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Spring partitioning of Disko Bay, West Greenland, by Arctic and Subarctic baleen whales

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Movements of co-occurring bowhead (*Balaena mysticetus*) and humpback (*Megaptera novaeangliae*) whales in Disko Bay, West Greenland, were examined using satellite telemetry. Data on movements, habitat use, and phenology were collected from tagged 49 bowheads and 44 humpbacks during the transition from sea-ice breakup to open water between 2008 and 2010. Bowhead whales began their northward spring migration around 27 May (median day-of-the-year departure date = 147, interquartile range 141–153) and were distributed broadly in northern and central Disko Bay in water depths between 100 and 400 m. Humpback whales arrived in Disko Bay no later than 2 June and were located in shallow water (<100 m) along the coasts of the mainland or Disko Island. Trends in departure date from Disko Bay were significant for bowhead whales (∼15 d later, $p < 0.001$) between two periods: 2001–2006 and 2008–2010. Many species are predicted to arrive earlier in the Arctic and to expand their range northwards with reduced sea ice and increasing temperatures under climate change. Quantifying the spatial and temporal relationships between co-occurring Arctic and Subarctic top predators allows for baseline insight to be gained on how climate change might alter interspecies interactions.

Keywords: Arctic, bowhead whale, Greenland, humpback whale, interspecies interactions, migration.

Introduction

Foodweb interactions in marine ecosystems with strong physical drivers, such as the Arctic, generally have some dramatic and predictable trophic level responses (Paine, 1980), which will be amplified and altered with a changing climate. One of the primary predictions of climate change is an expected increased influx of Subarctic species to the Arctic. Subarctic or temperate species are expected to arrive earlier in northern areas, to spend longer periods at higher latitudes, and to shift their ranges north, resulting in increased or new competition and shifts in community composition (Parmesan and Yohe, 2003; Root *et al.*, 2003; Rosenzweig *et al.*, 2008; Chen *et al.*, 2011). Given the loss of Arctic sea ice and changes in the marine ecosystem, similar trends are expected for Arctic and Subarctic marine mammals (Laidre *et al.*, 2008; Kovacs *et al.*, 2011), and in some cases, there are already indicators of change (Heide-Jørgensen *et al.*, 2010, 2011a, b; Scheinin *et al.*, 2011).

The coast of West Greenland is the longest continuous stretch of Subarctic to Arctic coastline in the world. When the annual winter sea-ice cover retreats, it triggers a large bloom of primary production on the shelf, attracting high densities of lower-trophic-level forage fish and zooplankton (Laidre *et al.*, 2008). This ultimately attracts large numbers of top marine predators, including more than ten species of baleen and toothed whales. Disko Bay, located on the west coast at ∼69°N, attracts some of the highest densities and diversity of marine mammals in Greenland. There, annual to decadal variations in the extent of the sea-ice cover influence the timing of the diatom-dominated spring bloom (Hansen *et al.*, 2006; Heide-Jørgensen *et al.*, 2007a). This spring phytoplankton bloom is closely coupled to the distribution, development, feeding, and reproduction of *Calanus* species, forming the base of the marine food chain in the region (Madsen *et al.*, 2001; Niehoff *et al.*, 2002).

The influx of baleen whales to Disko Bay typically begins in February with the arrival of bowhead whales (*Balaena mysticetus*), a high-Arctic zooplankton-feeder that target *Calanus* copepods (Laidre *et al.*, 2008). Bowhead whales are the Arctic's largest and most-dependent marine mammal predator of zooplankton (Laidre *et al.*, 2007), so the food chain leading up to this species is short and is strongly impacted by physical variables such as sea-ice cover and temperature. An estimated 1400 ($CV = 0.23$) bowhead whales occupy Disko Bay in spring (Heide-Jørgensen *et al.*, 2007b; Wiig *et al.*, 2011), and they depart from West Greenland predictably in late May and early June (Heide-Jørgensen *et al.*, 2006).

