

Divergent movements of walrus and sea ice in the northern Bering Sea

Chadwick V. Jay^{1,*}, Mark S. Udevitz¹, Ron Kwok², Anthony S. Fischbach¹,
David C. Douglas³

¹US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA

²Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive, Pasadena, California 91109, USA

³US Geological Survey, Alaska Science Center, 3100 National Park Road, Juneau, Alaska 99801, USA

ABSTRACT: The Pacific walrus *Odobenus rosmarus divergens* is a large Arctic pinniped of the Chukchi and Bering Seas. Reductions of sea ice projected to occur in the Arctic by mid-century raise concerns for conservation of the Pacific walrus. To understand the significance of sea ice loss to the viability of walruses, it would be useful to better understand the spatial associations between the movements of sea ice and walruses. We investigated whether local-scale (~1 to 100 km) walrus movements correspond to movements of sea ice in the Bering Sea in early spring, using locations from radio-tracked walruses and measures of ice floe movements from processed synthetic aperture radar satellite imagery. We used generalized linear mixed-effects models to analyze the angle between walrus and ice floe movement vectors and the distance between the final geographic position of walruses and their associated ice floes (displacement), as functions of observation duration, proportion of time the walrus was in water, and geographic region. Analyses were based on 121 walrus–ice vector pairs and observations lasting 12 to 36 h. Angles and displacements increased with observation duration, proportion of time the walrus spent in the water, and varied among regions (regional mean angles ranged from 40° to 81° and mean displacements ranged from 15 to 35 km). Our results indicated a lack of correspondence between walruses and their initially associated ice floes, suggesting that local areas of walrus activities were independent of the movement of ice floes.

KEY WORDS: Pacific walrus · *Odobenus rosmarus* · Bering Sea · Sea ice · Telemetry · RADARSAT · RGPS · SAR

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INTRODUCTION

The Pacific walrus (*Odobenus rosmarus divergens*) is a large Arctic pinniped that forages on the seafloor of the continental shelves of the Chukchi and Bering Seas. The species is a vital subsistence resource to coastal communities in Alaska and Russia (Metcalf & Robards 2008) and can substantially affect the structure of benthic communities (Oliver et al. 1983, Oliver et al. 1985, Nelson & Johnson 1987, Nelson et al. 1987, Nelson et al. 1994, Born et al. 2003, Ray et al. 2006).

Sea ice is used by walruses as a platform for giving birth, nursing young, molting, resting between feeding forays, accessing offshore foraging areas, and avoiding

nearshore predation and disturbance (Fay 1982). The large losses of sea ice that are projected to occur in the Arctic by mid-century (Maslanik et al. 2007, Overland & Wang 2007, Stroeve et al. 2007, Wang & Overland 2009) raise concerns for the conservation of the Pacific walrus and is the basis of a recent non-governmental petition to the US Fish and Wildlife Service to list the Pacific walrus population as threatened or endangered under the US Endangered Species Act. To understand the significance of sea ice loss to the viability of walruses, it would be useful to better understand the spatial associations between the movements of sea ice and walruses. Broad-scale seasonal associations are known (Fay 1982), but local within-season associations are poorly understood.

*Email: cjay@usgs.gov

Seasonal movements of sea ice over the Chukchi and Bering Seas allow walrus to occupy a wide area over the continental shelf during the year. Walrus typically occur in areas of unconsolidated ice, open leads, and thin ice where they can create breathing holes (Burns et al. 1980, 1981, Fay 1982). In winter, the entire Pacific walrus population resides in the Bering Sea, and it is here on the sea ice that breeding courtships (January to February) and most of the calving (April to June) occur. Most adult female and young walrus prefer to use sea ice for hauling out throughout the year. In spring, they follow the receding ice pack northward to summer in the Chukchi Sea. Unlike females, most adult male walrus summer near coastal areas of the Bering Sea, using land haul-outs to rest between foraging trips. In autumn, the female and young walrus in the Chukchi Sea migrate with the developing sea ice southward into the Bering Sea, where they are joined in late autumn and winter by the males that summered there (Fay 1982, Jay & Hills 2005).

The Bering Sea has relatively steady-state sea ice conditions in winter until the disintegration and northward retreat of sea ice in spring (Burns et al. 1981). Regions of relatively homogeneous ice habitats are formed each year in the Bering Sea from regionally specific winds, currents, and land configurations (Muench & Ahlnas 1976, Burns et al. 1980, 1981). St. Lawrence Island is a major land form affecting movements of ice in the northern Bering Sea. Most of the ice in this region forms in the northern Bering Sea, but some originates from the Chukchi Sea. The ice is driven southward by northerly winds from November to December until mid- to late April (Burns et al. 1981). In winter, winds from the north and northeast prevail about 60% of the time, typically with speeds near 10 m s⁻¹. The northerlies compress ice floes against the north side of St. Lawrence Island, and create a polynya on the island's south side. The polynya can extend along nearly the entire 150 km length of the island and as much as 25 km offshore (Danielson et al. 2006), and is associated with high benthic production (Grebmeier & Cooper 1995). As the ice is pushed southward, it is deflected around the narrower passages of the east and west sides of the island where the ice is compressed and deformed. The ice diverges as it moves farther south and into the wider parts of the Bering Sea. There are periods of northward ice drift during winter and early spring, but they are of short duration. Late spring is characterized by melting ice and the northward retreat of sea ice with rising air temperatures (Burns et al. 1981).

