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Movements of Walruses Radio-tagged in Bristol Bay, Alaska

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ABSTRACT. Satellite radio-location data from 57 adult male Pacific walruses (*Odobenus rosmarus divergens*) were used to estimate haul-out fidelity, broadly describe seasonal foraging distributions, and determine the approximate timing of autumn migration from Bristol Bay, Alaska. Data were collected intermittently during 1987–91 and 1995–2000, primarily during the period from May to October. Transmitter longevity ranged from less than 1 day to 560 days (median 75 d). The four tagging sites were the only haul-outs that were commonly used in the bay from spring through autumn. Mean fidelity, defined as the chance that an animal will return to an area where it previously hauled out, was 0.56 (SE = 0.09). However, small sample sizes precluded comparisons of fidelity among years and among haul-outs by season. No tagged animals migrated out of the bay between spring and early autumn. Combined monthly locations suggest that foraging occurred primarily in the southern and eastern areas of the bay in spring and gradually shifted towards northwestern areas in late autumn and winter. Ninety-eight percent of the in-water locations were in waters under 60 m deep, which account for 76% of the study area. Some animals migrated out of the bay in late autumn and winter; others remained within the bay throughout the year. Those making long-range migrations departed the bay during November and December.

Key words: walrus, *Odobenus rosmarus*, haul-out, fidelity, Bristol Bay, foraging, seasonal, distribution, transmitters

RÉSUMÉ. On a utilisé des données de radiolocalisation satellitaire provenant de 57 morses du Pacifique (*Odobenus rosmarus divergens*) mâles afin d'évaluer la fidélité au site d'échouerie, de décrire sommairement la distribution saisonnière des aires d'alimentation et d'établir le moment approximatif de la migration automnale partant de la baie Bristol, en Alaska. Entre 1987 et 1991, puis entre 1995 et 2000, on a recueilli des données par intermittence, essentiellement durant la période allant de mai à octobre. La longévité des émetteurs allait de moins de 1 jour à 560 jours (médiane de 75 jours). Les quatre sites de marquage étaient les seules échoueries couramment utilisées dans la baie, du printemps à la fin de l'automne. La fidélité moyenne, définie comme la probabilité qu'un animal réutilise un site d'échouerie donné, était de 0,56 (erreur-type = 0,09). La petite taille des échantillons a cependant empêché une comparaison saisonnière de la fidélité d'une année à une autre et d'une échouerie à une autre. Aucun animal marqué n'a migré hors de la baie entre le printemps et le début de l'automne. Un regroupement mensuel des localisations suggère qu'au printemps, les aires d'alimentation se trouvaient surtout dans les zones méridionales et orientales de la baie, et qu'elles se déplaçaient graduellement vers des zones situées dans la partie nord-ouest à la fin de l'automne et en hiver. Quatre-vingt-dix-huit p. cent des localisations au large se trouvaient dans des eaux d'une profondeur supérieure à 60 m, ce qui représente 76 % de la zone d'étude. Quelques animaux émigraient de la baie à la fin de l'automne et en hiver, tandis que d'autres restaient dans la baie tout au long de l'année. Ceux qui effectuaient des migrations sur une longue distance quittaient la baie durant les mois de novembre et décembre.

Mots clés: morse, *Odobenus rosmarus*, échouerie, fidélité, baie Bristol, alimentation, saisonnier, distribution, émetteurs

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INTRODUCTION

Pacific walruses (*Odobenus rosmarus divergens*) are segregated by gender for much of the year as they migrate over vast areas of the Chukchi and Bering seas (Fay, 1982). Adult females and dependent young remain with the sea ice year-round, traveling to the north in the Chukchi Sea in summer and to the south in the Bering Sea in winter. In contrast, adult males generally abandon the sea ice in spring for land haul-outs along the coasts of Russia and Alaska. During summer, the adult males rest at the land haul-out sites for up to several days at a time between offshore foraging trips lasting 4–10 days (Hills, 1992; Jay et al., 2001). Bristol Bay has long been recognized as the most important area for summering adult males in Alaskan waters. In the mid-1980s, these animals comprised roughly 7% of the total Pacific walrus population, then estimated at 232 518 (Gilbert, 1989). However, little is known about the exchange of animals between haul-out sites, the location of foraging areas within the bay, or the timing of autumn migration from the bay. This information is important in developing policies to conserve essential coastal

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and offshore walrus habitats (U.S. Fish and Wildlife Service, 1994).

The use of Alaskan coastal haul-outs has been shown to change with the size of the Pacific walrus population. Fay (1957) and Fay et al. (1989) provide a detailed history of the exploitation and ensuing distribution of walruses during three periods of commercial harvests from the mid-1800s to the 1980s. In the Bristol Bay region, during the mid-1950s decline from the last period of commercial harvests, no walruses were observed along the Alaska Peninsula, and only about a thousand animals were recorded at the Walrus Islands (Fig. 1). By about 1960, protective measures had been established in Russia and Alaska, and by the 1980s, the population had apparently increased to its pre-exploitation levels (Fay et al., 1989). Concurrently, walruses reoccupied Amak Island and Port Moller in the southern part of Bristol Bay, and walrus numbers at the Walrus Islands (mostly Round Island) grew from about 3000 animals in the late 1950s to about 12 000 in the early 1980s (Frost et al., 1982; Fay et al., 1984). Three other Bristol Bay haul-outs, Cape Seniavin, Cape Peirce, and Cape Newenham, were reoccupied between the late 1970s and early 1980s (Frost et al., 1982; Mazzone, 1986). During this same time, Round Island was the only Walrus Island haul-out being used regularly, and Cape Seniavin became the major haul-out on the Alaska Peninsula (Frost et al., 1982). Thus, four major haul-outs in Bristol Bay were recognized by the early 1980s (several years before the current study): Cape Seniavin (CS), Round Island (RI), Cape Peirce (CP), and Cape Newenham (CN) (Frost et al., 1982; Fay et al., 1984).

