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RESEARCH ARTICLE

Reproductive biology in two species of deep-sea squids

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Abstract Deep-sea squids, *Moroteuthis ingens* and *Gonatus antarcticus*, were collected in the slope waters off the Falkland Islands and their reproductive systems preserved and investigated onshore. Changes in oocyte length-frequencies at maturation and spawning, and their fecundity were studied. These squids, as well as many other species, are characterised by a synchronous oocyte growth and ovulation. Oviducts are not used for ripe egg accumulation and consequently the universal scale of Lipinski (1979) cannot be applied to assign female maturity. *M. ingens* spawns near the bottom; its fecundity is 168–297 thousand eggs. Maximum egg size is 1.8–2.7 mm. *G. antarcticus* spawns midwater; its fecundity is 10–25 thousand eggs. Egg size is 3.2–3.3 mm. In *M. ingens* spawning takes place in the austral autumn and winter, in *G. antarcticus*—in austral winter. Our data and the literature data show that the so-called "synchronous ovulation" probably occurs in all deepwater squids. This pattern is very rare among fish, but is quite common among benthic octopods that brood their egg masses.

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Introduction

Cephalopod reproduction has been investigated since Aristotle, and by the end of the twentieth century oogenesis, ovary maturation and spawning patterns have been studied in many cuttlefish, octopod and squid species, commercially exploited ones in particular. It has been found that squid reproducing on the shelf, slope and in epi-mesopelagic layers of the open ocean (Loliginidae, Ommastrephidae, Enoploteuthidae, Thysanoteuthidae, Ancistrocheiridae, Architeuthidae and *Berrytheuthis*, Gonatidae) are characterised by asynchronous vitellogenesis (Burukovsky and Vovk 1974; Burukovsky et al. 1977; Nigmatullin et al. 1996; Nigmatullin and Arkhipkin 1998; Laptikhovsky 1999a; Hoving et al. 2004). Oocytes mature and ovulate at different times, after which they are transferred and accumulated in oviducts until those are full and ready to spawn. After the eggs are released during spawning (in single or multiple batches), the oviducts receive a fresh influx of ripe oocytes. It was suggested that the oviducts represent a compromise between the inherited ancestral asynchronous pattern of yolk accumulation and the subsequently evolved intermittent batch spawning strategy (Burukovsky et al. 1977). This principle was used to develop a universal maturity scale by Lipinski (1979) and its later revision (Lipinski and Underhill 1995). According to this scale, all female squid without eggs in the oviducts are assigned to either immature or early maturing, those with a few eggs in the oviducts (stage IV) as late maturing, and those with full oviducts (stage V) as mature.

Casual reports on squid spawning in deep waters (Onychoteuthidae, Gonatidae, Histioteuthidae, and Cranchiidae) revealed evidence of synchronous ovary maturation. In maturing and mature females of *Teuthowenia megalops* and *T. pellucida*, all oocytes were found to be of

the same size (Muus 1956; Voss 1985). Synchronous egg development has also been discovered in immature and maturing tropical and subtropical bathypelagic spawners—*Onychoteuthis banksi* and different *Histioteuthis* spp. (Arkhipkin and Nigmatullin 1997; Laptikhovsky 2001a). It was suggested that in some deepwater-spawning squid, oocytes start to develop synchronously at the very late stages of vitellogenesis, which allows the species to release its eggs in separate batches (Nigmatullin and Piatkowski 1997; Nigmatullin 2004). Another interesting feature, post-spawning egg care and brooding, was discovered and photographed in deepwater-spawning gonatids (Okutani et al. 1995; Seibel et al. 2005). This was confirmed by the presence of egg-mass remnants on the arms of spent females of *Gonatus fabricii* (Björke et al. 1997).

Around the Falkland Islands, there are two abundant squid species that spawn in deep waters, *G. antarcticus* Lönnberg 1898 (Gonatidae) and *Moroteuthis ingens* (Smith 1881) (Onychoteuthidae). Their juveniles and subadults inhabit shelf and slope waters and play an important role in food chains of these ecosystems (Jackson et al. 1998; Nesis 1999).

The present study aims to describe the maturation and fecundity of these two squid species and to discuss reproductive strategies of deepwater spawning squid.

Materials and methods

A total of 203 immature, maturing, mature, and spent female *M. ingens* (mantle length, ML 6.3–51.5 mm, body weight, BW 12–4,418 g) were collected and frozen onboard commercial fishing vessels and RV "*Dorada*" fishing between 138 and 934 m depth around the Falkland Islands in February, March, July, August, and November 1999–2006 (Fig. 1). Commercial vessels used different types of bottom trawls with minimum mesh sizes of 90 mm in the codend and 135 mm in chafers. Towing speed was 3.5–4.2 kt. A semipelagic trawl, used onboard RV "Dorada", had 40 mm mesh size in the codend, polyvalent doors with a spread of 97 m and towing speeds of 3.3–3.6 kn. The bottom temperature decreased with depth from 7° (139–143 m) to 3.5°C (877–907 m).

