

North American Brant: effects of changes in habitat and climate on population dynamics

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Abstract

We describe the importance of key habitats used by four nesting populations of nearctic brant (*Branta bernicla*) and discuss the potential relationship between changes in these habitats and population dynamics of brant. Nearctic brant, in contrast to most geese, rely on marine habitats and native intertidal plants during the non-breeding season, particularly the seagrass, *Zostera*, and the macroalgae, *Ulva*. Atlantic and Eastern High Arctic brant have experienced the greatest degradation of their winter habitats (northeastern United States and Ireland, respectively) and have also shown the most plasticity in feeding behavior. Black and Western High Arctic brant of the Pacific Flyway are the most dependent on *Zostera*, and are undergoing a shift in winter distribution that is likely related to climate change and its associated effects on *Zostera* dynamics. Variation in breeding propensity of Black Brant associated with winter location and climate strongly suggests that food abundance on the wintering grounds directly affects reproductive performance in these geese. In summer, salt marshes, especially those containing *Carex* and *Puccinellia*, are key habitats for raising young, while lake shorelines with fine freshwater grasses and sedges are important for molting birds. Availability and abundance of salt marshes has a direct effect on growth and recruitment of goslings and ultimately, plays an important role in regulating size of local brant populations.

Keywords: brant, *Branta bernicla hrota*, *Branta bernicla nigricans*, breeding, climate change, migration, molting, North America, winter

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Introduction

Brant (*Branta bernicla*; brent geese in Europe) are small-bodied geese that migrate long distances from holarctic nesting areas to temperate wintering habitats of the northern hemisphere. They are among the most marine of all geese and are associated with coastal wetlands throughout their range. Brant are herbivorous, but differ from other geese in that they still almost completely rely on native plants through the full annual cycle.

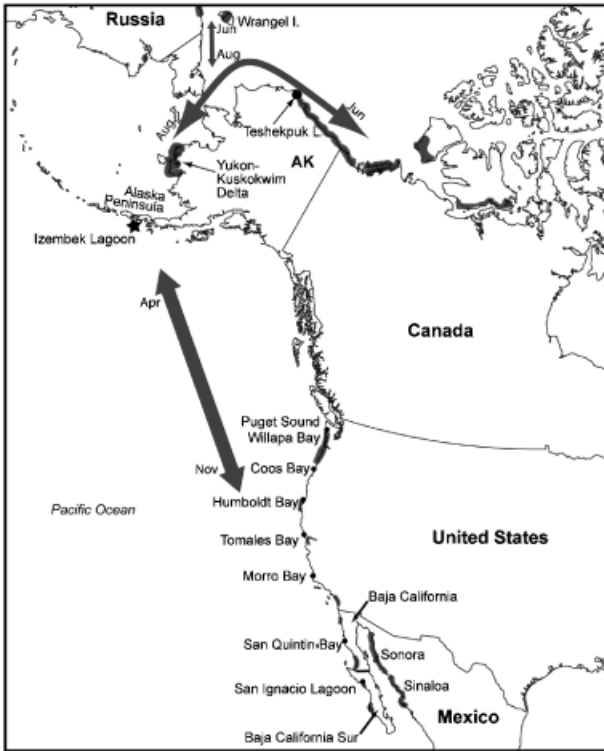
Two of the three recognized subspecies of brant breed in North America (*B. b. nigricans* and *B. b. hrota*). These subspecies are separated into four breeding populations based on genetics, location of breeding and wintering areas, and migration routes (Reed *et al.*,

1998). Two of the populations occur in the Pacific Flyway (Fig. 1). Black Brant breed from the western North America low Arctic to the eastern Russian Arctic, and winter along the Pacific coast of North America from Alaska to Mexico. Western High Arctic (WHA) Brant nest on islands in the western North American high Arctic and winter mainly in Puget Sound, Washington (Reed *et al.*, 1998). The other two populations occur in the Eastern Canadian Arctic (Fig. 1). Atlantic Brant breed in the eastern Canadian low Arctic and winter on the Atlantic coast from Massachusetts to North Carolina, and Eastern High Arctic (EHA) Brant nest on islands in the eastern Canadian high Arctic and winter primarily on the coast of Ireland (Reed *et al.*, 1998).

