Reproductive strategy of deep-sea and Antarctic octopods of the genera *Graneledone, Adelieledone* and *Muusoctopus* (Mollusca: Cephalopoda)

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ABSTRACT: Reproductive systems of spent brooding octopodid females of *Muusoctopus longi-brachus akambei*, *Adelieledone polymorpha* and *Graneledone macrotyla* (Eledoninae) were collected in Southwest Atlantic and Antarctic waters. Their study demonstrated that the size distribution of post-ovulatory follicles (POF) is mostly unimodal, suggesting that they only lay 1 batch of eggs. These data, together with a reevaluation of the literature, revealed that deep-sea and polar benthic octopods are generally not multiple spawners. Females spawn a single egg mass simultaneously or as a series of several consequent mini-batches separated by short periods of time, making it difficult to distinguish them by either size or condition of their POF. Analysis of the length–frequency distribution of POF is a useful tool to reconstruct the spawning history of brooding females of cold-water octopods.

KEY WORDS: Octopus · Spawning · Post-ovulatory follicle · POF · Reproductive strategy · Deep sea · Antarctic

INTRODUCTION

Most benthic octopods brood a single egg mass, and the female dies as the eggs hatch. This egg mass (clutch) might be laid in one bout or in several consecutive egg batches separated by fairly short time periods (Rocha et al. 2001). In some small-sized shallow-water tropical species, such as *Octopus chierchiae* (Rodaniche 1984), *O. micropyrsus* (Hochberg, pers. comm. in von Boletzky 2003) and possibly *O. kagoshimensis* (Salman et al. 2005), spawning is intermittent. In *O. chierchiae*, the interval between these batches might be long enough for the previous batch to hatch ca. 40 d before the next one is laid (Table 1 in Rodaniche 1984).

Cold-water, deep-sea and polar octopods have very large eggs (10–30 mm in length), and a fecundity of a few dozen to a few hundred oocytes (Hochberg et al. 1992, Laptikhovsky 1999a, 2001, Barratt et al. 2007,

2008). Growth of ovarian eggs is generally synchronous, although in maturing females the oocyte size distribution might be bimodal or polymodal (Kuehl 1988, Laptikhovsky 1999a, 2001, Önsoy & Salman 2004, Bello 2006, Barratt et al. 2007, 2008).

However, as has been shown in the large-egged octopod genera *Muusoctopus* (formerly *Benthoctopus*), *Eledone* and *Sasakiopus*, smaller oocytes might never grow to maturity and are subject to atresia because of intra-gonad competition for nutrient supply (Boyle & Chevis 1992, Laptikhovsky 1999a, 2001). Before degenerating, these oocytes could be confused with eggs from a newly developing batch. One approach to determine the frequency of batch laying is to study the ovaries of brooding and spent females, where the size distribution of resorbing post-ovulatory follicles (POF) may provide information about how many eggs were actually laid and in how many batches. Only 4 ovaries of spent females have been

described in the literature, not only among deep-sea octopods but for the entire order Octopoda. The ovary of a spent female of the Antarctic species *Adelieledone polymorpha* was described previously (Daly 1996). Two spent brooding females of *Graneledone pacifica* were collected together with 2 non-brooding animals by a submersible from a depth of ca. 2600 m (Voight & Grehan 2000), and a spent female of *Pareledone turqueti* was mentioned by Barratt et al. (2008). Also, spent females of *Muusoctopus*, *Sasakiopus* and *Graneledone* are known from the Okhotsk Sea, but their ovaries were not described (Nesis 1989).

Spent and brooding females of deep-sea octopodids are difficult to collect, particularly in *Muusoctopus* and *Graneledone.* These deep-sea cephalopods attach their eggs to rocky outcrops and ledges (Voight & Grehan 2000, Drazen et al. 2003, Voight & Drazen 2004), where fishing nets are impossible to deploy. In respect to shallow-water species, it is surprising that the ovaries of spent females kept in captivity have not been investigated, despite egg brooding and development being monitored and described in numerous octopods.

