

## Change in Abundance of Pacific Brant Wintering in Alaska: Evidence of a Climate Warming Effect?

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**ABSTRACT.** Winter distribution of Pacific Flyway brant (*Branta bernicla nigricans*) has shifted northward from low-temperate areas to sub-Arctic areas over the last 42 years. We assessed the winter abundance and distribution of brant in Alaska to evaluate whether climate warming may be contributing to positive trends in the most northern of the wintering populations. Mean surface air temperatures during winter at the end of the Alaska Peninsula increased about 1°C between 1963 and 2004, resulting in a 23% reduction in freezing degree days and a 34% decline in the number of days when ice cover prevents birds from accessing food resources. Trends in the wintering population fluctuated with states of the Pacific Decadal Oscillation, increasing during positive (warm) phases and decreasing during negative (cold) phases, and this correlation provides support for the hypothesis that growth in the wintering population of brant in Alaska is linked to climate warming. The size of the wintering population was negatively correlated with the number of days of strong northwesterly winds in November, which suggests that the occurrence of tailwinds favorable for migration before the onset of winter was a key factor in whether brant migrated from Alaska or remained there during winter. Winter distribution of brant on the Alaska Peninsula was highly variable and influenced by ice cover, particularly at the heavily used Izembek Lagoon. Observations of previously marked brant indicated that the Alaska wintering population was composed primarily of birds originating from Arctic breeding colonies that appear to be growing. Numbers of brant in Alaska during winter will likely increase as temperatures rise and ice cover decreases at high latitudes in response to climate warming.

**Key words:** Alaska Peninsula, abundance, *Branta bernicla nigricans*, climate warming, distribution, Izembek Lagoon, Pacific brant, Pacific Decadal Oscillation, wintering

**RÉSUMÉ.** Au cours des 42 dernières années, la répartition de la bernache cravant du Pacifique (*Branta bernicla nigricans*) s'est déplacée vers le nord en hiver, passant ainsi de régions faiblement tempérées à des régions subarctiques. Nous avons évalué l'abondance et la répartition de la bernache en Alaska l'hiver afin de tenter de déterminer si le réchauffement climatique contribue aux tendances positives au sein des populations d'hivernage les plus au nord. Les températures moyennes de l'air à la surface en hiver se sont accrues d'environ 1°C entre 1963 et 2004, ce qui s'est traduit par une réduction de 23 % du nombre de jours atteignant le point de congélation et d'une diminution de 34 % du nombre de jours pendant lesquels la couverture de glace empêche les oiseaux d'avoir accès aux ressources alimentaires. Les tendances caractérisant la population d'hivernage fluctuaient en fonction des états de l'oscillation pacifique décennale en ce sens qu'elles augmentaient pendant les phases positives (tièdes) et qu'elles baissaient pendant les phases négatives (froides). Cette corrélation vient appuyer l'hypothèse selon laquelle la croissance de la population d'hivernage de la bernache en Alaska est liée au réchauffement climatique. L'effectif de la population d'hivernage a été négativement corrélé au nombre de jours de vents forts en provenance du nord-ouest en novembre, ce qui laisse croire que l'occurrence de vents arrière favorables à la migration avant le début de l'hiver constituait un facteur-clé déterminant si une bernache migrerait de l'Alaska ou y restait pendant l'hiver. Dans la péninsule de l'Alaska, la répartition de la bernache en hiver variait énormément et dépendait de la couverture de glace, surtout à la lagune Izembek particulièrement achalandée. Les observations de bernaches déjà marquées ont permis de constater que la population d'hivernage de l'Alaska était principalement composée d'oiseaux provenant des colonies de reproduction de l'Arctique qui semblent prendre de l'ampleur. Le nombre de bernaches en Alaska pendant l'hiver augmentera vraisemblablement au fur et à mesure que les températures augmenteront et que les couvertures de glace diminueront en haute latitude en raison du réchauffement climatique.

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## INTRODUCTION

Rapid climate warming is occurring in the Arctic and sub-Arctic (ACIA, 2004). Over the past 100 years, average Arctic air temperatures have increased by 1.4°C, a rate that is nearly twice the global average (0.7°C; IPCC, 2007). Most of the warming during this period has occurred since 1976, at rates higher than at any other time during the past 1000 years (IPCC, 2001). As a consequence, most high-latitude regions are experiencing increasing periods of above-freezing temperatures and diminishing snow and ice cover (Stone et al., 2004).

Climate affects the movement and distribution of fauna, often directly through species-specific physiological tolerances to temperature and precipitation, but also indirectly, through impacts on the availability and abundance of food resources (Root, 1988; Hoffman and Parsons, 1997). In the current global warming scenario (IPCC, 2007), the expectation is that species will respond to warming trends by shifting their distributions to higher latitudes or elevations (but see Helmuth et al., 2002). Northward shifts in the breeding ranges of many species of birds have been reported in Europe (Burton, 1995) and North America (Hitch and Leberg, 2007). In Britain, Thomas and Lennon (1999) found that 59 species of birds had shifted the northern boundaries of their breeding ranges an average of 19 km northward over a 20-year period (i.e., 1968–72 to 1988–91). Some evidence also points towards a poleward movement in winter distribution of temperate species of birds in North America (Johnson, 1994; Root and Weckstein, 1995; LaSorte and Thompson, 2007), although published accounts are relatively sparse. Nevertheless, shifts in distribution of animals may be more evident in migratory birds than in resident birds because the migrators are more apt to move in response to environmental and climatic changes (Parmesan et al., 1999; LaSorte and Thompson, 2007). Also, shifts in distribution are likely to be more apparent during winter (January to March) because over the last 100 years, average daily temperatures have increased more rapidly in that season than in other seasons (IPCC, 2007).

Pacific brant (*Branta bernicla nigricans*; hereafter brant) winter along the Pacific coast of North America, over a wide geographic range extending from Alaska (55° N) to Sinaloa, Mexico (24° N). Until recently, however, more than 70% of this population had traditionally wintered in Mexico (Reed et al., 1998). Brant are currently exhibiting a northward shift from their primary wintering areas in Baja California that appears related to changes in the availability and abundance of eelgrass (*Zostera marina*), their primary food during the nonbreeding season (Ward et al., 2005). Numbers of brant are increasing throughout their northern wintering

range, with greatest gains occurring in Alaska relative to the other sites north of Mexico. In Alaska, brant are increasing along the Alaska Peninsula at Izembek Lagoon and adjacent embayments, where virtually the entire eastern Pacific Flyway population stages in fall prior to trans-oceanic migration to wintering areas (Reed et al., 1989, 1998; Dau, 1992). This increase in wintering numbers has coincided with a general warming of temperatures in the North Pacific (Zveryaev and Selemenov, 2000; Mantua and Hare, 2002), suggesting that environmental conditions may have changed for one of the northernmost-wintering populations of geese.

Here, we examine 42 years of observational data on wintering brant in Alaska to determine whether climatic conditions may be contributing to positive trends in this population. Specifically, we assess winter use patterns and long-term trends in abundance of brant along the Alaska Peninsula to ascertain when this population increased and to understand whether growth in the Alaska population was influenced by environmental (e.g., ice-cover, temperature) changes resulting from climate warming. We also examine the breeding origin of the birds in the Alaska wintering population to determine whether growth in the winter population was related to increases in particular segments of the breeding population.

