers clean sandy bottoms. It is epibenthic, but has been collected in midwater during both night and day (Collins *et al.*, 2001). Bruun (1945) commented that most specimens recorded around Iceland were caught pelagically. The species is stenohaline and not found in areas with high salinity variation (Guerra, 1992; Rodrigues *et al.*, 2011d). Collins *et al*. (2002), in their study on the distribution of cephalopods from plankton surveys around the British Isles, found that *S. atlantica* was the most abundant cephalopod in samples from the North Sea.

10.6.2   Migrations

Seasonal migrations have been observed in the waters around Anglesey (north Wales; Jones and Richardson, 2012), where *S. atlantica* migrates inshore in July, reaching peak abundance between July and August, declining in numbers between September and October, and migrating offshore in late October. These movements are probably related to feeding strategies, because of the abundance of prey such as shrimps in shallow water in summer, and, more generally, to take advantage of environmental conditions favourable for enhanced growth and maturation. In addition, congregation in shallow waters may favour encounters with mates.

Seasonal differences in abundance were also recorded in the Areamilla area (Galician waters, northwestern Spain; Rodrigues *et al.*, 2011b), where, however, lowest abundance was recorded in summer. It was proposed that this seasonal pattern of abundance was due to migration of individuals from shallow to deeper waters, related to changes in bottom temperature.

10.7 Trophic Ecology

10.7.1 Prey

The main prey species of *S. atlantica* are mysids and decapod shrimps. Foraging primarily takes place at dawn and dusk, and prey are taken above the seabed (Yau, 1994).

10.7.2 Predators

Sepiola atlantica is the most frequently recorded cephalopod in the diet of harbour porpoise in Scottish waters. The sepiolids are probably detected by porpoises directing their sonar into the substratum, detecting the acoustic signal given by the hole in which the animal lies (Santos and Pierce, 2003; Santos *et al.*, 2004b). In Galician waters, the species has been recorded in the stomach contents of hake and gurnards (Á. Guerra, pers. comm.). Known predators of this species are listed in Table 10.2.

Table 10.2. Known predators of *Sepiola atlantica* in the Northeast Atlantic.

Taxon	Species	References
Myxini	Hagfish (*Myxine glutinosa*)	Shelton (1978)
Chondrich-thyes	Lesser spotted dogfish (*Scyliorhinus canicula*)	Ellis *et al.* (1996)
	Greater spotted dogfish (*Scyliorhinus stellaris*)	Ellis *et al.* (1996)
	Spotted ray (*Raja montagui*)	Ellis *et al.* (1996)
	Spurdog (*Squalus acanthias*)	Ellis *et al.* (1996)
	Thornback ray (*Raja clavata*)	Ellis *et al.* (1996)
	Tope shark (*Galeorhinus galeus*)	Ellis *et al.* (1996)
Osteichthyes	European hake (*Merluccius merluccius*)	P. Torres, pers. comm.
	Gurnards: family Triglidae	Á Guerra, pers. comm.
Cetacea	Common dolphin (*Delphinus delphis*)	González *et al.* (1994a), Silva (1999a), De Pierrepont *et al.* (2005)
	Harbour porpoise (*Phocoena phocoena*)	Santos and Pierce (2003), Víkingsson *et al.* (2003), Santos *et al.* (2004b), Jansen *et al.* (2013)

10.8 Other ecological aspects

10.8.1 Behaviour

Sepiola atlantica may bury itself in the sand by day to hide from predators and as a technique for hunting. The burying behaviour in natural substrata in the aquarium was described by Rodrigues *et al.* (2010a). After a short period in an alert position, the animal starts burying itself, and on average the whole process taking 21.9 (± 4.93) s. Burial time does not appear to be related to size. Burying behaviour is accompanied by a display of colour changes peculiar to the species.

In the laboratory, the entire body of newly hatched individuals is yellow and covered with expanded dark brown chromatophores. Individuals often assume a "flamboyant" arm display (as shown and described in Mauris, 1989, for *Sepiola affinis*). This posture consists of stretching the dorsal and latero-dorsal arms upwards perpendicular to the body axis, while the latero-ventral and ventral arms together are stretched downwards on each side of the body; all arm tips are rolled inwards.

Hatchlings are generally less active during daylight and attempt to bury themselves in the sand immediately after hatching (see Rodrigues *et al.*, 2011a). Although equipped with yolk reserves, they are ready to hunt mysid shrimp of equal size soon after hatching, and display a characteristic pattern of expanded dark brown chromatophores when focusing on prey. Prior to attacking prey, all chromatophores are contracted and, consequently, the animal turns virtually transparent. Arms are spread to form a circular crown, enabling the tentacles to be shot out rapidly (generally to the dorsal side, towards the middle of the mysid shrimp). If the attack is successful, tentacles are quickly retracted with the prey. When the tentacles are retracted (with or without prey), animals regain the dark brown colour (Rodrigues *et al.*, 2011a).

10.9 Fisheries

Bobtail squids *Sepiola* spp. are not usually identified in fishery landings (ICES, 2010). However, they are known to be landed and sold in fish markets in southern Europe (Reid and Jereb, 2005).

10.10 Aquaculture

Although of no commercial value, *S. atlantica* is a potential species for experimental work under controlled conditions. For that reason, the University of Vigo and the Instituto de Investigaciones Marinas-CSIC are developing sepiolid culture techniques (Rodrigues *et al.*, 2011d).

10.11 Future research, needs, and outlook

Despite *S. atlantica* being a relatively common nearshore species, information on its biology, ecology, and life history was, until very recently, limited to waters around Scotland (e.g. Yau, 1994; Yau and Boyle, 1996). More recently, there has been research on the species in Wales (Jones and Richardson, 2010, 2012) and Galicia (Rodrigues *et al.*, 2009, 2010a, b, c, 2011a, b, c, d, 2012). However, life cycle biology and ecology remain poorly known through most of its range, and more research is needed.

Cephalopod biology and fisheries in European waters: species accounts

Loligo vulgaris

European squid
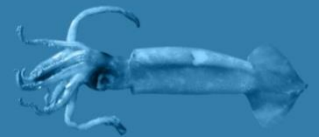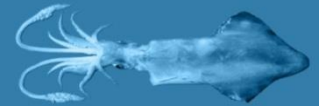
11   *Loligo vulgaris* Lamarck, 1798

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).

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).

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

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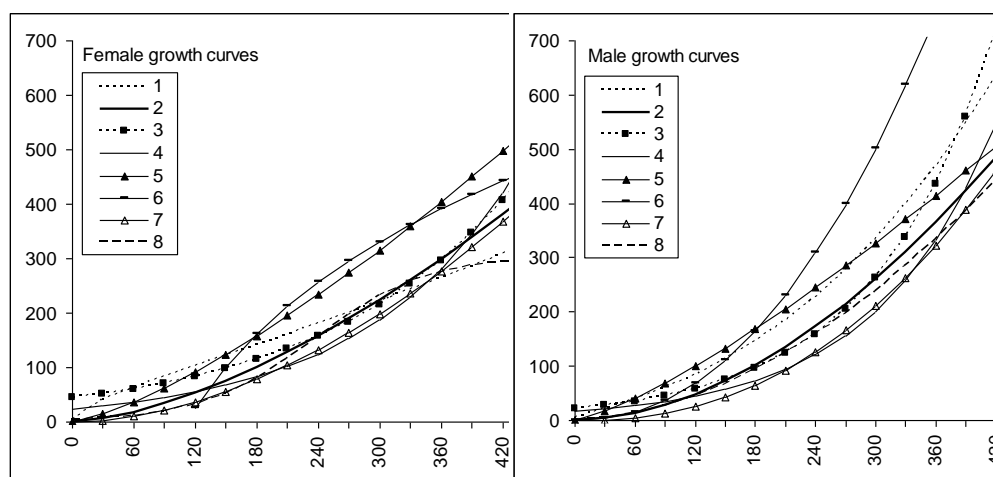
Figure 11.6. *Loligo vulgaris.* **Growth curves (length in mm vs. age in d), according to 1, Natsukari and Komine (1992); 2, Arkhipkin (1995); 3, Rocha and Guerra (1999); 4, Rocha and Guerra (1999) autumn-winter hatchers; 5, Bettencourt *et al.* (1996), spring-summer hatchers; 6, Raya *et al.* (1999);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

Cephalopod biology and fisheries in European waters: species accounts

Loligo forbesii

Veined squid
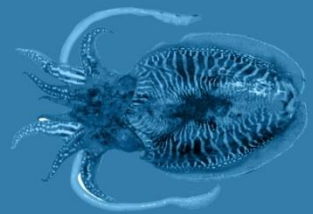
12 *Loligo forbesii* Steenstrup, 1856

Graham J. Pierce, Lee C. Hastie, Evgenia Lefkaditou, A. Louise Allcock, Jennifer M. Smith, Sansanee Wangvoralak, and Patrizia Jereb

Common names

Encornet veiné (France); Καλαμάρι [calamary] (Greece); calamaro venato, occhione (Italy); lula-riscada (Portugal), calamar veteado (Spain); veined squid, European northern squid (UK) (Figure 12.1).

Synonyms

Loligo fusus Risso, 1854, *Loligo moulinsi* Lafont, 1871.

12.1 Geographic distribution

The veined squid, *Loligo forbesii* Steenstrup, 1856, is found in the Northeast Atlantic, from ca. 60°N to ca. 20°N, and throughout the Mediterranean (Jereb *et al.*, 2010) (Figure 12.2). A neritic and mainly near-bottom species, it lives in coastal waters and continental shelf seas of the Northeast Atlantic, from the Faroe Islands (Howard, 1979; Gaard, 1987) and the northern North Sea (Howard *et al.*, 1987) to the southwest coast of Norway (Grieg, 1933), where it has been recorded as far north as Trondjemsfjord (Nordgård, 1923). The species was considered absent from the Baltic Sea by Roper *et al.* (1984) and Jereb *et al.* (2010), but old records exist of

Figure 12.1. *Loligo forbesii*. **Dorsal view. From Roper *et al.* (1984).**

the species in the Kattegat and western Baltic Sea (Grimpe, 1925) and are supported by recent observations (Hornbörg, 2005), although the presence of the species is considered extremely variable in those areas. *Loligo forbesii* inhabits the central and southern North Sea (De Heij and Baayen, 2005; Oesterwind *et al.*, 2010) and is common in British and Irish waters (Holme, 1974; Howard, 1979; Howard *et al.*, 1987; Pierce *et al.*, 1994b, 1998; Collins *et al.*, 1995b*)*. It also extends south through French and Spanish waters to the west coast of Africa, around and south of the Canary Islands, to ca. 23–24°N according to FAO (1979) or even to 18°N according to Roper and Sweeney (1981), and west to Madeira (Clarke and Lu, 1995) and the Azores (Martins, 1982). Although the southern limits of its distribution remain unknown (Guerra, 1992), the Azores Islands are considered its western limit in the Northeast Atlantic. *Loligo forbesii* has been recorded throughout the Mediterranean Sea (Mangold and Boletzky, 1987; Bello, 2004; Salman, 2009), although it is scarce in the northwestern Mediterranean, but more abundant in the Strait of Sicily (in the early 1990s) and in the northeastern Ionian Sea (Naef, 1921/1923; Mangold-Wirz, 1963a; Boletzky and Mangold, 1985; Ragonese and Jereb, 1986; Jereb and Ragonese, 1994; Lefkaditou *et al.*, 2003a). Its occurrence in the Adriatic Sea is limited to central and southern areas (Casali *et al.*, 1988; Bello, 1990; Krstulović Šifner *et al.* 2005), is found in the Aegean Sea and the Levant Basin (D'Onghia *et al.*,

1992; Salman *et al.*, 1997, 1998; Lefkaditou *et al.*, 2003b), but has not been recorded in the Sea of Marmara (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

Figure 12.2. *Loligo forbesii*. **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

12.2 Taxonomy

12.2.1 Systematics

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

12.2.2 Type locality

North Sea, Denmark (exact position not known).

12.2.3 Type repository

Kobenhavns Universitet, Zoologisk Museum, Universitetsparken 15, DK 2100 Copenhagen, Denmark. Syntype [fide Kristensen and Knudsen (1983)]. *Loligo forbesii* Steenstrup, 1856, Danske videnskabernes selskabs skrifter (5) 4:189.

12.3 Diagnosis

12.3.1 Paralarvae

Hatchlings of this species are differentiated from their congener species *Loligo vulgaris* by their larger size; mean ML of *L. forbesii* hatchlings is 3.7 mm (range 3.5–4.9 mm) compared with 3.1 mm (2.8–3.3 mm) for *L. vulgaris*. Note, however, that hatchling size apparently varies regionally in *L. vulgaris* (González *et al.*, 2010), and this may also be true for *L. forbesii.* The chromatophore patterns are highly variable, and the number of chromatophores decreases from the ventral to the dorsal side in hatchlings of both species. Fins are paddle-shaped, broad with short bases, and each fin is much wider than

long. The tentacular clubs are broad and much wider than the tentacular stalks (Segawa *et al.*, 1988; Hanlon *et al.*, 1989; Sweeney *et al.*, 1992; Yau, 1994).

12.3.2 Juveniles and adults

The body form of juveniles is bullet-shaped, with well-developed, paddle-shaped, terminal fins. The ventral arms and tentacles are also well developed, and the tentacular club suckers are like those of the adult, i.e. median suckers slightly larger (1.5-fold) than marginal suckers (Yau, 1994).
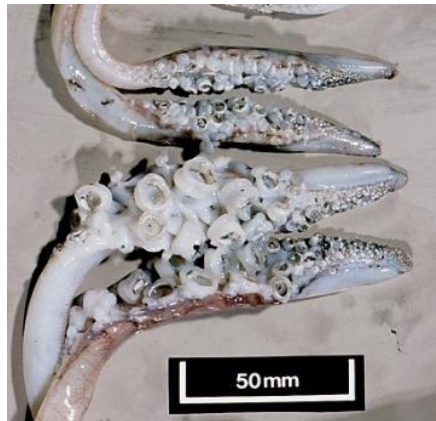
Figure 12.3. Details of the tentacular clubs of *L. forbesii* (above) and *L. vulgaris* (below), showing the enlarged central series of suckers in *L. vulgaris.* Photo: Andy Lucas

The mantle of adults is long, moderately slender, muscular, and cylindrical; the fins are rhomboid, with slightly concave posterior borders, and their length is ca. 75% the length of the mantle. A cornea covers the eye. The arms have two series of suckers. The species lacks the markedly enlarged medial suckers typical of the tentacular club of *L. vulgaris*. Instead, the suckers on the manus of the tentacular club of *L. forbesii* are subequal in size (Figure 12.3). The sucker rings on the tentacular club have 13–18 sharp conical teeth. The largest sucker rings on the arms have 7–8 teeth. In mature males, the left ventral arm (IV) is hectocotylized in its distal third by modification of suckers into long papillae that gradually decrease in size distally. The locking cartilage is simple (Naef, 1921/1923; Roper *et al.*, 1984; Guerra, 1992; Jereb *et al.*, 2010).

Loligo forbesii has "prominent longitudinal flame-like stripes of purplish dark chromatophores on the anterior and ventrolateral surfaces of the mantle" (Jereb *et al.*, 2010), although Holme (1974) describes them as orange-red in colour. This feature is also sometimes seen in large mature males of *L. vulgaris*, although the stripes are usually much smaller and less numerous. In general, the mantle colour is more orange in *L. forbesii* and more violet or purple in *L. vulgaris* (Figure 12.4).

12.4 Life history

The life cycle of *L. forbesii* is annual, and maximum lifespan is ca. 16 months. It usually spawns in winter, but summer breeders have also been described in some areas.

12.4.1 Egg and juvenile development

The size of the egg string or egg size itself is generally used to distinguish *L. forbesii* eggs from those of *L. vulgaris* (Naef, 1921/1923; Sacarrão, 1956–1957; Boletzky, 1987b). The egg strings of *L. forbesii* are larger and contain fewer eggs of greater volume than those of *L. vulgaris* (Martins, 1997). Grimpe (1925) stated that *L. forbesii* egg strings contain an average of 54 eggs, ca. half the number of eggs in *L. vulgaris* egg strings. However, Holme (1974) found egg strings to contain 50–130 eggs per string. Eggs of *L. forbesii* are large and supplied with a large quantity of yolk relative to many marine fish eggs (Boletzky, 1987b; Hanlon *et al.*, 1989). They are packed and wrapped in gelatinous substances produced by the oviducal and nidamental glands, forming finger-like

egg strings. The number of egg strings in a cluster is variable, and a cluster may contain egg strings spawned and deposited by one or several females. A single egg string may be fertilized by more than one male and hence be multipaternal (Shaw and Boyle, 1997). Clusters of these egg strings are normally attached to substrata that include algae, shells, rock crevices, nets, ropes, creels, and other fishing gear (e.g. Holme, 1974; Lum-Kong *et al.*, 1992).

Figure 12.4. External appearance of large, mature males of *Loligo forbesii* (above) and *L. vulgaris* (below), showing the more prominent "flame-like" stripes on the mantle of the former. These two specimens were caught in Scottish waters in early 1990. Differences in colouration of the mantle and stripes are also evident. Photo: Andy Lucas.

Records of egg masses of *L. forbesii* originate primarily from inshore areas. Collins *et al.* (1995c) recovered egg masses from static fishing gear over rocky ground at 10–50 m off the south coast of Ireland. There are numerous incidental and anecdotal records of egg masses attached to fixed fishing gear in UK waters at various times of year, and Holme (1974) reported egg masses attached to fishing floats, rope moorings, and crab pots in inshore areas off the coast of Plymouth. Lum-Kong *et al.* (1992), Martins (1997), and Craig (2001) found egg masses attached to inshore creel lines in Scottish waters over muddy and rocky substrata in depths of 30–110 m in both winter and summer. Fishers interviewed about the distribution of squid in the Moray Firth (North Sea coast, UK) reported egg masses from all around their coast in water as shallow as 2 m along moorings and piers, but also from the middle of the Moray Firth attached to creel lines (Smith, 2011). Regardless of distance from the coast, egg masses in the Moray Firth tend to be found over rocky bottoms. Lordan and Casey (1999) argue that the species is more likely to spawn over rocky bottoms where opportunities to attach eggs to the substratum are more numerous.

In Portugal, based on the distribution of spawning females, egg strings of *L. forbesii* are believed to be deposited farther offshore than those of *L. vulgaris* (Cunha *et al.*, 1995). Recently, an *L. forbesii* egg mass was recovered on the west coast at 240 m (A. Moreno, pers. comm.). From egg masses recovered on octopus traps, spawning activity in the Azores is known to take place at depths of 25–144 m (Porteiro and Martins, 1992; Pham *et al.*, 2009). The deepest record of an egg mass of this species in the Azores, and the only record from the area to date not obtained from fish traps, was a group of 2–30 egg strings seen in a rocky crevice at 373 m depth using an ROV (Carreira *et al.*, 2011).

Lum-Kong *et al.* (1992) suggested that most spawning could take place outside coastal waters because commercial samples containing fully mature squid originate largely from fishing areas some distance from the coast. Although several records point to spawning in deeper waters of both the Atlantic and Mediterranean (e.g. Lordan and Casey, 1999; Salman and Laptikhovsky, 2002; Carreira *et al.*, 2011), the general lack of data on eggs from such areas could be due to egg masses trawled offshore going unreported and/or the preference of squid spawning over rocky substratum, making spawning areas largely inaccessible to trawling (Holme, 1974; Lordan and Casey, 1999). The deepest record to date (730 m) is one from the Aegean Sea (eastern Mediterranean; Salman and Laptikhovsky, 2002), at a bottom water temperature of 13°C.

Observations in captivity show that the timing of development and hatchling emergence of *L. forbesii* depends on both egg size and temperature (Paulij *et al.*, 1990b; Gowland, 2002). Size at hatching varies inversely with temperature and is significantly less at 16°C than at 8°C. Duration of the embryonic phase increases as temperature decreases: 140 d at 8°C, 60 d at 12°C, and 36 d at 16°C (Martins, 1997; Gowland *et al.*, 2002). Growth patterns also change with varying temperature. Hatchlings reared at 12°C have long, narrow mantles consistent with normal development, whereas hatchlings reared at both higher and lower temperatures have shorter and wider mantles. Craig (2001) found that all hatchlings emerged during darkness. Hatchlings from each string emerge over a period of ≥2 days. At hatching, *L. forbesii* paralarvae exhibit positive phototaxis, and swim actively. From 2 d on, swimming near the surface is rare (Martins, 1997). The statolith shape of *L. forbesii* hatchlings is different from that of juveniles (>50 mm ML) and adults. Martins (1997) postulated that if changes in swimming behaviour (ontogenetic descent, dexterity, and velocity) were related to changes in statolith shape, then the stage at which the form of the statolith changes could be indicative of the end of the planktonic life phase. However, Collins *et al.* (2002) suggested that the general absence of this species from plankton samples could indicate that the paralarva is not planktonic. Using an epibenthic sled, Robin and co-workers caught hundreds of squid paralarvae in the English Channel during surveys in June 2011 and March 2013, mostly *Alloteuthis* and a few *L. vulgaris*, but no *L. forbesii* paralarvae (J.-P. Robin, pers. comm.).

Statolith length is highly correlated with dorsal mantle length, larger hatchlings having larger statoliths. Gowland (2002) found that deformities in hatchlings increased with increasing temperature, whereas Martins (1997) found more deformed hatchlings in *L. forbesii* acclimated to temperatures <13°C. This suggests a relatively narrow temperature optimum for normal hatchling development. Deformities in development may also be caused by hypoxia or abnormal ion concentrations (Hanlon *et al.*, 1989). Detailed descriptions of embryonic stages of *L. forbesii* can be found in Segawa *et al.* (1988).

12.4.2   Growth and lifespan

Loligo forbesii is one of the largest members of the family Loliginidae. Male *L. forbesii* can grow considerably larger and heavier than females and have faster growth rates. Typically, adult body size reaches 100–650 mm ML in males (weight range 155–3700 g) and 175–350 mm ML in females (weight range 200–1150 g) throughout the species' range. However, there is wide variation within both sexes and, in particular, some males mature at ca. 120 mm long and probably never grow much larger (Pierce *et al.*, 1994c; Porteiro and Martins, 1994; Boyle *et al.*, 1995).

Females as large as 420 mm ML and 1.5 kg and males of 735 mm and 4.3 kg have been recorded in Scottish waters (G. J. Pierce, pers. comm.). In the Azores population, males

reach 937 mm ML and 8.3 kg, compared with 462 mm ML and 2.2 kg for females (Martins, 1982). Genetic differences between the Azores and mainland coastal samples indicate that the former may represent a separate subspecies (Brierley *et al.*, 1995; Shaw *et al.*, 1999). However, the large size of squid observed in Azorean waters may also be at least partly due to sampling bias, because the squid sampled in the above-mentioned studies were caught by jigging. Very large individuals (males >500 mm ML) appear occasionally in commercial trawl catches landed in other areas, e.g. the records for Scotland, and a large male of 560 mm ML found at the fish market in Sicily (Jereb and Ragonese, 1986), but it is not certain that they are as rare as they appear to be, because they may simply not often be caught by trawling.

Several techniques have been used to determine the growth characteristics of *L. forbesii*, including observations in captivity (Forsythe and Hanlon, 1989), length frequency analysis (Pierce *et al.*, 1994c), and estimates based on growth increments in the statoliths (Collins *et al.*, 1995c) and the gladius (Hughes, 1998). The gladius extends the entire length of the mantle, and a growth increment of 1 mm in the gladius therefore represents ca. a 1-mm increase in mantle length.

Modal progression analysis of length frequency data, whereby the growth of putative cohorts is followed through most of the post-recruit life cycle, along with plotting of maturity ogives, has revealed the presence of two or more size modes at maturity, apparently corresponding to different growth strategies, in both sexes (Holme, 1974; Boyle and Ngoile, 1993a; Pierce *et al.*, 1994c; Boyle *et al.*, 1995; Collins *et al.*, 1995c, 1999). Males consistently exhibit at least two alternative growth strategies, with some maturing very small; these probably correspond to different reproductive strategies: mateguarding by large males and sneaking by small males (Hanlon and Messenger, 1998). However, some studies have suggested as many as 3–4 cohorts (or "microcohorts"), with different growth trajectories in males and 2–3 in females (e.g. Collins *et al.*, 1999). It should be noted, however, that reliable resolution of multiple modes in length frequency data requires large samples and regular sampling.

Boyle *et al.* (1995) suggested that the different size modes in mature males of this species could reflect differences in age or growth rate and could be of environmental or genetic origin. Wangvoralak (2011) showed that if males sampled in Scotland during 2007–2008 were divided into two groups based on hatching dates, evidence of two sizes at maturity was then seen only in animals hatched in cold months and not in those hatched during warm months. The same author showed that maturity ogives calculated in terms of age rather than length were simpler in form, with no evidence of two modes, i.e. that all individuals tended to mature at similar ages.

Temperature is known to affect the development time of embryos (Boletzky, 1987b). The development time of *L. forbesii* is 75 d at 12.5°C (Hanlon *et al.*, 1989). Based on the report of a viable egg mass remaining at a particular site for 6 months at temperatures of 8–10°C, Boyle *et al.* (1995) suggested that, in Scottish waters, the development of *L. forbesii* eggs may be held in stasis over the coldest period of winter, generating two cohorts from a single breeding population with an extended spawning period.

Statoliths of *L. forbesii* were first used for age determinations by Martins (1982); subsequent studies include those by Gaard (1987), Guerra and Rocha (1994), Collins *et al.* (1995c), Hughes (1998), Rocha and Guerra (1999), and Wangvoralak (2011). Increments in squid statoliths are proposed to be formed daily (Kristensen, 1980; Lipiński, 1986, 1993; Rodhouse and Hatfield, 1990). In *L. forbesii*, daily deposition of statolith increments has been validated in aquarium-based studies (Hanlon *et al.*, 1989), and has been supported by increment counts in statoliths of squid from successive monthly fishery

samples (Collins *et al.*, 1995c). Based on the results from counting growth increments on statoliths (Gaard, 1987; Guerra and Rocha, 1994; Boyle *et al.*, 1995; Collins *et al.*, 1995c; Rocha and Guerra, 1999; Wangvoralak, 2011) and aquarium studies (Hanlon *et al.*, 1989), there is general consensus that *L. forbesii* can live 15–16 months, with most sampled animals being no more than a year old. The largest male recorded in Scotland to date (ML = 735 mm) was estimated to be 420 d old (i.e. ca. 14 months; G. J. Pierce, pers. comm.).

The growth pattern in loliginid squid appears to comprise two distinct phases: an early rapid, "exponential" phase, followed by a secondary, slower, "logarithmic" phase (Forsythe and van Heukelem, 1987; Forsythe and Hanlon, 1989). During the exponential phase, juvenile *L. forbesii* can achieve daily growth rates of 8% of body mass (Forsythe and Hanlon, 1989; Grist and Des Clers, 1998). However, that phase generally lasts no more than 2–4 months (Jackson, 1994). Over the course of the life cycle, growth rate gradually declines, from 5.4% BW d^{-1} in the smallest individuals to 1.4 in the largest (Forsythe and van Heukelem, 1987). Forsythe and Hanlon (1989) give the final growth rate as 1–2% BW d^{-1}.

Based on statolith data collected from post-recruit animals, Collins *et al.* (1995c) reported growth rates of 0.98% ML d^{-1} and 2.48% BW d^{-1} in males, and 0.85% ML d^{-1} and 2.26% BW d^{-1} in females. This corresponded to growth of ca. 1 mm d^{-1} for females and 1–5 mm d^{-1} for males. Growth rates estimated from modal progression analysis using monthly length frequency data were slightly lower (e.g. female growth rate was 30 mm month^{-1} from statoliths and 15–30 mm month^{-1} from length frequency data).

Individual growth rates in squid are highly variable, as revealed by both rearing studies and analysis of market sample data on length, weight, age, and gladius increments. Factors affecting growth rate include food availability and water temperature, as well as sex, maturity, season, and hatching time (Forsythe and van Heukelem, 1987; Rodhouse and Hatfield, 1990; Bettencourt *et al.*, 1996; Hughes, 1998; Smith *et al.*, 2005, 2011; Wangvoralak, 2011). Cephalopods are poikilotherms and, as such, temperature is thought to be one of the main external factors determining growth rate prior to sexual maturity, although the logarithmic phase is apparently less temperature-dependent than the earlier exponential phase (Forsythe, 1993; Grist and Des Clers, 1998). In captivity, when food is not limited, temperature is positively related to growth rate up to optimal values (Forsythe and van Heukelem, 1987). However, squid that experience colder temperatures prior to hatching may ultimately attain adulthood at larger size (and/or older ages) (Wangvoralak, 2011).

Comparisons of length–weight relationships from different studies (see Table 12.1) are generally difficult, in this species as in many others, because of the use of different length–weight models, the fact that confidence limits are rarely indicated, and, often, an absence of information on the model fitting-procedures. Nevertheless, it is clear that there are sex-related differences in the length–weight relationship (Holme, 1974; Martins, 1982; Gaard, 1987; Ngoile, 1987; Boyle and Ngoile, 1993b; Pierce *et al.*, 1994c; Guerra and Rocha, 1994; Moreno *et al.*, 1994). Although there is some overlap in values for the exponent *b*, it is consistently higher in females (*b* = 2.18–2.66) than in males (*b* = 2.00–2.58), indicating that female *L. forbesii* are relatively heavier at a given length. This feature has also been noted in *L. vulgaris* (Coelho *et al.*, 1994; Guerra and Rocha, 1994; Moreno *et al.*, 2002).

Table 12.1. *Loligo forbesii.* **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), ML is dorsal mantle length (cm), and a and b are the coefficients.**

Region	a	b	Sex	Reference
Faroe Islands	0.074–0.088	2.61–2.66	F	Gaard (1987)
	0.133–0.180	2.30–2.45	M	
Rockall (ICES Division VIb)	0.113	2.61	F	Ngoile (1987)
	0.175	2.43	M	
Scotland	0.201	2.33	All	Young *et al.* (2004)
Scotland west coast	0.151	2.51	F	Ngoile (1987)
	0.214	2.37	M	
Scotland	0.138	2.49	F	Boyle and Ngoile (1993b)
	0.192	2.36	M	
Scotland	0.151	2.43	F	Pierce *et al.* (1994c)
	0.206	2.29	M	
Northern North Sea	0.161	2.53	F	Ngoile (1987)
	0.268	2.33	M	
Middle North Sea	0.164	2.45	F	Ngoile (1987)
	0.232	2.55	M	
English Channel	0.449	2.43	F	Holme (1974)
	0.527	2.29	M	
Northwestern Spain	0.111	2.57	F	Guerra and Rocha (1994)
	0.138	2.44	M	
Portugal	0.102	2.60	F	Moreno *et al.* (1994)
	0.103	2.58	M	
Portugal	0.104	2.59	F	Cunha (2000)
	0.111	2.54	M	
Azores	0.425	2.18	F	Martins (1982)
	0.548	2.08	M	
Northeastern Mediterranean Sea	0.141	2.46	All	E. Lefkaditou, pers. comm.

12.4.3 Maturation and reproduction

There seems to be an annual cycle in the sex ratio, females being more abundant than males during the spawning season, e.g. November–February in Scotland. There is also evidence of males outnumbering females during the recruitment period in Scotland and Spain (Holme, 1974; Guerra and Rocha, 1994; Pierce *et al.*, 1994c; Collins *et al.*, 1999). Holme (1974) speculated that large males are better able to avoid trawls, but Collins *et al.* (1999) indicate that abundance of males declines earlier than that of females in the breeding season.

The maturation process in *L. forbesii* is affected by both intrinsic factors (e.g. age, body size, and sex) and external factors (e.g. hatching season, temperature, daylight, food supply). In Scottish waters, gonad weight in both sexes is related to calendar month, consistent with seasonal triggering of maturation, and to digestive gland weight, indicating an effect of nutritional status, as might be expected if energy for gonad growth is derived primarily from food (Smith *et al.*, 2005). Once animals have reached maturity,

there is evidence of a decline in gonad growth in males, whereas females apparently continue to invest energy to grow gonads (Wangvoralak, 2011), presumably because eggs continue to grow and mature within the ovary.

As noted above, male *L. forbesii* exhibit at least two different growth and reproduction strategies, individuals maturing over two different size ranges (Guerra and Rocha, 1994; Moreno *et al.*, 1994; Boyle *et al.*, 1995; Collins *et al.*, 1995d), although apparently at similar ages (Wangvoralak, 2011), and a similar phenomenon is sometimes encountered in females. As a consequence, standard population reproductive parameters such as size-at-50%-maturity ($MLm_{50\%}$) can be misleading, at least in males. Published results on the range of size at maturity, nevertheless, make clear the variability of the growth and maturation process (Table 12.2).

Loligo forbesii has an annual life cycle and is generally described as semelparous (Lum-Kong *et al.*, 1992; Pierce *et al.*, 1994c; Collins *et al.*, 1995d), with an extended spawning season or "intermittent, terminal spawning", i.e. the females lay eggs in batches and die shortly after completion of spawning (Rocha *et al.*, 2001). The timing of peak spawning activity varies across the range, and additional peaks are observed in some areas (Roper *et al.*, 1984; Lum-Kong *et al.*, 1992; Boyle and Ngoile, 1993a; Guerra and Rocha, 1994; Moreno *et al.*, 1994; Pierce *et al.*, 1994c; Boyle *et al.*, 1995; Collins *et al.*, 1995d), possibly because of the presence of both winter and summer breeders (Holme, 1974). In Scottish waters, *L. forbesii* spawns mainly in December–February, although at least some mature specimens can be found throughout the year (Pierce *et al.*, 1994c).

Demersal trawl survey results from 2004 (Stowasser *et al.*, 2005) indicated that the greatest abundance of *L. forbesii* in autumn was along the shelf edge west of Scotland and Ireland. As the spawning season progressed (January–March), locations of high squid abundance shifted from offshore to inshore, with abundance greatest in the Minch (northwestern Scotland) and Moray Firth (northeast Scotland) and south along the east (North Sea) coast of the UK.

Table 12.2. Reported ranges of size-at-maturity for male and female *L. forbesii* (from size at first detection of maturity to 100% of sample mature). Where multiple microcohorts were detected, separate estimates are given for each.

Area	Male ML (mm)	Female ML (mm)	Reference
Faroe Islands	200–250	180–200	Gaard (1987)
Scotland + Faroe Islands		220	Howard (1979)
Scotland (west coast)	120–450	160–310	Boyle *et al.* (1995)
Scotland (west coast)	180–220, 250–320, >400	180–220, 280–320	Collins *et al.* (1999)
Scotland (North Sea)	180–350	192–250	Wangvoralak (2011)
Ireland	120–400	150–300	Collins *et al.* (1995a)
England (southwest)	130–420	160–320	Holme (1974)
Galicia (northwestern Spain)	160–380	160–380	Guerra and Rocha (1994)
Portugal	145–450	175–315	Moreno *et al.* (1994)
Azores Islands	<310–490	<250–326	Martins (1982)
Azores Islands	<240–611	<200–390	Porteiro and Martins (1994)

In summer, mature specimens were found only in the English Channel. In an analysis of historical data, Pierce *et al.* (2005) found high autumn/winter temperatures (high winter NAO values) to be associated with high squid abundance and precocious maturation, which tended to favour high abundance in the following year, along with increased body weight at length and a decrease in the proportion of animals breeding in December. High abundance in summer, conversely, was correlated with lower body weight at length the following year.

