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WINTER ECOLOGY OF SPECTACLED EIDERS: ENVIRONMENTAL CHARACTERISTICS AND POPULATION CHANGE

MARGARET R. PETERSEN[1] AND DAVID C. DOUGLAS[2]
U.S. Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, AK 99503

Abstract. We described characteristics of the wintering area used by Spectacled Eiders (*Somateria fischeri*) in the Bering Sea, Alaska, and evaluated these characteristics in relation to long-term population trends. Remoteness, limited daylight, and extreme weather conditions precluded direct observations, so we derived the location of the wintering area from satellite telemetry, ice conditions from remotely sensed data, weather conditions from archived data sets, and benthic communities from the literature. Based on analyses of two indices spanning 1957–2002 and 1988–2002, we identified no single environmental parameter that explained the precipitous decline in nesting populations in western Alaska. In general, we found that the number of days with extreme sea ice in winter, extreme winds, and winds in spring explained the greatest variability in annual indices. These analyses support the conclusion that annual population estimates on the breeding grounds can be negatively impacted by extended periods of dense sea-ice concentration and weather during the previous winter. Examination of population indices did not support the hypothesis that changes in benthic community on the wintering grounds have contributed to the decline or inhibited the recovery of the Spectacled Eider breeding population in western Alaska.

Key words: *Bering Sea, ice concentration, population variability, remote sensing, Spectacled Eider, weather, winter.*

Ecología Invernal de *Somateria fischeri*: Características Ambientales y Cambio Poblacional

Resumen. Describimos las características del área de invernada utilizada por *Somateria fischeri* en el Mar de Bering, Alaska, y evaluamos estas características con relación a tendencias poblacionales a largo plazo. La lejanía, la limitación en las horas de luz y las condiciones climáticas extremas imposibilitaron realizar observaciones directas, por lo que calculamos la localización de los sitios de invernada basándonos en telemetría satelital, las condiciones del hielo a partir de información remota, las condiciones del tiempo basándonos en archivos de datos y las comunidades bénticas a partir de la literatura. El análisis de dos índices que se extendieron entre 1957–2002 y 1988–2002 no permitió identificar un parámetro ambiental único que explicara la declinación precipitada en las poblaciones nidificantes en el oeste de Alaska. En general, encontramos que el número de días del invierno con mucho hielo en el mar, los vientos extremos y los vientos en la primavera explicaron la mayor variabilidad en los índices anuales. Estos análisis apoyan la conclusión de que las estimaciones poblacionales anuales en las áreas de cría pueden estar afectadas negativamente por largos períodos de concentraciones densas de hielo marino y de tiempo durante el invierno previo. El examen de los índices poblacionales no apoyó la hipótesis de que los cambios en las comunidades bénticas en las áreas de invernada hayan contribuido a la declinación o hayan inhibido la recuperación de las poblaciones reproductivas de *S. fischeri* en el oeste de Alaska.

INTRODUCTION

Loss of body condition by sea ducks in winter can result in death by starvation (Barry 1967, Fournier and Hines 1994) or dispersal to more favorable areas (Nilsson 1970, 1972, Systad et al. 2000). To meet daily energy costs when conditions in winter restrict prey availability, sea ducks may use stored nutrient reserves, increase feeding time during the day (Beauchamp et al. 1992, Systad et al. 2000), forage at night, or forage in areas with high prey densities (Paulus 1988, Guillemette et al. 1993, Guillemette 1998).

For sea ducks, unless they winter in areas accessible to observers, the variables in winter that affect food availability and feeding behavior are unknown. Many sea ducks winter in northern coastal and marine environments, and face harsh

Manuscript received 30 January 2003; accepted 22 August 2003.
[1] E-mail: margaret_petersen@usgs.gov
[2] Present address: U.S. Geological Survey, Alaska Science Center, 3100 National Park Road, Juneau, AK 99801.

weather conditions that influence their survival (Barry 1967, Fournier and Hines 1994) and reproductive output (Coulson 1984, 1999). An understanding of conditions that constrain recovery of populations should improve management of these populations.

The numbers of Spectacled Eiders (*Somateria fischeri*) on the Yukon-Kuskokwim (Y–K) Delta in western Alaska have declined precipitously since the 1970s (Stehn et al. 1993, Ely et al. 1994, USFWS 1996). The Spectacled Eider was listed as threatened under the Endangered Species Act (Federal Register 1993); however, too little information, especially away from their breeding grounds, existed to determine causes of the decline (Stehn et al. 1993, USFWS 1996). More recent data suggests that the Y-K Delta breeding population is stable (T. D. Bowman, unpubl. data). Recent (1993–2002) aerial survey results from northern Alaska suggest this breeding population is also stable; W. W. Larned (unpubl. data) detected no significant difference from a growth rate of 1.0. Additionally, surveys conducted from 1993–1995 on the eastern arctic coast of Russia resulted in an estimate of 146 245 Spectacled Eiders (Hodges and Eldridge 2001), which is probably not different from the provisional estimate of 47 000 to 58 000 pairs (Dau and Kistchinski 1977).

The Spectacled Eider spends 9–12 months of the year at sea (Dau and Kistchinski 1977, Petersen et al. 1999) and winters only in the Bering Sea (Petersen et al. 1999). Recent studies of annual survival of birds breeding in western Alaska (Flint and Grand 1997, Grand et al. 1998) suggest that almost half of the mortality of adult females occurs during their nine or more months away from the breeding grounds (Flint et al. 2000). However, little is known about factors within the wintering area that may influence survival.

Here we focus on aspects of the marine environment in winter that likely have the most immediate, direct effects on variation in annual population indices of breeding Spectacled Eiders. Our objectives are to describe the location and selected environmental characteristics of the wintering area of Spectacled Eiders in the Bering Sea, and evaluate variability of weather and sea ice in relation to annual variability in populations. To evaluate the hypothesis that changes in food resources in the wintering area contributed to the decline in Spectacled Eiders (Stehn et al. 1993, USFWS 1996), we discuss changes in invertebrate species composition at the wintering area and their relationship to recent and expanded population indices.

METHODS

STUDY AREA

The Bering Sea consists of a shallow, gradually sloping (0.24 m km^{-1}) shelf with a steep drop into deeper waters; about half of it consists of waters <200 m deep. It extends from the Bering Strait between the Chukchi Peninsula and the Seward Peninsula south to the Aleutian Islands, and from western coastal Alaska to eastern coastal Russia. On 21 December, St. Lawrence Island (63.78°N, 171.74°W) has about four hours of daylight.

Weather in the northeastern Bering Sea during winter is harsh (Karpova 1963, Brower et al. 1977). The locations and strength of the Aleutian Low and the Arctic High atmospheric pressure systems are primary factors influencing weather (Sharma 1976, Niebauer 1983). November through April is a period of frequent storms with high winds and rough seas; rain, fog, and snow are common (Karpova 1968, Brower et al. 1977). Sea ice moves into the area during late December, and the mean extent of ice cover with >63% (5/8) concentration occurs south of 60°N from January through April (Brower et al. 1977). The concentration of sea ice is the proportion of ice, regardless of its thickness, within an area. This measure incorporates open areas within the ice (polynyas, open leads, and holes) as well as the extent of ice cover (edge of the pack ice).

Community structure in the Bering Sea is dynamic and varies in response to decadal (15–25 or 50–70 year) regime shifts (Hare and Mantua 2000). The National Research Council (1996) summarizes long-term climate information from the North Pacific and shows an increasingly cool period in the 1950s and 1960s. Based on a detailed analysis of over 100 physical and biological time series collected during 1965–1997 from the Bering Sea and Pacific Ocean, Hare and Mantua (2000) provided evidence of a regime shift beginning about 1977 to a warmer period with higher values of productivity or biomass, and another shift in 1989 to a cooler period that resulted in decreased productivity or biomass. Recent analyses of benthic communities in the Bering Sea also show decreased trends in productivity and biomass as well as high annual variability during the cooler period beginning in 1989 (Grebmeier and Dunton 2000).

Benthic communities and biomass are heterogeneous and variable throughout the Bering Sea shelf (Neiman 1963, Stoker 1981, Grebmeier et al. 1988, Kolesnikova et al. 1990, Grebmeier and Cooper 1995). In general, benthic communities in the area south of St. Lawrence Island include combinations of amphipods, bivalves, and polychaetes in high densities, and these communities and their biomass have varied over several decades (Sirenko and Koltun 1992, Grebmeier 1993, Grebmeier and Cooper 1995). This variation may ultimately be the result of cyclic changes in intensity and position of the Aleutian Low pressure system (Niebauer 1983, Niebauer and Day 1989, National Research Council 1996, Grebmeier and Dunton 2000).

