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A metapopulation model for Canadian and West Greenland narwhals

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Abstract

A model of the metapopulation structure of narwhals *Monodon monoceros* in Baffin Bay, Hudson Bay and adjacent waters is proposed based on satellite telemetry data collected over two decades from six coastal aggregations of narwhals in the eastern Canadian high Arctic, Hudson Bay and West Greenland. In addition, data on seasonal catches of narwhals in 11 Inuit communities are used to provide information on the occurrence of narwhals. The tracking data suggest that disjunct summer aggregations of narwhals are, to some extent, demographically independent subpopulations, with minimal or no exchange with other summering aggregations. We propose that these should be considered separate stocks for management purposes. Year-round satellite tracking of individuals demonstrates that whales return to the same summering areas the following year, suggesting inter-annual site fidelity. We propose that the narwhals in Canada constitute five separate stocks, with limited exchange between three of the stocks. Coastal summer aggregations in Greenland constitute two stocks in addition to two fall and winter aggregations supplied by narwhals from several summering areas. Several narwhal stocks mix on the wintering areas in Baffin Bay, but the metapopulation structure is likely maintained through a combination of life-history traits and migratory routes, as mating most likely occurs after the initiation of the return migration toward summering areas. The metapopulation structure in Baffin Bay narwhals will be impacted differentially by Inuit subsistence hunting, depending on the migratory schedule of narwhals and dates at which whales occur in different seasonal hunting areas. It is therefore important to identify which narwhal stocks contribute to which subsistence hunts in order to assess the sustainability of those hunts. This paper proposes a preliminary stock model for this purpose.

Introduction

Understanding population structure of a species is vital for the conservation and management of factors affecting its demography. This is particularly important in the case of species hunted for subsistence, such as the narwhal *Monodon monoceros*. Metapopulation theory was developed to study population structure and demography of spatially segregated populations of a single species (Levins, 1970; Hanski & Gilpin, 1991). In essence, a metapopulation is a 'population of populations' (Levins, 1970) or a collection of spatially separated subpopulations that have a degree of demographic independence but also some degree of exchange of animals. A species with metapopulation structure may therefore exhibit dynamics that are different from the dynamics of a collection of completely isolated populations or a single extensively mixed (panmictic) population.

The narwhal is an ice-associated cetacean that inhabits Arctic seas bordering the Atlantic Ocean. During summer, narwhals visit inshore bays and fjords in the Canadian Arctic archipelago and Greenland (Fig. 1). In the autumn, upon the formation of fast ice, narwhals are forced to move east and south and spend the winter in ice-covered areas where they are widely dispersed in Baffin Bay and Davis Strait with the highest aggregations between 55–64°W and 68–71°N and off Disko Bay (Heide-Jørgensen *et al*., 1993, 2002, 2003; Koski & Davis, 1994; Dietz & Heide-Jørgensen, 1995; Dietz *et al*., 2001; Heide-Jørgensen & Acquarone,

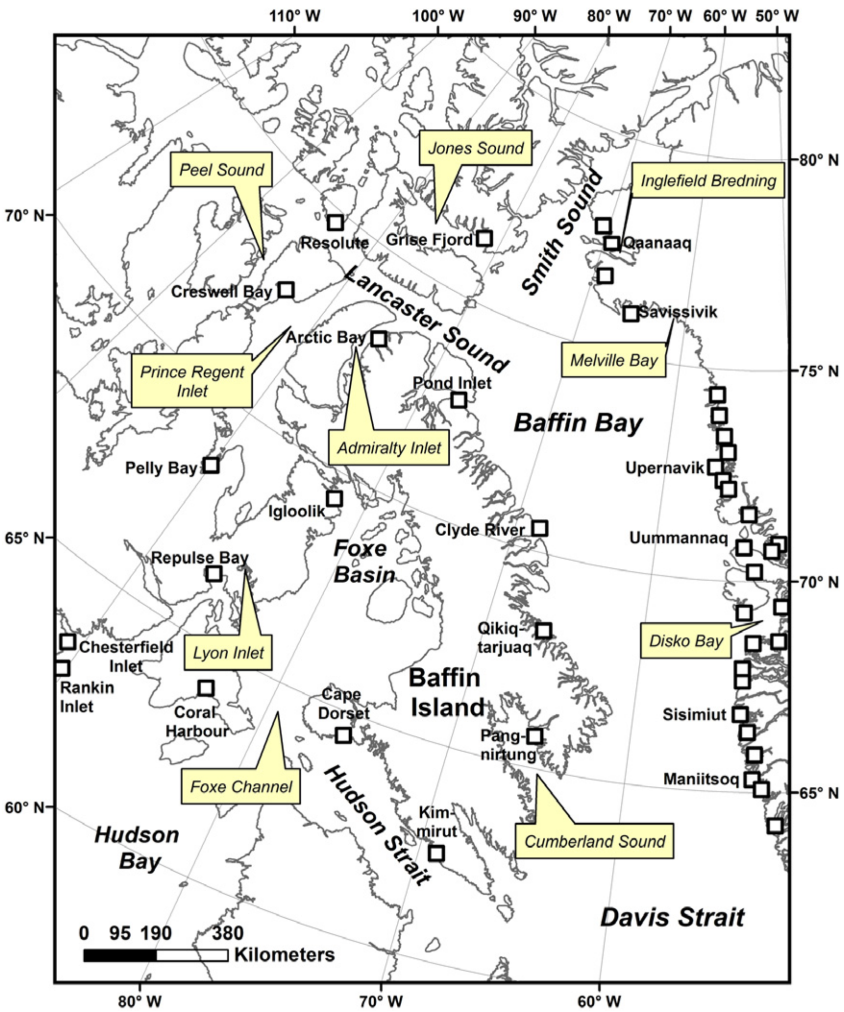

Figure 1 Map of Nunavut and West Greenland with localities, towns and settlements where narwhal *Monodon monoceros* hunting occur indicated. The four towns in Disko Bay where narwhal hunting occurs are Qeqertarsuaq, Ilulissat, Qasigiannguit and Aasiaat.

2002). During spring, aggregations of narwhals are seen along ice edges on the east coast of Baffin Island, at the entrances of Lancaster and Jones Sound, and in Smith Sound (e.g. Bradstreet and Cross, 1982). Narwhals are also known to move along the ice edges along West Greenland and to aggregate in the North Water in spring before entering Inglefield Bredning (Heide-Jørgensen, 2004). Narwhals spend the summer in bays and fiords of north-west Greenland, Hudson Bay and the north-eastern Canadian archipelago (Richard, 1991; Heide-Jørgensen *et al.*, 2010; Richard *et al.*, 2010).

