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Decadal Bering Sea seascape change: consequences for Pacific walruses and indigenous hunters

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Abstract. The most significant factors currently affecting the Pacific walrus (*Odobenus rosmarus divergens*) population are climate change and consequent changes in sea-ice morphology and dynamics. This paper integrates recent physical sea-ice change in the Bering Sea with biological and ecological conditions of walruses in their winter–spring reproductive habitat. Historically, walrus in winter–spring depended on a critical mass of sea-ice habitat to optimize social networking, reproductive fitness, feeding behavior, migration, and energetic efficiency. During 2003–2013, our cross-disciplinary, multiscale analysis from shipboard observations, satellite imagery, and ice-floe tracking, reinforced by information from indigenous subsistence hunters, documented change of sea-ice structure from a plastic continuum to a "mixing bowl" of ice floes moving more independently. This fragmentation of winter habitat preconditions the walrus population toward dispersal mortality and will also negatively affect the availability of resources for indigenous communities. We urge an expanded research and management agenda that integrates walrus natural history and habitat more completely with changing sea-ice morphology and dynamics at multiple scales, while also meeting the needs of local communities.

Key words: Bering Sea; climate change; Odobenus rosmarus divergens*; Pacific walrus; sea ice; seascape; subsistence hunting*

Introduction

Loss of sea ice is considered to be the most significant factor affecting Arctic ice-dependent marine mammals, including the Pacific walrus, *Odobenus rosmarus divergens*. Much evidence makes clear that Bering Sea sea ice has been breaking up earlier in spring and undergoing structural change. Naturalists have generally agreed that walruses are distributed in accord with the character of the pack ice to meet life history needs (e.g., Burns 1970, Fay 1974, 1982, Burns et al. 1981). For walruses, most attention so far has been drawn to the accelerating retreat of summer sea ice in the Chukchi Sea that has forced walruses to haul out on land, which risks overconsumption of food supply (Jay et al. 2011, MacCracken 2012). However, social structure of the summer population in the Chukchi Sea depends on reproductive success in the Bering Sea, as well as during migration, especially for females and calves. Therefore, the effects of sea-ice change on the winter–spring walrus population in the Bering Sea and the overall effects of climate change on walrus natural history requirements there are important to consider.

Ray et al. (2010) proposed that the spatial relationships of walruses are dependent on sea-ice structure and that the effects of sea-ice change are best studied through "seascape" concepts, following principles of landscape ecology (Wu and Hobbs 2007). Ray and Hufford (1989) provided the basis for this approach, by describing six seascape types, with "broken pack" as the major walrus habitat. (Fig. 1, Table 1); notably, the names given for these types are new to current nomenclatures (e.g., NOAA 2000,

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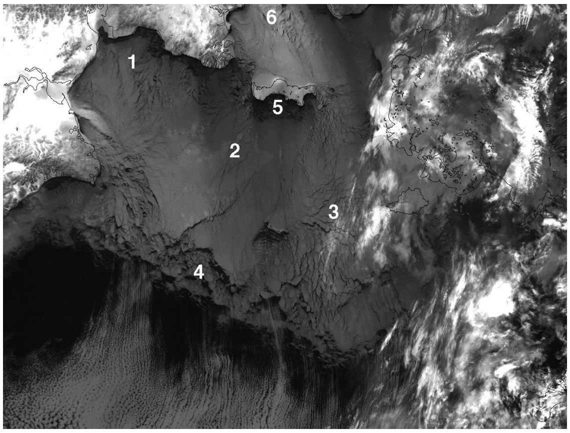

Fig. 1. March 1988 sea-ice seascapes (from Ray and Hufford 1989). Seascapes are not strictly bounded due to ecotone effects and inclusion of other types within them (analogously to terrestrial landscapes, e.g., "taiga" and "tundra"). Also, southeastern Bering Sea ice, occupied by a relatively small population of walruses, remains to be classified. Sea-ice types (see Table 1) are: (1) broken pack, west-central Bering Sea to northwest of St. Lawrence Island (SLI); (2) pack ice with leads, in the coldest, northwestern part of the Bering Sea; (3) rounded pack, eastern Bering Sea; (4) loose pack, at sea-ice margin; (5) polynya, usually on south sides of peninsulas and islands; (6) continuous ice, Bering Sea Strait region and northward into the Chukchi Sea.

WMO). From 2003 to 2013, we used MODIS satellite imagery to trace change of the Bering Sea seascape. And in 2006–2009 we had the opportunity to observe walrus–sea-ice association from the icebreaker *Healy*. In combination, these observations, reinforced by knowledge from subsistence hunters, enabled us to identify and interpret sea-ice conditions at seascape and local scales, and to compare these observations with historic spatial distributions of walruses.

Dynamics of Sea-ice Change

Prior to about the mid-1990s, Bering Sea sea ice in March had usually covered ~75% of the Bering Sea shelf (Stabeno et al. 2012). Winter sea ice has maintained this historical cover through 2013, except for June, when sea-ice cover has declined slightly (Fig. 2). This is due to the southern Bering Sea being mostly governed by shifts in North Pacific weather (Overland et al. 2014), in contrast to dramatic summer sea-ice loss north of Bering Strait. McNutt and Overland (2003) observed that sea ice formerly performed as a "plastic continuum" governed primarily by fracture mechanics. Also, a 6-yr warm period in 2000–2005 with less winter–spring ice cover has been followed by a transition in 2006 to a cold period with greater ice cover in 2007–2013, except for 2011 (Overland et al. 2012). Maximum sea-ice cover in March, however, is not the best index for our study. Rather, rapid melt and thin sea ice in late spring have contributed to a shortened the sea-ice season by 3–4 weeks (Walsh 2008).

Table 1. Attributes of midwinter seascape types of the Bering Sea, with ice types from Ray and Hufford (1989).

Ice type	Dominant species and other species	Seascape description
Broken pack (see Figs. 1 and 3)	Walrus, bearded seal; benthic feeders that require dispersed floes on which to rest over relatively shallow shelf water; open water, thin ice, leads, and small polynyas required for access to benthic food supply	Central Bering Sea; pack broken into angular floes with intersecting leads and polynyas, due to low-frequency forces from winds, waves, and ocean currents; open water and/or thin ice continuously available
Loose pack, including remnant ice (see Figs. 1 and 3)	Ribbon seal mostly westward toward Bering Sea basin; spotted seal mostly eastward over shelf and toward coastal lands; small seals that cannot break ice and require easy access to open water; occur in ice where polar bears are rare	Southernmost extent of the pack; small to medium-sized, dispersed floes due to interactions with wind, waves, and oceanic forces; floes often flat and rounded from continuous collisions
Pack ice with leads (see Figs. 1 and 3)	Walrus; can be continuous with broken pack; ribbon seal later in spring	Gulf of Anadyr and Koryak coast; floe distribution constrained by coastal configuration; large, congealed floes frequent; winds create leads nearly perpendicular to wind direction
Rounded pack (see Figs. 1 and 3)	Very few pinnipeds due to restricted open water	Eastern Bering Sea; thick, ridged, concentrated, rounded floes that are mostly highly concentrated due to opposing north winds and the north-flowing coastal stream
Continuous pack (see Figs. 1 and 3)	Ringed seal; make breathing holes in shorefast or continuous ice up to 2 m thick; may also occur on open, flat floes with pressure ridges in broken pack and elsewhere	Bering Strait region, shores; semi-continuous, highly concentrated ice, fractured in all directions due to continuous, opposing stresses
Polynyas (see Figs. 1 and 3)	Few pinnipeds on isolated floes, remnant ice, or swimming	Large open-water or thin ice south or north of land masses, due to winds that force sea ice away from coasts; small polynyas are distributed in all portion of pack

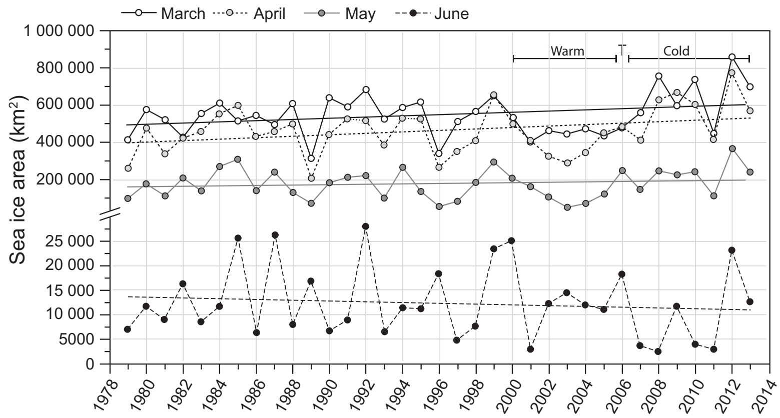

FIG. 2. Total March–June sea-ice cover (km^2) over the Bering Sea during March–June 1978–2013. Dashed lines indicate decadal trends. Cover for the 2000–2005 warm period is relatively low, but relatively high for the 2007–2013 cold period; 2006 is transitional and 2011 is anomalous. Slight decreases in sea-ice area occur in June (−744 km^2/decade), while slight increases occur during March (+32775 km^2/decade), April (+39915 km^2/decade), and May (+10752 km^2/decade); only March and April are statistically significant ($P < 0.1$). Areas are based on sea-ice concentrations derived from SMMR and SSM/I passive microwave satellite time series (Cavalieri et al. 1996, Maslanik and Stroeve 1999). Due to the low resolution of the imagery, small and highly dispersed floes are not detected.

