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Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea

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Abstract Ontogenetic changes in morphometric and reproductive indices were studied using 166 individuals of the arctic gonatid squid *Gonatus fabricii* (7.3–322 mm pen length) collected in the southern part of the Norwegian Sea. Body proportions and consistency of the mantle and fins did not change in maturing and mature males. In contrast, during maturation the females first lost their tentacles, then the horny rings of their 4th arm suckers, and the muscular part of their body turned watery and gelatinous. Unlike most squid, *G. fabricii* females start mating at maturity stage III, and all but one female at stage IV had mated, as well as all spent females. Females had high values of both gonadosomatic index and maturity indices compared to those of the North Pacific gonatids, whereas gonadosomatic index values of males were low, probably due to slow functioning of both testis and spermatophoric gland, and long accumulation of spermatophores in the Needham's sac. It is suggested that the breakdown of female body tissues is an adaptation for a deepwater bathypelagic "brooding" of the negatively buoyant egg-mass caused by the high specific density of the secretion from the nidamental glands in gonatids.

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Introduction

Gonatus fabricii (Lichtenstein 1818) is widely distributed in arctic and subarctic waters of the North Atlantic, occurring from the North Pole to the southern Norwegian and Irminger Seas and Newfoundland (Nesis 1971; Kristensen 1983). Juveniles of 0.3–4.0 cm pen length (PL) live in shoals in the uppermost 80 m of the water column (Kristensen 1983). The species shows an ontogenetic downward migration, and specimens larger than 200 mm PL have been caught at depths from 400 m and downwards to 1200 m (maximum depth fished) (Bjørke and Gjøsæter 1998). Due to its high abundance, *G. fabricii* is one of the important components of the arctic food web, being a common prey for marine fishes and mammals (Clarke 1966). Occasionally, young *G. fabricii* are fished by local fishermen in Greenland and northern Norway (Nesis 1965; Wiborg 1979), and it is considered as a potential fishery resource of the Norwegian Sea (Wiborg 1979).

The biology of *G. fabricii* is well studied. However, these studies have focused predominantly on the paralarval and juvenile epipelagic phases that are most available to capture by pelagic nets and trawls. Deepwater trawlings have seldom been performed in the Norwegian Sea, and until now there have been morphometric and sexual data on only a few dozen specimens >150 mm PL (Kristensen 1981a, 1983). Multivariate discriminant analysis of various morphometric parameters showed an existence of several well-distinguished local populations even in geographically closed areas (Kristensen 1982). *G. fabricii* exhibits a sexual dimorphism in body shape at the adult phase. Males remain muscular with a rocket-shaped body until the end of their life, whereas maturing and mature females (caught at great depths) become gelatinous with flaccid mantle and fins and lost tentacles (Kristensen 1981b; Bjørke and Hansen 1996). The reproductive parameters investigated in previous studies included only relationships between pen length, testis weight and penis length in males, and ovary weight and nidamental gland length in females, and were mainly in immature and just starting to mature animals (Kristensen 1983, 1984). However, for estimation of both fecundity and reproductive strategy it is necessary to have access to sufficient material from mature animals, and this has not yet been available for *G. fabricii* (Bjørke 1995).

In spring 1998, the authors had a good opportunity to get a representative sample of all ontogenetic stages of *G. fabricii*, including several dozen mature and spent males and females, which were taken from deepwater trawls in the southern part of the Norwegian Sea. Studies of ontogenetic changes of various morphometric and reproductive parameters enabled us to subdivide the whole ontogenesis of *G. fabricii* into several ecological phases and to put forward a hypothesis on evolutionary reasons for muscle degeneration of the mantle and fins in mature and spent females.

Materials and methods

Individuals of *G. fabricii* were captured during an experimental pelagic trawl survey carried out in the southern part of the Norwegian Sea off Møre by the R/V "G.O. Sars" between 8 and 18 April 1998 (Fig. 1). Thirty-five 2-h hauls were performed at depths between 200 and 1200 m (mainly 700–900 m) so that each depth sector (with depth interval of 100 m) was represented at least once both at night and in the daytime. All deepwater hauls (>1000 m) were made at least 200 m above the bottom. A rope pelagic Åkra trawl was used (20 mm mesh-size in the cod-end) at a trawling speed of 3 knots (5.5 km h^{-1}) (Valdemarsen and Misund 1995).

After sorting the catch, squid were identified as *G. fabricii* using Nesis's key (1987). All squid were analysed immediately on board ship. A total of 166 specimens including 11 juveniles (47–92 mm pen length), 79 females (75–322 mm pen length) and 76 males (72–254 mm pen length) were caught. Dorsal mantle length (ML), pen length (PL), nidamental gland and Needham's sac lengths were measured (whenever possible) to the nearest 1 mm. Body weight (BW) and other weight characters were weighed to the nearest 0.1 g using a special anti-rolling electric balance. Maturity stages (juveniles; immature, I, II; maturing, III, IV; mature, V, spent, VI) were assigned using the VI-stage scale of Nigmatullin (1989). The following observations were made for 119 specimens >100 mm ML: the presence of tentacles, consistency of the mantle and fins (muscular or "watery"), and presence of suckers on the 4th arms. Presence of spermatangues (sperm reservoirs) on the buccal membrane (indicating previous matings) were also recorded in females.