## METHODS

### *Study Area*

We analyzed data collected on brant during winter (1 December–15 March) between 1963 and 2004 at the western end of the Alaska Peninsula (162.5–163.5° W longitude), a narrow landmass that separates the Bering Sea from the Pacific Ocean (Fig. 1). This remote region of tundra and steep volcanic mountains is edged by shallow-water embayments containing extensive intertidal stands of eelgrass (Ward et al., 1997). These areas are accessible to feeding brant when tide height falls about 1.0 m below mean lower low water (Ward and Stehn, 1989). In winter, diurnal feeding opportunities are further limited by reduced periods of daylight. The average daily number of daylight hours when eelgrass is available for foraging ranges from about two hours in December to seven hours in March (Mason et al., 2006). Nocturnal foraging may also occur (Lane and Hassall, 1996), but it has not been detected on the Alaska Peninsula.

Izembek Lagoon supports the majority of the birds staging on the Alaska Peninsula in fall (> 80%) and spring (100%) (Ward and Stehn, 1989). Most birds arrive

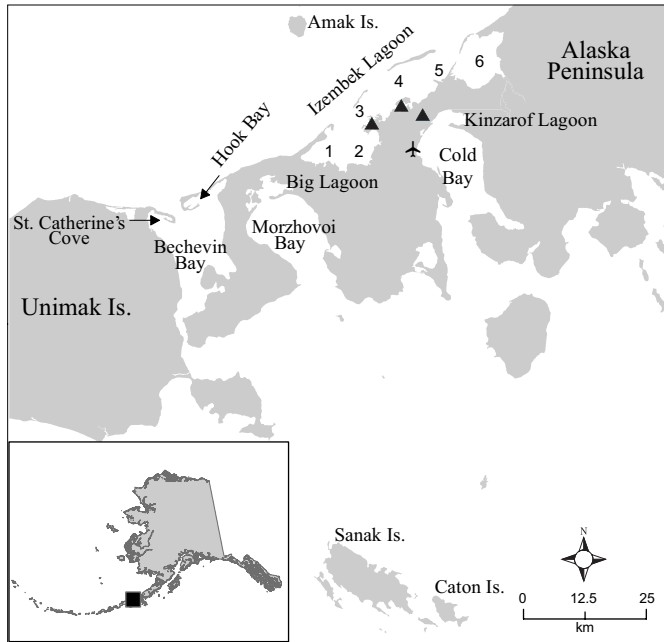


FIG. 1. Wintering sites used by Pacific brant on the Alaska Peninsula. Numbers one to six indicate the areas surveyed during aerial counts of brant in Izembek Lagoon, and triangles mark locations where brant were counted during the annual Christmas Bird Count of Izembek and Kinzarof lagoons.

at Izembek Lagoon by early October and depart by late November (Reed et al., 1989). Spring migrants begin returning to the lagoon in early April (Mason et al., 2007). Winter distribution of brant on the Alaska Peninsula is largely confined to four embayments (Dau and Ward, 1997): Izembek Lagoon, Kinzarof Lagoon, Big Lagoon in northern Morzhovoi Bay, and northern Bechevin Bay (including Hook Bay and St. Catherine's Cove; Fig. 1). Brant also use intertidal areas adjacent to the Sanak Islands and Caton Island (Jones, 1952; Dau and Chase, 1995), but survey data there are limited by the remoteness of these islands, which are located 75 km south of the study area. Winter observations of brant have been rare at other coastal areas on the Alaska Peninsula, and when birds were observed, flock sizes were small (< 100 birds) (Boden, 1994; Larned, 2000).

The climate in this region is maritime, but it becomes more continental in winter when Arctic sea ice extends south into the Bering Sea (Brower et al., 1977). Winter weather is harsh and highly influenced by the position and strength of the Aleutian Low and the Arctic High atmospheric pressure systems (Niebauer, 1983; Overland et al., 1999; Rodionov et al., 2005). Storms and high winds are frequent, and the ubiquitous precipitation fluctuates almost continually between rain and snow (Brower et al., 1977). Arctic sea ice (concentrations of more than 70% cover) generally moves south into the Bering Sea beginning in November, reaching an average southern extent at about 57° N in February (National Ice Center, unpubl. data). Only twice in the last 30 years (winters of 1971–72 and 1973–74) has sea ice extended south to the tip of the Alaska Peninsula (55° N). Shorefast ice, however, is a regular feature of shallow-water embayments in the region between November and April.

Shorefast ice forms initially in protected shallow estuaries before expanding into the more exposed and deeper water areas, where ice formation can be disrupted by winds and currents. The extent of shorefast ice cover in estuaries on the Alaska Peninsula is highly variable, and it is greater on the north side of the peninsula (Brower et al., 1977).

Marine ecosystems of the North Pacific and Bering Sea vary with interdecadal (15–25 or 50–70 years) climatic shifts, commonly described by the Pacific Decadal Oscillation (PDO; Mantua and Hare, 2002). The PDO is a large-scale ocean-atmospheric phenomenon that is measured by an index derived from temporal (monthly) and spatial changes in the sea surface temperatures and sea-level pressure in the North Pacific (above 20° N). Three climate shifts (warm vs. cold phases) in the 20th century were described by the PDO index; the most recent occurred in winter of 1976 (Minobe, 1997; Hare and Mantua, 2000). Analyses of long-term biological and physical data provide evidence that the North Pacific and Bering Sea experienced a cold phase (negative PDO values) and a period of low productivity and biomass in fish stocks and zooplankton between 1964 and 1977 (Anderson and Piatt, 1999; Hare and Mantua, 2000). After this period, the region entered a warm phase (positive PDO values) and a period of enhanced biological productivity and biomass. This warm phase has persisted through the 2000s except for short-term cold periods in 1989–91 and 1998–2001 (Hare and Mantua, 2000).

#### *Environmental Data*

To examine long-term variation in climatic conditions within the winter range of brant on the Alaska Peninsula, we obtained daily weather records (i.e., surface air temperature, precipitation, and surface wind direction and speed) collected at the Cold Bay airport (55.13° N, 162.44° W) between 1963 and 2004 from the National Climatic Data Center (2004). The airport is near (< 13 km) to Izembek and Kinzarof lagoons, which form the northeastern portion of the wintering range of brant on the Alaska Peninsula (Fig. 1). From this dataset we used daily air temperature to calculate freezing degree days (FDD) per year by summing the daily mean air temperatures of days with mean temperatures below 0°C. FDD were given a plus sign for purposes of analysis and display. Additionally, we estimated the percent cover of shorefast ice in each embayment during the periodic aerial surveys to census brant.

