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Reproductive biology and ecology of the boreoatlantic armhook squid *Gonatus fabricii* (Cephalopoda: Gonatidae)

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ABSTRACT

The squid *Gonatus fabricii* (Lichtenstein, 1818) is the most abundant pelagic cephalopod in the Arctic and the only squid to spend all of its life cycle in this region. Despite being highly abundant, its reproductive biology remains poorly known, and data on large maturing and mature specimens are especially rare. This study, based on extensive material (51 large specimens and >35,000 specimens in all), fills major gaps in the knowledge of the reproductive biology and ecology of *G. fabricii*. The fecundity of females ranged from 8,862 to 16,200 oocytes, with mature and late maturing specimens having between 8,862 to *c.* 10,000 and 11,402 oocytes, respectively. Oogenesis was synchronous, and oocyte resorption was observed; resorbed oocytes constituted up to 23.5% of fecundity. Between two to five ripe oocytes were observed, and these were 4.0–5.5 mm in diameter (maximum dimension). Males possessed between 77 and 257 spermatophores (length = 5.8–10.8 mm). Spermatophores were characterized by a cement body with well-developed collar and discs at the oral end, an ejaculatory apparatus longer than the cement body and the lack of a tapered, sharp tip to the cement body. Spermatophore size showed a uniform increase in relation to increasing male size. In newer spermatophores, the length, width and volume of the seminal reservoir also increased. Females possessed between 62 and 84 spermatangia (length = 1.8–2.6 mm); the spermatangia were present on the buccal membranes and lacked special attachment structures. Seminal receptacles were not found on the buccal membranes of females. Our findings are consistent with the hypothesis of geographically restricted spawning in *G. fabricii*. The study found evidence for one new breeding area in south-eastern Greenland. No differences in sizes at maturity were found between the breeding areas. Such geographically localized reproduction is relatively common in non-deep-water squids, but is much less common in deep-water squids. Localized reproduction may be especially important for *G. fabricii* because increased food availability in the epipelagic layers would likely increase the survival of epipelagic juveniles, with surface currents potentially aiding in their dispersal.

INTRODUCTION

The squid *Gonatus fabricii* (Lichtenstein, 1818) is by far the most abundant cephalopod species in the Arctic (Bjørke, 2001; Golikov, Sabirov & Lubin, 2017). This species is the only pelagic decapodiform cephalopod that is confined to the Arctic for the entirety of its life cycle (Kristensen, 1981, 1984; Nesis, 1987; Bjørke & Hansen, 1996; Bjørke, Hansen & Sundt, 1997; Arkhipkin & Bjørke, 1999; Golikov *et al*., 2013b; Xavier *et al*., 2018). Despite the abundance of this species, our knowledge of its reproductive biology is largely limited to data on the growth dynamics of the reproductive system during maturation (Arkhipkin & Bjørke, 1999). *Gonatus fabricii* has a well-documented ontogenetic downward migration from epipelagic (<100 m depth) to bathypelagic (>800 m depth) layers (Kristensen, 1981, 1984; Bjørke, 2001). Deep-living maturing and mature specimens, with a mantle length (ML) >200 mm in females

and >130 mm in males, are captured far less often than are shallow-living immature ones, which are numerous in trawls (Arkhipkin & Bjørke, 1999; Golikov, Sabirov & Lubin, 2012). Bjørke & Hansen (1996) presented data for all large maturing and mature specimens that had been caught up to and during 1995. More specimens have been caught since then (Bjørke *et al.*, 1997; Arkhipkin & Bjørke, 1999; Vecchione & Pohle, 2002; Shea *et al.* 2017). Current knowledge of the reproductive biology of *G. fabricii* consists of a few, scattered details, such as the length of individual spermatophores (6–10 mm) (Kristensen, 1984; Bjørke & Hansen, 1996), the number (varies from a 'few' to 70) and length (*c.* 2.5 mm) of spermatangia present on the buccal membranes of females (Kristensen, 1981; Bjørke & Hansen, 1996) and estimates of individual female fecundity (*c.* 10,000 oocytes; Kristensen, 1981). Although males remain active during maturation, females undergo gelatinous degeneration, becoming incapable of active movement and feeding, as they transform into flotation devices for the negatively buoyant eggs that they brood (Kristensen, 1981; Bjørke & Hansen, 1996; Bjørke *et al.*, 1997; Arkhipkin & Bjørke, 1999). Underwater observations of other gonatid females in this state indicate that they remain alive (Seibel, Hochberg & Carlini, 2000; Seibel, Robison & Haddock, 2005). Current knowledge suggests that *G. fabricii* reproduces in only a few specific geographic areas (e.g. the northeastern part of the Greenland Sea, the border between the Greenland and Norwegian Seas, the northeastern and southernmost parts of the Norwegian Sea and the southwestern part of the Davis Strait), but this needs to be clarified (Bjørke, 1995, 2001; Bjørke & Gjøsaeter, 1998). Some authors have indicated that this species may reproduce throughout its distributional range (Nesis, 1965, 1971, 1987).

Recent surveys of the coastal waters around Greenland, Baffin Bay/Davis Strait, the Barents Sea and adjacent areas have yielded 51 squid exceeding the minimum mature size. Using these specimens, we fill major gaps in the current understanding of the reproductive biology and ecology of *G. fabricii*, the only squid reproducing in the Arctic.

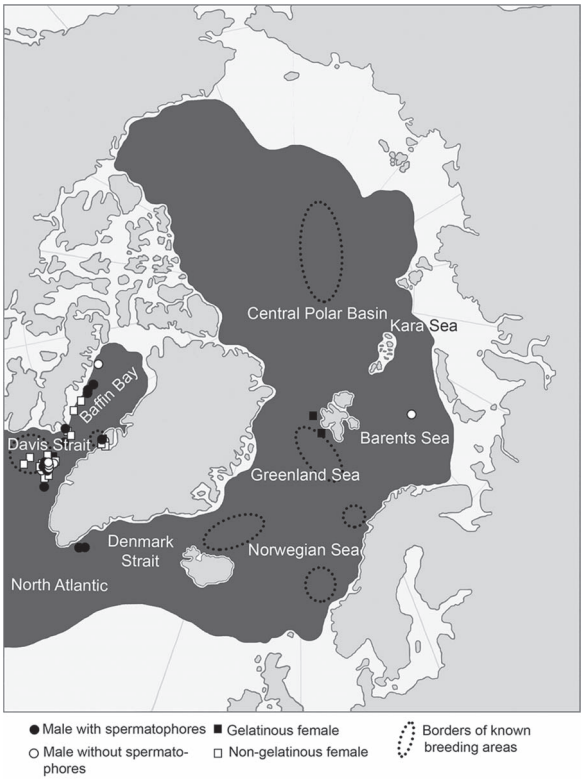

Figure 1. Localities of *Gonatus fabricii* sampled in the study and breeding areas known prior to our study. The limits of the breeding areas are based on the following: Nesis (1971, 1987); Young (1973); Kristensen (1984); Bjørke (1995, 2001); Bjørke & Hansen (1996); Bjørke *et al.* (1997); Bjørke & Gjøsaeter (1998); Arkhipkin & Bjørke (1999); Vecchione & Pohle (2002); Zumholz & Frandsen (2006); and Gardiner & Dick (2010). The area south of Nova Scotia is not shown.

MATERIAL AND METHODS

Specimens of *Gonatus fabricii* were collected on shrimp-fish trawl surveys in the Arctic region. The surveys were conducted from May–October in the period 2005–2016, in depths ranging from sea level to 1514 m (Fig. 1). The areas sampled, along with corresponding details of timing and institutions involved, are as follows: (1) Barents Sea and surroundings from 4°E to 77°E and as far as 83°N (sampled in 2005–2016 by the Polar Research Institute of Marine Fisheries and Oceanography and Institute of Marine Research); (2) coastal waters around Greenland, as far as 73°N on the western side and 67°N on the eastern side (sampled in 2014–2016 by the Greenland Institute of Natural Resources); and (3) Canadian side of the Davis Strait and the Baffin Bay, from 61°N to 73°N (sampled in 2016 by Fisheries and Oceans Canada).