After defrosting, ML was measured to the nearest 1 mm, body weight (BW), stomach weight (SW) and ovary, oviducts and nidamental gland weight—within 0.1 g. A total of 32 reproductive systems (from females of ML 195–515 mm) were then preserved in 10% buffered formalin solution for fecundity studies. From each ovary, three subsamples of about 300–2,000 oocytes were taken and weighed to the nearest 0.001 g. All oocytes in the subsample were counted and the longest axis of at least 100 was measured. Oviducts were investigated for the presence of eggs. The size of the largest, and not misshaped oocytes, was used as the maximum oocyte size.

A total of 56 immature, maturing, and spent females of *G. antarcticus* were collected by RV "Dorada" in October 2001 and October 2002 on the Falkland slope above depths of 1,017–2,378 m (trawl horizon = 738–975 m). They were also frozen and then fixed in 10% formalin ashore. A total of nine ovaries of immature (2), maturing (5), and spent (2) squids (270–395 mm ML) were investigated. In this species, upon removal of the excess preservative, a large piece (5–10% of ovary) was sampled for fecundity studies. Both ovary and sample were weighed to the nearest 0.001 g. All oocytes in the subsample were counted, and the maximum oocyte size was measured for about 100 oocytes from the subsample. Fecundity was assumed to be equal to a total number of normal oocytes in the ovary; total oocyte stock represented the sum of fecundity and total number of resorpting oocytes.

Gonado-somatic index (GSI) was calculated as:

$$\mathrm{GSI} = \mathrm{RSW}/(\mathrm{BW} - \mathrm{SW}),$$

where RSW is total reproductive system weight.

Statistical package Graph Pad Prism Version 3.00 was used for statistical estimations.

Results

Moroteuthis ingens

Female maturity

Analysis of the reproductive system growth with increasing ML (Fig. 2) demonstrated that both oocyte size and ovary weight increased only slightly during most of their ontogenesis. The "avalanche" like yolk accumulation in oocytes occurred in squid more than 450 mm ML, resulting in a drastic increase of the ovary weight to 14.5–27.7% BW (mean 19.7%) and the whole reproductive system to 21.5–37.5% BW (mean 26.1%). Sizes of mature females ranged between 475 and 515 mm ML (3,280–4,418 g BW). In these females, the ovary occupied literally the whole posterior part of the mantle cavity. Oviducts looked like straight tubes without any loops (Fig. 3). Females that were categorised "mature" did not have any eggs in the oviducts; however, ripe eggs in their ovaries were often ovulated and fell loose during dissection, similar to mature *M. ingens* from South Australian and New Zealand waters (Jackson et al. 2004). The inner side of the mantle wall was reddish-brown. All mature females had flaccid mantles and numerous spermatangia embedded

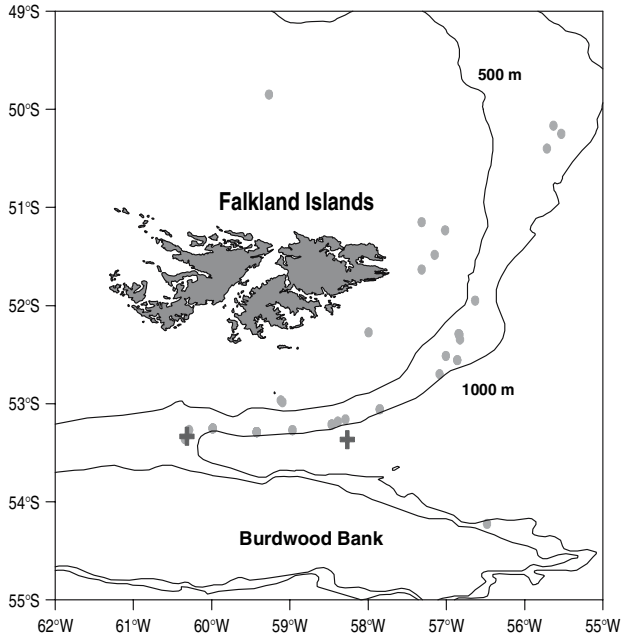

Fig. 1 Position of sampling sites (*Moroteuthis ingens*—dots, *Gonatus antarcticus*—crosses)

into tissues both around and in the funnel, and sometimes in the coelomic membranes and the inner side of the mantle wall. Ripe egg size ranged between 2.0 and 2.7 mm (mean 2.4 mm).

Ovary maturation and fecundity

Analysis of the oocyte length frequency in the ovaries showed that oocyte growth is synchronous (Fig. 4). All oocytes grow as a single batch up to a maximum size of 0.5–0.6 mm and then, due to partial oocyte resorption, the total number of oocytes decreases whilst the rest continue to grow. Consequently, the total number of oocytes decreases with squid growth (Fig. 5). Yolk accumulation begins at an oocyte size of ~0.7 mm. The greatest resorption occurs at the maximum size of normal oocytes of 0.7–1.5 mm. The oocyte stock to be released (the fecundity) continues growing synchronously and is not subjected to any further resorption until the oocytes achieve about 1.5 mm.

Fecundity in mature females (maximum egg size 1.8–2.7 mm with no resorption of main oocyte stock) was 168–297 (mean 249) thousand eggs (Fig. 6). There is a positive correlation between fecundity and ML ($r = 0.77$, $P = 0.0002$). Relative fecundity was 53–84 (mean 66.1) eggs/g.

