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Male reproductive system and spermatophores production and storage in *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae): A look into deep-sea squids' reproductive strategy



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ABSTRACT

Coleoid cephalopods go through a single breeding period in their life cycle, i.e., they are semelparous, although a great flexibility has been observed in their reproductive strategies, which range from simultaneous terminal spawning over a short period at the end of the animal's life to continuous spawning over a long period of the animal's life. So far, the information available on deep-sea species reproductive strategies is still poor and most of our knowledge about squid reproduction relates to females. In particular, not much is known on what strategy male squids have evolved to store sperm into spermatophores and adapt to semelparity. In this study an investigation of male reproductive strategy of the deep-sea umbrella squid *Histioteuthis bonnellii* (Férussac, 1835) is presented. The reproductive system was examined in 119 males caught in the Sardinian waters (Central Western Mediterranean) and is described for the first time. Results indicate that this species produces and stores spermatophores over a considerable period of time. The total number of spermatophores found in the reproductive system ranged between 12 and 3097 and the size of spermatophores stored by a single individual varied greatly, up to over 300%. Spermatophore length (SpL) gradually decreased towards the distal end of the reproductive system, so that spermatophores found in the proximal part of Needham's Sac were larger than those found in the terminal organ. Body size and SpL of spermatophores from the proximal part of Needham's Sac were positively correlated. Both indices of the sperm mass and of the ejaculatory apparatus decreased with the increase of SpL, while the cement body index increased, indicating that larger spermatophores contain less sperm and are equipped with larger cement bodies. Up to 64 spermatangia were found, exclusively in the terminal organ. The large size range of mature males (ML: 60.0–198.0 mm; TW: 113.50–2409.00 g) and the variation in spermatophore number and size indicate that in *H. bonnellii* males the allocation and storage of sperm start early in the individual life and extends in time, while animals continue to grow and produce spermatophores presumably more successful in attaching to female tissues. This pattern enlarges the time window available for reproduction and likely maximizes the percentage of mating success as the animals grow older and chances of mating events become comparatively lower, due to the basic low density of specimens in the deep-sea environment. Both aspects are potentially indicative of adaptation to the deep sea.

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1. Introduction

Maximizing the production of viable offspring is the outcome of sexual and natural selection, reached through complex adaptations encoded in the genetic heritage of each species. Also called "reproductive strategies" (Stearns, 1992), these adaptations consist

of a broad variety of physiological and behavioral mechanisms, which allow individuals to reach their reproductive goal and make the best use of the environment they live in.

Given the successful colonization by cephalopods of virtually all marine habitats, from very shallow waters to the deep-sea environment, it is reasonable to expect that their reproductive strategies may be variable. Indeed, though a general consensus exists on the fact that coleoid cephalopods are semelparous (Boyle and Rodhouse, 2005; Nesis, 1987), there is accumulating evidence that very different timing, mode and behavior of mating, maturing

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and spawning also exist (Boyle and Rodhouse, 2005; Hanlon and Messenger, 1996; Nesis, 1995; Rocha et al., 2001).

Due to the increased importance of cephalopods as fisheries resources in the past decades (Jereb and Roper 2005, 2010; Jereb et al., 2014) and to the key role of many cephalopod species in the marine environment (Clarke, 1996; Piatkowski et al., 2001; Sinclair and Valdimarsson, 2003), understanding cephalopods' reproductive strategies has become increasingly important for the understanding of the marine system and to attempt managing important fisheries.

While much of the available knowledge on squid reproductive strategies relates to females and to species inhabiting neritic environments, less information exists on males and deep-sea species, for which recent investigations have evidenced peculiar reproductive tactics and adaptations (Hoving et al., 2008a, 2008b, 2009, 2012; Laptikhovskiy et al., 2007; Seibel et al., 2005).

Histioteuthid squids are deep-sea species known for their importance in the oceanic realm, where they are actively predated upon by cetaceans and other top predators (e.g., Clarke, 1996). The umbrella squid *Histioteuthis bonnellii* (Férussac, 1834), in particular, turned out to play a major role in the marine food chain both as predator and as prey (Bello, 1996; Blanco et al., 2006; Quetglas et al., 1999). In addition, this species has been shown to represent an intermediate paratenic host in the transmission of Anisakidae (Culurgioni et al., 2010; Hochberg, 1983; Oshima, 1972), which draws increasing attention on its ecological role, due to man's potential utilization of fish.

Broadly distributed in the north temperate hemisphere (Voss et al., 1998), *H. bonnellii* was once considered poorly represented in the Mediterranean Sea, being seldom caught by trawlers. However, increasing evidence has been gathered with time that this species is rather common throughout the Mediterranean basin (see Bello, 2000 and Quetglas et al., 2010 for reviews), where it usually occurs between 500 and 1500 m, only occasionally extending beyond 2000 m (Cuccu et al., 2007b; Jereb and Roper, 2010; Quetglas et al., 2010; Voss et al., 1998).

