

Predicting impacts of food competition, climate, and disturbance on a long-distance migratory herbivore

R. A. STILLMAN ^{1,†} E. M. RIVERS ¹ W. GILKERSON,² K. A. WOOD ³ B. A. NOLET ^{4,5}
P. CLAUSEN ⁶ H. M. WILSON,⁷ AND D. H. WARD ⁸

¹Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, Dorset BH12 5BB UK

²Merkel and Associates, 5434 Ruffin Road, San Diego, California 92123 USA

³Wildfowl and Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT UK

⁴Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, Wageningen 6708 PB The Netherlands

⁵Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, Science Park 904, Amsterdam 1098 XH The Netherlands

⁶Department of Bioscience—Wildlife Ecology, Aarhus University, Grenåvej 14, Rønne 8410 Denmark

⁷U.S. Fish and Wildlife Service, Migratory Bird Management-Region 7, 1011 E. Tudor Road, Anchorage, Alaska 99503 USA

⁸Alaska Science Center, U.S. Geological Survey, 4210 University Drive, Anchorage, Alaska 99508 USA

Citation: Stillman, R. A., E. M. Rivers, W. Gilkerson, K. A. Wood, B. A. Nolet, P. Clausen, H. M. Wilson, and D. H. Ward. 2021. Predicting impacts of food competition, climate, and disturbance on a long-distance migratory herbivore. *Ecosphere* 12(3):e03405. 10.1002/ecs2.3405

Abstract. Climate change is driving worldwide shifts in the distribution of biodiversity, and fundamental changes to global avian migrations. Some arctic-nesting species may shorten their migration distance as warmer temperatures allow them to winter closer to their high-latitude breeding grounds. However, such decisions are not without risks, since this intensifies pressure on resources when they are used for greater periods of time. In this study, we used an individual-based model to predict how future changes in food abundance, winter ice coverage, and human disturbance could impact an Arctic/sub-Arctic breeding goose species, black brant (*Branta bernicla nigricans*, Lawrence 1846), and their primary food source, common eelgrass (*Zostera marina* L.), at the Izembek Lagoon complex in southwest Alaska. Brant use the site during fall and spring migrations, and increasingly, for the duration of winter. The model was validated by comparing predictions to empirical observations of proportion of geese surviving, proportion of geese emigrating, mean duration of stay, mean rate of mass gain/loss, percentage of time spent feeding, number of bird days, peak population numbers, and distribution across the complex. The model predicted that reductions >50% of the current decadal (2007–2015) mean of eelgrass biomass, which have been observed in some years, or increases in the number of brant, could lead to a reduction in the proportion of birds that successfully migrate to their breeding grounds from the site. The model also predicted that access to eelgrass in lagoons other than Izembek was critical for overwinter survival and spring migration of brant, if overall eelgrass biomass was 50% of the decadal mean biomass. Geese were typically predicted to be more vulnerable to environmental change during winter and spring, when eelgrass biomass is lower, and thermoregulatory costs for the geese are higher than in fall. We discuss the consequences of these predictions for goose population trends in the face of natural and human drivers of change.

Key words: black brant; climate change; eelgrass; human disturbance; individual-based model; mechanistic modeling; migration; winter.

Received 13 November 2019; revised 18 September 2020; accepted 6 October 2020; final version received 21 December 2020. Corresponding Editor: Brooke Maslo.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** rstillman@bournemouth.ac.uk

INTRODUCTION

Unprecedented ecological shifts are occurring worldwide in response to climate change, with many avian species transitioning to more northerly breeding and wintering areas (Berthold et al. 1992, Hitch and Leberg 2007, La Sorte and Thompson 2007, Chen et al. 2011, Lehtikoinen et al. 2013). Species that would previously have migrated long distances may winter closer to their breeding grounds, and take advantage of warmer weather conditions. This would allow them to avoid the energetic penalties of a costly migration (Klaassen 1996, Mason et al. 2006), and benefit from earlier arrival on the breeding grounds (Bearhop et al. 2005, Visser et al. 2009). These changes in distribution may lead to seasonal conflicts between different species whose natural ranges are shifting, potentially bringing together species or metapopulations that may never have occurred together before (Urban et al. 2012, Van Hemert et al. 2015). For long-distance migrants, these changes may also place greater demands on stopover and staging areas that are used for longer periods during the nonbreeding season, thus intensifying pressures on food resources and vulnerable systems such as coastal wetlands (Jefferies et al. 2006, Viaroli et al. 2007).

Although the choice of some migratory birds to spend the nonbreeding season closer to the poles may be associated with energetic savings (Root 1988, Mason et al. 2006), the risks of unexpectedly cold winters and potential food shortages are ever present (Kirby and Obrecht 1982, Camphuysen et al. 2002, Ward et al. 2009). Individuals may burn fat stores during inclement weather to the point their body condition is so reduced that they may become unable to leave a site to seek further resources (Mason et al. 2006). Concurrent human exploitation of a site can compound the situation, whether through exclusion from resources, disturbance or direct loss through hunting (Stock 1993, Ward et al. 1994, Riddington et al. 1996). New human disruptions may increase energetic pressures on birds through increases in avoidance and vigilance behaviors, and changes to normal patterns of activity (Madsen 1995, Gill et al. 2001, Mini and Black 2009, Desmots et al. 2009). In addition, climate change is anticipated to lead to increasingly

extreme weather patterns, such as exaggerated climatic oscillations (Cai et al. 2015, EPA 2016). This would induce more uncertainty in animal decision making about whether to migrate or remain at high latitudes (Suter and Van Eerden 1992), with higher mortality risks during severe northern winters (Clausen et al. 2001). At migration stopover sites which host mass staging of many species, phenological overlaps between groups competing for the same resources could bring novel conflicts and reduce individual fitness (e.g., Rudolf 2019).

In this study, we examine potential threats to a migratory bird species dependent upon an Alaskan estuarine lagoon complex during the nonbreeding season by predicting how multiple changes in environmental conditions could impact their survival and ability to migrate. Our study species, the black brant (*Branta bernicla nigricans*, Lawrence 1846; hereafter 'brant'), is a small migratory coastal goose, which depends almost entirely upon common eelgrass (*Zostera marina* L.) for nutrition during the nonbreeding period (August–May; Ward et al. 2005, Lewis et al. 2013). Our study system comprises Izembek Lagoon and adjacent embayments (hereafter "Izembek complex"; Fig. 1), where virtually the entire Pacific Flyway population of brant stages annually in fall and spring, prior to transoceanic, long-distance migrations to and from wintering areas primarily in Mexico (Reed et al. 1989, Dau 1992, Sedinger et al. 1993, Lewis et al. 2013). Increasingly, however, ~30% of fall-staging brant are short-stopping their southward migration to overwinter in the Izembek complex for up to 7 months of the year (Ward et al. 2009, Wilson 2017a). Eelgrass is abundant in the Izembek complex with one of the largest beds in the world located in Izembek Lagoon (Ward et al. 1997, Hogrefe et al. 2014). However, variability in the annual abundance of eelgrass in Izembek Lagoon (Ward and Amundson 2019) may have far-reaching consequences for the entire brant population.

We parameterized an individual-based model (IBM, called MORPH; Stillman 2008), to simulate the study system, and validated predictions against empirical values derived from the literature. Such IBMs predict behavior and its population-level consequences from individual-level (or groups of individuals) properties and

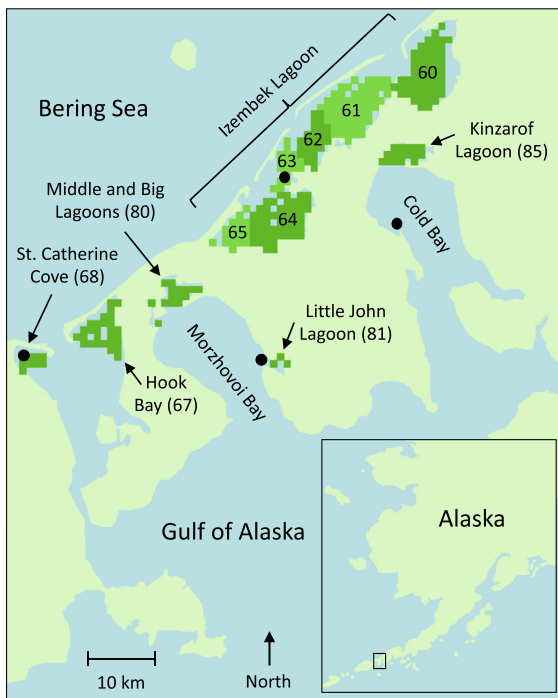


Fig. 1. Map of the Izembek complex, and its location within Alaska, showing the sites used in the model (numbers; different hues of green in Izembek Lagoon), the distribution of eelgrass beds used in present-day simulations (as eelgrass distribution was different in future simulations), and the location of tidal gauge stations (solid circles).

interactions, together with decision rules based on fitness maximization. The parameters define the behavior and energetics of foragers, including daily energy expenditure, typical response to disturbance, rate of feeding and assimilation, and the availability of food across a study site. A range of possible future environmental conditions can then be simulated so that species responses can be predicted at the individual and population level. Our model also incorporated Taverner's cackling goose (*Branta hutchinsii taverneri*, Delacour 1951; hereafter "cackling goose") to account for interspecific competition, as these geese are numerous in the Izembek complex during fall migration and also feed on eelgrass (Hupp et al. 2013). Thus, our model predicts how brant survival and successful migration depends on the number of geese, changes in eelgrass abundance, climate-induced variation in winter ice coverage, and disturbance.

METHODS

Study system

The Izembek complex (Fig. 1) comprises several shallow embayments at the end of the Alaska Peninsula ($55^{\circ}15' N$, $163^{\circ}00' W$), adjoining the Bering Sea to the north, and the Gulf of Alaska to the south. The complex supports ~31,000 ha of eelgrass, with the greatest area of eelgrass in Izembek Lagoon (17,000 ha; Hogrefe et al. 2014). During freezing conditions, sea ice builds along shorelines and in shallow offshore areas. Sea ice levels frequently vary among the discrete embayments with those situated along the Gulf of Alaska side of the peninsula remaining largely ice-free when Izembek Lagoon is frozen (Ward et al. 2009). Therefore, the distribution of geese within the Izembek complex during winter is heavily influenced by the prevailing sea ice conditions, and consequently, accessibility of eelgrass beds.

Modeling time, space, and environmental variables

The model simulated 319 d, from 1 August to 15 June, encompassing the period of all levels of brant usage of the area (Table 1a; see Appendix S1: Table S1a for details). The model defined fall as 1 August–15 December, winter as 16 December–31 March, and spring as 1 April–15 June (Table 1a; see Appendix S1: Table S1a for details), corresponding to the periods of brant fall-staging, overwintering, and spring staging, respectively (Reed et al. 1989, Mason et al. 2006, 2007, Baldassarre 2014). The model ran until 15 June to ensure that all simulated spring migrants could potential emigrate, as some did not arrive until 27 May (Table 1c; see Appendix S1: Table S1c for details). Time was divided into discrete 1-h time steps, within which environmental conditions were assumed to remain constant. We used a 1-h time step, rather than a longer duration, as the model needed to represent the exposure and covering of the eelgrass food resource during the tidal cycle between time steps. The model incorporated the diurnal cycle, with hours of daylight or night based on predicted times of civil twilight at sunrise and sunset for the Izembek complex (Table 1a; see Appendix S1: Table S1a for details). It was assumed that geese could feed by day and by night.