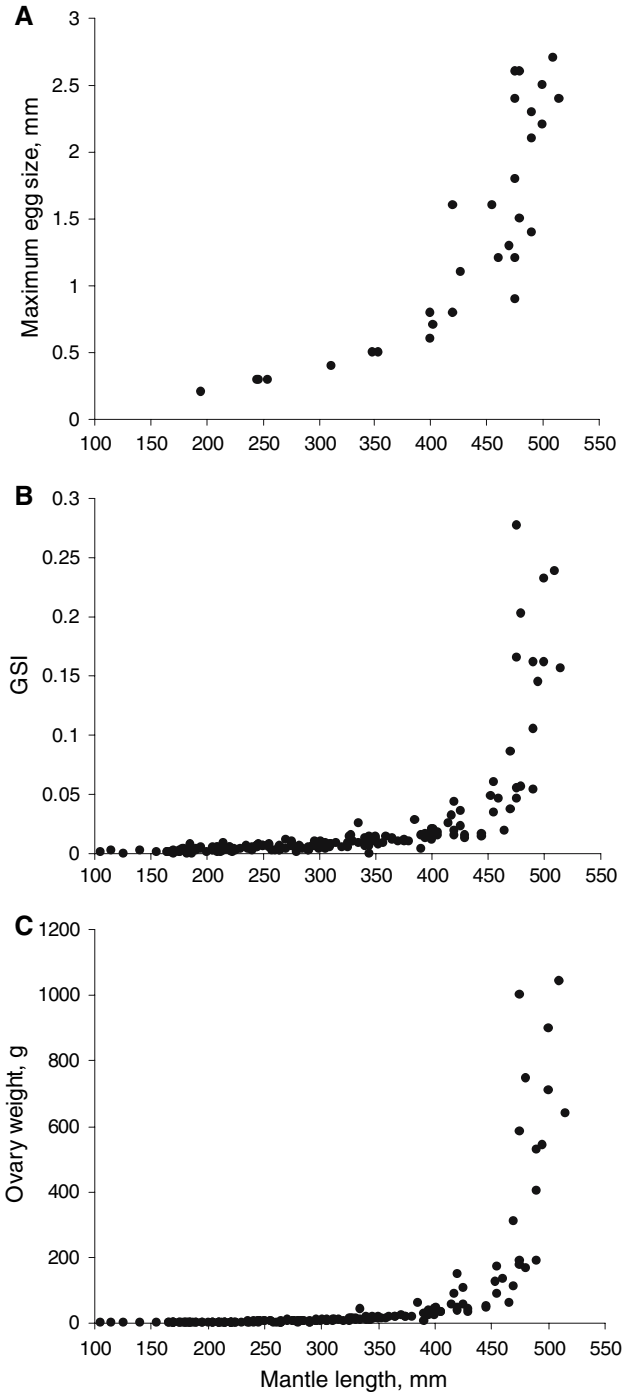

Fig. 2 Changes in **a** size of the largest egg; **b** GSI; and **c** ovary weight with growth in females of *M. ingens*

Spawning habitat

Large mature and spent *M. ingens* were caught near the bottom at depth range 739–889 m on 13–23 March 2006 at 53°10′–53°31′S; 57°00′–59°59′W. Mature males were

Fig. 3 Sac-like oviduct in *M. ingens* (no extendable loops)

present in all these catches. This indicates that spawning takes place deeper than 700 m in the austral autumn.

Gonatus antarcticus

Female maturity

There were no fully mature squids sensu Lipinski (1979) scale, nor did we collect squid ready to spawn immediately. In the most advanced maturing female (275 mm ML) with the largest eggs of 1.65 mm, the ovary was 4.1% BW (total reproductive system—7.0% BW). The largest maturing female was 300 mm ML. The sizes of two spent females were 380 and 395 mm (523 and 597 g BW, respectively). Both of them had remnants of dark greenish slime on their arms (similar to brooding *G. fabricii*—Björke et al. 1997) indicating that they might have recently been brooding. Each one had about a hundred empty spermatangia bases attached to the buccal membrane.

Ovary maturation and fecundity

Oocyte development is synchronous, even prior to yolk accumulation which begins at an egg size of 0.7 mm. Upon maturation, oocytes continued to grow synchronously, the largest of them being about 50% larger than the smallest ones. In the most advanced maturing female, oocyte size varied from 1.1 to 1.65 mm, being mostly 1.3–1.6 mm (Fig. 7).

Oocyte maturation was accompanied by resorption of the excess oocyte stock, which was evident at all stages of the gonad development. In squid of 270–300 mm ML, the potential fecundity decreased from about 30,000 eggs at an oocyte size of 0.6 mm to some 10,000 eggs at an oocyte size of 1.3–1.6 mm. Larger females probably have higher fecundity; the two spent females of 380 and 395 mm ML had some 22,000 and 25,000 empty follicles and 100 and 375 yolk oocytes of 0.7–1.0 mm, respectively. This