Using Alfredo and Cosmos trawls in Greenland and Campelen-1800 bottom shrimp trawls in the Barents Sea and adjacent areas, a total of 7,300 stations were sampled. Collected squid specimens were fixed in 6% formalin solution while still at sea. All squid exceeding the minimum size of mature *G. fabricii* were used in this study, that is males with a ML > 160 mm (Arkhipkin & Bjørke, 1999) and females with a ML > 200 mm (Bjørke & Hansen, 1996; Arkhipkin & Bjørke, 1999). In total, 51 specimens from 38 stations met these size criteria (Table 1). Overall, >35,000 specimens, which did not meet these criteria, were sampled in our study area. The localities from which mature animals were collected are shown in Figure 1.

After preservation, ML and total weight were recorded for all specimens. The sex and maturity stage were identified for each specimen, and an analysis of the reproductive system was carried out. Maturity stages (m. st.) were assigned using the scale based on Sauer & Lipinski (1990), Nigmatullin, Laptikhovsky & Sabirov (1996) and Nigmatullin, Sabirov & Zalygalin (2003) for squids. The maturity stages are as follows: 0 m. st., juvenile; I m. st., early immature; II m. st., late immature; III m. st., early maturing; IV m. st., late maturing; V_1 m. st., pre-mature; V_2 m. st., mature; V_3 m. st., sub-spent; and VI m. st., spent. Finally, the reproductive system and body condition (the latter in females only) were described. The total number of oocytes in the ovary, oocyte phase distribution (i.e. previtellogenic, early vitellogenic, midvitellogenic, late vitellogenic and ripe, as determined by visual analysis and measurements) and the proportion of oocytes undergoing resorption were assessed using five subsamples (each consisting of 5–8% of the total number of oocytes) from each ovary. Oocyte diameter (OD) was measured for all subsamples. All ripe or late vitellogenic oocytes in the ovary were measured. For oval-shaped oocytes, OD was considered to be equivalent to the maximum length.

While we largely followed Nigmatullin *et al.*'s (2003) terminology for spermatophore morphology, we used the term 'ejaculatory apparatus' instead of 'ejaculatory tube' and the term 'tubular extension' for the appropriate part of the cement body (Hoving, Lipinski & Videler, 2008; Marian & Domaneschi 2012). The total number of spermatophores was counted and the length of individual spermatophores was measured. In eight of the males all the spermatophores were in an ejaculated state; this is probably an artefact of fixation (all of these individuals were collected in 2016). In these specimens, the number of spermatophore heads was taken to represent the total number of spermatophores. From each of four males with intact spermatophores, 56 randomly sampled intact spermatophores were extracted from different parts of the spermatophoric sac (Fig. 2). The following details were documented

Table 1. Studied specimens of *Gonatus fabricii*.

Sex and mating status	Specimen code	Location	Depth (m)	ML (mm)	Weight (g)	Maturity stage
Females without	6–19	SDS	849	194	158	II (immature)
spermatangia	1–114–6	NEDS	507	192	130	
	6–77	SDS	1184	228	183	III (maturing)
	8–122		876	232	202	
	6–26–2		692	239	198	
	6–31		810	239	145	
	6–51		1121	247	207	
	6–56		1443	249	239	
	6–75		1105	249	164	
	8–170		956	306	342	
	1–113	NEDS	1368	226	164	
	1–114–8		507	226	166	
	1–114–9		507	236	160	
	8–11	NWDS	1358	238	239	
	8–72		1237	244	320	
	8–2		1304	247	264	
	8–55		665	257	228	
	6–26–1	**SDS**	**692**	**225**	**212**	**IV (maturing)**
Females with	**248–2012**	**NEGS**	**1229**	**215**	**273**	
spermatangia	**31–2011**		**840**	**221**	**209**	**V_2 (mature)**
Male without	178–2016	EBS	348	185	78	III (maturing)
spermatophores	6–9	SDS	967	160	82	
	6–34		746	214	191	
	1–102–10	NEDS	490	163	119	
	1–102–6		490	171	103	
	1–115		282	172	114	
	1–102–3		490	213	154	
	1–102–9		490	218	141	
	1–114–4		507	218	135	
	1–114–1		507	219	149	
	1–114–5		507	229	168	
	6–6	SDS	1073	208	134	IV (maturing)
	6–14		877	233	133	
	6–57		1429	261	173	
	1–84	NEDS	368	198	124	
	1–114–2		507	230	233	
	1–102–4		490	241	256	
	1–114–3		507	249	214	
	8–33	SWBB	1326	269	218	
Male with spermatophores	6–5*	SDS	1132	257	228	
	1–102–5**	NEDS	490	236	248	V_1 (pre-mature)
	4–21	NA	1449	178	100	V_2 (mature)
	4–18		1414	285	318	
	8–73	NWDS	957	221	188	
	8–24	SWBB	1102	241	200	
	6–43	SDS	769	232	341	V_3 (sub-spent)
	8–125		876	256	223	
	6–69		1264	273	362	
	8–4	NWDS	1148	325	294	
	8–51	SWBB	942	224	191	
	8–28		1330	298	34	

Sampled regions are abbreviated as follows: EBS, eastern Barents Sea; NA, North Atlantic (southeastern Greenland); NEDS, northeastern Davis Strait (Disko Bay); NEGS, northeastern Greenland Sea (Western Spistbergen); NWDS, northwestern Davis Strait; SDS, southern Davis Strait; SWBB, southwestern Baffin Bay. Females with a gelatinous body are indicated in bold font. The presence of only tentative spermatomophores is indicated by a single asterisk and the presence of both tentative and normal spermatophores by two asterisks.

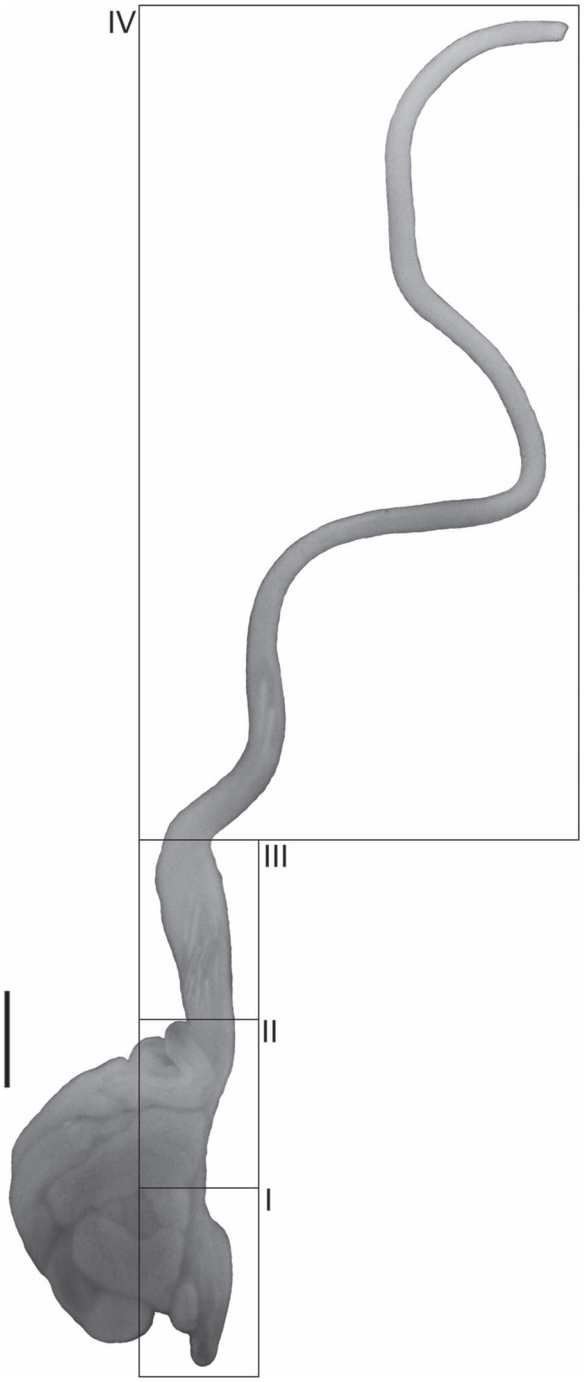

Figure 2. Parts of the spermatophoric sac of *Gonatus fabricii*. These are indicated as follows: I, fundus (proximal part); II, central part (posterior); III, central part (anterior); IV, penis (muscular distal part with the capacity to elongate). Scale bar = 5 mm.

