ORIGINAL PAPER

# Reproductive strategies in female polar and deep-sea bobtail squid genera *Rossia* and *Neorossia* (Cephalopoda: Sepiolidae)

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**Abstract** Female reproductive features have been investigated in five polar and deep-sea bobtail squid genera *Rossia* and *Neorossia* (*R. macrosoma*, *R. moelleri*, *R. pacifica*, *N.c. caroli* and *N.c. jeannae*). These species are characterized by asynchronous ovary maturation, very large eggs (>10% ML), fecundity of several hundred oocytes, very high reproductive output, and continuous spawning with low batch fecundity. This adaptive complex of reproductive traits evolved in these small animals as an optimum strategy for polar and deep-water habitats.

**Keywords** *Neorossia* · *Rossia* · Spawning ·
Reproduction · Polar · Deep-sea

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## Introduction

Cuttlefish of the family Sepiolidae, commonly known as "bobtail squid", inhabit tropical, temperate and polar waters of all oceans. The family has three subfamilies including the oceanic and pelagic Heteroteuthinae and the benthic Sepiolinae and Rossiinae which inhabit continental shelf and slope waters. Sepiolinae are common on tropical and temperate shelves and on the upper part of the continental slope (down to depths of about 400 m). Rossiinae are generally associated with cold water. They occur on polar shelves and in deep seas between 200 and 2,000 m, usually deeper than 500 m, though not south of the Antarctic Polar Front (Reid and Jereb 2005).

Because species belonging to the Sepiolinae occur in relatively shallow waters, are easy to catch and are reared quite successfully in aquaria, reproduction in sepiolids is best studied in this subfamily (Arnold et al. 1972; Boletzky 1975, 1983a, b; Bergstrom and Summers 1983; Gabel-Deickert 1995; Yau and Boyle 1996; Bello and Deickert 2003; Salman and Önsoy 2004). Fecundity in Sepiolinae is generally several hundred eggs and the number of eggs laid at a spawning event (batch size) varies from 1 to 176. Egg length is 2–4 mm and spawning is continuous with decreasing intensity, though some individual females in captivity have been reported as single spawners (Gabel-Deickert 1995). A similar continuous spawning pattern was found in Heteroteuthinae (Hoving et al. 2008).

In contrast, little is known about the female reproductive biology of Rossiinae, except that they produce relatively large eggs (egg length 7–12 mm) (Okutani and Sasaki 2007). One female *Rossia pacifica* was kept in captivity and laid two batches of 50 and 35 eggs each. The laying of the first and the second batch was separated by an interval of 3 weeks and the female died after the last eggs were

spawned (Summers 1985). Pre-spawning large females of this species may have 50–200 well-developed oocytes in the ovary (Summers and Colvin 1989; Shevtsov and Mokrin 2000). The western Mediterranean mature female *Rossia macrosoma* may have 120–150 large yolk oocytes in their ovaries and ripe eggs are laid in clusters of 30–40 (Gabel-Deickert 1995; Reid and Jereb 2005). Data on the ovulation pattern and actual fecundity are absent for both the species, because smaller eggs were never taken into consideration during fecundity analysis. Recent research on the female reproductive biology of *Neorossia caroli* from the western Mediterranean (Cuccu et al. 2007) demonstrated that mature females have between 24 and 611 oocytes while more than 100–200 oocytes are present in immature bobtail squid. An egg clutch deposited on a piece of hard substrate consisted of 13 eggs. Following the classification proposed by Rocha et al. (2001) the spawning pattern of *N. caroli* is continuous. To increase the knowledge of reproductive strategies within the family Sepiolidae this paper provides information on the fecundity, ovary development, female reproductive strategies and spawning patterns of five Rossiinae species and subspecies (genera *Rossia* and *Neorossia*).

## Materials and methods

A total of 64 females belonging to five species and subspecies of the polar and deep-sea bobtail squid genera *Rossia* and *Neorossia* were collected in the different geographical areas (Fig. 1; Table 1). From the North Atlantic, we examined *Rossia macrosoma* (delle Chiaje, 1830) and *Rossia moelleri* Steenstrup, 1856. *R. macrosoma* inhabits waters from East Greenland and Iceland to the Mediterranean Sea and Northwest Africa and occurs at depths between 30 and 900 m (Reid and Jereb 2005). *R. moelleri* occurs in the