The number of POF might provide precise information about the number of eggs that have been recently laid in deep-sea and Antarctic squid (Nesis et al. 1998, Laptikhovsky et al. 2007, Bush et al. 2012). Initially these follicles in fish and cephalopods are distinct 3-dimensional structures, but they rapidly deteriorate and are resorbed, which makes them a very convenient tool with which to study spawning frequency. Decreasing temperatures increase the time that POF can be detected. In small-egged (eggs of 1–2 mm) fish and squid species, POF degenerate in less than 24 h (tropical species, spawning temperature 20–25°C) to ~48 h (temperate species, spawning temperature 10–19°C), and up to 6 wk at 9°C (Hunter & Macewicz 1985, Fitzhugh & Hettler 1995, Sauer et al. 2002, Macchi & Pájaro 2003, Macewicz et al. 2003, Whittames 2003). In Atlantic cod they are easily identifiable even 3 mo after the spawning season ends in the Flemish Cap area (Lowerre-Barbieri et al. 2011), where bottom temperatures are 3–4°C (Stein 1996). In Antarctic fish it takes several months — up to 7 in *Notothenia neglecta* — for POF to degen-erate at negative temperatures (Everson 1970, Butskaya & Faleeva 1987, La Mesa et al. 2007), so complete degeneration of POF in giant-egged (eggs of 10–30 mm) cold-water octopods that reproduce at 0–4°C is likely to take a similar amount of time.

Spent females of 3 deep-sea and Antarctic octopod genera *Muusoctopus*, *Adelieledone* and *Graneledone* were collected by chance during research cruises in Falkland and Antarctic waters. The present study aims to investigate POF length–frequencies and condition, as well as the number and condition of residual oocytes to shed some light on how individual spawning occurs in deep-sea and polar octopods.

MATERIALS AND METHODS

Three spent females of the recently described species *Muusoctopus longibrachus akambei* Gleadall, Guerrero-Kommritz, Hochberg, Laptikhovsky 2010 (Octopodidae, Bathypolypodinae) of 105–115 mm mantle length (ML) and 596–782 g body mass (BM), were captured on 28 October 2010 onboard the RV 'Castelo' (48° 40′ S, 60° 23′ W, depth range from 316 to 324 m) by a bottom trawl with a codend mesh size of 90 mm (Fig. 1). The trawl was towed across muddy bottom with large sponges and Actiniaria (found in catch). No additional sampling of the reproductive
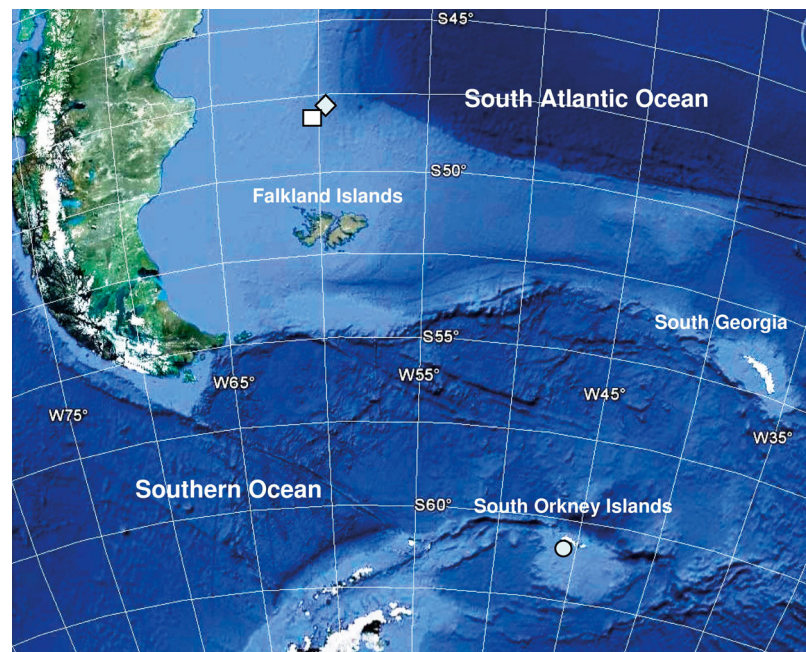

Fig. 1. Sampling locations of spent females *Graneledone macrotyla* (diamond), *Muusoctopus longibrachus akambei* (square) and *Adelieledone polymorpha* (circle)

systems of maturing and mature females of this species was carried out, because ovaries at these ontogenetic stages and fecundity were already described by the author as 'Benthoctopus eureka' (Laptikhovsky 2001).