Burns et al. (1980) delineated 4 regions of marine mammal ice habitats around St. Lawrence Island based on major features of March–April ice cover. These are (1) a region north of the island characterized by a com-

pact mass of heavy, pressure-ridged ice extending northward for >100 km; (2) a region south of the island characterized by broken to rounded pack ice, usually with a well developed polynya; (3) a region east of the island characterized by continuous ice, most often consisting of pack ice and broken pack ice with leads and angular floes, and with heavy ice occupying >85% of the surface; and (4) a region west of the island characterized by broken, rounded, or loose ice, often associated with open water or thin ice, and often lacking heavy ice. Ice to the south, east, and west of the island is usually active and forming new leads.

Although walrus movements are determined by the movement of sea ice when they are hauled out on the ice, their movements in water may be affected by water currents, which are also regionally variable. The general flow of water through the Bering Sea is northward from the North Pacific towards the Arctic Ocean. The flow is intensified in the areas northwest, north, and east of St. Lawrence Island, with average speeds of ~20 cm s⁻¹ along Anadyr Strait to the northwest and 10 to 15 cm s⁻¹ along Shpanberg Strait to the east (Danielson et al. 2006). To the south of the island, 3 bands of currents have been described. One is a nearshore band extending out to ~60 to 70 km, flowing eastward or southeastward at ~5 cm s⁻¹; the second is a transitional band extending out about another 100 km from the nearshore band, with a northward, but weak flow of <2 cm s⁻¹; and the third is an outer band over the central shelf out to at least mid-way between St. Lawrence and St. Matthews Islands with a westward or north-westward flow of 5 to 10 cm s⁻¹ (Danielson et al. 2006).

Walrus movements throughout the year are likely to be associated with particular activities, including breeding, socialization, predator avoidance, migration, foraging, and traveling between foraging areas. We investigated whether local-scale (~1 to 100 km) walrus movements correspond to movements of sea ice in the Bering Sea in early spring, using location data from radio-tracked walrus and measures of ice floe movements from processed synthetic aperture radar satellite imagery. A lack of correspondence would suggest that areas of walrus activity are not dependent on the movement of ice at this scale. Further, we test whether local correspondence of walrus–ice movements varied among regions that have been recognized by others as having unique ice types and movement patterns (Burns et al. 1980, 1981).

MATERIALS AND METHODS

Walrus tracking. Forty adult walrus were tracked with satellite-linked radio-tags (hereafter referred to as 'tags') (Telonics) in the northern Bering Sea as part

of an abundance survey conducted in spring 2006. The tags were similar to the post-type tags described in Jay et al. (2006) and were deployed with a crossbow from a distance of ~10 m. Each tag was fitted with a barbed head that embedded in the walrus's blubber layer on impact. We attempted to place each tag on the individual's dorsum, midway between the shoulders.

We deployed tags opportunistically as walrus groups were encountered, while attempting to distribute tags as widely as possible among walruses within the tagging region south of St. Lawrence Island. Our deployment technique involved the targetting of individuals that were lying with their back to the approaching tagging team, and that could be approached from downwind and without obstruction from neighboring walruses. The barbed heads were too large for the thin skin and blubber layers of young animals (Jay et al. 2006), so we deployed tags on adult walruses, except parturient females. Selections were also tempered by daily weather and ice conditions and overall availability of walruses. In most cases, the sex of tagged walruses was classified either from sexually dimorphic features (Fay 1982, Fay & Kelly 1989), or genetic determination of sex from remotely collected biopsies (Fischbach et al. 2008). If neither of these methods successfully determined sex, the animal was classified as undetermined sex.

Haul-out chronologies from tagged walruses were derived from data collected by a conductivity sensor on the walrus's tag. The conductivity sensor detected whether the tag was in or out of salt water. Conductivity was measured every second and the results were summarized over 30 min intervals. If $\geq 90\%$ of the measurements for a given interval indicated the tag was out of water, the walrus was classified as being hauled out during that interval.

Tags had battery capacities that allowed transmissions for at least 3 to 4 weeks. Transmissions were suspended whenever the tag was submerged to conserve battery life. Information from 232 consecutive 30 min behavioral intervals was encoded in each transmission. Thus, the data from any given behavioral interval were received if there was at least one successful transmission during the 4.8 d (116 h) period while this information was stored onboard the tag. This provided considerable redundancy and allowed for collection of a nearly continuous record of haul-out behavior. We only retained data from transmissions that passed a checksum test designed to identify transmission errors.

Records of haul-out data were received and geographic locations of tagged walruses were estimated by the Argos location and data collection system (Collecte Localisation Satellites 2007). Because these locations are subject to errors, they were filtered, using the Douglas Argos Filter (Douglas 2006), to retain only

those locations with spatial errors expected to average $< \sim 5$ km. This filter assesses the plausibility of locations based on spatial redundancy, Argos location quality, maximum rate of movement, and turning angles of successive movements. We set the algorithm to retain (1) all standard class locations, (2) non-standard class locations within 2 km of the previous or subsequent location, and (3) remaining locations based on a distance-angle-rate filter that accepted a maximum walrus speed of 10 km h^{-1} and rejected locations at the apex of highly acute angles (RATECOEF = 25, Douglas 2006). Other marine animal tracking studies have used the same algorithm, but with different user-defined settings (Andrews et al. 2008, Eckert et al. 2008), or an algorithm with a very similar approach (Freitas et al. 2008). Despite a lack of evidence that tagging alters the animal's behavior, we elected to exclude all data from the first 24 h after deployment of each tag in case there was any short-term effect of the tagging procedure.