Although data on food habits of Spectacled Eiders are limited, when in the Bering Sea they eat bivalves, mollusks, and crustacea (Cottam 1939, Petersen et al. 1998). Twelve Spectacled Eiders collected in the Bering Sea wintering area (March 2001) had eaten bivalves, primarily *Nuculana radiata* (Lovvorn et al. 2003).

IDENTIFICATION OF WINTERING AREA

The wintering area used by Spectacled Eiders was determined by satellite telemetry from locations of adult male and female eiders from 21 November to 31 January 1993–1997 (Petersen et al. 1999). Thirteen individuals (37 locations) provided data during winter. Fixed kernel analysis (Seaman et al. 1998) was used to delineate the area of utilization. More efficient transmitters provided more locations, which would disproportionately weight a kernel analysis. Thus, no more than three randomly selected locations per individual were used for this analysis. The 99% utilization distribution was considered an estimate of total distribution, and the contour encompassing greater than average observed density was considered the core area. The eiders' persistent use of the core area during late winter and spring (1 February–31 March and April, respectively) was verified from aerial surveys (Petersen et al. 1999).

ENVIRONMENTAL DATA

Bathymetric characteristics of the core wintering area were investigated using a global model developed by Smith and Sandwell (1997). We resampled their raster map with 2-minute resolution in Mercator projection to an Alber's Equal Area projection with 1.8-km resolution and then derived 10-m isobaths.

Historic sea-ice conditions were quantified using 25-km-resolution sea-ice concentration maps derived from passive microwave satellite data (Comiso 2002). The data set had advantages for long-term, interannual comparisons because the tie points used by the bootstrap ice-concentration algorithm had been standardized to compensate for significant differences between the Scanning Multichannel Microwave Radiometer (SMMR) and Special Sensor Microwave/Imager (SSM/I) sensors (Comiso et al. 1997, Cavalieri et al. 1999). To match the 2-day temporal resolution of the SMMR maps (1978–1987), we used every other day from the daily SSM/I ice concentration maps (1987–2002), and considered each map representative of 2 days. For analyses of sea-ice conditions, we considered only the four 25 $\times$ 25 km pixels that spatially overlapped the Spectacled Eider's core wintering area. We used the arcsine transformation of minimum ice concentration in the four pixels as our daily estimate of ice concentration in all analyses.

High-resolution European Remote Sensing Satellite (1993–1996) and Japanese Earth Resources Satellite synthetic aperture radar (SAR) images were acquired from the Alaska SAR Facility (ASF), Fairbanks, Alaska, to qualitatively characterize fine-scale sea-ice features during periods of extensive ice concentration. All images were received from ASF in standard format with 12.5-m pixel resolution. Each image was radiometrically calibrated to Sigma-0 dB units and georeferenced to polar stereographic projection (ASF 2000).

Speed and direction of sea-ice movements were from 24-hr ice-drift forecasts (1993–2002) distributed by NOAA (2001a) that were calculated using the ice-drift model by Grumbine (1998). This model is based on geostrophic wind speed and direction. We analyzed the daily predictions from the forecast point at 61.24°N, 170.00°W.

Daily weather records for the St. Paul Island airport (57.17°N, 170.22°W) and Gambell (63.78°N, 171.74°W) were obtained from the National Climate Data Center (2002). Gambell was the nearest weather station to the eider win-

TABLE 1. Parameters considered in models accounting for variation of Spectacled Eider population indices. Ice data sets were derived from daily ice maps from Comiso (1999); weather data sets were derived from NCDC (2002) and NOAA (2001b). Parameters were used to analyze population estimates from two indices: the Breeding Pair Survey Index (1957–2002; Hodges et al. 1996, B. Conant, unpubl. data) and the Nest Plot Index (1988–2002; T. D. Bowman, unpubl. data).

Parameter	Description	Analysis
Extreme ice	Number of days with ≥95% sea-ice concentration in *Year*	Nest Plot Index
Spring ice	Number of days with ≥95% sea-ice concentration in April (spring) of *Year*	Nest Plot Index
Winter ice	Number of days with ≥95% sea-ice concentration in Dec–Mar of *Year*	Nest Plot Index
Extreme temp	Number of days at St. Paul Island with ≤5% minimum temperatures in *Year*	Both analyses
Spring temp	Average minimum daily temperature in April at St. Paul Island	Both analyses
Winter temp	Average minimum daily temperature in Dec–Mar at St. Paul Island	Both analyses
Extreme winds	Number of days with ≥95% maximum wind speed at St. Paul Island in *Year*	Both analyses
Spring winds	Average wind speed at St. Paul Island in April	Nest Plot Index
Winter winds	Average wind speed at St. Paul Island in Dec–Mar	Nest Plot Index
Year	Year of observation (Dec–April). *Year* for December calculated as year + 1	Breeding Pair Survey Index
$Year^2$	*Year* squared	Breeding Pair Survey Index

tering area; however, data were discontinuous (1982–1988, 1994–1998). St. Paul Island was the nearest Bering Sea weather station to the eider wintering area that had a continuous archive of data. To examine long-term annual variation of winter weather in the greater Bering Sea region, daily temperatures (1949–2002) and wind speeds (1984–2002) from St. Paul Island were analyzed. To extend the NCDC data set for St. Paul Island, daily wind speed data (1946–1982) was used from a moored meteorology station located at 62°N, 171°W (NOAA 2001b). December data were pooled with January–April, and the January calendar year was used for reporting results.

POPULATION INDICES

We examined the relationship of abundance indices of the population of Spectacled Eiders breeding on the Y-K Delta to ice and weather variables (Table 1). Two measures of population abundance were used: (1) the Breeding Pair Survey Index for Stratum 9 (Hodges et al. 1996; B. Conant, unpubl. data; 1957–2002), and (2) the Nest Plot Index (T. D. Bowman, unpubl. data; 1988–2002). Stratum 9 is a specific geographical delineation of tundra habitat in western Alaska (Hodges et al. 1996) between and including the Yukon and Kuskokwim River drainages. The Breeding Pair Survey Index includes both Spectacled and Common (*S. mollissima*) Eiders (Hodges et al. 1996), but is considered the best indication of the long-term trend of Spectacled Eiders breeding in western Alaska (Stehn et al. 1993, USFWS 1996). No similar, long-term data exist for birds nesting in northern Alaska or arctic Russia.

As the population on the Y-K Delta declined (Fig. 1), fewer birds were recorded each year and the resulting annual variability in the Breeding Pair Survey Index (an aerial survey) suggested that it became biologically unrealistic. Beginning in 1988, a combination of ground surveys for nests and aerial surveys for pairs was used to derive an annual index (Nest Plot Index) of the number of nesting females on the Y-K Delta (T. D. Bowman, unpubl. data); this index is currently being used by the Spectacled Eider Recovery Team to assess current trends in this breeding population. We used this more precise estimate to evaluate recent indices of the breeding population in relation to weather and ice.

STATISTICAL ANALYSIS

Akaike's Information Criterion modified for small sample size (AIC_c) was used to identify

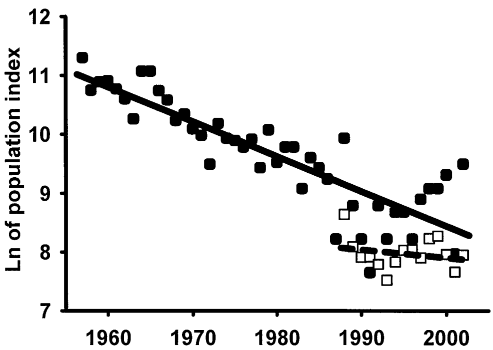

FIGURE 1. Evidence for the population decline of Spectacled Eiders breeding on the Yukon-Kuskokwim Delta, Alaska. Data points are the natural logarithm of estimates from the Breeding Pair Survey Index (black squares and solid regression line; Hodges et al. 1996, B. Conant, unpubl. data) and the Nest Plot Index (clear squares and dashed regression line; T. D. Bowman, unpubl. data). The Breeding Pair Survey Index indicated a significant decline ($r^2 = 0.74$, $P < 0.001$, $y = -0.06x + 126.45$, $n = 46$ years); but the Nest Plot Index did not ($r^2 = 0.42$, $P = 0.46$, $y = -0.01x + 32.24$, $n = 15$ years).

the best models (Anderson and Burnham 2002, Burnham and Anderson 2002) of population indices. The natural log of the population index was used in all regression models. Model selection using SAS software (SAS Institute 1990) was done separately for each data set: (1) variation in the Breeding Pair Survey Index (1957–2002) included the effects of year and weather; and (2) variation in the Nest Plot Index (1988–2002) included the effects of ice and weather. Candidate models were ranked based on AIC_c differences (ΔAIC_c; Anderson et al. 2000, Burnham and Anderson 2002), and the evidence regarding model selection was examined following Burnham and Anderson (2002). For each model, we report AIC_c, ΔAIC_c, model weight (w_i), number of parameters (k) (Anderson et al. 2001, Burnham and Anderson 2002), and coefficient of determination (r^2) values. The number of parameters includes a parameter for the intercept and a parameter for the variance of the regression model. The relative importance of parameters was evaluated by ranking the summed Akaike weights (w_i) of models that included each variable (Burnham and Anderson 2002). In each AIC_c analysis, we examined models containing each parameter (Table 1) and all possible combinations of these parameters, plus the null model. We discuss only the models with substantial levels of empirical support (ΔAIC_c 0–2; Burnham and Anderson 2002) and present all models with $\Delta AIC_c < 4$.