Table 1. Parameter values used in the model.

Parameter	Value(s)
(a) Time and environmental parameters	
Time step length (hours)	1
Model length (days)	319
Seasons	Fall, 1 Aug–15 Dec Winter, 16 Dec–31 Mar Spring, 1 Apr–15 June
Duration of daylight (hours)	8.7–19.4
Percentage and duration of ice coverage in Izembek Lagoon	0% 25%, 40 d 50%, 40 d 100%, 27 d
Mid-point of icing conditions	Early, 15 Jan Mid, 14 Feb Late, 15 Mar
Hunting and boating disturbance rate (h^{-1})	Fall, 0.00, 0.30, 0.60, or 0.42 Winter, 0.00 or 0.06 Spring, 0.00
Natural disturbance rate (h^{-1})	Fall, 0.13–0.32 Winter/Spring, 0.32 all areas
(b) Patch and eelgrass parameters	
Patch size (m^2)	$1000 \times 1000 = 1,000,000$
No. patches	308
No. sites	11
Patch elevation (m MLLW)	–2.43 to 0.87
Water level (m MLLW)	Varies
Eelgrass initial biomass (B) ($g DM m^{-2}$)	
Bering Sea sites	$B = 169.27 - 120.15H - 8.7932H^2$
Gulf of Alaska sites	$B = 198.93 - 94.75H - 72.4132H^2$ where $H =$ patch elevation (m MLLW)
Eelgrass initial shoot length (L) (m)	
Bering Sea sites	$L = 0.56279 - 0.39378H$
Gulf of Alaska sites	$L = 0.48837 - 0.25641H$ where $H =$ patch elevation (m MLLW)
Eelgrass seasonal changes in biomass independent of depletion by the geese	
End of biomass decline, day 138	Proportional change per time step, 0.9996361223
Start of biomass growth, day 245	Proportional change per time step, 1.0003706031
Eelgrass seasonal changes in shoot length (L_{rel})	$L_{rel} = (136.23 - 1.1294D + 0.0027D^2)/136.23$ where D = Days since 1 August
Eelgrass metabolizability (%)	51
Eelgrass energy content ($kJ g^{-1} DM$)	16.8
Eelgrass floating biomass (percentage of rooted biomass in patch)	Fall, 5% of rooted biomass Winter/spring, no floating biomass
(c) Goose parameters	
Population size (number passing through sites)	Brant fall, 160,736 Brant winter, 43,210 Brant spring, 52,058 Cackling fall, 34,648
Size of flocks	1000 individuals
First and last arrival dates	Brant fall, 25 Aug–8 Oct Brant winter, 25 Aug–8 Oct Brant spring, 1 Apr–27 May Cackling fall, 2 Sep–6 Sep

(Table 1. Continued.)

Parameter	Value(s)
Departure date	Brant fall, 4 Nov Brant winter, 15 May Brant spring, 15 May Cackling fall, 29 Oct
Initial distribution across sites (proportion in each site; sites, 60, 61, 62, 63, 64, 65, 67, 68, 80, 81, 85, 100)	Brant fall/winter 0.086, 0.280, 0.081, 0.093, 0.156, 0.215, 0.007, 0.035, 0.022, 0.000, 0.025, 0.000 Brant spring 0.059, 0.101, 0.087, 0.008, 0.477, 0.161, 0.073, 0.008, 0.026, 0.000, 0.000, 0.000 Cackling fall 0.383, 0.117, 0.042, 0.009, 0.107, 0.133, 0.007, 0.139, 0.062, 0.00, 0.001, 0.000
Body mass on arrival (g)	Brant fall, 1369 Brant winter, 1369 Brant spring, 1522 Cackling fall, 2202
Energy density of fat (kJ g ⁻¹)	Brant/Cackling, 34.3
Starvation mass (g)	Brant, 964 Cackling, 161
Target body mass during staging (g)	Brant fall, 1752 Brant winter, 1715 (start of winter) to 1585 (end of winter) Brant spring, 1611 Cackling fall, 2529
Departure body mass (g)	Brant fall, 1752 Brant winter, 1611 Brant spring, 1611 Cackling fall, 2529
Maximum foraging depth (m)	Brant, 0.40 Cackling, 0.52
Rate of consuming eelgrass biomass (g DM h ⁻¹) (C)	Brant C = $60 \times (0.419B)/(20.2 + B)$ Cackling C = $60 \times (0.659B)/(20.2 + B)$ where B = eelgrass biomass (g DM/m ²).
Maximum energy assimilation (KJ d ⁻¹) (E _{max})	$E_{max} = 1713M^{0.72}$ where M = body mass Brant fall M = 1597 Brant winter M = 1585 Brant spring M = 1491 Cackling fall M = 2366
Energy expenditure while foraging (J s ⁻¹)	Brant fall, 13.5 Brant winter (ice free), 15.3 Brant winter (25% ice), 17.1 Brant winter (50% ice), 17.1 Brant winter (100% ice), 19.9 Brant spring, 14.4 Cackling fall, 18.4
Energy expenditure while resting (J s ⁻¹)	Brant fall, 12.8 Brant winter (ice free), 15.3 Brant winter (25% ice), 17.1 Brant winter (50% ice), 17.1 Brant winter (100% ice), 19.9 Brant spring, 14.4 Cackling fall, 18.4
Time cost per disturbance event (s) (D _T)	$D_T = p_R d_T$ where p_R = probability of responding to disturbance and d_T = time cost of response Land-based disturbance $p_R = 0.824$; $d_T = 139$ Boat disturbance $p_R = 0.931$; $d_T = 224$ Natural disturbance $p_R = 0.980$; $d_T = 206$

(Table 1. Continued.)

Parameter	Value(s)
Energy cost per disturbance event (KJ) (D_E)	$D_E = p_F d_E$ where p_F = probability of flying due to disturbance and d_E = energy cost of response
Land-based disturbance	$p_F = 0.900$ Brant fall $d_E = 10.23$, brant winter $d_E = 10.38$, brant spring $d_E = 10.27$ Cackling fall $d_E = 15.50$
Boat disturbance	$p_F = 0.944$ Brant fall $d_E = 17.02$, brant winter $d_E = 17.27$, brant spring $d_E = 17.08$ Cackling fall $d_E = 25.78$
Natural disturbance	$p_F = 0.917$ Brant fall $d_E = 10.50$, brant winter $d_E = 10.65$, brant spring $d_E = 10.53$ Cackling fall $d_E = 15.90$

Note: See Appendix S1: Table S1 for sources.

The model included 11 sites, comprising the following embayments on the Alaska Peninsula: Izembek Lagoon, Hook Bay, St. Catherine Cove, Middle Lagoon, Big Lagoon, Little John Lagoon, and Kinzarof Lagoon. Izembek Lagoon was divided into 6 subsites (termed “sites” henceforth; Fig. 1; see Data S1 for details) comprising locations where population counts are made in the lagoon (Wilson and Dau 2016). Each site was divided into 1x1 km square patches. Patches were the unit of space that birds occupied and moved between.

Tidal height (in meters, at mean lower low water; m MLLW) during each time step within each site was measured from the nearest tidal gauge (Fig. 1), considering the following observed offsets in the timing of tidal curves. These were Izembek Lagoon, Grant Point gauge; Hook Bay and St. Catherine Cove, St. Catherine Cove gauge; Middle Lagoon and Little John Lagoon, Morzhovoi Bay gauge; and Kinzarof Lagoon, Cold Bay with 1-h lag, and Big Lagoon, Morzhovoi Bay gauge with 2-h lag (Table 1b; see Appendix S1: Table S1b for details). The water depth over each patch during each time step was calculated as the difference between tidal height during the time step, and the elevation of the patch (see Data S1 for details). Patches were assumed to be exposed when the elevation of the patch was higher than tidal height.

The model simulated four types of winter sea ice conditions, when eelgrass was partly or wholly inaccessible to geese in Izembek Lagoon:

ice-free, and 25%, 50%, and 100% ice cover following Petrich et al. (2014). In general, patches with a higher elevation, and hence shallower water depth, were more susceptible to freezing. Sites other than Izembek Lagoon always maintained some ice-free patches of eelgrass, even when Izembek Lagoon was completely ice-covered (Petrich et al. 2014; see Data S1 for details). The duration of sea ice conditions was taken as the mean observed for different extents of ice coverage (Petrich et al. 2014, Wilson and Dau 2016; Table 1a; see Appendix S1: Table S1a for details), or presumed to occur throughout the entire winter as an extreme assumption. In simulations where ice coverage did not last throughout winter, three alternative timings of ice were assumed, early, mid, and late, based on the observed variations in ice timing (Table 1a; see Appendix S1: Table S1a for details).

The model incorporated human (primarily land- and boat-based hunting) and natural (primarily bald eagles *Haliaeetus leucocephalus* Linnaeus 1766) disturbances (Table 1c; see Appendix S1: Table S1c for details) with the frequency and distribution of events based on empirical data and observations (Ward et al. 1994, Daniels 2014).

Each patch had a season-specific disturbance rate which, in combination, affected the time and energy costs of the geese (see Data S1 for details). Human-induced disturbance events (hunting and boating) followed the legal hunting periods (permitted in fall and spring but not winter), and

were more frequent closer to road-based access points. Natural disturbances were more frequent away from road-based access points, and in winter and spring when eagles are most abundant (Ward et al. 1994, Daniels et al. 2019).

Modeling eelgrass biomass and shoot length

The eelgrass food supply at each site was modeled as the spatial arrangement of eelgrass across the grid of 1-km² patches (Fig. 1). Each patch had a fixed elevation (which determined its water depth through the tidal cycle), and when

eelgrass was present, it contained a specific aboveground biomass and shoot length of eelgrass, which combined with elevation determined the availability of food for geese (see Data S1 for details). The mean elevation of each patch was calculated from a Digital Elevation Model (DEM) of the Izembek complex using ArcGIS 10.1 (ESRI, Redlands, California, USA).

Eelgrass shoot length (m, meristem to tip of longest ungrazed leaf) and aboveground biomass (g/m²) were derived from embayment-wide boat surveys using a systematic point-sampling design (Ward and Amundson 2019). Surveys were conducted during peak biomass and shoot length of eelgrass in July–September, between 2007 and 2015 (Izembek 2007–2011 and 2015; Kinzarof 2008–2010; all others 2012; Hogrefe et al. 2014). A separate quadratic regression was used to relate aboveground biomass to elevation for sites bordering the Gulf of Alaska and the Bering Sea, because tidal regimes and coastal geomorphic characteristics influencing eelgrass growth differed between these two sides of the Alaska Peninsula (Hogrefe et al. 2014; Table 1b; see Appendix S1: Table S1b for details). Similarly, separate linear regressions were used to express shoot length in terms of elevation (Ruesink et al. 2010; Table 1b; see Appendix S1: Table S1b for details). These relationships were then used to predict the eelgrass summer (1 August) aboveground biomass, and shoot length relative to mean elevation (m MLLW) of each patch.

Even though there has not been a recent systematic decline in eelgrass biomass within the Izembek complex, there has still been considerable year to year variation, with the minimum over a ten-year period around 50% of the mean (2007–2018; Ward and Amundson 2019). We therefore ran two alternative model simulations for eelgrass biomass to account for the temporal variation in eelgrass abundance within the Izembek complex: mean biomass simulations based on the mean biomass of eelgrass during the embayment-wide surveys, and minimum biomass simulations based on 50% of the mean biomass of these surveys. The mean and minimum biomass simulations accounted for the variation in eelgrass biomass observed (Ward and Amundson 2019).

