

## EFFECTS OF EL NIÑO ON DISTRIBUTION AND REPRODUCTIVE PERFORMANCE OF BLACK BRANT

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**Abstract.** Climate in low-latitude wintering areas may influence temperate and high-latitude breeding populations of birds, but demonstrations of such relationships have been rare because of difficulties in linking wintering with breeding populations. We used long-term aerial surveys in Mexican wintering areas and breeding areas in Alaska, USA, to assess numbers of Black Brant (*Branta bernicla nigricans*; hereafter brant) on their principal wintering and breeding area in El Niño and non-El Niño years. We used Pollock's robust design to directly estimate probability of breeding and apparent annual survival of individually marked brant at the Tutakoke River (TR) colony, Alaska, in each year between 1988 and 2001. Fewer brant wintered in Mexico during every El Niño event since 1965. Fewer brant were observed on the principal breeding area following each El Niño since surveys began in 1985. Probability of breeding was negatively related to January sea surface temperature along the subtropical coast of North America during the preceding winter. Between 23% (five-year-olds or older) and 30% (three-year-olds) fewer brant nested in 1998 following the strong El Niño event in the winter of 1997–1998 than in non-El Niño years. This finding is consistent with life history theory, which predicts that longer-lived species preserve adult survival at the expense of reproduction. Oceanographic conditions off Baja California, apparently by their effect on *Zostera marina* (eelgrass), strongly influence winter distribution of brant geese and their reproduction (but not survival), which in turn affects ecosystem dynamics in Alaska.

**Key words:** Arctic; Black Brant; *Branta bernicla nigricans*; breeding; demography; El Niño; herbivore; population; robust design; sea surface temperature; *Zostera marina*.

### INTRODUCTION

Understanding the population dynamics of long-distance migrants has been limited by the difficulty of directly linking the status of individuals on winter or migration areas to survival and reproductive success of these same individuals on breeding areas. The use of stable isotopes has suggested a relationship between timing of arrival on temperate breeding areas and win-

ter habitat (Mora et al. 1998). Resighting of uniquely marked individuals, combined with modern analytical methods (Lebreton et al. 1992), has improved our ability to understand how survival probability varies with individual state (Cam et al. 2002), climate (Sillett et al. 2000), or other environmental variables (Sedinger et al. 2002). Small passerines experienced reduced survival and fecundity in El Niño southern oscillation (El Niño) years compared to other years (Sillett et al. 2000).

Winter condition is an especially important determinant of subsequent reproductive success in relatively large-bodied birds, like waterfowl, that carry stored nutrients from wintering or migration areas to breeding sites thousands of kilometers distant (Drent and Daan 1980). These stored nutrients are known to influence the likelihood of breeding and reproductive investment (Ankney and MacInnes 1978, Ebbinge and Spaans 1995, Feret et al. 2003, Gauthier et al. 2003). Both climate and habitat change in temperate and subtropical

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PLATE 1. (Top left) Female Black Brant near her nest, standing on a map of her nesting area in the Tutakoke River colony, Alaska, USA. This female was marked in 1986 and was at least 20 years old at the time of the photo. (Top right) Female Black Brant defending her nest in the Tutakoke River colony. (Lower left) A pair of Black Brant at their nest site in the Tutakoke River colony. (Lower right) Female Black Brant with her brood immediately following hatch in the Tutakoke River colony. This female was at least 10 years old when the photo was taken. Photo credits: top left, Benjamin Sedinger; all others, J. Sedinger.

areas potentially influence population dynamics, even of long-distance migrants breeding in pristine arctic environments, because of the reliance of individuals on nutrients acquired at lower latitudes for migration and reproduction (Alisauskas 2002). Accumulation of lipid reserves can influence the number of goslings adult geese return with to the wintering grounds (Prop et al. 2003). Bêty et al. (2003) showed that spring nutrient reserves influenced clutch size in Greater Snow Geese (*Anser caerulescens atlantica*), but it is generally not known whether variation in breeding probability, clutch size, nest success, or gosling survival contributed to variation in recruitment of young. Because geese substantially impact vegetation in high-latitude ecosystems where they breed (Kotanen and Jefferies 1997, Jefferies and Rockwell 2002, Person et al. 2003), the linkage between winter habitats and reproductive performance of geese also has important implications for ecological connections between temperate ecosystems and those in the arctic.