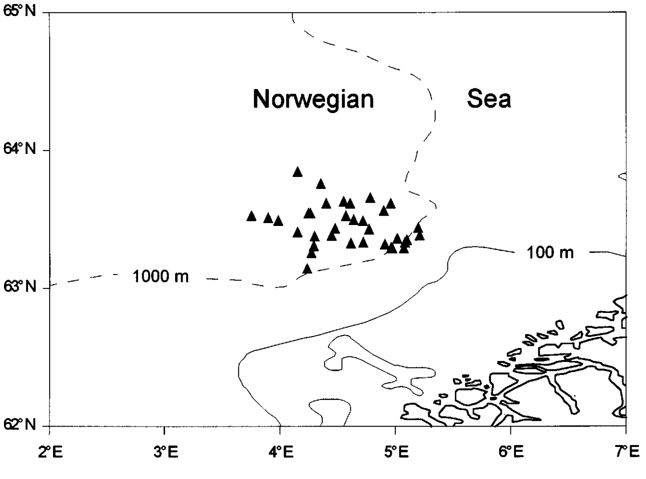


Fig. 1 Sampling locations of the squid *Gonatus fabricii* in the southern part of the Norwegian Sea in April 1998

Furthermore, six paralarvae of *G. fabricii* (7.3–32 mm ML) were caught in three plankton net tows (Munk 1993), which were performed in epipelagic water layers.

The gonadosomatic index (GSI), maturity index (MI) and stomach index (SI) were calculated for each specimen as:

$$\mathrm{GSI_W} = \mathrm{GW/BW} \times 100$$

$$\mathrm{MI_W} = \mathrm{SSW/BW} \times 100$$

$$\mathrm{SI} = \mathrm{SW/BW} \times 100$$

where GW is a gonad weight, SSW is total weight of the sexual system, SW is stomach weight and BW is body weight of a squid excluding a weight of stomach contents.

In addition, other parameters ($\mathrm{GSI_{PL}}$ and $\mathrm{MI_{PL}}$, g $\mathrm{mm^{-1}}$) were used for description of the reproductive process in females because of the rapid increase of their somatic weight due to breakdown of the mantle and fins with maturity:

$$\mathrm{GSI_{PL}} = \mathrm{GW/PL}$$

$$\mathrm{MI_{PL}} = \mathrm{SSW/PL}$$

where PL is pen length of squid.

Results

Morphometric indices

The relationship between pen length and dorsal mantle length was well approximated by the power function with the power coefficient being quite close to 1 (Fig. 2A). Similar to other gonatids (Nesis 1987), *G. fabricii* is characterized by the presence of a muscular "tail" at the posterior part of the mantle. This tail is often torn in animals that have been caught by trawl, making it impossible to measure their dorsal mantle length. The revealed relationship between PL and ML shows that during the whole ontogenetic range studied (50–322 mm PL), the dorsal mantle length was greater (by about 13%) than the pen length, both in males and females.

The length-weight relationship was also best described by the power equation with a low value of power coefficient (2.47, Fig. 2B). Sexual dimorphism in length-weight relationship was not revealed.

Allometric growth of both mantle and fins (in respect to the pen length) was the same in immature females and all maturity stages of males (Fig. 3). However, maturing females had mantle and fins about 1.5–2 times heavier than the same-sized immature females and males. Weight of the mantle and fins of spent females increased sharply even compared to maturing females (Fig. 3A, C). Such a dramatic increase in weight of the mantle and fins in maturing and spent females was not due to somatic growth. At these ontogenetic stages, the tissues of the mantle and fins became flaccid and gelatinous. The mantle itself (without skin) became semi-transparent with ovary and nidamental glands visible through it. The

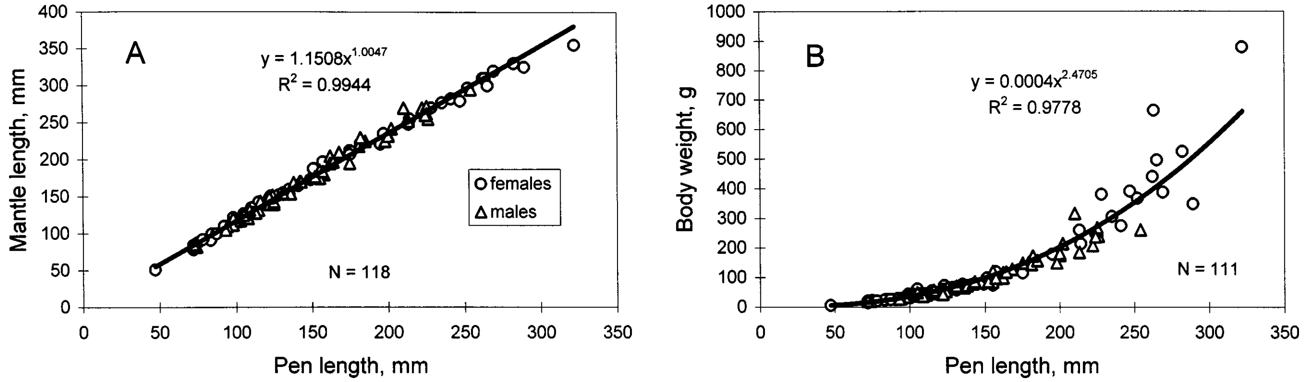


Fig. 2 The relationships between pen length and mantle length (**A**) and pen length and body weight (**B**) for *Gonatus fabricii*

breakdown of the muscular tissues of the mantle and fins started at maturity stage III and continued through maturity stage IV. All spent females had gelatinous mantle and fins, but none of the maturing and mature males (Table 1).