A spent female of *Graneledone macrotyla* Voss 1976 (Octopodidae, Eledoninae), 105 mm ML and 655 g BM, was sampled on 12 July 2008 onboard the FV 'Jose Antonio Nores' (47° 43′ S, 59° 39′ W, depth range from 798 to 812 m), which also operated a commercial bottom trawl with a codend mesh size of 90 mm (Fig. 1). No information about the bottom was available. Six maturing and mature females of the same species (ML 105–130 mm, BM 562–1198 g) were collected in 2007–2009 onboard the FVs 'Manual Angel Nores' and 'Jose Antonio Nores' and the PV 'Dorada' (from 46° 55.5′ S, 59° 52.8′ W to 53° 29.3′ S 60° 25.5′ W, depth range from 481 to 965 m) using a bottom trawl with a codend mesh size of 90 mm.

A spent brooding female of *Adelieledone polymorpha* (Robson, 1930) (Octopodidae, Eledoninae), 54 mm ML and 90.9 g BM, was collected onboard the RV 'James Clark Ross' at the South Orkney Islands (60° 55′ S, 45° 45′ W, depth range from 242 to 245 m) on 19 October 2011 by Agassiz trawl (mesh size 10 mm, horizontal opening 2 m, 3 min haul at 0.34 kn) that was towed on muddy bottom (Figs. 1 & 2). Together with this female, 3 developing octopus eggs were found in the catch. No additional sampling of maturing and mature specimens was carried out
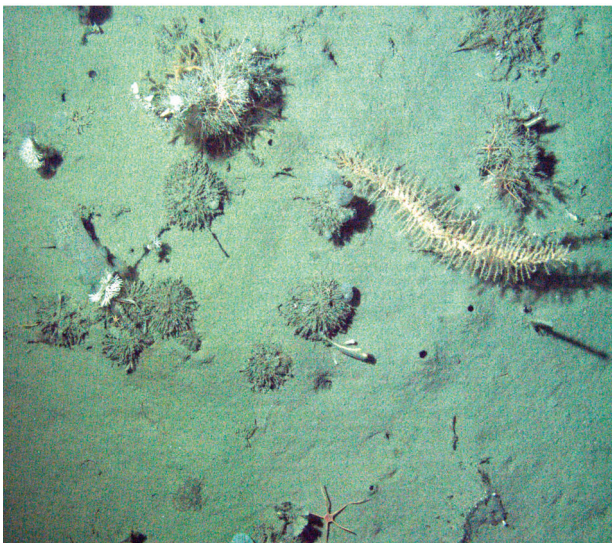

Fig. 2. Bottom view of the location where a spent female *Adelieledone polymorpha* was collected. The photo was taken using the Shallow Underwater Camera System onboard the RSS 'James Clark Ross' (courtesy of David Barnes, British Antarctic Survey)

because these ontogenetic stages and the fecundity of this species has been well studied by other authors (Kuehl 1988, Barratt et al. 2008).

Ovaries of *Graneledone macrotyla* and *Muusoctopus longibrachus akambei* were preserved in 10 % buffered formalin solution (BFS) after being opened to prevent oocyte shape distortion. *Adelieledone polymorpha* was preserved whole in 6 % BFS.

In the laboratory, the ovaries were soaked in water for 24 h, and then all oocytes and POF were measured to the nearest 1 mm under a dissecting microscope (×10) and counted. The POF were easily recognisable from intact oocytes: they were flat, empty follicular sheaths with no content inside, but with a wide opening on their distal end where oocyte broke through at ovulation. Their numbers were supposed to reflect the numbers of eggs that were spawned. If other ovarian ova were in a developing or an atretic state, it was possible to infer whether that individual would be able to produce another batch of eggs, or whether it produced a single clutch that was already laid by a particular spent female. Potential fecundity in pre-spawning animals was estimated as the total number of all eggs. Actual fecundity was estimated as the number of presumably viable eggs without signs of degeneration.