Changes in eelgrass biomass from fall to spring were determined from monthly sampling

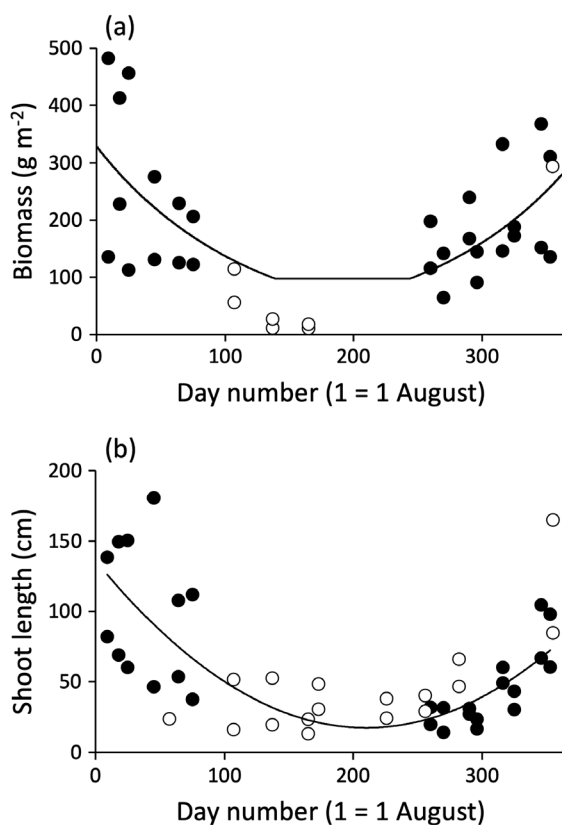


Fig. 2. Seasonal changes in (a) eelgrass biomass and (b) shoot length within Izembek Lagoon independent of grazing by geese. The solid symbols show values from 2010 and 2011, through which relationships were fitted. The open symbols show present-day (2016–2017) values when eelgrass biomass was 50% of the current, 2007–2015, decadal mean values. The solid lines show the fitted relationships used to determine seasonal changes in biomass and shoot length (see Table 1b and Appendix S1: Table S1b for details).

of eelgrass in a meadow that received little or no grazing by geese in Izembek Lagoon during 2010 and 2011 (Fig. 2a). This relationship was used to calculate rates of eelgrass change during three periods of the year: fall biomass decline (1 August–15 December); winter stable biomass (16 December–31 March); and spring biomass increase (1 April–31 May; Fig. 2a; Table 1b; see Appendix S1: Table S1b for details). Changes in eelgrass shoot length through time were determined from the same monthly sampling of eelgrass in 2010–2011 (Fig. 2b). Relative eelgrass shoot length was calculated as a proportion of the annual maximum shoot length. A quadratic equation was fitted to relative shoot length to determine the relationship between shoot length and day (Fig. 2b; Table 1b; see Appendix S1: Table S1b for details).

Geese primarily feed on eelgrass rooted to the substrate when it is exposed and within reach at low tides, but also may consume eelgrass that becomes displaced and floats to the water surface as the tide rises above eelgrass beds (e.g., Moore 2002, Elkinton et al. 2013). During each time step, birds were assumed to feed on either rooted or floating eelgrass, depending on which yielded the highest rate of energy consumption.

Modeling goose migration, energetics, and behavior

The model considered three types of brant: fall migrants—geese that passed through the sites during southward migration; spring migrants—geese that passed through the sites during northward migration; and over-winterers—geese that spent the winter in the sites. Although in reality fall and spring migrants are the same geese, these were considered separately in the model as it did not incorporate other staging and wintering sites to the south. Cackling geese were only included in the fall, since they do not winter or stop at the Izembek complex in spring. Cackling geese are known to feed to some degree on food other than eelgrass (Hupp et al. 2013), but to explore the full potential impact of cackling geese on brant through inter-species food competition, we assumed that cackling geese obtained all of their energy requirements from eelgrass. The sizes of the modeled goose populations were based on the mean count of surveys, made during fall staging (Wilson 2017b, 2019), wintering

(Wilson 2017a), and spring staging (Wilson 2017c) in 2010–2016 (Table 1c; see Appendix S1: Table S1c for details).

Due to the large population size of geese in the sites, rather than simulating each individual goose, most model simulations used flocks comprised of 1000 individuals. This assumption was realistic, as geese within sites tend to concentrate in large flocks rather than being spread individually throughout the sites (Ward and Stehn 1989). However, to test the effect of this assumed flock size, we also ran one set of simulations with a flock size of 100 to compare predictions (see below for results). Individuals within flocks were assumed to have identical behavior, amounts of energy, and shared fates (i.e., they either all survived, or all died). Each model flock was randomly assigned a date when it arrived at Izembek, drawn from a uniform distribution between the observed first and last arriving geese of the three season types (Table 1c; see Appendix S1: Table S1c for details). A uniform distribution was assumed for simplicity and as limited data were available to determine the precise distribution of arrival dates. Each flock was also assigned an arrival site, derived from the mean proportion of geese counted in each site (including the subsites of Izembek Lagoon) throughout fall, winter, and spring (Table 1c; see Appendix S1: Table S1c for details). Flocks remained in their arrival site unless their energy reserves fell below a threshold amount (see below for details of the movement between sites).

The model tracked the amount of energy stored by each goose, calculated as body mass minus lean body mass, and multiplied by the energy content of fat (Table 1c; see Appendix S1: Table S1c for details). Geese of each type were also assigned a body mass at arrival in the system (Table 1c; see Appendix S1: Table S1c for details). Geese were assumed to remain in the system until a type-specific departure day and departure energy store were reached (Table 1c; see Appendix S1: Table S1c for details). Geese emigrated from the system after the departure day was reached, but only if they had reached their departure body mass.

Daily energy expenditure for each season was calculated following Nolet et al. (2016), using raw data body mass estimates from Mason et al.

(2007), which included approximately 30% juveniles in the sample. Two possible values of daily energy expenditure were initially calculated: Field Metabolic Rate (FMR), incorporating the costs of activity but excluding any additional costs of thermoregulation, and Heating Metabolic Rate (HMR), incorporating the costs of thermoregulation. FMR was calculated from basal metabolic rate (BMR), and the behavior of the birds (Table 1c), and BMR itself was calculated from body mass (Bruinzeel et al. 1997). The energy expenditure of different behaviors was calculated from multipliers of BMR (Nolet et al. 2016, excluding flight, which was addressed in more detail; Table 1c). HMR was calculated with environmental adjustments to consider the predominantly marine nature of the environment. This method considers multiple factors in avian thermoregulation, including individual body temperature (T_b), ambient temperature (T_a), solar radiation (R_g), wind speed (u), and the impact of environmental conditions. As energy expended through activity can substitute heat production through regulatory thermogenesis (Swanson 2010), either HMR or FMR was selected with preference to the highest value during each season. Therefore, in brant, FMR was the highest value during fall, while HMR was the highest value during winter and spring, when brant were regularly exposed to temperatures below their zone of thermoneutrality. Cackling geese were only present during fall and did not experience environmental conditions requiring additional thermoregulation.

Although waterfowl are well adapted to maintaining body heat in water, a small thermoregulatory cost has been demonstrated when the water temperatures dropped below 15°C (Jennsen et al. 1989). Water temperatures in this region of Alaska during the study periods are usually well below this, so this additional factor was calculated following Wood et al. (2013),

$$\text{Cost (W/kg)} = 1.80 - (0.09t)$$

where t refers to water temperature in °C, taken from mean sea surface temperatures in each season (NOAA National Centers for Environmental Information; <https://www.ncei.noaa.gov>; data from 2017). In all seasons, the cost of roosting fell below that of heating metabolism, so this was not included in the model.

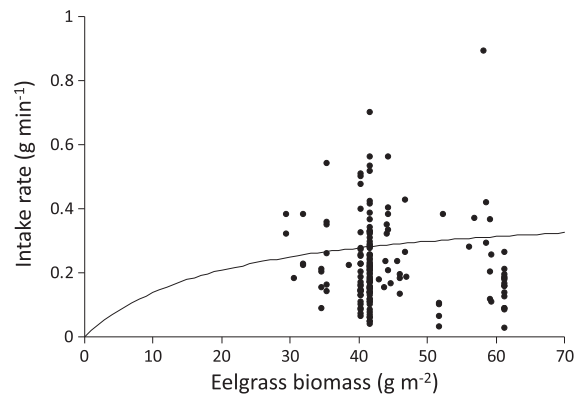


Fig. 3. Relationships between eelgrass biomass and brant intake rates. The symbols show observations of brant intake rates recorded in Humboldt Bay (Stillman et al. 2015). The curve shows the predicted functional response of brant feeding on eelgrass while swimming (Clausen 2013; see Table 1c and Appendix S1: Table S1c for details).

We assumed rooted eelgrass was available to the geese if it was within the maximum foraging depth of geese, 40 cm (Clausen 1994, 2000). Cackling geese are about 12 cm longer than brant from mid-belly to beak tip, so were assumed to gain 12 cm greater foraging depth. For each time step, the water depth on each patch was calculated as the difference between water level and the elevation of the patch, both measured relative to MLLW. This assumes that the eelgrass is standing upright in the water column, and does not bend, due to water current, for example. To test the model's sensitivity to this assumption, we included eelgrass height in the sensitivity analysis of the model (see below for results). Rooted eelgrass was classed as either fully available to geese, or not available to geese, depending on whether it was within reach from the water surface or exposed by the tide (Table 1c; see Appendix S1: Table S1c for details). Floating eelgrass, when present in fall, was assumed to be available to the geese at all times.

The rate at which the model geese could consume eelgrass, during the day or at night, was calculated using a functional response derived from light-bellied brant geese (*Branta bernicla hrota*) feeding on *Z. marina* in Europe (Clausen 2013). Fig. 3 shows this relationship in comparison to intake rates of brant swim-feeding on

eelgrass in Humboldt Bay (Stillman et al. 2015). We use the functional response curve from Clausen (2013) that has been derived from studies on light-bellied brant geese swim-feeding on submerged *Z. marina* beds in the Limfjord, Denmark (57° N; Clausen 1998, 2000), and from dark-bellied brant geese feeding on submerged *Z. marina* in the White Sea, Russia (65° N; Clausen 1997). These birds were thus feeding on the same and submerged *Zostera* species as the birds do in the Izembek complex (55° N). Intake rates in the Limfjord were assessed from indirect measurements, that is, by fecal dropping rates on flocks that occasionally went ashore after longer extensive feeding bouts on *Zostera*. Intake rates were then estimated following the approach of Prop and Deerenberg (1991)—with details given by Clausen (1994). The available biomass during feeding days on *Zostera* was derived by interpolation from known biomass, leaf-length and water-levels (data from Clausen 1998, 2000). In the White Sea, intake rates were estimated from direct measurement, where feeding birds were observed at close range (<100 m) with a 20–60 × telescope from an observation tower, and their intake in terms of entire plants or single leaves were counted per unit time. Biomasses of plants and leaves were measured from sampled plants, and available biomass during feeding days on *Zostera* estimated from leaf lengths and water levels following the same methods as Clausen (2000). Data on the intake rate of brant swim-feeding on eelgrass in Humboldt Bay are variable and show no relationship with eelgrass biomass, but the relationship used by Clausen (2013) predicts intake rates within the range observed (Fig. 3). Following Wood et al. (2013), the consumption rate of cackling geese was allometrically scaled from brant rates.

