

BLACK BRANT WINTER AND SPRING-STAGING USE AT TWO WASHINGTON COASTAL AREAS IN RELATION TO EELGRASS ABUNDANCE¹

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Abstract. We monitored numbers of Black Brant (*Branta bernicla nigricans*) in Washington from fall 1980 through spring 1992 at Willapa Bay, and from fall 1986 through spring 1993 in the Dungeness area. We estimated brant use by converting the counts into use days. Coincidentally we also monitored variations in the extent of eelgrass (*Zostera marina*) beds by remote sensing techniques. At Willapa, brant use was positively correlated with the total extent of eelgrass beds and negatively correlated with the extent of oyster beds that were located within eelgrass beds, and where eelgrass had been removed by mechanical means. A 52% decline in brant use was associated with a 22% decline in eelgrass. At Dungeness there was a significant negative trend in spring-staging brant use. Overall a 63% decline in brant use coincided with a 31% decline in eelgrass. The Dungeness eelgrass beds may have declined because of natural factors. In both areas, brant use during the spring-staging period was more related to eelgrass extent than brant use during the winter months. These results suggest that Black Brant use in coastal Washington is limited by eelgrass availability. Immatures averaged 10.4% of the population at Willapa and 9.9% at Dungeness and are amongst the lowest reported. A shortage of eelgrass during the critical spring-staging period may have led to reduced endogenous reserves and associated low reproductive success of Black Brant that staged in coastal Washington. The shortage of eelgrass may have contributed to the observed southward shift to Mexico by wintering brant.

Key words: Black Brant; eelgrass; age composition; remote sensing; oyster culture; human disturbance; Washington.

INTRODUCTION

The Black Brant (*Branta bernicla nigricans*), one of two North American brant races, typically winters and stages on the west coast of North America (Bellrose 1976). In Washington, Black Brant arrive in the fall after migrating non-stop from staging areas at Izembek Lagoon, Alaska (Dau 1992), and then spend the winter and spring in traditional coastal areas (Reed et al. 1989). There is considerable evidence that a major southward shift to Mexico in wintering quarters of Black Brant has occurred since the 1950s (Ball et al. 1989). While the reasons for this change in distribution are unknown on the Pacific coast, similar changes documented on the Atlantic coast (Erskine 1988, Kirby and Obrecht 1982) have been linked to changes in food availability. The preference and dependence of brant on eelgrass (*Zostera marina*) as a major food source are well

known (Cottam et al. 1944, Charman 1977, Einarson 1965). Because there have been no studies relating changes in brant use patterns and eelgrass abundance at key Black Brant wintering and spring-staging areas, we investigated this subject on the Washington coast.

METHODS

We studied two principal Black Brant use areas in Washington, Willapa Bay and the Dungeness Bay area. Willapa Bay (46°30'N, 124°W), on the Pacific coast of southwestern Washington, is the state's largest and most pristine bay. With a total size of 300 km², 66% of which are exposed intertidal flats at low tide, the bay has extensive beds of eelgrass and supports large numbers of wintering waterfowl. Many of the bay's intertidal areas are under intensive aquaculture use by numerous oyster companies. Willapa Bay was open to brant hunting for 18 days during the fall of 1980 and 1981, for five days during the fall of 1989 and 1990, and for 11 days in the fall of

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1991. Hunting pressure during these periods was low, and only rarely did we witness any associated disturbance to the birds.

The Dungeness Bay area (48°10'N, 123°09'W), on the shore of Juan de Fuca Strait on the northern Olympic peninsula, extends from the base of Dungeness Spit east-southeast to Grays Marsh. Approximately 28 km² in size, about half the area is exposed intertidal flats at low tide. The area supports numerous eelgrass beds and a relatively small oyster industry. Brant hunting was not allowed during this study. The brant at Dungeness, however, were subjected to more human disturbance than the birds at Willapa, primarily due to the area's high recreational use and more developed shoreline.

