B. A. Seibel · F. G. Hochberg · D. B. Carlini

Life history of Gonatus onyx (Cephalopoda: Teuthoidea): deep-sea spawning and post-spawning egg care

Received: 22 February 1999 / Accepted: 25 May 2000

Abstract A reproductive strategy consisting of deep-water spawning and egg-care was inferred for the midwater squid Gonatus onyx Young, 1972. Brooding females and associated eggs and hatchlings, captured between 1250 and 1750 m depth off southern California, are described. Brooding females appear to be senescent and lack tentacles. Large eggs of this species (3 mm) at cold temperatures (3 °C at capture depth) may require as long as 9 mo to develop. The high lipid content of the digestive gland in adult females of this species may provide fuel to support such an extended “brooding” period.

Introduction

The life-history strategies of oceanic cephalopods are largely unknown. Based primarily on knowledge of a few shallow-living and commercially important squids (order Teuthoidea), it has been assumed that post-spawning egg-care is limited to the order Octopoda (Young 1972; von Boletzky 1992). As a result, egg-brooding and related characteristics have been used to derive evolutionary relationships between the squids and octopods (von Boletzky 1992). However, two squid photographed in the Sea of Okhotsk carrying large egg masses were recently reported (Okutani et al. 1995). Although the specimens were not captured, they were, based on the absence of tentacles, tentatively identified as squids in the genus Gonatopsis (Gonatidae).

Gonatus onyx Young, 1972 is among the most abundant cephalopods off the coast of California (Roper and Young 1975). Because of an ontogenetic descent to great depths (Hunt and Seibel 2000), spawning, egg masses, eggs and hatchlings have never been observed for this species. The present study provides the first report of brooding behavior in the mesopelagic squid, G. onyx. Two senescent females, eggs (in addition to fragments of the egg mass) and hatchlings captured between 1250 and 1750 m off southern California are described. The energetic and evolutionary advantages of the observed life-history characteristics are discussed.

Materials and methods

Collection

Specimens of Gonatus onyx Young, 1972 were captured in an opening-closing Mother Tucker trawl equipped with a thermally-protecting cod-end (Childress et al. 1978). BESS (biological environmental sampling system) pressure and salinity and SEA BIRD temperature sensors, which relay data to a computer-controlled shipboard acquisition controller via a single-conductor armored cable, were deployed with the net. Specimens were captured 160 km west of Point Conception, California (35°0’N; 123°02’W) and over the San Clemente Basin off San Diego, California (32°27’W; 117°57’W). Live specimens were weighed on a motion-compensated, precision, ship-board balance system (Childress and Mickel 1980). Tissue samples were taken and frozen in liquid nitrogen for gene-sequencing and biochemical analysis. Specimens were then preserved in 5% formalin in seawater, and are presently archived in the collections of the Santa Barbara Museum of Natural History, Santa Barbara, California (SBMNH). Morphometric and meristic measurements were made according to Roper and Voss (1983) on preserved specimens and eggs.
Gene-sequencing

Nucleotide sequence of the cytochrome-C oxidase (CCO) gene was determined for *Gonatus onyx* and additional gonatid species following the methods described in Carlini and Graves (1999). The LCO 1490 and HCO 2198 polymerase chain-reaction (PCR) primers designed by Folmer et al. (1994) were used to amplify the cytochrome oxidase I (COI) gene in gonatids. DNA sequences were aligned by eye and compiled in MacClade 3.0 (Maddison and Maddison 1992). Alignment was straightforward, as there were no apparent insertion/deletion events or alignment ambiguities, a finding consistent with the results of Folmer et al., whereby no gaps were introduced in the alignment of COI sequences from diverse metazoan phyla. Non-gonatid COI sequences obtained by Carlini and Graves were included in the analyses, and were used as out-group sequences. Phylogenetic analysis of the aligned sequences (657 bp, base excluding the primer sequences) was conducted using the branch-and-bound search option in PAUP* (phylogenetic analysis using parsimony: Swofford 1993). Both parsimony and maximum-likelihood were implemented as the optimality criteria in tree searches. Maximum-likelihood analysis was conducted using the nucleotide substitution model of Hasegawa et al. (1985), with gamma-distributed rates partitioned into four discrete categories.

**Fig. 1** *Gonatus onyx*. A Vento-lateral view of two mature female specimens; Specimen No. 1 (right, SBMNH 345288) has a mantle length (ML) of 132 mm; this specimen was captured with an egg mass (B). Specimen No. 2 (left, SBMNH 345289) has a ML of 145 mm; this specimen was captured with hatching squids (C). The digestive gland (cytochrome oxidase I) of specimen No. 2 is smaller and degenerate relative to that of specimen No. 1. B Fragment of an egg mass containing some eggs. C Hatchlings (preserved in formalin) with a ML of 3.4 mm (Yang 1994). Support for phylogenetic trees was examined using the branch-and-bound bootstrap search command (1000 replicates) in PAUP*, which was also used to calculate uncorrected sequence divergences for pairwise comparisons among taxa.

**Results**

**Material examined**

**Brooding females** (*Fig. 1a; Table 1*)

Two mature female *Gonatus onyx* were captured off California. Specimen No 1 (SBMNH 345288) was collected on 21 September 1995 in an oblique tow between 1250 and 1750 m off Point Conception, California, over a bottom depth of ≃4100 m. It had a mantle length (ML) of 132 mm and a wet weight of 99.7 g. Associated with this specimen were eggs embedded in a fragile black gelatinous material. Specimen No. 2 (SBMNH 345289) was collected on 22 May 1996 between 1350 and 1420 m depth in the San Clemente Basin off San Diego, California, over a bottom depth of 2100 m. It had a mantle length of 145 mm and a wet weight of 138.6 g. Associated with this specimen were ≃2000 hatchlings.