We examined measurements of winds and temperatures from St. Paul Island and Gambell and excluded highly correlated variables in our analysis. Different types of wind measurements were highly correlated within and among weather stations ($r = 0.88$–0.96), as were temperature measurements ($r = 0.79$–0.96). The variables *average daily wind speed* and *minimum temperature* from St. Paul Island were included in the models since these represented extremes in weather and had the fewest missing data points. Ice variables were used only in the analysis of the Nest Plot Index since ice data were not available from 1957–1979. Other environmental measurements were not included in either model analysis because they were not measured each year (i.e., benthic fauna), or they were insufficiently variable within and among years (i.e., water depths).

Since inclement weather or reduced food availability in spring has been reported to reduce survival (Barry 1967, Fournier and Hines 1994) and breeding propensity (Coulson 1984) in other sea ducks, two sets of weather variables were created representing the months December to March and the month of April using these same daily weather variables. The weather variables representing extreme conditions during 1950–2002 were defined as the total number of days within a year and period with mean daily temperatures -13°C and lower (lowest 5% of all years combined) and mean daily wind speed ≥ 15.0 m sec^{-1} (highest 5% of all years combined). The index of extreme ice conditions was defined as the number of days within the year and period with ≥ 95% minimum ice concentration. Data are presented as means $\pm$ SE unless otherwise stated.

RESULTS

EXTENT OF WINTERING AREA

Spectacled Eiders from Alaskan and Russian breeding areas repeatedly used the same area south of St. Lawrence Island during winter and consistently arrived during late November and December (Petersen et al. 1999) to a very specific area about 100 km west-southwest of St. Lawrence Island (Fig. 2). The total extent of this area was about 2900 km^2, with the core area

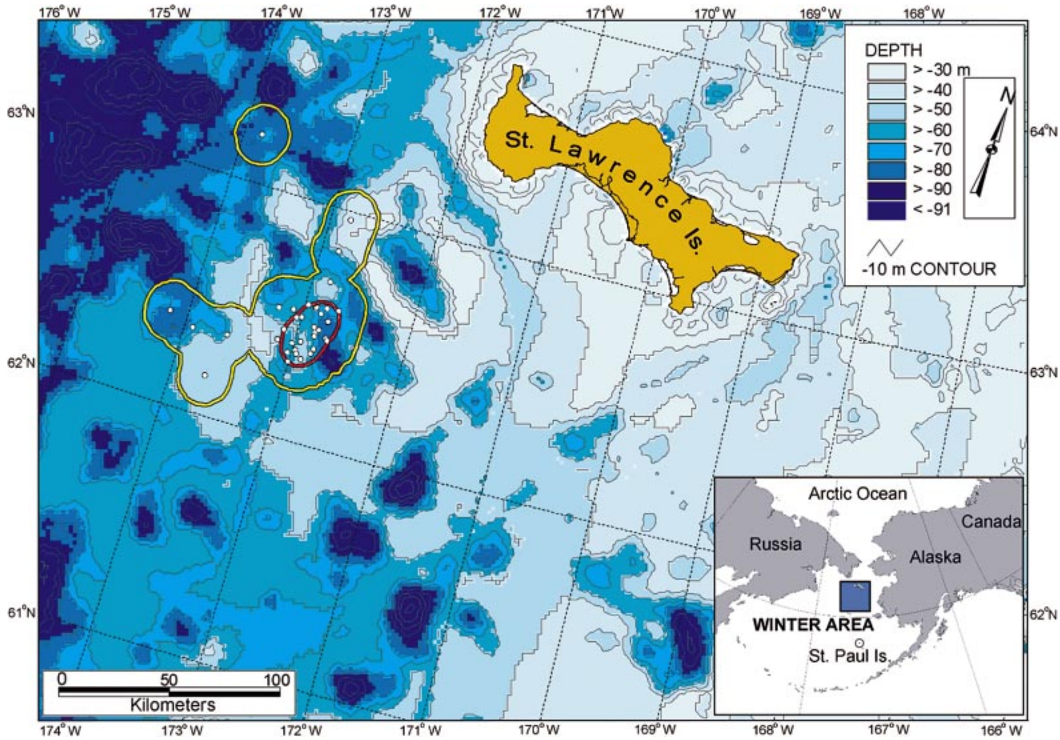

FIGURE 2. Bathymetric features of Spectacled Eider wintering area and surrounding regions in the Bering Sea. Depths shown in shades of blue with 10-m contours. White circles are locations of individuals (Petersen et al. 1999). Fixed kernel analysis was used to delineate the area of utilization: red polygon (84% contour) encompasses the core area (greater than average observed density); yellow polygons are the 99% contours.

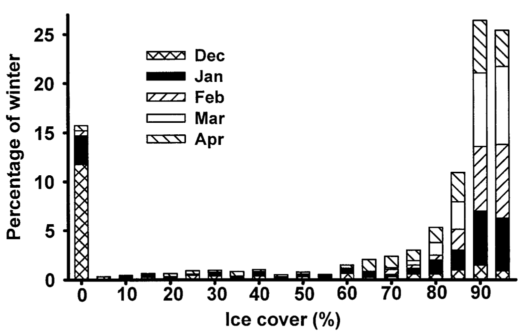

FIGURE 3. Relative occurrence by month of sea-ice concentrations on the Spectacled Eider core wintering area (Fig. 2) during winters of 1979–1999. Data were derived from remote sensing information obtained from the National Snow and Ice Data Center (Comiso 1999) for the four 25 × 25 km pixels that overlapped the core area.

(84% distribution) encompassing approximately 570 km^2. Within the total area, the telemetry locations of eiders corresponded to water depths of 60.9 ± 0.5 m (n = 39, range 49–68 m).

WINTER ENVIRONMENT

The core winter area contained waters 40–90 m in depth within a large, undulating basin (Fig. 2). This basin was relatively broad, with gentle slopes, and heterogeneous compared to nearby basins which tended to be steeper sided and deeper. Furthermore, the basin had distinct openings at its southwest and northern peripheries, whereas adjacent basins had a more closed, pit-like character.

Sea ice extended south of St. Lawrence Island beginning in mid- to late December and was a dominant feature of the environment. On average, the core winter area was ≥90% covered by sea ice for >50% of the winter, mostly during the months of January through April (Fig. 3). Sea ice was typically either absent (<5%) or dense (≥85%).

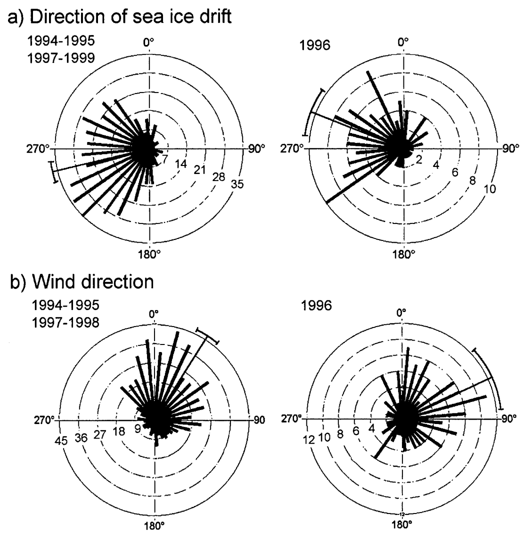

FIGURE 4. Directional histograms of the 24-hr ice-drift forecasts from the point at 61.24°N, 170.00°W for December–April 1993–1999: (a) daily direction of ice drift; (b) average originating wind direction at St. Paul Island. Pooled years were not statistically different. Axes represent compass bearings, circles represent sample sizes (days), and thinner lines extending beyond the outer circle represent the mean compass bearing ±95% CI.