The relative use of these four haul-outs by walruses varies both seasonally and from year to year. Concern to protect walruses from disturbance and illegal harvesting prompted state and federal resource agencies to set up annual field camps at RI, CP, and CN. From these camps, daily counts of walruses have been recorded at RI from roughly May through August since 1977 (Taggart and Zabel, 1980; VanDaele et al., 1990; Cody, 2002), at CP from June through September since 1985 (Mazzone, 1986; MacDonald, 2002), and at CN from May through August since 1991 (Jemison, 1992; MacDonald, 2002). At CS, similar data have been collected regularly during July since 1998 (Kruse and Jack, 1998; Barnum, 2001). Annual maximum counts during these years ranged from about 1500 walruses to well over 10 000 walruses at RI (VanDaele et al., 1990; MacDonald, 2002) and CP (Mazzone, 1986; Raymond and Stroka, 1998; MacDonald, 2002), from about 1000 to 1500 at CS (in July) (Kruse and Jack, 1998; Snyder, 1999; Barnum, 2001), and from zero to 5000 at CN (Jemison, 1993; MacDonald, 2002).

The degree to which animals move among haul-out sites in the bay is unclear, although some exchange is known to occur between RI and CS (Frost et al., 1982; Hills, 1992) and RI and CP (Taggart, 1987; Hills, 1992). It has been reported, but not well documented, that peaks in walrus abundance at CP typically occur later in the year (July–August) than do peaks at RI (May–early July), perhaps reflecting a progressive northerly movement of animals in autumn (Jemison, 1991).

Seasonal in-water locations (presumably foraging locations) of walruses in Bristol Bay are poorly known. Monthly aerial surveys of Bristol Bay in 1980–81 by Fay and Lowry (1981) provide the only information available on in-water locations before the use of radio-tags. The surveys covered the bay east of 161° W, which does not include the CP and CN areas in the current study, and the authors recognized that, in some months, a substantial number of animals may have been present west of their survey area. Walruses were sighted in the bay throughout the year. Their numbers were highest in the southern portion of the bay for a short period peaking in April, but shifted northward thereafter (Fay and Lowry, 1981).

In late autumn and winter, the number of walruses in the bay declines, in part because adult males move out of the bay to join females for breeding (Fay and Lowry, 1981; Fay, 1982; Frost et al., 1982). Initial radio-tagging work by Taggart (1987) suggests that in autumn, a significant number of adult males undertake long-range northward migrations to the vicinity of St. Lawrence Island.

In this paper, we report on the movements of adult male walruses in Bristol Bay, using satellite radio transmitter data collected intermittently between 1987 and 2000. Although these data came from studies with various objectives, we used them to the extent possible to estimate haul-out fidelity, describe the seasonal distribution of walruses, and comment on autumn migrations from the bay.

METHODS

The primary study area was Bristol Bay, defined here by the area east of 164° W and bounded by the mainland coastline (Fig. 1). A few additional observations were made of several animals migrating outside the bay. Data came from Argos satellite-linked radio transmitters fitted to 59 adult male walruses, during the periods 1987–91 and 1995–2000, at four principal haul-out sites (Fig. 1). All animals were captured by chemical immobilization, and a transmitter was attached with stainless steel bands to one tusk of each animal. Walruses typically began using the Cape Seniavin (CS) and Round Island (RI) sites in early spring and the Cape Peirce (CP) and Cape Newenham (CN) sites in mid-summer; therefore, most transmitters were deployed either at CS and RI in May and early June (37%) or at CP in August (49%); three transmitters were deployed at CN.

Transmitter configurations varied considerably; however, all transmitters had a conductivity sensor that disabled transmissions when the device was underwater to conserve battery life. Various duty cycles were used, and expected battery life ranged from a few months to over one year.

Large errors can occur in Argos location data. For example, an average error of over 10 km was reported for

