ORIGINAL ARTICLE

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Seagrass (*Zostera* spp.) as food for brent geese (*Branta bernicla*): an overview

Abstract Brent geese (called brant in North America) are among the smallest and the most marine of all goose species, and they have very long migration routes between high Arctic breeding grounds and temperate wintering grounds. Like all other geese, brent geese are almost entirely herbivorous. Because of these ecological characteristics they have a high food demand and are strongly dependent on stopover sites to "refuel" during the migration period. Three subspecies of brent geese are distributed around the Holarctic, forming seven populations with distinct migration routes. Most or all of these populations make heavy use of *Zostera* spp. during migratory stopovers on spring and/or autumn migration. Examples of *Zostera* stopover areas being used by large numbers of brent geese for several weeks each year are Izembek Lagoon (Alaska), lagoons in Baja California, the German/Danish Wadden Sea, the Golfe du Morbihan (France), British estuaries, and the White Sea (Western Russian Arctic). Brent geese feed on *Zostera* wherever they can, but they can only reach the plants at low tide or in shallow water. Changes in *Zostera* abundance affect brent goose distribution, and the "wasting disease" affecting Atlantic *Zostera* stocks during the 1930s was at least partly responsible for a steep decline in brent goose population sizes on both sides of the Atlantic. While *Zostera* is of outstanding importance as food for brent geese, the impact of the geese on *Zostera* stocks seems to be less important – at many sites, the geese consume only a small amount of the available *Zostera*, or, if they consume more, the seagrass can regenerate fully until the following season.

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Introduction

Where the seagrass *Zostera* spp. occurs in intertidal or shallow-water areas of the north-temperate regions it can be used as a food source by herbivorous water birds during certain times of their annual cycle. Among the species that exploit *Zostera* either occasionally or regularly are coots (*Fulica atra*), swans (*Cygnus* spp.), dabbling ducks (*Anas* spp.) and brent geese or brant (*Branta bernicla*). This short review will focus on interactions between brent geese and *Zostera*. Brent geese are more dependent on *Zostera* as a food source than are the other bird species, and can consume large amounts of both above- and below-ground *Zostera* biomass at certain times of the year.

Brent geese are Arctic-breeding, migratory water birds. Three subspecies (dark-bellied brent goose, *B. b. bernicla*; light-bellied brent goose, *B.b. hrota*; and black-bellied brent goose or black brant, *B. b. nigricans*) are distributed around the Holarctic, forming seven populations with distinct breeding ranges and migration routes (Owen 1980; Madsen et al. 1996; Fig. 1, Table 1). Population sizes range from about 5,000 to about 300,000 birds (Table 1). In their habitat use, brent geese are confined to coastal areas throughout the annual cycle; they are the most marine of all goose species. The breeding grounds of brent geese are mostly situated in the high Arctic, and distances to wintering areas along temperate coasts are very long – up to 8,900 km in Canadian high Arctic *B. b. nigricans* (Reed et al. 1998).