Maturing and spent females had other characteristic features distinguishing them from immature females and all males. At stage III (and even in one female at stage II), the tentacles were missing and stalks of the tentacles were freshly cut with flat and sharp edges. The length of these freshly cut stalks was equal to the distance between the stalk base and squid mandibles. All females at stages IV and VI had cut stalks of tentacles with rounded tips and diminished in size compared to those of stage III (Table 1). Three mature males (from a total of 29 specimens) also had cut stems of tentacles. Females at stages III and IV started to lose the horny rings of suckers on their 4th arms. All spent females had only buds on their 4th arms instead of suckers. Only one mature male had buds on its 4th arms (Table 1).

Thus during maturation, females lose their tentacles first, then the horny rings of their 4th arm suckers, and their mantle and fin muscles break down and become gelatinous.

The weight of the digestive gland increased with pen length in immature and maturing females. Maturing females had the largest digestive glands (in terms of its absolute weight). Spent females had digestive glands similar in weight to immature females, which were half as heavy (Fig. 4A). In contrast, the heaviest male digestive glands were in mature specimens (Fig. 4B). The maximum weight of the digestive gland was approximately the same in females (95 g) and males (97 g).

Relative weights of the digestive glands (in respect to mantle weight) showed a different pattern of growth

Fig. 3 The relationships between pen length and mantle weight (**A**, **B**) and pen length and fin weight (**C**, **D**) for females and males of *Gonatus fabricii*

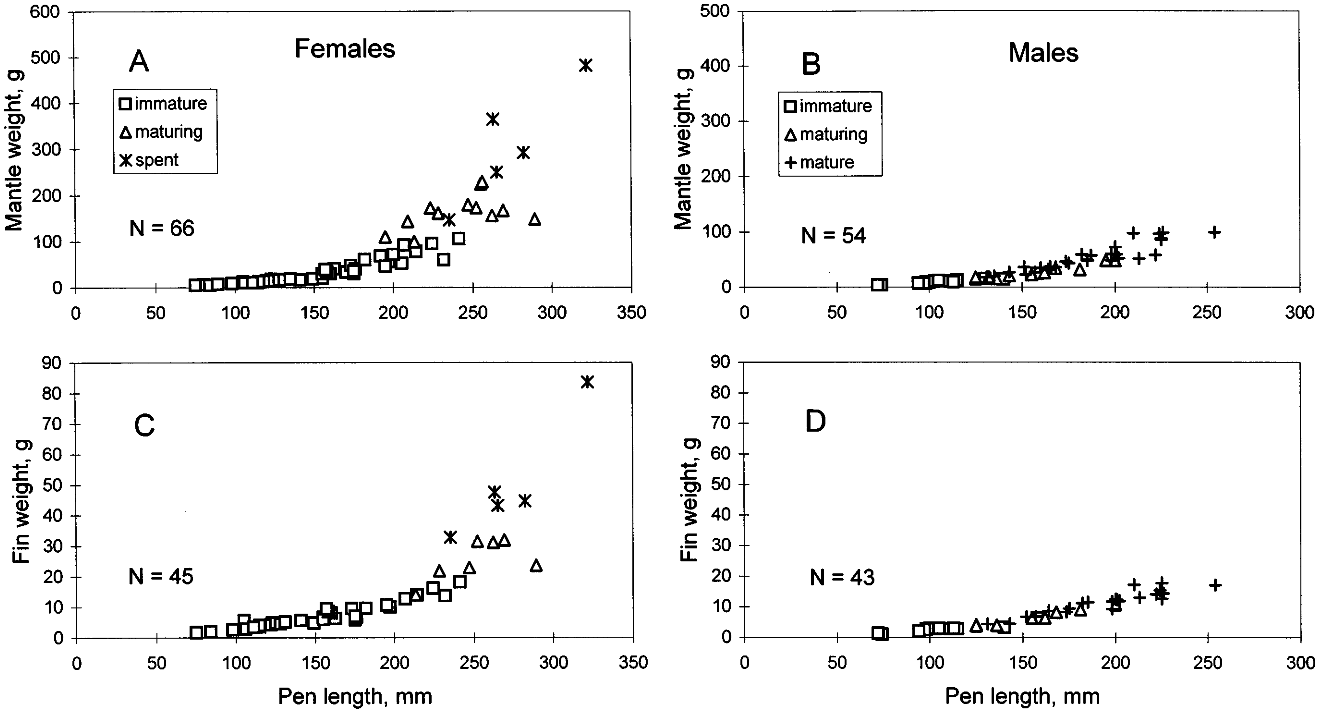


Table 1 *Gonatus fabricii*. Number of females and males with intact and cut tentacles, muscular and flaccid mantle, and with suckers or buds on the 4th arms at different maturity stages. Note that there were no females at stage V in our samples

	Maturity stage	Tentacles		Mantle		Fourth arms with		Mating traces		Total
		Intact	Cut	Muscular	Flaccid	Suckers	Buds	No	Yes	
Females	I	31	0	31	0	31	0	31	0	31
	II	16	1	17	0	17	0	17	0	17
	III	2	4	4	2	5	1	3	3	6
	IV	0	6	2	4	4	2	1	5	6
	VI	0	5	0	5	0	5	0	5	5
Males	I	10	0	10	0	10	0	–		10
	II	4	0	4	0	4	0	–		4
	III	4	0	4	0	4	0	–		4
	IV	7	0	7	0	7	0	–		7
	V	26	3	29	0	28	1	–		29