North Atlantic and the Arctic Ocean northward to 82°N from northeast Canada to the Laptev Sea between 17 and 250 m (Nesis 2001; Reid and Jereb 2005). *Rossia pacifica* Berry, 1911 inhabits the North Pacific from Japan and California to the Bering Strait between 30 and 1,350 m (Nesis 1989; Reid and Jereb 2005). The species *Neorossia caroli* (Joubin, 1902) is the most bathyal sepiolid and is also the most common cephalopod between 1,000 and 2,000 m (Reid and Jereb 2005). The species consists of two subspecies (Reid and Jereb 2005): *N.c. caroli* (Joubin, 1902) that inhabits the East Atlantic from Iceland to Namibia from 40 to 1,744 m; and *N.c. jeannae* (Nesis et al., 2001) which occurs around the Falkland Islands between 474 and 670 m.

An egg mass of *R. pacifica* was sampled onboard RV "Kayo Maru" on 24 November 1997. The vessel was operating a bottom trawl between 61°06′–61°34′N and 179°15′–178°12′E (depth range 210–280 m).

Captured animals were preserved whole in 6–10% formalin. In preserved squid, the dorsal mantle length (ML) was measured to be within 1 mm, and total body mass (BM) was estimated to be within 0.1 g. Animals were assigned as immature, maturing, mature and spent animals (Table 2). The ovary and accessory glands were weighed to be within 0.0001 g. All oocytes from the ovary and the oviduct were separately counted and measured along the major axis to the nearest 0.1 mm. The gonadosomatic index (GSI) was calculated as a ratio between the gonad mass (GM) to the BM (GSI = (GM/BM) × 100) and the reproductive system index (RSI), as a ratio between reproductive system mass (RSM), and BM (RSI = (RSM/BM) × 100) (Bakhayokho 1983; Gabr et al. 1998). Total number of oocytes in the ovary and ripe eggs in oviduct was considered to be the potential fecundity (PF). The number of follicular sheaths together with PF, minus the number of ovulated ripe eggs was assumed to represent maximum potential fecundity, MPF. Relative fecundity (RF) was



**Fig. 1** Position of sampling sites of *R. moelleri* (*diamonds*), *Rossia macrosoma* and *Neorossia c.caroli* (*circles*), *Rossia pacifica* (*squares*) and *N.c. jeannae* (*crosses*)
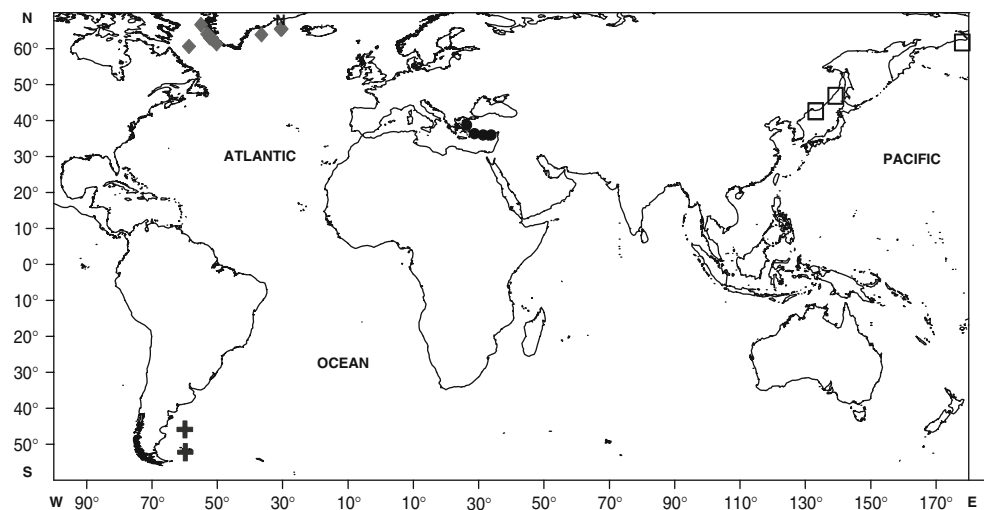
**Table 1** Locality data for female *Rossia* spp and *Neorossia* spp examined