The model incorporated competition due to resource depletion, with each model flock depleting 1000 times the amount of eelgrass consumed by a single individual goose. Both brant and cackling geese therefore competed with themselves and each other for food. Furthermore, resource competition occurred both within and between simulated flocks through the successive depletion of eelgrass between time steps. Other types of competition, such as aggression or competitor avoidance, were not modeled explicitly, as they were not considered important in this

system, and would have been incorporated to some extent in the functional response as it was based on observations of real geese. No limit was set on the number of geese that could potentially occur a single patch.

The rate at which model geese could assimilate energy from feeding was calculated from the rate at which they could feed, the eelgrass energy content, and their digestive efficiency in assimilating eelgrass (Table 1c). A limit was placed on the maximum possible daily intake of energy, based on an allometric equation following Kirkwood (1983).

Model geese had a target size of energy (e.g., fat) store that they attempted to achieve (Table 1c; see Appendix S1: Table S1c for details). Target energy store size was assumed to change linearly between the arrival and departure days for geese arriving and departing within a season (i.e., fall brant and cackling geese, and spring brant). The target energy store of brant staying throughout winter changed linearly between fixed points in the seasons: fall arrival through to the end of fall; the end of fall through to the end of winter; and then the end of winter through to their departure energy store.

The target energy store size of overwinter brant was assumed to decrease through winter, to mimic the reduction in body mass of brant observed wintering in the Izembek complex (Mason et al. 2007). Reasons for this phenomenon, in addition to reduced caloric intake, may include enhancement of flight performance to avoid predators (e.g., Zimmer et al. 2010). Bald eagles are especially numerous in the study area during winter and spring staging (Daniels 2014, Wilson et al. 2017a); therefore, avoidance of predation could be an important factor in the management of body mass by the geese.

On reaching their target energy store, model geese regulated the amount of food they consumed by reducing the amount of time they spent feeding and hence increasing resting time. However, if model geese were unable to meet their energy requirements, they drew energy from their store, thus decreasing the overall size of the store. Geese that could not reach their departure energy store remained in the system. If a bird's energy store fell to zero, it died of starvation. Therefore, mortality due to starvation was incorporated as an all-or-nothing response to

reduction in energy store size, in which birds survived if the size of their energy store was greater than zero but died as soon as the store size fell to zero. Direct sources of mortality through hunting or predation were not incorporated into the model and were assumed to be constant between model simulations.

Disturbance within patches incurred time and energy costs for the geese. The total time cost was calculated from the sum of the periods lost due to different types of human and natural disturbances, while accounting for their rate (disturbance events/h) and the proportion of geese responding to the event (Table 1c; see Appendix S1: Table S1c for details). The same time costs were assumed for brant and cackling geese and were taken from empirical evidence on brant responses to human and natural disturbance during fall at Izembek Lagoon (Ward et al. 1994). The subsequent energy costs were calculated based on the average mass of birds through the seasons (Gudmundsson 1995, Nudds and Bryant 2000, Mason et al. 2006, 2007).

The time cost due to disturbance reduced the time geese was able to feed within a time step. The total energy cost was calculated as the sum of the energy cost due to each disturbance type, while accounting for rates of disturbance, flight time of geese, the energy demands of flight, and the proportion of geese responding to the disturbance (Table 1c; see Appendix S1: Table S1c for details). Flight costs were assumed to comprise 10 s of energetically intensive take-off flight, combined with less intensive steady state flight. This was calculated using the available literature (Gudmundsson et al. 1995, Nudds and Bryant 2000) as a function of phylogeny, mass, and flight style. The energy cost of disturbance increased the amount of energy expended by geese within a time step.

During each time step, model geese could choose to move to a new patch or remain in their current position. If they were able to maintain the size of their energy store to within 95% of their target energy store, model geese only moved to patches within their current site. In this case, geese moved to the patch that maximized their net rate of energy consumption, taking account of energy assimilation and energy costs of foraging and resting, but not accounting for the distance to the patch. If their energy store

was lower than 95% the size of their target energy store size, model geese considered patches within a fixed distance of 20 km, that is, the distance that geese could move within 0.5 h. (half a time step). When moving between sites, model geese still moved to the patch that maximized their net rate of energy consumption. This reflects the choices made by real geese (Moore and Black 2006) to minimize unnecessary energy expenditure. The distance and energetic cost of moving between patches was not incorporated into the model.

Model simulations

The model incorporated stochasticity in terms of the arrival dates and sites of geese, and the movement of geese between patches yielding equal net energy gain. Therefore, five replicate simulations were run for each combination of model parameter values, with mean predictions and associated 95% confidence intervals presented. For clarity, and as 95% confidence intervals were often small relative to means, 95% confidence intervals are not shown on figures. Instead, the 95% confidence intervals are stated in figure legends. In total, 170 simulations were run.

Model validation and sensitivity analysis

The model was tested by comparing its predictions to the following observed field data; proportion of geese surviving, proportion of geese emigrating, proportion of time spent feeding by geese, mean rate of body mass change, mean staging duration, peak number of birds, number of bird use days, diversity of sites occupied, and distribution of birds across all sites. To assess the effect of the flock size assumed in the model, two sets of predictions were tested based on either a flock size of 1000 or 100. The individual parameter perturbation method was used to assess the sensitivity of the model predictions to adjustments in parameter values. We assessed the amount of change that occurs in the proportion of time feeding due to plus or minus 25% changes in individual parameter values. We chose to vary each parameter value by a fixed amount, rather than by the amount by which the parameter varies in the real system, because the amount of variation has not been measured in all cases.

Scenario I: changes in eelgrass biomass

To examine the effects of changes in the biomass of eelgrass, we ran simulations in which the eelgrass biomass of each patch was sequentially varied in 10% increments from 10% to 100% of the mean biomass measured (Ward and Amundson 2019). Subsequent simulations (i.e., Scenarios II–V) were based on both the mean biomass (mean biomass simulations) and a 50% biomass reduction in this value (minimum biomass simulations) to represent the average and lower limit of biomass observed within the Izembek complex over the decadal study period. Simulations were run for two alternative winter sea ice conditions, ice-free simulations, and 50% Izembek coverage occurring late in winter (termed 50% late ice simulations henceforth).

Scenario II: changes in eelgrass distribution

To assess the importance of sites other than Izembek Lagoon, simulations were run in which eelgrass biomass was set to zero in areas outside of Izembek Lagoon: Hook Bay, St. Catherine Cove, Middle Lagoon, Big Lagoon, Little John Lagoon, and Kinzarof Lagoon. Although we excluded these sites by setting eelgrass biomass to zero, these simulations represent a scenario in which these areas could become unavailable due to a combination of factors (e.g., habitat loss, increased disturbance, reduction in eelgrass biomass). All combinations of the mean biomass, minimum biomass, ice-free, and 50% late ice simulations were run.

Scenario III: changes in goose population size

We assessed the effect of potential increases in goose population size by changing the size of populations in 20% increments from the current day population sizes—from 120% to 200% of the present-day populations. Three sets of simulations were run in which (1) the populations sizes of both goose species were changed in all seasons (i.e., fall, winter and spring brant, and fall cackling goose); (2) brant population size in winter was changed alone (i.e., the number that overwintered rather than migrating); or (3) cackling goose population size in fall was changed alone. All combinations of the mean biomass, minimum biomass, ice-free, and 50% late ice simulations were run.

Scenario IV: changes in the coverage and timing of ice

Changes in ice cover conditions were simulated by varying both the overall extent (none, 25%, 50% and 100% within Izembek Lagoon) and timing (early, mid, late during winter, and throughout winter; Table 1a) of ice coverage. The model assumed that the thermoregulatory energy costs of the geese were higher in simulations with higher ice coverage. We did not simulate the effects of ice cover in the spring, because this condition has been rare since the 1980s (Petrich et al. 2014). Both the mean biomass and minimum biomass simulations were run.

Scenario V: changes in disturbance

The effect of changes in disturbance was predicted by varying disturbance rate from zero to five times the current disturbance rate. For simplicity, we assumed that the distribution and timing of disturbances were unchanged. Simulations either varied both human and natural disturbance or varied human disturbance alone. All combinations of the mean biomass, minimum biomass, ice-free, and 50% late ice simulations were run.

RESULTS**Model validation and calibration**

We validated the model for brant and cackling geese by comparing 8 predictions to observations (Table 2; Figs. 4, 5). It was important to validate the model for cackling geese to determine whether the amount of interspecific competition from this species was likely to be similar in the model to reality. Predictions were virtually identical with either a flock size of 100 or 1000 (Table 2), and so a flock size of 1000 was used in all subsequent simulations due to the reduced duration of simulations (around 12 min per simulation with a flock size of 1000, compared to around 120 min with a flock size of 100). Overall, there was a close match between predictions and observations, with general observed patterns being accurately predicted. All model geese could survive and emigrate, and observations show that all or virtually all of real birds do also. The predicted and observed proportions of time spent feeding were lower in fall than in winter and spring and differed by 0.04 at most. This

Table 2. Tests for 8 properties of the system.

Test	Species/season	Predicted flock size		Observed
		100	1000	
Proportion of geese surviving	Fall brant	1 ± 0	1 ± 0	0.99
	Winter brant	1 ± 0	1 ± 0	1.00
	Spring brant	1 ± 0	1 ± 0	0.99
	Fall cackling	1 ± 0	1 ± 0	?
Proportion of geese emigrating	Fall brant	1 ± 0	1 ± 0	~1
	Winter brant	1 ± 0	1 ± 0	~1
	Spring brant	1 ± 0	1 ± 0	~1
	Fall cackling	1 ± 0	1 ± 0	~1
Proportion of time spent feeding (over 24 h)	Brant in fall	0.43 ± 0.00	0.43 ± 0.00	0.48
	Brant in winter	0.72 ± 0.01	0.73 ± 0.00	0.73
	Brant in spring	0.72 ± 0.02	0.72 ± 0.01	0.68
	Cackling in fall	0.29 ± 0.00	0.29 ± 0.00	?
Mean rate of body mass change (g/day)	Brant in fall	7.11 ± 0.04	7.06 ± 0.19	5.7
	Brant in winter	-1.20 ± 0.00	-1.20 ± 0.00	-0.82
	Brant in spring	6.29 ± 0.28	6.51 ± 0.25	4.00
	Cackling in fall	5.94 ± 0.01	5.95 ± 0.01	9.5
Staging duration (days)	Fall brant	48.7 ± 0.3	49.4 ± 1.3	46
	Winter brant	240.0 ± 0.6	240.1 ± 1.8	247.3
	Spring brant	17.9 ± 0.9	17.3 ± 0.9	17.3
	Cackling in fall	54.1 ± 0.1	54.0 ± 0.0	56
Peak count (no. of geese)	Brant in fall	160,700 ± 0	161,000 ± 0	175,222
	Brant in winter	43,200 ± 0	43,000 ± 0	41,728
	Brant in spring	83,020 ± 694	82,800 ± 1900	49,622
	Cackling in fall	34,600 ± 0	35,000 ± 0	41,971
No. of bird days	Brant in fall	9,771,380 ± 51,035	9,862,800 ± 143,239	7,304,246
	Brant in winter	4,622,400 ± 0	4,601,000 ± 0	4,084,552
	Brant in spring	2,841,460 ± 46,138	2,800,200 ± 49,041	858,466
	Cackling in fall	1,904,960 ± 2,237	1,924,000 ± 1,640	1,920,812
Diversity of sites occupied	Brant in fall	5.76 ± 0.04	5.82 ± 0.04	5.75
	Brant in winter	4.37 ± 0.37	4.34 ± 0.24	4.55
	Brant in spring	4.02 ± 0.27	4.13 ± 0.42	3.56
	Cackling in fall	4.64 ± 0.01	4.63 ± 0.02	4.66

