Trends in sea-ice cover within bowhead whale habitats in the Pacific Arctic

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Abstract

The range of the Bering-Chukchi-Beaufort (BCB) population of bowhead whales (*Balaena mysticetus*) extends across the seasonally ice-covered waters of the Pacific Arctic region. The majority of whales summer in the eastern Beaufort Sea and winter in the Bering Sea, migrating across the Chukchi Sea in fall and spring. As arctic sea-ice extent rapidly diminishes, the increasing length and variability of the open water season is changing bowhead habitat substantially, with many areas now regularly ice-free when whales are present. This study examines changes in the number of open water days (OWD) between 1979 to 2014 within annual bowhead whale core-use areas as defined by satellite tagging data, and within the western Beaufort Sea (140°W-157°W; to 72°N) sampled by fall aerial surveys. Ice cover has decreased more in the core-use areas in the northern extent of the range than in core-use areas in the southern extent. The numbers of OWD within the core-use areas near Point Barrow and along the northern Chukotka Coast during peak use have increased by 13 and 10 days/decade, respectively. The most dramatic reductions in sea-ice cover have taken place in the western Beaufort Sea where the number of OWD on the shelf and slope have increased by 20 and 25 days/decade, respectively. In contrast, sea-ice cover has not significantly changed within the winter core-use area near the Gulf of Anadyr. Using aerial survey data, we found that bowheads in the Beaufort Sea during the fall migration have a preference for being closer to shore than to the ice edge, and that their distance to shore decreases as the fraction of open water increases. This distribution may be due to increased feeding opportunities closer to shore as a result of greater upwelling along the shelf break when the ice cover is farther from shore. Furthermore, the aerial survey data also revealed a substantial shift westward toward Point Barrow in the whales' use of the western Beaufort Sea during fall in the period 1997-2014 compared to 1982-1996. The extent and timing of sea-ice coverage has changed relatively little over time in the Bering Sea. Bowheads typically migrate north prior to spring ice melt and retreat; therefore, large changes in the timing of the spring migration are not expected. We anticipate that bowheads will spend increasingly more time within summer and fall feeding areas, delaying their arrival to wintering areas in the Bering Sea. Reduced ice coverage and thickness in the southern Chukchi Sea may make wintering there more common in the future. Summer and fall movements may be more variable as productivity and zooplankton aggregations in existing

feeding areas are altered in response to sea ice thinning and retreat, and as new areas become available.

Keywords

Bowhead whales, arctic sea ice, Beaufort Sea, Chukchi Sea, Bering Sea

1. Introduction

Sea ice is important for the ecology and evolution of arctic marine mammal species. These species exhibit a range of adaptations for living in ice-covered waters, such as thick blubber, no dorsal fin (beluga—*Delphinapterus leucas*, narwhal—*Monodon monoceros*, and bowhead whales—*Balaena mysticetus*), or cryptic coloration as seen in young seals (i.e. white lanugo) or the white pelage of polar bears (*Ursus maritimus*). Sea ice, due to its roles both as a structural element in the Arctic environment and as an ecological driver of prey populations, is also thought to be an important factor for determining the seasonal range of arctic marine mammals. For pinnipeds, such as ice seals and walruses (*Odobenus rosmarus*), sea ice provides a platform for resting, pupping, molting, and feeding. For polar bears, sea ice provides the substrate on which they hunt. For cetaceans, sea ice may provide refuge from predators, such as killer whales (*Orcinus orca;* e.g. Shelden et al., 2003; Higdon and Ferguson, 2009). However, too much sea ice may also pose a risk of entrapment for cetaceans (e.g. beluga whales; Heide-Jørgensen et al., 2002; Ivashin and Shevlyagin, 1987) or limit gene flow between populations (e.g. Dyke et al., 1996; Alter et al., 2012). In contrast, the presence of sea ice may foster connectivity between populations for species that travel on the ice, such as the Arctic fox (e.g. *Alopex lagopus*; Geffen et al., 2007).

The spatial extent of arctic sea ice has declined at a rate of 14% per decade since the beginning of the satellite record in 1979 (Stroeve et al., 2014). This decline has been especially evident in recent years with the ten lowest September minimum ice extents having all occurred in the last ten years (2007-2016). Furthermore, the Arctic has experienced over a 60% reduction in annual mean sea-ice thickness over the last 30-40 years (Lindsay and Schweiger, 2015). There are several identified causes of the recent arctic sea-ice decline, including warming trends

(Overland et al., 2008), atmospheric circulation and wind patterns (Nghiem et al., 2007), a thinner more mobile ice cover (Maslanik et al., 2007), increased inflow of warm water (Woodgate et al., 2006), and the ice albedo feedback (Perovich, 2011). Given that most of these drivers are either projected to continue (e.g. warming trends) or are positive feedback mechanisms (e.g. increased ice mobility and the ice albedo feedback), it is unlikely that the current declining trends in sea-ice extent will abate before a nearly ice-free Arctic Ocean is observed in summer.

In this paper, we examine how sea ice has changed the habitat of the Bering-Chukchi-Beaufort (BCB; aka Western Arctic) stock of bowhead whales. Bowheads have long been considered ice-associated whales (e.g. Haldiman and Tarpley, 1993; Moore and Reeves, 1993; George, 2009) that have a range restricted to areas with seasonal ice cover, seek refuge within pack-ice from predators, migrate through seasonal flaw lead systems in spring, and have a protruding rostrum capable of breaking ice up to 60 cm thick to breathe (George et al., 1989). The majority of the BCB stock spends summers in the Beaufort Sea (Moore and Reeves, 1993; Harwood et al., 2010) and winters in the Bering Sea, migrating through the Chukchi Sea in both fall and spring. The most recent abundance estimate for the stock was approximately 17,000 whales in 2011 (Givens et al., 2013). Whales that summer in the eastern Beaufort Sea have been observed in deep waters beyond the continental shelf (Moore et al., 2000); however, the majority feed in shallower waters over the continental shelves (e.g. Moore and Reeves, 1993; Moore et al., 2000; Ashjian et al., 2010; Harwood et al., 2010; Citta et al., 2015) where summer sea ice has substantially diminished over recent decades. In a typical year, the majority of bowheads remain in the eastern Beaufort Sea until late summer or early fall, when they begin their fall migration across the western Beaufort Sea and Chukchi Sea. Most whales arrive at, and pass by, Point Barrow from late August through mid-October. By mid to late fall, bowhead whales are well into the Chukchi Sea, where their migration is broadly distributed (Quakenbush et al., 2010; Clarke et al., 2016). Most whales linger along the northern Chukotka coast before arriving in the Bering Sea, where they remain from December to April.

Our understanding of how sea ice is thought to affect the distribution of bowhead habitat has changed over the last several decades, concurrently with diminishing arctic sea ice. Researchers initially believed that bowheads in winter were largely restricted to polynyas—areas of open water usually formed downwind from land masses (Niebauer and Schell, 1993)—

because polynyas provided open water for surfacing (e.g. Bogoslovskaya et al., 1982; Brueggeman et al., 1987) and because bowheads targeted the ice edge for feeding. Recent studies indicate that bowhead whales are much less limited by sea ice than originally thought, although this assertion is confounded by lighter ice conditions in recent years. Satellite tagging has shown that most bowheads do not rely on polynyas in winter (Citta et al., 2012) and that they are capable of migrating through very heavy sea ice in spring (Zeh et al., 1993; Quakenbush et al., 2012). Genetic studies indicate that the dispersal of bowheads is not as limited by sea ice as previously believed (Alter et al., 2012). Although bowheads may sometimes target the ice edge for feeding, many feeding areas are completely devoid of sea ice when whales are present (Moore et al., 1995; Ashjian et al., 2010; Walkusz et al., 2012; Citta et al., 2015; Okkonen et al., this issue). Bockstoce et al. (2005) summarized catch data from historical whaling ship logs indicating that thousands of bowheads summered in the Bering Sea in the 1850s, which was presumably ice-free, at least in some years (e.g. see Mahoney et al., 2011). This does not mean that bowhead habitat is independent of sea-ice conditions; rather, that the relationship between bowheads and ice is more subtle.

The current decline in sea ice is thought to have had a positive influence on bowhead whale habitat in the Pacific Arctic region (Moore and Stabeno, 2015). Declining sea ice is associated with an increase in net primary productivity due to more photosynthetically active radiation entering the ocean (e.g. Arrigo et al., 2008) and a longer growing season (e.g. Arrigo and van Dijken, 2011; 2015). These changes may translate into enhanced secondary production, including faster growth rates of zooplankton (Matsuno et al., 2011; Ershova et al., 2015) that bowhead whales consume. George et al. (2015) found that sub-adult whales in particular gain more mass, an indicator of improved body condition, during years with less sea ice. Improved body condition, however, may be linked to other factors as well, including prey aggregation through increases in upwelling favorable winds (Pickart et al., 2013) or increased transport of zooplankton through Bering Strait (Woodgate et al., 2012; Ershova et al., 2015). Despite these mechanisms for advantage, it is unclear if continued rapid declines in sea ice will remain advantageous for bowhead whales. For example, bowhead whales are known to target large zooplankton, yet warming may favor smaller-sized species, which appears to be the case in the Bering Sea where bowheads winter (Eisner et al., 2014). Declining sea-ice habitat may expose bowhead whales to more competition as sub-arctic species of whales, such as humpback whales

(*Megaptera novaeangliae*), or predators, such as killer whales (*Orcinus orca*), expand into the bowhead whales' summer and fall range.

In this paper, we examine sea-ice conditions within known bowhead whale habitats by analyzing long-term (1979-2014) changes in sea-ice concentration and timing within the areas of the Alaskan Beaufort Sea where whales are counted via aerial surveys during the fall migration (Clarke et al., 2015) and within core-use areas delineated by satellite telemetry studies (e.g. Citta et al., 2015). Within the aerial survey zone, we examine how the presence and location of sea ice influence the observed locations of bowhead whales relative to the coast. We then synthesize this information to discuss how the distribution of bowhead whales and the timing of their migration may change as sea ice continues to decline.

2. Methods

This section describes the three primary datasets used in this study, each corresponding to a different period. The sea-ice data span 1979-2014 (see Section 2.1) and begin at the start of the satellite record; thus providing consistency with most studies of long-term changes in arctic sea-ice concentration. Due to our focus on long-term changes in the ice cover, we did not constrain the years of sea-ice data to align with the period of either the aerial survey data (1982-2014; see Section 2.2) or the satellite tagging data (2006-2012; see Section 2.3).

2.1. Satellite-derived sea-ice coverage (1979-2014)

We derived values for the open water fraction (OWF; 1 minus the sea-ice fraction) within the whale core-use areas and over the western Beaufort Sea shelf and slope using the daily and monthly averaged passive microwave datasets from the Nimbus-7 Scanning Multi-channel Microwave Radiometer (SMMR) and the Defense Meteorological Satellite Program (DMSP) Special Sensor Microwave Imager (SSM/I) and Special Sensor Microwave Imager/Sounder (SSMIS) (Cavalieri et al., 1996) for years 1979-2014. All data were accessed from the National Snow and Ice Data Center, where they had been processed using the NASA Team algorithm (Comiso et al., 1997) for relating brightness temperatures to sea-ice concentration. Data were provided in the polar stereographic projection with a grid cell size of 25 km x 25 km. Prior to August 19, 1987, daily sea-ice coverage was observed every-other day; thus, we used interpolated values for days without observations.

Several different ice condition values were calculated for whale use locations and times of the year. First, mean monthly OWF were extracted for all months to examine long-term changes in sea-ice cover. Second, using the daily ice concentrations, we calculated mean weekly OWF. Third, the number of open water days (OWD) annually and during peak-use periods were calculated as the total number of days when the OWF was greater than 0.85, which is the typical threshold used to define open water (e.g. by the National Snow and Ice Data Center). All data were processed in R (Ver. 3.2.2) using the *raster* package (Hijmans et al., 2016) for reading and analyzing gridded spatial data.

2.2. Aerial survey data (1982-2014) in the western Beaufort Sea

This study used aerial survey data from the Aerial Surveys of Arctic Marine Mammals (ASAMM) program, obtained from the National Oceanographic Data Center. ASAMM, which is a continuation of the Bowhead Whale Aerial Survey Project (BWASP) and Chukchi Offshore Monitoring in Drilling Area (COMIDA), has documented the distribution and relative abundance of marine mammals in the western Beaufort and eastern Chukchi Seas, focusing on areas of potential oil and natural gas activities. A primary ASAMM objective is to document inter-annual differences and long-term trends in the spatial distribution and timing of the annual bowhead whale fall migration. Through aerial surveys from fixed-winged aircraft, ASAMM records data on bowhead whales and a variety of other cetaceans, ice seals, walruses, and polar bears (Clarke at al., 2015).