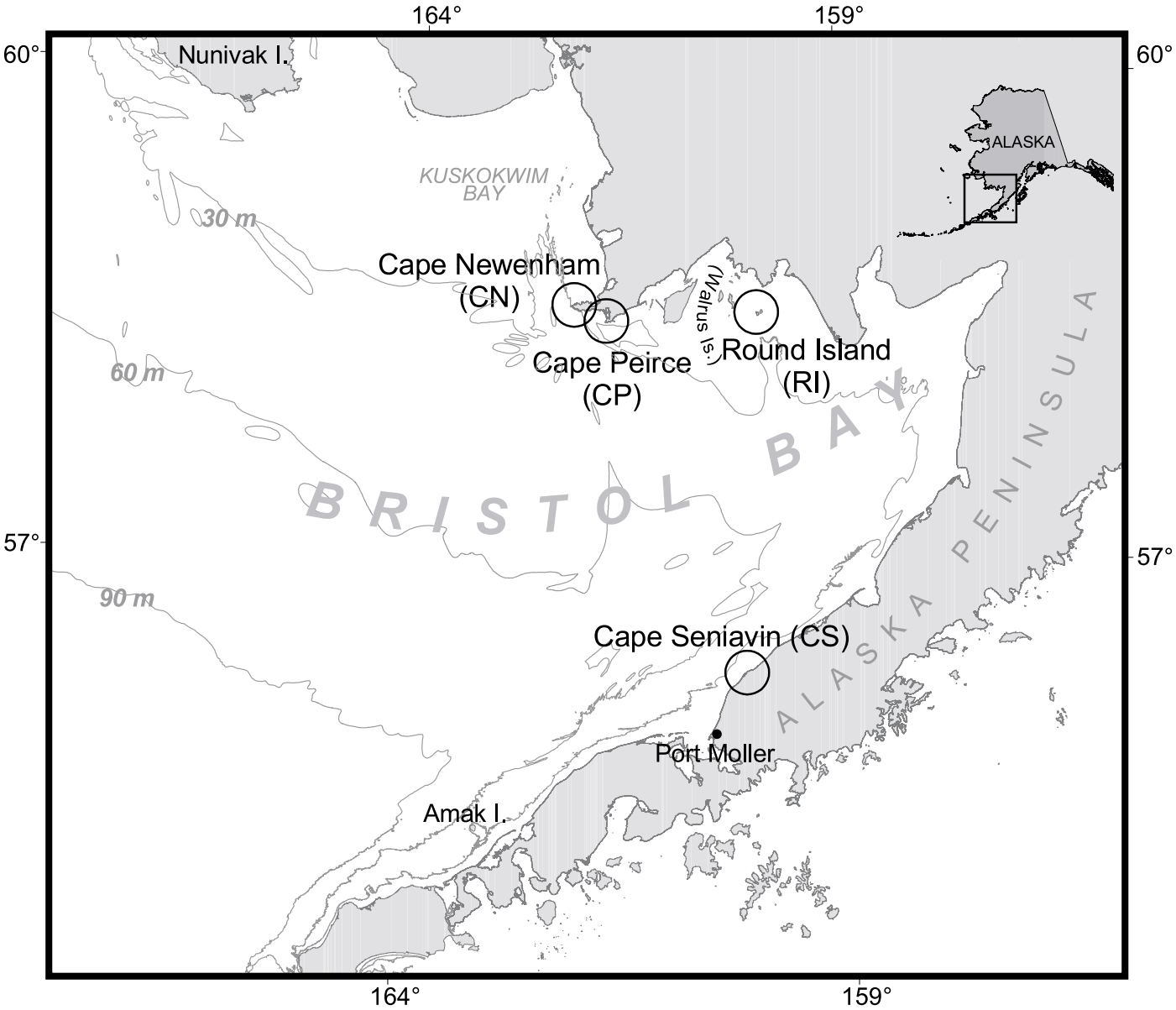

FIG. 1. Map of study area. Haul-out areas were delineated by a 15 km radius around haul-out sites.

low-class (nonstandard) locations in a tracking study of the Atlantic walrus (*O. r. rosmarus*) (Born and Knutsen, 1992). In the current study, to exclude locations with potentially large errors, we accepted a nonstandard location (equivalent to post-1994 LC < 1) only if it could be confirmed to within 15 km of a preceding or subsequent location using an iterative process of evaluating the distance between three locations at a time (D. Douglas, USGS, Alaska Science Center, unpubl. algorithm, 2000). Argos location quality designations changed from time to time during the study period, however nonstandard locations were always distinguishable in the data. All standard locations and GPS-acquired locations from satellite-linked GPS transmitters (Jay and Garner, 2002) were retained.

Here, we define fidelity as the chance that an animal will return to an area where it previously hauled out. We estimated fidelity to a haul-out area rather than to a specific point, because even after we filtered large location errors from the data, some unknown amount of location error remained. Also, we wanted to measure fidelity on the basis of substantial dispersals from a haul-out site because they would most likely be associated with foraging trips. Therefore, we delineated haul-out areas by a 15 km radius around observed haul-out sites using GIS (ArcView, ESRI, Redlands, CA) and classified each location either as belonging to one of the haul-out areas or as "offshore." Eleven locations fell within an overlap region between the CP and CN haul-out areas (Fig. 1), so each was assigned to the area associated with the haul-out site nearest the location. We used these location classifications to estimate the dates of each walrus's departure from a haul-out area and its arrival at the next haul-out area.

We restricted our estimates of fidelity to May–October, because the formation of coastal ice generally prevented

TABLE 1. Summary of satellite radio transmitter locations from walruses in Bristol Bay, Alaska, 1987–2000.[1]