Notes: Predicted values are mean ±95% confidence intervals from 5 replicate simulations, assuming either a flock size of 100 or 1000. The predicted and observed distributions of geese are shown in Figs. 4, 5. Question marks indicate unknown observed values. See Appendix S1: Table S2 for sources of observations.

suggests that the model and real geese had to spend a similar amount of time feeding to meet their energy demands. We did not test tidal or time-of-day variation in the proportion of time feeding as suitable observed data were not available. Both model and real geese gained mass during the fall and spring, but lost mass during the winter. Predicted rates of mass gain were higher than observed for brant in fall and spring, and lower than observed in cackling goose in fall. The predicted rate of mass loss in brant in winter was higher than observed. The model closely predicted staging duration, being within 3 d of observations for fall and spring migrant brant and cackling goose, and 7 d for overwintering

brant. Predicted peak counts and bird days showed similar overall patterns to observations, although the spring peak count and bird days of brant differed more greatly from observations than other predictions.

The predicted and observed site use diversities were similar, with a higher diversity of sites being used in the fall (Table 2). Model geese, when they first entered the system, were assumed to arrive at a target site based on the observed distribution of geese. They only moved between sites if they were not able to maintain the size of their energy store. During fall, both brant and cackling geese achieved their target energy store size; thus, the

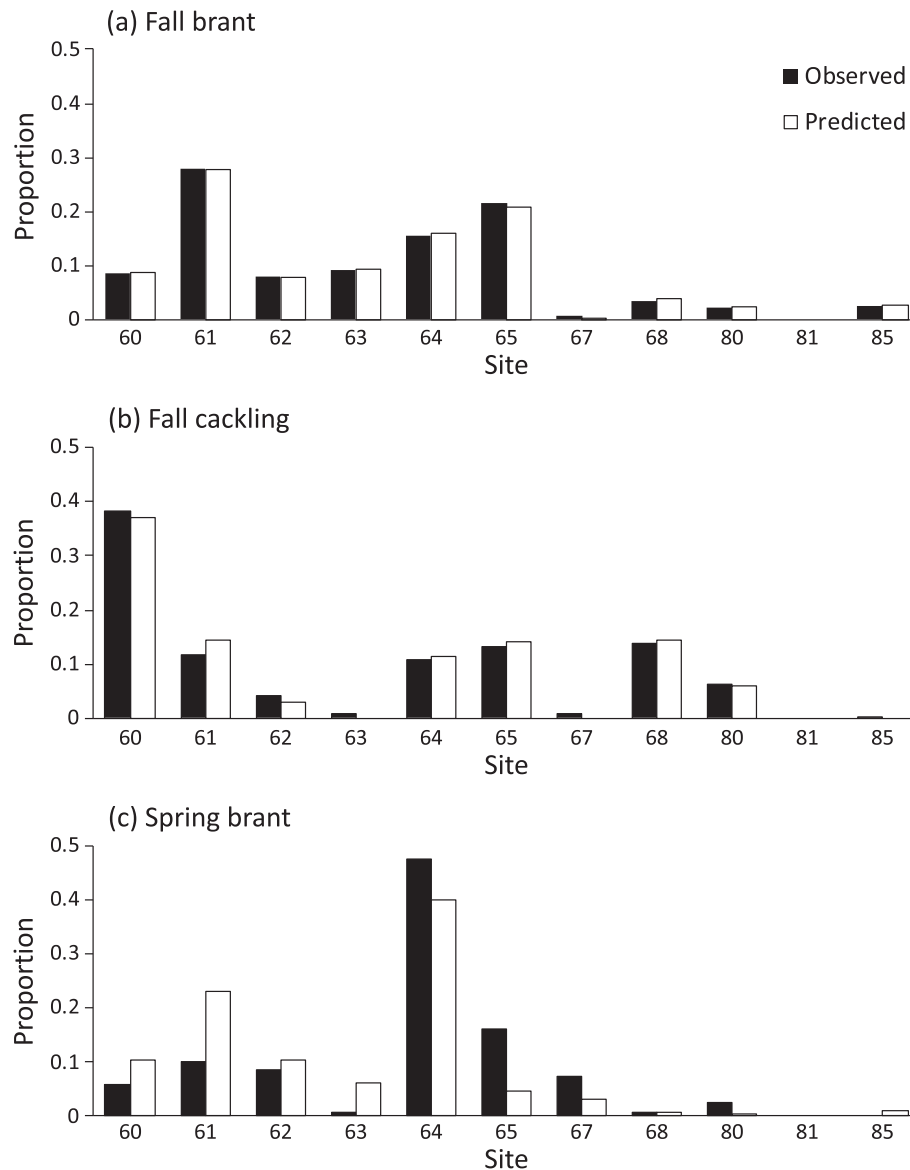


Fig. 4. Predicted (open bars) and observed (black bars) distributions of brant and cackling geese in fall and spring assuming an ice-free winter: (a) brant during fall; (b) cackling geese during fall; (c) brant during spring. The bars show the proportion of the total population within each site. Predictions are the mean of 5 replicate simulations (mean 95% confidence interval of predicted proportion across all sites = 0.006). See Fig. 1 for the distribution of sites.

predicted and observed distribution of geese were similar during this season (i.e., very few geese needed to move from their arrival site; Fig. 4). Similarly, in spring, brant were able to achieve their target energy store size, and the predicted and observed distributions were also similar (Fig. 4).

During winter, even for ice-free winters, brant were not able to maintain their energy store size across sites, and therefore moved between sites, leading to greater deviations between the observed and predicted distributions (Fig. 5). The most consistent deviation was for site 65, which was predicted to hold fewer geese than observed.

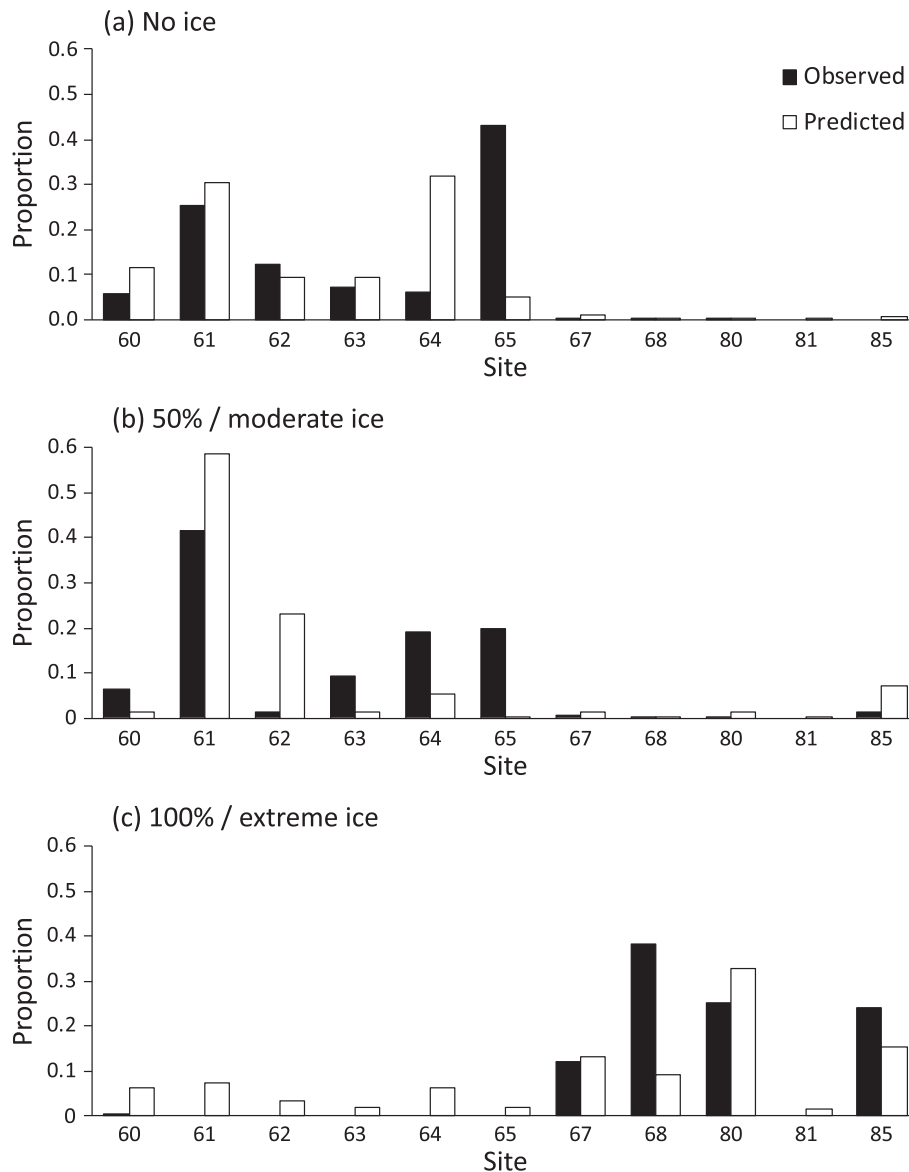


Fig. 5. Predicted (open bars) and observed (black bars) distributions of brant during winter relative to varying ice coverage: (a) no ice; (b) 50%/moderate ice; (c) 100%/extreme ice. For simulations including ice, predictions are for the period of ice coverage, rather than the overall winter period. The bars show the proportion of the total population within each site. Predictions are the mean of 5 replicate simulations (mean 95% confidence interval of predicted proportion across all sites = 0.008). See Fig. 1 for the distribution of sites.

The extent of ice coverage affected both the predicted and observed distribution of brant in winter in broadly similar ways (Fig. 5); when ice coverage was 100%, fewer geese were predicted and observed to occur in Izembek Lagoon. However, there were differences with comparisons made on a site by site basis, with sites 61, 63, 64,

65, and 68 showing the largest differences between predictions and observations.