Satellite imagery for the Bering Sea in March–May 2003–2013 (Fig. 3a–c) illustrates the recent high variability of sea-ice cover and changes in the seascape. First, southward sea-ice extent has varied significantly (Fig. 3, March for all years). Second, major melt-outs have left large expanses of open water (Fig. 3, April–May of several years), with the effect of dispersing floes over large areas. Even during cold years, notably 2007 and 2008, numerous melting and freezing events have occurred as early as February, resulting in large expanses of young ice (<0.3 m thick), setting the stage for rapid melting from May onward. Third, advection of warming North Pacific water and storm events have mixed upper ocean waters, shifting the morphology of sea ice toward smaller floes (Bond et al. 1994). Fourth, when winds are northerly, very large areas of near-open water (polynyas) have occurred in the central shelf and Gulf of Anadyr (Fig. 3; March and April of many years), increasing melt and resulting in significant reductions of ice by mid-May.

Importantly for the seascape, when sea-ice concentration is diminished, the speed and direction of individual floe movements, influenced by different proportions of sail or keel, cause floes to react more independently, producing what we call a "mixing-bowl effect" (groupings of floe sizes and thickness from different seascapes). Floe tracking demonstrates this effect (Fig. 4). Feature recognition technology (Fily and Rothrock 1990, Holt et al. 1992) enabled tracking of 42 floes during 2006–2009, 36 with walrus present or on adjacent occupied floes, four for "rounded" pack, and two very large, concentrated floe associations that moved eastward from the Gulf of Anadyr (Figs. 2a and 3b). This technology also revealed variability among years due to differing weather and ice conditions.

In 2006, we tracked 10 floes associated with walrus during migration for 3–15 d from 8 May to 1 June, a time of ice retreat and extensive open water. All floes moved generally northward at different speeds, mainly in response to ocean circulation. Winds were generally light, but when greater than 27 km/h, floes moved greater distances, especially when they were in very loose pack or surrounded by open water. Two floes from rounded pack illustrated the effect of the northward-moving Alaska Current on floe movement. One area 2 June near the International Dateline, provides an example of the combined effects of winds and currents. Earlier imagery identified the floe's origin off the mouth of the Anadyr River on 9 May. Storm winds beginning 12 May rapidly pushed the floe association southeast, where it lingered for 14 d as ocean currents balanced wind stress. Ocean currents then pushed the floe association slowly northeast until 2 June, when another wind event pushed it northeast toward St. Lawrence Island, where it grounded and melted in place.

In 2007, we tracked 11 floes of the broken pack associated with walruses for 5–11 d from 9 April to 4 June. This was a cold year with four storms, cloudy days, and predominately northerly winds until mid-April, which kept the ice pack relatively consolidated. These combined conditions limited floe tracking. In late April into May, three additional storms brought warm temperatures and a rapid melt-out. A very large, consolidated floe (SL; Fig. 3; 2007) provides another example of the combined effects of winds and currents. This floe from the central Gulf of Anadyr was tracked from 14 March to 5 June. Storm winds pushed it eastward into the central-western Bering Sea, when

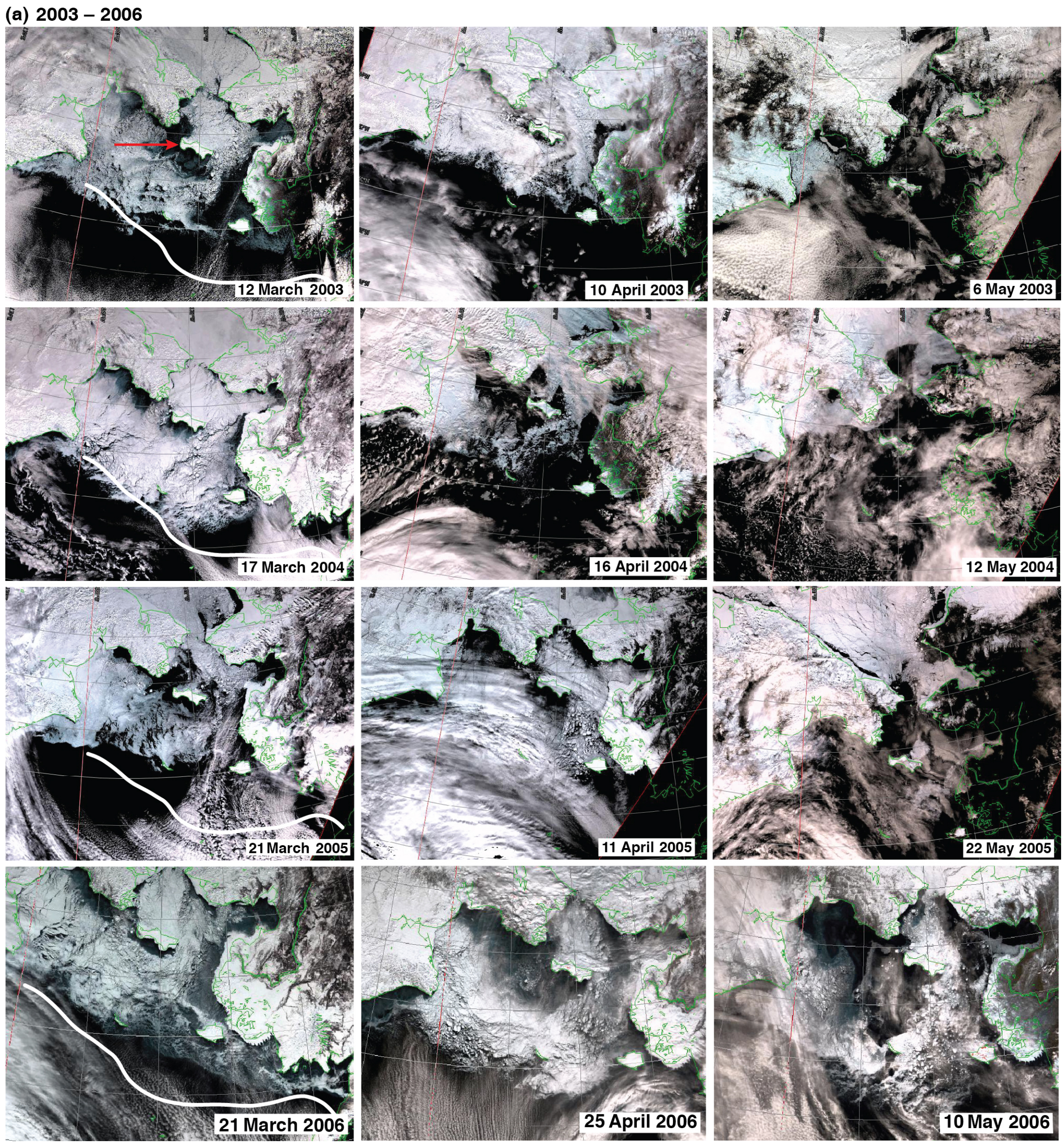

Fig. 3. (a) MODIS satellite imagery showing sea-ice conditions for March, April, and May; floes of small size and low concentration are not detected. The white lines on March images indicate the climatological norm and allow high variability of extent among years to be assessed. The red arrow on March 2003 indicates St. Lawrence Island as a reference point for all images. Years 2003–2006 represent a portion of the warm period when sea-ice extent and cover were less than the norm; 2006 was transitional. In 2003, the maximum extent occurred on 21 March. Melting then began and by mid-May the Bering Strait was open; an event that normally occurs in late June. In 2004, maximum sea-ice extent occurred on 3 April, and was near average except for the southeast Bering Sea. Rapid melting occurred so that by mid-May only scattered patches of sea ice were left except for the Gulf of Anadyr, and the Bering Strait was partially open. In 2005, maximum ice extent occurred on 8 April, well north of the climatological norm; this was the warmest year on record, as also reflected by ice conditions. The pack was generally unconsolidated, and only patches of sea ice were present throughout April–May. The Bering Strait was virtually ice-free by 22 May. 2006 was a transitional year, moving from a warm period to a cold period. Maximum extent occurred on 2 February, but showed a lag in extent for that period, probably due to warm ocean waters. Cold northerly winds, indicated by long, parallel "cloud streets" over open water south of the ice edge (25 April), continued to push the pack southward, However, the ice edge never reached the February maximum. Rapid melting did not occur until late April, with extensive open water appearing in mid-May in the central Bering Sea and Gulf of Anadyr.

northeast and then southeast currents dominated floe movement. By 5 June, the floe had finally drifted near SLI, where it began to break up and melt in place.