for each of the extracted spermatophores: width of spermatophore, length of head, length of ejaculatory apparatus, length of cement body, length and width of seminal reservoir and length of posterior hollow part of spermatophore (Fig. 3). The volume of the seminal reservoir was calculated using the formula for the volume of a cylinder:

$$V = 3.14 \times i^2 \times \frac{1}{4}$$

where V = seminal reservoir volume (mm^3), i = seminal reservoir width (mm) and l = seminal reservoir length (mm). The total volume of sperm in all spermatophores carried by one male was estimated by multiplying the number of spermatophores in the male by the mean volume estimated from the 56 seminal reservoirs examined. For females, the following details were recorded: total number of spermatangia on the buccal membrane of individual females, total length of individual spermatangia and length of oral and aboral parts of individual spermatatangia (Fig. 4D).

Dispersion analysis was used to assess differences in mean values. Nonparametric Kruskal–Wallis *H* and Mann–Whitney *U* tests (Zar, 2010) were used to compare groups. Regression analysis was used to calculate equations between variables (Zar, 2010). Statistical analyses and other calculations were performed with Statistica v. 10 (Statsoft), PAST v. 3.15 (Hammer, Harper & Ryan, 2001) and MS Excel 2010. Photographic images were taken with an optical microscope AxioImager A2 and digital video microscope Hirox KH-7700; all images were of fixed material. The samples for scanning electron microscopy were carefully washed with distilled water, placed in 70% ethanol, then in 96% ethanol and finally critical point dried before analysis under a Hitachi TM-1000.

RESULTS

Distribution and sizes

The sampling yielded a total of 35,000 small, immature specimens of *Gonatus fabricii*, with between 1 and >150 immatures being sampled per station from nearly all the 7,300 stations. Large specimens were much rarer (Table 1). ML was 160 mm in the smallest maturing male and 215 mm in the smallest maturing female.

Twenty large females were collected. All of these, except the early maturing (III m. st.) individuals from the northeastern part of Davis Strait (Disko Bay), were found at bathyal depths (Table 1). Most of the large females did not show any sign of gelatinous degeneration. Their tentacles were either still present, or were missing, possibly due to damage caused during trawling. The reproductive system of the large females was in late immature (II m. st.; ML = 192–194 mm) or early maturing (III m. st.; ML = 226–306 mm) stages (Fig. 1; Table 1). Females showing gelatinous degeneration were found only in the southern part of Davis Strait and in the northeastern region of the Greenland Sea (Fig. 1); their reproductive system was in late maturing (IV m. st., ML = 215–225 mm) or mature (V_2 m. st., ML = 221 mm) stages (Fig. 1; Table 1). Many early maturing females were larger (up to 1.4×) than the gelatinous ones. The early maturing group showed a 1.5-fold range in size. Judging by the presence of stomach contents, many of these individuals had fed recently and, despite having a ML >300 mm, may have possibly still been growing in size.

Thirty one large males were collected; all, except those from Disko Bay and the eastern Barents Sea, were found at bathyal depths (Table 1). They were maturing (III and IV m. st.) or premature (V_1 m. st.) specimens (Fig. 1; Table 1). Maturing males showed a 1.6-fold range in size and many were larger than some mature (V_2 st.) specimens. However, unlike the females, the largest males were mature or sub-spent (V_3), with these two male groups showing a 1.6-fold and 1.5-fold range in size, respectively. The sub-spent males had the greatest ML.

Female reproductive system and fecundity

The female reproductive system of *G. fabricii* had a typical oegopsid structure, that is a single ovary with paired oviducts, paired oviducal and nidamental glands were present (Fig. 5A, D). Fecundity at II m. st. (n = 2) ranged from 13,750 to 13,932 oocytes. All oocytes observed in the ovaries were similar in size and were at the previtellogenic phase, with OD ranging from 0.15 to 0.30 mm

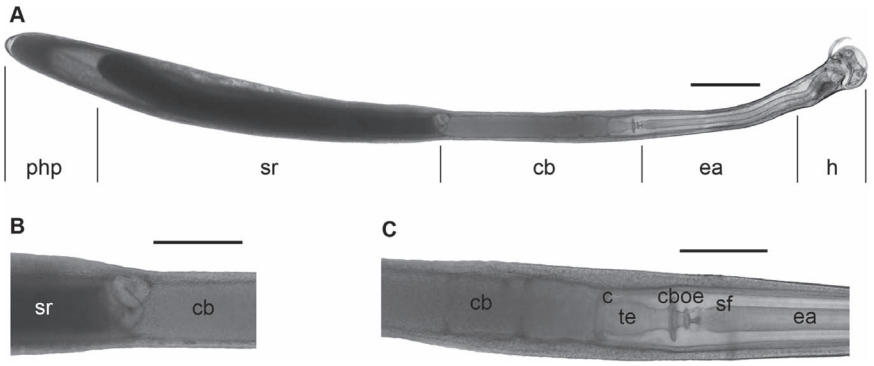

Figure 3. Spermatophores of *Gonatus fabricii*. **A.** Entire spermatophore. **B.** Junction of cement body and seminal reservoir. **C.** Junction of ejaculatory apparatus and cement body. Abbreviations: c, collar; cb, cement body; cboe, oral end of cement body; ea, ejaculatory apparatus; h, head; php, posterior hollow part; sf, spiral filament; sr, seminal reservoir; te, tubular extension. Scale bars: **A** = 0.5 mm; **B, C** = 0.2 mm.

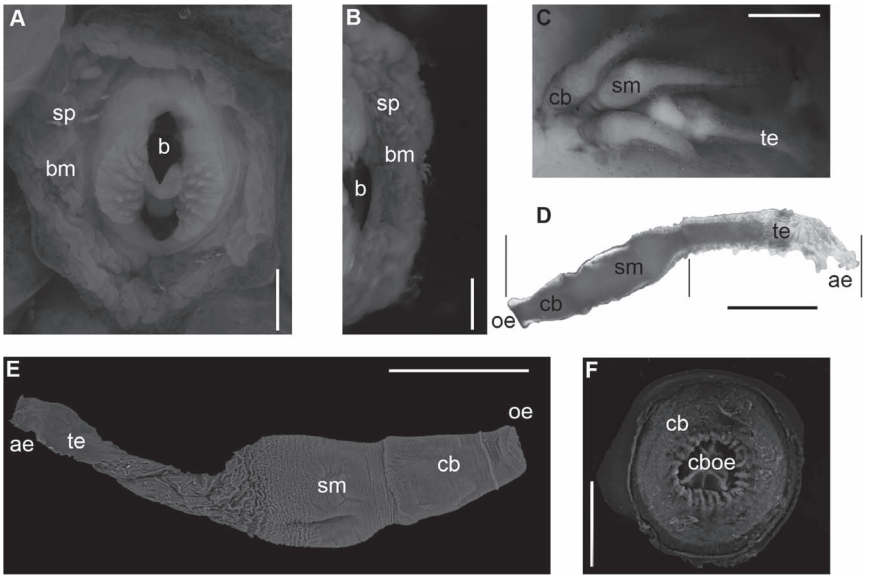

Figure 4. Spermatangia of *Gonatus fabricii*. **A.** Spermatangia implanted in the buccal membrane of a late maturing female (IV m. st.; ML = 215 mm). **B.** Spermatangia implanted in the buccal membrane of a mature female (V_2 m. st.; ML = 221 mm). **C.** Close-up view of implanted spermatangia. **D.** An extracted spermatangium as viewed under the light microscope. **E.** SEM image of an extracted spermatangium. **F.** SEM image of the flattened disk at the oral end of a spermatangium. Abbreviations: ae, aboral end of spermatangium; b, beak; bm, buccal membrane; cb, cement body; cboe, oral end of cement body; oe, oral end of spermatangium; sm, sperm mass; sp, spermatangia; te, trailing end. Scale bars: **A, B** = 5 mm; **C–E** = 0.5 mm; **F** = 0.05 mm.