#### *Population Indices*

We assessed trends in population size of brant wintering in Alaska using two long-term indices: aerial survey data and Christmas Bird Count (CBC) data. Since 1986, systematic aerial surveys of wintering brant have been conducted annually along the Alaska Peninsula. These replicate surveys (≥ 2 counts in most winters) include coverage of the four main embayments used by brant in winter and provide the most complete estimate of the total number of brant in

Alaska (Pacific Flyway Council, 2002). Counts of brant at Izembek Lagoon were divided further into six survey areas (Fig. 1) to differentiate use within this lagoon. These areas were delineated by physiographic features, such as tidal channels, peninsulas, or islands. The CBC, which has been conducted annually since 1963 (except in 1967, 1970, and 1971) at Izembek and Kinzarof lagoons, provides a long-term index of brant abundance in these lagoons. The CBC is made in late December–early January by staff of the Izembek National Wildlife Refuge, who scan the central portion of Izembek Lagoon and western Kinzarof Lagoon from basically the same vantage points each year (Fig. 1). The CBC data were correlated positively with the aerial survey data ( $r = 0.49$ ,  $n = 19$ ,  $p = 0.03$ ; Pearson product-moment correlation coefficient test), indicating that the CBC was a reasonably good index of the number of brant in the region and a gauge to trends in the brant population on the Alaska Peninsula before systematic aerial surveys began in 1986.

Trends were also examined in a third population index for brant, the Pacific Flyway midwinter count, to examine changes in Alaska winter population relative to the overall size of the population. The Pacific Flyway population estimate (Pacific Flyway Council, 2002) is a compilation of aerial survey and ground counts of brant collected from Alaska to Mexico in mid-January each year. This estimate has proven to be reasonably accurate for evaluating changes in overall size of the entire population (Sedinger et al., 1994).

### *Breeding Origin*

We resighted color-marked brant at Kinzarof Lagoon during February 1994, 1996, 1997, and December 1999 to determine the breeding origin of birds in the wintering population. Adults and goslings had been marked previously with uniquely encoded, colored tarsus bands (Sedinger et al., 1997) at one sub-Arctic site, the Yukon-Kuskokwim Delta (YKD), Alaska, where about 80% of the Pacific Flyway population breeds (Pacific Flyway Council, 2002), and two Arctic sites, the Arctic coastal plain of Alaska (ACP) and the western Canadian Arctic (WCA), including Liverpool Bay and Banks Island, Northwest Territories, Canada. Tarsus bands were observed through variable-power spotting scopes during high ebb tides, when birds stood on sand bars to preen and acquire grit (Ward et al., 2004).

### *Data Analysis*

We used linear regression models to examine trends across the 42-year study period in average daily winter temperatures, number of FDD, and estimated number of days with extreme ice conditions. We were unable to use satellite imagery to measure the extent of shorefast ice because such images were lacking for much of the western end of the Alaska Peninsula during the study period. Therefore, we estimated extreme ice conditions in Izembek Lagoon by developing a model of FDD (Eicken, 2003). Extreme ice

conditions were defined as days when eelgrass beds became inaccessible to brant at Izembek Lagoon or when shorefast ice covered more than 70% of the eelgrass in the lagoon as determined by observations of ice cover relative to the known distribution of eelgrass in this lagoon (Ward et al., 1997). To account for the considerable lag in the formation and melting of ice caused by both wind and heat stored in the water, we used a lag time of four days and calculated a modified estimate of FDD using below-freezing temperatures with no above-freezing episodes longer than four days (FDD-4d). We tested the relationship of FDD-4d to our observed estimates of ice cover at Izembek Lagoon by plotting the maximum ice cover for each year as a function of the FDD-4d for the time interval prior to the observations. FDD-4d was a reasonably good predictor ( $F = 12.3$ ,  $df = 12$ ,  $p < 0.001$ ) of shorefast ice cover, explaining 67% of the variance in the percent of peak ice cover in this lagoon (Fig. 2). Using this relationship, we determined that FDD-4 values higher than 60 indicated more than 70% ice cover for that day in Izembek Lagoon (Fig. 2). We then calculated FDD-4d for all years and used FDD-4d values of more than 60 to estimate the number of days with extreme ice conditions on the Alaska Peninsula. We used the Kruskal-Wallis test to compare average ( $\pm$  SE) daily temperatures and number of days with extreme ice cover between cold phases (< 1977, 1989–91, and 1998–2001) and warm phases (1978–88, 1992–97, and 2002–04) of the PDO.

We assessed trends in the three population indices using loglinear Poisson regression models in program TRIM v3.53 (Pannekoek and van Strien, 2000; van Strien et al., 2001). Trends were estimated using a times-effect model adjusted for serial correlation and lack of model fit (overdispersion). Missing values in the CBC data were handled by producing a model based on existing counts and using this model to predict those values that were missing. Trends were then calculated for the entire dataset using predicted counts from the model in place of the missing values.

Brant counted during winter surveys represented birds that had already decided to winter in Alaska. To assess the influence of climatic variability on annual changes to the winter brant population in Alaska (aerial survey data), therefore, we examined models of climatic parameters occurring during fall staging (September–November) that may act as cues to birds in deciding whether to stay in or migrate from Alaska. For this analysis, we used the winter aerial survey data as the dependent variable and explored the influence of four climatic parameters during September–November: mean surface air temperatures, FDD, values of the PDO-index (<http://jisao.washington.edu/pdo/PDO.latest>), and the number of days of northwesterly (270–360°) winds in November (our proxy for weather conditions favorable to migration). Dau (1992) showed that the majority of brant migrate from Alaska in November, when strong Aleutian Low pressure systems generate powerful tailwinds that can aid southward migration. We defined a day of northwesterly winds as one when average daily surface winds exceeded 18 km/hr, a minimum wind speed at peak departure of

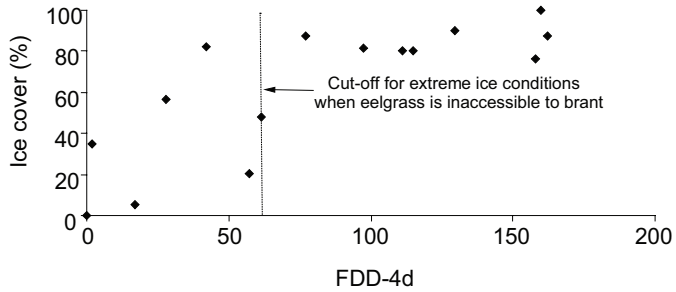


FIG. 2. Relationship between freezing degree-days with no above-freezing episodes longer than four days (FDD-4d) and peak ice cover observed each winter between 1986 and 2004 at Izembek Lagoon. FDD-4d values to the right of the dashed line represent extreme ice conditions, when ice covered 70% or more of the lagoon and eelgrass was inaccessible to brant.

brant from Izembek Lagoon (Dau, 1992). We developed candidate models from all possible combinations of the four parameters and ranked models based on the Akaike Information Criterion adjusted for sample size ( $AIC_c$ ; Burnham and Anderson, 2002). We calculated  $AIC_c$  weights ( $w_i$ ) to compare the relative support for each model and  $R^2$  values to indicate overall model fit. Finally, we calculated model-averaged parameter estimates and unconditional standard errors based on Akaike weights for parameters of interest (Burnham and Anderson, 2002).

Using the winter aerial survey data, we evaluated the distribution of brant among the four embayments and within the six areas of Izembek Lagoon by comparing means and overlap of 95% confidence intervals. The influence of ice cover on the distribution of brant at Izembek Lagoon and the other three embayments was tested using regression analysis.

