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First record of an egg mass of *Loligo forbesi* (Cephalopoda: Loliginidae) in the Ligurian Sea, with notes about egg laying patterns in southern populations

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Abstract
During the trawl survey MEDITS 2005, an egg mass of *Loligo forbesi* was collected in the western Ligurian Sea, on a muddy bottom at about 600 m of depth. This record, the first in the study area, is discussed taking into account general information about spawning in *L. forbesi* Mediterranean and Macaronesian populations. The occurrence of different reproductive patterns in *Loligo* species are underlined and in *L. forbesi* the existence of egg strands heavier and lighter than the sea water is considered indicative of a spawning strategy evolving with time and age of the female.

Riassunto
Si riporta il primo ritrovamento di uova di *L. forbesi* su fondi fangosi batiali del Mar Ligure occidentale, a circa 600 m di profondità. Per commentare questo reperto ed inquadrarlo nella biologia della specie, si riassumono le informazioni sulla riproduzione reperibili nella letteratura relativa al Mediterraneo e all'Atlantico adiacente. Queste riguardano: 1) la presenza di zone di deposizione in prossimità del limite piattaforma/scarpata, che fu accertata circa un secolo fa dai ricercatori della Stazione Zoologica di Napoli; 2) l'associazione delle capsule ovigere a celenterati coloniali che risulta dalle stesse ricerche; 3) lo sviluppo embrionale, con simili dimensioni alla schiusa in materiale del Mediterraneo e delle Azzorre; 4) osservazioni sul comportamento condotte alle Azzorre sia su individui marcati, sia su individui in cattività: di questi ultimi è stato osservato l'accoppiamento e la deposizione delle uova; 5) un recente ritrovamento di uova deposte a circa 730 m di profondità nell'Egeo. Questa rassegna degli aspetti riproduttivi è suggerita dal fatto che *L. forbesi* del Mediterraneo e del nord Europa sarebbero distinti a livello di sottospecie e che nelle due sottospecie della congenere *L. vulgaris* (*L. v. vulgaris*, *L. v. reynaudii*) vengono descritti comportamenti riproduttivi sostanzialmente differenti. Si conclude che nelle popolazioni meridionali di *Loligo forbesi*, le capsule ovigere possono essere deposte in un intervallo di profondità di oltre 500 m; le capsule ovigere possono presentare diverse tipologie, cioè essere più dense o meno dense del mezzo ambiente, verosimilmente in funzione dell'età delle femmine. Capsule ovigere erette sul fondo, rispondenti ad esigenze di visibilità, suggeriscono comportamenti riproduttivi complessi come quelli descritti in specie o sottospecie di Loliginidae non presenti nel Mediterraneo (*Loligo pealei, L. opalescens, L. vulgaris reynaudii* ecc.).

Key words
Loligo forbesi, Mediterranean, egg capsules, spawning strategies, Cephalopoda.

Introduction

The veined squid *Loligo forbesi* Steenstrup, 1856 (Cephalopoda: Loliginidae), is distributed throughout the Mediterranean and adjacent Eastern Atlantic, in the latitudinal range 20°-60° N, with the Azores Islands as its western boundary (Roper et al., 1984). This species, which is often confused and/or dealt with together *L. vulgaris*, represents a valuable fishery resource in the Atlantic, while in the Mediterranean it is an irregular by-catch of trawl fisheries.

Clearly, the knowledge about the populations living in this large range of latitude and longitude (**Fig. 1**) is unbalanced, with a pole of intensive research in Scotland and scarce data in the South: such a polarity reflects the economic importance of the species in the NE Atlantic, with the largest landings in the UK. On the other hand, both morphometric and genetic studies, have indicated relevant differences in northern and southern populations (Guerra, 1992; Pierce et al., 1994; Brierley et al., 1995).

The aim of this note is to describe a recent record of *L. forbesi* eggs in the Ligurian Sea and to report old and recent data, from Mediterranean and adjacent Atlantic waters. Available literature about reproductive patterns, which are supposed to be conservative, are re-examined in detail to clarify similarities and/or differences with respect to northern populations. The description of the "state of the art" about reproduction in the southern populations of *L. forbesi* also shows uncertainties or gaps of knowledge as well as providing indications for future research.