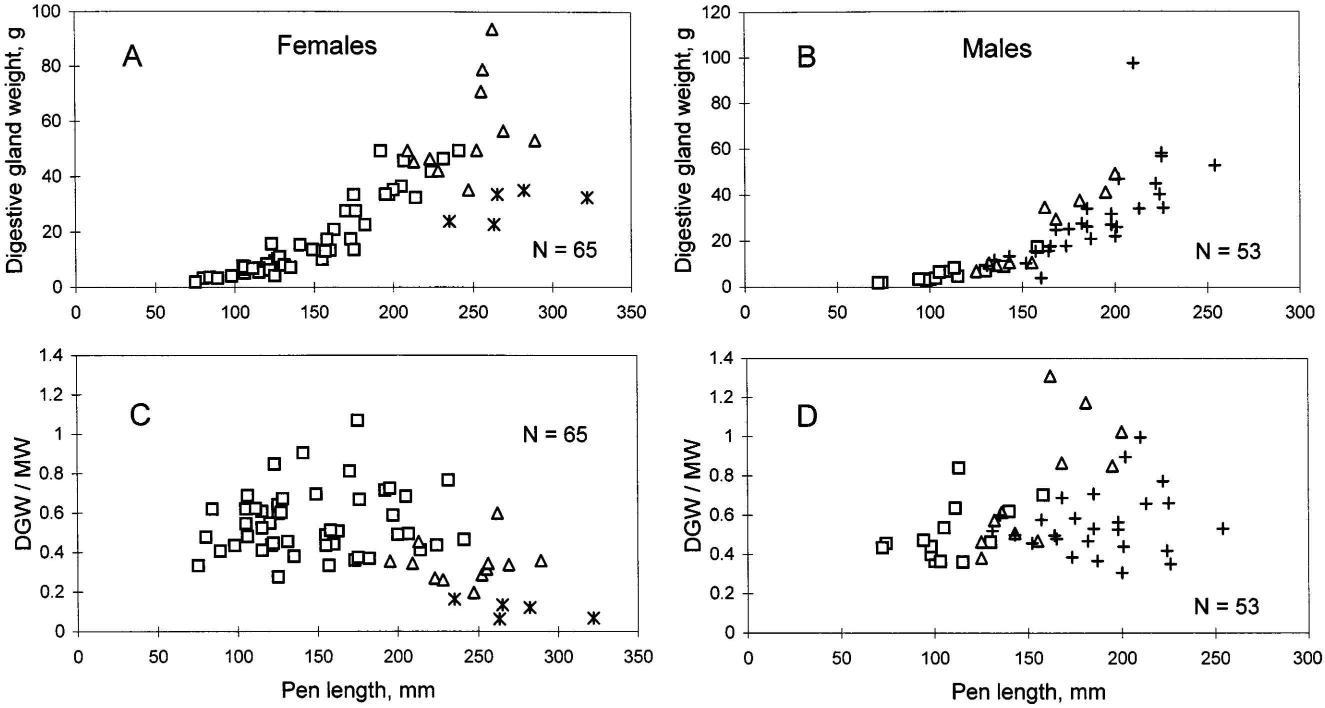


Fig. 4 The relationships between pen length and digestive gland weight (**A**, **B**) and pen length and ratio digestive gland/mantle weight (**C**, **D**) for females and males of *Gonatus fabricii*. *Symbols* are the same as in Fig. 3

during ontogenesis. In females, digestive glands were relatively small in small immature females (0.4–0.6 of MW); then they increased and attained their maximum values in immature females of 160–170 mm PL, decreased again in maturing females and dropped dramatically in weight in spent females (Fig. 4C). Generally, males showed the same trend in relative growth of the digestive gland. However, weights were maximum in maturing males, and decreased again in mature males. It seems that males had relatively larger digestive glands than females (Fig. 4C, D), but the data set was too small for statistical comparisons. The largest digestive gland in females weighed approximately the same as the mantle, whereas in two males digestive gland weights were 1.16 and even 1.3 times higher than mantle weight (Fig. 4D).

The stomach index was maximum in juvenile squid, and then it gradually decreased attaining minimum values in large spent females (Fig. 5).

Reproductive parameters

As in other squid, the reproductive parameters of *G. fabricii* changed during ontogenesis with maximum values in mature squid (Figs. 6, 7, 8, 9).

In females, nidamental glands grew in length in concert with pen length, and attained 30–35 mm in large immature specimens. The same-sized maturing females had nidamental glands 2–2.5 times longer than immature ones. In spent females, these glands decreased in absolute length (Fig. 6A). Weight indices of different

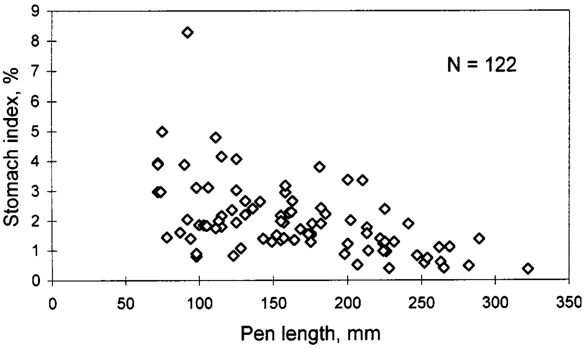


Fig. 5 The relationship between pen length and stomach index for *Gonatus fabricii* (females and males pooled)

parts of the female sexual system (nidamental glands, ovary, oviducal glands) changed similarly during ontogenesis, being minimum in immature females, then increasing dramatically (up to 40 times) in maturing females and diminishing again in spent females (Fig. 6B–D). It was notable that the female (255 mm PL with a gelatinous mantle) that had the largest ovary (126.3 g), filled however with large trophoplasmatic oocytes (but not ripe eggs), and with empty oviducts, was almost mature, but still at maturity stage IV.