Black Brant (*Branta bernicla nigricans*; hereafter brant; see Plate 1) are a small, colonially breeding goose that nests predominately in four major colonies on the Yukon-Kuskokwim (Y-K) Delta (Sedinger et al. 1993). Brant are strictly herbivorous, grazing on terrestrial grasses and sedges during the breeding season (Person et al. 1998, 2003) and marine plants, primarily *Zostera marina* (eelgrass), during the remainder of the year (Reed et al. 1998). Most brant fly directly from an autumn migratory staging area on the Alaska Peninsula, USA, to wintering areas in Mexico (Einarsen 1965). About 75% of the entire population winters in bays and estuaries in western Mexico, and 25% winter along the Pacific coast from California to Alaska (Subcommittee on Pacific Brant 2002).

Abundance and distribution of eelgrass is negatively influenced by sea surface temperatures (SST), such that the biomass and spatial extent of intertidal beds generally decreases along a latitudinal gradient as SST increases in a southward direction (Cabello-Pasini et

al. 2003, Thom et al. 2003). During El Niño years, when SST rises in the north Pacific (Philander 1990), eelgrass biomass is reduced along the Pacific coast of North America compared to non-El Niño years (Cabello-Pasini et al. 2002, Thom et al. 2003, Ward et al. 2005). Eelgrass reductions likely have greater effect on brant populations wintering in southern areas because these areas, especially those in Mexico where eelgrass is already at its southern limit in the northern hemisphere, contain less intertidal eelgrass than more northern areas (e.g., Cabello-Pasini et al. 2003). Because brant use of bays along the Pacific coast is directly related to eelgrass abundance (Moore et al. 2004), we hypothesized that brant numbers decline in Mexico during El Niño years in response to reduced eelgrass in southern areas. Further, we hypothesized that this reduction reflects a northward shift in distribution out of Mexico rather than a decrease in survival. We also hypothesized that fewer brant breed in El Niño years because of reduced food abundance on wintering and migration areas.

We examined the association between El Niño and numbers of brant wintering in Mexico, combined with demographic patterns, to explore the hypothesis that brant shifted their wintering distribution north in El Niño years. We used observations and reencounters since 1987 of uniquely marked individual brant combined with a robust design analysis (Kendall et al. 1997) to test hypotheses about the effects of El Niño years and SST on breeding probability and apparent annual survival of brant on the Y-K Delta in western Alaska. We augmented our robust design analysis of breeding probabilities with annual surveys of numbers of brant breeding on the Y-K Delta between 1985 and 2000.

#### METHODS

Numbers of brant present on the Y-K Delta, Alaska, breeding areas were counted during annual surveys for all geese nesting on the Y-K Delta during June 1985–2000 (Butler et al. 1995). Surveys followed standard aerial-survey techniques, which consisted of 400 m wide transects spaced at 0.8–12.9 km intervals, flown at 40 m altitude in fixed-wing aircraft. Approximately 100 transects up to 60 km long were flown annually, resulting in 8% of the 12 800 km<sup>2</sup> being sampled annually. Surveys of wintering areas in Mexico were conducted by a pilot and observer using fixed-wing aircraft in January of each year between 1961 and 2001 (Conant and Voelzer 2001). Because brant were in flocks in winter, each bay was flown in its entirety, enabling the pilot and observer to estimate the number of individuals in each flock. Aerial surveys in Mexico were not replicated within years because of logistical, time, and financial constraints. Duplicate surveys of bays in Mexico in 1994 and 1995, however, showed that counts of individuals were precise to within  $\pm 16\%$  of the count (Conant and Hodges 1995). We report total counts for

Baja California for 1961–2001. We assessed the probability that numbers in Mexico declined by chance during all six El Niño events during the winter survey period by raising 0.5 to the sixth power, assuming that (1) the a priori probability of decline during each El Niño was 0.5 and (2) that population change during the six El Niño events represented independent events.

