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Arctic cephalopod distributions and their associated predators

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Abstract

Cephalopods are key species of the eastern Arctic marine food web, both as prey and predator. Their presence in the diets of Arctic fish, birds and mammals illustrates their trophic importance. There has been considerable research on cephalopods (primarily *Gonatus fabricii*) from the north Atlantic and the west side of Greenland, where they are considered a potential fishery and are taken as a by-catch. By contrast, data on the biogeography of Arctic cephalopods are still incomplete. This study integrates most known locations of Arctic cephalopods in an attempt to locate potential areas of interest for cephalopods, and the predators that feed on them. International and national databases, museum collections, government reports, published articles and personal communications were used to develop distribution maps. Species common to the Canadian Arctic include: *G. fabricii*, *Rossia moelleri*, *R. palpebrosa* and *Bathypolypus arcticus*. *Cirroteuthis muelleri* is abundant in the waters off Alaska, Davis Strait and Baffin Bay. Although distribution data are still incomplete, groupings of cephalopods were found in some areas that may be correlated with oceanographic variables. Understanding species distributions and their interactions within the ecosystem is important to the study of a warming Arctic Ocean and the selection of marine protected areas.

Cephalopods are found in all marine habitats of the world, and are prey for a variety of commercial and culturally significant species. Cephalopod distributions are correlated (Hjort & Ruud 1929; Bjørke 2001) with predators such as narwhals (*Monodon monoceros* L.) (e.g., Finley & Gibb 1982; Bjørke 2001) and Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) (e.g., Orr & Bowering 1997; Dawe et al. 1998; Bjørke 2001). A species of interest is the squid *Gonatus fabricii* Lichtenstein, which is considered a keystone species in several Arctic food webs (Chambers & Dick 2007). *Gonatus fabricii* are high in lipids and an excellent source of energy (Hooker et al. 2001; Frandsen & Wieland 2004). These squid are also predatory on a variety of fish and other marine invertebrates (e.g., Nesis 1965), enabling a transfer of energy from the productive epipelagic zone to benthic waters through ontogenetic migrations (Sennikov et al. 1989).

A significant body of research has been conducted on cephalopods around Greenland (e.g., Collins 2002; Zumholz & Frandsen 2006), Norwegian (Kristensen 1977; Wiborg et al. 1982) and Russian waters (e.g., Nesis 1965, 2001). However, cephalopods of the Canadian Arctic (above 60°N) are not well known. Most reports (e.g., Clarke 1966; Kristensen 1983; O'Dor & Macalaster 1983; Nesis 2001) have focused on potential commercial species (e.g., *G. fabricii*) and their presence or absence in an area, whereas others have been general surveys.

The objectives of this work are to: (1) consolidate all distributional data to a single source; (2) present maps to identify areas of biodiversity interest and potential feeding areas (i.e., predator–prey interactions); and (3) establish a baseline for future comparisons, including climate change effects in the Arctic.

Materials and methods

Initial queries into Arctic cephalopods were conducted using the Global Biodiversity Information Facility website (http://www.gbif.org/). All cephalopod records for areas north of 60°N were acquired, and five taxa were determined to be the most abundant. Of those taxa, records were obtained through contacts with museums (the Canadian Museum of Nature [CMNML] in Ottawa, Ontario, and the Atlantic Reference Centre [ARC] in St. Andrew's, New Brunswick), organizations such as Arctic Ocean Diversity (ArcOD, at the University of Alaska

Table 1 Additional reported cephalopod species from the circumpolar Arctic.

Species	Locations
Architeuthis sp.[a,b,c]	Iceland, Norwegian coast, south-west Greenland
Bathypolypus sp.[d,e,f]	Baffin Bay, Hudson Strait, south-west Greenland
Bathypolypus bairdii[d,e,g,h]	Baffin Bay, Davis Strait, Denmark Strait, east Greenland, south-west Greenland, Iceland, Norwegian coast, south of Svalbard
Bathypolypus pugniger sp.[e,h]	Baffin Bay, Denmark Strait, Faroe Islands, Iceland, south-west Greenland
Benthoctopus sp.[b,i,j,k]	Faroe–Shetland Strait, Kara Sea, Norwegian coast, Resolute Bay (Nunavut), east Svalbard
Benthoctopus hokkaidensis[l]	Point Barrow, Alaska
Benthoctopus profundorum[l]	Point Barrow, Alaska
Benthoctopus sibericus[b,j]	east Siberian and Laptev seas
Brachioteuthis riisei[b]	Faroe Islands, Norwegian coast, Norwegian Sea, south Iceland
Eledone cirrhosa[b,m]	Iceland, Norwegian coast, Norwegian sea, Svalbard
Gonatus sp.[d,e,f,i,n,o]	Baffin Bay, east Baffin Island, Cumberland Strait (mouth), Foxe Basin, southern tip of Greenland, south-west Greenland, Hudson Strait, Point Barrow (Alaska)
Graneledone verrucosa[b]	south of Iceland
Grimpoteuthis sp.[i,p]	Denmark Strait
Illex illecebrosus[a,b]	south Greenland (Frederikshaab), Iceland
Loligo forbesii[q,r]	North Sea, Norwegian coast, Norwegian Sea
Moroteuthis robusta[s]	Gulf of Alaska
Ommastrephes bartrami[b]	north-east Greenland, Norwegian Sea
Onychoteuthis banski[b]	south of Iceland, north coast of Norway
Opisthoteuthis sp.[t,u]	Davis Strait, Gulf of Alaska, south Iceland
Opisthoteuthis borealis[v]	south-west Greenland, south Iceland
Rossia sp.[e,f,w]	Baffin Bay, Denmark Strait, Hudson Strait, north Somerset Island (Nunavut)
Rossia glaucopis[b,g,m,n,q,r,x]	Barents Sea, around the Faroe Islands, east Greenland, Kara Sea, Iceland, North Sea, Svalbard
Rossia macrosoma[b]	Faroe Islands, Norwegian coast
Rossia megaptera[a,y]	Davis Strait
Semirossia tenera[b]	Laptev Sea, Norwegian coast
Sepiola atlantica[b,m]	south of Iceland, Iceland
Sepiola rondeletti[y]	Ellesmere Island, Jones Sound
Stauroteuthis syrtensis[t]	Davis Strait, Denmark Strait
Teuthowenia megalops[b,g,i,z]	Denmark Strait, south-west Greenland, south Iceland
Todarodes sagittatus[b,m]	Faroe Islands, Iceland, north coast of Norway
Todaropsis elbanae[aa]	North Sea, Norway

[a] Berry 1925; [b] Grimpe 1933; [c] Nesis et al. 2003 (1985); [d] Northwest Atlantic Fisheries Organization (NAFO) fishery survey of 2004 (M. Treble, pers. comm.); [e] Treble 2007; [f] NAFO survey of 2007 (M. Treble, pers. comm.); [g] Muus 1962; [h] Muus 2002; [i] Smithsonian National Museum of Natural History Invertebrate Zoology Collections; [j] Nesis 2001; [k] Muus (2002) reported that the *Benthoctopus* type specimen is actually a *Bathypolypus* spp. Therefore any mention of *Benthoctopus piscatorum* has been listed as *Benthoctopus* sp.; [l] Mercer 1968; [m] Taxonomic Information System for the Belgian Coastal Area database; [n] Atlantic Reference Centre database; [o] Piatkowski & Wieland 1993; [p] Referred to in this article as *Opisthoteuthis megaptera*, an invalid species name according to the Integrated Taxonomic Information System (2008); [q] Historical Benthic Dredge Samples from the Southern Baltic and the North Sea database; [r] Kondakov 1937; [s] North Pacific Groundfish Observer database; [t] Collins 2002; [u] Nesis 2003 (1989); [v] Collins 2005; [w] D. Hardie (pers. comm. 2007); [x] Atlantic Reference Centre; [y] Academy of Natural Sciences Malacology Database; [z] Nesis 1965; [aa] Swedish Museum of Natural History: Invertebrates database.

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Fairbanks) and the US National Oceanic and Atmospheric Administration (NOAA) Ocean Explorer project, and unpublished data of one of the authors (TAD) as well as unpublished data provided in 2007 by L. Harwood, B. Bluhm and D. Hardie. Data and locations were also obtained from published literature (e.g., Wiborg et al. 1982; Nesis 2001; Muus 2002; Raskoff et al. in press). The GeoNames website was used to determine the most likely latitude and longitude in lieu of the given place name. All samples listed from Arctic communities were assumed to be caught at the nearest marine location. Additional locations were identified from published, geo-referenced maps (Nesis 1965; Kristensen 1977, 1982; Wiborg et al. 1982; Sennikov et al. 1989). If the identification from a location was questionable (e.g., fishery survey) the specimens were listed as unidentified. If a specimen was described from a broad region (e.g., bay, sea, ocean), it was not mapped but was listed in Table 1. Specific sites were averaged from start and end trawl locations. Sample numbers were denoted with incrementally larger markers.

All specimens from the Northwest Atlantic Fisheries Organization (NAFO) fishery survey of 2007 (M. Treble, pers. comm.) were identified by one of the authors (KG). Specimens from the CMNML collection from Frobisher Bay (CMNML 35058) and Cape Parry (CMNML 37887, 37897, 37891) were examined to verify the original identification, and were found to be correct. The identification of ARC specimens, primarily from the Mercer collection,

Table 2 Percentages of cephalopod prey items reported from the stomachs of Arctic predators.