Narwhals in Baffin Bay and adjacent waters are an example of a migratory species, where different stocks are hunted over varying temporal and spatial scales. Narwhals are hunted during both their northbound spring and southbound autumn migrations and during their stay at summering or wintering areas. In addition to summer stocks, there are also segments of the population that are observed as 'aggregations' outside the summer season. Following this, the total allowable narwhal catch should be allocated to individual whaling areas based on the information on the distribution and movement patterns of each stock, reducing the risk of local overexploitation. Allocation of allowable catches to aggregations or stocks can only safely be performed when the relationship between catches and stocks of known abundance has been established. Persistence and integrity of subpopulations rely on reproductive isolation of subpopulations maintained by strong philopatry, that is, seasonal homing to specific habitats.

Metapopulation theory has largely been applied to non-migratory species, where subpopulations are defined geographically. Nevertheless, the theory offers a valuable conceptual framework for migratory species as well (Esler, 2000). In this paper, we present evidence for the metapopulation structure of narwhals in the Canadian Arctic and West Greenland. We propose the distinction of a number of subpopulations or 'stocks' of narwhals to be used for conservation and subsistence hunt management. We also discuss spatial, temporal, genetic and behavioral factors that affect the demographic independence of narwhal subpopulations throughout the year.

Material and methods

Temporal and spatial distribution of the hunt for narwhals in Canada and West Greenland

Data on the seasonal occurrence of the narwhal subsistence hunt in Canada for the period 1979–2002 and for Greenland during 1993–1999 were extracted from Romberg & Richard (2005) and Piniarneq (1993–1999), respectively. Catch data before the installation of quotas were chosen because they show a better picture of the seasonality of both catches and occurrence of narwhals at the hunting localities. In the more recent catch data, the catches are stopped before the whales leave the hunting areas.

Historical data on satellite tracking of narwhals 1993–2004

Satellite-tagging studies of narwhals were initiated in 1993 to determine the movement patterns and migratory routes of narwhals in Canada and Greenland (Dietz & Heide-Jørgensen, 1995; Dietz *et al.*, 2001). In 1993 and 1994, nine whales from Melville Bay, West Greenland (Fig. 1), were tracked from late August to early December. Between 1997 and 1999, 17 narwhals were tracked from Eclipse Sound, Canada (Dietz *et al.*, 2001; Heide-Jørgensen *et al.*, 2002). In 2000 and 2001, 16 narwhals were tagged in Creswell Bay (Prince Regent Inlet), on the coast of Somerset Island, Canada (Heide-Jørgensen *et al.*, 2003). In August 2003–2004, 20 narwhals were tagged in Admiralty Inlet, the third summering aggregation in the Canadian high Arctic (Dietz *et al.*, 2008). These data were analyzed and published in several papers between 1995 and 2009 and provided background on the movements of narwhals from four of their largest summering areas.

Satellite tracking data from narwhals 2005–2009

An additional 22 narwhals were captured and instrumented with satellite-linked transmitters in Admiralty Inlet, Canada, August 2005 ($n = 14$) and 2009 ($n = 8$) as well as five in the Eclipse Sound area in 2010 (Table 1), following methods similar to previous live captures in the Inlet (Heide-Jørgensen *et al.*, 2002; Dietz *et al.*, 2008). Seven narwhals were instrumented at Fisher Islands (7606.965°N, 6142.453°W) Melville Bay, West Greenland in September 2006 and 2007, supplementing the tagging information from the area from 1993 to 1994 (Dietz & Heide-Jørgensen, 1995). Two narwhals were instrumented in Uummannaq in November 2007 and 2008 (Table 1) using nets set at the promontory of Niaqornat (7047.600°N, 5338.600°W). A total of nine narwhals were tagged over 2 years in Repulse Bay and Lyon Inlet using set nets in the same way as the other tagging projects above (Westdal, Richard & Orr, 2010).

The amount and quality of location data obtained from the satellite telemetry studies varied during the studies because of improvements in satellites' transmitter functionality and attachments over time, but also because of improved performance of the Argos Data Collection and Location System. Here, we only use good quality positions, that is, location class 1, 2 and 3 with estimated precision of < 500 m.

Results

Timing, locations and magnitude of the hunting of narwhals

Hunting along the east coast of Baffin Island (Qikiqtarjuaq and Clyde River) occurs between July and October [annual average of catches (AAC) 1996–2000: 18], except for the community of Pangnirtung (AAC = 23), which has an extended hunting period ranging from March to November (Fig. 2; Ditz, 2001). The majority of the Pond Inlet (AAC = 116) hunt occurs between May and September. The hunt in Arctic Bay (AAC = 99) is shorter, taking place between June and September, and the hunt at Somerset Island takes place in July–August (Resolute and Creswell Bay; AAC = 6). The hunt in Grise Fjord (AAC = 7) takes place between July and September. Catches in Pelly Bay, Igloolik and Hall Beach are low (AAC = 11).

Catches in Hudson Bay were taken in Chesterfield Inlet, Coral Harbour, Rankin Inlet and Repulse Bay. Most catches in Hudson Bay were taken by Repulse Bay in July–August. Only 2% ($n = 347$) were taken in June or September.

In West Greenland, catches reported from Sisimiut and south (AAC 1993–1998: 40; Figs 1 and 2) include whales taken further north. Hunting in Disko Bay (AAC = 154) takes place from late autumn throughout the winter and peaks in spring (April–May). The hunting in Uummannaq (AAC = 315) takes place in October–December, with lower catches during winter and spring. Hunting statistics identify that the largest catch in Upernavik (AAC = 81) takes place between August and November. Hunters from Qaanaaq sometimes see narwhals in the Smith Sound area in winter and spring (January–June); however, most hunting takes place between May and September with peaks in July–August (AAC = 106).

Results of narwhal tracking studies in the eastern Canadian Arctic and West Greenland

Satellite tracking data from 107 individual narwhals from six different coastal localities in Arctic Canada (Somerset Island, Admiralty Inlet, Eclipse Sound and North Hudson Bay) and West Greenland (Melville Bay and Uummannaq) were available for this analysis (Figs 3–8).