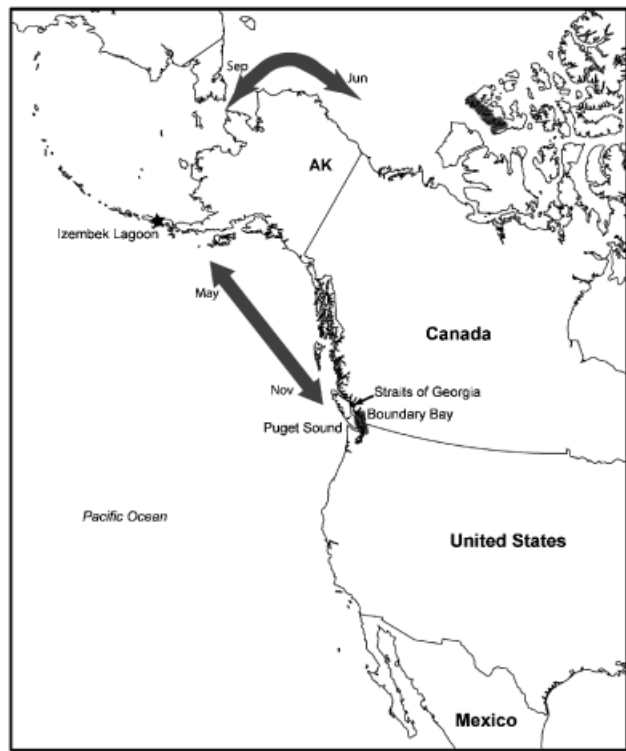
All populations, except EHA Brant, are 20–50% below levels in the early 1950s and 1960s, when winter inventories were first initiated. Two populations are considered to be stable. Black Brant number about

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Black Brant



Western High Arctic Brant



Atlantic Brant



Eastern High Arctic Brant



Fig.1 Breeding and wintering areas, and migration routes of nearctic brant populations.

120 000 individuals (Pacific Flyway Council, 2002) and EHA Brant total about 20 000 birds (Merne *et al.*, 1999; O. Merne, personal communication). Atlantic Brant, the largest population in North America, number about 160 000 individuals and are experiencing a period of growth (Atlantic Flyway Council, 2002), while WHA Brant are in decline with a population size of about 6000 birds (Pacific Flyway Council, 2002).

Environmental change over the last half of the 20th century, driven both by human perturbations and/or natural events, has had a great impact on wetland habitats in North America and these changes have affected brant. Effects include changes in distribution, survival and fitness, and breeding propensity (e.g., Hestbeck *et al.*, 1991; Cooch *et al.*, 1993; Schamber, 2001; Person *et al.*, 2003). Although environmental change is ongoing, current global warming predictions indicate that the rate of change is likely to accelerate (Folland & Karl, 2001).

Anthropogenic changes to marine and freshwater wetlands in the temperate regions have caused most species of geese to abandon or alter their food preferences during migration and winter from native plants in natural habitats to agricultural plants and seeds in cultivated fields (e.g., Abraham *et al.*, 2005; Fox *et al.*, 2005; Gauthier *et al.*, 2005; van Eerden *et al.*, 2005). Species have undergone this adjustment with differing degrees of success but most with favorable results. In contrast to other geese, including the European populations of brant (Madsen *et al.*, 1999), brant wintering in North America have, for the most part, not switched to agricultural and cultivated plants. North American brant still depend on native marine macrophytes, especially their preferred forage species of seagrass, *Zostera marina*. No other species of goose relies so heavily on a single plant species.

This paper offers insight into the current situation and conservation challenges faced by brant in North America. We do this by describing the significance of key wetland habitats in the annual cycle of the four populations of brant. We characterize the relationship between brant and their wetland habitats by presenting examples of variation in brant population dynamics (i.e., distribution, migration patterns, population parameters) with respect to habitat parameters (i.e., abundance, availability, and quality) and climatic variability.

Methods

To compare use of key habitats among the four nearctic populations of brant during nonbreeding and breeding periods we summarized data from the literature. We conducted trend analyses of count data from mid-winter surveys to examine changes in overall population size and shifts in winter distribution of Atlantic and Black

brant with respect to variation in winter climatic conditions. These standardized surveys have been conducted annually across the entire nonbreeding range of Atlantic and Black brant populations and have proven to be reasonably accurate estimates for evaluating trends in overall population size and winter distribution (Kirby & Obrecht, 1982; Sedinger *et al.*, 1994). We used multiple linear regression of the log-transformed annual totals to assess trends in overall population size and shifts in winter distribution of Atlantic and Black brant.

To examine the influence of climatic variations on shifts in winter distribution, we tested for a correlation between annual population counts of brant and a measure of climatic variability, the North America Oscillation (NAO) for Atlantic Brant and El Niño Southern Oscillation (ENSO) for Black Brant, using the Pearson product-moment correlation coefficients. The NAO and ENSO are large-scale atmospheric phenomenon that are associated with the intra- and inter-annual changes in temperature and precipitation in the north Atlantic (Hurrell, 1995), and central and eastern Pacific (Philander, 1990), respectively. A monthly index value has been developed using several large-scale atmospheric measures, and in the case of ENSO, also oceanic measures to monitor the state of each phenomenon. We used values of the NAO index averaged over the winter months of December to March 1960–2003 (Hurrell, 1995; <http://www.cgd.ucar.edu/~jhurrell/noa.stat.winter.html#winter>) as an indicator of climate variability during winters in the northeastern United States. Positive values of the NAO index are associated with above-normal temperatures during winters in northeastern North America, whereas negative values are associated with below-normal temperatures, and above-normal snowfall during winters in the region (Hurrell, 1995). For an indicator of climate variability during winters in Mexico, we used values from the multivariate index of the ENSO (MEI) for the months of December and January combined (http://www.cdc.noaa.gov/ENSO/enso.mei_index.html). Positive MEI values, or El Niño events, are associated with above-normal sea surface temperatures and precipitation along the Pacific coast of southern California and northern Mexico, and negative MEI values, or La Niña events, are associated with below-normal sea surface temperatures in this region (Philander, 1990; Minnich *et al.*, 2000).