During several Mediterranean trawl surveys, both national and European, *L. forbesi* has been caught from 50 to 600 m at the Balearic islands (Quetglas et al., 2000), from 84 to 115 m off the French coast (Boletzky & Mangold, 1985); from the range 50-100 m to the range 500-650 m in the Ligurian Sea (Relini et al., 2002); from 100 to 400 m in the North Tyrrhenian sea (Mannini & Volpi, 1989; Belcari & Sartor, 1993); from 40 to 620 m in Sardinia (Cuccu et al., 2003); from 70 to 560 m in the Sicilian Channel (Ragonese & Jereb, 1986); from 75 to 425 m in the

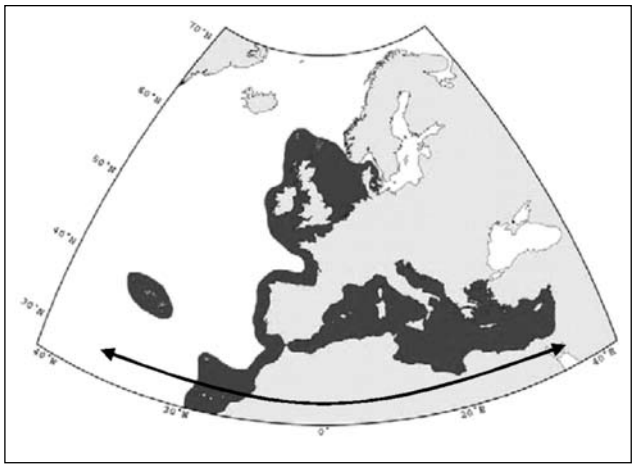

Fig. 1. Distribution area of *Loligo forbesi*. Southern populations live along an axis about 6,000 Km long.

Fig. 1. Areale di *Loligo forbesi*. Le popolazioni meridionali sono distribuite lungo un asse esteso per circa 6.000 km.

North Ionian sea (D'Onghia et al., 1995); from 276 to 715 m in the North Eastern Ionian sea (Lefkatidou et al., 2003). In the southern Ligurian Sea, a recent mapping of the distributions of *L. vulgaris* and *L. forbesi* shows the latter squid located from 80 to 600 m (Ria et al., 2005). *Loligo forbesi* therefore appears to be a circalittoral and bathyal species, which is mostly separated from the strictly coastal *L. vulgaris*.

In the Atlantic, such a separation disappears progressively to the north and *L. forbesi* extends its range to shallow coastal waters: thus, near Plymouth, where it coexists with *L. vulgaris*, it has been trawled up from 13 to 104 m of depth (Holme, 1974) and in Scotland, where the presence of *L. vulgaris* is scarce, from 18 to 371 m (Lum-Kong et al., 1992). In the Moray Firth (Scotland) a specific trawling for juveniles is carried out in autumn at only 10 m (Pierce et al., 2006).

Material and methods

The egg mass described herein was collected on the 12 July 2005 during the trawl survey MEDITS (Bertrand et al., 2002), by a haul located off the Gallinara Island (Fig. 2). It lasted one hour, the starting positions was 43°57'91" N - 08°18'19" E, the ending position 43°56'00" N - 08°17'68" E, the average depth 614 m; the sea bottom temperature 13.6°C.

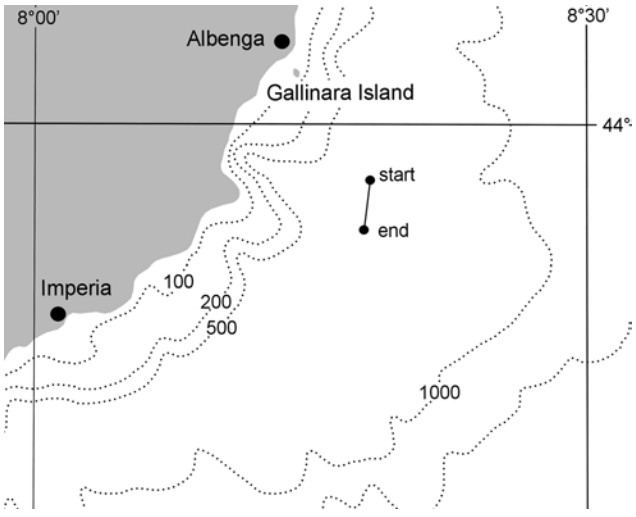

Fig. 2. Location where the eggs of *Loligo forbesi* were caught by trawl.