In 2008, northerly winds predominated. During late winter to early breakup, we tracked eight floes from 16 March to 14 April for periods of 3–6 d. Sea-ice

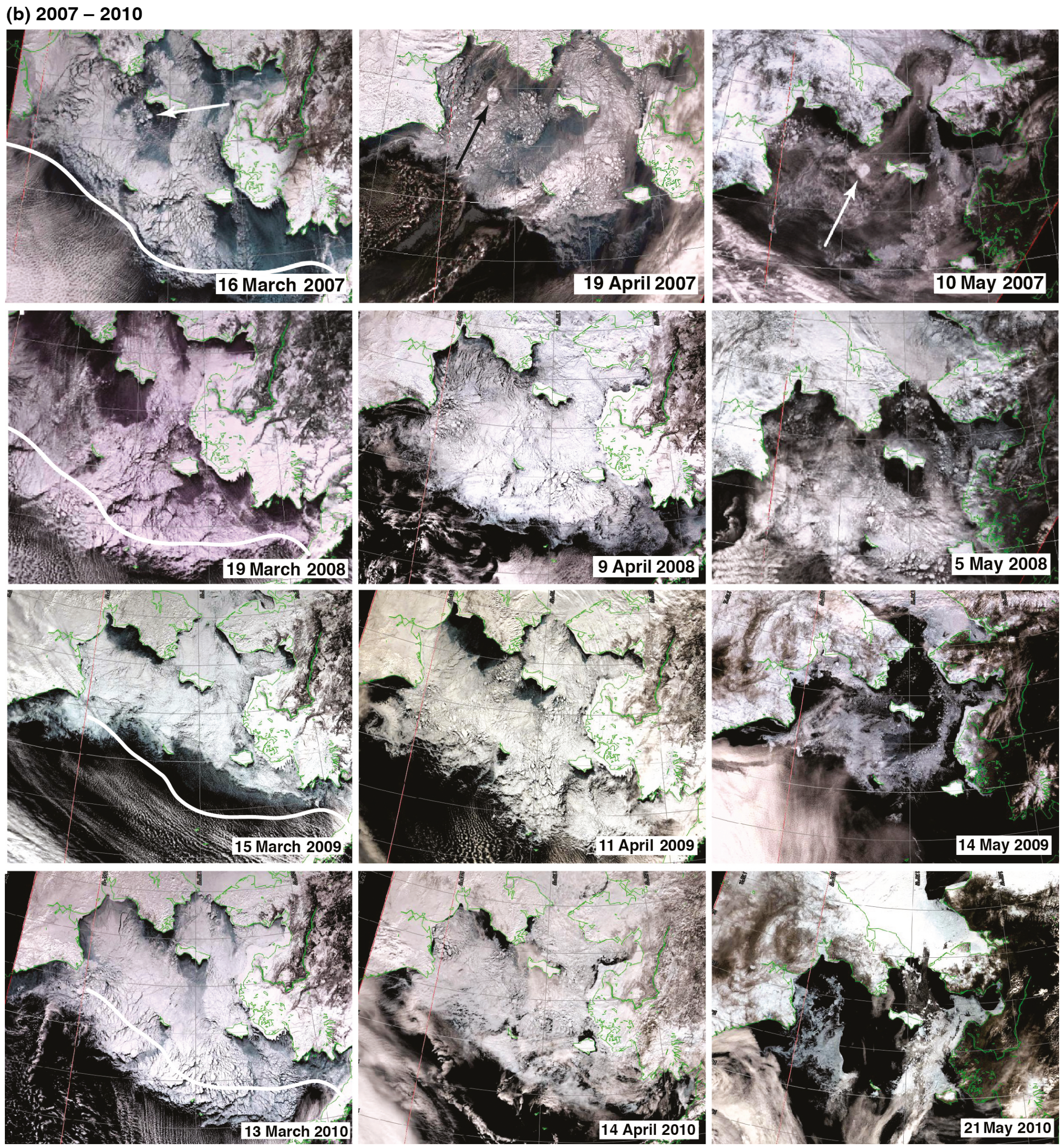

FIG. 3. (b) The years 2007–2010 were a cold period; melt and retreat were quite different in May for the 4 yr. 2007 was the first year to show clear effects of the cold period. Sea-ice extent on 16 March was near the climatological norm, although there were light ice conditions in the Bristol Bay area. Even with cold winter–early spring temperatures, ice melt and retreat were very rapid in late April and early May. The Bering Strait was mostly open by 10 May. The arrow in the 16 March image points to an area of broken pack containing many small groups of walruses. Arrows on 19 April and 10 May images indicate the large, concentrated floe mass that was tracked from the Gulf of Anadyr to SLI (see Fig. 4b). In 2008, winter and spring were anomalously cold due to persistent cold northerly winds. Sea-ice maximum occurred on 31 March and exceeded the climatological norm. On 3 April a major storm moved across the southern Bering Sea. Melt and retreat of sea ice increased substantially in May, with major open water in the Chirikov Basin. In 2009, under strong northerly winds, March sea-ice extent reached a maximum greater than the norm and remained at or near the maximum into early April, similar to conditions observed in the 1970–1980s. But from mid-April, sea-ice melt and retreat were extensive, creating large areas of open water. Ice cover in April was very similar to conditions in April 2008. However, there was a consistency in the melt-out patterns in the northern Bering Sea, but with a shift in timing. In 2010, ice extent on 13 March exceeded the climatological norm, with ice cover similar to conditions observed in the 1970–1980s. Ice cover in April was very similar to April 2008 and 2009. Sea-ice retreat and melt-out in April was very slow, with significant ice still present in the central Bering Sea, especially around St. Lawrence Island, in late May.

conditions ranged from consolidated ice with many fractures and open leads to very compact pack. Persistent, strong, northerly winds pushed many floes southward for several days and the southern edge of the polynya extended southward from SLI to just east of St. Matthew Island. A strong storm in early March