Location	Predators	Cephalopod prey	% of diet (weight)
Bering Sea	Baird's beaked whale (*Berardius bairdii*)[a]	cephalopods	90%
	bearded seals (*Erignathus barbatus*)[a]	octopods	<1%
	beluga whale (*Delphinapterus leucas*)[a]	cephalopods	2%
	Bering Sea beaked whale (*Mesoplodon stejnegeri*)[a]	cephalopods	90%
	Dall's porpoise (*Phocoenoides dalli*)[a]	squid	50%
	fin whale (*Balaenoptera physalus*)[a]	cephalopods	2%
	harbour porpoise (*Phocoena phocoena*)[a]	squid	1%
	harbour seal (*Phoca vitulina*)[a]	squid	4%
	humpback whale (*Megaptera novaeangliae*)[a]	cephalopods	1%
	killer whale (*Orcinus orca*)[a]	cephalopods	20%
	minke whale (*Balaenoptera acutorostrata*)[a]	cephalopods	1%
	northern fur seal (*Callorhinus ursinus*)[a]	squid	33%
	northern sea lion (*Eumetopias jubatus*)[a]	squid	3%
	Pacific walrus (*Odobenus rosmarus*)[a]	octopods	1%
	ribbon seal (*Histriophoca fasciata*)[a]	squid	1%
	sperm whale (*Physeter macrocephalus*)[a]	cephalopods	82%
	spotted seal (*Phoca largha*)[a]	squid	<1%
Bjørnøya and Bleiksøy islands	thick-billed murre (*Uria lomvia*)[b]	squid	30%
	common murre (*Uria aalge*)[b]	*Gonatus fabricii*	40%
Clyde	bearded seal (*Erignathus barbatus*)[c,d]	*Bathypolypus arcticus*	<1%
		Gonatus sp.	<1%
Grise Fjord	bearded seal (*Erignathus barbatus*)[c,e]	*Bathypolypus arcticus*	<1%
		Gonatus sp.	<1%
Iceland	hooded seal (*Cystophora cristata*)[f]	*Gonatus* sp.	79%
Norwegian waters	sperm whale (*Physeter macrocephalus*)[g]	*Gonatus* sp.	96%
		Haliphron	1.60%
		Histioteuthis	1.20%
		Teuthowenia	0.34%
		Todarodes	0.43%
eastern Norwegian waters	sperm whale (*Physeter macrocephalus*)[f]	Cranchiidae	25%
		Gonatus sp.	9%
		Histioteuthis	38%
Pond Inlet	bearded seal (*Erignathus barbatus*)[c,h]	*Bathypolypus arcticus*	<1%
		Gonatus sp.	<1%
	narwhal (*Monodon monoceros*)[i,j,k]	squid	<5%

[a] Perez 1990; [b] Barrett et al. 1997; [c] Finley & Evans 1983; [d] Finley & Evans (1983) reported that bearded seals from the Clyde had a 57% occurrence of *B. arcticus* and *Gonatus* sp. in their stomachs. [e] Finley & Evans (1983) also reported bearded seals from Grise Fjord, NU, had a 67% occurrence of *B. arcticus* and a 71% occurrence of *Gonatus* sp. in their stomachs. [f] Bjørke 2001; [g] Santos et al. 2001; [h] Finley & Evans (1983) described an occurrence of 85% *B. arcticus* and 77% *Gonatus* sp. in the stomachs of bearded seals caught off Pond Inlet, NU. [i] Finley & Gibb 1982; [j] Estimates from Pond Inlet in 1978 described a 92% occurrence of *G. fabricii* and a 16% occurrence of *B. arcticus* in the stomachs of narwhals caught. In 1979, 79% of narwhals had *G. fabricii* and 17% had *B. arcticus* remains in their stomachs (Finley & Gibb 1982). [k] Finley & Gibb (1982) reported that narwhals in Pond Inlet were feeding on cephalopods, in particular, *G. fabricii*.

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was previously verified by the senior author. Although location data were only used from reputable sources, there is the chance of mis-identifications, especially with *Bathypolypus arcticus* Prosch. Holdings of this particular species should be re-examined to verify its speciation. The names of all species were validated, and those considered invalid were listed as their synonym in accordance with the Integrated Taxonomic Information System.

Beaks and specimens from stomach content analyses were recorded as such in the data set. Locations were obtained from published literature, government documents, surveys, Arctic expeditions (e.g., Wacasey et al. 1979; Nesis 2001; Cephbase) and unpublished data (T.A. Dick; L. Harwood, pers. comm. 2007) (Tables 1–4). Each predator species was identified with a unique symbol that differed from specimens recovered from trawls. Again, if a location was described from a broad region, it was not mapped. Predators and capture locations are listed in Tables 2–4.

All locations were mapped using ArcMap 9 (ESRI GIS mapping software).

Results

Specimens described in this paper were collected between 1856 and 2007. The five most prominent species from the

Table 3 Percentage occurrences of cephalopod prey items from the stomachs of Arctic predators (percentages of predators sampled with cephalopods in their stomachs).

Location	Predators	Cephalopod prey	% occurrence in stomachs
Andenes	sperm whale (*Physeter macrocephalus*)[a]	squid	83.3
Baffin Bay, Greenland	narwhal (*Monodon monoceros*)[b]	*Gonatus fabricii*	35
Barrow (Alaska)	bearded seal (*Erignathus barbatus*)[c]	*Octopus* spp.	69.4
Barrow (Alaska), Holman (Canada)	ringed seal (*Pusa hispida*)[c]	cephalopods	2.6
Davis Strait	Greenland halibut (*Reinhardtius hippoglossoides*)[d,e]	cephalopods	2
Greenland Sea pack ice	harp seal (*Phoca groenlandica*)[f]	*Gonatus* sp.	40
	hooded seal (*Cystophora cristata*)[f]	*Gonatus* sp.	82
Hendrickson Island	beluga whale (*Delphinapterus leucas*)[g]	cephalopods	3
Jan Mayen	northern bottlenose whale (*Hyperoodon ampullatus*)[a]	cephalopods	75
Kendall Island Bird Sanctuary	beluga whale (*Delphinapterus leucas*)[g]	cephalopods	3
Little Diomede Island (Alaska)	spotted seal (*Phoca largha*)[c]	squid	2.6
north-east Iceland	northern bottlenose whale (*Hyperoodon ampullatus*)[a]	*Gonatus* sp.	100

[a] Bjørke 2001; [b] Laidre et al. 2004; [c] Dehn et al. 2007; [d] Orr & Bowering, 1997; [e] Orr & Bowering (1997) also commented that Greenland halibut preyed on *Gonatus* sp. in the Davis Strait; [f] Haug et al. 2004; [g] L. Harwood (pers. comm. 2007).

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Canadian Arctic are *G. fabricii*, *Rossia moelleri* Steenstrup, *R. palpebrosa* Owen, *B. arcticus* and *Cirroteuthis muelleri* Eschricht.

Gonatus fabricii distribution

Gonatus fabricii has a circumpolar distribution, extending from Alaska north to the high Arctic (Fig. 1). The Canadian range extends from the Dolphin and Union Strait, Northwest Territories (NWT), north to Cape Vera, Nunavut (NU), and Pond Inlet, NU, and south through the Hudson Strait (Fig. 1). *G. fabricii* also extends along the coasts of Greenland, through the Denmark Strait, Norwegian Sea, off the Norwegian shore, around the Faroe Islands and Svalbard, and into the Barents Sea (Figs. 1, 2).

Because of the number of groundfish and shrimp surveys in the Norwegian Sea and west coast of Greenland, there are numerous records of *G. fabricii* (Nesis 1965; Kristensen 1977; Wiborg et al. 1982; Sennikov et al. 1989). Other areas of interest include Cape Vera (190 specimens) and Pond Inlet (46 specimens) (Figs. 1, 2). Wiborg et al. (1982) also identified potential spawning sites in the Norwegian Sea (Fig. 2).

Distributions around Greenland and Hudson Strait are based on samples collected in trawls, whereas those from Cape Vera and Pond Inlet are from stomach contents of northern fulmars (*Fulmarus glacialis* L.) and narwhals, respectively (Fig. 3). Several Hudson Strait locations are from the stomachs of thick-billed murres (*Uria lomvia* L.), whereas most of the locations in the eastern Arctic are based on stomach contents from commercially fished haddock (*Melanogrammus aeglefinus* L.), Greenland halibut and cod (*Gadus* sp. L.) (Fig. 3).

Rossia moelleri distribution

Rossia moelleri has a circumpolar distribution, with a range extending from Cape Parry, NWT, through the Dolphin and Union Strait, NWT, to Foxe Basin, Frobisher Bay and north to Slidre Fjord, Ellesmere Island (Fig. 4). It was also recorded from western Greenland and Denmark Strait (Fig. 4). There are records from the Norwegian Sea north to Svalbard, with one specimen reported from the Laptev Sea (Fig. 4).

Cape Parry (12 records) and Slidre Fjord (nine records) have the greatest number of recorded specimens (Fig. 4).

Most records are from trawls. One beak was collected from a walrus (*Odobenus rosmarus* L.) off the north-west tip of Greenland (Fig. 5). Records from the Norwegian Sea and Denmark Strait are primarily from the stomachs of cod. One was from the stomach of a haddock (Fig. 5).

Rossia palpebrosa distribution

Most records of *R. palpebrosa* are reported from the junction of the East Siberian and Laptev seas and the Laptev Sea proper (Fig. 6). Individuals were recorded from Svalbard, the Kara and Barents seas, as well as from the northern tip of Greenland to Disko Bay, across Davis to the Hudson Strait (Fig. 6). Individuals were also collected from Slidre Fjord, Ellesmere Island, Frobisher Bay and the east coast of Somerset Island (Fig. 6).

There are no records of predators for this species.

Bathypolypus arcticus distribution

The Arctic range of *B. arcticus* extends from Frobisher Bay north through Davis Strait to Pond Inlet, Devon Island

Table 4 Anecdotal accounts of cephalopods as prey species from the Arctic.