Mean directions (azimuths) of sea-ice drift during the winters of 1994–1999 were statistically similar among all years except 1996, which was significantly different than all other years (Watson's F-test for two circular means, $P \leq 0.01$). Mean sea-ice drift was toward the northwest during 1996 ($\mu = 292°$) and more southwesterly in other years ($\mu = 257°$; Fig. 4a). Wind direction at St. Paul Island (1994–1999) was also significantly different in 1996 ($\mu = 65°$) compared to all other years ($\mu = 32°$, $P \leq 0.03$) except 1999 ($\mu = 47°$, $P = 0.25$). Winds were typically from the north-northeast at St. Paul Island, but were more easterly in 1996 (Fig. 4b). The average estimated distance of daily sea-ice drift varied annually, with slightly faster drifts during 1994–1996 compared to 1997–1999 (Table 2). In general, average movement of sea ice in the eider's wintering region was westerly and ranged from 7.9–10.4 km day^{-1}, with daily distances ≥15 km occurring about 10% of the time during an average winter.

High-resolution satellite images illustrated the diversity and dynamics of sea-ice conditions at the eider wintering area during periods of relatively dense ice concentration. Figure 5a depicts a mixture of ice formations, where older leads and fractures had refrozen (darker intermediate gray areas) and newer leads of open water had recently formed by movement and shearing (black linear features). In Figure 5b, relatively uniform consolidated sea ice had undergone some shearing, resulting in several long, narrow leads of open water. Figure 5c shows open-water patches that were possibly beginning to freeze (slight gray texturing within the dark areas of open water) as well as recent shearing and formation of new leads. Figure 5d depicts less consolidated sea ice with increased water fractions toward the west that were showing signs of either freezing or being roughened by surface winds. Manual interpretation of additional SAR images corroborated a highly dynamic sea-ice environment and a scarcity of open water during periods of heavy ice cover.

TABLE 2. Annual variation in daily sea-ice drift estimated in the north-central Bering Sea grid location 61.2°N, 170.0°W (derived from daily forecasts; NOAA 2001a). The number of forecasts includes those from December of the previous year plus the number from January through April. Years followed by the same letter were not significantly different (one-way ANOVA, $F_{8,1212} = 5.2$, $P \leq 0.05$; Duncan's multiple range test, $P \leq 0.05$).

Year	No. of forecasts	Daily ice movement (km day^{-1}) mean ± SE	Range (km day^{-1})
1994 a,b	145	10.0 ± 0.4	1.7–22.8
1995 b	88	10.4 ± 0.5	2.8–22.4
1996 a,b,c	145	9.5 ± 0.3	0.9–21.5
1997 d	149	7.9 ± 0.3	0.4–19.3
1998 c,d	131	8.6 ± 0.4	1.6–23.5
1999 d	121	8.2 ± 0.4	0.9–18.7
2000 a,c,d	140	8.9 ± 0.3	1.1–18.7
2001 a,b,c	151	9.8 ± 0.4	1.3–21.5
2002 d	151	8.2 ± 0.4	0.7–21.3

Satellite-derived estimates of ice concentration throughout the winter at the eiders' core wintering area showed considerable annual variation (Fig. 6). Average ice concentration and the number of days with extreme ice conditions were highly correlated ($r = 0.79$). During 1990–2002, 9 and 8 of 13 winters were above the median number of days with extreme ice conditions (39.5, $n = 24$) and median average ice concentration (76%, $n = 24$), respectively. In comparison during 1979–1989, only 3 and 5 of 11 winters were above these respective medians.

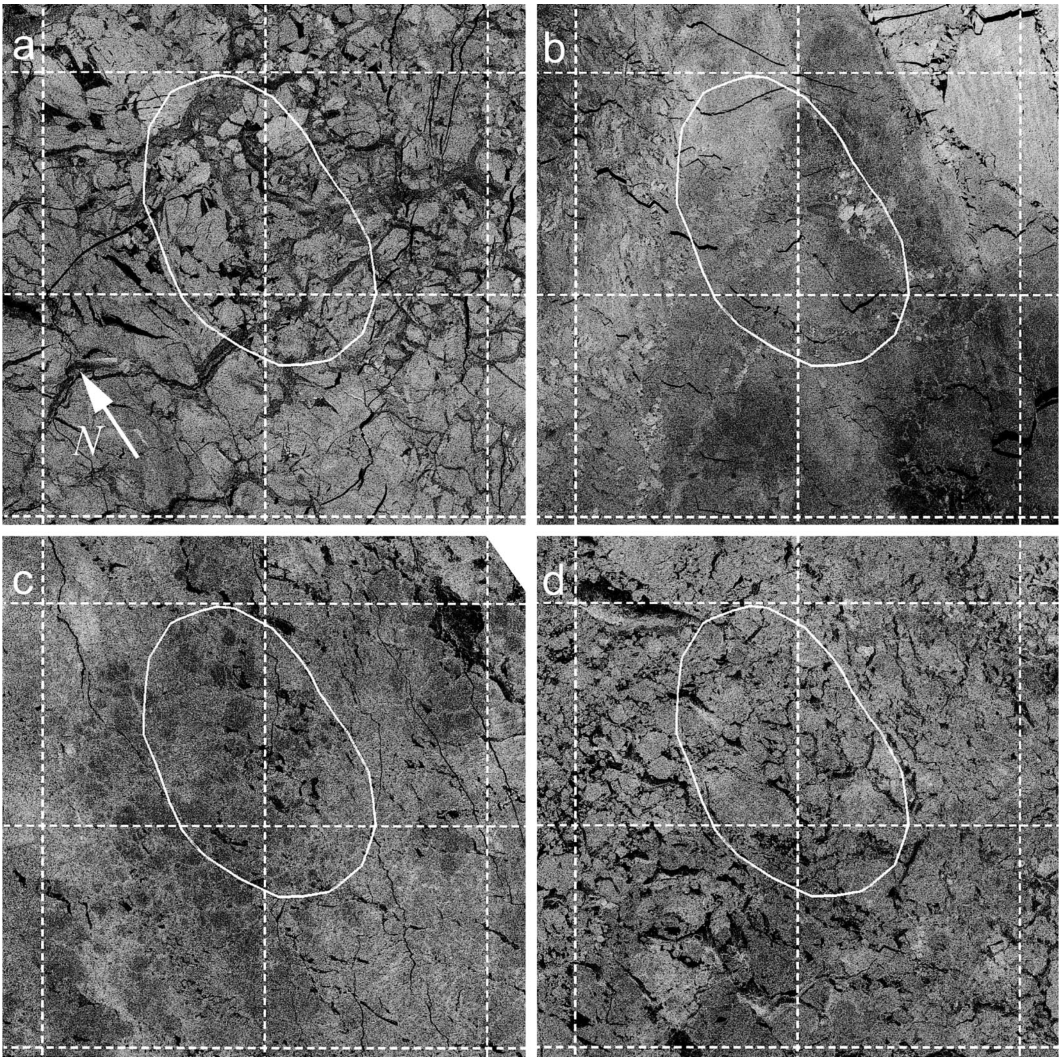

FIGURE 5. Synthetic aperture radar images (ASF 2000) of the Spectacled Eider wintering area in the Bering Sea showing configurations of open water (dark areas) and ice (light areas). Solid line indicates eider core wintering area. Dashed lines indicate the 25 × 25 km pixels used to calculate sea-ice concentrations (mean ± SD): (a) 27 January 1993, 96 ± 1%; (b) 3 March 1993, 98 ± 2%; (c) 18 February 1995, 95 ± 7%; and (d) 15 March 1996, 92 ± 1%.

The annual time-sequences of the winter days when ice concentration was ≥95% at the core wintering area (Fig. 7) suggests that, although 1980, 1990–1992, 1995, and 2000 had the greatest number of days with extreme ice conditions, the timing of occurrence of consecutive days with extreme ice varied among these years. Most other years had fewer days with extreme ice conditions (Fig. 6), and they also were characterized by a variety of temporal distributions (Fig. 7). For example, consecutive days of extreme ice began in December of 1982, 1989, and 1993, but not until February of 1984–1985, and 1987.