We collected data on brant use by counting the birds from observation points (Willapa $n = 10$, Dungeness $n = 5$), located along the shorelines of the study areas. Surveys were conducted from late October 1980 through early May 1992 at Willapa Bay, and from late October 1986 through May 1993 at Dungeness. The 1985/1986 and 1990/1991 survey years were excluded from the Willapa data set because too few surveys were conducted for assessing brant use. The average number of surveys each survey year at Willapa was 18 (Range = 15–26), and at Dungeness was 19 (Range = 14–22). Observations from 1980/1981–1982/1983 were made with a Bausch and Lomb SR60 spotting scope equipped with a 20× eyepiece, while all subsequent observations were made with Questar Field Model spotting scopes equipped with 16 mm and 24 mm (magnification 50×–130×) eye pieces. Because considerably more brant were seen with the Questar scope, it was necessary to adjust the previous brant estimates for comparisons. During the 1983/1984 survey year we obtained 67 duplicate counts using both scopes. By tallying the birds counted with each scope over the survey year, we determined that on average we saw 1.692 more brant with the Questar scope than with the Bausch and Lomb scope. We therefore corrected earlier counts by multiplying them by 1.692. We estimated brant use days (UD) by multiplying the counts by the number of days before the next census, and by tallying the results over time. Thus, brant UD are essentially a histogram approximation of the area under the curve obtained by plotting census counts over time. To assess the reproductive success of brant using the two areas, we determined the percentage of immatures during

January and February. Immatures (<12 months) are easily distinguished from older birds by the presence of white-edged greater and middle wing coverts (Bellrose 1976).

We employed remote sensing to determine the extent of the eelgrass beds within the two study areas. Because of the large size of Willapa Bay, an eelgrass sample area was selected, based on knowledge of eelgrass distribution and brant use patterns. The area selected extends from Goulter's Slough, on the Long Beach Peninsula, south to Long Island's Jensen Point, with its easterly boundary being a line running north from Long Island's most northerly point. This area covers approximately 44 km² (15%) of Willapa Bay. An examination of 1974 aerial photographs suggested that this area contained approximately 40% of the bay's eelgrass beds. Four of the 10 brant observation points covered this area. The entire Dungeness Bay area was surveyed for eelgrass. Remote sensing involved photographing the eelgrass beds (Holz 1973, Kelly 1978) during July or August at low tide when there was little or no surface wind and when the horizontal sun angle was between 30° and 50°. A 23 × 23 cm aerial mapping-camera and regular color film was used. The scale of the photos was 1:24,000 at Willapa, and 1:18,000 at Dungeness. Eelgrass beds were photographed at Willapa in 1981, 1982, 1984, 1989, and 1991, and at Dungeness in 1987 and 1993 by the Washington Department of Transportation photogrammetry branch. To assure reliable identification of eelgrass beds, numerous sites at Willapa were visited at low tide each survey year. During 1982 and 1991, we also checked the beds from a Cessna 172 at low level with the photos in hand. Because the Dungeness beds were considerably more fragmented, the entire area was checked at low tide with the photos in hand from a Hughes 500D helicopter at an altitude of 10–300 m. Because of the high quality of the aerial photographs, we estimated the potential error in the size of the eelgrass beds at <5%. We distinguished between dense beds (>75% coverage) and patchy beds (<75% coverage). At Willapa, we were also able to identify and measure oyster beds located within eelgrass beds. The eelgrass beds were in stark contrast to the square shapes of the oyster beds, where eelgrass had been removed by mechanical means. Maps were later prepared from the photos and accompanying notes, and the total extent of eelgrass calculated with a polar planimeter.