Location	Predators	Cephalopod prey
Admiralty Inlet	narwhal (*Monodon monoceros*)[a]	squid
Akpatok Island	thick-billed murre chicks (*Uria lomvia*)[b]	*Gonatus fabricii*
Arctic/sub-Arctic waters of North America and Eurasia	beluga whale (*Delphinapterus leucas*)[c]	cephalopods
Atlantic side of Arctic	narwhal (*Monodon monoceros*)[d]	squid
Barents Sea	harp seal (*Phoca groenlandica*)[c]	squid
	hooded seal (*Cystophora cristata*)[c]	*Gonatus* sp.
Barrow (Alaska)	bearded seals (*Erignathus barbatus*)[e]	*Octopus* sp.
Barrow (Alaska), Holman (Canada)	ribbon seal pups (*Histriophoca fasciata*)[e]	cephalopods
	spotted seals (*Phoca largha*)[e]	cephalopods
	walrus (*Odobenus rosmarus*)[e]	*Octopus* sp.
Barrow Strait	narwhal (*Monodon monoceros*)[a]	Squid
Canadian Arctic	bearded seals (*Erignathus barbatus*)[e]	*Octopus* sp.
Coats Island	thick-billed murre chicks (*Uria lomvia*)[b]	*Gonatus fabricii*
Digges Island	thick-billed murre chicks (*Uria lomvia*)[b]	*Gonatus fabricii*
east coast of Greenland, Denmark Strait	harp seal (*Phoca groenlandica*)[f]	*Gonatus fabricii*
	hooded seal (*Cystophora cristata*)[f]	*Gonatus fabricii*
eastern Bering Sea	beluga whale (*Delphinapterus leucas*)[d]	cephalopods
	Greenland halibut (*Reinhardtius hippoglossoides*)[d]	squid
	harp seal (*Phoca groenlandica*)[d]	squid
	hooded seal (*Cystophora cristata*)[d]	squid
	sperm whale (*Physeter macrocephalus*)[d]	squid
Eclipse Sound	narwhal (*Monodon monoceros*)[a]	squid
Greenland	beluga whale (*Delphinapterus leucas*)[g]	cephalopods
Hantzsch Island	thick-billed murre chicks (*Uria lomvia*)[b]	*Gonatus fabricii*
High Arctic	northern bottlenose whale (*Hyperoodon ampullatus*)[h]	*Gonatus* sp.
	long-finned pilot whale (*Globicephala melas*)[i]	*Gonatus* sp.
	sperm whale (*Physeter macrocephalus*)[i]	*Gonatus* sp.
Iceland–Faroe Ridge	cod (*Gadus* sp.)[h]	*Gonatus* sp.
		Ommastrephidae
	Halibut sp.[h]	*Gonatus* sp.
		Ommastrephidae
Irminger Sea, south Iceland	northern bottlenose whale (*Hyperoodon ampullatus*)[j]	*Gonatus* sp.
Lancaster Sound	narwhal (*Monodon monoceros*)[a]	squid
Navy Board Inlet	narwhal (*Monodon monoceros*)[a]	squid
northern Bering and Chukchi seas	beluga whale (*Delphinapterus leucas*)[g]	*Gonatus* sp.
		Octopus sp.
Norwegian Sea	beluga whale (*Delphinapterus leucas*)[j]	*Gonatus* sp.
	blue ling (*Molva dypterygia*)[j]	*Gonatus* sp.
	cod (*Gadus* sp.)[j]	*Gonatus* sp.
	Greenland halibut (*Reinhardtius hippoglossoides*)[j]	*Gonatus* sp.
	Greenland shark (*Somniosus microcephalus*)[j]	*Gonatus* sp.
	grenadier fish sp.[j]	*Gonatus* sp.
	harp seal (*Phoca groenlandica*)[j,k]	*Gonatus* sp.
		squid
	hooded seal (*Cystophora cristata*)[j,k]	*Gonatus* sp.
		Gonatus sp.
	narwhal (*Monodon monoceros*)[j]	*Gonatus* sp.
	northern bottlenose whale (*Hyperoodon ampullatus*)[j]	*Gonatus* sp.
	long-finned pilot whale (*Globicephala melas*)[j]	*Gonatus* sp.
	saithe (*Pollachius virens*)[j]	*Gonatus* sp.
	sea perch sp.[j]	*Gonatus* sp.
	seabirds[j]	*Gonatus* sp.
	Sowerby's beaked whale (*Mesoplodon bidens*)[j]	*Gonatus* sp.
	sperm whale (*Physeter macrocephalus*)[j]	*Gonatus* sp.
Peel Sound	narwhal (*Monodon monoceros*)[a]	squid
Pond Inlet, Eclipse Sound, Admiralty Inlet	narwhal (*Monodon monoceros*)[l]	squid
Prince Regent Inlet	narwhal (*Monodon monoceros*)[a]	squid

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Table 4 *Continued*

Location	Predators	Cephalopod prey
southern Greenland	Greenland halibut (*Reinhardtius hippoglossoides*)[m]	squid
Tremblay Sound, Creswell Bay	narwhal (*Monodon monoceros*)[i]	*Gonatus* sp.
Uummannaq (north-west Greenland)	narwhal (*Monodon monoceros*)[n]	*Gonatus fabricii*
western Alaska	beluga whale (*Delphinapterus leucas*)[g]	*Gonatus* sp.
		Octopus sp.
Within the predators' natural range	harbour seal (*Phoca vitulina*)[d,o]	squid
	ribbon seal (*Histriophoca fasciata*)[d,o]	squid
	spotted seal (*Phoca largha*)[d,o]	squid
	narwhal (*Monodon monoceros*)[d,o]	*Gonatus fabricii*

[a] Welch et al. 1992; [b] Gaston 1985; [c] Stewart & Stewart 1989; [d] Loeng et al. 2005; [e] Dehn et al. 2007; [f] Haug et al. 2004; [g] Dahl et al. 2000; [h] Hjort & Ruud 1929; [i] Laidre et al. 2004; [j] Bjørke 2001; [k] Dommasnes et al. 2001; [l] Hay & Mansfield 1989; [m] Woll & Gundersen 2004; [n] COSEWIC 2004; [o] Tomilin 1967 (1957).

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and Lady Ann Strait, and along the west coast of Greenland (Fig. 7). Records exist from the middle of the east coast of Greenland through Denmark Strait to Iceland, and down to the Faroe Islands (Fig. 7). *Bathypolypus arcticus* is also found offshore of Norway and in the Norwegian Sea to Svalbard (Fig. 7). There are also reports from the Kara and Laptev seas (Fig. 7). The most western distribution is from the Canada Basin, north of Alaska (Fig. 7). Areas of interest are Kap Powlett, Greenland and the Laptev Sea (Fig. 7).

Specimens are typically recovered from trawls. One was found in the stomach of a narwhal caught at Pond Inlet (Fig. 8). The specimen from Lichtenaufjord, Greenland, was from the stomach contents of a Greenland halibut (Fig. 8).

Cirroteuthis muelleri distribution

The majority of *C. muelleri* specimens are from Baffin Bay, and the Norwegian and Greenland seas, with a few records from the Laptev Sea (Fig. 9). *C. muelleri* is also reported from the deep water of the Canada Basin (Raskoff et al. in press; B. Bluhm, pers. comm. 2007), and from Davis Strait and Baffin Bay (Fig. 9).

Unidentified cephalopods

Although not much cephalopod research has been conducted in the Canadian Arctic, there are records of unidentified cephalopods (typically from fishery or bird surveys) from areas such as Pond Inlet, Arctic Bay, Cape Vera, Somerset Island and Peel Sound, NU, with other records from Liverpool Bay, southern Banks and Victoria islands, NWT (Fig. 10).

Rare species of the Canadian Arctic Ocean and adjacent areas

Deep-sea squid like the giant squid (*Architeuthis* sp. Steenstrup) and temperate species such as *Illex illecebrosus* Lesueur and *Sepiola atlantica* D'Orbigny have been reported from Greenland (e.g., Berry 1925; Grimpe 1933; Nesis 1987; Table 1). *Architeuthis* sp. have also been reported from Iceland and the Norwegian coastline, wheras *Loligo forbesi* Steenstrup has been reported from the Norwegian Sea (Table 1). *Rossia glaucopis* Loven is reported along the eastern shore of Greenland, and its presence was noted in Svalbard, the Faroe Islands, and the Barents and Kara seas (Table 1). *Bathypolypus bairdii* Verrill and Muus's (2002) proposed species *Bathypolypus pugniger* were found through the Denmark Strait and around Greenland, with *B. bairdii* extending west into the Davis Strait (Table 1). Both were reported (Treble 2007) from Baffin Bay in the 2006 NAFO fishery survey (Table 1). Numerous *Gonatus* sp., *Bathypolypus* sp. and *Rossia* sp. were also collected throughout the Hudson Strait (Table 1).

Cephalopod–predator interactions

The percentage of diets comprising cephalopods of various Arctic species is listed in Table 2. Cephalopods comprised ca. 90% of the diet of Bering Sea beaked (*Mesoplodon stejnegeri* True) and Baird's beaked (*Berardius bairdii* Stejneger) whales (Table 2). The diet of sperm whales is ca. 72–96% cephalopods (Table 2). Santos et al. (2001) reported that 96% (by weight) of prey items in stranded sperm whale stomachs from Norwegian waters were *Gonatus* sp. Other mammalian predators from the Bering Sea, such as northern fur seals (*Callorhinus ursinus* L.) and Dall's porpoise (*Phocoenoides dalli* True), have 33–50% of their diets made up of squid (Table 2). Thick-billed and common murres (*Uria* spp.) off Bjørnøya and Bleiksøy, Norway, have 30% and 40% of their diets represented by squid and *G. fabricii* (Table 2).

