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II. Species Accounts.

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Cephalopod biology and fisheries in European waters: species accounts

Gonatus fabricii

Boreoatlantic armhook squid

19 *Gonatus fabricii* (Lichtenstein, 1818)

Uwe Piatkowski, Karsten Zumholz, Patrizia Jereb, Sonia Seixas, Daniel Oesterwind, Evgenia Lefkaditou, A. Louise Allcock, Graham J. Pierce, and Oleg Katugin

Common names

Encornet atlantoboreal (France), gonalura atlantoboreal (Spain), Boreoatlantic gonate squid or Boreoatlantic armhook squid (UK) (Figure 19.1).

Synonyms

Onychoteuthis fabricii Lichtenstein, 1818, *Onychoteuthis amoena* Möller, 1842, *Cheloteuthis rapax* Verrill, 1881 in 1880–1881. See Kristensen (1981a) for full details of synonomy.

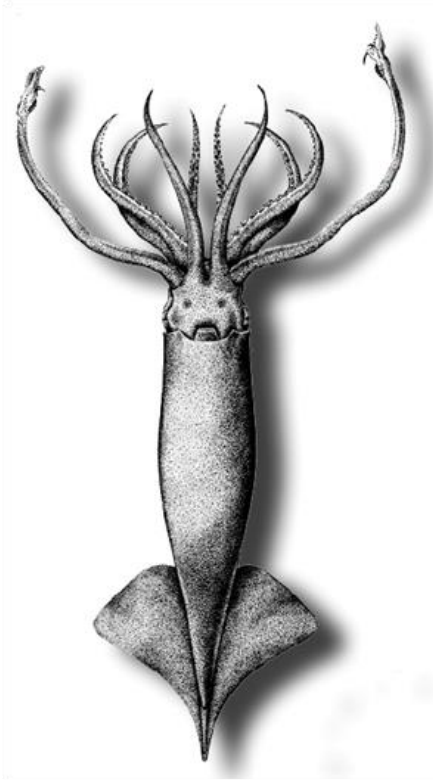

Figure 19.1. *Gonatus fabricii*. Ventral view. From Kristensen (1981a).

19.1 Geographic distribution

The boreoatlantic gonate squid, *Gonatus fabricii* (Lichtenstein, 1818), is widely distributed in offshore Arctic and subArctic waters of the North Atlantic, and its distribution also extends into the western Barents Sea (Arctic Ocean). In the Northeast Atlantic, it is found in the Norwegian Sea, westwards around Greenland to Baffin Bay and the Newfoundland Basin, and southwards to southern Cape Cod in the Northwest Atlantic (Nesis, 1971; Wiborg, 1979b; Kristensen, 1981a, 1983; Bjørke and Gjøsæter, 2004; Roper *et al.*, 2010b; Golikov *et al.*, 2013) (Figure 19.2).