The resulting ASAMM dataset includes bowhead whale sighting location (latitude and longitude), the number of whales observed in each sighting, whale behavior, and distance to shore. Whale behavior is reported as swimming, diving, resting, feeding, milling, or several other descriptors related to display (e.g. breaching, tail slapping, or spy hopping). Feeding behavior, in particular, is challenging for aerial observers to characterize. Whales are seen for brief periods and some feeding modes are easier to identify than others. For example, the presence of mud in the water or on a whale's rostrum indicates benthic feeding, and visibly open mouths indicate surface feeding. In contrast, mid-water feeding has no significant indicator. The distance-to-shore measurement, d_{shore}, is defined as the shortest distance between the sighting and a normalized coastline within the ASAMM study area. The normalized coastline, which was based on the World Vector Shoreline produced by the U.S. Defense Mapping Agency, is a standardized, stationary feature that coarsely defines the coastline and offshore extent of bays and barrier islands (Clarke et al., 2015).

ASAMM transect data for years 1982-2014 were compiled and subsampled to include all bowhead whale sightings in the western Beaufort Sea (140°W-157°W) for the months of August to October. The earliest ASAMM data for years 1979-1981 were excluded due to differences in methodology during those years compared to the longer-term record. We only used sightings that were systematically collected during the survey transects and excluded sightings made at other times during flight (e.g. while navigating to transect start and end locations). The geographic range of our study region included 91% of the total transect sightings during August-October for these years. Sightings (n=2679) ranged in size from 1 to 70 individual whales, yet the mean number of whales per sighting was only 1.9. Criteria for delineating groups of whales over the duration of the study varied due to data recording limitations. However, we avoided any associated bias by using a normalized value for total whales sighted (W_N), computed as the total number of whales sighted divided by survey effort:

$$W_N = W_T / T_x ,$$

where W_T is the total whales observed per sighting and T_x is the distance (km) of transect effort flown within the corresponding 25-km x 25- km grid cell for the corresponding month and year of the sighting. The effort grid matched the scale and location of the passive microwave sea-ice data used in this study (see Section 2.1). The resulting analysis examines the relationship between W_N and various metrics related to ice conditions and distance to shore.

For the aerial survey data, the peak-sighting period during which sea-ice conditions were analyzed was defined as when at least 5% of the normalized total whale sightings pooled from all years occurred within a weekly period. We also calculated the distance from each whale sighting to the sea-ice edge (d_{ice}), which is here defined as at least 15% ice concentration. The R software *raster* package's distance function was used to determine d_{ice} as the distance between the center of the passive microwave sea-ice data grid cell that corresponded with the whale sighting location to the center of the nearest grid cell with at least 15% sea ice. Therefore, the minimum distance to the ice edge for whale sightings outside the ice edge is 25 km (i.e. the grid cell resolution).

Using the whale distance from shore, d_{shore}, and the calculated distance to the ice edge, d_{ice}, we additionally computed the ratio of d_{shore} to $d_{shore} + d_{ice}$ for each whale sighting from the aerial surveys. This ratio effectively describes whether the whale is relatively closer to shore (lower ratio) versus closer to the ice edge (higher ratio). For example, a sighting with a ratio value of 0 describes a sighting at the shoreline, while values approaching 1 represent sightings that are nearer the ice edge.

2.3. Whale core-use areas defined by satellite tagging data (2006-2012)

This study characterizes sea-ice and open water trends for the six core-use areas for BCB bowhead whales as defined by Citta et al. (2015), shown in Fig. 1. These six areas are (1) adjacent to Cape Bathurst at the western entrance to Amundson Gulf, (2) along the Tuktoyaktuk Peninsula, (3) north and northwest of Point Barrow, (4) along the northern Chukotka Coast and extending into Bering Strait, (5) Anadyr Strait, and (6) the Gulf of Anadyr. Using the locations of whales carrying satellite tags, Citta et al. (2015) defined these areas as the 25% density contours of probability distributions of locations using the lattice-based approach of Barry and McIntyre (2011). Whale locations were obtained using the Argos system of satellites from 54 individually tagged whales. Quakenbush et al. (2012) summarize the Alaska Department of Fish and Game's whale tagging program and methodology, while Citta et al. (2015) present details of the obtained data (location, dive, and oceanographic information), the statistical and geographic approach for determining the core-use areas across the whales' annual range, and oceanographic and wind conditions during the tagging period between May 2006 and October 2012. The core-use areas derived from the satellite tagging data (Citta et al., 2015) are generally consistent with past studies of BCB bowhead whale range (e.g. Moore and Reeves, 1993; Bockstoce et al., 2005).

The numbers of whale location "sightings" for each core-use area, aggregated by week, are shown in Fig. 1. These weekly aggregations, defined as when five or more location transmissions were received within a defined weekly period, were based on the estimated daily locations by Citta et al. (2015) that controlled for minor differences in tag transmission rates due to tag functionality. These peak-use periods do not directly correspond to the peak-use periods defined by Citta et al. (2015), where data were presented by day. The first, second, third, and fourth weekly periods of each month, except February, were defined by days-of-month 1-7, 8-15, 16-23, and 24-30 or 24-31, respectively. For February, these weekly aggregations were for days 1-7, 8-14, 15-21, and 22-28 or 22-29.

3. Results

3.1. Sea-ice trends in the western Beaufort Sea and shifts in bowhead distribution as observed through aerial surveys

The most dramatic and statistically significant observed reductions in sea-ice cover have taken place along the western Beaufort Sea in fall where the numbers of OWD on the shelf and slope have increased by 20 and 25 days/decade, respectively (Table 1). Within both regions, roughly half of these increases have taken place during the peak period of total whale sightings from 1 September to 23 October (see Fig. 2). In recent years, the peak-use period has been entirely ice-free on the shelf for years 2009-2014 and on the slope for years 2003-2014 (not shown). These trends in sea-ice conditions during August-October correspond to when whales are predominantly migrating westward, but include periods of loitering and non-directional movements during which the whales may be feeding, resting, or socializing.

During the months of August through October, the OWF over the shelf is very similar to the OWF over the slope; when sea ice is absent over the shelf, the ice edge is almost always farther offshore and not over the slope (Fig. 3). Since 1997, September has been entirely ice-free over the shelf, and nearly ice-free over the slope of the western Beaufort Sea. Since 2002, October, which is the month with the greatest inter-annual variability in ice cover throughout the satellite record for this region, has shown significant trends toward more open water with much less inter-annual variability.

We explored the influence of these reductions in ice coverage in the western Beaufort Sea relative to the proximity of whales to shore between two periods: 1982-1996 and 1997-2014. During the earlier period, more aerial survey transect effort occurred in the eastern than western portion of the survey area, and there was effort farther (75-100 km) offshore in the western portion near Point Barrow (Fig. 4). During the later period, slightly more survey effort occurred in the western portion of the survey area, and there was no effort far offshore near Point Barrow. Based on normalized total whales sighted (W_N; see Section 2.2), relatively more whales were observed in the waters over the slope in the eastern portion of the study area (i.e. out to approximately 125 km off Kaktovik) during the earlier years, and significantly more whales were observed in the waters between Point Barrow and Harrison Bay during the later years (Fig. 4).

The average distance from shore of normalized whale sightings decreased during the 1982-2014 study period within the western Beaufort Sea (Fig. 5). There is a significant downward trend in the average whale distance from shore during the fall season (August to October) by about 8 km/decade. These results prompt the question of whether the observed reductions in regional sea ice are influencing the whales' distance from shore.

Using the d_{shore} to $d_{shore} + d_{ice}$ ratio, we found that whales prefer to be nearer to shore than to the ice edge (Fig. 6). Due to the coarseness of the determined ice edge location, this analysis excluded whales that were within 100 km of the ice edge (i.e. $d_{ice} \leq 100$ km), which accounted for 28% of all individual whales sighted. This omission; however, did not change the overall relationship shown in Fig. 6, except for removing a single interval peak at 1 for whales at or within the ice edge (11% of all whales sighted). Moore et al. (2000) similarly found that bowheads in the western Beaufort Sea in September and October were observed more often over the shelf than the slope and basin waters. The distance to shore for each normalized whale sighting was also analyzed across different intervals of OWF over the western Beaufort Sea shelf and slope (Fig. 7). Although whales appear to generally favor proximity to shore (see Fig. 6), they are more likely to be found offshore when there is less open water over the shelf and slope, as opposed to when the there is more open water and the ice edge is beyond the continental slope (see Fig. 7). We have not examined in detail how bowhead whale behavior relates to the whales' proximity to shore; however, results show no overwhelming difference between d_{shore} for all observed whales and those that were observed to be foraging (milling or feeding) (Fig. 8). Yet, a relatively tighter distribution closer to shore for foraging whales is observed.

3.2. Sea-ice trends within whale core-use areas

The long-term trends and variability in sea-ice conditions (1979-2014) in the whale core-use areas at Cape Bathurst, Tuktoyaktuk Peninsula, Point Barrow, and the northern Chukotka Coast/Bering Strait are summarized in Figs. 9 to 12, respectively. These core-use areas, which were defined by satellite tagging data, represent summer and fall locations where either sea ice is retreating (Cape Bathurst), largely absent (Tuktoyaktuk Peninsula), or advancing (Point Barrow and northern Chukotka Coast/Bering Strait). Similarly, sea-ice conditions for the largely ice-covered winter core-use areas at Anadyr Strait and the Gulf of Anadyr are summarized in Figs. 13 and 14. This section describes the observed changes in ice cover for each core-use area in more detail, while Table 2 summarizes the corresponding trends in the number of OWD.

The peak-use period at Cape Bathurst (1 May to 15 July; i.e., when ≥ 5 whale locations were observed per week) coincides with the area's transition from a nearly 100% ice cover in early May to nearly 100% open water in early to mid-July (Fig. 9). There is no significant trend ($p > 0.05$) toward more OWD during the peak-use period, which has much greater inter-annual variability relative to the fall transition period. Although also not statistically significant ($p > 0.05$), there has been an increase of 11 OWD/decade in this area overall, primarily due to later freeze-up in late October and early November.

For the Tuktoyaktuk Peninsula, there is a significant increase ($p < 0.05$) of 10 OWD/decade, but only about half of this increase occurred within the peak-use period of 8 July to 15 October (Fig. 10). In contrast, for Point Barrow, there has been a substantial and significant ($p < 0.001$) increase of 20 OWD/decade during the study period, which has more than doubled the total number of OWD since 1979 (Fig. 11). Here, the majority of the increase (13 OWD /decade) has taken place within the peak-use period between 16 August and 7 November. Similarly, a highly significant increase ($p < 0.001$) in OWD was observed for the northern Chukotka Coast/Bering Strait core-use area. The peak-use period coincides with the timing of ice advance within this area; however, the ice advance is occurring later in fall (Fig. 12). During the period of peak-use (8 October to 15 January), OWD increased by 10 days/decade. Over the course of the entire year, the increase is 18 OWD/decade.

The winter ice-covered periods for the Anadyr Strait and Gulf of Anadyr core-use areas largely coincide with when the whales are present (Figs. 13 and 14). For Anadyr Strait, the number of OWD increased annually by 8 days/decade, with 4 days/decade occurring during the peak-use period of 24 November to 15 April. On the contrary, no trend was detected for the number of OWD in the Gulf of Anadyr, either annually or during the peak-use period (1 December to 7 April). In general, these findings suggest that ice conditions have changed less substantially within the bowhead southern (winter) range in comparison to their northern (summer and fall) range.