Being almost exclusively herbivorous and unable to dive, brent geese are restricted to feeding on either intertidal vegetation (*Zostera* and green algae such as *Ulva* spp. and *Enteromorpha* spp.) at low water levels, on submerged vegetation in shallow water areas, or on salt marshes. Feeding in upland areas such as pastures or even cereal fields occurs relatively infrequently in this
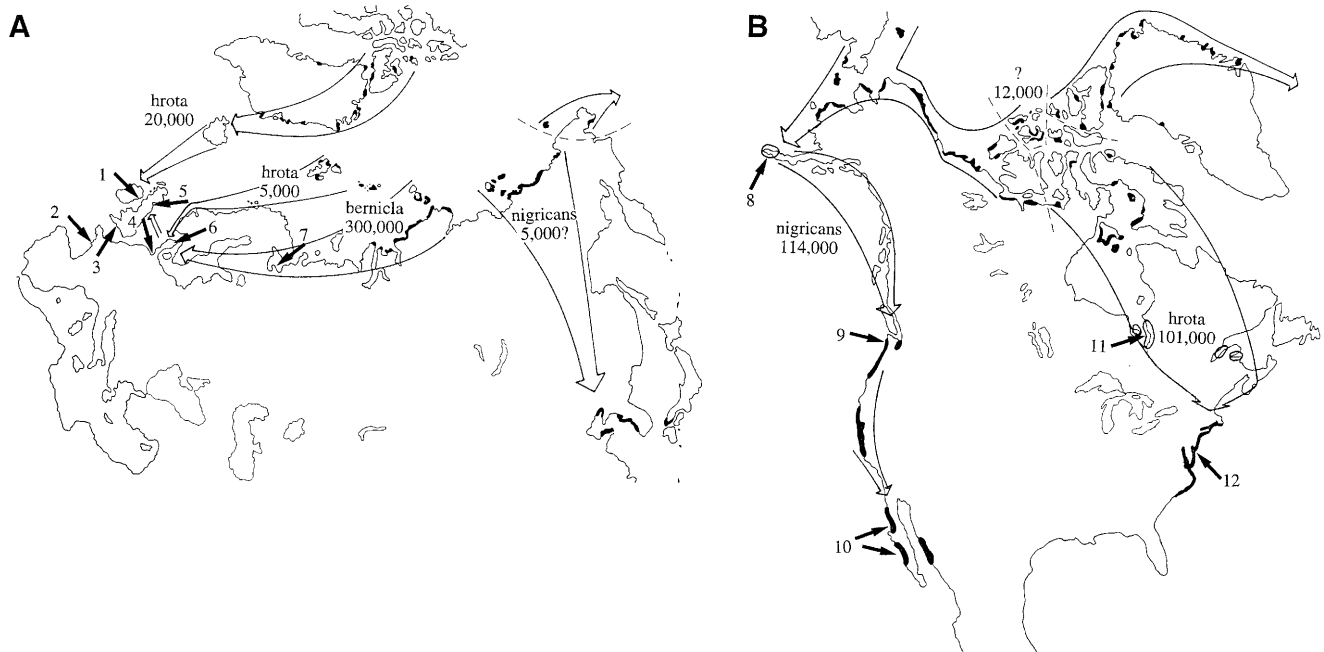
A

B

Fig. 1 Breeding grounds and migration routes of populations of brent geese in the Palaearctic (**A**) and brant in the Nearctic (**B**), with subspecies names and approximate population sizes (after Owen 1980, Madsen et al. 1996). "?" in **B**: "Grey-bellied Brent Goose" population. *Small numbered arrows* indicate important *Zostera* staging and wintering areas (see text and Table 1): *1* Strangford Lough; *2* Golfe du Morbihan; *3* English south coast; *4* Lindisfarne; *5* Wadden Sea; *6* Danish fjords; *7* White Sea; *8* Izembek Lagoon; *9* Washington coast; *10* Baja California lagoons; *11* James Bay; *12* Chesapeake Bay

Table 1 Breeding ranges, wintering ranges, and important *Zostera* staging areas of all populations of brent geese (*Branta bernicla*)

Subspecies	Population size (approx.)[a]	Breeding range[b]	Wintering range	*Zostera* staging/wintering areas[c]
B.b. bernicla	300,000	Taymyr Peninsula (Russia)	England (east and south coasts), France	Wadden Sea – A; British Estuaries, Golfe du Morbihan, other French estuaries – A, W; White Sea – A, S
B.b. nigricans	5,000?	Eastern Asian Arctic	Korea, Japan	? (very little known about this population)
B.b. nigricans	114,000	Russian Far East, Alaska, Western Canadian Arctic	US and Mexico Pacific coast	Izembek Lagoon (Alaska) – A,S; Washington & Oregon coast – A; Baja California coast – W
? ("Grey-bellied brent goose")	12,000	Western Canadian High Arctic	US Pacific coast	Washington coast – A, W, S
B.b. hrota	101,000	Eastern Canadian Arctic	US Atlantic coast	James Bay – A, S; Chesapeake Bay, other areas along U.S. Atlantic coast – W
B.b. hrota	20,000	Eastern Canadian High Arctic	Ireland	Iceland – A, S; Strangford Lough (Northern Ireland), Irish estuaries – A
B.b. hrota	5,000	Svalbard	Denmark, Northeast England	Lindisfarne (northeast England), Danish Wadden Sea – A; Danish fjords – A, W, S