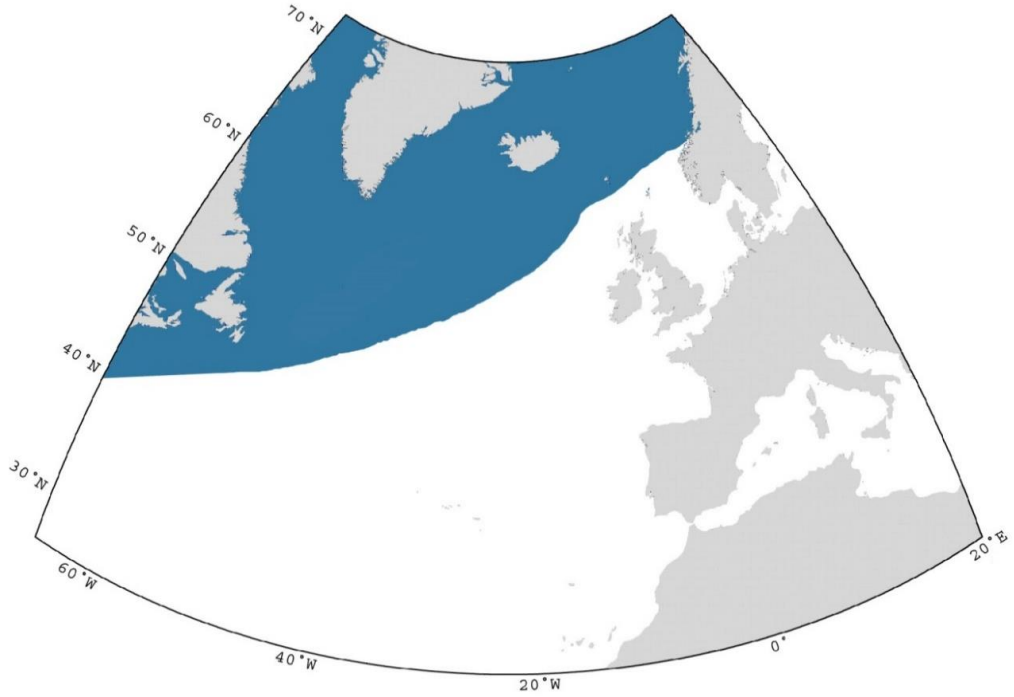

Figure 19.2. ***Gonatus fabricii*****. Geographic distribution in the North Atlantic.**

19.2 Taxonomy

19.2.1 Systematics

Coleoidea – Decapodiformes – Oegopsida – Gonatidae – *Gonatus.*

19.2.2 Type locality

Amerdloq Fjord, Holsteinsborg (ca. 67°N 54°W), West Greenland, 457–521 m [fide Kristensen and Knudsen (1983)].

19.2.3 Type repository

Kobenhavns Universitet, Zoologisk Museum, Universitetsparken 15, DK 2100 Copenhagen, Denmark. Neotype [fide Kristensen (1981a: 66)].

19.3 Diagnosis

19.3.1 Paralarvae

Paralarvae are characterized by the presence of a pair of round or oblong chromatophores on the ventral surface of the head, slightly anterior to the ocular axis, and by a dorsal pad on the funnel organ with an inverted V-shape, with straight lateral sides (Kristensen, 1981a; Falcon *et al.*, 2000). The presence of chromatophores can be used as the primary character to identify even very small specimens (ML <3.6 mm), in which the funnel organ is too small to verify confidently its shape (Falcon *et al.*, 2000). The onset of formation of hooks from suckers, both on the tentacular clubs and arms I–III, is at ML >20 mm (Falcon *et al.*, 2000). This seems to be a good character to define the end of what is now termed the paralarval phase and the beginning of the juvenile phase in gonatids (Young, 1972; Kristensen, 1977a); in fact, the presence of hooks is likely to indicate a change in feeding habits and, therefore, a change in the ecological position of the squids.

19.3.2 Juveniles and adults

Figure 19.3. *Gonatus fabricii*. Tentacular club showing the two larger hooks. Photo: Karsten Zumholz.

Figure 19.4. *Gonatus fabricii*. Lower beak (left) and upper beak (right). Photo: Uwe Piatkowski.

In juveniles, one large hook is generally present on the club, with three small hooks proximal to it and a moderately large hook distal to it (see Figure 19.3); several small suckers are present on both dorsal and ventral sides of the club, especially at the proximal end, where they form a large cluster (Kristensen, 1977a; Falcon *et al.*, 2000).

Adult maximum mantle length is 385 mm, which was reported for a female in the Barents Sea (Sennikov *et al.*, 1989), although the largest individual recorded by Arkhipkin and Bjorke (2000) was 322 mm ML. The mantle is long, slender, conical, slightly wider at its midpoint, tapering to a sharp point posteriorly, its muscular part ending at the conus, with a fleshy, tapered column extending posteriorly as the tail. Fins are heart-shaped, with anterior lobes free and lateral margins rounded, their length <50% of ML, their width slightly less than their length. Tentacular clubs are small and slender, their length ca. 12–20% of ML, with one very large, central hook followed proximally by three small hooks and distally by one moderately large hook. Nine to 13 tetraserial rows of suckers and hooks are present on the proximal half of arms III, and 14–17 tetraserial rows of suckers (no hooks) on the proximal half of arms IV (Kristensen, 1981a; Roper *et al.*, 2010b). Note that tetraserial armature on the arms is characteristic of the Gonatidae (Roper *et al.*, 1969). Beaks are illustrated in Figure 19.4.

19.4 Remarks

Gonatus fabricii and *G. streenstrupi* are similar species, and confusion between the two may arise in areas of the (North) Atlantic where they overlap, such as the Irminger Sea (Kristensen, 1981a). Whereas *G. fabricii* is thought to be the most abundant squid in the high latitudes of the Atlantic and the only native pelagic squid in the Arctic (Nesis, 2001; Golikov *et al.*, 2013), *G. steenstrupi* lives in the boreal zone of the Atlantic, especially in the eastern part off the United Kingdom, Ireland, and Spain (Kristensen, 1981a). *Gonatus steenstrupi* was also the most abundant squid in a comprehensive collection of oceanic cephalopods from an RV "G. O. Sars" expedition in summer 2004 to the northern and central regions of the Mid-Atlantic Ridge, including the Reykjanes Ridge and the Charlie Gibbs Fracture Zone (Vecchione *et al.*, 2010).