(Fig. 6A, B). Fecundity at III m. st. (n = 15) ranged from 12,633 to 13,832 (mean ± SE = 13,052 ± 71 mm). Almost all oocytes (i.e. 90–97%, mean = 94.8%) observed at this maturity stage were at the early vitellogenic phase, with OD ranging from 0.5 to 0.7 mm (Figs. 5E, 6C); the remaining 3–10% of oocytes were at the previtellogenic phase. The fecundity of one of the two gelatinous females at maturity stage IV was 11,402 (the mantle of the other gelatinous female at this stage had been perforated and its gonad lost during trawling). Most oocytes (73.8%) at maturity stage IV were at midvitellogenic phase, with OD ranging from 1.8 to 1.9 mm (Fig. 6D); oocytes in this phase differed from the younger ones in being much larger and having an elongated, oval shape (Fig. 5A–C, F). The remaining oocytes at maturity stage IV were either late vitellogenic oocytes (2.7%, OD = 1.6–2.3 mm) or oocytes undergoing resorption (23.5%, OD = 0.5–0.6 mm; Fig. 6D). The late vitellogenic oocytes were present throughout the ovary and were especially prevalent in the peripheral areas (Fig. 6D). They had an intense yellow colour due to yolk accumulation and were longer and more rounded in shape (Fig. 5A–C, G) than younger oocytes, with OD ranging from 1.6 to 2.3 mm. These late vitellogenic oocytes were significantly greater in length than the midvitellogenic oocytes (U = 577.5, P = 0.009). Despite the similarity in size to early vitellogenic oocytes, oocytes undergoing resorption were distinguished by their transparency, flaccidity and, sometimes, also by other characters (irregular shape, cytoplasm partly detached from the cell membrane; Fig. 5F). Two ripe yet unovulated oocytes were attached in the distal ovary (Fig. 5C); these had an OD of 4 mm. These two oocytes were completely surrounded by follicles and had no inner follicle folds. No empty follicles were found in the ovary, nor were any ripe oocytes found in the oviducts.

The mature female (n = 1) had a fecundity of 8,862, with 79% of oocytes being at midprevitellogenic phase (OD = 1.3–1.6 mm), 4.9% at late vitellogenic phase (OD = 1.4–2.1 mm) and 16.1% being oocytes under resorption (OD = 0.5–0.6 mm; Fig. 6E). The late vitellogenic phase oocytes were observed mostly in the peripheral areas of the ovary and were significantly larger than the oocytes belonging to the previous phase (U = 514.5, P = 0.005). Five ripe oocytes were found: two in the distal part of the ovary

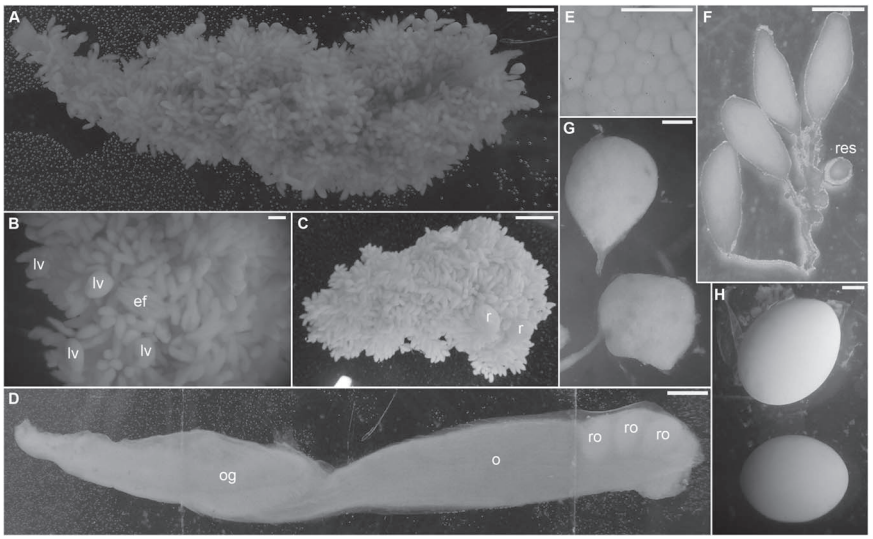

Figure 5. Female reproductive system of *Gonatus fabricii*. **A, B.** Intact ovary of mature female (V_2 m. st.; ML = 221 mm). Note that no ripe oocytes are visible. **C.** Intact ovary of late maturing female (IV m. st.; ML 215 mm). **D.** Right oviduct of mature female with ripe oocytes. **E.** Early vitellogenic oocytes. **F.** Midvitellogenic oocytes and oocytes undergoing resorption. **G.** Late vitellogenic oocytes. **H.** Ripe oocytes. Abbreviations: ef, empty follicle; lv, late vitellogenic oocyte; o, oviduct; og, oviducal gland; r, ripe oocyte; res, resorbing oocyte; ro, ripe oocyte in the oviduct. Scale bars: **A, C, D** = 5 mm; **B, F, H** = 1 mm; **E, G** = 0.5 mm.

(unovulated; similar to those in the female described above) with an OD of 4.5 mm and 5 mm, respectively; and three in the basal part of the right oviduct (Fig. 5D, H), with two oocytes having an OD of 5.0 mm, and one oocyte having an OD of 5.5 mm. All of these lacked an epithelium and lay freely in the oviduct cavity (Fig. 5D). Three empty follicles, each measuring 3.2 mm in length, were present in the distal ovary; they were oval and transparent with folds on the surface (Fig. 5B).

Male reproductive system

The male reproductive system of *G. fabricii* had a typical oegopsid structure, that is it consisted of a single sperm duct, and a spermatophoric complex comprising six glands and a spermatophoric sac (Fig. 2). The spermatophoric sac was long: up to 84.5% of ML (this sac can be as much as 106.8% of ML; see Arkhipkin & Bjørke, 1999). This sac was divided into four well-distinguished inner portions (Fig. 2). The first portion, the fundus (proximal part of spermatophoric sac), held between 4.8–19.1% (11.6 ± 1.6%) of all the spermatophores in a single male. The central part of the spermatophoric sac consists of two portions, the central-posterior and central-anterior, which accounted for 3.6–58.0% (21.4 ± 6.7%) and 24.9–73.3% (53.3 ± 5.6%) of all spermatophores, respectively. The fourth portion of the spermatophoric sac was the penis, a narrow muscular tube-like structure forming the distal spermatophoric sac and reaching up to 72.7% of the length of the spermatophoric sac; the penis contained 0–25.4% (13.8 ± 3.3%) of all spermatophores. Two males lacked spermatophores inside the penis. In nearly all cases, the largest part of the spermatophoric sac was the central-anterior part. In one male, however, it was the central-posterior part that was the largest (Fig. 7A).