[a]After Madsen et al. (1996)   [b]After Owen (1980)   [c]*A* autumn, *W* winter, *S* spring

goose species. This pattern of habitat choice applies throughout the non-breeding season; during the breeding season, the brent geese feed on a variety of plant species (mostly graminoids) in the Arctic nesting and brood-rearing areas (Spilling et al. 1994; Reed et al. 1998). Throughout the non-breeding season, *Zostera* is a preferred food for brent geese wherever it is available; reasons for this are the high digestibility and nutritive value of *Zostera* compared with other potential food plants, but also the comparatively low levels of human and other disturbance in *Zostera* feeding areas (Madsen 1988; Clausen 1994). Moreover, where *Zostera* occurs it is usually abundant and easy to ingest in large quantities during periods of body reserve build-up.

The combination of herbivory, long migration routes and the relatively small body size of brent geese (their body mass of about 1,300 g being among the lowest of all goose species) leads to a high food demand of the birds both in winter – small body size resulting in increased costs of thermoregulation – and on migration. Good body condition of adults upon departure from temperate staging areas in spring is mandatory for subsequent successful breeding in the summer (Ebbinge and Spaans 1995). However, because of their relatively small structural size and high wing load, brent geese are unable to carry enough body reserves with them to allow a non-stop migration from wintering to breeding grounds and also to leave some reserves for the early stages of breeding (Ebbinge and Spaans 1995). Therefore, a number of stopover areas on the different flyways are visited both in autumn and in spring migration; here, the birds stage for periods up to several weeks to feed and replenish their fat reserves.

Use of *Zostera* by brent geese on wintering and stopover sites

World-wide, all populations of brent geese use one or more species of *Zostera* at one or more stages of the annual cycle, either in their wintering areas or during longer staging periods or shorter migration stopovers both in autumn and spring (Table 1). The seasonal pattern of *Zostera* use along the migration routes depends solely on the seasonal availability of *Zostera* biomass, which varies according to the topography of the coastal area and the species of *Zostera* present. Below are some examples of patterns of *Zostera* utilisation by different brent goose populations throughout the year.

Dark-bellied brent geese, *B. b. bernicla*

At the end of the breeding season, the birds of this largest population of brent geese migrate from their breeding areas on the Taymyr peninsula in central Siberia to the White Sea in western Russia, where they stage for 1–2 weeks, feeding on abundant supplies of *Z. marina* (Clausen 1997). From the White Sea they move on to the next staging area in the Wadden Sea along the coast of Denmark, Germany and The Netherlands. Here they feed on intertidal stands of *Z. noltii* (where available; mainly in the Danish and northern German parts of the Wadden Sea) until the supply is depleted, and then switch to salt marshes or move on to England and France, where they spend the winter. In French and English estuaries they again feed on *Zostera* as long as it is available, then switch to feeding on green algae, to salt marsh feeding or (especially in England) upland feeding (e.g. Tubbs and Tubbs 1982). The Golfe du Morbihan on the northern French Atlantic coast is the single most important *Zostera* feeding area for this population after they have left the Wadden Sea: up to 20% of the total population were present here in the 1970s (Maheo 1976), and in the 1990s with a much larger total population the Golfe du Morbihan still holds more than 10% of all dark-bellied brent geese (van Nugteren 1997). In the spring, dark-bellied brent geese move back to the Wadden Sea for pre-migratory fattening; however, no *Zostera* is available in the Wadden Sea in spring, and the birds feed on salt marsh vegetation instead. On the way to the breeding grounds, dark-bellied brent geese stop once more in the White Sea. Here, perennial stands of *Z. marina* are preserved under the sea ice and become available as soon as the ice breaks up in late May. The stopover and refuelling periods in the White Sea on both autumn and spring migration are essential because the geese are not capable of 5,000 km non-stop migration between the breeding grounds and the Wadden Sea, and the White Sea is situated about half way between the two (Ebbinge and Spaans 1995).