Somerset Island

For management purposes, we refer to narwhals occupying that area as the 'Somerset Island stock'. Narwhals tagged on

Table 1 List of narwhals *Monodon monoceros* tagged in this study. Whale ID # 37235 had a 225-cm long calf

Tagging locality	Tagging date	Transmitter ID #	Sex	Standard length (cm)	Tusk length (cm)
Admiralty Inlet	14 Aug 2005	20685	F	360	–
Admiralty Inlet	14 Aug 2005	20686	M	483	194
Admiralty Inlet	17 Aug 2005	20689	F	360	–
Admiralty Inlet	17 Aug 2005	37235	F	358	–
Admiralty Inlet	17 Aug 2005	37236	F	380	–
Admiralty Inlet	17 Aug 2005	37280	F	380	–
Admiralty Inlet	17 Aug 2005	37282	F	364	–
Admiralty Inlet	21 Aug 2005	37283	F	390	–
Admiralty Inlet	21 Aug 2005	20688	F	386	–
Admiralty Inlet	21 Aug 2005	7928	F	373	–
Admiralty Inlet	21 Aug 2005	20696	M	453	179
Admiralty Inlet	21 Aug 2005	20158	F	330	–
Melville Bay	9 Sept 2006	3960	F	372	–
Melville Bay	9 Sept 2006	3962	F	390	–
Melville Bay	13 Sept 2006	3964	M	437	187
Melville Bay	26 Aug 2007	7618/10946	F	390	100
Melville Bay	3 Sept 2007	6335/20162	F	420	100
Melville Bay	4 Sept 2007	3965	F	390	99
Melville Bay	4 Sept 2007	7617/37227	M	490	110
Uummannaq	15 Nov 2007	3961/3962	M	462	200
Uummannaq	24 Nov 2008	3961	F	406	–
North Hudson Bay	11 Aug 2006	57595	M	437	152 (broken)
North Hudson Bay	11 Aug 2006	57596	F	396	–
North Hudson Bay	11 Aug 2006	57597	M	262	27
North Hudson Bay	11 Aug 2006	57598	M	353	91
North Hudson Bay	11 Aug 2006	57599	F	396	–
North Hudson Bay	8 Aug 2007	36641	F	400	–
North Hudson Bay	9 Aug 2007	40152	M	375	98
North Hudson Bay	9 Aug 2007	37024	M	385	110
North Hudson Bay	10 Aug 2007	40622	M	364	101
Admiralty Inlet	15 Aug 2009	39290	F	374	–
Admiralty Inlet	15 Aug 2009	39309	M	376	79
Admiralty Inlet	16 Aug 2009	39313	F	391	–
Admiralty Inlet	17 Aug 2009	39256	M	450	165
Admiralty Inlet	17 Aug 2009	39287	M	439	150
Admiralty Inlet	17 Aug 2009	39211	M	307	51
Admiralty Inlet	17 Aug 2009	39312	M	455	211
Admiralty Inlet	18 Aug 2009	39249	F	386	–
Eclipse Sound	21 Aug 2010	51871	M	444	156
Eclipse Sound	21 Aug 2010	51872	M	461	100
Eclipse Sound	22 Aug 2010	51873	F	400	–
Eclipse Sound	22 Aug 2010	51874	F	390	–
Eclipse Sound	24 Aug 2010	51875	F	380	–

the east coast of Somerset Island in August ranged over waters on both sides of Somerset Island, including Prince Regent Inlet, Peel Sound and adjacent waters (Heide-Jørgensen *et al*., 2003; Dietz *et al*., 2008; magenta lines in Fig. 3). In September and October, the Somerset Island stock of narwhals were tracked leaving Peel Sound and Prince Regent Inlet and moving east along the southern and the northern coast of Lancaster Sound. The whales moved further east across Baffin Bay to the western side of the deep basin toward West Greenland and continued south to a wintering area centered at 71°N and 62°W where they remained stationary through March, after which the whales still transmitting ($n = 2$) began a return migration through Lancaster Sound along the southern shoreline of Devon to the Somerset Island summering area (Heide-Jørgensen *et al*., 2003; Dietz *et al*., 2008).

Admiralty Inlet

We refer to narwhals in Admiralty Inlet during summer as the 'Admiralty Inlet stock' (black lines in Fig. 3). Tracking studies of narwhals from Admiralty Inlet in 2003–2004

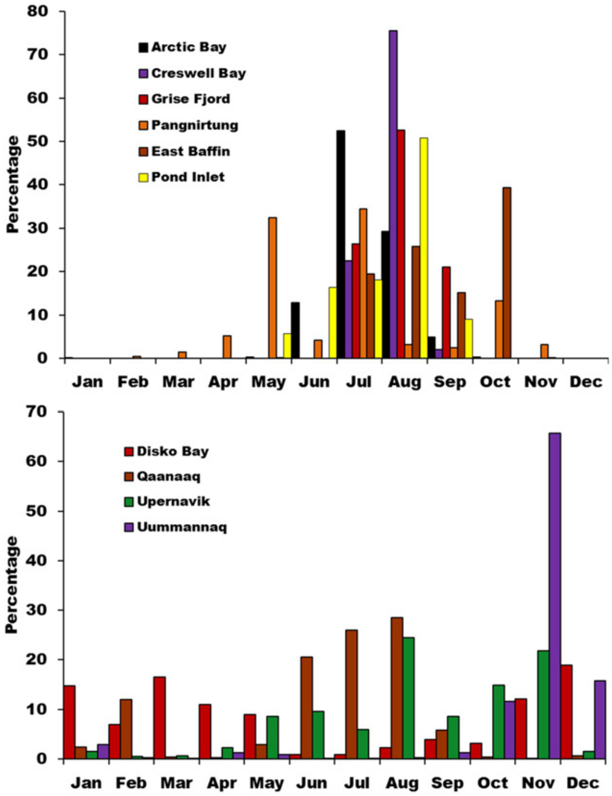

Figure 2 Upper panel: the five primary hunting areas in the Canadian high Arctic and the distribution of catches by month ($n = 2890$). Catches in Pangnirtung are considered part of East Baffin Island catches. Lower panel: the four primary hunting areas in West Greenland and the distribution of catches by month ($n = 4877$). The area from Sisimiut and south is considered mainly to consist of catches in the Disko Bay area because the hunters in this area are highly mobile and narwhals *Monodon monoceros* are rare in the area south of Disko Bay (Sources: Department of Fisheries and Oceans for Canada for the period 1979–2002 and *Piniarneq* for 1993–1999; Greenland Home Rule, http://www.nanoq.gl).