The departure of bowhead whales coincides with the arrival of several Subarctic cetacean species, including the humpback whale (*Megaptera novaeangliae*). An estimated 3299 ($CV = 0.57$) humpbacks occupy the coast of West Greenland (Heide-Jørgensen *et al.*, 2012), and the species has been increasing annually at 9.4% per year (s.e. = 0.01) since 1984. Humpback whales feed on various species of schooling fish, especially capelin (*Mallotus villosus*), which aggregate at productive sites on the banks and in shallow areas, where they feed on recently ascended zooplankton. Humpback whales in Greenland also feed on sandeels (*Ammodytidae* spp.) and krill (*Meganyctiphanes norvegica* and *Thysanoessa* sp.; Laidre *et al.*, 2010).

During spring, the ecosystem in Disko Bay goes through a transition from the dense sea-ice cover in March and April to complete open water by late June and remains open until January. Disko Bay is currently the only location in the world where bowhead and humpback whales predictably overlap in distribution, although this may change in other areas with climate warming (Moore and Huntington, 2008). Predation by these two cetacean species moves sequentially up the foodweb, with bowheads first preying on zooplankton and, after their departure, humpbacks preying on schooling forage fish. In this study, we investigated area use, spatial overlap, and the arrival and departure dates of bowhead and humpback whales using satellite telemetry on the movements of individual whales tagged between 2001 and 2010. The overlap between the two species is discussed, and implications drawn for changes with both population growth and climate warming.

Methods

Instrumentation

Between April and July of 2008–2010, 84 bowhead whales and 63 humpback whales were instrumented with Argos satellite-linked radio transmitters off West Greenland. Three types of satellite transmitter were used: SPOT5, MK10, and SPLASH (Wildlife Computers, Redmond, WA, USA). The SPOT5 tag (120 g) was a stainless steel cylinder of dimension 20 × 113 mm mounted with a stopping plate 38 mm below the distal end (where the antenna was positioned). The proximal end had a threaded bolt that mounted to a stainless steel spear of 8 × 160 mm equipped with foldable barbs. The MK10 implant (125 g) was similar in dimension except that it had a diameter of 22 mm. The SPLASH tag had an external epoxy mould that sat outside the skin of the whale (8.5 × 5 × 2.5 cm). These transmitters were anchored in the blubber of the whale by a cylindrical spear 23.5 cm long and 8 mm wide equipped with barbs (total weight 294 g). All tags provided positions between 08:00 and 20:00 GMT (250 transmissions between these hours). Tags were deployed with a pneumatic gun (SPOT5, MK10 tags; Heide-Jørgensen *et al.*, 2001) or a 6-m carbon fibre pole (SPLASH tags).

The tags were all deployed on adult bowhead and humpback whales within Disko Bay, <30 nautical miles from the towns of Qeqertarsuaq (along the south coast of Disko Island) or Aasiaat (along the mainland coast). Instrumented bowhead whales ranged between 12 and 17 m long, and humpback whales between 10 and 14 m, when length was estimated visually (relative to the tagging boat). Several instrumented whales were resighted near Qeqertarsuaq during the field season, and tag attachment was examined photographically if possible. Resighted tags were still well placed on the whale, and there was no indication of physiological rejection at the tagging site.

Data analysis

Data on the geographic positions of whales were collected using the ARGOS system (Service Argos, 1989; Harris *et al.*, 1990). Location data were filtered such that the best quality location (LC 3, 2, 1) closest to noon each day was used for each individual whale to reduce the autocorrelation bias. Days with no high-quality locations were discarded.

The species-specific monthly area use in Disko Bay was examined between April and July each year along with the overlap in the area use by bowheads and humpbacks in each month. This was conducted by calculating the 50% kernel home range for each month (for each species) using the single good-quality location each day with the land area removed. This area represented a defined region in which 50% of the locations were located for each month. Fixed-kernel range estimates were obtained using the Animal Movement and Spatial Analyst extensions in ArcView using least squares cross-validation (Hooge and Eichenlaub, 1997). We also compared the use of habitats within Disko Bay by examining the distribution of locations by water depth in May for bowheads and in June for humpbacks (source: srtm30 bathymetric GRID from USGS EROS; Becker *et al.*, 2009). A normalized density function was created by bathymetric depth for each species.