Results and discussion

Key habitats during nonbreeding

During the nonbreeding season, nearctic brant are found exclusively in coastal areas, where they typically

feed within the intertidal zone of shallow, protected embayments that contain beds of seagrasses (*Z. marina*, *Ruppia maritima* and *Z. japonica* in North America, and *Z. marina* and *Z. noltii* in western Europe) and/or green macroalgae (*Ulva* spp. and *Enteromorpha* spp.). For all populations, *Zostera* is the preferred food during fall and spring migration and winter (Reed *et al.*, 1998). Patterns of use of *Zostera* and other intertidal plants are primarily dictated by tides and by the plant's distributional range and seasonal availability and abundance.

All populations use a network of staging areas during migration to obtain their nutrient reserves for the annual cycle. These networks consist of one major staging area and varying number of ancillary sites. Eastern populations rely on only a few sites and tend to concentrate in fall and spring at single major staging areas that are rich in *Zostera*; James Bay, Quebec (Atlantic Brant) and western Iceland (EHA Brant) (Fig. 1). Black and WHA brant stage at more sites but also concentrate at a single staging area, Izembek Lagoon, Alaska, in fall, prior to a >2000 km flight to their primary wintering area (e.g., Dau, 1992). During spring migration, western populations generally disperse across several staging areas and travel shorter distances between stops in a stepping stone approach. This movement pattern presumably conserves nutrient reserves for breeding. Moore *et al.* (2004) showed that portions of the Black Brant population use no fewer than 67 different bays and estuaries during spring migration and variation in bird numbers among eight of the major staging areas was best explained by *Z. marina* abundance and distance to the next large (containing >500 ha of *Z. marina*) estuary to the north (Fig. 2).

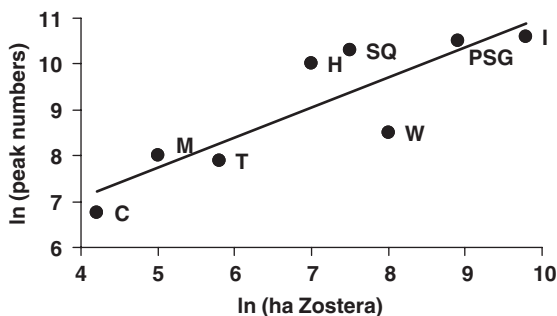


Fig. 2 Linear regression of log-transformed data: peak brant numbers vs. eelgrass abundance at eight pooled spring staging areas throughout the Pacific Flyway ($R^2 = 0.79$, $F_{1,6} = 21.91$, $P = 0.003$). C, Coos Bay; H, Humboldt Bay; I, Izembek Lagoon; M, Morro Bay; PSG, Puget Sound and Strait of Georgia area; SQ, San Quintin Bay; T, Tomales Bay; W, Willapa Bay. The regression indicates a positive relationship between peak brant numbers and eelgrass. From Moore *et al.* (2004).

Wintering Black and WHA brant are more dependent on *Zostera* than the other two populations, probably because this seagrass has two to three times the spatial extent on the Pacific coast (>1000 km²) than along the Atlantic coasts of North America (ca. 600 km²) and western Europe (<350 km²) (Green & Short, 2003). Populations from eastern North America still feed on *Zostera* when available, but also consume *Ulva* and *Enteromorpha* (green algae now dominates the diet of wintering Atlantic Brant), as well as, some salt marsh plants (*Spartina alterniflora* for Atlantic Brant and *Festuca rubra* and *Puccinellia maritima* for EHA Brant) (Penkala, 1976; Smith *et al.*, 1985; Merne *et al.*, 1999). Since the 1970s, both eastern populations have used inland sites that contain cultivated grasslands. Currently, this behavior is displayed by about 5% of the wintering Atlantic Brant and is generally confined to sites within 1–2 km of the coast, where birds feed on school fields and golf courses (P. Castelli, unpublished data). In Ireland, where intertidal foods are more limited, inland feeding is an important activity for about 25% of the EHA Brant and birds may travel up to 20 km inland to feed on farmlands, managed grasslands, and cereal crops (Merne *et al.*, 1999).