Climate data from St. Paul Island indicated that winters in the Bering Sea during the 1970s were more severe than others during the 50-year record. The consecutive winters of 1971–1972 and 1975–1976 had significantly colder mean temperatures (Fig. 8a) than all other years, except 1954 and 1956 (ANOVA, $F_{1,49} = 16.1$, $P < 0.001$; Duncan's multiple-range test, $P <$

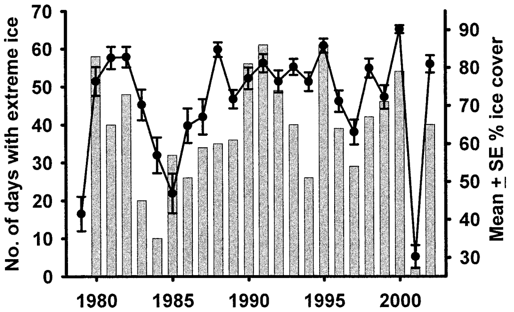

FIGURE 6. Annual variation in ice concentration at the Spectacled Eider core wintering area (red polygon, Fig. 2) for the winters of 1979–2002. Bars indicate the number of days with extreme (≥95%) ice concentration; points indicate the yearly mean ± SE percentage of ice concentration. No days with extreme ice concentration occurred in 1979.

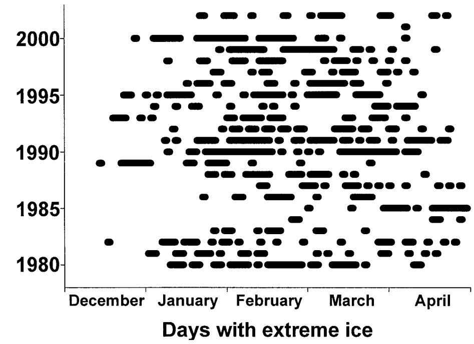

FIGURE 7. Temporal distribution of extreme (≥95%) ice concentration at the Spectacled Eider core wintering area (red polygon, Fig. 2) for the winters 1979–2002. No days with extreme ice concentration occurred in 1979.

0.05). In addition to having the lowest mean temperatures, the winters of 1975 and 1976 had the highest number of extremely cold (lowest 5%) days. The 1970s also recorded the windiest conditions of the 50-year climate history (Fig. 8b), especially during 1975–1977 when the number of extremely windy days (upper 5%) exceeded all other years.

EIDER POPULATION CHANGES

There was no evidence for a single best model that described the trend in the long-term Breeding Pair Survey Index (1957–2002; Table 3), although there was substantial empirical support for two models including (1) the parameters *year*, *year squared*, and *number of days with extreme winds*, and (2) *year* and *year squared.* The three parameters included in these two models had the greatest relative weight among all variables (sum of AIC_c weights: *year* = 1.00, *year squared* = 1.00, *number of days with extreme winds* = 0.72). Despite the high coefficient of determination values of these two models, the minimal difference between these values implies that much of the variation in the data is not explained by the number of days with extreme winds.

No single best model could be selected to describe the more recent (1988–2002) Nest Plot Index, although there was substantial empirical support for two (Table 4). The ice parameter *number of days in winter with ≥95% ice concentration* and the weather parameters *temperature* and *average wind speed in spring* were more important relative to other variables (sum of AIC_c weights: *number of days in winter with ≥95% ice concentration* = 0.16, *average wind speed in spring* = 0.77, *average minimum temperature in spring* = 0.68). The temperature and wind variables in spring were negatively correlated with the index. Ice variables and drift

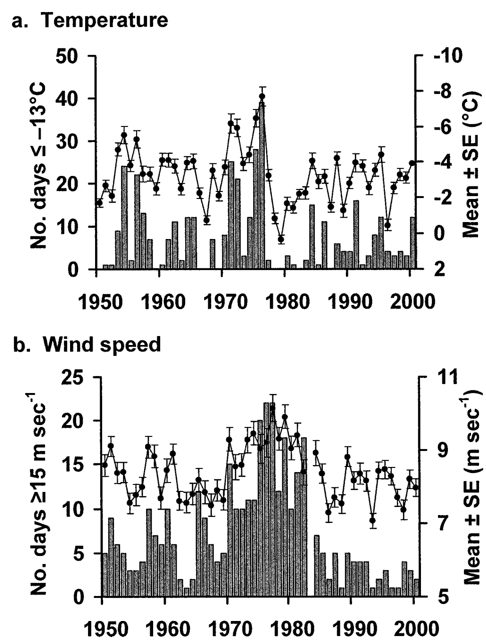

FIGURE 8. Annual variation in mean (a) temperature and (b) wind speed at St. Paul Island during December–April. Bars indicate the number of days of extreme weather (mean daily temperature within the lowest 5% of all years combined [−13°C]; mean daily wind speed within the highest 5% [15 m sec^{-1}]). Points indicate the yearly mean ± SE.

TABLE 3. Models fitted to determine the sources of variation in numbers of Spectacled Eiders breeding on the Yukon-Kuskokwim Delta, based on the Breeding Pair Survey Index (1957–2002; $n = 46$ years), using four weather variables and *year* and *year*^{2} as parameters. Models were evaluated using Akaike's Information Criterion adjusted for small sample size (AIC_c), number of estimated parameters (k), difference in AIC_c (ΔAIC_c), model weight (w_i), and coefficient of determination (r^2). Only models with ΔAIC_c values <4.0 are presented. Models with $\Delta AIC_c \leq 2$ are considered to have substantial levels of empirical support (Burnham and Anderson 2002). See Table 1 for parameter definitions.

Model	k	AIC_c	ΔAIC_c	w_i	r^2
Year, Year^2, Extreme winds	5	–70.35	0.0	0.33	0.79
Year, Year^2	4	–68.48	1.9	0.13	0.76
Year, Year^2, Extreme winds, Extreme temp	6	–68.12	2.2	0.11	0.79
Year, Year^2, Extreme winds, Spring temp	6	–67.78	2.6	0.09	0.79
Year, Year^2, Extreme winds, Winter temp	6	–67.77	2.6	0.09	0.79
Year, Year^2, Extreme winds, Extreme temp, Winter temp	7	–67.51	2.8	0.08	0.80
Year	3	–66.92	3.4	0.06	0.74
Year^2	3	–66.78	3.6	0.06	0.74
Year, Year^2, Winter temp	5	–66.36	3.9	0.05	0.77
Null model of no factors	2	–7.35	63.0	0.00	0.00

speed were negatively correlated with the index, as were all other ice parameters in relation to longer-term (1979–2002) population indices.

DISCUSSION

The location and depth of the Aleutian Low, the Arctic oscillation, terrestrial river flow, sea surface temperatures, ice cover and thickness, upwelling, and currents either directly or indirectly affect benthic communities in the Bering Sea (Niebauer 1983, Niebauer and Day 1989, Kolesnikova et al. 1990, Sirenko and Koltun 1992, National Research Council 1996, Grebmeier and Dunton 2000, Cooper et al. 2002). However, these indices reflect conditions throughout the Bering Sea that determine weather and ice conditions and do not necessarily reflect the conditions experienced by Spectacled Eiders on their core wintering area. Thus, we focused our analyses on ice extent and weather parameters that we believe best reflected the conditions experienced by eiders, and examined how these parameters may influence the number of Spectacled Eiders that survive the winter or return to the nesting area (as reflected by annual breeding population indices) the following summer. We will also compare long-term population indices to changes in benthic communities within the core wintering area (see below).

Implicit in our analysis is the assumption that the current wintering area has remained the same from 1950–2001. There is no evidence to support or reject the assumption of no change in distribution of eiders. It is possible that the wintering area of Spectacled Eiders was in an entirely different location during the cold period prior to 1977. They may have changed distribution during the warm period of 1977–1988, and then moved to yet another area with the shift to a cooler climate that began in 1989. However,

TABLE 4. Models fitted to determine the sources of variation in numbers of Spectacled Eiders breeding on the Yukon-Kuskokwim Delta, based on the Nest Plot Index (1988–2002; $n = 15$ years), in relationship to six weather and two ice variables. k, AIC_c, ΔAIC_c, w_i, and r^2 are defined in Table 3. Only models with ΔAIC_c values <4.0 are presented. Models with $\Delta AIC_c \geq 2$ are considered to have substantial levels of empirical support (Burnham and Anderson 2002). See Table 1 for parameter definitions.

Model	k	AIC_c	ΔAIC_c	w_i	r^2
Spring temp, Spring winds	4	–38.75	0.0	0.09	0.49
Winter ice, Spring winds, Spring temp	5	–36.98	1.8	0.08	0.57
Spring winds	3	–36.65	2.1	0.08	0.24
Winter temp, Spring winds	4	–36.49	2.3	0.08	0.40
Winter ice, Spring winds	4	–35.32	3.4	0.08	0.36
Spring winds, Winter temp, Spring temp	5	–35.08	3.7	0.08	0.52
Null model of no factors	2	–34.71	3.7	0.07	0.00

since 1993, Spectacled Eiders have wintered in the same area (this study, Petersen et al. 2000).

