

Staging of Pacific flyway brant in relation to eelgrass abundance and site isolation, with special consideration of Humboldt Bay, California

Jeffrey E. Moore*, Mark A. Colwell, Ryan L. Mathis, Jeffrey M. Black

Department of Wildlife, Humboldt State University, Arcata, CA 95521, USA

Received 16 January 2002; received in revised form 11 February 2003; accepted 13 February 2003

Abstract

Spring distributions of black brant (*Branta bernicla nigricans*) are closely related to that of their primary food plant, eelgrass (*Zostera marina*). Using historical (1931–2001) brant data from Humboldt Bay, California, we show that proportional use of two main feeding areas in the bay strongly reflects food abundance. We used multiple regression to investigate whether the spatial relationship between brant and eelgrass holds at the flyway level. We related peak brant numbers at 11 staging areas in the Pacific flyway to the sites' *Z. marina* abundance and isolation from other important staging areas. We explained 90% of the variation in peak brant numbers across sites with these variables; isolated bays with high eelgrass abundance supported the most brant. Our results emphasize the importance of protecting large eelgrass habitats along the Pacific Coast, particularly in bays that are geographically isolated from other large staging areas.

© 2003 Elsevier Ltd. All rights reserved.

Keywords: Abundance; Black brant; Distribution; Eelgrass; GIS; Humboldt Bay; Isolation; Pacific flyway; Spring staging

Brant geese (*Branta bernicla*) have one of the most specialized diets of all goose species during the non-breeding season. Unlike many other geese, which have abandoned traditional feeding habitats in favor of agricultural foods (Krapu and Reinecke, 1992), brant still utilize their native coastal habitats and feed preferentially on intertidal (or shallow subtidal) eelgrass (*Zostera* spp.) from autumn through late spring. All seven brant populations worldwide (from three recognized subspecies) utilize eelgrass at some period in their annual cycle (Ganter, 2000), and Reed et al. (1998) stated that “no other goose species relies so heavily on a single native food plant”. Hence, distributions of brant and eelgrass are closely tied, and changes in the distribution or abundance of eelgrass have had dramatic effects on brant populations. For example, the loss of eelgrass stocks due to “wasting disease” in Europe and the Atlantic coast of North America in 1931 (Moffit and

Cottam, 1941; Rasmussen, 1977) resulted in as much as a 90% reduction in the population sizes of light-bellied *B. b. hrota* and dark-bellied *B. b. bernicla* subspecies (Cottam et al., 1944; Ogilvie and Matthews, 1969). Populations of both subspecies have since recovered, but incomplete eelgrass recovery in Europe has led to a habitat shift by the dark-bellied population, which now feeds on salt-marsh vegetation rather than eelgrass in spring (Ganter, 2000). Human-induced eutrophication and changes in sediment processes off the coasts of Denmark and northeast England have also reduced the distribution and abundance of eelgrass, resulting in a distribution and habitat shift of the Svalbard population of light-bellied brant (Clausen et al., 1998; Clausen and Percival, 1998).

The dependence of brant on eelgrass is equally exemplified by the Pacific subspecies, black brant (*B. b. nigricans*), which rely almost exclusively on eelgrass *Z. marina* throughout the entire non-breeding period. Alternative foods, such as wigeongrass, surfgrass *Phyllospadix* spp., eelgrass *Z. japonica*, green algae, salt-marsh and upland vegetation, are also consumed by black brant, but only at a few flyway locations or in

* Corresponding author. Present address: Department of Forestry, Natural Resources, Purdue University, West Lafayette, IN, 47907, USA.

E-mail address: jmoore@fnr.purdue.edu (J.E. Moore).

years of poor *Z. marina* production (Moffit, 1941; Moffit and Cottam, 1941; Cottam et al., 1944; Ward, 1983; Baldwin and Lovvorn, 1994b).

In this paper, we provide a detailed account of historical brant distributions in relation to eelgrass abundance on Humboldt Bay, California, an important spring staging site in the Pacific flyway. We compare our results to data from other bays that document this brant–eelgrass relationship, and then address whether such patterns hold at the level of the entire flyway. To do this, we relate brant use at spring staging areas throughout the Pacific flyway to two site-specific attributes: eelgrass abundance and the degree of isolation from other staging areas. Our goals are to (1) synthesize the available information concerning distributions of eelgrass and brant throughout the Pacific flyway, (2) elucidate further evidence of the brant's dependence on eelgrass, and (3) draw attention to Humboldt Bay's importance as a spring staging area for black brant. We emphasize the need to protect eelgrass habitats along the Pacific coast of North America, and hope this information will be useful to flyway managers in establishing winter and spring population goals for black brant at important migration areas.

1. Study areas and methods

1.1. Brant use of Humboldt Bay

During the non-breeding season, black brant feed in eelgrass habitats of shallow bays and estuaries along the west coast of North America. Most brant winter in Baja California, Mexico, and at other sites along Mexico's western mainland coast, although small numbers winter along the Pacific coast north to Alaska (Reed et al., 1998). In fall, most brant migrate nearly non-stop from their main staging site at Izembek Lagoon, Alaska, to Mexico (Dau, 1992). Northward migration begins as early as mid-December, and consists of several stopovers en route to breeding grounds in western and northern Alaska (Fig. 1, Table 1).

Humboldt Bay (Fig. 1) is the second largest estuary in California, with a water surface area of 62.4 km² at mean high tide (MHW) (Proctor et al., 1980). Based on data for peak brant numbers, it is the fourth most utilized spring staging area in the Pacific flyway (Table 1), and Lee (2001) estimated that approximately 60% of the black brant population stopped there during spring 2001. The Humboldt Bay National Wildlife Refuge (HBNWR) recognizes it as one of the most important sites in the USA for black brant (US Fish and Wildlife Service, 1989). Humboldt Bay is influenced by mixed semi-diurnal tides, and consists of three sections: Arcata Bay and South Bay, which are wide and shallow, and a smaller, deeper Entrance Bay. Both South Bay and

Arcata Bay consist of extensive tidal flats, accounting for approximately 80% of their MHW areas (Barnhart et al., 1992). Much of the flats are interlaced with an extensive network of drainage channels, and are nearly all exposed at low tides below the mean lower low water datum (MLLW, i.e. 0.0 m) (Moore, 2002). Below about +0.3 to +0.4 m MLLW, intertidal flats support large areas of *Z. marina*, the extent of which varies annually.

