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Fisheries Research 52 (2001) 113–120

FISHERIES RESEARCH

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Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea

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Abstract

Gonatus fabricii is the most abundant squid of the Arctic and sub-Arctic waters of the North Atlantic and, during the summer months, young specimens can be found in the upper 60 m over large areas of the Norwegian Sea. In the summer of 1994, the biomass of young *G. fabricii* in this area was calculated to be at least 1.5 million tons. When the young squids reach a mantle length (ML) of 50–60 mm, they disappear from the surface and can be found at depths greater than 400 m. The life span of both sexes probably does not exceed 2 years, and the largest specimen ever recorded was a female of 385 mm ML. The biomass production of this species represents a considerable food resource and their consumption by known predators such as sperm whales (*Physeter macrocephalus*), northern bottlenose whales (*Hyperoodon ampullatus*), long-finned pilot whales (*Globicephala melaena*) and hooded seals (*Cystophora cristata*) is discussed. It is concluded that the distribution of *G. fabricii* in the Norwegian Sea and its importance as food for sperm whales and northern bottlenose whales could, to a great extent, explain the presence of these species in the Norwegian Sea.

Keywords: *Gonatus fabricii*; Norwegian Sea; Biomass; Predation

1. Introduction

Gonatus fabricii is the most abundant squid of the Arctic and sub-Arctic waters of the North Atlantic (e.g. Nesis, 1965; Kristensen, 1981a, 1983). It was studied intensively in the 1980s. In his work on the biology of *G. fabricii* in Greenland waters, Kristensen (1983) concludes: "*G. fabricii* hatch at a size of 0.3 cm PL (pen or gladius length). As juveniles of 0.3–4.0 cm, the species lives in shoals in the uppermost 80 m of the water column. At increasing size they are found deeper, and as sub-adults and adults they live above the bottom from 200 m downwards, but migrate upwards at night. Growth is about 8 mm/month and they reach a size of about 10 cm PL in the first year."

Until 1995, only seven mature specimens of *G. fabricii* had been recorded and only one specimen described in detail (Kristensen, 1981b, 1984; Sennikov et al., 1989). These specimens were recorded as being caught at depths varying from 160 to 2700 m. In 1995, three mature males and two mature females were caught with a pelagic trawl at depths between 270 and 820 m in an area off Andenes, with a bottom depth of 1350 m (Fig. 1) (Bjørke and Hansen, 1996).

In the Norwegian Sea, larger *G. fabricii* is one of the main items in the diet of sperm whales, bottlenose whales, and narwhals, and is also consumed by pilot whales, white whales, Sowerby's whales and other cetaceans, harp seals, hooded seals, seabirds, cod, saithe, sea perch, the Greenland shark, grenadiers,

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0165-7836/01/$ – see front matter
PII: S0165-7836(01)00235-1