Linking walrus and ice movements. Daily synthetic aperture radar (SAR) images of the Bering Sea, coincident with areas and times of the walrus tracking data, were acquired from NASA through the University of Alaska Fairbanks, Alaska Satellite Facility. The SAR imagery was processed with the RADARSAT Geophysical Processor System (RGPS) at the Jet Propulsion Laboratory, California, to produce motion vectors for individual ice floes by tracking common image features (< 150 m location error) (Kwok 1998).

Successive walrus locations were usually acquired within a few hours of one another (85th percentile of time between locations = 3 h), whereas RADARSAT images were acquired at ~ 12 h intervals (± 2 h). We used the following procedure to obtain a set of walrus-ice vector pairs for analysis. We identified each of as many walrus locations as possible associated with an underlying ice floe within ~ 12 h of the walrus location that could be distinguished and tracked through at least one subsequent RADARSAT image. Each match constituted the start of a walrus-ice vector pair. The ice floe was followed through as many subsequent RADARSAT images as possible. The ice floe in the last image defined the location and time for the end of the ice vector, and the walrus's location closest in time to the end of the ice vector defined the location and time for the end of the walrus vector. We selected for our analysis only those vector pairs where the difference in time between the walrus and ice start times, and between the walrus and ice end times, were within 10% of the duration of the ice vector. We refer to the tracked ice floe as the walrus's initially associated ice floe.

Analysis. We used 2 statistics to characterize the relation between the walrus and ice vectors in each

pair: the internal angle formed by the 2 vectors (hereafter referred to as 'angle') and the distance between the end points of the 2 vectors (hereafter referred to as 'displacement'). Also, for each walrus–ice vector pair, we estimated the proportion of time the walrus was in water from its associated haul-out chronology (hereafter referred to as 'walrus time-in-water').

In addition, we investigated the possibility of differences in the correspondence of walrus–ice movements among regions of ice habitat in the northern Bering Sea that were identified by Burns et al. (1980). Most of our walrus–ice vector pairs fell within, or near to, 4 of these regions around St. Lawrence Island, and we assigned each vector pair to one of the 4 regions based on the pair's start location, except for 10 pairs, as described below (Fig. 1). We recognize that ice habitat boundaries probably shifted during our study with wind reversals and as the region transitioned from cold and consistent ice conditions in very early spring to more dynamic melting ice conditions in late spring. Five walrus–ice vector pairs were slightly north of the western region and were assigned to that region (Fig. 1). We assigned 5 vector pairs that were outside the boundaries of the eastern region to that region

because the ice vectors and locations from these pairs appeared to be most closely associated with the region's character of having a high rate of southward ice motion around the eastern side of St. Lawrence Island (Burns et al. 1980).

We used generalized linear mixed-effects models (McCullagh & Nelder 1999, Littell et al. 2006) to model angles and displacements as functions of tracking duration, proportion of walrus time-in-water, and region. We considered Normal, Poisson, and Gamma distributions with canonical links to cover a range of possible variance structures. We used plots of residuals to select the final form of the model (McCullagh & Nelder 1999). We initially included a random effect for walrus to account for the fact that we had multiple observations for many walruses. We removed this effect from the final model if the estimate of the final variance component associated with this effect had a 95% confidence interval that included zero. We used Type III *F*-tests for significance of fixed effects and 95% confidence intervals for their least-squares means to assess effects of tracking duration, proportion of walrus time-in-water, and region. Separate analyses were conducted for angle and displacement. Finally, we used mean directions and mean resultant lengths (Fisher 1993) to characterize direction of movement for walruses and ice floes in each region.