Fig. 2. Luogo di raccolta a strascico delle uova di *Loligo forbesi*.

The MEDITS project (Mediterranean International Trawl Surveys) (Bertrand et al., 2002), which presently concerns 10 European countries, is based on a spring-summer survey which is primarily aimed at obtaining estimates of abundance indexes for a series of target species. The selected stations are based on a depth stratified sampling scheme that includes five depth strata: 10-50, 50-100, 100-200, 200-500 and 500-800 m. The trawl net has 20 mm stretched mesh size in the codend. During the haul continuous measures of temperature and depth are recorded. The GRUND project (Italian Trawl Surveys) has similar aims and a similar depth stratified sampling scheme, with more numerous hauls which are carried out in autumn. In the present study area the GRUND net mesh has the same size than the MEDITS net.

The egg mass was frozen on board and, once transferred to the laboratory, it was thawed and fixed in 10% formalin. Eggs were observed with a video camera attached to a stereo microscope. Counts and measurements were taken from the images by means of the LeicaQWin software.

Results

The egg mass comprised 13 capsules, 8-8.5 cm long, each containing 36-40 eggs. The egg capsules merged at the base in a common point which retained a small quantity of mud, thus suggesting that the group was attached to some hard object laying on the bottom; however no part of any object was found.

Six eggs were randomly extracted from the jelly mass and measured; the largest diameter was ca. 3 mm. The developmental stages of embryos appeared to be very similar in all the eggs and corresponded to stage 16 of Segawa et al. (1988).

We assigned the egg mass to *L. forbesi* on the basis of the following combination of characteristics: 1) egg size; 2) number of eggs per capsule; 3) general aspects of the capsule, such as transparency of the jelly and irregular surface (see further below); 4) depth of the record.

Discussion

First observations on *L. forbesi* egg masses were carried out at the Zoological Station of Naples. Jatta (1896), describing the species, stated that eggs were unknown; however he figured, in plate 3 fig. 1 of his monograph, a group of five capsules laid on a thin branch of the bamboo coral *Isidella elongata* (**Fig. 3 A**) and wrote: "these eggs must be assigned to a Myopsid squid; they are found at 150-200 m depth and are collected in the vicinity of Capri island. Such masses are very similar to those of *L. vulgari*s and I think they belong to *L. forbesi*". Later

on both Lo Bianco (1909) and Issel (1932) confirmed Jatta's identification.
Lo Bianco (1909) noted that egg masses were found on branches of *Isidella* and other gorgonians and also on *Corallium rubrum* in the period from April to June: "they are opalescent, rather trasparent, cylindrical with an irregular surface and two tapering ends. The length of the capsule ranges from 8 to 11 cm, with a diameter of about 15 mm; it is very similar to the capsule of *L. vulgaris*, but it is more transparent and larger. Capsules are laid on muddy bottoms and on coralligenous reefs, at 150-200 m depths".
The notes of Lo Bianco (1909) placed the spawning area of *L. forbesi* approximately at the shelf break, while the indicated spawning season is spring, so that the presence of recruits should occur in the following summer. However Lo Bianco (1909) noted also that *L. forbesi* was not a species continually present in the Gulf of Neaples. It could appear in September, sometimes in large numbers, but not in all the years. The association of eggs with gorgonians is not mentioned in any further paper and is intriguing. In particular *I. elongata*, standing on compact muddy bottoms in a large depth range of the slope (Pérès & Picard, 1964), in the past should have offered to the squid large quantities of living hard substratum, but at present it almost disappeared from trawled bottoms, including their deepest range at about 700 m depth, where the trawlers target the red shrimps *Aristeus antennatus*.
Other basic studies carried out in Naples regarded the comparative anatomy of the Loliginidae. Naef (1923), describing the general morphology of *L. forbesi*, mentioned the occurrence in males of accessory glands with a possible content of luminescent bacteria, a feature which, in modern taxonomical approaches, might remove this species from the genus *Loligo* (Alexeyev, 1992). Naef noted that juveniles of this species have a thicker head than *L. vulgaris* of the same size. He could not observe fully mature animals, but wrote: "The mature male is much slenderer, the length of the mantle is at least 6 times its width". Naef's observations were confirmed when Martins (1982) described for the first time the fishery and the biological characteristics of *L. forbesi* at the Azores Islands, where very large specimens were found.
Martins (1982) examined 1/3 of the total annual catch of an artisanal fishery using hand lines in Horta, Faial, for a total of 622 specimens. The jigging had taken place at 215-270 m of depth. The catch consisted of a majority of mature individuals (80.2%) whose length range was 31-90 cm DML in males and 25-41 cm in females. During the year of the study the highest degree of maturity was observed in spring and the lowest in autumn.
From the notes of Martins (1982), several affinities with the Mediterranean population are evident as well as differences from populations of Northern Europe. As to the latter, beside having a different depth distribution, as previously noted, they are characterized by smaller sizes (Holme, 1974), by a different reproductive season (i.e. from December to June in coastal water of Scotland, according to Lum-Kong et al., 1992) and, what is more relevant, a smaller size of hatchlings in respect of southern populations (see later), i.e. 3.26 and 3.13 mm at the temperatures of 8 and 12°C (Gowland et al., 2002).