| Species | N | Date | Mantle length, ML (mm) | Body mass, BM (g) | Vessel | Locality | Position | Fishing gear | Depth (m) |
|---|---|---|---|---|---|---|---|---|---|
| *Rossia macrosoma* | 21 | II–X 1991–1993 | 24–59 | 5.9–89.4 | RV "Koca Piri Rejs" | Aegen and Mediterranean Seas | 34°26'–40°28'N 24°50'–34°51'E | Bottom trawl | 180–340 |
| *R. moelleri* | 11 | II–XI 2003–2006 | 26–44 | 6.6–38.7 | RV "Walter Hervig" | Greenland Arctic | 61°38'–66°40'N 30°34'–58°31'W | Bottom trawl | 91–400 |
| *R. pacifica* | 5 | VIII–XII 1995–1196 | 61–86 | 90–195 | FV "Kayo Maru" | Bering Sea | 60°40'–61°45'N 178°E–179°45'W | Bottom trawl | 176–455 |
| – | 2 | VIII–X 1995 | 25–41 | 9.7–28.2 | RV "TINRO" | Sea of Japan | 42°37'–46°56'N 133°12'–139°15'E | Pelagic trawl | 200 and 200 |
| *Neorossia caroli caroli* | 3 | VII–X 1992 | 27–36 | 9.5–19.2 | RV "Koca Piri Rejs" | Aegen and Mediterranean Seas | 38°04'–39°50'N 24°35'–25°58'E | Bottom trawl | 450–480 |
| *N. caroli jeannae* | 22 | IX–XI 2006–2007 | 25–63 | 6.6–163.3 | FVs "Antonio Nores", "Manuel Angel Nores" | Subantarctic waters off the Falkland Islands | 45°18'–59°56'S 52°15'–59°46'W | Bottom trawl | 733–845 |

calculated as the ratio of MPF to BM (RF = MPF/BM). Index of potential reproductive investment (PRI) was calculated as the product of RF to an individual egg weight.

## Results

*Rossia macrosoma.* The gonad maturation is asynchronous with small oocytes predominating at all stages of maturation and maturity, although the number of large eggs becomes relatively high in the short period prior the first ovulation (Fig. 2). Presence/absence of copulation traces were not recorded.

Potential fecundity in immature and maturing females was 382–837 (Fig. 3; Table 3). Mean ripe egg length increased with female length (Fig. 4). The PF in two advanced spawning females was only 106–155 eggs indicating that most of it (probably 200–700 eggs) had already been released during spawning and the empty follicular sheaths had degenerated.

*Rossia moelleri.* As in the previous species, the gonad maturation was asynchronous with small oocytes predominant at all stages of maturation and maturity. Oocyte growth and subsequent ovulation proceed independently with no defined batches. Eggs accumulate in the oviduct until an egg mass is released. Females did not have a bursa copulatrix. The number of implanted spermatangia in females ranged from 6 to 21 (mean $14 \pm 5$; $n = 10$). Spermatangia were mainly implanted on the left side of the females' bodies, where the distal oviduct opened (Hoving et al. in prep).

The PF of prespawning females (no empty follicles found) is about 200–400 oocytes (Fig. 3). In contrast to the relatively high potential fecundity, the maximum number of ripe eggs in oviducts was 18. Ripe egg length was similar between females of different body size (Fig. 4). PRI was 1.8–7.9 (mean 3.58). Low values of PRI were found in large mature females with low fecundity that probably released most of their eggs prior the capture. This suggests that the total weight of female generative production would exceed its own weight at least by a factor of 3–4.

*Rossia pacifica.* Gonad maturation was asynchronous. Modal oocyte length increases at approaching maturity. The PF is about 300–1,300 oocytes (Fig. 3). In mature females there were up to 40–60 ripe eggs in the ovarian coelom and oviduct combined. PRI was about 0.6–1.0.

Copulation traces were found in all four mature females and one advanced maturing animal of 72 mm ML. The number of spermatangia varied from 4 to 13. Spermatangia were attached on/at the oviducal gland and on the funnel. After being attached, sperm penetrates deep into tissues forming very visible white patches under the skin extending to the surface layers of the oviducal gland.

**Table 2** Maturity scale for sepiolid squid family Rossiinae

| Stage | Female | Male |
|---|---|---|
| Immature | Accessory nidamental glands (ANG) are not visible by the naked eye. No large yolk eggs in ovary | No spermatophores. No sperm in spermaduct |
| Maturing | ANG well seen, white-yellowish, large yolk eggs in ovary, no ripe eggs in oviduct | There is sperm in spermaduct. Usually a few spermatophores in the Needham sac. Normal testis |
| Mature | ANG reddish. Reproductive system of a normal "adult" size, a few ripe eggs in oviduct | Needham sac is densely packed with spermatophores |
| Spent | Just a few eggs left in the reproductive system. Ovary shrank | Testis degenerated. A few residual spermatophores left |