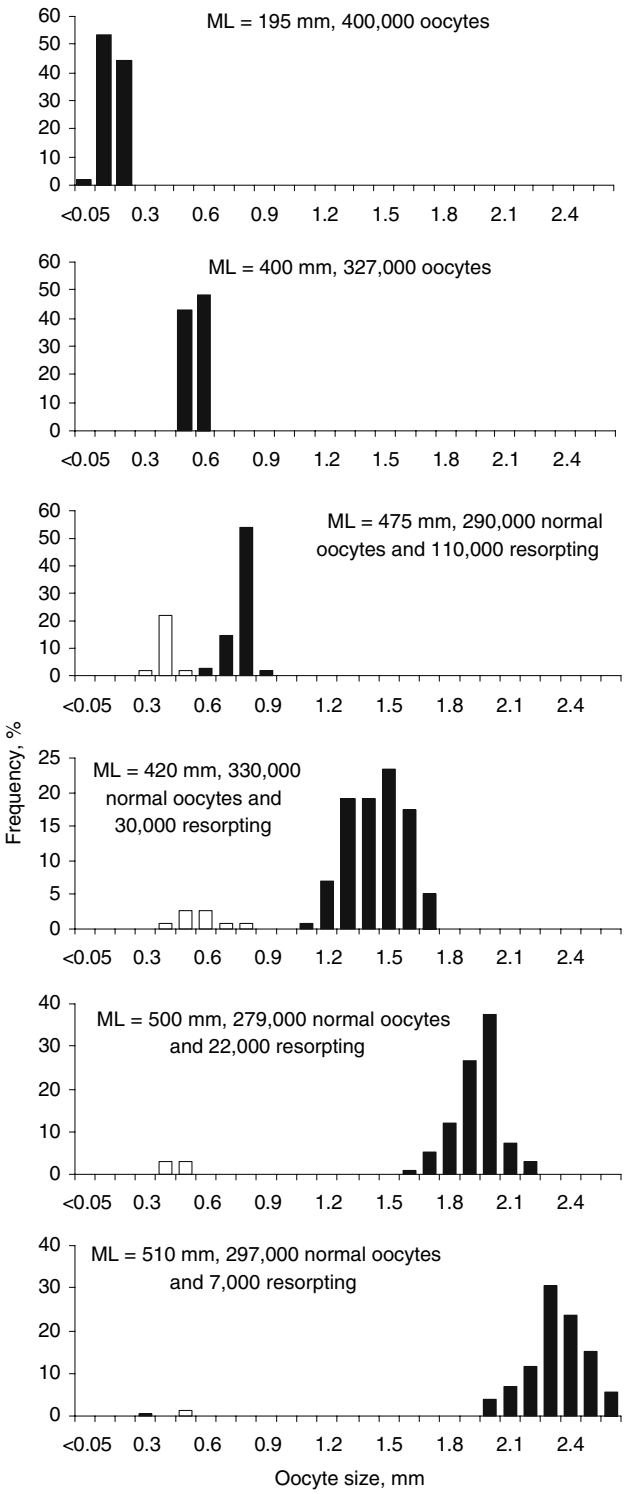

Fig. 4 Oocyte size distribution by squid size showing oocyte growth and resorption at maturation of *M. ingens* (resorpting oocytes are shown by *empty boxes*)

indicated that their fecundity was more than twice as large with respect to maturing animals of 270–300 mm ML. The largest of spent females had nine ripe eggs in the oviducts, which were probably left after spawning. Egg size was 3.2–

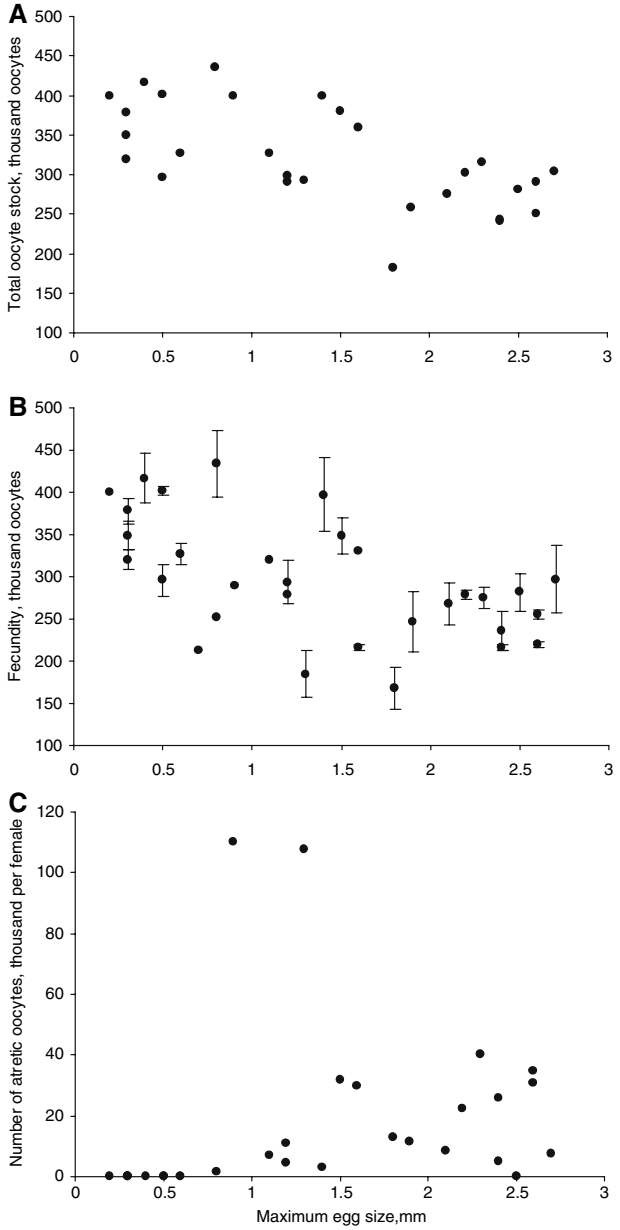

Fig. 5 Changes in oocyte numbers at maturation of *M. ingens*. **a** Total oocyte stock (including resorpting oocytes) plotted against maximum egg size of the individual (i.e. of the largest spherical, not misshapen oocytes); **b** Fecundity (resorpting oocytes excluded), *error bars* show confidence limits at $\alpha = 0.05$; **c** Changes in number of atretic oocytes with ovary maturation

3.3×2.5–2.9 mm. The absence of eggs in oviducts of another spent female indicated that the squid could utilise up to 100% of their fecundity.