The two species can be separated on the basis of the two large chromatophores present on the ventral surface of the head in *G. fabricii*, and absent in *G. steenstrupi*; this character can also be used to distinguish paralarvae of the two species (Falcon *et al.*, 2000; Vecchione and Young, 2006). Other useful characters to separate the two species are the numbers of tentacular club hooks proximal to the large central hook: three hooks in *G. fabricii*, 4–5 hooks (the largest is the most distal) in *G. steenstrupi* (Kristensen,

1981a). A possible complication is mentioned by Boyle (2009). Vecchione and others participating in the RV "G. O. Sars" expedition in 2004 (Vecchione *et al.,* 2010) found several specimens in which one tentacular club displayed the characteristics of *G. fabricii*, whereas the other club was consistent with *G. steenstrupi.* Boyle suggests that genetic studies are needed to resolve the issue. Kristensen (1981a) also mentioned the relative size of the club as a potentially useful character: *G. fabricii* has a relatively smaller club [12–20% of pen length (PL)], and *G. steenstrupi* has a relatively larger club (20–35% of PL). As noted by Arkhipkin and Bjorke (1999), *G. fabricii* has a muscular "tail" at the posterior end of the mantle; hence, ML exceeds PL by ca. 13%. This tail is often damaged in trawl-caught animals, making it impossible to measure their dorsal mantle length. Hence, PL is often used as the standard measurement.

19.5 Life history

The life cycle of *G. fabricii* probably does not exceed 2 years. Spawning takes place from winter to summer, and females die soon after egg development is completed.

19.5.1 Egg and juvenile development

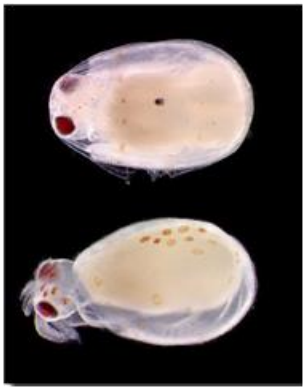

Figure 19.5. *Gonatus fabricii*. Egg and hatchling. Egg diameter 5.5 mm. Photo: Lars Are Hamre (from Bjørke and Gjøsæter, 2004).

Eggs are translucent, light blue, and roughly spherical (elliptical), with maximum egg diameter of 4–6 mm (Kristensen, 1981b; Bjørke and Hansen, 1996; Bjørke *et al.*, 1997). Nesis (1999) suggests that embryonic development takes ca. 4 months. However, this conclusion is based on a formula developed for warm-water species, and the real development time may be much longer (O. Katugin, pers. comm.). Hatching size is ca. 3 mm ML (see Figure 19.5). Paralarvae may be found widely in the water column, but usually at depths <400 m in spring and mainly within the upper 100 m in summer (Falcon *et al.*, 2000). Juveniles are found in large shoals in the uppermost 100 m of the water column over deep water (Nesis, 1965). South of the polar circle, juveniles are reported to perform upward diurnal migrations at night (Kristensen, 1977b). By the time the hook on the tentacular club starts to develop (20 mm ML), the adult proportions of the body become recognizable. At that stage, the squids are very mobile and swim like adults (Kristensen, 1977b).

19.5.2 Growth and lifespan

As in other squid species (e.g. *Illex coindetii*, Jereb and Ragonese, 1995; Arkhipkin *et al.*, 1998), different methods to investigate growth and age give different results for *G. fabricii*. Analysis of length frequency data suggests a rather long life cycle (2–3 years, Muus, 1962; Zumholz and Frandsen, 2006). Slow growth rates of 4–5 mm (Piatkowski and Wieland, 1993; Zumholz and Frandsen, 2006) and 8–9 mm month^{-1} (Kristensen 1977b, 1984) were proposed for animals from West Greenland waters. This would not be so unlikely for a polar species, given that cold-water species grow more slowly and live longer than species from lower latitudes. Statolith microstructure analysis of juveniles and immature squids revealed four growth zones, and daily, weekly, and fortnightly increment bands in the statoliths have been proposed (Kristensen, 1980).