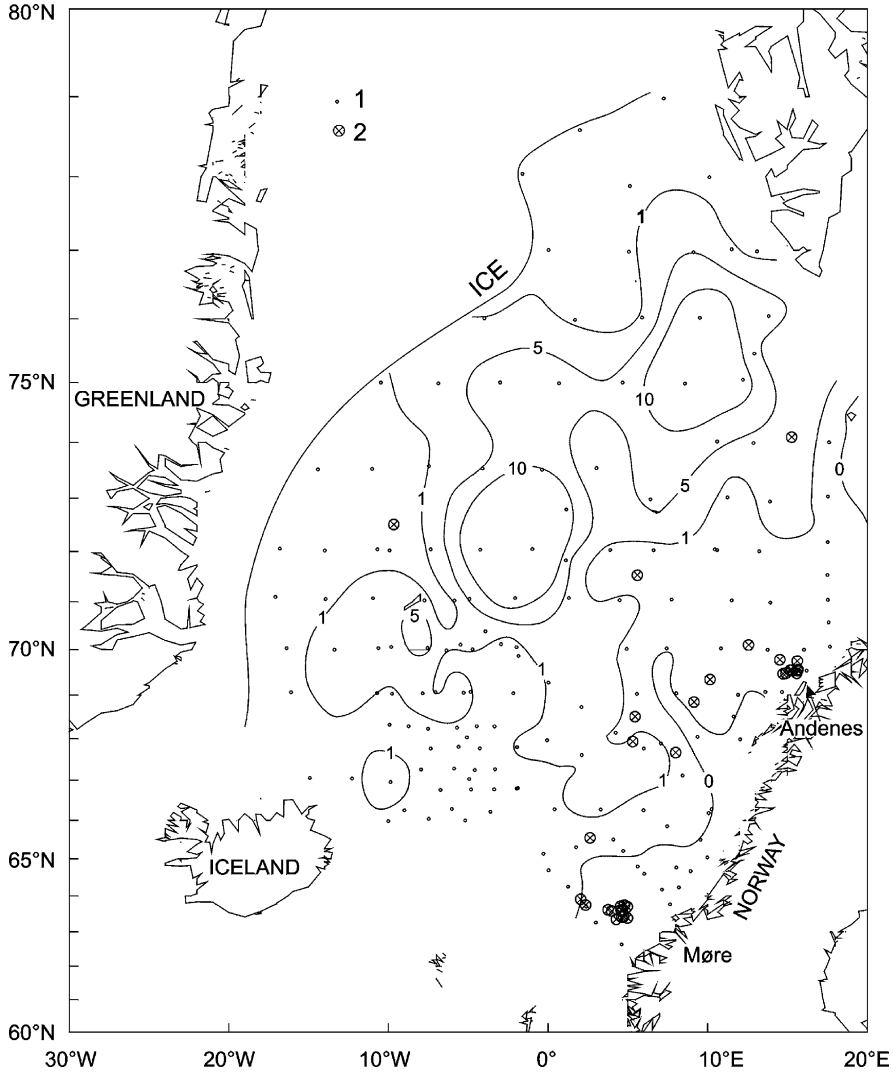

Fig. 1. Distribution of young *G. fabricii* during summer 1994. Isolines show catch of *G. fabricii* in kilograms per 30 min trawl haul in the surface layers. Symbols: 1, trawl stations in 1994; 2, recordings of *G. fabricii* larger than 200 mm ML in the Norwegian Sea from Norwegian investigations and from the literature (Kristensen, 1981a,b; Sennikov et al., 1989).

blue ling and Greenland halibut (Nesis, 1965; Kristensen, 1983; Wiborg et al., 1984; Santos et al., 1999).

Recently, abundance estimation of whales has been carried out in the Norwegian Sea (Anon., 1998). The present paper reviews current knowledge about the biology of *G. fabricii* and uses the new information on the abundance of its main predators to evaluate its ecological importance as food in the Norwegian Sea.

2. Biology of *G. fabricii*

2.1. Distribution

G. fabricii is found in offshore Arctic and sub-Arctic waters of the northern North Atlantic from the Newfoundland Basin, around Greenland and eastwards to the Barents Sea (Kristensen, 1981a, 1983; Roper et al., 1984; Nesis, 1987).

2.2. Vertical distribution of early stages G. fabricii

In the Norwegian Sea, smaller *G. fabricii* (<50 mm) appear in the surface layers during May. The distribution of *G. fabricii* in the upper 30 m during the summer 1994 is shown in Fig. 1. At a dorsal mantle length of 50–60 mm (ML), the specimens disappear from the surface layers, although smaller specimens can be found there until September (Bjørke, 1995).

2.3. Growth

Arkhipkin and Bjørke (1999, 2000) found that males started to mature and became mature at lengths between 130 and 200 mm PL and that females were maturing, mature and spent at lengths >200 mm PL. During this phase, the females' mantle and fins become gelatinous and relatively thicker compared to those of immature females due to a disintegration of muscle tissue and their absorption of sea water. Because of the flaccid tissue, the females have lost their capability for active locomotion, they have reduced specific density, and float in the water column like an air ship. They also mate during this phase. Dorsal mantle length exceeds the pen length by about 13% both in males and females (Arkhipkin and Bjørke, 1999, 2000). The life span of both sexes probably does not exceed 2 years (Arkhipkin and Bjørke, 2000). The largest specimen ever recorded was a female of 385 mm ML (Sennikov et al., 1989).

2.4. Vertical distribution of larger G. fabricii

During the preliminary sampling in 1997 off Andenes, individuals larger than 200 mm ML were found only at depths greater than 1000 m. The sampling took place during 24 h daylight (Bjørke and Gjøsæter, 1998). *G. fabricii* larger than 200 mm ML have, however, been sampled in shallower depths (Sennikov et al., 1989) and, during a cruise in April 1998, *G. fabricii* larger than 200 mm DL were found as shallow as 400 m during both day and night (Bjørke and Gjøsæter, 1998). This was at the bottom of a scattering layer extending from 250 to 400 m (Skjoldal et al., 1993). However, *G. fabricii* larger than 200 mm ML were recorded at all depths from 400 m down to 1200 m, which was the maximum depth fished (Bjørke and Gjøsæter, 1998).