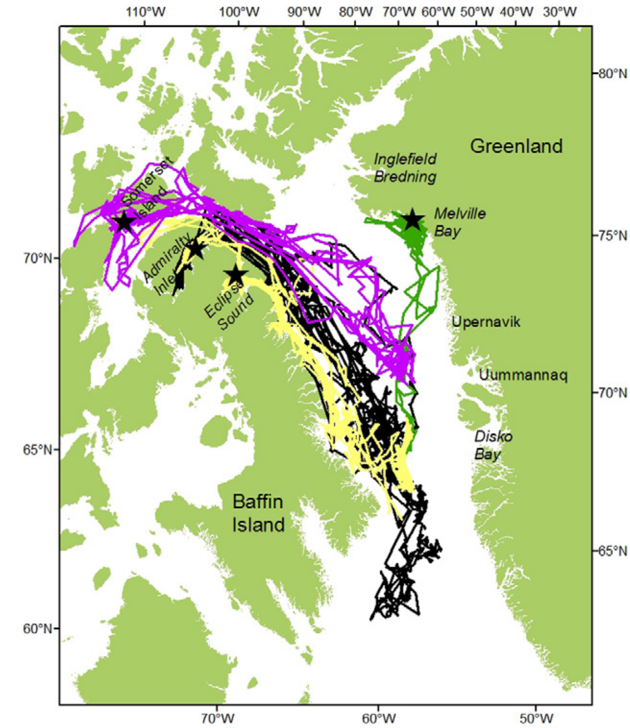

Figure 3 Tracklines of narwhals *Monodon monoceros* tagged from 1993 to 2004 (after Dietz et al., 2008). The black stars indicate the tagging positions.

showed that the whales remained in the Inlet for the summer through August and early September. However, in 2005, one Admiralty Inlet whale visited Prince Regent Inlet ('Somerset Island stock') in early September before heading east with the other whales from Admiralty Inlet (Fig. 4). This was also observed in 2009, where five out of seven tracked whales went to Prince Regent Inlet between early to mid-September before heading east (Fig. 5). Except for one whale that moved through the Furry and Hecla Strait into Foxe Basin in November (and remained there throughout the winter), all other whales from the Admiralty Inlet stock moved eastward through Lancaster Sound in late September, and southward along the east coast of Baffin Island. They eventually terminated their migration offshore in the northern part of Davis Strait. One male moved to the coastal areas close to Disko Island and Uummannaq in West Greenland during the month of January 2006 (Fig. 4).

Eclipse Sound

The geographic range of narwhals from Eclipse Sound did not generally overlap with that of narwhals from other aggregations during August and they are therefore referred to as the 'Eclipse Sound stock' (yellow lines in Figs 3 and 6). One exception to this was, in 1999, three tagged whales from Eclipse Sound moved to Admiralty Inlet and Prince Regent Inlet before returning east toward Baffin Bay (Dietz *et al.*, 2001; Heide-Jørgensen *et al.*, 2002). In late September, tagged narwhals from Eclipse Sound began to depart on their autumn migration. They moved south along the east coast of Baffin Island and visited several of the fjords along the way. In November, several of these whales moved into a wintering area in central Davis Strait (yellow tracks in Fig. 3), whereas others (Fig. 6) continued south toward southern Davis Strait. Two whales entered Cumberland Sound in late fall, and of them, a male crossed Davis Strait and entered Disko Bay in December 2010. Most narwhals from Eclipse Sound wintered in central Baffin Bay, roughly between 69°N and 60°W in the same area as narwhals tracked from Melville Bay, but some chose a more southern wintering area in northern Davis Strait (Figs 3 and 6).

Northern Hudson Bay

Narwhals tagged in northern Hudson Bay in 2005 and 2006 remained in the area between Repulse Bay, Lyon Inlet and western Foxe Channel until the end of October, at which

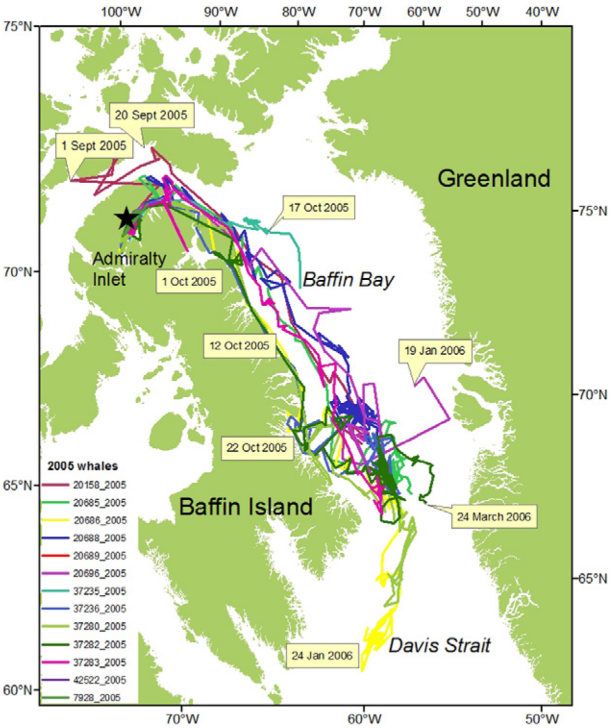

Figure 4 Tracklines of 14 narwhals *Monodon monoceros* tagged in Admiralty Inlet in 2005 (data from this study). The black star indicates the tagging positions.

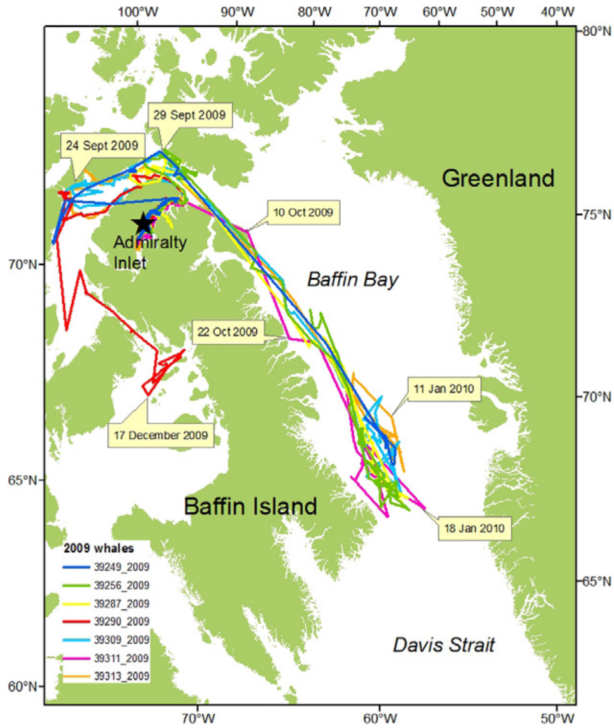

Figure 5 Tracklines of eight narwhals *Monodon monoceros* tagged in Admiralty Inlet in 2009 (data from this study). The black star indicates the tagging positions.

time they started moving eastward toward Hudson Strait (Westdal, 2008; Westdal *et al*., 2010; Fig. 7). They transited through Hudson Strait during the months of November and early December. Four animals were tracked throughout the winter months east of Hudson Strait. Two of them transmitted long enough to be tracked returning westward into Hudson Strait in June, which suggests that they were on their way back to their previous year's summering range in northern Hudson Bay. The narwhals that summer in northern Hudson Bay and winter off Hudson Strait do not seem to be overlapping year-round with any of the other stocks. They are referred to as the 'Hudson Bay stock'.