Key habitats during breeding

Nesting. Brant nest predominantly in wet graminoid meadows adjacent to coastal salt marshes (Reed *et al.*, 1998). At the low Arctic nesting sites of Black and Atlantic brant, meadows are relatively extensive allowing these birds to nest in colonies (Reed *et al.*, 1998), and are dominated by sedges (*Carex* spp.) and grasses such as *Poa eminens* and *Calamagrostis deschampsoides* (Jorgenson, 2000). At the Arctic sites of WHA and EHA brant, graminoid meadows are less extensive and consequently, nesting is more dispersed, often occurring inland near freshwater lakes or in braided river beds (Boyd & Maltby, 1979; Merne *et al.*, 1999). For all populations, distribution of nests is likely influenced by the typical distribution of predators, especially arctic foxes (*Alopex lagopus*), because brant are incapable of defending their nests from foxes. Nonetheless, all principal nesting areas occur in close proximity to salt marshes dominated by *C. subspathacea* and *Puccinellia* spp. (Merne *et al.*, 1999; Jorgenson, 2000; Person & Ruess, 2003), where females feed predominantly during incubation (Eichholz & Sedinger, 1999). Availability of foraging habitat in close proximity to nests is essential for brant because females begin breeding with nutrient reserves to meet only about 20% of their needs during breeding (Ankney, 1984) and females must continue feeding throughout the incubation period to maintain their body mass (Eichholz & Sedinger, 1999).

Following hatch in the low Arctic, broods also feed primarily in salt marshes, where they maintain grazing lawns (Person *et al.*, 2003) containing plant leaves with high concentrations of protein (Sedinger *et al.*, 2001). Abundance and quality of plants in salt marshes govern growth of brant goslings (Sedinger *et al.*, 2001; Herzog, 2002), which, in turn, controls recruitment (Sedinger *et al.*, 1995). Consequently, availability of salt marsh plays an important role in regulating brant populations (Sedinger *et al.*, 1998; Person *et al.*, 2003). In the high Arctic, where salt marshes are limited, many broods are raised along rockier shorelines or at inland freshwater lakes (O'Briain *et al.*, 1998). Maintaining population size in this harsh region is also likely influenced by available salt marsh habitat; however, weather is likely equally or possibly more important and can in some years cause complete breeding failure (O'Briain *et al.*, 1998).

Molting. Many brant that lose their clutches and those that do not attempt to nest, emigrate from breeding areas to high Arctic molting sites in June and July. Brant molting areas are reused year after year when undisturbed, and these long-standing traditions are thought to reduce intraspecific competition for food between unsuccessful breeders and nonbreeders and breeding pairs (Salomonsen, 1968). Two key areas of concentration for molting Pacific Flyway brant, in Alaska and Russia, have been identified and their habitats described. No exclusive molting areas have been discovered for Atlantic and EHA brant, but nonbreeders and failed breeders do molt at nesting areas on Southampton and Bathurst islands, Canada, respectively (Reed *et al.*, 1998).

In northcentral Alaska, the large, oriented thaw lakes north and east of Teshekpuk Lake provide molting habitat for an average of 14% (17500 birds) of the Pacific Flyway population of brant (King & Hodges, 1979; Derksen *et al.*, 1979; King & Derksen, 1979; E. Mallek, unpublished data), although numbers of flightless birds vary considerably between years depending, at least in part, on nest success at breeding colonies in western Alaska (Sedinger *et al.*, 1994). Flightless brant feed primarily along moss/peat shorelines immediately adjacent to open water rather than along the little used sedge zones more distant from the security of the lake (Derksen *et al.*, 1982; Weller *et al.*, 1994). These relatively narrow moss flats support fine grasses (*Deschampsia caespitosa*, *Dupontia fisheri*) and sedges (*Carex* spp.) preferred by brant and the birds spend up to 52% of the 24 h cycle in foraging behavior (Derksen *et al.*, 1982). Importantly, the availability of moss/peat flats along shorelines of thaw lakes is very limited – only about 2% (about 8 km²) of all habitats

classified in the Teshekpuk Lake molting area (over 4000 km²) consisted of this land cover class (Markon & Derksen, 1994).

Another important, but less well known, molting area for Pacific Flyway brant occurs on Wrangel Island, Russia. An estimated 4200 molting brant were counted during the first survey of the island in 1990 (Ward *et al.*, 1993). The freshwater lakes used by molting brant on Wrangel Island have vegetation zones similar to those of the Teshekpuk Lake area. The largest and most heavily grazed community was a moist, moss-dominated zone immediately adjacent to lake shorelines, where brant primarily foraged on *Dupontia fisheri* and *F. rubra* (Ward *et al.*, 1993).

Variation in brant use of wintering grounds and migration routes with respect to habitat change

Shifts in distribution and behavior caused by food depletion or habitat degradation. The nonbreeding distribution of nearctic brant is largely dictated by the distribution and abundance of *Z. marina* (Ganter, 2000; Moore *et al.*, 2004); therefore, changes in abundance and availability of *Zostera* have implications for brant distribution, survival, and reproductive output. An example of food depletion resulting in a large-scale, long-term shift in brant distribution and behavior occurred in 1931–1932 (Table 1) when a pathogenic slime mold, *Labyrinthula zosterae*, caused an extensive die-off of *Z. marina* in the north Atlantic (Rasmussen, 1977). This die-off was followed by an apparent 80–90% decline in the Atlantic Brant population (Cottam *et al.*, 1944; Kirby & Obrecht, 1982). Loss of *Z. marina* throughout its nonbreeding range caused many Atlantic Brant to move north to areas where *Z. marina* was more abundant and/or to switch to alternative foods (Cottam *et al.*, 1944). Although some birds may have starved (Cottam *et al.*, 1944), the greatest influence on population size was likely through reduced breeding effort by malnourished birds (Kirby & Obrecht, 1982). A concurrent rapid decrease in numbers of EHA Brant, as well as, populations of brant wintering in Europe was also attributed, in part, to this wasting disease event (Merne *et al.*, 1999).