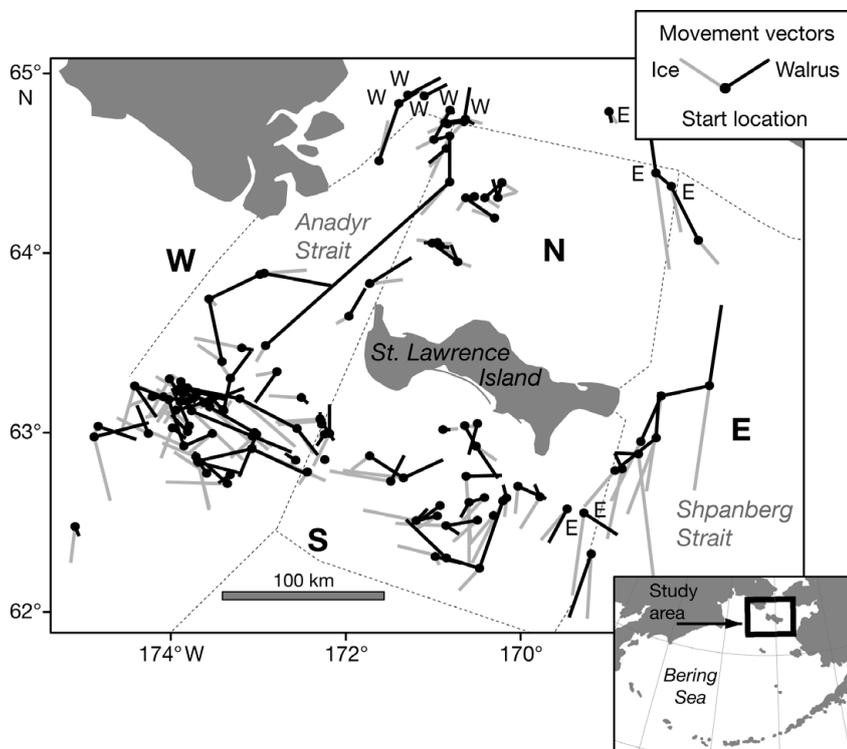


Fig. 1. *Odobenus rosmarus divergens*. Walrus–ice vector pairs derived from walrus and ice movements observed in 4 regions of the northern Bering Sea (N, S, E, W: north, south, east, west regions, respectively; delineated by Burns et al. 1980), 26 March to 10 May 2006. Small 'W's and 'E's indicate vector pairs that were re-assigned to a region (see: 'Materials and methods: Analysis')

RESULTS

Analyses were based on data from 22 walruses (17 female, 4 male, and 1 undetermined) and 121 walrus–ice vector pairs; almost 80% of the vector pairs were from the southern and western regions (Table 1, Fig. 1). Walrus location estimates were mostly of Argos location quality B, and roughly an equal number of location estimates were of quality A, 1, 2, and 3 (number of locations per quality type were: 1/Z, 142/B, 24/A, 6/0, 25/1, 25/2, and 19/3). Most vector pair observations were of 36 h duration (Table 2).

Observations were obtained from 26 March to 10 May 2006 (Fig. 2), which corresponds to a period from very early spring, when most walruses are still within their winter breeding areas, to late spring, when many walruses are migrating with the disintegration of ice. Vast ice fields of variable concentration and thickness were available to wal-

Table 1. *Odobenus rosmarus divergens*. Number of walrus–ice vector pairs derived from walrus and ice movements observed in 4 regions of the northern Bering Sea, 26 March to 10 May 2006

Walrus Tag no.	Region				Total
	North	South	East	West	
7603	0	2	0	0	2
7604	0	4	3	0	7
7606	0	3	0	2	5
7614	4	0	0	2	6
10953	0	0	0	5	5
10955	0	0	0	3	3
10956	0	1	0	0	1
10959	0	1	0	5	6
10961	0	1	0	0	1
10962	1	0	0	18	19
10963	0	0	0	5	5
62646	0	0	0	8	8
62647	0	1	0	1	2
62648	0	0	0	1	1
62651	0	1	1	0	2
62652	0	2	7	0	9
62656	6	0	0	2	8
62658	0	5	2	0	7
62665	0	1	0	8	9
62671	0	1	0	6	7
62672	0	5	0	0	5
62674	0	2	1	0	3
Total	11	30	14	66	121

Table 2. *Odobenus rosmarus divergens*. Duration of walrus–ice vector pair observations in 4 regions of the northern Bering Sea, 26 March to 10 May 2006

Region	Duration (h)		
	12	24	36
North	1	1	9
South	6	3	21
East	0	1	13
West	2	18	46
Total	9	23	89

ruses during this period (National Ice Center, www.natice.noaa.gov). Most walrus–ice vector pairs in the southern region were observed in the first part of the study period, whereas most vector pairs in the eastern region were observed in the latter part of the study period (Fig. 2). Vector pairs in the northern and western regions were observed over a relatively wide time period.

Walrus were in the water >50% of the time for most walrus–ice vector pairs (Fig. 3). Vector pair angles ranged from 1° to 180° (median = 63°, Fig. 3) and vector pair displacements ranged from 1 to 164 km (median = 17 km, Fig. 3).

The directions of ice and walrus movements were highly variable, but showed tendencies within regions (Fig. 4). In the northern region, ice tended to flow in

the eastern, southeastern, and western directions and walrus showed no directional tendencies. In the southern region, ice moved primarily in the southern, southwestern, and western directions and walrus showed no directional tendencies. In the eastern region, ice tended to flow to the south and walrus tended to move to the north. In the western region, ice tended to flow in the southeastern, southwestern, and northwestern directions and walrus moved mostly in the northwestern, eastern, and southeastern directions.

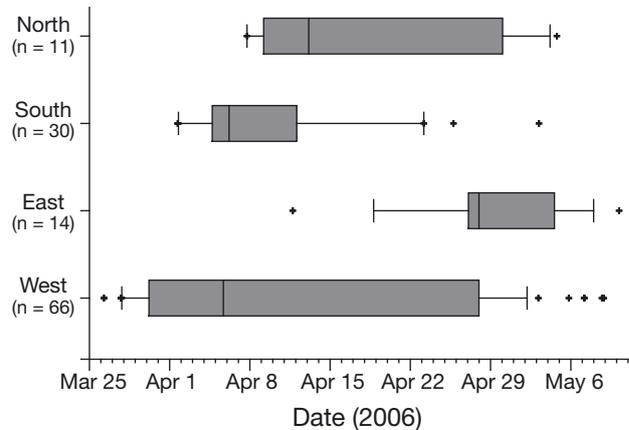


Fig. 2. *Odobenus rosmarus divergens*. Starting date of walrus–ice vector pairs observed in 4 regions of the northern Bering Sea, 26 March to 10 May 2006. Outliers (+) and the 25th, 50th, 75th (box), and 10th and 90th (whiskers) percentiles are indicated. n: number of walrus–ice vector pairs