Eelgrass is consistently more abundant on South Bay than Arcata Bay (Keller, 1963; Waddell, 1964; Harding and Butler, 1979; Bixler 1982), covering approximately 720 and 309 ha in the 2 areas, respectively (Terra-mar 1997 image data, classified by the California Department of Fish and Game). A small amount of eelgrass (~15 ha) occurs in the entrance channel (Arcata Channel), which connects Arcata Bay to Entrance Bay. Harding and Butler (1979) estimated that 78–95% of the total dry weight of eelgrass occurred on South Bay. Potential factors explaining the disparity in eelgrass abundance between Arcata Bay and South Bay have been poorly studied. It is known that a large oyster culture industry on Arcata Bay has degraded eelgrass habitat there (Waddell, 1964), but data are lacking to describe the condition of eelgrass prior to oyster culture, so it is difficult to assess the full degree to which this human activity has impacted the system.

We compared historical (1931–2001) spring brant use between Arcata Bay and South Bay; these 2 areas support about 99% of the bay's total brant use (HBNWR unpublished data 1992–2000). Brant census data were available for both Arcata Bay and South Bay from 1931–1936, 1940–1941, 1976–1977, and 1992–2001 (Moffit, 1931, 1932, 1933, 1934, 1935, 1936, 1940, 1941; Henry, 1980; HBNWR unpublished data 1979–2000, Moore, 2002). Data from the 1930s and 1940s consisted of counts on a single date only (conducted around 10 February of each year), so we limited our comparisons in all years to data collected on or near 10 February. Thus, measures of brant use on the two bays were consistent and comparable through time. To determine whether this single-date index accurately reflected the proportion of spring brant use (i.e. proportion of use-days from January through May) occurring on each of the two bay sections, we performed a Wilcoxon signed-rank test on post-1975 data, for which actual use-day estimates were available ($n=11$ years). Use-days were calculated by first multiplying weekly counts by seven to obtain weekly-use estimates, and then summing these over the survey period. Each year we paired the proportion of brant counted on South Bay on or near 10 February, with the proportion of spring use-days estimated on South Bay (Table 2). No significant difference was detected ($Z=0.04$, $P=0.96$), indicating that a 10 Feb measure adequately described proportional use of the two bays. We thus proceeded to use a Wilcoxon signed-rank test to compare the number of brant counted on

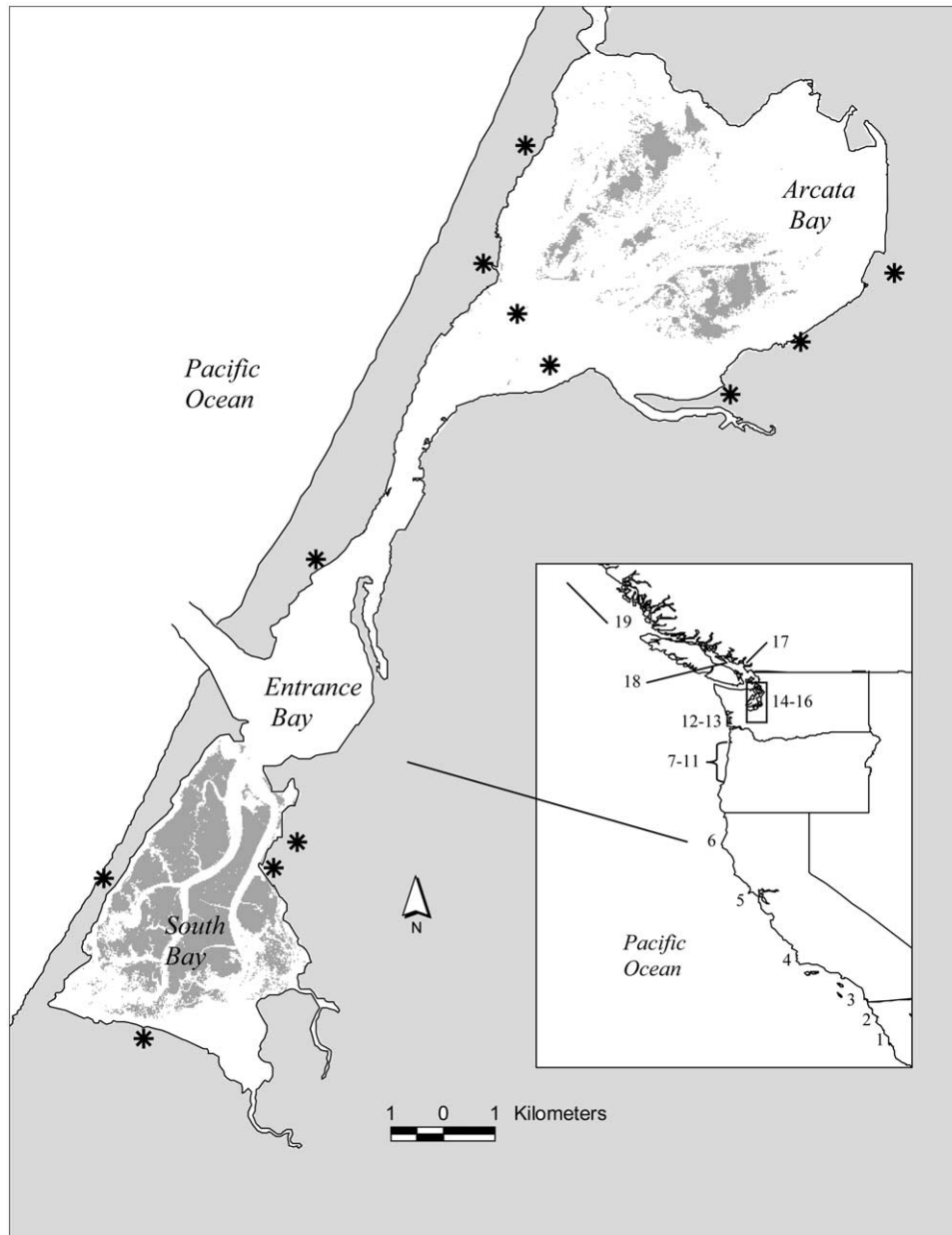


Fig. 1. Map of Humboldt Bay, indicating the distribution of eelgrass beds (shaded) according to image classification by California Department of Fish and Game of Terra-mar remote sensing data (1997). Stars indicate observer locations for brant surveys in a related study. Locations of spring staging areas south of Alaska are noted in inset map; see Table 1 for key to locations.

Arcata Bay with the number counted on South Bay each 10 February from 1931 to present ($n = 19$ years).