Depletion of eelgrass

To predict the depletion of eelgrass caused by brant and cackling geese, we ran simulations with either the observed number of geese, or no

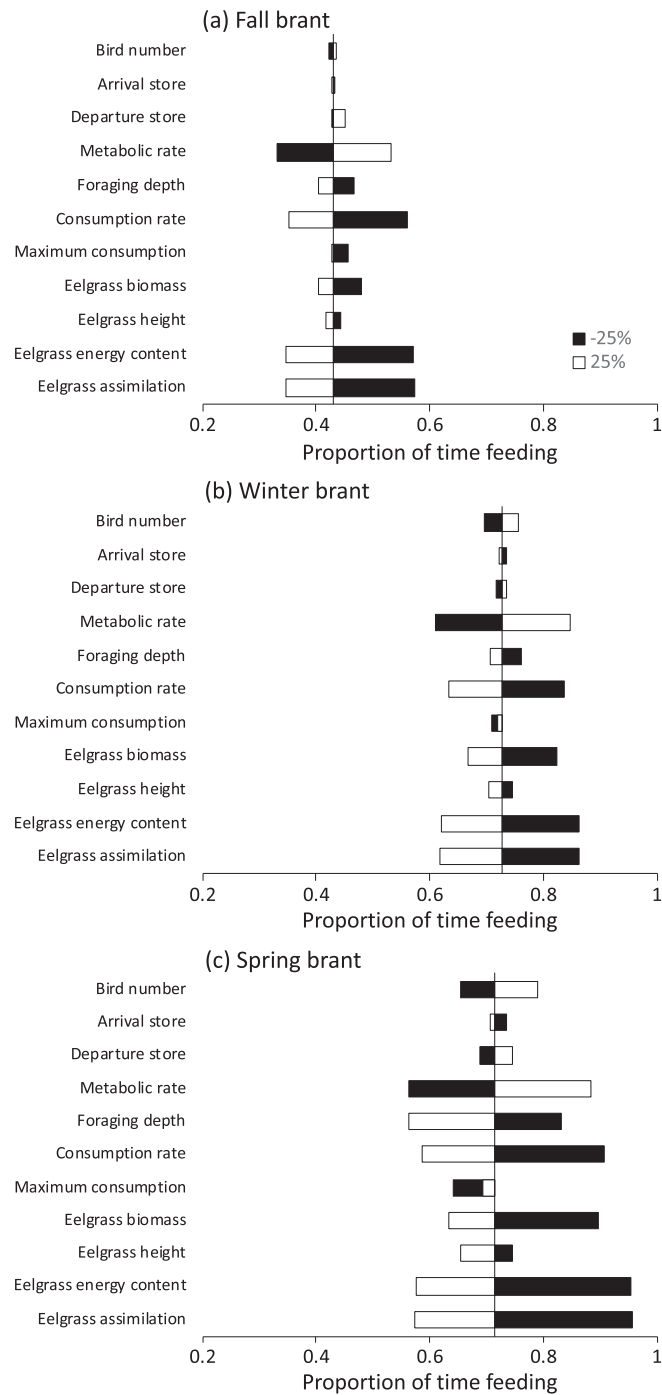


Fig. 6. Predicted effects of $\pm 25\%$ change in key parameters on model predictions of mean proportion of time feeding assuming an ice-free winter: (a) brant during fall; (b) brant during winter; (c) brant during spring. Black bars show predictions when a parameter value was decreased, and open bars show predictions when a parameter value was increased. Bars are shown relative to predictions with the default parameter values. Predictions are the mean of 5 replicate simulations (mean 95% confidence interval of proportion of time feeding across all parameters = 0.004).

geese. We then compared the mean biomass of eelgrass at the end of fall, winter, and spring predicted in these simulations. Mean predicted biomasses across all sites in the presence or absence of geese, respectively, were as follows: start of fall (1 August) 163.3/163.3 g/m²; end of fall (16 December) = 45.3/49.3 g/m²; end of winter (31 March) = 42.8/49.4 g/m²; and end of spring (31 May) = 70.1/83.5 g/m². The geese, therefore, reduced eelgrass biomass by 8%, 13% and 16% in fall, winter, and spring, respectively, with offtake increasing through time due to depletion by geese in earlier seasons.

Model sensitivity analysis

The sensitivity analysis, and all subsequent predictions, was restricted to brant. The predicted proportion of time spent feeding varied with changes in key parameters (Fig. 6). For all seasons, but particularly in spring, the proportion of time spent feeding was most sensitive to variation in parameters directly related to the flow of energy from eelgrass to geese or the energy requirements of geese: increasing with increased metabolic rate, and decreasing with decreased consumption rate, eelgrass energy content, and eelgrass assimilation efficiency. The proportion of time feeding was also relatively sensitive to foraging depth, which determined the proportion of the time for which geese could reach rooted eelgrass, and eelgrass biomass, which determined the total amount of food available and the rate at which geese were able to consume food. Proportion of time spent feeding decreased with increases in either of these parameters. The proportion of time feeding was relatively insensitive to the arrival and departure energy store sizes, the maximum rate at which eelgrass could be consumed and eelgrass height.

Scenario I: changes in eelgrass biomass

Any reduction in eelgrass biomass was predicted to increase the proportion of time spent feeding by brant during all seasons in both the ice-free (Fig. 7a–c) and 50% late ice simulations. A reduction in eelgrass biomass lowered the rate at which geese consumed eelgrass and therefore increased the proportion of time the geese needed to spend feeding to compensate for loss in eelgrass abundance. In both the ice-free and 50% late

ice simulations, a more than 70% reduction in eelgrass biomass reduced the proportion of brant that could successfully emigrate in fall, and a more than 50% reduction in eelgrass biomass reduced the proportion of winter and spring brant that could successfully emigrate in spring (Table 3). In addition, in both the ice-free and 50% late ice simulations, a more than 70% reduction in eelgrass biomass reduced brant survival in fall and spring, and a more than 50% reduction in eelgrass biomass reduced brant survival in winter (Table 3). Emigration and/or survival were reduced when increased feeding time was not sufficient to compensate for the reduction in consumption rate caused by reduced biomass.

Scenario II: changes in the distribution of eelgrass

These simulations restricted eelgrass to Izembek Lagoon (by setting eelgrass biomass in other sites to zero), which reduced the number of sites geese could feed and increased eelgrass depletion. Predicted impacts were largely restricted to overwintering brant and in the minimum biomass simulations (Table 3). Overwintering brant were already in the system at a time when eelgrass biomass was at a minimum, energy demands were greatest and ice coverage could potentially reduce the area available for feeding (especially in Izembek Lagoon). No simulations predicted any effect on the emigration or survival of fall migrants, and none of the mean biomass simulations predicted any impacts on brant during any season. Eelgrass biomass was highest during the fall and in the mean biomass simulations, suggesting that even in the absence of alternative sites to Izembek Lagoon, enough food was available for the geese under these conditions.

Scenario III: changes in goose population size

The mean biomass simulations, for both ice-free and 50% late ice conditions, predicted that the Izembek complex could support at least a doubling of the number of brant and cackling geese or the number of overwintering brant (Table 3). The eelgrass biomass in these simulations was predicted to be sufficient to support the increased population sizes of the geese. Similarly, for fall-staging birds, both the minimum and mean biomass simulations, for both ice-free and 50% late ice conditions, predicted that the complex could support at least a

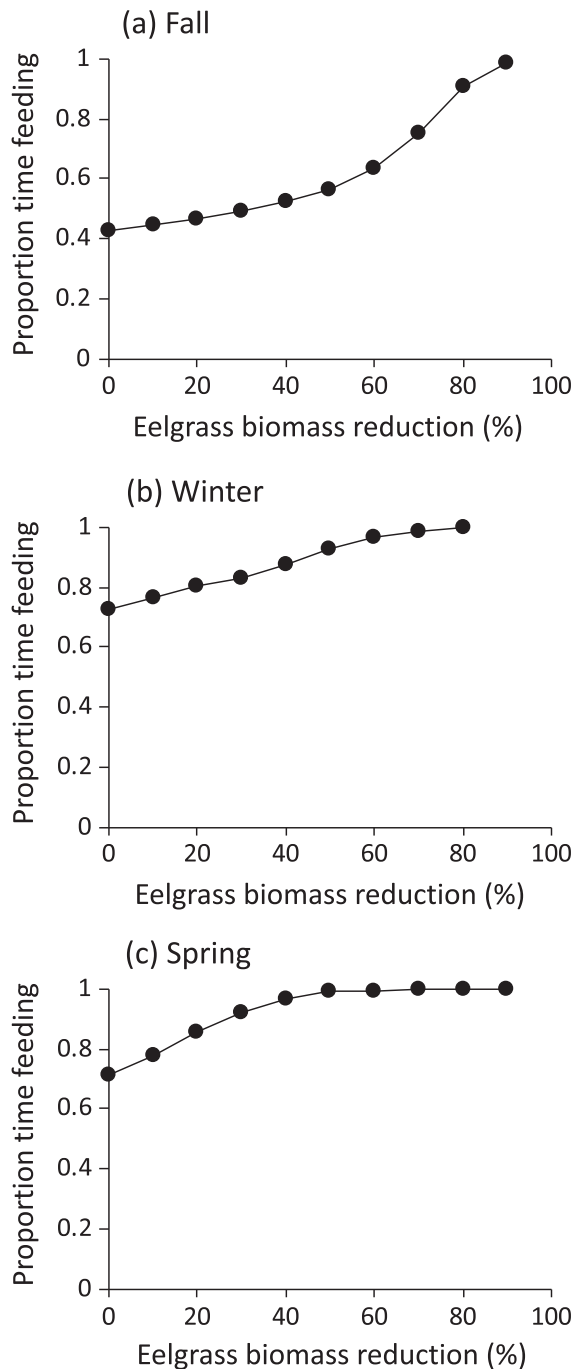


Fig. 7. Predicted effects of percentage reductions in eelgrass biomass from the 2007–2015 decadal mean (i.e., the value used in mean biomass simulations) on brant mean proportion of time spent feeding in fall assuming an ice-free winter: (a) brant during fall; (b) brant during winter; (c) brant during spring. A value of 50% indicates half of the 2007–2015 decadal mean (i.e., the value used in the minimum biomass simulations). Predictions are the mean of 5 replicate simulations (mean 95% confidence interval of proportion of time feeding across all biomasses = 0.003).

biomass simulations predicted that increases in the number of brant and cackling geese, or the number of overwintering brant, could potentially reduce the number of overwintering and spring brant that emigrated and survived, with effects being greatest for overwintering brant (Table 3). The emigration of overwintering brant was reduced with 1.2 times the total number of brant and cackling goose, or 1.4 times the number of overwintering brant (Table 3). Overwintering birds were more affected by increased population size because during winter, eelgrass biomass was at a minimum, the energy demands of the geese were at a maximum and feeding habitat could be lost due to ice coverage, meaning that the food supply was insufficient to support goose populations much greater than those currently observed. The emigration of spring migrant brant could potentially be affected by increases in the number of overwintering brant due to increased depletion of eelgrass (Table 3). The size of effect tended to be greater if the increased number of brant survived winter (as depletion was greater), and relatively less if this was not the case. Up to a doubling of the number of cackling goose alone was not predicted to affect the emigration or survival of brant in any simulation (Table 3). The default population size of cackling geese in the model was much smaller than the population size of brant and cackling geese combined, meaning that increased depletion (and hence potential for effects on emigration or survival) due to increases in the number of cackling geese alone was much smaller.

Scenario IV: changes in the coverage and timing of ice

The mean biomass simulations predicted that the presence of ice had no effect on the survival

doubling of the number of brant and cackling geese (Table 3). Eelgrass biomass was greatest during this period, and overall depletion with the default number of geese was lowest; hence, there was sufficient food to support a larger population of geese and birds could successfully gain mass to migrate. In contrast, the minimum

Table 3. Predicted effect of simulated change scenarios on brant emigration and survival during fall, winter, and spring.