**Fig. 2** Oocyte length–frequencies in *R. macrosoma*
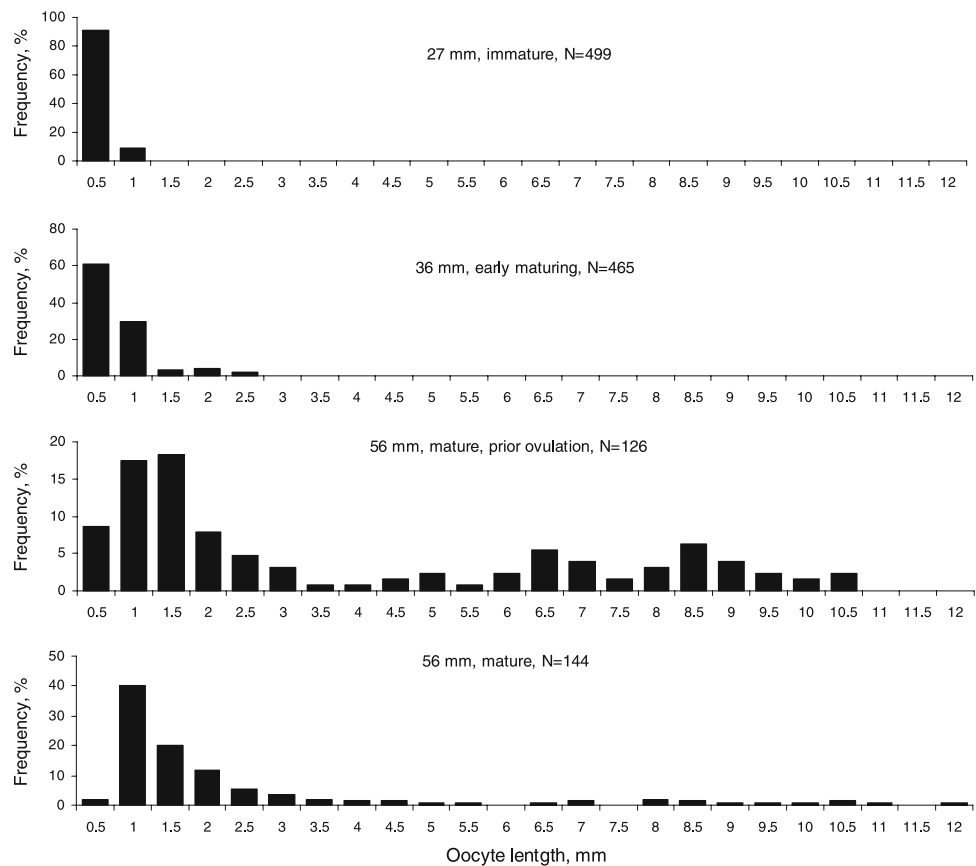


An egg mass was found to be laid inside a misshaped iron tray that fishing vessels use to freeze catch (73 × 38 × 6 cm). The egg mass occupied a surface of about 30 × 40 cm and consisted of exactly 700 whitish eggs including 119 empty shells, among which 15 were unambiguously hatched, whereas the remaining 104 could be either the remains of hatched eggs or damaged at hauling. Embryos were immersed into translucent gel and identical as those described by Nesis (1989) and Shevtsov et al. (2000) for *R. pacifica*. Eggs were attached in 2–3 layers in the center of the egg mass, and in a single layer toward the edges. Capsule size was 17–20 × 14–15 mm. Embryos were at

different stages of development (scale of Arnold et al. 1972) and their size increased with developmental stage (Table 4).

*Nerossia caroli caroli.* Ovaries of this species exhibited the same pattern of maturation as in the genus *Rossia*, though the egg size was smaller and the relative fecundity was higher (Table 3). The only mature female had nine eggs in the oviduct and exactly nine empty follicles which allows the assumption it had not spawned before.