We were also interested in whether proportional brant use of Arcata Bay and South Bay (based on 10 February counts) was similar during the first and most recent decades of brant census. In part, this was an attempt to indirectly determine whether the relative abundance of eelgrass on Arcata Bay and South Bay has changed over time, since no early (pre-1970s) eelgrass data are available for Humboldt Bay. This approach is somewhat circular, because it assumes what we set out to test in this study: that brant use reflects eelgrass abundance. However, since we know that

Arcata Bay eelgrass has been affected by oyster culture over the past several decades (Waddell, 1964), a large decrease in proportional brant use of Arcata Bay over time could suggest that eelgrass there was historically more expansive. We used a Mann–Whitney U -test to compare the mean proportion of brant counted on South Bay from 1931–1941 ($n = 7$ years) with that from 1992–2001 ($n = 10$ years). We did not use data from 1933 in this analysis because an unusually small proportion (0.10) of brant were counted on South Bay during that year's 10 February survey, which was very unrepresentative of actual brant use on South Bay in that (Moffit, 1933) or any other years.

Table 1
Known spring staging areas for black brant in the Pacific Flyway (listed generally from south to north)^a

Geographic region	Map Ref ^b	Staging area	Area of eelgrass (ha)	Peak brant numbers	Brant use-days	Sources
Baja California	1	San Quintin Bay	1800	38,000	2,991,000 (January–April)	D. Ward (pers. comm.)
	2	Ensenada Bay				
California	3	San Diego and Mission Bays				
	4	Morro Bay	140	3100	226,000 (January–April)	Roser (unpublished), Chesnut (unpublished)
	5	Marin County Bays Bolinas Lagoon Drakes Estero Tomales Bay*	325	3000		Spratt (1989), Fourqurean et al. (1997), Kelly (unpublished)
		Bodega Bay				
	6	Humboldt Bay	1045	25,250	1,277,000 (January–June)	Terra-mar (1997), Humboldt Bay NWR (unpublished reports)
Oregon	7	Coos Bay (South Slough)	65	800		Contreras (1998), South Slough NWR (unpublished)
	8	Yaquina Bay		600		Bayer (1996), Merrifield (1998)
	9	Tillamook Bay	360			Strittholdt and Frost (1996)
	10	Netarts Bay	335			Phillips (1984)
	11	Nehalem Bay				
Washington	12	Willapa Bay	3000	6900	675,000 (December–May)	Wilson and Atkinson (1995), WA Dept. Fish Wildl. (unpublished)
	13	Grays Harbor	3350			Proctor et al. (1980), Phillips (1984)
	14	Dungeness and Sequim Bays	555 (Dungeness only)	4800	256,000 (December–May) (Dungeness only)	Wilson and Atkinson (1995), WA Dept. Fish Wildl. (unpublished)
	15	Puget Sound (south of Skagit Co.) and Hood Canal areas (about 20 sites)				

(continued on next page)

Table 1 (continued)

Geographic region	Map Ref ^b	Staging area	Area of eelgrass (ha)	Peak brant numbers	Brant use-days	Sources
	16	Skagit and Whatcom County Bays Fidalgo Bay Padilla Bay Samish Bay Bellingham Bay Lummi Bay Birch Bay	3125	37,700 (includes Fidalgo and Samish Bays)		Thom (1990), Padilla Bay NERR, WA Dept. Fish Wildl. (unpublished)
British Columbia	17	Boundary Bay and Roberts Bank	3320 745	1660 3560		Ward (1992), Baldwin and Lovvorn (1994a), K. Hagmeier (unpublished) Ward (1992), K. Hagmeier (unpublished)
	18	Southeast Coast of Vancouver Island Sooke Basin Victoria and Saanich Peninsula areas Parksville-Qualicum Beach area Baynes Sound- Comox Harbor Campbell River area		6160		K. Hagmeier (unpublished)
	19	Queen Charlotte Islands Skidegate Inlet area Masset Inlet area		2100 7000		Vermeer et al. (1991), Goudie and Hearn (1997) Goudie and Hearn (1997)
Alaska		Izembek Lagoon Chagvan and Nanavak Bays	16,000	52,000	2,116,000 (February–May)	Ward et al. (1997), D. Ward (pers. comm.)

^a Brant data are for spring migration, and therefore do not include available midwinter count information. Mean eelgrass and brant values are presented for locations with multiple years of data.

^b See Fig. 1 for location of each staging site in the Pacific Flyway

Table 2

Proportion of Humboldt Bay's black brant use that occurs in South Bay, estimated by the number of brant counted on 10 February, and by the number of brant-days during migration^a

Year	February 10 count			January–June use-days		
	South Bay	Arcata Bay	Prop on S Bay	South Bay	Arcata Bay	Prop on S Bay
1976	720	8	0.989	803,845	102,569	0.887
1977	670	14	0.980	714,560	102,800	0.874
192	2200	500	0.815	866,301	242,685	0.781
1993	6200	1313	0.825	938,423	248,241	0.791
1994	5300	1040	0.836	1,042,048	301,607	0.776
1995	6620	1510	0.814	1,067,325	225,425	0.826
1996	4808	1523	0.759	814,913	233,874	0.777
1997	6440	1804	0.781	744,981	188,867	0.789
1998	8100	2200	0.768	1,476,741	191,128	0.885
1999	8100	963	0.894	1,354,829	93,622	0.935
2000	6380	3665	0.635	1,330,338	238,131	0.837
Mean	5049	1322	0.829	1,004,019	197,177	0.833
SD	2688	1044	0.100	254,715	69,346	0.055

^a Data are from Henry 1980 and from Humboldt Bay NWR (unpublished data).

1.2. Brant use throughout the Pacific flyway

In addition to Humboldt Bay, published studies of black brant are available for just a handful of stopover areas (listed from south to north): San Quintin Bay in Mexico, Willapa, Dungeness and Padilla Bays in Washington, Boundary Bay and Parksville-Qualicum Beach in the Strait of Georgia, British Columbia, and Izembek Lagoon in Alaska. These locations constitute most of the heaviest use-areas, yet several other sites in the Pacific flyway also support significant brant numbers [e.g. Morro Bay, Tomales Bay, and Queen Charlotte Islands (Table 1); Chagvan and Nanavak Bays, (Subcommittee on Pacific Brant, 1992)]. Dozens of additional areas support smaller numbers of brant each spring (Table 1). All of these sites contain *Z. marina*, however there are many areas along the North American coast containing small amounts of eelgrass that are not reported to be used by brant (see Phillips, 1972, 1984).

We used multiple linear regression to examine spring brant use at stopover sites throughout the flyway in relation to the sites' eelgrass abundance and isolation from other staging areas. We used data from locations for which data on both brant use and eelgrass abundance were available (Table 1). For our dependent variable (brant use) we would have liked to use the number of spring use-days at each site, but for most staging areas, only peak numbers were available. Therefore, we used this latter metric as our index of brant use; limited data throughout the flyway (Table 1), as well multiple years of data for Morro Bay and Humboldt Bay (Roser, 2001, Moore and Black, in review), suggest that the 2 measures are closely correlated.