Data collected from bowhead whales in this study between 2008 and 2010 were augmented with an earlier time-series of satellite tracking data from whales tagged in Disko Bay in spring of 2001–2006 ($n = 18$ whales; see Heide-Jørgensen *et al.*, 2003, 2006). These two datasets were used to examine long-term trends in spring departure date from Disko Bay between 2001 and 2010. Bowhead departure date was calculated as the day after which an individual crossed the 55°W longitude line and remained west of that longitude. Only whales with a series of positions representing the departure period were used. If an individual whale had a >7 d gap (referred to here as departure gap) in locations during the period the whale crossed 55°W, that individual was not used in the analysis. If the gap was <7 d, the date of crossing 55° was interpolated based on the available locations. Analyses were conducted using R (R Development Core Team, 2011). The 55°W longitude line was selected because it represented the eastern threshold point at which whales were located completely outside Disko Bay. This line allowed comparison with historical accounts of bowhead whale departure dates (Eschricht and Reinhardt, 1861). We also tested the sensitivity of departure results to the selection of longitude by running the analysis for both 56 and 57°W and comparing the results for all three longitude thresholds.

Results

General movements of bowhead whales

All bowheads were tagged in Disko Bay between February and May of 2008–2010. In all years, the whales remained in Disko Bay until late May or early June. Whales were concentrated in the northern part of Disko Bay, near the south coast of Disko Island, but extending offshore around small islands in the opening of the bay or in the eastern part of the bay towards Ilulissat. After departure from Disko Bay in late May and early June, the migration route was northwestwards through leads and cracks in the Baffin Bay pack ice or north in the open water along the Greenland coast.

In May, the 50% kernel home range for bowhead whales in all years was focused entirely within Disko Bay proper. The region used in 2008 was 20 340 km^2 ($n = 8$ whales) and covered the entire bay down to the south coast. In May of both 2009 and 2010, the area used was smaller (2009: 7810 km^2, $n = 18$ whales; 2010: 6830 km^2, $n = 35$ whales; Figure 1a).

The area used by bowhead whales increased in June after their departure from Disko Bay. Whales were broadly dispersed across Baffin Bay as they moved north during their spring migration. The bowheads used an area of 24 000 km^2 in June 2008 ($n = 9$ whales), 41 200 km^2 in June 2009 ($n = 16$ whales), and 35 160 km^2 in June 2010 ($n = 29$ whales; Figure 1b). Although there was no spatial overlap between the June 50% kernel home ranges for bowheads and humpbacks, primarily because the migration was concentrated towards eastern Canada, bowheads were still located in Disko Bay ($<55°$W) in June when humpbacks were present (three bowhead whales in 2008, three in 2009, and one in 2010).

General movements of humpback whales

Of the humpback whales tagged during this study, all were instrumented primarily in the southern part of Disko Bay (near Aasiaat) in early June. This tagging locality was chosen because humpbacks have known affinity to the mainland coast along southern Disko Bay, and densities of whales have been predictably high in recent years. The earliest date a humpback whale was tagged in this study was 2 June, soon after first sightings were reported in Disko Bay. It was not possible to confirm the exact arrival dates for humpbacks in Disko Bay, however, and they may have been present earlier than the start of the tagging efforts.

Humpback whales tagged in southern Disko Bay moved back and forth rapidly between several smaller focal feeding areas along the south and north coast of Disko Bay, as well as to the banks of the outer mainland coast. The 50% kernel home range for humpbacks in June 2008 was focused in the southern half of Disko Bay (3350 km^2, $n = 9$ whales). In 2009, the 50% home range was concentrated in two distinct regions: one in the southern half of Disko Bay (2500 km^2, $n = 14$ whales) and one off the mainland coast at ~66.5°N (2930 km^2). The 50% region in 2010 was similar, with 22 whales using one area along the south coast of Disko Island (2200 km^2) and other whales along the north mainland coast (2700 km^2; Figure 1b). Humpbacks continued to use Disko Bay through August, although movements and the area use are not reported here.