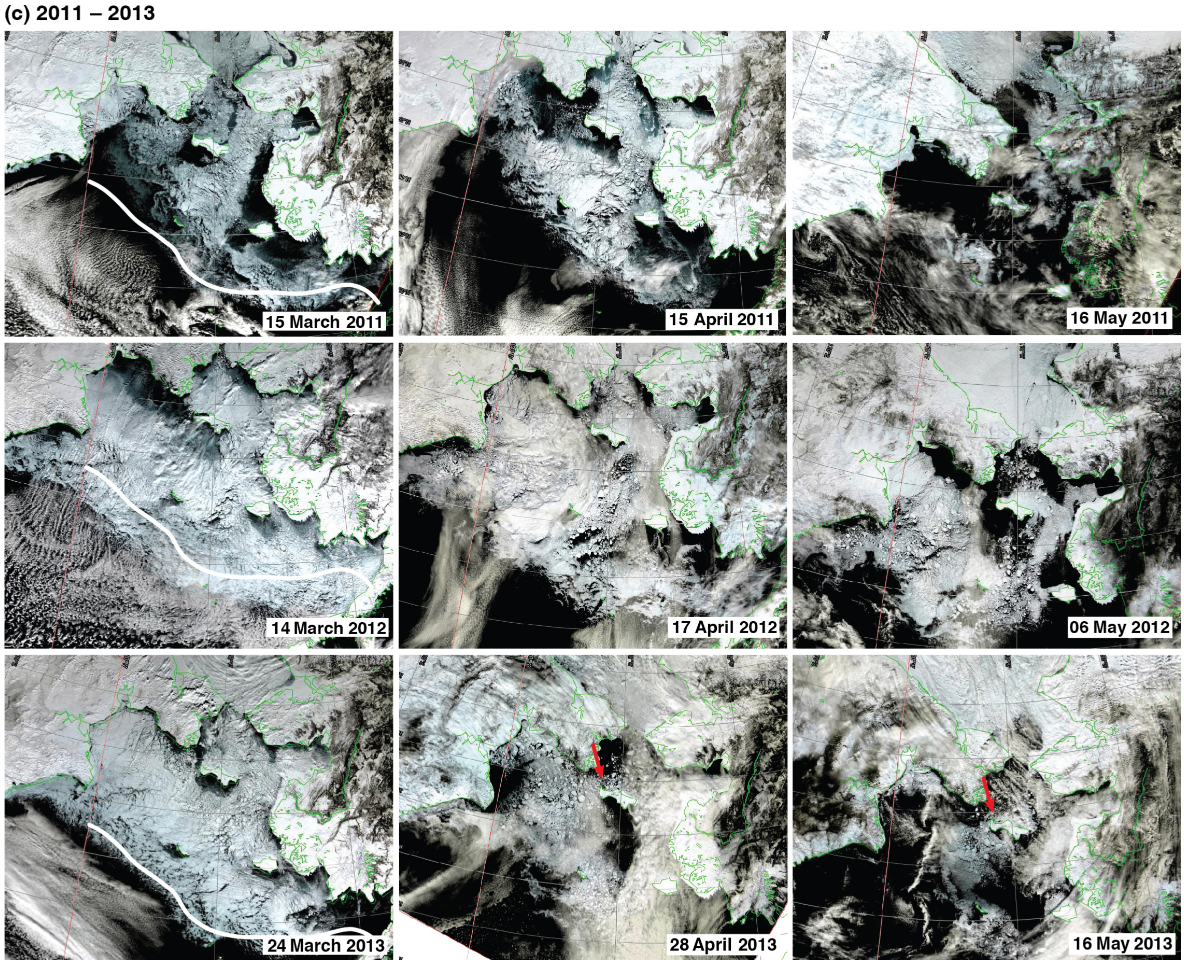

FIG. 3. (c) The period 2012–2013 continued the cold period dominated by northerly winds, but very warm temperatures in 2011 in part of the Bering Sea interrupted this period. Ice conditions in 2011 exceeded the norm in the central and eastern Bering Sea, but were below average in the western Bering, where warm air temperatures prevailed. The overall ice pack was unconsolidated with many leads. This pattern continued into early April, but by mid-April melting and retreat were evident. By mid-May, most of the northern Bering Sea was open water that extended north into the Chukchi Sea. In 2012, anomalous cold air temperatures returned across the Bering Sea. Sea-ice extent in February was the second highest on record, and the extent continued to be greater than average into mid-April. However, rapid melt and retreat began so that by mid–May there was extensive open water and any remaining sea ice was very thin. In 2013. strong southwest winds pushed ice onshore at the western end of SLI on 11 May (arrow), preventing hunting; this condition of southerly winds originated in late April and persisted through May, which kept the sea-ice pack compacted in the northern Bering Sea.

produced westerly winds that pushed the sea ice eastward, especially in the southern Bering Sea. A major melt-out occurred in May. The overall result was to push broken pack into the south-central and eastern Bering Sea, producing a mix of sea-ice types in and near the marginal ice zone.

During March to early April 2009, we tracked nine floes for periods of 4–8 d. This year was exceptional. The Bering Sea was covered by ~75% of concentrated ice in mid-April, much reduced by mid-May, and nearly ice-free by early June. Northerly winds dominated and sea-ice conditions ranged from consolidated with many fractures and open leads to very compact pack. All floes moved slowly in numerous directions and for relatively short distances. In late May, some areas retained considerable ice, especially around St. Lawrence Island.

In sum, floe rates and distances traveled are consistent with diminishing sea ice and earlier spring melting, except for 2009, when relatively concentrated sea ice was reminiscent of former conditions (e.g., Fig. 1). Worth noting is that tracks for 2006 and 2007 differ in direction and distance of floe movement, according to monthly differences in winds and currents and times of sea-ice break-up and melting. However, the many physical factors that influence sea-ice motion and melt make it difficult to determine which factors are primarily affecting drift speed and direction of any floe

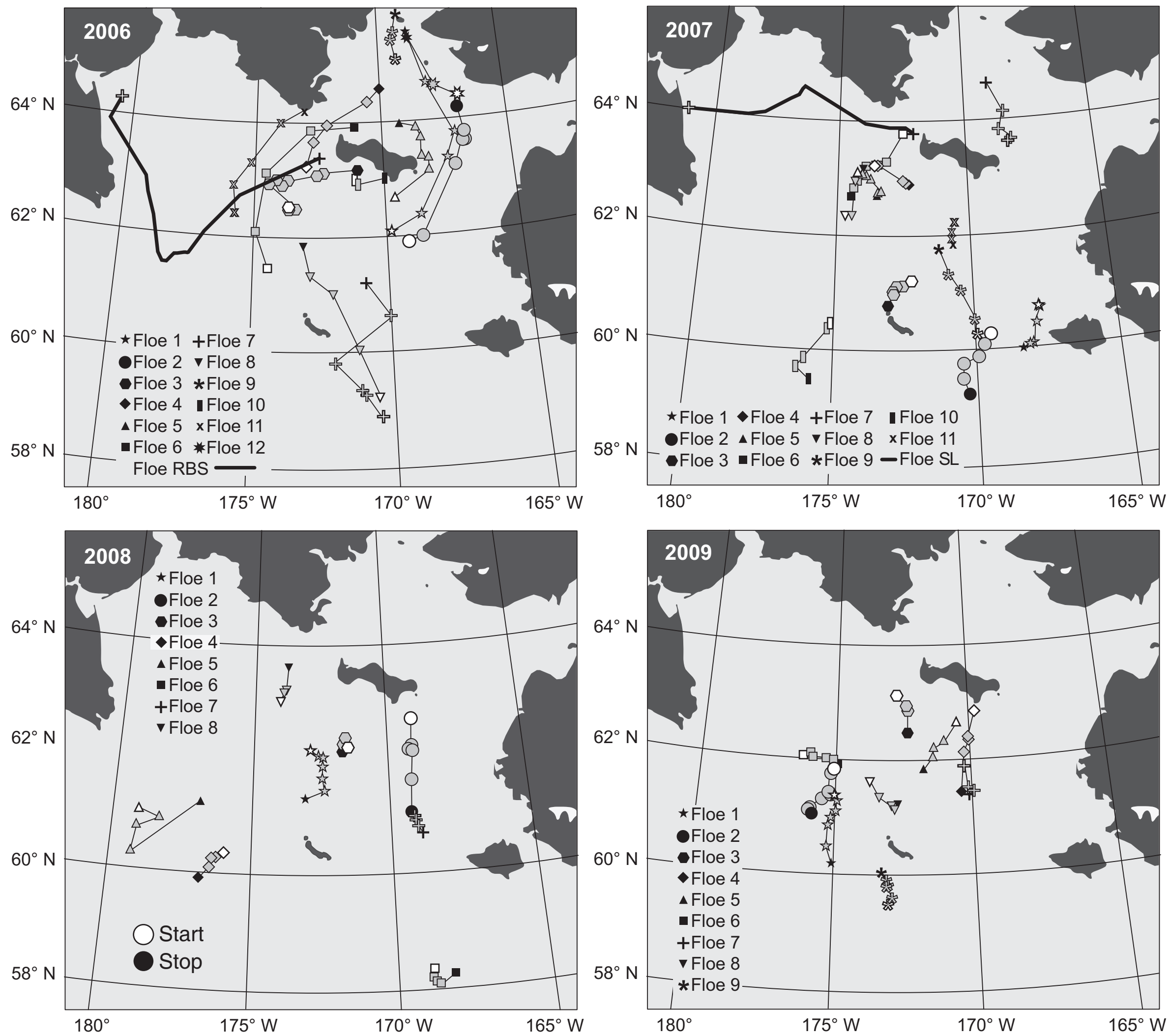

FIG. 4. Floe tracking, where open circles indicate track start and closed indicates end. Worth noting is that 2006 and 2007 tracks are during migration and differ in direction and distance of floe movement; 2006 appears to be a favorable year for walrus northward migration. Floe movements for 2008 and 2009 are less extensive due the more consolidated ice. In 2006, 10 floes of the broken pack moved 7.2–43.2 km/d. Floes 1 and 2 were tracked to determine the effect of the Alaska Current on floe movement; their rates of dispersal ranged from ~17 to 98 km/d with an average of 69.6 km/d. Floe RBS (dark line) was tracked over a very long distance; overall, this floe moved a total of 674 km in 33 d, averaging 20.4 km/d. In 2007, floes tracked in April moved southward at rates of 4.8–28.8 km/d. Floes in late May moved northward at an average speed of 14.4 km/d. A large, consolidated floe (RS, dark line) moved a total of 593 km in 54 d, averaging 11 km/d. In 2008, all floes moved southward except floe 8, which moved northward at 2.4 km/d. Speeds for other floes ranged from 4.8 km/d in concentrated ice to 16.8 km/d in lighter ice. Floe 3 on the eastward side of the polynya moved rapidly south because of less consolidated ice and very strong northerly winds. In 2009, floe movement was restricted by very heavy, consolidated ice pack in mid-March to early April. Nine floes were tracked and the speed averaged only 4.8 km/d, with the general direction to the south. Melting and retreat remained slow though April and into May. Considerable ice was still present, especially around St. Lawrence Island, in late May.

at any one time. Within season variability rather than mean drift or overall sea-ice extent is likely to be the dominant factor in establishing seascape associations. Significantly for the seascape, floes can move in numerous directions and at higher speeds when the pack is less concentrated or has many open-water areas. During 2006-2009, floes appeared to be traveling at more rapid rates and for greater distances under the forces of winds and currents than formerly, and are intermingling with floes of other sizes and types: a "mixing bowl" that disrupts seascape habitats.