RESULTS

Graneledone macrotyla

Potential fecundity varied from 101 to 166 eggs (mean 121.5 eggs), and actual fecundity varied from 75 to 134 eggs (mean 92.0 eggs). Oocytes of the smaller maturing female exhibited an extended size distribution (Fig. 3A). In the more advanced maturing octopus of 100 mm ML (Fig. 3B), these small eggs had already begun to shrink and degenerate, they were flaccid with cytoplasm, losing contact with the follicular envelope, and the nucleus often misshaped (early atretic). In more advanced mature animals, these eggs were already ca. 1–3 mm in length and no well defined structures were seen inside (late atretic). The ovary of a spent female (Fig. 3E & 4A) contained 83 POF, which ranged in length from 19 to 32 mm, one yolk oocyte of 20 mm (not seen on the photo) and 29 late atretic oocytes ~2 mm in length. POF were whitish and flattened, with an opening on the distal end and some scarce longitudinal folds. The length–frequency distribution of POF appeared to be bimodal, with modes of 22–23 and 26 mm, but this might be a single extended mode of 22–27 mm.
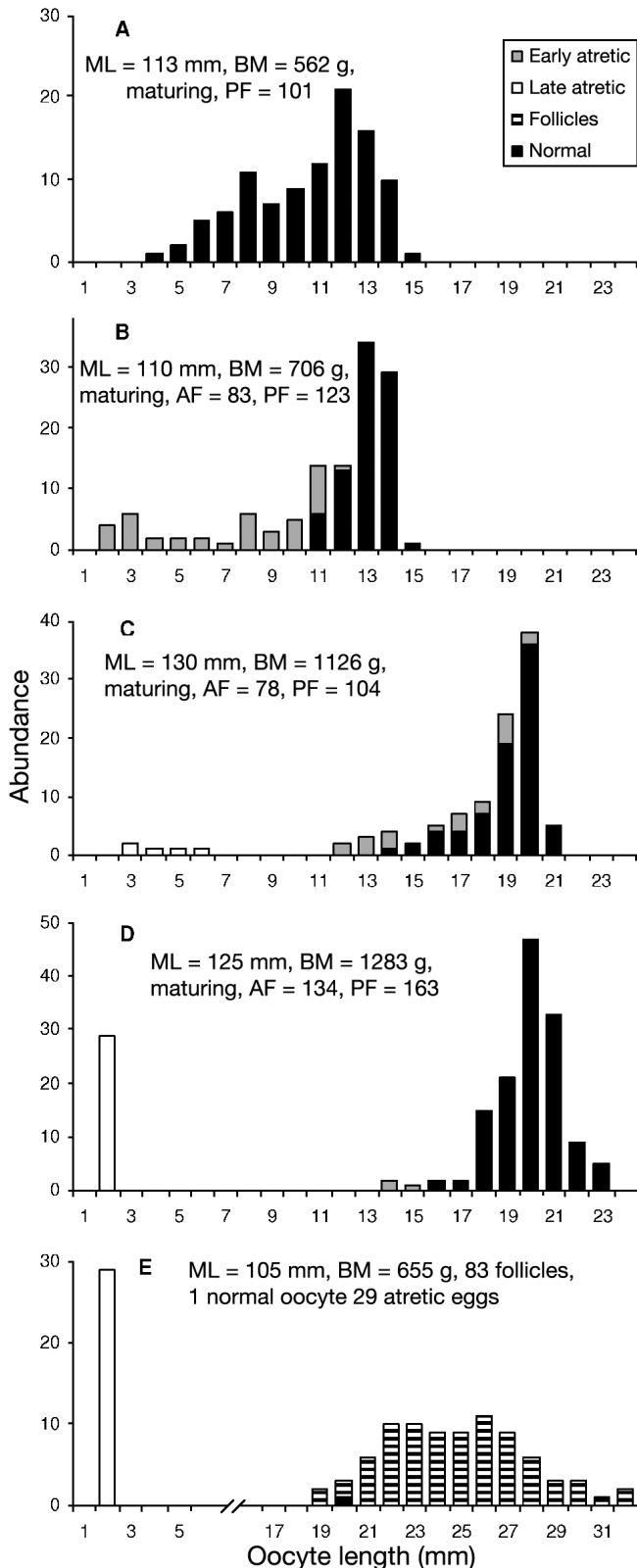
Fig. 3. *Graneledone macrotyla*. Length–frequency distribution of oocytes and post-ovulatory follicles in 5 females. ML: mantle length; BM: body mass; AF: actual fecundity (no. of eggs); PF: potential fecundity (no. of eggs)

Oviductal glands of the spent female were pale yellow-pinkish, in contrast to dark purple in mature prespawning specimens. The animal itself did not look different from mature females showing no signs of exhaustion. No spermatophores were found in the ovaries of any of the females.