Atlantic Brant fed primarily on *Z. marina* (85% of their diet) prior to the event. After the onset of the wasting disease, brant diet consisted mostly of *Ulva* (75%), and much less so on *Z. marina* (9%; Cottam *et al.*, 1944). The Atlantic Brant population gradually increased concomitant with the *Z. marina* recovery and a sport-hunting moratorium between 1933 and 1952. By the mid-1950s, Atlantic Brant reached the level present before the *Z. marina* die-off (Atlantic Flyway Council, 2002). Lack of historical data makes it

Table 1 Changes in brant population dynamics and use of nonbreeding and breeding areas with respect to habitat change

| Event | Date/location | Population affected | Duration of effect | Effect on brant | Population effect | Reference |
|---------------------------------------|---------------------------------------|-----------------------------|--------------------|---|--|---|
| Nonbreeding areas Wasting disease | 1931–1932 North Atlantic | Atlantic brant EHA brant | Decadal | Starvation Fewer feeding opportunities | Flyway-wide shift in distribution Reduced breeding Lower population size | Cottam <i>et al.</i> (1944), Kirby & Obrecht (1982) |
| Other eelgrass declines | 1999–2000 James Bay, Quebec | Atlantic brant | Not yet known | Diet switch to salt marsh vegetation? | Unknown | Lemieux & Lalumière (2001) |
| Habitat degradation | > 1970 North Atlantic | Atlantic brant EHA brant | Ongoing? | Diet switch to algae and upland grasses Fewer feeding opportunities | Flyway-wide shift in distribution Change in migration corridor | Kirby & Obrecht (1982), Green & Short (2003) |
| Severe weather | 1976–1977 1977–1978 Northeastern U.S. | Atlantic brant | 2 winters | Starvation Fewer feeding opportunities | Flyway-wide shift in distribution Reduced breeding Lower population size | Kirby & Obrecht (1982), Kirby & Ferrigno (1980) |
| El Niño Southern Oscillation | 1997–1998 North Pacific | Black brant | Usually 1 winter | Fewer feeding opportunities | Flyway-wide shift in distribution Reduced breeding Greater winter movement | Ward <i>et al.</i> (1999), Schamber (2001) |
| Climate change? | > 1980 North Pacific | Black brant WHA brant | Ongoing | Fewer feeding opportunities | Lower population size Flyway-wide shift in distribution | Ward <i>et al.</i> (1999, 2003), Dau & Ward (1997) |
| Oyster aquaculture | 1987–1993 Willapa Bay, WA | Black brant | Annual | Fewer feeding opportunities | Local shift in distribution | Wilson & Atkinson (1995) |
| Breeding areas Habitat degradation | 1980–1985 YKD, AK | Black brant | Decadal | Reduced gosling growth rates Increased food competition Lower carrying capacity | Reduced breeding Reduced recruitment Lower population size | Sedinger <i>et al.</i> (1993, 1998) |

YKD, Yukon–Kuskokwim Delta; EHA, Eastern high arctic; WHA, Western high arctic.

impossible to know whether *Z. marina* along the Atlantic coast has ever recovered to its prewasting disease abundance and spatial extent. However, based on behavior of brant, it appears that *Z. marina* has not recovered to its full extent. Atlantic Brant have maintained a diet consisting primarily of *Ulva* and alternative foods through the 1970's and 1980's (Penkala, 1976; Smith *et al.*, 1985; Hindman & Ferrigno, 1990) and up to the present (Reed *et al.*, 1998; P. Castelli, unpublished data).

The dependence of Atlantic Brant on *Ulva* is likely related to the increase in abundance and availability of this macroalgae and a corresponding degradation and loss of *Z. marina* habitats along the United States Atlantic coast (Green & Short, 2003). Over the last 20–30 years, water quality of shallow estuaries and lagoons has declined because of inputs of nutrients and sediment loads associated with upland development and shoreline construction (Short & Wyllie-Echeverria, 1996). *Zostera* losses have been attributed largely to nutrient over-enrichment that can stimulate the proliferation of fast growing phytoplankton and filamentous algae like *Ulva* and *Enteromorpha* (McGlathery, 2001). If blooms of macroalgae are extensive and persistent enough, they can eventually displace seagrasses as the dominant macrophyte in eutrophic waters (Hauxwell *et al.*, 2000).