Change simulated	Eelgrass biomass†	Ice cover‡	Fall brant		Winter brant		Spring brant	
			Emig.	Surv.	Emig.	Surv.	Emig.	Surv.
Percentage reduction of eelgrass biomass		Ice-free	-80%	-80%	-60%	-70%	-60%	-80%
		50% late	-80%	-80%	-60%	-60%	-70%	-80%
Eelgrass removed from all sites except Izembek Lagoon§	Mean	Ice-free	No	No	No	No	No	No
	Mean	50% late	No	No	No	No	No	No
	Minimum	Ice-free	No	No	Yes	No	Yes	No
	Minimum	50% late	No	No	Yes	Yes	No	No
Relative increase in brant and cackling goose population sizes	Mean	Ice-free	>2x	>2x	>2x	>2x	>2x	>2x
	Mean	50% late	>2x	>2x	>2x	>2x	>2x	>2x
	Minimum	Ice-free	>2x	>2x	1.4x	1.6x	>2x	>2x
	Minimum	50% late	>2x	>2x	1.2x	1.4x	1.2x	>2x
Relative increase in overwintering brant population size	Mean	Ice-free	>2x	>2x	>2x	>2x	>2x	>2x
	Mean	50% late	>2x	>2x	>2x	>2x	>2x	>2x
	Minimum	Ice-free	>2x	>2x	1.6x	2x	1.6x	>2x
	Minimum	50% late	>2x	>2x	1.4x	1.6x	>2x	>2x
Relative increase in cackling goose population size	Mean	Ice-free	>2x	>2x	>2x	>2x	>2x	>2x
	Mean	50% late	>2x	>2x	>2x	>2x	>2x	>2x
	Minimum	Ice-free	>2x	>2x	>2x	>2x	>2x	>2x
	Minimum	50% late	>2x	>2x	>2x	>2x	>2x	>2x
Izembek percentage early-winter ice cover¶	Mean		No	No	No	No	No	No
	Minimum		No	No	100%	100%	No	No
Izembek percentage mid-winter ice cover¶	Mean		No	No	No	No	No	No
	Minimum		No	No	100%	100%	No	No
Izembek percentage late-winter ice cover¶	Mean		No	No	No	No	No	No
	Minimum		No	No	100%	100%	No	No
Izembek percentage all-winter ice cover¶	Mean		No	No	100%	100%	No	No
	Minimum		No	No	50%	50%	No	No
Relative increase in disturbance from both human and natural sources	Mean	Ice-free	>5x	>5x	>5x	>5x	>5x	>5x
	Mean	50% late	>5x	>5x	>5x	>5x	>5x	>5x
	Minimum	Ice-free	>5x	>5x	4x	>5x	4x	>5x
	Minimum	50% late	>5x	>5x	3x	5x	4x	>5x
Relative increase in disturbance from humans alone	Mean	Ice-free	>5x	>5x	>5x	>5x	>5x	>5x
	Mean	50% late	>5x	>5x	>5x	>5x	>5x	>5x
	Minimum	Ice-free	>5x	>5x	>5x	>5x	>5x	>5x
	Minimum	50% late	>5x	>5x	>5x	>5x	>5x	>5x

Notes: Predicted effects (i.e., emigration or survival below 100%) are shown in bold with numeric values indicating the percentage or rate when emigration and survival would be affected. Non-bold values show the maximum amount of change that did not have an effect or if the change did not have an effect (i.e., emigration or survival remained at 100%).

† Indicates whether predictions are for mean or minimum biomass simulations.

‡ Indicates whether predictions are for ice-free or 50% late ice simulations.

§ "No" indicates no effect on emigration or survival of removing eelgrass from all sites except Izembek Lagoon.

¶ "No" indicates no effect on emigration or survival within simulated range of ice coverage (i.e., ice coverage at sites other than Izembek Lagoon would need to exceed that simulated when Izembek Lagoon had 100% ice coverage).

or emigration of brant, irrespective of the amount of ice coverage and timing of ice, unless 100% ice occurred throughout winter, in which case emigration and survival of overwintering brant were zero (Table 3). The minimum biomass simulations predicted that the presence of ice increased the rate of body mass loss of geese over winter compared to simulations in which ice was absent

(Fig. 8). The rate of body mass loss was greatest in simulations of 100% ice cover of Izembek Lagoon, and for these simulations, the model also predicted that no brant would be able to survive the winter (Table 3). Additionally, no geese were predicted to survive if 50% ice occurred throughout winter (Table 3). The rate of mass loss was measured from the start of winter, until either the

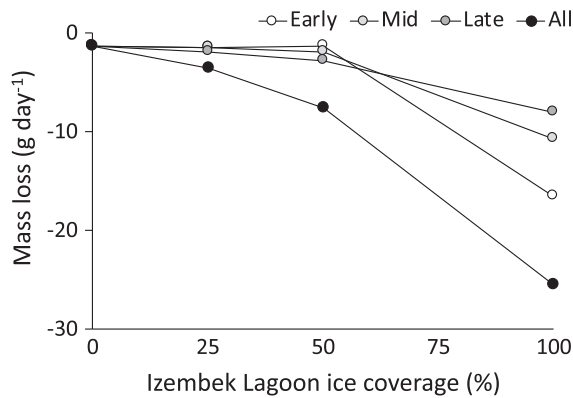


Fig. 8. Predicted effects of changes in ice coverage on the rate of mass loss of brant during winter derived from the minimum biomass simulations (i.e., biomass 50% of the current, 2007–2015, decadal mean). For each goose, the rate of mass loss was measured from the start of winter until either the end of winter or the time step on which the geese starve. Symbol shading shows the timing of ice (see Table 1a and text for more details). Predictions are the mean of 5 replicate simulations (mean 95% confidence interval of mass loss across all ice combinations = 0.175).

end of winter, or until a goose died. With 100% ice, all geese died during the winter, and so the rate of mass loss was measured from the start of winter until a goose died. In this case, the rate of mass loss was lower when ice occurred later in winter because it was measured incorporating a longer period of ice-free conditions (Fig. 8).

Scenario V: changes in disturbance

Disturbance increased the energy demands of model geese and reduced their time available for feeding, and so could potentially reduce their net rate of gaining energy to the point at which emigration or survival would be reduced. The mean biomass simulations predicted that increased disturbance up to five times of the default rate had no effect on the survival or emigration of brant (Table 3). The minimum biomass simulations, for both ice-free and 50% late ice, predicted that the proportion of time spent feeding increased as the combined rate of natural and human disturbances increased (Fig. 9). In these simulations, the emigration or survival of overwintering and fall migrant brant were predicted to be reduced by increases in the combined rate of human and natural disturbance of 1.3 times or more

(Table 3), whereas no effects on emigration or survival were predicted for fall migrants with increases of up to 5 times the default rate (Table 3). Increases in the disturbance rate from humans alone of up to five times the default rate were not predicted to reduce survival or emigration in any simulation (Table 3). During simulations, the model assumed that natural disturbance occurred throughout the study site, whereas human disturbance was restricted to current access points and close to the shore.

DISCUSSION

In this paper, we used a process-based model for a migratory goose species, black brant, at a critically important staging site, to assess the likely effects of changes in eelgrass food abundance and availability, winter ice coverage, and disturbance, on the ability of the site to support this species. These findings were then validated against a range of observations from the real system.

Overall, there was a relatively close match between the model predictions and observations from the study system. Therefore, the model contained appropriate parameters, which could accurately predict observed goose behavior, making it a practically applicable model for predicting responses to future scenarios of environmental change. As with any model, some simplifying assumptions were required to make the model tractable, given the availability of suitable data on which to base assumptions and parameters, and the complexity and size of the real system. Furthermore, we decided to only include processes and parameters if their values could be estimated from observed data, rather than including parameters that needed to be calibrated. For example, the model assumed that eelgrass was upright in the water column, whereas, in reality, it will be curved at times due to water currents, meaning that it would be slightly less available to the geese. In contrast, the model assumed that food was evenly distributed and available within 1-km² patches, whereas, in reality, geese will forage at a finer scale and will be able to find areas of higher biomass or increased availability than assumed. It was not practical, due to the time taken to run simulations, to

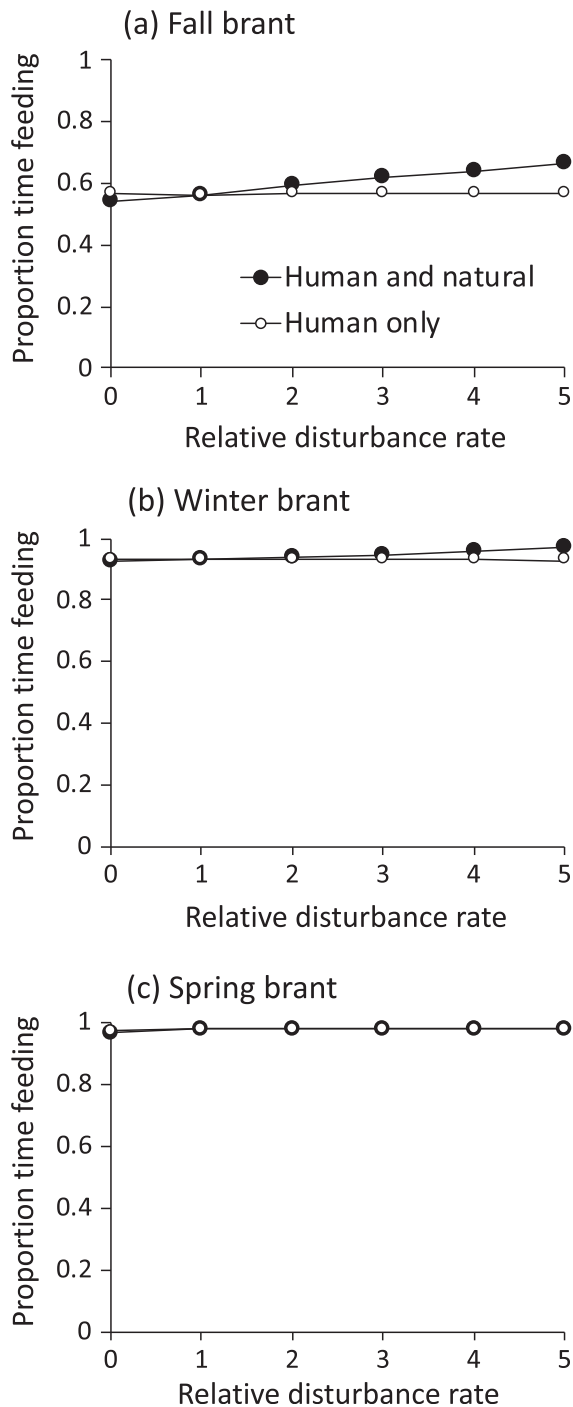


Fig. 9. Predicted effects of changes in disturbance rate on the mean proportion of time spent feeding derived from the minimum biomass simulations (i.e., biomass 50% of the current, 2007–2015, decadal mean) under 50% late ice conditions. A relative disturbance rate of 1 was used in the default simulations. Relative disturbance rates above 1 indicate an increase in disturbance rate (up to five times), and a value of 0 indicates the absence of disturbance. Solid symbols represent changes in the rate of both human and natural disturbance, and open symbols represent changes in the rate of human disturbance alone. Predictions are the mean of 5 replicate simulations (mean 95% confidence interval of proportion of time feeding across all disturbances = 0.002).

traditional use of sites, time, and energy costs of travel between patches, which may account for differences in the detail of patches used in the model. Again, due to time constraints, the model simulated flocks of geese rather than individual geese, but its predictions were not sensitive to changes in flock size from 1000 to 100. The model did not include Sanak and Caton islands, 100 km south of the complex in the Gulf of Alaska, which contain some eelgrass beds, used by some brant temporarily, especially during periods of ice coverage during winter (Wilson and Larned 2020). These islands were not included due to uncertainties in the decision rules birds would use in moving to and returning from them, and as the purpose of the study was to assess the value of the Izembek complex for the geese. Despite such simplifying assumptions, the model still accurately predicted observations from the real system. Especially, important was the accuracy with which the model predicted the proportion of time spent feeding by the geese, meaning that model geese were having a similar amount of difficulty meeting their requirements than the real geese were, and so both model and real geese would have similar abilities to adapt to environmental change.