Pham *et al.* (2009) were the first to describe spawning behaviour of this species in the wild and noted that the "chromatic, locomotor and postural components were very similar to those of other coastal loliginids observed on spawning grounds". They describe a range of behaviours including "'pair formation', 'mate guarding', 'egg holding', 'egg touching', 'white arms', 'red accessory nidamental glands', 'accentuated testis', and 'jockeying and parrying'".

Although they are relatively short-lived species, fecundity in loliginid squids is surprisingly low. Female *L. forbesii* apparently produce only a few thousand eggs in their lifetime (Boyle *et al.*, 1995). Mature females exhibit asynchronous oocyte maturation, with oocytes found in various stages of development at any one time (Ngoile, 1987; Collins *et al.*, 1995a). The number of oocytes present (or potential fecundity) in *L. forbesii* females has been estimated to range from 1000 to 23 000 eggs (Guerra and Rocha, 1994; Boyle *et al.*, 1995). A weak positive relationship between ML and potential fecundity is reported, although small mature females may have relatively more oocytes than larger females as a proportion of body weight (Boletzky, 1987b; Hanlon *et al.*, 1989; Guerra and Rocha, 1994; Boyle *et al.*, 1995; Collins *et al.*, 1995a).

12.5 Biological distribution

12.5.1 Habitat

Jereb *et al.* (2010) indicate that the species can be found down to >700 m, based on captures from bottom-trawl surveys in the Sicilian Channel and records of egg masses, both in the Mediterranean and Atlantic.

The main population in UK waters is distributed over the continental shelf and shelf edge, mostly in water 50–250 m deep and within ca. 200 km of the coast (Pierce *et al.*, 1994b). Oesterwind *et al.* (2010) recorded *L. forbesii* at depths of 20–171 m in the North Sea during bottom-trawl surveys. At Rockall Bank, 200 miles west of Scotland, survey catches were mostly in shallow water <150 m (Pierce *et al.*, 1998). Moreno *et al.* (1994) reported *L. forbesii* at depths of 100–200 m in Portuguese waters. Mangold-Wirz (1963a) described the vertical distribution of *L. forbesii* as between 15 to 150 m in the North Sea and eastern Atlantic, and 150–400 m in the Mediterranean.

Several published records show that the species can extend into deeper water. Lordan and Casey (1999) found egg masses at ca. 500 m depth in the Celtic Sea, Ragonese and Jereb (1986) reported *L. forbesii* to be commonly captured at 560 m depth in the Sicilian Channel, Salman and Laptikhovsky (2002) recorded egg masses at a depth of 730 m in the Aegean Sea, Lefkaditou *et al.* (2003a) refer to its capture at 715 m in the Ionian Sea, and Orsi Relini *et al.* (2009) report an egg mass from 600 m in the Ligurian Sea. In the Azores, the species is recorded over water depths >1000 m, although such depths are close to the coast, and there is no published evidence that the species descends to the seabed at such depths; it is normally fished near the surface by jigging (Martins, 1982).

Where its distribution overlaps with that of *L. vulgaris*, *L. forbesii* tends to be found in deeper water. According to Ragonese and Jereb (1986), in the Sicilian Channel (central

Mediterranean), the switch from dominance by one species to the other is at ca. 70–80 m; *L. vulgaris* was seldom found deeper and *L. forbesii* was never captured shallower. A similar situation is described by Ria *et al.* (2005) in the southern Ligurian Sea (Mediterranean), where *L. forbesii* is found at depths of 80–600 m, whereas *L. vulgaris* is in shallow coastal waters (<60 m depth).

Studies on temporal trends in abundance of *L. forbesii* in UK waters show that both the timing of migration into the English Channel and winter abundance in the North Sea are related to sea surface temperature (SST) (Pierce *et al.*, 1998; Waluda and Pierce, 1998; Sims *et al.*, 2001; Pierce and Boyle, 2003). Squid abundance in the English Channel peaks when bottom temperature is 13°C, independent of time of year (Sims *et al.*, 2001). Zuur and Pierce (2004) found that squid abundance was related to both strength of the North Atlantic Oscillation (NAO) and SST, proposing that both the inflow of Atlantic water (with associated nutrients, prey organisms, and squid) and favourable growth conditions (i.e. temperature) are important in determining abundance, as measured by catch per unit effort.

The distribution of *L. forbesii* in the North Sea in winter seems to be strongly correlated with seabed temperatures (SBT) and, to a lesser extent, salinity (i.e. more squid in more saline waters), with *L. forbesii* generally not being found at temperatures <7°C (Pierce *et al.*, 1998). Bellido *et al.* (2001) found that commercial fishery catch rates of *L. forbesii* in UK waters were best when SST was ca. 11°C. Oesterwind *et al.* (2010) found *L. forbesii* at temperatures (SBT) of 6.3–9.4°C in winter and 8.1 and 18.2°C in summer in the North Sea. In Portuguese waters, catches of loliginid squid were best when SST was in the range 13–16°C (Moreno and Sousa-Reis, 1995). Georgakarakos *et al.* (2002) found a positive correlation between loliginid landings and SST in nutrient-rich areas.

12.5.2 Migrations

Migratory patterns have been described for the species, but are poorly understood. One issue is the low spatial and temporal resolution of data available from both trawl surveys and commercial fisheries (trawl surveys tend to include only a single haul per ICES rectangle, and commercial catch data are normally aggregated to this spatial scale). In addition, movements have been inferred from shifts in distribution rather than directly observed and, finally, there is evidence that distribution and movements vary between years (see Waluda and Pierce, 1998; Viana *et al.*, 2009).

Several authors have reported evidence of inshore–offshore movement associated with the breeding cycle in Scottish waters (Pierce *et al.* 1998; Stowasser *et al.*, 2005; Viana *et al.*, 2009), and there is also evidence of movements parallel to the coast in several regions (Holme, 1974; Waluda and Pierce, 1998; Sims *et al.*, 2001; Oesterwind *et al.*, 2010). Most evidence seems to suggest that post-hatching *L. forbesii* migrate away from the coast, moving offshore as they grow, but subsequently returning to shallow water to breed. There are few records of capture of post-spawning squid, and it is most likely that they die soon after spawning, although post-breeding offshore migration of adults has also been proposed.

Holme (1974) reported that *L. forbesii* hatched in the western English Channel and migrated east, appearing in trawls off Plymouth around May. After a few months of rapid growth in the English Channel and the southern North Sea, the squid moved back to the Western Approaches to spawn, and died during the following December–January (although he also noted the presence of summer spawners). Sims *et al.* (2001) showed that the annual timing of the arrival of *L. forbesii* in trawls off Plymouth varied according to sea temperature.

Waluda and Pierce (1998) interpreted month-to-month trends in catch locations from UK fishery data as implying west–east migrations over the course of the breeding cycle, with squid moving from deeper water in the west to spawn in coastal water in the east, subsequently moving offshore again. However, subsequent analysis of commercial fishery catch data for Scotland, from a longer series of years, by Viana *et al.* (2009) indicated that inshore–offshore movements with no important east–west component were more common.

Distribution maps based on trawl survey data collected by Scottish vessels during the years 1980–1994 confirm the existence of centres of abundance north of Shetland and at ca. 56°N in both February and April, whereas the only centre of abundance in August and October was around the Moray Firth (Pierce *et al.*, 1998). These findings are consistent with observations by fishers that high concentrations of juveniles are found close inshore in the Moray Firth (Scotland) in summer, where they are targeted by a small directed fishery (Young *et al.*, 2006a, b).

Trawl survey data from UK waters for 2004–2005 showed that squid were predominantly found in deeper water along the shelf edge (100–200 m) at the beginning and end of the winter spawning season (November and March), and that most squid were caught in water shallower than 50 m during the peak of winter spawning (Stowasser *et al.*, 2005). Trawl survey data from 2007 to 2009 indicate that *L. forbesii* concentrate mainly in the northern part of the North Sea in winter, especially around Shetland, and that the centre of abundance shifts south to ca. 56°N in summer (Oesterwind *et al.*, 2010).

12.6   Trophic ecology

12.6.1   Prey

Loligo forbesii is a highly mobile, opportunistic predator that will attack and consume any potential prey that it can overcome (including members of its own species). Dietary studies have covered various parts of its range, including the UK (Ngoile, 1987; Pierce *et al.*, 1994a; Collins and Pierce, 1996; Pierce and Santos, 1996; Stowasser, 1997, 2004; Wangvoralak *et al.*, 2011), Ireland (Collins *et al.*, 1994; Collins and Pierce, 1996), Spanish Atlantic waters (Pierce *et al.*, 1994a; Rocha *et al.*, 1994), and Portugal (Martins, 1982; Porteiro *et al.*, 1990; Pierce *et al.*, 1994c).

A large number of different prey species, including various fish, crustaceans, and cephalopods, as well as polychaetes and other molluscs, have been identified in *L. forbesii* stomachs (Table 12.3). In most locations, fish are the main prey, with crustacean, cephalopod, and polychaete species also present in the diet to varying degrees. The most prominent fish species in the diet belong to the families Gadidae, Clupeidae, Ammodytidae, and Gobiidae (Collins *et al.*, 1994; Rocha *et al.*, 1994; Collins and Pierce, 1996; Pierce and Santos, 1996; Wangvoralak *et al.*, 2011).

There are ontogenetic shifts in diet, from a crustacean-dominated one in juvenile squid to a predominance of fish in the diet of adult squid (Pierce *et al.*, 1994a). Rearing studies showed *L. forbesii* paralarvae to feed mainly on copepods, juvenile mysids, and palaemonid larvae (Forsythe and Hanlon, 1989; Hanlon *et al.*, 1989). In Spanish waters, cephalopods also make up a greater component of the diet of *L. forbesii* as the squid grow (Rocha *et al.*, 1994). Cannibalism in *L. forbesii* appears to be limited to large squid (>150 mm ML) feeding on much smaller ones (20–50 mm ML) (Collins *et al.*, 1994).

The same broad prey taxa are important in the diet of *L. forbesii* throughout its geographic range (Pierce *et al.*, 1994a). However, regional differences in the diet have also

been identified. For example, in Scottish waters, whiting (*Merlangius merlangius*), *Trisopterus* spp., and sandeels (Ammodytidae) are the principal fish prey (Pierce *et al.*, 1994a), whereas in Irish waters, the dominant prey species are sprat (*Sprattus sprattus*) and *Trisopterus* spp. (Collins *et al.*, 1994). Prey composition may vary seasonally, probably because of changes in prey availability (Collins *et al.*, 1994; Pierce *et al.*, 1994a; Rocha *et al.*, 1994).

No significant differences have been found between the diets of male and female *L. forbesii* (Pierce *et al.*, 1994a; Rocha *et al.*, 1994) or animals of different maturity stages (Rocha *et al.*, 1994). However, Howard *et al.* (1987) observed seasonal differences in stomach emptiness, with a higher frequency of empty stomachs in winter, and Gaard (1987) noted that *L. forbesii* probably feeds mainly by day, because full stomachs and less-digested contents were more frequent in samples taken in the evening. Rocha *et al.* (1994) observed more empty stomachs in immature females than in mature females and in mature females than in mature males.

Investigations into the trophic ecology of *L. forbesii* through fatty-acid and stable-isotope analysis have shown that *L. forbesii* is mainly associated with the benthic foodweb and also confirmed that both diet composition and dietary variability change with increasing body size. Application of these methods has also made it possible to infer ontogenetic movements from offshore to more coastal waters and to determine the diet of individuals that have no food in their stomachs (Stowasser, 2004). Chouvelon *et al.* (2011) reported a positive correlation between $\delta^{15}N$ values and ML in this species, implying an ontogenetic trend of increasing prey size (and trophic level).

Table 12.3. List of identified prey types and species from *Loligo forbesii* stomach contents (compiled from Martins, 1982[1]; Collins *et al.*, 1994[2]; Guerra and Rocha, 1994[3]; Pierce *et al.*, 1994a[4]; Stowasser, 1997[5], 2004[6]; Hastie *et al.*, 2009a[7]; Wangvoralak *et al.*, 2011[8]).

Taxon	Species
Osteichthyes	
Agonidae	*Agonus cataphractus* (hooknose)[2]
Ammodytidae	*Ammodytes marinus* (lesser sandeel)[8], *Ammodytes* spp.[2,4,5,8], *Gymnammodytes semisquamatus* (smooth sandeel)[3], *Hyperoplus lanceolatus* (greater sandeel)[8], indet.[2,3,4]
Argentinidae	*Argentina silus* (greater argentine)[8], *Argentina sphyraena* (argentine)[2,3,8], *Argentina* spp.[4], indet.[2]
Atherinidae	*Atherina* spp.[3]
Belonidae	*Belone belone* (garfish)[1]
Bothidae	*Arnoglossus laterna* (Mediterranean scaldfish)[8]
Callionymidae	*Callionymus lyra* (dragonet)[2,3,8], *C. maculatus*[2], *Callionymus* spp.[3,4,8], indet.[2,5]
Caproidae	*Capros aper* (boarfish)[1,4]
Carangidae	*Trachurus picturatus* (blue jack mackerel)[1,8], *T. trachurus* (Atlantic horse mackerel)[2,3,4,5], *Trachurus* spp.[4]
Centriscidae	*Macroramphosus scolopax* (longspine snipefish)[4]
Cepolidae	*Cepola macrophthalma* (red bandfish)[2,3]
Clupeidae	*Clupea harengus* (Atlantic herring)[2,4,5,6], *Sardina pilchardus* (European sardine or pilchard)[3], *Sprattus sprattus* (European sprat)[2,5], indet.[2,4,5,8]
Cyclopteridae	*Cyclopterus lumpus* (lumpfish)[4]

Gadidae	*Gadiculus argenteus* (silvery pout)[2,4,6], *Gadus morhua* (Atlantic cod)[4,5,8], *Melanogrammus aeglefinus* (haddock)[4,5,8], *Merlangius merlangus* (whiting)[2,4,5,8], *Micromesistius poutassou* (blue whiting)[3,4,5,8], *Phycis phycis* (forkbeard)[1], *Pollachius virens* (saithe)[4], *Trisopterus esmarkii* (Norway pout)[2,5,8], *T. minutus* (poor cod)[2,8], *Trisopterus* spp.[2,3,4,5,6,8], indet.[2,3,4,5,6,8]
Gobiidae	*Aphia minuta* (transparent goby)[2,3,6,8], *Crystallogobius* spp.[3], *Lesueurigobius friesii* (Fries' goby)[2], *Gobiusculus flavescens* (two-spotted goby)[8], *Gobius niger* (black goby)[2], *Pomatoschistus minutus* (sand goby)[2,3], *Pomatoschistus* spp.[3,8], indet.[2,3,4,5,6,8]
Lotidae	*Enchelyopus cimbrius* (four-bearded rockling)[2,8], indet.[4]
Merlucciidae	*Merluccius merluccius* (European hake)[3]
Pholidae	*Pholis gunnellus* (rock gunnel)[8]
Pleuronectidae	*Hippoglossoides platessoides* (Long rough dab)[8], *Pleuronectes platessa* (European plaice)[2], indet.[2]
Scombridae	*Scomber scombrus* (Atlantic mackerel)[4], *Scomber* spp.[4]
Sebastidae	*Helicolenus dactylopterus* (blackbelly rosefish)[4], *Sebastes norvegicus* (as *S. marinus*) (Norway redfish)[4]
Serranidae	*Anthias anthias* (swallowtail seaperch)[1]
Sparidae	*Boops boops* (bogue)[1]
Sternoptychidae	*Maurolicus muelleri* (pearlside)[2,4]
Trichiuridae	*Lepidopus caudatus* (silver scabbardfish), indet.[1,4]
Triglidae	*Eutrigla gurnardus* (grey gurnard)[2], indet.[2]
Chondrichthyes	
Etmopteridae	*Etmopterus* spp.[1]
Crustacea	indet.[4]
Decapoda	indet.[5,6,8]
Dendrobranchiata-Penaeiodea	indet.[1]
Pleocyemata-Anomura	Paguridea indet.[2]
Pleocyemata-Brachyura	*Maja* spp.[1], indet.[1,3]
Pleocyemata-Caridea	Crangonidae indet.[2], *Dichelopandalus bonnieri*[2], Hippolytidae indet.[3], Oplophoridae indet.[2], Palaemonidae indet.[2,5], Pandalidae indet.[5,6], *Pasiphaea sivado*[2], Processidae indet.[3], indet.[3]
Macrura reptantia-Astacidea	*Nephrops norvegicus* (Norway lobster)[2]
Euphausiacea	*Meganyctiphanes norvegica*, indet.[1,2,3,6]
Mysida	indet.[3]
Amphipoda	indet.[1,5]
Cumacea Isopoda	Dyastilidae spp.[5]
Cymothoida	Gnathiidae spp.[5], *Gnathia* spp. (larvae)[2]
Copepoda	
Calanoidea	Calanoidae spp.[5,6], *Temora turbinata*[8], indet.[3]
Cephalopoda	

Myopsida	*Alloteuthis subulata*[3,4], *Alloteuthis* spp.[3], *Loligo forbesii*[1,4], *L. vulgaris*[3], Loliginidae indet.[2]
Sepioidea	Sepiolidae indet.[2], *Sepiola* spp.[5], *Sepietta* spp[5]., indet.[4]
Octopoda Teuthida	*Eledone cirrhosa*[5], *Octopus vulgaris*[3], Octopodidae indet.[2,5], indet.[1,2,4] Ommastrephidae indet.[5]
Gastropoda	*Calliostoma zizyphinum*[2], indet.[2]
Bivalvia	*Chlamys* spp.[2], indet.[3]
Nematoda	indet.[6]
Polychaeta	indet.[4,5]
Phyllodocida	*Nereis pelagica*[2], *Nereis* spp.[8], Nereidae indet.[1]
Terebellida	Sternaspidae indet.[1]
Chaetognatha	
Sagittoidea	*Sagitta* spp.[1]
Foraminifera	*Miniacina* spp.[1]
Bryozoa	indet.[1]
Algae	indet.[2]

12.6.2 Predators

Loligo forbesii forms a component of the diet of a number of marine predators including some large demersal fish and marine mammals (Table 12.4). The great skua (*Catharacta skua*) is the only bird species from Northeast Atlantic waters for which beaks of *Loligo* sp. have been reported in its stomach contents (Furness, 1994), but because sampling was carried out in Shetland, it is reasonable to assume that the beaks were from *L. forbesii.*

Identification of the stomach contents in the majority of predatory fish and marine mammals is at the level of the genus *Loligo* or family Loliginidae and, consequently, although in many cases the predators probably eat *L. forbesii*, we cannot rule out predation on *L. vulgaris.* Confusion with predation on *Alloteuthis* spp. is less likely because the beaks of this genus are distinguishable (see Clarke, 1986). Loliginid beaks have been reported from the stomachs of pygmy sperm whale (*Kogia breviceps*), northern bottlenose whale (*Hyperoodon ampulatus*), common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), bottlenose dolphin (*Tursiops truncatus*), Atlantic white-sided dolphin (*Laganorhynchus acutus*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melas*), and Risso's dolphin (*Grampus griseus*) (as seen in, for example, De Pierrepont *et al.*, 2005; Santos *et al.*, 2014). None of these predators were considered to be a major cause for mortality of *Loligo* species. In some cases, the geographic location from which samples were obtained makes it reasonably certain that the beaks were from *L. forbesii* (MacLeod *et al.*, 2014). Pierce and Santos (1996) note that the species is also eaten by grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) and suggested that marine mammals could consume a greater amount than is taken by fisheries in Scotland. Cannibalism is known for the species, and it is also preyed upon by its congener *L. vulgaris* (Guerra and Rocha, 1994).

Table 12.4. Known predators of *Loligo forbesii* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalopoda	European squid (*Loligo vulgaris*)	Guerra and Rocha (1994)

Chondrich-thyes	Blonde ray (*Raja brachyura*)	Farias *et al.* (2006)
Osteichthyes	Atlantic cod (*Gadus morhua*)	Daly *et al.* (2001), Magnussen (2011)
	Atlantic lizardfish (*Synodus saurus*)	Soares *et al.* (2003)
	Monkfish (*Lophius piscatorius*)	Daly *et al.* (2001)
	Swordfish (*Xiphias gladius*)	Salman (2004)
Aves	Great skua (*Catharacta skua*)	Furness (1994)
Pinnepedia	Grey seal (*Halichoerus grypus*)	Pierce *et al.* (1991a)
	Harbour seal (*Phoca vitulina*)	Brown and Pierce (1998)
Cetacea	Harbour porpoise (*Phocoena phocoena*)	Rogan and Berrow (1996), Santos *et al.* (2005b)
	Risso's dolphin (*Grampus griseus*)	Bearzi *et al.* (2011)
	Sperm whale (*Physeter macro-cephalus*)	Clarke and Pascoe (1997), Santos *et al.* (1999*, 2001b)
	Striped dolphin (*Stenella co-eruleoalba*)	Würtz and Marrale (1993)

*This was a single beak

12.7 Fisheries

Loligo forbesii is one of the two loliginid species of significant commercial importance in the Northeast Atlantic. As noted in the account for *L. vulgaris*, landings are not routinely recorded by species, and both FAO and ICES report figures for long-finned squid (Loliginidae); sometimes even this level of taxonomic disaggregation is unavailable. Scotland is probably the only reporting unit with significant catches for which it can be safely assumed that most long-finned squid landings reported to ICES are *L. forbesii*. Between 2000 and 2010, landings from the northern North Sea fluctuated from ca. 350 t in 2001 to 21 000 t in 2010, with a further 70–450 t arising from the west coast (ICES Division VIa). Interestingly, landings from the offshore ICES Division VIb, which includes Rockall, rose from <100 t annually to >700 t in 2008, possibly indicating the re-emergence of the Rockall fishery, which last generated substantial landings in the 1980s (see below). Although landings dipped to slightly over 200 t in 2009, they increased to 700 t again in 2011 (ICES, 2012). Note that these trends in landings in Scotland do not follow the overall trends for loliginid landings in the European ICES Area which, over the same time-period, show a peak in 2003 (ICES, 2012). Although this trend should not be overinterpreted, it is likely that the two *Loligo* species show different abundance trajectories (see also Chen *et al.*, 2006).

Records of landings in Scotland go back to the early 20th century (Thomas, 1969), although the quantities landed remained small for several decades, and dropped to a few tens of tonnes during the two world wars. The species supported a directed fishery by Denmark and Sweden in the North Sea and Skagerrak in the years 1948–1953 (Arnold, 1979). The fishery in Scotland expanded in the mid-1950s, facilitated by the advent of deep-freeze facilities and exports to continental Europe, and targeted fishing from small boats emerged in the English Channel in the mid-1970s (Arnold, 1979). Since the rise and fall of the short-lived fishery for *Todarodes sagittatus* in Norway, *L. forbesii* has been the dominant squid species fished north of the English Channel.

The seasonality of fishing is related to the seasonality of recruitment. Depending on the area, there are one or several associated pulses of recruitment. Two main pulses of recruitment have been reported in Scotland in April and November, though with small

numbers of recruits present throughout most of the year (Lum-Kong *et al.*, 1992; Boyle and Pierce, 1994; Pierce *et al.*, 1994b; Collins *et al.*, 1997, 1999). The April recruitment may represent summer spawners. Shifting seasonal patterns in historical fishery landing data for Scotland are consistent with the relative importance of summer and winter breeding seasons having fluctuated since the 1970s (Pierce *et al.*, 2005).

In northern Europe and beyond the coastal zone in southern Europe, *L. forbesii* is mainly taken as bycatch in demersal trawl fisheries (e.g. Pierce *et al.*, 1994b). The importance of directed fishing may be limited by the wide fluctuations in abundance reported (Young *et al.*, 2004; 2006b), and there also appear to have been historical shifts in distribution (e.g. a disappearance from the southern part of its range in Atlantic coastal waters for several years; Chen *et al.*, 2006).

In Scotland, some trawl landings originate from 480 km west of mainland Scotland around Rockall. Although fishing in the area is mainly targeted at whitefish (e.g. haddock), it appears that squid have been targeted when abundant. Catches of *L. forbesii* at Rockall are made mainly in July and August when only the smallest recruits are caught in coastal waters, so possibly representing exploitation of a different stock. Catches from Rockall were greatly reduced after the mid-1980s (Pierce *et al.*, 1994b, 2005). A small directed trawl fishery for squid exists close inshore in the Moray Firth (North Sea, Scotland). This fishery is strongly seasonal (September–November) and usually involves only a few small trawlers between 10 and 17 m in length (Anon., 2000). In the mid-2000s the number of trawlers taking part in this fishery increased dramatically (Young *et al.*, 2006b), but subsequently decreased again (Smith, 2011).

In Portuguese and Galician waters, although official fishery statistics indicate that *L. forbesii* is mainly taken as a bycatch in the multispecies trawl fisheries, local artisanal fisheries employing handjigs also exist (Cunha and Moreno, 1994; Guerra *et al.*, 1994; Rocha *et al.*, 1994). *Loligo forbesii* is the only squid species of economic importance in the Azores, where it is fished by an artisanal fleet equipped with handlines and homemade jigs (Martins, 1982; Porteiro, 1994). There is also some jigging for the species in the English Channel (Hamabe *et al.*, 1982).

Investigation of morphometric variation throughout the range, coupled with the development of molecular markers for this species, suggests no significant separation of stocks throughout the range of its distribution on mainland coasts (Pierce *et al.*, 1994d, e; Brierley *et al.*, 1995; Collins *et al.*, 1997, 1999; Shaw *et al.*, 1999). There is, however, some evidence that animals from offshore, sampled around Rockall Bank west of the UK, may be distinct from the coastal population. Boyle and Ngoile (1993b) recorded morphometric differences between coastal and offshore squid, and Shaw *et al.* (1999) confirmed differences at the molecular level. In the Azores, the degree of morphometric and genetic difference suggests a highly isolated population based on an introductory event up to 1 million years ago (Shaw *et al.*, 1999); the differences may be sufficient to justify recognition of a separate subspecies (Brierley *et al.*, 1995).

12.8 Future research, needs, and outlook

It is a common theme across all the exploited cephalopod species in European waters, but there is a clear and urgent need for routine identification of all landed cephalopods to species level. This is of particular concern in *L. forbesii* and *L. vulgaris* which, despite their superficial morphological similarity, have different habitat preferences and show distinct population trends (see Chen *et al.*, 2006); therefore, assessment of the combined stocks would not be meaningful. Robin and Boucaud-Camou (1995) have shown that

market sampling could be used to quantify monthly changes in proportions of the two *Loligo* species landed along the French coast of the English Channel.

There is a need to develop routine stock assessment for loliginid squid fisheries in Europe, along with appropriate management measures. If squid fishing is to expand, there will need to be more use of selective gear such as jigs, because the bycatch of finfish could be an issue where there is targeted trawling. In the UK, trials to test jigs for squid catching in the 1970s and 1980s were largely unsuccessful (see Pierce *et al.*, 1994b), but it seems likely that this was, to a large extent, a consequence of poor knowledge of squid distribution and abundance fluctuations.

More studies are also needed on the artisanal fisheries that harvest this species (among other loliginids) in coastal waters of southern Europe. In the Azores, depredation by Risso's dolphins (*Grampus griseus*) has the potential to cause significant economic losses in the jig fishery. Such issues would need to be managed if jig fishing for squid were to expand into the larger-scale fishing sectors.

Finally, much more could be learned about the distribution and migration of this species, given access to logbook and VMS position data that are potentially available for a large proportion of the European fishing fleet.

Cephalopod biology and fisheries in European waters: species accounts
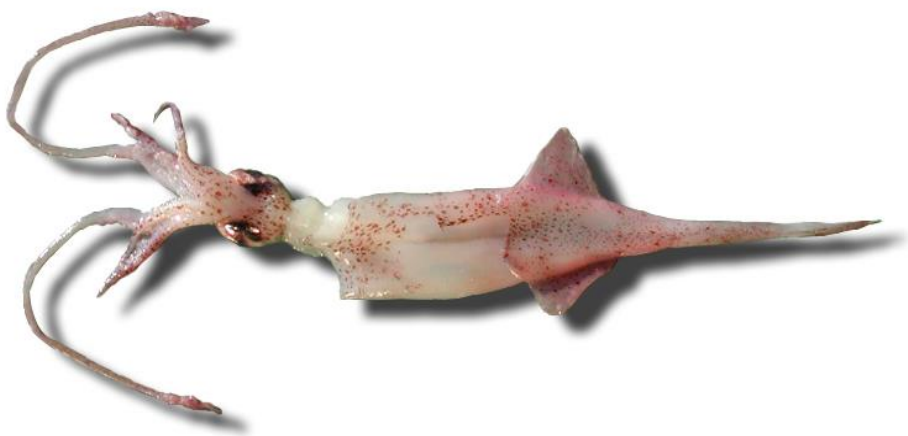
Alloteuthis subulata

European common squid
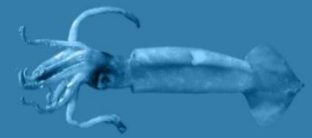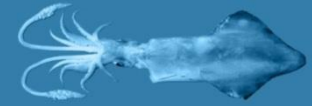
13 *Alloteuthis subulata* (Lamarck, 1798)

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Common names

Casseron commun (France), calamaretto (Italy), lula-bicuda-comprida (Portugal), calamarín picudo (Spain), European common squid (UK) (Figure 13.1).

Synonyms

Loligo subulata Lamarck, 1798, *Sepia subulata*: Bosc (1802), *Sepiola subulata*: Gervais and Beneden (1838).

13.1 Geographic distribution

The European common squid, *Alloteuthis subulata* (Lamarck, 1798) is found in the Northeast Atlantic from ca. 60°N to 20°N and has been reported from several areas of the Mediterranean (Figure 13.2), although it is considered to be absent from the Sea of Marmara and the easternmost parts (Jereb *et al.*, 2010). In the Northeast Atlantic, the species is particularly abundant in Irish waters (Massy, 1928; Lordan *et al.*, 1995; Nyegard, 2001) and the English Channel (Rodhouse *et al.*, 1988). It is common in the North Sea (De Heij and Baayen, 2005; Oesterwind *et al.*, 2010), from northern Scottish waters (Stephen, 1944) and the southwest coast of Norway (Grieg, 1933) to the English Channel, and is considered the dominant cephalopod species in the southern North Sea (De Heij and Baayen, 1999). It is present in the Kattegat, where it is regularly caught in Swedish waters (Hornbörg, 2005), and it enters the western Baltic Sea occasionally (Herrmann *et al.*, 2001). Distributed along the

Figure 13.1. *Alloteuthis subulata.* **Dorsal view. From Guerra (1992).**

French, Spanish, and Portuguese coasts, it extends south onto the Sahara Bank, and, according to Adam (1952), to Rio de Oro waters (Cape Blanc, southwestern Sahara, see also Balguerias *et al.*, 2000). *Alloteuthis subulata* has been found in the western and central Mediterranean (Mangold-Wirz, 1963a; Belcari and Sartor, 1993; Jereb and Ragonese, 1994; Relini *et al.*, 2002; Cuccu *et al.*, 2003a) and in the eastern Ionian Sea (Kaspiris and Tsiambaos, 1986; Lefkaditou *et al.*, 2012). A few records of the species from the northern Aegean Sea exist from trawl surveys (D'Onghia *et al.*, 1996; Salman *et al.*, 1997), but these have not been confirmed by the most recent investigations (Lefkaditou *et al.*, 2012), so remain questionable. Although Zuev and Nesis (1971) refer to the presence of *A. subulata* in the Sea of Marmara, it has not been recorded during recent studies in that sea (Katağan *et al.*, 1993; Ünsal *et al.*, 1999). Also, old records of this species from the Levantine basin remain questionable (see **Remarks**).

Figure 13.2. *Alloteuthis subulata.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

13.2 Taxonomy

Loliginid squids have been under constant systematic revision for many years. Two species placed in the genus *Alloteuthis* Wülker, 1920, *Alloteuthis subulata* and *A. media*, have been the object of numerous morphological and molecular studies in recent years (see **Remarks** for details). Results confirmed that two species exist in European waters, but, given that the type specimen of *subulata* is not extant and the whereabouts of the type specimen of *media* has not been confirmed, taxonomic issues abound (Allcock, 2010). Clearly, further studies are required to help define the whole species complex. Until the taxonomic situation with *A. media* and *A. subulata* is resolved, we elect to retain them here as separate entities (see also Jereb *et al.*, 2010).

13.2.1 Systematics

Coleoidea – Decapodiformes – Myopsida – Loliginidae – *Alloteuthis.*

13.2.2 Type locality

Mediterranean Sea.

13.2.3 Type repository

Assumed to have originally been Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France. However, type specimen has not been found here [fide Lu *et al.* (1995)].

13.3 Diagnosis

13.3.1 Paralarvae

Paralarvae are not described, but embryonic statoliths are documented (Morris, 1993). The young stages are visually almost indistinguishable from *Loligo* spp. (Grimpe, 1925; Hanlon *et al.*, 1992). However, compared with *Loligo forbesii*, hatchlings of *A. subulata* have a different chromatophore arrangement, with more yellow chromatophores (Degner, 1925; Hanlon *et al.*, 1992). Sizes of hatchlings are given as 1.5–2.2 mm ML by Jereb and Roper (2010), with most guides citing a size of ca. 2 mm. However, Yau (1994) indicated mean hatching size to be 2.0–2.8 mm. This is smaller than the typical hatching size for *L. forbesii* of ca. 4.5 mm (Boletzky, 1987b; Hanlon *et al.*, 1989), although Gowland (2002) quotes 3 mm for hatching size in *L. forbesii*, suggesting some potential for confusion.