Gonadosomatic and maturity indices showed similar trends at different maturity stages of females, being maximum in maturing specimens (Fig. 7A, C). GSI_{PL} and GSI_{ML} attained the highest levels (0.5 and 0.64 g/mm, respectively) in a maturing female at stage III (255 mm PL) (Fig. 7B, D).

Mating of females (indicated by presence of spermatangues on the buccal membrane) started at maturity stage III. All but one female at stage IV had mated already, and all spent females had mated also (Table 1).

The Needham's sac was short (40–55 mm in length) in immature and maturing (38–80 mm) males. Its length greatly increased in mature males, being even more than pen length (171 mm) in a mature male of 160 mm PL. The Needham's sac length varied considerably (60–175 mm) (Fig. 8A). Such variation depended on the physiological status of the terminal organ (penis). In dead animals it was relaxed and rather short, whereas in live males it became rigid and elongated when it was touched with tweezers, for example.

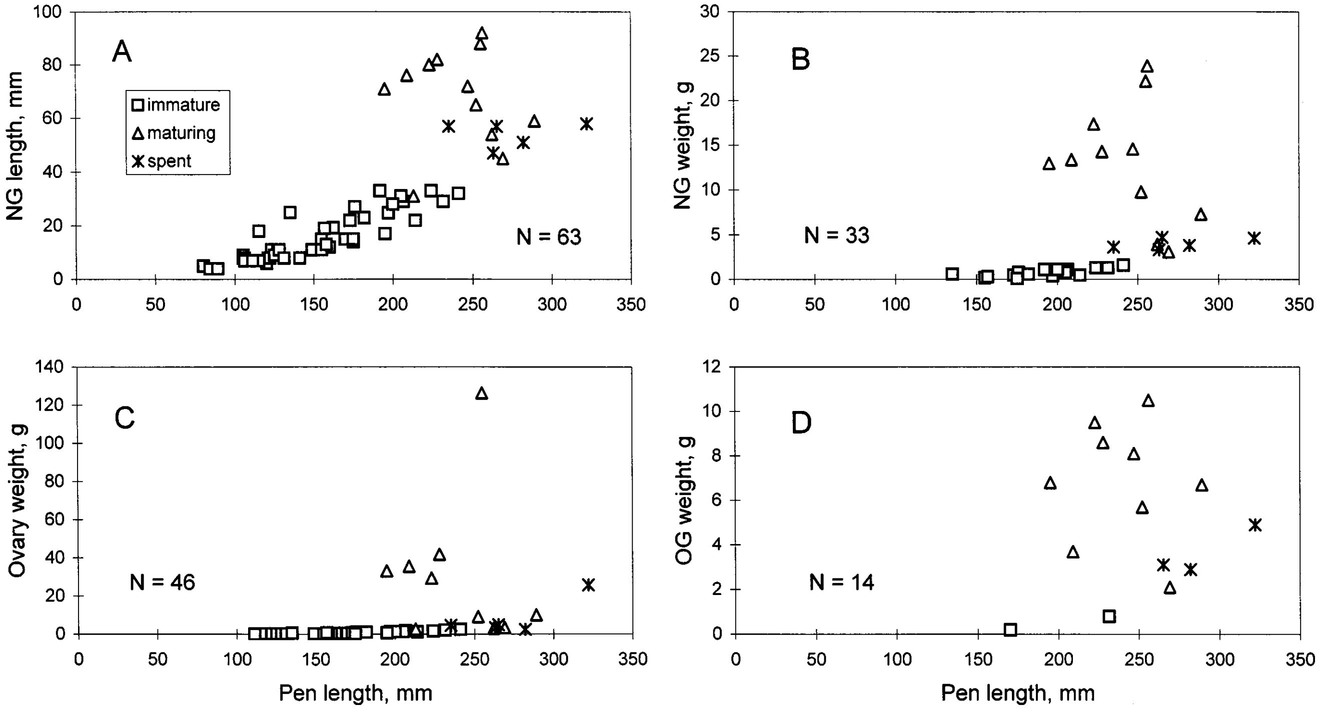
The testis was relatively small at all maturity stages, not exceeding 0.5 g in weight. Both maximum and minimum testis weights were observed in mature males, indicating a good physiological condition of the gonad in the first case and an almost spent gonad in the second case (Fig. 8B). Weight of spermatophoric complex of organs (SCO) increased with the PL, attaining maximum values (4.2 g) in large mature males (Fig. 8C).

The gonadosomatic index of males gradually decreased during ontogenesis (Fig. 9A) due to the almost constant weight of the gonad in mature males, whereas the maturity index gradually increased mainly due to an accumulation of physiologically mature spermatophores in the Needham's sac of the SCO (Fig. 9B).