Svalbard light-bellied brent geese, *B. b. hrota*

Outside the breeding season, this small population of brent geese (numbering only about 5,000 individuals) is restricted to only a few sites in Denmark and one site (Lindisfarne) in northeast England (Clausen et al. 1998). Throughout the non-breeding season the birds rely heavily on *Zostera* spp. After arrival in autumn, *Z. noltii* stands in the northern part of the Danish Wadden Sea are used for a short time by a part of the population, while others move on directly to other Danish sites or to Lindisfarne (Clausen et al. 1998). Throughout autumn, winter and spring, the birds use several sites in sequence, feeding on *Zostera* at every one of them. All Danish sites outside the Wadden Sea are shallow fjord areas with submerged *Z. marina*, the availability of which depends on local water levels (Clausen 1994). At Lindisfarne, the birds feed on intertidal stands dominated by *Z. noltii* until they are depleted (Percival and Evans 1997). When *Zostera* is temporarily unavailable due to high water levels, and after *Zostera* stands have been depleted, the brent geese either switch to feeding on green algae or salt marshes, or move on to other areas.

Greenland/Canadian light-bellied brent geese, *B. b. hrota*

These birds stop in Iceland on both autumn and spring migration to forage on seagrass beds along the coast on the way to and from their winter quarters in Ireland. For about 6–8 weeks after arrival in autumn, more than 75% of this population totalling about 20,000 birds are concentrated on the *Zostera* beds of Strangford Lough, Northern Ireland (O'Briain and Healy 1991). Later in the autumn, most of the birds disperse to other Irish estuaries. By midwinter, only about 25% of the population are left at Strangford Lough. At all sites, birds continue to feed on *Zostera* until it is depleted by a combination of the birds' feeding activities and damage through wave

action. After depletion of *Zostera* in late autumn or winter, the birds switch to feeding on green algae and, even later, to salt marshes (O'Briain 1991).

Atlantic brant, *B. b. hrota*

Atlantic brant, breeding around Foxe Basin in the Canadian Arctic, winter along the North American Atlantic coast where *Zostera* is a main food. Pre-migratory body reserves built up in spring are not sufficient to carry the birds non-stop from wintering to breeding grounds (Vangilder et al. 1986), but are sufficient to reach a major staging area on the northeast coast of James Bay. Here, birds feed to more than 95% on *Zostera* in spring and again during a stopover on autumn migration (Reed et al. 1996).

Pacific black brant, *B. b. nigricans*

Like the dark-bellied brent geese of the Palaearctic, this large population makes use of a chain of *Zostera* stop-over and wintering sites which are separated by rather large distances along the long migration route. The most northerly area, used by probably the entire population in both autumn and spring, is Izembek Lagoon near the tip of the Alaska peninsula. According to Jones and Jones (1966), Izembek Lagoon harbours the most extensive *Z. marina* beds in the world, totalling 16,300 ha. This vast area not only supports the entire population of Pacific black brant, but also very large numbers of Canada geese (*Branta canadensis*), emperor geese (*Anser canagicus*) and pintail (*Anas acuta*) (Jones and Jones 1966). The breeding range of the brant using Izembek Lagoon extends from the low Arctic Yukon–Kuskokwim Delta in western Alaska to the central Canadian high Arctic. In autumn, brant from different breeding areas arrive at Izembek Lagoon at different times according to the distance they have to cover before reaching the lagoon: birds from the low Arctic arrive several weeks earlier than those from the high Arctic; however, the early arrivals also leave the area earlier in November, so that the staging period for both groups comes to about 7 weeks (Reed et al. 1989). From Izembek, birds move on to wintering areas along the Pacific coast of North America, ranging from southern British Columbia to Mexico. Only a minority of birds winter in the more northerly areas (British Columbia, Washington and Oregon); most birds have their final wintering areas in California and in several large lagoons along the coast of Baja California, Mexico (Baldassare and Bolen 1994). *Zostera* (mainly *Z. marina*, but also the introduced *Z. japonica*) is the main food for brant in all wintering areas, although in Baja California birds can also feed on green algae. In spring, the birds move back north along the Pacific coast, and the more northerly wintering areas can also be used as stopover sites by brant wintering further south (e.g. Wilson and Atkinson 1995). The *Zostera* beds of Izembek Lagoon, as the vital last refuelling site before reaching the breeding grounds, are used again in spring.