2.5. Hatching and spawning area

Nesis (1965) assumed that *G. fabricii* did not make any significant spawning migration. Fig. 1 shows records of mature *G. fabricii* by other authors (Kristensen, 1981a,b; Sennikov et al., 1989) and of specimens larger than 200 mm ML sampled in 1995–1998. Larger *G. fabricii* seem to be widely distributed over the Norwegian Sea, and are usually caught wherever a trawl haul is made at depths of 1000 m or greater (Bjørke and Gjøsæter, 1998). This distribution of larger specimens and the distribution of younger specimens (Fig. 1) indicate that spawning and hatching take place over large areas. Wiborg (1979) suggested that areas with high abundance of bottlenose whales could be spawning grounds for *G. fabricii* since it is the main food item for bottlenose whales (Fig. 2).

2.6. Hatching period

By back-calculating the length distribution, Bjørke (1995) suggested that hatching took place during most of the year with a maximum in January–February. Specimens of *G. fabricii* smaller than 10 mm ML; i.e. less than 1 month old, have been recorded in plankton sampled off the Norwegian shelf in January, April and July (B. Endresen, IMR, pers. comm.). Bjørke et al. (1997) found eggs of *G. fabricii* off Andenes (Fig. 1) in July.

2.7. Shoaling

Nesis (1965) and Kristensen (1983) reported that *G. fabricii* is a shoaling squid. When trawling at random in the Norwegian Sea at depths exceeding 1000 m (Fig. 1), from one to four *G. fabricii* larger than 200 mm ML were usually caught per trawl haul. From this it can be concluded that *G. fabricii* does not seem to be shoaling when it becomes larger (Bjørke and Gjøsæter, 1998).

3. Predators

Of the mammals mentioned above which prey upon larger *G. fabricii*, the abundance of sperm whales, bottlenose whales and hooded seals in the Norwegian

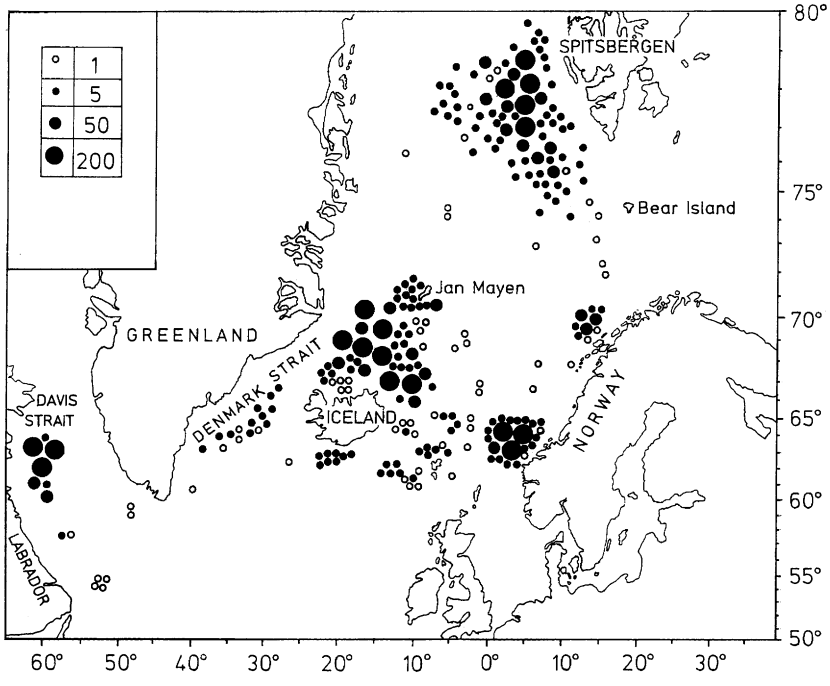

Fig. 2. Localities of northern bottlenose whales (*Hyperoodon ampullatus*) caught by Norwegian whalers in the period 1938–1972 (Benjaminsen and Christensen, 1979).