Discussion

The length-weight relationship obtained previously for juvenile and immature *G. fabricii* (< 150 mm PL,

Fig. 6 The relationships between pen length and nidamental gland length (**A**) and weight (**B**), ovary weight (**C**) and oviducal gland weight (**D**) for females of *Gonatus fabricii*



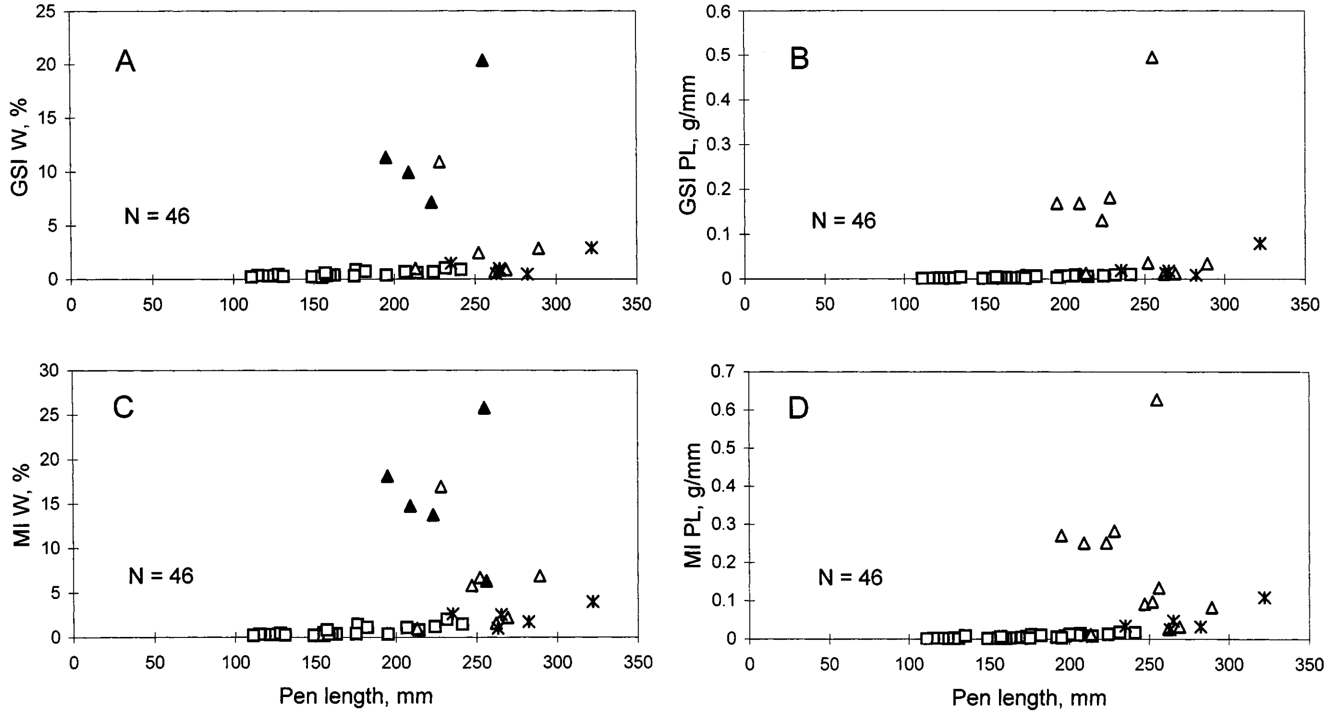


Fig. 7 Gonadosomatic index (**A**), ratio gonad weight to pen length (GSI PL) (**B**), maturity index (**C**) and ratio sexual system weight to pen length (**D**) for females of *Gonatus fabricii* (black triangles indicate maturing females which had been caught without a tail, and their total body weight was calculated). Symbols are the same as in Fig. 6

Kristensen 1984) was very similar to our values which included maturing and spent individuals. The low value of the power coefficient "*b*" in both studies (2.43 and 2.47, respectively) indicates that the body of *G. fabricii* becomes more elongate during ontogenesis, which is a characteristic feature of many other North Pacific gonatids (Okutani et al. 1988). However, the proportion of the "tail" on the posterior tip of the mantle does not differ in adult (13%, our data) and juvenile squid (approximately 11%, Wiborg 1982).

Ontogenetic changes in body shape and, correspondingly, in different morphometric parameters (i.e. lengths of different parts of the body) of juvenile and immature (< 150 mm ML) *G. fabricii* have been well described in the literature (Kristensen 1981a, 1982). Therefore, we used only weight indices to describe the hitherto poorly understood maturation process both in males and females of *G. fabricii*. It is known that one of the main functions of the squid digestive gland is to provide an effective storage for the energy which is spent on generative growth during maturation (Nesis 1987). It is notable that the inflection point of the digestive gland growth of *G. fabricii* practically coincides with the start of the growth of all parts of the sexual system in females (maturity stage II–III, 180–190 mm PL), and with the spermatophore accumulation in the Needham's sac in males (maturity stage V, 150–160 mm PL).

Body proportions and integrity of the mantle and fins do not change in maturing and mature males. They remain capable of active locomotion, which is necessary for chasing prey (their tentacles are not lost) and mating, similar to mature males of other gonatid species (Okutani et al. 1988; Nesis 1997). In contrast, maturing females start to convert to inactive planktonic animals, losing their tentacles and suckers on the 4th arms, and markedly increasing the weight of their mantle and fins; this, however, is not due to somatic growth, but to degeneration of muscle tissues (gelatinization). Such a remarkable gelatinous transformation of the body flesh has also been observed in maturing, mature and spent females of other pelagic gonatids such as *Gonatus madokai*, *Gonatopsis makko* and *Gonatopsis octopedatus* (Nesis 1997). Females of neritic gonatids (*Berryteuthis magister*, *Gonatopsis borealis*), as well as those of nektonic ommastrephids and onychoteuthids, do not have degenerated bodies at the mature stage. Only in spent and, sometimes, already spawned mature animals do the mantle and fins become thin and flaccid, with degenerated muscle fibres, as in the ommastrephid *Illex argentinus* (Nigmatullin 1989) and onychoteuthid *Onychoteuthis banksi* (= *Chaunoteuthis mollis*, Arkhipkin and Nigmatullin 1997).