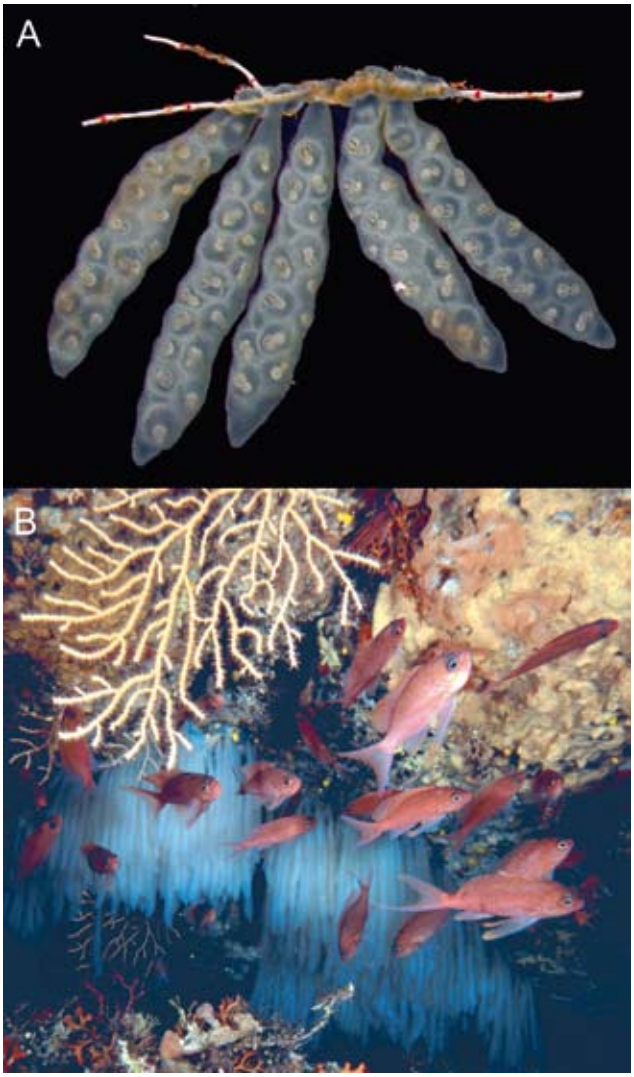

Fig. 3. Loliginid egg capsules lighter and heavier than sea water. **A.** Egg capsules of *Loligo forbesi* in the figure from Jatta (1896); the capsules are attached to a very thin branch of the bamboo coral *Isidella elongata*, suggesting that they are lighter than sea water. **B.** Egg capsules of *Loligo vulgaris* – clearly heavier than sea water – in a sheltered location on rocky bottom.