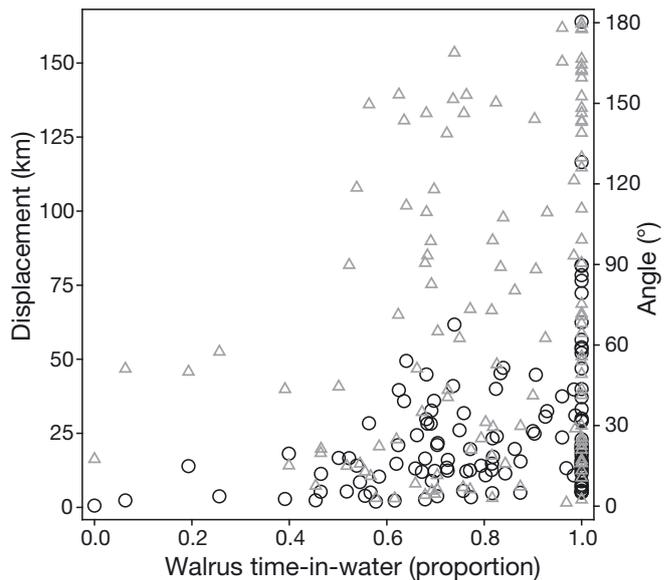


Fig. 3. *Odobenus rosmarus divergens*. Walrus–ice vector pair angle (Δ) and displacement (O) and associated walrus time-in-water observed in the northern Bering Sea, 26 March to 10 May 2006

The rates of ice movements were also highly variable (Fig. 5), but were comparatively slow in the northern region and fast in the eastern region, which is consistent with general descriptions of ice motion within the Bering Sea (Burns et al. 1981). Rates of walrus movements were somewhat slower in the northern region than in the other 3 regions.

Variance of walrus–ice vector pair angles increased approximately in proportion to their mean, as suggested by the plot of angle versus walrus time-in-water (Fig. 3). Examination of residuals indicated that this variance function was adequately fit with an over-dispersed

Poisson distribution. Over-dispersion was modeled by including the random effect of walrus (variance estimate = 0.46, SE = 0.17). A plot of predicted versus observed angle indicated that a large proportion of the total variation in angle between walrus and ice vectors remained unexplained (Fig. 6). Nevertheless, the model indicated that angle increased with duration of the observation ($F_{1,95} = 314.1$, $p < 0.01$; Fig. 7) and with the proportion of time the walrus spent in the water ($F_{1,95} = 240.2$, $p < 0.01$). Least-squares mean estimates of vector pair angles ranged from 40° to 81° among regions (Table 3). Vector pair angles were similar in the northern and west-