Animal	Tagging location	Tagging date	Last location	Number of locations	Transmitter longevity (d)	Rate of locations (loc/d)	Number of haul-out returns observed May – October				Animal observed outside bay (Yes/No)
							CS	RI	CP	CN	
CS88001	CS	12 MAY 88	01 SEP 88	41	112.52	0.36	2	0	0	0	N
CS90003	CS	07 MAY 90	18 AUG 90	59	102.28	0.58	0	3	0	0	N
CS90004	CS	08 MAY 90	14 OCT 90	376	159.04	2.36	1	2	0	0	N
CS90007	CS	08 MAY 90	08 SEP 90	117	122.25	0.96	10	0	0	0	N
CS90009	CS	08 MAY 90	28 MAY 90	19	19.58	0.97	0	1	0	0	N
CS90011	CS	09 MAY 90	10 JUL 90	189	61.21	3.09	0	1	0	0	N
CS90012	CS	10 MAY 90	06 OCT 90	245	149.67	1.64	7	10	0	0	N
RI87001	RI	14 AUG 87	14 NOV 87	40	91.42	0.44	0	2	2	0	N
RI90001	RI	22 MAY 90	01 FEB 91	441	255.08	1.73	0	10	0	0	N
RI90003	RI	22 MAY 90	16 NOV 90	473	177.93	2.66	0	14	1	0	N
RI90006	RI	23 MAY 90	25 SEP 90	395	125.68	3.14	0	14	0	0	N
RI97031	RI	30 MAY 97	17 DEC 97	36	200.39	0.18	0	0	2	0	N
RI97033	RI	30 MAY 97	12 JUN 97	4	12.21	0.33	–	–	–	–	N
RI97034	RI	30 MAY 97	17 DEC 97	60	200.15	0.30	0	1	6	0	N
RI97035	RI	31 MAY 97	15 JUN 97	5	15.68	0.32	–	–	–	–	N
RI97037	RI	31 MAY 97	18 DEC 97	27	200.08	0.13	0	0	2	0	N
RI98062	RI	10 JUN 98	03 DEC 98	43	176.08	0.24	0	0	4	1	N
RI98064	RI	10 JUN 98	14 JUN 98	1	3.59	0.28	–	–	–	–	N
RI98065	RI	11 JUN 98	18 JUN 98	3	7.11	0.42	–	–	–	–	N
RI98068 *	RI	12 JUN 98	25 DEC 99	69	560.24	0.12	3	0	2	1	Y
RI98069	RI	12 JUN 98	18 AUG 98	9	66.92	0.13	–	–	–	–	N
RI98070 *	RI	13 JUN 98	15 NOV 99	127	520.17	0.24	3	2	1	0	N
CP95003	CP	30 JUL 95	13 SEP 95	29	44.85	0.65	0	0	3	0	N
CP95005	CP	02 AUG 95	19 DEC 95	56	138.78	0.40	0	1	2	1	N
CP95006	CP	03 AUG 95	07 AUG 95	21	4.14	5.08	–	–	–	–	N
CP95007	CP	04 AUG 95	23 AUG 95	28	19.04	1.47	0	0	2	0	N
CP95009	CP	04 AUG 95	19 SEP 95	29	46.75	0.62	0	0	4	0	N
CP95010	CP	05 AUG 95	02 SEP 95	11	28.19	0.39	0	0	0	1	N
CP95011	CP	05 AUG 95	18 NOV 95	83	105.75	0.78	1	0	7	1	N
CP95014	CP	07 AUG 95	15 SEP 95	6	38.70	0.16	0	0	0	1	N
CP96017	CP	02 AUG 96	15 FEB 97	78	197.77	0.39	0	1	5	1	Y
CP96019	CP	15 AUG 96	07 SEP 96	25	22.25	1.12	0	0	2	2	N
CP96020	CP	16 AUG 96	06 SEP 96	18	21.00	0.86	–	–	–	–	N
CP96021	CP	16 AUG 96	17 AUG 96	2	0.10	20.82	–	–	–	–	N
CP96022	CP	19 AUG 96	23 SEP 96	100	35.60	2.81	1	0	4	1	N
CP96023	CP	19 AUG 96	01 NOV 96	40	74.69	0.54	0	0	3	1	N
CP96024	CP	22 AUG 96	21 DEC 96	51	120.14	0.42	1	1	1	0	N
CP96025	CP	22 AUG 96	26 JAN 97	86	156.06	0.55	0	0	1	0	Y
CP97047	CP	10 JUL 97	10 DEC 97	30	152.28	0.20	–	–	–	–	N
CP97049	CP	06 AUG 97	07 SEP 97	8	31.92	0.25	–	–	–	–	N
CP97050	CP	06 AUG 97	10 OCT 97	36	64.44	0.56	0	0	3	0	N
CP97051	CP	06 AUG 97	02 OCT 97	18	56.36	0.32	0	0	2	0	N
CP97052	CP	07 AUG 97	12 SEP 97	13	36.03	0.36	–	–	–	–	N
CP97055	CP	11 AUG 97	01 DEC 97	15	111.98	0.13	0	0	2	0	N
CP97059	CP	14 AUG 97	27 AUG 97	3	12.34	0.24	–	–	–	–	N
CP97060	CP	15 AUG 97	11 SEP 97	10	27.78	0.36	–	–	–	–	N
CP97061	CP	15 AUG 97	27 AUG 97	14	12.06	1.16	0	0	1	0	N
CP98072	CP	11 AUG 98	18 NOV 98	7	99.11	0.07	0	0	1	1	Y
CP98075	CP	12 AUG 98	12 AUG 98	1	0.03	33.83	–	–	–	–	N
CP98078	CP	13 AUG 98	11 JAN 99	15	151.20	0.10	–	–	–	–	N
CP98080	CP	14 AUG 98	03 DEC 98	39	110.27	0.35	2	0	0	0	N
CP98083	CP	15 AUG 98	08 SEP 98	12	23.36	0.51	–	–	–	–	N
CP98084	CP	29 SEP 98	23 JAN 99	24	116.17	0.21	0	0	1	3	N
CP98085	CP	29 SEP 98	19 JAN 99	19	112.51	0.17	–	–	–	–	N
CP99093	CP	23 AUG 99	07 FEB 00	32	168.28	0.19	0	1	1	0	Y
CN97041	CN	03 JUL 97	03 JUL 97	1	0.01	77.01	–	–	–	–	N
CN97042	CN	03 JUL 97	09 SEP 97	30	68.15	0.44	0	0	1	0	N

[1] CS = Cape Seniavin, RI = Round Island, CP = Cape Peirce, CN = Cape Newenham.

* tabulated haul-out returns are for two years combined.

animals from using land haul-outs in late autumn, winter, and early spring. Furthermore, fidelity was estimated for two three-month periods (May–July and August–October) because most animals were tagged in May or August and the transmitters usually remained active for three months or less.

In our analysis of fidelity among haul-out areas and between periods, the experimental unit was the animal and the sampling unit was an indicator of fidelity (1 if the animal returned to the area where it had previously hauled out; 0 otherwise). Many animals used more than one haul-

out area, and the number of observed haul-out returns from each animal varied from 1 to 17 (Table 1). Therefore, we used only the first observed haul-out return from each animal, so that observations were weighed equally among animals.

Fidelity could vary with different combinations of haul-out, period, and year; however, the data were insufficient to analyze for these potential interactions. Therefore, we performed separate analyses, using logistic regression, to compare fidelity among haul-outs and between periods, where fidelity was the response variable, and haul-out and period were the predictor variables. Data were insufficient to analyze for a potential year effect.

In addition to location data, eight of the transmitters provided dive data, which we used to confirm foraging and non-foraging locations. The satellite-linked time-depth recorders (SLTDRs), which were deployed on walruses at Cape Peirce in late June to mid-August of 1995 and 1996, reported the accumulated time spent in 15 m depth classes over periods of one hour (3 SLTDRs) and six hours (5 SLTDRs). Walruses regularly haul out to rest between periods of offshore foraging on the seafloor. A study of walrus dive behavior within the current study area indicated that maximum dive depth was bimodal, with very few dives between 10 and 20 m depth. The deeper dives were primarily foraging dives (> 94% of all deep diving time) (Jay et al., 2001). Therefore, in the current study, each one-hour and six-hour period was assigned to a behavior category: foraging if the animal spent at least one-third of the period at a depth of 15 m or more, or non-foraging otherwise. Subsequently, each period was linked to locations that were acquired within three hours of the mid-point of the period.