In spite of its ecological importance, the biology of *H. bonnellii* is still poorly known. Preliminary investigations on reproductive aspects of this species in the western Mediterranean have been carried out (Quetglas et al., 2010), and additional scattered information exists for the Italian waters (Cuccu et al., 2007b; Capua et al., 2009; Lazzaretti et al., 1995). However, no mature females have been caught, and no mature, mated specimens have been examined, only a few spent females have been found floating in the Ligurian Sea (Quetglas et al., 2010). Indeed, the capture of fully mature females of this species seems a very rare event, and only two records exist to date: one refers to a 330 mm ML specimen caught off west Greenland (Kristensen, 1980), and the other to a 225 mm ML female caught in the North Atlantic at 37°N 56°W (Stephen, 1982). This lacking of mature females to examine hampers females' reproductive strategy investigation.

As for males, observations on *H. bonnellii* spermatophores revealed intraspecific variations that “could prove valuable in identifying genetically separate populations” (Voss et al., 1998), but studies on sperm allocation and spermatophore production and storage have not been carried out for this species so far.

In this paper we offer a contribution to improve our knowledge of male deep-sea squids' reproductive strategies by studying *H. bonnellii* from Sardinian waters (central western Mediterranean Sea). To this goal, male reproductive system has been investigated and spermatophore production, morphometrics and storage are described.

2. Materials and methods

A total of 119 males were collected during commercial bottom fishing carried out in the Sardinian waters (western Mediterranean)

from 2005 to 2012, at depth ranging between 400 and 700 m. Hauls were performed by daylight and a bottom otter trawl with a 20 mm cod-end stretched mesh size was used.

Dorsal mantle length (ML, to the nearest mm) and total weight (TW, to the nearest 0.1 g) were recorded on fresh specimens. Maturity stages were assigned using a four-stage scale (I, immature; II, maturing; III, mature; IV, spent); specimens were considered mature when spermatophores were packed in Needham's sac.

Size at maturity ($ML_{50\%}$) was estimated by fitting the mantle length–frequency distribution of the proportion (P_i) of mature and spent specimens (stages: III and IV), grouped in 20 mm ML classes, to the logistic model:

$$P_i = 1/[1 + \exp(-\alpha + \beta ML_i)]$$

where $ML_{50\%} = -\alpha/\beta$.

Total weight at maturity ($TW_{50\%}$) was also estimated following the same procedure, grouped in 100 g TW classes.

The following measurements were recorded on reproductive systems: total gonad weight (GW), testis weight (TeW) and spermatophoric complex weight (SpCW) to the nearest 0.01 g and terminal organ length (TOL) to the nearest mm. Gonadosomatic ($GSI = GW * 100 / TW$) and Hayashi [$HI = SpCW / (SpCW + TeW)$] indices also were computed.

A sample of 18 mature specimens was selected and the reproductive systems were removed and preserved in 5% saline formalin for further examination. The total number of spermatophores and spermatangia (when present) were recorded and total length of both structures was measured to the nearest 0.01 mm (i.e., SpL and SgL, respectively).

A subsample of 13 mature specimens was used to investigate spermatophore length distribution within the reproductive system; Needham's sac was subdivided into 3 sections of approximately equal volume (Sections 1, 2 and 3; Fig. 3a) followed by a fourth section made up by the terminal organ (Section 4; Fig. 3a). SpL was measured on samples of spermatophores ($N = 5-20$; usually 20) extracted from each section; spermatophore length index also was computed ($SpLI = SpL * 100 / ML$), accordingly. The non-parametric Kruskal–Wallis test and the Mann–Whitney pairwise comparisons were performed to investigate differences in spermatophores size within the four sections and between the proximal (1) and distal (4) sections, respectively.

A subsample of 8 reproductive systems was used to investigate spermatophores structure; 10 spermatophores from each of the 4 selected sections of above, for a total of 320 spermatophores, were extracted and the following measures were taken: ejaculatory apparatus length (EAL), cement body length (CBL) and sperm mass length (SML) (Fig. 3b and 3c). Corresponding relation of each spermatophore section with spermatophore total length was computed as a percentage index (SpL; EALI, CBLI, SMLI, respectively).

Oral sperm mass length (OSML) and trailing end length (TEL) were also recorded (Fig. 3d) on spermatangia. Mean SpL of the spermatophores from each section of Needham's sac (SpLS1, SpLS2, SpLS3 and SpLS4) was plotted against body size (ML and TW) to investigate SpL relationship with the animal growth.

3. Results

3.1. Male maturity condition and reproductive morphology

Data on maturity stages and size of the analyzed sample are reported in Table 1. The majority of the examined specimens was mature (i.e., 62 over the total 119 males analyzed; 52%), 34 were maturing, 18 were immature and 5 were spent. Both GSI and HI mean values increased from immature (0.10% and 0.49, respectively) to mature males (0.85% and 0.76, respectively) and decreased again

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