Fig. 3. Capsule ovariche di loliginidi meno e più dense dell'acqua del mare. **A.** Capsule ovariche di *Loligo forbesi* in una figura da Jatta (1896); le capsule aderiscono ad un sottilissimo ramo del corallo-bambù *Isidella elongata*, mostrando una minore densità rispetto all'acqua del mare. **B.** Capsule ovariche di *Loligo vulgaris* – chiaramente più dense dell'acqua del mare – in un posto protetto su fondo roccioso.

In Naples fishermen never confused the two species of *Loligo*: *L. forbesi* was called "occhione" (= big eye) because of its large eyes (Naef, 1923). The distinction was probably related to the respective commercial value: in fact because of their large size and tough flesh, *L. forbesi* are cheaper than *L. vulgaris* (Nesis, 1971). At present (end of 2005) in the Ligurian landings of cephalopods, the small catch of *L. forbesi* (**Fig. 4**) is divided into two commercial categories, the large and the small specimens, the latter being also the most expensive.
After these first studies, apparently the reproductive biology of Mediterranean *L. forbesi* was neglected for many years. Mangold-Wirz (1963) observed very rare speci-

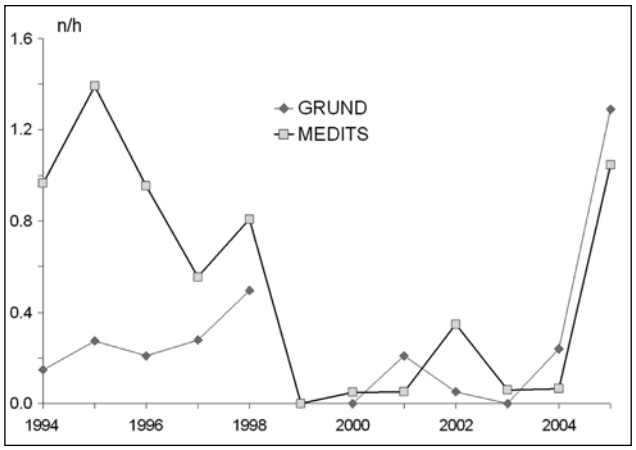

Fig. 4. Catches of *Loligo forbesi* observed in the Ligurian Sea during the trawl survey MEDITS (end of spring) and GRUND (autumn), during the period 1994-2005.

Fig. 4. Catture di *Loligo forbesi* effettuate nel Mar Ligure nell'ambito del trawl survey MEDITS (tarda primavera) e GRUND (autunno), nel periodo 1994-2005.

mens of *L. forbesi* in the Catalan Sea fisheries, but about twenty years later, the squid appeared with interesting numbers on the Provencal coast (Boletzky & Mangold, 1985); in trawls carried out between 85 and 115 m, both adults and juveniles were observed. Similar events occurred in the Ligurian Sea. In the period 1977-81 during a study of bathyal fishing grounds no *L. forbesi* was found. During the '80s some specimens began to appear in the trawl catches and at present with the trawl surveys of the Italian project GRUND and those of the international project MEDITS, started in 1994, catches remain very variable (**Fig. 4**).

In the '80s substantial information on eggs and embryos of *L. forbesi* were achieved both on Mediterranean and Azorean material. In both cases, females captured alive laid egg capsules which were raised in the laboratory to hatching; although egg laying may have been triggered by stress, the development was apparently normal. Boletzky (1987) observed that a female caught by trawl at 95-105 m in November and maintained in a tank onboard, deposited two capsules before dying. The capsules were brought to the laboratory of Banyuls-sur-Mer and raised together with freshly laid capsules of *L. vulgaris*. Eggs of *L. forbesi* hatched 60 days after the deposition, at a temperature varying from 12 to 15°C; hatchlings measured 4.5 mm ML and thus corresponded to juvenile *L. vulgaris* one to several weeks old (Boletzky, 1987). Egg strands were obtained also from mature females in captivity in a wooden cage maintained for this purpose in the Horta harbour (Porteiro & Martins, 1992). Live eggs, after 11 days at about 15°C in the harbour, were transported to Texas and raised there at 12.5°C. Segawa et al. (1988) illustrated 30 embryonic stages and observed a range of DML of hatchling (4.3-4.9 mm) in the same size range as indicated by Boletzky (1987). The size of embryos of *L. forbesi* mirrors the fact that this species is considered the largest Loliginid squid (Nesis, 1971).