For one independent variable (eelgrass abundance), we used the number of ha of *Z. marina* at each site.

Where estimates of eelgrass or brant numbers were available for more than 1 year at a particular location, the mean of all available estimates was used. We only used post-1980 data (for eelgrass, $n=1-5$ year; for brant, $n=1-13$ year for each area), except for brant data at Padilla/Samish/Fidalgo Bays, for which April count data (when peak numbers occur) were only available from 1971–1980. For our second independent variable (site isolation), we did not know a priori which measures would best describe the insularity of a stopover site from a brant's perspective, so several measures were independently tested. These included distances to the nearest staging areas to the north and to the south, the minimum of these values (nearest site in either direction), the maximum of these, and the sum of these. In one set of tests, the nearest staging area was considered to be that of any size. In a second set of tests, the nearest staging area was considered to be that with > 500 ha eelgrass.

We selected as our best regression model that which maximized Adj. R^2 , subject to the constraint that $P < 0.10$ for each variable in the model and $P < 0.05$ for the full regression model.

2. Results

2.1. Brant use on Humboldt Bay

Based on counts each 10 Feb, the proportion of brant using Humboldt Bay was consistently greater on South Bay than Arcata Bay from 1931–2001 ($\bar{X}_{\text{South}} \pm \text{SE} = 0.81 \pm 0.02$, $\bar{X}_{\text{Arcata}} \pm \text{SE} = 0.19 \pm 0.02$, $Z = 3.82$, $P = 0.001$, $n = 19$ years). Further, the proportion of brant observed on South Bay was not statistically different in 1931–1941 ($\bar{X} = 0.77$, range = 0.64–0.89,

$n=7$ years) than in 1992–2001 ($\bar{X}=0.80$, range = 0.64–0.89, $n=10$ years) ($Z=-0.84$, $P=0.42$), indicating that relative proportions of brant using these two sections of the bay have probably not changed over the last 70 years.

2.2. Brant use throughout the Pacific flyway

We used data from 11 staging areas in our regression analyses. Although these locations were not randomly selected from the “population” of staging areas, they represented the full range of eelgrass abundance, brant use, geographic isolation and latitude of stopover sites within the Pacific flyway. Eelgrass abundance at sites ranged from 65 to 16,000 ha, average peak brant numbers ranged from 800 to 52,000, and locations included the southernmost (San Quintin Bay) and second northernmost (Izembek Lagoon) staging areas (Table 1). Treating all 11 staging areas as statistically independent locations, peak brant numbers at a staging area were positively related to eelgrass abundance (Fig. 2 a, Table 3), and to distance from the nearest staging area to the north with > 500 ha eelgrass (Table 3). Brant numbers were not related to any other measures of location isolation when eelgrass abundance was included in the multiple regression models (i.e. all $P>0.10$ for t -tests of the isolation variables, and Adj R^2 of model with isolation variables $< R^2$ for eelgrass abundance alone).

We considered that for staging areas that are very close together, brant use might not be independent, i.e. from a migrating bird’s perspective, nearby sites might all be extensions of a single area. Therefore, we repeated the above analyses after pooling all nearby stopover sites (arbitrarily designated as those separated by < 100 km) into single locations, with peak brant numbers and eelgrass abundance represented by the sum of their component sites. This not only affected the brant numbers and eelgrass abundance for a given data point, but also the measure of distance to the nearest site. For example, the nearest bay to the north of Willapa Bay was no longer Grays Harbor (40 km), but instead the collective Puget Sound and Strait of Georgia area (approx. 330 km coastline distance). This reduced our sample size from 11 to 8 stopover areas, but peak brant numbers were significantly related to the same variables as in the previous tests, with an even greater amount of variation in the data explained (Fig. 2b, Table 4).

3. Discussion

3.1. Brant use on Humboldt Bay

Given the specialized diet of black brant during the nonbreeding season, we would expect the number of

geese staging at a particular location to be influenced by the abundance and availability of eelgrass at that site. We found clear evidence of this occurring over both spatial and temporal scales. Humboldt Bay provides a spatial example. From 1931 to 2001, 81% of the observed brant use occurred on South Bay, reflecting Harding and Butler’s (1979) estimate that 78–95% of the eelgrass biomass occurred there. Thus the number of brant using South Bay and Arcata Bay appears to be directly related to eelgrass abundance in each of those areas.

An example of temporal response by brant to eelgrass abundance comes from Wilson and Atkinson (1995), who found that the annual variation in abundance of spring staging brant on Willapa and Dungeness Bays in Washington was positively correlated with the extent of eelgrass. Further support comes from Roser (2001), who found a similar trend on Morro Bay, California; brant use and eelgrass abundance simultaneously increased each year from 1998 to 2001 (Fig. 3). Interestingly, this temporal relationship between brant use and eelgrass abundance does not seem to hold for Humboldt Bay. Anecdotes indicate severe eelgrass shortages in Humboldt Bay during the winter/spring periods of 1937/1938, 1940/1941, 1951/1952, 1952/1953, 1957/1958, and 1997/1998 (Moffit, 1938, 1941; Murrell, 1962; Yocum and Harris, 1975, HBNWR unpublished data), yet in none of these years was brant use notably lower than in surrounding years (Moore and Black, in review). In fact, in spring 1998, the highest brant-use on Humboldt Bay in several decades was recorded (HBNWR unpublished data). In this, and in other years of poor eelgrass production, thousands of brant fed in the salt marshes and pastures surrounding the bay. We suggest that brant use on Humboldt Bay does not decline in years of reduced eelgrass abundance because of the bay’s relative isolation within the Pacific flyway (see below), and the constraint this may impose on brant migration. If Humboldt Bay cannot provide enough eelgrass for the thousands of birds that stop there, many individuals may not have the option to simply move on to the next site. Rather, this staging area may serve as a bottleneck for migrating geese, such that large numbers of individuals may choose to remain on the bay until adequate nutrient reserves have been accumulated, whether from eelgrass or from surrounding habitats. Prop et al. (in press) showed that barnacle goose *Branta leucopsis* stopover at spring staging sites is related to foraging performance, where lower intake rates yielding minimal fat and nutrient accumulation results in a longer stopover duration and later departures.

The relative constancy in proportional use of South and Arcata bays through time suggests that eelgrass has long been less abundant in the latter area (i.e. since before the establishment of a large oyster culture industry).