Spawning habitat

The two spent (brooding?) female *G. antarcticus* were caught at a horizon of 976–1,001 m over 1,848–2,381 m bottom depths on 1 October 2002 at 53°24′–53°29′S,

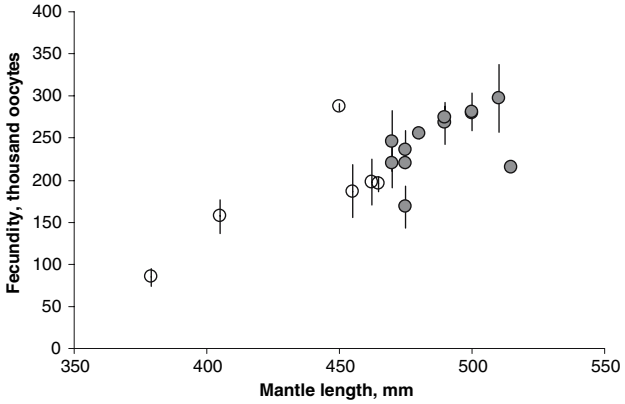

Fig. 6 Fecundity of mature female *M. ingens*; *error bars* show confidence limits at $\alpha = 0.05$; *empty circles* maturing females, *filled circles* mature animals

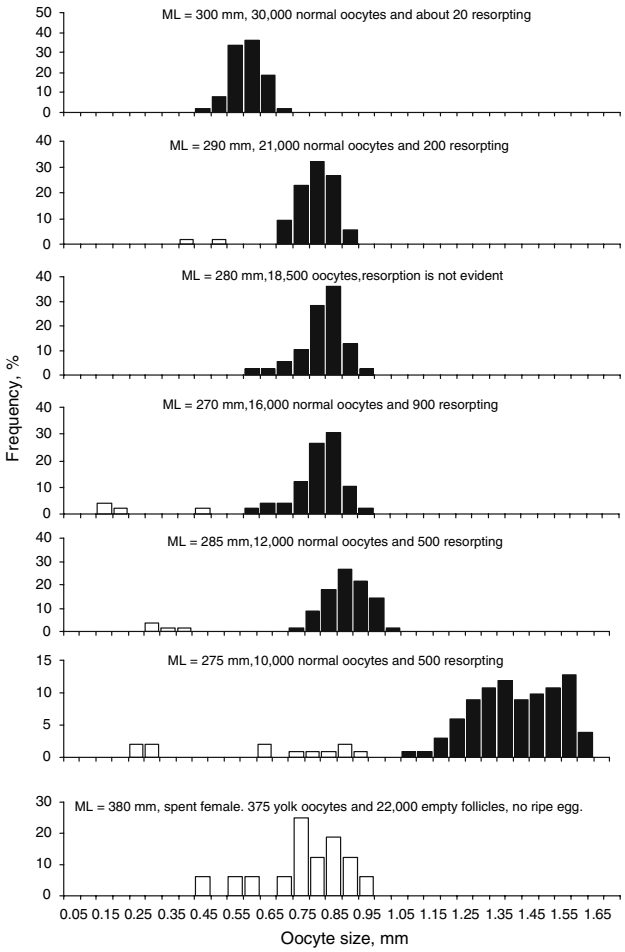

Fig. 7 Oocyte size distribution by squid size showing oocyte growth and resorption at maturation of *G. antarcticus* (resorpting oocytes are shown by *empty boxes*)

58°13′–58°04′W. "Mature–spent" males of 210–280 mm ML (53–204 g BW) were collected on 8 October 2001 at 53°20′S to 60°20′–59°57′W (horizon 700–750 m over

905–1,017 m depths). These males were neither mature nor spent: their testes were virtually absent and hardly thicker than the central blood vessels, whereas their spermatophoric sacs were tightly packed with spermatophores. As well as females, they were ready for a single (or a few consequent) spawning events and their maturity status also did not fit into the Lipinski universal maturity scale. Their occurrence at these stations suggested that copulation, spawning, and egg brooding probably take place in the water column, well off both the sea bottom and surface.

Discussion

Size of mature animals

The "avalanche-like" maturation in the Falkland *M. ingens* begins at a larger size (about 450 mm) than in New Zealand female squids, which began to mature at about 400 mm (Jackson 1997). Because of this, mature Pacific squids were also smaller: 425–488 (mean 445) mm vs. 475–515 (mean 491) mm in this study. It is likely that the smaller size of the New Zealand females was caused by higher water temperatures and respective earlier maturation that was observed in other squid species in which populations living at warmer temperatures mature earlier (Mangold 1987).