Accessibility of *Zostera* to brent geese

Where brent geese and *Zostera* are present in the same general area, the *Zostera* is only accessible to the geese if certain conditions are met, most of which are related to water level. A brent goose can reach about 40 cm below the water surface when up-ending (Clausen 1994), which sets a limit to the water depths at which the bird can exploit *Zostera* (or other submerged plants).

In tidal areas, *Zostera* is usually unavailable to the birds at high tide (usually twice, but sometimes once a day depending on the tidal regime of the area), and the length of the period of accessibility depends on topography of the area and on the tidal regime. Sub-littoral stands of *Zostera* can be exposed for short periods at low spring tides (Tubbs and Tubbs 1982), and even when not exposed, parts of these stands can be accessed by up-ending geese during low tide. The degree to which night-time low tides are used for feeding appears to vary between areas: Madsen (1988) and Percival and Evans (1997) report that feeding activity at night was the same as during the day, while Jacobs et al. (1981) and O'Briain (1991) state that birds did not feed at night. In areas where tidal elevations fluctuate seasonally, *Zostera* accessibility can be restricted further during certain periods of the year (Einarsen 1965; Baldwin and Lovvorn 1994a).

Brent geese have adapted their behaviour to the tidal changes to maximise the time of *Zostera* exploitation: during the falling tide, they fly out to the *Zostera* beds from their roosts and swim on the water until *Zostera* can be reached by up-ending (Einarsen 1965; Jacobs et al. 1981; Madsen 1988). During the course of the tidal cycle, different feeding techniques are used depending on the actual water level: up-ending; dabbling; wading in shallow water with ingestion of partially submerged *Zostera* leaves; pecking leaves from completely exposed *Zostera* stands; grubbing and trampling in the substrate to access *Zostera* rhizomes (Jacobs et al. 1981; Madsen 1988). Reed et al. (1998) describe how the geese feed on the long leaves of *Z. marina*: "A brant feeding on leaves of eelgrass appears to suck it in rapidly, but the blades must be manipulated within the buccal cavity, because blades are stored in the oesophagus in neatly folded clumps". In some areas feeding, either by grazing, up-ending or pecking *Zostera* leaf fragments from the water surface, is possible at all stages of the tide (O'Briain 1991; Reed et al. 1996). In early spring in James Bay, birds also feed along the edges of retreating ice flows, pecking off *Zostera* leaves that had been imprisoned in the ice over winter (Reed et al. 1996).

In shallow, non-tidal areas with submerged *Zostera*, feeding is only possible by up-ending or dabbling. In Danish fjords with only a weak tidal influence, the water levels are strongly dependent on wind conditions. At

high water levels, brent geese cannot reach the *Zostera* beds and have to switch to salt marsh feeding; as soon as water levels are favourable again, the birds immediately switch back to feeding on *Zostera* (Clausen 1994). An additional problem of accessibility occurs when brent geese graze submerged stands of *Zostera* (the leaves of which stand vertically in the water column) down to levels beyond their own reach (Clausen 1994).

Even in deeper water areas where *Zostera* grows beyond the reach of brent geese at all times, the birds can sometimes feed on floating *Zostera* parts that have been accidentally uprooted by the activities of other species foraging on the sea floor. Brent geese have been reported to follow diving ducks or oyster dredgers (Cottam et al. 1944), and even approach clam fishermen to a distance of less than 2 m (Kirby and Obrecht 1980). These behaviours have been reported especially in periods of severe food shortage (Cottam et al. 1944; Einarsen 1965). Frequently, brent geese also glean fresh leaves of *Zostera* from shore drifts at high tide (Cottam et al. 1944; Baldwin and Lovvorn 1994b).

Apart from water levels, another factor potentially restricting the access of brent geese to *Zostera* is disturbance. By influencing the distribution of the birds, hunting disturbance in particular can greatly restrict the use of parts of *Zostera* beds (Einarsen 1965; Madsen 1988; Percival and Evans 1997).