Sea can be estimated. The cephalopod consumption by sperm whales, bottlenose whales and hooded seals is further investigated. Hence it is possible to make a rough estimation of the consumption of *G. fabricii* by these predators. Arkhipkin and Bjørke (1999) suggested that *Gonatus*-eating whales and dolphins were attracted to the high concentrations of easily caught non-active gelatinous females of *G. fabricii* in their spawning sites instead of hunting single very active non-aggregated squid during their feeding season.

3.1. Sperm whales as predators

Fig. 3 shows the distribution of sperm whales in the Norwegian Sea during summer 1995 (N. Øien, IMR, pers. comm.). They are distributed all over the Norwegian Sea, with a tendency to concentrate in the eastern part. Usually cephalopods have been reported to be the main diet of sperm whales (e.g. Kawakami, 1980), but Roe (1969) found that fish was the dominant food of sperm whales caught off Iceland. This was later confirmed by Martin and Clarke (1986), who noted that squids belonging to the families Cranchiidae and Histioteutidae contributed 25 and 38% to the weight of cephalopods eaten and Gonatidae 9%.

The food of the sperm whale from the Norwegian Sea is not well investigated, but Hjort and Ruud (1929) classified it as large fish and squids. Benjaminsen (IMR, Bergen, pers. comm.) investigated the stomach contents of 12 sperm whales caught off Andenes (Fig. 1) during the summer of 1971. Two of the stomachs were empty, four contained beaks of squids only, and six both beaks and fish remains. Santos et al. (1999) found that *Gonatus* sp. constituted more than 95% of the stomach content in weight of 17 sperm whales stranded in Scotland and Denmark, and presumed to have been feeding in Norwegian waters. They suggested that concentrations of spawning *G. fabricii* probably represent an important food resource for sperm whales in the North Atlantic. This is also suggested by Clarke (1996), and it may be suggested that *G. fabricii* is the main food item for the sperm whales in the Norwegian Sea.

Christensen et al. (1992) estimated the abundance of sperm whales in the northern part of the Norwegian Sea to be 2500 individuals. Øien (IMR, Bergen, pers.