Spent females of *G. antarcticus* in our samples were larger than the largest female ever reported (about 350 mm ML—Nesis 1999), but still smaller than that reconstructed from the beak found in the stomach of a wandering albatross—440 mm ML (Nesis 1999).

Ovary maturation and spawning

Our data showed that the maturation pattern in the Falkland Islands' population of *M. ingens* which results in a sudden increase in the ovary weight is very different from that of squids with asynchronous egg maturation, such as warm-water small-egged species like *Dosidicus gigas*, Ommastrephidae (Markaida and Sosa-Nishizaki 2001), and also coldwater large-egged squids *Loligo forbesi* and *L. gahi*, Loliginidae (Guerra and Castro 1994; Smith et al. 2005; our data) and sepiolids (Salman 1998). In all these cephalopods, the ovary increases in weight slowly while the animal is still growing in length. Our results are in agreement with a small data set on 29 squids at the different maturity stages from another *M. ingens* population from around Chatham Rise, New Zealand (Jackson 1997). The only cephalopod species in which a similar pattern of reproductive system growth has been described before is *G. fabricii* (Arkhipkin and Bjorke 1999).

Mature females of *M. ingens* in our study had large ovaries with gonadal and reproductive indices similar to those sampled off New Zealand (average 20 and 26%, respectively) (Jackson et al. 2004). Conversely, gonadal and reproductive indices were much smaller (2–9 and 10–20% in average) in the majority of mature females of species with asynchronous oocyte development (e.g. families Loliginidae, Enoploteuthidae, and Ommastrephidae) (Zuev et al. 1985; Pierce et al. 1994; Laptikhovsky 1999a; Markaida and Sosa-Nishizaki 2001; Collins et al. 1995; our data). Asynchronous ovulations allow both shelf and epipelagic squid to increase their fecundity despite the restrictions imposed by the volume of the coelomic cavity (Fig. 8). The relatively small size of the reproductive system allows squid with asynchronous oocyte development to maintain their nektonic life style and continue feeding whilst being mature and spawning without drastic changes in body shape, which would make them much less active.

Because of the larger body size of mature specimens, the fecundity of the Falkland Islands' *M. ingens* was higher than that of the New Zealand squid: mean 249,464 vs. 189,609 eggs. The mean egg size was also larger—2.4 mm vs. 2.1 mm, respectively (Jackson 2001 and this study). Fecundity values were quite similar to those observed in the intermittent spawning species reproducing on the shelf edge and in the upper part of temperate and polar continental slopes: *Todarodes sagittatus*, *T. angolensis*, and *M. hyadesi* (Nigmatullin and Laptikhovsky 1999).

Gonatid squids (except *Berryteuthis*) possess a peculiar reproductive strategy, which is very different from that in other oegopsid squids, including *Moroteuthis* spp. It involves the production of large eggs and results in a brooding behaviour (Seibel et al. 2005). Our data on maturation and fecundity in *G. antarcticus* are similar to those observed in the north Atlantic *G. fabricii*, although in the latter species their ripe eggs are larger at about 5 mm whereas the fecundity is similar—about 10,000 (Kristensen 1981). There are no data for other gonatid squid with this strategy. Reproduction of *Berryteuthis*, which spawns on the upper part of continental slope, is generally similar to that in other squids (Nigmatullin et al. 1996).

It is likely that the ovary maturation process is similar in all deepwater squids. Initially, a high oocyte stock (about 400,000 in *M. ingens*, about 20,000—in *G. antarcticus*) begins to develop synchronously until the onset of maturation. Restrictions on fecundity by the volume of the coelomic cavity are resolved by the resorption of excessive oocytes as it occurs in octopods (Laptikhovsky 1999b, 2001b). Because larger females have larger coelomic cavities, their fecundity is higher. This ovary development and fecundity formation is also exhibited by other deepwater spawners: Histioteuthidae (Laptikhovsky 2001a), Batoteuthidae (our data), and probably Cranchiidae (Nesis et al. 1998) as well as semelparous teleost fish like Pacific salmon *Oncorhynchus* spp. (Ivankov 1985). In all deep-sea

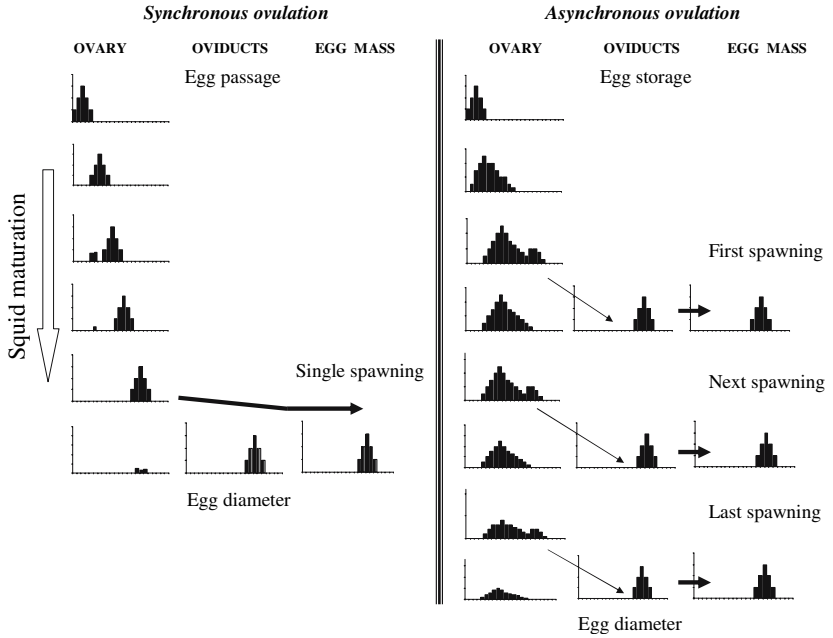

Fig. 8 Scheme of asynchronous and synchronous ovulation and spawning in squids. *Thin arrows* egg accumulation in oviducts, *thick arrows* egg release at spawning