*Neorossia caroli jeannae.* Ovary maturation and ovulation in *N.c. jeannae* is similar to the other subspecies with protoplasmic oocytes predominating during the entire ontogenesis. The modal length of these small oocytes slightly
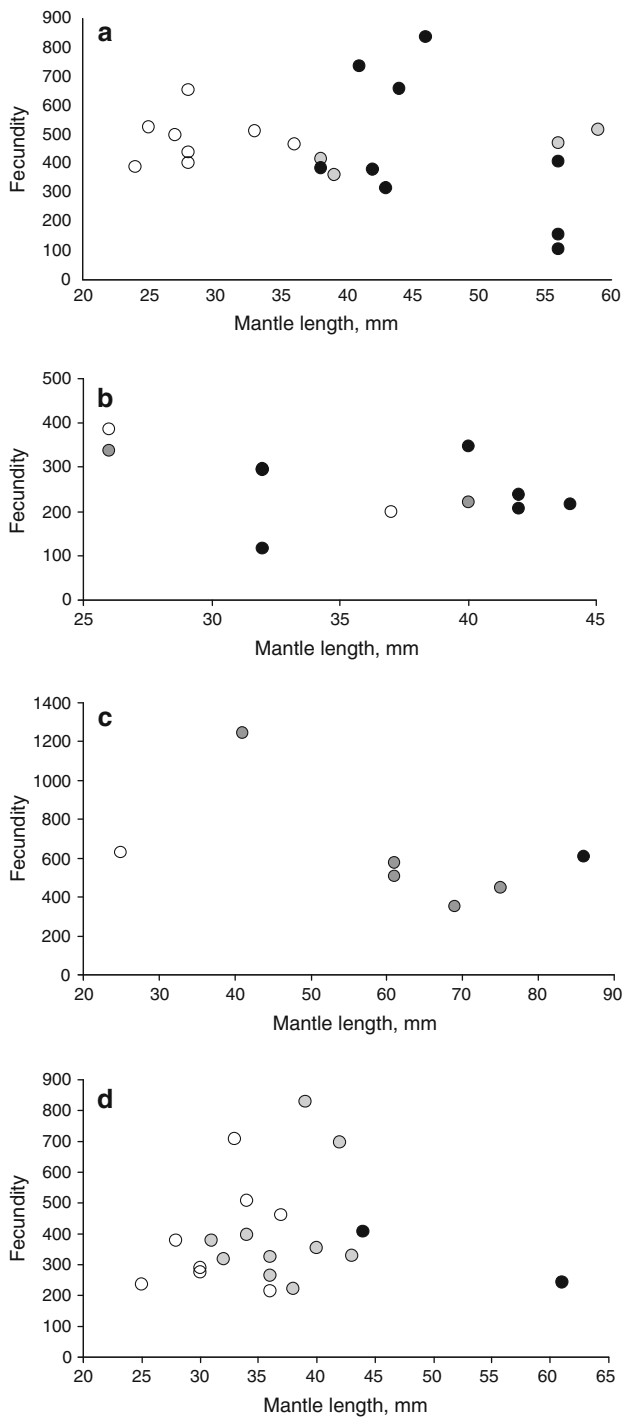
**Fig. 3** Fecundity of bobtail squid genera *Rossia* and *Neorossia* (**a** *R. macrosoma*, **b** *R. moelleri*, **c** *R. pacifica*, **d** *N. caroli jeannae*); *Empty circles* immature, *gray circles* maturing, *black circles* mature

increases in mature animals. A smaller female had only one ripe egg in the oviduct and presumably had not spawned before. The larger female had 17 ripe eggs in the oviduct and 2 more in coelomic cavity, as well as 49 empty follicles in the ovary, which indicates previous egg release. Egg size was similar between females of the different ML (Fig. 4).

## Discussion

Gonad maturation in bobtail squid subfamily Rossiinae is asynchronous as in most coleoid cephalopods from the different taxonomical, ecological and zoogeographical groups (Rocha et al. 2001; Nigmatullin 2002). Particularities of oocyte length frequency distributions indicate continuous spawning as in representatives of subfamilies Heteroteuthinae and Sepiolinae (Gabel-Deickert 1995; Hoving et al. 2008).