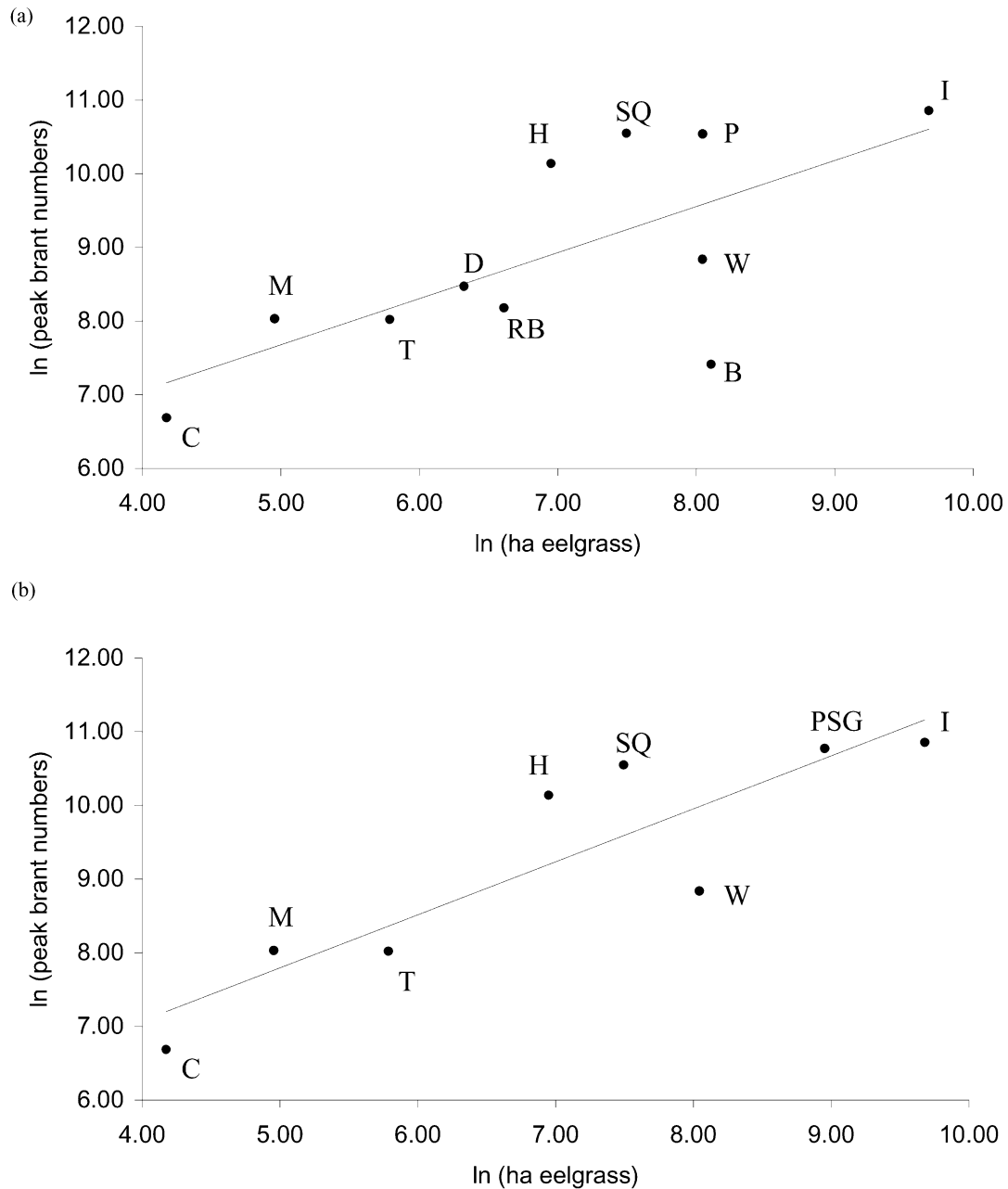


Fig. 2. Linear regression of log-transformed data: peak brant numbers vs. eelgrass abundance. For sites with > 1 year of data available, data points indicate the mean values for eelgrass abundance or brant numbers. Graph A shows data for 11 spring staging areas throughout the Pacific flyway ($R^2=0.49$, $F_{1, 9}=8.55$, $P=0.017$); B=Boundary Bay, C=Coos Bay, D=Dungeness Bay, H=Humboldt Bay, I=Izembek Lagoon, M=Morro Bay, P=Padilla Bay, RB=Robert's Bank, SQ=San Quintin Bay, T=Tomaes Bay, W=Willapa Bay. Graph B shows data for 8 pooled spring staging areas ($R^2=0.79$, $F_{1, 6}=21.91$, $P=0.003$); PSG=Puget Sound and Strait of Georgia area, which includes Boundary, Dungeness, Padilla, and Robert's Bank.

Table 3

Results of multiple linear regression analysis, testing for effects of eelgrass abundance and a measure of isolation on peak brant numbers at 11 spring staging areas in the Pacific Flyway^a

Independent variable	β	t	P	Partial R^2
Eelgrass abundance (ha)	0.645	3.52	0.008	0.61
Distance to nearest bay to north with > 200 ha eelgrass (km)	0.494	2.07	0.072	0.35

^a Statistics for full model: Adj $R^2=0.58$, $F_{2,8}=8.00$, $P=0.012$. Dependent and independent variables were all \log_e transformed.

Table 4

Results of multiple linear regression analysis, testing for effects of eelgrass abundance and a measure of isolation on peak brant numbers at eight spring staging areas in the Pacific Flyway^a

Independent variable	β	T	P	Partial R^2
Eelgrass abundance (ha)	0.526	4.60	0.006	0.90
Distance to nearest bay to north with >200 ha eelgrass (km)	1.197	3.21	0.024	0.82

^a Statistics for full model: Adj $R^2 = 0.90$, $F_{2,5} = 8.00$, $P = 0.01$. Dependent and independent variables were all \log_e transformed.

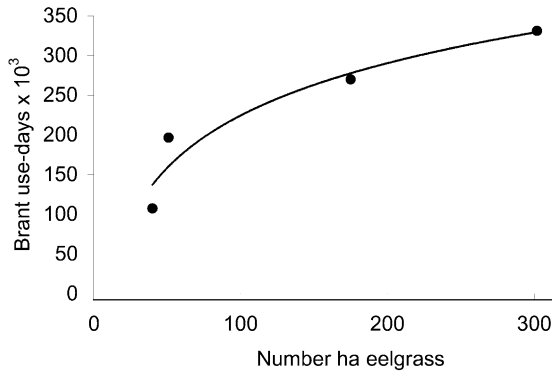


Fig. 3. Logarithmic relationship between eelgrass extent and brant use-days (January–April) on Morro Bay, California, 1998–2001; $R^2 = 0.92$. Data are from J. Roser and J. Chesnut, with permission.