Indigenous Hunters' Observations

Indigenous subsistence hunters provide the most complete, continual, and long-term observations of local walrus–sea-ice associations (Krupnik and Ray 2007), using extensive nomenclatures for ice-related phenomena (Oozeva et al. 2004, Weyapuk and Krupnik 2012). The Sea Ice Knowledge and Use (SIKU) project of the International Polar Year (Krupnik et al. 2010*a,b*) provided more than 250 monthly logs during winter–springs of 2006–2012 that constitute a database of local ice and weather conditions, records of subsistence activities, and interpretations of sea-ice change (Krupnik 2009, 2013, Kapsch et al. 2010, Krupnik et al. 2010*a*, Eicken et al. 2014). More than 50 monthly logs from Gambell (Sivuqaq) on St. Lawrence Island (SLI) represent one of the most active walrus-hunting communities. Most of the walrus catch was from late April to early June, 2006–2012 (Table 2), but whether this timing was due to local sea-ice conditions or social causes, or both, requires understanding of how hunting is conducted (Oozeva et al. 2004), in order to establish relationships between sea ice, weather, and walrus availability (Krupnik and Ray 2007, Metcalf and Robards 2008, Kapsch et al. 2010, Krupnik et al. 2010*a*, Huntington et al. 2013, Robards et al. 2013).

Hunters use specific indicators to assess seasonal dynamics. The mid-March to mid-June transition from winter to spring is seen by hunters to progress through shifts in sea-ice concentration, triggered by combinations of winds, currents, and ice movements. Some of these patterns are episodic and hardly predictable; others occur regularly and have established names. The most common features are short-term events of strong southerly winds that move large floes in from the western and southern sides of SLI (*ivghaghutkak*), and the formation of a large polynya that extends southward every year, usually in early May (*kelliighineq*), from SLI and as far south as St. Matthew Island (Krupnik et al. 2010*a*). Commonly, hunters expect walrus and bearded seals to be abundant on western and southern floes. They explain the formation of *kelliighineq* by strong northerly winds on the already fractured sea ice.

Most hunting is conducted when the northern wind subsides and the polynya is replaced by floes drifting from the south, when the main mass of pack ice retreats north with southerly winds and currents, carrying migrating walrus from the western and central Bering Sea. This retreat of ice "loaded with game" has usually occurred in May. Occasionally under strong westerly winds, another type of ice comes from the Gulf of Anadyr. These conditions record what scientists call the "spring retreat" of sea ice, but to hunters is a series of individual events and distinctive seascape changes. Gambell hunters anticipate the first wave of walrus migrating north around the first and second weeks of May, corresponding to a shift in the prevailing wind from northerly to southerly, accompanied by a 2–5°C upward spike in daily air temperature. A second wave of walrus, probably from the southeastern Bering Sea subpopulation, occurs about 2 weeks later, followed in late May to early June by "last ice" reportedly coming from the Gulf of Anadyr and often carrying ribbon seals, *Histriophoca fasciata* (Krupnik et al. 2010*a*). The peak of walrus migration had usually occurred around 15 May, corresponding to a few days of active hunting, when up to 200–300 walruses were often killed. If the ice retreats northward earlier, hunters will have to make ever longer trips to get to the retreating pack ice; by late May, they may have to travel 80–110 km north to reach the ice. By early-mid June, the ice is usually gone.

Gambell hunters also use several proxies, not necessarily related to walrus, to track local-scale seasonal changes; e.g., arrival of certain birds, sightings of seals, melting of snow on the ground, etc. A proxy used by U.S. Fish and Wildlife Service monitors in Gambell is the numbers of walrus killed by week or season. However, Table 2 indicates no marked shifts in the timing of walrus migration for 2006–2013, yet the number of walruses killed in "peak days" or "last weeks of active hunting" fluctuated dramatically. Attempts have been made to explain these fluctuations by correlating results of hunts with reported ice

Table 2. Dynamics of spring walrus hunting in Gambell, Alaska, USA, 2006–2013, with weekly harvest data, according to UFWS monitoring program, where "Wk" is calendar week and *N* is number of walrus taken.

Year	First week of active spring hunting		Peak of walrus migration		Last week of active hunting		Total spring catch, Wk17–23
	Wk	*N*	Wk	*N*	Wk	*N*	*N*
2006	19	104	21–22	197	22	82	342
2007	18	235	18–19	360	22	94	612
2008	20	307	20–22	519	22	102	536
2009	18	37	21–22	574	23	42	685
2010	19	102	21	291	23	26	457
2011	18	34	19	274	21	47	404
2012	17	57	20	381	22	45	684
2013	17	10	21–23	70	23	20	114

concentration, strength of wind or wind direction, and other environmental factors (Kapsch et al. 2010, Huntington et al. 2013, Robards et al. 2013). Rather, social factors often override effects of environmental conditions; for example, sky-rocketing gasoline prices (Alaska Fuel Price Report 2012) transform into fewer trips, fewer boats hunting, and shorter distances over which hunters can hunt. What hunters now report is a shift to thinner, weaker, unstable ice conditions with an increased unpredictability of familiar patterns of spring break-up. Despite this, there is a strong priority given to attaining an ample food supply, which tends to cancel out other conditions.

Unusual mismatches can conflict with generation-based experience, e.g., substantial shifts in ice and weather conditions, timing of appearance of valued species, etc. Hunters now refer to an earlier and shorter break-up and more rapid northern retreat of seasonal pack ice, such that spring walrus migration can take place 3–4 weeks earlier than previously (Krupnik 2000, Metcalf and Krupnik 2003, Krupnik and Weyapuk 2010, Wisniewski 2010, Robards et al. 2013). Also, the strength and timing of any trend related to weather or sea ice differs substantially from place to place. In 2007 and 2011, spring walrus hunting in Gambell started in late April because of earlier break-up, whereas in 2009, 2010, and 2012 the ice remained well into the month of June, as was normal in previous decades; the only noticeable change in spring ice conditions there is the increasingly common absence of the late-season ice coming from the Gulf of Anadyr. In contrast, at Savoonga, Diomede, Uelen, and Wales, the peak of spring walrus catch and disintegration of the shore-fast ice now takes place almost 15 d earlier than previously (Krupnik and Weyapuk 2010, Golbtseva 2013, Robards et al. 2013).

A mismatch of a different sort occurred during the late April to early June 2013 hunting season, between hunters' expectations and public perceptions. Media reports and a declaration by the Governor of Alaska in 2013 spoke of a "historically low walrus harvest" and an impending "food crisis" on an unprecedented scale due to an exceptionally poor hunting season (Table 2; USFWS 2007, Caldwell 2013*a,b*, Carlton 2013, Torquiano 2013). Yupik hunters were keen to report that conditions in spring 2013 were neither "unprecedented" nor "catastrophic", as news reports had indicated. Inclement weather for most of April and light winds from the southwest during the first 2 weeks of May pushed the ice on shore and prevented hunting (Fig. 3c; 28 April and 16 May 2013). "By the time the floes finally gave way to scattered ice, much of the game had gone past already…." (Paul Apangalook to Igor Krupnik, 30 October 2013). Gambell hunters had missed their best hunting window. This experience presents an example of the need to incorporate hunters' knowledge into research and monitoring.

Responses of Walruses to Sea-ice Change

Here, we have observed that sea ice has undergone a transition from a "plastic continuum" governed primarily by fracture mechanics (McNutt and Overland 2003) to a less structured, fragmented sea ice, to a pattern of relatively independent, free-moving floes that we call a "mixing bowl." Observations from satellite imagery, floe tracking, and indigenous sources point in the same direction: that seascape changes have affected walrus winter–spring habitat concurrently with times of reproduction and migration. This situation suggests that walruses are vulnerable to phenological and structural habitat effects occurring as a result of climate change. We propose that top-down, physical forcing at the regional scale imposes structural changes at the seascape-habitat scale, which affects Pacific walruses, whose life history encompasses cross-scale integration of the physical environment and physiological and behavioral needs, such as social networking, food finding, reproduction, migration, and energetics. The overall effect is, predictably, higher dispersal mortality, which also reduces the availability of resources for native subsistence hunters.

With respect to habitat, development of our hypothesis that walruses prefer "broken pack" in winter–spring began with Burns et al. (1981), who first noted that annually recurring features of the Bering Sea ice sheet "exhibit a high degree of organization," that "wind and ocean current regimes produce different habitats, which are spatially and temporally repetitive and predictable," and that ice-inhabiting mammals "tend to partition their environment." Fay's (1982) records of past walrus distributions (Fig. 5, March) reinforced the conclusion that walruses prefer broken pack. Subsequently, Braham et al. (1984) recorded habitat partitioning for five species of ice-dependent pinnipeds (Fig. 6), showing that walruses occurred in the same general areas as Fay's (1982) historical records. This information prompted Ray and Hufford (1989) to perform a statistical analysis of 10 yr of March AVHRR satellite imagery, concluding that most walruses occurred in the same general area as "broken pack" (Fig. 1, Table 1) during their winter–spring reproductive period. Recently, in situ observations from icebreakers of floe size, shape, and thickness during northward migration into the Chukchi Sea (G. C. Ray, *personal observation*) indicated that floes were derived from broken pack seascape.Fig. 6. Spatial distributions of all five species of pagophilic pinnipeds illustrate habitat partitioning in early- to mid-April 1976. These species occupy different areas of pack ice; walrus distributions are roughly equivalent to those in Fig. 3. From Braham et al. (1984).