Adelieledone polymorpha

Ovary of a spent female (Fig. 4B) contained 87 POF of 6–9 mm in length (Fig. 5) and neither eggs nor atretic oocytes. Three ripe eggs — leftovers of the destroyed egg mass captured with the female — were 18 mm in length, much larger than the POF. Their outer envelope was rigid and opaque, not transparent. However, it cannot be completely excluded that eggs belonged to another brooding female of the same or different species that escaped the fishing gear. The length–frequency distribution of POF was unimodal. This female appeared absolutely normal (Fig. 6), though after opening there was an impression that its digestive gland was a bit smaller than it should be. Oviductal glands were deep purple (Fig. 4B). No spermatophore was found in the ovary.

Muusoctopus longibrachus akambei

Ovaries of spent females (Fig. 4C) contained 139 to 251 POF that were 12–21 mm in length, and up to 8 yolky eggs 21–25 mm long. The eggs exhibited patchy colouration and large separated yolk droplets that may have been signs of degeneration, because those patterns have never been seen in mature ovaries preserved the same way (author's pers. obs.). Two females also had one residual atretic oocyte each (Fig. 5). The POF length–frequency distribution in every female was unimodal. Females themselves looked normal, their digestive glands being of the same size as in mature animals. Their oviductal glands were pale brownish-purple, in contrast to deep purple in mature pre-spawning females. No spermatophores were found inside the oviductal glands or in the ovary.

DISCUSSION

Brooding deep-sea octopodids are extremely difficult to obtain. However, analysis of existing literature has shown that 4 spent females of deep-sea eledonins were caught by bottom trawls, but not all of
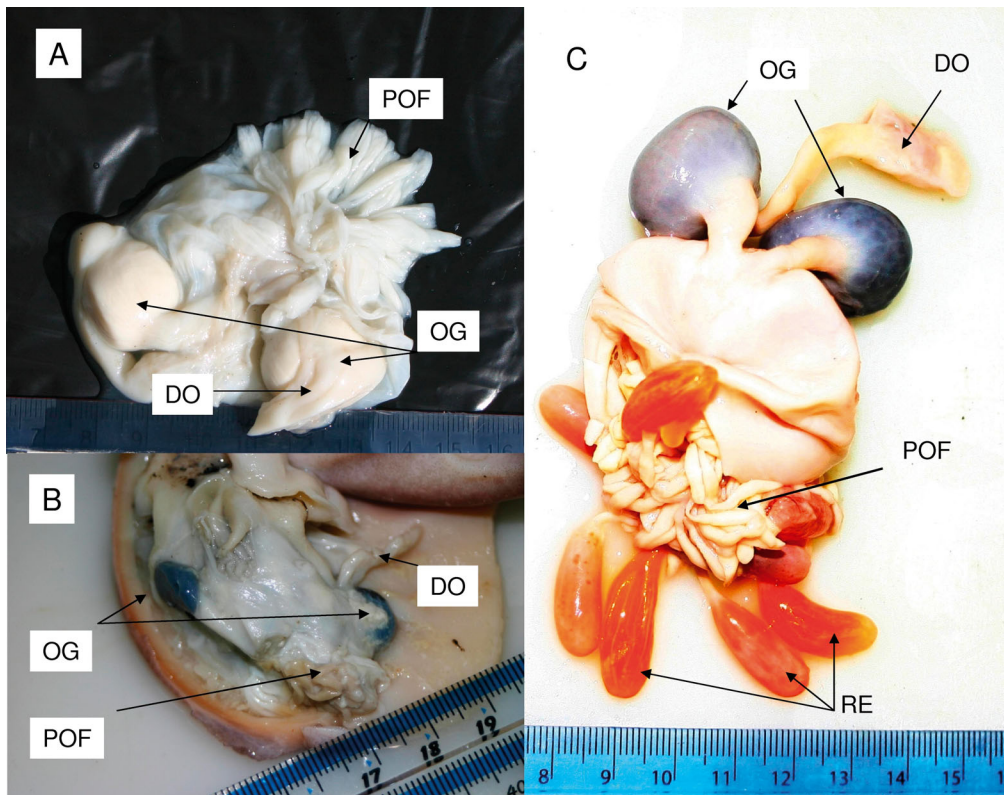
Fig. 4. Spent ovaries of (A) *Graneledone macrotyla*, (B) *Adelieledone polymorpha* and (C) *Muusoctopus longibrachus akambei*. DO: distal oviduct; OG: oviductal glands; POF: post-ovulatory follicles; RE: residual ripe oocytes