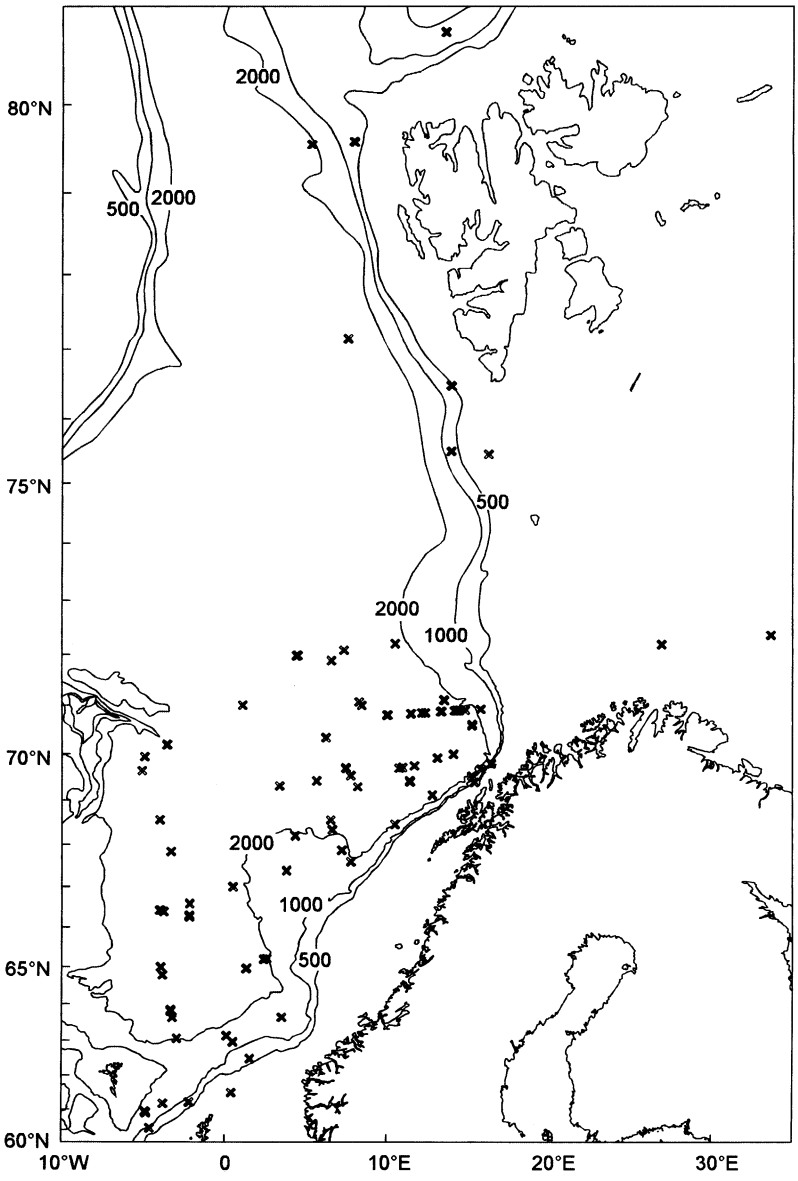

Fig. 3. Distribution of sperm whale sightings in the Norwegian Sea in 1995 (N. Øien, IMR, Bergen, pers. comm.).

comm.) estimated the average weight of the sperm whales to be around 30 t with a daily consumption of 3% of body weight, and he supposed that the sperm whales stayed in the Norwegian Sea for about 6 months/year, although there were indications that some were to be found there for a longer period. Using the numbers above and the Santos et al. (1999) estimates of *G. fabricii* in the diet (95%), the total consumption of *G. fabricii* by sperm whales is calculated to be 384 750 t/year.

3.2. Northern bottlenose whales as predators

Anon. (1998) estimated the number of northern bottlenose whales in the North Atlantic to be around 40 000 animals. *G. fabricii* is known to be the major

prey of northern bottlenose whales (Hjort and Ruud, 1929). Benjaminsen and Christensen (1979) investigated the stomach contents of 46 northern bottlenose whales caught off northeast Iceland in 1976. Of these, 40 had eaten only *G. fabricii* while four had eaten fish and *G. fabricii*. The importance of *G. fabricii* as food for this whale was confirmed by Lick and Piatkowski (1998). The northern bottlenose whale sightings for the 1995 surveys show that they were also observed outside the Norwegian Sea, i.e. in the Irminger Sea and south of Iceland (Anon., 1998). In this area the distribution of *Gonatus steenstrupi* overlaps with that of *G. fabricii* and theoretically some of the 40 000 whales could have eaten *G. steenstrupi*. Sigurjónsson and Vikingsson (1992) assumed that 95% of the prey of the northern bottlenose whales consisted of cephalopods. In the 1987 surveys, the area northeast of Iceland towards Jan Mayen had by far the greatest abundance of northern bottlenose whales (75%) (Sigurjónsson and Vikingsson, 1992). Assuming the same distribution in the 1995 surveys, this means that at least 75% of the 40 000 whales recorded in the North Atlantic were recorded in the Norwegian Sea where only *G. fabricii* is found. Estimating the number of northern bottlenose whales around Iceland and adjacent waters to be 41 625 whales, Sigurjónsson and Vikingsson (1992) estimated the consumption of cephalopods to be 650 851 t. This means that at least 480 000 t (75%) of *Gonatus* sp. eaten by the northern bottlenose whales is *G. fabricii*.

3.3. Hooded seals as predators

Hooded seals (*Cystophora cristata*) of the West Ice stock, which spend most of their life in the Norwegian Sea, may number in the order of 250 000 animals, with an average weight of 170 kg (Folkow and Blix, 1995).

Potelov et al. (1997) investigated stomach contents of hooded seals during moulting off the east coast of Greenland and found that *G. fabricii* constituted 79.2% of the prey biomass in the few non-empty stomachs. Polar cod (*Boreogadus saida*) and the amphipod *Themisto* sp. constituted 15.7 and 5.1%, respectively. During moult the seals eat very little. Folkow and Blix (1995) examined the distribution and diving behaviour of hooded seals and found that they may dive repeatedly to >1000 m, but usually dive to 100–600 m depth. After moult, the satellite-tagged seals performed excursions, lasting approximately 3–7 weeks, to such distant areas as the waters off the Faroe Islands, the Irminger Sea, north/northeast of Iceland, areas in the Norwegian Sea and along the continental edge from Norway to Bear Island. Investigations of the seals' diet in these areas have not been made, but the authors suggested that the spatial and temporal distribution of the seals off the Faroe Islands and west of Ireland correlated well with the known distribution of the blue whiting (*Micromesistius poutassou*). The tagged seals spent 600 (16%) of the almost 3800 seal days which were recorded during the tracking period, in these areas. Seal days are the number of tagged seals recorded per day multiplied by the number of days. The seals were calculated to consume 105 000 t of blue whiting during this period. The seals spent 3.8% of seal days in the Irminger Sea and the authors suggested that, in this area, the seals most likely fed on redfish (18 000 t). In the ice-covered area off east Greenland, the tagged seals spent 38% of seal days. This is much more than needed for breeding and moulting when the seal is fasting. It is thus reasonable to believe that at least 100 000 t of *G. fabricii* is consumed by the hooded seal in this area.