Our data show that the fecundity of all five studied representatives of the subfamily can be several hundred eggs, which is much higher than previously estimated by yolk egg counts in *R. macrosoma* and *R. pacifica* (review: Reid and Jereb, 2005) but in agreement with the data on *N. caroli caroli* from the West Mediterranean (Cuccu et al. 2007), assuming that some mature females with very low fecundity (24–169 eggs) from that study probably released a significant amount of mature eggs prior capture.
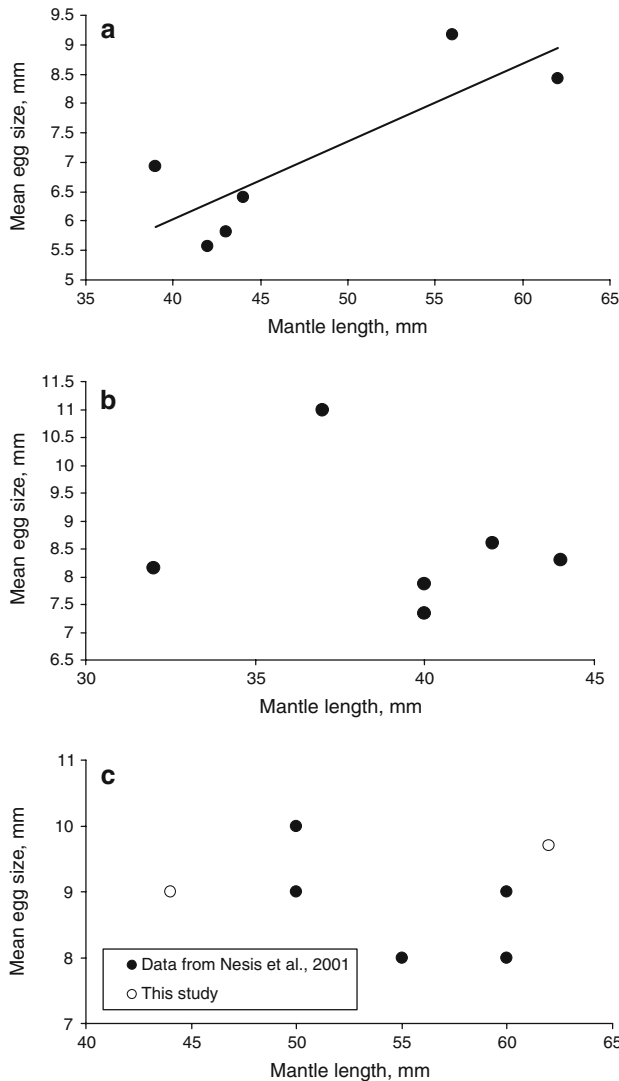
Within species across a wide variety of taxa, offspring size is positively correlated with maternal size (Stearns 1992). In subtropical deep-sea *R. macrosoma,* larger females invest more energy into an individual egg. This trend was confirmed for Mediterranean *N. caroli caroli* where a small female (36 mm ML) produced smaller eggs than normal sized females (50–70 mm ML) (Mangold-Wirz 1963; Reid, 1991). An increase of egg length/weight with female size is also common in other warm-water cuttlefish, such as the subtropical shelf *Sepia officinalis* (Boletzky 1983; Laptikhovsky et al. 2003). This trend is less obvious in individuals with eggs of intermediate size, like *Loligo gahi* (Laptikhovsky et al. 2002) and negligible in cephalopods with small eggs like ommastrephid and enoploteuthid squid. It is consistent with a general trend that the highest level of within-population variation in offspring size is observed in large-egged species, particularly in direct developers that display a fourfold difference between the largest and smallest offspring in a population. It possibly occurs because offspring size–performance relationships are likely to be stronger and more consistent in direct developers (Marshall and Keough 2008), which have no larval stage that can be affected unpredictably by environmental variability. In small-egged species with planktonic larvae or paralarvae, there is less advantage for larger females to invest more energy into an individual offspring at costs to fecundity because the risk of sudden mass mortality at early stages is too high.

Although egg length in the polar and subpolar sepiolids *N. caroli jeannae* or *R. moelleri*, is large and similar to that of deep-sea sepiolids, there is no positive correlation between body size and egg length. This suggests that in spite of similarities between the cold-water environments of both polar and deep seas, where hydrobionts produce

**Table 3** Reproductive parameters in mature bobtail squids genera *Rossia* and *Neorossia*: min–max (mean)

| Species | ML | BM | Egg length (mm) | Egg weight (g) | PF* | RF* | GSI | RSI |
|---|---|---|---|---|---|---|---|---|
| *Rossia macrosoma* | 24–59 | 5.9–89.4 | 5.6–9.2 | | 382–837 | 4.9–22.1 (12.9) | 6.1–20.2 (10.6) | 9.7–29.4 (17.2) |
| *R. moelleri* | 32–44 | 7.3–26.8 | 7–11 | 0.13–0.27 | 200–385 | 8.0–39.7 (18.2) | 13.8–45.9 (28.5) | 19.1–52.4 (33.7) |
| *R. pacifica* | 69–86 | 110–195 | 7.9–9.1 | 0.18–0.22 | 355–1246 | 3.2–4.8 (3.7) | 7–9 | 18–25 |
| *Neorossia caroli caroli* | 36 | 19.2 | 4.7–6.6 | 0.05 | 551–609 | 38–51 | 3.5 | 8.7 |
| *N. caroli jeannae* | 44–62 | 28.7–163.3 | 8.5–10.6 | 0.28 | 215–827 | 1.8–14.2 | 10.4–10.7 | 14.6–14.8 |