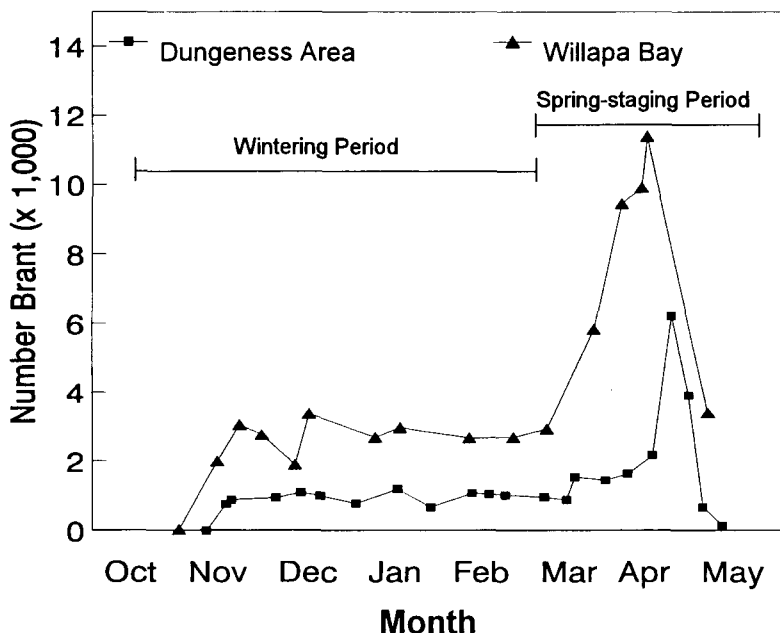


FIGURE 1. Typical Black Brant use pattern at Willapa Bay and the Dungeness Bay area, Washington (data are from the 1989/1990 season).

RESULTS

Brant arrived between late October and mid November, and numbers usually remained relatively constant through February (Fig. 1). During March, the numbers began to increase gradually with the arrival of north-bound migrants. Peak numbers during staging typically occurred during the last week of April, and by mid May only a few stragglers remained in the area. We named October through February the "wintering period," and March through May the "spring-staging period."

Black Brant use at Willapa Bay varied considerably over the study period (Fig. 2). Peak total UD occurred during the 1981/1982 season (874,226 UD), then declined until 1984/1985 (415,621 UD). Beginning in 1985/1986 brant use increased again to 771,715 UD in 1989/1990. Brant use during the spring-staging period followed the same pattern, and accounted for the majority of UD in seven out of the 10 years studied. However, brant use during the wintering period varied less between years. Over the entire period there was no significant trend with time in total UD, spring-staging UD, or wintering UD (Spearman rank correlation, $n = 10$: $r_s = -0.006$,

$P > 0.5$; $r_s = -0.176$, $P > 0.5$; $r_s = -0.091$, $P > 0.5$, respectively).

The Pacific flyway brant population index varied irregularly between 103,153–194,197 birds during 1981–1992 (U.S. Fish and Wildlife Service unpubl. data). There was no significant correlation between these estimates and Willapa's total UD, spring-staging UD, and wintering UD (Spearman rank correlation, $n = 10$: $r_s = 0.273$, $P > 0.2$; $r_s = -0.042$, $P > 0.5$; $r_s = 0.333$, $P > 0.2$, respectively).

The total extent of eelgrass at Willapa varied in a fashion to that of total UD and spring-staging UD (Fig. 2). During 1981–1984, eelgrass beds declined from 1,383 ha, to 1,081 ha, and then increased again to 1,372 ha in 1989. The extent of dense beds varied similarly, and accounted for most of the beds (Fig. 2). Patchy beds at Willapa were located around the edges of dense beds, and their total extent varied approximately inversely with the extent of the dense beds. Oyster beds, located within eelgrass beds, varied between 233 and 69 ha during the five years examined (Fig. 2). Oyster beds were negatively correlated with the extent of total and dense eelgrass beds (Spearman rank correlation, $n = 5$: $r_s = -0.900$, $P = 0.05$; $r_s = -0.900$, $P = 0.05$, respectively), and