4. Discussion and Synthesis

This investigation characterized observed changes in ice conditions within spatially and temporally identified bowhead whale habitat and use areas. In general, the two primary datasets used to define whale locations—the aerial surveys and the satellite tagging data—are notably different in their capacity to depict the movement and behavior of the BCB bowhead population. The aerial surveys provide information on a potentially large number of whales within a determined survey region (here, the western Beaufort Sea) at a given time of year (here, August to October), but provide no information beyond the survey region. Alternatively, the tagging data provides high-resolution information on individually tagged whales as they migrate across their range. The acquired locations from a small subset of the population are then used to spatially and temporally define core-use areas, which are believed to represent the use of a larger portion of the population (see Citta et al., 2015). The differences between these two approaches to examine whale locations are important, yet the relative merits and limitations of each are beyond the scope of this study and do not factor into how we examined sea-ice concentration and timing within the defined areas. Is it important to highlight, however, that the core-use areas were defined using satellite tagging data from years 2006 to 2012, a time by which substantial reductions in sea ice had already occurred, especially at Tuktoyaktuk Peninsula, Point Barrow, and the northern Chukotka Coast/Bering Strait core-use areas (see Figs. 10-12, respectively). We found that sea-ice conditions remain relatively unchanged in the Bering Sea core-use areas of BCB bowhead whales. Ice conditions in the Bering Sea are largely decoupled from those in the Arctic Ocean (e.g. Stabeno et al., 2012; Laidre et al., 2015; Frey et al., 2015). As such, it is unlikely that the southern extent of the bowhead whales' range will change greatly relative to the northern extent where sea-ice retreat is most pronounced in summer and fall. Bowheads begin to migrate north prior to ice retreat in the Bering Sea (Citta et al., 2012). Therefore, we do not expect the timing of the spring migration to alter significantly in the near future; although, there is a trend toward earlier spring arrival of bowheads at Utqiaġvik (previously Barrow), since 1978 (George et al., 2011). Rather, we expect that northern core-use areas will be available to bowheads for longer periods, resulting in bowheads lingering in regions farther north through late fall, prior to entering the Bering Sea. For example, shifts in bowheads away from the northern coast of Chukotka into the Bering Sea are correlated with ice formation and the breakdown of the strong salinity front observed by Citta et al. (2015). Freeze-up restricts the input of fresh water entering the Siberian Coastal Current, weakening the salinity front (see Fig. 8 in Citta et al., 2015) and possibly reducing the density of zooplankton. We would expect that a later freeze-up (as shown in Fig. 12) would lead to whales feeding along the northern Chukotka Coast for a longer period in fall. Citta et al. (2012) indicate some bowheads winter in the vicinity of St. Lawrence Island and Bering Strait in recent years, and there is evidence of similar wintering behavior during surveys in the 1970s-1980s (Moore and Reeves, 1993; see p.344).

Likewise, the feeding area near Point Barrow is available for a longer period than it once was, which may account for the notable shift west in bowhead whale sightings within the western Beaufort Sea in recent years (Fig. 4). Ashjian et al. (2010) and Okkonen et al. (2011) have shown stable concentrations of advected prey near Point Barrow in fall (i.e. the ‘‘Barrow krill trap’’) as a result of the local bathymetry, geography, and wind driven oceanographic processes. While Ashjian et al. (2010) concluded there is no known influence of climate variability on the presence of favorable fall feeding conditions near Point Barrow, it is reasonable to assume that the duration of the favorable feeding conditions may have been constrained in the early 1980s as ice either remained in the area into late August or returned abruptly in early October to inhibit upwelling. The aerial survey data also suggest that use of the western Beaufort Sea in general may have increased over time (Fig. 4), although it is difficult to determine if this is an increase in the total number of whales using the area or a shift in the timing of migration. Indeed, aerial survey sighting rates are higher in most of the western Beaufort Sea in the later time period (1997-2014), which is influenced to some degree by the three-fold increase in bowhead whale population size over the entire study period (Givens et al., 2016). However, it should also be noted that several of the ASAMM surveys conducted during the earlier time period (1982-1996) used an aircraft that lacked bubble windows and flew at a faster speed (Clarke et al., 2016). Both factors likely led to lower sighting rates in earlier years.

In addition to ice conditions, the feeding habitat of bowhead whales is largely defined by water depth and oceanographic fronts (Moore and Reeves, 1993; Moore et al., 2000; Ashjian et al., 2010). At a fundamental level, bowhead whale feeding habitat is simply localized areas with a high density of zooplankton that the whales can access. While bowhead whales are probably limited in their diving depth, their affinity for shelf waters is likely more related to the availability of better feeding conditions there than to their diving ability. Shelf waters sometimes have an elevated density of zooplankton near the seafloor, as this is a lower boundary for the diurnal migration of zooplankton and where zooplankton are expected to aggregate during diapause (Smith and Schnack-Schiel, 1990; Falk-Petersen et al., 2009). Zooplankton within shelf waters are further aggregated by fronts and stratified layers (e.g. pycnoclines), which, along with upwelling and advection, create situations where zooplankton aggregate in sufficient densities for bowheads to target (e.g. Moore et al., 1995; Ashjian et al., 2010; Walkusz et al., 2012; Citta et al., 2015; Citta et al., this issue; Okkonen et al., this issue).

Given what is known about bowhead feeding requirements, we do not expect the range of BCB bowhead whales to change greatly in the near future by simply shifting northward with declining sea ice. First, the current mechanisms that deliver and aggregate zooplankton are expected to continue, such as the advection of zooplankton from the Bering Sea into the Chukchi Sea, upwelling and advection of zooplankton onto the shelf, and the formation of fronts. However, shifts in wind patterns may also alter the amount or timing of upwelling and advection, resulting in prey aggregating differently or at different times. Also, as certain areas are open longer and earlier in the season, nutrient depletion may occur, impacting lower trophic dynamics. Thus, we expect that summer and fall movements may become less predictable, because bowheads will have more feeding areas to choose from or the quality of those areas will be more variable, at least until bowheads identify optimal foraging areas under an altered ice regime. Second, bathymetric features necessary to aggregate zooplankton are largely absent in the deep Arctic Basin. Third, recent work suggests that the western boundary of BCB bowhead whales in the Chukchi Sea may be defined by the location of relatively fresh Siberian Shelf water (Citta et al., this issue), which is known to have the lowest biomass of zooplankton in the Chukchi Sea (Ershova et al., 2015). Although the area west of Wrangel Island is now ice-free in summer, satellite-tagged whales have not spent much time west of the island. Lastly, bowhead whales are largely found in the same places observed by Yankee whalers in the mid- to late-1800s and early

1900s (e.g. Bockstoce et al., 2005), although ice conditions have changed drastically (Mahoney et al., 2011).

If the range of bowhead whales does expand, we would expect the expansion to follow features that help aggregate zooplankton, such as areas near the shelf break where upwelling can deliver zooplankton onto the shelf where they aggregate on the seafloor or along frontal features. As such, we would expect the range of BCB bowheads to expand along the shelf break, northwest of Wrangel Island and northeast into the Canadian Archipelago. Both places were covered in multi-year ice until recently. Satellite-tagged whales have been tracked near the shelf break north of Wrangel Island (Citta et al., 2015) and into the Northwest Passage (Heide-Jørgensen et al., 2011). Currently, these areas do not appear to be used by many bowheads, but this could change in the future.

When examining the distribution of bowhead whale sightings from aerial survey data in the western Beaufort Sea, we found that bowheads were more likely to be observed nearer the coast when there was less sea-ice cover on the shelf and slope (see Fig. 7), further supporting the argument that bowheads will not simply move north with further reductions in sea ice. Pickart et al. (2013) showed that upwelling and phytoplankton blooms have increased on the Beaufort Sea shelf in recent decades and that upwelling events along the shelf are more common when ice is farther offshore. Accordingly, we suspect that foraging may be better nearshore when sea ice is farther offshore. Using a subset (1982-1991) of the same aerial survey data as this study, Moore et al. (2000) identified a comparable pattern during September to October and, similarly, attributed their observation to improved feeding opportunities along the coast when the ice is farther offshore. It may also be that bowheads are avoiding the risk of ice-entrapment by staying relatively farther offshore when the ice is nearer the coast. A sudden shift in winds can pile ice onshore, which can be harmful, especially for young whales. Blackwell et al. (2007) also associated the whales' nearer-shore presence with fewer or no sea-ice impediments to migration. Therefore, we do not think the risk of ice entrapment should be discounted completely.

Having too little ice may also directly affect the distribution of bowhead whales if the risk of predation increases. Bowheads are rarely found south of the marginal ice edge in winter, even over shelf waters (e.g. Citta et al., 2012), and this may be to avoid predation by killer whales, which are known to attack bowhead whales (e.g. Finley, 1990; George et al., 1994). Although summer and fall feeding areas are largely devoid of sea ice, the occurrence of killer whales is relatively rare in the northern Chukchi and Beaufort seas (George et al., 1994: Higdon et al., 2012), where bowhead whales are located in summer and fall. However, the occurrence of killer whales is increasing in the eastern Canadian Arctic as sea ice declines (Higdon and Ferguson, 2009) and a similar trend may be occurring in the Pacific Arctic (e.g. O'Corry-Crowe et al., 2016). DeMarban (2015) documents three bowhead whales thought to have been killed by killer whales in the last few years. George et al. (2017) provide evidence that the frequency of killer whale predation scars on harvested bowhead whales has increased statistically in the second decade of their study (1990 to 2012). The summer and fall distribution of bowhead whales may change if killer whales become more common in the northern Chukchi and Beaufort Seas.

It is important to note that the largest area of unoccupied bowhead habitat in which we know BCB bowhead whales could survive is in the Bering Sea in summer (i.e. south of their current summer range). Yankee whalers found bowhead whales during summer in the Bering and Chukchi seas in 1848. By 1853, this segment of the population was either extirpated or possibly displaced to summer grounds in the Canadian Beaufort Sea (Bockstoce and Botkin, 1983; Bockstoce et al., 2005). As a result, bowhead whales, which are believed to have life-spans greater than 100 years of age (George et al., 1999), may simply migrate to the Canadian Beaufort Sea each spring because they have become behaviorally entrained to do so. If bowhead whales could survive year-round in the Bering Sea in 1848, they can probably do so today. The population of BCB bowhead whales is increasing (Givens et al., 2016) and does not appear to be negatively affected by declines in sea ice observed to date (George et al., 2015). Even now, some whales spend summer in the Chukchi Sea (e.g., Melnikov and Zeh, 2007; Citta et al., 2012). That BCB bowhead whales could expand their range southward in the face of ice retreat is somewhat counter-intuitive, but definitely possible.

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Tables

Table 1. Linear regression results of the number of OWD (>85% open water) annually for the western Beaufort shelf and slope during years 1979-2014.

Area	R^2	Slope	Std err	p-value
W Beaufort shelf	0.398	2.025	0.427	3.67e-5
W Beaufort slope	0.449	2.451	0.466	7.93e-6

Table 2. Linear regression results of the number of OWD (>85% open water) annually for each core-use area both during the entire year and the defined peak-use periods, during years 1979-2014.

Area	Area (km^2)	Time period	R^2	Slope	Std err	p-value
Cape Bathurst	5,399	*Annually:*	0.1048	1.121	0.562	0.0541
		1-May to 15-Jul:	0.0785	0.505	0.297	0.0978
Tuktoyaktuk Peninsula *	7,238	*Annually:*	0.134	0.961	0.419	0.0283
		8-Jul to 15-Oct:	-	-	-	-
Point Barrow	5,479	*Annually:*	0.412	1.965	0.402	2.42e-5
		16-Aug to 7-Nov:	0.351	1.29	0.30	0.00014
Northern Chukchi Coast/Bering Strait	18,281	*Annually:*	0.316	1.773	0.447	0.00036
		8-Oct to 15-Jan:	0.389	1.010	0.217	4.76e-5
Anadyr Strait	6,348	*Annually:*	0.239	0.825	0.253	0.00249
		24-Nov to 15-Apr:	0.179	0.375	0.138	0.0101
Gulf of Anadyr	15,080	*Annually:*	0.00030	-0.035	0.350	0.921
		1-Dec to 7-Apr:	0.00056	-0.033	0.2371	0.891

** A linear regression was not applied for the peak-use period because the number of OWD frequently equaled the duration of the peak-use period.*

Figure Captions

Fig. 1. *Top*: Map of study region showing bowhead whale core-use areas (colored polygons) derived from satellite tag data (from Citta et al., 2015) and the mean monthly sea-ice extent (≥ 15% ice concentration) in September and March for years 2006-2012, derived from passive microwave satellite imagery (see Section 2.1). The dark gray polygons represent the western Beaufort Sea shelf and slope used to summarize ice conditions within the aerial survey region, and mark the longitudinal boundaries (157°W and 140°W) between which the aerial survey data were analyzed. *Bottom*: Stacked weekly counts of satellite tagged whale location transmissions by core-use area (colors correspond to the areas mapped at top) for years 2006-2012.

Fig. 2. Open water conditions over the western Beaufort Sea shelf. *Top*: Open water fraction (OWF) by week (y-axis) and year (x-axis) alongside the weekly sightings of whales during fall aerial surveys (August to October) over the western Beaufort Shelf (1982-2014). The horizontal red lines define the peak-sighting period where at least 5% of the total normalized whale sightings occurred per week between 157°W and 140°W, either over the shelf or slope. *Middle*: Yearly time series of number of open-water days (> 0.85 OWF) annually. *Bottom*: Yearly time series of number of open-water days within the peak-sighting period (1 September to 23 October).

Fig. 3. Trends in monthly open water fraction (OWF) from 1979 to 2014 over the western Beaufort Sea shelf and slope regions (see Fig. 1) for August to October.