them were recognised. Two of them were thought to be aberrant maturing animals, and because of this their ovaries were illustrated, allowing proper identification of their reproductive status. One of these ovaries was from *Adelieledone polymorpha* (Fig. 4A in Barratt et al. 2008) and one was from *Graneledone macrotyla* (Fig. 9D in Guerra et al. 2012). Empty POF in these ovaries were considered to be: (1) smaller oocytes of another batch (Barratt et al. 2008) and (2) oocytes with widely opened cases in the distal pole and with a flaccid consistency — either an artefact of freezing, apoptosis or atresia (Guerra et al. 2012). Because both spent females had a few residual post-spawning eggs that were interpreted as the most advanced batch, both groups of authors came to the conclusion that there was a possibility of multiple egg release by these eledonins, at least by some individuals. This supposition might be checked by comparing the number of POF with actual fecundity.

Spent and brooding females found in the present study looked like normal mature octopuses. This is similar to the observation of a spent specimen of *Pareledone turqueti*, 'which did not appear to differ noticeably in condition to other specimens' (p. 588,

Barratt et al. 2008). This is not surprising for species surviving for more than 1 yr after spawning. Spent females might differ from mature animals in terms of the colour of oviductal glands, which were paler in brooding animals of *Graneledone macrotyla* and *Muusoctopus longibrachus akambei* but not in *Adelieledone polymorpha*.

The present study shows that numbers of POF found in spent brooding females of all 3 species were very similar to actual fecundity of pre-spawning females (Kuehl 1988, Laptikhovsky 2001, Barratt et al. 2008, present study). In *Graneledone macrotyla*, respective values were 84 POF vs. 75–134 (mean 92.0) eggs.

Spent females of *Adelieledone polymorpha* had 87 POF (present study) and 75 POF with 6 residual yolk oocytes, 2 of which already began to degenerate (Barratt et al. 2008), compared with an actual species fecundity of 71 to 128 eggs (Barratt et al. 2008). The specimen described by H. I. Daly had 9 mature oocytes and 30 POF of 3–6 mm length in the ovary (Daly 1996 cited in Barratt et al. 2008).

In *Muusoctopus longibrachus akambei*, the total number of POF (139–251) was also similar to the fecundity of mature females (75–234 eggs; Laptik-
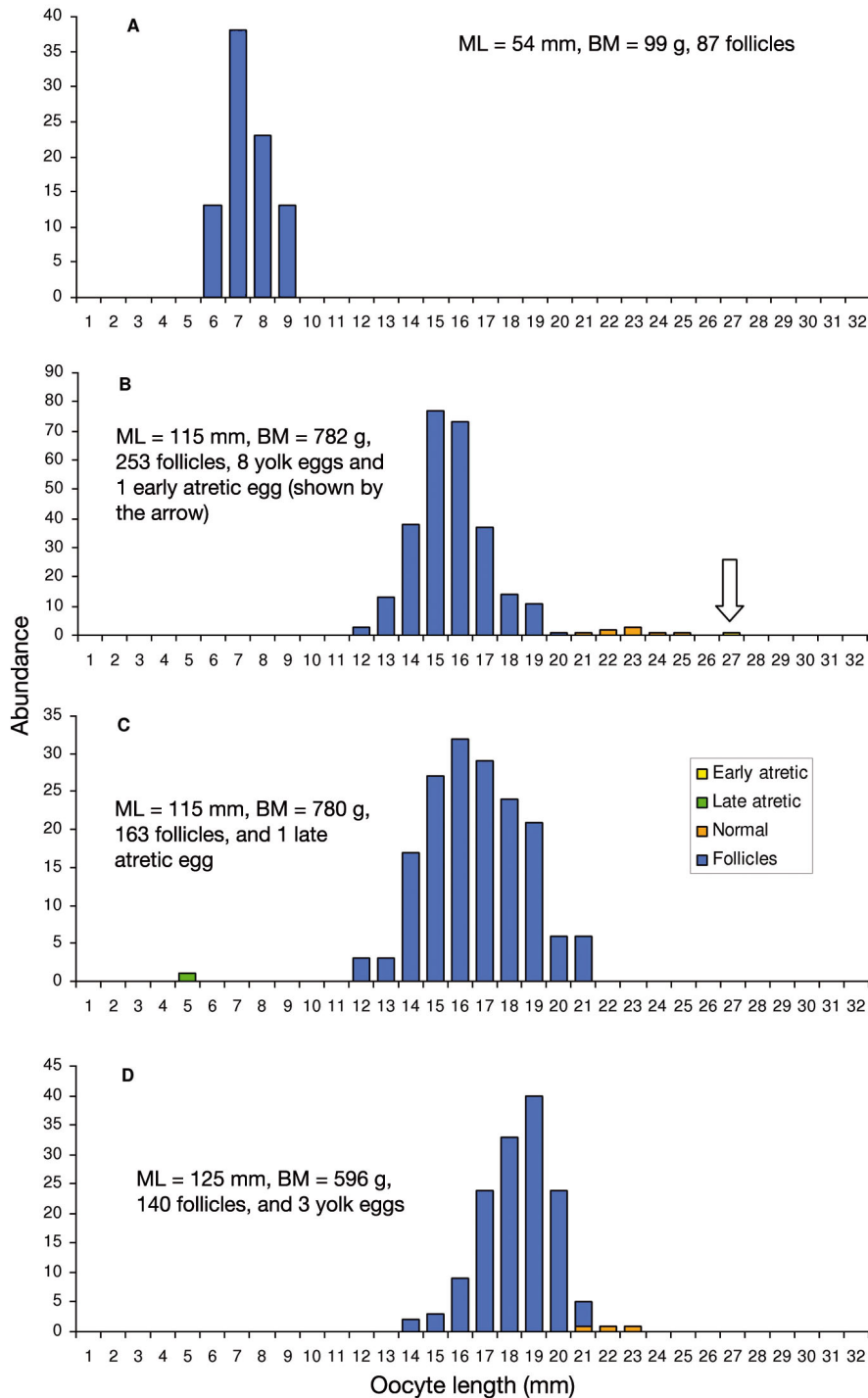
Fig. 5. Length–frequency distribution of post-ovulatory follicles in (A) *Adelieledone polymorpha* and (B–D) *Muusoctopus longibrachus akambei*. ML: mantle length; BM: body mass