13.3.2 Juveniles and adults

Juvenile *A. subulata* have a bullet-shaped body, with well-developed, paddle-shaped, terminal fins coming to a simple point at the apex. This apex develops into a tail in the subadult stage (Yau, 1994). Although young stages are similar to those of *Loligo* spp., the chromatophore arrangement still differs, with more yellow chromatophores than in *L. forbesii* (Degner, 1925; Hanlon *et al.*, 1992; Yau, 1994). Like all squid in the family Loliginidae, adult *A. subulata* are muscular, with elongated mantles and clearly-defined fins (Nesis, 1982/1987). The fins are situated on the posterior half of the mantle, reaching its posterior end. The arms have two series of suckers, and the tentacles widen into clubs at the ends with four series of suckers. Members of the genus *Alloteuthis* can be separated from other genera of the family Loliginidae based on their small size as adults (although care must be taken to avoid confusion with young *Loligo*) and a mantle that is 6- to 15-fold longer than its width. The fins are ca. rhomboidal, longer than wide, and end far from the anterior edge of the mantle; they are convex on the anterior edge and attenuate posteriorly into a long, slender tail, which can be more than 50% of the mantle length in males. The fin width is >25% of the mantle length and the longest arm is 20–25% of the mantle length. The tentacles are considerably shorter than the head and mantle combined, with narrow clubs that have pairs of central suckers attached obliquely to the club axis at an angle of ca. 45° (Nesis, 1982/87). The tentacle club arrangement is similar in juveniles and adults, with median series of suckers three- to fourfold larger than marginal suckers (Yau, 1994). The left ventral arm (IV) is hectocotylized in mature males, with 6–8 pairs of normal suckers proximally followed by two longitudinal series of fine papillae distally (Yau, 1994).

Within the genus *Alloteuthis, A. subulata* has traditionally been separated from other members of the genus (*A. media* and *A. africana*) based on the length of the tail and fins; a tail up to 20 mm long in females, and 50–60 mm long in males, and fins that are more that 50% of ML, are reported by Nesis (1982/1987). Recent studies, however, suggest that these characters offer a doubtful and unreliable tool for separating the species (Laptikhovsky *et al.*, 2002, 2005; Anderson *et al.*, 2008). First, these characters are evident only upon attainment of maturity (Laptikovsky *et al.*, 2005). Second, the nature of morphometric sexual dimorphism differs between species; females grow larger in *A. media*, whereas males develop a longer mantle and tail in *A. subulata* and *A. africana* (Arkhipkin and Nekludova, 1993; Lefkaditou *et al.*, 2012). According to Nesis (1982/1987), Laptikovsky *et al.* (2002), and Anderson *et al.* (2008), the relative size of club suckers (as described by Naef, 1921/1923) is informative for separating *A. subulata* and *A. media* (the suckers are smaller in *A. subulata*). In addition, Lefkaditou *et al.* (2012) showed that, using the length of the anterior part of the mantle, i.e. mantle length (ML)

minus fin length (FL), as a reference length, the relative arm length (much shorter in *A. subulata*) can be used to distinguish this species from *A. media* (see the *A. media* account in the present volume for additional details). In addition, Muus (1963) indicated that at 30–50 mm ML, *A. subulata* has a shorter tentacular club than *A. media* (club no more than 11 mm compared with at least 12 mm).

According to Roper *et al.* (1984), maximum ML is ca. 200 mm. Hastie *et al.* (2009b) give maximum ML as 215 mm in males and 150 mm in females, whereas Jereb *et al.* (2010) reported maximum ML as 184 mm for males and 140 mm for females; in both cases, values are based on examination of available literature. Regional studies give various maximum lengths (unless otherwise stated, these refer to males), but differences may reflect relatively limited sampling periods or areas. Moreno (1995) reports a maximum size in Portuguese waters of 183 mm ML. The largest individuals sampled in the English Channel during 1985 and 1986 measured ca. 160 mm ML (Rodhouse *et al.*, 1988). Arkhipkin and Nekludova (1993) mention individuals up to 180 mm ML off West Africa. Nyegaard (2001) reported mean sizes in the Irish Sea as 55–87 mm ML for males and 58–108 mm for females, depending on the month. In a more recent study (G. Stowasser, pers. comm.), the species was sampled in three areas, and size ranges for mature specimens were 80–120 mm in females and 90–160 mm in males in the Irish Sea, 60–90 mm in females and 70–120 mm in males in the northern North Sea, and 60–100 mm in females and 50–120 mm in males in the German Bight. In another North Sea study, maximum length of females in winter was 113 mm and that of males was 151 mm, but in summer, both sexes were larger on average (females, maximum 117 mm; males, maximum 160 mm) (Oesterwind *et al.*, 2010).

13.4 Remarks

Although it appears to be safe to conclude that there are two distinct morphotypes of *Alloteuthis* in European waters, real doubts remain as to the true taxonomic affiliation of the animals we currently think of as *A. subulata* and *A media*. Assuming that there are two distinguishable European species, there is a strong likelihood that past misidentifications have resulted in mixing of information on both species. Laptikhovsky *et al.* (2002) suggested that *A. subulata* and *A. media* are intraspecific forms rather than true species, although the large degree of sympatry between the two types indicates that this is not simply a case of minor differences between allopatric populations. Anderson *et al.* (2008) supported a sister-species relationship between *A. media* and *A. subulata*. According to those authors, who analysed both morphometric and DNA sequence data from *Alloteuthis* specimens from several localities, central club sucker size can be used to separate *A. media* from *A. subulata*, but relative fin length, an easily diagnosable character often used to distinguish *Alloteuthis* species, appears to be of little taxonomic value. As type specimens of neither *A. media* nor *A. subulata* can be located, there are real nomenclatural issues. Anderson *et al.* (2008), considering morphometric and genetic characters, assigned three specimens from the Adriatic to *A. subulata*, but without recourse to type material, the validity of these assignations is impossible to verify. Further details of the issues are given in the **Remarks** section of the *A. media* account.

As a consequence of the above-mentioned taxonomic issues, the exact geographic limits of the distributions of *A. media* and *A. subulata* remain uncertain. The remainder of this account assumes that the morphotypes we think of as representing the two species have been correctly assigned. However, it remains probable that there has been confusion over the years. Hence, Llewellyn (1984) comments that *A. subulata* was reported as *Loligo media* by Beauchamp (1912).

Old records of this species in the eastern Mediterranean, Sea of Marmara, and Levantine Basin (i.e. Gruvel, 1931; Ruby and Knudsen, 1972) remain questionable (see Lefkaditou *et al.*, 2012, for additional details). Studies of morphometric characters and maturation, based on *Alloteuthis* samples collected from the Levant, Aegean, and Marmara seas, noting also the wide range of size at maturity for both females and males that might lead to species misidentification, suggested that the genus *Alloteuthis* is represented by a single taxonomic unit in the eastern Mediterranean, which should be *A. media* (Laptikhovsky *et al.*, 2002; 2005). The mention of the presence of the species as *Loligo subulata* (Gruvel, 1931) in Syrian waters is also questionable (Lefkaditou *et al.*, 2012) and probably refers to *A. media*. Two female *A. subulata* (one from off Haifa, the other from an unknown locality) are listed by Ruby and Knudsen (1972) for the waters off Israel, but the only other mention of *Alloteuthis* specimens from that area refers to *A. media* (Adam, 1966; one male). Therefore, the presence of *A. subulata* in the easternmost waters of the Mediterranean remains questionable.

13.5 Life history

Alloteuthis subulata is a typical small, fast-growing, short-lived cephalopod. Its life cycle can be as short as 6 months (Arkhipkin and Nekudova, 1993) and possibly sometimes as long as 12 months, but there may be several spawning seasons, each probably associated with a different "microcohort".

13.5.1 Egg and juvenile development

Mature ova are reported to measure 1.55 mm (Hastie *et al.*, 2009b). During spawning, gelatinous capsules 30–50 mm long and containing a number of eggs are usually attached to a solid substratum (Yau, 1994). Mantle length of *A. subulata* on hatching is reported to be 1.5–3.2 mm (Mangold-Wirz, 1963a; Yau, 1994; Jereb and Roper, 2010).

Incubation time for eggs is 2–3 weeks at 15–18°C (Lipiński, 1985), but could be longer in cooler waters. Paralarvae and juveniles are planktonic at first, but shift to a near-bottom mode of life 15–30 d after they first appear in the plankton (Yau, 1994). Based on observations of an egg mass kept in an aquarium, Yau (1994) estimated the time of hatching in Scottish waters (North Atlantic) to be around May.

13.5.2 Growth and lifespan

Males and females have similar length–weight relationships until ca. 70 mm ML, when females become relatively heavier than males of a similar length, as reflected in the higher slope coefficients in females (Table 13.1). However, males generally achieve larger body sizes overall (Rodhouse *et al.*, 1988; Hastie *et al.*, 2009b).

Table 13.1. *Alloteuthis subulata.* **Length–weight relationships in different geographic areas for females (F) and males (M). Original equations converted to W = aML^b where W is body mass (g) and ML is dorsal mantle length (cm). From Hastie *et al.* (2009b).**

Region	a	b	Sex
Irish Sea	0.291	1.39	M
Irish Sea	0.150	1.84	F
North Sea	0.184	1.59	M
North Sea	0.160	1.77	F
Portugal	0.420	1.20	M
Portugal	0.167	1.83	F

As in other loliginids, length frequency data for the North Sea suggest the existence of several microcohorts, representing animals with different growth rates and/or hatching times (and potentially also mapping onto different spawning periods), which might be attributable to different spatial variation in water temperatures within the species range (Oesterwind *et al.,* 2010). Oesterwind *et al.* (2010) described five cohorts for males and four cohorts for females in summer. There were two cohorts of males and females in the entire North Sea in winter. Differences between summer and winter length frequency distributions presumably reflect the annual nature of the life cycle.

Growth increments in the statoliths are thought to be deposited daily (Lipiński 1985, 1986; Morris 1993). This provides growth estimates of between 0.03 and 0.1 cm d^{-1}. On the West African shelf, absolute growth rates ranged between 0.5 and 1.0 mm d^{-1} in length and from ca. 0.03 to 0.06 g d^{-1} in weight. Instantaneous relative daily growth rates fell from ca. 2.2% ML d^{-1} and 3.5% BW d^{-1} at 90 d of age to ca. 0.8% ML d^{-1} and 0.5% BW d^{-1} at 210 d (Arkhipkin and Nekludova, 1993; see their Figures 8 and 9).

Rodhouse *et al.* (1988) indicate a lifespan of ca. 12 months in northern temperate waters, but Arkhipkin and Nekudova (1993) proposed a lifespan of 6 months for the population off Northwest Africa, based on statolith analysis.

13.5.3   Maturation and reproduction

Hastie *et al.* (2009b) reported seasonal variation in sex ratio, with a slight overall preponderance of males (M:F = 1.04–1.14 depending on region), although females were relatively more abundant in spring in Portugal (M:F = 0.76) and during summer in the North Sea and Irish Sea (M:F = 0.76 and 0.78, respectively).

Progressive maturation in *A. subulata* occurs from winter to late spring or summer, beginning when the animals reach 30–40 mm ML. Sexual maturity can be reached at 40–50 mm ML in both sexes (North Sea: 44 mm ± 9 mm in females; 43 mm ± 10 mm in males). Some 50% of females are mature at a length of 75–80 mm, and MLm$_{50\%}$ for males is 70–75 mm. However, the length of mature animals varies considerably in both sexes, with mature males having a wider range of sizes (39–183 mm) than mature females (54–104 mm) (Moreno, 1995).

Males mature slightly earlier than females, and the majority of the population reaches maturity by late spring (Portugal) or summer (English Channel and North Sea) (Rodhouse *et al.*, 1988; Moreno, 1990, 1995; Oesterwind *et al.*, 2010). Relatively large immature males (120 mm ML) and females (75 mm ML) are sometimes caught in Portuguese waters in winter, indicating that there may be variations in the life cycle described above (Moreno, 1995).

Within any year, there may be several more or less distinct spawning periods. For example, in the English Channel, there are three spawning groups of females that spawn in spring, summer, and autumn, respectively[1], with young individuals being recruited to the population twice during the year, in spring and summer. In the Irish Sea, spawning takes place in spring and summer, with a possible minor spawning period in autumn (Nyegaard, 2001). In the North Sea, spawning is in June–July, with hatchlings appearing in plankton samples towards the end of July (Yau, 1994). Spawning probably takes place earlier off the west coast of Scotland than in the North Sea (Yau, 1994). The polymodal egg size frequency distribution seen in ovaries might be explained by batch spawning (Hastie *et al.* (2009b).

Based on examination of 11 female *A. subulata* ranging in size from 8 to 12.1 cm ML, the average number of oocytes present (potential fecundity) is 5705 (range = 1234–18 770). This contrasts with "batch counts" that indicate an average of 148 eggs laid in any one session and that actual fecundity is between 400 and 1500 eggs (Nyegaard, 2001). Perhaps each female lays a number of batches of eggs throughout her lifetime, possibly as many as 40 batches. Whether this maximum number of batches is finally produced may depend on female condition and mortality during the spawning season (Nyegaard, 2001).

13.6 Biological distribution

The biology and ecology of this species were reviewed in Hastie *et al.* (2009a), and reproductive biology was described by Hastie *et al.* (2009b); these papers may be consulted for further details.

13.6.1 Habitat

Alloteuthis subulata is a near-bottom species that lives in shelf waters, particularly in the North Sea (Grimpe, 1925; Steimer, 1993), Kattegat, and western Baltic Sea (e.g. Jaeckel, 1937; Herrmann *et al.*, 2001; Hornbörg, 2005). In UK waters, the species is abundant in the English Channel (Rodhouse *et al.*, 1988) and the Irish Sea (Nyegaard, 2001). It is found from the coast out to ca. 500 m depth (Guerra, 1992), although mainly between 20 and 120 m, and captures below 300 m are sporadic (Roper *et al.*, 1984; Jereb *et al.*, 2010). In Portuguese waters, it is often abundant at 20–200 m (Moreno, 1990, 1995). In the western Mediterranean, it is primarily recorded at depths of 34–278 m (González and Sánchez, 2002).

13.6.2 Migrations

In some parts of its range, *A. subulata* is present year-round (e.g. in the English Channel; Rodhouse *et al.*, 1988), but in other parts, it is thought to be migratory. For example, in the North Sea, juveniles are reported to leave the area at an age of ca. 3 months in November and return the following spring at a size of ca. 5 cm. Both males and females move inshore in early summer (Yau, 1994). However, studies along eastern North Sea coasts (and recent trawling surveys) suggest that juvenile *A. subulata* migrate from the spawning grounds in the southeast to the deeper (and, in winter, relatively warmer) waters in the central parts during late autumn/winter, perhaps as a response to cooling.

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[1] Such apparently contradictory life-cycle features have also been noted in other loliginids such as *L. forbesii*, with various explanations being proposed for the mismatch of spawning and recruitment periods.

In spring, as the waters warm, the young adults return from the Danish coast to shallow waters off the Belgian and southeast British coasts to spawn (De Heij and Baayen, 1999, 2005; Oesterwind *et al.*, 2010).

13.7 Trophic ecology

13.7.1 Prey

The main prey species of *A. subulata* in the Irish Sea are reported to be clupeid fish and crustaceans (Nyegaard, 2001). In the North Sea, fish prey consists mainly of Gobiidae, but Clupeidae, Gadidae, and sandeels (Ammodytidae) are also common (Table 13.2). Diet composition varies significantly in relation to body size (ML). Small *A. subulata* feed mainly on crustaceans, but fish remains are increasingly commonly found in the stomachs of larger individuals. Larger *A. subulata* also eat larger prey (Oesterwind, 2011). *Alloteuthis subulata* feeds in the pelagic zone rather than close to bottom (Hastie *et al.* 2009a). The estimated maximum length of fish prey is ca. 7 cm in the North Sea (Oesterwind, 2011).

Llewellyn (1984) observed the feeding behaviour of the species in aquaria, noting that squid fed readily on "prawns, shrimps, mysids and gobies" introduced into the tanks, although such prey were ignored if they were on the bottom of the tank. "Food capture was effected by the squid darting forward in a straight line from as far as ca. 20 cm from the prey; the prey was held between the arms and tentacles and then usually swallowed within a few seconds."

Table 13.2. Prey composition of *Alloteuthis subulata*, as known from studies in the Northeast Atlantic (compiled from Lipiński, 1985[1]; Nyegard, 2001[2]; Hastie *et al.*, 2009a[3], Oesterwind, 2011[4], pers. comm.[5]).

Taxon	Species
Osteichthyes	
Ammodytidae	*Ammodytes tobianus* (sandeel)[3], indet.[4]
Clupeidae	*Sprattus sprattus* (European sprat)[3], indet.[2,4]
Gadidae	indet.[4]
Gobiidae	*Pomatoschistus minutus* (sand goby)[1,5], *Crystallogobius linearis* (crystal goby)[5], *Gymnammodytes semisquamatus* (smooth sandeel)[5], *Aphia minuta* (transparent goby)[5]
Polychaeta	indet.[4]
Crustacea	Mysida indet.[1], indet.[2,4]
Cephalopoda	indet. squids[1]

13.7.2 Predators

Alloteuthis subulata is an important item in the diet of many predatory fish in the Northeast Atlantic, North Sea, and adjacent waters, including cod, hake, whiting, ling, tuna, sharks, halibut, wolfish, and plaice (Zuev and Nesis, 1971; Hislop *et al.*, 1991; Daly *et*

al., 2001; Velasco *et al.*, 2001). It is the most commonly recorded cephalopod species in stomach contents of demersal fish in UK waters (Hislop *et al.*, 1991; Daly *et al.*, 2001). Several marine mammals and larger cephalopod species are also recorded as feeding on *A. subulata* (Table 13.3; see also Hastie *et al.*, 2009a). In some studies, *Alloteuthis* spp. was recorded; for example, the genus was found in 6 of 10 stomachs of striped dolphin sampled in Galicia during the years 1990–2009 (Sollmann, 2011).

Table 13.3. Known predators of *Alloteuthis subulata* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalopoda	European squid (*Loligo vulgaris*)	Pierce *et al.* (1994a), Rocha *et al.* (1994)
	Veined squid (*Loligo forbesii*)	Pierce *et al.* (1994a), Rocha *et al.* (1994)
Chondrichthyes	Blonde ray (*Raja brachyuran*)	Farias *et al.* (2006)
	Milk shark (*Rhizoprionodon acutus*)	Patokina and Litvinov (2005)
	Spotted ray (*Raja montagui*)	Farias *et al.* (2006)
	Thornback ray (*Raja clavata*)	Farias *et al.* (2006)
Osteichthyes	Albacore (*Thunnus alalunga*)	Consoli *et al.* (2008), Romeo *et al.* (2012)
	Brill (*Scophthalmus rhombus*)	Vinagre *et al.* (2011)
	European hake (*Merluccius merluccius*)	Daly *et al.* (2001)
	Red gurnard (*Chelidonichthys cuculus*)	Lopez-Lopez *et al.* (2011)
	Tub gurnard (*Chelidonichthys lucerna*)	Lopez-Lopez *et al.* (2011)
	Whiting (*Merlangius merlangus*)	Hislop *et al.* (1991), Pedersen (1999)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	Santos *et al.* (2001b, 2005a)
	Common dolphin (*Delphinus delphis*)	González *et al.* 1994a), Meynier (2004), Santos *et al.* (2013)
	Striped dolphin (*Stenella coeruleoalba*)	Sollmann (2011)
	Harbour porpoise (*Phocoena phocoena*)	Börjesson *et al.* (2003), Santos *et al.* (2005b), Jansen *et al.* (2013)
	Northern bottlenose whale (*Hyperoodon ampullatus*)	Santos *et al.* (2001c)
Aves	Puffin (*Fratercula arctica*)	Hislop and Harris (1985)

13.8 Other aspects of biology and ecology

13.8.1 Parasites

According to Zuev and Nesis (1971), the trematode (monogenean) *Isancistrum loliginis* has been noted on gills (it was originally described by Beauchamp, 1912) and the nematode *Filaria loliginis* in the mantle cavity and ovary. Llewellyn (1984) described a new

monogenean species, *Isancistrum subulatae*, mainly on the arms and tentacles of *A. subulata* (and probably never on the gills). González *et al.* (2003) recorded the copepod *Pennella* sp. on a range of cephalopods in Galicia, including *A. subulata.*

13.8.2 Behaviour

Llewellyn (1984) recorded the shoaling behaviour of *Alloteuthis* in aquaria, noting that under bright artificial light: "the squid frequently swam in loosely-regimented shoals of ca. 5–10 individuals with an interval between individuals of ca. 10–20 cm, and with each shoal being confined usually to a volume of ca. 40 × 40 × 40 cm. Occasionally individuals strayed from the shoal, but they very soon rejoined it". In darkness, the squid scattered, but they reassembled into a shoal within a few minutes of the light being turned on. In addition, mating was observed on one occasion; two squid "were seen to copulate by frontal approach and mutual intermingling of the arms and tentacles... The coupling lasted for... ca. 20 seconds".

13.9 Fisheries

Alloteuthis subulata is not currently the main target of any directed fishery and is of relatively low commercial value because of its small size (Moreno, 1995). However, *Alloteuthis* spp. are landed and marketed as a secondary target or bycatch in Spain, Portugal, and Italy. As commented elsewhere, landings of loliginid squids in Europe are usually not identified to species, and *Alloteuthis* spp. are probably also frequently landed (unrecognized) in commercial trawl catches of *Loligo* spp. throughout their ranges.

During certain years, both *A. subulata* and *A. media* can be important components of Portuguese cephalopod catches, although they do not appear in commercial fishery statistics (Moreno, 1995). Both *Alloteuthis* species are also landed in Galicia (northwestern Spain). In 2010, 13 t of *Alloteuthis* were landed in Galicia, but most originated from distant fishing grounds (data from www.pescadegalicia.com). Landings from Galician fishery grounds (900 kg) were recorded, mainly in summer and autumn, presumably as a secondary target species (after *Loligo vulgaris*) in the *boliche* (boat seine net) fishery (Tasende *et al.*, 2005) inside the Galician rías (500 kg, M. G. Tasende, pers. comm.). The remainder was caught with trawl (200 kg) or purse-seine (200 kg) in grounds outside the rías. *Alloteuthis subulata* may also be caught and misidentified as juvenile *L. forbesii* in directed fisheries for that species (e.g. in the Moray Firth, Scotland).

In some southern European countries, a minimum landing size (MLS) is set for *Loligo* spp. (for example, 10 cm in Portugal; Fonseca *et al.*, 2008) and in Galicia, there is also a MLS (6 cm) for *Alloteuthis (*Tasende *et al.*, 2005). In general, given the intraspecific variability in growth patterns in loliginids, it is arguably difficult to set a meaningful MLS. In addition, in the future, it may be useful to consider protecting spawning areas.

There is currently no information on whether *A. subulata* is a single, continuous, mixed population or is divided into a number of smaller populations with limited gene flow between them. However, as previously noted, larger taxonomic issues remain unresolved.

13.10 Future research, needs, and outlook

Despite being one of the more common squid species in European waters, relatively little is known about *A. subulata*. This is probably because it is currently of little commercial fishery interest in most of Europe. However, if this situation changes, it will be

important to increase current knowledge of the biology of this species to allow adequate management procedures to be introduced. In addition, it will be necessary to distinguish *Alloteuthis* species routinely within landings data for loliginid squid. As noted above, the taxonomy of the genus *Alloteuthis* remains unresolved, and further work is urgently needed to confirm which *Alloteuthis* species are actually present and their distributions in European waters.

Cephalopod biology and fisheries in European waters: species accounts

Alloteuthis media

Mid-sized squid

14 *Alloteuthis media* (Linnaeus, 1758)

Evgenia Lefkaditou, Cleopatra Alidromiti, Lee C. Hastie, Graham J. Pierce, A. Louise Allcock, and Patrizia Jereb

Common names

Casseron bambou (France), Καλαμαράκι [kalama-raki] (Greece), calamaretto comune (Italy), lula-bicuda-curta (Portugal), calamarin menor (Spain), midsize squid (UK) (Figure 14.1).

Synonyms

Sepia media Linnaeus, 1758, *Loligo parva* Leach, 1817, *Loligo subulata*: Delle Chiaje (1831), *Loligo marmorae* Verany, 1837, *Loligo urceolatus* Risso, 1854, *Loligo media*: Jeffreys (1869), *Acroteuthis media*: Naef (1916).

14.1 Geographic distribution

The midsize squid, *Alloteuthis media* (Linnaeus, 1758), is reported in the Northeast Atlantic and Mediterranean (Nesis, 1982/1987; Roper *et al.*, 1984; Guerra, 1992; Jereb *et al.,* 2010; Figure 14.2), but the limits of its distribution range in the Northeast Atlantic are not well documented and remain unclear, partly because of the difficulties in correctly identifying *Alloteuthis* species using morphometric

Figure 14.1. *Alloteuthis media.* **Dorsal view. From Guerra (1992).**

characters only (see **Remarks**); hence, confusion exists in some of the old records of both species. *Alloteuthis media* is considered "rare" in the North Sea, but was specifically mentioned by Grimpe (1925) in the waters of the Helgoland archipelago (54°11′N 7°53′E) and reported to be present in the southern North Sea "only in small numbers in summer" by Zuev and Nesis (1971). It was not included in the cephalopods of Scottish waters by Stephen (1944) nor mentioned by Grieg (1933) for the waters of the west coast of Norway. Records by Russell (1922) in Scottish waters probably refer to *A. subulata*, as do the records of Massy (1909) along the Irish coasts (Massy, 1928). The presence of the species was mentioned in the Irish Sea by Moore (1937; Isle of Man) in Stephen (1944) and Zuev and Nesis (1971). *Alloteuthis media* is found in the English Channel, according to Stephen (1944), Zuev and Nesis (1971), and, more recently, Anderson *et al.* (2008). It is particularly abundant off the western Iberian coasts (Coelho and Borges, 1982; Moreno, 1990) and was also reported as abundant on the Sahara Bank (in the area between Cape Blanc, 21°N, and Cape Bojador, 26°N; Balguerias *et al.,* 2000). *Alloteuthis media* is abundant and widely distributed throughout the Mediterranean Sea (Mangold and Boletzky, 1987; Bello, 2004; Salman, 2009), and it is found in the western part of the Sea of Marmara (Katağan *et al.,* 1993; Ünsal *et al.,* 1999) (see **Remarks**).

Figure 14.2. *Alloteuthis media*. **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

14.2   Taxonomy

As further discussed in the **Remarks** section below, the two species placed in the genus *Alloteuthis* (Wülker, 1920) have been the subject of numerous morphological and molecular studies in recent years. Results have confirmed that two species exist in European waters, but the type specimen of *subulata* is not extant, and the whereabouts of the type specimen of *media* has not been confirmed (Allcock, 2010). Further studies are required, but until the taxonomic situation with *A. media* and *A. subulata* is resolved, we elect to retain them here as separate entities (see also Jereb *et al*., 2010).

14.2.1   Systematics

Coleoidea – Decapodiformes – Myopsida – Loliginidae –*Alloteuthis.*

14.2.2   Type locality

"Pelago" (Linnaeus, 1758) – literally "the sea".

14.2.3   Type repository

Unknown. The original description cites Rondelet (1554), which has a figure and detailed description. The Linnean Society of London was tentatively proposed as the repository of that specimen by Sweeney and Roper (1998), but enquiries to the Linnean Society suggest that no type is held in that repository (A. L. Allcock, pers. comm.).

14.3 Diagnosis

14.3.1 Paralarvae

The mantle length (ML) of hatchlings is 2.8 mm (Zuev and Nesis, 1971). A detailed description of *A. media* paralarvae is not yet available, and according to Sweeney *et al.* (1992), they are nearly indistinguishable from *Loligo* spp.

14.3.2 Juveniles and adults

Alloteuthis media is a small member of the Loliginidae, not exceeding 13.2 cm ML (Laptikhovsky *et al.*, 2002). There is morphometric sexual dimorphism, with females attaining larger size than males (Katsanevakis *et al.*, 2008; Alidromiti *et al.*, 2009). Similar to *A. subulata,* it has a narrow elongated mantle, with its posterior ending in a narrow, pointed tail, and the heart-shaped fins, with their lateral angles rounded, extending posteriorly along the tail. Very large and small chromatophores alternate on the mantle.

When the length of the anterior part of the mantle (from the upper edge of the fins to the mantle opening) is used as a reference length, the arm length index ranges between 81 and 167% for *A. media* and 25 and 52% for *A. subulata* (Lefkaditou *et al.*, 2012). For individuals of equal size, the tentacular club of *A. media* is 50–75% longer and 50% broader than that of *A. subulata* (Naef, 1921/1923; Zuev and Nesis, 1971). According to Muus (1963), in animals 30–50 mm ML, the tentacular club of *A. media* is at least 12 mm long as opposed to no more than 11 mm in *A. subulata.* The suckers of both arms and tentacles in *A. media* are larger than in *A. subulata.* Males lack the very long tails seen in *A. subulata.* On the hectocotylus, the apical suckers are larger, coarser, and fewer, whereas the median row in the proximal part has only 10–12 suckers. The beaks of *A. media* are transparent, with darkening limited to around the rostral tip in both the upper and lower mandibles (Figure 14.3). Pigmentation does not seem to be related to maturation (Mangold and Fioroni, 1966). The crest length is almost double the hood length, and the jaw angle is approximately a right angle in both mandibles. The hood and crest of the upper beak are considerably larger, reaching double the size of those in the lower beak (Mangold and Fioroni, 1966).
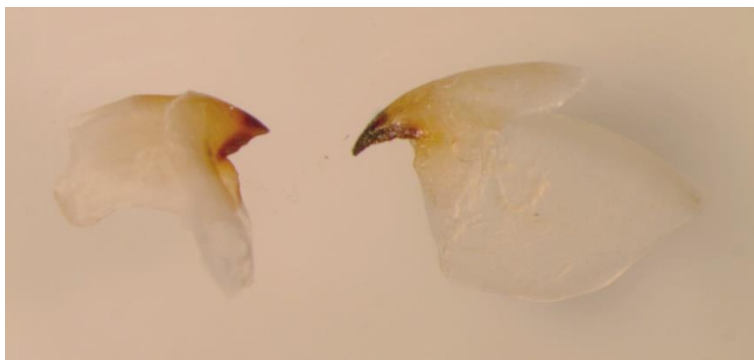
Figure 14.3. *Alloteuthis media*. **Lower beak (left) and upper beak (right) of a female (78 mm ML), from the Aegean Sea. Photo: Evgenia Lefkaditou.**

14.4 Remarks

While it appears to be safe to conclude that there are two distinct morphotypes of *Alloteuthis* in European waters, real doubts remain as to the true taxonomic affiliation of the animals we currently think of as *A. subulata* and *A media*, and (assuming that there

are two distinguishable European species) there is a strong likelihood that past misidentifications have resulted in mixing of information on both species.

As noted by Naef (1921/1923), the congeneric species *A. media* and *A. subulata* were not distinguished before his studies in 1912, so specimens described before that date probably included individuals of two species. However, in spite of Naef's research and description, there has been continued confusion over the identification of the two species in the eastern Mediterranean, where the occurrence of *A. media* was considered questionable until the late 1980s (Mangold and Boletzky, 1987). The few individuals reported by Adam (1966) and, subsequently, by Ruby and Knudsen (1972) in the Levant basin were considered as possibly *Loligo* juveniles or *A. subulata*. Since the early 1990s, the occurrence and distribution of *A. media* in the Aegean Sea has been confirmed by research cruises (Katağan and Kocatas, 1990; D'Onghia *et al.*, 1992, 1996; Salman *et al.*, 1997; Lefkaditou *et al.* 2004). The species was first mentioned as present in the Sea of Marmara by Digby (1949), although more extensive trawl surveys in the1990s have shown that its distribution is limited to the southwest part of the Sea of Marmara, reflecting the species' tolerance of a moderately brackish environment, but intolerance of waters with low levels of dissolved oxygen, such as those in the eastern part of the Sea of Marmara (Katağan *et al.*, 1993; Ünsal *et al.*, 1999).

Morphometric studies on hundreds of *Alloteuthis* specimens collected from the Levant and Aegean seas suggested that the genus *Alloteuthis* is represented by a single taxonomic unit in the eastern Mediterranean, which should be *A. media* (Laptikhovsky *et al.*, 2002, 2005). Analyses of DNA sequence data from *Alloteuthis* specimens collected from different subareas of the Mediterranean Sea indicated two distinct clades, confirming that two species exist (Anderson *et al.*, 2008). Based on the description of the club by Naef (1921/1923), Anderson *et al.* (2008) considered that the clade extending throughout the eastern (Aegean Sea) and western (Catalan Sea) Mediterranean and several areas of the Northeast Atlantic corresponded to *A. media.* Those authors referred the clade sampled only from the Adriatic Sea (i.e. three specimens only) to *A. subulata*, which is also believed to live in the Ionian Sea (Lefkaditou *et al.*, 2012). Despite following the morphological diagnostic characters used by Naef (1921/1923), Anderson *et al.* (2008) obtained conflicting results, because Naef considered *A. subulata*, with its smaller club suckers, to extend throughout the Atlantic (including the North Sea) and Mediterranean, and *A. media*, with its larger club suckers, to have a restricted distribution in the Mediterranean. Without recourse to type material, assigning names to morphotypes is extremely difficult. As noted above, the type of *A. media* appears not to be held at the Linnean Society. Linnaeus may not have deposited a specimen, because he refers to the drawing in Rondelet (1554). The type of *A. subulata* is presumed lost, because it could not be located at the Muséum National d'Histoire Naturelle in Paris (fide Lu *et al.*, 1995).

14.5   Life history

The lifespan of *A. media* is probably 9–11 months. Depending on the region, spawning may take place year–round, or there may be an extended spawning season.