Fig. 4. Aerial survey transect effort and normalized sighting rate in the western Beaufort Sea during fall (August to October). *Top panels*: Bowhead whale aerial survey transect effort (km) per 25 km x 25 km grid cell for years 1982-1996 (left) and 1997-2014 (right). *Bottom panels*: The normalized total whales observed (whales/km) per grid cell for years 1982-1996 (left) and 1997-2014 (right) in fall. The grid corresponds to the passive microwave sea-ice data grid between 157°W and 140°W. The 200 m and 2000 m isobaths define the outward limits of the shelf and slope, respectively.

Fig. 5. Trend in the average distance offshore of the normalized total whales sighted per year in the western Beaufort Sea. Yearly averages represent all normalized sightings between 157°W and 140°W during fall (August to October). Red data points denote sightings from 1982-1996 and black denotes those from 1997-2014, corresponding to the time periods in Fig. 4. Gray bars represent standard deviations.

Fig. 6. Histogram of the % of normalized total whales sighted by ice-shore distance ratio for all years, 1982-2014, in the western Beaufort Sea (excluding whales within 100 km of the ice edge). The inset schematic illustrates the distance measurements used to calculate the ice-shore distance ratios, where the grid lines reference the 25 km x 25 km passive microwave grid cells.

Fig. 7. The relationship between whale sighting distance to shore (d_{shore}) and the average open water fraction (OWF) over the western Beaufort Sea shelf and slope for years 1982-2014. Box width is proportional to the square-root of the number of observations in the interval.

Fig. 8. Whale sighting distance to shore for all whales and for foraging whales within the western Beaufort Sea (between 157°W and 140°W) in fall (August-October) for years 1982-2014. *Left and bottom axes*: Histogram of the % of normalized total whales sighted at intervals of distance from shore for both all whales (light gray) and milling and feeding whales (dark gray). *Right and top axes*: Boxplots of the same frequency distributions, where box width is proportional to the square-root of the percentage of total normalized observations in the group.

Fig. 9. Open water conditions at the Cape Bathurst core-use area. *Top*: Open water fraction (OWF) by week (y-axis) and year (x-axis) alongside the weekly counts of whale location transmissions for this core-use area. The horizontal red lines define the peak-use period (weeks when ≥ 5 whales were located). *Middle*: Yearly time series of number of open-water days (> 0.85 OWF) annually. *Bottom*: Yearly time series of number of open-water days within the peak-use period (1 May to 15 July).

Fig. 10. Open water conditions at the Tuktoyaktuk Peninsula core-use area. *Top*: Open water fraction (OWF) by week (y-axis) and year (x-axis) alongside the weekly counts of whale location

transmissions for this core-use area. The horizontal red lines define the peak-use period (weeks when ≥ 5 whales were located). *Middle*: Yearly time series of number of open-water days (> 0.85 OWF) annually. *Bottom*: Yearly time series of number of open-water days within the peak-use period (8 July to 15 October).

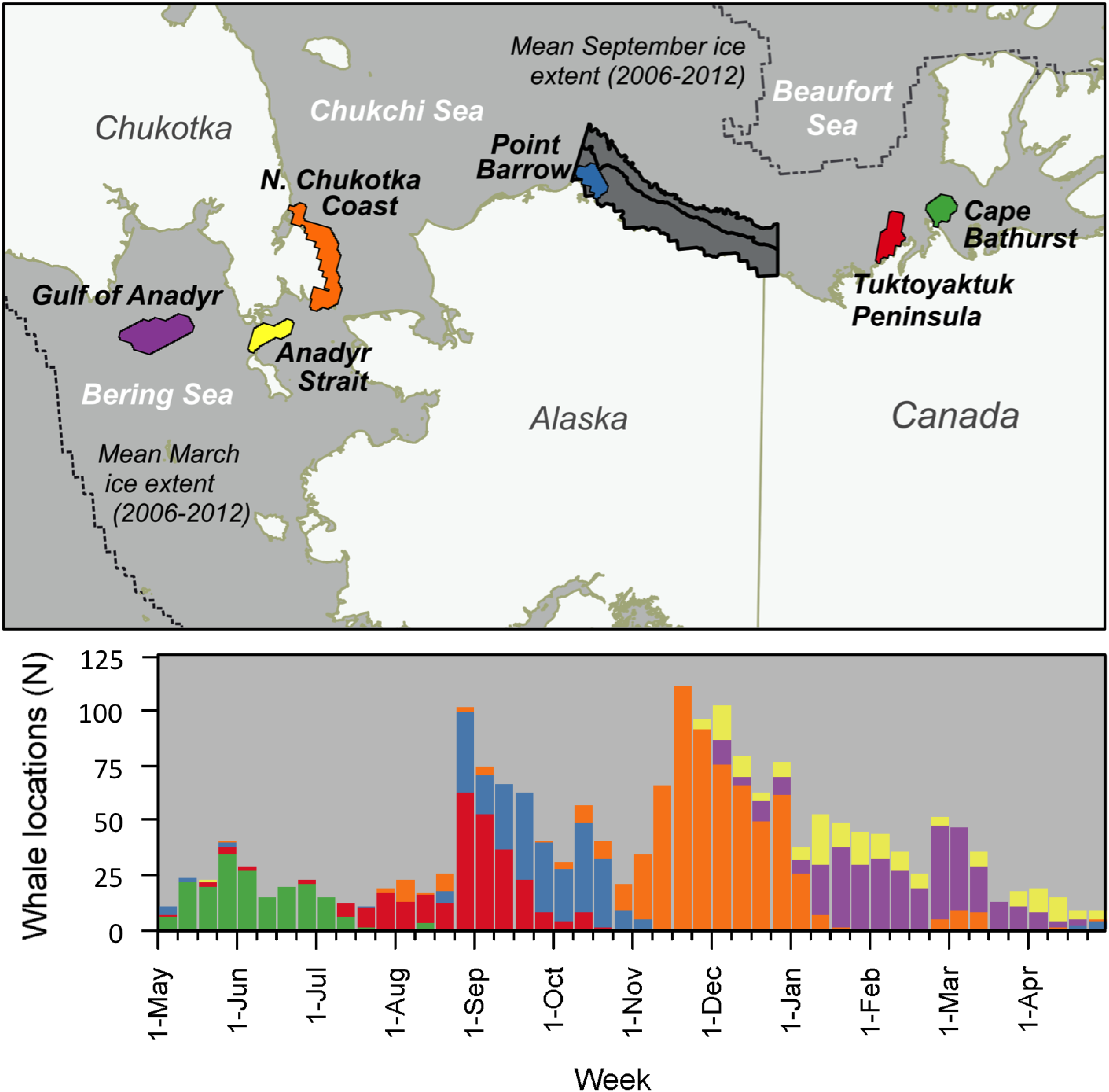
Fig. 11. Open water conditions at the Point Barrow core-use area. *Top*: Open water fraction (OWF) by week (y-axis) and year (x-axis) alongside the weekly counts of whale location transmissions for this core-use area. The horizontal red lines define the peak-use period (weeks when ≥ 5 whales were located). *Middle*: Yearly time series of number of open-water days (> 0.85 OWF) annually. *Bottom*: Yearly time series of number of open-water days within the peak-use period (16 August to 7 November).

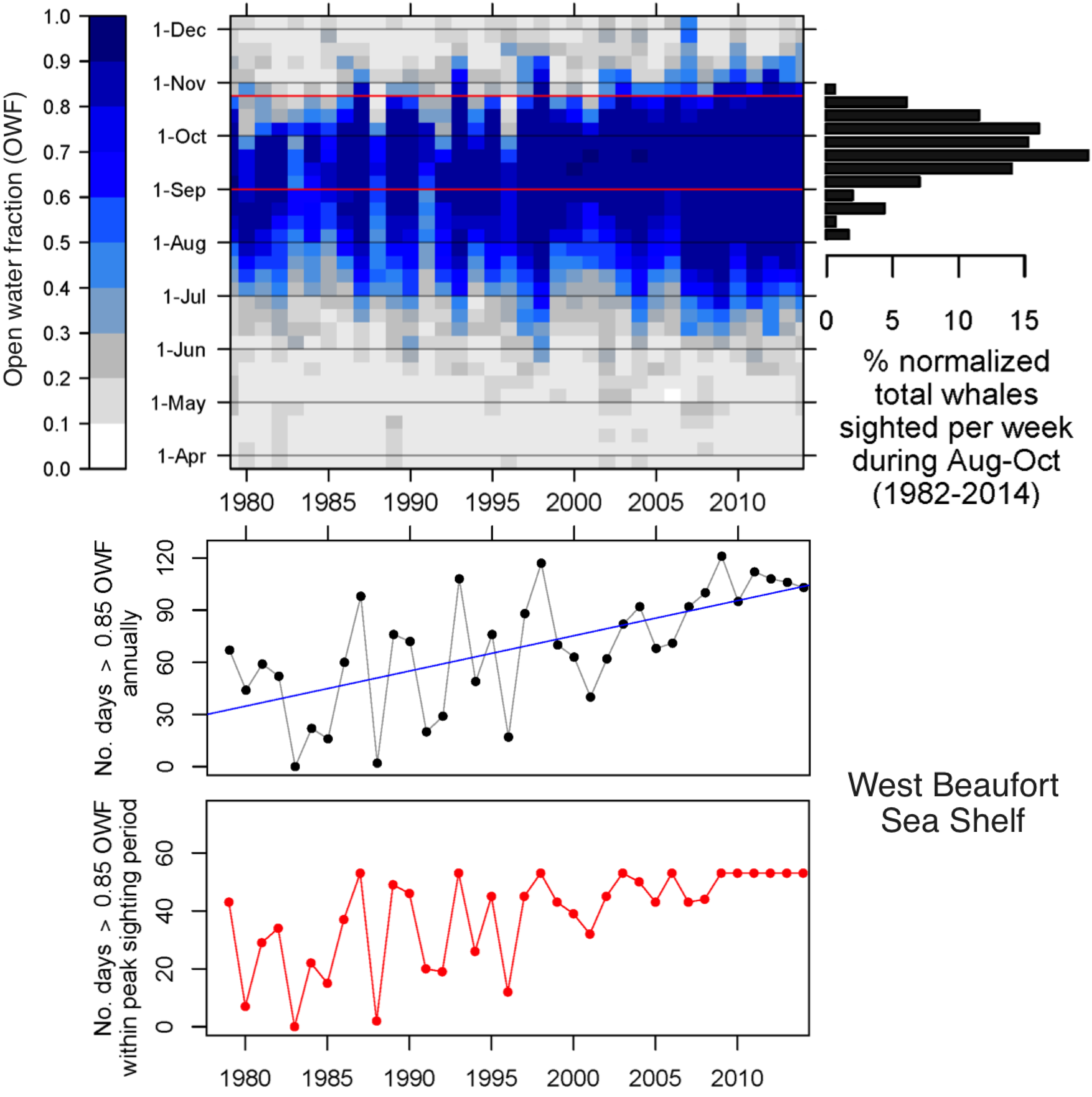
Fig. 12. Open water conditions at the northern Chukotka Coast/Bering Strait core-use area. *Top*: Open water fraction (OWF) by week (y-axis) and year (x-axis) alongside the weekly counts of whale location transmissions for this core-use area. The horizontal red lines define the peak-use period (weeks when ≥ 5 whales were located). *Middle*: Yearly time series of number of open-water days (> 0.85 OWF) annually. *Bottom*: Yearly time series of number of open-water days within the peak-use period (8 October to 15 January).

Fig. 13. Open water conditions at the Anadyr Strait core-use area. *Top*: Open water fraction (OWF) by week (y-axis) and year (x-axis) alongside the weekly counts of whale location transmissions for this core-use area. The horizontal red lines define the peak-use period (weeks when ≥ 5 whales were located). *Middle*: Yearly time series of number of open-water days (> 0.85 OWF) annually. *Bottom*: Yearly time series of number of open-water days within the peak-use period (24 November to 15 April).