Loss of *Z. marina* in northeastern North America may also influence spring migration routes of Atlantic Brant. Traditionally, large numbers of these birds migrated along two main fronts: one up the Atlantic coast from the United States to the gulf and estuary of the St. Lawrence River, and the other overland, also to the St. Lawrence, but further west near the confluence with the Ottawa River and in eastern Lake Ontario (Fig. 1; Reed *et al.*, 1998). From the St. Lawrence staging areas both groups move to James Bay. However, a radio telemetry study (2002–2004) indicated that a minority of Atlantic Brant now uses the coastal New England route (P. Castelli, unpublished data), even though it was once predominant (Palmer, 1976). Extensive declines in *Zostera* have occurred along the coastal route (Green & Short, 2003) and have been especially severe at Monomoy Point, Cape Cod, Massachusetts (P. Castelli personal observation), which has traditionally been a primary spring staging area for Atlantic Brant (Fig. 1; Palmer, 1976). With the continued low availability of *Zostera* along the Atlantic coast and in the St. Lawrence estuary, and with further recent declines in *Zostera*, the coastal route has become less advantageous than the direct inland flight, even if the latter route offers no coastal feeding areas before James Bay.

Atlantic Brant have experienced other instances of food depletion causing large-scale changes in their

distribution and abundance. During the winters of 1976–1977 and 1977–1978, severe weather at the main brant wintering sites in New York and New Jersey covered intertidal habitats with ice and prevented birds from feeding on seagrasses and macroalgae (Kirby & Ferrigno, 1980). In each of these winters, there was about a 30% decline in brant use of estuaries in the north and a corresponding increase in more southerly wintering areas (Fig. 3; Atlantic Flyway Council, 2002) where intertidal areas were ice-free. This was also the first time that brant were recorded feeding on cultivated grasses and clover on golf courses (Hindman & Ferrigno, 1990). Reduced food resources in the 1970s combined with hunting pressure and reduced recruitment were likely responsible for a crash in the Atlantic population (1960–1979: $R^2 = 0.68$, $F_{1,18} = 38.56$, $P < 0.001$; Fig. 3) similar to the 1930s crash (Kirby & Obrecht, 1982). The population has steadily increased from its lowest count of 42 000 birds in 1979 to 165 000 birds in 2003 (1980–2003: $R^2 = 0.45$, $F_{1,22} = 17.80$, $P < 0.001$; Fig. 3), but is still 20–25% below levels of the 1960s (Fig. 3). An important decline in *Z. marina* has been reported for James Bay (Lemieux & Lalumière, 2001), but the effects on brant have not been determined.

We found no correlation between the winter NAO index and Atlantic Brant wintering in areas north ($r = -0.03$, $P = 0.84$) or south ($r = 0.22$, $P = 0.15$) of their core habitats in New Jersey since 1960. Moreover, the direction of the relationship in each case was opposite what one would expect if a positive winter NAO index caused an increase in brant numbers at northern wintering areas and a negative winter NAO index led to an increase in brant at southern wintering areas. The lack of correlation is not surprising given the low power of these types of analyses; however, except for extreme climatic events, other factors, such as hunting pressure, and/or other human activities, may have greater influence on winter distribution of Atlantic Brant.

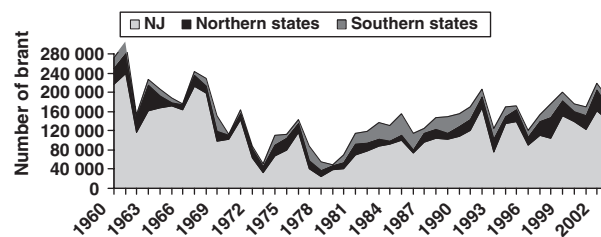


Fig. 3 Change in abundance and distribution of Atlantic Brant across the winter range 1960–2003. Trends were evaluated on log-transformed data using multiple linear regression analyses. Atlantic Brant populations were assessed across three geographical regions: NJ (New Jersey), northern states (New York to Maine), and southern states (Delaware to North Carolina).