To determine the breeding origin of birds, we used chi-square contingency tests to compare the distribution of tarsus-marked brant from the different breeding areas. We used only direct resightings (i.e., observations of individuals that were marked in the previous summer) to eliminate uncertainty introduced by breeding dispersal (Lindberg et al., 1998; Sedinger et al., 2008). The expected number of tarsus-marked birds in the winter population was based on the total number of brant tarsus-marked in the summer preceding the winter observations. We assumed that adult survival between banding and arrival on the Alaska Peninsula was similar among breeding populations, because Sedinger et al. (2002) found adult annual survival was similar among sub-Arctic and Arctic breeding populations. Because juvenile survival between banding and arrival on the Alaska Peninsula differs between sub-Arctic and Arctic populations (Ward et al., 2004), we adjusted the expected number of juveniles in the winter population for differential seasonal survival using Ward et al.'s (2004) monthly survival estimates of 0.68 for juveniles from the sub-Arctic (YKD) and 0.94 for juveniles from the Arctic (ACP and WCA) calculated over the 2.33 month period between banding and arrival on the Alaska Peninsula. Because the number of direct observations was small in any given year, we conducted the analysis on data combined across the four winters.

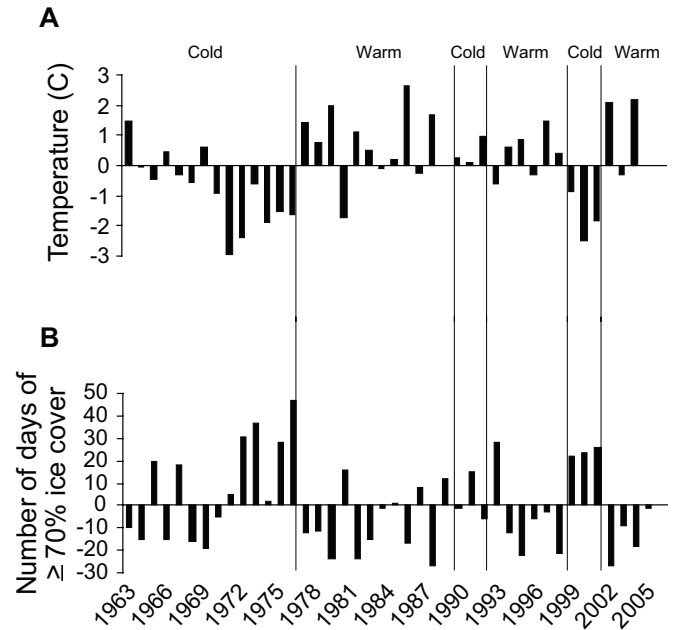


FIG. 3. Deviations from the 1963–2004 mean in (A) average daily surface air temperatures and (B) number of days of extreme ( $\geq 70\%$ ) ice conditions during winter at Izembek Lagoon. Vertical lines separate cold phases (before 1977, 1989–91, and 1998–2000) and warm phases (1978–97 and after 2000) of the Pacific Decadal Oscillation.

## RESULTS

Between 1963 and 2004, average daily surface air temperature in winter increased by  $1^\circ\text{C}$ , resulting in a 10-day reduction (23% decline) in FDD. Periods of warm temperatures (Fig. 3A) and reduced ice cover (Fig. 3B) were evident after the 1976 climate shift except during the short-term climate shift of 1998–2001, when average daily winter temperatures dropped below the long-term mean. On average, days with extreme ice cover occurred 1.5 times as often ( $p = 0.03$ ) before 1977 (mean =  $41 \pm 5$  days,  $n = 14$  years) than after 1976 (mean =  $27 \pm 3$  days,  $n = 28$  years) (Fig. 3B).

### Population Changes

A strong positive trend ( $p < 0.01$ ;  $7 \pm 1\%$  growth per year) existed in the aerial counts of brant along the Alaska Peninsula between 1986 and 2004 (Fig. 4A). The Alaska wintering population was generally larger than predicted during warm phases and smaller than predicted during cold phases of the PDO. Mean number of brant from the CBC data was significantly lower ( $p = 0.02$ ) before 1977 (mean =  $110 \pm 51$  birds,  $n = 14$ ) than after 1976 (mean =  $1331 \pm 413$  birds,  $n = 28$ ). Positive trends in the Alaska wintering population were also apparent in the longer-term CBC data ( $p < 0.01$ ;  $11 \pm 1\%$  growth per year; Fig. 4B). Where years of the two indices overlapped, patterns of change in the CBC index were similar to that of the aerial survey data. Gains in the Alaska wintering population occurred despite an overall stable trend in the entire wintering population of brant in the Pacific Flyway ( $p = 0.63$ ; Fig. 4A).

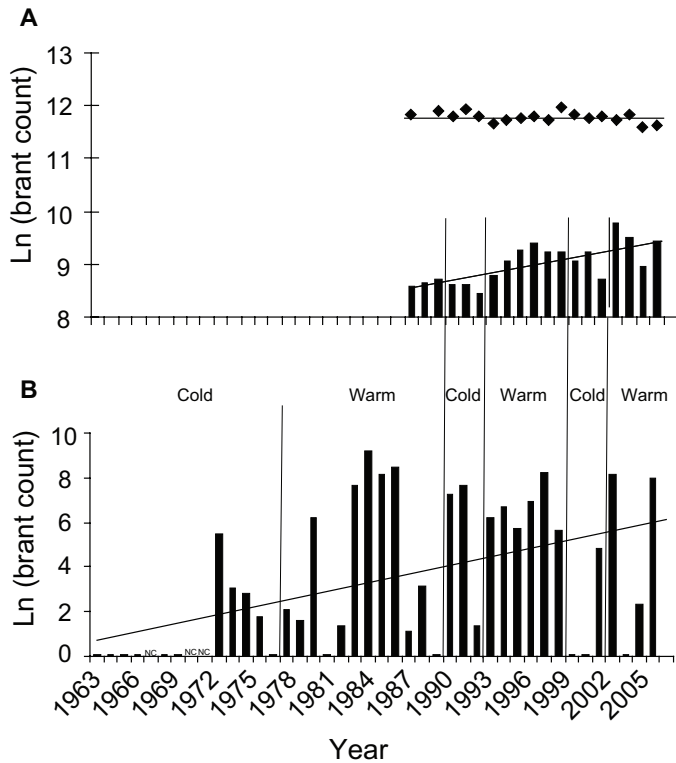


FIG. 4. Change in number of wintering Pacific brant counted during aerial surveys in the Pacific flyway (Alaska to Mexico; A-top) and along the Alaska Peninsula (A-bottom) between 1986 and 2004, and during the Christmas Bird Counts at Izembek and Kinzarof lagoons between 1963 and 2004 (B). NC indicates no count. Vertical lines separate cold phases (before 1977, 1989–91, and 1998–2000) and warm phases (1978–97 and after 2000) of the Pacific Decadal Oscillation. Horizontal lines indicate trends in survey data, either stable (A-top) or increasing (A-bottom and B).

Our examination of variation in the number of brant wintering on the Alaska Peninsula showed there is strong support for its relationship to the number of days with strong northwesterly winds in November. This parameter was included in the five top models (combined  $AIC_c$  weight = 0.87; Table 1) and when examined as a single variable, explained the greatest proportion of the variation in the aerial survey data ( $R^2 = 0.27$ ) of the four fall climatic variables tested, nearly twice that of the next most important fall climatic parameter, FDD\_fall ( $R^2 = 0.14$ ). The population of brant wintering in Alaska increased as the number of days with strong northwesterly winds in November decreased (model averaged estimate =  $-446.5 \pm 176.7$ ; note SE did not overlap 0). On average, November had six fewer days with strong northwesterly winds during warm phases of the PDO (mean =  $9 \pm 1.0$  days) than during its cold phases (mean =  $15 \pm 1.2$  days) (Fig. 5).