3.4. Long-finned pilot whales as predators

The long-finned pilot whale (*Globicephala melaena*) is known to be a squid eater (Nesis, 1965; Desportes and Mouritsen, 1993). Desportes and Mouritsen (1993) investigated the diet of pilot whales caught around the Faroe Islands. In years when the European flying squid *Todarodes sagittatus* was present, beaks of this species were found in all the stomachs, and represented 96% of the beaks recovered. *Gonatus* sp. appeared in 40% of the stomachs but contributed for only 4% of the beaks. In years when no *T. sagittatus* were landed, *Gonatus* sp. was recorded in 87% of the stomachs and represented 80% of the beaks. The *Gonatus* sp. eaten was most probably *G. fabricii* since the whales were reported to feed north of the Faroe Islands. However, the long-finned pilot whale is not common in the Norwegian Sea (Christensen, IMR, Bergen, pers. comm.). Although it most probably feeds on *G. fabricii* in the Norwegian Sea occasionally, the biomass consumed is small compared to that consumed by the sperm whale.

4. Conclusions

The epipelagic phase of the life of *G. fabricii* is relatively well-known and its ecological importance has been mentioned by Nesis (1965) and Wiborg et al. (1984). The distribution of smaller *G. fabricii* and the records of larger *G. fabricii* at depths between 400 and 1100 m indicate that larger *G. fabricii* is distributed over a greater part of the Nordic Seas. This distribution and the importance of *G. fabricii* as food for sperm whales and northern bottlenose whales could to a great extent explain the presence of these species in the Norwegian Sea. *G. fabricii* probably constitutes an important part of the food of the hooded seal.

References

Anon., 1998. Report of the scientific committee working group on abundance estimates. NAMMCO Annual Report 1997, Tromsø, pp. 173–202.

Arkhipkin, A., Bjørke, H., 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. Polar Biol. 22, 357–365.

Arkhipkin, A., Bjørke, H., 2000. Statolith shape and microstructure as indicators of ontogenetic shifts in the squid *Gonatus fabricii* (Oegopsida, Gonatidae) from the Norwegian Sea. Polar Biol. 23, 1–10.

Benjaminsen, T., Christensen, I., 1979. The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Foster). In: Winn, H.G., Olla, B.L. (Eds.), Behavior of Marine Animals, Vol. 3. Plenum Press, New York, pp. 143–164.

Bjørke, H., 1995. Norwegian investigations on *Gonatus fabricii* (Lichtenstein). ICES CM 1995/K: 12.

Bjørke, H., Gjøsæter, H., 1998. Who eats the larger *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea? ICES CM 1998/M: 10.

Bjørke, H., Hansen, K., 1996. Recordings of mature *Gonatus fabricii* (Lichtenstein) off the Norwegian coast. ICES CM 1996/K: 17.

Bjørke, H., Hansen, K., Sundt, R.C., 1997. Egg masses of the squid *Gonatus fabricii* (Cephalopoda, Gonatidae) caught with pelagic trawl off northern Norway. Sarsia 82, 149–152.

Christensen, I., Haug, T., Øien, N., 1992. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. ICES J. Mar. Sci. 49, 341–355.

Clarke, M.R., 1996. Cephalopods as prey. III. Cetaceans. Phil. Trans. R. Soc. Lond. B 351, 1053–1065.

Desportes, G., Mouritsen, R., 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Rep. Int. Whal. Commn. Spec. Iss. 14, 305–324.

Folkow, L.P., Blix, A.S., 1995. Distribution and diving behavior of hooded seals. In: Blix, A.S., Walløe, L., Ulltang, Ø. (Eds.), Whales, Seals and Man. Proceedings of the International Symposium on the Biology of Marine Mammals in the North East Atlantic, Tromsø, Norway, November 29–December 1, 1994. Elsevier, Amsterdam, pp. 193–202.

