



RESEARCH NOTE

FIRST CASE OF POSSIBLE ITEROPARITY AMONG COLEOID CEPHALOPODS: THE GIANT WARTY SQUID *KONDAKOVIA LONGIMANA*

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Modern teleost fish and coleoid cephalopods (squid, cuttlefish and octopods) share the same ecological niche as meso- and macronektonic predators of the World Ocean. In spite of convergence of their lifestyles (Packard, 1972), some important differences exist between these taxa, one being their respective reproductive patterns, particularly semelparity *vs* iteroparity. Following Rocha, Guerra, & González (2001) who refined the original definition of iteroparity (Cole, 1954), we use the term iteroparous for species that “spawn once a year, survive, feed, grow and regenerate their gonads for a further reproductive event the following year” (Rocha *et al.* 2001: 292). Animals that have short lifespans are automatically eliminated from this category regardless of their spawning pattern. This definition restricts the possibility of iteroparity to those few cephalopods that live for many years.

The vast majority of fish are iteroparous and reproduce several times during their lives; semelparous reproduction, as in Pacific salmon, is a rare phenomenon among them. In contrast, the only cephalopods known to breed over several seasons are ectocochleate species of *Nautilus*. All known endocochleate coleoid cephalopods are semelparous: they reproduce just once and their gonad never returns to an immature condition between spawning events (Rocha *et al.*, 2001), as it does in iteroparous fishes (Wallace & Selman, 1981).

The capture of a large female of the giant warty squid *Kondakovia longimana* Filippova, 1972 (Oegopsida: Onychoteuthidae) questions this established point of view. Endemic to the Antarctic epi- and mesopelagic water masses, this squid also occurs near-bottom, attaining 1,100 mm mantle length (ML) (more than 2 m total length and ca. 30 kg in body weight) and living between 4 and 10 years (Bizikov 1991; Jarre, Clarke, & Pauly, 1991; Vacchi, Greco, & La Mesa, 1994; Lynnes & Rodhouse, 2002). Adult *Kondakovia* are an important prey of sperm whales and elephant seals, and juveniles are preyed upon by albatrosses and penguins (Collins & Rodhouse, 2006). Nothing is known about reproduction of this species.

An adult female of this species was captured by the longliner *Argos Froyanes* on 15 February 2012 in the Ross Sea at 70°24'S, 122°42'W at 1,700 m depth (Fig. 1) and was brought frozen to Stanley, Falkland Islands. Dorsal mantle length was 890 mm (measured frozen) and total weight was 18.1 kg. Its extended oviducts were simple elongated tubes, relatively larger than those of a mature *Onykia ingens* (Laptikhovskiy, Arkhipkin, &

Hoving, 2007), with no meandering as is seen in such batch spawners as the squid families Ommastrephidae and Loliginidae. Their walls were relatively flabby. The proximal oviducts held 12 ripe ovulated eggs, measuring 4.0 × 2.5 mm. The ovary of the *Kondakovia* (Fig. 2) did not contain post-ovulatory follicles (POF). The ovary itself was in good condition and contained some 2,522,532 ± 355,419 protoplasmic oocytes of about 0.5 mm modal length (Fig. 2). The nidamental glands were 317 mm long (35.6% ML), similar to those in mature female *O. ingens* (32.3–58.9%, mean 42.8% ML; A. Arkhipkin & V. Laptikhovskiy, unpublished) and much larger than in immature *K. longimana* (9.8–14.0%; Filippova, 1972). The oviductal glands were also much enlarged, similar to those of maturing squids of *O. ingens*. The stomach contained some fish scales. Inspection of inner and outer body surfaces, on which spermatophores are normally attached in this family (Hoving & Laptikhovskiy, 2007; Bolstad & Hoving, 2011), as well as of the arms, buccal membrane and other possible sites of spermatophore attachment, revealed no trace of spermatangia.

There was no evidence of body degeneration and in every respect this appeared to be a healthy active squid, despite the 12 ripe eggs in the proximal oviduct. What evidence indicates this species has an iteroparous life history? First, spent representatives of the family Onychoteuthidae are typified, in for example the squid genus *Onychoteuthis*, by a thin and flaccid mantle with its relative proportions as well as those of fins greatly distorted. This can occur to such a degree that post-spawning animals were described as different genus and species “*Chaunoteuthis mollis* Appellöf, 1891” (Arkhipkin & Nigmatullin, 1997). Similar processes of mantle degeneration are known in other onychoteuthid genera such as *Onykia*, *Notonykia* and *Callimachus* (Bolstad & Hoving, 2011).

Second, if the 12 eggs found in oviducts were just a small part of the portion that had previously been spawned, we might suppose that POF were already resorbed—an indication that spawning happened some time ago. In Antarctic fish POF atresia can take up to 5–7 months (Everson, 1970; Butskaya & Faleeva, 1987; La Mesa, Caputo & Eastman, 2007).

Third, the walls of the oviducts were relatively flabby, not straight and rigid as might be expected in immature or early maturing squid that had never held mature eggs, supporting the supposition that this animal had spawned before.