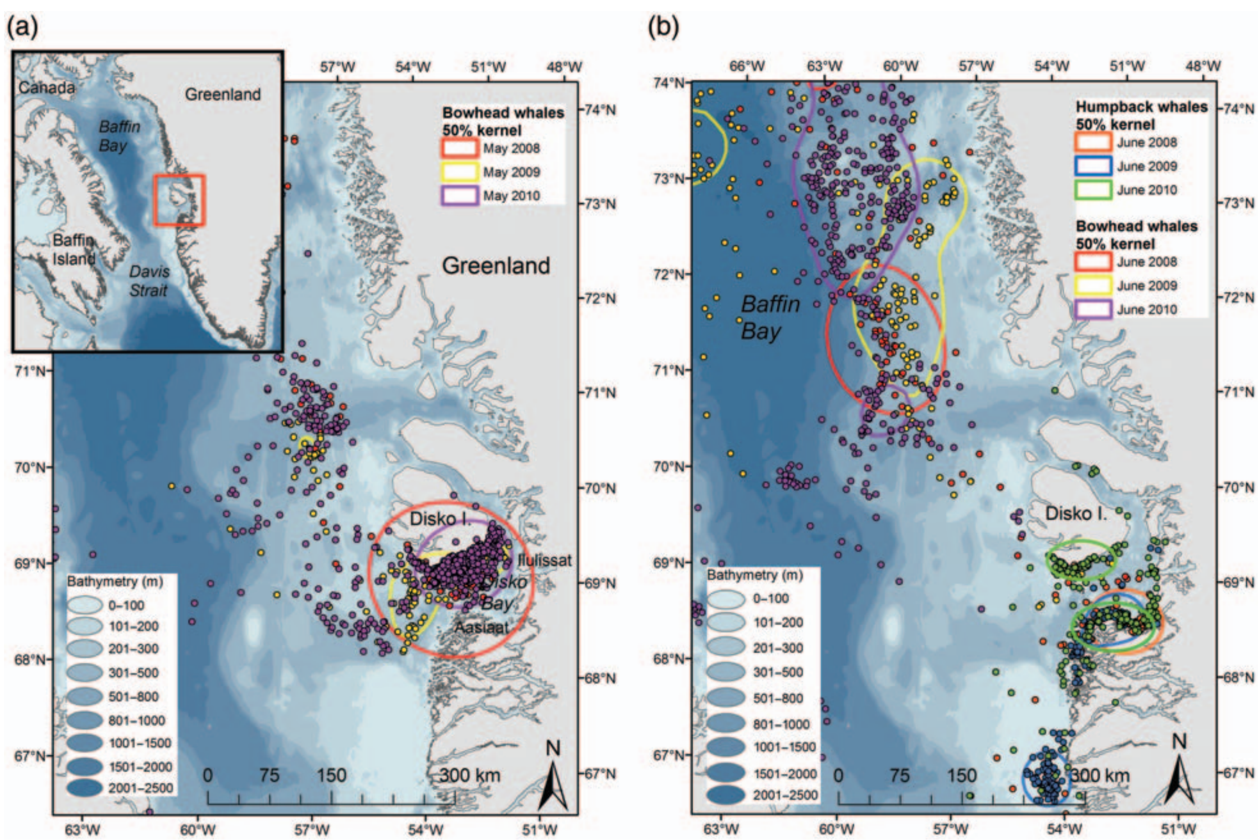

Figure 1. Map of the study area with the Disko Bay region shown in the red box. Kernel home ranges (50%) for (a) bowhead whales in May (2008, 2009, and 2010 shown separately), and (b) for bowhead and humpback whales in June in West Greenland between 67 and 74°N (2008, 2009, and 2010 shown separately).