hovsky 2001), and no oocytes for the second batch were found in pre-spawning or spent ovaries.

The number of POF might be a good tool to estimate actual fecundity in brooding deep-sea and polar octopodids when egg mass is not available, as

was shown for some deep-sea and Antarctic squids (Nesis et al. 1998, Laptikhovsky et al. 2007, Bush et al. 2012). In these studies, the unimodal distribution of their size indicated that eggs were released more or less as a single batch or a few mini-batches separated by very short periods of time.

The number of residual eggs in all known spent females of deep-sea and Antarctic octopods varies from 0 to 9 (Barratt et al. 2008, Guerra et al. 2012, present study). Patchy colouration, large separated yolk droplets and other abnormal features (see also Fig. 9D in Guerra et al. 2012) might be signs of degeneration. Among all 6 studied individuals in which POF were counted (all species combined), 5 in the present study and 1 studied by Barratt et al. (2008), a total of 92.6–100% (mean 97.6%) of the eggs representing actual fecundity were laid. In a variety of large-egged octopodids, from the deep-sea Arctic *Bathypolypus bairdii* (Wood et al. 1998), to the shelf temperate *Eledone cirrhosa* (Mangold et al. 1971) and the intertidal zone subtropical *Octopus digueti* (De Rusha et al. 1987), the entire process of egg laying from the first to the last batch takes approximately 2–3 wk. For cold-water octopuses such as *Bathypolipus bairdii* and *Enteroctopus dofleini*, this is a very short time frame with respect to embryonic development. The latter takes as much as 13–18 mo at developmental temperatures (5–11°C) that are far from being the coldest among octopodids (von Boletzky 1994, Wood et al. 1998). Duration of embryogenesis in *Muusoctopus* and *Sasakiopus*, which brood much larger eggs of 16–27 mm at a year-round bottom temperature of 2–4°C in the Bering Sea was estimated, using an equation relating these 3 parameters, to be 19–21 mo (Laptikhovsky 1999a,b). For *Graneledone pacifica* living at 2°C, this estimation was almost 4 yr (Voight & Grehan 2000). For the entire 4 yr the clutch is brooded by a female that occasionally eats available prey to support ener-

Fig. 6. A spent female *Adelieledone polymorpha*

getic requirements (Wood et al. 1998), so it can be concluded that the duration of life in these octopods is several years. The spawning period of 2–3 wk is just a short episode in such a life span.