Massive die-offs of *Z. marina* have not been documented on the Pacific coast; nevertheless, shifts in distribution of brant related to loss of *Z. marina* have occurred. Currently, Black Brant are experiencing a flyway-wide shift in distribution (Ward *et al.*, 2002) that is likely related to changing environmental conditions such as those that influence the abundance and availability of *Z. marina* (e.g., irradiance and water temperature; Hemminga & Duarte, 2000). Over the last 20 years, there has been a rise in sea-surface temperatures and sea level in the north Pacific (Zveryaev & Selemenov, 2000; Cabannes *et al.*, 2001), and recent assessments of seagrass at the major brant wintering areas along this coast have revealed a decline in *Z. marina* abundance and spatial extent between 1980 and 2000 (Ward *et al.*, 2002, 2003; S. E. Ibarra-Obando, unpublished data). Between 1980 and 2000 and during a period of population stability for Black Brant, inventories showed a negative trend in numbers of Black Brant wintering in Mexico ($R^2 = 0.35$, $F_{2,20} = 10.59$, $P < 0.01$; Fig. 4a) and a positive trend in numbers in the United States and Canada ($R^2 = 0.69$, $F_{2,20} = 44.71$, $P < 0.01$; Fig. 4b). Brant reductions in Mexico have largely occurred at the southern wintering sites (Fig. 4a) where *Z. marina* reaches the southern extent of its range in the northern hemisphere and air and sea surface temperatures already limit *Z. marina* growth to low intertidal and subtidal areas (Melting-López & Ibarra-Obando, 1999; Cabello-Pasini *et al.*, 2003). Shifts in distribution also coincided with a period of increased El Niño activity (Fig. 4c). Between 1960 and 2003, we found a weak, but nonsignificant, negative correlation ($r = -0.20$, $P = 0.22$) between the winter MEI and number of brant wintering in Mexico. Nevertheless, seven out of the 10 lowest counts of Black Brant in Mexico were associated with positive winter MEI values (0.39–2.74; Fig. 4c). Effects of changing environmental conditions on *Z. marina* are exacerbated during strong El Niño events, such as in 1997–1998, when a sharp rise in sea level (up to a 20 cm above mean sea level) and increased sea-surface temperatures (1–3 °C) were associated with dramatic declines (up to 50% decrease) in *Z. marina* abundance at brant southern wintering sites (Ward *et al.*, 1999).

Increased numbers of brant at wintering sites has been most evident in Alaska (Fig. 4B). Recent studies of the Alaskan wintering population (Dau & Ward, 1997; D. Mather, unpublished data) indicate that a portion of the increase may be attributed to an influx of WHA Brant that traditionally wintered exclusively in Puget Sound (Pacific Flyway Council, 2002). The reasons for some WHA Brant shifting their winter distribution northward are unclear. Estuaries along the Alaska Peninsula contain extensive beds of *Z. marina* (Ward

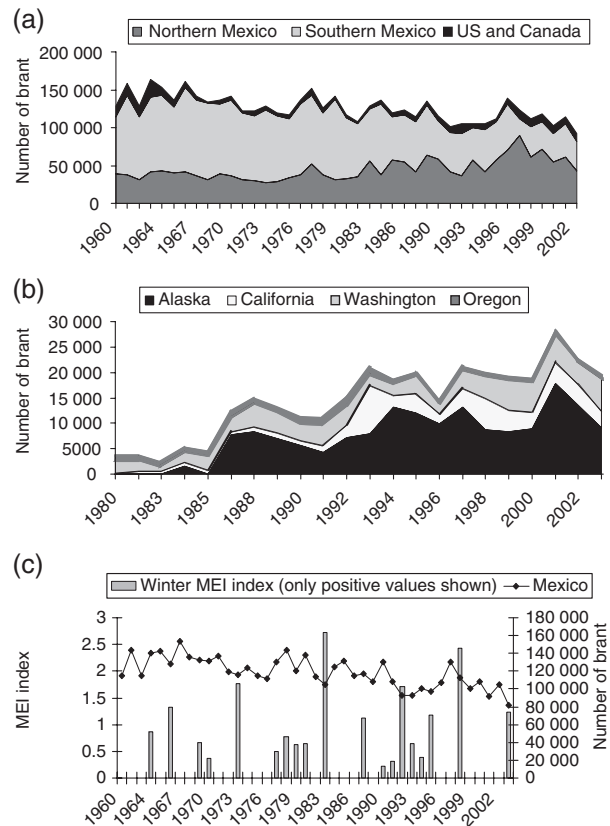


Fig. 4 Change in abundance and distribution of Black Brant across the entire winter range 1960–2003 (a), within the US 1980–2003 (b), and in Mexico 1960–2003 with respect to the winter MEI (c). Black Brant populations were assessed across four geographical regions: southern Mexico (Mexican states of Baja California Sur, Sonora, and Sinaloa), northern Mexico (Baja California), and US/Canada (California, Oregon, Washington, British Columbia, and Alaska). Three counts in Mexico were excluded from the analysis because they were either conducted outside the winter period in February (1962 and 1987) when Black Brant begin northward migration from Mexico or were considered unrealistic counts (1981) (Sedinger *et al.*, 1994).

et al., 1997) and support virtually the entire populations of Black and WHA brant in fall. However, prior to the 1980s, these estuaries were believed to winter fewer than 1000 brant (Dau, 1992), presumably because *Z. marina* beds were often covered by ice and inaccessible to birds. Brant numbers in Alaska have steadily increased in winter to 18000 birds in 2001 (Pacific Flyway Council, 2002) coincident with a warming trend in the north Pacific (Zveryaev & Selemenov, 2000). Warmer temperatures appear to have reduced the period and frequency of ice cover in coastal areas along the Alaska Peninsula (Dau & Ward, 1997), thus, increasing food availability and reducing energy costs for wintering birds.