We used January mean SST data from ship track 1, between 20° S and 20° N along the Pacific coast of the Americas (Rasmusson and Carpenter 1982) to assess oceanographic conditions along the Pacific coast of North America. Mooers et al. (1986) demonstrated strong correlation between January SST at La Jolla, California, USA, and sites along the Pacific coast between 18° and >45° N. Thus, we believe the index we used provided a reasonable proxy for SST dynamics in winter areas used by brant.

About 2,000 brant have been uniquely marked annually since 1987 at the Tutakoke River (TR) colony (61°15' N, 165°37' W), Y-K Delta, Alaska, with plastic bands containing alphanumeric codes. Brant were captured by herding them into corral traps during the adult remigial molt in mid to late July each year (Sedinger et al. 1997). During the study, ~2000 previously marked individuals were identified annually on the breeding area. Breeding individuals were identified by flushing them from nests and reading the codes on their plastic bands using binoculars or 15–60× telescopes. We also recorded breeding brant accompanying broods by observing them from 3–7 m tall towers with blinds on top and by capturing them in banding drives during the flightless period in mid- to late July. Only female brant with a brood patch, indicating they had nested that summer, were recorded as present for our analysis. We restricted our analysis to female brant (1) to avoid pseudoreplication associated with treating both members of a pair as independent and (2) because females were faithful to their colony of origin, whereas males may disperse following a change in mates (Linberg et al. 1998).

We used Pollock's robust design (Pollock 1982, Kendall et al. 1997) to estimate probability of being present on the breeding colony each summer, which, based on our sampling protocols, was synonymous with breeding (Sedinger et al. 2001). In robust design terminology (Kendall et al. 1997), the entire breeding season corresponded to a primary encounter period. We used samples from nesting (May–early June), brood-rearing (late June–early July) and banding (late July) as our secondary-encounter occasions within each primary occasion (Kendall et al. 1997). Robust design assumed that the population was closed between secondary samples. Because most individuals were initially marked during banding drives at the end of the breeding season, they were not available to be encountered during the earlier secondary samples in that year. Therefore, we conditioned our encounter history on the first reencounter of each individual so they were available to be

encountered in all three of the secondary samples during the breeding season in which they first appeared. Despite this precaution, we knew, based on radiotelemetry data, that our population was not closed because some females that failed in their breeding attempt left the colony for molting areas in the arctic (Flint et al. 1995). Simulation of this problem, however, indicated that, while it produced bias in our estimates of conditional encounter probability for the third secondary-encounter occasion (i.e., banding), bias in our estimates of breeding probability were <2% (Sedinger et al. 2001).

Because our encounter histories were conditioned on first reencounter, no individuals in our sample were less than one year old. Previous analyses indicated minimal age-related variation in survival after the first year (Sedinger et al. 2001), so we excluded age structure from models of survival. We allowed apparent annual survival, estimated in the robust design models we considered, to be fully time (year) specific in all models. Because permanent emigration cannot be distinguished from mortality in these models, we estimated apparent, rather than true, survival. Hereafter, we refer to apparent annual survival as annual survival.

Earlier analyses showed that breeding probabilities increased up to age five, secondary-encounter probabilities varied among years, and secondary-encounter occasions, and increased up to age three (Sedinger et al. 2001). We therefore maintained full-time variation and age-related variation up to age three in conditional secondary-encounter probabilities, and maintained five age classes in all models of breeding probability. The robust design actually estimated the probability of being absent,  $\gamma$ , and we estimated breeding probability as  $1 - \gamma$ . We used Program MARK to estimate parameters in models of breeding probability (White and Burnham 1999). Program MARK allowed for Markovian models of breeding probability, in which it was possible to distinguish between the probability of being absent from the sampled area conditioned on being either present during the previous primary sampling period,  $\gamma''$ , or absent during the previous primary sampling period,  $\gamma'$  (Kendall et al. 1997). We set  $\gamma''$  equal to  $\gamma'$  in all models because we were interested only in the effects of oceanographic conditions in the wintering range of brant on breeding probability.