However, given the negative impact of oyster culture practices on eelgrass in Arcata Bay (Murrell, 1964), and the strong relationship between brant numbers and eelgrass abundance, it is surprising that proportional brant use of Arcata Bay has not declined since the 1930s. One possible explanation is that since brant numbers on Humboldt Bay were much greater 70 years ago than today (Moore and Black, in review), brant distributions that were once dictated by food abundance (e.g. ideal-free) are currently maintained simply by traditional use patterns. We expect that if brant numbers increase substantially on Humboldt Bay, a lower proportion of these will be supported on Arcata Bay than in the past years.

3.2. Brant use throughout the Pacific flyway

Data collected throughout the Pacific flyway over the past 2 decades strongly suggest that the brant–eelgrass relationships evident within particular staging areas also apply at the scale of the entire flyway. Even when ignoring the isolation of a particular staging area, we found that sites with larger eelgrass beds generally accommodate higher brant numbers (Fig. 2). However, when describing brant use according to eelgrass abundance alone, San Quintin Bay, Padilla Bay, and Morro Bay, in addition to Humboldt Bay, receive larger than expected numbers of brant, while Boundary Bay, and to a lesser extent Willapa Bay, Roberts Bank, and Coos Bay, receive lower than expected brant numbers. Incorporating a measure of isolation for each staging area accounted for some of these discrepancies (Table 3). If isolation of a site

can be described as its distance to the nearest large staging area (> 500 ha eelgrass) to the north, then three of the four sites yielding higher than expected brant numbers (San Quintin Bay, Humboldt Bay, and Morro Bay) are among the most isolated (~600 to 1400 km from nearest large northerly area) in the flyway. Similarly, the four staging areas receiving lower than expected use are all relatively close (<250 km) to the nearest large northerly staging site, and three of these (Boundary Bay, Roberts Bank, and Willapa Bay) are among the least isolated (<100 km) stopover locations (for which we had both brant and eelgrass data) in the flyway.

When all bays within 100 km of each other were pooled, brant numbers in the collective Puget Sound–Strait of Georgia staging area were well described by eelgrass abundance alone (Fig. 2b), yet site isolation still explained additional variation in brant numbers throughout the flyway. Willapa Bay and Coos Bay remained the two least isolated areas (<350 km from nearest large northerly area) and were the only two bays with brant numbers considerably lower than expected according to eelgrass abundance-based predictions. Humboldt and San Quintin Bays remained among the most isolated areas, and still contained higher brant numbers than would be predicted solely by eelgrass abundance.

Additional factors may of course contribute to brant use at a particular location in the Pacific flyway, including the level of disturbance at a site, and the extent to which food at a particular staging area is actually available to brant. As an example of the latter factor, Boundary Bay contained lower than expected brant numbers, based on predictions from eelgrass abundance alone, but this may be because a large proportion of *Z. marina* in Boundary Bay is inaccessible to brant. During a study by Baldwin and Lovvorn (1994a) at this site, the lowest tides observed (–1.1 m MWL) would have left nearly all pure stands of *Z. marina* (which occurred at –1.8 m to –5.5 m MLW) submerged and unavailable to foraging geese. Their study took place in the late fall, when low tides on the Pacific Coast are not as low as during spring months. However, tides in spring would have to have been a great deal lower to expose most or all of the *Z. marina*, so a significant area of eelgrass was probably still inaccessible during peak brant migration. In Humboldt Bay, by contrast, the lowest tides in spring expose nearly all eelgrass beds to brant (Moore, 2002).

Another factor affecting food availability is the proportion of eelgrass constituted by the exotic *Z. japonica*, rather than *Z. marina*. Baldwin and Lovvorn (1994a) found that in Boundary Bay only 51% (1760 ha) of the area covered by *Z. marina* (3444 ha) was pure *Z. marina* stand, and this was all in the lowest intertidal and subtidal areas (−1.8 to −5.5 m MLW). The remaining 49% (1684 ha) of *Z. marina*, which grew between −0.9 and −1.8 m MLW, was mixed with *Z. japonica*. Although the energy content of *Z. japonica* may be slightly higher than that of *Z. marina* (Baldwin and Lovvorn, 1994a), *Z. japonica* is a much smaller plant than *Z. marina* (Phillips, 1984), growing at much lower shoot densities and biomass per unit area (Thom, 1990; Baldwin and Lovvorn, 1994a). Further, *Z. japonica* is an annual plant, occurring at very low abundance in winter and early spring (Baldwin and Lovvorn, 1994a; Thom, 1990). *Zostera marina*, by contrast, is perennial. Thus, values for eelgrass abundance at various staging areas may be misleading as predictors of brant use if a smaller food plant (*Z. japonica*) makes up a significant fraction of the eelgrass. *Zostera japonica*, to our knowledge, is only abundant at staging sites north of California.

Our study highlights the need to conserve large eelgrass habitats along the Pacific Coast, and we suggest this may be exceptionally important for isolated staging areas, such as Humboldt Bay and San Quintin Bay. Since large, alternative feeding locations are not nearby, these remote bays may serve as critical sites for birds to better accumulate nutrient for migration and successful reproduction (Ankney, 1984; Ebbinge and Spaans, 1995; Prop and Black, 1998; Reed et al., 1998). Geese using these bays in years when food is very limiting will likely forego or fail in breeding attempts, as evidenced for barnacle geese staging at a site with degraded spring staging habitat (Prop and Black, 1998). Further, loss of important eelgrass habitats will likely result in increased use of agricultural fields by brant, as has occurred in Europe and the eastern coast of U. S., leading to economic problems associated with crop damage (Owen, 1990; Ganter et al., 1997). These implications are particularly relevant for Humboldt Bay, which is surrounded by pasturelands, considering that 30–60% of the entire Pacific flyway population used the bay in 2000 and 2001, with individuals staging there for a mean of 50 days during migration (Lee, 2001).

Eelgrass integrity is threatened to varying degrees throughout the Pacific coast, including at some of the most heavily utilized brant-staging areas. The most widespread concerns include eelgrass loss to expanding oyster culture practices (Wright, 2001; Alliance for Responsible Shellfish Farming, 2001; Ward et al., 2002) and high sediment and chemical loading (Morro Bay National Estuary Program, 2000; Wright, 2001; Ward et al., 2002). The latter has resulted from runoff from upland watersheds, due to industrial practices and chan-

ging land-use such as logging and clearing for agriculture. Additional threats to eelgrass habitats include oil spills and dredging activities (Wright, 2001), encroachment of invasive exotics such as *Spartina alterniflora* (e.g. in Willapa Bay, Jacques, 2001), and rising water temperatures associated with El Niño events and global climate warming (Wright, 2001; Ward et al., 2002).