#### Distribution Patterns

Brant were not distributed evenly among the four embayments between 1986 and 2004 (Fig. 6A). Mean numbers of brant were greater at Bechevin Bay and Izembek Lagoon than at the other sites. Within Izembek Lagoon, brant tended to use area 5 the most, and areas 6 and 2 the least

(Fig. 6B). Ice cover did not affect brant numbers similarly among the four embayments (Fig. 6C). At Izembek Lagoon, brant numbers decreased as ice cover increased ( $F = 5.27$ ,  $df = 1$ ,  $p = 0.03$ ,  $R^2 = 0.15$ ), while at the other three sites combined, brant numbers rose slightly with increasing ice cover, though this change was not significant ( $F = 2.29$ ,  $df = 1$ ,  $p = 0.14$ ).

#### Breeding Origin

Over four winter seasons, we resighted 290 color-marked brant, representing 227 individuals. A greater proportion of the resighted brant were from the two Arctic breeding colonies than from the one sub-Arctic colony (samples pooled across years:  $\chi^2 = 11.1$ ,  $p = 0.004$ ). Observations were equally distributed between ACP and WCA, the two Arctic breeding colonies where birds were marked; each accounting for 34% of the resightings.

## DISCUSSION

The shift in climate to a positive (warm) phase of the PDO after 1976 had a well-documented impact on the abundance and distribution of a variety of marine species (e.g., pandalid shrimp, *Pandalus* spp.; walleye pollack, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*; kittiwake gulls, *Rissa* spp.; thick-billed murre, *Uria lomvia*; northern fur seals, *Callorhinus ursinus*) in the Bering Sea and Gulf of Alaska (Mantua et al., 1997; Anderson and Piatt, 1999; Hunt et al., 2002). Effects on organisms restricted to estuarine ecosystems have not yet been investigated. Our study provides evidence that the growth in the brant population wintering on the Alaska Peninsula was linked to this same climate shift. This linkage is based on two lines of evidence. First, although records are sparse, few (< 3000 birds) brant were detected wintering in Alaska prior to 1977 from CBC surveys (Fig. 4B), boat surveys by Jones (1952, 1955), and anecdotal accounts from residents of the region (Dau and Ward, 1997). Second, numbers of brant increased after 1976, and fluctuations in winter population indices coincided with the phases of the PDO, increasing during warm phases and decreasing during cold phases (Fig. 4).

We suggest that a large portion of the increase in the wintering brant population is related to a general improvement in coastal environmental conditions for brant at the western end of the Alaska Peninsula. Our findings of increased air temperatures, decreased number of FDD, and reduced extent of shorefast ice are consistent with a general change in climatic patterns that has resulted in warmer winters in southwestern Alaska (Zveryaev and Selemenov, 2000; Hartman and Wandler, 2005). We contend that the milder winter conditions and reductions in ice cover have improved the accessibility of eelgrass and reduced thermoregulatory demands for wintering brant in Alaska. Accessibility (i.e., availability and abundance) of eelgrass is a major factor affecting movements, distribution, and abundance of brant at other areas during

TABLE 1. Selection of models to assess the influence of climatic variability in fall on annual winter population size for Pacific brant on the Alaska Peninsula, 1986–2004.

Model <sup>1</sup>	K <sup>2</sup>	AIC <sub>c</sub> <sup>3</sup>	ΔAIC <sub>c</sub> <sup>4</sup>	w <sub>i</sub> <sup>5</sup>	R <sup>2</sup>
Days_NWwind_Nov, PDO_fall	4	309.15	0	.401	0.43
Days_NWwind_Nov	3	310.76	1.61	.179	0.27
Days_NWwind_Nov, AirTemp_fall	4	312.38	3.23	.080	0.33
Days_NWwind_Nov, PDO_fall, AirTemp_fall	5	312.52	3.37	.074	0.44
Days_NWwind_Nov, PDO_fall, FDD_fall	5	312.79	3.64	.065	0.44
FDD_fall	3	313.81	4.66	.039	0.14
Days_NWwind_Nov, FDD_fall	4	313.94	4.79	.037	0.27
PDO_fall, FDD_fall	4	314.37	5.22	.029	0.25
Days_NWwind_Nov, FDD_fall, AirTemp_fall	5	314.76	5.61	.024	0.37
FDD_fall, AirTemp_fall	4	314.88	5.73	.023	0.23
PDO_fall	3	315.18	6.03	.020	0.07
Days_NWwind_Nov, PDO_fall, FDD_fall, AirTemp_fall	6	316.16	7.01	.012	0.47
AirTemp_fall	3	316.63	7.48	.010	0.01
PDO_fall, FDD_fall, AirTemp_fall	5	317.25	8.10	.007	0.29
PDO_fall, AirTemp_fall	4	318.06	8.91	.005	0.09

<sup>1</sup> Model parameters included Days\_NWwind\_Nov, number of days of northwesterly winds in November with average daily surface wind speed over 18 km/hr and direction between 270° and 360°; PDO\_fall, average values of the Pacific Decadal Oscillation index during fall (September–November); AirTemp\_fall, average air surface temperatures during fall; FDD\_fall, average sum of the freezing degree days during fall.

<sup>2</sup> Number of parameters in each model.

<sup>3</sup> Akaike's Information Criterion value adjusted for small sample size.

<sup>4</sup> Difference in AIC<sub>c</sub> value relative to the model with the lowest AIC<sub>c</sub>. A ΔAIC<sub>c</sub> of 0 indicates the best model.

<sup>5</sup> The Akaike weight of each model.

winter (Lindberg et al., 2007) and spring staging (Wilson and Atkinson, 1995; Moore et al., 2004). Thermoregulatory demands are relatively high for wintering brant in Alaska (Mason et al., 2006), and undisturbed access to sufficient amounts of eelgrass is likely crucial to their winter survival, especially considering the access limitations imposed by short daylight foraging opportunities and regular periods of extreme ice cover in December and January. There are no published data to indicate whether eelgrass accessibility or brant survival has increased in Alaska. Nevertheless, Mason et al. (2006), who compared the nutritional condition of wintering brant in Alaska and Mexico under the current climatic conditions, found that physiological demands were similar for the two wintering populations, indicating that the birds were capable of employing either wintering strategy (i.e., winter residency or migration). Further, with the relatively higher nutritious value of eelgrass in Alaska and its closer proximity to breeding areas, recent milder conditions on the Alaska Peninsula may provide a selective advantage for brant to stay north (Mason et al., 2006).

The increase in wintering brant in Alaska is likely a result of birds “short-stopping” on their southward migration flight and remaining north of their traditional wintering areas. This behavior is not uncommon in Arctic-nesting geese and has been documented in association with, among other factors, increases in food availability and temperature at northern sites (see Calvert et al., 2005). Individual brant also appear capable of changing their migration strategy between years, as evidenced by the 15% (34 of 227) of individuals resighted in different years at either an Alaskan or a southern wintering site (D. Ward, unpubl. data).