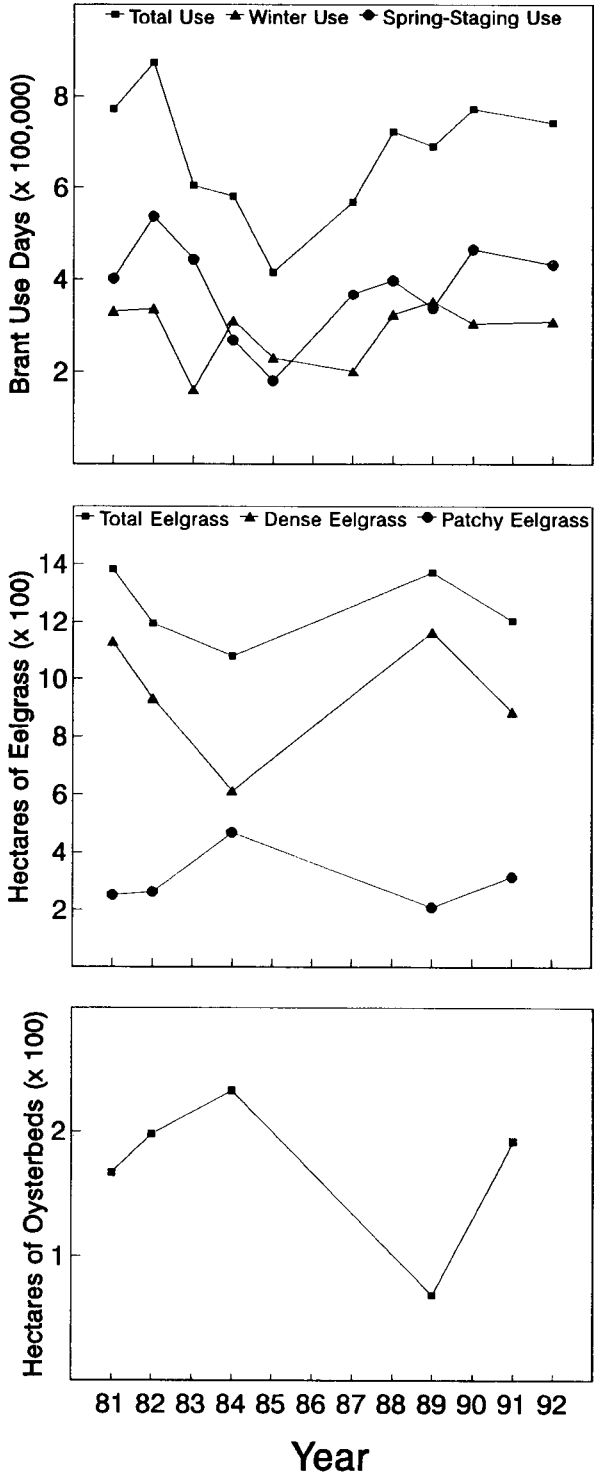


FIGURE 2. (Top) Black Brant total, winter and spring-staging use days at Willapa Bay, Washington, 1980/1981-1991/1992. (Middle) Extent of total, dense and patchy eelgrass beds at Willapa Bay, Washington, 1981-1991. (Bottom) Extent of oyster beds, within eelgrass beds at Willapa Bay, Washington, 1981-1991.