We inferred seasonal foraging areas and estimated the approximate timing of migration from the bay qualitatively, from pooled locations of all animals in all years, because the sampling rate and period of locations varied substantially among walruses. Several walruses provided locations for exceptionally long periods, and we briefly described their movements.

RESULTS

Two of the 59 transmitters failed to provide animal locations, and 22% of the Argos locations from the remaining 57 animals did not meet the filtering criteria and were omitted from further analysis. A total of 3667 Argos locations and 102 GPS locations were retained.

Transmitter longevity (time of deployment to last filtered location) and the rate of acquiring locations varied considerably among animals (Table 1). Transmitter longevity ranged from less than 1 day to 560 days (median 75 d). Since the transmitters usually functioned for only a few months, and most were deployed in May or August, we obtained the preponderance of location data from May through October (90% of all filtered locations, Fig. 2).

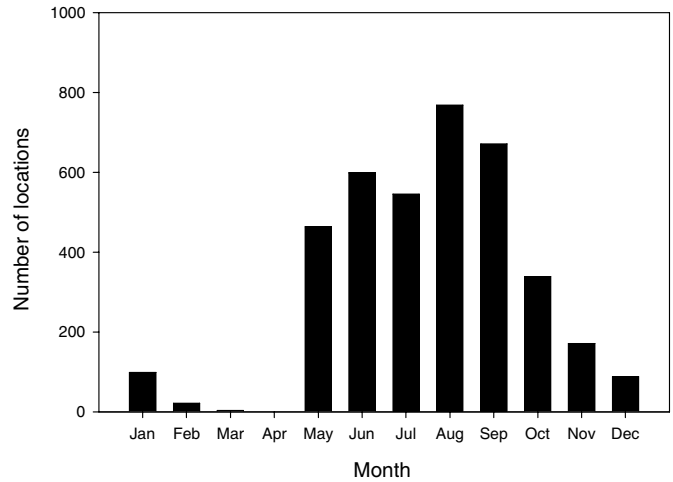

FIG. 2. Number of locations (after filtering) each month from satellite radio-tagged walruses, 1987–2000.

Most animals were tracked for 255 days or less. Two animals (RI98068 and RI98070) were tracked for 520 days or more.

Locations within the bay indicated that the tagging sites (CS, RI, CP, and CN) were the only land haul-out sites commonly used in the bay. Almost all the in-water locations (98%) were in waters under 60 m deep, which account for 76% of the study area (Fig. 1, east of 164° W). (bathymetry data from U.S.G.S. Alaska Science Center, 1997).

We found no evidence of a difference in level of fidelity among the CS (0.50), RI (0.67), and CP (0.57) haul-outs (χ^2 = 0.50, df = 2, n = 38, p = 0.78; CN was excluded because there was only one observation), nor between the May–July (0.56) and August–October (0.57) periods (χ^2 = 0.0003, df = 1, n = 39, p = 0.99). Thus, pooling across haul-out and time periods, mean fidelity for the tagged walruses was 0.56 (SE = 0.09, n = 39). Since these estimates used the first haul-out return from each animal, they may be artificially low if capture of the animal deterred the animal from immediately returning to the same haul-out.

Differences in the duration and location of haul-out preference were apparent from nine animals from which 6 to 17 haul-out returns were observed between May and October (Table 1). For example, walrus RI90003 returned almost exclusively (14 times) to RI through both periods (May–October), whereas walrus CS90012 returned exclusively to CS during May–June (7 times), then exclusively to RI thereafter through at least September (10 times) (Table 1, sequence of returns not shown).

Locations associated with confirmed foraging behavior were observed throughout most of the distribution of the combined offshore locations of the eight walruses with satellite-linked time-depth-recorders (Fig. 3). All these animals were tagged at CP in late July and August. Foraging was confirmed to within about 10 km of CP and 45 km of CS, and across the entire bay, as far as 130 km from the nearest haul-out site. One foraging location was identified in the shallow waters of Kuskokwim Bay.

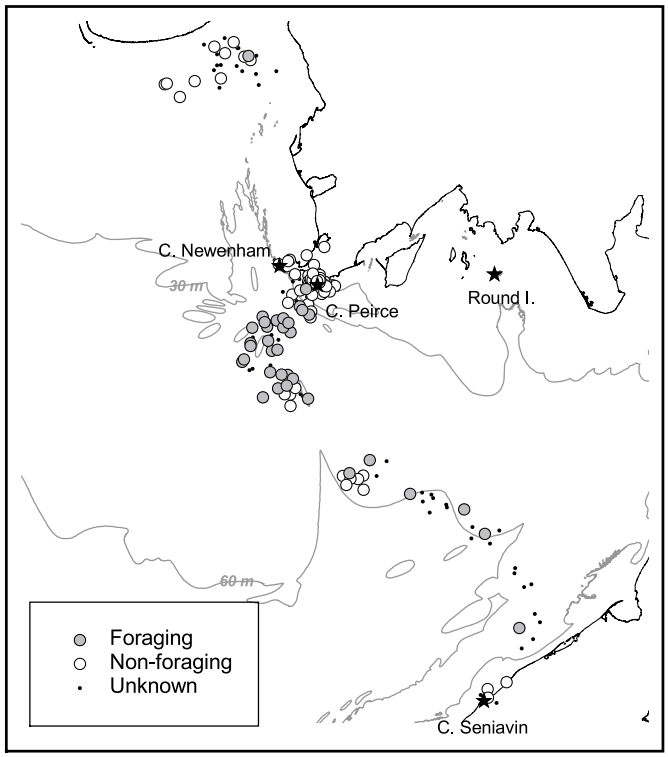

FIG. 3. Confirmed foraging and non-foraging locations of eight walruses with satellite-linked time-depth recorders.

The percentage of tagged animals occupying the bay each month (Table 2) suggests that animals did not migrate from the bay from spring through early autumn (the one animal that was observed outside the bay in May was returning to the bay) and that those animals that did migrate from the bay did so after October.