14.5.1   Egg and juvenile development

The eggs are shed in several batches and are encapsulated in rather short gelatinous strings laid on hard substrata such as stones and shells. An egg string consists of ca. 12 capsules containing 6–30 eggs each, giving a total of 200–300 eggs. The string resembles the string of *A. subulata,* but the capsules are broader with shorter stalks, and the string

itself is smaller. The eggs measure 1.0–1.5 mm along their major axis, and the egg capsules are 3–4 cm long. The eggs apparently mature in batches, but the duration of embryonic development is unknown (Zuev and Nesis, 1971). According to the description of the last embryonic stages of *A. media* by Capua *et al.* (2005), an external yolk sac is still present in embryos up to 2.4 mm ML, when rudimentary arms, funnel, and eyes are already clearly visible (Figure 14.4).
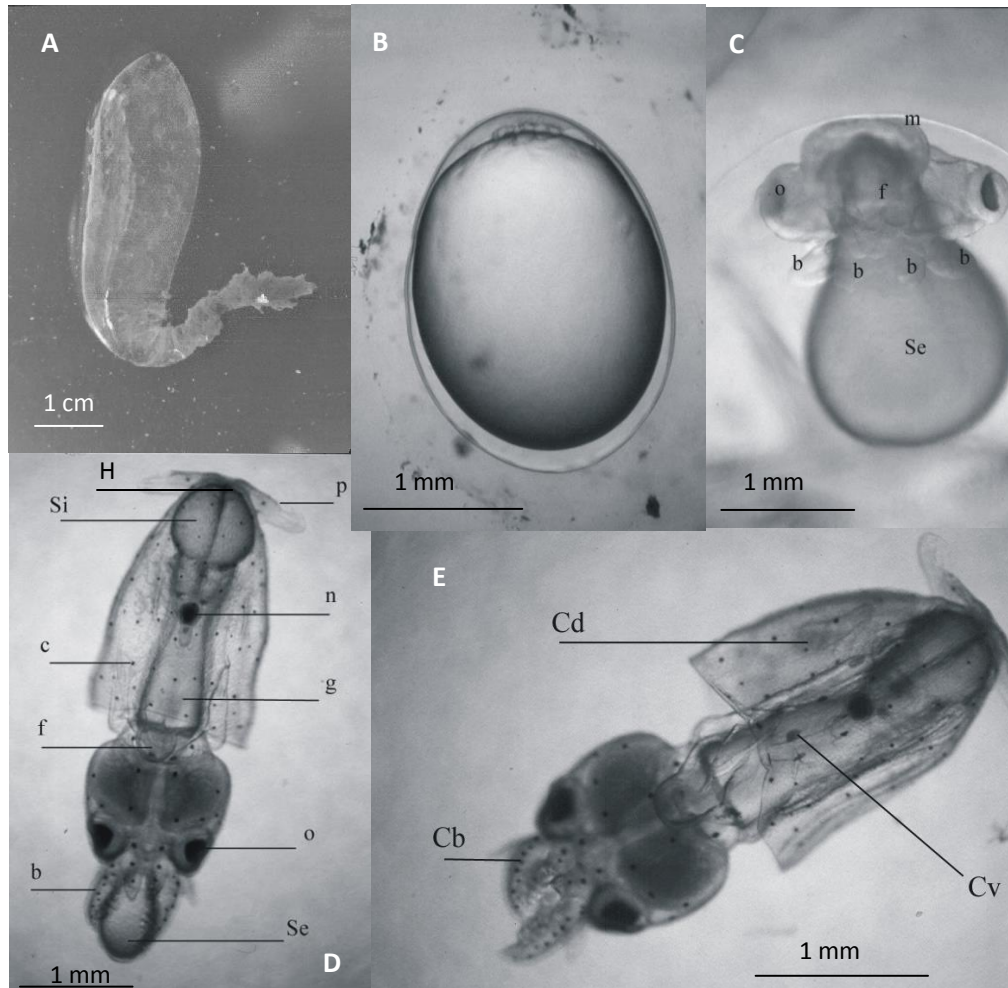
Figure 14.4. *Alloteuthis media.* **Embryonic stages described by Capua *et al.* (2005) from an egg mass collected by trawl in the Ligurian sea, fixed in 4% formalin. (A) An egg string containing rows of eggs in a gelatinous matrix and showing the basal apparatus by which the string is connected to the substratum, (B) Detail of an egg at developmental stage 10–11, with blastoderm seen at the germinative pole, (C) embryonic form still enclosed into the egg (stage 23–24) with visible rudimentary arms (b), funnel (f), mantle (m) and external yolk sac (Se), (D) embryo (stage 29 of Arnold) with visible arms (a), eyes (e), funnel (f), digestive gland (g), ink sac (n), chromatophores (c), external (Se) and internal (Si) yolk sacs, (E) embryo (stage 30 of Arnold) showing brachial (Bc), dorsal (Cd) and ventral (Cv) chromatophores. Photos: Domenico Capua.**

14.5.2 Growth and lifespan

Alloteuthis media is a species of small size, with females reaching 120 mm ML and males 90 mm ML. The tail appears and grows during maturation (Laptikhovsky *et al.*, 2002). Based on length frequency analyses, the longevity of *A. media* had been estimated to be ca. 1 year for males and 18 months for females, with a monthly growth rate decreasing from 7–8 mm in the first summer of life to 2–5 mm during the second year (Mangold-

Wirz, 1963a; Zuev and Nesis, 1971; Auteri *et al.*, 1987). However, recent direct age determination of *A. media* in the northwestern Aegean Sea, based on enumeration of daily increments in statoliths, has shown that the lifespan of females reaches up to 11 months, whereas the males can reach 9 months of age (Alidromiti *et al.*, 2009). Growth rate (mantle length vs. age) is faster in females, which also reach a larger size. Best fit growth equations (ML in mm and age in days) according to Alidromiti *et al.* (2009) are as follows:

$$\text{Females: ML} = 1.096 \times \text{Age}^{0.7538} \ (\text{ML} = 1.096 \times \text{Age}^{0.7538} r = 0.830, n = 73)$$

$$\text{Males: ML} = 0.911 \times \text{Age}^{0.7666} \ \text{ML} = 0.911 \times \text{Age}^{0.7666} \ (r = 0.841, n = 46)$$

In terms of length–weight relationships (see Table 14.1), females display higher values for the slope coefficient *b* (Belcari, 1999b).

Table 14.1. *Alloteuthis media.* **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
Southern Portugal	0.099	2.22	F	Moreno (1990)
	0.185	1.79	M	
Northern Aegean	0.106	2.07	F	E. Lefkaditou, pers. comm.
	0.143	2.01	M	
Southeastern Aegean	0.244	1.76	All	Akyol and Metin (2001)

Research on age and growth of *A. media* in the northern Aegean Sea (Alidromiti, 2007) showed that growth rates of both sexes were faster in the eastern basin, which is characterized by relatively low temperature as a consequence of the cold and nutrient-rich Black Sea water inflow throughout the year. Hence, food availability, particularly the zooplankton biomass associated with Black Sea waters (Isari *et al.*, 2007), is an important influence on *A. media* growth in this area.

14.5.3   Maturation and reproduction

Individual maturity is reached over a wide range of mantle lengths, but mainly when the animals reach ca. half of the maximum mantle length. The MLm$_{50\%}$ estimated for *A. media* in the Tyrrhenian and the Adriatic Seas is ca. 50 mm in males and 60 mm in females (Auteri *et al.*, 1987; Soro and Piccinetti-Manfrin, 1989). Note, however, that the existence of multiple sizes at maturity in loliginid squids, especially males, can mean that such values are misleading.

As in other cephalopods, it appears that there is a gradient of decreasing minimum mantle length at maturity from the western to the eastern basins of the Mediterranean. In the western basin, the smallest mature females measure 80 mm ML, and the smallest mature males 50 mm ML, relative to 37 mm ML for females and 32 mm ML for males in the eastern basin (Jereb *et al.*, 2010).

During the reproductive period, adults migrate to shallow water. Spawning in the Mediterranean is at depths of 10–100 m on sand, seagrass meadows, etc. The spawning season lasts from March to October in the western Mediterranean (Mangold-Wirz, 1963a), but is year-round in the central and eastern regions (Lo Bianco, 1909; Naef, 1921/1923; Laptikhovsky *et al.*, 2002; Lefkaditou *et al.*, 2007). In the North Sea, spawning takes place in June and July (Zuev and Nesis, 1971).

Oocyte maturation occurs in batches. The potential fecundity has been estimated at ca. 950–1400 eggs for the western Mediterranean, whereas typical values in the eastern Mediteranean (1500–2500) are higher. Ripe egg size in the eastern Mediterranean (1.5–2.3 mm along the major axis) is somewhat larger than in females from the western area (1.4–1.6 mm) (Laptikhovsky *et al.*, 2002). Larger females produce larger and heavier eggs.

14.6 Biological distribution

14.6.1 Habitat

Alloteuthis media is among the most abundant demersal cephalopod species of the shelf community, as demonstrated by studies in the Gulf of Cádiz (Silva *et al.*, 2011), the Iberian Mediterranean coast (González and Sánchez, 2002), the Tyrrhenian (Sánchez *et al.*, 1998a), Adriatic and eastern Ionian seas (Ungaro *et al.*, 1999; Krstulovic-Šifner *et al.*, 2005), and the northern Aegean Sea (Lefkaditou, 2006); see also Katsanevakis *et al.* (2008). Generally, *A. media* inhabits a wide depth range from the coast down to 500–600 m (Lefkaditou, 2007), although it is most common in water >150 m deep over sandy and muddy grounds. It is also found in brackish water (Ünsal *et al.*, 1999).

14.6.2 Migrations

Alloteuthis media undertakes seasonal migrations between offshore (in winter) and inshore (in spring) areas, where juveniles recruit mainly during summer and autumn (Mangold-Wirz, 1963a; Belcari, 1999b). Diel vertical migrations have also been described (Zuev and Nesis, 1971).

14.7 Trophic ecology

14.7.1 Prey

Zuev and Nesis (1971) report that the diet of *A. media* from the Adriatic Sea consists of larvae and juveniles of fish, copepods, and euphausiids (Table 14.2). According to Guerra (1992), its diet off the Iberian Peninsula also includes molluscs. In the Aegean Sea, decapod crustaceans, mysids, and hydrozoans were identified among prey items (Vafidis *et al.*, 2008).

Table 14.2. Prey composition of *Alloteuthis media*, as known from studies in the eastern Mediterranean Sea (compiled from Zuev and Nesis, 1971[1]; Vafidis *et al.*, 2008[2]).

Taxon	Orders
Oste-ichthyes	Larvae indet.[1]
Crusta-cea	Decapoda-Natantia indet.[2], Decapoda-Brachyura indet.[2], Euphausiacea indet.[1,2], Mysida indet.[2], Amphipoda indet.[2], Copepoda indet.[1,2], indet.[1]
Cni-daria	Hydrozoa indet.[2]

14.7.2 Predators

Alloteuthis media is potentially available to demersal fish of medium and large size. The species is eaten by several fish species (Zuev and Nesis, 1971; Mienis, 1980; Matallanas *et al.*, 1995; Bello, 1997; Capapé, 1977; Velasco *et al.*, 2001; Morte *et al.*, 2001, 2002; Cartes *et al.*, 2004; Bozzano *et al.*, 2005; Carpentieri *et al.*, 2005, 2007; Valls *et al.*, 2011) (Table

14.3). It is also identified in a fish-stomach-contents database for UK waters (Cefas[2]), but *Alloteuthis* beaks in stomach contents are usually not identified to species level because of the difficulty of distinguishing the beaks of the two species. Velasco *et al.* (2001) recorded *Alloteuthis* sp. in the diet of 16 fish species, and it was the most important cephalopod category in the diet of blue whiting (*Micromesistius poutassou*).

Table 14.3. Known predators of *Alloteuthis media* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalopoda	Common octopus (*Octopus vulgaris*)	Quetglas *et al.* (1998a)
	Musky octopus (*Eledone moschata*)	Krstulović Šifner and Vrgoč (2009b)
Chondrichthyes	Lesser spotted dogfish (*Scyliorhinus canicula*)	Cefas[1]
	Longnose spurdog (*Squalus blainville*)	Mienis (1980)
	Bull ray (*Pteromylaeus bovinus*)	Capapé (1997)
	Thornback ray (*Raja clavata*)	Bello (1997), Valls *et al.* (2011)
Osteichthyes	Bicoloured false moray (*Chlopis bicolor*)	Carpentieri *et al.* (2007)
	Blacktailed conger (*Gnathophis mystax*)	Carpentieri *et al.* (2007)
	European hake (*Merluccius merluccius*)	Cartes *et al.* (2004), Bozzano *et al.* (2005), Carpentieri *et al.* (2005)
	Geater amberjack (*Seriola dumerili*)	Matallanas *et al.* (1995)
	Greater forkbeard (*Phycis blennoides*)	Morte *et al.* (2002)
	Poor cod (*Trisopterus minutus capelanus*)	Morte *et al.* (2001)
Cetacea	Striped dolphin (*Stenella coeruleoalba*)	Würtz and Marrale (1993)

14.8 Other ecological aspects

14.8.1 Parasites

Anisakis simplex (a nematode of the Anisakidae family) has been identified in *A. media* from the Northeast Atlantic, for which, however, it is not considered an important host parasite (Smith, 1984). Gestal *et al.* (1999) reported the copepod *Pennella* sp. on the gills of several cephalopod species in the Tyrrhenian Sea, including *A. media.*

14.9 Fisheries

Alloteuthis media is taken as bycatch in bottom trawl and beach-seine fisheries. Studies on bottom trawl discards have shown that the species is totally discarded in the northeastern Mediteranean (Machias *et al.*, 2001), whereas it seems to be discarded only accidentally during the fast sorting operations on deck of fishing vessels in the western

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[2]http://www.cefas.defra.gov.uk/our-science/fisheries-information/fish-stomach-records/predators-of-specified-prey.aspx

Mediterranean (Sartor *et al.*, 1998a). In the Gulf of Cádiz, the annual landings of *Alloteuthis* sp. during the period 1996–2004 oscillated between 55 and 290 t, of which 55% were found to correspond to *A. media*, according to trawl survey data (I. Sobrino, pers. comm.). In general, separate statistics by species are not provided, and where there is an attempt to identify catches to species, catches of *A. media* are probably reported as *Loligo* sp. or *Alloteuthis* sp.

14.10 Future research, needs, and outlook

Clarification of the status of the species (and morphotypes) of the genus *Alloteuthis* is urgently needed. In addition, as with most cephalopod fishery catches, there is a need to ensure that reporting is at species level. This would also facilitate stock assessment of these species, should it be needed. Given their apparent abundance in continental shelf communities, it is likely that they have an important ecological role, and this also merits further studies.

Because of its small size, high growth plasticity, and easily interpretable statolith microstructure, *A. media* might be an ideal species for laboratory studies to investigate how cephalopod growth and life history respond under different temperature and environmental regimes. Such work, as suggested by Jackson (2004), may also help to establish the extent to which loliginids may serve as useful indicators of ecosystem health and climate change.

Cephalopod biology and fisheries in European waters: species accounts
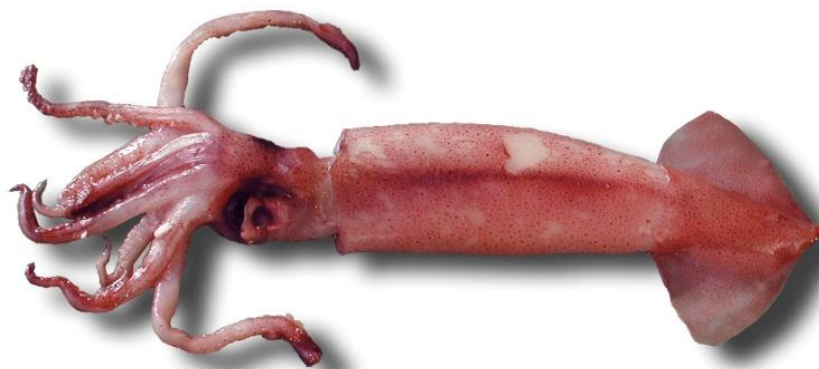
Illex coindetii

Broadtail shortfin squid
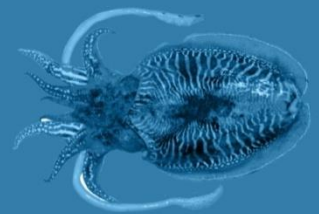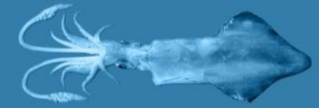
15   *Illex coindetii* (Vérany, 1839)

Patrizia Jereb, Drosos Koutsoubas, Paola Belcari, Graham J. Pierce, Roger Villanueva, A. Louise Allcock, and Evgenia Lefkaditou

Common names

Faux encornet (France), θράψαλο [thrapsalo] (Greece), Totano (Italy), pota-voadora (Portugal), volador (Spain), broadtail shortfin 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).
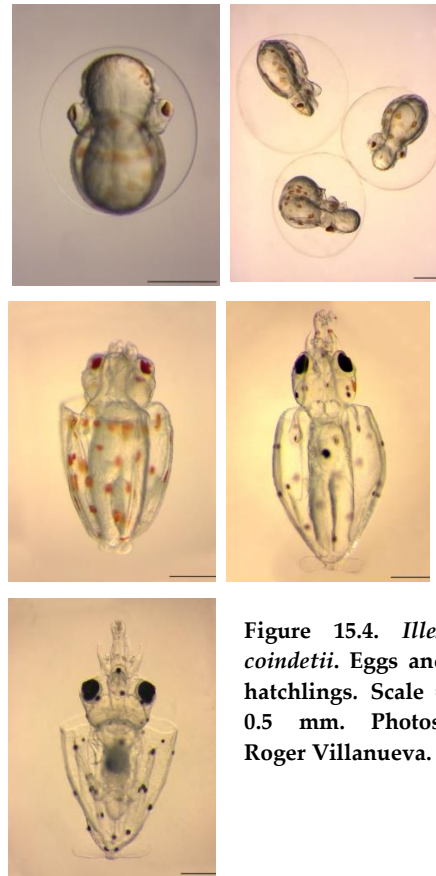
Figure 15.4. *Illex coindetii.* **Eggs and hatchlings. Scale = 0.5 mm. Photos: Roger Villanueva.**

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 = aML^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)
Chondrichthyes	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 (*Globicephala 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.

Cephalopod biology and fisheries in European waters: species accounts

Todarodes sagittatus

European flying squid
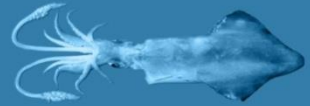
16   *Todarodes sagittatus* (Lamarck, 1798)

Uwe Piatkowski, Karsten Zumholz, Evgenia Lefkaditou, Daniel Oesterwind, Patrizia Jereb, Graham J. Pierce, and A. Louise Allcock

Common names

Toutenon commun (France), Θράψαλο [thrap-salo] (Greece), totano viola (Italy), pota europeia (Portugal), pota europea[3] (Spain), European flying squid (UK) (Figure 16.1).

Synonyms

Loligo sagittata Lamarck, 1798, *Ommastrephes sagittatus* (Lamarck, 1798), *Loligo todarus* Rafinesque, 1814, *Sthenoteuthis todarus* (Rafinesque, 1814), *Ommastrephes todarus* (Rafinesque, 1814), *Loligo aequipoda* Rüppell, 1844, *Sepia minor* Seba, 1758, *Loligo brasiliensis* Férussac, 1823, *Sepia loligo* Gmelin, 1789.

16.1   Geographic distribution

The European flying squid (*Todarodes sagittatus* Lamarck, 1798) has been identified in the North Atlantic from the northeast coasts of Europe to ca. 62°W (Figure 16.2), where it is found associated with the Mid-Atlantic Ridge (Korzun *et al.*, 1979; Vecchione *et al.*, 2010), and from the Arctic Ocean south to the waters off Guinea (Clarke, 1966; Nigmatullin *et al.*, 1998), including northeastern Norway and the Barents Sea (Grieg, 1933; Sennikov and Bliznichenko, 1985), Iceland (Nielsen, 1930; Jonsson, 1998; Figure 16.3), and throughout Norwegian waters (Nordgård, 1923; Grieg, 1933; Wiborg and Beck, 1984). Old records from the Skagerrak (Grimpe, 1925; Jaeckel, 1958) are confirmed

Figure 16.1. *Todarodes sagittatus.* Dorsal view. From Guerra (1992).

by recent information (Hornbörg, 2005), but occasional incursions into the southwestern Baltic Sea (old record in Grimpe, 1925) are rare. *Todarodes sagittatus* has been recorded in the North Sea, although it is probably limited to the northern area (Oesterwind *et al.*, 2010), and extends past northern Scotland to Shetland waters (Stephen, 1944; Joy, 1990) and south to the west Irish coast (Massy, 1928; Wiborg and Beck, 1984; Lordan *et al.*, 2001a, b), where it is particularly abundant in deep water off the northwest coast (Lordan *et al.*, 2001b). Recorded in the Celtic Sea (Lordan *et al.*, 2001a, b), it extends south through French and Spanish waters, including those of the Azores and Madeira (Magaz, 1934; Bouxin and Legendre, 1936; Rees and Maul, 1956; Piatkowski *et al.*, 1998). Its southernmost records are at 11°N off Guinea (V. Laptikhovsky, pers. comm.). *Todarodes sagittatus* is widely distributed in the Mediterranean (Mangold and

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[3] Other common names are also used, e.g. calamar volador (i.e. flying squid).

Boletzky, 1987; Bello, 2004; Salman, 2009**),** including western and central Mediterranean parts (Mangold-Wirz, 1963a; Sánchez, 1986a; Jereb and Ragonese, 1994; Giordano and Carbonara, 1999; Relini *et al.,* 2002; Cuccu *et al.,* 2003a), the Adriatic Sea (Bello, 1985; Casali *et al.,* 1988; Krstulović Šifner *et al.,* 2005), 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). Reference to its presence in the Sea of Marmara exists (Demir, 1952, in Ünsal *et al.,* 1999), but it was not recorded during more recent research carried out in those waters (Katağan *et al.,* 1993; Ünsal *et al.,* 1999).
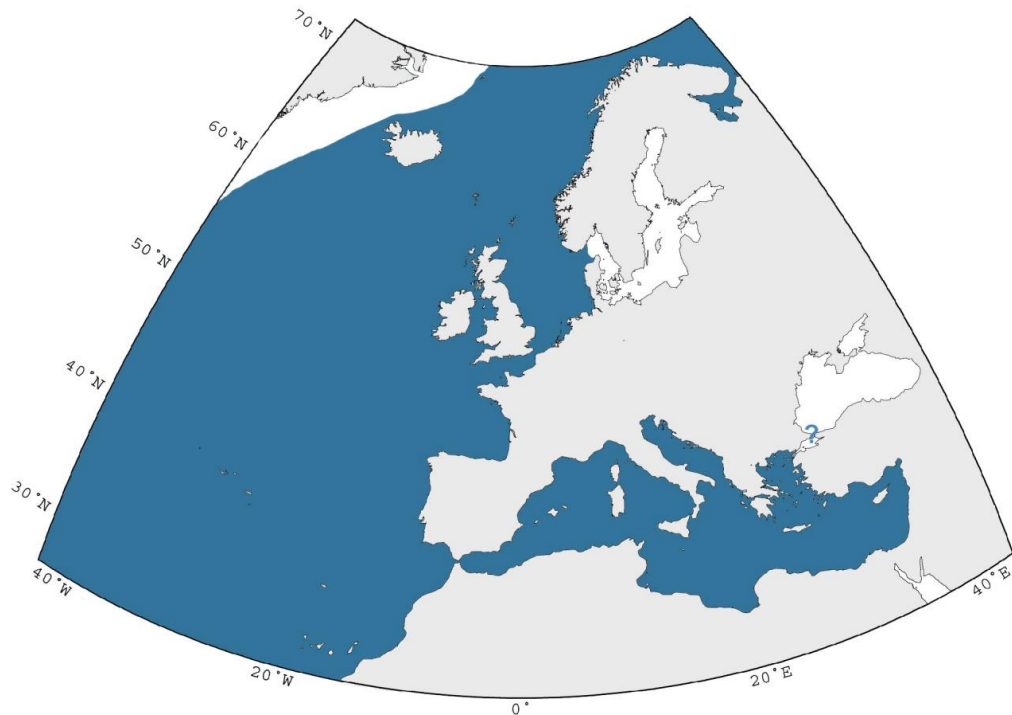
Figure 16.2. *Todarodes sagittatus.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

16.2   Taxonomy

16.2.1   Systematics

Coleoidea – Decapodiformes – Oegopsida – Ommastrephidae – Todarodinae – *Todarodes.*

16.2.2   Type locality

Atlantic Ocean: "sur les côtes de l'Ocean de l'Europe et de l'Amerique", fide Lamarck (1799: 14).

Figure 16.3. *Todarodes sagittatus.* **Stamps document its distribution in the Northeast Atlantic.**

16.2.3   Type repository

Originally Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertebres Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France. MNHN Synypes; specimens not extant [fide Lu *et al.* (1995)].

16.3 Diagnosis

16.3.1 Paralarvae

Early life stages of *T. sagittatus* (Figure 16.4) are not well known. Key characters that would allow the distinction of early stages and particularly its paralarvae from those of the other common ommastrephid species in European waters, *Illex coindetii* and *Todaropsis eblanae,* have not yet been established (Sweeney *et al.,* 1992; Villanueva *et al.,* 2011). Although the paralarvae of *T. sagitattus* have not been described, records exist from various regions of the Northeast Atlantic as well as speculations about the location of spawning grounds (e.g. Shimko, 1989; Collins *et al.,* 2002).

Figure 16.4. *Todarodes sagittatus.* **Early life stage, 18 mm total length, sampled off Messina, Sicily. Photo: Alberto Villari.**

16.3.2 Juveniles and adults

This squid is one of the typical muscular cephalopods inhabiting open waters of the high seas (Clarke, 1966; Zuev *et al.,* 1976).
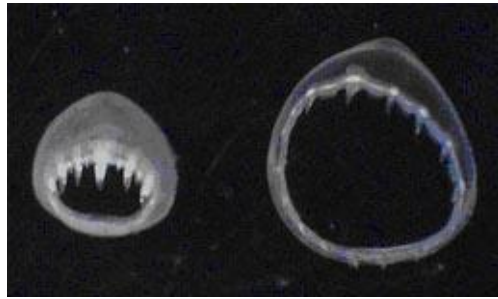
Figure 16.5. *Todarodes sagittatus.* **Sucker rings of arm (left) and tentacle (right). Photo: Evgenia Lefkaditou.**

The fins are wide and strong, with fin length up to 45% of mantle length. The funnel groove has a foveola without side pockets. The suckers on the dactylus of the tentacular club are arranged in four series. The carpus is elongated with 10–12 pairs of suckers. The entire club is relatively long, extending along the stalk. The arm sucker rings have an enlarged central tooth, 7–9 regular teeth, and virtually no small alternating teeth (Figure 16.5).
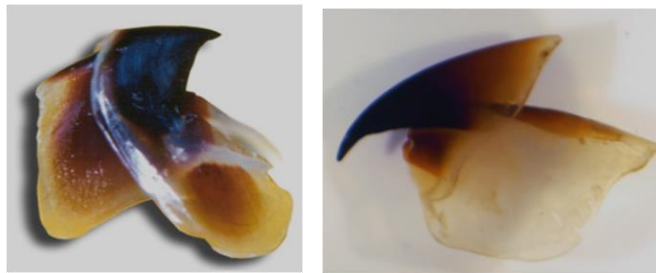
Figure 16.6. *Todarodes sagittatus.* **Lower beak (left) and upper beak (right). Photo: Karsten Zumholz.**

There are no light organs on the viscera. Right arm IV is hectocotylized in males by the modification of terminal suckers into fleshy papillae (Roper *et al.,* 1984; Warneke-Cremer and Dzwillo, 1993; Roper *et al.,* 2010a). Sexual dimorphism in *T. sagittatus* results in relatively longer arms and tentacular clubs in females than in

males, contrary to the situation in the other two common ommastrephids of European waters, *I. coindetii* and *T. eblanae* (Mangold-Wirz, 1963b). The appearance and growth of the mandibles (beaks, Figure 16.6) are described by Hernández-García *et al.* (1998b).

16.4 Life history

Most individuals probably live 12–14 months, but the lifespan of the largest individuals may approach 2 years. Spawning is seasonal, its timing varying with geographic location.

16.4.1 Egg and juvenile development

There is no information available on egg and juvenile development.

16.4.2 Growth and lifespan

A maximum mantle length of 75 cm was reported for an unsexed specimen from North Atlantic waters (probably a female; Herzenstein, 1885), whereas the maximum recorded mantle length for a male in this area is currently 64 cm (Fridriksson, 1943). In the Mediterranean, the maximum sizes recorded are 60 cm (females) and 38.5 cm (males) (Cuccu *et al.* 2005). In the North Sea, maximum reported mantle length is 49 cm, and females are larger than males in winter (Oesterwind, 2011), as also reported for several different areas (ICES Divisions IV, V, VI) of the Northeast Atlantic by Lordan *et al.* (2001b). Common sizes range in general between 35 and 40 cm and 20 and 25 cm for females and males, respectively.

The periodicity of statolith increment formation has not been yet validated for the species, although daily growth rings have been confirmed for the congeneric *Todarodes pacificus* (Nakamura and Sakurai, 1991), as well as for several other ommastrephids, and might, therefore, be assumed for this species. However, assuming that growth increments in statoliths are daily, Rosenberg *et al.* (1981) estimated a mean absolute growth rate of 2 mm d^{-1} for individuals with a dorsal mantle length range of 15–52 cm. Moustahfid (2002) estimated that growth rates in squid aged 4–6 months ranged from 0.4 mm d^{-1} to 1.3 mm d^{-1} and 0.3 g d^{-1} to 2.7 g d^{-1}. Instantaneous relative growth rates (G) were 0.6% for ML and 3.4% for BW. Borges and Wallace (1993) estimated growth rates in Norwegian waters from monthly length frequency distributions. Results varied between years, being 0.8–1.2 mm d^{-1} in females and 0.6–1.0 mm d^{-1} in males. Instantaneous growth rates (in terms of weight) were estimated as 1.1–1.6% BW d^{-1} for animals in the weight range 252–322 g.

Length–weight relationships have been documented for several geographic areas (Table 16.1).

Table 16.1. *Todarodes sagittatus.* **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
North Sea	0.0078	3.29	F	Oesterwind (2011)
	0.0075	3.27	M	
Off Norway	0.0091	3.23	F	Borges and Wallace (1993)
	0.0111	3.17	M	
Off Scotland	0.0071	3.33	F	

	0.0061	3.39	M	
Southwestern Portugal, Madeira	0.0158	3.12	F	Piatkowski *et al.* (1998)
	0.0164	3.09	M	
Northwest African waters	0.0423	2.803	All	Arkhipkin *et al.* (1999)
	0.0326	2.991	F	Nigmatullin *et al.* (2002)
	0.0314	2.845	M	
Western Mediterranean	0.009	3.334	F	Quetglas *et al.* (1998b)
	0.011	3.282	M	
Eastern Mediterranean	0.0193	3.11	F	E. Lefkaditou, pers. comm.
	0.0081	3.39	M	

Prior to statolith studies, individuals >50 cm were believed to be at least 2 years old (Nesis, 1982/1987), but most recent studies based on statolith increments have suggested a longevity of not more than 14 months for individuals reaching up to 47 cm ML (Rosenberg *et al.,* 1981; Wiborg *et al.,* 1982; Arkhipkin *et al.,* 1999; Lordan *et al.,* 2001b; Quetglas and Morales-Nin, 2004; Potoschi *et al.,* 2009).

16.4.3 Maturation and reproduction

Females generally outnumber males in catches outside the breeding areas because they are larger and faster and can migrate farther to forage. Borges and Wallace (1993) found that the average percentage of males in samples from Norway ranged from 4 to 18%, as compared with 3– 29% in Scotland. Quetglas *et al.* (1998b) found that males were significantly more abundant than females during winter in the western Mediterranean. Ripe males are present during most of the year in the southernmost areas of the Northeast Atlantic and the western Mediterranean (Quetglas *et al.*, 1998b; Nigmatullin *et al.*, 2002). In the northernmost regions of the species' distribution, male maturity precedes that of females (Piatkowski *et al.*, 1998; Lordan *et al.*, 2001b).

Differences observed in age and size at maturity (Table 16.2) between different geographic areas suggest that southern populations reach maturity and decrease somatic growth at younger ages and smaller sizes than northern ones, which attain larger sizes as a result of maintaining fast growth and delaying maturation (Arkhipkin *et al.*, 1999; Quetglas and Morales-Nin, 2004).

Table 16.2. *Todarodes sagittatus.* **Minimum size of mature females and males (with values of MLm$_{50\%}$, when known, in parentheses) in populations from different geographic areas.**

Region	ML (mm)		Reference
	Females	Males	
Off Norway	350	300	Wiborg *et al.* (1982)
Northeast Atlantic	310 (~480)	280 (340)	Lordan *et al.* (2001b)
Northwest African waters	200	170	Arkhipkin *et al.* (1999)
Western Mediterranean	318 (337)	196 (232)	Quetglas *et al.* (1998b)

Spawning probably takes place on the continental slope in late winter or early spring off northern Europe, in March and April off France, and between September and November in the western Mediterranean (Piatkowski *et al.*, 1998; Quetglas *et al.*, 1998b; Arkhipkin *et al.*, 1999; Lordan *et al.*, 2001b; Roper *et al.*, 2010a). The main spawning grounds are probably situated on the Mid-Atlantic Ridge between the Azores and 45°N (Sennikov *et al.*, 1986).

Potential fecundity (PF) estimates were considerably lower in squid from the Northeast Atlantic, ranging from 205 000 to 532 500 for females of 415–520 mm ML (Lordan *et al.*, 2001b), than in mature females from the Sahara Bank (ML, 253–341 mm; PF, 215 000–950 000) and in an immature female from the western Mediterranean (ML 288 mm; PF, 2 370 000) (Laptikhovsky and Nigmatullin, 1999). Spawning depth is 70–800 m off Portugal and >500 m in the western Mediterranean.

16.5 Biological distribution

16.5.1 Habitat

Todarodes sagittatus may be found both in the open ocean and near the coast. It is known to migrate vertically between the surface at night and near-bottom waters by day (Mangold-Wirz 1963a; Clarke 1966; Korzun *et al.*, 1979; Nesis, 1982/87; Vecchione *et al.*, 2010); it can be found in surface waters above depths of 4595 m (Collins *et al.*, 2001) and as deep (ROV observation) as 1947 m (Moiseev, 1991).

16.5.2 Migrations

Todarodes sagittatus undertakes pronounced migrations, probably mainly related to feeding and spawning (Shimko, 1989). Foraging shoals of *T. sagittatus* have been reported from the Arctic since the late 1800s (see Golikov *et al.*, 2013, for detail). Such excursions are described to last for long periods of time and to arise with a certain periodicity. Interestingly, these foraging shoals have not been recorded in Arctic waters between the early 1980s and recent years, apparently reappearing only in 2010 (Golikov *et al.*, 2013). This finding is consistent with the highly unpredictable nature of the fishery (see below).

From June on, large schools appear off the south and southwest coasts and in the northwestern fjords of Iceland and off the Faroe Islands, Norway, and, in some years, Scotland, where they stay until ca. December (Stephen 1937; Wiborg 1972, 1979a, 1987; Sundet, 1985; Joy, 1990; Boyle *et al.*, 1998; Jonsson, 1998; Lordan *et al.*, 2001b; Bjørke and Gjøsæter, 2004; Roper *et al.*, 2010). In early winter, the animals migrate into deeper offshore water. On the fishing grounds around Madeira and other parts of the eastern Central Atlantic, the species is found in large numbers only between March and May (Borges and Wallace, 1993; Piatkowski *et al.*, 1998; Arkhipkin *et al.*, 1999; Lordan *et al.*, 2001b). In the Mediterranean, a similar migration pattern is suggested by the higher catch per unit effort observed during July–August in the artisanal handjig fishery in the southern Tyrrhenian Sea (Potoschi and Longo, 2009) and the relatively more frequent occurrence noted in trawl catches during summer and autumn in the eastern basin (Katsanevakis *et al.*, 2008).