Our finding of a negative correlation between the size of the Alaska wintering population and the number of days with strong northwesterly winds in November corroborates a recent theoretical evaluation of migration strategies of Pacific brant. Purcell and Brodin (2007) found that changes in the occurrence of tailwinds prior to onset of winter, in combination with even a slight increase in survival (resulting from milder winters), could cause a sudden shift in wintering strategy from a long-distance migration to either a short-distance detour migration or winter residency on the Alaska Peninsula. Together, these investigations emphasize the importance of tailwinds for successful brant migration from Alaska, an event that is characterized by a long period (ca. two months) of slow fuel gain before departure and an initial non-stop flight across the Gulf of Alaska (without the possibility of refueling) of at least 2000 km for detour migrants and up to 5500 km for long-distance migrants (Ward and Stehn, 1989; Dau, 1992). We anticipate that brant numbers will continue to increase during winter in Alaska given climate predictions for increasing temperatures and decreasing ice at high latitudes (IPCC, 2007) and a northward shift in the storm track of the Aleutian Low pressure system (McCabe et al., 2001; Salanthé, 2006) that will likely reduce the opportunities for wind-aided migration. As more brant opt to winter in Alaska, more of the population will be put at risk should mild winters be punctuated by any extended periods of severe cold weather and extreme shorefast ice cover, as occurred in winter of 1991–92 (Fig. 3B). Such scenarios are likely to become more frequent if predictions that couple climate warming to greater climate variability and a rise of extreme weather events prove accurate (IPCC, 2007).

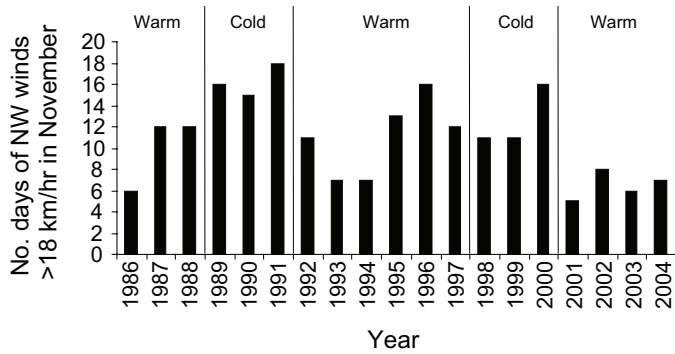


FIG. 5. Frequency of days with strong (> 18 km/hr) northwesterly (270–360°) winds in relationship to cold phases (1989–91 and 1998–2000) and warm phases (1986–88 and after 2000) of the Pacific Decadal Oscillation.

*Breeding Origin*

Most brant in the Alaska winter population were from Arctic breeding colonies. We believe this interpretation to be accurate for two reasons. First, while observations were made at only one embayment, Kinzarof Lagoon, we regularly observed flocks of brant moving between Kinzarof and Izembek lagoons and between Izembek and western embayments, which suggests that breeding populations were mixing among wintering locations on the Alaska Peninsula. Second, we were conservative in our test of the relative contributions of the different breeding colonies to the wintering population because in calculations of bands available for observation from the respective populations, we used the lowest survival estimate for birds from the larger sub-Arctic colony and the highest survival estimate for birds from the smaller Arctic colonies (Ward et al., 2004).

We cannot rule out that a portion of the increase in the Alaska wintering population has been caused by growth in the Arctic breeding population. Although this component of the brant breeding population, which represents more than 15% of the overall Pacific Flyway population of nesting brant (Sedinger et al., 1993; Pacific Flyway Council, 2002), has never been systematically surveyed, there is indirect evidence that it has grown since the mid 1990s. For instance, on the Arctic Coastal Plain of Alaska, numbers of brant nests were stable from the mid 1970s to the early 1990s (Stickney and Ritchie, 1996), but increased in the mid 1990s (Sedinger and Stickney, 2000). A similar pattern of stability followed by a slight positive trend was evident in the number of brood flocks in the Arctic between 1976 and 2005 (Flint et al., 2008). Consistent with the notion of a growing Arctic population, survival of western Canadian Arctic brant improved for adults (> 15%) and juveniles (> 40%) between the 1960s and 1970s and 1991–2001 (Hines and Brooks, 2008). Together these trends suggest that the Arctic population has grown, particularly since the early 1990s, and that if these birds have a propensity to stay north during winter (as band resightings suggest), it has contributed to the increase in the Alaska wintering population.

Our study shows that the western end of the Alaska Peninsula has become an important wintering area for

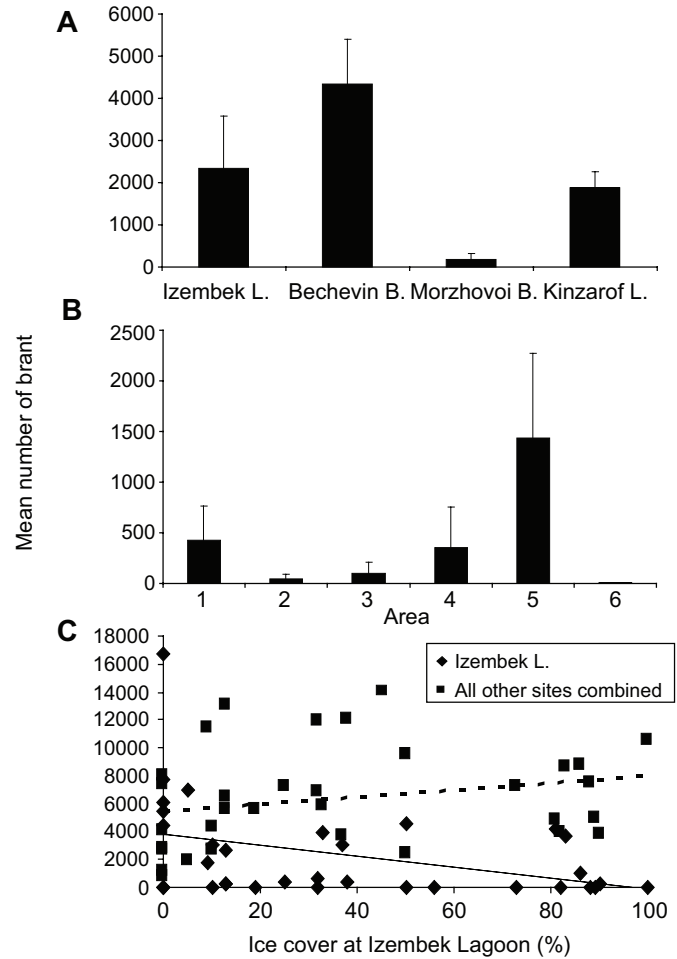


FIG. 6. Mean number ( $\pm$  95% CI) of brant counted on 33 aerial surveys in four embayments on the Alaska Peninsula (A) and within six areas of Izembek Lagoon (B) between 1986 and 2004. Also shown is the relative pattern of brant use at Izembek Lagoon and the three other wintering areas combined in relation to shorefast ice cover in Izembek Lagoon (C). Locations of embayments and survey areas within Izembek Lagoon are shown in Figure 1.

brant and that they are capable of adapting to the changing environmental conditions in the region. Since the end of our study in 2004, numbers of wintering brant in Alaska have continued to rise, highlighting the increased importance of the region. Currently, the Alaska Peninsula supports 25–30% (up to 40 000 birds) of the entire Pacific flyway population of brant during winter and contains the greatest concentration of brant outside of Mexico (Drut and Trost, 2008). Given that significant numbers of brant now regularly use the Alaska Peninsula for up to eight months of the year, it would be prudent to determine the region’s carrying capacity for brant and assess patterns of local movements by birds in relation to the abundance and distribution of eelgrass in all embayments and on the nearshore islands. It is also important to understand the effects (whether positive or negative) on the region’s carrying capacity related to increasing climate change pressures (e.g., increasing sea levels, coastal erosion, temperatures, and CO<sub>2</sub> levels) and proposed nearshore and coastal development (e.g., oil and gas development in the North Aleutian Basin; Minerals



Management Service, 2007). Finally, any threats to the Alaska wintering population have implications for the entire Pacific Flyway population; therefore, further monitoring of brant in Alaska in winter is warranted, especially given that this species is experiencing a long-term decline and is of conservation concern across its range (Pacific Flyway Council, 2002; Ward et al., 2005).