Melville Bay

Narwhals tracked from Melville Bay in 1993, 1994, 2006 and 2007 spent the summer in that bay without visiting other areas with narwhal summer aggregations and we refer to these animals as the 'Melville Bay stock' (Figs 3 and 8). Their fall migration began in October, when some individuals took a southern route along the 1000-m depth contour, while the others moved south but remained closer to land. Most of them arrived in central Davis Strait in mid-November where they presumably spent the winter. One of them left the wintering area late December 2006 and moved to the south end of Disko Bay where it stayed until 13 January 2007 before returning to the central Davis Strait wintering area.

Uummannaq

A male narwhal tagged in November 2007 spent the entire winter inside Uummannaq Fjord or just outside the Uummannaq area after in late January (Fig. 6). On 13 March 2008, it headed north (< 72°N) along the West Greenland coast, but contact was lost on 4 April 2008. A 2008 female also tagged in November immediately left Uummannaq Fjord after tagging and spent December through mid-February 2009 off the banks west of Disko Island (Fig. 6). On 24 March, it started moving north along West Greenland reaching northern Baffin Bay in early April where it remained through May. In late May, it migrated westward, moved through Lancaster Sound and ended in Peel Sound where contact was lost on 24 July. Based on the track of this narwhal, it is reasonable to assume that some narwhals from the Uummannaq fall aggregation belong to the Somerset Island stock.

Evidence for inter-annual site fidelity

Eight satellite-linked tags on narwhals transmitted for a full year, allowing for the assessment of inter-annual site fidelity to be based on individuals that returned in spring to the summering area where they were tagged the previous year (Table 2). At least six of the eight whales re-entered the area where they were tagged the previous year. The two other whales were close to (and heading toward) the summering

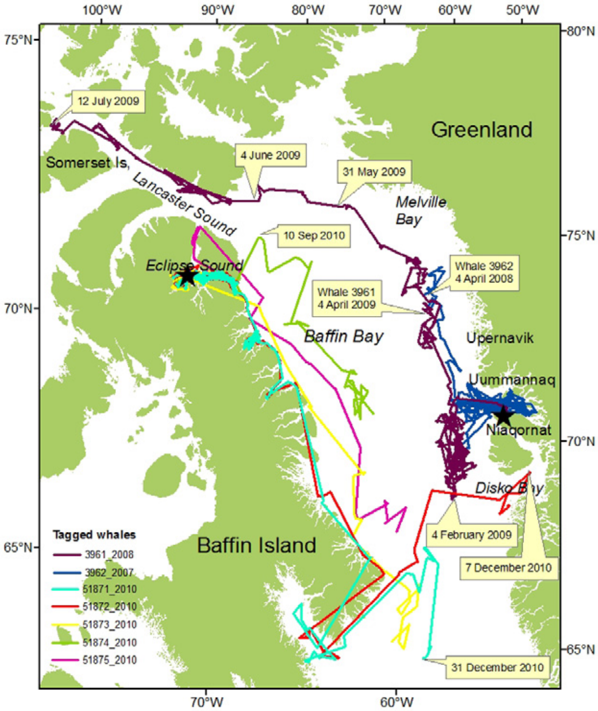

Figure 6 Tracklines of five narwhals *Monodon monoceros* tagged in Eclipse Sound in August 2010 and of two narwhals tagged in Uummannaq: one in November 2007 (blue) in November 2008 (purple). The black stars indicate the tagging positions.

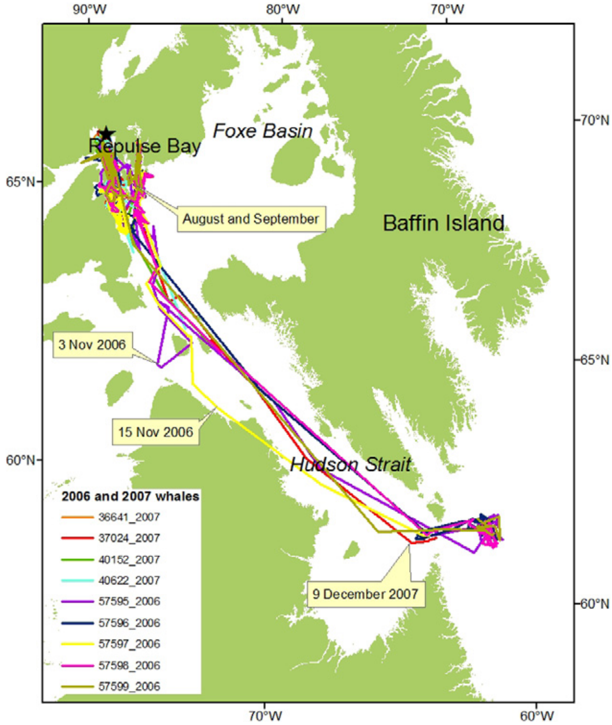

Figure 7 Tracklines of nine narwhals *Monodon monoceros* tagged in Northern Hudson Bay in 2006 and 2007 (data from this study). The black star indicates the tagging positions.

area where they were tagged, but contact with the transmitter was lost before they were inside the summering ground range.

Proposed relationship between summering area and subsistence harvest

The proposed metapopulation structure of the narwhal population in Baffin Bay and adjacent waters (Fig. 9) has important implications for the management of narwhal hunting in Canadian and West Greenland communities (Fig. 10). Occurrence in summering areas defines the stock unit, and the utilization of the narwhals in each stock must be balanced against the productivity of those local summer stocks and their exposure to hunting in other seasons and areas (Table 3). At least two additional putative stocks for the areas of 'East Baffin Island' (east of Pond Inlet to Cumberland Sound) and 'the North Water' (i.e. Smith Sound, Jones Sound and Inglefield Bredning) that have not been studied by satellite-linked tracking need to be considered as well. Three of the hunting communities (Grise Fjord, Qaanaaq, Arctic Bay and Creswell Bay/Resolute) rely on summer catches of these narwhals when their local subpopulations (stocks) are present in the area. However, when narwhals depart from the summering areas, they are exploited in other communities that only have narwhal subsistence harvests during winter months (e.g. Uummannaq and Disko Bay) or communities that hunt them during the fall and spring migrations (e.g. East Baffin Island). In several cases, the hunt outside the summering areas constitutes a mix of whales from different stocks (e.g. Melville Bay, Somerset Island and Eclipse Sound narwhals in Disko Bay, Admiralty Inlet, Eclipse Sound along East Baffin Island); in other situations, the migrations are unknown (e.g. Qaanaaq and East Baffin stocks), and in one case, there is evidence for a connection between a summering ground (Somerset Island) and a fall aggregation that is being hunted (Uummannaq). Only in Hudson Bay and Strait communities are the annual catches attributable to a single stock, the Northern Hudson Bay narwhal stock.