16.6 Trophic ecology

16.6.1 Prey

The diet of *T. sagittatus* consists mainly of fish, crustaceans, cephalopods, and polychaete worms, usually in the above-mentioned order of importance; cannibalism has also been noted by several authors (Table 16.3). In the eastern Atlantic, *T. sagittatus* feeds primarily on small mesopelagic fish such as pearlside and lanternfish, as well as on small gadoids and herring (Breiby and Jobling, 1985; Hernández-García, 1992; Lordan *et al.*, 2001b), whereas in the western Mediterranean, silver scabbardfish appear to be the preferred prey species (Marabello *et al.*, 1996; Quetglas *et al.*, 1999). The prey spectrum found in different size classes reflects both increased body size and the ontogenetic migration of the species to deeper water (Quetglas *et al.*, 1999; Lordan *et al.*,

2001b). Differences are also reported between the diets of males and females (Wiborg *et al.*, 1982; Quetglas *et al.*, 1999).

Table 16.3. Prey composition of *Todarodes sagittatus*, as known from studies in different regions of the eastern Atlantic and the western Mediterranean (compiled from Wiborg *et al.*, 1982[1], Breiby and Jobling, 1985[2]; Joy, 1990[3]; Hernández-García, 1992[4]; Marabello *et al.*, 1996[5]; Stowasser, 1997[6], 2004[7]; Piatkowski *et al.*, 1998[8]; Quetglas *et al.*, 1999[9]; Lordan *et al.*, 2001b[10]).

Taxon	Species
Osteichthyes	
Acropomatidae	*Synagrops microlepis* (thinlip splitfish)[4]
Alepisauridae	*Alepisaurus ferox* (lancerfish)[10]
Ammodytidae	*Ammodytes tobianus* (sandeel)[1,2], *Ammodytes* spp.[6,7]
Argentinidae	*Argentina sphyraena* (lesser argentine)[1], *Argentina* spp.[10], *Glossanodon leioglossus* (smalltoothed argentine)[9]
Belonidae	*Belone belone* (garfish)[10]
Caproidae	*Capros aper* (boarfish)[4,8,]
Carangidae	*Trachurus trachurus* (Atlantic horse mackerel)[10]
Centracanthidae	*Centracanthus cirrus* (curled picarel)[9], *Spicara smaris* (picarel)[9]
Chauliodontidae	*Chauliodus sloani* (Sloane's viperfish)[5]
Clupeidae	*Clupea harengus* (Atlantic herring)[1,2,10], *Sprattus sprattus*[6], indet.[6,9]
Epigonidae	*Epigonus telescopus* (black cardinal fish)[8]
Gadidae	*Gadiculus argenteus* (silvery pout)[10], *Gadus morhua* (Atlantic cod)[2], *Melanogrammus aeglefinus* (haddock)[2,6,7], *Merlangius merlangus* (whiting)[3,10], *Micromesistius poutassou* (blue whiting)[1,2,6,7,10], *Pollachius virens* (saithe)[2], *Trisopterus esmarkii* (Norway pout)[1,2,3], *Trisopterus minutus* (poor cod)[6], *Trisopterus* spp.[6,10], indet.[6,7]
Macrouridae	Macrourinae indet.[8], *Nezumia aequalis* (common Atlantic grenadier)[9], indet.[4]
Merlucciidae	*Merluccius merluccius* (European hake)[9]
Myctophidae	*Benthosema glaciale* (glacier lantern fish)[1,9,10], *Ceratoscopelus maderensis* (Madeira lanternfish)[9], *Diaphus dumerilii*[4], *Diaphus raffinesquii*[5], *Diaphus* spp.[4,10], *Hygophum benoiti* (Benoit's lanternfish)[5], *Hygophum hygomii* (Bermuda lantern fish)[9], *Lampanyctus crocodilus* (jewel lanternfish)[5,9], *Myctophum punctatum* (spotted lanternfish)[5,10], *Notoscopelus elongatus*[9], *Symbolophorus veranyi* (large-scale lanternfish)[9], indet.[4,7,8,10]
Moridae	*Lepidion lepidion* (Mediterranean codling)[9], *Mora moro* (common mora)[9]
Notacanthidae	*Polyacanthonotus rissoanus* (smallmouth spiny eel)[9]
Osmeridae	*Mallotus villosus* (capelin)[2]
Paralepididae	*Arctozenus risso* (spotted barracundina)[1,9], *Paralepis* spp.[10], *Sudis hyalina*[5], indet.[5]
Phosichthyidae	*Ichthyococcus ovatus*[5], *Vinciguerria poweriae* (Power's deep-water bristle-mouth fish)[5], *Vinciguerria attenuata*[5]
Scombridae	*Scomber scombrus* (Atlantic mackerel)[10]
Sebastidae	*Sebastes* spp.[1,2]
Soleidae	*Microchirus boscanion* (Lusitanian sole)[8]

Sparidae	*Boops boops* (bogue)[9]
Sternoptychidae	*Argyropelecus hemigymnus* (half-naked hatchetfish)[5,9,10], *Maurolicus muelleri* (pearlside)[1,2,5,7,9,10]
Stichaeidae	*Leptoclinus maculatus* (daubed shanny)[2]
Stomiidae	*Chauliodus sloani* (Sloane's viperfish)[9], *Stomias boa* (boa dragonfish)[5,9]
Trichiuridae	*Lepidopus caudatus* (silver scabbardfish)[9]
Chondrichthyes	
Scyliorhinidae	*Galeus melastomus* (black-mouthed dogfish)[9], indet.[9]
Crustacea	
Decapoda	
Dendrobranchiata-Penaeiodea	*Aristeus antennatus*[9], Penaidea indet.[4]
Macrura reptantia-Astacidea	*Nephrops norvegicus* (Norway lobster)[9], indet.[4]
Pleocyemata-Anomura	Galatheidae indet.[8], *Munida iris*[9], *Munida* spp.[4,9]
Pleocyemata-Caridea	*Alpheus glaber*[9], Crangonidae indet.[9], Oplophoridae indet.[4], *Pasiphaea multidentata*[9], *P. sivado*[4,9], *Pasiphaea* spp.[2,9,10], *Plesionika giglioli*[9], *P. heterocarpus*[4,9], *Plesionika* spp.[4,8,9], *Processa canaliculata*[9], *Processa* spp.[9], indet.[8]
Euphausiacea	*Meganyctiphanes norvegica*[2], indet.[8,10]
Amphipoda	Lyssianassidae indet.[6], *Parathemisto* spp.[1,10], *Phrosina semilunata*[5], *Phronima* spp.[5], *Themisto abyssorum* (as *Parathemisto abyssorum*)[2], indet.[1,3,10]
Isopoda	*Cirolana* sp.[5], *Idothea* spp.[1], indet.[1,9]
Copepoda	Calanoidea indet.[2], *Pareuchaeta* spp.[1], indet.[1,3,6,7,10]
Cephalopoda	Indet.[9]
Myopsida	*Loligo forbesii*[9], Loliginidae indet.[5,7]
Oegopsida	*Abralia veranyi* (eye-flash squid)[8], *Abraliopsis* spp.[4], *Ancistroteuthis lichtensteini* (angel squid)[9], *Brachioteuthis riisei*[8], Cranchiidae indet.[4,8], *Histioteuthis bonnellii* (umbrella squid)[5,9], *H. reversa* (elongate jewel squid)[9], *Gonatus* spp.[1,10], *Illex coindetii* (broadtail shortfin squid)[9,10], Ommastrephidae indet.[4,6,7,8], *Onychoteuthis banksii* (common clubhook squid)[5,9], Onychoteuthidae indet.[4], *Thysanoteuthis rhombus* (diamond squid)[9], *Todarodes sagittatus* (European flying squid)[1,2,5,9,10], *Todaropsis eblanae* (lesser flying squid)[8], indet.[8]
Sepioidea	*Heteroteuthis dispar* (odd bobtail)[9], *Neorossia caroli* (carol bobtail)[9], *Sepia orbignyana*[4], *Sepia* spp.[4,8], *Sepietta neglecta*[9], *Sepiola atlantica*[3], Sepiolidae indet.[7,9]
Octopoda	*Bathypolypus sponsalis* (globose octopus)[9], *Eledone cirrhosa* (horned octopus)[6], Octopodidae indet.[6]
Gastropoda	indet.[7]
Thecosomata	*Limacina retroversa* (retrovert pteropod)[2,10]
Bivalvia	indet.[7]
Polychaeta	indet.[3]
Eunicida	*Eunice* spp.[2]
Phyllodocida	*Nereis pelagica* (bristlerworm)[2,10], *Nereis* spp.[1],

Chaetognatha	
Sagittoidea	*Parasagitta elegans* (as *Sagitta elegans*)[2], *Sagitta* spp.[1,2]

16.6.2 Predators

Todarodes sagittatus is an important prey item of many marine top predators. In the Northeast Atlantic and Mediterranean, its beaks have been found in the stomachs of cetaceans, seals, and fish (Table 16.4).

Table 16.4. Known predators of *Todarodes sagittatus* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	Reference
Chondrichthyes	Black-mouthed dogfish (*Galeus melastomus*)	Carrasson *et al.* (1992), Villanueva (1992), Bello (1996), Kabasakal (2002), Valls *et al.* (2011)
	Blue shark (*Prionace glauca*)	Macnaughton *et al.* (1998)
	Cuckoo ray (*Leucoraja naevus*)	Farias *et al.* (2006)
	Greater lantern shark (*Etmopterus princeps*)	Jakobsdottir (2001)
	Portuguese dogfish (*Centroscymnus coelolepis*)	Clarke and Merrett (1972), Carrasson *et al.* (1992)
	Shortfin mako (*Isurus oxyrinchus*)	Maia *et al.* (2006)
	Smooth lanternshark (*Etmopterus pusillus*)	Xavier *et al.* (2012)
Osteichthyes	Albacore (*Thunnus alalunga*)	Bello (1999), Salman and Karakulak (2009), Romeo *et al.* (2012), Goñi *et al.* (2011)
	Alfonsino (*Beryx splendens*)	Dürr and González (2002)
	Atlantic bluefin tuna (*Thunnus thynnus*)	Karakulak *et al.* (2009), Logan *et al.*, (2011), Romeo *et al.* (2012), Battaglia *et al.* (2013)
	Cod (*Gadus morhua*)	Zuev and Nesis (1971)
	Common dolphinfish (*Coryphaena hippurus*)	Massutí *et al.* (1998)
	European hake (*Merluccius merluccius*)	Guichet (1995)
	Greenland halibut (*Reinhardtius hippoglossoides*)	Hovde *et al.* (2002)
	Lancetfish (*Alepisaurus* sp.)	Zuev and Nesis (1971)
	Mediterranean spearfish (*Tetrapturus belone*)	Romeo *et al.* (2012)
	Roundnose grenadier (*Coryphaenoides rupestris*)	Bergstad *et al.* (2010)
	Saithe (*Pollachius virens*)	Zuev and Nesis (1971)
	Swordfish (*Xiphias gladius*)	Bello (1985, 1991b, 1996), Guerra *et al.* (1993), Clarke *et al.* (1995), Hernández-García (1995), Ribeiro and Andrade (2000), Peristeraki *et al.* (2003, 2005), Salman (2004), Chancollon *et al.* (2006), Romeo *et al.* (2012)

Aves	Barolo shearwater (*Puffinus baroli*)	Neves *et al.* (2012)
Pinnipedia	Harbour seal (*Phoca vitulina*)	Bjørge *et al.* (1981)
	Harp seal (*Pagophylus groenlandicus*)	Hauksson and Bogason (1995)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	Orsi Relini *et al.* (1994), González *et al.* (1994a), Blanco *et al.* (2001), Santos *et al.* (2001a, 2005a)
	Common dolphin (*Delphinus delphis*)	Orsi Relini and Relini (1993), González *et al.* (1994a), Santos *et al.* (2013)
	Cuvier's beaked whale (*Ziphius cavirostris*)	Blanco *et al.* (1997), Lefkaditou and Poulopoulos (1998), Blanco and Raga (2000), Santos *et al.* (2001d), Spitz *et al.* (2011)
	Long-finned pilot whale (*Globicephala melas*)	Orsi Relini and Garibaldi (1992), Spitz *et al.* (2011)
	Northern bottlenose whale (*Hyperoodon ampullatus*)	Clarke and Kristensen (1980), Santos *et al.* (2001c)
	Pygmy sperm whale (*Kogia breviceps*)	Spitz *et al.* (2011)
	Risso's dolphin (*Grampus griseus*)	Clarke and Pascoe (1985), Bello (1992b, 1996), Carlini *et al.* (1992), Würtz *et al.* (1992b), Bearzi *et al.* (2011)
	Short-finned pilot whale (*Globicephala macrorhynchus*)	Hernández-García and Martín (1994)
	Sperm whale (*Physeter macrocephalus*)	Clarke and MacLeod (1976), Clarke *et al.* (1993), Clarke and Pascoe (1997), Santos *et al.* (1999, 2002), Simon *et al.* (2003), Spitz *et al.* (2011)
	Striped dolphin (*Stenella coeruleoalba*)	Bello (1992c), Würtz and Marrale (1993), Blanco *et al.* (1995)

16.7 Other ecological aspects

16.7.1 Parasites

Todarodes sagittatus is an important parasite host, representing a trophic bridge for parasite flow within marine ecosystems (Smith, 1984; Abollo *et al.*, 1998; Gestal *et al.*, 2000). Parasites recorded include the protozoan *Aggregata sagitatta*; the cestodes *Phyllobothrium dohrni, P.* sp., *Nybelinia lingualis*, and *Amphistoma loliginis*; the nematode *Anisakis simplex* B; and probably dicyemids (Zuev and Nesis, 1971; Pascual *et al.*, 1996a; Gestal *et al.*, 2000; González *et al.*, 2003).

16.7.2 Environmental effects

The abundance of *T. sagittatus* on the European shelf increases in colder years, the opposite situation to that of *T. eblanae* (Hastie *et al.*, 1994). However, the relationships between its distribution and environmental factors, such as temperature and hydrological regimes, are still largely unknown (Golikov *et al.*, 2013). Strandings on the beaches of the Strait of Messina (central Mediterranean) are probably related to unusual conditions such as a shift in currents (Berdar and Cavallaro, 1975).

16.8 Fisheries

Common fishing methods include jigging off Norway (Sundet, 1985) and artisanal hand-jigging in parts of the Mediterranean (Ragonese and Bianchini, 1990; Potoschi and Longo, 2009; Battaglia *et al.*, 2010) and Canary Islands (Escánez Pérez *et al.*, 2012), where there are directed artisanal fisheries. Over much of its distribution, it is taken mainly as bycatch in trawl fisheries (Joy, 1990; Jonsson, 1998; Lordan *et al.*, 2001b; González and Sánchez, 2002).

In several areas *T. sagittatus* caught by bottom trawling are either discarded (Sartor *et al.*, 1998a; Machias *et al.*, 2001) or sold cheaply as line bait (Thomas, 1973, as cited in Arnold, 1979). Indeed, Stroud (1978) noted that *T. sagittatus* was discarded by UK fishers when caught in the Northeast Atlantic and was probably an important underutilized species that could provide raw material for squid products.

In general, the quality of fishery data is poor; data are not fully reported, and the various ommastrephid squids are often not separated. *Todarodes sagittatus* is reported as a separate category in FAO statistics (FAO, 2011), but such data have to be considered with caution. This is particularly true for the Mediterranean, where there has been confusion in the past about species reported in the FAO database under the general category "ommastrephids", because other species, such as *I. coindetii* and *T. eblanae*, have been recorded as *T. sagittatus* (P. Jereb, pers. comm.). Also, there are discrepancies between and within the current available fishery statistics databases (i.e. the older FISHSTAT Plus and the more recent FISHSTAT J; FAO 2011), in relation to landings of this species.

As is typical of ommastrephids, there can be wide fluctuations in catches between years, and recruitment to the fishery is probably highly variable. Mantle length of the exploited population ranges from ca. 20 to 40 cm (Norway) and from ca. 14 to 34 cm (Canary Islands). The body mass of fished specimens ranges from 150 g to 4 kg. Recruitment to the fishery begins at ca. 3 months of age.

As with all European squid fisheries, there is currently no routine stock assessment for *T. sagittatus*.

An important fishery for the species has existed intermittently off Norway. Fishing is concentrated during the months August–December in ICES Division IIa. FAO data (FAO, 2011) show that, since 1950, reported landings from this fishery were zero in several years, but there were occasional years of big landings, e.g. ca. 10 000 t in 1958 and 1965. The peak years of the fishery were during 1981–1985, with more than 18 000 t landed annually in both 1982 and 1983, but by 1989, annual landings had dropped to a mere 5 t, and the fishery effectively disappeared (see Wiborg, 1972, 1979a, 1987; Besteiro, 1985; Sundet, 1985; Bjørke and Gjøsæter, 2004; FAO, 2011). During the peak of the Norwegian fishery, the species was also frequently caught by trawlers based in Shetland (UK) (Joy, 1989, 1990).

In some Mediterranean countries, the commercial value of *T. sagittatus* is relatively high. The main directed fishery operates in Italian waters, particularly in the Aeolian Islands (southern Tyrrhenian Sea). It is an artisanal handjig fishery in which fishers use handjig lines with a small blinking light. Fishers can achieve a catch per unit effort of 8.35 ± 2.55 kg d^{-1}, with total catches reaching ca. 3000 t year^{-1}, assuring a good income (Battaglia *et al.*, 2010). In most areas, however, hand-jigging for *T. sagittatus* is practiced by professional and sport fishers only during late summer (Escánez Pérez *et al.* 2012; E. Lefkaditou, pers. comm.).

Todarodes sagittatus is consumed fresh or boiled, although the flesh of large individuals has been described as tough. It is also marketed frozen, salted, or dried and is used as bait in finfish fisheries. Apart from it being an active predator on commercially important finfish species, the species has occasionally been considered a nuisance because of its competition with finfish for baited hooks.

According to Nigmatullin *et al.* (2002), based on a study of the biology and ecology, the *T. sagittatus* inhabiting the outer shelf and upper slope of Northwest African waters (between ca. 10 and 26°N) are an isolated population differing from those in the North Atlantic and the Mediterranean. That population has a 1-year life cycle and spawns year-round, with a winter peak. It is suggested that the Northwest African squids represent a separate stock unit for fishery–biological management purposes and even, probably, a separate systematic unit, species, or subspecies. However, Martina Roeleveld (pers. comm. to Vladimir Laptikhovsky), upon studying a sample of mature males and females from the African population, found no distinctive features that would allow morphological separation of these squids from the North Atlantic population.

16.9 Future research, needs, and outlook

Biological information on this species remains sparse. Important questions for future studies concern stock identification, the location of spawning grounds, description of egg development and the juvenile phase, as well as the validation of daily growth increments in statoliths. Results of such studies could provide a basis for the prediction of the vast migrations undertaken by this species, which are vaguely described, but not yet understood.

Cephalopod biology and fisheries in European waters: species accounts

Todaropsis eblanae

Lesser flying squid
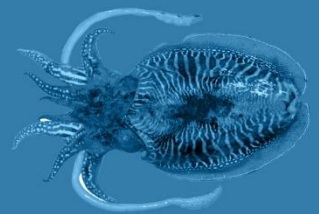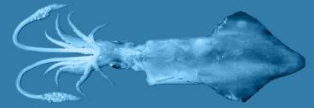
17   *Todaropsis eblanae* (Ball, 1841)

Paola Belcari, Uwe Piatkowski, Karsten Zumholz, Paolo Sartor, Evgenia Lefkaditou, Graham J. Pierce, Lee C. Hastie, A. Louise Allcock and Patrizia Jereb

Common names

Toutenon souffleur (France), Θράψαλο [thrapsalo] (Greece), totano tozzo (Italy), pota costeira (Portugal), pota costera (Spain), lesser flying squid (UK) (Figure 17.1).

Synonyms

Loligo eblanae Ball, 1841, *Ommastrephes eblanae* (Ball, 1841), *Sthenoteuthis eblanae* (Ball, 1841), *Todaropsis veranyi* Girard, 1890.

17.1   Geographic distribution

The lesser flying squid (*Todaropis eblanae* Ball, 1841), exhibits a disjunct geographic distribution, being found in the eastern Atlantic and the entire Mediterranean (Figure 17.2), and in the West Indian Ocean, West Pacific Ocean, and eastern and northwestern Austalian waters (Roper *et al.*, 2010a). In the eastern Atlantic, it has been recorded from the Shetland Islands and northeastern Scotland (e.g. Grimpe, 1921 in Grimpe, 1925; Stephen, 1944) down to South Africa (Roeleveld, 1998), where it is reported off Cape Town and the Cape of Good Hope (see references in Adam, 1952). However, very recent findings extend its distribution north to the Arctic, where it has been recorded since 2006 at distances >2500 km outside its previously documented range (Golikov *et al.*, 2013).

Figure 17.1. *Todaropsis eblanae.* **Dorsal view. From Guerra (1992).**

Todaropsis eblanae is present in the North Sea, Skagerrak, and Kattegat (Grimpe, 1925; Jaeckel, 1958; Hornbörg, 2005; Zumholtz and Piatkowski, 2005), with occasional incursions into the northern North Sea (Stephen, 1944; Hastie *et al.*, 1994) and off the east and west coasts of Ireland (Massy, 1928; Lordan *et al.*, 1995). It is particularly abundant off the southwest coast of Ireland and in the Celtic Sea (Lordan *et al.*, 2001a). It is widely distributed off the French, Spanish, and Portuguese coasts (Bouxin and Legendre, 1936; González *et al.*, 1994b; Robin *et al.*, 2002; Moreno *et al.*, 2009), and down to West Africa (Hernández-García, 1991) and farther south. It is also distributed throughout the Mediterranean (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 (Casali *et al.*, 1998; Krstulović Šifner *et al.*, 2005, 2011; 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, 2002; Lefkaditou *et al.*, 2003b). It has also been recorded in the Sea of Marmara (Katağan *et al.*, 1993).
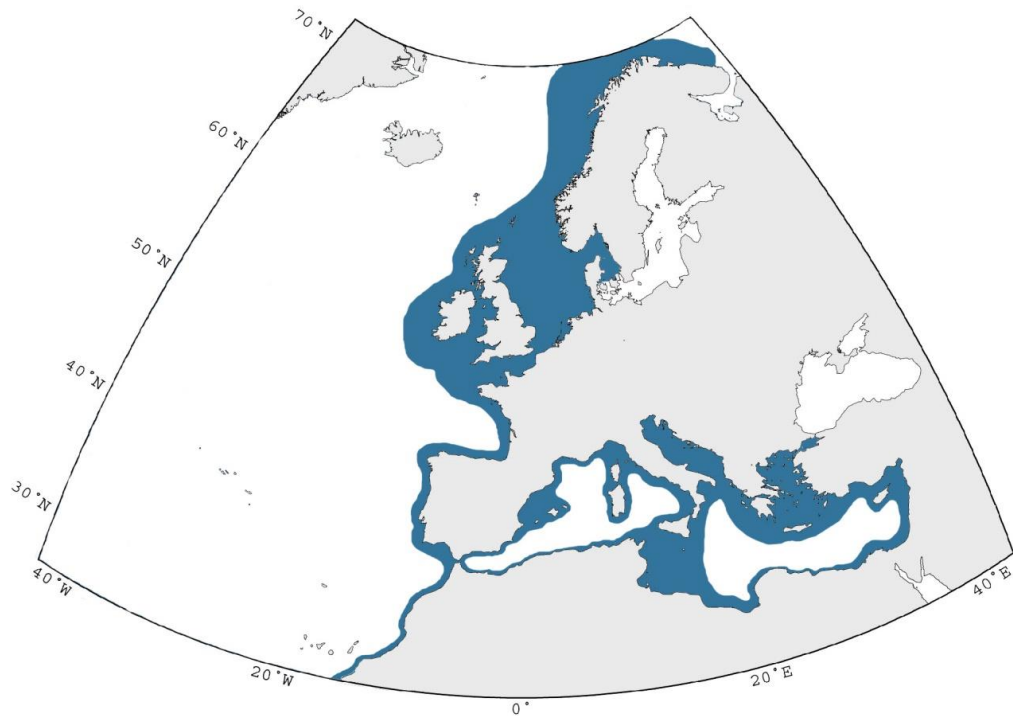
Figure 17.2. *Todaropsis eblanae.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

17.2 Taxonomy

17.2.1 Systematics

Coleoidea – Decapodiformes – Oegopsida – Ommastrephidae – Todarodinae – *Todaropsis.*

17.2.2 Type locality

Dublin Bay, Ireland.

17.2.3 Type repository

Natural History Museum, National Museum of Ireland, Merrion St Upper, Dublin 2. Holotype [fide Hoyle (1903)].

17.3 Diagnosis

17.3.1 Paralarvae

No description of the paralarva (rhynchoteuthion) is yet available. Taxonomic characters permitting distinction of *T. eblanae* parlarvae from those of co-familiar species have been investigated very recently, based on *in vitro* fertilization experiments (Petroni *et al.*, 2012). The skin sculpture of the external mantle surface, bearing a network of hexagonal cells, absent in *Illex coindetii,* seems the most promising character for the distinction of fresh rhynchoteuthions of *T. eblanae* from those of *I. coindetii.*

17.3.2 Juveniles and adults

Adult external mophology is illustrated in Figure 17.3. Fin length is <50% of dorsal mantle length (ML), and fin width ranges between 75 and 90% of ML. Fins are rhomboid, with the anterior border more convex than the posterior border. Mantle width is >33% of ML. The head is wide and robust, with four nuchal folds in the neck region. The funnel groove lacks a foveola and side pockets. The funnel-locking cartilage is inverse T-shaped. The arms bear two longitudinal series of suckers. Sucker rings of the largest arm suckers bear one large pointed median tooth and 3–4 smaller pointed teeth (Figure 17.4a). The dactylus of the tentacular club (Figure 17.4b) bears four longitudinal series of small suckers. The manus of the club bears six transverse rows of four suckers, each with median pairs up to fourfold larger in diameter than the lateral suckers. Sucker rings of largest median club suckers are armed with ca. 30 short, pointed teeth, occasionally alternating with much smaller teeth (Figure 17.4a).
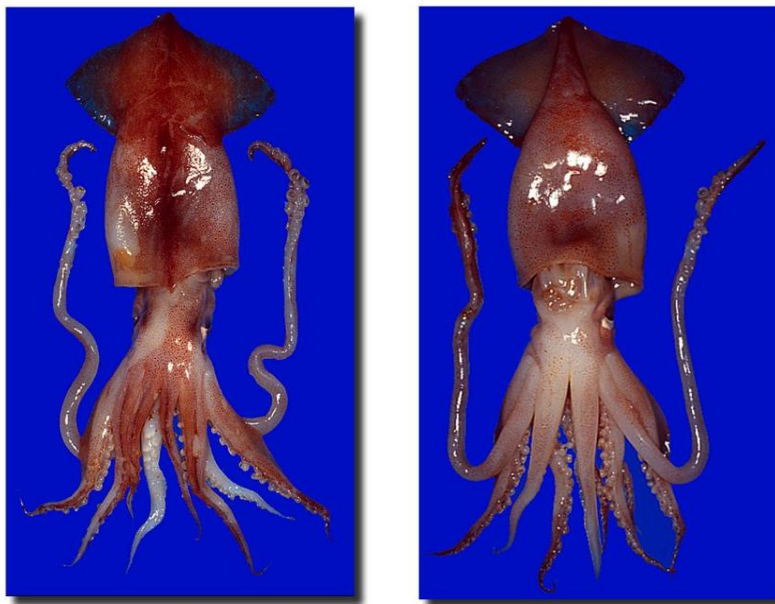
Figure 17.3. *Todaropsis eblanae.* **Dorsal (left) and ventral (right) views. Photos: Domenico Capua.**

Figure 17.4. *Todaropsis eblanae.* **(a) Sucker rings of arm (left) and tentacle (right). Photo: Evgenia Lefkaditou. (b) Detail of the tentacular club. Photo: Domenico Capua.**

Left and right ventral arms (IV) of mature males are hectocotylized (Figure 17.5) by modification of suckers into cirrate lappets with transverse lamellae and an expanded protective membrane (Roper *et al.* 1984; Guerra, 1992; Roper *et al.*, 2010a). Upper and lower beaks are illustrated in Figure 17.6.
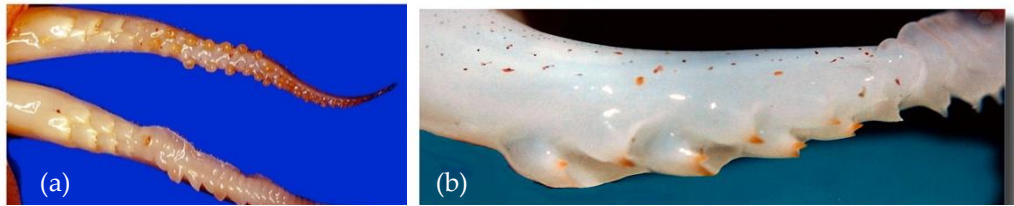
Figure 17.5. *Todaropsis eblanae.* **(a) Hectocotylized ventral arms of male. Photo: Domenico Capua. (b) Detail of hectocotylized arm (right IV) base with transverse lamellae. Photo: Evgenia Lefkaditou.**
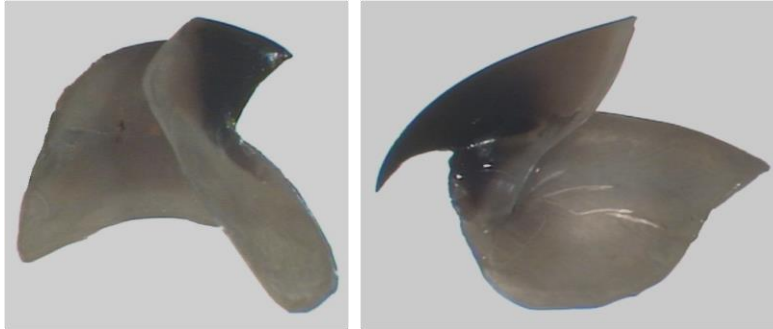
Figure 17.6. *Todaropsis eblanae.* **Lower beak (left) and upper beak (right). Photos: Evgenia Lefkaditou.**

17.4 Life history

The life cycle of *T. eblanae* is probably annual, because estimated values for the lifespan range from 7–8 months to 1 year. Spawning is year-round, with different seasonal peaks in different geographic areas.

17.4.1 Egg and juvenile development

No records have been published on eggs in the wild. It is presumed that the species spawns pelagic egg masses, similar to many of its relatives within the family Ommastrephidae. Oocyte size in mature females varies between 0.8 and 2.5 mm along the principal axis throughout the species' range, with a mean of 1.2 mm in West African waters (Laptikhovsky and Nigmatullin, 1999) and in the Mediterranean (Mangold-Wirz, 1963a) and a mean of 1.57 mm in Scottish waters (Hastie *et al.*, 1994). The duration of embryological development is unknown. The hatching season extends from October to March in British waters (Hastie *et al.*, 1994; Collins *et al.*, 2002) and from March to July, with a peak in May, in Northwest African waters (Laptikhovsky and Nigmatullin, 1999).

17.4.2 Growth and lifespan

Maximum mantle lengths have been registered in North Atlantic waters: 290 and 220 mm for females and males, respectively (Robin *et al.*, 2002). There is morphometric sexual dimorphism, with females attaining larger size than males (Mangold-Wirz, 1963a) (see Table 17.1).

Table 17.1. *Todaropsis eblanae.* **Maximum mantle length (mm) for females (F) and males (M) in different geographic areas of the eastern Atlantic and Mediterranean Sea.**

Region	ML (mm)		Reference
	F	M	
Scottish waters	205	141	Hastie *et al.* (1994)
North Sea	190	160	Zumholz and Piatkowski (2005)
Bay of Biscay – Celtic Sea	290	220	Robin *et al.* (2002)
Northwestern Spain	219	169	González *et al.* (1994b)
Northwest Africa (16–26°N)	250	200	Arkhipkin and Laptikhovsky (2000)
Northwest Africa (3–35°N)	215	164	Hernández-García (2002a)
Western Mediterranean	204	156	Mangold-Wirz (1963a)
Eastern Mediterranean	170	143	Zikos (2006), Lefkaditou (2006)

Significant differences between sexes have been found in length–weight relationships in most of the studied regions (Table 17.2). In general, the values of the regression coefficient *b* are lower than 3 in both sexes.

Table 17.2. *Todaropsis eblanae.* **Length–weight relationships in different geographic areas for females (F), males (M), and sexes combined (All). Original equations were converted to W = aML^b, where W is body mass (g) and ML is dorsal mantle length (cm).**

Region	a	b	Sex	Reference
Scottish waters	0.126	2.723	F	Hastie *et al.* (1994)
	0.115	2.777	M	
North Sea	0.142	2.660	F	Zumholz and Piatkowski (2005)
	0.094	2.854	M	
Bay of Biscay – Celtic Sea	0.330	2.41	F	Robin *et al.* (2002)
	0.670	2.15	M	
Northwestern Spain	0.148	2.671	F	González *et al.* (1994b)
	0.088	2.917	M	
Portuguese waters	0.0004	2.620	F	J. Pereira, pers. comm.
	0.0003	2.687	M	
Northwest African waters	0.224	2.505	All	Arkhipkin and Laptikhovsky (2000)
South African waters	0.110	2.67	All	Cooper (1979)
Western Mediterranean Sea	0.039–0.246	2.43–3.16	F	Belcari *et al.* (1999)
	0.163–0.680	2.11–2.64	M	
Eastern Mediterranean Sea	0.141	2.704	All	E. Lefkaditou, pers. comm.

The most statolith increments counted has been 255 (Robin *et al.*, 2002), suggesting a lifespan not exceeding 1 year. Growth rates calculated from monthly changes in average ML are 0.76 cm month^{-1} (95% *CL* 0.12–1.24) in males and 1.22 cm month^{-1} (1.18–1.86) in females, compared with 1.86 cm month^{-1} in males and 3.41 cm month^{-1} in females based on statolith data (Robin *et al.*, 2002). As with other cephalopods, it is likely

that asynchronous hatching and recruitment make it difficult to interpret changes in average ML in samples from consecutive months. Daily growth rate is faster in females (Table 17.3), and instantaneous relative growth rate decreases with increasing size in both sexes (Arkhipkin and Laptikhovsky, 2000).

Table 17.3. *Todaropsis eblanae.* **Daily growth rate (DGR, mm d⁻¹) and lifespan (months) of females (F) and males (M) in populations from the eastern Atlantic and Mediterranean Sea. (DA = direct ageing, MPA = modal progression analysis)**

Method	DGR		Lifespan		Region	Reference
	F	M	F	M		
DA	1.14	0.62	8.5	7.7	Southern Celtic Sea – Bay of Biscay	Robin *et al.* (2002)
DA	0.7–1.8	0.85–1.6			Northwest Africa	Arkhipkin and Laptikhovsky (2000)
MPA	0.41	0.25	8.5		Southern Celtic Sea – Bay of Biscay	Robin *et al.* (2002)
MPA	0.2	0.15			Western Mediterranean	Mangold-Wirz (1963a)

17.4.3 Maturation and reproduction

Most authors report that the sex ratio of *T. eblanae* is not substantially different from 1:1. Arkhipkin and Laptikhovsky (2000) found that the sex ratio was ca. 1:1 in winter and summer off Northwest Africa, but that there was a slight predominance of females in autumn (1.2:1). However, Zumholz and Piatkowski (2005) found an overall female:male ratio of 0.78:1 in research cruise catches in the North Sea. Given the existence of sexual dimorphism in size, these discrepancies might be caused by the use of sampling gears with different selectivities.