spawners studied to date, eggs are released at one time, contrary to previous points of view (Nigmatullin and Piatkowski 1997; Nesis 1999; Nigmatullin 2004). Because of this, the oviducts in these squids do not function as storage devices, as noted before for *M. ingens* (Jackson et al. 2004).

This type of ovary development could be assigned to the so-called "synchronous ovulation" that may be found in teleosts that spawn once and then die (Wallace and Selman 1981; Ivankov 1985). This pattern is very rare among fish, but is quite common among benthic octopods that brood their egg masses (Rocha et al. 2001; Laptikhovsky 1999b, 2001b). This type of ovulation was also thought to occur in two squid species: *L. opalescens* and *T. pacificus* (Rocha et al. 2001). However, *L. opalescens* was recently found to be a intermittent batch spawner (Hanlon et al. 2004; Macewicz et al. 2004) and *T. pacificus* has asynchronous ovary maturation like any other ommastrephid squid (see Fig. 3 in Ikeda et al. 1993). Also, not only is ovulation in this species asynchronous, but at least some animals can spawn twice in captivity (Ikeda et al. 1993), perhaps even more times in the wild. Therefore, *M. ingens* and *G. antarcticus* are the first examples of synchronous ovulation by squids.

Spawning seasonality

Moroteuthis ingens was reported to have a winter spawning season over the species range including the Falkland waters (Cherel and Weismerkirch 1999; Jackson et al. 1998; Jackson 2001). Our data show that the species reproduces also in early autumn, although it probably spawns during the entire cold season. Spent *G. antarcticus* were caught in late winter which also indicates winter spawning. This is consistent with the intensive predation by penguins on juveniles of 20–50 mm ML in November–January (Thompson 1994). Because both species have pelagic juveniles foraging in the 0–200 m layer including shelf waters (Nesis 1999; our data), the winter peak of spawning presumably maximises survival of paralarvae and juveniles during their feeding on the spring zooplankton bloom.

Spawning habitats and predatory impact

Spawning and spent female *M. ingens* were caught by bottom trawl with a small vertical opening (3 m). Squid were found in the cod-end rather than entangled in the trawl wings, indicating that the squid were not captured during the net hauling through pelagic layers, but near the bottom. Spawning and spent squids from the Chatham Rise were also sampled by a bottom trawl (Jackson 2001), suggesting that spawning takes place near the sea floor. However, egg masses could develop in pelagic layers as it occurs with eggs of many deep-sea near-bottom fish like grenadiers and toothfish (Merrett and Haedich 1997).

Another reproductive strategy was found in *G. antarcticus*. Some species of this genus are known to brood their egg masses for a very long time, perhaps several months (Bjorke et al. 1997; Arkhipkin and Bjorke 1999; Seibel et al. 2000, 2005). Initially, females are active, muscular, and neutrally buoyant; but, while during brooding, they become progressively gelatinous and passive. Observation from ROA demonstrated that a specimen bearing undeveloped eggs made a vigorous escape by using fin and mantle contractions, whereas those with advanced embryos

showed only respiratory mantle contractions and did not move away. Activities of metabolic enzymes in locomotory muscles of spawned female *G. onyx* are lower in specimens that have more advanced embryos (Seibel et al. 2005). Despite retaining some capacity for swimming, the relatively immobile brooding squids become an easy prey, particularly when eggs are at late stages of development. Near-bottom layers with abundant predators are not a convenient long-term habitat for these slow moving squids with degenerated muscles. For this reason, egg brooding takes place in pelagic layers about one kilometre off both the bottom and surface. These regions do fall within the usual diving range of whales and elephant seals and so squids may provide an easy target for such "mesopelagically hunting" mammals (Seibel et al. 2005), but these predators are evidently not as abundant as fish and their searching time under water is restricted.

In spite of the very different spawning habitats, the fate of moribund female squid of both species is the same. They float to the surface where they become subjected to albatross and petrel scavenging, a common fate for many deep-sea spawning squids (Croxall and Prince 1994, 1996). After spawning the spent females (not males!) of Ancystrocheiridae, Octopoteuthidae, Gonatidae, Histioteuthidae, Cranchiidae, and of some other families lose their neutral buoyancy and float passively to the surface (Nesis 1996). These unusual looking squids have been known for a long time and were described as new taxa three times (Nesis 1996). Moribund females probably float up because of a change in buoyancy just after the egg mass release in *M. ingens* and after egg hatching and subsequent destruction of egg mass remnants at the end of brooding in *G. antarcticus* (Arkhipkin and Björke 1999). In gonatid squid, the buoyancy of female probably turns positive at the start of hatching from egg mass which she carries. Perhaps this is why a moribund gonatid female that carried a hatching egg mass was spotted at just 13-m depth, with another squid having just remnants of the egg mass (Okutani et al. 1995). On the contrary, males do not accumulate large amounts of sexual products at one time and therefore do not need to change the composition of their body as females do to keep neutral buoyancy. It is also quite unlikely that after death, decomposing bodies of deepwater squid acquire positive buoyancy and float to the surface as deep-sea scavengers consume carrion very quickly (Collins et al. 1999; Bozzano and Sarda 2002).