Cephalopods have very flexible reproductive strategies, often exhibiting a variety of spawning patterns between individuals (von Boletzky 1986, 1988, Gabel-Deickert 1995), so there is a possibility for some individuals to spawn eggs in 2 (perhaps even more) batches separated by a long period of time. Such a gap would be necessary for the second batch do grow due to a restricted body capacity. Bimodal size distribution of viable eggs was found in a single female of both *Sasakiopus salebrosus* (Laptikhovsky 1999a) and *Adelieledone polymorpha* (Barratt el al. 2008) and a possibility of multi-batch spawning was corroborated by a extended POF distribution in a spent female *A. polymorpha* (present study). It is likely that such a strategy represents an individual variation, such as in the large-egged cuttlefish *Sepia officinalis*, in which most females are simultaneous terminal spawners, but some individuals spawn intermittently (von Boletzky 1986, 1988).

Among the 2 sampled brooding females of *Graneledone pacifica* (Voight & Grehan 2000), one had 3 residual oocytes of 21.5 mm and 63 flattened oocytes. The latter likely were POF and their number was similar to the fecundity observed in a pre-spawning animal. Eggs were probably laid as a single batch because all the POF were of the same size (10 mm).

Thus, it can be concluded that deep-sea and polar (both Arctic and Antarctic) octopodids normally are not multiple spawners, as has been suggested (Rocha et al. 2001, Bello 2006, Guerra et al. 2012), though they can lay a single clutch as several mini-batches during to 1–3 wk. These actual mini-batches are formed from a single large batch growing more or less synchronously in the ovary. Atresia of yolk oocytes probably plays an important role in the size segregation of batches at early and advanced maturation stages in Antarctic fish through the selective reabsorption of oocytes of intermediate size (La Mesa et al. 2007 and references therein). This process has never been seen in deep-sea and cold-water octopods and squid, in which early maturation stages are invariantly to degenerate, whereas intermediate stages develop into the actual fecundity (Laptikhovsky 1999a, Laptikhovsky et al. 2007). However, some individual females can probably spawn this synchronously developed egg portion as several batches with a significant time gap in between.

The problem with interpretation of the type of spawning from length–frequencies of oocytes is complicated by the fact that maturing females always have an extended range of oocyte sizes, often polymodal. This might lead to the incorrect perception of egg maturation as occurring in separate, distinctive batches. Such an extended range of egg sizes has been described in every large-egged deep-sea octopodid where the process of oocyte growth has been studied: *Eledone moschata* (Önsoy & Salman 2004), *Graneledone pacifica* (Bello, 2006), *Muusoctopus* spp. and *Sasakiopus salebrosus* (Laptikhovsky 1999a, 2001), *Muusoctopus* spp. and *Bathypolypus sponsalis* (Barratt et al. 2007, González et al. 2008), *Adelieledone polymorpha* and *Pareledone turqueti* (Barratt et al. 2008), and *Graneledone macrotyla* (present study). In all cases where pre-spawning females were available to study, it was shown that only one viable batch eventually remained in their ovaries, aside from a few small mostly already atretic oocytes.

Larger egg size and hence higher parental investment into individual offspring at the cost of lower fecundity are particular for cephalopods in relatively stable environments (Nigmatullin & Laptikhovsky 1994, Rocha et al. 2001), so it is not surprising to find these characteristics in deep-sea and polar octopodids. However, terminal spawning seems to be a strange evolutionary choice for these habitats, particularly because cirrate octopods that live at similar depth ranges and produce eggs of similar size exhibit continuous spawning with eggs laid

individually (Villanueva 1992, Laptikhovsky 1999a). A phenomenon similar to single-batch terminal spawning also exists in the deep-sea squid families Onychoteuthidae, Cranchidae, Gonatidae and Bathyteuthidae (Seibel et al. 2000, Laptikhovsky & Arkhipkin 2003, Laptikhovsky et al. 2007, Bush et al. 2012), of which at least Gonatidae and Bathyteuthidae are also brooders. In contrast to octopods, females of these squid families carry the egg mass in their arms, so they are not able to feed even occasionally during the incubation period. However, their eggs are smaller and developmental time is presumably shorter, which makes female survival until hatching possible, based totally on expenditures of stored food reserves. Brooding may restrict both deep-sea squid and octopods to a simultaneous terminal spawning strategy because of the costs in terms of energy, time and predation risk associated with parental care (Wood et al. 1998, Barratt et al. 2007). In this case, the flexibility of reproductive strategy to ensure reproductive success might be achieved by an extended spawning period of the entire population rather than of individuals.

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