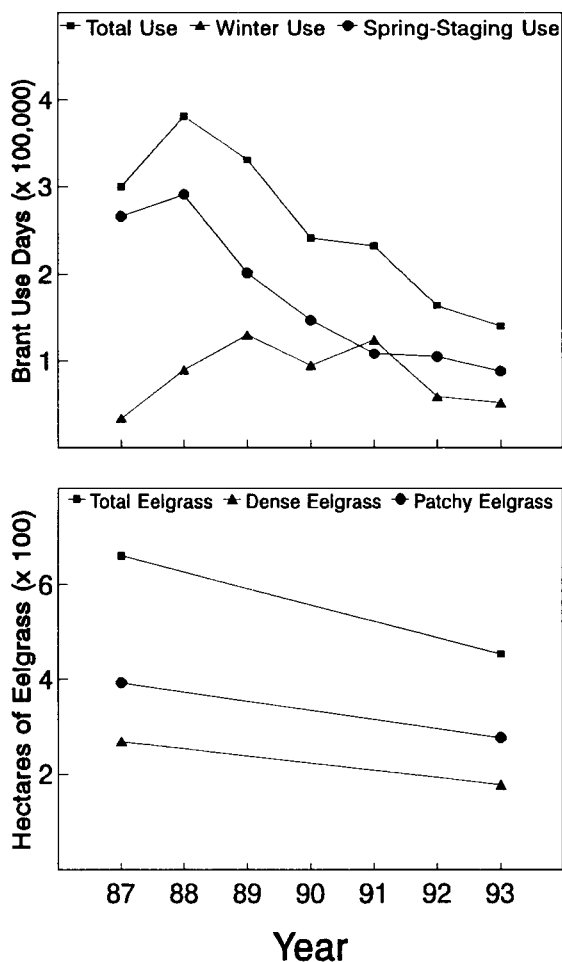


FIGURE 3. (Top) Black Brant total, winter and spring-staging use days at the Dungeness Bay area, Washington, 1986/1987–1992/1993. (Bottom) Extent of total, dense and patchy eelgrass beds at the Dungeness Bay area, Washington, 1987 vs. 1993.

positively correlated with the extent of patchy beds (Spearman rank correlation, $n = 5$, $r_s = 0.900$, $P = 0.05$).

At Willapa, Black Brant total UD were positively correlated with the total extent of eelgrass beds (Spearman rank correlation, $n = 5$, $r_s = 1.000$, $P = 0.01$), and negatively correlated with the extent of oysterbeds (Spearman rank correlation, $n = 5$, $r_s = -0.900$, $P = 0.05$). Black Brant spring-staging UD were also positively correlated with the extent of total and dense eelgrass beds (Spearman rank correlation, $n = 5$: $r_s = 0.900$, $P = 0.05$; and $r_s = 0.900$, $P = 0.05$, respectively). On the other hand, wintering UD were not significantly correlated with the extent of eelgrass. Overall, a 52% decline in brant UD coincided with a 22% decline in the area of eelgrass beds.

At Dungeness, Black Brant total UD declined from a peak of 381,148 in 1987/1988 to 139,898 in 1992/1993 (Fig. 3). Spring-staging UD followed the same pattern and accounted for most of the use except during 1990/1991. Similar to Willapa, brant UD during the winter varied less between years. There was a significant negative trend in time of total UD and spring staging UD (Spearman rank correlation, $n = 7$: $r_s = -0.893$, $P < 0.05$; $r_s = -0.964$, $P < 0.025$, respectively). There was no significant correlation between the Pacific flyway population index and Dungeness' total UD, spring-staging UD, and wintering UD (Spearman rank correlation, $n = 7$: $r_s = 0.429$, $P > 0.2$; $r_s = 0.286$, $P > 0.5$; $r_s = 0.679$, $P > 0.1$, respectively). During the study period, the total extent of eelgrass at Dungeness declined from

TABLE 1. Comparisons of Black Brant age composition counts, Willapa Bay and Dungeness Area, Washington vs. Izembek Lagoon, Alaska, 1983/1984–1992/1993.

Year	Willapa Bay	Dungeness Area	Izembek Lagoon*
	% Immatures (n)	% Immatures (n)	% Immatures (n)
1983/1984	14.5 (1,148)	—	24.0 (8,096)
1984/1985	8.8 (2,856)	—	13.7 (10,950)
1986/1987	8.8 (2,111)	5.2 (1,222)	15.3 (18,444)
1987/1988	16.4 (1,193)	16.6 (1,846)	31.2 (25,293)
1988/1989	13.6 (1,351)	16.8 (1,677)	19.2 (19,985)
1989/1990	8.2 (1,070)	9.4 (2,463)	23.9 (17,935)
1990/1991	3.4 (684)	4.2 (2,101)	19.2 (29,965)
1991/1992	9.6 (1,315)	11.9 (1,036)	27.8 (43,559)
1992/1993	—	5.2 (885)	16.5 (66,839)

* Data supplied by Izembek National Wildlife Refuge, Alaska.

660 to 454 ha (Fig. 3). Both dense and patchy beds declined although, in contrast to Willapa, patchy beds accounted for most of the observed eelgrass. At Dungeness, there were no signs of oyster culture disturbance to the beds. Overall, a 63% decline in brant use coincided with a 31% decline in the area of eelgrass beds.