It is noteworthy that all families where spent squids float to the surface either after egg release or brooding consist of single-batch spawners with synchronous egg development. In either plankton or less agile cephalopods with watery tissues (Cranchiidae, Histioteuthidae, adult female Gonatidae, Psychroteuthidae, and Onychoteuthidae), buoyancy should be very close to neutral. A sudden release of a large amount of eggs (about 25% of BW) that are heavier than seawater certainly changes buoyancy to a positive value. Gonatidae, keeping their egg mass in arms, remain brooding in deep-sea, whereas Psychroteuthidae, Histioteuthidae, and Onychoteuthidae float up and become easy prey for sea birds.

In contrast to the squid described above, species with intermittent spawning that release eggs in numerous relatively small batches, like *Illex* and *Loligo*, do not float. Their eggs are heavier than sea water (5% heavier in *Illex*), although the entire egg mass density is only 0.005% higher than seawater used to form the surrounding gel (O'Dor and Balch 1985). But batch size is relatively small (Fig. 8) and does not impact squid buoyancy to such an extent, as in the situation for "big-bang" spawners. In the most advanced pre-spawning female *L. gahi* (copulation traces inside mantle cavity), the weight of the full oviduct was 1.7–5.5 (mean 2.7) % BW (our data). In fully mature female *Illex*, a species that possess two functional oviducts, this value was about 6–7% only (Laptikhovsky and Nigmatullin 1993). The nektonic life style of these females would also help to cope with minor changes in buoyancy during the spawning period.

Maturity scale problems

Our data (as well as previous observation of Jackson et al. 2004) demonstrated that maturity of some female and male deepwater squids cannot be described by the universal scale (Lipinski 1979; Lipinski and Underhill 1995). Arkhipkin (1992) provides an alternative scale, which facilitates comparative investigations of the different cephalopod taxa because it accounts for the fact that the functional maturity can occur at different stages of reproductive development. In this case, both *Gonatus* and *Moroteuthis* with octopus-like reproductive strategies (Jackson et al. 2004) fit perfectly into the octopod part of the maturity scale.

Similarity in cephalopod and fish styles of ovary maturation

Cephalopods and fish occupy the same broad adaptive zone despite differences in morphology and life cycle strategies and have evolved a range of similarities despite different organisational types (Packard 1972). However, both groups were supposed to have "modal differences in reproductive habits". In contrast to this, our data show that the similarity between coleoid cephalopods and fish is even deeper than it was previously believed (Packard 1972).

In spite of the very different oogenesis, both groups are characterised by the same three types of ovary maturation and spawning (Marza 1938 cit. from Wallace and Selman 1981) though combinations of maturation and spawning patterns could be different between fish and cephalopods. Also, the presence/absence of growth between spawning

Table 1 A generalised classification of teleost fish and cephalopod maturation and spawning patterns

Strategy	Diagnosis	Examples	
		Fish	Squid
Synchronous vitellogenesis and simultaneous terminal spawning	All oocytes, once formed, grow and ovulate in unison; no replenishment of the oocyte fund takes place	*Oncorhynchus* spp.	Deepwater spawning squids and most of the Octopodidae
Group-synchronous vitellogenesis and polycyclic batch spawning	At least two groups of oocytes can be distinguished: a fairly synchronous group of large oocytes (batch) and more heterogenous group of smaller protoplasmic oocytes from which the batch is recruited	Most of teleost fish	*Nautilus* spp.
Asynchronous (or quasi-asynchronous) vitellogenesis and batch spawning	Oocytes of all stages are present in the ovary. Batches, if present, are usually not well defined, and ovulate rather asynchronously. In those species, the batches could be accumulated either in oviducts or in the coelom	Not found	Ommastrephidae, Loliginidae and Enoploteuthidae, and cuttlefishes Sepiidae, peagic octopod superfamily Argonautoidea, and some benthic species of Octopodidae (e.g. *O. chierchiae*)
Asynchronous vitellogenesis and intermittent spawning with individual egg release	Oocytes of all stages are present without dominant populations. Eggs are laid one-by-one	Killifish, *Fundulus heteroclytus*, pipe fishes, and seahorses	Cirrata

events become important in cephalopods requiring a separate cephalopod reproductive strategies classification (Rocha et al. 2001). A general classification for fish and squid combined is given in Table 1.

In spite of differences in the occurrence of the different types of oogenesis, a common trait is that both taxa do not have a proper larval stage and early stages of cephalopods larvae are ecologically close to those of teleost fish, and not to those of other mollusks (Nesis 1979). Both teleost fish and cephalopods produce eggs of similar size ranges and have similar ranges of fecundity. Such a similarity could be explained by the fact that early stages of ontogenesis of both cephalopods and fish inhabit the same set of habitats with certain ranges of egg and larval mortality sharing the same adaptive zone.

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