Other aspects of egg laying where observed in Horta (Porteiro et al., 1990). Mating occurred in captive specimens – male 46 cm DML, female 35 cm DML – which were kept in a tank of 3 m in diameter. After 13 days the female laid 50 strands of eggs (80-100 eggs per strand), most of which where fixed to small stones on the bottom. The female died two days after spawning. In the same locality, eggs were found also on a artificial substratum (Porteiro & Martins, 1992), an octopus trap, formed by a segment of tubular PVC, with a diameter of 13.5 cm and one end sealed with concrete. The trap was placed at 25-30 m depth and, at recovering, it contained 20 capsules, each with 39 to 50 eggs. This record seemed surprising to the authors: in fact, in the Azores, squids bearing acoustic transmitters, tracked both day and night, had been observed to move between 20 and 550 m, so the authors considered surprising that and adult squid would come up to lay eggs in shallow waters. However this record and others to be mentioned later on, suggest that egg laying can occur at any level of their depth distribution.

The two clearly different egg masses of *L. forbesi* observed in Horta (*L. vulgaris* is not present in the Azores), deserve some further comments. Spawnings of about 4,500 and 900 eggs respectively, could be due to spawners of different size, a large and a small female respectively (*de facto* the former was due to a large female, 35 cm ML). However also the modes of egg laying changed completely: inside a hollow object and on stones on the bottom, respectively.

In the literature, such different modalities of egg laying are generally ascribed to different species or subspecies of Loliginid squids: the two subspecies of *L. vulgaris* can serve as examples.

In *L. vulgaris vulgaris* of the Mediterranean the eggs are commonly observed on rocky areas at about 20-30 m depth (**Fig. 3B**): they are heavier than the sea water and their placement apparently scarcely fulfils the need of visibility. Social interaction during spawning are apparently limited to the fact that females, in presence of laid eggs strings, add their own to those previously fixed on the substratum (Mangold, 1963, 1989).

On the contrary, in the other subspecies, namely *L. vulgaris reynaudii*, the mating process is very complex and there are three different ways of sperm transmission. Females, already mated and bearing sperm in a buccal receptacle, reach mating arenas, i.e. areas covered by several egg mops (1-3 m diameter). Around each mop agonistic behavior of large males and intrusion of sneaker males are observed (Sauer et al., 1997; Hanlon et al., 2002). Winner males transfer their spermatophores inside the mantle of the female; sneaker males to the egg mass which is forming in the arms of females. The result is that multiple paternity is assured to eggs of a single capsule (Shaw and Sauer, 2004). The egg masses erected on the bottom, are very visible and they represent important visual signals for the spawners. In fact, large males wait for the arrival of females remaining near egg masses and after mating they escort the female to the mops (Hanlon et al., 2002). Touching egg strands, males also take specific reproductive pheromones (Buresh et al., 2003).

In southern populations of *L. forbesi* two modes of egg laying have been observed: a) egg capsules heavier than sea water which hang from the substratum like those of *L. vulgaris*: examples can be found in the egg capsule figured by Boletzky (1987) and those found in the octopus trap of Horta (Porteiro & Martins, 1992); b) egg capsules lighter than sea water which are standing on the substratum: examples are egg masses adhering to small stones of the bottom (Porteiro et al., 1990), as well as those laid on *Isidella elongata* (**Fig. 3A**). The latter capsules had to be light, otherwise a more robust part of the colony should have been used. This kind of egg strands suggest their collocation in mating fields. May these different modalities of egg laying be related to the age of females? Taking into account that an intermittent terminal spawning occurs in Loliginidae (Rocha & Guerra, 1996) and that the firmness of body tissues of the spawners declines with time (Macewicz et al., 2004) this supposition seems reasonable. Older females, i.e. those engaged in the last steps of spawning, might produce a lighter jelly and buoyant egg strands, which could be more suitable for mating arenas. Loliginid squids show the most complex social behavior, particularly in the genus *Sepioteuthis* (Moyniham & Rodaniche, 1982); in the genus *Loligo* top performances are assigned to older and larger individuals, in particular to large males which are the leaders of nuptial choreographies (Sauer et al., 1997) but could also be assigned to large females. If it is so, it is not surprising to find such strategy in *L. forbesi*, the species that reaches the largest sizes and the most important sexual dimorphism. However, many questions remain to be answered: why sometime egg laying seems occasional and sometime so "organized"? Are the latter phenomena related to population densities?