If the assumption of 1 increment d^{-1} is true for *G. fabricii*, as has been shown for other species, based on the total number of increments counted in adult specimens, the lifespan would not exceed 2 years (Arkhipkin and Bjørke, 2000).

Sources differ as to whether the length–weight relationship differs between sexes. Arkhipkin and Bjorke (2000) reported no differences, whereas Zumholz and Frandsen (2006) found sexual dimorphism in the growth pattern (Table 19.1).

Table 19.1. *Gonatus fabricii*. Length–weight relationships in different geographic areas for females (F), males (M), and sexes combined (All). Original equations converted to $W = aML^b$, where W is body mass (g) and ML is dorsal mantle length (cm).

Region	*a*	*B*	Sex	Reference
West Greenland	0.269	2.050	F	Zumholz and Frandsen (2006)
	0.053	2.648	M	
	0.101	2.412	All	
	0.138	2.43	All	Kristensen (1984)
Norwegian Sea	0.118	2.47	All	Arkhipkin and Bjørke (1999)

19.5.3 Maturation and reproduction

Many aspects of the biology of this species have been described only relatively recently. As noted by Bjørke (2001), only seven mature specimens had been recorded and only one described in detail.

Development of the testis begins at a pen length of ca. 80–100 mm, and maturity is reached at a pen length of ca. 200 mm (Kristensen, 1983). Spermatophores measure 6–10 mm. The ovary begins to develop at a pen length of 60–90 mm and increases in weight until maturity. Spermatophores have been found attached onto the buccal membrane of maturing and ripe females, indicating head-to-head copulation (Arkhipkin and Bjørke, 1999; Zumholz and Frandsen, 2006). Individual fecundity is estimated to be ca. 10 000.

Female *G. fabricii* undergo considerable degenerative changes before spawning; the tentacles are lost, the arm and mantle tissues swell, the suckers on the arms are lost, and the animals lose their capability for active locomotion. It has been hypothesized (Arkhipkin and Bjørke, 1999) that these degenerative changes are related to the important activity of the nidamental glands in these species, i.e. the secretion of a peculiarly dense matter that envelops the eggs within the egg mass; this, in turn, would make the egg masses negatively buoyant, and bound to sink unless they are carried in the arms of "brooding", light, and positively buoyant females.

Gonatus onyx females are known to "brood" their eggs (Okutani *et al.*, 1995; Seibel *et al.*, 2000, 2005). Females use hooks on their arms to hold the egg mass, apparently contracting and extending the arms repeatedly to aerate the eggs (Siebel *et al.*, 2005). This may also be the case in *G. fabricii.* Bjorke *et al.* (1997) caught egg masses and mature females together in pelagic trawls and speculates that females may have been egg brooding.

Adult mature male *G. fabricii* show no signs of degeneration and seem likely to mate several times during their life cycle (Kristensen, 1984).

It is speculated that the squid spawn in the Norwegian Sea from winter to summer and that the eggs hatch from late March to June or July (Bjørke and Gjøsæter, 2004). Spawning is suggested to take place at great depths, in oceanic waters. As noted above, females probably brood the eggs, although free egg masses have been found among

spent females, possibly because the egg masses had become detached from the females during capture. The eggs are kept together in a single layer between two mucous membranes (Bjørke *et al.*, 1997; Bjørke and Gjøsæter, 2004). Off Greenland in the Davis Strait, hatching is believed to take place in spring and early summer, whereas the eggs hatch in Disko Bay in autumn and early winter (Kristensen, 1984).

19.6 Biological distribution

19.6.1 Habitat

Gonatus fabricii is an oceanic species that exists commonly between the surface and 500–1000 m; records from depths of 2700 m exist, however. Adults are common at the bottom and in midwater layers in Arctic and subArctic waters, whereas juveniles live within a very wide range of depths from 2000 m to the surface, to where they may undertake diel migrations. Adults hunting for prey near the surface at night are reported from West Greenland (Kristensen, 1981b, 1983; O. Katugin, pers. comm.).

19.6.2 Migrations

This species undertakes vertical migrations and, possibly, horizontal migrations. Kristensen (1977b) reports dispersal of young squid by the West Greenland Current from zone 1 to zone 2, although no other extensive horizontal migrations are reported. Variation in the barium:calcium ratio in the statoliths of this species suggests that juveniles inhabit surface waters and that larger specimens move to deeper waters. In addition, increases in the uranium:calcium and strontium:calcium ratios towards the outer part of the statolith suggested migration of adult squid into colder water (Zumholz *et al.*, 2007b).