The percentage occurrence of indigestible cephalopod parts (mostly beaks) and flesh from the stomachs of sampled predators is listed in Table 3. These records indicate cephalopod remains, but not the relative proportion

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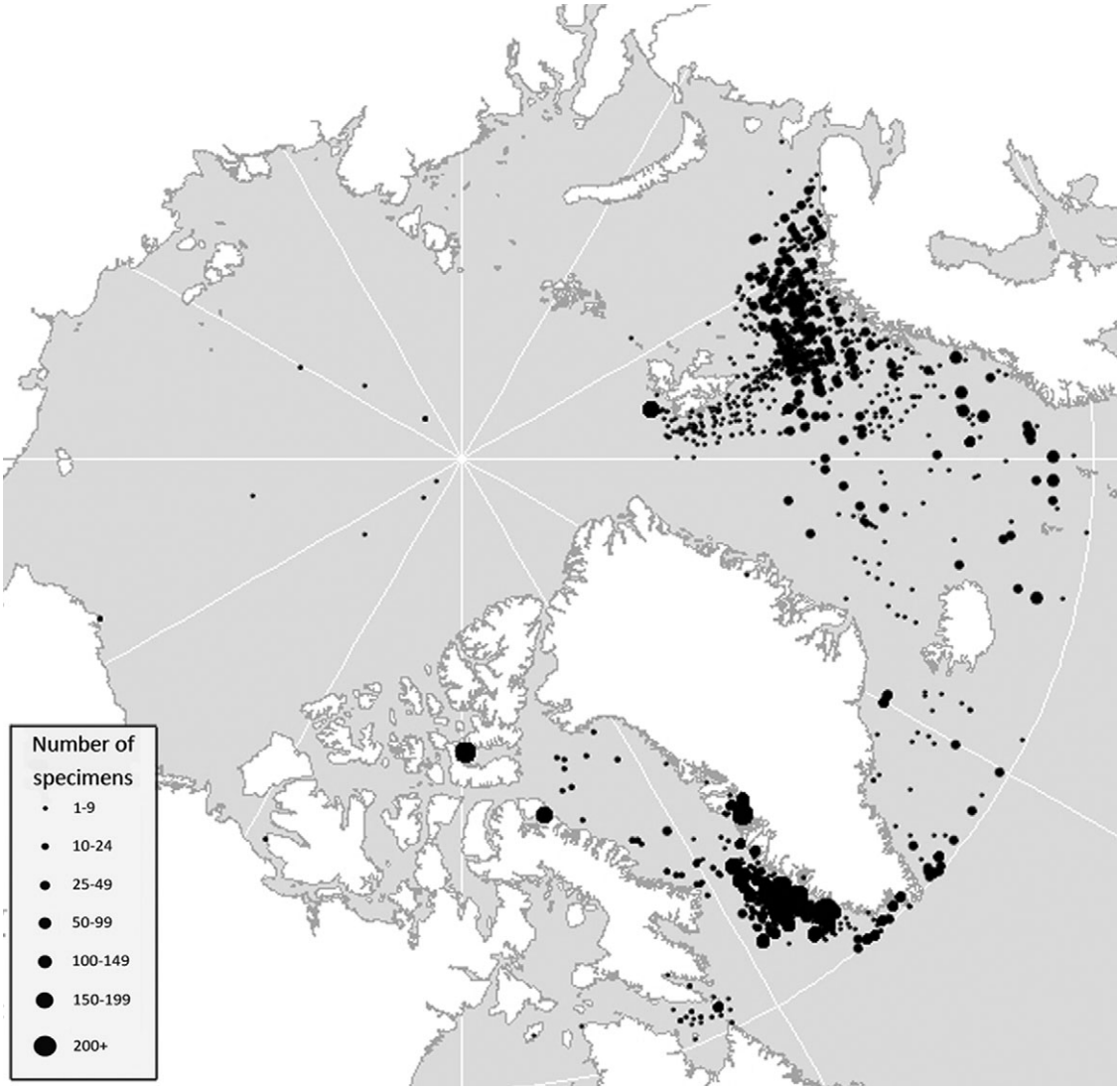

Fig. 1 Circumpolar records of *Gonatus fabricii.* Sources: Berry (1925); Hjort & Ruud (1929); Grieg (1930) and Kubodera & Tsuchiya (1993), as cited in Cephbase; Grimpe (1933); Muus (1962); Nesis (1965, 2001, 2003 [1971]); Young (1973); Kristensen (1977, 1982); Finley & Gibb (1982); Wiborg et al. (1982); Gaston (1985); Sennikov et al. (1989); Piatkowski & Wieland (1993); Barrett et al. (1997); B. Bluhm (pers. comm. 2007); Zumholz et al. (2007); Atlantic Reference Centre collection; Canadian Museum of Nature collection; Atlantic Reference Centre online database; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) fishery survey of 2004 (M. Treble, pers. comm.); NAFO survey of 2007 (M. Treble, pers. comm.); Raskoff et al. in press; and T.A. Dick (unpubl. data). Forty-two specimens were collected during the NAFO trawl surveys in 2006. They were caught along the west side of Baffin Bay between depths of 425.5 and 1482.5 m (Treble 2007).

in the diets. All bottlenose whales (*Hyperoodon ampullatus* Forster) sampled around Iceland had squid remains in their stomachs, and 92% of narwhals caught off Pond Inlet in 1978 had *G. fabricii* parts in their digestive tracts (79% in 1979) (Table 2). Cephalopods comprised 67–71% of the diet of bearded seals (*Erignathus barbatus* Erxleben) from Grise Fjord (Table 2), and 69.4% of the diet was unidentified octopods near Barrow, Alaska (Table 3). Of the sperm whales collected off Andenes, Norway, in 1971, 83% had squid beaks in their stomachs (Table 3).

More than 50% of the anecdotal accounts of diets of Arctic predators list *Gonatus* sp. (likely to be *G. fabricii* based on locations) in the diets, indicating its importance as a prey species (Table 4).

Discussion

Recent studies have shown that cephalopods, specifically the high-energy keystone species *G. fabricii*, are important prey for a variety of Arctic predators (Frandsen & Wieland 2004; Chambers & Dick 2007). With increasing water

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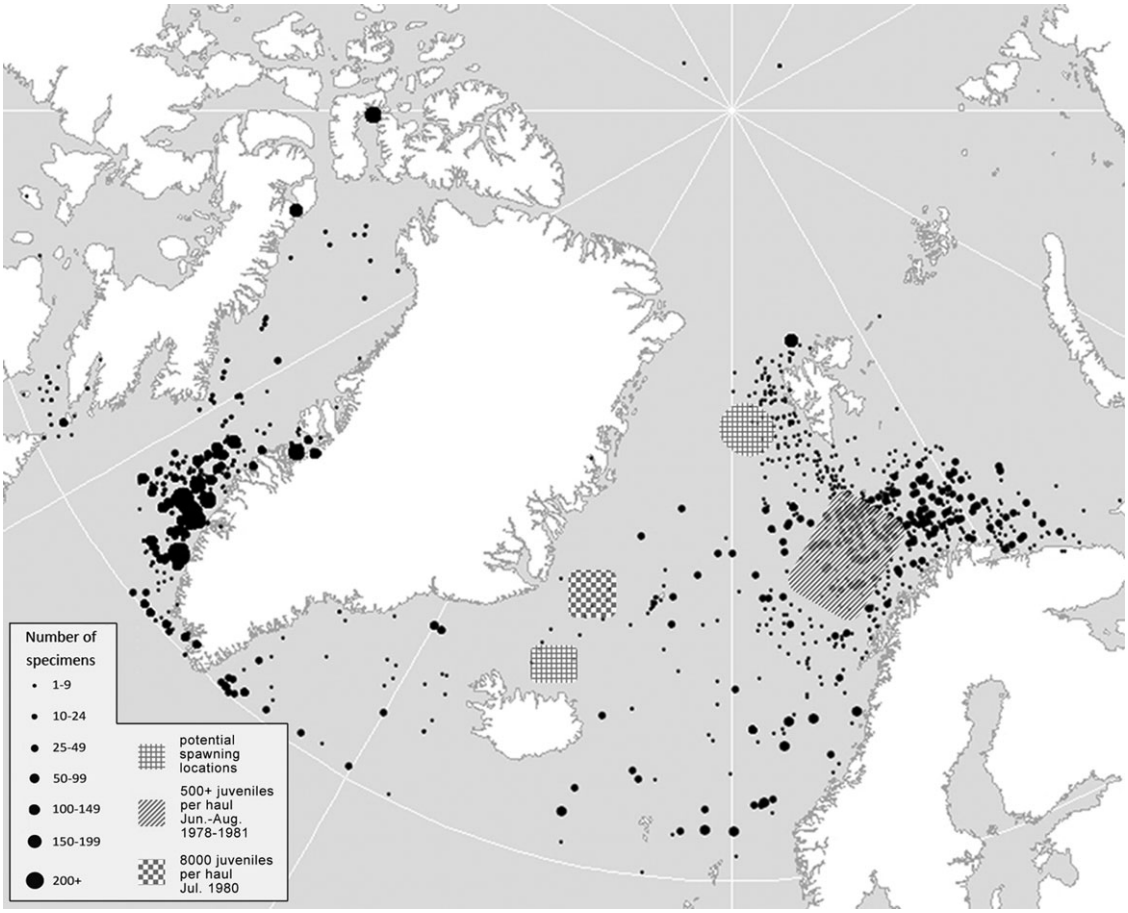

Fig. 2 Distribution of *Gonatus fabricii* in the western European Arctic with reference to potential spawning locations, areas of 500+ juveniles per haul caught between June and August 1978–1981 and a region where 8000 juveniles per haul were recorded in July 1980 (Wiborg et al. 1982). For a more accurate representation of the juvenile distribution of *G. fabricii*, see Wiborg et al. (1982: fig. 1).

temperatures, more temperate species, such as *I. illecebrosus* and *L. forbesi*, are likely to become more common, thereby increasing the competition for prey and adding to the predation pressure on such species as *G. fabricii* (O'Dor 1983). It is unknown what impact these potential shifts in predator–prey interactions might have on the overall food web.

Arctic cephalopod range extensions

Gonatus fabricii. We extend the range of *G. fabricii* from that described by Clarke (1966). This new distribution includes the eastern Siberia Sea, the Beaufort Sea (Canada Basin) (Raskoff et al. in press; B. Bluhm, pers. comm. 2007), Pond Inlet (stomach contents of narwhals) and the most northern Canadian Arctic location, Cape Vera (T.A. Dick, unpubl. data; Fig. 1). Although not reported by Nesis (2001), specimens from the Dolphin and Union Strait (ARC; Fig. 1) give validity to Nesis's description of a circumpolar species.

Discrepancies have been noted between the range described in this study and previously reported distributions, especially from the Pacific Ocean. Other regions of the Pacific Ocean probably represent a different species of gonatid (Wiborg et al. 1982).

Rossia moelleri. Nesis (2001) noted that *R. moelleri* is not typically found south of 75°N, although a "questionable" specimen from Franklin Bay was reported. The present range includes specimens collected south of 75°N near Cape Parry and Coronation Gulf, and extending into waters around Iceland (Fig. 4). The range also extends to the interior of Frobisher Bay and Melville Island (Fig. 4).