Bowhead and humpback spatial and temporal overlap

In all 3 years, humpback whales instrumented in southern Disko Bay moved to the northern bay (specifically the southern coastline of Disko Island), starting in early June (6 June 2008, 4 June 2009, and 1 June 2010). The area use and arrival time of humpback whales coincided almost precisely with most bowheads leaving the bay in June (Figure 2), and there was no spatial overlap in the 50% core ranges for the two species. The same general area is used extensively by bowheads until the end of May, although they also use a larger area of the bay and deeper water.

In general, there was a clear shift of the core range of bowhead whales northwestwards out of Disko Bay precisely when humpback whales arrived during the first week of June. The latest departure date of any bowhead tagged in Disko Bay between 2001 and 2010 was 10 June (two whales in 2009), but 80% of the departure dates for bowhead whales were before 1 June or before humpback whales moved into their preferred habitat.

Bowhead whale departure

Bowheads have been tagged with satellite transmitters in Disko Bay since 2001 (Heide-Jørgensen *et al.*, 2003). To estimate as precisely as possible the date of departure of bowheads, we used data from 58 whales that transmitted data continuously over the traditional period of departure from Disko Bay, i.e. May–June. As stated above, the criterion for continuous transmission was that no temporal gap in location transmissions could be >7 d.

Using 55°W as the threshold for departure, the median day-of-the-year departure date for bowhead whales between 2001 and 2006 was day 132 (12 May; $n = 18$ whales, interquartile range 129–135). The median day-of-the-year departure date between 2008 and 2010 was day 147 (27 May; $n = 40$ whales, interquartile range 137–150). Differences in departure date between the early and late parts of the decade were significant (Mann–Whitney, $p < 0.002$), with bowhead whales departing ~15 d later in 2008–2010 than in 2001–2006 (Figure 3). Significant trends towards later departure were insensitive to the selection of the western longitude: bowhead whales departed significantly later in 2008–2010 using 56°W (14-d difference, Mann–Whitney, $p = 0.003$) or 57°W (10-d difference, Mann–Whitney, $p < 0.002$).

Habitat preference

The normalized distribution of location data by bathymetric depth in Disko Bay revealed a clear difference in habitat selection by species. The mean depth used by bowheads was 233 m (s.d. = 100 m, $n = 49$ animals, May 2008–2010), and the mean depth used by humpbacks was 82 m (s.d. = 84, $n = 44$ animals, June 2008–2010), with a significant difference ($p < 0.001$). The