We assessed the impact of El Niño events on breeding probability of brant in two ways. One set of models included El Niño years as a fixed effect; that is, we allowed breeding probability to differ between El Niño and non-El Niño years. Hypotheses about the mechanism by which El Niño events affect brant winter distribution and breeding probability involve the effect of greater SST on eelgrasses in Baja California. (Ward et al. 2005). We, thus, also considered models in which breeding probability varied as a function of January SST along the tropical Pacific coast of the Americas. Apparent nest success of brant at Tutakoke was typi-

cally high (>75%), but brant experienced catastrophic failure in a few years associated with tidal flooding or high rates of predation by arctic foxes (*Alopex lagopus*; e.g., Anthony et al. 1991). We recorded most marked females during late incubation, hatching, or when recaptured during banding drives in July (Sedinger et al. 2001). Consequently, we likely underestimated breeding probability in years of high nest failure. Therefore, we considered models including apparent nest success to control for effects of nest success on our estimates of breeding probability. Apparent nest success was calculated as the proportion of nests that hatched, which were monitored from egg laying until hatching or failure. The most complex model we considered contained five age classes for estimates of breeding probability, effects of nest success on estimates of breeding probability, an additive effect of January SST on breeding probability (SST effects were parallel across age classes), and an interaction between the effects of January SST and nest success on breeding probability. We considered all models containing additive effects of nest success, and both additive and interactive effects of SST on breeding probability. Continuous variables were transformed to standard normal distributions. We used the logit-transformation to relate independent variables to parameters estimated in our models.

Encounter-reencounter data are typically overdispersed compared to the theoretical expectation (Burnham and Anderson 2002). This extra-binomial variation is accounted for in model selection using quasi-likelihood by adjusting Akaike Information Criteria (AIC) scores using a variance inflation factor,  $\hat{c}$ , producing QAIC scores (Burnham and Anderson 2002). We estimated  $\hat{c}$  from  $\chi^2/df$ , using the goodness-of-fit test for Program RDSURVIV (Hines 1996) applied to the most general model excluding covariates. This procedure was likely conservative (overestimated true  $\hat{c}$ ) because RDSURVIV did not incorporate effects of age-specific variation or covariates on parameters that existed in the models we ran. Not including covariates or age effects would have reduced model fit, producing a larger estimate of  $\hat{c}$ , and more conservative analysis, than was necessary for the most general model we actually considered. Program MARK adjusted AIC and QAIC scores for small sample size, producing AIC<sub>c</sub> and QAIC<sub>c</sub> scores (White and Burnham 1999). We report model-averaged estimates of the  $\beta$  parameters and their standard errors relating logit-transformed estimates of breeding probability to independent variables such as SST (Burnham and Anderson 2002). Because these estimates include the effects of uncertainty about the "true" model, they are more conservative than estimates based only on the best model among those considered (Burnham and Anderson 2002).

## RESULTS

January SST varied from 22.6°C (1999) to 27.2°C (1998) during the years of this study for which we

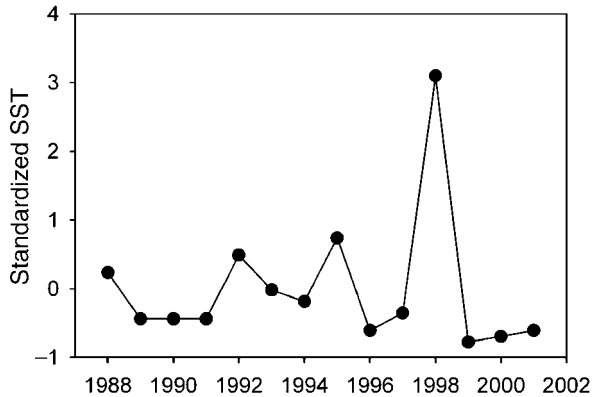


FIG. 1. Standardized sea surface temperatures (SST) during January along the tropical Pacific coast of the Americas between 1988 and 2001. Mean  $\pm$  SE SST was  $23.5 \pm 0.32^\circ\text{C}$  between 1988 and 2001.

estimated breeding probability for brant at the TR colony (Fig. 1). Highest SST occurred in 1998, followed by 1995 and 1992. Numbers of brant wintering in Mexico declined relative to the previous year during all six El Niño events since 1965 (Fig. 2). Probability of decline in every El Niño year occurring by chance was  $(0.5)^6 = 0.016$ . Numbers in Mexico recovered in the year following four of six El Niño events; exceptions followed the 1992 and 1998 El Niño events.