Consequences for brent geese of changes in *Zostera* abundance

Because of their heavy reliance on *Zostera* as a main food source, the distribution of brent geese outside the breeding season is to a large extent determined by the distribution of *Zostera* (e.g. Prokosch 1984; Clausen 1994). Consequently, changes in *Zostera* abundance will impact the distribution or, if changes occur on a large enough scale, the population size of the birds. The most prominent example of changes in *Zostera* abundance affecting brent goose populations was the "wasting disease" of Atlantic *Zostera* in the early 1930s.

In 1931–1932, a disease associated with the mycetozoan *Labyrinthula* led to the abrupt and almost complete destruction of *Z. marina* beds along the entire east coast of North America and, at about the same time, a marked decline of the species in Europe (Cottam et al. 1944; Cottam and Munro 1954; Rasmussen 1977). The sudden decline of *Zostera* coincided with population crashes of brent geese on both sides of the Atlantic. Although exact counts of the total population are missing, the reduction in the population size of Atlantic brant on the east coast of North America was estimated to be as much as 90% (Cottam et al. 1944). Estimates for the population losses of dark-bellied brent geese in Europe range from 75% to 90% (Ogilvie and Matthews 1969), with only about 15,000 birds left in the early 1950s.

Before the "wasting disease", 85% of the diet of Atlantic brant consisted of *Zostera* (Cottam et al. 1944); after the disease, when the birds were deprived of their main food source, "large flocks wandered from place to place and many perished" (Cottam and Munro 1954). In the years after the disease, *Zostera* only averaged about 9% of the brant's diet, the major proportion now consisting of *Ulva*, *Enteromorpha* and other algae (Cottam et al. 1944). Eventually, the birds were able to switch to alternative habitats, using meadows and upland areas for feeding, a behaviour that had never been observed before (Cottam et al. 1944). However, owing to the traditional behaviour of the birds, this switch only occurred after a considerable time lag, during which the recovery of the population was halted (Smith et al. 1985). By the early 1950s, a considerable recovery of *Zostera* along the North American side of the Atlantic had occurred (Cottam and Munro 1954); this was followed by a recovery of the brant population, which now numbers more than 100,000 again (Madsen et al. 1996).

In the European range of the dark-bellied brent goose the "wasting disease" led to changes in *Zostera* availability that still have not been reversed. Before the 1930s, *Z. marina* used to be the main food of brent geese during spring as well as autumn staging in the Wadden Sea (Drent 1996); today, no *Zostera* is available for the birds in the Wadden Sea in spring because the overwintering stands of *Z. marina* did not recover. Brent geese now almost exclusively forage on salt marshes in spring. Upland feeding, although still rare on the whole, has also become more common in some areas, especially in England. Although the sudden crash in the abundance of *Zostera* in the 1930s certainly played a role in the decline of the dark-bellied brent goose population, it was probably not the sole cause responsible for very low levels and slow recovery of the population. Human persecution may have been especially severe on the breeding grounds of dark-bellied brent geese during the 1930s and 1940s, moulting birds being caught in large numbers both by indigenous people (Ogilvie and Matthews 1969) and inhabitants of prison camps (Nowak 1995). Additional strong hunting pressure on migration and in winter in Europe kept the population at a low level of around 25,000 birds, a marked recovery not taking place until the early 1970s, when hunting was banned in nearly all of the range states and a series of successful breeding seasons allowed a rapid population increase (Ebbinge 1991; Summers and Underhill 1991). Since then the population has recovered to a level – unprecedented during this century – of nearly 300,000 birds (Madsen et al. 1996), despite the lack of *Zostera* feeding opportunities in spring. This is an example of a successful habitat shift by an entire population of migratory birds.

In addition to the massive changes brought about by the "wasting disease", there are various examples of smaller-scale changes in *Zostera* abundance and their impact on brent goose distribution. In a study of black brant stopover and wintering sites in the state of Washington, Wilson and Atkinson (1995) report that at one site there was a negative relationship between the area covered by *Zostera* and the area used for oyster cultures;

numbers of wintering brant were unaffected by annual changes in *Zostera* area, but numbers of spring staging birds were correlated with the amount of *Zostera* available. Similar competition between commercial shellfisheries and *Zostera* was reported for the Golfe du Morbihan in France where *Zostera* recovery is prevented in some places by the establishment of oyster cultures (Maheo 1976). At a second site studied by Wilson and Atkinson (1995) there was a long-term decline in *Zostera*, the cause of which was not clear, but could have been increased turbidity after clearcutting and erosion of the surrounding hilllsides; again, numbers of wintering brant were not affected, but those of spring-staging birds were.