Although walrus locations were obtained infrequently in winter months (particularly February–April), monthly locations for all years combined suggest a broad pattern of seasonal distribution of walruses in the bay (Fig. 4). These observations should be viewed cautiously, however, because of unbalanced sampling among walruses, seasons, and years. In May, walruses occurred in their most eastern extent in the bay and were observed over large areas of the bay between CS to the south and RI to the north. The numerous locations that were obtained in May corresponded to the deployment time of a large portion of the transmitters, mainly at CS and RI (Table 1). Some locations in early spring of some years were probably from animals on sea ice. Evidence is a very linear sequence of locations obtained from an animal in May 1999 (RI98070) in the far eastern portion of the bay, during a time when sea ice was still present in that area. In addition, many of the locations were of a high quality (LC ≥ 1),which is more prevalent from walruses hauled out on ice or land (Born and Knutsen, 1992).

Tagged walruses were evident near CP as early as June, and by July they were observed near all four haul-out sites (Fig. 4). Many more locations near CP were transmitted in August, when we deployed another large portion of the transmitters at that site (Table 1). Tagged walruses began occupying Kuskokwim Bay in September and continued to do so through December. Locations in Kuskokwim Bay were represented by five different animals, all tagged at CP, in three different years (1995, 1996, and 1998). No animals were evident in the far eastern portion of the bay at this time. Although locations transmitted in October and November were fewer in number, their distribution was similar to that in September. In December, most walrus locations were confined to the northwest portion of the bay, and in January, no animals were observed in the Kuskokwim Bay region. In general, the combined monthly locations suggest that walruses primarily used the southern and eastern areas of the bay in spring, then gradually shifted toward northwestern areas in late autumn and winter.

Ten animals were radio-tracked long enough to determine their winter destinations. Five migrated out of the bay in late autumn and winter (Fig. 5), and the other five remained in the bay. Six departures were observed from the five migrating animals (two observed from animal RI98068 in two years). Four departures occurred by December, one by November, and one by early February. The latter was associated with a movement only slightly west of the bay. The northern limits of travel were variable between years, and the northernmost location was near the north coast of the Chukotka Peninsula in Russia, ~1000 km from the bay. Animal RI98068 was the only migrating animal that was tracked long enough to determine a destination the following summer. It returned in May to the haul-out where it was tagged the previous year (RI), and then left the bay again the following winter. Year-round residence in the bay was evidenced by four animals that were tracked through January or February (RI90001, CP98078, CP98084, and CP98085) and one animal that was tracked through November of the following year (RI98070) (Table 1).

DISCUSSION

Fay (1982) postulated the existence of three main breeding aggregations of walruses in the Bering Sea in winter: a southeast aggregation in the vicinity of Bristol Bay, a northern aggregation just southwest of St. Lawrence Island, and a smaller western group in an area southwest of Anadyr Gulf, Russia. He suggested that many of the animals that arrive at coastal sites in Bristol Bay in spring come from the nearby southeastern winter aggregation. Our study supports this theory, but we show further that animals also come from wintering aggregations in the northern Bering Sea, which was demonstrated by a tagged walrus that returned to the bay after overwintering in the north. The degree of interannual fidelity of individuals to Bristol Bay remains unknown because individuals are seldom tracked over multiple years. Although annual variation in walrus abundance in Bristol Bay has not been

TABLE 2. Percent of tagged animals occupying Bristol Bay each month, all animals and years combined.

Month[1]	%	n
January	66	9
May	94	18
June	100	19
July	100	17
August	100	48
September	100	41
October	100	22
November	95	18
December	84	19

[1] Insufficient data ($n \leq 4$) were available for February, March, and April.

clearly quantified, daily animal counts in summer by resource agency personnel at RI and CP suggest that the number of males entering the bay each spring may vary substantially between some years. For example, the sums of the highest counts during summer at RI and CP in 1994, 1995, and 1996 were 5968, 10 471, and 6447, respectively (Wilson, 1995, 1996; Moran and Wilson, 1996).

Walruses tended to show preferences for haul-out areas, but a certain amount of exchange occurred among all four haul-outs (Table 1). Few animals were tracked long enough for us to observe potential shifts in haul-out preference over time, but one animal (CS90012) clearly demonstrated such a shift (from CS to RI). Conversely, preference for a single haul-out throughout May–October was also demonstrated (e.g., the near exclusive use of RI by animal RI90003).

Our data indicate that migration out of the bay does not occur through the summer months. There are no documented observations of mass movements of animals into the bay from coastal routes during summer; in some years, however, large groups of walruses have been observed in June along the Alaskan coast from Kuskokwim Bay to Norton Sound (Fay, 1982). It seems likely that the bay encompasses a closed population from spring through early autumn, but the lack of migration into the bay during summer has not been verified.

Movements on and off the haul-out sites in Bristol Bay during the summer months are primarily associated with foraging trips (Jay et al., 2001). In the current study, the considerable overlap of confirmed foraging locations with other at-sea locations from walruses tagged with SLTDR transmitters at CP suggests that offshore locations obtained from other animals probably represented foraging areas as well. Foraging was confirmed as close as 10 km to one of the haul-outs (CP) in this study, but foraging may not be prevalent in waters from 10 to 20–35 m deep (Jay et al., 2001). Atlantic walruses have been observed foraging in waters 15–30 m deep in Greenland and Svalbard (Born and Knutsen, 1997; Gjertz et al., 2001) and within 2 km of a haul-out site in Svalbard (Gjertz et al., 2001).

The distance that walruses move from their haul-out sites during foraging trips is likely related to prey density, but information on prey density is lacking (Born and Knutsen, 1997; this study). In our study, walruses moved a considerable distance offshore to feed, up to 130 km from their nearest haul-out site. However, offshore locations were conspicuously absent from areas beyond about 50 km west-southwest of CS and 100 km west-southwest of CP and in waters more than 60 m deep (consistent with Jay et al., 2001). The fact that depths in these areas are apparently within the aerobic dive limits of the animals (Jay et al., 2001), and less than maximal foraging depths observed for Pacific walruses (Fay and Burns, 1988), would suggest that these areas had insufficient prey densities or patch sizes for effective foraging.