Hjort, J., Ruud, J.T., 1929. Whaling and fishing in the North Atlantic. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 56, 1–123.

Kawakami, T., 1980. A review of sperm whale food. Sci. Rep. Whales Res. Inst. Tokyo 32, 199–218.

Kristensen, T.K., 1981a. The genus *Gonatus* Gray, 1948 (Mollusca: Cephalopoda) in the North Atlantic: a revision of the North Atlantic species and description of *Gonatus steenstrupi* n. sp. Steenstrupia 7, 61–99.

Kristensen, T.K., 1981b. First record of a mature female of the squid *Gonatus fabricii* (Lichtenstein 1818) (Cephalopoda: Teuthoidea). Steenstrupia 7, 101–108.

Kristensen, T.K., 1983. *Gonatus fabricii*. In: Boyle, P.R. (Ed.), Cephalopod Life Cycles, Vol. 1. Species Accounts. Academic Press, London, pp. 159–173.

Kristensen, T.K., 1984. Biology of *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. Meddr. Grønland, Biosci. 13, 3–17.

Lick, R., Piatkowski, U., 1998. Stomach contents of a northern bottlenose whale (*Hyperoodon ampullatus*) stranded at Hiddensee, Baltic Sea. J. Mar. Biol. Assoc. UK 78, 643–650.

Martin, A.R., Clarke, M.R., 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. J. Mar. Biol. Assoc. UK 66, 779–790.

Nesis, K.N., 1965. Distribution and feeding of young squids *Gonatus fabricii* (Licht.) in the Labrador Sea and the Norwegian Sea. Oceanology 5, 102–108.

Nesis, K.N., 1987. Cephalopods of the World: Squids, Cuttlefishes, and Allies (English translation). TFH Publications, Neptune, NJ, 351 pp.

Potelov, V., Nilssen, K.T., Svetochev, V., Haug, T., 1997. Feeding habits of harp *Phoca groenlandica* and hooded seals *Cystophora cristata* during moult (April–June) in the Greenland Sea. NAMMCO, SC/5/ME/8.

Roe, H.S.J., 1969. The food and feeding habits of the sperm whale (*Physeter catodon* L.) taken off the west coast of Iceland. J. Cons. Int. Explor. Mer. 33, 93–102.

Roper, C.F.E., Sweeney, M.J., Nauen, C.E., 1984. FAO Species Catalogue, Vol. 3. Cephalopods of the World: An Annotated and Illustrated Catalogue of Species of Interest to Fisheries. FAO Fisheries Synopsis No. 125, pp. 1–277.

Santos, M.B., Pierce, G.J., Boyle, P.R., Reid, R.J., Ross, H.M., Patterson, I.A.P., Kinze, C.C., Tougaard, S., Lick, R., Piatkowski, U., Hernández-García, V., 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. Mar. Ecol. Prog. Ser. 183, 281–294.

Sennikov, A.M., Muchin, S.G., Bliznichenko, T.E., 1989. Distribution and trophic importance of juvenile squid (*Gonatus fabricii*, Lichtenstein) in the Norwegian and Barents Seas in 1986–1988. ICES CM 1989/K: 15.

Sigurjónsson, J., Vikingsson, G.A., 1992. Investigations on the ecological role of cetaceans in Icelandic and adjacent waters. ICES CM 1992/N: 24.

Skjoldal, H.R., Noji, T.T., Giske, J., Fosså, J.H., Blindheim, J., Sundby, S., 1993. Mare cognitum. Science plan for research on marine ecology of the Nordic Seas (Greenland, Norwegian, Iceland Seas). Institute of Marine Research, Bergen, Norway.

Wiborg, K.F., 1979. *Gonatus fabricii* (Lichtenstein), en mulig fiskeriressurs i Norskehavet (*Gonatus fabricii* (Lichtenstein), a possible fishery resource in the Norwegian Sea). Fisken Hav. 1, 33–46 (in Norwegian with English abstract).

Wiborg, K.F., Beck, I.M., Gjøsæter, J., 1984. The squid *G. fabricii* (Lichtenstein), investigations in the Norwegian Sea and western Barents Sea, 1983–1983. ICES CM 1984/K: 19.