The extent and thickness of sea ice in the Northern Hemisphere has decreased since about 1952 (Vinnikov et al. 1999). However, satellite data from the Bering Sea during 1979–1996 showed wide interannual variability with the extent and amount of sea ice and no trend of reduction in ice cover (Parkinson 2000). Similarly, we could not document a trend based on the remotely sensed sea-ice data of the core winter area from 1978–2002. Thus, we assumed that the distribution of Spectacled Eiders during the 52-year period we examined did not change in response to long-term trends in ice. Anecdotal information from walrus (*Odobenus rosmarus*) and other marine mammal surveys since the 1970s (Petersen et al. 1999) also suggests that Spectacled Eiders were in or near the general wintering area we identified.

Although ice data corresponding with the Spectacled Eider wintering area are not available before 1979, it is reasonable to infer that ice conditions on the wintering area during 1972–1976 were severe. Macklin and Stabeno (2000) analyzed ice maps for 1972–1998 and reported that during the cold 1972–1976 period, ice in the Bering Sea persisted 2–4 weeks longer than during the warmer 1977–1988 period. After 1989, a weaker cold period returned during which ice was more extensive, but not as extensive as the early 1970s (Macklin and Stabeno 2000). Wyllie-Echeverria and Wooster (1998) investigated the same maps and found that the southernmost latitude of seasonal sea-ice extent along the 169°W meridian was over two standard deviations (± 0.37°) farther south than average (57.25°N) during the winters of 1972, 1974–1976, and 1995.

BATHYMETRIC IMPACT

The southward currents south of St. Lawrence Island may influence benthic communities within this region by transporting nutrients and sediments (Grebmeier and Cooper 1995, Grebmeier and Dunton 2000). The bathymetric character of the core wintering area is unique compared to surrounding regions south of St. Lawrence Island. The underwater openings at the southern and northern peripheries of this core wintering area (Fig. 2) could funnel water from the generally south-southwestern ocean current (illustrated in Macklin and Stabeno 2000) and thus promote nutrient exchange within that area. Also, the undulating benthic surface would provide a greater diversity of habitats, and thus variability in the density and species composition of invertebrates (McDonald et al. 1981, Stoker 1981).

EFFECTS OF ICE

The presence and dynamic nature of ice in the core wintering area may decrease total energy costs of Spectacled Eiders that would otherwise occur during winter. The energetic cost of complete contact with water (diving) is much greater than having no contact (roosting; de Vries and van Eerden 1995). By wintering in open areas within the ice, eiders may lower daily maintenance costs by roosting on the ice. In addition, the ice pack may dampen the effects of winter storms. Wave height in the ice pack is lower than in open waters (Divoky 1981), allowing birds to feed in conditions that otherwise might be considered severe.

As the amount of ice cover increases in winter, the amount of foraging area may become restricted. Spectacled Eiders form dense flocks in open holes and leads in the ice (hundreds to 10 000s birds; Petersen et al. 1999). Dense flocks of birds feeding in such small areas under most conditions would quickly deplete available prey (Doleman and Southerland 1997). However, the constant movement of the ice may ameliorate this restriction. The ice moves about 9 km day^{-1} providing access to resources throughout the wintering area. Thus, the daily travel costs associated with finding new patches of prey (Bernstein et al. 1991) approaches zero. However, given the small size of the core wintering area, because of sea-ice drift, eiders would have to relocate to their core wintering area every few days.

We found that both population indices were negatively correlated with extreme ice concentration. Ice conditions may affect distribution and survival of sea ducks by constricting the availability of foraging areas (Pehrsson 1975). Several species of sea ducks leave wintering areas in conjunction with ice formation or cold temperatures (Nilsson 1970, 1972). In most years, Spectacled Eiders were not exposed to more than 60% ice cover until January (Fig. 3), two months into their five-month winter. In addition, we found no evidence that eiders moved as ice began to cover the core winter area. As with Common Eiders (*Somateria mollissima*) (Guillemette et al. 1993), our data suggest that ice rarely completely covered the core wintering area and, if so, only for short periods (Fig. 7). In the extreme weather associated with severe ice conditions, Spectacled Eiders probably cease feeding and use reserves until conditions improve, as has been shown with other ducks (Goudie and Ankney 1986, Suter and van Eerden 1992, Lovvorn 1994). It is unlikely that birds move to distant areas during these short, extremely cold periods (Suter and van Eerden 1992). However, in spring (April) 1995 a portion of the Spectacled Eider population was found in open holes and leads in the ice about 100 km southeast of the core area (Petersen et al. 1999), suggesting that some birds may move in some particularly harsh periods.

If Spectacled Eiders feed diurnally, as do other species of sea ducks (Nilsson 1972, Stott and Olson 1973, Goudie and Ankney 1986, Guillemette 1998), their daily foraging time in winter would be only about four hours in late December and early January. However, the most severe weather occurred in February to March when daylight periods were increasing rapidly; thus the additional time available to forage may offset restrictions related to severe conditions (Systad et al. 2000).

CHANGES IN POPULATIONS

We found that, in general, indices of the number of Spectacled Eiders returning to the Y-K Delta were negatively correlated with parameters of extreme ice concentrations during winter, and cold temperatures in winter and spring. This suggests that annual survival and breeding propensity of adult Spectacled Eiders may have been affected by the severity of ice conditions and temperatures, and that more birds returned to nest in years when weather patterns may have resulted in broken and dispersed ice in spring.

Annual survival of subadult Spectacled Eiders at sea is difficult to determine since they do not return to the breeding grounds until their third or fourth summer (Petersen et al. 2000). Thus, low subadult survival could only be detected by differences in annual recruitment in subsequent years. Hatching and brood success of Spectacled Eiders can be highly variable within the breeding grounds and among years and are influenced by predators, weather, and time of nest initiation (Dau 1976, Flint and Grand 1997, Grand and Flint 1997). Thus, it does not always follow that a mild winter corresponds to a large recruitment two or three years later.

Since Spectacled Eiders are well adapted to harsh winter environments, we would not expect significant mortality unless conditions exceed some unknown threshold. Nesting eider abundance on the Y-K Delta was negatively correlated with extreme ice concentration on the core wintering area, and our results show that the prevalence of extreme ice concentration was associated with conditions that directly or indirectly affected survival. This relationship suggests the possibility of a single-variable threshold. More conservatively, our data indicate that the largest annual decreases in eider nest abundance on the Y-K Delta followed winters that had the highest frequency of days with extreme ice concentration. Premised on a threshold principle, rather than a continuous effect, our results support the general conclusion that eider survival can be influenced by extended periods of extreme sea ice on the wintering area.

The impact of weather on subsequent reproductive effort of Spectacled Eiders and other sea ducks is difficult to determine. It is assumed that weather or other disturbances at locations where sea ducks put on reserves for breeding can influence clutch size, timing of nesting, and the proportion of pairs attempting to nest (Coulson 1984, 1999, Fox 1996). This is especially true for many birds in the Arctic that must arrive to the breeding grounds with most or all of their reserves necessary for successful nesting (Raveling 1979, Ankney 1982, Owen and Black 1990, Fox 1996).

Based on our models, we conclude that the long-term decline of Spectacled Eiders breeding on the Y-K Delta during 1957–2002 was not strongly related to annual variation of weather in the Bering Sea. Unknown causes associated with year accounted for a large fraction of the variation in the data. However, extreme wind conditions explained some of the variation of this 46-year index. Very cold temperatures during the 1970s and persistent winds in winter suggest that environmental conditions in the Bering Sea during this period were the worst of the past 50 years (Trenberth and Hurrell 1994) and could have significantly affected annual changes in population indices. However, the Y-K Delta population began to decline at least by 1957, continued during the colder regime ending in 1976 and during the warmer regime of 1977–1988, and stabilized during the cooler regime beginning in 1989.

It has been hypothesized that changes in benthic fauna in the Bering Sea influenced population changes of Spectacled Eiders (Stehn et al. 1993, USFWS 1996). Such a change could, in part, account for the low explanatory power of weather in our models of the Breeding Pair Survey Index. Although benthic sampling was not conducted annually, and thus cannot be incorporated into our models, maps published as figures and data from fixed locations can be used to describe benthic species assemblages in the wintering area. A species assemblage dominated by the bivalve *Macoma calcarea* covered the Spectacled Eider core wintering area during 1950–1984 (Neiman 1963, Stoker 1981, Sirenko and Koltun 1992); the bivalve *Nuculana rediata* dominated on a portion of the area by 1988 (Sirenko and Koltun 1992); and Nuculidae, Nuculanidae, Tellinidae, and polychaetes dominated in the entire wintering area from 1990–2001 (Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Lovvorn et al. 2003). A decline in benthic fauna biomass was recorded from 1988–1999 (Grebmeier and Dunton 2000).