Sexual maturation starts at a larger size in females than in males. Estimates of the size at maturity in different areas range from 120 to 150 mm ML for males and from 140 to 200 mm ML for females (Table 17.4) (Mangold-Wirz, 1963a; González *et al.*, 1994b; Hastie *et al.*, 1994; Joy, 1989; Arkhipkin and Laptikhovsky, 2000; Robin *et al.*, 2002; Zumholz and Piatkowski, 2005). Mature females are reported to have particularly large nidamental glands, ranging from 7.5 to 27.7% of the total body weight in mature animals (Hastie *et al.*, 1994).

The spawning season probably extends throughout the year, with peaks varying according to geographic location (Belcari, 1999d). *Todaropsis eblanae* spawns mainly during summer and early autumn in the Catalan Sea (Mediterranean) (Mangold-Wirz 1963a) and in northern Atlantic waters (Hastie *et al.*, 1994; Robin *et al.*, 2002; Zumholz and Piatkowski, 2005; Oesterwind *et al.*, 2010), whereas it spawns in early spring and early autumn in Atlantic waters south of 44°N (González *et al.*, 1994b; Arkhipkin and Laptikhovsky, 2000).

Table 17.4. *Todaropsis eblanae.* **Minimum size at maturity and MLm$_{50\%}$ (in parentheses) for females and males of populations from different geographical areas.**

Region	ML (mm)		Reference
	Females	Males	
Scottish waters	110 (157.3)	92 (120.8)	Hastie *et al.* (1994)
North Sea	120 (164)	85 (123)	Zumholz and Piatkowski (2005)
Southern Celtic Sea – Bay of Biscay	(165)	(135)	Robin *et al.* (2002]
Northwestern Spain	140 (180–199)	104 (130–149)	González *et al.* (1994b)
Northwest Africa (16–26°N)	150	120	Arkhipkin and Laptikhov-sky (2000)
Northwest Africa (3–35°N)	128 (168)	109 (130)	Hernández-García (2002a)
Western Mediterranean	160	110	Mangold-Wirz (1963a)

The spawning grounds are still unknown. However, a possible location was identified in Northwest Iberian waters, where paralarvae matching the spawning season of *T. eblanae* were collected during plankton cruises in many years (Rocha *et al.*, 1999; Moreno *et al.*, 2009).

Potential fecundity (PF) varies from 4500 to 28 000 for mature females in Scottish waters (Hastie *et al.*, 1994), from 99 979 to 143 792 for females of 136–196 mm ML caught off Northwestern Spain (Rasero *et al.*, 1995), and from 43 000 to 275 000 off West Africa (Laptikhovsky and Nigmatullin, 1999). Actual fecundity has been estimated in a number of ways. The number of ripe oocytes in the oviduct ranges from 5000 to 10 000 eggs in the western Mediterranean (Mangold-Wirz, 1963a), the number of mature (orange) eggs ranges from 355 to 13 157 in Scottish waters (Hastie *et al.*, 1994), and the number of eggs in the oviducts ranges from 3600 to 34 400 off Northwest Africa (Laptikhovsky and Nigmatullin, 1999). For Galician waters, Rasero *et al.* (1995) report an average of 12 167 oocytes in the oviducts. Trends in both PF and numbers of ripe oocytes suggest a trend of decreasing egg numbers with increasing latitude, at least in the Atlantic. However, eggs from *T. eblanae* captured in Scottish waters are larger than from those captured in the Mediterranean and off West Africa (1.6 vs. 1.22 mm) (Laptikhovsky and Nigmatullin, 1999), suggesting that total reproductive output may be similar in northern and southern areas. The species can be considered an intermittent terminal spawner. Spent females are rarely found.

The average number of spermatophores in the Needham's sac is ca. 100, with a maximum of 269 in Northwest African waters (Hernández-García, 2002a; Sabirov *et al.*, 2012) and 12–130 (mean = 60) in Scottish waters (Hastie *et al.*, 1994). The number and length of spermatophores increases with the size of males. Males copulate several times, and spermatophores continue to be produced for further mating.

17.5 Biological distribution

17.5.1 Habitat

Todaropsis eblanae is a demersal species associated with sandy and muddy bottoms, mainly in the lower sublittoral and upper bathyal over the continental shelf, usually not ascending to the surface or approaching the shore. It seems to live within a temperature range of 9–18°C and inhabits a wide range of depths (Guerra, 1992), being

more abundant in highly productive areas around the shelf break (Colloca *et al.*, 2004). In the Mediterranean, it has been observed at depths of 200–600 m in the western area (Quetglas *et al.*, 2000) and 30–700 m in Italian waters (Belcari and Sartor, 1993; Belcari, 1999d), but in the central basin and Hellenic seas, it has been recorded at 100–850 m and more frequently on the upper slope of regions with steep slopes (Krstulovic-Šifner *et al.*, 2005; Lefkaditou, 2006; Katsanevakis *et al.*, 2008).

17.5.2   Migrations

Unlike other ommastrephid species, there is no evidence that *T. eblanae* regularly ascends to the surface or approaches shorelines (Hastie *et al.*, 2009a; Oesterwind *et al.*, 2010), although it is occasionally caught in coastal waters (Hastie *et al.*, 1994). It is probably the least mobile of the ommastrephid squids in terms of migratory habits and is more likely to behave like neritic loliginid squid species than the sympatric ommastrephid species *I. coindetii* and *Todarodes sagitattus* (Lordan *et al.*, 2001a; Roper *et al.*, 2010a).

17.6   Trophic ecology

17.6.1   Prey

The diet is composed, in decreasing order of importance, of fish, crustaceans, and cephalopods. *Todaropsis eblanae* is clearly an opportunistic predator, taking a wide variety of prey, particularly the most abundant in its habitat, e.g. blue whiting (*Micromesistius potassou*) made up nearly 50% of the diet off the Galician coast (Rasero *et al.*, 1996) and Mueller's pearlside (*Maurolicus muelleri*) much of the diet off the southwest Irish coast (Lordan *et al.*, 1998b). Cannibalism has been also recorded (Table 17.5).

Table 17.5. Prey composition of *Todaropsis eblanae*, as known from studies in different regions of the Northeast Atlantic and the eastern Mediterranean (compiled from Hernández-García, 1992[1]; Rasero *et al.*, 1996[2]; Lordan *et al.*, 1998b[3]; Lelli *et al.*, 2005[4]; Vafidis *et al.*, 2008[5]).

Taxon	Species
Osteichthyes	
Acropomatidae	*Synagrops microlepis* (thinlip splitfish)[1]
Argentinidae	*Argentina sphyraena* (argentine)[2], *Argentina* spp.[3], *Glossanodon leioglossus* (small-toothed argentine)[4]
Callionymidae	*Callionymus* (dragonets) spp.[2]
Caproidae	*Capros aper* (boarfish)[4]
Carangidae	*Trachurus trachurus* (Atlantic horse mackerel)[2,3]
Cepolidae	*Cepola macrophthalma* (red bandfish)[2]
Clupeidae	*Clupea harengus* (Atlantic herring)[3], *Sprattus sprattus* (European sprat)[3], indet.[3,4]
Congridae	indet.[4]
Gadidae	*Gadiculus argenteus* (silvery pout)[2,3,4], *Micromesistius poutassou* (blue whiting)[2,3], *Trisopterus* spp.[3], indet.[2]
Gobiidae	*Aphia minuta* (transparent goby)[2,3] , indet.[2,3,4]
Lotidae	*Gaidropsarus biscayensis* (Mediterranean bigeye rockling)[2], Lotinae indet. larvae[3]
Macrouridae	indet.[4]
Merlucciidae	*Merluccius merluccius* (European hake)[2,3]
Myctophidae	*Diaphus* spp.[1], indet.[1]

Pleuronectiformes	indet.[2]	
Sternoptychidae	*Maurolicus muelleri* (pearlside)[3,4]	
Crustacea		
Decapoda		
Dendrobranchiata-Penaeiodea	indet.[1]	
Macrura reptantia	indet.[2]	
Pleocyemata-Anomura	Galatheidae indet.[2], *Munida* spp.[1], indet.[1]	
Pleocyemata-Brachy-ura	indet.[2,5]	
Pleocyemata-Car-idea	*Dichelopandalus bonnieri*[3], Pandalidae indet.[1], *Pasiphaea si-vado*[1], *Pasiphaea* spp.[1,2,3], *Plesionika* spp.[1], indet.[1]	
Euphausiacea	*Meganyctiphanes norvegica*[2,3], indet.[3]	
Mysida	indet.[5]	
Amphipoda	indet.[4]	
Cephalopoda		
Myopsida	*Alloteuthis* spp.[2,4], *Loligo forbesii*[3], *Loligo* spp.[2]	
Oegopsida	*Abraliopsis* spp.[1], *Illex coindetii*[2,3], *Todaropsis eblanae*[2,3], Om-mastrephidae indet.[1,2]	
Octopoda	*Eledone cirrhosa*[2], indet.[4]	
Sepioidea	*Sepietta oweniana*[4]	
Gastropoda	*Heliconoides inflatus*[4], *Limacina retroversa*[3], indet.[4]	
Bivalvia	indet.[4]	

17.6.2 Predators

Toothed whales and dolphins are considered to be the most important predators of this species, but it is also preyed on by a wide variety of birds, fish and cephalopods (Roper *et al.*, 1984, 2010a; Guerra, 1992; Table 17.6).

Table 17.6. Known predators of *Todaropsis eblanae* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Cephalopoda	Clubhook squid (*Onychoteuthis banksii*)	Hastie *et al.* (2009a)
Chondrich-thyes	Black-mouthed dogfish (*Galeus me-lastomus*)	Kabasakal (2002)
	Blue shark (*Prionace glauca*)	Clarke and Stevens (1974)
	Portuguese shark (*Centroscymnus coelolepis*)	Hastie *et al.* (2009a)
	Shortfin mako shark (*Isurus oxyrinchus*)	Hastie *et al.* (2009a)
	Sleeper shark (*Somniosus* spp.)	Hastie *et al.* (2009a)
	Smooth hammerhead (*Spyrna zi-gaena*)	Hastie *et al.* (2009a)
	Smooth lanternshark (*Etmopterus pusil-lus*)	Xavier *et al.* (2012)
Osteichthyes	Albacore (*Thunnus alalunga*)	Hastie *et al.* (2009a)

	Atlantic bluefin tuna (*Thunnus thynnus*)	Karakulak *et al.* (2009), Romeo *et al.* (2012)
	Swordfish (*Xiphias gladius*)	Hernández-García (1995), Salman (2004), Hastie *et al.* (2009a)
Aves	Great albatross (*Diomedea* spp.)	Hastie *et al.* (2009a)
	Sooty albatross (*Phoebetria fusca*)	Hastie *et al.* (2009a)
Cetacea	Bottlenose dolphin (*Tursiops truncatus*)	Santos *et al.* (1997, 2007), Blanco *et al.* (2001)
	Common dolphin (*Delphinus delphis*)	Pascoe (1986)
	Northern bottlenose whale (*Hyperoodon ampullatus*)	Santos *et al.* (2001c)
	Risso's dolphin (*Grampus griseus*)	Clarke and Pascoe (1985), Bearzi *et al.* (2011), Bloch *et al.* (2012)
	Sperm whale (*Physeter macrocephalus*)	Hastie *et al.* (2009a)
	Spotted dolphin (*Stenella attenuata*)	Hastie *et al.* (2009a)
	Striped dolphin (*Stenella coeruleoalba*)	Würtz and Marrale (1993), Blanco *et al.* (1995)

17.7 Other ecological aspects

17.7.1 Parasites

Todaropsis eblanae can host at least six species of helminth: three tetraphyllidean cestodes (*Phyllobothrium* sp., *Pelichnibothrium speciosum*, *Dinobothrium* sp.); two trypanorhynchidean cestodes (*Nybelinia yamagutii*, *Nybelinia lingualis*); and one ascaridoid nematode (*Anisakis simplex*) (Smith, 1984; Pascual *et al.*, 1996a, b, c; 1999). *Todaropsis eblanae* is the most important paratenic host for *Anisakis* (Abollo *et al.*, 1998, 2001), but it is only occasionally infected in regions of strong coastal upwelling (Pascual *et al.*, 2007). Copepods *(Pennella* sp.) (Pascual *et al.*, 1997*)* and isopods (Pascual *et al.*, 2002) have also been recorded in this species. Additional studies on *T. eblanae* and *I. coindetii* parasites (Pascual *et al.*, 1996b) suggest 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.

17.7.2 Environmental effects

Abundance indices of *T. eblanae* derived from 21 cruises off northwestern Spain (30–500 m depth) were significantly positively related with the upwelling index (Lavín *et al.*, 1991) for this area (Rasero, 1994, 1996; Rocha *et al.*, 1999). This relationship might be due to the increased survival rates of hatchlings and prerecruits when abundance of prey inceases as a consequence of greater productivity caused by seasonal upwelling. These conclusions are supported by results achieved from 57 plankton cruises carried out during a 19-year research programme in Iberian waters (Moreno *et al.*, 2009).

The species is scarce in the northern North Sea, although there may be occasional huge aggregations. These historical phenomena may be linked to hydrographical anomalies such as incursions of warm, high-salinity Atlantic seawater into the North Sea (Rae and Lamont, 1963; Hastie *et al.*, 1994).

The very recent findings of *T. eblanae* in the Arctic Sea described by Golikov *et al.* (2013) seem to be connected to the continuous warming of those waters as a consequence of climatic change recently. *Todaropsis eblanae* appears to have spread into the Barents Sea via the eastern branch of the Norwegian Current and farther by the southern branch of the North Cape coastal current as far as the Murman shelf (Golikov *et al.*, 2013).

17.8 Fisheries

Recruitment is year-round, with a peak in autumn–early winter (Rasero, 1996; Belcari, 1999d; Rocha *et al.*, 1999; Robin *et al.*, 2002).

Todaropsis eblanae is taken throughout the year as bycatch in otter trawl fisheries, and, to a lesser extent, by gill- and trammelnets, longlines, and jigging at depths of 100–400 m in the Mediterranean, off West Africa, and in the Northeast Atlantic. Most catches are made at ca. 200 m in the North Atlantic (Robin *et al.*, 2002) and at 200–800 m in Italian waters, with wide annual fluctuations in catches presumably reflecting high between-year variability in abundance (González *et al.*, 1994b; Hastie *et al.*, 1994; Belcari, 1999d).

Few official fishery statistics are available for the species. Landings from the ICES Area and the Mediterranean are usually pooled for different ommastrephid squid species, including lesser flying squid (*T. eblanae*), broadtail shortfin squid (*I. coindetii*), European flying squid (*T. sagittatus*), and neon flying squid (*Ommastrephes bartramii*). However, the species has been identified in commercial landings in Ireland, UK, France, Spain, and Portugal in the North Atlantic, and in Spain, Italy, and Greece in the Mediterranean; some data on its landings are available from market sampling in France, Spain, and Portugal (Robin *et al.*, 2002; Bruno, 2008; Bruno and Rasero, 2008; Bruno *et al.*, 2009).

Todaropsis eblanae is less important than *I. coindetii* in shortfin squid landings in France (Robin *et al.*, 2002) and northern Spain (Bruno and Rasero, 2008). It does make up ca. 40% of ommastrephid landings along the Spanish Atlantic coast (Bruno and Rasero, 2008), although those authors reported both seasonal variation and differences between gears: *T. eblanae* made up 81% of pair-trawl ommastrephid landings. Further analysis by Bruno *et al.* (2009) showed that *T. eblanae* was relatively more common in ICES Division VIIIc-W than in Division IXa-N, i.e. it formed a greater proportion of landings farther north.

Total landings of shortfin squids from the Mediterranean and Iberian Atlantic waters can be fairly consistent from year to year. The species is a minor component of the catch of the French fishery operating in the northern Bay of Biscay and Celtic Sea. Farther north, landings have generally been sporadic. At present, *I. coindetii*, *O. bartramii* and *T. eblanae* are not exploited commercially by UK fleets. However, reports from adjacent waters indicate that, at times, they can be widespread and abundant in the Northeast Atlantic and may represent a significant potential fishery resource (Hastie *et al.*, 2009a).

17.9 Stock identity

Results of molecular investigations suggest the presence of at least three genetically isolated populations across the species' distribution range in the eastern Atlantic (Dillane *et al.*, 2005), a fact that has important implications for sustainability of the resource, although it is important to note that fishing on this species is not currently regulated and is unlikely to be managed in the immediate future. The substantial genetic differences existing among samples from European waters (Northeast Atlantic and Mediterranean), from Southeast Atlantic waters off Mauritania, and off South Africa may explain the geographic variation observed in the hectocotylized arm morphology, as well

as in spermatophore morphology among animals from the Atlantic and Indian oceans (Sabirov *et al.*, 2012). The presence of the species in the Southwest Indian Ocean (Saya de Malha and Nazareth banks, Mascarene Ridges) was recorded by Korzun *et al.* (1979). It has also been reported in the South China Sea (Chen and Guo, 2001; Shevtsov and Katugin, 2006) and in Australian waters from the Timor Sea (Nesis, 1979a) down along the east and west coasts of Australia (Lu, 1982; Dunning, 1998; Wormuth, 1998). However, no data on the genetic identity of these populations are available to date.

17.10 Future research, needs, and outlook

Important topics for future research include further investigation of intraspecific divergence of *T. eblanae*, stock separation, detection of spawning sites, and description of early life stages. Further studies on parasites could explore their use as indirect indicators of the species' migratory habits (Pascual *et al.*, 1996b). In addition, there is a need to study the effect of parasites on squid growth (Pascual *et al.*, 2005).

For assessment and management purposes, cephalopod species should be adequately identified in landings. It is also recommended that sampling of cephalopods in EU waters is stratified by métier and that sampling frequency and intensity are sufficient to follow the growth of different microcohorts. In addition, data on maturation and length composition by microcohort from research surveys should be analysed to assess trends in recruitment and length at 50% maturity ($MLm_{50\%}$).

Cephalopod biology and fisheries in European waters: species accounts

Ommastrephes bartramii

Red flying squid
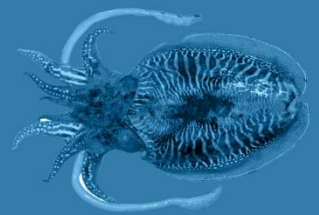
18 *Ommastrephes bartramii* (Lesueur, 1821)

A. Louise Allcock, Patrizia Jereb, Evgenia Lefkaditou, Graham J. Pierce, Lee C. Hastie, and Uwe Piatkowski

Common names

Encornet volant, encornet carol (France); Θράψαλο [thrapsalo], Καταμάχι[4] [katamachi] (Greece); totano, totano nero[4] (Italy); pota saltadora (Spain); pota-saltadora, pota-de-orelhas (Portugal); neon flying squid, red flying squid (UK) (Figure 18.1).

Synonyms

Loligo bartramii Lesueur, 1821, *Sthenoteuthis bartramii* (Lesueur, 1821), *Stenoteuthis bartrami* (Lesueur, 1821), *Loligo vitreus* Rang, 1835 in Férussac and d'Orbigny, 1834–1848, *Ommastrephes cylindraceu*s d'Orbigny, 1835 in 1834–1847, *Onychoteuthis brevimanus* Gould, 1852, *Loligo pironneauii* Souleyet, 1852, *Loligo touchardii* Souleyet, 1852, *Ommastrephes caroli* Furtado, 1887, *Ommatostrephes caroli* Furtado, 1887, *Ommastrephes caroli stenodactyla* Rancurel, 1976, *Ommastrephes caroli stenobrachium* Rancurel, 1976.
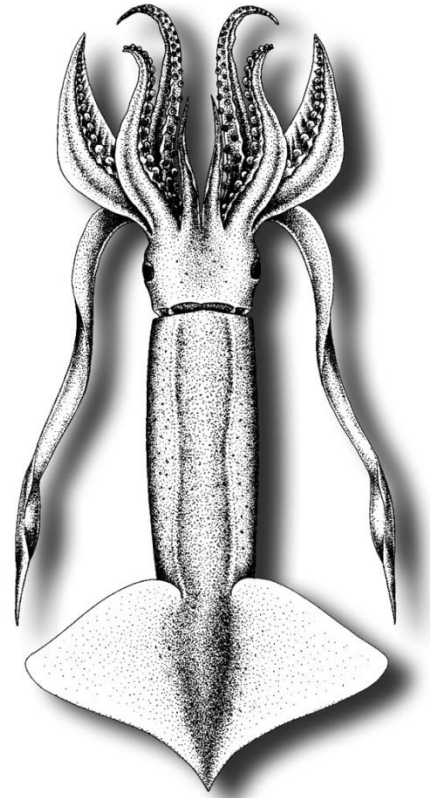
Figure 18.1. *Ommastrephes bartramii*. Dorsal view. From Guerra (1992).

18.1 Geographic distribution

The neon flying squid (*Ommastrephes bartramii* Lesueur, 1821) has a circumglobal, subtropical, and partly temperate distribution, but is excluded from the equatorial waters of all three major oceans (Roper *et al.*, 2010a). It has the greatest geographic range of all ommastrephids (Dunning, 1998), although its distribution is discontinuous between the southern and northern hemispheres. In the South Pacific, it extends from Chile in the east to the Tasman Sea in the west (Polezhaev, 1986; Dunning, 1998). In the Southeast Indian Ocean, it has been reported from off Western Australia (Filippova, 1968, 1971) and from the Great Australian Bight (Nesis, 1979a). In the South Atlantic, it is found from 14 to 27°S off Africa (Roeleveld, 1998) and from 27 to at least 45°S off South America (Zuev *et al.*, 1976; Roper *et al.*, 1984), with recent coastal records from Argentina (Ré *et al.*, 2002). In the North Pacific, *O. bartramii* is particularly abundant off the Pacific coast of Japan (Okutani *et al.*, 1981). In the North Atlantic, *O. bartramii* ranges from the Caribbean coast of Central America, north to the Grand Banks, across the Atlantic as far north as Iceland, east to the British Isles and the western North Sea, as far south as Madeira, and into the Mediterranean (Clarke, 1966; Zuev and Nigmatullin, 1975) (Figure 18.2). *Ommastrephes bartramii* is widespread throughout the Mediterranean (Torchio, 1968; Bello, 1986, 2004;

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[4] Names used by fishers, not official names

Salman, 2009; Lefkaditou *et al.*, 2011), including western and central Mediterranean parts (Biagi, 1990; Orsi Relini, 1990; Ragonese and Jereb, 1990, Ragonese *et al.*, 1992; Sanchez *et al.*, 1998a; Cuccu *et al.*, 2009c), the Gulf of Taranto (Torchio, 1967; Bello, 2007), the Adriatic Sea (Guescini and Manfrin, 1986b; Bello, 1990), the whole of the Aegean Sea (Akyol and Şen, 2004; Lefkaditou *et al.*, 2011), and the Levantine Basin (Katağan *et al.*, 1992; Lefkaditou *et al.*, 2011). Lefkaditou *et al.* (2011) provides a list of the Mediterranean records to date.
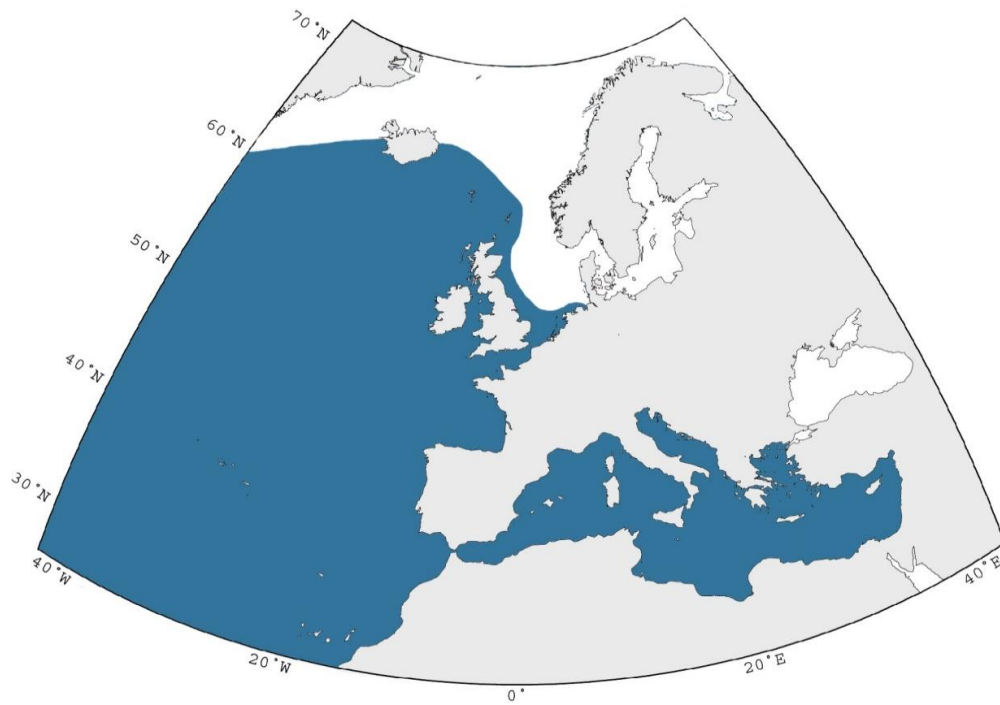
Figure 18.2. *Ommastrephes bartramii.* **Geographic distribution in the Northeast Atlantic and Mediterranean Sea.**

18.2   Taxonomy

18.2.1   Systematics

Coleoidea – Decapodiformes – Oegopsida – Ommastrephidae – Ommastrephinae – *Ommastrephes.*

18.2.2   Type locality

Type Locality not indicated.

18.2.3   Type repository

Specimen no longer extant [fide Voss (1962) and Lu *et al.*, 1995)]. Originally in Academy of Natural Sciences, 19th and The Parkway, Philadelphia, Pennsylvania, 19103, USA.

18.3   Diagnosis

18.3.1   Paralarvae

Detailed descriptions of paralarvae from the Pacific are available (Okutani, 1968, 1969; Young and Hirota, 1990; Wormuth *et al.*, 1992; Sakurai *et al.*, 1995). The following diagnosis of Atlantic paralarvae is abbreviated from Nesis (1979b); see also Figure 18.3 below. The mantle is narrow, barrel-like in early larvae, cup-shaped or semi-fusiform

later. The head is narrow, not retracting into the mantle. Arms III develop at 1.5 mm, arms IV at 2.5–3 mm ML. The proboscis is narrow, slender, longer than the arms in early larvae; lateral suckers at the tip are larger than those in the middle; it splits when animals measure between 5 and 9 mm. Chromatophores are small, closely packed, brown and carmine in colour.
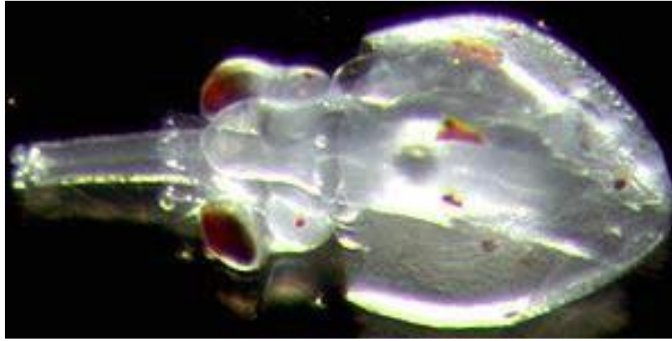
Figure 18.3. *Ommastrephes bartramii.* **Four-day-old hatchling off Hawaii. Photo: Yasunori Sakurai.**

18.3.2   Juveniles and adults

Dunning (1998) gives the following description: "Funnel groove with foveola and side pockets; tetraserial suckers on dactylus of tentacular club; medial manus-sucker rings with one tooth in each quadrant greatly enlarged; carpal-fixing apparatus consisting of smooth-ringed suckers and knobs on tentacular stalk; small, irregularly shaped, sub-cutaneous photophores present in adults, embedded in ventral mantle and ventrally in head; no photophores in paralarvae; either left or right arm IV hectocotylized by complete loss of suckers and sucker bases distally in mature males; mantle-funnel locking apparatus not fused." The tentacular clubs (Figure 18.4), suckers on arms and tentacular clubs (Figure 18.5), and beaks (Figure 18.6) are illustrated below.

Figure 18.4. *Ommastrephes bartramii.* **Tentacular club. Photo: Evgenia Lefkaditou.**

Figure 18.5. *Ommastrephes bartramii.* **Sucker rings from arm (left) and tentacular club (right). Photos: Evgenia Lefkaditou.**

Figure 18.6. *Ommastrephes bartramii.* **Lower beak (left) and upper beak (right). Photos: Evgenia Lefkaditou.**

18.4 Remarks

Nesis (1982/1987) considered that the southern hemisphere populations were likely to represent a separate subspecies, and that the North Atlantic and North Pacific populations, separated by the land barrier (the Americas), were also likely to merit subspecific status. Pinchukov (1975) also considers the North Atlantic and South Atlantic populations to be separate subspecies. Nesis (cited in Dunning 1998) suggested that a cold-water barrier prevents the mixing of the South Pacific and Indian Ocean populations, indicating that the Indian Ocean population might represent another subspecies. Nesis (1979a) also suggested that two populations may exist in the South Atlantic (separate eastern and western populations) and that two populations may exist in the Indian Ocean (again, separate eastern and western populations). However, Shevtsova *et al.* (1977) showed that the cholinesterases from squid from the Southeast Atlantic populations and the Great Australian Bight had identical properties, suggesting occasional genetic exchange between the populations. The cholinesterases of North Atlantic, North Pacific, and southern hemisphere squids all differed from each other (Shevtsova *et al.*, 1979). A study also found differences in spermatophore morphology (Nigmatullin *et al.*, 2003).

The distribution of *O. bartramii* was believed neither to extend into the Mediterranean nor as far north as Iceland (Roper *et al.*, 1984), its niche in these areas instead being occupied by *Ommastrephes caroli*. However, revisions of the Ommastrephidae by Zuev *et al.* (1975, 1976) and Nigmatullin (1979, 2007) determined that *O. caroli* was, in fact, a junior synonym of *O. bartramii*. Naef (1921/1923) specifically referred to this species as

"much more frequently found" on the market in Naples than *Todarodes sagittatus*; however, *O. bartramii* has long been considered uncommon in the Mediterranean, given the sporadic captures of isolated specimens (Torchio, 1967). Subsequent findings and records of young specimens suggest the species to be more common than sometimes suggested (Orsi Relini, 1990; Katağan *et al.*, 1992; Ragonese *et al.*, 1992; Bello, 2007), and recent observations suggest that the abundance of *O. bartramii* is currently increasing in the Mediterranean (see Lefkaditou *et al.*, 2011, for a review).

18.5 Life history

Ommastrephes bartramii is believed to live for ca. 1 year, with females reaching markedly larger size than males. Reproduction has a seasonal periodicity, which varies between areas across the distribution.

18.5.1 Egg and juvenile development

There are few data available on development of *O. bartramii* from the North Atlantic. Naef (1921/1923) describes the development of ommastrephid embryos from egg masses found floating in surface waters near Naples that he considers are "highly likely" to be attributable to *O. bartramii.* He describes the formation of the typical rhynchoteuthis larva with tentacles fused into a "proboscis", which is characteristic of ommastrephids. Wormuth *et al.* (1992) suggest that Naef's egg masses are, in fact, probably attributable to *Illex coindetii*, and it is now thought that wild-spawned *O. bartramii* egg masses have never actually been seen. Detailed information on embryonic development through hatching was provided by artificial fertilization of Pacific stock. Eggs measured 0.9 × 1.1 mm; they hatch into rhynchoteuthis paralarvae (Sakurai *et al.*, 1995). There are various estimates of hatchling size at proboscis separation. Splitting appears to begin at 4–5 mm ML (Shea, 2005), but estimates of size at completion of this process range from 7 (Wormuth *et al.*, 1992) to 12 mm (Bigelow and Landgraf, 1993). Around this time, growth changes from an exponential to a linear pattern (Yatsu and Mori, 2000; Bigelow and Landgraf, 1993). Although the tentacles are still very underdeveloped at this stage (Shea, 2005), the change in growth patterns indicates a change in feeding habits, and this may correspond with the end of the paralarval stage (Anon., 2005).

There are several records of rhynchoteuthis paralarvae from the North Atlantic (e.g. Rocha *et al.*, 1999; Collins *et al.*, 2002), but these are rarely identified to species (although see Diekmann and Piatkowski, 2002). Nigmatullin (1987) suggests that newly hatched *Ommastrephes* rhynchoteuthis paralarvae have a mantle length of ca. 1 mm. They inhabit the surface layers to depths of ca. 250 m (Zuev and Nesis, 1971). The best descriptions of paralarvae are from the Pacific (see above), where research is driven by the needs of the commercial fishery. The artificial fertilization technique developed by Sakurai *et al.* (1995) has led to paralarvae being readily available on board research vessels in the Pacific.

18.5.2 Growth and lifespan

Ommastrephes bartramii females reach markedly larger size than males. Females also have narrower fins and larger suckers. Males reach a maximum mantle length of 45 cm, but two size groups of females can be distinguished: one maturing at 36–65 cm ML, and the other at >70 cm ML. In the North Atlantic, the maximum documented ML of a female is 90 cm (BW 25 kg) and of a male is 42 cm (BW 2.2 kg) (Nigmatullin, 1989). Around Madeira, females reach a maximum size of 69 cm ML and males a maximum size of 36 cm ML; Lefkaditou *et al.* (2011) give maximum sizes for the Mediterranean

as 66 and 32 cm ML, respectively. Guerra *et al.* (2010b) listed a specimen of 102 cm ML and BW of ca. 35 kg captured in the eastern tropical Pacific.

Research from the Pacific suggests that *O. bartramii* live for ca. 1 year (Yatsu *et al.*, 1997; Yatsu, 2000). However, for larger females, lifespan is not known and may be longer.

Most available information on length–weight relationships and growth refers to this species in the Pacific (e.g. Yatsu and Mori, 2000; Chen and Chiu, 2003). Growth of females is slightly more rapid than for males, as expected from the marked sexual dimorphism (Yatsu *et al.*, 1997; Yatsu, 2000). There are again few available data on growth in European waters. Lefkaditou *et al.* (2011) report a length–weight relationship for the Mediterranean, based on a sample of 30 individuals of both sexes, using an exponential model, because this had a slightly higher r^2 value than the traditional power equation. For consistency, we include the power equation version here: BW = $0.310 \times$ ML$^{3.044}$.