Rossia palpebrosa. With a distribution throughout most of the Arctic Ocean (Nesis, 2001), *R. palpebrosa* has a similar range to *R. moelleri*. The present distribution reflects that described by Nesis (2001), with the exception of no records from Iceland or the Danish Strait

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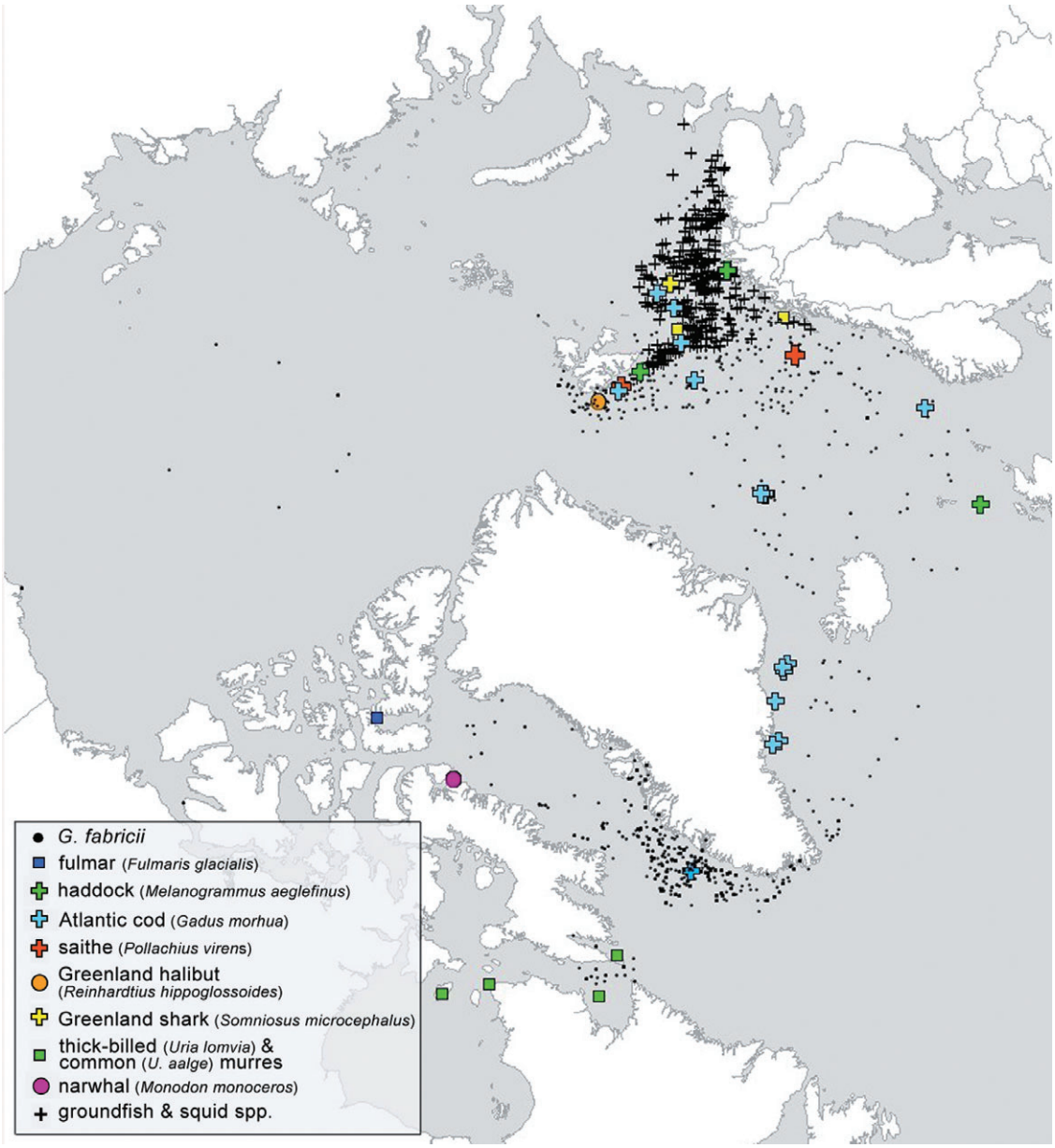

Fig. 3 Occurrence records of *Gonatus fabricii* specimens, including remains in the stomach contents of predators. Sources: Berry (1925); Hjort & Ruud (1929); Grieg (1930) and Kubodera & Tsuchiya (1993), as cited in Cephbase; Grimpe (1933); Muus (1962); Nesis (1965, 2001, 2003 [1971]); Young (1973); Kristensen (1977, 1982); Wiborg et al. (1982); Finley & Gibb 1982; Gaston 1985; Sennikov et al. (1989); Piatkowski & Wieland (1993); Barrett et al. (1997); B. Bluhm (pers. comm. 2007); Zumholz et al. (2007); Atlantic Reference Centre collection; Canadian Museum of Nature collection; Atlantic Reference Centre online database; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) (M. Treble pers. comm.); NAFO survey of 2007 (M. Treble, pers. comm.); Raskoff et al. in press; and T.A. Dick (unpubl. data).

(Fig. 6). The range is extended in the Canadian Arctic to Hudson Strait, the mouth of Cumberland Sound, Frobisher Bay, and Somerset and Ellesmere islands (Fig. 6).

Bathypolypus arcticus. Muus's (2002) re-description of the *B. arcticus* complex requires most museum specimens to be re-examined and identified under the new criteria. Based on current museum records, our map shows a distribution south from Hudson Strait to Frobisher Bay, southern Davis Strait and north to Lady Ann Strait (Fig. 7). The species identification of samples collected around the United Kingdom, Norway and southern Greenland are questionable, as they occur in areas of

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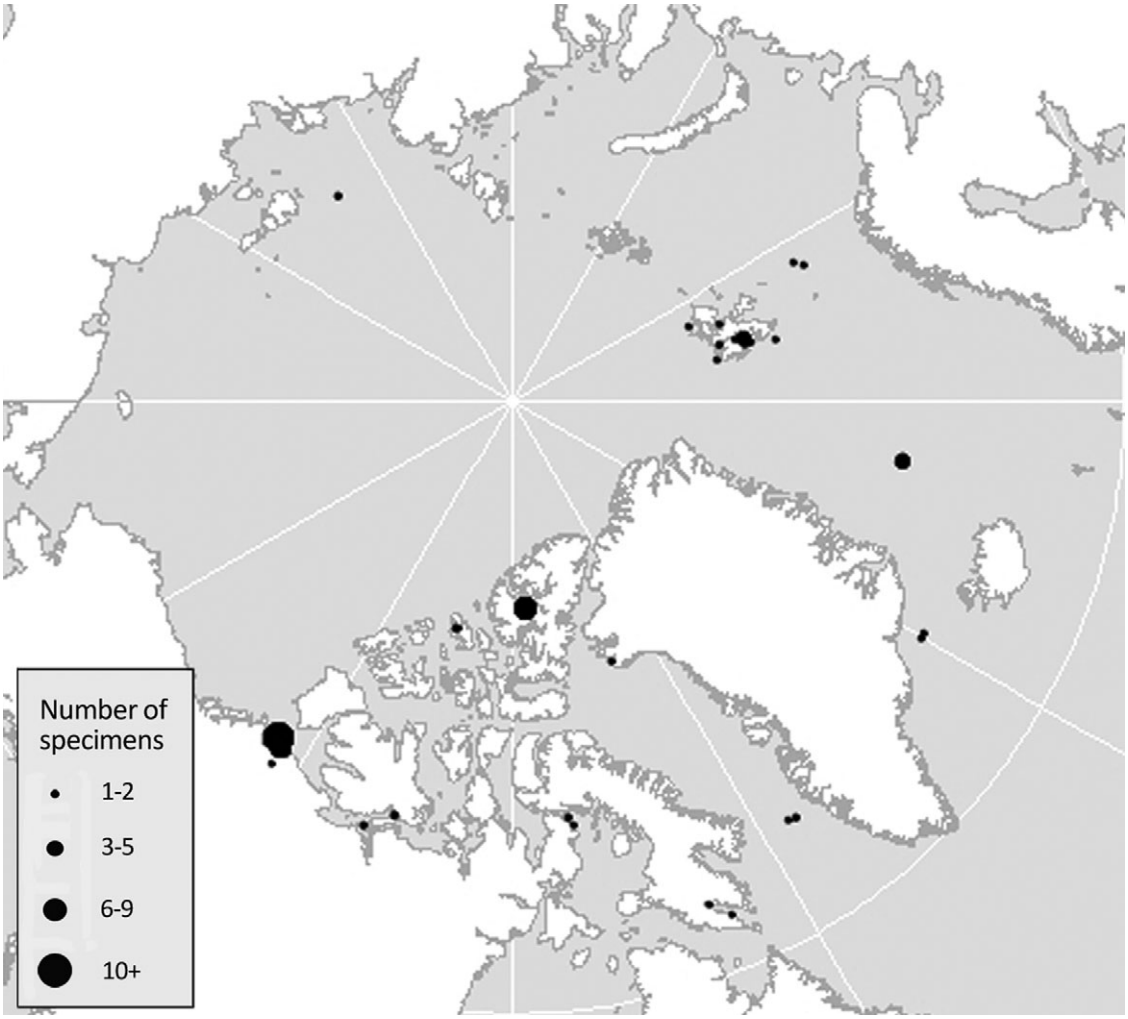

Fig. 4 Circumpolar records of *Rossia moelleri*. Sources: Grieg (1930), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962); Wacasey et al. (1979); Atkinson & Wacasey (1989); Nesis (2001); Canadian Museum of Nature collection; and Atlantic Reference Centre online database. One specimen of *R. moelleri* was caught between a depth of 139 and 150.5 m from the western side of Baffin Bay during Northwest Atlantic Fisheries Organization trawl surveys in 2006 (Treble 2007).

potential overlap between *B. arcticus*, *B. bairdii* and *B. pugniger* sp. (Fig. 7) (Muus 2002).

A specimen from Cape Parry (CMNML) (Fig. 7) was confirmed as the westernmost Canadian distribution of *B. arcticus*; however, records extend the range further west to Point Barrow, Alaska, and the Canada Basin (Fig. 7). These locations extend the range west from Muus's (2002) original description. Only two specimens were recorded by Muus (2002) from Canadian waters, one from Devon Island and the other just off the Cumberland Peninsula, Baffin Island. The current map extends the species to Pond Inlet and Frobisher Bay. Our distribution re-affirms O'Dor & Macalaster's (1983) and Nesis's (2001) claim of a western Canadian distribution.