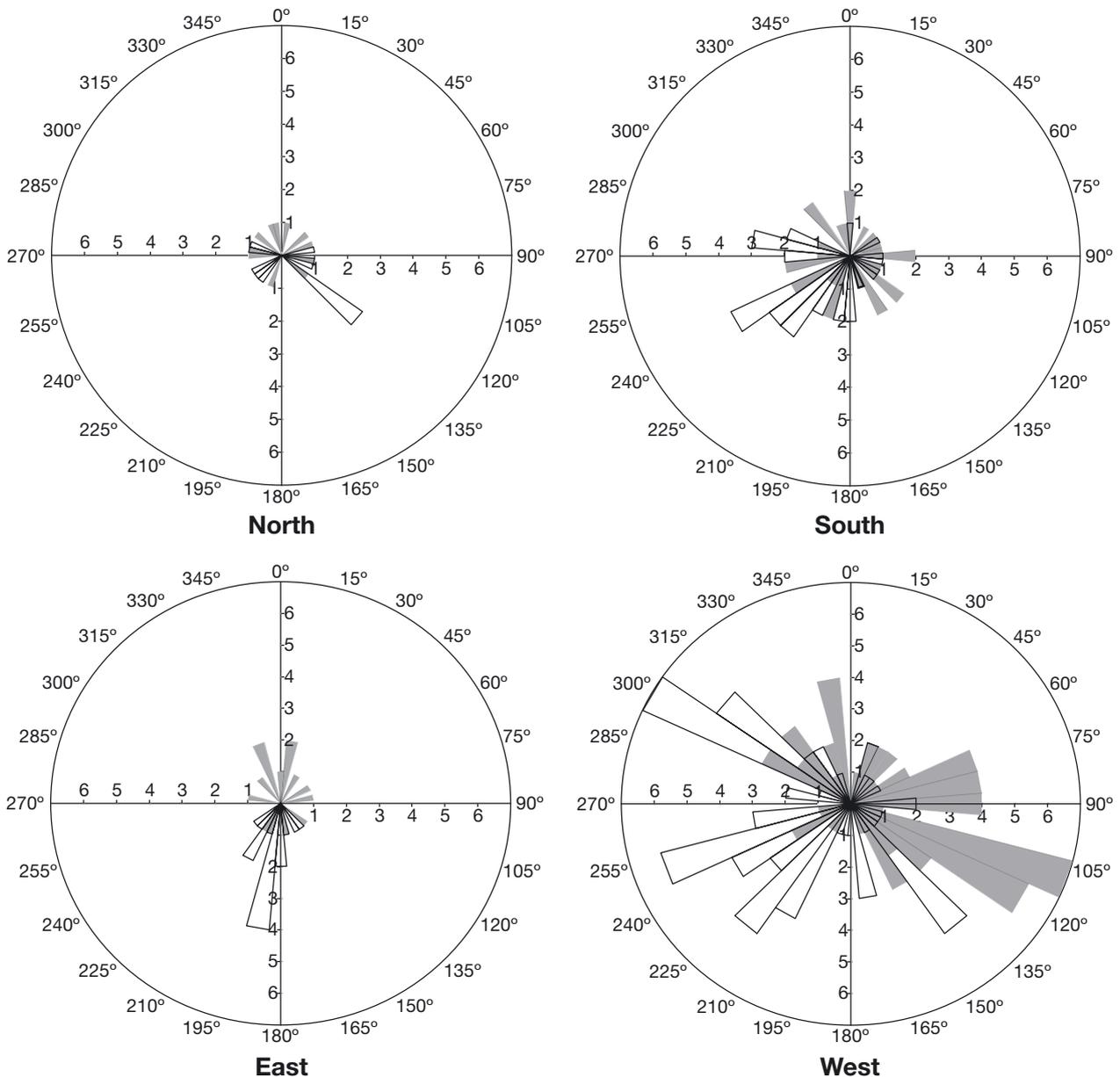


Fig. 4. *Odobenus rosmarus divergens*. Directions of walrus (solid bars) and sea ice (open bars) movements from walrus–ice vector pairs in 4 regions of the northern Bering Sea, 26 March to 10 May 2006. The length of a bar indicates the number of observations within that 10° bin

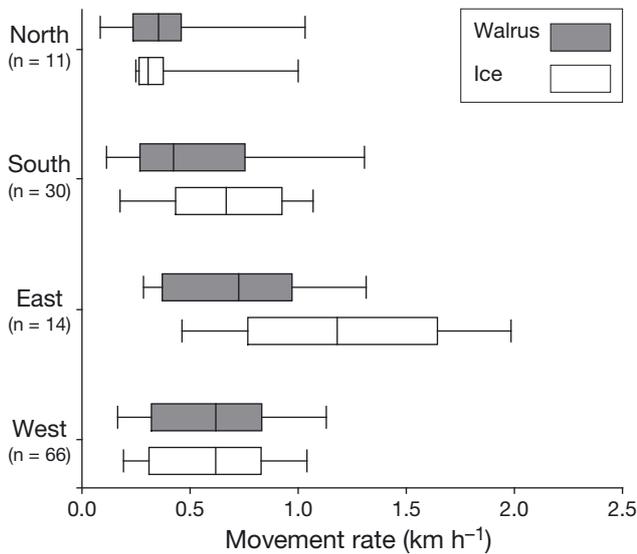


Fig. 5. *Odobenus rosmarus divergens*. Rates of walrus and sea ice movements from walrus–ice vector pairs in 4 regions of the northern Bering Sea, 26 March to 10 May 2006. The 25th, 50th, 75th (box), and 10th and 90th (whiskers) percentiles are indicated. N: number of walrus–ice vector pairs

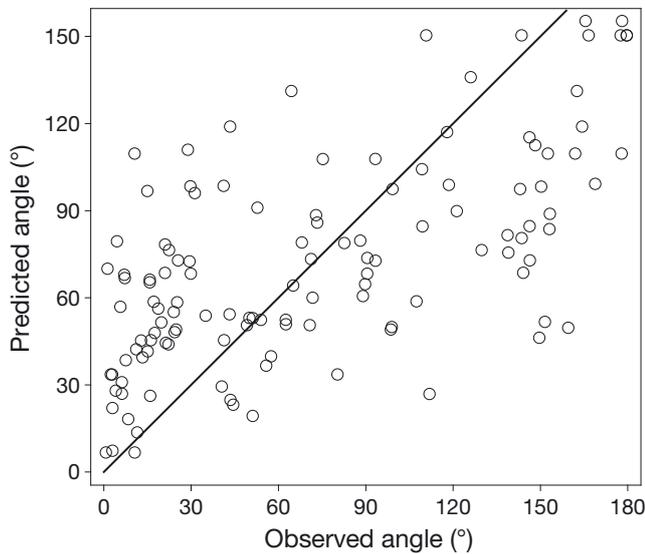


Fig. 6. *Odobenus rosmarus divergens*. Comparison of predicted and observed angles of walrus–ice vector pairs observed in the northern Bering Sea, 26 March to 10 May 2006. Predictions that exactly match observations would lie on the indicated 45° line

ern regions, but tended to be larger in the southern (difference of least-squares means $\geq 32^\circ$, 95% CI = 25–38) and eastern (difference of least-squares means $\geq 39^\circ$, 95% CI = 31–48) regions. Vector pair angles in the eastern region also tended to be larger than angles in the southern region (difference of least-squares means = 8° , 95% CI = 7–9) (Fig. 7, Table 3).