The monthly at-sea distribution of locations in Bristol Bay suggests that foraging shifted from the eastern part of the bay in early spring to northwestern areas in late autumn and early winter, although considerable overlap occurred. This pattern is consistent with the annual build-up of animals observed at the northwestern haul-outs (CP and CN) in June and July over many years of monitoring (MacDonald, 2002). The reasons for these shifts are unclear.

In the longer term, patterns of walrus distribution and haul-out use in Bristol Bay have apparently changed over the past 20 years. During a systematic survey of the seasonal abundance and distribution of walruses in Bristol Bay in 1980–81, Fay and Lowry (1981) observed a marked decline in the number of walruses in the southern portion of the bay off the north coast of the Alaska Peninsula after April. In contrast, tagged animals from the current study indicate that the southern region of the bay was occupied by walruses through as late as November, and in recent years, thousands of animals have been observed at CS during haul-out monitoring counts in July (Kruse and Jack, 1998; Barnum, 2001). Furthermore, other haul-out monitoring counts show a large decline in the use of the CP and CN haul-outs beginning in 1999 (MacDonald, 2002).

The reasons for long-term changes in walrus distribution and haul-out use are almost certainly complex. Factors that could affect these patterns include prey abundance and distribution, walrus density, and physical alteration or chronic disturbance at the haul-outs. Historical accounts of intense commercial exploitation of walruses beginning in the mid-1800s document shifts in population range, including areas within Bristol Bay, and attribute these shifts to changes in population density (Fay, 1957; Fay et al., 1989). The fact that RI has been the only haul-out consistently used during periods of dramatic population-wide declines during past commercial harvests (Fay, 1957; Frost et al., 1982; Fay et al., 1984, 1989) might suggest that RI is the most preferred site in Bristol Bay. Since it is unlikely that food was a limiting factor during the population declines associated with commercial harvests, it is possible that RI and its adjacent islands offer more favorable conditions to walruses, such as higher levels of protection from adverse weather and disturbance, than haul-outs along the mainland coastline. The status of the Pacific walrus population from the late 1980s to the present is unknown.

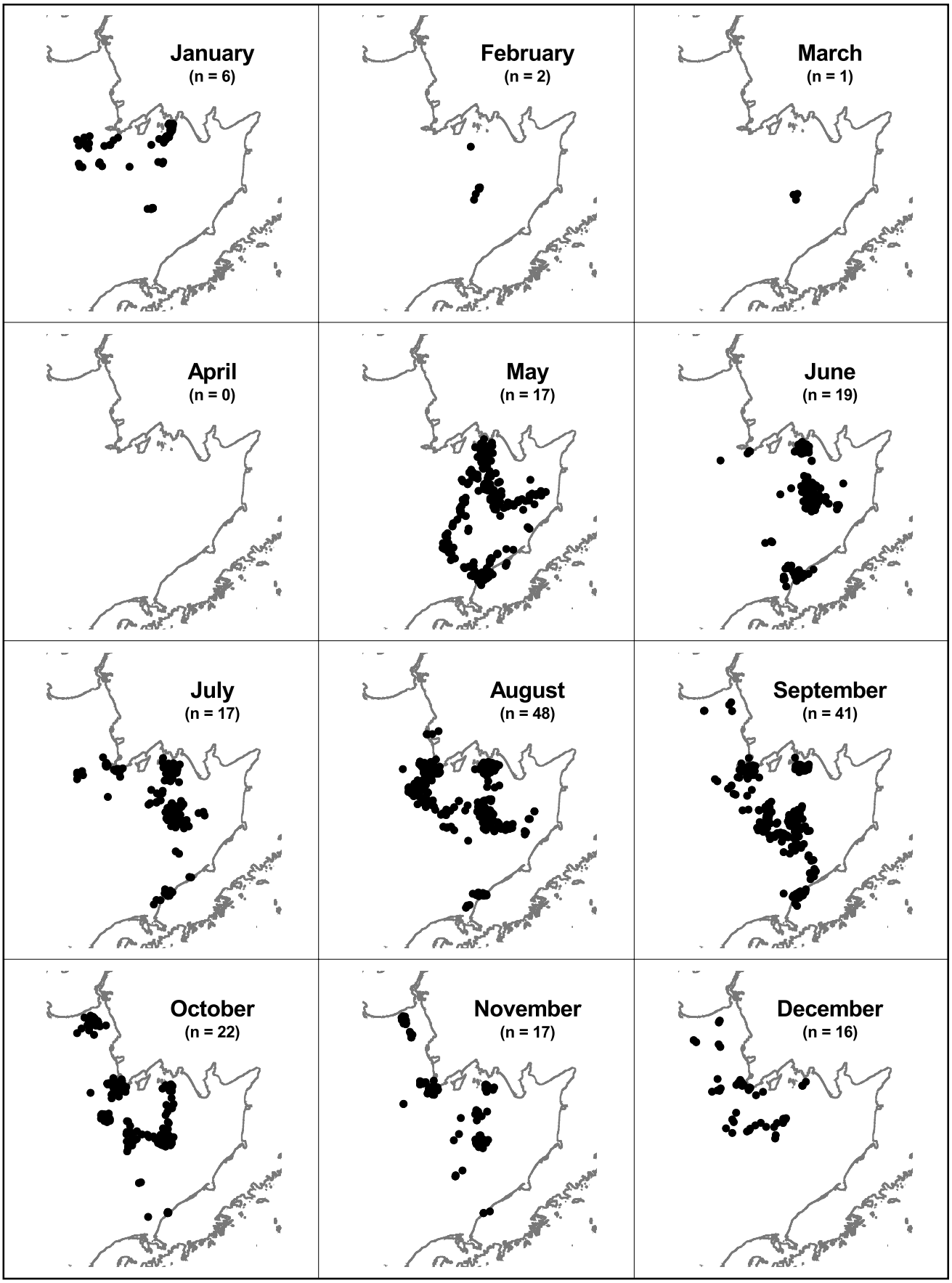

FIG. 4. Monthly locations of satellite radio-tagged walruses in Bristol Bay, 1987–2000 (n = number of animals).