Spermatophores were elongate, cylindrical, slightly curved structures (Fig. 3A). In freshly fixed squid, they were white in colour. Spermatophore length varied among specimens (Table 2; Supplementary Material Table S1). The oral end of the spermatophore had a relatively short, smooth head; the head was covered by a cap, to which a long spermatophoric thread was attached. The ejaculatory apparatus was quite long for a squid (Fig. 3A; Supplementary Material Table S1). The spiral filament was clearly visible inside the ejaculatory apparatus in freshly fixed squid; it almost reached the loops of the ejaculatory apparatus inside the head of the spermatophore. However, following preservation, the spiral filament became increasingly invisible with the passing of time. Stellate particles were not found inside the ejaculatory apparatus. The cement body was not divided and was 5–6× thinner near its aboral end; this thin part formed a few loops near the junction of the cement body and the seminal reservoir (Fig. 3B). The oral region of the cement body was characterized by a well-developed collar and a tubular extension that was half the width of the cement body (Fig. 3C). The oral end of the cement body did not taper to a sharp tip. Two discs were located at the oral end of the cement body, near its junction with the ejaculatory apparatus (Fig. 3C); the disc closest to the aboral end was larger. The posterior hollow part of the aboral region of the spermatophore was well developed. The largest part of the spermatophore was the single, slightly curved seminal reservoir (Fig. 3A; Table 2; Supplementary Material Table S1).

The ontogenetic increase in spermatophore size was clearly seen inside the spermatophoric sac, with the oldest and smallest spermatophores being in the penis (or in the central-anterior part of the sac, if the penis was empty), while the youngest and largest spermatophores were in the fundus (Fig. 7B; Table 2). Young and old spermatophores differed significantly in length and to a lesser extent in width; all the dimensions increased gradually during ontogenesis (Table 2; Supplementary Material Table S1). Ontogenetic increase of 17–86% was observed for spermatophore length and of 25–100% for spermatophore width. The length, width and volume of seminal reservoirs also showed a significant increase (Table 2; Supplementary Material Table S1), with the length increasing by 17–118%, the width by 17–100% and the volume by 59–757% (Table 2). Thus, the length of the seminal reservoir increased to a relatively greater degree than the width. The width of the seminal reservoir was less variable. The length of the head, length of the ejaculatory apparatus, length of the cement body and length of the posterior hollow part of the spermatophore also increased during ontogenesis; in almost all of the males, these parts were significantly larger in young spermatophores (Table 2; Supplementary Material Table S1). The length of the cement body and the length of the spermatophore's hollow posterior part increased relatively more than did the length of the seminal reservoir.

Table 2. Ontogenetic changes in spermatophore size in three specimens of *Gonatus fabricii*.

Measurement (mm)	**Specimen 6–69 ($n = 56$)**			**Specimen 6–43 ($n = 56$)**		**Specimen 4–21 ($n = 56$)**			
	Central-anterior	Central-posterior	Fundus	Penis	Central-anterior	Penis	Central-anterior	Central-posterior	Fundus
Spermatophore length		$H = 7.632$, $\mathbf{P = 0.021}$		$U = 44.2$, $\mathbf{P = 0.014}$			$H = 14.241$, $\mathbf{P = 0.033}$		
	8.00 ± 1.87	9.59 ± 0.94	10.36 ± 0.42	9.00 ± 0.06	10.40 ± 0.10	7.10	7.49 ± 0.48	8.20 ± 0.25	8.58 ± 0.31
Spermatophore width		$H = 5.441$, $\mathbf{P = 0.039}$		-			$H = 5.34$, $P = 0.07$		
	0.43 ± 0.04	0.50	0.60	0.50	0.50	0.40	0.45 ± 0.05	0.45 ± 0.05	0.50
Length of head		$H = 7.001$, $\mathbf{P = 0.028}$		$U = 9.0$, $\mathbf{P = 0.046}$			$H = 5.34$, $P = 0.07$		
	0.56 ± 0.02	0.61 ± 0.02	0.75 ± 0.05	0.87 ± 0.03	0.9	0.70	0.75 ± 0.05	0.75 ± 0.05	0.80
Length of ejaculatory		$H = 8.789$, $\mathbf{P = 0.017}$		$U = 52.1$, $\mathbf{P = 0.033}$			$H = 14.946$, $\mathbf{P = 0.035}$		
apparatus	1.58 ± 0.10	1.69 ± 0.07	1.95 ± 0.05	2.13 ± 0.03	2.37 ± 0.03	1.40	1.45 ± 0.05	1.61 ± 0.09	1.75 ± 0.05
Length of cement		$H = 9.334$, $\mathbf{P = 0.013}$		$U = 41.0$, $\mathbf{P = 0.023}$			$H = 14.745$, $\mathbf{P = 0.033}$		
body	0.92 ± 0.07	1.21 ± 0.09	1.45 ± 0.05	1.00 ± 0.06	1.80 ± 0.06	1.20	1.29 ± 0.02	1.37 ± 0.03	1.45 ± 0.05
Length of seminal		$H = 7.984$, $\mathbf{P = 0.020}$		$U = 44.4$, $\mathbf{P = 0.029}$			$H = 13.572$, $\mathbf{P = 0.030}$		
reservoir	3.60 ± 0.36	4.02 ± 0.74	4.70 ± 0.10	3.37 ± 0.03	4.10 ± 0.06	3.20	3.15 ± 0.05	3.22 ± 0.09	3.35 ± 0.25
Width of seminal		$H = 4.251$, $\mathbf{P = 0.041}$		-			$H = 3.18$, $P = 0.08$		
reservoir	0.25 ± 0.02	0.30	0.39 ± 0.01	0.30	0.30	0.30	0.30	0.32 ± 0.01	0.35
Length of posterior		$H = 7.298$, $\mathbf{P = 0.024}$		$U = 40.1$, $\mathbf{P = 0.024}$			$H = 11.644$, $\mathbf{P = 0.044}$		
hollow part	0.86 ± 0.12	1.02 ± 0.11	1.11 ± 0.18	-	0.86 ± 0.12	1.02 ± 0.11	1.11 ± 0.18	-	0.86 ± 0.12

Values are mean ± SE. A Kruskal–Wallis *H* test of within-male differences was used when three or more groups were considered, and a Mann–Whitney *U* test was used when the comparison was based on two groups. Significant *P* values are shown in bold font.