Immature brant varied between 5.4 and 16.4% of the population at Willapa, and 4.2 and 16.8% at Dungeness (Table 1). The counts of both areas were correlated (Spearman rank correlation, $n = 6$, $r_s = 0.886$, $P = 0.025$), and were not significantly different (Mann Whitney U -test: $U = 15$, $P > 0.2$), suggesting the same stocks of Black Brant used both areas. There was no significant correlation between percent immatures at Izembek Lagoon, Alaska, and those at Willapa and Dungeness (Spearman rank correlation: $n = 8$, $r_s = 0.578$, $P > 0.05$; $n = 7$, $r_s = 0.564$, $P > 0.1$, respectively). The percent immatures of the Willapa and Dungeness brant populations were significantly below those of Izembek Lagoon (Mann Whitney U -test: $U = 60.5$, $P < 0.001$; $U = 38$, $P < 0.01$, respectively).

DISCUSSION

Results at both Willapa and Dungeness indicate that in Washington Black Brant use is limited by the extent of eelgrass beds. Because >90% of the beds were accessible to brant at low tide, the extent of the beds presumably determined how much eelgrass was available to the birds. While this study represents the first quantitative assessment of the effect of eelgrass on the distribution of Black Brant outside the breeding season, the brant/eelgrass relationship has been reported previously (North America: Bellrose

1976, Cottam et al. 1944, Moffitt 1941; Europe: Charman 1977, Jepsen 1984, Ogilvie and Matthews 1969, Prokosch 1984). Madsen (1989) and Summers (1990) also demonstrated that variations in salt marsh vegetation and beds of green algae were responsible for seasonal variations in brant numbers.

The positive correlation of spring-staging brant UD with the extent of eelgrass beds, and the lack of correlation between winter UD and eelgrass indicate that the demands on eelgrass are greatest during spring. Because brant use during spring-staging accounts for the majority of brant UD during most years, a positive correlation between total brant UD and eelgrass extent was also realized in the Willapa data set. During spring-staging, brant increase their food intake considerably in order to build up energy reserves important for migration and breeding success during the coming summer (Boudewin 1984, Bruns and Thoren 1988, Prokosch 1984, Vangilder et al. 1986). Large flocks of arriving spring migrants rapidly deplete *Zostera* stocks (also observed by Goss-Custard and Charman 1976), that may already have been reduced by the grazing of wintering brant and other waterfowl, or that have suffered from the impacts of winter storms. Thus, on the Washington coast, brant use during the winter period appears to be less limited by eelgrass extent than during the critical spring-staging period.

The negative correlations at Willapa between brant use and extent of oyster beds, and between the sizes of oyster beds and extent of eelgrass beds, emphasize the adverse impact the oyster industry has on brant, and may explain why a 22% decline in eelgrass coincided with a dispro-

portionate 52% decline in brant use. Within the Willapa eelgrass study area oyster beds were usually located in the shallower areas of the eelgrass beds. These areas are critical to brant because they are most frequently exposed at low tides.

At Dungeness a 31% decline in eelgrass coincided with a 63% decline in brant use. While the reasons for this decline in *Zostera* are unknown, the fragmented nature of the beds indicate possible damage by winter storms. The Dungeness area is located along the southern shore of Juan de Fuca Strait, and thus is exposed to large storm waves. These waves are most damaging to *Zostera* beds located in the more shallow intertidal flats, which, because of their more frequent exposure during low tides, are also the most important brant feeding areas.

Other factors that may have influenced brant use on the Washington coast include flyway-wide population fluctuations, periods of low breeding success, and human disturbance. The lack of correlation between the Pacific flyway population index and brant use at Willapa and Dungeness however, points to a more local cause. This is also supported by the significant difference and lack of correlation in the percent immatures, between Izembek Lagoon, Alaska, and the two Washington areas. Since hunting at Willapa only occurred at a low level in the fall of some years, and at Dungeness was absent, it is unlikely that the observed brant use patterns were influenced by it. Other types of human disturbances were rare at Willapa, but were more frequent at Dungeness.