We released 5348 uniquely marked females that were reencountered at least once between 1986 and 2000. We estimated  $\hat{c} = 1.34$ . The best performing model of breeding probability contained nest success, an additive relationship between age and SST (effects of SST were parallel across age classes) and an interaction between nest success and SST (Table 1). Five of the top seven models contained a term for SST or a distinction between El Niño and non-El Niño years. Models with either an SST or an El Niño effect had a combined model weight of 0.86, indicating strong support for effects of oceanographic conditions in the tropical east Pacific on breeding by brant. Models that did not contain either a January SST or El Niño effect were not supported. All of the top four models also contained a term for nest success (combined model weights 0.83), indicating that our estimates of breeding probability were affected by nest success. The model-averaged estimate of  $\beta$  ( $\pm$ SE) for the effect of SST,  $0.206 \pm 0.125$ , indicated that  $\gamma$ , probability of being absent from TR, increased as SST increased. Because breeding probability equaled  $1 - \gamma$ , breeding probability declined as SST increased. Our estimate of  $\beta$  ( $0.310 \pm 0.125$ ) for the relationship between breeding probability and SST, based on the best model in Table 1, indicated a somewhat stronger relationship between breeding probability and SST.

As we expected, the model averaged estimate of  $\beta$  ( $\pm$ SE) for the effect of nest success on  $\gamma$  was  $-0.251 \pm 0.125$ , indicating that our estimate of breeding prob-

ability declined as nest success declined. When controlled for nest success, predicted breeding probability ranged from 0.84 to 0.70 for female brant five years old or older and from 0.71 to 0.52 for two-year-old female brant (Fig. 3). Calculated breeding probabilities in Fig. 3 were based on model-averaged estimates of the  $\beta$  relating breeding probability to January SST. Model-averaged estimates of breeding probability (Fig. 4) reflected annual variation in January SST; breeding probability was substantially lower in 1998 and somewhat lower in 1992 and 1995 than in other years of the study. Consistent with our estimates of breeding probability, fewer brant were counted on the entire Y-K Delta in each of the three El Niño years since 1985 than in the year preceding the El Niño event (Fig. 5). Because of the limited duration of surveys on the breeding area, inference is somewhat limited, but patterns from the aerial-survey data suggest that our observations from the TR colony apply generally to the entire breeding population on the Y-K Delta. Annual survival fluctuated within a relatively narrow range (Fig. 6). Annual survival did not decline coincident with El Niño events. In fact, two of the highest estimates of annual survival coincided with El Niño events (1991–1992 and 1997–1998; Fig. 6).

## DISCUSSION

Breeding probability of brant on the Y-K Delta, Alaska, was negatively related to SST along the Pacific coast of the Americas between  $20^\circ$  S and  $20^\circ$  N during the previous January. The strong El Niño event of 1997–1998 reduced numbers of breeding brant the following summer by up to 30%, depending on age class. We are unaware of other direct assessments of the impact of El Niño events on reproductive performance of

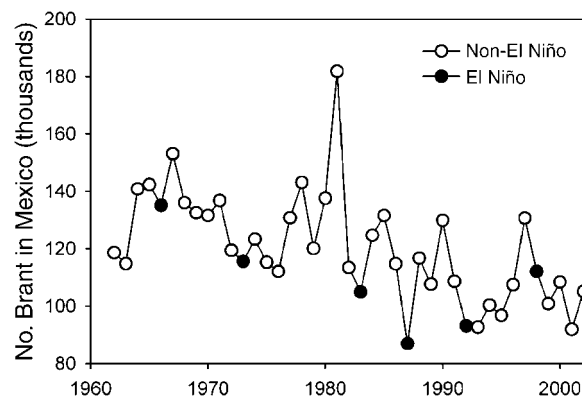


FIG. 2. Number of brant counted in Mexico during U.S. Fish and Wildlife Service surveys flown during January (February in 1987) of each year. Brant were counted by flying at low level over bays on the mainland coast of Mexico from Isla Tiburon, through Bahía de Santa María, and on the Pacific coast of Baja California (Magdalena, San Ignacio, Ojo de Liebre, San Quintín). Counts during El Niño years are indicated by solid symbols, while other years are represented by open symbols.