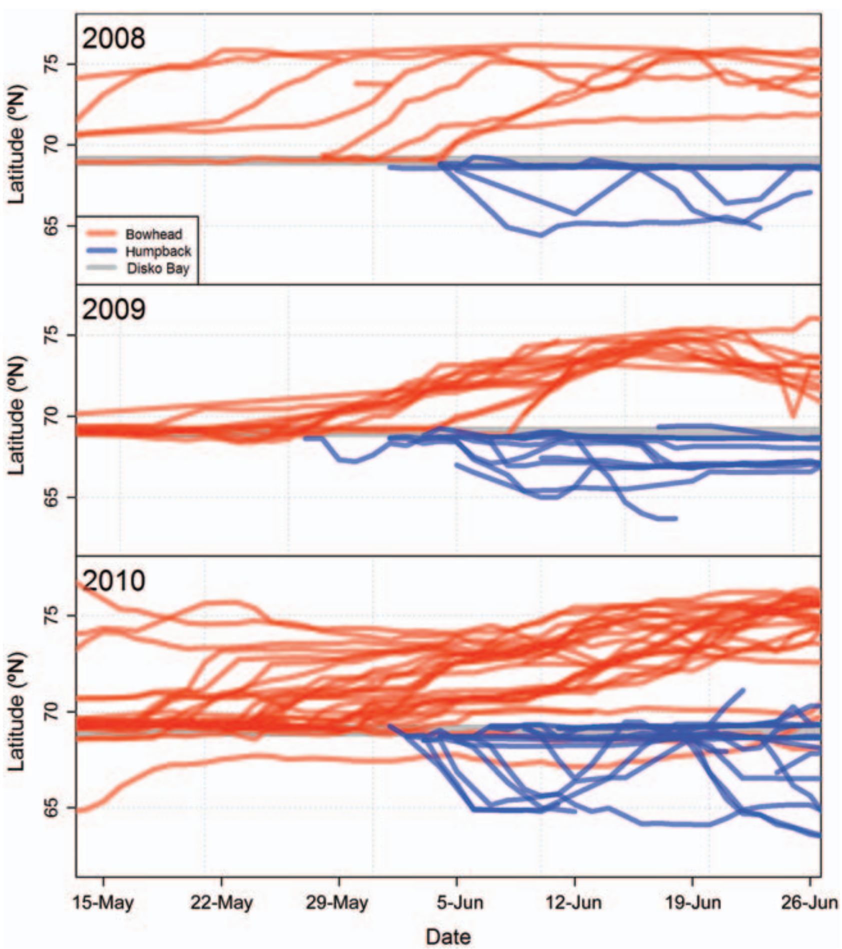

Figure 2. Latitudinal overlap between bowhead whales (red) and humpback whales (blue) in West Greenland using one location per day per animal. Each line represents a single whale. Bowhead whales arrive in February and March and depart from Disko Bay in late May. The latitude of Disko Bay is shaded grey.

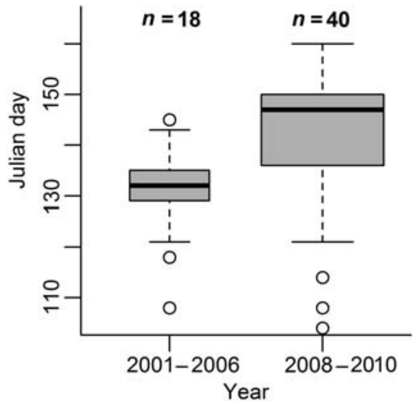

Figure 3. Median day-of-the-year departure for two periods, 2001–2006 and 2008–2010, showing the sample size of individual whales crossing longitude 55°W. The difference in departure date for bowhead whales was 15 d later during the years 2008–2010 ($p = 0.001$).

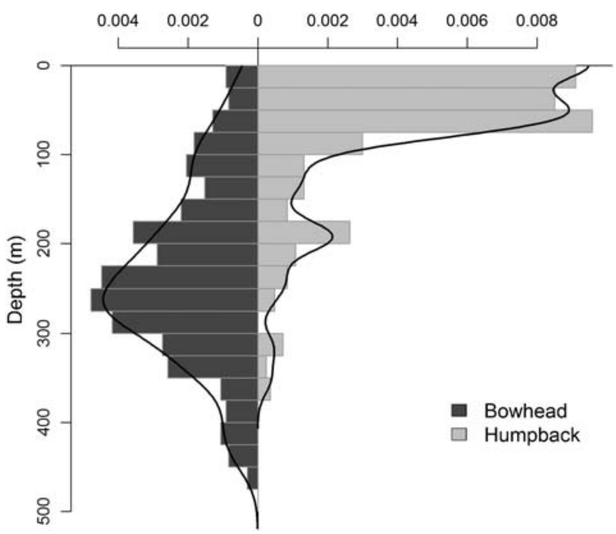

Figure 4. Vertical histogram of normalized densities of bowhead whales in May (left) and humpback whales in June (right) based on maximum bathymetric depths at locations of whale observations within Disko Bay. The solid black line represents the kernelized estimate of the probability distribution function of depth.

distribution of bowhead locations by depth was unimodal and covered a broad range between 0 and 350 m, with a peak near 250 m. In contrast, the locations of humpbacks by depth were skewed and bimodal, and focused in waters between 0 and 100 m, with a small secondary peak around 200 m, likely representing movements between areas (Figure 4).

Discussion

It is increasingly recognized that fluxes of organisms across ecosystem boundaries can have major consequences for community dynamics. Understanding the spatial and temporal overlap of Arctic and temporal/boreal species is therefore important for assessing changes in competition or interspecies interactions caused by climate change.