19.7 Trophic ecology

19.7.1 Prey

Juveniles feed on copepods, euphausiids, amphipods, pteropods, and chaetognaths (Table 19.2). Adults can feed on prey larger than themselves (Kristensen, 1984), and the diet consists of macroplanktonic crustaceans (amphipods, euphausiids), fish [e.g. capelin (*Mallotus villosus*), redfish (*Sebastes marinus*), and lanternfish], and cephalopods (occasionally including bottom-dwellers such as octopuses). Cannibalism also takes place (Nesis, 1965; Zuev and Nesis, 1971; Wiborg, 1980; Kristensen, 1984). Although crustaceans are the main prey of both juveniles and adults, the importance of fish and cephalopods in the diet increases with age. Fish start to become more important in the diet after the hooks on the tentacular clubs have developed (Kristensen, 1984).

Table 19.2. Prey composition of *Gonatus fabricii*, as known from studies in different regions of the eastern Atlantic (compiled from Nesis, 1965[1]; Zuev and Nesis, 1971[2]; Wiborg; 1980[3], 1982[4], 1984[5]; Kristensen, 1984[6]).

Taxon	Species
Osteichthyes	
Myctophidae	indet. lanternfish[2]
Sternoptychidae	*Maurolicus muelleri* (pearlside)[4]
Osmeridae	*Mallotus villosus* (capelin)[6]
Sebastidae	*Sebastes norvegicus* (as *S. marinus*) (redfish or rose fish)[3]
Crustacea	
Decapoda	*Pasiphaea* sp.[6], indet. shrimps[3,6]

Euphausiacea	*Meganyctiphanes norvegica*[3,4,5], *Thysanoessa longicaudata*[1], indet.[2]
Mysida	indet.[6]
Amphipoda	*Hyperia galba*[1], Hyperiidae indet.[6], *Parathemisto abyssorum*[4], *Parathemisto* spp.[3,4,5], *Pseudalibrotus* spp.[1], *Themisto gaudichaudi (as P. gaudichaudii)*[4], *T. libellula (as P. libellula)*[4], indet.[3]
Isopoda	indet.[3,6]
Copepoda	*Calanus finmarchicus*[1,3,4,5], *C. hyperboreus*[1,3], *Euchaeta* sp.[5], *Paraeuchaeta norvegica*[1,3,4], *Metridia* spp.[1], *Temora* sp.[5], indet.[3]
Cephalopoda	*Gonatus fabricii*[2,3,4,6], Octopoda indet.[2], Oegopsida indet.[2], indet.[6]
Gastropoda	*Clione limacina*[3], *Limacina retroversa* (retrovert pteropod)[1,3,4,5]
Chaetognatha	*Eukrohnia* spp.[3,4,5], *Sagitta* spp.[1,3,4,5]

19.7.2 Predators

Gonatus fabricii is one of the most abundant food resources for virtually all top predators in the North Atlantic (Bjørke, 2001; Bjørke and Gjøsæter, 2004; Table 19.3) and a key species in the eastern Arctic foodweb (Gardiner and Dick, 2010). It is taken by large pelagic cephalopods and fish, seabirds, and marine mammals (Table 19.3). Beaks in stomach contents of predators are often only identified to genus (i.e. *Gonatus* sp.), and the inference that it is *G. fabricii* that has been eaten then depends to some extent on knowledge of its distribution and abundance. However, as noted above under **Remarks**, the distribution overlaps with that of *G. steenstrupii*, and both species are found around Iceland and southeast Greenland (see maps in Frandsen and Zumholz, 2004; Jereb and Roper, 2010), so there is scope for misidentification.

Table 19.3. Known predators of *Gonatus fabricii* in the North Atlantic.