TABLE 1. Deviance, QAIC<sub>c</sub>, and Akaike weights for models of the relationships between breeding probability ( $1 - \gamma$ ) and age, January sea surface temperature (SST), El Niño years, nest success, and year based on the robust design.

Model†	No. parameters	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	Akaike weight
{Age+nest,age+sst,nest*sst}	142	-51 947.27	0	0.4306
{Age+nest,age+sst}	141	-51 946.18	1.092	0.2494
{Age+nest}	140	-51 944.11	3.164	0.0885
{Age+nest+El Niño}	141	-51 943.29	3.987	0.0586
{Age+sst}	140	51 943.20	4.073	0.0562
{Age+El Niño}	140	-51 943.10	4.173	0.0534
{Age}	139	-51 942.97	4.307	0.0500
{Nest,age*sst}	141	-51 937.18	10.095	0.0028
{Age*nest,age*sst}	146	-51 937.06	10.210	0.0026
{Age,age*sst}	144	-51 936.24	11.029	0.0017
{Age+nest,age*El Niño}	145	-51 935.45	11.823	0.0012
{Age*sst}	140	-51 932.55	14.721	0.0003
{t}	94	-51 023.31	923.961	<0.0001
{.}	45	-47 170.12	4777.148	<0.0001

Notes: All models of breeding probability, except the {t} and {.} models, included five age classes. Annual survival was allowed to be year- but not age-specific for all models. Detection probabilities were allowed to be year-, secondary period-, and age-specific for all except the {t} and {.} models based on earlier analyses (Sedinger et al. 2001). All analyses used Program MARK.

† Notation generally followed Lebreton et al. (1992). Models in which variable effects were additive were indicated with a “plus” (+), while interactions between variables were indicated using “asterisks” (\*). For example, the model age+sst specified the model in which SST effects were parallel across the five age classes. “Nest” indicated that nest success, a continuous covariate, was included in the model, while “sst” was January SST along the tropical Pacific coast of the Americas. The variable “El Niño” indicated that El Niño years were included as a fixed factor with two levels: El Niño vs. non-El Niño years. The {t} was a model in which  $\gamma$  varied only among years. QAIC<sub>c</sub> values were calculated based on  $\hat{c} = 1.34$ .

high latitude breeders. Survival rates, in contrast, were not lower during El Niño years. Response of brant to El Niño conditions is fundamentally different from that for passerines, which had reduced survival in El Niño years (Silllett et al. 2000). Response of brant is characteristic of long-lived species that preserve adult survival but forego reproduction when dictated by environmental conditions. The contrast between brant and passerines is consistent with predictions from life-history theory (Charlesworth 1994) and suggests that population demographic responses to El Niño and climate change may reflect general variation expected from theory.

El Niño events and climate change influence sea-grasses, including *Z. marina*, by changes in SST, and sea level (Short and Neckles 1999), which in turn influence light availability (Moore et al. 1997). All of these factors alter the balance between photosynthesis and respiration (Moore and Wetzel 2000), thereby affecting standing crop (Moore and Wetzel 2000, Plus et al. 2001), nutrient content (Plus et al. 2001), and survival (Moore et al. 1997) of *Z. marina* in brant wintering areas. Consistent with expectation, Ward et al. (2005) reported that *Z. marina* biomass in Baja California was reduced during El Niño events. Availability of *Z. marina* to brant is directly related to their use of embayments outside the breeding season (Wilson and Atkinson 1995, Moore et al. 2004). Thus, oceanographically mediated changes in *Z. marina* could explain changes in winter distribution of brant during El Niño

years, which was reflected in reduced counts in Mexico during El Niño winters.