The loss of *Zostera* through eutrophication in some areas in Denmark has led to a redistribution of the Svalbard population of light-bellied brent geese. While Nissum Fjord used to support the entire population in the spring until the 1960s, this area now holds only a few geese following the rather rapid and complete disappearance of *Zostera* beds between 1966 and 1988, which is attributed to severe eutrophication of the fjord (Clausen and Percival 1998). The geese subsequently switched to a previously unused area where, due to a combination of factors (including reduction of eutrophication), a positive development of *Zostera* stocks has taken place in the 1980s and 1990s. However, similar to the situation in Atlantic brant after the wasting disease, this switch only occurred after a time lag during which the growth of this very small population may have been hampered by declining food resources in the traditional areas (Clausen 1994).

The spread of the exotic species *Z. japonica* along the northern Pacific coast of North America has also had consequences for herbivorous water birds including black brant. Because *Z. japonica* occupies a previously unused niche in the middle to upper zone of tidal estuaries, vast areas of seagrass habitat accessible at low tide have been added to the previously present subtidal and lower intertidal stands of *Z. marina* (Baldwin and Lovvorn 1994b). This has enormously increased the feeding opportunities for herbivorous water birds, although the changes have not been quantified for black brant alone. In contrast to dabbling duck species, which use the intertidal stands of *Z. japonica* exclusively, brant still have a high proportion of *Z. marina* in their diet because they can reach down into the shallow subtidal zone (Baldwin and Lovvorn 1994b).

Impact of brent goose feeding activities on *Zostera* stocks

Although it is quite clear that brent geese (and other herbivorous water birds) can consume significant amounts of *Zostera* biomass in some areas at certain times of the year, quantification of this consumption relative to other factors reducing *Zostera* biomass is difficult to achieve. In a number of studies the decline of *Zostera* biomass or leaf cover during the presence of the birds was determined without measuring how much of the decline was due to grazing activities (e.g. Baldwin and Lovvorn 1994b; Fox 1996), while only a few studies estimated more closely the amount consumed by birds using exclosures which were inaccessible to grazing birds. Most of these studies relate to dark-bellied brent geese in autumn and winter.

In an exclosure study in southern England, Tubbs and Tubbs (1982) found that inside exclosures (i.e. without grazing) the percentage of cover of *Zostera* leaves declined from 85% to 20% between October and January, whereas outside the exclosures the cover declined to less than 5%; however, they did not quantify how much *Zostera* was taken by brent geese outside the exclosures, or measure any effects on below-ground biomass of *Zostera* by feeding geese. For the autumn period on a *Zostera* bed in the Dutch Wadden Sea, Jacobs et al. (1981) recorded a decrease from 60% to 55% cover inside exclosures between August and early November whereas outside the exclosures only about 20% cover remained. Here, brent geese were only responsible for about 19% of biomass consumption, the remainder being taken by three species of dabbling ducks. In total, Jacobs et al. (1981) estimated that 50% of maximum above-ground standing stock (or 26% of total annual production) of *Zostera* was taken by birds during autumn and winter. In addition, intensive feeding occurred on *Zostera* rhizomes, but was not quantified. In another exclosure study in the Danish Wadden Sea, Madsen (1988) found a reduction in above-ground biomass of *Zostera* of 59% inside and 89% outside exclosures between August and early December; below-ground biomass decreased by 29% outside exclosures while it increased by 26% inside exclosures. Brent geese and wigeon (*Anas penelope*) were estimated to consume 45% and 33% of the total annual production of *Zostera* in 2 years of study, corresponding to 91% or 66% of maximum standing crop; brent geese were responsible for about three-quarters of the consumption.