At least ten species of cetacean move in from the North Atlantic to take the advantage of the explosion in primary and secondary production on the shelves off south and central West Greenland. In addition to humpback whales, fin whales (*Balaenoptera physalus*), minke whales (*Balaenoptera acutorostrata*), and sei whales (*Balaenoptera borealis*) all migrate to feed in the waters of West Greenland, and all have been sighted in Disko Bay. The seasonal shift in Baffin Bay–Davis Strait from a dominance of Arctic cetaceans in winter (bowhead whale, narwhal, beluga) to high densities of temperate cetaceans in summer (humpback whale, blue whale, *Balaenoptera musculus*, harbour porpoise, *Phocoena phocoena*) has been observed since the 18th century by the offshore fishery and land-based stations. Eschricht and Reinhardt (1861) reported that during winter (December–April), bowheads were located between 65 and 69°N along the West Greenland coast, departing in mid-June. At that time, both blue and humpback whales moved into Greenlandic waters as far north as 76°N in August–September, departing south in autumn and disappearing from Baffin Bay–Davis Strait by late November.

The dates reported by Eschricht and Reinhardt (1861) were the last day when the managers of the whaling station (approximate range, 10 km from Qeqertarsuaq) documented a sighting in their area. These dates suggest that bowheads remained in Disko Bay with a median departure day around day 156 (interquartile range 141–164) or 5 June. In the present study, and from observations made over the past decade, bowhead whales depart 1.5–3 weeks earlier than during the period 1780–1837 (Eschricht and Reinhardt, 1861).

Bowhead whale numbers in West Greenland are increasing, but current abundance (around 1400 animals; Wiig *et al.*, 2011) is still well below the abundance before 1840 (tens of thousands). The observed differences in the timing of departure of bowhead whales 200 years ago compared with today's timing are possibly related to the overall reduced abundance, with a similar smaller variability in behaviour. Reduced abundance is also often accompanied by a contraction in range or a shift towards areas of optimal habitat (Rugh *et al.*, 2010), which would explain the highly focused distribution in prime habitat within Disko Bay.

The results of the present study suggest a trend towards later departure from Disko Bay over the past decade—with a net change of ∼15 d. During the same period, Disko Bay has experienced significant changes in the physical environment attributable to changes in climate. Specifically, reduced sea-ice coverage has led to earlier and longer spring production blooms (Heide-Jørgensen *et al.*, 2007a). Bowheads may now feed in Disko Bay for longer periods because the extended open-water season provides access to areas rich in their preferred prey, calanoid copepods (Heide-Jørgensen *et al.*, in press). If this trend continues, the spatial and temporal overlap with humpback whales arriving to feed on capelin in June is likely to increase.

The departure of bowhead whales from Disko Bay coincides almost precisely with the arrival of humpback whales. Although not quantified in this study, the arrival of spawning capelin in the bay, harvested annually by local fishers, also coincides largely with the arrival of humpbacks. We cannot determine conclusively the exact date of the arrival of humpbacks in late May or early June, but tags were placed on them as soon as sighting reports were made from either Qeqertarsuaq or Aasiaat, so it is unlikely that humpback whales were present in Disko Bay for more than a few days before tagging. Sighting networks in Disko Bay are extensive and thorough as a consequence of intense activity by local hunters and fishers.

Humpback whales arrive in West Greenland in spring and feed on spawning concentrations of capelin in the shallow areas at many localities along the coast West Greenland (Heide-Jørgensen and Laidre, 2007; Hedeholm *et al.*, 2010; Laidre *et al.*, 2010). Whales often follow the capelin close to sandy beaches in early summer, explaining the coastal focus of humpbacks in southern and northern Disko Bay in June (Heide-Jørgensen and Laidre, 2007). Humpback whales also feed in areas outside Disko Bay during summer, e.g. the banks of West Greenland. Sightings of humpback whales in Upernavik (72°N) in 2010 may suggest that whales make exploratory visits farther north (Greenland Institute of Natural Resources, unpublished data). In general, the continental shelves (<200 m) and offshore edge of the shelves off West Greenland are regions with significant upwelling (Ribergaard *et al.*, 2006), and this important feeding habitat supports high densities of sandeels (*Ammodytes* spp.), another prey species.