Walrus observations from the icebreaker *Healy* during late winter to early spring of 2006 through 2009 (Fig. 7) generally agree with this historical pattern, although the timing of ice break-up and melting is different than recorded by Fay (1982). In March–April,

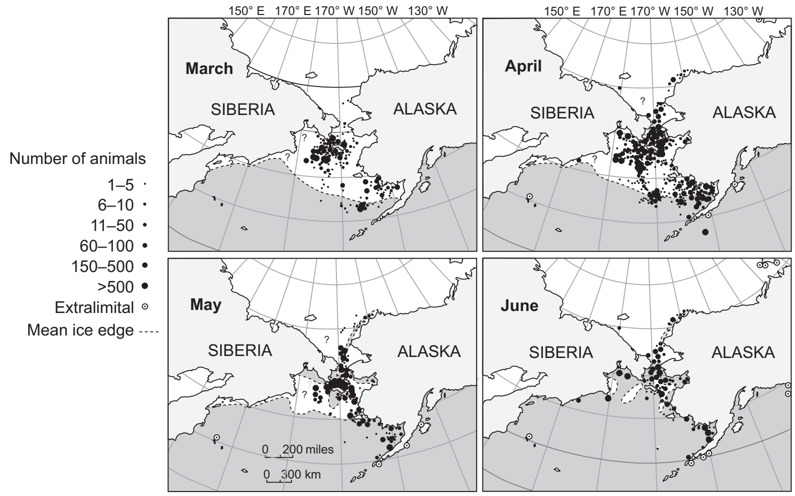

Fig. 5. March–June walrus distributions based on 50 yr of published and unpublished data (1930–1978), with indications of sea-ice extent. Clearly, walruses remained in the northern Bering Sea later than presently (see Fig. 7). In March-April, two subpopulations are evident. The majority of walruses occur north- and southwest of St. Lawrence Island. A smaller subpopulation is southeast near Bristol Bay. In April, migration into the Chukchi Sea has begun, but the majority of the population remains in the Chirikov Basin north of St. Lawrence Island. May is the height of the migration period. A substantial number of walruses remain in the Chirikov Basin. In June, most walruses have migrated into the Chukchi Sea, but many remain in the Chirikov Basin, including males that occupy land haul-outs in both the Bering and Chukchi seas. From Fay (1982).

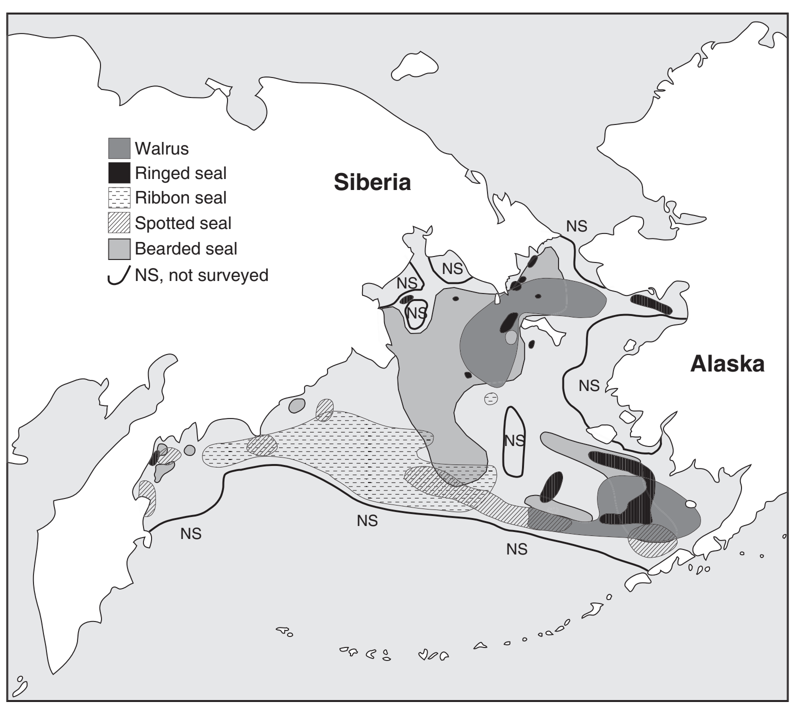

Fig. 6. Spatial distributions of all five species of pagophilic pinnipeds illustrate habitat partitioning in early- to mid-April 1976. These species occupy different areas of pack ice; walrus distributions are roughly equivalent to those in Fig. 3. From Braham et al. (1984).

most walruses occurred in the area of broken pack, and in May most occurred southwest to northwest of St. Lawrence Island. A smaller number of walruses also occurred southeast near Bristol Bay. Distributions in the northwest-central and southeast Bering Sea suggest a metapopulation structure consistent with Jay et al. (2008) and with subsistence hunters' records of "two waves" of walruses passing SLI during migration.

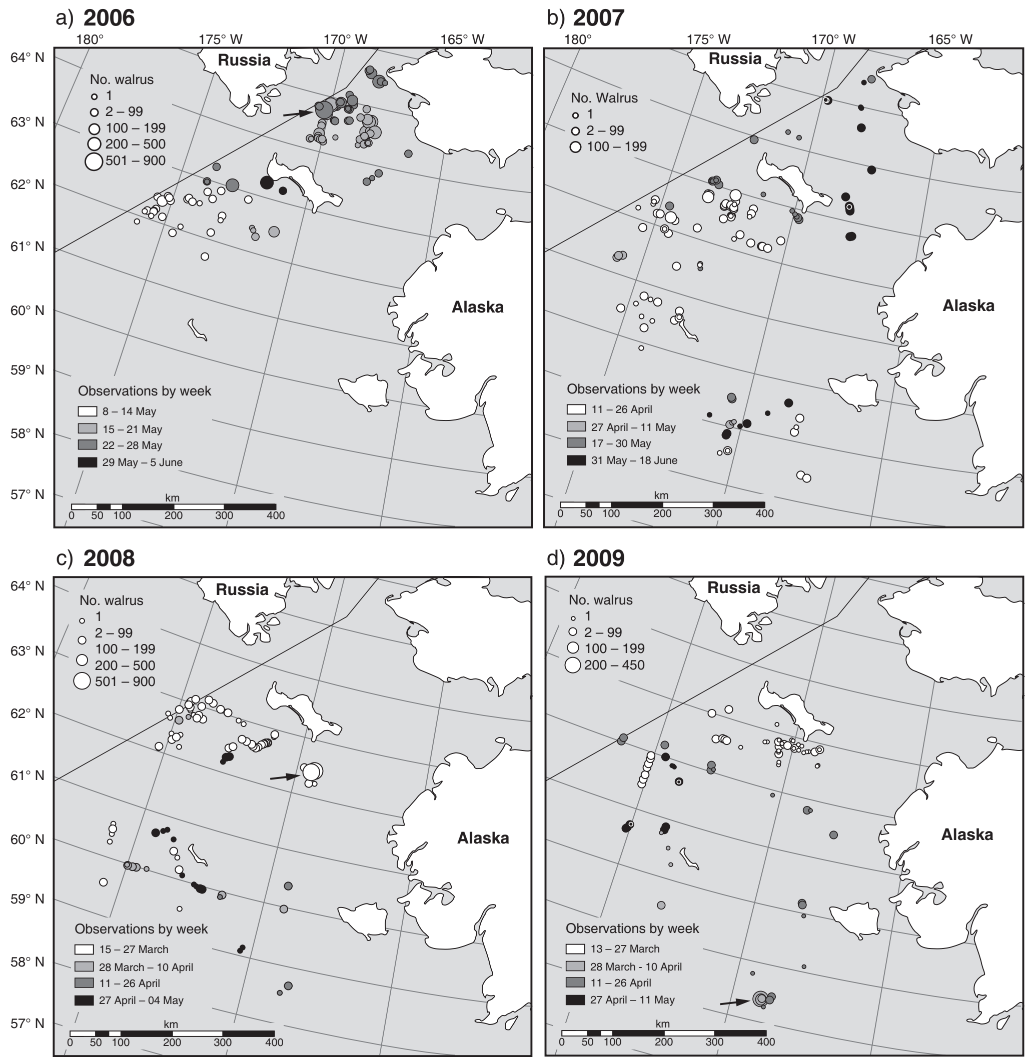

FIG. 7. Observations from the icebreaker *Healy*, 2006–2009, supplemented by helicopter observations and sightings from the U.S. Fish and Wildlife Service, the U.S. Geological Survey, and the NOAA National Marine Mammal Laboratory. The area sampled included 1141200 km^2 from the shelf break north to Bering Strait and between the Alaskan coast and the International Date Line at 166° W; the area west of the Date Line could not be surveyed. Areas sampled represent 2.0–3.8% of the total observation area, within the 1.3–7.3% range of previous aerial walrus assessments to 1995 (Gilbert 1999). Observations were made from the ship's bridge 20 m above the water's surface; helicopter sightings were from 150–200 m altitude. Small groups of walruses could be detected on clear days to at least 4 km distance. Locations of groups were determined from the ship's GPS records and from tracking the helicopter from the ship. Most observations are of groups of <50 individuals. Herds of >500 were rare, contrary to Fay's (1982) historical record (Fig. 5) and our personal experience (see Fig. 8). (a) Observations 8 May–5 June 2006 during migration of ~5310 walruses, the majority in a single herd of >4500 animals (arrow). Observations by week trace northward migration and clustering of groups in the Chirikov Basin. By late May–early June, only one large group (large black dot) remained near the southwest cape of SLI. (b) Observations 11 April–18 June 2007, early spring to migration, of ~1550 walruses. Small groups were widely scattered in April. Groups to the southeast are from the Bristol Bay subpopulation. No herds were observed. Very few animals, likely males, lingered in the Chirikov Basin and Bristol Bay area until mid-June. (c) Observations 15 March–4 May 2008, late-winter breakup to early migration, with 805 walruses clustered south to southwest of St. Lawrence Island and east–west of St. Matthew representing two subpopulations. One herd of ~1000 animals (arrow) observed March 22 made up >50% of observations. (d) Observations 13 March–11 May 2009, late-winter breakup to early migration, with ~5370 walruses. Groups were widely scattered in moderate-sized groups mostly of <50 individuals; some groups southeast of SLI may indicate a dissociated herd. Also, a possible herd had emerged from the Bristol Bay area (arrow).