The percent immatures averaged 10.4% at Willapa and 9.9% at Dungeness, and were considerably below the 21.2% average determined at Izembek Lagoon during the same time span. The estimates for the Washington coast are also lower than those reported in the literature. For the Pacific coast, Jones (1970) gave a range of 18–40% (average 24.7%), while averages for Atlantic brant were 39% (Bellrose 1976), and 26% (Kirby et al. 1985). Studies from Europe also indicate higher proportions of immatures. Madsen (1984) gave an average of 15%, Ogilvie and Matthews (1969) an average of 22%, and the considerable data base of Prokosch (1984) an average of 21% (range 0–52%). While brant populations with few immatures are frequently associated with problems on the breeding grounds (Anthony et al. 1991, Barry 1962, Bellrose 1976), the quality of the wintering and spring-staging

areas also influences brant breeding success. Eb-binge et al. (1982) found brant that were heavier on the spring feeding grounds in Europe had a greater probability of returning with offspring the following fall, and Teunissen et al. (1985) showed that pairs that used plots enhanced in biomass and protein content in spring were accompanied by more young in autumn. The *Zostera* stocks of Willapa Bay and the Dungeness area may be so limiting as to adversely affect the breeding success of brant that winter and stage on the Washington coast. If this were the case when eelgrass declined in Washington, brant may have been forced to shift their wintering quarters to Mexico where eelgrass may be more available. The Pacific coast situation may be similar to the Atlantic coast where brant apparently changed their migration patterns in response to changes in availability and distribution of food resources (Erskine 1988, Smith et al. 1985).

The historical brant use of the two study areas was undoubtedly much higher. The numbers of brant counted during mid-winter waterfowl surveys in Washington during the past averaged 23,393 birds during 1936–1960, 19,513 birds during 1961–1970, 8,779 birds during 1971–1980, and 11,708 brant during 1981–1990 (U.S. Fish and Wildlife Service, unpublished data). If Washington Black Brant are currently limited by the extent of *Zostera* stocks, then eelgrass abundance was likely much higher in the past, in order to have supported their numbers. Phillips (1984) mentioned dredging and filling as the most severe negative human impacts on eelgrass, but also stated that sedimentation and turbidity brought about by logging are major limiting factors of eelgrass growth. The watersheds of Willapa and Dungeness have been extensively clearcut, perhaps explaining vast areas that are devoid of eelgrass at Willapa, and the unusually patchy and fragmented nature of the beds at Dungeness.

Data on the historical extent of eelgrass are virtually nonexistent, and current monitoring and conservation efforts are inadequate. As Kelly (1978) pointed out, we need a better understanding of the ecology of eelgrass, which requires knowledge of its distributional patterns. Since transplanting of eelgrass is not feasible on a large scale (Phillips 1984), we need to better protect our remaining eelgrass beds from the ever-increasing industrial demands on coastal and estuarine environments. To what degree Black Brant will be part of Washington's coastal avi-

fauna in the future may well depend on the success of resource managers in conserving *Zostera* stocks adequate for the birds' support.