Taxon	Species	References
Cephalopoda	European flying squid (*Todarodes sagittatus*)	Wiborg (1972)
Osteichthyes	Atlantic cod (*Gadus morhua*)	Grimpe (1933)
	Atlantic salmon (*Salmo salar*)	Lear (1980)
	Deep water arrowtooth eel (*Histiobranchus bathybius*)	Martin and Christiansen (1997)
	Greater amberjack (*Seriola dumerili*)	Matallanas *et al.* (1995)
	Greenland halibut (*Reinhardtius hippoglossoides*)	Dawe *et al.* (1998), Hovde *et al.* (2002), Michalsen *et al.* (1998)
	Redfish (*Sebastes marinus*)	Nesis (1965)
	Roundnose grenadier (*Coryphaenoides rupestres*)	Bergstad *et al.* (2010)
Aves	Atlantic puffin (*Fratercula arctica*)	Falk *et al.* (1992)
	Common murre (*Uria aalge*)	Barrett *et al.* (1997)
	Northern fulmar (*Fulmarus glacialis*)	Lydersen *et al.* (1989), Garthe *et al.* (2004)
	Thick-billed murre (*Uria lomvia*)	Barrett *et al.* (1997)
Pinnipedia	Harp seal (*Phoca groenlandica*)	Lydersen *et al.* (1991), Potelov *et al.* (2000), Haug *et al.* (2004)

	Hooded seal (*Cysophora cristata*)	Potelov *et al.* (2000), Bjørke (2001), Haug *et al.* (2004)
Cetacea	Blue whale (*Balaenoptera musculus*)	Hjort and Ruud (1929)
	Northern bottlenose whale (*Hyperoodon ampullatus*)	Benjaminsen and Christensen (1979), Clarke and Kristensen (1980), Lick and Piatkowski (1998), Bjørke and Gjøsæter (1998), Bjørke (2001), Hooker *et al.* (2001), Santos *et al.* (2001c)
	Cuvier's beaked whale (*Ziphius cavirostris*)	Blanco *et al.* (1997), Santos *et al.* (2001d)
	Long-finned pilot whale (*Globicephala melas*)	Nesis (1965), Desportes and Mouritsen (1988, 1993), Bjørke (2001)
	Narwhale (*Monodon monoceros*)	Grimpe (1933), Laidre and Heide-Jørgensen (2005)
	Sperm whale (*Physeter macrocephalus*)	Clarke and Macleod (1976), Clarke (1997), Bjørke and Gjøsæter (1998), Santos *et al.* (1999, 2002), Bjørke (2001), Simon *et al.* (2003), Mendes *et al.* (2007)

19.8 Fisheries

Gonatus fabricii is considered to have some fishery potential. It is the most abundant squid of the Arctic and subArctic waters of the North Atlantic, it has a high lipid content, the flesh, at least of younger animals, has a good consistency, and the species attains a desirable size (Nesis, 1965; Wiborg, 1979b; Kristensen, 1984; Frandsen and Wieland, 2004; Roper *et al.*, 2010b). According to Kristensen (1984), the very high lipid content of the digestive gland (ca. 63%) makes it suitable for industrial use as well, although the abundance of lipases in the midgut may be problematic (see Okuzumi and Fujii, 2000). Piatkowski and Wieland (1993) suggested that the species might be of commercial interest, based on the abundance of early life stages of *G. fabricii* off West Greenland. Bjørke and Gjøsæter (1998) suggested that there was surplus production of this species in the Norwegian Sea, which could be exploited by the fisheries. However, because females undergo significant tissue degradation as they mature (Arkhipkin and Bjorke, 1999), fisheries might logically target immature animals, although it is possible that mature females could be marketed for animal feeds, while retaining males for human consumption.

As noted by Frandsen and Wieland (2004), there have been at least two unsuccessful experimental fisheries for this species. In 1998, an experimental fishery targeted adult *G. fabricii* in the Norwegian Sea using a pelagic trawl, but catches were small (no more than 10 kg haul^{-1}). An experimental bottom-trawl fishery for cephalopods conducted off West Greenland during a period of two months in 2003 achieved a total catch of oegopsid squid (probably *Gonatus* sp.) of only 4.7 kg. However, *G. fabricii* is used by Greenland Inuit as bait in the cod and shellfish fisheries and for human food. It is also regularly taken as bycatch in shrimp trawls in Greenland (Frandsen and Wieland, 2004; Roper *et al.*, 2010b).

19.9 Stock identity

Off West Greenland, at least two distinct populations exist (Disko Bay and Davis Strait), with differences in time of spawning and morphometric measurements (Kristensen, 1982). Another, probably separate, population is found in the Norwegian Sea

(Bjørke and Gjøsæter, 2004). However, genetic methods for stock separation have not yet been applied to *G. fabricii*.

19.10 Future research, needs, and outlook

Considering the possible fishery potential of this species, improved knowledge on distribution, aggregation patterns, and migrations would be useful. Molecular genetic identification of remains in predator stomach contents would supplement the (incomplete) information on identity available from beaks.