* in prespawning females (including late maturing animals)



**Fig. 4** Egg size in bobtail squid genera *Rossia* and *Neorossia* (**a** *R. macrosoma*, **b** *R. moelleri*, **c** *N. caroli jeannae*)

**Table 4** Egg size at the different stages of embryonic development in *Rossia pacifica* and it's percentage in a random sample (120 eggs)

| Stage | Embryo size (mm) | Percentage in the sample |
|---|---|---|
| <11 | 7.0–8.0 × 6.5–7.5 | 25 |
| 11–18 | 7.5–8.5 × 7.1–8.2 | 18.5 |
| 19–22 | 8.0–8.5 × 7.3–7.7 | 12.5 |
| 23–24 | 8.0–8.7 × 7.2–8.2 | 22 |
| 25–27 | 9.0–9.6 × 8.4–9.2 to 9.8–10.2 × 9.0–9.2 | 22 |

egg size. The egg size becomes more important in polar seas where all females produce similar sized eggs. Also, if competition between siblings is likely then larger, more fecund mothers would be expected to produce larger offspring to compensate for increased levels of competition (Parker and Begon 1986). This hypothesis may be applied to the *Rossia* and *Neorossia* genera, because in nutrient-poor deep seas an increase in egg size may reduce mortality among hatchlings. In seasonally very productive polar seas the increase in egg size is apparently less important.

We may conclude that among Sepiolidae, the large sized polar and deep-water bobtail squid subfamily Rossiinae (*Rossia*, *Neorossia*) have generally the same fecundity as the small-sized subtropical and temperate shallow-water bobtail squid subfamily Sepiolinae (*Sepiola*, *Sepietta*, *Euprymna*), as well as the same continuous spawning pattern. However, they are very different in egg length: in Rossiinae eggs are 3–4 times larger (Table 5) and 10–30 times heavier than in Sepiolinae (see: Bergstrom and Summers 1983; Salman and Önsoy 2004). Relative egg length is not so different between subfamilies though Rossiinae produce eggs generally larger than 10% ML whereas Sepiolinae are less than 10%ML with some rare exceptions.

The production of larger eggs is particular to inhabitants of both polar and deep seas (Marshall 1953), and may have ensured the evolutionary success of Rossiinae in these waters. Small–sized Sepiolinae with also relatively small eggs occupy the "sepiolid" niche on shelves and on the upper part of slopes of tropical and temperate latitudes.

relatively large eggs (Marshall 1953), reproductive strategies are still different. In subtropical continental slope sepiolid hatchlings from relatively small eggs may have higher chances of survival and females maximize their reproductive effort by increasing egg numbers rather than