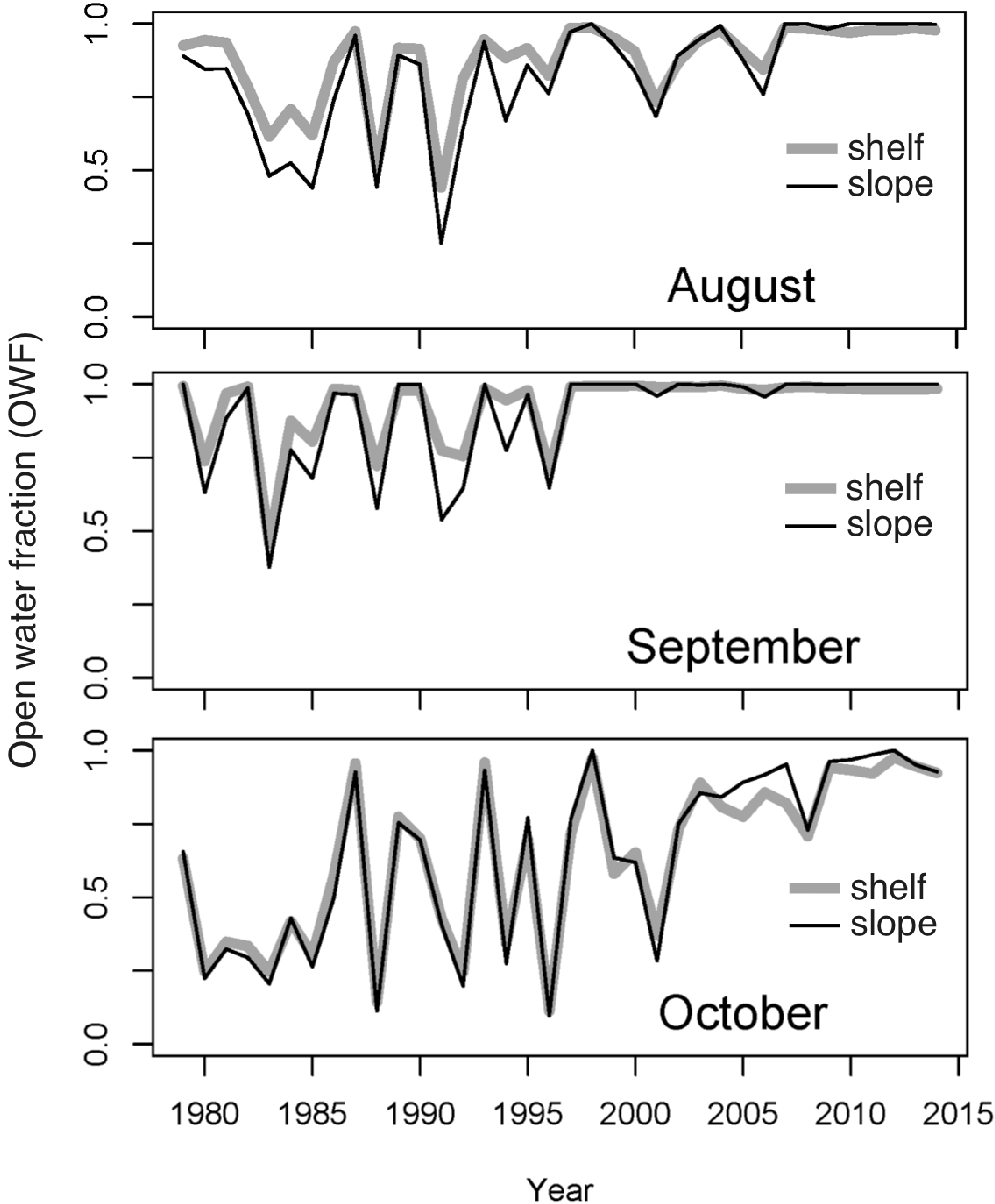
Fig. 14. Open water conditions at the Gulf of Anadyr core-use area. *Top*: Open water fraction (OWF) by week (y-axis) and year (x-axis) alongside the weekly counts of whale location transmissions for this core-use area. The horizontal red lines define the peak-use period (weeks when ≥ 5 whales were located). *Middle*: Yearly time series of number of open-water days (> 0.85

OWF) annually. *Bottom*: Yearly time series of number of open-water days within the peak-use period (1 December to 7 April).

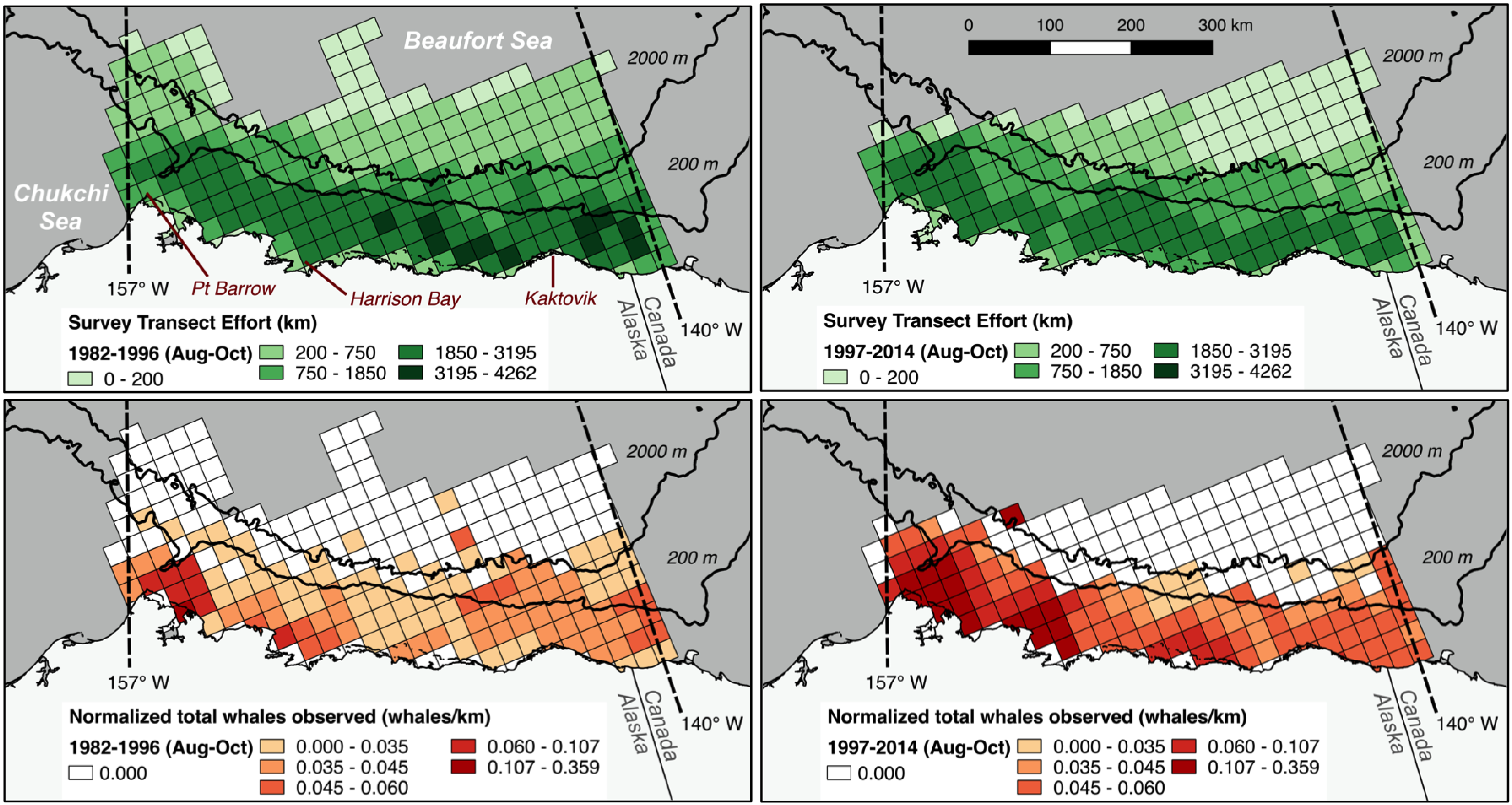

Mean September ice extent (2006-2012)
Chukchi Sea
Beaufort Sea
Chukotka
Point Barrow
N. Chukotka Coast
Cape Bathurst
Tuktoyaktuk Peninsula
Gulf of Anadyr
Anadyr Strait
Bering Sea
Alaska
Canada
Mean March ice extent (2006-2012)
Whale locations (N)
125
100
75
50
25
0
1-May
1-Jun
1-Jul
1-Aug
1-Sep
1-Oct
1-Nov
1-Dec
1-Jan
1-Feb
1-Mar
1-Apr
Week



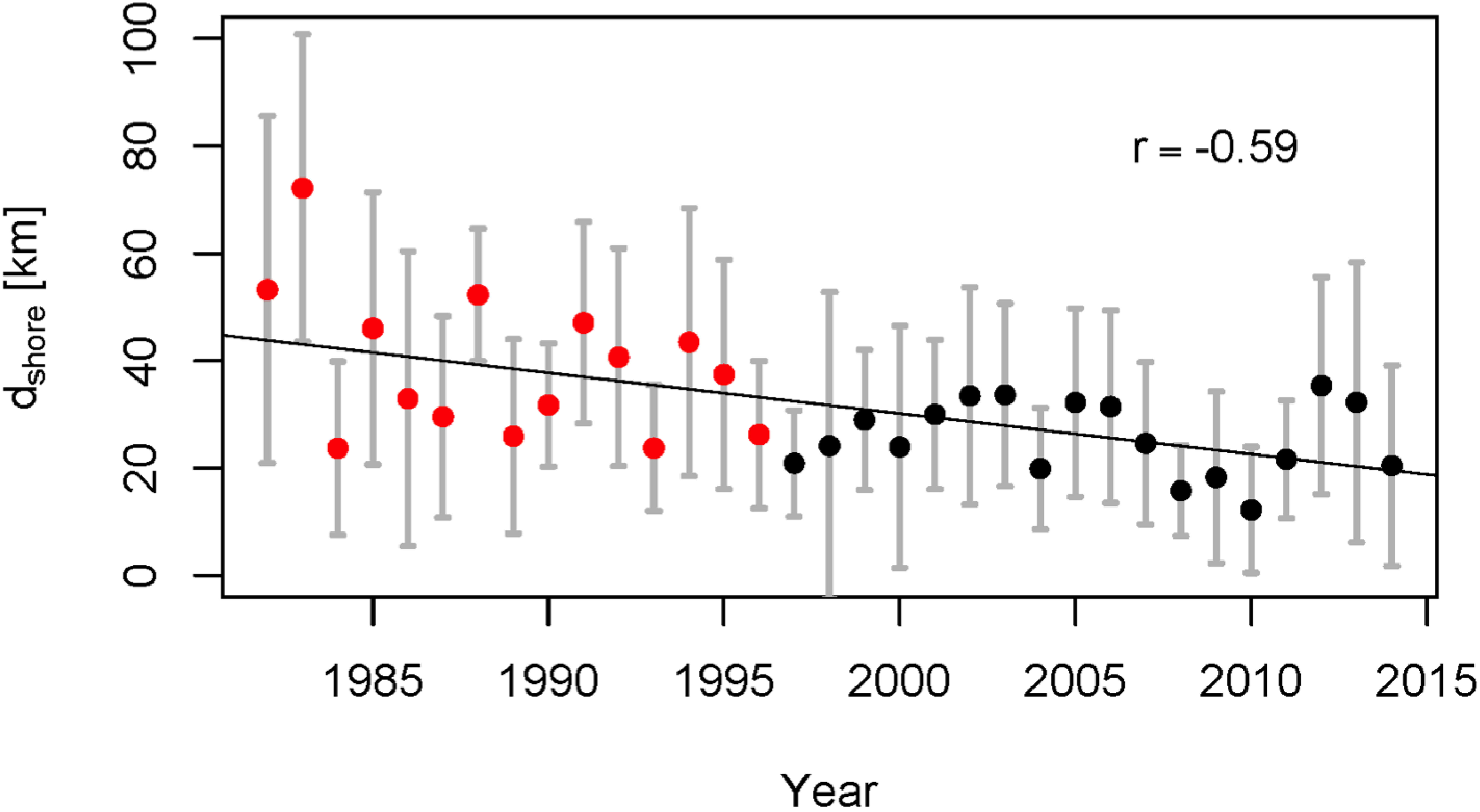
Open water fraction (OWF)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1-Dec
1-Nov
1-Oct
1-Sep
1-Aug
1-Jul
1-Jun
1-May
1-Apr
1980
1985
1990
1995
2000
2005
2010
0
5
10
15
% normalized total whales sighted per week during Aug-Oct (1982-2014)
No. days > 0.85 OWF annually
0
30
60
90
120
No. days > 0.85 OWF within peak sighting period
0
20
40
60
West Beaufort Sea Shelf