Discussion

Among marine mammal species, metapopulation models has so far only been described for pinnipeds, such as sea lions or gray seals (*Eumetopias jubatus, Halichoreus grypus*) (Harwood *et al.*, 1996; York, Merrick & Loughlin, 1996). Most cetaceans range widely over offshore areas that are difficult to access and it is often a complicated task to observe the underlying population structure. Although metapopulation structures has been suggested for several species of cetaceans (e.g. Pirzl *et al.*, 2009; Heide-Jørgensen *et al.*, 2011), metapopulation models have yet to be developed for cetaceans, and the spatial model proposed here for narwhals is the first attempt to develop such a model. Traditional methods of comparing genetic traits by hypothesis testing alone have failed to clarify the stock structure of narwhals in the Baffin Bay region (Palsbøll, Heide-Jørgensen & Dietz, 1997); however, the satellite tracking results presented here provide insight into the metapopulation structure for a species that aggregates in coastal areas and island passages in summer.

Esler (2000) suggested that the applicability of metapopulation theory as a conceptual framework for understanding the population structure and dynamics of migratory animals requires consideration of spatial, temporal and behavioral factors that affect demographic independence throughout the year. Following Esler (2000), we propose that narwhal population structure in the eastern Canadian Arctic and West Greenland consists of separate summering stocks, which probably also represent separate breeding units, with little dispersal between them.

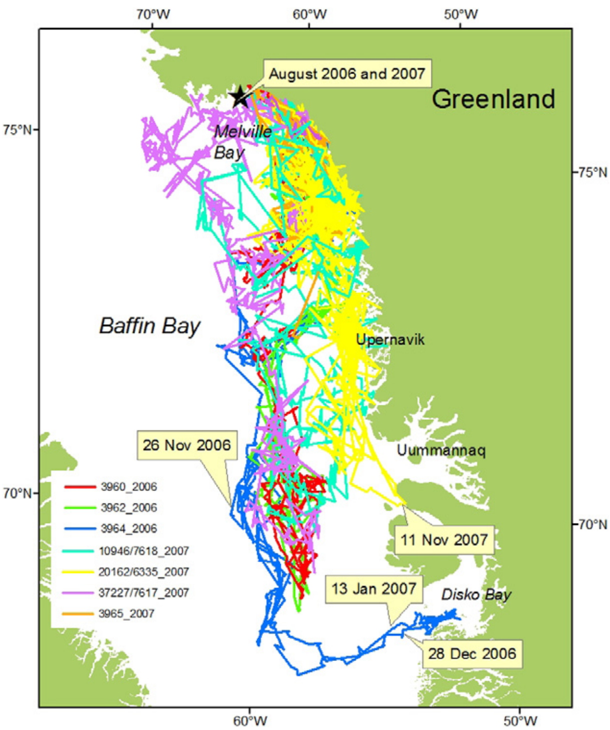

Figure 8 Tracklines of seven narwhals *Monodon monoceros* tagged in Melville Bay in 2006 and 2007 (data from this study). The black star indicates the tagging positions.

This study presents a conceptual model of narwhal population structure. Some narwhal subpopulations may be more isolated than others and there are subpopulations (stocks) for which movements remain unknown (e.g. Inglefield Bredning, East Baffin). Nevertheless, the metapopulation approach is a proposed framework for studying those relationships and should serve as a basis for conservation and management of narwhals.

Tracking data and observational evidence for population structure

The observations presented here suggest that at least some of the narwhal summer aggregations in eastern Canada and West Greenland are, to some extent, demographically independent subpopulations. The evidence for this includes regular occurrence of stable numbers of narwhal aggregating in summering areas, minimal movements out of summering sites during summer months, fall migration routes that differ between subpopulations and return spring migrations of some animals to the same summering area where they originated. The observation that animals from identified stocks are local in summer and do not appear to overlap in their range with adjacent stocks suggests that narwhals in other not-yet-studied summering areas should also be considered separate summer stocks.

A growing number of satellite tags deployed on narwhals in summering areas have transmitted long enough to show that the majority of them return to the

Table 2 Examples of evidence for site fidelity obtained from satellite-tracked narwhals *Monodon monoceros* returning to the tagging locality the subsequent year or later

Stock	Years	Observation	Reference
Somerset Island	2001–2002	Two whales tagged in 2001 returned to the summering area the following year	Heide-Jørgensen *et al.*, 2003
Somerset Island	2001–2006	One whale tagged in 2001 was resighted in Lancaster Sound 5 years later on its return migration toward Somerset Island	Heide-Jørgensen *et al.*, 2008
Admiralty Inlet	2004–2005	One whale tagged in 2004 returned to the ice edge at Admiralty Inlet in June–July 2005 but departed again and went east in Lancaster Sound passing the ice edge at Navy Board Inlet en route to the north coast of Baffin Island. Contact was lost before the August destination could be determined.	Dietz *et al.*, 2008
Admiralty Inlet	2009	One whale migrated back to the mouth of Admiralty Inlet and was last recorded a few tens of kilometers inside the inlet in June 2010	This study
Melville Bay	2007–2008	One whale tagged in 2007 returned the following year to the exact same area	This study
Northern Hudson Bay	2008	Two whales tagged in and Lyon Inlet in 2006 were tracked back to the same general area in June the following year	Westdal *et al.*, 2010