In some areas, steps have been taken to reduce threats to eelgrass. For example, in the southern section of Humboldt Bay, eelgrass is protected from aquaculture, and oyster growers in the northern section of the bay are managing their industry to reduce impacts on eelgrass habitats there (Coast Seafood Company, 1997). Also in Humboldt Bay, a local management plan has led to two initial years of monitoring of eelgrass distribution and condition by a consortium of workers. Boundary Bay in western Canada is designated as a Provincial Wildlife Management Area, and the nearby Roberts Bank area has some protection under the Fraser River Estuary Management Program (Harrison and Dunn, unpublished). However, we found little documentation of similar protection or management at other locations in the flyway, although conservation groups have formed to identify and begin addressing local issues (e.g. Wright, 2001; Morro Bay NEP, 2000). Still, coordinated efforts to regularly monitor eelgrass condition or share research and management information throughout the flyway are very much lacking.

Acknowledgements

We thank P. Clausen and an anonymous reviewer for their comments on a previous version of this manuscript. N. E. Pappani digitized eelgrass data from south Humboldt Bay into a GIS. M. Dunn, K. Hagmeier, HBNWR, D. Jacques, J. Kelly, D. Kraege, L. Moore, J. Roser, D. Ward, U. Wilson, and N. Wright provided us with data or other information concerning brant and eelgrass at various staging areas. Our work was partially funded by the California Department of Fish and Game and its Duck Stamp Account, and the California Waterfowl Association, the Humboldt State University Foundation, and California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis.

References

- Alliance for Responsible Shellfish Farming. 2001. Shellfish farm expansion: a case study in the neglect of public process and the vital need for scientific assessment as the basis for decision making. Unpublished report, prepared for the Ministry of Sustainable Resource Management, British Columbia.

- Ankney, C.D., 1984. Nutrient reserve dynamics of breeding and molting brant. *Auk* 101, 361–370.
- Baldwin, J.R., Lovvorn, J.R., 1994a. Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. *Marine Ecology Progress Series* 103, 119–127.
- Baldwin, J.R., Lovvorn, J.R., 1994b. Habitats and tidal accessibility of the marine foods of dabbling ducks and brant in Boundary Bay, British Columbia. *Marine Biology* 120, 627–638.
- Barnhart, R. A., Boyd, M. J., Pequegnat, J. E. 1992. The Ecology of Humboldt Bay, California: An Estuarine Profile. US Fish and Wildlife Service Biological Report 1.
- Bayer, R., 1996. Census of black brant at Yaquina Estuary, Lincoln County, Oregon. *Journal of Oregon Ornithology* 6, 723–780.
- Bixler, R. P. 1982. Primary productivity of eelgrass *Zostera marina* L.: comparative rates and methods. Master's Thesis, Humboldt State University, Arcata, California.
- Clausen, P., Madsen, J., Percival, S.M., O'Connor, D., Anderson, G.Q.A., 1998. Population development and changes in winter site use by the Svalbard light-bellied brent goose, *Branta bernicla hrota* 1980–1994. *Biological Conservation* 84, 157–165.
- Clausen, P., Percival, S.M., 1998. Changes in distribution and habitat use of Svalbard light-bellied brent geese *Branta bernicla hrota*, 1980–1995: driven by *Zostera* availability? *Norsk Polarinstittut Skrifter* 200, 253–276.
- Coast Seafood Company, 1997. Management plan for Coast Seafood Company commercial shellfishing in Humboldt Bay, California. Eureka, California.
- Contreras, A. 1998. Birds of Coos County, Oregon: Status and Distribution. Cape Arago Audubon Society and Oregon Field Ornithologists Special Publication No. 12, Eugene, Oregon.
- Cottam, C., Lynch, J.J., Nelson, A.L., 1944. Food habits and management of American sea brant. *Journal of Wildlife Management* 8, 36–56.
- Dau, C.P., 1992. The fall migration of Pacific flyway brent *Branta bernicla* in relation to climatic conditions. *Wildfowl* 43, 80–95.
- Ebbinge, B.S., Spaans, B., 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology* 26, 105–113.
- Fourqurean, J.W., Moore, T.O., Fry, B., Holligbaugh, J.T., 1997. Spatial and temporal variation in C:N:P ratios, delta N, and delta C of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. *Marine Ecology Progress Series* 157, 147–157.
- Ganter, B., 2000. Seagrass (*Zostera* spp.) as food for brent geese (*Branta bernicla*): an overview. *Helgoland Marine Research* 54, 63–70.
- Ganter, B., Prokosch, P., Ebbinge, B.S., 1997. Effect of saltmarsh loss on the dispersal and fitness parameters of dark-bellied brent geese. *Aquatic Conservation: Marine and Freshwater Ecosystems* 7, 141–151.
- Goudie, R.I., Hearne, M., 1997. Aspects of the distribution and ecology of brant in the Queen Charlotte Islands. *Canadian Wildlife Service Occasional Paper* No 93, 94–101.
- Harding, L.W., Butler, J.H., 1979. The standing stock of production of eelgrass, *Zostera marina*, in Humboldt Bay, California. *California Fish and Game* 65, 151–158.
- Harrison, P. G., Dunn, M. 1999. The Fraser Delta seagrass ecosystems: importance to migratory birds and changes in distribution. Unpublished manuscript.
- Henry, W. G. 1980. Populations and behavior of black brant at Humboldt Bay, California. Master's Thesis, Humboldt State University, Arcata, California.
- Jacques, D. 2001. Black brant at Willapa Bay: the 1999–2000 season and trends since 1979. Unpublished report, Willapa National Wildlife Refuge Complex, Ilwaco, Washington.
- Keller, M. 1963. The growth and distribution of eelgrass *Zostera marina* L. in Humboldt Bay, CA. Master's thesis, Humboldt State University, Arcata, California.
- Krapu, G.L., Reinecke, K.J., 1992. Foraging ecology and nutrition. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A., Krapu, G.L. (Eds.), *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minnesota, pp. 1–29.
- Lee, D. E. 2001. Immigration, emigration, stopover duration, and volume of black brant migrating through Humboldt Bay, California. Master's thesis. Department of Wildlife, Humboldt State University, Arcata, California.
- Merrifield, K. 1998. Waterbird censuses of Yaquina Bay, Oregon: March 1993–February 1994. Oregon Department of Fish and Wildlife Technical Report 98-1-01.
- Moffit, J., 1931. First annual black brant census in California. *California Fish Game* 17, 396–401.
- Moffit, J., 1932. Second annual black brant census in California. *California Fish Game* 18, 298–310.
- Moffit, J., 1933. Third annual black brant census in California. *California Fish Game* 19, 255–263.
- Moffit, J., 1934. Fourth annual black brant census in California. *California Fish Game* 20, 355–364.
- Moffit, J., 1935. Fifth annual black brant census in California. *California Fish Game* 21, 343–350.
- Moffit, J., 1936. Sixth annual black brant census in California. *California Fish Game* 22, 295–300.
- Moffit, J., 1938. Eighth annual black brant census in California. *California Fish Game* 24, 341–346.
- Moffit, J., 1940. Tenth annual black brant census in California. *California Fish Game* 26, 381–389.
- Moffit, J., 1941. Eleventh annual black brant census in California. *California Fish Game* 27, 216–223.
- Moffit, J., C. Cottam. 1941. Eelgrass depletion on the Pacific coast and its effect upon black brant. US Fish and Wildlife Service, Wildlife Leaflet No. 204.
- Moore, J. E. 2002. Distribution of spring staging black brant *Branta bernicla nigricans* in relation to feeding opportunities on South Humboldt Bay, California. Master's thesis, Humboldt State University, Arcata, California.
- Moore, J. E., Black, J. M., In review. Historical changes in black brant use on Humboldt Bay, California. *Journal of Wildlife Management Morro Bay National Estuary Program*. 2000. Comprehensive conservation and management plan. Available at <http://www.mbne-p.org/plan.htm>.
- Murrell, S. L. 1962. A study of crippling loss, kill and aging techniques of black brant (*Branta nigricans*), at Humboldt Bay, California. Master's thesis, Humboldt State University, Arcata, California.
- Ogilvie, M.A., Matthews, G.V.T., 1969. Brent geese, mudflats and man. *Wildfowl* 20, 119–125.
- Owen, M., 1990. The damage-conservation interface illustrated by geese. *Ibis* 132, 238–252.
- Phillips, R. C. 1972. Ecological life history of *Zostera marina* L. (eelgrass) in Puget Sound, Washington. Doctoral Dissertation, University of Washington, Seattle, Washington.
- Phillips, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: a community profile. US Fish and Wildlife Service. FWS/OBS-84/24.
- Proctor, C. M., Garcia, J. C., Galvin, D. V., Lewis, G. B., Loehr, L. C., Massa, A. M. 1980. An ecological characterization of the Pacific Northwest coastal region. US Fish and Wildlife Service, FWS/OBS-79/11-15.
- Prop, J., Black, J.M., 1998. Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. *Norsk Polarinstittut Skrifter* 200, 175–193.
- Prop, J., Black, J.M., Shimmings, P. in press. Migration schedules to