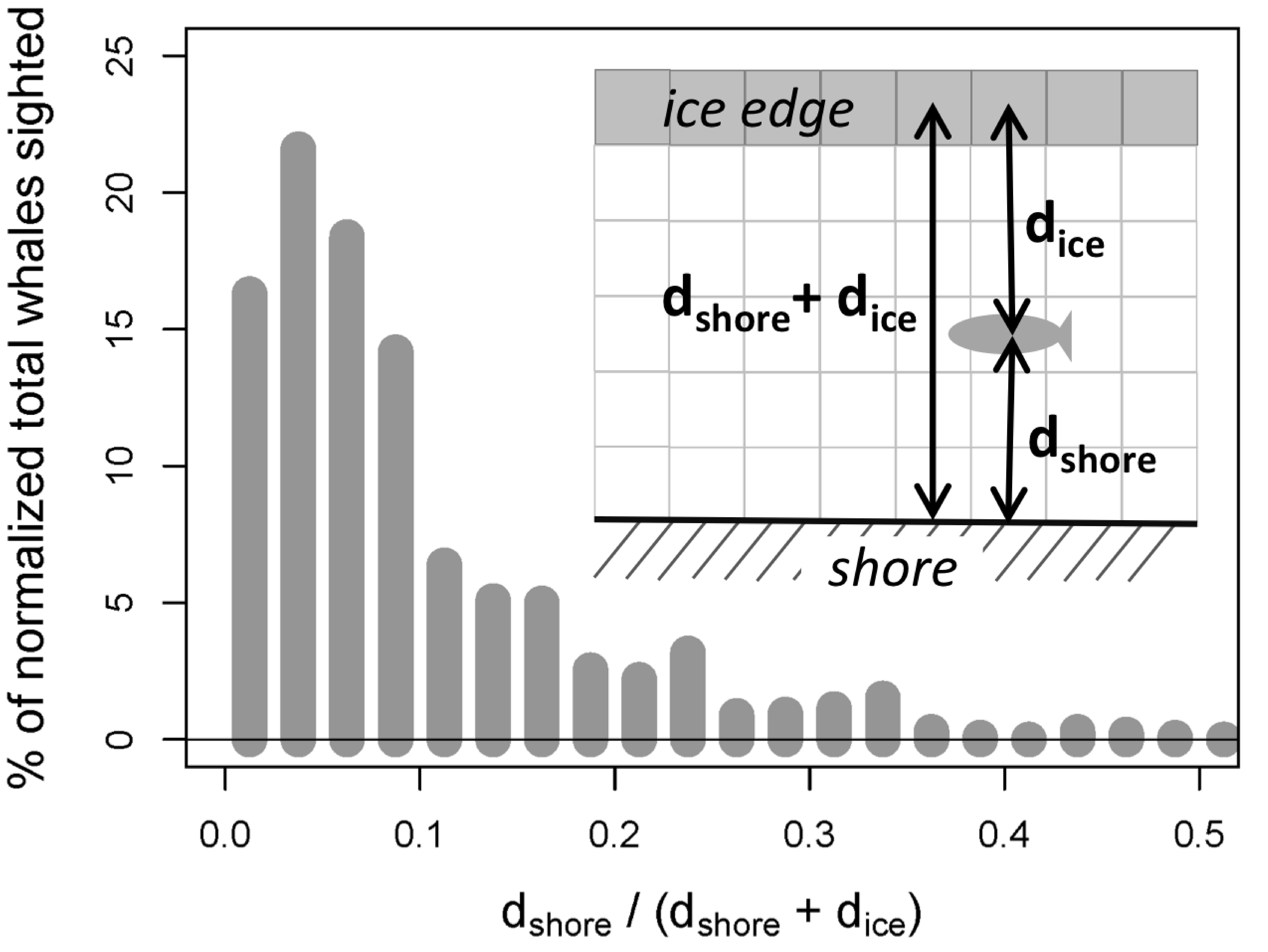
Open water fraction (OWF)
1.0
0.5
0.0
shelf
slope
August
September
October
1980
1985
1990
1995
2000
2005
2010
2015
Year



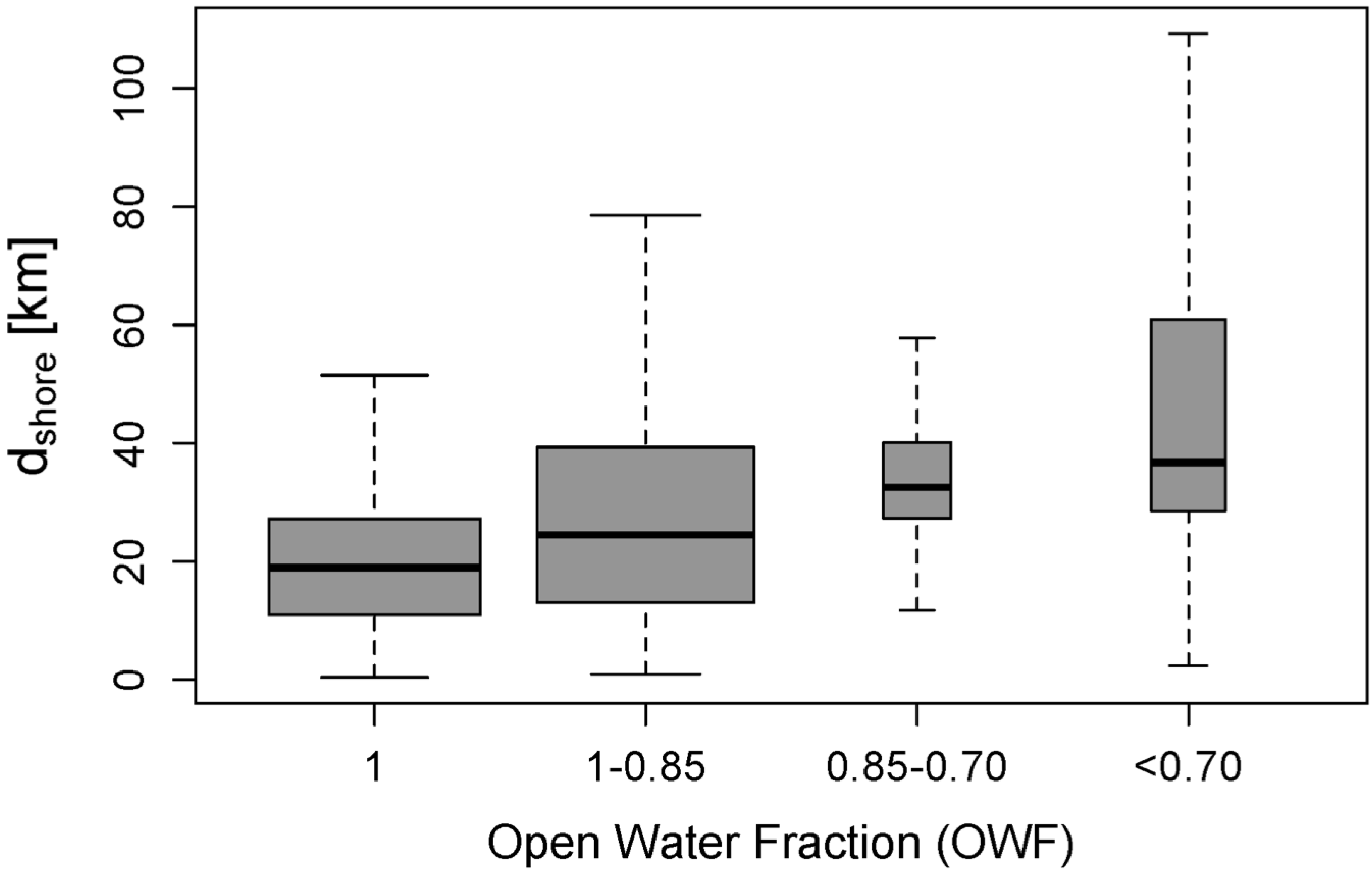
Beaufort Sea
Chukchi Sea
2000 m
200 m
157° W
140° W
Pt Barrow
Harrison Bay
Kaktovik
Alaska
Canada
0
100
200
300 km
Survey Transect Effort (km)
1982-1996 (Aug-Oct)
0 - 200
200 - 750
750 - 1850
1850 - 3195
3195 - 4262
Survey Transect Effort (km)
1997-2014 (Aug-Oct)
0 - 200
200 - 750
750 - 1850
1850 - 3195
3195 - 4262
Normalized total whales observed (whales/km)
1982-1996 (Aug-Oct)
0.000
0.000 - 0.035
0.035 - 0.045
0.045 - 0.060
0.060 - 0.107
0.107 - 0.359
Normalized total whales observed (whales/km)
1997-2014 (Aug-Oct)
0.000
0.000 - 0.035
0.035 - 0.045
0.045 - 0.060
0.060 - 0.107
0.107 - 0.359



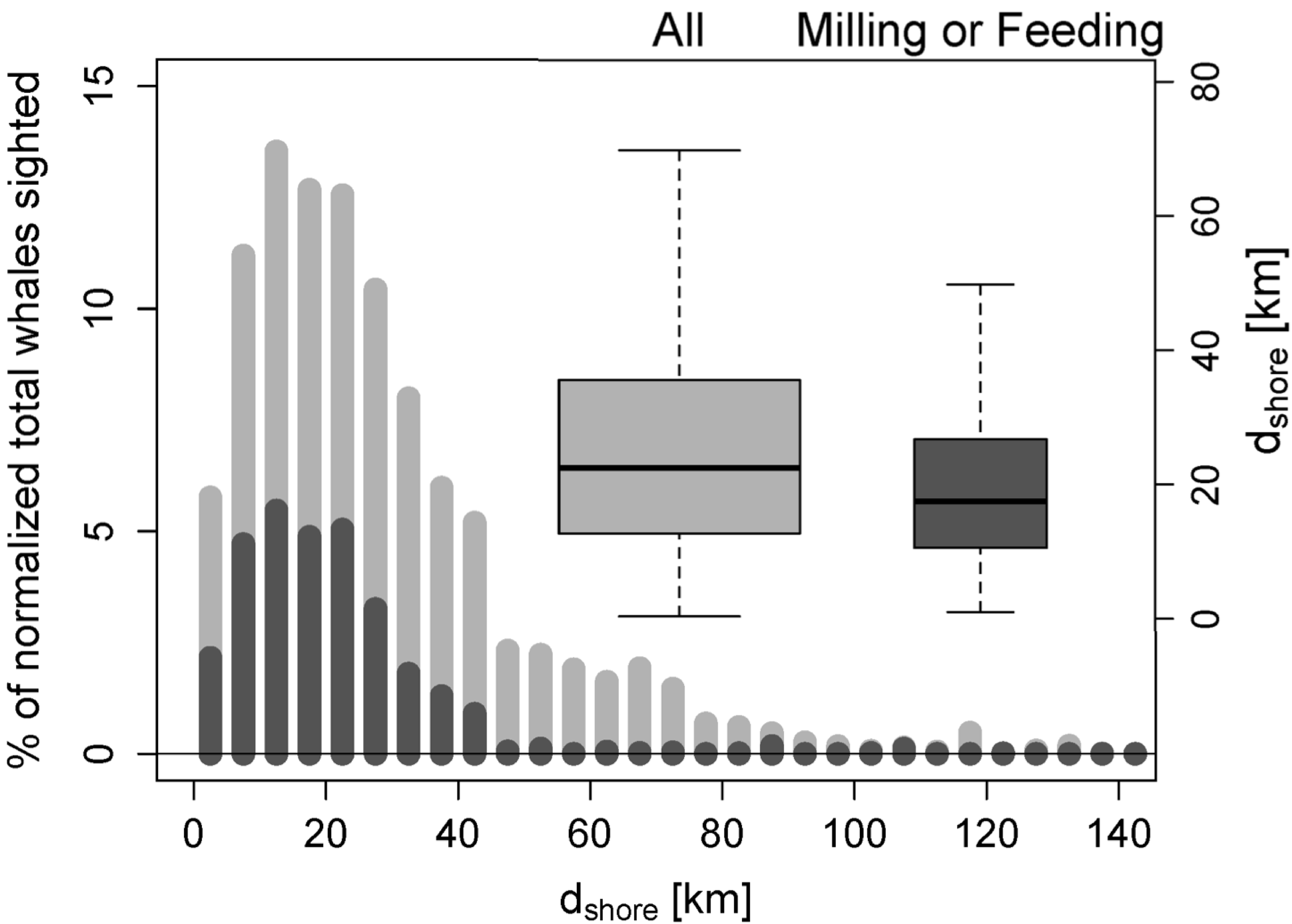
r = -0.59
d_{shore} [km]
0
20
40
60
80
100
1985
1990
1995
2000
2005
2010
2015
Year