**Table 5** Absolute and relative egg size and fecundity in some Sepiolid cuttlefish

| Species | Egg size (mm) | Fecundity | Source | Maximum female size (ML) (Reid and Jereb 2005) | Relative egg size (% ML) |
|---|---|---|---|---|---|
| Rossiinae | | | | | |
| *Neorossia leptodons* | 12 | | Reid 1991 | 77.5 | 15.1 |
| *Neorossia c. caroli* | 9.9 | >115; up to 611 in mature | Reid 1991; Cuccu et al. 2007 | 83 | 11.9 |
| *N c. jeannae* | 8.5–10.6 | 215–827 | This study | | |
| *Rossia australis* | 10 | | Reid 1991 | 63 | 15.1 |
| *Rossia moelleri* | 7–8.7 | 200–385 | This study | 70* | 10.0–12.4 |
| *Rossia macrosoma* | 6–9 | 382–837 | Mangold-Wirz 1963; This study | 85 | 8.2–9.4 |
| *Rossia pacifica* | 7.9–9.1 | 355–1,246 | This study | 90 | 8.9–10.0 |
| *Semirossia patagonica* | 3.4–5.0 | 527–766 | Önsoy et al. (2008) | 35 | 9.7–14.3 |
| Sepiolinae | | | | | |
| *Rondeletiola minor* | 1.4–1.8 | | Salman and Katagan 1996 | 23 | 6.0–7.8 |
| *Sepietta oweniana* | 1.4–3.4 | 719–1,613 | Salman 1998; Bello and Deickert 2003 | 40 | 3.5–8.5 |
| *S. neglecta* | 1.4–2.8 | | Lefkaditou and Kaspiris 1998 | 33 | 4.2–8.4 |
| *Euprymna scolopes* | 2 | | Arnold et al. 1972 | 30 | 6.7 |
| *Sepiola atlantica* | 2.5–3 | | Yau and Boyle 1996 | 21 | 11.9–14.3 |
| *S. affinis* | 3.2 | 25–349** | Boletzky 1975; Gabel – Deickert 1995 | 25 | 12.8 |
| *S. intermedia* | 2.2–2.9 | 47–407** | Gabel – Deickert 1995; Salman and Önsoy 2004 | 28 | 7.9–10.4 |
| *S. ligulata* | 2.6 | | Naef 1928 | 25 | 10.4 |
| *S. robusta* | 2.2–2.4 | 117–245 | Boletzky 1983; Salman and Önsoy 2004 | 28 | 7.9–8.6 |
| *S. rondeletii* | 2.5–3 | 302** | Mangold-Wirz, 1963; Gabel – Deickert, 1995 | 60 | 4.2–5 |
| *S. steenstrupiana* | 2.8–4.8 | 163–191 | Salman and Önsoy 2004 | 30 | 9.3–16.0 |

* Nesis 2001; ** actual fecundity in captivity

Both groups may have inherited the same family–specific ancestral range of potential fecundity. This range is determined by gonial activity at the early stages of development. Large–sized Rossiinae were able to invest more energy into an individual egg as a result of evolving to larger sizes. It is possible then, that the ensuing evolution of their reproductive strategies tended towards even larger eggs. This trend may have been partially a result of the relative stability of deep-sea and polar environments supporting K-selection. In contrast to this, ommastrephid squid during their ecological expansion into the open ocean evolved higher fecundity and smaller eggs, due perhaps to the high environmental instability of the high seas and unpredictability of mortality at early stages of development (Nigmatullin and Laptikhovsky 1994).

A dwarf *Semirossia patagonica* in the southwest Atlantic shelf evolved as an ecological sibling of Sepiolinae that are absent in this region (Önsoy et al. 2008), and its eggs, though relatively small for Rossiinae, are still larger that in any Sepiolinae species (Table 5).

Reproductive output in Rossiinae is enormous. The index of potential reproductive investment in both myopsid and oegopsid squid is approximately an order of magnitude lower: it is 0.25–0.5 in squid genus *Illex* (Laptikhovsky and Nigmatullin 1993), 0.3 – 1.0 in *Sthenoteuthis pteropus* (Laptikhovsky and Nigmatullin 2005), 0.7–1.7 in *Abralia veranyi* (Laptikhovsky 1999), 0.29–0.71 in *Loligo vulgaris* (Laptikhovsky 2000), and 0.20–1.14 in *Loligo gahi* (Laptikhovsky et al. 2002). The first three of these squid spawn their eggs pelagically while *Loligo* attaches eggs to substrate.

*Rossia* produce large eggs with rigid egg shells, which do not decay after hatching nor are they colonized by sessile organisms (Boletzky 1994). The shells protect the eggs effectively against predators. The production of large eggs and extraordinary egg protection are beneficial during the long embryonic development, which lasts from 4.5 to more than 9 months in *Rossia pacifica* (Summers and Colvin 1989).

Deep seas and polar Rossiinae are continuous spawners like their warm-water relatives of the subfamily Sepiolinae. We observed that eggs are released in numerous batches and are often added to batches previously laid by other

females. Because of this, embryos at different stages of development could be found within a single large egg mass. This also occurs in Sepiolinae, in which polyspecific egg masses (even *Sepietta + Rossia*) are not uncommon (Deickert and Bello 2005). It is possible that egg masses (even of a different species) could be a visual stimulus to spawn as reported in cuttlefish (Mangold-Wirz 1963) and loliginid squid (Arnold 1962; Larcombe and Russel 1971).

The main reproductive strategy traits of Rossiniae include asynchronous ovary maturation, very large eggs (>10% ML), fecundity of several hundred oocytes and high reproductive output, continuous spawning with low batch fecundity, reliable protection of embryos by hard shells as well as often hiding egg masses in sheltered places. This adaptive complex of reproductive traits evolved in these small animals as an optimum strategy for polar and deep-water habitats.

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