Future increases in temperature will likely continue to reduce the extent of the sea-ice cover in Disko Bay. Such changes are expected to expand the timing, duration, and spatial extent of the spring bloom and potentially could cause a shift in the composition of the *Calanus* spp. community (Swalethorp *et al.*, 2011). Smaller *C. finmarchicus*, containing fewer lipids, are likely to thrive with a more-predictable bloom (Madsen *et al.*, 2008), and the larger lipid-rich *C. glacialis* and *C. hyperboreus*, adapted to a short, intense feeding season, are probably incapable of fully utilizing a prolonged season of food availability. Consequently, the copepod community is predicted to be dominated by lipid-poorer species in warmer Disko Bay, with less sea-ice cover (Swalethorp *et al.*, 2011). It is unknown how shifts in the community composition would cascade to top predators such as bowheads and humpbacks.

The extent to which capelin distribution in West Greenland has expanded with change in temperature is unknown. Rose (2005) found a northward shift in the distribution of capelin with increasing sea temperature. Capelin are also efficient predators of copepods (Hassel *et al.*, 1991). Earlier arrival of the capelin in spring, with warmer temperatures (Rose, 2005), and increased predation on copepods could shift the transfer of production from the Arctic chain (copepods to bowheads) to a more Subarctic chain (copepods–capelin–humpback whales).

Conclusions

Population monitoring studies conducted over the past 20 years have demonstrated that populations of both bowhead and humpback whales have been increasing in West Greenland. Bowhead whales in Disko Bay have been increasing at a rate of ∼5% per year (Heide-Jørgensen *et al.*, 2007b; Wiig *et al.*, 2011), and humpback whale numbers have been increasing at 9.4% per year since 1984 (Larsen and Hammond, 2004; Heide-Jørgensen *et al.*, 2012).

Although the spring distribution of bowhead whales has remained relative consistent with historical records (with whales concentrated in central west Greenland and Disko Bay in spring), recent evidence of bowheads moving through the Northwest Passage suggests that the species may indeed be expanding its distribution (Heide-Jørgensen *et al.*, 2011a). Similarly, the distribution of humpback whales has also expanded along the west coast of Greenland during the past 30 years. Studies in the 1980s and 1990s showed humpback whales to be most abundant between 62 and 66°N (Larsen and Hammond, 2004), and Heide-Jørgensen and Laidre (2007) reported that humpbacks in the early 2000s moved as far north as 69°N and even crossed Baffin Bay, with a northward range extension between 1984 and 2007 (Heide-Jørgensen *et al.*, 2012). In this study, humpback whales migrated as far north as 69°N, but it is difficult to quantify the northward shift in distribution because effort has not been allocated consistently over the past few decades.

Niche segregation and spatial separation between species with similar ecology is not uncommon (Schoener, 1983), and some studies have provided evidence of small-scale niche segregation in baleen whales, including foraging at different depths, occupying different habitats, or targeting prey of different sizes (Murase *et al.*, 2002; Friedlaender *et al.*, 2009; Skern-Mauritzen *et al.*, 2011). Bowhead whales feed exclusively on copepods and amphipods, whereas humpback whales target schooling fish and krill (Laidre *et al.*, 2010). It is therefore unlikely that the two species would experience increased competition for prey associated with increasing population densities and/or increased overlap in spatial distribution in Disko Bay. However, earlier sea-ice breakup and warming conditions are expected to bring large changes to Arctic ecosystems, including more temperate species arriving earlier in spring (Root *et al.*, 2003; Chen *et al.*, 2011). The results here suggest a clear trend towards later departure of bowhead whales from Disko Bay over the past decade. Changes in spatial and temporal overlap between bowheads and humpbacks within Disko Bay and in other areas of the Arctic can be expected in future, so increased monitoring of co-occurrence and overlap in distribution is needed.

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