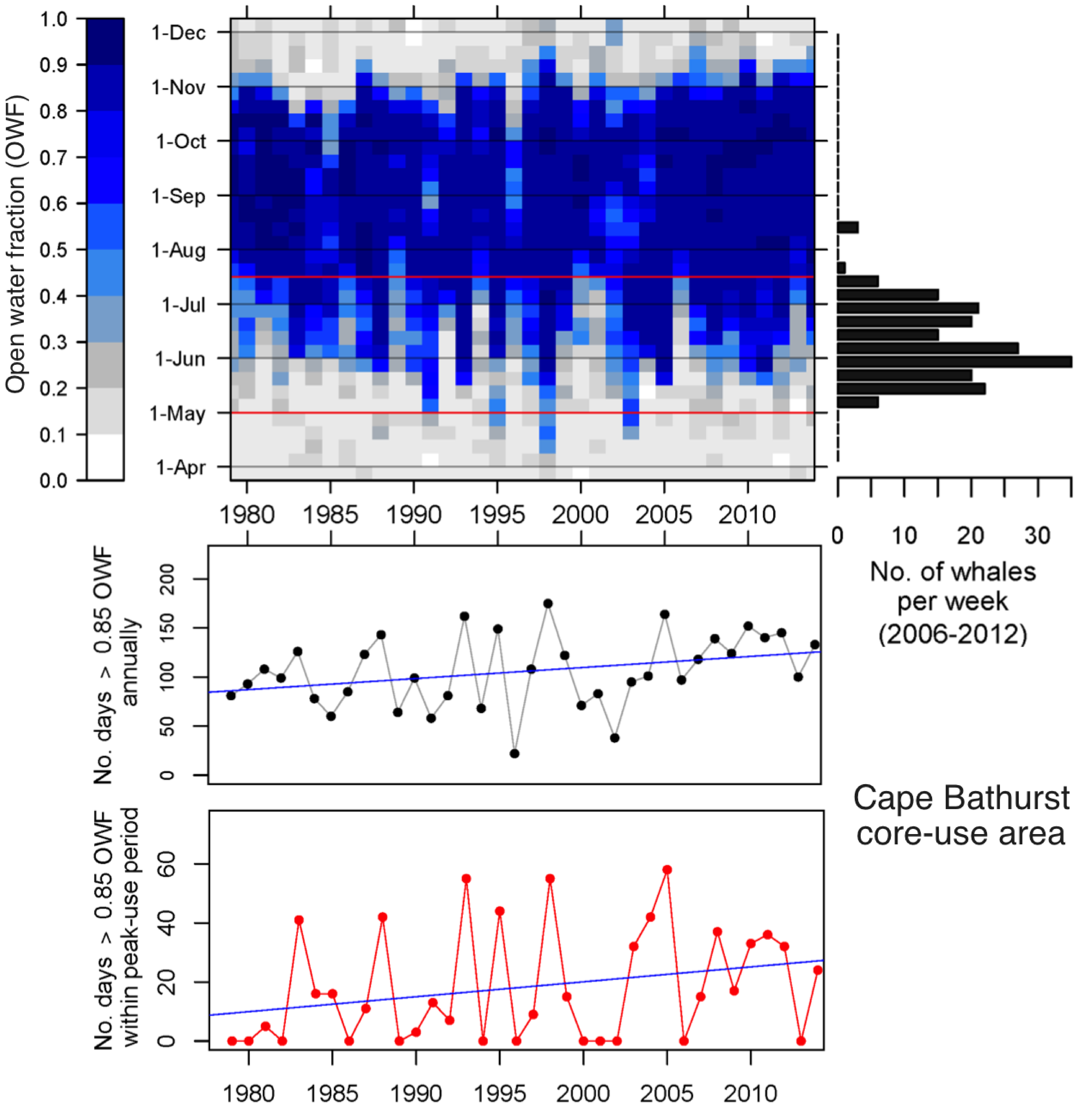
% of normalized total whales sighted
0
5
10
15
20
25
ice edge
d_ice
d_shore + d_ice
d_shore
shore
0.0
0.1
0.2
0.3
0.4
0.5
d_shore / (d_shore + d_ice)



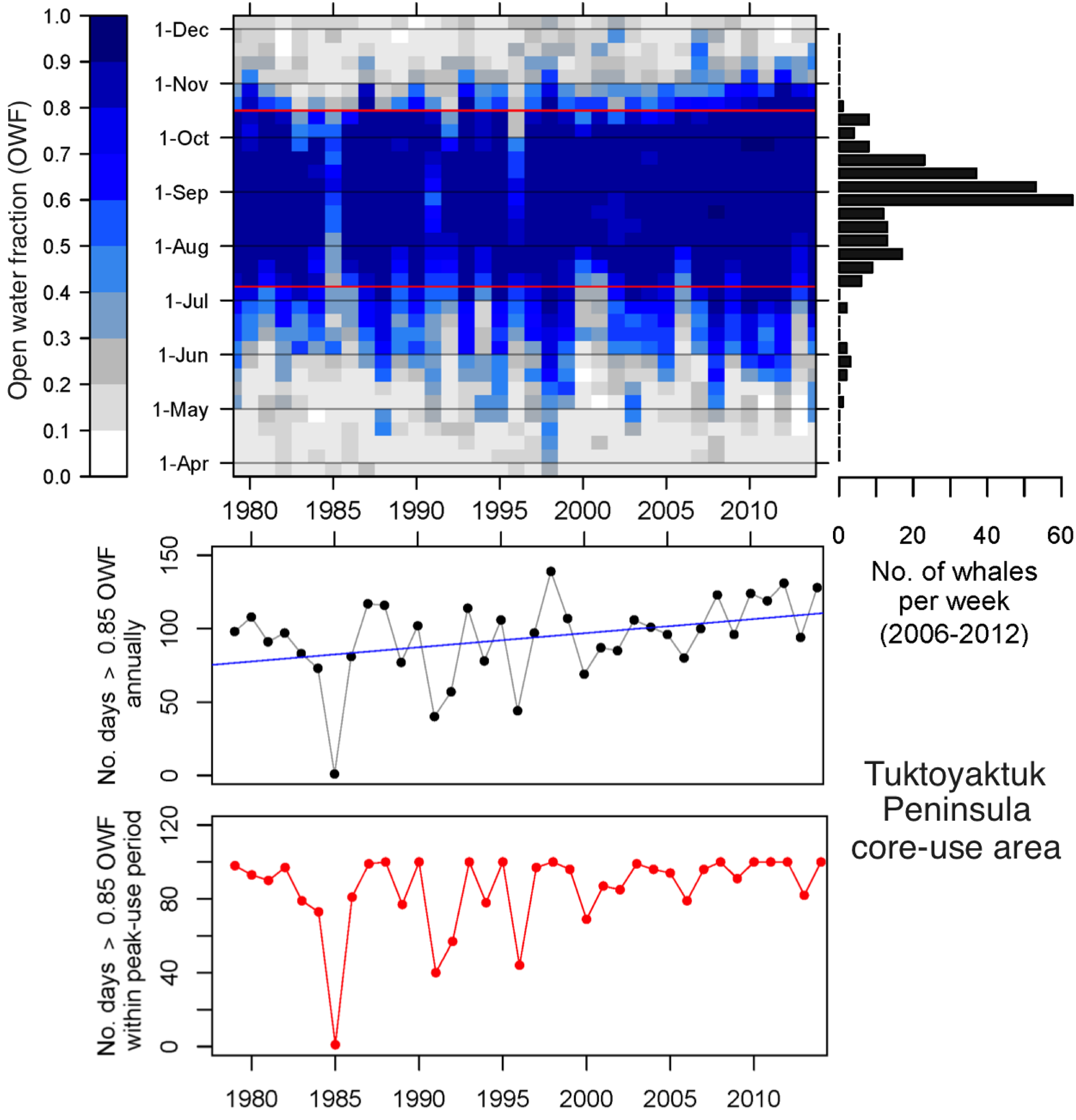
d_shore [km]
0
20
40
60
80
100
1
1-0.85
0.85-0.70
<0.70
Open Water Fraction (OWF)



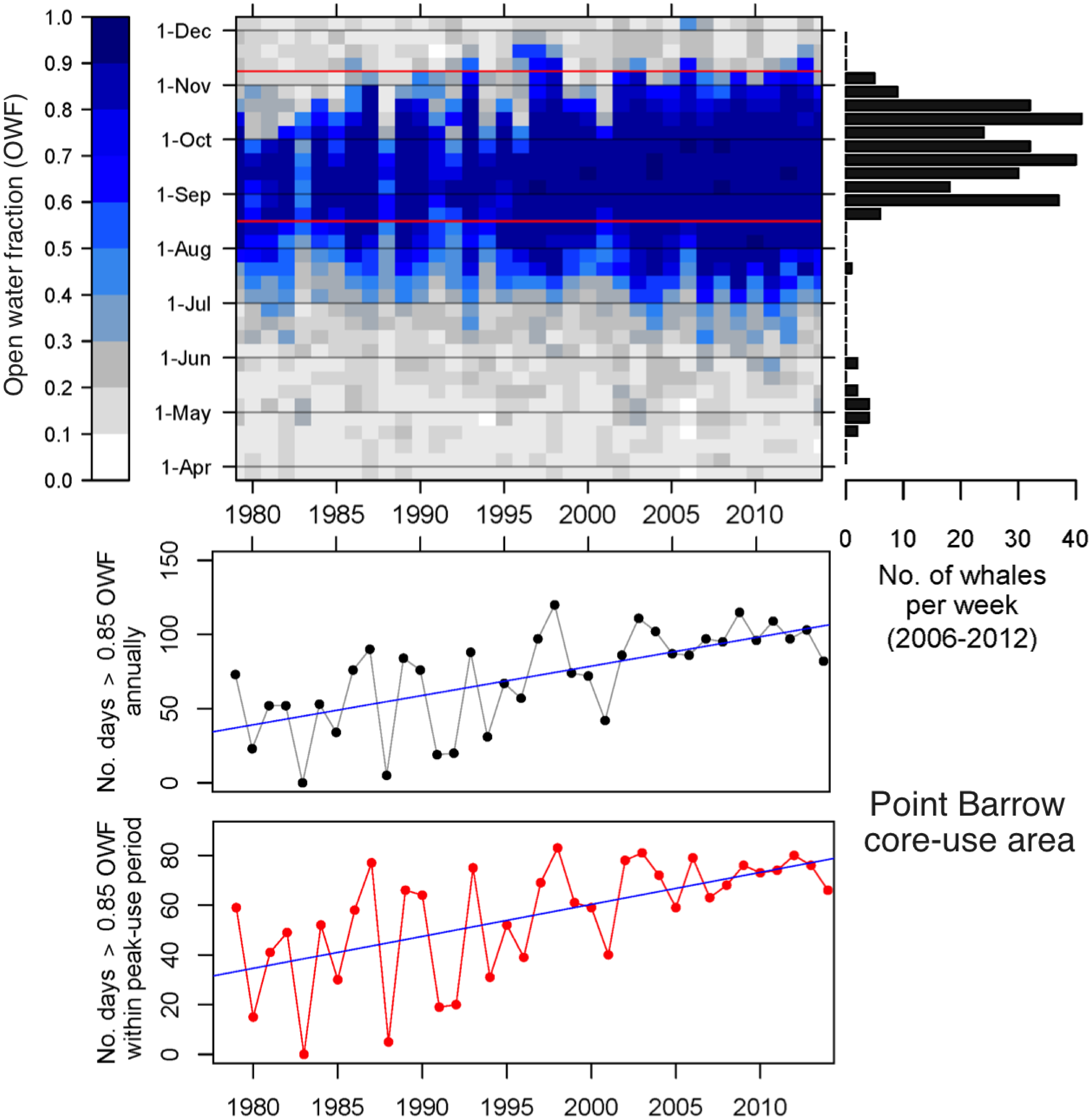
All
Milling or Feeding
% of normalized total whales sighted
0
5
10
15
0
20
40
60
80
d_{shore} [km]
0
20
40
60
80
100
120
140
d_{shore} [km]