Cirroteuthis muelleri. Nesis (2001) described *C. muelleri* as a circumpolar species found in deep water (500–3786 m), and our range agrees, with the exception of specimens from the shallower Laptev Sea (Fig. 9). Additional locations were identified from the Canada Basin, based on plankton samples and remotely operated vehicle surveys by ArcOD and the NOAA Ocean Explorer (Raskoff et al. in press; B. Bluhm, pers. comm. 2007; Fig. 9). The greatest number of samples caught in one location ($n = 63$) were caught in northern Baffin Bay (Fig. 9).

Additional Arctic cephalopod distributions. Several other species have been reported from the Arctic (Table 1), and of these *B. bairdii* and *R. glaucopis* were the

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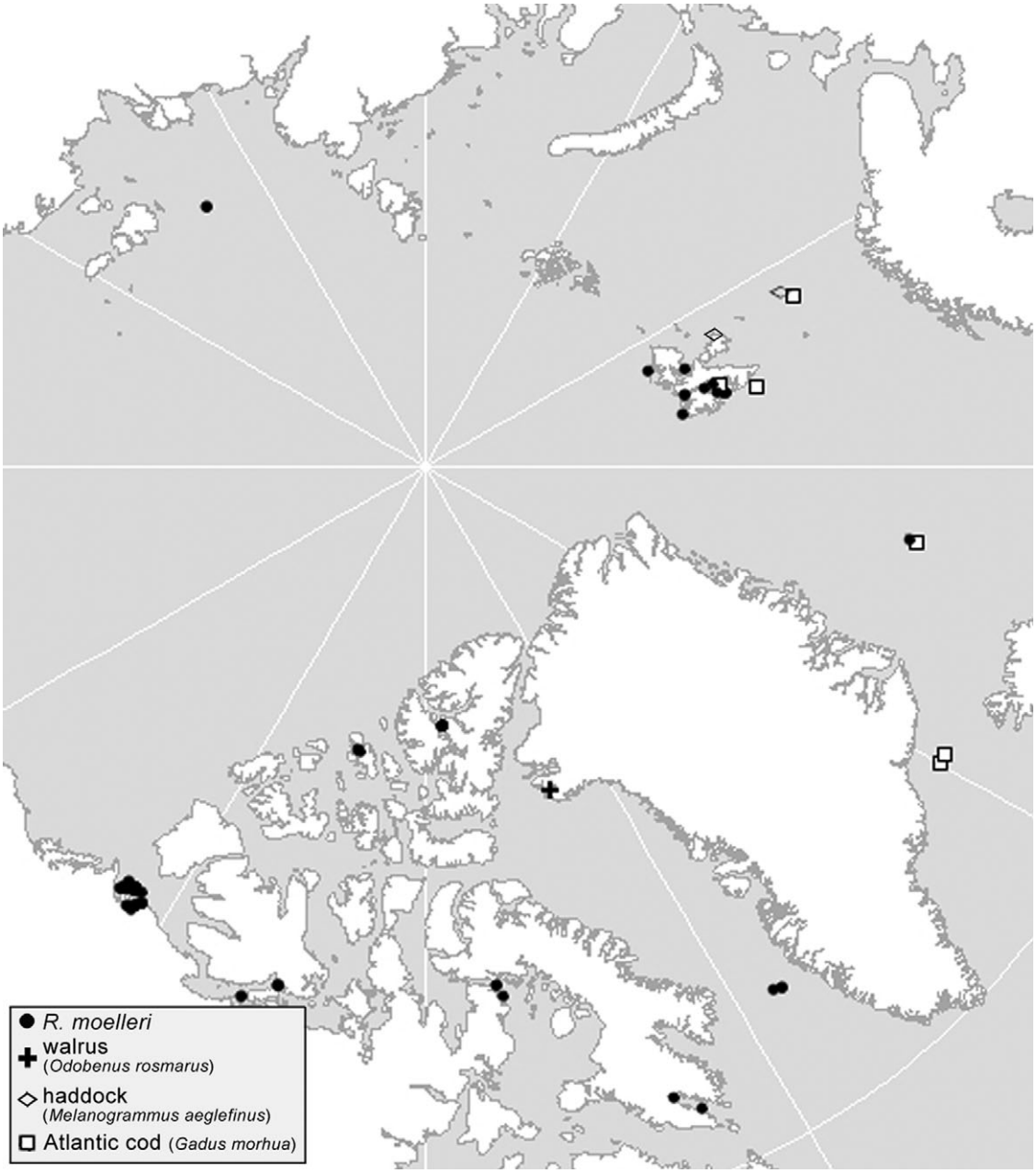

Fig. 5 Circumpolar records of *Rossia moelleri* specimens, including remains in the stomach contents of predators. Sources: Grieg (1930), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962); Wacasey et al. (1979); Atkinson & Wacasey (1989); Nesis (2001); Canadian Museum of Nature collection; and Atlantic Reference Centre online database.

most abundant (Table 1). The remaining species are listed in Table 1.

Predator–prey relationships

Arctic predators of cephalopods are often large and mobile. Consequently, the source of samples collected needs to be considered when designating an "area of interest". Areas with large numbers of recorded specimens may indicate a greater abundance of cephalopods or may be associated with an active sampling programme of a nearby field station or traditional hunting grounds. The latter may also indirectly reflect an abundance of prey in that particular region.

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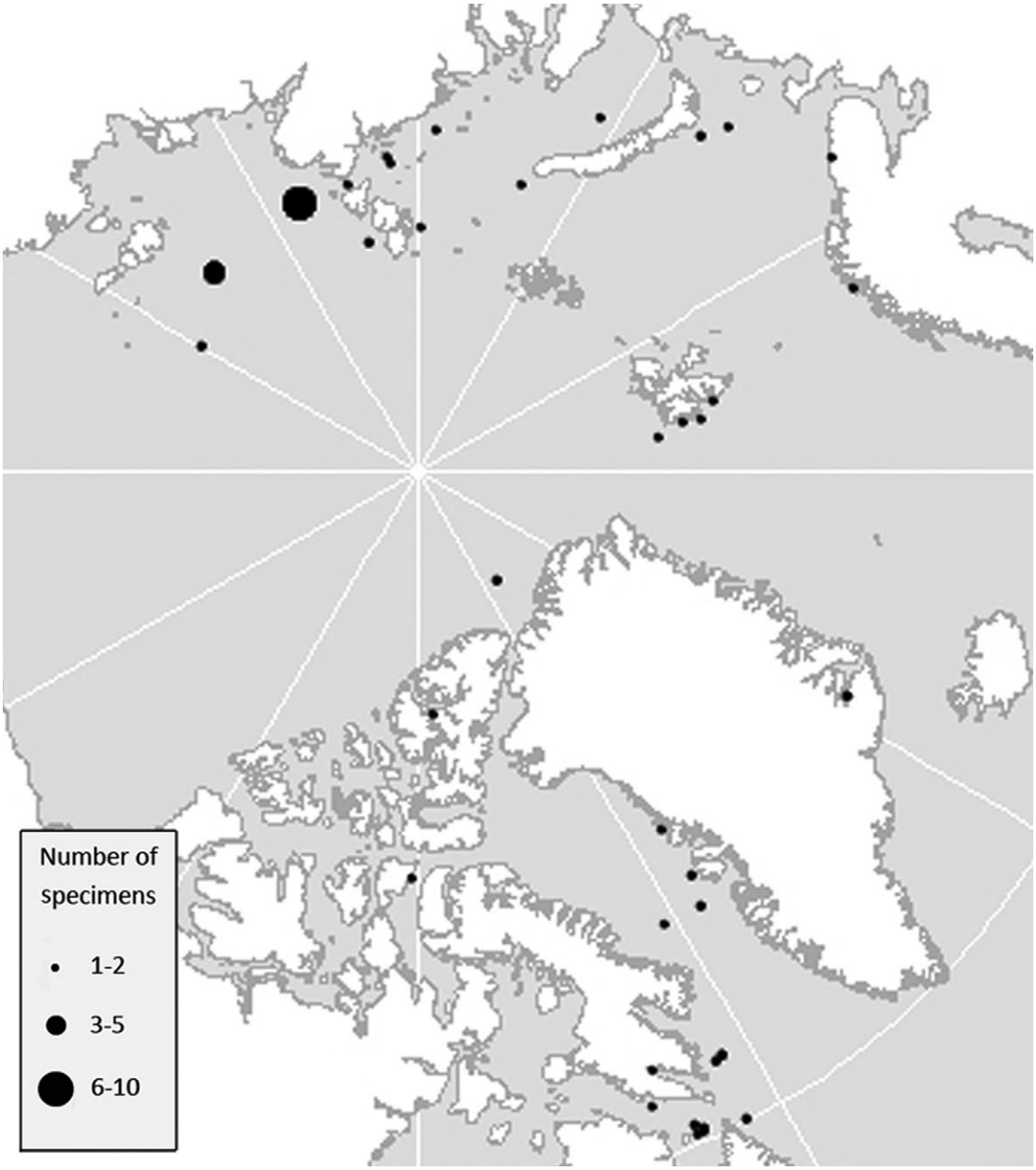

Fig. 6 Circumpolar records of *Rossia palpebrosa.* Sources: Grimpe (1933); Kondakov (1937); Wacasey et al. (1979); Nesis (2001); Canadian Museum of Nature collection; and Atlantic Reference Centre online database. Seven specimens were collected from the western side of Baffin Bay during Northwest Atlantic Fisheries Organization trawl surveys in 2006. They were all caught between depths of 123 and 611.5 m (Treble 2007).