Females of *Gonatus fabricii* mate by maturity stage III (at the start of maturation) unlike females of most other squids, which mate only after complete maturation (*B. magister*, Nesis 1997; many ommastrephids and loliginids, Mangold 1987). The process of sexual system development and the accumulation of ripe sexual products in both sexes of *Gonatus fabricii* generally followed the characteristic pattern of most decapods: gradual growth of the different parts of the reproductive system during maturation, sharp increase of reproductive indices at maturity stage V, followed by an even sharper decrease in spent animals (Mangold 1987). Females of *Gonatus fabricii* have high values of both GSI and maturity indices compared to other North Pacific gonatids (Nesis 1997), which appear to be even higher if the relation between the gonad weight and pen length is taken into account (because of breakdown of the body muscles which diminishes the "real GSI"). Owing to the early gelatinization of the body, massive accumulation of ripening oocytes in the ovaries of maturing females and their practical absence in spent females, *Gonatus fabricii* appears to be a terminal spawner like other species with an early degeneration of the body (*Gonatopsis octopedatus*, Nesis 1997; *Moroteuthis ingens*, Jackson and Mladenov 1994). Females with a late degeneration of the body usually spawn several times before death (*B. magister*, Nesis 1997; *I. argentinus*, Nigmatullin 1989).

Males of *Gonatus fabricii* are characterized by a rather unusual feature among squid; the weight of their testis remains practically constant in maturing and mature specimens. Testis weight in males of most other squid increases considerably during maturation and sharply decreases at the end of maturity stage V (Mangold 1987; Jackson and Mladenov 1994). Probably, such an uncommon feature can be explained by the slow and prolonged functioning of both testis and spermatophoric gland in producing spermatophores, and their long accumulation in the Needham's sac.

Based both on our data and data available from the literature on ontogenetic changes in body shape, weight and reproductive indices (Kristensen 1982, 1983, 1984; Bjørke and Hansen 1996), it is possible to subdivide the whole ontogenesis of *Gonatus fabricii* into several well-distinguished phases:

1. Planktonic epipelagic paralarvae (3.5–15 mm PL). They have a bell-shaped mantle and small fins, and empty stomachs (probably due to high digestive rates). They occur solely in epipelagic waters and do not have marked vertical migrations (Nesis 1965; Kristensen 1983).
2. Micronektonic epipelagic juveniles (15–65 mm PL). Their body acquires a roughly torpedo-like form with wide fins. Active feeding is observed during this ontogenetic phase; stomachs of almost all juveniles were full of food. At the end of the phase squid start to descend to mesopelagic waters (Nesis 1965; Kristensen 1983; Bjørke 1995).
3. "Swimming stomachs" (nektonic mesopelagic immature squid, 65–130 mm PL). After descending to mesopelagic waters, squid continue active feeding,

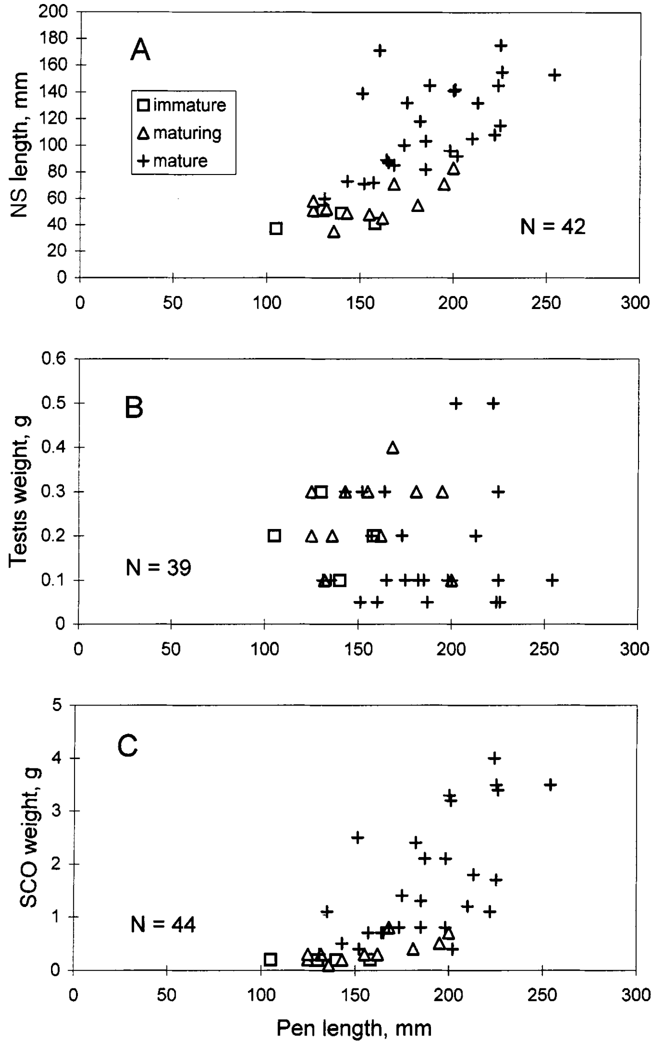
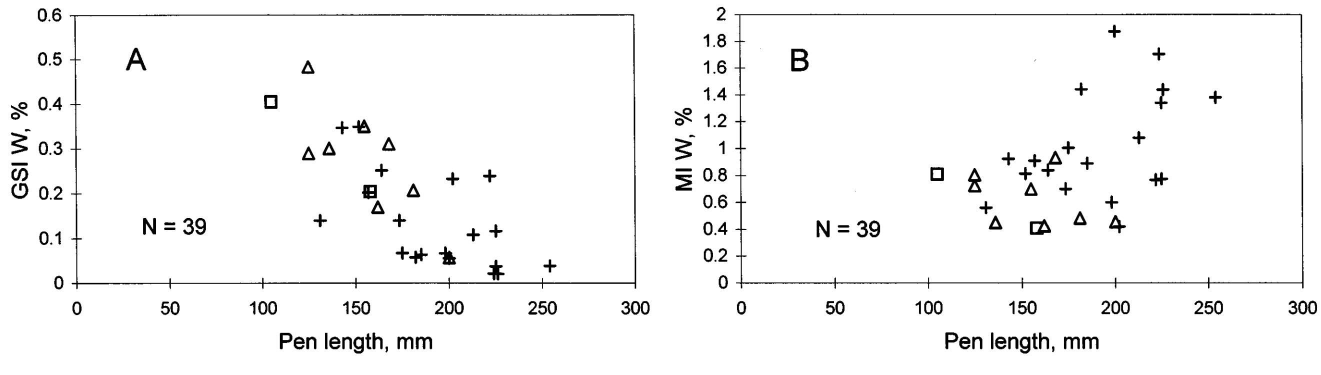