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LITERATURE CITED

- ANTHONY, R. M., P. I. FLINT, AND J. S. SEDINGER. 1991. Arctic Fox removal improves nest success of Black Brant. *Wildl. Soc. Bull.* 19:176-184.
- BALL, I. J., R. D. BAUER, K. VERMEER, AND M. J. RABENSBERG. 1989. Northwest riverine and Pacific coast, p. 429-449. *In* L. M. Smith, R. T. Pederson, and R. M. Kaminski [eds.], *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech Univ. Press, Lubbock, TX.
- BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26:19-26.
- BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.
- BOUDEWIN, T. 1984. The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl* 35:97-105.
- BRUNS, K., AND B. T. THOREN. 1988. Zugvorbereitung und Zugenruhe bei der Ringelgans *Branta bernicla bernicla*. Proc. Int. 100 DO-G Meeting, Current Topics Avian Biol., Bonn 1988, Germany.
- CHARMAN, K. 1977. The grazing of *Zostera* by wildfowl in Britain. *Aquaculture* 12:229-233.
- COTTAM, C., J. J. LYNCH, AND A. L. NELSON. 1944. Food habits and management of American sea brant. *J. Wildl. Manage.* 8:36-55.
- DAU, C. P. 1992. The fall migration of Pacific Brent *Branta bernicla* in relation to climatic conditions. *Wildfowl* 43:80-95.
- EBBINGE, B., A. ST. JOSEPH, P. PROKOSCH, AND B. SPAANS. 1982. The importance of spring staging areas for arctic-breeding geese wintering in western Europe. *Aquila* 89:249-258.
- ENARSEN, A. S. 1965. Black brant sea goose of the Pacific coast. Univ. of Washington Press, Seattle, WA.
- ERSKINE, A. J. 1988. The changing patterns of brant migration in eastern North America. *J. Field Ornithol.* 59:110-119.
- GOSS-CUSTARD, J. D., AND K. CHARMAN. 1976. Predicting how many wintering waterfowl an area can support. *Wildfowl* 27:157-158.
- HOLZ, R. K. 1973. *The surveillance science: remote sensing of the environment*. Houghton Mifflin, Boston.
- JEPSEN, P. U. 1984. Protection and management of arctic goose populations in Denmark. *Nor. Polarinst. Skr.* 181:153-160.
- JONES, R. D. 1970. Reproductive success and age distribution of Black Brant. *J. Wildl. Manage.* 34:328-333.
- KELLY, M. G. 1978. Remote sensing of seagrass beds, p. 69-85. *In* R. C. Phillips and C. P. McRoy [eds.], *Handbook of seagrass biology: an ecosystem perspective*. Garland Press, New York.
- KIRBY, R. E., AND H. H. OBRECHT, III. 1982. Recent changes in the North American distribution and abundance of wintering Atlantic Brant. *J. Field Ornithol.* 53:333-341.
- KIRBY, R. E., T. W. BARRY, R. H. KERBES, AND H. H. OBRECHT, III. 1985. Population dynamics of North American Light-bellied Brent Geese as determined by productivity and harvest surveys. *Wildfowl* 36:49-52.
- MADSEN, J. 1984. Status of the Svalbard population of Light-bellied Brent Geese *Branta bernicla hrota* wintering in Denmark 1980-1983. *Nor. Polarinst. Skr.* 181:119-124.
- MADSEN, J. 1989. Spring feeding ecology of Brent Geese *Branta bernicla*: annual variation in salt marsh food supplies and effects of grazing on growth of vegetation. *Dan. Rev. Game Biol.* 13:1-16.
- MOFFITT, J. 1941. Eelgrass depletion on the Pacific coast and its effect upon Black Brant. U.S. Dept. Int. Fish and Wildl. Serv. Wildlife Leaflet 204.
- OGLIVIE, M. A., AND G. V. T. MATTHEWS. 1969. Brent Geese, mudflats and man. *Wildfowl* 20:119-125.
- PHILLIPS, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: a community profile. U.S. Dept. Int. Fish and Wildl. Serv. report FWS/OBS-84/24.
- PROKOSCH, P. 1984. Population, annual cycle and traditional relationships to feeding areas of the Dark-bellied Brent Goose (*Branta b. bernicla*, L. 1917 58) in the Northfrisian Waddensea. *Ecol. Birds* 6:1-99.
- REED, A., M. A. DAVISON, AND D. K. KRAEGE. 1989. Segregation of Brent Geese *Branta bernicla* wintering and staging in Puget Sound and the Strait of Georgia. *Wildfowl* 40:22-31.
- SMITH, L. M., L. D. VANGILDER, AND R. A. KENNER. 1985. Food of wintering brant in eastern North America. *J. Field Ornithol.* 56:286-289.
- SUMMERS, R. W. 1990. The exploitation of beds of green algae by Brent Geese. *Est., Coast. and Shelf Sci.* 31:107-112.
- TEUNISSEN, W., B. SPAANS, AND R. DRENT. 1985. Breeding success in brant in relation to individual feeding opportunities during spring in the Wadden Sea. *Ardea* 73:109-119.
- VANGILDER, L. D., L. M. SMITH, AND R. K. LAWRENCE. 1986. Nutrient reserves of premigratory brant during spring. *Auk* 103:237-241.