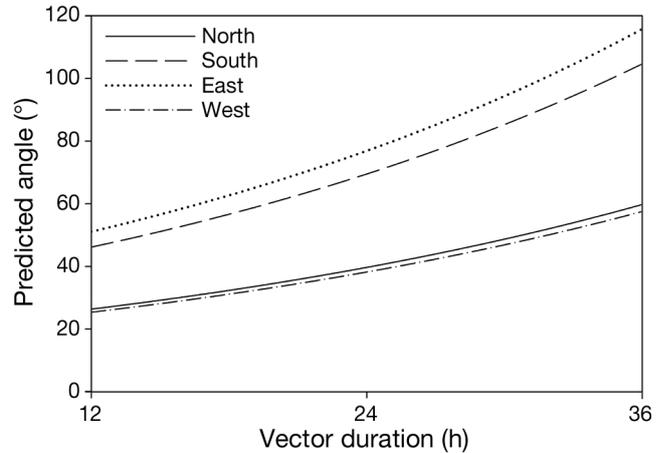


Fig. 7. *Odobenus rosmarus divergens*. Model predictions of angle of walrus–ice vector pairs observed in 4 regions of the northern Bering Sea, 26 March to 10 May 2006. Predictions are estimated for a walrus time-in-water value of 1.0

Table 3. *Odobenus rosmarus divergens*. Least-squares mean estimates of the angle and displacement of walrus–ice vector pairs observed in 4 regions of the northern Bering Sea, 26 March to 10 May 2006

Region	Angle (degrees)		Displacement (km)	
	Mean	95% CI	Mean	95% CI
North	42	30–58	14.5	9.8–21.6
South	74	55–99	21.9	17.2–28.0
East	81	60–111	34.6	23.9–50.2
West	40	30–55	20.3	17.2–23.8

Variance of walrus–ice vector pair displacements increased approximately with the square of their mean (Fig. 3). Examination of residuals indicated that this variance function was adequately fit with a gamma distribution. The estimate of the variance component associated with the random walrus effect converged to zero, so we eliminated it from the final model. As with the model for angles, the final gamma model for displacements left a large amount of variation unexplained (Fig. 8), but it indicated that displacement increased with duration of the observation ($F_{1,117} = 29.7$, $p < 0.01$; Fig. 9) and with the proportion of time the walrus spent in the water ($F_{1,117} = 35.1$, $p < 0.01$), and that there were differences among regions (Table 3). Least-squares mean estimates of vector pair displacements ranged from 15 to 35 km among regions (Table 3). Vector pair displacements tended to be larger in the eastern than in the northern (difference of least-squares means = 20.1 km, 95% CI = 9.2–31.0), southern (difference of least-squares means = 12.7 km, 95% CI = 7.0–18.4), and western (difference of least-squares means = 14.4 km, 95% CI = 8.6–20.1) regions (Fig. 9, Table 3).

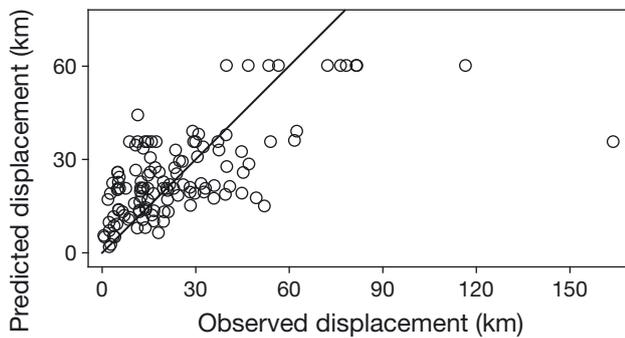


Fig. 8. *Odobenus rosmarus divergens*. Comparison of predicted and observed displacement of walrus-ice vector pairs observed in the northern Bering Sea, 26 March to 10 May 2006. Predictions that exactly match observations would lie on the indicated 45° line

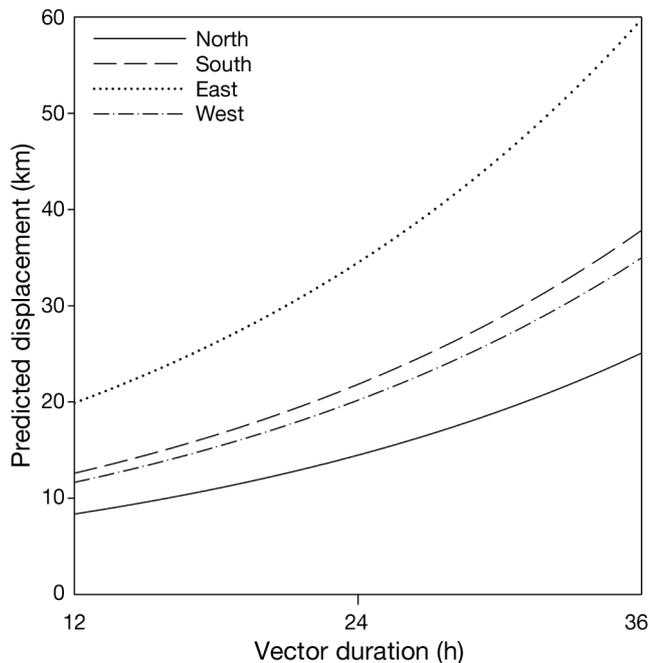


Fig. 9. *Odobenus rosmarus divergens*. Model predictions of displacement of walrus-ice vector pairs observed in 4 regions of the northern Bering Sea, 26 March to 10 May 2006. Predictions are estimated for a walrus time-in-water value of 1.0

DISCUSSION

We observed substantially divergent movement (angle and displacement) between walrus and their initially associated ice floes in all 4 regions of the study area. The magnitude of divergence varied among regions, which can be attributed to regional differences in the direction and rate of walrus and ice movements.