Fewer brant were counted in Mexico during each El Niño event since 1961 than in the year preceding the El Niño event. Brant numbers in Mexico recovered

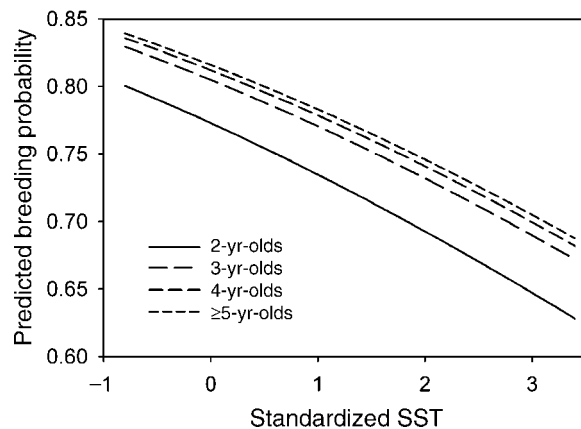


FIG. 3. Estimated relationship between breeding probability of brant at the Tutakoke River colony on the Yukon-Kuskokwim (Y-K) Delta, Alaska, USA, and standardized January SST at La Jolla, California, USA. Breeding probability was estimated by back-transforming the logit. We set standardized nest success equal to zero to remove effects of variation in nest success and used a model-averaged estimate for the  $\beta$  relating  $\gamma$  ( $1 - \text{breeding probability}$ ) to January SST. We also used model-averaged estimates for  $\beta$ 's adjusting  $\gamma$ 's for each age class.

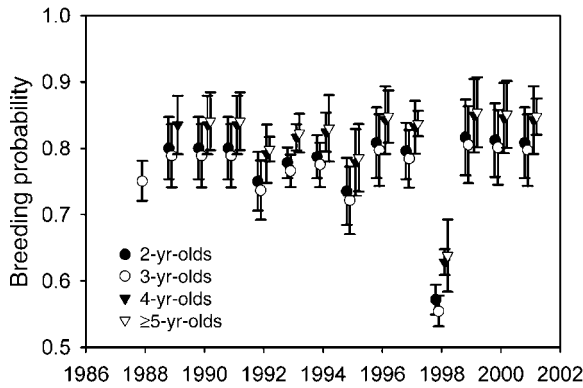


FIG. 4. Estimates of breeding probability for brant 2–5+ years old from the Tutakoke River colony, Alaska. Estimates (mean  $\pm$  SE) represent averages across models in Table 1 and their unconditional variances.

following four of the six El Niño events in this study. Of the two exceptions, 1993, followed the 1992 breeding season, one of the latest on record in the arctic (Ganter and Boyd 2000), and 1999 followed the 1998 El Niño event, one of the strongest of the 20th century, for which our study shows an especially strong reduction in breeding. We hypothesize that declines in Mexico during El Niño events reflect a shift in winter distribution because dynamics of the population in Mexico are inconsistent with observed demography. Our estimates of annual survival tended to be higher during El Niño years (1991–1992, 1997–1998) when SST was warm along the tropical Pacific coast of the Americas. (Fig. 6). Thus, lower numbers in Mexico during El Niño winters were not a result of reduced survival before January surveys.

We show in this paper that breeding probability was lower following El Niño events, which would have reduced the number of young produced in summers following El Niño events. Reduced density of broods during these summers might have resulted in higher growth rates for goslings (Sedinger et al. 1998, 2001, Person et al. 2003), which in turn could have increased their survival during their first fall (Owen and Black 1989, Schmutz 1993, Sedinger et al. 1995). Reduced brood densities associated with El Niño events would be expected to increase mean gosling size by <20 g (Sedinger et al. 1998, Person et al. 2003), producing <10% increase in expected first-year survival (J. S. Sedinger, unpublished data). Consequently, increased juvenile survival associated with reduced brood densities during summers following El Niño events was insufficient to compensate for the production of fewer goslings and recruitment was reduced following El Niño events. Thus, it is difficult to envision how numbers in Mexico increased following four of six El Niño events since 1960 if declines during the El Niño resulted from reduced survival, rather than a shift in distribution. We cannot, therefore, envision a demographic mechanism that could explain reduced numbers of