Shifts in distribution can also occur at a more local scale such as when human activities influence seasonal use patterns. For example, in an important spring staging area for Black Brant in Washington, Wilson & Atkinson, (1995) showed that oyster farming activities were correlated with reductions in *Z. marina* abundance and in turn, significant decreases in brant use-days.

Variation in habitat condition at nesting areas and its effect on brant population dynamics

Black Brant nesting on the Yukon–Kuskokwim (Y–K) Delta declined by >60% between about 1980 and 1985, primarily as a result of intensive arctic fox predation (Sedinger *et al.*, 1993). Subsequent increases in the brant population created a natural experiment by which regulation of this population could be studied, similar to the case for several European populations of geese (Larsson & Forslund, 1994; Loonen *et al.*, 1997; Black *et al.*, 1998). A retrospective analysis combined with studies of vegetation dynamics during the population increase indicated that Black Brant maintain grazing lawns of *C. subspathacea* through their foraging activity (Person *et al.*, 2003). Reduced grazing intensity during the early 1980s allowed most of these grazing lawns to ‘escape’ to a taller growth form that could no longer be eaten by goslings. Consequently, carrying capacity was reduced and density dependent effects on growth and recruitment of Black Brant were observed at population sizes >30% below historic levels (Sedinger *et al.*, 1993, 1998). Growth rates of goslings increased steadily throughout the late 1990s, corresponding to increased areal extent of grazing lawns (Person *et al.*, 2003). Association between gosling growth and recruitment (Sedinger *et al.*, 1995) suggests that local recruitment rates also increased during this period. These results directly link recruitment, hence local population dynamics, to the availability of intensively grazed salt marsh vegetation in the vicinity of the breeding colony.

Black Brant goslings on the North Slope of Alaska grew substantially faster than those on the Y–K Delta, because there was substantially greater biomass of salt marsh vegetation on the North Slope of Alaska compared with the Y–K Delta (Sedinger *et al.*, 2001). Greater biomass of salt marsh vegetation on the North Slope of Alaska was associated with lower local densities of Black Brant there, which is probably a result of high nest predation rates in the adjacent oilfields (Sedinger & Stickney, 2000). Black Brant goslings from the North Slope of Alaska survived their first fall at higher rates than those from the Y–K Delta (Ward *et al.*, 2004). This was consistent with their higher growth rates and provides additional support for a linkage between salt marsh vegetation and population

dynamics of Black Brant. Comparison of Black Brant populations from the Y–K Delta and the North Slope of Alaska shows that regulation of local populations represents a balance between habitat availability and predation rates. On the Y–K Delta, where nest success has been high (75–83%) in most years since the mid-1980s, recruitment is heavily influenced by gosling size, which is regulated by availability of salt marsh vegetation. In contrast, on the North Slope of Alaska, high nest predation rates reduce the number of goslings foraging in salt marsh habitats, increasing per capita food abundance, growth rates, and first-year survival.

Links between wintering conditions and population dynamics

Cross-seasonal effects. Variation in reproductive performance associated with wintering location and winter climate strongly suggests that quality of winter habitat plays an important role in population dynamics of Black Brant. Schamber, (2001), using observations of individually marked Black Brant, showed that birds wintering in southern Baja California were less likely to nest the next summer than those wintering in northern Baja California and British Columbia. Individuals wintering in the southern areas that did breed initiated their nests later than birds using more northern wintering areas. This effect was especially pronounced in the ENSO year of 1997–1998 when fewer than 10% of Black Brant wintering in San Ignacio Lagoon, the most southern area studied, were observed nesting the next summer. This contrasts with 39% of individuals wintering in Boundary Bay, British Columbia, and 28% of birds wintering in San Quintin Bay, Baja California breeding the following summer (Schamber, 2001). Reduced breeding in the ENSO year was directly related to reduced production of *Z. marina*, especially in more southern bays and estuaries (Ward *et al.*, 1999; Cabello-Pasini *et al.*, 2003), suggesting that food abundance at wintering areas had a direct effect on reproduction at the population level. Numbers of Black Brant nesting on the Y–K Delta have declined in each ENSO year since aerial surveys of nesting Black Brant began in the mid-1980s (W. Eldridge & W. Butler, unpublished data) indicating that the relationship between winter food and subsequent reproductive performance is a general phenomenon.

Reduced ability of adults to breed associated with declines in winter food availability have the potential to decrease the size of the Black Brant population that can be sustained along the Pacific Coast of North America. Brant management plans for both flyways (Atlantic Flyway Council, 2002; Pacific Flyway Council, 2002) recognize this potential and point out the need to

maintain the integrity of *Z. marina* and other intertidal plants, particularly in bays that are geographically isolated from other large staging areas (Moore *et al.*, 2004), and to reduce human disturbance at goose feeding and roosting areas where grit is obtained. The dependence of brant on *Z. marina* and other intertidal habitats leaves them vulnerable to the human activities that increasingly impact shallow bays and estuaries along North America's coasts (e.g., oil spills, sediment runoff, channel dredging, pollution, and mariculture).

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