The most comprehensive data are probably those of Pinchukov (1975), who studied maturation, fecundity, and horizontal migrations, sampling >400 *O. bartramii* from the North Atlantic and an additional 25 specimens from the Mediterranean. However, those data are in an unpublished Master of Arts thesis in Russian and were not available for this review. Nigmatullin (1987) summarizes the changes in body size and ecological niche as *O. bartramii* develops (Table 18.1).

Table 18.1. Ecological changes in *Ommastrephes bartramii* with growth. Data from Nigmatullin (1987).

Habitat	Maturity Stage	Size (mantle length)	Food
Plankton	Egg mass	1 mm	n/a
Plankton	Paralarva	1–8 mm	Macroplankton
Plankton	Juvenile	1–2.5 cm	Mesozooplankton
Micronekton	Juvenile	3–8 cm	Macrozooplankton
Nekton	Subadult/adult	>15 cm	Fish and squid

Rostral length of the lower beak (LRL) increases linearly with increasing mantle length (ML). In the Northeast Atlantic, this relationship is described by the equation ML = 8.55 + 40.72LRL ($r^2 = 0.98$), based on 57 *O. bartramii* (59–590 mm ML). Lefkaditou *et al.* (2011) indicate that a power regression better fits data from the Mediterranean: ML = 36.2613 $\times$ LRL$^{1.069}$ ($r^2 = 0.95$, $n = 11$).

18.5.3 Maturation and reproduction

Sexual maturation in the female begins when it reaches a length of ca. 40 cm ML. Females produce 3–8 million eggs or more (Nigmatullin and Laptikhovsky, 1994) ca. 1 mm long, which they are thought to lay in underwater floating ribbons (Hastie *et al.*, 2009a). Reproduction takes place towards the end of summer and at the beginning of autumn. In the North Atlantic, two groups of females mature at different sizes: the middle-sized group is mature at 36–65 cm of ML and larger-sized group at >70 cm ML (Gaevskaeya and Nigmatullin, 1976; Nigmatullin, 1989). North Atlantic males start maturing at 27–30 cm ML, and all males >32 cm are mature.

Spawning is throughout the year in the North Atlantic, with some seasonal activity from spring to the beginning of autumn (Gaevskaya and Nigmatullin, 1976; Roper *et al.*, 2010a). In the North Pacific population, there are two cohorts, one that begins spawning in September, the other with a winter spawning season, with females beginning their spawning activity in November–December (Bower and Ichii, 2005).

18.6 Biological distribution

18.6.1 Habitat

Individuals of *O. bartramii* are rare in the North Sea and are thought only occasionally to pursue fish to this region. They perish in cold waters and may be found on the shore in The Netherlands following cold stormy weather (Zuev and Nesis, 1971); at least one specimen has been stranded as far north as Yorkshire in Great Britain (Robson, 1925). The greatest abundance of *O. bartramii* in the North Atlantic is thought to be in the Madeira-Azores–Canary Islands region (Zuev and Nigmatullin, 1975). *Ommastrephes bartramii* have been caught at 400–500 m over the Mid-Atlantic Ridge at 44–47°N (Khromov, 1987b) and at other ridge locations in the North Atlantic (Zuev *et al.*, 1976).

Despite the wide distribution of *O. bartramii*, reproduction appears to be limited to areas between 25 and 40°N and south of the equator, with foraging taking place elsewhere throughout its known range (Aleksandronetz *et al.,* 1983). Zuev *et al.* (1976) suggest that it is limited to waters of 14–17°C. Shoals of *O. bartramii* rarely comprise more than 30 individuals (Zuev and Nigmatullin, 1975). At night, they appear to avoid areas where the water depth is exceptionally shallow directly above seamounts (review: Moiseev and Nigmatullin, 2002).

18.6.2 Migrations

Individual *O. bartramii* have been observed from manned submersibles (Sever-2, TINRO-2, and Tethys) over the Mid-Atlantic Ridge and adjacent areas (including Croner Rise, Josephine Seamount, and the South Azores Seamount complex). They have been recorded near the surface at night (down to 100 m), and at 560–1050 m by day (Moiseev, 1987, 1991). They are believed to undergo diel vertical migrations of 1000–1500 m. Upward (night-time) migration is at speeds of up to 5 m m^{-1}, with migrations taking between 30 min and 2.5 h, depending on the starting daylight depth (Moiseev, 2001). In the North Atlantic, shoals of larger squid, mainly females, make a feeding migration at the beginning of the summer to areas north of 40°N, including the North Sea and Newfoundland, and then return in autumn to lower latitudes to the reproductive part of their range (Zuev and Nigmatullin, 1975; Gaevskaya and Nigmatullin, 1976; Zuev *et al.*, 1976).

18.7 Trophic ecology

18.7.1 Prey

Ommastrephes bartramii takes mainly fish (especially myctophids, garfish, flying fish, and mackerel); squids, including its own species; crustaceans (amphipods, decapod larvae, euphausiids, and shrimps); and heteropods in the Northeast Atlantic (Table 18.2) and in other parts of its range, e.g. the Southwest Atlantic (Lipiński and Linkowski, 1988).

Table 18.2. Prey composition of *Ommastrephes bartramii*, as known from studies in the Northeast Atlantic and eastern Mediterranean Sea (compiled from Zuev and Nesis, 1971[1]; Ch. Nigmatullin, pers. comm. (based on Gaevskaya and Nigmatullin, 1976, and Nigmatullin and Pinchukov, 1976; both papers in Russian)[2]; Vafidis *et al.*, 2008[3]).

Taxon	Families and species
Osteich-thyes	Beloniformes indet. (garfish, flying fish)[1], Myctophidae indet. (lanternfish)[1,2], Scombri-dae indet. (mackerel)[1], indet.[1,2,3]
Crusta-cea	Decapoda indet. larvae [2], Euphausiacea indet.[2], Mysida indet.[3], Amphipoda indet.[2], Hyperiidae indet.[2], Phronimidae indet.[2], Copepoda indet.[2]
Cepha-lopoda	*Onychoteuthis banksii*[2], Enoploteuthidae indet.[2], Oegopsida indet.[1,2] , indet.[3]
Gas-tropoda	Limacinidae indet. (pteropod)[1], Pterotracheoidea indet.[2]

18.7.2 Predators

Ommastrephes bartramii is preyed upon by a variety of cetaceans, but also by large fish such as tuna and swordfish (Table 18.3).

Table 18.3. Known predators of *Ommastrephes bartramii* in the Mediterranean Sea and Northeast Atlantic.

Taxon	Species	References
Chondrich-thyes	Portuguese dogfish (*Centroscym-nus coelolepis*)	Carrasson *et al.* (1992)
Osteichthyes	Albacore (*Thunnus alalunga*)	Salman and Karakulak (2009)
	Atlantic bluefin tuna (*Thunnus thynnus*)	Battaglia *et al.* (2013), Romeo *et al.* (2012)
	Swordfish (*Xiphias gladius*)	Bello (1991b), Guerra *et al.* (1993), Hernández-García (1995), Salman (2004), Chancollon *et al.* (2006), Romeo *et al.* (2009, 2012)
Cetacea	Cuvier's beaked whale (*Ziphius cavirostris*)	Carlini *et al.* (1992)
	False killer whale (*Pseudorca cras-sidens*)	Hernández-García (2002b)
	Pygmy sperm whale (*Kogia brevi-ceps*)	Martins *et al.* (1985)
	Sperm whale (*Physeter macro-cephalus*)	Clarke *et al.* (1993)
	Risso's dolphin (*Grampus griseus*)	Bearzi *et al.* (2011)

18.8 Other ecological aspects

18.8.1 Parasites

Parasites of *O. bartramii* in the North Atlantic include two species of didymozoid trematode, larvae of three species of cestode, two species of nematode, and one acanthocephalan (Gaevskaya and Nigmatullin, 1976). The helminth fauna is identical in the South Atlantic, and Gaevskaya and Nigmatullin (1976) suggest that the parasitic relationships were established prior to the geographic separation of the North and South Atlantic forms of *O. bartramii*.

18.8.2 Environmental effects

Zuev *et al.* (1976) reported that, in the Atlantic, these squid forage in the productive zones found seawards of upwelling areas, and concentrations can be found in the North Atlantic from the Canary Islands to Cape Blanc, around Madeira, and around the Azores. Lefkaditou *et al.* (2011) attributed the apparent increase in abundance of this species in recent years in the Mediterranean to warming of upper sea layers since the 1980s.

18.9 Fisheries

Although this species is fished primarily in the Pacific (for details see Bower and Ichii, 2005), there are estimated to be 2.5 million t of *O. bartramii* in the North Atlantic (Nigmatullin, 1989; Nigmatullin *et al.*, 1991). In the ICES Area, landings of *O. bartramii* are reported as mixed landings together with *I. coindetii*, *Todaropsis eblanae*, and *Todarodes sagittatus*. Although Spanish landings of this group have reached several thousand tonnes in some years, it is unlikely that much of this biomass is attributable to *O. bartramii*. Nigmatullin (1989, 2004) notes that consistently occurring concentrations of *O. bartramii* have not been found in the North Atlantic, and it is, therefore, unlikely to represent a viable fishery resource in this area.

18.10 Stock identity

The North Pacific population of *O. bartramii* consists of two stocks that are spatially separated on the feeding grounds, reproduce at different times and which have recently exhibited opposite trends in abundance (Chen and Chiu, 2003; Chen, 2010). There is no evidence yet to suggest that the North Atlantic population consists of more than one stock, but there is a general lack of research on this species in the North Atlantic.

18.11 Future research, needs, and outlook

Much of the basic biology of *O. bartramii* in the North Atlantic is not known. Considering that several authors (see above) consider the North Atlantic population to be a separate subspecies, it is not appropriate to assume that data from the Pacific populations are representative of the North Atlantic. The translation of the comprehensive Russian literature from the 1960s to 1990s on oceanic ommastrephid squids into English would supply a wealth of new information to the international scientific community.

Cephalopod biology and fisheries in European waters: species accounts

Gonatus fabricii

Boreoatlantic armhook squid
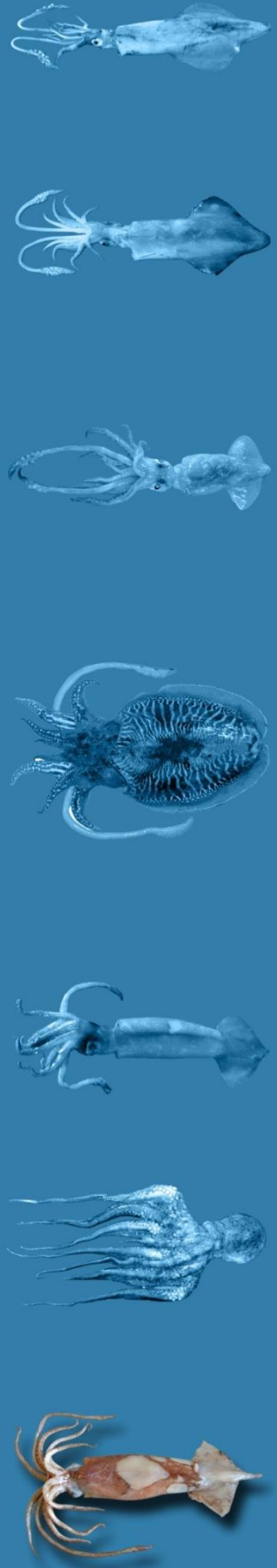
19 *Gonatus fabricii* (Lichtenstein, 1818)

Uwe Piatkowski, Karsten Zumholz, Patrizia Jereb, Sonia Seixas, Daniel Oesterwind, Evgenia Lefkaditou, A. Louise Allcock, Graham J. Pierce, and Oleg Katugin

Common names

Encornet atlantoboreal (France), gonalura atlantoboreal (Spain), Boreoatlantic gonate squid or Boreoatlantic armhook squid (UK) (Figure 19.1).

Synonyms

Onychoteuthis fabricii Lichtenstein, 1818, *Onychoteuthis amoena* Möller, 1842, *Cheloteuthis rapax* Verrill, 1881 in 1880–1881. See Kristensen (1981a) for full details of synonomy.

19.1 Geographic distribution

The boreoatlantic gonate squid, *Gonatus fabricii* (Lichtenstein, 1818), is widely distributed in offshore Arctic and subArctic waters of the North Atlantic, and its distribution also extends into the western Barents Sea (Arctic Ocean). In the Northeast Atlantic, it is found in the Norwegian Sea, westwards around Greenland to Baffin Bay and the Newfoundland Basin, and southwards to southern Cape Cod in the Northwest Atlantic (Nesis, 1971; Wiborg, 1979b; Kristensen, 1981a, 1983; Bjørke and Gjøsæter, 2004; Roper *et al.*, 2010b; Golikov *et al.*, 2013) (Figure 19.2).
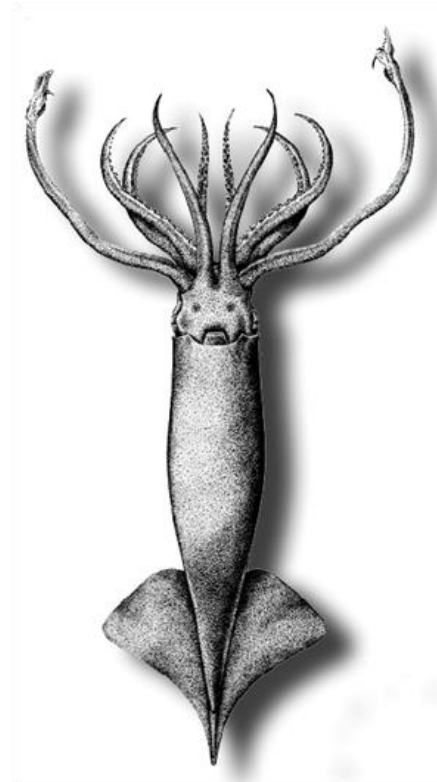
Figure 19.1. *Gonatus fabricii.* **Ventral view. From Kristensen (1981a).**
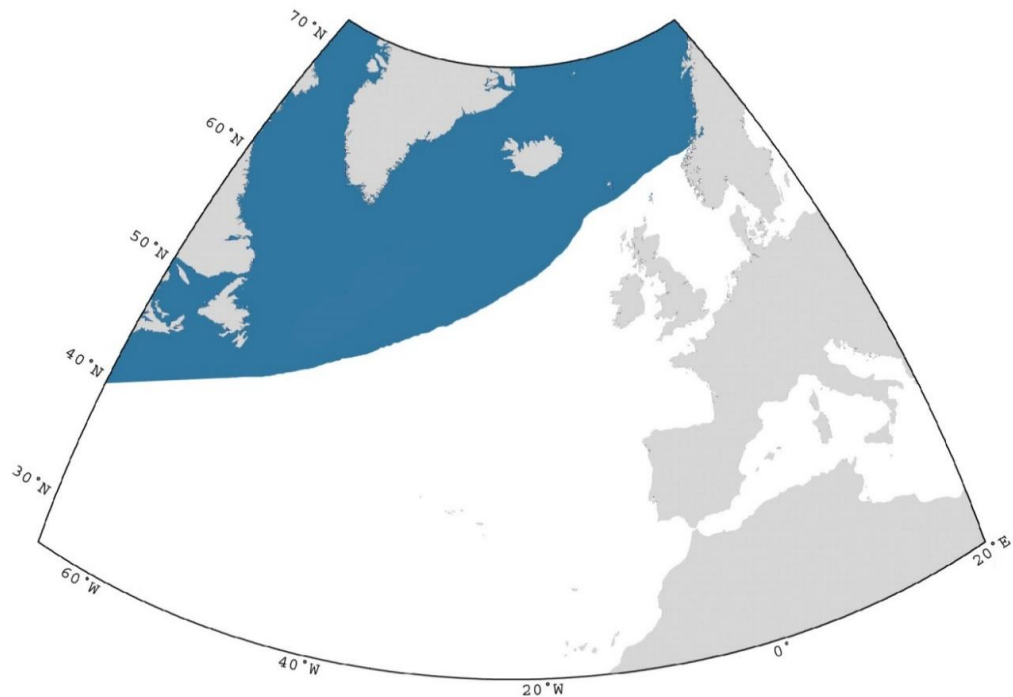
Figure 19.2. *Gonatus fabricii.* **Geographic distribution in the North Atlantic.**

19.2 Taxonomy

19.2.1 Systematics

Coleoidea – Decapodiformes – Oegopsida – Gonatidae – *Gonatus.*

19.2.2 Type locality

Amerdloq Fjord, Holsteinsborg (ca. 67°N 54°W), West Greenland, 457–521 m [fide Kristensen and Knudsen (1983)].

19.2.3 Type repository

Kobenhavns Universitet, Zoologisk Museum, Universitetsparken 15, DK 2100 Copenhagen, Denmark. Neotype [fide Kristensen (1981a: 66)].

19.3 Diagnosis

19.3.1 Paralarvae

Paralarvae are characterized by the presence of a pair of round or oblong chromatophores on the ventral surface of the head, slightly anterior to the ocular axis, and by a dorsal pad on the funnel organ with an inverted V-shape, with straight lateral sides (Kristensen, 1981a; Falcon *et al.*, 2000). The presence of chromatophores can be used as the primary character to identify even very small specimens (ML <3.6 mm), in which the funnel organ is too small to verify confidently its shape (Falcon *et al.*, 2000). The onset of formation of hooks from suckers, both on the tentacular clubs and arms I–III, is at ML >20 mm (Falcon *et al.*, 2000). This seems to be a good character to define the end of what is now termed the paralarval phase and the beginning of the juvenile phase in gonatids (Young, 1972; Kristensen, 1977a); in fact, the presence of hooks is likely to indicate a change in feeding habits and, therefore, a change in the ecological position of the squids.

19.3.2 Juveniles and adults

Figure 19.3. *Gonatus fabricii.* **Tentacular club showing the two larger hooks. Photo: Karsten Zumholz.**

In juveniles, one large hook is generally present on the club, with three small hooks proximal to it and a moderately large hook distal to it (see Figure 19.3); several small suckers are present on both dorsal and ventral sides of the club, especially at the proximal end, where they form a large cluster (Kristensen, 1977a; Falcon *et al.*, 2000).

Adult maximum mantle length is 385 mm, which was reported for a female in the Barents Sea (Sennikov *et al.*, 1989), although the largest individual recorded by Arkhipkin and Bjorke (2000) was 322 mm ML. The mantle is long, slender, conical, slightly wider at its midpoint, tapering to a sharp point posteriorly, its muscular part ending at the conus, with a fleshy, tapered column extending posteriorly as the tail. Fins are heart-shaped, with anterior lobes free and lateral margins rounded, their length <50% of ML, their width slightly less than their length. Tentacular clubs are small and slender, their length ca. 12–20% of ML, with one very large, central hook followed proximally by three small hooks and distally by one moderately large

Figure 19.4. *Gonatus fabricii.* **Lower beak (left) and upper beak (right). Photo: Uwe Piatkowski.**

hook. Nine to 13 tetraserial rows of suckers and hooks are present on the proximal half of arms III, and 14–17 tetraserial rows of suckers (no hooks) on the proximal half of arms IV (Kristensen, 1981a; Roper *et al.*, 2010b). Note that tetraserial armature on the arms is characteristic of the Gonatidae (Roper *et al.*, 1969). Beaks are illustrated in Figure 19.4.

19.4 Remarks

Gonatus fabricii and *G. streenstrupi* are similar species, and confusion between the two may arise in areas of the (North) Atlantic where they overlap, such as the Irminger Sea (Kristensen, 1981a). Whereas *G. fabricii* is thought to be the most abundant squid in the high latitudes of the Atlantic and the only native pelagic squid in the Arctic (Nesis, 2001; Golikov *et al.,* 2013), *G. steenstrupi* lives in the boreal zone of the Atlantic, especially in the eastern part off the United Kingdom, Ireland, and Spain (Kristensen, 1981a). *Gonatus steenstrupi* was also the most abundant squid in a comprehensive collection of oceanic cephalopods from an RV "G. O. Sars" expedition in summer 2004 to the northern and central regions of the Mid-Atlantic Ridge, including the Reykjanes Ridge and the Charlie Gibbs Fracture Zone (Vecchione *et al.*, 2010).

The two species can be separated on the basis of the two large chromatophores present on the ventral surface of the head in *G. fabricii*, and absent in *G. steenstrupi*; this character can also be used to distinguish paralarvae of the two species (Falcon *et al.,* 2000; Vecchione and Young, 2006). Other useful characters to separate the two species are the numbers of tentacular club hooks proximal to the large central hook: three hooks in *G. fabricii*, 4–5 hooks (the largest is the most distal) in *G. steenstrupi* (Kristensen,

1981a). A possible complication is mentioned by Boyle (2009). Vecchione and others participating in the RV "G. O. Sars" expedition in 2004 (Vecchione *et al.*, 2010) found several specimens in which one tentacular club displayed the characteristics of *G. fabricii*, whereas the other club was consistent with *G. steenstrupi.* Boyle suggests that genetic studies are needed to resolve the issue. Kristensen (1981a) also mentioned the relative size of the club as a potentially useful character: *G. fabricii* has a relatively smaller club [12–20% of pen length (PL)], and *G. steenstrupi* has a relatively larger club (20–35% of PL). As noted by Arkhipkin and Bjorke (1999), *G. fabricii* has a muscular "tail" at the posterior end of the mantle; hence, ML exceeds PL by ca. 13%. This tail is often damaged in trawl-caught animals, making it impossible to measure their dorsal mantle length. Hence, PL is often used as the standard measurement.

19.5 Life history

The life cycle of *G. fabricii* probably does not exceed 2 years. Spawning takes place from winter to summer, and females die soon after egg development is completed.

19.5.1 Egg and juvenile development
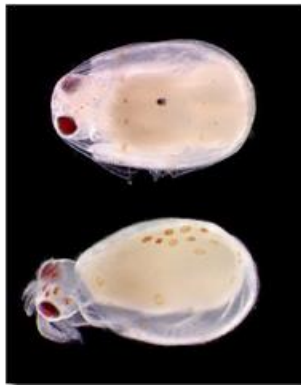
Figure 19.5. *Gonatus fabricii.* Egg and hatchling. Egg diameter 5.5 mm. Photo: Lars Are Hamre (from Bjørke and Gjøsæter, 2004).

Eggs are translucent, light blue, and roughly spherical (elliptical), with maximum egg diameter of 4–6 mm (Kristensen, 1981b; Bjørke and Hansen, 1996; Bjørke *et al.*, 1997). Nesis (1999) suggests that embryonic development takes ca. 4 months. However, this conclusion is based on a formula developed for warm-water species, and the real development time may be much longer (O. Katugin, pers. comm.). Hatching size is ca. 3 mm ML (see Figure 19.5). Paralarvae may be found widely in the water column, but usually at depths <400 m in spring and mainly within the upper 100 m in summer (Falcon *et al.*, 2000). Juveniles are found in large shoals in the uppermost 100 m of the water column over deep water (Nesis, 1965). South of the polar circle, juveniles are reported to perform upward diurnal migrations at night (Kristensen, 1977b). By the time the hook on the tentacular club starts to develop (20 mm ML), the adult proportions of the body become recognizable. At that stage, the squids are very mobile and swim like adults (Kristensen, 1977b).

19.5.2 Growth and lifespan

As in other squid species (e.g. *Illex coindetii*, Jereb and Ragonese, 1995; Arkhipkin *et al.*, 1998), different methods to investigate growth and age give different results for *G. fabricii*. Analysis of length frequency data suggests a rather long life cycle (2–3 years, Muus, 1962; Zumholz and Frandsen, 2006). Slow growth rates of 4–5 mm (Piatkowski and Wieland, 1993; Zumholz and Frandsen, 2006) and 8–9 mm month[-1] (Kristensen 1977b, 1984) were proposed for animals from West Greenland waters. This would not be so unlikely for a polar species, given that cold-water species grow more slowly and live longer than species from lower latitudes. Statolith microstructure analysis of juveniles and immature squids revealed four growth zones, and daily, weekly, and fortnightly increment bands in the statoliths have been proposed (Kristensen, 1980).

If the assumption of 1 increment d^{-1} is true for *G. fabricii*, as has been shown for other species, based on the total number of increments counted in adult specimens, the lifespan would not exceed 2 years (Arkhipkin and Bjørke, 2000).

Sources differ as to whether the length–weight relationship differs between sexes. Arkhipkin and Bjorke (2000) reported no differences, whereas Zumholz and Frandsen (2006) found sexual dimorphism in the growth pattern (Table 19.1).

Table 19.1. *Gonatus fabricii*. Length–weight relationships in different geographic areas for females (F), males (M), and sexes combined (All). 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
West Greenland	0.269	2.050	F	Zumholz and Frandsen (2006)
	0.053	2.648	M	
	0.101	2.412	All	
	0.138	2.43	All	Kristensen (1984)
Norwegian Sea	0.118	2.47	All	Arkhipkin and Bjørke (1999)

19.5.3   Maturation and reproduction

Many aspects of the biology of this species have been described only relatively recently. As noted by Bjørke (2001), only seven mature specimens had been recorded and only one described in detail.

Development of the testis begins at a pen length of ca. 80–100 mm, and maturity is reached at a pen length of ca. 200 mm (Kristensen, 1983). Spermatophores measure 6–10 mm. The ovary begins to develop at a pen length of 60–90 mm and increases in weight until maturity. Spermatophores have been found attached onto the buccal membrane of maturing and ripe females, indicating head-to-head copulation (Arkhipkin and Bjørke, 1999; Zumholz and Frandsen, 2006). Individual fecundity is estimated to be ca. 10 000.

Female *G. fabricii* undergo considerable degenerative changes before spawning; the tentacles are lost, the arm and mantle tissues swell, the suckers on the arms are lost, and the animals lose their capability for active locomotion. It has been hypothesized (Arkhipkin and Bjørke, 1999) that these degenerative changes are related to the important activity of the nidamental glands in these species, i.e. the secretion of a peculiarly dense matter that envelops the eggs within the egg mass; this, in turn, would make the egg masses negatively buoyant, and bound to sink unless they are carried in the arms of "brooding", light, and positively buoyant females.

Gonatus onyx females are known to "brood" their eggs (Okutani *et al.*, 1995; Seibel *et al.*, 2000, 2005). Females use hooks on their arms to hold the egg mass, apparently contracting and extending the arms repeatedly to aerate the eggs (Siebel *et al.*, 2005). This may also be the case in *G. fabricii.* Bjorke *et al.* (1997) caught egg masses and mature females together in pelagic trawls and speculates that females may have been egg brooding.

Adult mature male *G. fabricii* show no signs of degeneration and seem likely to mate several times during their life cycle (Kristensen, 1984).

It is speculated that the squid spawn in the Norwegian Sea from winter to summer and that the eggs hatch from late March to June or July (Bjørke and Gjøsæter, 2004). Spawning is suggested to take place at great depths, in oceanic waters. As noted above, females probably brood the eggs, although free egg masses have been found among

spent females, possibly because the egg masses had become detached from the females during capture. The eggs are kept together in a single layer between two mucous membranes (Bjørke *et al.*, 1997; Bjørke and Gjøsæter, 2004). Off Greenland in the Davis Strait, hatching is believed to take place in spring and early summer, whereas the eggs hatch in Disko Bay in autumn and early winter (Kristensen, 1984).

19.6   Biological distribution

19.6.1   Habitat

Gonatus fabricii is an oceanic species that exists commonly between the surface and 500–1000 m; records from depths of 2700 m exist, however. Adults are common at the bottom and in midwater layers in Arctic and subArctic waters, whereas juveniles live within a very wide range of depths from 2000 m to the surface, to where they may undertake diel migrations. Adults hunting for prey near the surface at night are reported from West Greenland (Kristensen, 1981b, 1983; O. Katugin, pers. comm.).

19.6.2   Migrations

This species undertakes vertical migrations and, possibly, horizontal migrations. Kristensen (1977b) reports dispersal of young squid by the West Greenland Current from zone 1 to zone 2, although no other extensive horizontal migrations are reported. Variation in the barium:calcium ratio in the statoliths of this species suggests that juveniles inhabit surface waters and that larger specimens move to deeper waters. In addition, increases in the uranium:calcium and strontium:calcium ratios towards the outer part of the statolith suggested migration of adult squid into colder water (Zumholz *et al.*, 2007b).

19.7   Trophic ecology

19.7.1   Prey

Juveniles feed on copepods, euphausiids, amphipods, pteropods, and chaetognaths (Table 19.2). Adults can feed on prey larger than themselves (Kristensen, 1984), and the diet consists of macroplanktonic crustaceans (amphipods, euphausiids), fish [e.g. capelin (*Mallotus villosus*), redfish (*Sebastes marinus*), and lanternfish], and cephalopods (occasionally including bottom-dwellers such as octopuses). Cannibalism also takes place (Nesis, 1965; Zuev and Nesis, 1971; Wiborg, 1980; Kristensen, 1984). Although crustaceans are the main prey of both juveniles and adults, the importance of fish and cephalopods in the diet increases with age. Fish start to become more important in the diet after the hooks on the tentacular clubs have developed (Kristensen, 1984).

Table 19.2. Prey composition of *Gonatus fabricii*, as known from studies in different regions of the eastern Atlantic (compiled from Nesis, 1965[1]; Zuev and Nesis, 1971[2]; Wiborg; 1980[3], 1982[4], 1984[5]; Kristensen, 1984[6]).

Taxon	Species
Osteichthyes	
Myctophidae	indet. lanternfish[2]
Sternoptychidae	*Maurolicus muelleri* (pearlside)[4]
Osmeridae	*Mallotus villosus* (capelin)[6]
Sebastidae	*Sebastes norvegicus* (as *S. marinus*) (redfish or rose fish)[3]
Crustacea	
Decapoda	*Pasiphaea* sp.[6], indet. shrimps[3,6]

Euphausiacea	*Meganyctiphanes norvegica*[3,4,5], *Thysanoessa longicaudata*[1], indet.[2]
Mysida	indet.[6]
Amphipoda	*Hyperia galba*[1], Hyperiidae indet.[6], *Parathemisto abyssorum*[4], *Parathemisto* spp.[3,4,5], *Pseudalibrotus* spp.[1], *Themisto gaudichaudi (as P. gaudichaudii)*[4], *T. libellula (as P. libellula)*[4], indet.[3]
Isopoda	indet.[3,6]
Copepoda	*Calanus finmarchicus*[1,3,4,5], *C. hyperboreus*[1,3], *Euchaeta* sp.[5], *Paraeuchaeta norvegica*[1,3,4], *Metridia* spp.[1], *Temora* sp.[5], indet.[3]
Cephalopoda	*Gonatus fabricii*[2,3,4,6], Octopoda indet.[2], Oegopsida indet.[2], indet.[6]
Gastropoda	*Clione limacina*[3], *Limacina retroversa* (retrovert pteropod)[1,3,4,5]
Chaetognatha	*Eukrohnia* spp.[3,4,5], *Sagitta* spp.[1,3,4,5]

19.7.2 Predators

Gonatus fabricii is one of the most abundant food resources for virtually all top predators in the North Atlantic (Bjørke, 2001; Bjørke and Gjøsæter, 2004; Table 19.3) and a key species in the eastern Arctic foodweb (Gardiner and Dick, 2010). It is taken by large pelagic cephalopods and fish, seabirds, and marine mammals (Table 19.3). Beaks in stomach contents of predators are often only identified to genus (i.e. *Gonatus* sp.), and the inference that it is *G. fabricii* that has been eaten then depends to some extent on knowledge of its distribution and abundance. However, as noted above under **Remarks**, the distribution overlaps with that of *G. steenstrupii*, and both species are found around Iceland and southeast Greenland (see maps in Frandsen and Zumholz, 2004; Jereb and Roper, 2010), so there is scope for misidentification.

Table 19.3. Known predators of *Gonatus fabricii* in the North Atlantic.

Taxon	Species	References
Cephalopoda	European flying squid (*Todarodes sagittatus*)	Wiborg (1972)
Osteichthyes	Atlantic cod (*Gadus morhua*)	Grimpe (1933)
	Atlantic salmon (*Salmo salar*)	Lear (1980)
	Deep water arrowtooth eel (*Histiobranchus bathybius*)	Martin and Christiansen (1997)
	Greater amberjack (*Seriola dumerili*)	Matallanas *et al.* (1995)
	Greenland halibut (*Reinhardtius hippoglossoides*)	Dawe *et al.* (1998), Hovde *et al.* (2002), Michalsen *et al.* (1998)
	Redfish (*Sebastes marinus*)	Nesis (1965)
	Roundnose grenadier (*Coryphaenoides rupestres*)	Bergstad *et al.* (2010)
Aves	Atlantic puffin (*Fratercula arctica*)	Falk *et al.* (1992)
	Common murre (*Uria aalge*)	Barrett *et al.* (1997)
	Northern fulmar (*Fulmarus glacialis*)	Lydersen *et al.* (1989), Garthe *et al.* (2004)
	Thick-billed murre (*Uria lomvia*)	Barrett *et al.* (1997)
Pinnipedia	Harp seal (*Phoca groenlandica*)	Lydersen *et al.* (1991), Potelov *et al.* (2000), Haug *et al.* (2004)

	Hooded seal (*Cysophora cristata*)	Potelov *et al.* (2000), Bjørke (2001), Haug *et al.* (2004)
Cetacea	Blue whale (*Balaenoptera musculus*)	Hjort and Ruud (1929)
	Northern bottlenose whale (*Hyperoodon ampullatus*)	Benjaminsen and Christensen (1979), Clarke and Kristensen (1980), Lick and Piatkowski (1998), Bjørke and Gjøsæter (1998), Bjørke (2001), Hooker *et al.* (2001), Santos *et al.* (2001c)
	Cuvier's beaked whale (*Ziphius cavirostris*)	Blanco *et al.* (1997), Santos *et al.* (2001d)
	Long-finned pilot whale (*Globicephala melas*)	Nesis (1965), Desportes and Mouritsen (1988, 1993), Bjørke (2001)
	Narwhale (*Monodon monoceros*)	Grimpe (1933), Laidre and Heide-Jørgensen (2005)
	Sperm whale (*Physeter macrocephalus*)	Clarke and Macleod (1976), Clarke (1997), Bjørke and Gjøsæter (1998), Santos *et al.* (1999, 2002), Bjørke (2001), Simon *et al.* (2003), Mendes *et al.* (2007)

19.8 Fisheries

Gonatus fabricii is considered to have some fishery potential. It is the most abundant squid of the Arctic and subArctic waters of the North Atlantic, it has a high lipid content, the flesh, at least of younger animals, has a good consistency, and the species attains a desirable size (Nesis, 1965; Wiborg, 1979b; Kristensen, 1984; Frandsen and Wieland, 2004; Roper *et al.*, 2010b). According to Kristensen (1984), the very high lipid content of the digestive gland (ca. 63%) makes it suitable for industrial use as well, although the abundance of lipases in the midgut may be problematic (see Okuzumi and Fujii, 2000). Piatkowski and Wieland (1993) suggested that the species might be of commercial interest, based on the abundance of early life stages of *G. fabricii* off West Greenland. Bjørke and Gjøsæter (1998) suggested that there was surplus production of this species in the Norwegian Sea, which could be exploited by the fisheries. However, because females undergo significant tissue degradation as they mature (Arkhipkin and Bjorke, 1999), fisheries might logically target immature animals, although it is possible that mature females could be marketed for animal feeds, while retaining males for human consumption.