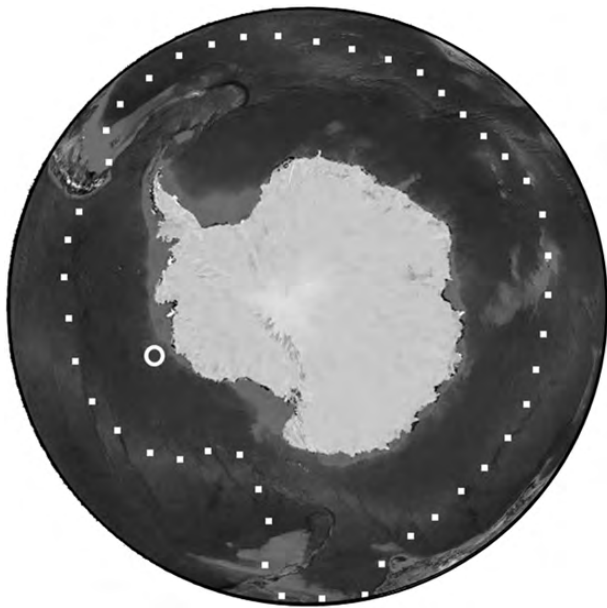


Figure 1. Geographical range of *Kondakovia longimana* and position of capture of the sampled female.

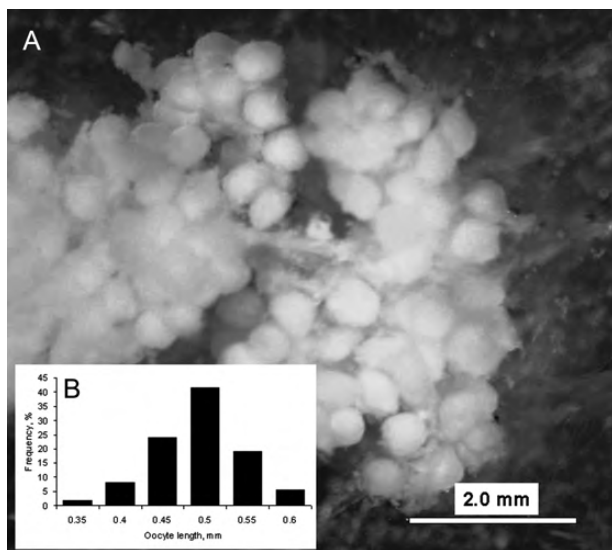


Figure 2. A. Piece of ovary of *Kondakovia longimana*. B. Frequency of oocyte lengths.

Fourth, the absence of any trace of copulation in the form of spermatangia or scars in this post-spawning squid is not entirely surprising, because spermatangium implantation was also not observed in spent females of the onychoteuthid genera *Notonykia* or *Callimachus* (Bolstad & Hoving, 2011). This phenomenon remains unexplained.

Fifth, the good condition of the ovary, with 2.5 million protoplasmic oocytes, suggests that the ova would develop in the next spawning season.

The specimen likely was not brooding eggs—it was actively hunting and attacked a baited hook of a longline. Its arms lacked any traces of the egg mass, which have invariably been found in all studied brooding squids of the families Gonatidae and Bathyteuthidae (Bjørke, Hansen & Sundt, 1997; Seibel, Hochberg, & Carlini, 2000; Laptikhovskiy *et al.*, 2007; Bower *et al.*, 2012; Bush *et al.*, 2012).

Moribund *Kondakovia* float up to the surface, where they are scavenged by seabirds. The occurrence of their beaks in stomachs of wandering albatross indicates that spawning takes place in winter (Cherel & Weimerskirch, 1999), a suggestion supported by the capture of this squid without POF, but with mature eggs in the oviducts, in summer. It also explains why the oocytes are still protoplasmic, far from their mature size. In most cases Antarctic fish have a biannual gonad cycle and advanced oocytes of 0.5–0.7 mm length are stored in gonads for next year's spawn. In some fish species, including *Notothenia rossi* and *N. neglecta*, with eggs (4.5–5 mm) even larger than those of *Kondakovia*, the gonad achieves the fully mature condition for only a few months (Everson, 1970; Kock & Kellermann, 1991). Therefore, we might assume that a *Kondakovia* with eggs of *c.* 0.5 mm in summer can mature by the austral winter.

The 12 ripe eggs in the oviduct of this single specimen of *Kondakovia*, which otherwise appears to be immature with flabby oviducts, do not prove this species to be iteroparous. They are likely to be the remnants of a previous spawning; such remnant eggs are known in spent oegopsid squids of other families: Ommastrephidae, Enoploteuthidae and Acistrocheiridae (Laptikhovskiy & Nigmatullin, 1993; Laptikhovskiy, 1999). In representatives of these three families, residual oocytes and POF quickly degenerate. Eventually, in spent squids of these families, only a few ovulated (therefore not subjected to atresia) eggs can be found freely floating in the mucus that fills the gonadal coelom where the ovary had been. Nothing equivalent was found in our mature specimen of *Kondakovia*, the only adult specimen of the species studied to date. Perhaps, at least some squid of this species survive for several months after spawning and maintain an important oocyte stock that potentially could be laid during the next reproductive season. As the lifespan of *Kondakovia* might exceed 5 years (Bizikov, 1991; Jarre *et al.*, 1991), it is possible using the definition of iteroparity above that the species qualifies for iteroparity.

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