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#### REFERENCES

- ACIA (Arctic Climate Impact Assessment). 2004. Impacts of a warming Arctic: Arctic climate impact assessment. Cambridge: Cambridge University Press. 140 p.
- Anderson, P.J., and Piatt, J.F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117–123.
- Boden, K. 1994. Comparative results from aerial waterfowl surveys of the Alaska Peninsula, March–May 1993. Unpubl. USFWS report. Available from U.S. Fish and Wildlife Service, Migratory Bird Management-Region 7, 1011 East Tudor Road, Anchorage, Alaska 99503.
- Brower, W.A., Jr., Diaz, H.F., Prechtel, A.S., Searby, H.W., and Wise, J.L. 1977. Climatic atlas of the outer continental shelf waters and coastal regions of Alaska. Vol. II, Bering Sea. Alaska Outer Continental Shelf Environmental Assessment Program. Final Report. Research Unit No. 347. Anchorage: U.S. Department of Commerce, National Oceanic and Atmospheric Administration.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. New York: Springer-Verlag.
- Burton, J.F. 1995. Birds and climate change. London: Christopher Helm.
- Calvert, A., Gauthier, G., and Reed, E. 2005. Spatiotemporal heterogeneity of greater snow geese harvest and implications for hunting regulations. *Journal of Wildlife Management* 69:561–573.
- Dau, C.P. 1992. The fall migration of Pacific Flyway brent *Branta bernicla* in relation to climatic conditions. *Wildfowl* 43: 80–95.
- Dau, C.P., and Chase, M.A. 1995. Aerial survey of wintering birds and mammals in the Sanak Islands. Unpubl. USFWS report. Available from U.S. Fish and Wildlife Service, Migratory Bird Management-Region 7, 1011 East Tudor Road, Anchorage, Alaska 99503.
- Dau, C.P., and Ward, D.H. 1997. Pacific brant wintering along the lower Alaska Peninsula: Population size, age composition and breeding derivation. Unpubl. USFWS report. Available from U.S. Fish and Wildlife Service, Migratory Bird Management-Region 7, 1011 East Tudor Road, Anchorage, Alaska 99503.
- Drut, M.S., and Trost, R.E. 2008. Annual summary of goose population monitoring programs in the Pacific Flyway, 2007–2008. Annual report. Portland, Oregon: U.S. Fish and Wildlife Service.
- Eicken, H. 2003. From the microscopic to the macroscopic to the regional scale: Growth, microstructure and properties of sea ice. In: Thomas, D.N., and Dieckmann, G.S., eds. *Sea ice—an introduction to its physics, biology, chemistry and geology*. London: Blackwell Science. 22–81.
- Flint, P.L., Mallek, E.J., King, R.J., Schmutz, J.A., Bollinger, K.S., and Derksen, D.V. 2008. Changes in abundance and spatial distribution of geese molting near Teshekpuk Lake, Alaska: Interspecific competition or ecological change. *Polar Biology* 31:549–556.
- Hare, S.R., and Mantua, N.J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103–145.
- Hartmann, B., and Wendler, G. 2005. The significance of the 1976 Pacific climate shift in the climatology of Alaska. *Journal of Climate* 18:4824–4839.
- Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E., and Blanchette, C.A. 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298:1015–1017.
- Hines, J.E., and Brooks, R.W. 2008. Changes in annual survival estimates for black brant from the western Canadian Arctic, 1962–2001. *Waterbirds* 31(2):220–230, doi:10.1675/1524-4695(2008)31[220:CIASEF]2.0.CO;2.
- Hitch, A.T., and Leberg, P.L. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* 21:534–539.
- Hoffman, A.A., and Parsons, P.A. 1997. *Extreme environmental change and evolution*. Cambridge: Cambridge University Press.
- Hunt, G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., and Bond, N.A. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Research Part II: Topical Studies in Oceanography* 49: 5821–5853.
- IPCC (Intergovernmental Panel on Climate Change). 2001. *Climate change 2001: Synthesis report*. Third Assessment Report of the IPCC, edited by Watson, R.T. and the Core Writing Team. Cambridge: Cambridge University Press.
- . 2007. *Climate change 2007: Synthesis report*. Fourth Assessment Report of the IPCC, edited by the Core Writing Team, Pachauri, R.K., and Reisinger, A. Cambridge: Cambridge University Press.
- Johnson, N.K. 1994. Pioneering and natural expansion of breeding distributions in western North American birds. *Studies in Avian Biology* 15:27–44.