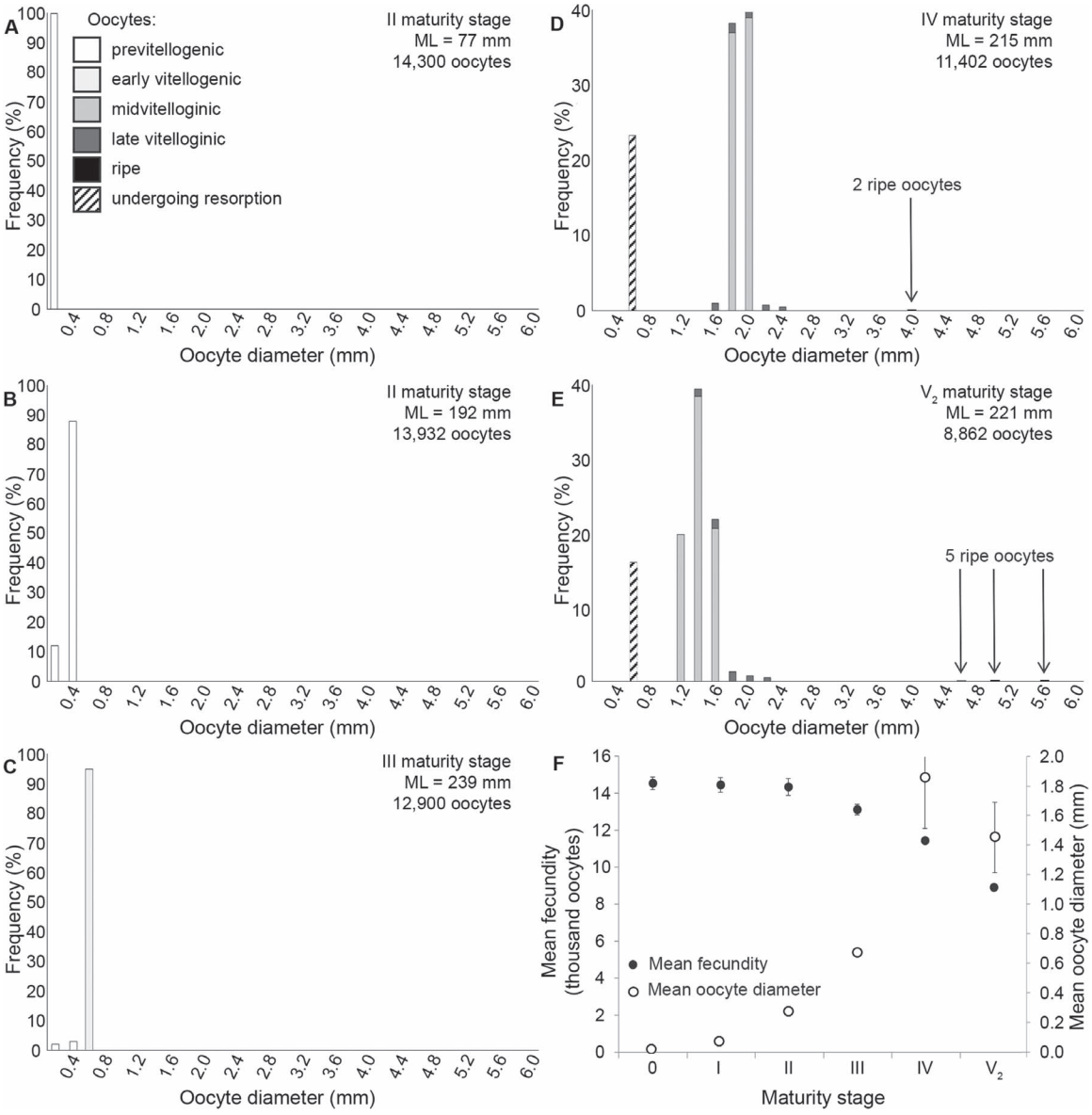

Figure 6. Fecundity of *Gonatus fabricii*. **A–E.** Fecundity of females at different maturity stages. **F.** Ontogenetic changes in fecundity and oocyte diameter. Values are mean ± SE. Sources: **A**, Golikov (2015); **B–E**, this study.

The number of spermatophores carried by a single male ranged from 77 to 257 (185 ± 18), with smaller males generally having fewer spermatophores. Nonetheless, a significant correlation was not found between ML and the number of spermatophores (number of spermatophores = $25.31 \times ML^{0.35}$, $R^2 = 0.299$, $P = 0.13$). Mature males (V_2 m. st.) were smaller than pre-spent ones (V_3 m. st.; Table 1) and usually had fewer spermatophores. Although the mean number of spermatophores was 146 ± 24 in the former and 211 ± 20 in the latter, the difference was not significant ($U = 2.13$, $P = 0.07$). The estimated total volume of sperm in all spermatophores carried by an individual male ranged from 44.12 to 80.46 mm^3.

Tentative spermatophores were found only in one of the late maturing males (ML = 257 mm; southern Davis Strait) and in the only available pre-mature male (V_1 m. st.; ML = 236 mm; northeastern Davis Strait). The late maturing male had 27 tentative spermatophores (length = 5.2–5.8 mm), most of which were in the central-anterior part of the spermatophoric sac (the penis contained no spermatophores). The pre-mature male had 27 normal spermatophores, as well as five tentative spermatophores (length = 6.2–6.4) within the penis. Tentative spermatophores differed from normal ones in being shorter in length, having a semi-transparent seminal reservoir with hardly any sperm, a relatively long ejaculatory apparatus, a relatively short cement body and a more transparent appearance throughout.

Spermatangia

Only two gelatinous females, both from the northeastern Greenland Sea (Fig. 1), carried spermatangia; one specimen had 62 spermatangia and the other had 84. The spermatangia were implanted throughout the buccal membrane. No structures resembling seminal receptacles were found on the buccal membranes (Fig. 4A, B). Spermatangium length varied from 1.8 to 2.6 (2.2 ± 0.12) mm. Spermatangia were clearly divided into oral (length = 0.8–1.2 mm, 1.0 ± 0.06 mm) and aboral (length = 1.0–

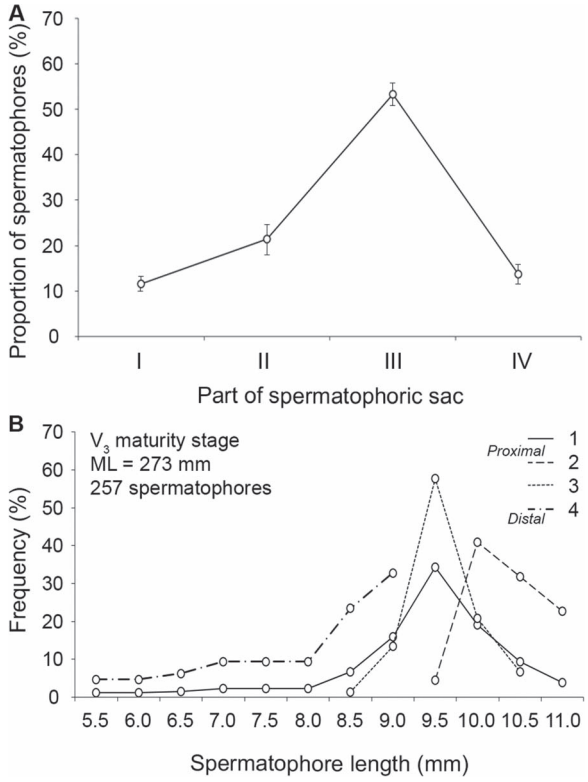

Figure 7. Spermatophores of *Gonatus fabricii*. **A.** Proportion of spermatophores inside each section of the spermatophoric sac in 12 of the males examined. Values are mean ± SE. The following parts of the spermatophoric sac are shown: I, fundus (proximal part); II, central-posterior part; III, central-anterior part; IV, penis (distal part). **B.** Ontogenetic changes in spermatophore length. The trends shown are as follows: 1, all spermatophores; 2, spermatophores in the fundus (proximal part) of the spermatophoric sac; 3, spermatophores in the central-posterior part of the spermatophoric sac; 4, spermatophores in the central-anterior part of the spermatophoric sac.

1.4, 1.2 ± 0.06 mm) parts (Fig. 4C–E). The oral part (this penetrates the female tissues) was surrounded by the remains of the cement body for 40% of its length, starting from the oral side. The flattened, disc-shaped oral end of the spermatangium constituted the thickest part of the cement body. An opening was located at the disc-shaped end; the oral end of the cement body protruded slightly from this opening (Fig. 4F). The main part of the spermatangium's oral half was composed of an elongated oval sperm mass, covered by an inner tunic. The aboral part of the spermatangium consisted of a long protruding tube, with spermatozoa exiting via its trailing end.

DISCUSSION

Size in relation to maturity, and gelatinous degeneration

To date, no gelatinous females of *Gonatus fabricii* with a ML <200 mm have been reported (Kristensen, 1981, 1984; Bjørke & Hansen, 1996; Arkhipkin & Bjørke, 1999; Tables 1, 3). While many early maturing females from the Davis Strait were much larger (the maximum ML recorded was 306 mm) than the gelatinous ones, they lacked any sign of gelatinous degeneration and were apparently still actively feeding and growing. Similar size differences have been described for the Norwegian Sea (Arkhipkin & Bjørke, 1999). There, females mated as early as maturity stage III, and almost all gelatinous females carried spermatangia (Arkhipkin & Bjørke, 1999). In our samples, regardless of size, early maturing females showed no evidence of having mated. We also found that one of the two late maturing specimens included in our study lacked spermatangia.

Table 3. Size and fecundity of *Gonatus fabricii* at different maturity stages.