Cape Vera and Pond Inlet are areas where northern fulmars are studied and narwhals are traditionally hunted. Records from both locations indicate that more than 100 samples of *G. fabricii* were collected from individual fulmar and narwhal stomachs (Figs. 1, 3). This distribution may indicate areas of greater cephalopod concentrations where predators congregate to feed. However, cephalopod beaks can accumulate in stomachs over time, with unknown expulsion rates (Lowry et al. 1986), which could result in an overestimation of predation pressure (Santos et al. 2001). Arctic predators are also migratory, and beaks collected from a sample from one location may be acquired from a different region. In the case of Cape Vera, the northern fulmars were believed to not travel great distances to forage, but a recent survey of the area found only a few individuals hunting in the

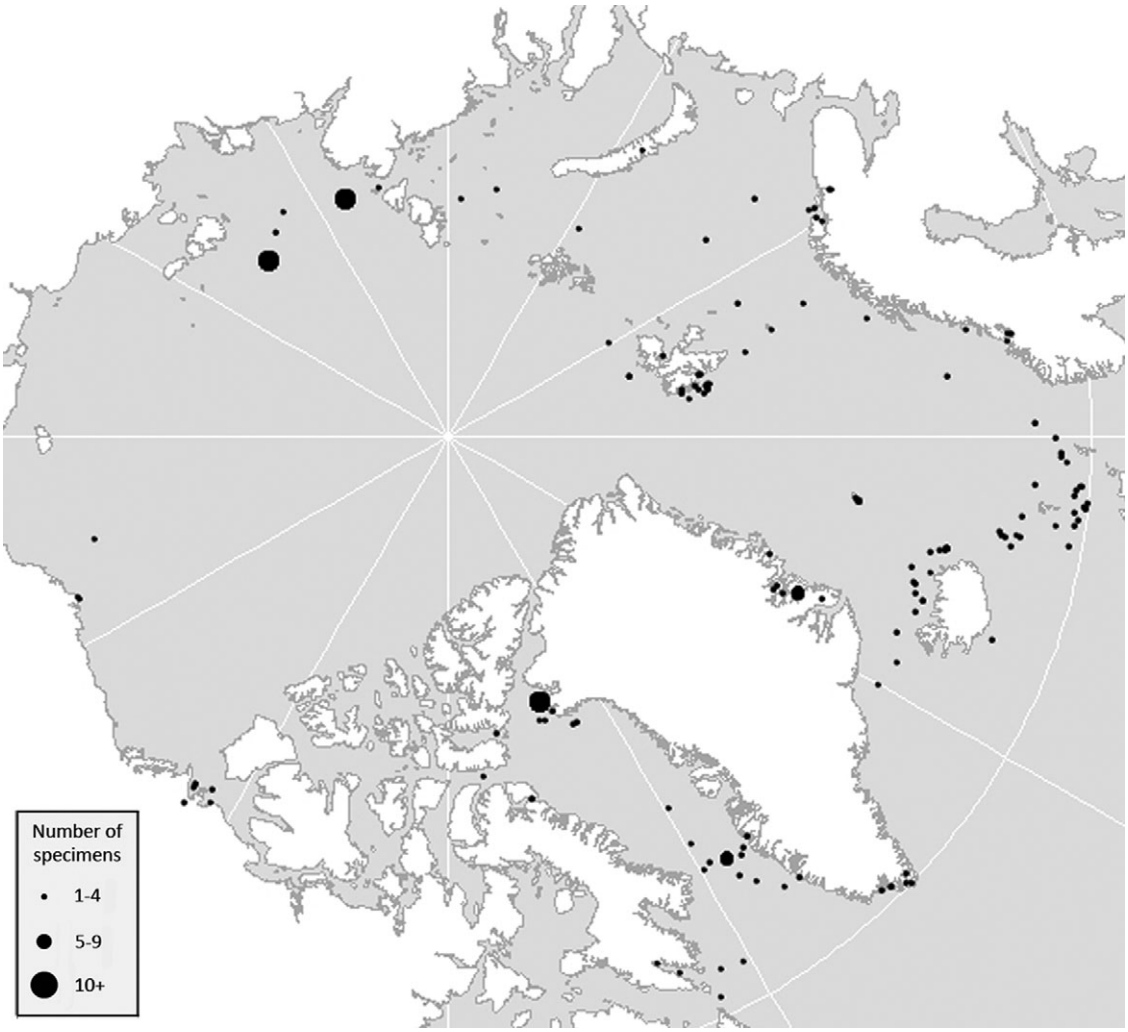

Fig. 7 Circumpolar records of *Bathypolypus arcticus*. Not included is a record (Taxonomic Information System for the Belgian Coastal Area online database) from the centre of Iceland. Sources: Hoyle (1886), Grieg (1930), Robson (1931), Adam (1939) and Macalaster (1976), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962, 2002); Wacasey et al. (1979); Finley & Gibb (1982); Atkinson & Wacasey (1989); Stewart et al. (1993); Nesis (2001); Canadian Museum of Nature collection; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) survey of 2004 (M. Treble, pers. comm.); and NAFO survey of 2007 (M. Treble, pers. comm.).

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nearby Hell Gate polynya, suggesting foraging trips of greater distances (Mallory & Gilchrist 2005). However, as Cape Vera is a breeding colony, it is unlikely that the birds would venture too far in search of food while caring for their young. Also, beaks may indirectly enter a predator's stomach when the animal feeds on a teuthophagus predator (Santos et al. 2001).

Increased sample numbers from a region may also reflect an active commercial fishery with a substantial bycatch. Large numbers of *G. fabricii* are reported from trawls along the south-west coast of Greenland (Fig. 1), and are frequently recovered as bycatch in the shrimp fishery (Kristensen 1983; Piatkowski & Wieland 1993; Zumholz & Frandsen 2006). Similarly, *B. arcticus* distribution is frequently reported from trawls (Stewart et al. 1993) (Figs. 7, 8).

Oceanographic variables and distributions

Many species of cephalopod have planktonic life stages, and ocean currents influence dispersal and local retention. Reports from the Norwegian Sea (between Jan Mayen and Vesterålen) indicate high densities of cephalopods, particularly *G. fabricii*, in areas with eddies (Figs. 2, 3; Wiborg et al. 1982). Larval *G. fabricii* cannot contract mantle muscles to drive active locomotion (e.g.,

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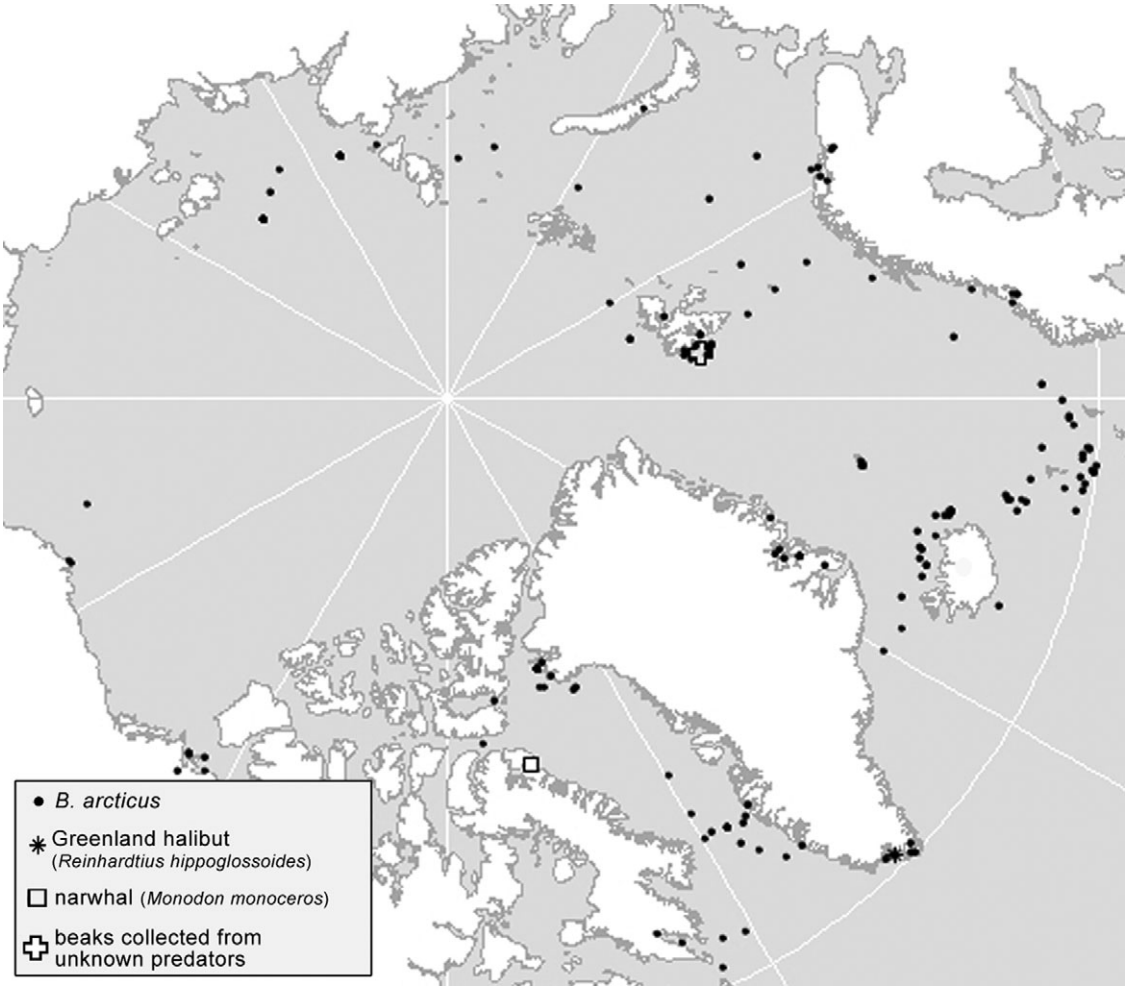

Fig. 8 Circumpolar records of *Bathypolypus arcticus* specimens, including remains in the stomach contents of predators. Sources: Hoyle (1886), Grieg (1930), Robson (1931), Adam (1939) and Macalaster (1976), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962, 2002); Wacasey et al. (1979); Finley & Gibb (1982); Atkinson & Wacasey (1989); Stewart et al. (1993); Nesis (2001); Canadian Museum of Nature collection; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) survey of 2004 (M. Treble, pers. comm.); and NAFO survey of 2007 (M. Treble, pers. comm.).

Nesis, 1965; Kristensen, 1983; Arkhipkin & Bjørke 1999), and, similarly, mature females lose musculature and revert back to a planktonic way of life (e.g., Clarke 1966; Kristensen 1983; Arkhipkin & Bjørke 1999). By contrast, *B. arcticus* and *Rossia* species lack a planktonic stage, and are not greatly influenced by currents (Sweeney et al. 1992; Wood 2000).