After the breeding period in winter, many adult male Pacific walruses migrate into Bristol Bay in spring to forage on benthic invertebrates and replenish their fat reserves. Similarly, Atlantic walruses off northeast Greenland migrate during spring into a bay, where they forage extensively during summer. In autumn, the formation of land-fast ice forces the walruses out of the bay, and subsequently they migrate north to winter in leads and cracks in the pack ice (Born and Knutsen, 1992).

The migration of some males from Bristol Bay in autumn is most likely associated with the impending breeding season (January–February; Fay, 1982). The abandonment of coastal haul-out sites in late autumn is prompted by the development of shore ice and the sudden long-range migration of some individuals. Wiig et al. (1996) suggest that certain long-range, round-trip movements by some male Atlantic walruses from southern areas of Svalbard, observed during autumn and winter, were not directly connected with breeding activity, but rather a sort of reconnaissance in search of females. In our study, departure from the bay by some individuals as early as November might suggest that similar behaviors exist in this population, since travel distance from the bay to the ice front increases with earlier departures, and breeding does not occur until January.

Walruses in Bristol Bay were thought to move primarily westward in late autumn and winter to join adult females on the sea ice during the breeding season (Fay and Lowry, 1981; Frost et al., 1982), forming the southeast breeding aggregation (Fay, 1982). In our study, the males that overwintered in the Bristol Bay region would have comprised part of the southeast breeding aggregation; however, at least some of the males migrated long distances and would have comprised part of the southwest St. Lawrence Island aggregation. This idea is consistent with observations by Taggart (1987), who tagged nine walruses with VHF radio transmitters at RI in the summer of 1981 and observed three of these animals in November about 850 km north of the tagging location.

Although we observed several animals migrating northward from the bay, our small sample size precluded a precise estimate of the proportion of Bristol Bay animals that did so. The percentage of tagged animals outside the bay from all years combined suggests that perhaps as many as one-third of the animals migrated from the bay by January (Table 2). The mix of resident and long-range migration behaviors we observed from the Bristol Bay walruses is similar to behaviors observed in male Atlantic walruses at Svalbard, where some animals tend to overwinter in local areas while others make long-range migrations. However, some Svalbard walruses make multiple long-range, round-trip migrations within the same autumn and winter seasons (Wiig et al., 1996), a behavior we did not observe among the Bristol Bay walruses.

Considerable effort and resources were required to accomplish the tagging reported here. Capturing walruses by chemical immobilization was difficult, and transmit-

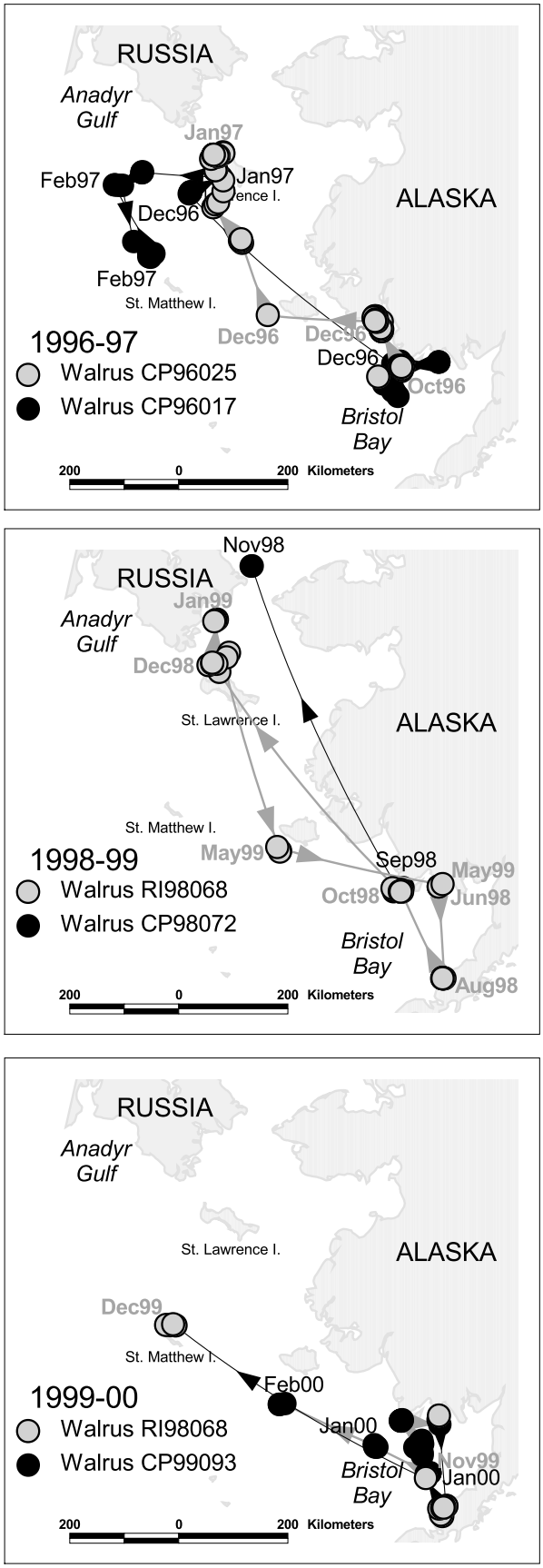

FIG. 5. Locations of five walruses observed migrating from Bristol Bay. One walrus (RI98068) is displayed in two panels because it was tracked over multiple years.

ters often failed much sooner than predicted from expected battery life. Until better methods for chemical restraint and more robust transmitters are developed, long-term tracking from a moderate sample of walruses will continue to be difficult. Future questions regarding the overall seasonal distribution and haul-out use of walruses in small areas such as Bristol Bay may be better addressed from a series of aerial surveys over the study area, perhaps in combination with haul-out counts made by land-based observers. However, such studies will not give an understanding of movements and haul-out use by individual walruses. An understanding of some of the causes of observed patterns would require comprehensive studies that include investigations into changes in prey density, distribution, and associated habitat.

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