Maturity stage	Females		Males
	ML (mm)	Fecundity	ML (mm)
0 (juvenile)	7–35	14,000–14,900	7–33
I (early immature)	31–73	13,200–16,200	36–75
II (late immature)	75–194	13,750–15,300	78–121
III (early maturing)	226–306	12,633–13,832	113–229
IV (late maturing)	200–288	11,402	198–269
V_1 (pre-mature)	no data	no data	236
V_2 (mature)	221–389	8,862 to *c.* 10,000	178–320
V_3 (sub-spent)	no data	no data	224–325
VI (spent)	239–322		no data

Sources: Nesis (1965); Kristensen (1981, 1984); Sennikov *et al.* (1989); Bjørke & Hansen (1996); Bjørke *et al.* (1997); Arkhipkin & Bjørke (1999); Zumholz & Frandsen (2006); Gardiner & Dick (2010); Golikov *et al.* (2012); and Golikov (2015); this study.

Large within-group size ranges (1.5–1.6×) were recorded for both mature and sub-spent males in all studied regions. Maturing males that were larger than the smallest mature ones occurred in all regions. The minimum size (i.e. ML) of mature males as reported in the literature is 160 mm for the Norwegian Sea (Arkhipkin & Bjørke, 1999) and 219 mm for Baffin Bay, western Greenland (Kristensen, 1984). Also, the size differences observed between mature males and between mature and maturing males in these areas (Kristensen, 1984; Bjørke & Hansen, 1996; Arkhipkin & Bjørke, 1999) are comparable to the differences observed in our study.

Our data show that size at maturity is not related to geographic area and this agrees with published studies: both the smallest and the largest mature specimens of *G. fabricii* have been reported from the Norwegian Sea (Sennikov, Muchin & Bliznichenko, 1989; Arkhipkin & Bjørke, 1999), and the size of immature and early maturing specimens (Kristensen, 1984; Arkhipkin & Bjørke, 1999; Zumholz & Frandsen, 2006; Golikov *et al.*, 2012; Golikov, 2015) shows no large-scale geographical pattern with regard to size distribution. Animals in all maturity stages overlapped broadly in size with those in the preceding and/or next stage (Table 3). In the stages following the late immature stage, females were consistently larger than males (Table 3).

Oogenesis and fecundity

Oogenesis in *G. fabricii* was synchronous: all oocytes in the ovary were nearly in the same phase and were the same size (Fig. 4A–E). Only previtellogenic oocytes were seen in the ovaries of immature females. In early maturing females, early vitellogenic oocytes constituted up to 97% of all oocytes (the remaining oocytes were previtellogenic). In late maturing and mature females, previtellogenic and early vitellogenic oocytes were absent, with most of the oocytes present being midvitellogenic (i.e. 73.8% and 79.0%, respectively). In late maturing and mature females, vitellogenic oocytes constituted just 2.7% and 4.9% of all oocytes, respectively. These oocytes were distributed throughout the ovary, but were most prevalent in the peripheral areas of the ovary. Ripe oocytes (numbering between 2 and 12) initially appeared in the distal ovary; some ripe oocytes (≤3) were also found in the oviducts of mature females (Kristensen, 1981; Bjørke & Hansen, 1996; this study). Empty follicles from ripe oocytes remained in the ovary. The OD of ripe oocytes ranged from 4 to 6 mm, accounting for 1.86–2.49% of ML (Kristensen, 1981; Bjørke & Hansen, 1996; Bjørke *et al.* 1997; this study). Mean OD increased as expected during ontogenesis (Fig. 6F), with the largest

increase being observed in gelatinous females as compared with nongelatinous females.

Species fecundity ranged from 8,862 to 16,200 (14,029± 120) ovarian oocytes, with 8,862 to *c.* 10,000 oocytes being found in mature females and 11,402 oocytes in a late maturing female (Kristensen, 1981; Golikov *et al*., 2012; this study). The overall trend throughout ontogenesis was that mean fecundity decreased slightly (but not significantly; $H = 60.12$, $P = 0.74$) during maturity stages 0–II and decreased significantly ($H = 32.005$, $P < 0.001$) at maturity stage III; a further decrease in mean fecundity was noted when two of the gelatinous females studied by us were added to the plot (Fig. 6F). Again, the most notable changes occurred in gelatinous females. So, while undergoing gelatinous degeneration, females decreased their fecundity due to oocyte resorption and increased mean OD (Fig. 6F). Oocytes undergoing resorbtion were found only in gelatinous females, with this type of oocytes accounting for 23.5% and 16.1% of fecundity in late maturing and mature specimens, respectively.

The reproductive strategy of female *G. fabricii* can be summarized in terms of the following characteristics: (1) comparatively low fecundity, (2) synchronous ovulation with clear evidence of oocyte resorption, (3) mating while still maturing, sometimes even before the onset of gelatinous degeneration and (4) terminal spawning (oviducts not used to store eggs), gelatinous degeneration and brooding of the egg mass (Bjørke *et al*., 1997; Arkhipkin & Bjørke, 1999; this study). Among other Gonatidae, gelatinous degeneration of females and/or brooding of the egg mass is known for *G. antarcticus*, *G. madokai*, *G. onyx*, *Gonatopsis makko* and *Gonatopsis octopedatus* (Young, 1973; Nesis, 1993, 1995, 1997, 1999; Okutani, Nakamura & Seki, 1995; Seibel *et al.* 2000, 2005; Laptikhovsky, Arkhipkin & Hoving, 2007; Bower *et al*., 2012; Kallqvist & Monllor, 2012; Hoving *et al*., 2017). Therefore, the same female reproductive strategy, with gelatinous degeneration, synchronous oogenesis and brooding, is hypothesized to occur in all species of *Gonatus*, *Eogonatus* and *Gonatopsis*, except for *Gonatopsis borealis*, which lacks female gelatinous degeneration (Nesis, 1997; Roper *et al*., 2010a). Synchronous ovulation involving oocyte resorption is known for the following deep-water squid families: the Gonatidae apart from the genus *Berryteuthis*, the Histioteuthidae, the Onychoteuthidae (resorption is not so evident in this group) and the Cranchiidae (Nesis, Nigmatullin & Nikitina, 1998; Laptikhovsky, 2001; Nigmatullin, 2002, 2007; Laptikhovsky *et al*., 2007; Hoving & Lipinski, 2009). The fecundity of *G. fabricii* is lower than all the species studied so far in these families.

Spermatophores and spermatangia

As observed in our study, spermatophore length in *G. fabricii* ranged from 5.8 to10.8 mm (8.3 ± 1.1 mm), and this agrees with previous studies (6–10 mm; Kristensen, 1984; Bjørke & Hansen, 1996). We found that the relative length of spermatophores in our samples ranged from 2.12% to 5.00% (3.90 ± 0.40%) of ML (Supplementary Material Table S1). The spermatophore morphology of *G. fabricii* clearly differs from that of *Berryteuthis magister*, the only other member of the Gonatidae to have been studied in detail (Hess, 1987; Nigmatullin *et al*., 1996; Voight, 1996). While *G. fabricii* possesses a single cement body with a well-developed collar and discs at the oral end of the cement body and an ejaculatory apparatus that is longer than the cement body, it lacks a tapered, sharp tip to the cement body. The spermatophore of this species resembles that of *Gonatopsis octopedatus* (see Okiyama, 1970) and clearly differs from those of other squid families, in the structure of the cement body (including the junction with the ejaculatory apparatus) and in possessing a relatively smaller head. There was a spiral filament under the inner tunic of the spermatophore of *G. fabricii*, but stellate particles were not found. Stellate particles have been reported from a few species of squids and sepiolids (e.g. Weill, 1927; Austin, Lutwak-Mann & Mann, 1964; Takahama *et al*., 1991; Marian & Domaneschi, 2012; Marian *et al*., 2012).