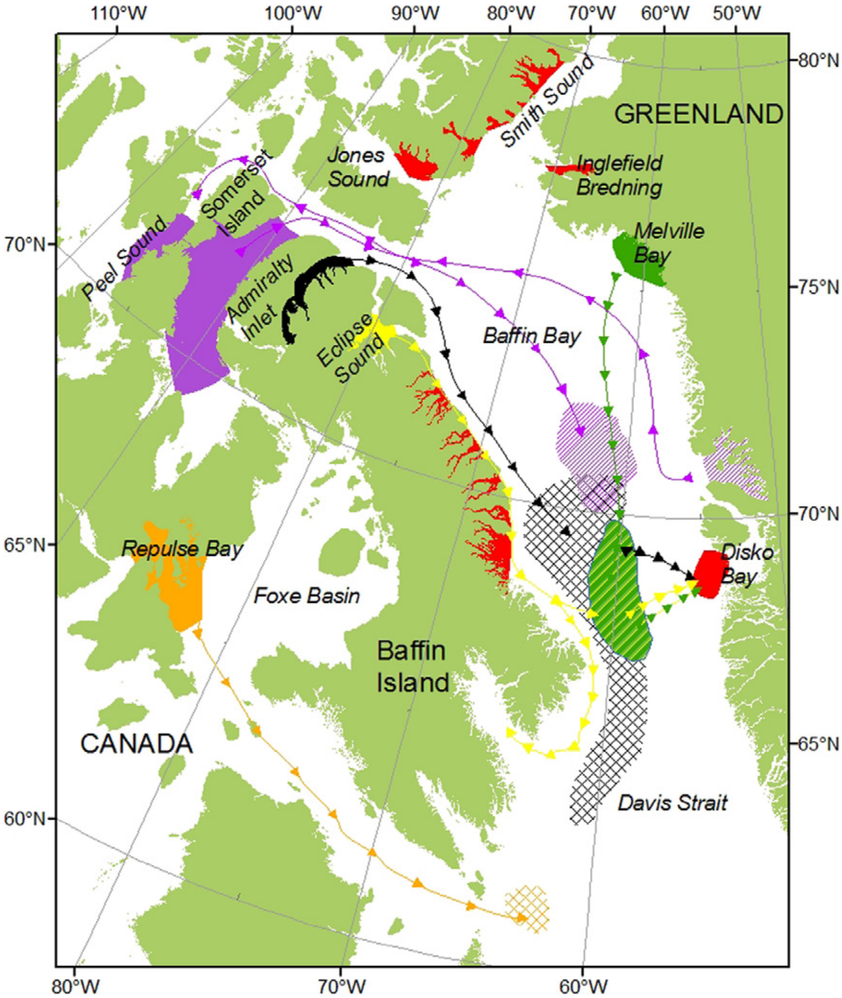

Figure 9 Map of the major summering aggregations (=stocks) of narwhals *Monodon monoceros*. Narwhals from the Melville Bay, the Eclipse Sound, the Somerset Island stock, the Admiralty Inlet and the Hudson Bay stocks (Repulse Bay) have been tracked by satellite and their late summer and autumn movements to four different wintering areas (cross-hatched) are shown. One narwhal from the Uummannaq November aggregation has been tracked to the summering area of the Somerset Island stock. Other localities that have not been studied (marked in red) include Disko Bay, Smith Sound and adjacent fjords, Jones Sound, Inglefield Bredning and fjords along the east coast of Baffin Island.

same summering areas the following summer. These tracking results, combined with the observations of recurring summer aggregations, lend support to the assumption that narwhalsummering stocks are philopatric aggregations and should be considered separate stocks for management and conservation purposes. Tagged narwhals leave these summering areas at about the same time each year and animals tagged in the same summering areas, with few exceptions, follow similar migration routes every year during their autumn, again suggesting philopatry to migration routes.

While summering aggregations are large and recurring in known areas as described earlier, there are occasional sightings of narwhals in areas not known to be aggregation areas. For example, narwhals are occasionally caught in Pangnirtung in August and September, but they are more often caught there in spring and fall. That catch is presumably supplied by narwhals from stocks further north, which winter in or migrate through that area. The low number of winter catches may be due to inclement weather, ice and light conditions. However, an aerial survey conducted in late March has documented the presence of many narwhal pods through the pack ice of Cumberland Sound (P. Richard, unpubl. data).

Genetic and contaminant lines of evidence

Palsbøll *et al*. (1997) described the genetic population structure of narwhals based on mtDNA and suggested that the three aggregations of narwhals in West Greenland (i.e. Inglefield Bredning, Melville Bay and Uummannaq) were genetically distinct. However, Palsbøll *et al*. (1997) also suggested that Disko Bay, the fourth aggregation, was a mixing area where narwhal pods from northern Baffin Bay and Melville Bay were wintering. A study of stable isotope ratios of $\delta^{15}N$ showed significant differences for narwhals in Inglefield Bredning and Uummannaq, and it was suggested this was due to a difference in short-term reflections of the trophic levels between the two areas (Dietz *et al*., 2004). The reflection of trophic level through stable isotope examination in muscle tissue likely result from short-term feeding and it is unknown exactly what time period these proxies are