As noted by Frandsen and Wieland (2004), there have been at least two unsuccessful experimental fisheries for this species. In 1998, an experimental fishery targeted adult *G. fabricii* in the Norwegian Sea using a pelagic trawl, but catches were small (no more than 10 kg haul[-1]). An experimental bottom-trawl fishery for cephalopods conducted off West Greenland during a period of two months in 2003 achieved a total catch of oegopsid squid (probably *Gonatus* sp.) of only 4.7 kg. However, *G. fabricii* is used by Greenland Inuit as bait in the cod and shellfish fisheries and for human food. It is also regularly taken as bycatch in shrimp trawls in Greenland (Frandsen and Wieland, 2004; Roper *et al.*, 2010b).

19.9 Stock identity

Off West Greenland, at least two distinct populations exist (Disko Bay and Davis Strait), with differences in time of spawning and morphometric measurements (Kristensen, 1982). Another, probably separate, population is found in the Norwegian Sea

(Bjørke and Gjøsæter, 2004). However, genetic methods for stock separation have not yet been applied to *G. fabricii*.

19.10 Future research, needs, and outlook

Considering the possible fishery potential of this species, improved knowledge on distribution, aggregation patterns, and migrations would be useful. Molecular genetic identification of remains in predator stomach contents would supplement the (incomplete) information on identity available from beaks.

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Annex 1: European and Mediterranean common names for cephalopods

Evgenia Lefkaditou, Roger Villanueva, Tooraj Valinassab, and Graham J. Pierce

This annex lists common names for cephalopods used in Europe and in non-European countries bordering the Mediterranean. These countries and their associated languages and dialects covered are listed in Table A1.1, along with the abbreviations used. Unless otherwise indicated, only the main official language is listed for each country. Abbreviations follow the ISO 639-2 codes as listed on the Library of Congress Standards webpage (http://www.loc.gov/standards/iso639-2/php/code_list.php). Some languages have different codes for bibliographic and terminology purposes.

The material has been compiled from various published general accounts (e.g. Jaeckel, 1958; Roper *et al.*, 1984; Jereb and Roper, 2005, 2010) and national lists, as well as information from colleagues and web sources, as listed in Table A1.2.

The common names of cephalopods appear in Table A1.3. Gaps indicate where we (and our listed sources) were unaware of common names for the species–country combinations in question. We can rarely be completely certain that no common name exists in these cases. We have not attempted to include all colloquial names (e.g. "inks" for squid in Scotland). We also excluded some names because their use is generic or ambiguous, such as the Icelandic "kolkrabbi" (octopus or flying squid) and "smockfiskur" (squid or cuttlefish) or the Norwegian "blekksprut" (octopus, cuttlefish, or sepiolid). However, we have included generic names where they were apparently the only name in use (e.g. kalamari for squid species in Israel). In the case of Arabic names, we list the most frequently used common names. Additional regularly used names in the Arabic-speaking countries are listed in Table A1.4.

Table A1.1. Names and codes of countries and languages (including widely spoken dialects) used along Mediterranean and Northeast Atlantic coasts. Some countries have two codes, here identified as "B" (bibliographic) or "T" (terminology).

Country			Language or dialect	
Code	Name	ISO 639-2 Code	Name	English translation
AL	Albania	Alb	Gjuha shqipe	Albanian
BE	Belgium	Dut	Belgisch-Nederlands [5]	Belgian Dutch, Flemish
CS	Serbia-Montenegro	Srp	Srpski	Serbian
CY	Cyprus	ell-cyp	Ελληνικά	Cypriot Greek
CZ	Czech Republic	ces (T); cze (B)	Čeština	Czech
DE	Germany	deu (T); ger (B)	Deutsch	German
DK	Denmark	Dan	Dansk	Danish
DZ	Algeria	Ara	العربية	Arabic
EG	Egypt	Ara	العربية	Arabic

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[5] The other official languages are French and German.

ES	Spain	Cat	Català	Catalan; Valencian
ES	Spain	Spa	Español; Castellano	Spanish; Castilian
ES	Spain	eus (baq)	Euskara	Basque
ES	Spain	Glg	Galego	Galician
FI	Finland	Fin	Suomi	Finnish
FO	Faroe Islands	Fao	Føroyskt	Faroese
FR	France	fra (T); fre(B)	Français	French
FR	France	Cos	Corse	Corsican
FR	France	Bre	Breton	Breton
FR	France	Mah	Marsall	Marshallese
GB	United Kingdom	Eng	English	English (UK)
GR	Greece	ell (gre)	Ελληνικά	Greek
HR	Croatia	Hrv	Hrvatski	Croatian
IE	Ireland	Gle	Gaeilge	Irish
IL	Israel	Heb	Ivrit	Hebrew
IS	Iceland	ice (B); isl(T)	Íslenska	Icelandic
IT	Italy	Ita	Italiano	Italian
IT	Italy	Scn	Sicilianu	Sicilian
IT	Italy	Srd	Sardu	Sardinian
LB	Lebanon	Ara	العربية	Arabic
LV	Latvia	Lav	Latviešu valoda	Latvian
LY	Libya	Ara	العربية	Arabic
MA	Morocco	Ara	العربية	Arabic
MT	Malta	Mlt	Malti	Maltese
NL	Netherlands	nld (T); dut (B)	Nederlands	Dutch; Flemish
NO	Norway	Nor	Nynorsk [6]	Norwegian
PL	Poland	Pol	Polski	Polish
PT	Portugal	Por	Português	Portuguese
RU	Russia	Rus	Russkij jazyk	Russian
SE	Sweden	Swe	Svenska	Swedish
SI	Slovenia	Slv	Slovenščina (slovenski jezik)	Slovenian
SY	Syria	Ara	العربية	Arabic
TN	Tunisia	Ara	العربية	Arabic
TR	Turkyie	Tur	Türkçe	Turkish

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[6] Norway has three official written languages, Bokmål, Nynorsk, and Sami.

Table A1.2. Additional sources for the common names listed in Table A1.3: published works, web resources, and communications from colleagues.

Country	Source
Albania	Dhora (2008). Fjalor i emrave të kafshëve të Shqipërisë (Emri shkencor – Shqip – Anglisht) / Dictionary of animal names of Albania (Scientific names – Albanian – English). Camaj – Pipa. Shkodër, Albania. pp. 288. (Cited at WoRMS - World Register of Marine Species - http://www.marinespecies.org/index.php).
Algeria	Wahid Refes, Ecole Nationale Supırieure des Sciences de la Mer et de l'Amınagememt du Littoral (ENSSMAL), Campus universitaire de Dıly Ibrahim, Alger, Algerie.
Belgium and The Netherlands	Dutch: WoRMS (see above), confirmed by Jan Mees, Director of Flanders Marine Institute, Belgium.
Croatia and Slovenia	Svjetlana Krstulović Šifner, Head of the Center of Marine Studies, University of Split, Croatia.
Cyprus	Cypriot Greek: Charis Charilaou, Department of Fisheries and Marine Research, Ministry of Agriculture, Nicosia, Cyprus.
Denmark	Ministry of Food, Agriculture and Fisheries, Danish Veterinary and Food Administration (March 2011)
Egypt	Official Egyptian language: Hatem Hanafy Mahmoud, National Institute of Oceanography and Fisheries (NIOF), Kasr El-Ainy Street, Cairo, Egypt. In Arabic from Bariche (2012).
Faroe Islands	Eilif Gaard, Faroe Marine Research Institute, Box 3051, FO-110 Torshavn, Faroe Islands.
Finland	Petri Suuronen, Finnish Game and Fisheries Research Institute, FI-00791 Helsinki, Finland.
France	Breton and Corsican language: Jean-Paul Robin, IBFA- Université de Caen Basse-Normandie Esplanade de la paix, Caen Cedex, France; Mediterranean French (Marshallese) : Angélique Jadaud, IFREMER, Sète Cedex, France.
Greece	Hellenic Statistical Authority http://www.statistics.gr/portal/page/portal/ESYE, except * which are unofficial names mentioned in the Pan-European Species directory Infrastructure (PESI) portal (http://www.eu-nomen.eu/portal) and ** which are names proposed to the Hellenic Ministry of Rural Development and Food, General Directorate for Fisheries common names, to be adapted as official common names.
Iceland	Jorge Fernandez, University of Aberdeen, UK
Ireland	Irish Statute Book, Office of the Attorney General, Ireland (March 2011) http://www.irishstatutebook.ie/2003/en/si/0320.html
Israel	Dor Edelist, Marine Ecologist, Haifa University, Israel.
Italy	Official Italian language: Bello and Borri (1990), except for * Roper *et al.* (2010); common names in Sicilian dialect provided by Fabio Fiorentino, Istituto per l'Ambiente Marino Costiero (IAMC), Mazara del Vallo, Sicily; common names in Sardinian dialect from the southern part of the island provided by Rita Cannas, University of Cagliari, Department of Life Sciences and Environment, Cagliari, Sardinia, Italy.
Latvia	Georgs Kornilovs, Institute of Food Safety, Animal Health and Environment "BIOR", Department of Fish Resources Research, Riga, Latvia.
Malta	Constantine Mifsud, Maltese taxonomist of molluscs.
Norway	Moen and Svendsen (1999), Gjøsæter *et al.* (2009), Terje van der Meeren, Institute of Marine Research, Austevol, Norway.

Portugal	Ministério da Agricultura, do Desenvolvimento Rural e das Pescas, Portugal; Sanches(1989).
Russia	Chingis Nigmatullin, Atlantic Research Institute of Fisheries and Oceanography, Kaliningrad, Russia.
Spain	Basque, Catalan, Galician: Ministerio de Medio Ambiente y Medio Rural y Marino, Gobierno de España
Sweden	Francesca Vitale, Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources, Institute of Marine Research, Lysekil, Sweden.
Syria and Tunisia	Arabic dialects: Bariche (2012).
Turkey	Alp Salman, Ege University, Faculty of Fisheries, Department of Hydrobiology, Izmir, Turkey.

Table A1.3. Common names of cephalopod species in different languages and dialects most widely spoken along Mediterranean and Northeast Atlantic coasts. Where specific and more generic common names are listed, the latter are given in parenthes (sic). Notes: (*) and (**) indicate names taken from different sources, as listed under the relevant country in Table A1.2.

Language	*Octopus vulgaris*	*Eledone cirrhosa*	*Eledone moschata*	*Sepia officinalis*	*Sepia elegans*	*Sepia orbignyana*
Ara	اخطبوط شائع	اخطبوط اقرن	اخطبوط مسكي	سيبيا شائع	سيبيا انيق	سيبيا زهري
AL-sqi	Tetëkëmbëshi; liku-rishtja; oktapodi i zakonshëm;		Octopod i eger	Sepia; supja; sipa; sepja	Sepja elegante	
BE-dut	Kraak; gewone octopus; gewone achtarm; achtarm	Kleine achtarm		Gewone zeekat; zeekat	Sierlijke zeekat	Gedoornde zeekat
CS-srp	Hobotnica	Muzgavac	Crni muzgavac			
CY-ell	Οχταπόδι		Μοσχοχτάποδο	Σουπιά (soupia)		
CZ-ces	Chobotnice pobřežní			Sépie obecná		
DE-deu	Gemeiner krake, oktopus	Zirrenkrake	Moschuskrake	Gemeiner tintenfisch	Kleine sepie, schlammsepie	Dornsepie
DK-dan	Almindelig ottearmet blæksprutte; ottearmet blæksprutte	Eledoneblæksprutte; ele-done	Moskusblæksprutte	Sepiablæksprutte; se-pia		
ES-cat	Pop roquer	Pop blanc	Pop mesquer	Sèpia	Castanyó	
ES-spa	Pulpo	Pulpo blanco	Pulpo almizclado, pulpo cabezón	Choco, jibia, sepia	Choquito, castaño	Choquito picudo

ES-eus	Olagarro, amor-rotza	Cabezón		Txautxa, jibia		
ES-glg	Polbo	Polbo cabezón	Polbo almiscrado	Choco	Choquiño	Choquiño picudo
FI-fin	Meritursas	Pikkumyskitursas	Myskitursas	Yleinen mustekala, se-pia		
FO-fao						
FR-fra	Pieuvre, poulpe	Elédone commune, poulpe, poulpe blanc	Elédone musquée	Seiche commune	Seiche élégante	Seiche rosée
FR-bre	Soavenn, morgazh			Morgad, margatte		
FR-cos	Polpu, pulpu, porpu			Seppia		
FR-mah	Poufre	Poulpe	Poulpe	Seiche	Sépions	Sépions
GB-eng	Common octopus	Horned octopus, lesser octopus	Dusky octopus	Common cuttlefish	Elegant cuttlefish	Pink cuttlefish
GR-ell	Χταπόδι (chta-podi)	Μοσκιός (moschios); λασπομοσχιός**	Μοσκιός (moschios)	Σουπιά (soupia)		Κοκκινοσουπιά*
HR-hrv	Hobotnica	Bijeli muzgavac	Crni muzgavac	Sipa	Sipica rumenka	Sipica iglata
IE-gle	Ochtapas			Cudal		
IL-heb	Tamnoon hakhof	Tamnoon	Tamnoon hamooshk	Dyonon rokhim (sabid-dah)	Sabiddah	Sabiddah
IS-ice		Mokkur				
IT-ita	Polpo commune	Moscardino bianco	Moscardino muschiato, moscardino rosso	Seppia comune	Seppia elegante Castagnola	Seppia pizzuta Castagnola
IT-scn	Purpu majulinu	Purpu jancu	Purpu nivuru	Siccia	Siccitedda	Castagnola
IT-srd	Pruppu	Pruppu biancu	Pruppu muscau	Seppia	Seppia	Seppia

LV-lav	Parastais astoņkājis	Mazais astoņkājis	Baltais astoņkājis	Parastā sēpija	Elegantā sēpija	Sārtā sēpija
MT-mlt	Qarnita	Frajjell tal-frilli	Qarnita ta-misk	Siċċa	Siċċa tat-tkarkir	Siċċa tax-xewka
NL-nld	Kraak; gewoone octopus; gewone achtarm; achtarm			Inktwise; zeekat; gewone zeekat; gewone inktvis	Sierlijke zeekat	Gedoornde zeekat
NO-nor	Blekksprut	Vanlig åttearmet bleksprut				
PL-pol	Ośmiornica zwyczajna			Matwa zwyczajna; matwa pospolita		
PT-por	Polvo-vulgar, polvo	Polvo-do-alto; polvo-cabeçudo	Polvo-mosqueado, polvo-de-cheiro, polvo cabeçudo	Choco-vulgar, choco	Choco-elegante	Choco-de-cauda
RU-rus	Obyknovennayj os'minog	Obyknovennayj malyj os'minog	Muskusnyj os'minog; мускусный осьминог	Obyknovennaya kara-katiza or sepia	Izjaschnaya kara-katiza or sepia	Sepia orbinji
SE-swe	Åttaarmad bläck-fisk	Eledone, åttaarmad bläckfisk		Sepia		
SI-slv	Hobotnica	Kodrasta hobotnica	Moškatna hobotnica	Sipa	Mala sipa	Bodičasta sipa
TR-tur	Ahtapot	Mis ahtapot; kancalı ahta-pot	Misk ahtapotu	Sübye, mürekkep balığı	Küçük sübye, mürekkep balığı	Dikenli sübye, mürekkep balığı

Language	*Sepietta ow-eniana*	*Sepiola atlantica*	*Sepiola* spp.	*Loligo vulgaris*	*Loligo forbesii*	*Alloteuthis media*	*Alloteuthis subu-lata*
Ara	حبار ابتر شائع	حبار ابتر	حبار ابتر	حبار مالوف	حبار اورده	حبار خيزراني	حبار اورده
AL-sqi				Kallamari; lignja; kal-mari; ulignja			
BE-dut	Langwerpige dwerginktvis	Kleine zeekat, gewone dwerginktvis, dwerginktvis	Dwerginktvis	Gewone pijlinktvis; pijlinktvis	Noordse pijlinktvis		Kleine pijlinktvis, dwergpijlinktvis
CS-srp							
CY-ell				καλαμάρι			
CZ-ces				Krakatice			
DE-deu	Große sepiette	Atlantische sepi-ole		Gemeiner kalmar	Nordischer kalmar	Großkeuliger mit-telländischer zwer-gkalmar	Geschwänzter At-lantischer zwer-gkalmar, gepfriemter zwer-gkalmar
DK-dan				Europæisk loligo; Eu-ropæisk loligoblæk-sprutte	Loligoblæksprutte; loligo	Dværgblæksprutte	
ES-cat				Calamar			Calamarsó
ES-spa	Globitos	Gobitos	Globitos	Calamar, calamar europeo	Calamar veteado	Calamarín menor	Calamarín picudo
ES-eus				Txipiron			
ES-glg			Chopiños	Lura	Lura colorada	Puntilla pequena	Puntilla común

FI-fin		Pikkuseepia		Kalmari		pikkukalmari, pohjanmerenkalmari
FO-fao		Lítil høgguslokkur			Mathøgguslokkur	
FR-fra	Sépiole commune	Sépiole grandes oreilles		Encornet européenne	Encornet veiné	Casseron bambou	Casseron comun
FR-bre				Stivell, stiogenn, sifoc'h		
FR-cos				Totanu		
FR-mah			Sépions	Encornet	Encornet	Piste; chipiron	Piste; chipiron
GB-eng	Common bobtail squid	Atlantic bobtail squid		European squid	Veined squid	Midsize squid	European common squid
GR-ell	Είδος σεπιέττας**		Είδος Σεπίολας**	Καλαμάρι	Καλαμάρι; Ψευτοκαλάμαρο*	Καλαμαράκι*	
HR-hrv	Obični bobić			Lignja	Lignja pučinka	Lignjica	Šiljasta lignja
IE-gle				Mathair shuigh na heorpa		
IL-heb	Sabiddah		Sabiddah	Loligo shakoof (kalamari)			Kalamari
IS-ice				Evrópskur smokkfiskur		
IT-ita	Seppiola commune		Seppiola	Calamaro comune	Calamaro venato	Calamaretto comune	Calamaretto puntuto
IT-scn	Confettura cappuccettu		Confettura cappuccettu	Calamaru	Calamaru	Calamaricchi	Calamaricchi
IT-srd	Seppiedda	Seppiedda	Seppiedda	Calamari	Calamari	Calamareddu	Calamareddu
LV-lav	Strupā sepieta	Atlantijas sepiola	Sepiola	Parastais kalmārs	Garspuru kalmārs	Vidējais kalmārs	Eiropas kalmārs
MT-mlt	Dakkru		Dakkru	Klamar	Klamar	Totlu	Totlu tal-fond

NL-nld	Langwerpige dwerginktvis	Kleine zeekat; gewone dwerginktvis; dwerginktvis		Pijlinktvis; gewone pijlinktvis	Noordse pijlinktvis		Kleine pijlinktvis; dwergpijlinktvis
NO-nor							
PL-pol				kałamarnice			
PT-por	Chopo-anão	Chopo-anão	Chopo-anão	Lula-comum, lula-vulgar, lula-legítima, lula	Lula-riscada	Lula-bicuda-curta	Lula-bicuda-com-prida
RU-rus	Sepietta ow-ena	Atlantichrskaya sepiola		Obyknovennayj dlinnoperyj kal'mar	Severnyj dlinnoperyj kal'mar	Allotevtis or dlinnohvostyj kal'mar	
SE-swe	Sepietta	Atlantsepiola		kalmar	Nordisk kalmar		Alloteuthis
SI-slv			Sipice	Ligenj		Pritlikavi ligenj	
TR-tur	Kulaklı sübye		Kulaklı sübye	Kalamar	Kalamar	Orta boy kalamar; Küçük kalamar	

Language	*Ommastrephes bartramii*	*Illex coindetii*	*Todarodes sagittatus*	*Todaropsis eblanae*	*Gonatus fabricii*	References
Ara	حبار	حبار احمر	حبار طيار	حبار طيار صغير	حـ بار	Bariche (2012)
AL-sqi						Dhora (2008)
BE-dut	Purperen pijlinktvis		Grote pijlinktvis	Kromme pijlinktvis		Adema *et al.* (1989)
CS-srp						
CY-ell		θράψαλο	θράψαλο βυθού			
CZ-ces						
DE-deu		kurzflossenkalmar	Europäischer flugkalmar	Kleiner flugkalmar	Nordischer köderkalmar	
DK-dan		Rød blæksprutte	Flyveblæksprutte			
ES-cat		Canana vera	Canana			
ES-spa	Pota saltadora	Volador	Volador	Pota costera		
ES-eus		Pota	Pota	Pota		
ES-glg		Pota común		Pota pequena		
FI-fin			Euroopanliitokalmari			European Commission (1998)
FO-fao			Agnhøgguslokkur			
FR-fra	Encornet volant	Encornet rouge	Toutenon commun	Toutenon soufleur		
FR-bre						
FR-cos						
FR-mah		Pisseur	Pisseur	Pisseur		

GB-eng	Neon flying squid	Broadtail shortfin squid	European flying squid	Lesser flying squid	Boreoatlantic gonate squid	Roper et al. (1984), Jereb and Roper (2010)
GR-ell	θράψαλο; καταμάχι ωκεανού **	θράψαλο; κόκκινο θράψαλο	θράψαλο πελαγικό; καταμάχι*	θράψαλο; πλατύουρο θράψαλο **		
HR-hrv	Lignjavac	Lignjun	Lignjun veliki	leteći lignjun		
IE-gle						Office of the Attorney General, Ireland (2003)
IL-heb	Kalamari	Kalamari	Kalamari	Kalamari		
IS-ice						
IT-ita	Totano nero (*)	Totano; todaro	Totano viola	Totano tozzo		Bello and Borri (1990), Jereb and Roper (2010)
IT-scn		Todaru di paranza	Todaru di lenza	Todaru di paranza		
IT-srd	Calamari	Calamari	calamari	Calamari		Marcialis (2005)
IS-ice		Beitusmokkur				
LV-lav	Sarkanais kalmārs	Īsspuru kalmārs	Parastais lidotājkalmārs	Mazais lidotājkalmārs	Ziemeļatlantijas kalmārs	
MT-mlt	Totlu	Totlu	Totlu	Totlu		
NL-nld	Purperen pijlinktvis		Grote pijlinktvis	Kromme pijlinktvis		de Bruyne et al. (1994), Hayward et al. (1999),

						Cattrijsse and Vincx (2001)
NO-nor			Akkar		Gonatus	Moen and Svendsen (1999), Gjøsæter *et al.* (2009)
PL-pol						
PT-por	Pota-saltadora, pota-de-orelhas	Pota-voadora, potra-voadora, charuto	Pota-europeia	Pota-costeira		Sanches (1989)
RU-rus	Kal'mar bartrama	Evropejskij or severoatlan-ticheskij korotkoperyj kal'mar	Severnyj kal'mar strelka	Korenastyj kal'mar or kal'mar-todaropsis	Kal'mar - gonatus severnyj	
As in RefsSE-swe						
Sl-slv		Kratkoplavuti ligenj	Puščičasti ligenj			
TR-tur	Bartram (only in SE Turkey, fethiye)	Erkek kalamar; Kirmizi kala-mar	Erkek kalamar; mızraklı kala-mar	Erkek kalamar; uçan kalamar	Kalamar	Bariche (2012)

Table A1.4. Additional Arabic dialect names, adapted from Bariche (2012) except as indicated in Table A1.2 above.

Species	DZ	EG	LB	LY	MA	SY	TN
Octopus vulgaris	Karnite	Okhtabute shaaea (بوط أخط)			رطالة	أخطبوط	
Eledone cirrhosa	Karnite hassi		قرنيط ابيض	خطبوطأ			بومسك
Eledone moschata	Karnite hassi	Okhtabute msky (بوط خط)		قرنيط مسكى	أةطالرط/طوب خط	بوط خط مِسكياً	بومسك
Sepia officinalis	Sepia; choubai	Sobbeit; طيب سد / بار حياب سد /	Sabbidije; حباب بد/صص/ارابح	Shouibia	Chubei; seiche; شوكو/ سد ب يا	صبيدج، حَبَّار	Choubei; شوب اي / سد ب يا / شواب ي / سوب يا
Sepia elegans	Sepia	سبيط	صبيدج/حبار/صبيضن بلدي			صبيدج، حَبَّار	شوابي صغير
Sepia orbignyana	Sepia		صبيدج/حبارا			صبيدج، حَبَّار	شوابي صغير
Sepiolidae	Sepia skhira						
Loligo vulgaris	Calmar	kalimary (يماري لك)	كالامار/قلم صبيدج/قلم صبيضن فرنجي			صبيدج	
Loligo forbesii	Calmar	kalimary (يماري لك)	كالامار/قلم صبيدج/قلم			صبيدج	
Alloteuthis media	Calmar hassi	كليماري	كالامار/قلم صبيدج/قلم			حَبَّار وَسَطي	
Alloteuthis subulata	Calmar hassi	كليماري	كالامار/قلم صبيدج/قلم			حَبَّار أوربي	
Illex coindetii	Calmar hmar	Kalimary	كالامار/قلم صبيدج/قلم/ صبيضن كاوتشوك			قلم	
Todarodes sagittatus	Calmar hmar	Kalimary; يماري لك	كالامار/قلم صبيدج/قلم	كليماري		حَبَّار طيار	
Todaropsis eblanae	Calmar hmar	كليماري	كالامار/قلم صبيدج/قلم	كليماري		حَبَّار طيار	

Annex 2: Regression equations used to estimate cephalopod sizes based on measurements of beaks

M. Begoña Santos and Graham J. Pierce

In studies of diets of marine predator (e.g. predatory fish, seabirds, marine mammals), cephalopods are often identified from their chitinous mandibles, because cephalopod flesh digests relatively rapidly, and the beaks are indigestible and may persist in the stomach for several days (possibly due to becoming lodged in the stomach lining (see Clarke, 1986; Santos *et al.*, 2001b).

As beaks are often well preserved, with little evidence of size reduction attributable to digestion (Tollitt *et al.*, 1997), measurements on the beaks can be used to estimate the original size of the cephalopods consumed. Squids and cuttlefish are generally identified from the lower beaks; consequently, most published regressions refer to lower beaks. Clarke (1986) gives regression equations for many species, but several other authors have subsequently compiled relevant regressions; these are all listed in Table A2.1. Additional regressions for *Eledone cirrhosa* are available in Lefkaditou and Bekas (2004), but they have not been included here because beak size is treated as the response variable and animal size as the predictor.

For squids and cuttlefish, the usual measurement is rostral length, whereas hood length is used for octopods. The measurements taken are illustrated in Figure A2.1.

Finally, we included regressions based on measurement of the cuttlebone in *Sepia officinalis* (from Almonacid Rioseco *et al.*, 2009).
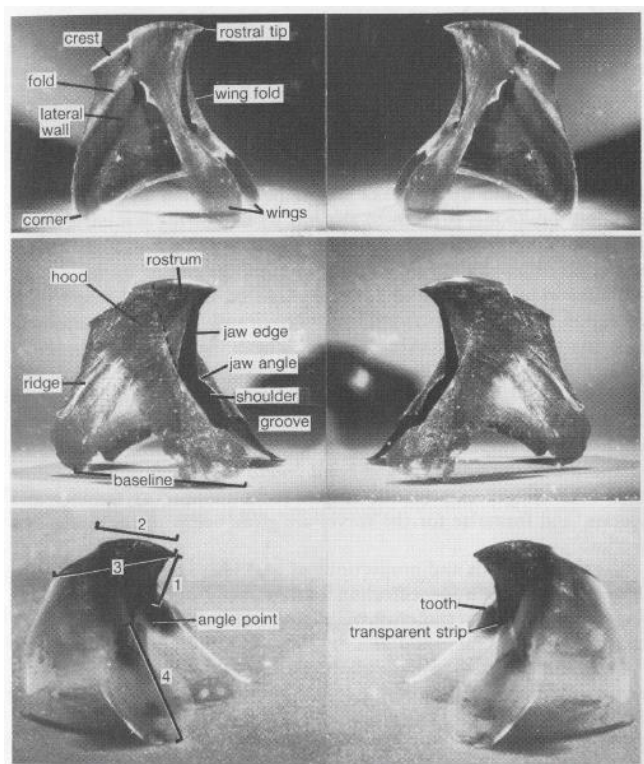

Figure A2.1. Stereoscopic images of decapod lower beaks from Clarke (1986), indicating features of a typical beak. Measurements illustrated are (1) rostral length, (2) hood length, and (3) crest length.

Table A2.1. Regression equations to estimate cephalopod sizes [ML, dorsal mantle length (mm); W, total weight (g)] from beak measurements: LHL, lower hood length; LRL, lower rostral length (mm); UHL, upper hood length; URL, upper rostral length; CL, cuttlebone length. Sources are as follows: AG, González (1994); Alm, Almonacid Rioseco *et al.* (2009); Br, Brown and Pierce (1998); Cl, Clarke (1986); Her, Hernández García (1995); PG, Pérez-Gándaras (1983); San, Santos (1998); Wf, Wolff (1984), Xav, Xavier *et al.* (2010). Where a regression refers to one sex only, this is indicated. Where known, sample size (*n*) and goodness of fit (*r²*) are given. The symbol * indicates combined data from more than one species.

Species	Mantle length (mm)	n	r²	Source	Body weight (g)	n	r²	Source
Octopus vulgaris					$W = 6.171858 \times LHL^{3.03000}$	108	-	PG
Eledone cirrhosa	$ML = 3.380 + LHL \times 26.570$	211	-	PG	$W = 5.365600 \times LHL^{2.85000}$	214	-	PG*
					$W = 8.250720 \times UHL^{2.33740}$			Br
Eledona moschata	$ML = 22.242 + LHL \times 28.230$				$W = 7.980491 \times LHL^{3.146}$			Xav
Sepia officinalis	$ML = -2.140 + LHL \times 21.890$	53	-	PG	$W = 0.123690 \times LHL^{4.06000}$	53	-	PG
	$ML = 0.0005 + CL \times 2.7142^{(males)}$	320	0.98	Alm				
	$ML = 0.0004 + CL \times 2.7451^{(females)}$	106	0.98	Alm				
Sepia elegans	$ML = 21.340 + LHL \times 13.560$	166	-	PG	$W = 5.312168 \times LHL^{1.56000}$	166	-	PG
Sepia orbignyana								
Sepietta oweniana	$ML = 22.060 + LHL \times 2.550$	67	-	PG	$W = 4.711470 \times LHL^{0.74000}$	67	-	PG
Sepiola atlantica	$ML = 15.020 + LHL \times 0.750$	60	-	PG*	$W = 1.491825 \times LHL^{0.35000}$	69	-	PG*
Loligo vulgaris	$ML = -42.220 + LRL \times 84.274$	129	-	PG*	$W = 8.331137 \times LRL^{2.91000}$	33	-	PG*
	$ML = 3.420 + URL \times 65.902$	29	-	San	$W = 12.335700 \times URL^{2.53290}$	29	-	San
Loligo forbesi	$ML = -42.220 + LRL \times 84.274$	129	-	PG*	$W = 19.10595 \times LRL^{2.39000}$	74	-	PG*
	$ML = -28.956 + URL \times 103.891$	232	-	San	$W = 31.09200 \times URL^{2.49712}$	233	-	San
Alloteuthis subulata	$ML = -30.990 + LRL \times 113.970$	135	-	PG*	$W = 7.389056 \times LRL^{2.75000}$	116	-	PG
Alloteuthis media	$ML = -30.990 + LRL \times 113.970$	135	-	PG*				
Illex coindetti					$W = 3.234906 \times LRL^{2.47000}$	14	-	Cl

					$W = 3.089471 \times LRL^{2.73500}$ (males)	157	0.916	AG
					$W = 2.664456 \times LRL^{2.88800}$ (females)	165	0.940	AG
	$ML = 56.849 \times LRL^{0.705}$ (males)	99	0.92	Her	$W = 3.460109 \times LRL^{2.60400}$ (males)	99	0.98	Her
	$ML = 57.812 \times URL^{0.656}$ (males)	99	0.92	Her	$W = 3.714336 \times URL^{2.41900}$ (males)	99	0.98	Her
	$ML = 52.557 \times LRL^{0.865}$ (females)	101	0.94	Her	$W = 3.339764 \times LRL^{2.67500}$ (females)	101	0.96	Her
	$ML = 53.006 \times URL^{0.827}$ (females)	101	0.94	Her	$W = 3.420203 \times URL^{2.55800}$ (females)	101	0.96	Her
					$W = 2.590886 \times URL^{2.70200}$ (males)	157	0.946	AG
					$W = 2.420563 \times URL^{2.77500}$ (females)	165	0.950	AG
Todaropsis eblanae	$ML = -10.320 + LRL \times 35.040$	194	-	PG	$W = 1.803988 \times LRL^{3.17000}$	194	-	PG
	$ML = 31.031 \times LRL^{0.953}$ (males)	55	0.92	Her	$W = 2.227545 \times LRL^{2.80000}$ (males)	99	0.98	Her
	$ML = 28.737 \times URL^{0.948}$ (males)	55	0.88	Her	$W = 1.732213 \times URL^{2.80200}$ (males)	55	0.91	Her
	$ML = 25.953 \times LRL^{1.095}$ (females)	59	0.97	Her	$W = 1.965998 \times LRL^{3.03300}$ (females)	59	0.96	Her
	$ML = 24.963 \times URL^{1.055}$ (females)	59	0.95	Her	$W = 1.440096 \times URL^{2.91700}$ (female)	59	0.95	Her
Todarodes sagittatus	$ML = -11.300 + LRL \times 41.360$	-	-	Cl	$W = 2.188027 \times LRL^{2.83000}$	-	-	Cl
	$ML = 62.396 \times LRL^{0.740}$ (females)	94	0.91	Her	$W = 3.386849 \times LRL^{2.48500}$ (female)	94	0.90	Her
	$ML = 62.465 \times URL^{0.728}$ (females)	94	0.91	Her	$W = 3.375016 \times URL^{2.44900}$ (female)	94	0.90	Her
Ommastrephes bar-trami	$ML = 52.7 + LRL \times 276.1$	-	0.96	Wf	$W = 735.095189 \times LRL^{2.0700}$	-	0.98	Wf
	$ML = 51.4 + URL \times 282.4$		0.94	Wf	$W = 812.405825 \times URL^{2.15000}$			Wf
Gonatus fabricii	$ML = -43.400 + LRL \times 42.870$	17	-	Cl*	$W = 0.520000 \times LRL^{3.33000}$	20	-	Cl*

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