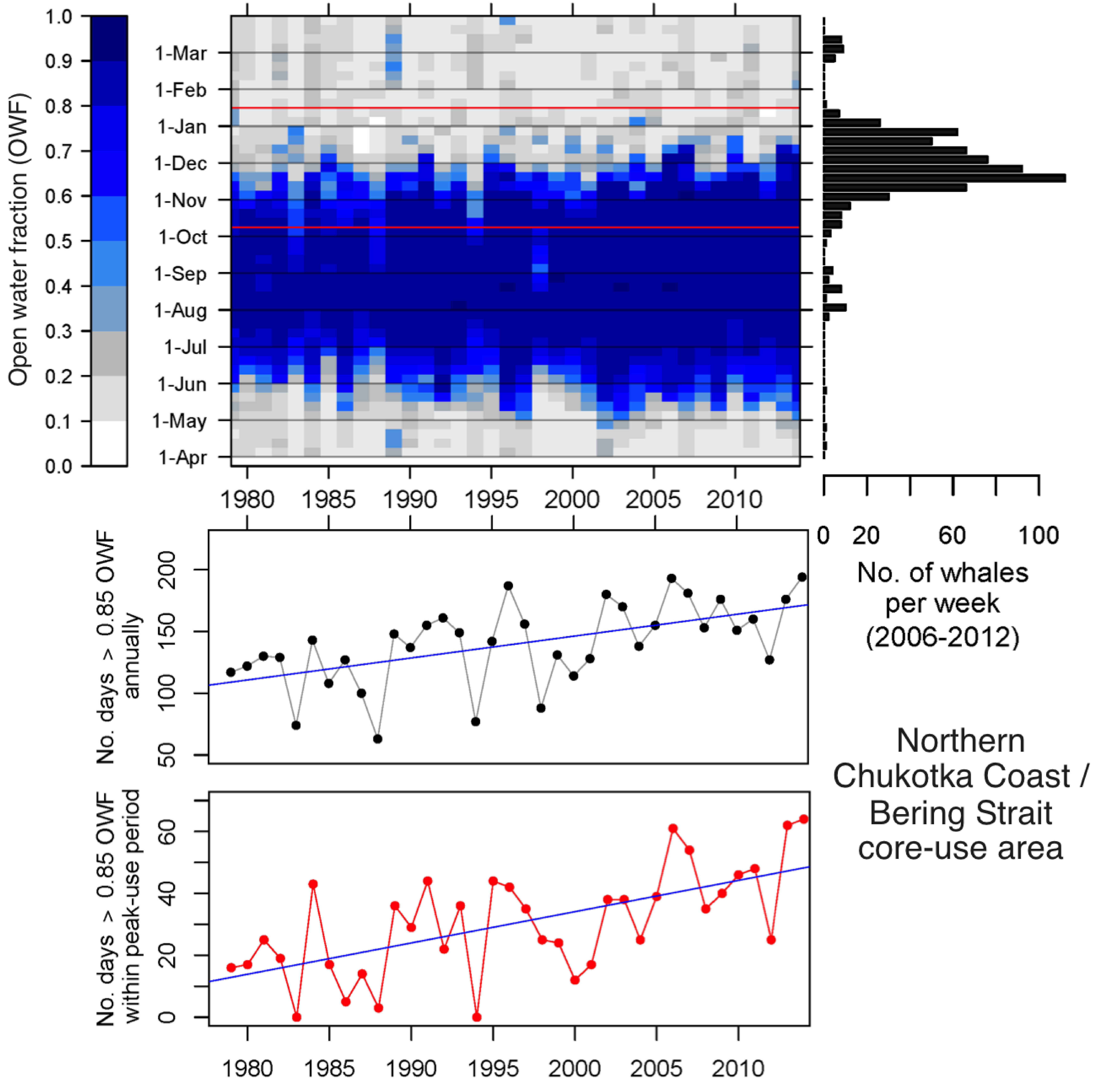


Open water fraction (OWF)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1-Dec
1-Nov
1-Oct
1-Sep
1-Aug
1-Jul
1-Jun
1-May
1-Apr
1980
1985
1990
1995
2000
2005
2010
0
10
20
30
No. of whales
per week
(2006-2012)
No. days > 0.85 OWF
annually
0
50
100
150
200
Cape Bathurst
core-use area
No. days > 0.85 OWF
within peak-use period
0
20
40
60

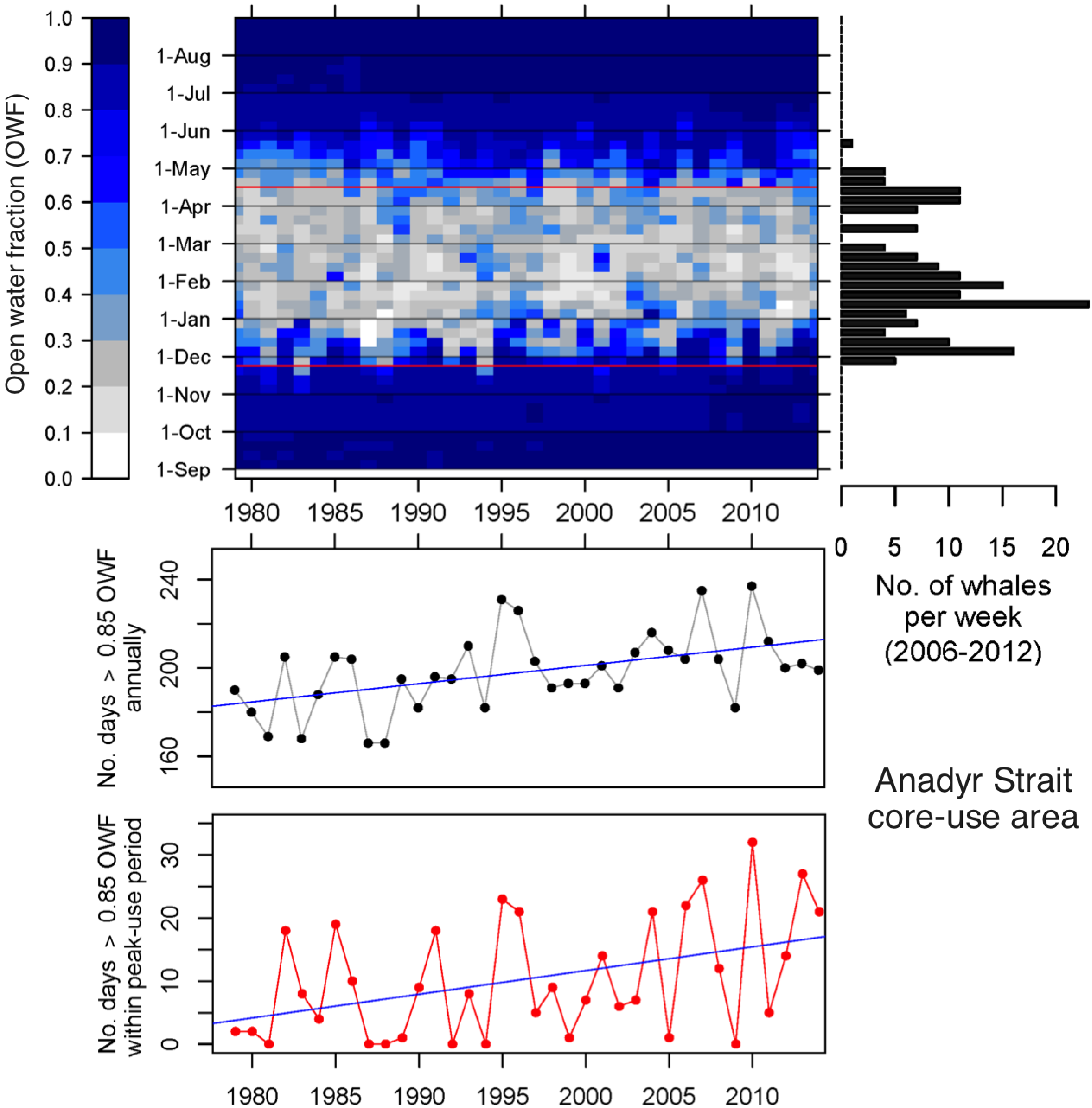


Open water fraction (OWF)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1-Dec
1-Nov
1-Oct
1-Sep
1-Aug
1-Jul
1-Jun
1-May
1-Apr
1980
1985
1990
1995
2000
2005
2010
0
20
40
60
No. of whales per week (2006-2012)
No. days > 0.85 OWF annually
150
100
50
0
No. days > 0.85 OWF within peak-use period
120
80
40
0
Tuktoyaktuk Peninsula core-use area

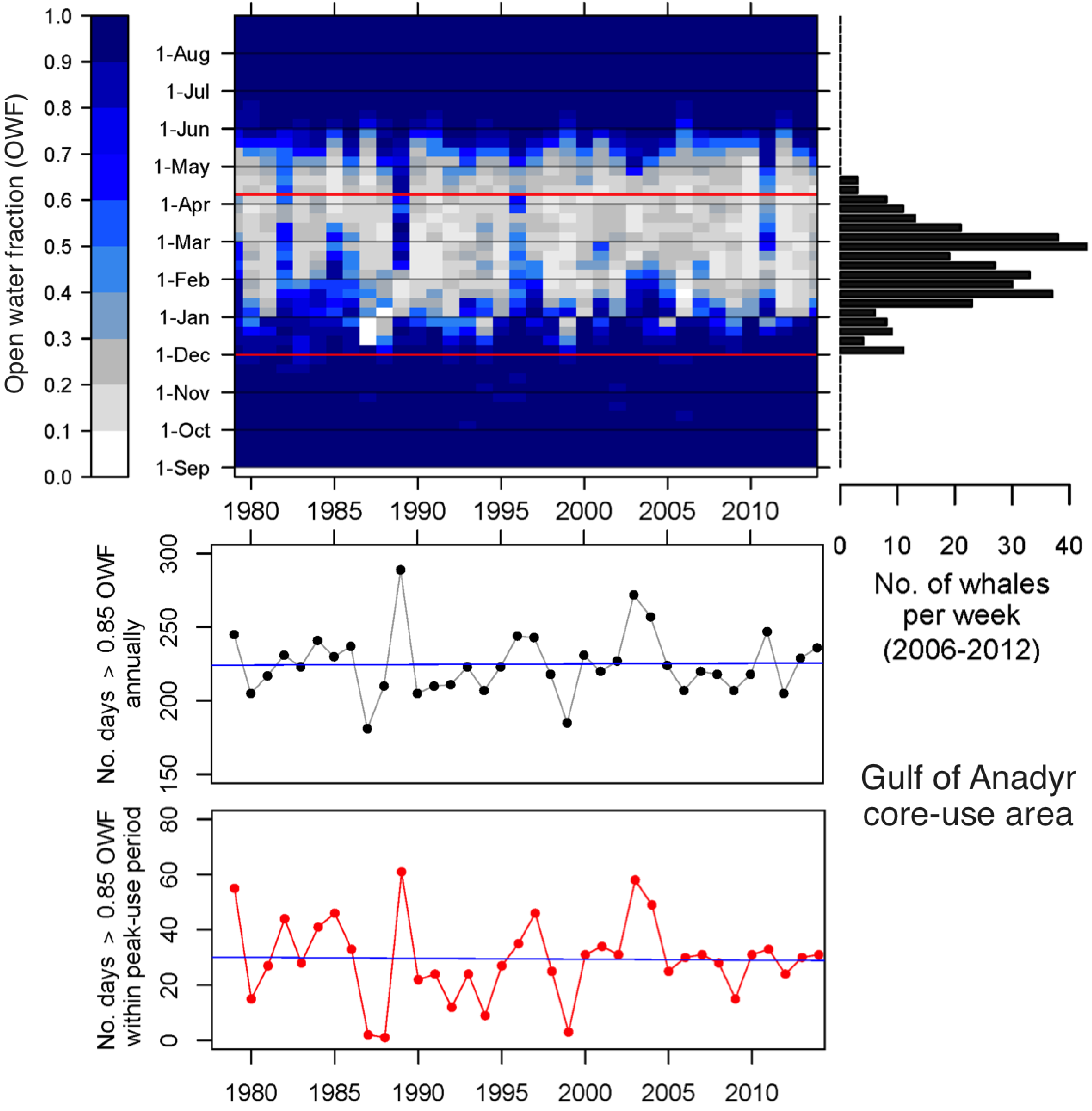

Open water fraction (OWF)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1-Dec
1-Nov
1-Oct
1-Sep
1-Aug
1-Jul
1-Jun
1-May
1-Apr
1980
1985
1990
1995
2000
2005
2010
0
10
20
30
40
No. of whales per week (2006-2012)
No. days > 0.85 OWF annually
150
100
50
0
Point Barrow core-use area
No. days > 0.85 OWF within peak-use period
80
60
40
20
0



Open water fraction (OWF)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1-Mar
1-Feb
1-Jan
1-Dec
1-Nov
1-Oct
1-Sep
1-Aug
1-Jul
1-Jun
1-May
1-Apr
1980
1985
1990
1995
2000
2005
2010
0
20
60
100
No. of whales per week (2006-2012)
No. days > 0.85 OWF annually
200
150
100
50
No. days > 0.85 OWF within peak-use period
60
40
20
0
Northern Chukotka Coast / Bering Strait core-use area



Open water fraction (OWF)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1-Aug
1-Jul
1-Jun
1-May
1-Apr
1-Mar
1-Feb
1-Jan
1-Dec
1-Nov
1-Oct
1-Sep
1980
1985
1990
1995
2000
2005
2010
0
5
10
15
20
No. of whales per week (2006-2012)
No. days > 0.85 OWF annually
240
200
160
No. days > 0.85 OWF within peak-use period
30
20
10
0
Anadyr Strait core-use area



Open water fraction (OWF)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1-Aug
1-Jul
1-Jun
1-May
1-Apr
1-Mar
1-Feb
1-Jan
1-Dec
1-Nov
1-Oct
1-Sep
1980
1985
1990
1995
2000
2005
2010
0
10
20
30
40
No. of whales per week (2006-2012)
No. days > 0.85 OWF annually
300
250
200
150
Gulf of Anadyr core-use area
No. days > 0.85 OWF within peak-use period
80
60
40
20
0