- Jones, R.D., Jr. 1952. Quarterly refuge narrative report for the Aleutian Islands National Wildlife Refuge, 1 Sept. to 31 Dec. 1952. Unpubl. USFWS report. Available from U.S. Fish and Wildlife Service, Migratory Bird Management-Region 7, 1011 East Tudor Road, Anchorage, Alaska 99503.
- . 1955. Refuge narrative report for the Aleutian Islands National Wildlife Refuge and Izembek Bay Area, Jan. to April 1955. Unpubl. USFWS report. Available from U.S. Fish and Wildlife Service, Migratory Bird Management-Region 7, 1011 East Tudor Road, Anchorage, Alaska 99503.
- Lane, S.J., and Hassall, M. 1996. Nocturnal feeding by dark-bellied brent geese *Branta bernicla bernicla*. *Ibis* 138:291–297.
- Larned, W.W. 2000. Aerial survey of Steller's eiders (*Polysticta stelleri*) and other waterbirds and marine mammals in southwest Alaska areas proposed for navigation improvements by the U.S. Army Corp of Engineers, Alaska. Unpubl. USFWS report. Available from U.S. Fish and Wildlife Service, Migratory Bird Management-Region 7, 1011 East Tudor Road, Anchorage, Alaska 99503.
- LaSorte, F.A., and Thompson, F.R. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88:1803–1812.
- Lindberg, M.S., Sedinger, J.S., Derksen, D.V., and Rockwell, R.F. 1998. Population structure and natal and breeding movements in a black brant metapopulation. *Ecology* 79:1893–1904.
- Lindberg, M.S., Ward, D.H., Tibbitts, T.L., and Roser, J. 2007. Winter movement dynamics of black brant. *Journal of Wildlife Management* 71:534–540.
- Mantua, N.J., and Hare, S.R. 2002. The Pacific decadal oscillation. *Journal of Oceanography* 58:35–44.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1079.
- Mason, D.M., Barboza, P.S., and Ward, D.H. 2006. Nutritional condition of Pacific black brant wintering at the extremes of their range. *Condor* 108:678–690.
- . 2007. Mass dynamics of wintering brant: Body, adipose tissue, organ, and muscle mass vary with location. *Canadian Journal of Zoology* 85:728–736.
- McCabe, G.J., Clark, M.P., and Serreze, M.C. 2001. Trends in Northern Hemisphere surface cyclone frequency and intensity. *Journal of Climate* 14:2763–2768.
- Minerals Management Service. 2007. Proposed final program Outer Continental Shelf Oil and Gas Leasing Program 2007–2012. Unpubl. report. Washington, D.C.: Department of Interior, Minerals Management Service. [www.mms.gov/5-Year/PDFs/MMSProposedFinalProgram2007-2012.pdf](http://www.mms.gov/5-Year/PDFs/MMSProposedFinalProgram2007-2012.pdf).
- Minobe, S. 1997. A 50–70 year climatic oscillation over the North Pacific and North America. *Geophysical Research Letters* 24:683–686.
- Moore, J.E., Colwell, M.A., Mathis, R.L., and Black, J.M. 2004. Staging of Pacific flyway brant in relation to eelgrass abundance and site isolation, with special consideration of Humboldt Bay, California. *Biological Conservation* 115:475–486.
- National Climatic Data Center. 2004. Online climate data directory. NOAA Satellite and Information Service, National Climatic Data Center, U.S. Department of Commerce. <http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html>.
- Niebauer, H.J. 1983. Multiyear sea ice variability in the eastern Bering Sea: An update. *Journal of Geophysical Research* 88:2733–2742.
- Overland, J.E., Adams, J.M., and Bond, N.A. 1999. Decadal variability of the Aleutian low and its relation to high-latitude circulations. *Journal of Climate* 12:1542–1548.
- Pacific Flyway Council. 2002. Pacific Flyway management plan for Pacific brant. Portland, Oregon: Pacific Flyway Study Committee, U.S. Fish and Wildlife Service.
- Pannekoek, J., and Van Strien, A. 2000. TRIM 3.04. Voorburg: Statistics Netherlands.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Purcell, J., and Brodin, A. 2007. Factors influencing route choice by avian migrants: A dynamic programming model of Pacific brant migration. *Journal of Theoretical Biology* 249:804–816.
- Reed, A., Stehn, R.S., and Ward, D.H. 1989. Autumn use of Izembek Lagoon, Alaska, by brant from different breeding areas. *Journal of Wildlife Management* 53:720–725.
- Reed, A., Ward, D.H., Derksen, D.V., and Sedinger, J.S. 1998. Brant (*Branta bernicla*). In: Poole, A., and Gill, F., eds. *The birds of North America*, No. 337. Philadelphia: The Birds of North America, Inc.
- Rodionov, S.N., Overland, J.E., and Bond, N.A. 2005. The Aleutian low and winter climate conditions in the Bering Sea. Part 1: Classification. *Journal of Climate* 18:160–177.
- Root, T.L. 1988. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography* 15:489–505.
- Root, T.L., and Weckstein, J.D. 1995. Changes in winter ranges of selected birds, 1901–89. In: LaRoe, E.T., Farris, G.S., Puckett, C.E., Doran, P.D., and Mac, M.J., eds. *Our living resources: A report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems*. Washington D.C.: U.S. Department of the Interior, National Biological Service. 386–389.
- Salanthé, E.P., Jr. 2006. Influences of a shift in North Pacific storm tracks on western North American precipitation under global warming. *Geophysical Research Letters* 33:1–4.
- Sedinger, J.S., and Stickney, A.A. 2000. Black brant. In: Truett, J.C., and Johnson, S.R., eds. *The natural history of an Arctic oil field development and the biota*. San Diego: Academic Press. 221–232.
- Sedinger, J.S., Lensink, C.J., Ward, D.H., Anthony, R.M., Wege, M.L., and Byrd, G.V. 1993. Current status and recent dynamics of the black brant breeding population. *Wildfowl* 44:49–59.
- Sedinger, J.S., Ward, D.H., Anthony, R.M., Derksen, D.V., Lensink, C.J., Bollinger, K.S., and Dawe, N.K. 1994. Management of Pacific brant: Population structure and conservation issues. *Transactions of the 59th North American Wildlife and Natural Resources Conference* 59:50–62.

- Sedinger, J.S., Lindberg, M.S., Rexstad, E.A., Chelgren, N., and Ward, D.H. 1997. Testing for handling bias in survival estimation for black brant. *Journal of Wildlife Management* 61:782–791.
- Sedinger, J.S., Chelgren, N.D., Lindberg, M.S., Obritchkewitch, T., Kirk, M.T., Martin, P., Anderson, B.A., and Ward, D.H. 2002. Life-history implications of large-scale spatial variation in adult survival of black brant (*Branta bernicla nigricans*). *Auk* 119:510–515.
- Sedinger, J.S., Chelgren, N.D., Ward, D.H., and Lindberg, M.S. 2008. Fidelity and breeding probability related to population density and individual quality in black brant geese (*Branta bernicla nigricans*). *Journal of Animal Ecology* 77(4): 702–712.
- Stickney, A.A., and Ritchie, R.J. 1996. Distribution and abundance of brant (*Branta bernicla*) on the central Arctic Coastal Plain of Alaska. *Arctic* 49:44–52.
- Stone, R.S., Belchansky, G., Drobot, S., and Douglas, D.C. 2004. Diminishing sea ice in the western Arctic Ocean. In: Levinson, D.H., and Waple, A.M., eds. *State of the climate in 2003*. *Bulletin of the American Meteorological Society* 85(6): 532–534.
- Thomas, C.D., and Lennon, J.J. 1999. Birds extend their ranges northwards. *Nature* 399:213.
- van Strien, A.J., Pannekoek, J., and Gibbons, D.W. 2001. Indexing European bird population trends using results of national monitoring schemes: A trial of a new method. *Bird Study* 48:200–213.
- Ward, D.H., and Stehn, R.A. 1989. Response of brant and other geese to aircraft disturbances at Izembek Lagoon, Alaska. U.S. Fish and Wildlife Service Final Report No. 14-12-0001-30332. Anchorage, Alaska: USFWS.
- Ward, D.H., Markon, C.J., and Douglas, D.C. 1997. Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. *Aquatic Botany* 58:229–240.
- Ward, D.H., Schmutz, J.A., Sedinger, J.S., Bollinger, K.S., Martin, P.D., and Anderson, B. 2004. Temporal and geographic survival of juvenile black brant. *Condor* 106:263–274.
- Ward, D.H., Reed, A., Sedinger, J.S., Black, J.M., Derksen, D.V., and Castelli, P.M. 2005. North American brant: Effects of changes in habitat and climate on population dynamics. *Global Change Biology* 11:869–880.
- Wilson, U.W., and Atkinson, J.R. 1995. Black brant and spring-staging use at two Washington coastal areas in relation to eelgrass abundance. *Condor* 97:91–98.
- Zveryaev, I., and Selemenov, K.M. 2000. Decadal scale changes in annual cycle of the North Pacific sea-surface temperatures. *International Journal of Climatology* 20:1639–1651.