Most groups were small, consisting of 1–100 individuals, and scattered; an exception was clusters of groups in the Chirikov Basin (Fig. 7; 2006, arrow), not surprising as the northward-moving ice converges as it approaches Bering Straight. Two smaller groupings occurred in 2008 and 2009 (Fig. 7; arrows). The dominance of scattered groups and the rarity of groups of >200 animals contrasts sharply with formerly frequent observations of very large herds (numbers of groups in close proximity) numbering in the thousands, consistent with walruses' strong gregarious behavior (Fig. 8; Wartzok and Ray 1980, Ray et al. 2006; G. C. Ray, *personal observation*).Fig. 7. Observations from the icebreaker *Healy*, 2006–2009, supplemented by helicopter observations and sightings from the U.S. Fish and Wildlife Service, the U.S. Geological Survey, and the NOAA National Marine Mammal Laboratory. The area sampled included 1141200 km^2 from the shelf break north to Bering Strait and between the Alaskan coast and the International Date Line at 166° W; the area west of the Date Line could not be surveyed. Areas sampled represent 2.0–3.8% of the total observation area, within the 1.3–7.3% range of previous aerial walrus assessments to 1995 (Gilbert 1999). Observations were made from the ship's bridge 20 m above the water's surface; helicopter sightings were from 150–200 m altitude. Small groups of walruses could be detected on clear days to at least 4 km distance. Locations of groups were determined from the ship's GPS records and from tracking the helicopter from the ship. Most observations are of groups of <50 individuals. Herds of >500 were rare, contrary to Fay's (1982) historical record (Fig. 5) and our personal experience (see Fig. 8). (a) Observations 8 May–5 June 2006 during migration of ~5310 walruses, the majority in a single herd of >4500 animals (arrow). Observations by week trace northward migration and clustering of groups in the Chirikov Basin. By late May–early June, only one large group (large black dot) remained near the southwest cape of SLI. (b) Observations 11 April–18 June 2007, early spring to migration, of ~1550 walruses. Small groups were widely scattered in April. Groups to the southeast are from the Bristol Bay subpopulation. No herds were observed. Very few animals, likely males, lingered in the Chirikov Basin and Bristol Bay area until mid-June. (c) Observations 15 March–4 May 2008, late-winter breakup to early migration, with 805 walruses clustered south to southwest of St. Lawrence Island and east–west of St. Matthew representing two subpopulations. One herd of ~1000 animals (arrow) observed March 22 made up >50% of observations. (d) Observations

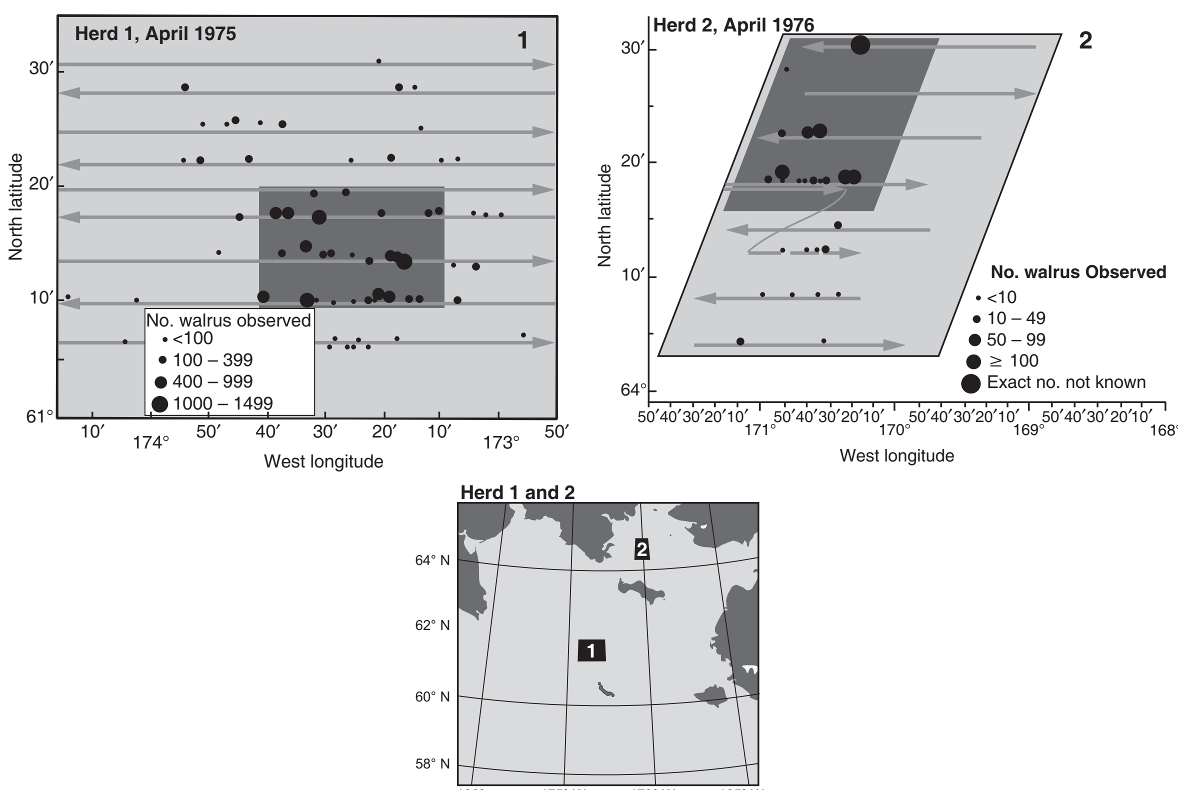

Fig. 8. In past years, very large herds of walruses appeared to be common (Fay 1982; *personal observations*). NASA CV-990 flights documented the spatial distributions of groups of walruses within herds. Arrows represent flight paths. (a) Herd 1: on 8 April 1975, a minimum of 9500 individuals hauled out following 3 d of warming weather. Typical of a "herd," the largest groups clustered at the center of concentrations (dark blue), with smallest groups (lighter blue) at the margins. The sea ice moved as a semi-continuous continuum at for 3 d at <11 km/d. (b) Herd 2: on 11 April 1976, ~1000 individuals occurred within a similar-sized area of broken pack as the previous year. (c) Locations of herds 1 and 2. From Wartzok and Ray (1980).

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Large herds demand large areas of semi-continuous habitat. A simple floe-stability calculation using the relative specific weights of sea ice (0.9) and sea water (1.025; Pounder 2013), sheds light on conditions required to support walrus herds. A one-ton walrus (a combined average body mass of one large female, one average male, and a large juvenile) requires ~12 m^2 of sea ice, two-thirds of a meter thick or heavily ridged, for support. How much ice-covered area is necessary for 1000 walruses is difficult to predict; nevertheless, this calculation is consistent with observations of 30–100 walruses assembled on floes 20–40 m in diameter, which where the ice may be distributed in variable concentrations. Fay (1982) observed that walruses tolerate ice concentrations of 20–80%, but if floes become too widely dispersed or represent mixed types, herd formation becomes unlikely. Therefore, the dispersion of floes into a mixing bowl of sea-ice types, as we suggest, may lead to unfavorable conditions for such gregarious species as walruses.

Potential effects on the walrus population related to fragmentation of habitat and consequent changes in social structure are predictable. Social networking is a central issue in ecology and evolution and has far-reaching implications for gene flow, frequency-dependent selection, information transfer, disease transmission, and the way animals exploit their environment (Foster et al. 2012). For example, walruses are highly vocal and their sounds have the potential for communication underwater over tens of kilometers, depending on depth (S. Ridgway, *personal communication*); for walruses, the "soundscape" concept (Garland et al. 2011, Servick 2014) has important implications. For example, adult, dominant male walruses engage in ritualized "song" displays to establish acoustic territories (Ray and Watkins 1975, Fay et al. 1984). Given sound transmission over 10-km distances, the arena within which male walrus acoustic territories could be established may encompass more than 300 km^2, approximating the dimensions of large herds (Fig. 8). Diminishment of sea ice and dispersal of floe structure would likely impede the formation of large reproductive arenas that could accommodate many territorial males. Smaller group sizes with fewer males could reduce male competition and promote "peripheral" (nonterritorial) males, as shown for other pinnipeds (e.g., Campagna et al. 1988, Gentry 1998). Thus, reduced group size resulting from unsuitable habitat could have significant implications for sexual selection and population fitness.