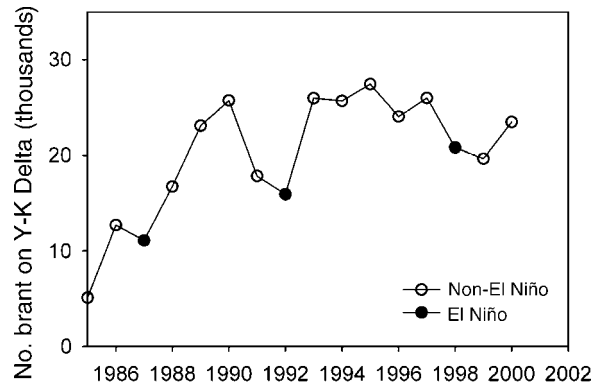


FIG. 5. Number of brant estimated to be on the Y-K Delta during the summer breeding season. Counts of brant were conducted by fixed-wing aircraft flown along random transects in the coastal zone of the Y-K Delta as part of annual surveys for all breeding geese on the Y-K Delta. Transects were flown during the middle of the incubation period each year.

brant in Mexico during El Niño winters other than a shift in distribution.

The effect of El Niño on reproduction in brant is generally consistent with the hypothesis that nutrients acquired on winter and spring migration areas affect reproductive performance in Arctic nesting geese (Davies and Cooke 1983, Ebbs and Spaans 1995, Alisauskas 2002). We cannot, however, distinguish between two more detailed hypotheses explaining the linkage between winter distribution and reproduction in brant. First, it is possible that reduced food abundance on wintering areas directly affected nutrient storage by brant using these areas. Second, displacement of wintering brant to the north may have depleted *Zostera* biomass in the bays where they wintered in El Niño years, thereby reducing food abundance and nutrient storage for spring migrants using the same bays later in the year during spring migration.

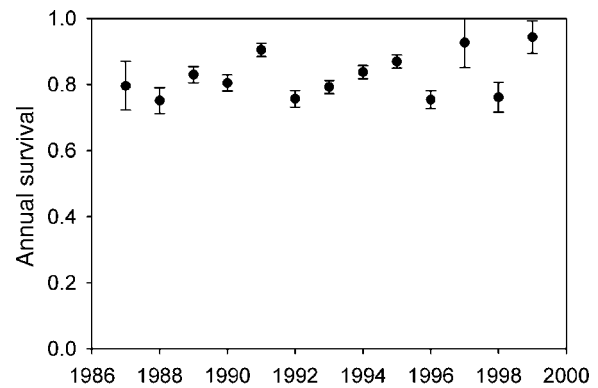


FIG. 6. Estimated annual apparent survival (mean  $\pm$  SE) of brant breeding at the Tutakoke River colony, representing averages across models in Table 1 and their unconditional variances. Survival was estimated for the year following the year indicated on the x-axis. For example, survival in 1998 was from summer 1998 to summer 1999.

Reduced breeding effort by brant following winters with El Niño conditions directly influences ecosystems on the Y-K Delta in Alaska because brant remove ~90% of aboveground primary production of preferred food plants (Person et al. 1998) and maintain these plants in grazing lawns in a high nutrient condition for growing young. Removal of such large amounts of primary production reduces litter accumulation and accumulation of organic matter that insulates the soil and eventually leads to development of permafrost (Jorgenson 2000). In the absence of grazing, lawns revert to taller forms of vegetation that are not extensively grazed and may require more than a decade to be reconverted to grazing lawns that will support goslings (Person et al. 2003). Thus, El Niño conditions directly affect reproduction in the brant population and in so doing, indirectly influence not only brant population dynamics but also ecosystem structure and function in their subarctic breeding area. The relationship between oceanographic conditions and brant winter distribution and reproduction suggests that long-term climate change may influence some subarctic ecosystems indirectly through impacts on migratory bird populations in addition to changes that may be directly mediated by climate change in the arctic (Walther et al. 2002).

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