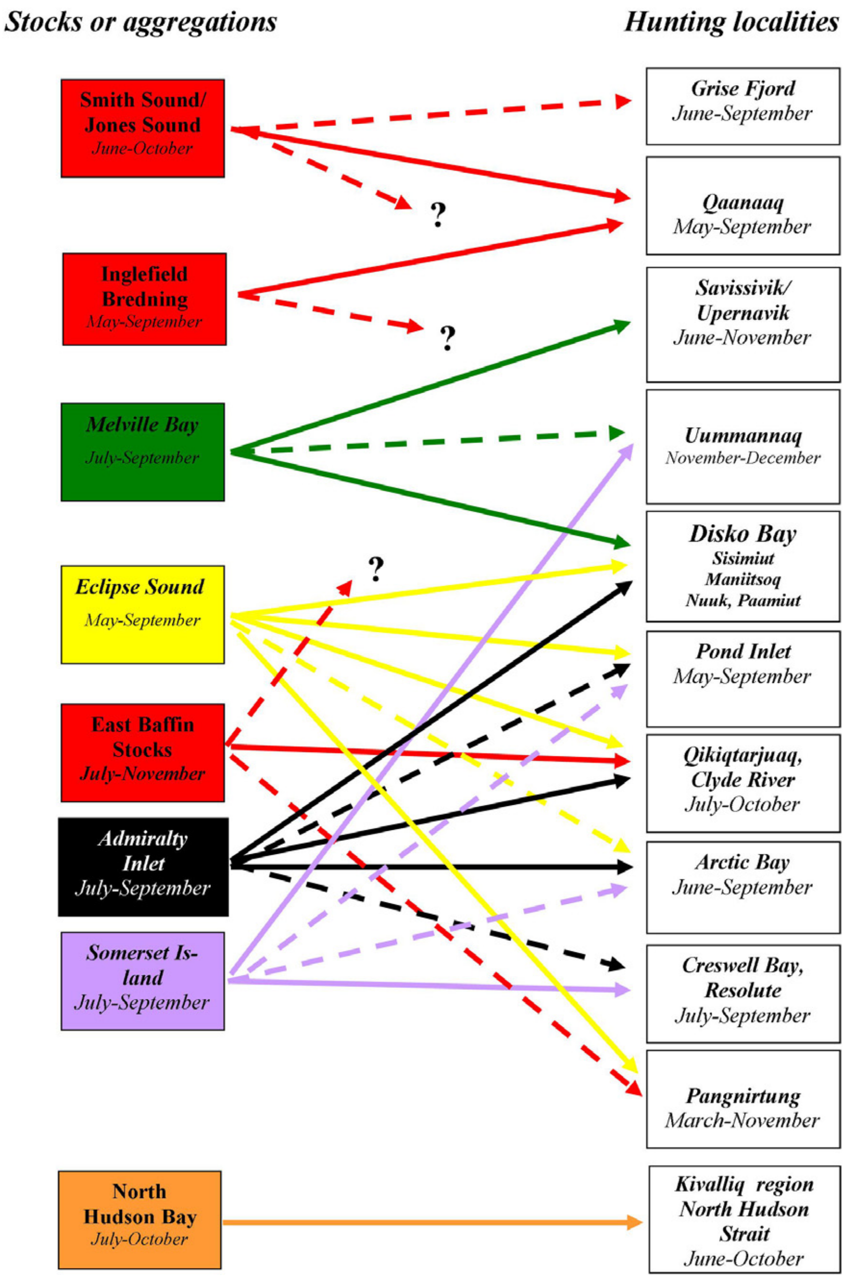

Figure 10 Hypothesized contribution to community catches in Canada and Greenland (right side) by stocks of narwhals *Monodon monoceros* (left side). Solid lines indicate catches by local communities adjacent to the stock's summering area. Broken lines indicate contribution of a stock to non-summer catches. Community names are given in italics to the right including Disko Bay that is a combination of several towns and the Kivallig region that includes Repulse Bay, Coral Harbour, Chesterfield Inlet, Rankin Inlet, and Arviat, and North Hudson Strait that includes Cape Dorset and Kimmirut. The month indicates the approximate time when the whales are present at their summering or aggregation areas and when they are available to the hunting communities. Question marks indicate unknown occurrence at other seasons.

Table 3 Approximate sizes of summering stocks of narwhals *Monodon monoceros* in Canada and West Greenland (Innes *et al.*, 2002; Heide-Jørgensen *et al.*, 2010; Richard, 1991; Westdal, 2008; Richard *et al.*, 2010). Confidence intervals (95%) are given in parenthesis

	Stock	Year	Stock size
Canada	Eclipse Sound stock	2004	20 225 (9471–37 096)
	Admiralty Inlet stock	2003	5362 (1920–12 199)
	Somerset Island stock	1996	45 358 (23 397–87 932)
	East Baffin Fiords stocks	2003	10 073 (5333–17 474)
	Northern Hudson Bay	2000	5627 (3543–8 935)
West Greenland	Inglefield Bredning stock	2007	8368 (5209–13 442)
	Melville Bay stock	2007	6024 (1403–25 860)

integrated over. Narwhals are thought to feed most heavily during winter and samples from stocks in summer do not necessarily reflect the prey choice and magnitude of feeding that occurs in winter (Laidre & Heide-Jørgensen, 2005).

Factors that may lead to demographic independence of subpopulations

Demographic independence between subpopulations of narwhals both on summering areas and, to a lesser extent, on the wintering areas is probably maintained through a combination of life-history traits and migratory routes. The mechanisms that lead to demographic independence of summering aggregations are probably related to nurturing and learning in mammals. Migratory and gregarious mammalian species, including odontocetes, tend to learn from one another and particularly from older experienced animals in their migrating group. Like other long-lived mammals, narwhal calves are believed to spend more than a year with their mother (Hay & Mansfield, 1989) and, consequently, learn from their migratory behavior. Although narwhals do not exhibit 'natal philopatry' in terms of calving and mating at the same locality, it is still conceivable that they learn their migration routes and the location of their summer and winter aggregation areas by following their mother and siblings, and, later on, other conspecifics from the same subpopulation.

While the extent of the mating season is not well known, it has been estimated that the average mating date is in the latter part of May (95% confidence interval: 1 May–12 June (Heide-Jørgensen & Garde 2011). Although some of the subpopulations utilize the same wintering areas and may be mating early in the season, other subpopulations are separated from April onward, when they are following migration routes to their summering areas and unlikely to encounter whales from other stocks. Some levels of cross-mating between stocks likely occur in late winter and low levels of cross-breeding are sufficient to dampen genetic differences between stocks, but animals composing a subpopulation (stock) are more related than in a perfect panmixia.

The degree of migratory divergence may vary between stocks, but evidently, some stocks are less likely to encounter whales from other stocks at that time of year. Mating is therefore likely to take place more between migrating whales and, consequently, with narwhals going to the same summering area (e.g. the three stocks that passes through Lancaster Sound in spring). This would contribute to maintain behavioral affinity for the same migration routes, probably a learned response, and philopatry to the same summering area.

The exception to the above seems to be the northern Hudson Bay narwhals, which segregate genetically from Baffin Bay narwhals (de March, Tenkula & Postma, 2003), probably because their seasonal distributions are separate year-round (Westdal *et al.*, 2010). These whales are also distinguished through contaminant analyses from other Canadian stocks (de March & Stern, 2003) and are therefore likely a population in the biological sense.

Three males were observed during winter to make incursions into other areas and they seem to be more likely to visit wintering areas of other stocks than the females. Satellite tracking provides insight into the coarse metapopulation structure, but estimation of the magnitude of exchange rates clearly would require substantially larger sample sizes to estimate exchange rates.

Management implications

This study proposes a metapopulation structure of narwhals in Baffin Bay and Hudson Bay, where discrete stocks are maintained through behavioral segregation. Panmixia is not supported by the data presented here on the relative stationary behavior in summer, and a return spring migration of individuals between years. The migratory destinations of narwhals from Inglefield Bredning and the East Baffin Stocks remain unknown and the association between the Uummannaq aggregation and the Somerset Island stock is based on limited information. However, for narwhal stocks, it is obvious that several stocks are hunted at many coastal locations in both Canada and Greenland, and that management action must take that into account (Fig. 8). From a management perspective, it is conservative to assume that stocks are demographically independent and therefore differentially exploited. Assuming that the Baffin Bay population is panmictic could lead to unsustainable catch levels at some localities or by some communities, which would severely affect these local narwhal stocks and the Canadian Inuit and Greenlandic populations that rely seasonally on those predictable aggregations.

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