The longer a walrus is in water, the more it can diverge from the movements of ice, which was reflected in our study by increased divergence with

duration of observation and walrus time-in-water. The rate and direction of walrus movements are probably associated with the type of activity in which the animal is engaged, an association observed in other marine mammals (Austin et al. 2004). In-water movements may be limited in some areas by thick and highly concentrated ice.

The period of our observations (26 March to 10 May) corresponds to a period from very early spring (when most walrus are still within their winter breeding areas [post-breeding]) to late spring (when walrus are migrating as the ice disintegrates). Other behaviors that walrus are engaged in during this period include calving (starting mid-April), foraging, and potentially, avoidance of subsistence hunting (Fay 1982). Since most tagged walrus were non-parturient adult females, most of the walrus in our study were likely engaged in behaviors related to familial social interactions, migration, and foraging.

The comparatively low walrus-ice divergence we observed in the northern region was associated with low rates of both walrus and sea ice movements. Although this region is characterized by having strong northward water currents (Danielson et al. 2006), the walrus did not show a strong tendency to travel north. Their movement may have been inhibited by difficulty in traveling amongst highly compressed ice, another characteristic of this region (Burns et al. 1980).

The relatively moderate walrus-ice divergence we observed in the southern region was associated with moderate rates of ice movements tending between the south and west, coupled with similar rates of walrus movements with no directional tendencies. Presumably, water currents in this region had little influence on walrus movement, since the area where most of our observations were made had only weak nearshore currents (Danielson et al. 2006).

The comparatively high walrus-ice divergence we observed in the eastern region was associated with comparatively high rates of southward ice drift and the tendency for walrus to move northward. Most of our observations in the eastern region were made from late-April through mid-May, a time when walrus are typically migrating northward, primarily by swimming (Fay 1982). Given the strong northward currents described for the central and northern areas of this region (Danielson et al. 2006), water currents may have contributed to the walrus' northward progression.

The relatively moderate walrus-ice divergence we observed in the western region was associated with moderate rates of ice movements tending from the southeast to northwest, and walrus movements tending from the northwest to southeast. As in the southern region, many of our observations in the southern part

of the western region were within the area of the nearshore band of weak flowing currents, and therefore walrus movements there were not likely to have been aided much by water currents. However, the strong water currents flowing northward through the central portion of this region (Anadyr Strait) (Danielson et al. 2006) may have aided in the northward progression of some walruses.

We recognize that our analyses included measurement error associated with Argos location estimates for walruses. However, the magnitude of the walrus and ice displacements were typically larger than those attributable to Argos measurement errors alone. The non-zero value for angle and displacement for the case when a walrus was hauled out on ice during the entire observation (i.e. walrus time-in-water = 0, Fig. 3) was the result of measurement errors. These measurement errors would include those associated with Argos walrus location estimates and relatively small spatial errors introduced from the inexact temporal match of walrus and ice floe locations.

We also recognize that the regions we used to assign walrus–ice vectors are rough approximations to ice habitat boundaries that occurred during our study. These boundaries probably shifted somewhat from short-scale fluctuations in ice drift. Although the net transport of ice is southward during winter and early spring, the rate and direction of drift are not uniform throughout the pack ice (Burns et al. 1981). Short-term (several days), small-scale fluctuations in ice drift occur, probably from variations in local winds, currents, and ice interactions (Muench & Ahlnas 1976).

Ice over the continental shelf affords walruses the ability to exploit benthic prey over large areas. It has been recognized that when walruses rest on moving ice they can be transported to new feeding areas (Fay 1982). It has been further suggested that, on a local scale (~1 to 100 km), walruses ‘home’ to specific or neighboring ice floes to haul out after bouts of benthic foraging, and that the continuously moving floes determine the areal extent of foraging by walruses, thereby dispersing benthic predation (Ray et al. 2006).

However, we observed substantial divergence between walruses and their initially associated ice floes, suggesting that areas of walrus activities were independent of the movement of ice floes at a local scale. Furthermore, in several walrus–ice vector pairs, the walrus was hauled out at the beginning and end of the walrus vector. The average walrus–ice displacement of these vector pairs was 19 km (SD = 11 km, n = 7), suggesting also that walruses were not homing to specific ice floes between in-water bouts. Lack of correspondence between walrus and sea ice movements suggests that sea ice movements do not necessarily determine the extent of walrus foraging and may not

prevent walruses from intensely feeding on local benthic prey. Local and regional heterogeneity in benthic biomass and community composition within our study area (Grebmeier et al. 2006) could lead walruses to preferentially select certain areas for foraging.

The magnitude of walrus–ice divergence may be partially dependent on the seasonal concentration and extent of useable ice. Although an extensive ice field was accessible to walruses during our study, in other places and times of year within the annual range of walruses, walrus–ice divergences may not occur to the same magnitude as we observed. For example, in the Chukchi Sea in late summer, ice extent over the continental shelf is sometimes reduced to very sparse ice (Jay & Fischbach 2008). During these times, walruses may be limited in their movements to areas where these ice floes are available, and in these cases, their movements may be more congruent with the movement of ice floes than what we observed here.

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