The most recent record of an egg mass of *L. forbesi* in the Mediterranean was reported in the Aegean Sea (Salman & Laptikhovsky, 2002). On March 1996, two egg masses were recovered from a depth of 720-740 m attached to small rubble; embryos were in an advanced phase of development. This record is very similar to the present one and for both the transport of detached materials cannot be excluded. However every new find of bathyal location of eggs reinforce the possibility of real very deep egg laying. Moreover, the detail of the small stones recall the existence of light egg strands, erect on the bottom, i.e. probably laid by old and/or large females which could live deeper than young females.

Conclusions

In conclusion, along the major axis of its distribution, from the Aegean Sea to the Azores, *Loligo forbesi* appears to be a deep water species – circalittoral and bathyal – which lives in a vertical space of about 500 meters and has spawning grounds around the shelf break and on the muddy bottoms of the slope. In the Mediterranean this habitat is homogeneous in terms of temperature (13-14°C); in fact, in this optimal temperature the development occurs in 60 days (Boletzky, 1987) and produces hatchlings measuring 4.5 mm ML.

Recruitment processes are not well known, however the distribution of young individuals is connected with the shallower levels at about 60-80 m. Sporadical observations on the behaviour of captive specimens suggest complex social interactions regarding mating and egg laying, in particular competition among large males, and the production of buoyant egg strings, suitable to assume maximum visibility on their substratum.

Are the above-mentioned features present also in the latitudinal axis of distribution of *L. forbesi*, from Morocco to Norway, and how far can they be tracked to the North?

Genetic studies have separated *L. forbesi* of the Azores from North European populations, from North Spain to the British Isles, at the level of subspecies (Brierley et al., 1995): have the two subspecies, which remain unnamed probably because of unresolved affinities of the genus (Vecchione et al., 1998), identical reproductive features?

Spawning areas similar, depth-wise, to the Mediterranean ones were reported by Lordan & Casey (1999) offshore the coast of Brittany. At the end of March 1995 a large amount of egg masses were found in a haul carried out at 135 m; the bottom temperature was about 11°C. This record may be very important to explain the reproductive biology of *L. forbesi*. In fact it represents the most recent documentation of the existence of spawning fields on muddy bottom, after those indicated by the use of *Isidella elongata* in the Mediterranean.

In the following years, two other records, less important as quantities, occurred west of Ireland, at 300 and 500 m, with bottom temperatures of 10.7°C and 10.8°C respectively (Lordan & Casey, 1999). These, in the opinion of the authors, could have been detached eggs that were not laid in the area where they were caught. All other egg masses mentioned in the literature of the British Isles (e.g. Lum-Kong et al., 1992; 1993; Collins et al., 1995; Gowland et al., 2003) were found in coastal shallow waters and frequently on artificial substrata, such as creels for lobsters. The possibility of two kinds of egg laying is thus confirmed also in NE Atlantic populations albeit at different latitudinal levels (North France and Ireland-Scotland respectively).

The Channel could be a significant boundary for *L. forbesi*, separating boreal neritic and deeper southern forms (Tait, 1968). However, as already noted, genetic studies contrast such hypothesis indicating a homogeneous population stretching from N Portugal to Scotland (Shaw et al., 1999). Unfortunately, southern continental populations, including all the Mediterranean ones, remain unexplored from a genetical point of view.

These brief notes on spawning characteristics of Loliginidae, indicate that many aspects, ranging from genetics to social behaviour, remain to be studied in the Mediterranean.

Reproductive strategies are certainly one of the most interesting aspects, because they can be related to the fishery management (Pierce et al., 2006) as well as to cephalopod general biology and evolution.

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