Fig. 8 The relationships between pen length and Needham's sac length (*NS*) (**A**), testis weight (**B**) and spermatophoric complex of organs (*SCO*) (**C**) for males of *Gonatus fabricii*

Fig. 9 Gonadosomatic index (**A**) and maturity index (**B**) for males of *Gonatus fabricii*. Symbols are the same as in Fig. 8



and usually their stomachs are full of food probably because of low digestive rates due to cold ambient temperatures (mean stomach index 3–4% BW).

4. "Swimming livers" (nektonic meso- and bathypelagic immature females and maturing and mature males of 130–200 mm PL). This phase is characterized by maximum rates of energetic storage in the digestive gland. Squid have a rocket-shape body, and the main part of their mantle cavity is occupied by the enlarged digestive gland (sometimes more than the mantle in weight).
5. "Swimming rockets" (nektonic bathypelagic mature males > 160 mm PL). The digestive gland decreases in weight due to diverting its nutritive substances to generative growth. Males remain active swimmers until the end of their life probably due to the necessity to seek females and mate with them.
6. "Floating dirigibles" (planktonic bathypelagic maturing, mature and spent females, > 200 mm PL). The digestive gland decreases in weight as in males. In this phase, females cease feeding (all stomachs were empty), and lose their tentacles and suckers on the arms. Their mantle and fins become gelatinous and relatively thicker compared to those of immature females due to a disintegration of muscle tissues and their "watering". Because of the tissue breakdown, the females lose their capability for active locomotion, their specific density decreases, and they float in the water column like dirigibles. They also mate at this phase.

The reasons for the gelatinous transformation of the body in maturing and mature females of pelagic gonatids have been unclear. Recently, it has been found that they possess a unique feature among decapod cephalopods, i.e. egg "breeding" (like most octopods; Mangold 1987). Spent females of oceanic gonatids *Gonatopsis* spp. (Okutani et al. 1995) and *Gonatus onyx* (B.A. Seibel, F.G. Hochberg, D.B. Carlini, unpublished work) were found with and (possibly) nesting egg-masses in their arms. In these egg-masses, the eggs were dipped into either a blackish or brownish secretion, probably from the nidamental glands (B.A. Seibel, F.G. Hochberg, D.B. Carlini, unpublished work). Similar egg-masses were found together with spent females of *Gonatus fabricii* off northern Norway, but none of the females carried these egg-masses probably because of detachment during the tow (Bjørke et al. 1997).

The dense secretion of the nidamental glands is possibly the main reason for the gelatinization of mature and spent females in pelagic gonatids. Both the extremely cold bathypelagic waters (from −0.68 to 0.84°C) and relatively large eggs of *Gonatus fabricii* (4.05–5.91 mm) (Bjørke and Hansen 1996; Bjørke et al. 1997) lead to a very long period of embryonic development (ca. 1 year, as calculated from the equation by Laptikhovsky 1991). Egg-masses of pelagic gonatids would sink into deep bathypelagic layers due to their negative buoyancy because of the dense secretion of the nidamental glands unless they were carried in the arms of "brooding", positively buoyant, gelatinous females. The females obviously cannot protect their egg-masses from predators, but they may passively support them at a certain depth until hatching of the paralarvae. Thus, females play a role of gelatinous "dirigible" (a float) for their egg-masses, which is usually accomplished by the gelatinous secretion of the nidamental glands during egg laying of pelagic ommastrephids and *Thysanoteuthis rhombus* (Mangold 1987). Our hypothesis explains the marked sexual dimorphism in mature pelagic gonatids; males do not have to carry the egg-masses and therefore they do not transform their body into a gelatinous condition. Females of near-bottom gonatids (*B. magister*, *Gonatopsis borealis*) attach their egg-masses to the bottom (Nesis 1997) and because of this, gelatinization of their body has not evolved.

It is possible that *Gonatus*-eating whales and dolphins (review: Bjørke and Gjøsæter 1998) are attracted to feed on the abundant concentrations of easily caught non-active gelatinous females of *Gonatus fabricii* in their spawning regions instead of hunting the active non-aggregated squid during the feeding season.

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