The breeding population of Spectacled Eiders on the Y-K Delta began to decline by 1957 (Hodges et al. 1996) and stabilized in 1989 (T. D. Bowman, unpubl. data). The number of breeding birds on the Y-K Delta declined while *Macoma calcarea* dominated on the core wintering area in the 1950s to 1984 and through periods of relatively high and low productivity or biomass; continued to decline during the change to *Nuculana rediata* (1988); and stabilized during its domination (1990–2001) and the period of declining biomass (1988–1999). This lack of concordance suggests that the change in benthic populations of bivalves in the wintering area may have had only a minor influence on the decline of the Y-K Delta breeding population. If changes in benthic fauna in the wintering area were a major factor influencing the decline of the Y-K Delta breeding population (Stehn et al. 1993, USFWS 1996), we would have expected similar major declines in the Russian breeding population. However, there is no evidence (Dau and Kistchinski 1977, Hodges and Eldridge 2001) that any such decline occurred in arctic Russia.

We show that extreme winter weather conditions contributed to annual variation in population indices. This variation, in part, was a reflection of reduced annual survival and reproductive effort of adult female Spectacled Eiders during those extreme winters. The decline of the Y-K Delta breeding population, however, was probably influenced most by reduced survival of adult females (USFWS 1996), including predation during the breeding season (Flint and Grand 1997, Flint et al. 2000). In addition, lead poisoning reduced survival of adult females an additional 35% each year (Grand et al. 1998). Thus, slow recovery of this breeding population would be expected in response to efforts to increase survival and reproductive success on the breeding grounds. As human-induced effects on survival continue to be reduced, variation in ice and weather on the wintering area may have a greater relative impact on annual population variability.

Except for the occasional extremely harsh winter, ice cover and weather on the wintering area during the past 25 years was relatively inconsequential to changes in population trends of Spectacled Eiders. However, managers should keep in mind that eiders could experience harsh conditions in some years, which may adversely affect the number of birds surviving or returning to nest. Increased winter temperatures associated with global warming could ameliorate the overall intensity of the latest cold regime, but the frequency of winters with very dense ice cover may still be higher than that observed during the warmer period of 1977–1989.

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LITERATURE CITED

ALASKA SAR FACILITY [ONLINE]. 2000. The Alaska Satellite Facility: synthetic aperture radar data. <http://www.asf.alaska.edu/getdata.html> (30 September 2003).

ANDERSON, D. R., AND K. P. BURHNAM. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66:912–918.

ANDERSON, D. R., K. P. BURNHAM, AND W. L. THOMPSON. 2000. Null hypothesis testing: problems, a prevalence, and an alternative. Journal of Wildlife Management 64:912–923.

ANDERSON, D. R., W. A. LINK, D. H. JOHNSON, AND K. P. BURNHAM. 2001. Suggestions for presenting the results of data analyses. Journal of Wildlife Management 65:373–378.

ANKNEY, C. D. 1982. Annual cycle of body weight in Lesser Snow Geese. Wildlife Society Bulletin 10: 60–64.

BARRY, T. W. 1967. Observations on natural mortality and native use of eider ducks along the Beaufort Sea coast. Canadian Field-Naturalist 82:140–144.

BEAUCHAMP, G., M. GUILLEMETTE, AND R. YDENBERG. 1992. Prey selection while diving by Common Eiders, *Somateria mollissima*. Animal Behaviour 44: 417–426.

BERNSTEIN, C., A. KACELNIK, AND J. R. KREBS. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. Journal of Animal Ecology 60:205–225.

BROWER, W. A. JR., H. F. DIAZ, A. S. PRECHTEL, H. W. SEARBY, AND J. L. WISE. 1977. Climatic atlas of the outer continental shelf waters and coastal regions of Alaska. Vol. II. Bering Sea. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Alaska Outer Continental Shelf Environmental Assessment Program. Final Report. Research Unit No. 347. Anchorage, AK.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

CAVALIERI, D. J., C. L. PARKINSON, P. GLOERSEN, J. C. COMISO, AND H. J. ZWALLY. 1999. Deriving long-term time series of sea ice cover from satellite passive-microwave multisensor data sets. Journal of Geophysical Research 104(C7):15803–15814.

COMISO, J. [ONLINE]. 2002. Sea ice products at NSIDC: bootstrap sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I. <http://nsidc.org/data/seaice/data.html> (30 September 2003).

COMISO, J. C., D. CAVALIERI, C. PARKINSON, AND P. GLOERSEN. 1997. Passive microwave algorithms for sea ice concentrations: a comparison of two techniques. Remote Sensing of the Environment 60:357–384.

COOPER, L. W., J. M. GREBMEIER, I. L. LARSEN, V. G. EGOROV, C. THEODORAKIS, H. P. KELLY, AND J. R. LOVVORN. 2002. Seasonal variation in sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. Marine Ecology Progress Series 226:13–26.

COTTAM, C. 1939. Food habits of North American diving ducks. USDA Technical Bulletin 643, Washington, DC.

COULSON, J. C. 1984. The population dynamics of the Eider Duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. Ibis 126: 525–543.

COULSON, J. C. 1999. Variation in clutch size of the Common Eider: a study based on 41 breeding seasons on Coquet Island, Northumberland, England. Waterbirds 22:225–238.

DAU, C. P. 1976. Clutch sizes of the Spectacled Eider on the Yukon-Kuskokwim Delta, Alaska. Wildfowl 27:111–113.

DAU, C. P., AND S. A. KISTCHINSKI. 1977. Seasonal movements and distribution of the Spectacled Eider. Wildfowl 28:65–75.

DE VRIES, J., AND M. R. VAN EERDEN. 1995. Thermal conductance in aquatic birds in relation to the degree of water contact, body mass, and body fat: energetic implications of living in a strong cooling environment. Physiological Zoology 68:1143–1163.

DIVOKY, G. J. 1981. Birds and the ice-edge ecosystem in the Bering Sea, p. 799–956. *In* G. L. Hunt, Jr. [ED.], The eastern Bering Sea shelf: oceanography and resources, section VI, marine birds. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Seattle, Washington.

DOLEMAN, P. M., AND W. J. SOUTHERLAND. 1997. Spatial patterns of depletion imposed by foraging vertebrates: theory, review and meta-analysis. Journal of Animal Ecology 66:481–494.

ELY, C. R., C. P. DAU, AND C. A. BABCOCK. 1994. Decline in a population of Spectacled Eiders nesting on the Yukon-Kuskokwim Delta, Alaska. Northwestern Naturalist 75:81–87.

FEDERAL REGISTER. 1993. Final rule to list the Spectacled Eider as threatened. Federal Register 58(88):27474–27480.

FLINT, P. L., AND J. B. GRAND. 1997. Survival of Spectacled Eider adult females and ducklings during brood rearing. Journal of Wildlife Management 61:217–221.

FLINT, P. L., J. B. GRAND, J. A. MORSE, AND T. F. FONDELL. 2000. Late summer survival of adult female and juvenile Spectacled Eiders on the Yukon-Kuskokwim Delta, Alaska. Waterbirds 23:292–297.

FOURNIER, M. A., AND J. E. HINES. 1994. Effects of starvation on muscle and organ mass of King Eiders *Somateria spectabilis* and the ecological and management implications. Wildfowl 45:188–197.

FOX, A. D. 1996. Factors affecting the reproductive output of Northern Hemisphere migratory Anatidae: the role of female condition (a review). Gibier Faune Sauvage, Game Wildlife 13:635–651.

GOUDIE, R. I., AND D. C. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

GRAND, J. B., AND P. L. FLINT. 1997. Productivity of nesting Spectacled Eiders on the lower Kashunuk River, Alaska. Condor 99:926–932.