Gonatus fabricii showed significant ontogenetic increase in the length and width of the spermatophore, and in the length, width and volume of the seminal reservoir, with spermatophores produced later in life being larger than those produced earlier. If, following Hoving, Lipinski & Dam (2010), we consider the volume of sperm in the seminal reservoir to indicate 'spermatophore quality', then our work shows that spermatophore quality increases during ontogenesis. This observation was reported for the first time by Drew (1919), but was only described in detail much later (Sabirov, 1995; Nigmatullin *et al*., 1996, 2003). The increase of spermatophore size was observed in all examined specimens of *G. fabricii*, without any detectable decline between stages. However, a decline in the rate of increase in spermatophore size has been observed later in ontogenesis in other squids and sepiolids (Sabirov, 1995; Nigmatullin *et al*., 2003; Hoving *et al*., 2010; Golikov *et al.* 2013a) and this probably also occurs in *G. fabricii*.

We found that a single male *G. fabricii* can carry between 77 and 257 spermatophores. The size of mature males does not influence the number of spermatophores in decabrachians (Nigmatullin, Arkhipkin & Sabirov, 1991; Sabirov, 1995; Nigmatullin *et al*., 1996, 2003; Hoving *et al*., 2004, 2008, 2010, 2016; Sabirov *et al*., 2012; Golikov *et al*., 2013a; Cuccu *et al*., 2014; Golikov, 2015). Instead, the number of spermatophores appears to be related to the number of spawning events and to the rate of spermatophore formation. Also, as shown for other squid species (Sabirov, 1995; Nigmatullin *et al*., 1996, 2003), young mature male *G. fabricii*, which are still accumulating spermatophores before starting reproduction, have fewer spermatophores. This could explain the substantial differences recorded among the specimens in our study.

The male reproductive strategy of *G. fabricii* can be summarized in terms of the following characteristics: (1) a long ontogenesis, with continuous production of spermatophores as males mature, and males feeding and growing while actively reproducing (Kristensen, 1984; Arkhipkin & Bjørke, 1999, 2000; this study); and (2) a significant increase in the length and width of spermatophores and in the length, width and volume of seminal reservoirs as males mature. A similar reproductive strategy occurs in other deep-water squids. For example, the number of spermatophores in species of the families Architeuthidae and Onychoteuthidae is similar to or lower than *G. fabricii* (Nesis, 1995; Hoving *et al*., 2004, 2016). In contrast, the deep-water squid family, the Histioteuthidae, has a different reproductive strategy, with many more spermatophores (up to *c.* 3000) being present in a single male (Hoving *et al*., 2010; Cuccu *et al*., 2014). *Berryteuthis*, the only other studied gonatid, has a reproductive strategy that differs from *G. fabricii* (Nigmatullin *et al*., 1996; Voight, 1996). Male *Berryteuthis* show only a slight ontogenetic increase in the length and volume of spermatophores and seminal reservoirs, with approximately 1000 spermatophores being present in a single male (Nigmatullin *et al*., 1996; Voight, 1996). This reproductive strategy is similar to that found in neritic or epipelagic squids, such as those belonging to the families Ommastrephidae, Thysanoteuthidae and Loliginidae (Nigmatullin *et al*., 1991, 2003; Sabirov, 1995; Sabirov *et al*., 2012).

The spermatangia of *G. fabricii* were long, with relatively well-defined oral and aboral parts and a well-developed trailing end. These spermatangia appear to be intermediate in structure to the two main types of spermatangia described from decapodiformes. The first type of spermatangia, as found in the Octopoteuthidae and Sepiolidae, has a massive/well-developed, oval-shaped sperm reservoir and a thin long trailing end. The second type, which is characterized by a long and tapering shape and poor differentiation of its component parts, occurs in the Loliginidae, Ommastrephidae, Enoploteuthidae, Architeuthidae, Cranchiidae, Thysanoteuthidae and the gonatid genus *Berryteuthis*. The two types of spermatangia also differ in the depth of implantation: for the second type, this can be either deep or shallow, whereas for the first type implantation is always deep (see the review by Marian, 2014). In *G. fabricii*, implantation of the spermatangia in the buccal membranes of

females was shallow, with no special attachment structures being observed. The spermatangia are characterized by a thick, flattened and disc-shaped oral end, with the oral end of the cement body protruding slightly from the opening at the centre of the disc-shaped area. The disc-shaped oral end of the spermatangium together with the protruding end of the cement body constitutes the most anterior part of the spermatangium; these are apparently the most robust and hardened regions of the spermatangium and are thus likely to have a key role in penetrating the tissues of the female.

Reproductive ecology

The extensive data presented here support the hypothesis that *G. fabricii* reproduces only in a few geographically restricted areas. Nesis (1965, 1971, 1987) argued that reproduction in *G. fabricii* takes place throughout the entire geographical range of the species and occurs mainly in March–June. However, Bjørke (1995, 2001) and Bjørke & Gjøsaeter (1998) have indicated that *G. fabricii* reproduces only in a few restricted parts of its vast range (Fig. 1). It is interesting to note that one of the breeding areas is in the centre of the Polar Basin, an area from which mature and spent females as well as newly hatched juveniles have been collected (Nesis, 1971, 1987; Young, 1973). There are two most important lines of evidence that are consistent with the hypothesis of restricted breeding areas within the wider range of *G. fabricii*. First, extensive sampling has almost completely failed to collect large maturing and mature specimens in deep waters outside the putative breeding areas. In our surveys we sampled a huge area with deep-water trawls (i.e. depths from 500 to 800 m), but such specimens formed less than 0.1% of all sampled *G. fabricii*. Second, except for the putative breeding area in the centre of the Polar Basin, the other breeding areas have large concentrations of the northern bottlenose whale *Hyperoodon ampullatus*, the main predator of *G. fabricii*.

Our findings indicate two previously unreported breeding areas for *G. fabricii*. The first of these lies in the North Atlantic near southeastern Greenland and is located far from any of the other breeding areas (Fig. 1). The second breeding area discovered by us is located in the northwestern part of the Davis Strait and in southwestern Baffin Bay. This area is contiguous with the well-known breeding area in the northeastern Davis Strait (Fig. 1). Given that the northern and southern parts of the Davis Strait are separated by a shallow-water central zone, the Davis Strait consists of two distinct breeding areas for *G. fabricii*. One breeding area is located in the southern Davis Strait. The second extends from the northern part of the Davis Strait to Baffin Bay. Further work may reveal that all currently known breeding areas may be greater in geographic extent than presently recognized, with some geographically proximate areas possibly being shown to be contiguous, as new data become available. No differences in maturity sizes were found among the distinct breeding areas.

Reproduction in geographically distinct areas, typically the most productive parts of the range, is well known for shelf and epi-mesopelagic oceanic squids of the families Loliginidae and Ommastrephidae (Jereb, Vecchione & Roper, 2010; Roper *et al*., 2010b) and for deep-water squids of the family Onychoteuthidae and the gonatid genus *Berryteuthis* (Nigmatullin *et al*., 1996; Roper & Jereb, 2010c). In deep-water squids belonging to the Architeuthidae and Histioteuthidae, mature specimens have been caught throughout the ranges of sampled species (Voss, Nesis & Rodhouse, 1998; Roper & Jereb, 2010a, 2010b; Roper & Shea, 2013). The same is true for the epipelagic oceanic species *Thysanoteuthis rhombus* (Thysanoteuthidae) (Nigmatullin, Arkhipkin & Sabirov, 1995). While reproduction in geographically distinct areas is relatively common in non-deep-water squids and less common in deep-water squids, it may be especially important for *G. fabricii*, as food resources are patchily distributed in the Arctic. The patchy distribution of food may importantly be the result of hydrographic processes, such as ocean currents, sea ice dynamics and upwelling and downwelling events. Key support for this hypothesis is the fact that the breeding areas of *G. fabricii*—and this includes the breeding area in the Central Polar Basin—are places with high surface current activity and high productivity in the epipelagic layers. Increased food availability in the epipelagic layers would contribute to increased survival of epipelagic juveniles, with surface currents potentially facilitating the dispersal and wider distribution of this species.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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