For brent geese feeding in intertidal areas, a number of studies report "giving-up densities" of *Zostera* cover, i.e. the percentage of leaf cover below which feeding on *Zostera* becomes unprofitable for brent geese. These densities are between 5% and 15% cover (Charman 1979; Jacobs et al. 1981; Tubbs and Tubbs 1982; Madsen 1988; O'Briain 1991; Percival and Evans 1997). At lower leaf cover values, brent geese either feed increasingly on *Zostera* rhizomes (Madsen 1988), switch to salt marsh or upland feeding, or leave the site. Percival and Evans (1997) observed that with declining cover of *Zostera* the geese increased the time spent feeding each day and also increased night-time feeding activity, before leaving the site completely. Where geese are disturbed by hunting, the giving-up densities can be much higher than 10–15% (Madsen 1988).

While brent geese may consume significant proportions of *Zostera* biomass in the intertidal areas in Europe investigated in the above studies, the impact of goose

grazing in Izembek Lagoon (Alaska) appears to be minimal: the consumption of 300,000 geese staging there for 60 days (and feeding exclusively on *Zostera*) was estimated to amount to 1.2% of the total summer standing stock of this extremely large *Zostera* area (Jones and Jones 1966).

For the slightly different situation of spring-grazing brent geese on submerged *Z. marina*, Clausen (1994) found that a reduction of the leaf length by about 2.5 cm through grazing of brent geese was followed by compensatory growth of the plants, with fewer flowering and more vegetative shoots being produced. The difference in biomass between grazed and ungrazed plots had disappeared by August. Thus, there were no long-term effects of brent goose grazing on *Zostera* standing stock, but possibly some effects on seed production and dispersal. In a study of spring-staging brent geese in the White Sea, it was estimated that the birds consumed 31–47% of the standing crop of *Z. marina* in the study area (Clausen 1997).

Where brent geese and other herbivorous water birds (such as wigeon) occur in the same *Zostera* feeding areas, it can be expected that some interspecific competition would occur, at least in those areas where the *Zostera* resource is limited. However, studies investigating possible competition between brent geese and wigeon have found little or no interaction between the species (Madsen 1988; Fox 1996; Percival and Evans 1997). While Fox (1996) reported almost no spatial overlap between wigeon and brent geese because wigeon fed exclusively by dabbling and had to follow the tide line to feed on partially submerged *Zostera*, Nacken (1998) observed wigeon feeding on *Zostera* rhizomes in depressions created by grubbing brent geese. In areas like the Izembek Lagoon with a very abundant food supply, no interspecific competition occurs despite very large numbers of different species of grazing birds being present (Jones and Jones 1966).

Conclusion

All populations of brent geese world-wide rely on *Zostera* as a food source during various periods of the annual cycle; thus, the opportunity to feed on *Zostera* is of outstanding importance to the species. This importance has declined somewhat for brent goose populations on both sides of the Atlantic after the dramatic changes brought about by the "wasting disease" with its catastrophic declines of *Zostera* stocks in the early 1930s. However, even the dark-bellied brent goose, which has undergone the largest and most lasting shift in feeding strategies after the "wasting disease", still relies on *Zostera* in autumn and before reaching the breeding grounds in spring.

From the opposite perspective, the impact of goose grazing on *Zostera* stocks seems to be much less important. The birds either remove only a small proportion of the biomass or they utilise *Zostera* at a time of the year when storms, wave action and senescence have at least as large an impact on the plants as grazing does. In no case have effects of grazing by brent geese (or other birds) on *Zostera* been reported which lasted longer than a season. This is in agreement with the general assumption summarised by Jacobs et al. (1981) "that the grazing of seagrasses by birds plays a minor role compared with the decomposition of tissues by microorganisms". Goose grazing may even have positive effects on *Zostera* beds by preventing excessive silting and thus maintaining a sediment level suitable for *Zostera* growth (Jacobs et al. 1981). The observation made by Nacken (1998) that *Z. noltii* plots where brent geese were excluded from feeding in autumn had sparser vegetation cover in the following spring than grazed plots had seems to support this speculation. Although Baldwin and Lovvorn (1994b) suggest that "the trophic role of avian herbivores in temperate seagrass food webs may often be underemphasized", restricted accessibility of *Zostera* and relatively short staging periods of the birds during the least productive times of the year still make it seem unlikely that they have a major impact on *Zostera* stocks in most of the areas used.

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