- the high arctic: barnacle geese trade off timing of migration for size of fat loads. *Oikos* 00:00-00.
- Rasmussen, E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: McRoy, C. F., Helfferich, C. (Eds.), *Seagrass Ecosystems—A Scientific Perspective*. Marcel Dekker, pp. 1–51.
- Reed, A., Ward, D. H., Derksen, D.V., Sedinger, J. S. 1998. Brant *Branta bernicla*. In: Poole, A., Gill, F. (Eds.), *The Birds of North America*. The American Ornithologists' Union, No.337.
- Roser, J. 2001. Brant observations from Morro Bay, California: a summary report 11/97–4/01. Unpublished report, 309 Binscarth Rd., Los Osos, California 93402.
- Spratt, J.D., 1989. The distribution and density of eelgrass, *Zostera marina*, in Tomales Bay, California. *California Fish and Game* 75, 204–212.
- Strittholt, J. R., Frost, P. A. 1996. Determining abundance and distribution of eelgrass (*Zostera* spp.) in Tillamook Bay Estuary, Oregon, using multispectral airborne imagery. Unpublished report prepared for Tillamook Bay National Estuary Project, Garibaldi, Oregon, by Earth Design Consultants, Inc.
- Subcommittee on Pacific Brant. 1992. Pacific flyway management plan for Pacific brant. Pacific flyway Study Committee (c/o USFWS, MBMO). Unpublished report, Portland, Oregon.
- Terra-Mar Humboldt Bay Orthophoto (USGS Map Ref. Ca0006-av3020). 1997. Vol. NCGIC 98.8-51. Distributed by North Coast Geographic Information Cooperative, Arcata, California.
- Thom, R.M., 1990. Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. *Botanica marina* 33, 497–510.
- Vermeer, K., Morgan, K. H., Bentley, M., Goodfellow, F., Beattie, N. 1991. The importance of spring staging areas of brant (*Branta bernicla*) and the distribution of other marine birds near Sandspit, Queen Charlotte Islands. Technical Report Series No. 136. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.
- Waddell, J. E. 1964. The effect of oyster culture on eelgrass *Zostera marina* L. growth. Master's thesis, Humboldt State University, Arcata, California.
- Ward, D. H. 1983. The relationship of two seagrasses: *Zostera marina* and *Ruppia maritima* to the black brant, *Branta bernicla nigricans*, San Ignacio Lagoon, Baja California, Mexico. Master's thesis, University of Oregon, Eugene, Oregon.
- Ward, D.H., Markon, C.J., Douglass, D.C., 1997. Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. *Aquatic Botany* 58, 229–240.
- Ward, P. 1992. Wetlands of the Fraser Lowland, 1989: summary report. Technical Report Series No. 156, Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.
- Ward, D.H., Morton, A., Tibbitts, T.L., Douglas, D.C., Carrera-González, E., 2002. Spatial change in seagrass extent in Bahía San Quintín, Baja California. In: Cabello-Pasini, A., García-Esquivel, Z. (Eds.), *Proceedings of the 2002 Meeting on Bahía San Quintín*. University of Baja California, Ensenada, Baja California, Mexico.
- Wilson, U.W., Atkinson, J.B., 1995. Black brant winter and spring-staging use at two Washington coastal areas in relation to eelgrass abundance. *Condor* 97, 91–98.
- Wright, N. 2001. Towards an eelgrass conservation initiative for the Strait of Georgia: a discussion paper. Unpublished report for the Canadian Wildlife Service, prepared by Sea-Change Marine Conservation Society, Victoria, British Columbia.
- Yocum, C. F., Harris, S. W. 1975. Status, habitats, and distribution of birds in northwestern California. Humboldt State University, Arcata, California.