GRAND, J. B., P. L. FLINT, M. R. PETERSEN, AND C. L. MORAN. 1998. Effect of lead poisoning on Spec-

tacled Eider survival rates. Journal of Wildlife Management 62:1103–1109.
GREBMEIER, J. M. 1993. Studies of pelagic-benthic coupling extended onto the Soviet continental shelf in the northern Bering and Chukchi Seas. Continental Shelf Research 13:653–668.
GREBMEIER, J. M., AND L. W. COOPER. 1995. Influence of the St. Lawrence Island polynya upon the Bering Sea benthos. Journal of Geophysical Research 100:4439–4460.
GREBMEIER, J. M., AND K. H. DUNTON. 2000. Benthic processes in the northern Bering/Chukchi seas: status and global change, p. 61–71. *In* Impacts of changes in sea ice and other environmental parameters in the Arctic. Report of the Marine Mammal Commission Workshop, 15–17 February 2000, Girdwood, Alaska. Marine Mammal Commission, Bethesda, MD.
GREBMEIER, J. M., C. P. MCROY, AND H. M. FEDER. 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Marine Ecology Progress Series 48:57–67.
GRUMBINE, R. W. 1998. Virtual floe ice drift forecast model intercomparison. Weather and Forecasting 13:886–890.
GUILLEMETTE, M. 1998. The effect of time and digestion constraints in Common Eiders while feeding and diving over blue mussel beds. Functional Ecology 12:123–131.
GUILLEMETTE, M., J. H. HIMMELMAN, C. BARBETTE, AND A. REED. 1993. Habitat selection by Common Eiders in winter and its interaction with flock size. Canadian Journal of Zoology 71:1259–1266.
HARE, S. R., AND N. J. MANTUA. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103–145.
HODGES, J. I., AND W. D. ELDRIDGE. 2001. Aerial surveys of eiders and other waterbirds on the eastern Arctic coast of Russia. Wildfowl 52:127–142.
HODGES, J. I., J. G. KING, B. CONANT, AND H. A. HANSON. 1996. Aerial surveys of waterbirds in Alaska 1957–94: population trends and observer variability. USDI National Biological Service Information and Technology Report 4.
KARPOVA, L. A. 1963. Principal climatic features of the Bering Sea, p. 95–109. *In* P. A. Moiseev [ED.], Soviet fisheries investigations in the northeast Pacific, Part I. Translated (1968), Israel Program for Scientific Translations, Jerusalem.
KOLESNIKOVA, H. A., N. G. SERGEVA, AND N. A. VALOVAYA. 1990. Benthos of the Bering Sea, p. 175–187. *In* P. F. Roscigno [ED.], Results of the second joint U.S.—U.S.S.R. Bering Sea expedition, summer 1984. U.S. Fish and Wildlife Service Biological Reports 90, Washington, DC.
LOVVORN, J. R. 1994. Nutrient reserves, probability of cold spells and the question of reserve regulation in wintering Canvasbacks. Journal of Animal Ecology 63:11–23.
LOVVORN, J. R., S. E. RICHMAN, J. M. GREBMEIER, AND L. W. COOPER. 2003. Diet and body condition of Spectacled Eiders wintering in pack ice of the Bering Sea. Polar Biology 26:259–267.
MACKLIN, S. A., AND P. J. STABENO. 2000. Marine ecosystem studies of physical and biological interactions in the eastern Bering Sea and western Gulf of Alaska. Arctic Research of the U.S. 14:25–32.
MCDONALD, J., H. M. FEDER, AND M. HOBERG. 1981. Bivalve mollusks of the southeastern Bering Sea, p. 1155–1204. *In* D. W. Hood and J. A. Calder [EDS.], The eastern Bering Sea shelf: oceanography and resources. Vol. 2. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of Marine Pollution Assessment, Washington, DC.
NATIONAL CLIMATE DATA CENTER [ONLINE]. 2002. NOAA satellite and information service; get/view online climate data. <http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html> (30 September 2003).
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION [ONLINE]. 2001a. National Centers for Environmental Prediction, Ocean Modeling Branch. <ftp://polar.wwb.noaa.gov/pub/history/ice/drift.data> (30 September 2003).
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION [ONLINE]. 2001b. Oceanographic *in-situ* time series data access. <http://www.epic.noaa.gov/epic/ewb/> (1 October 2003).
NATIONAL RESEARCH COUNCIL. 1996. The Bering Sea. National Academy of Sciences, National Academy Press, Washington, DC.
NEIMAN, A. A. 1963. Quantitative distribution of benthos on the shelf and upper continental slope in the eastern part of the Bering Sea, p. 143–217. *In* P. A. Moiseev [ED.], Soviet fisheries investigations in the northeast Pacific, part 1. Translated (1968), Israel Program for Scientific Translations, Jerusalem.
NIEBAUER, H. J. 1983. Multiyear sea ice variability in the eastern Bering Sea: an update. Journal of Geophysical Research 88:2733–2742.
NIEBAUER, H. J., AND R. H. DAY. 1989. Causes of interannual variability in the sea ice cover of the eastern Bering Sea. GeoJournal 18:45–59.
NILSSON, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145–154.
NILSSON, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. Ornis Scandinavica 3:55–78.
OWEN, M., AND J. M. BLACK. 1990. Waterfowl ecology. Chapman & Hall, New York.
PARKINSON, C. L. 2000. Variability of arctic sea ice: the view from space, an 18-year record. Arctic 53: 341–358.
PAULUS, S. L. 1988. Time-activity budgets of nonbreeding Anatidae: a review, p. 135–152. *In* M. W. Weller [ED.], Waterfowl in winter. University of Minnesota Press, Minneapolis, MN.
PEHRSSON, O. 1975. A ten-year fluctuation pattern of the Common Eider (*Somateria mollissima*) on the Swedish west coast as a result of food availability, p. 91–98. *In* X. Andersson and S. Fredga [EDS.], Proceedings from the symposium on sea ducks. June 16–17, 1975, Stockholm, Sweden. The Na-

tional Swedish Environmental Protection Board, Solna, Sweden.

PETERSEN, M. R., J. B. GRAND, AND C. P. DAU. 2000. Spectacled Eider (*Somateria fischeri*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 547. The Birds of North America, Inc., Philadelphia, PA.

PETERSEN, M. R., W. W. LARNED, AND D. C. DOUGLAS. 1999. At-sea distribution of Spectacled Eiders: a 120-year-old mystery resolved. Auk 116:1009–1020.

PETERSEN, M. R., J. F. PIATT, AND K. A. TRUST. 1998. Foods of Spectacled Eiders *Somateria fischeri* in the Bering Sea, Alaska. Wildfowl 49:124–128.

RAVELING, D. G. 1979. The annual cycle of body composition in Canada Geese with special reference to the control of reproduction. Auk 96:234–252.

SAS INSTITUTE. 1990. SAS/STAT user's guide. Version 6. 4th ed. SAS Institute Inc., Cary, NC.

SEAMAN, D. E., B. GRIFFITH, AND R. A. POWELL. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95–100.

SHARMA, G. D. 1976. Geology. *In* Bering Land Bridge Cultural Resource Study. Final Report. U.S. Bureau of Land Management, Outer Continental Shelf Office. Contract #08550-CT5–45. The University Museum, University of Alaska, Fairbanks, AK.

SIRENKO, B. I., AND V. M. KOLTUN. 1992. Characteristics of benthic biocenoses of the Chukchi and Bering Seas, p. 251–261. *In* P. A. Nagel [ED.], Results of the third joint US-USSR Bering and Chukchi Seas expedition (BERPAC), summer 1988. USDI Fish and Wildlife Service, Washington, DC.

SMITH, W. H. F., AND D. T. SANDWELL. 1997. Global seafloor topography from satellite altimetry and ship depth soundings. Science 277:1957–1962.

STEHN, R. A., C. P. DAU, B. CONANT, AND W. I. BUTLER JR. 1993. Decline of Spectacled Eiders nesting in western Alaska. Arctic 46:264–277.

STOKER, S. 1981. Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf, p. 1069–1090. *In* D. W. Hood and J. A. Calder [EDS.], The eastern Bering Sea shelf: oceanography and resources. Vol. 2. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of Marine Pollution Assessment, Washington, DC.

STOTT, R. S., AND D. P. OLSON. 1973. Food-habit relationship of sea ducks on the New Hampshire coastline. Ecology 54:996–1007.

SUTER, W., AND M. R. VAN EERDEN. 1992. Simultaneous mass starvation of wintering diving ducks in Switzerland and the Netherlands: a wrong decision in the right strategy? Ardea 80:229–242.

SYSTAD, G. H., J. O. BUSTNES, AND K. E. ERIKSTAD. 2000. Behavioral responses to decreasing day length in wintering sea ducks. Auk 117:33–40.

TRENBERTH, K. E., AND J. W. HURRELL. 1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9:303–319.

U.S. FISH AND WILDLIFE SERVICE. 1996. Spectacled Eider recovery plan. Recovery plan prepared for Region 7, U.S. Fish and Wildlife Service. USDI Fish and Wildlife Service, Anchorage, AK.

VINNIKOV, K. Y., A. ROBOCK, R. J. STOUFFER, J. E. WALSH, C. L. PARKINSON, D. J. CAVALIERI, J. F. B. MITCHELL, D. GARRETT, AND V. F. ZAKHARTOV. 1999. Global warming and Northern Hemisphere sea ice extent. Science 286:1934–1936.

WYLLIE-ECHEVERRIA, T., AND W. S. WOOSTER. 1998. Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fisheries Oceanography 7:159–170.