With respect to food-finding, social networking would allow walruses to explore very large areas of the benthos, where they feed on highly patchy prey, especially clams (Fay 1982, Sheffield et al. 2001, Born et al. 2003, McCormick-Ray et al. 2011). Social networking by sound communication is likely to assist food-finding (e.g., Evans and Evans 1999, Slocombe and Zuberbühler 2005, Clay et al. 2012). It follows that the greater the number of individuals that are seeking food over wide areas, the better the chance of communication of that information to others. Food-finding among walruses may also be facilitated by passive transport on moving sea ice, from which walruses disperse periodically to feed, then return to nearby floes of the same general area to rest (Wartzok and Ray 1980, Ray et al. 2006). This behavior suggests that walruses are "central-place foragers," common among pinnipeds that breed on land and feed at sea (e.g., Loughlin 2014). Negative effects of central-place foraging include over-exploitation of local food supply, which seems to be the case for Pacific walruses in summer (Jay et al. 2011, MacCracken 2012). However, passive transport avoids this effect because the "central place" of sea ice is in constant motion, allowing new food patches to be continuously exploited. As Fay (982) has noted: "By staying with the ice, they are able to exploit the benthic resources of almost the entire shelf…"

Other interpretations of feeding behavior are possible. Jay et al. (2010) found no correlation between dispersal "vectors" of tagged walrus and sea ice on which they hauled out. Walruses are well known to disperse from floes in small groups to feed, but whether the tagged walruses reaggregated following feeding was not investigated. Further, Jay et al. (2014) also propose that walruses seek "priority hot spots" with high "benthic production" to feed, notably the SLI polynya. However, walrus distributions, past (Fig. 5) and present (Fig. 7), do not support this preference. Nor do tracking data from Jay et al. (2014), who recorded only one in three occasions with walruses in the polynya area. To determine priority areas for feeding, examination of the entire range of walruses during all seasons is required, which has yet to be done. Furthermore, benthic production as measured by calories per gram (Jay et al. 2014) or grams of carbon per square meter (Grebmeier et al. 2006) obscures walrus food preferences. Walruses favor large clams, *Mya* spp. and others (Fay 1982, Sheffield et al. 2001), that are often deeply buried, patchily and subregionally distributed (cf. McCormick-Ray et al. 2011), and difficult to sample, but whether preferred walrus food and benthic production are correlated has yet to be determined. Nevertheless, both passive transport and cultural memory of "priority" feeding areas may both occur, and if so, would play reinforcing roles.

Finally, the effects of sea-ice change on walruses may be especially significant during spring migration, when birthing and nursing also occur. Females with newborns are reluctant to enter the water for some time (possibly during most of the 2-month migration period) when they nurse intensively, provide body warmth to vulnerable calves, and closely guard them. As noted previously, the floes on which walrus migrate are usually derived from the same broken pack on which birthing occurred. However, should the ice break up and melt out earlier, as is now usual, walrus groups would be forced to enter the water. And/or if the ice is moved south and large polynyas develop under the influence of northerly winds, (e.g., Fig. 2; May 2009–2011), a significant increase in migration distance and duration is imposed. That is, the availability of appropriate floes and the distances that walrus must travel during migration are critical, lest calves, especially, be forced to endure an energetically costly swim.

Reproductive fitness, food-finding, and the efficacy of migration are arguably the essence of Pacific walrus natural history, all of which bear the burdens of winter–spring sea-ice change. In all respects, we stress the particular importance of energetics. Fay and Ray (1968) reviewed walrus thermoregulatory behavior, and Ray and Fay (1968) examined physiological thermoregulation of calves, together stressing the need of walruses to haul out frequently on ice to rest. Recently, bioenergetics models have provided important physiological requirements of female walruses in particular, suggesting that changes in body condition could affect the population overall (Noren et al. 2012, 2014, Noren et al. 2015). We conclude that sea-ice habitat change as it affects walrus behavior is resulting in higher energetic costs during every season of the year, both in the Bering Sea during winter–spring, as indicated here, and in the Chukchi Sea in summer–fall (Jay et al. 2011, MacCracken 2012).

Future Directions

This paper provides evidence that the seascape concept is specific to the dynamics of sea-ice habitat structure and morphology, and provides a realistic way

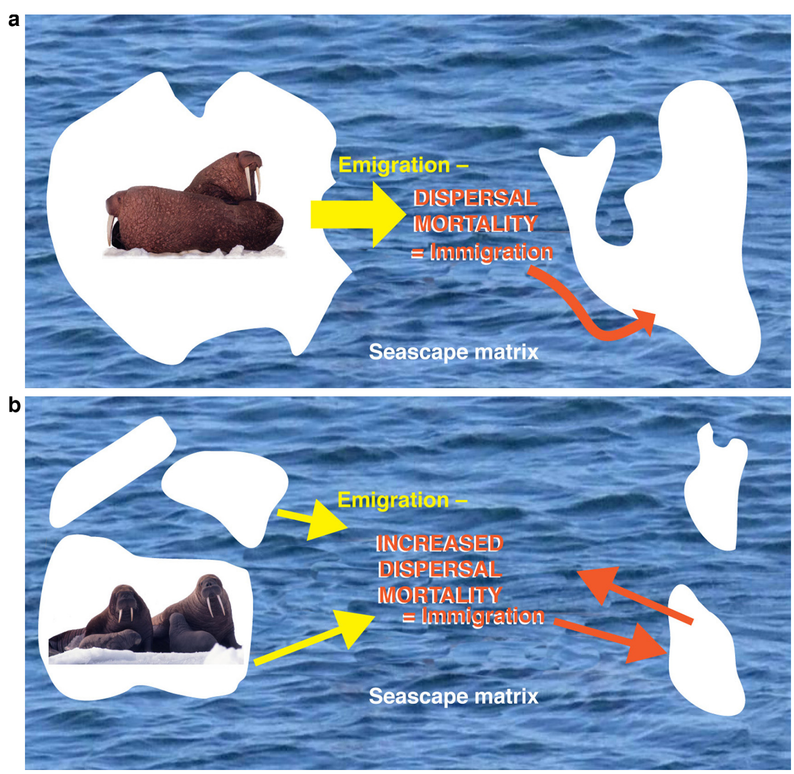

Fig. 9. Structural change resulting from sea-ice diminishment is hypothesized to increase walrus mortality. (a) Under a relatively high proportion of available sea-ice habitat to water, relatively low energetic cost and mortality are expected. (b) Under a relatively low proportion of available sea-ice habitat, dispersing walruses experience higher energetic cost while seeking appropriate sea-ice haul-outs, thereby experiencing increased mortality. Based on a concept from Fahrig (2007).

for evaluating the potential effects of climate change on Pacific walruses in the Bering Sea during winter–spring. Our data indicate that sea ice is undergoing a transition from a "plastic continuum" governed primarily by fracture mechanics (McNutt and Overland 2003) to a "mixing bowl" of less structured, fragmented, relatively independent, free-moving floes. This transition is producing structural changes at the seascape-habitat scale that has considerable potential to affect Pacific walruses in significant ways: i.e., social networking, food-finding, reproduction, migration, and energetics, with implications for their natural history.

Changes in seascape morphology are likely to become more evident in the future as climate change and sea-ice diminishment continue. Under these conditions, stresses on the Pacific walrus population during the winter–spring reproductive and migration period may affect the walrus population to at least the degree of sea-ice loss in summer. Taken together, landscape population models suggest that walruses are facing unfavorable habitats, higher energetic costs, and increasing dispersal mortality (Fahrig 2007, Fig. 9). Although inconclusive, the 2006 walrus assessment shows that population decline may already be underway (Speckman et al. 2010). The sustainability of Native subsistence hunting is no less at risk, as presently ~30 Beringian communities engage in walrus hunting.

The looming issue for the Bering Sea ecosystem, walruses, and its Native people concerns emergent conditions and lag effects caused by climate change, and how these impinge on Pacific walrus natural history. However, much research remains to unravel the complex relationships between walruses and their changing habitat, especially as to behavioral and energetic effects. Comprehensive, interdisciplinary research and monitoring programs are required, incorporating scientists, management agencies, and the knowledge of indigenous subsistence users. Especially, we emphasize the need to interpret seascape change through many lenses, and to consider data and indicators beyond usual disciplinary toolkits. Regional sea-ice attributes set the stage for assessing climate-change effects, and new tools and local observations are essential for revealing aspects of natural history. In this context, evaluation of the effects of environmental change on the Pacific walrus population, as well as all other pagophilic pinnipeds, requires integration of scales, whereby population dynamics is based on natural-history knowledge for anticipating effective conservation and management (cf. Scheffer et al. 2012).

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