Depth is another key variable, as *C. muelleri* is typically limited to deep water regions in the Arctic Ocean and Baffin Bay (Fig. 9).

Polynyas, regions with wind-induced upwellings and direct access to sunlight, have increased productivity (Brown & Nettleship, 1981). The Canadian Arctic has several polynyas, including the large North Water in Baffin Bay (Michel et al. 2006). The distributions of some cephalopod species may correlate with these open water areas. An example is cephalopods from Cape Parry, a potential "hotspot" affected by the Cape Bathurst flaw lead (Michel et al. 2006). This lead creates higher productivity and, in turn, provides greater quantities of prey for cephalopods. Large numbers of *B. arcticus* were also collected off Greenland near the North Water Polynya. Nesis (2003 [1971]) suggested that cephalopods caught in the High Arctic through holes in the ice from drifting stations may have been responding to increased light. If this is the case, polynyas are likely to be the areas with most light during the winter months in the Arctic Ocean, and may explain, at least in part, the occurrences of greater numbers of cephalopods and their predators.

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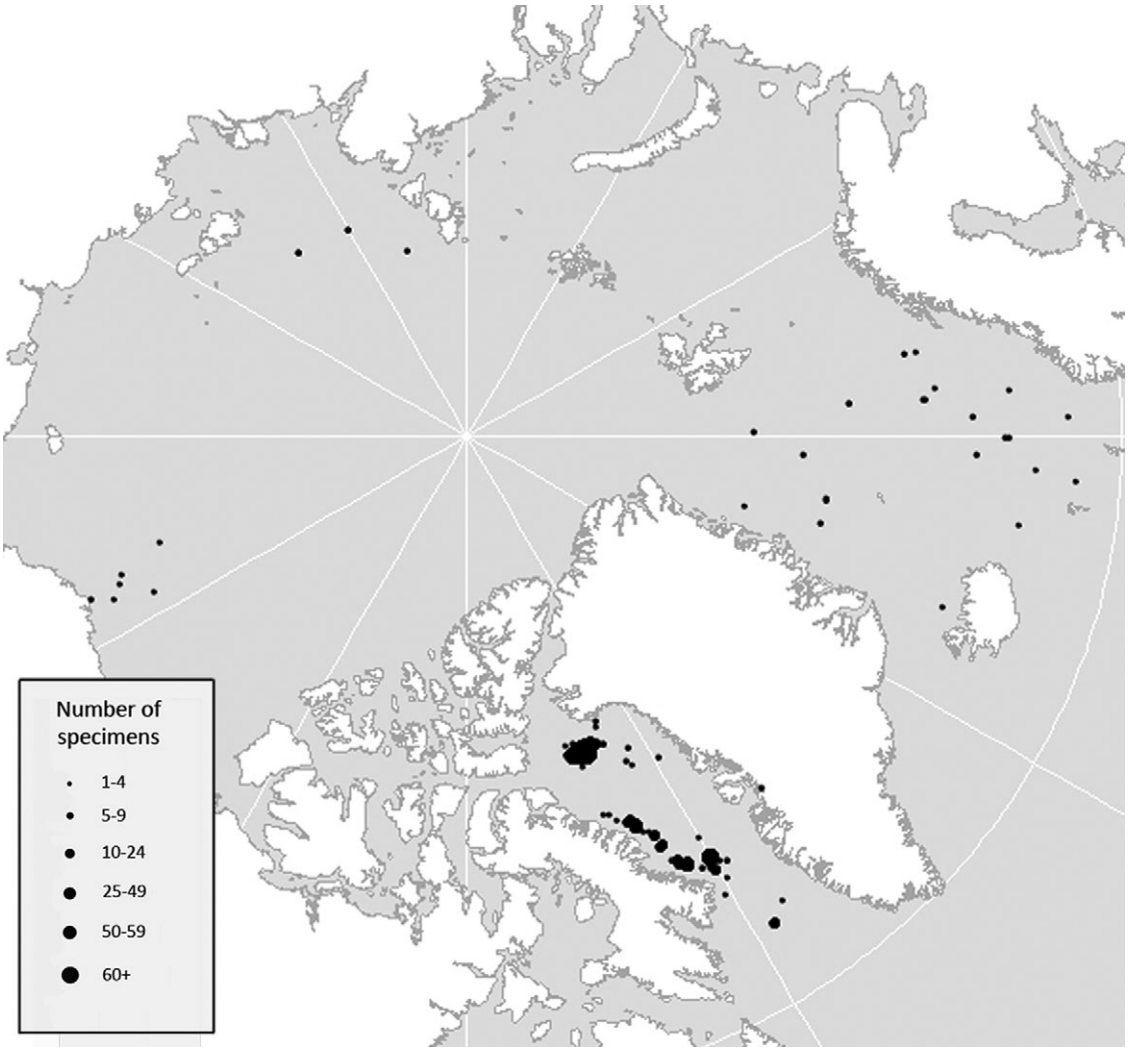

Fig. 9 Circumpolar records of *Cirroteuthis muelleri*. Forty-five individuals were collected from the western side of Baffin Bay during Northwest Atlantic Fisheries Organization (NAFO) trawl surveys in 2006. They were collected between the depths of 103 and 1482.5 m (Treble 2007). Sources: Grieg (1930) and Robson (1931), as cited in Cephbase; Grimpe (1933); Muus (1962); Nesis (1987, 2001); Collins (2002); B. Bluhm (pers. comm. 2007); Raskoff et al. in press; Ifremer BIOCEAN database 2007; Smithsonian National Museum of Natural History online database; Swedish Museum of Natural History online database; and NAFO survey of 2004 (M. Treble, pers. comm.).

Predator–prey distributions relative to ocean variables

Predators are often reported in areas with an abundance of cephalopods (Hjort & Ruud, 1929). Table 4 lists predators found in the Norwegian Sea near retention areas with strong circular currents (Wiborg et al. 1982; Dommasnes et al. 2001), where planktonic cephalopods (e.g., larvae) are likely to become concentrated. Narwhals feeding near Pond Inlet may be responding to greater prey abundance caused by currents in Baffin Bay and the local polynya (WHOI 2006; Barber & Massom 2007). Belugas have also been reported from the Amundsen Gulf (L. Harwood, pers. comm. 2007), which is an area of cephalopod aggregations (Figs. 1–10), possibly as a result of eddies formed by the influx of water from the Bering Sea (WHOI 2006) or by the retention from the Cape Bathurst polynya flaw lead (Barber & Massom 2007).

Summary

In summary, cephalopods play an important role in Arctic food webs, and are highly dependent on oceanographic processes for distribution. Further research on the collection of quantitative trawl data in biologically sensitive areas, in areas of active ocean currents and remote regions of the Canadian Arctic are urgently needed. Furthermore, a comprehensive compilation of community-

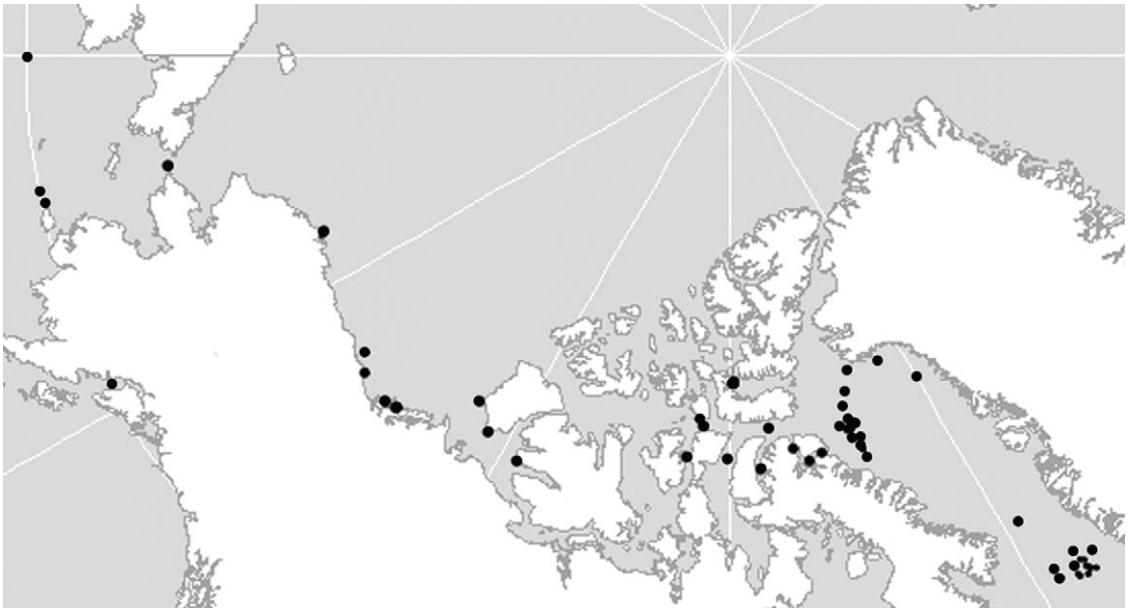

Fig. 10 Canadian records of unidentified cephalopods. Not included are a record of an unidentified cephalopod from central Norway and one from Alaska (coordinates not accurate). Sources: Hay & Mansfield (1989); Welch et al. (1992); Stewart et al. (1993); Dehn et al. (2007); L. Harwood (pers. comm. 2007); Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) survey of 2004 (M. Treble, pers. comm.); NAFO survey of 2007 (M. Treble, pers. comm.); and T.A. Dick (unpubl. data).

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based data on the diets of the commonly harvested marine predators will substantially increase the knowledge of this important group of invertebrates. Equally important is information on the physiological requirements of Arctic animals and climate change. Portner and Farrel (2008) discuss poleward shifts in the geographical distributions of animals, population collapses, changes in seasonal timing of biological events and changes in food-web structure, all of which are influenced by environmental temperatures. Cephalopods inhabit both deep and shallow waters, and some of their larvae are dispersed by surface waters, which make them vulnerable to temperature changes at all depths. Data are needed on cephalopod optimum temperature ranges and oxygen requirements. These baseline data are essential to clarify the importance and distribution of this nutrient-rich food source in Arctic marine food webs in the context of ice loss, warming waters, altered ocean currents, salinity and alien species invasions, including the large cephalopod predators.

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