The minimum biomass simulations accounted for the fact that even though there has not been a systematic decline in eelgrass biomass, there is still considerable year to year variation, with the minimum over this period about 50% of the mean (Ward and Amundson 2019). Our predictions showed that the survival and emigration of

include a smaller patch size within the model, given the overall size of the study area, and the spatial scale of the eelgrass survey data. Furthermore, patch usage by real geese depends on several factors not included in the model, including small-scale variation in predation risk, or

the geese was much more sensitive to environmental change in simulations assuming a lower eelgrass biomass. In contrast, the extent of environmental changes modeled had little effect on the birds in simulations assuming the higher eelgrass biomass, even if 50% ice coverage was assumed. We did not use higher ice coverage in these simulations, as the model predicted that 100% ice coverage would cause geese to die even in the absence of other types of change. The higher eelgrass biomass, in effect, buffered the birds against environmental change, as they had a greater capacity to compensate as they could consume food at a greater rate than when a lower eelgrass biomass was assumed.

The predicted proportion of time feeding, and probability of emigration and survival, were sensitive to changes in eelgrass aboveground biomass across the Izembek complex. Therefore, geese were vulnerable to any reduction in biomass below the decadal minimum, especially if change occurs within the winter or spring and is widespread throughout the Izembek complex. Dramatic losses of eelgrass in the Atlantic in the early 1930s caused the population collapse (~90%) of Atlantic light-bellied brant in North America, and dark-bellied brant geese in Europe (Ganter 2000), demonstrating their extreme sensitivity to losses of this target forage source. The observed global declines in eelgrass populations (Waycott et al. 2009), especially those in the north Pacific (Mexico, Ward et al. 2003, Muñiz-Salazar et al. 2006; California, Merkel 2015, Merkel and Gilkerson 2017; Alaska, Harris et al. 2012), represent a substantial threat to brant and other waterfowl that are obligate grazers of eelgrass or foods associated with eelgrass communities (e.g., fish, invertebrates, seaweeds). Ongoing monitoring of eelgrass within the study system (e.g., Ward and Amundson 2019) is important to identify potential threats (e.g., disease, invasive species) and early signs of eelgrass reduction, or to identify years of especially low eelgrass biomass.

We show that at the lower end of current levels of eelgrass biomass (i.e., 50% of the decade mean), a number of environmental changes could reduce the number of brant that could successfully migrate through the Izembek complex in winter and spring. Reduced eelgrass abundance in the Izembek complex has implications for breeding propensity, reproductive success and survival of brant (Sedinger et al. 2006, 2011,

Schamber et al. 2012), given the importance of this site as a final staging site before arrival on the breeding grounds for most of the Pacific Flyway population of brant (Lewis et al. 2013). Indeed, the variation in eelgrass abundance in Izembek Lagoon may be an important driver of current negative trends in range-wide rates of survival for both juveniles and adults (Sedinger and Nicolai 2011, Leach et al. 2017), and annual productivity of the brant population (Ward et al. 2018).

The model predicted that access to eelgrass in lagoons other than in Izembek Lagoon itself was critical for the overwinter survival and spring migration of brant. This was driven by the depletion of eelgrass in the fall by brant and cackling geese that mainly concentrate within Izembek Lagoon, and thus, a lower starting eelgrass biomass for overwintering brant and migrant brant arriving in spring than was available in the fall. In the Izembek complex, brant have few options to forage on alternative sources of food, such as green algae (e.g., *Ulva* spp.), other seagrasses (e.g., *Ruppia maritima*, *Phyllospadix* spp.) or salt marsh plants (e.g., *Triglochin maritima*), which brant may eat during eelgrass shortages in other parts of their wintering range (Moore et al. 2004, Ward et al. 2005). These alternative foods are scarce at the end of the Alaska Peninsula, and when present, occur in very low abundance (Hogrefe et al. 2014). In addition, there are few alternative sites containing ice-free eelgrass close to the Izembek complex should feeding conditions deteriorate for brant. The closest of these sites are the Sanak and Caton islands that are used by some brant during high ice winters (Wilson et al. 2017a). The next closest suitable sites are >500 km away. Therefore, any factors that reduce the biomass of eelgrass throughout the Izembek complex or prevent birds access to non-Izembek lagoons in the fall, could adversely affect the ability of brant to survive the winter, or migrate in the spring. This highlights the need to protect the network of feeding sites, rather than focusing purely on the main site.

Under the mean biomass simulations, brant were predicted to still successfully emigrate in fall with up to a doubling of population size. The abundance of eelgrass was greater in the fall than in other seasons and so could support a higher

number of both brant and cackling geese. In contrast, the minimum biomass simulations predicted that relatively small increases in population size of brant during the winter could reduce the number of brant that could be supported. A similar model of brant at another site on the Pacific flyway (Humboldt Bay, California, USA) predicted that the food supply was sufficient to support more than doubling of goose population size (Stillman et al. 2015). Clearly, different sites along the migratory pathway may vary in the number of geese that they may support in the future, and the ability of a site to support geese may also vary seasonally.

Frozen sea conditions can occur frequently within the study system and effectively reduce the amount of habitat available to the geese. Although global warming may eventually reduce the frequency of these events, some of the most extreme winters have occurred in recent years (Petrich et al. 2014, Wilson 2017a, Wilson and Larned 2020). Importantly, some access to alternative eelgrass meadows is available to geese when this habitat is inaccessible in Izembek Lagoon. The minimum biomass simulations predicted that in all but the most extreme simulations geese could survive frozen conditions by redistributing to other locations in or near the Izembek complex. Minimum biomass simulations of 100% ice cover in Izembek Lagoon indicated that geese would not be able to survive winter, due to a combination of food shortage and increased energy demands. Observations show that the real geese have been able to survive severe ice conditions, by temporally redistributing themselves to ice-free locations (Wilson 2017a, Wilson and Larned 2020), and in extreme situations, reducing the proportion of time spent feeding to minimize energy expenditure (Daniels et al. 2019). However, the model still predicts that 100% ice conditions, and its resulting reduced eelgrass biomass, poses a threat to the brant population. We think this prediction is reasonable given that in 2012 when 100% ice conditions occurred throughout winter and annual eelgrass biomass was among the lowest (Ward and Amundson 2019), brant productivity was 13%, half of the 53-yr mean and one of the lowest estimates ever recorded (Ward et al. 2018).

Brant are highly susceptible to adverse effects of disturbances, and particularly to eagles, boats and hunting (Kramer et al. 1979, Ward et al.

1994, Moore and Black 2006), which currently account for most disturbances in the Izembek complex (Daniels et al. 2019; P. Fitzmorris, U.S. Fish Wildlife Service, Izembek National Wildlife Refuge, *personal communication*). Rates of disturbances are relatively low in the Izembek complex, averaging less than one event per hour. But despite these low levels, the minimum biomass simulations predicted that increases in the combined rate of human and natural disturbances increased the proportion of time geese spent feeding and could prevent birds from emigrating. Brant are spending all or nearly all of their time feeding during these seasons and are therefore unable to compensate for lost foraging opportunities and increased energy expenditure (flight) by increasing rates of food intake. Increases in human population size and ability to access remote areas are bringing humans into more contact with wildlife in the area, increasing the chances that disturbance from human activities may be detrimental (Dickman 2010, Barua et al. 2013). The primary sources of disturbance in the study system were from either land- or boat-based hunting, and from bald eagles. Currently, both types of human disturbance occur within a few km of the shoreline, and hence geese are not subject to hunting in the majority of the Izembek complex. Disturbance was also restricted to daylight, allowing geese to potentially feed without disturbance at night. The present-day distribution of human disturbance is more restricted in extent than natural disturbance, and increases in the amount of human disturbance alone were not predicted to affect the probability of emigration. However, this assumes that the area over which disturbance occurs does not change, and the simulations including natural disturbance show that the geese may be vulnerable to increases in the area over which disturbance occurs. Indeed, there are indications that hunting disturbances are on the rise and more widespread in the Izembek complex given the 3- to 4-fold increase in recoveries of brant bands in the complex in recent years (Leach et al. 2019) and updated disturbance data are needed to more accurately assess its effects on brant in the complex.

Our study has highlighted the potential vulnerability of brant to combinations of low eelgrass biomass and natural and anthropogenic

environmental change while highlighting knowledge gaps that could be targeted by future research. For example, we assumed that a fixed number of brant would migrate south from the system in fall, but in reality, geese may be using eelgrass biomass, or a correlate of this, such as changes in the position of low pressure systems that reduce the frequency and strength of south-driven tailwinds (Purcell and Brodin 2007, Ward et al. 2009), as a cue for migration. This could mean that birds only migrate away from the site in years of lower eelgrass biomass, avoiding the risk of overwintering when eelgrass biomass is low. Even if such a pattern is not detected from current empirical data, it may be a pattern that emerges through time, as there would be a strong evolutionary selection pressure favoring individuals that only overwintered in years when eelgrass abundance was high. Incorporating such long-distance migration decisions and their evolutionary basis and consequences in the face of environmental change would be a logical next step in the construction of a flyway-wide model of the brant population.

ACKNOWLEDGMENTS

We are very grateful to Rick McKinney for his advice on the modeling of wildfowl energetics, D. Damberg, N. Hoffman, L. Melendez, and G. Risdahl, Izembek National Wildlife Refuge, for their support of the project, and C. Amundson, T. Lewis, and J. Pearce for reviews of earlier drafts of the manuscript. This study was funded by the U.S. Geological Survey and the U.S. Fish and Wildlife Service, Izembek National Wildlife Refuge. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Baldassarre, G. A. 2014. Ducks, Geese and Swans of North America. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Barua, M., S. A. Bhagwat, and S. Jadhav. 2013. The hidden dimensions of human-wildlife conflict: health impacts, opportunity and transaction costs. *Biological Conservation* 157:309–316.
- Bearhop, S., W. Fiedler, R. W. Furness, S. C. Votier, S. Waldron, J. Newton, G. J. Bowen, P. Berthold, and K. Farnsworth. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* 310:502–504.
- Berthold, P., A. J. Helbig, G. Mohr, and U. Querner. 1992. Rapid microevolution of migratory behavior in a wild bird species. *Nature* 360: 668–670.
- Bruinzeel, L. W., M. R. van Eerden, R. H. Drent, and J. T. Vulink. 1997. Scaling metabolizable energy intake and daily energy expenditure in relation to the size of herbivorous waterfowl: Limits set by available foraging time and digestive performance. Pages 111–132 in M. R. van Eerden, editor. *Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands*. Ministerie van Verkeer en Waterstaat, Directoraat-Generaal Rijkswaterstaat, Directie IJsselmergebied, Lelystad, The Netherlands.
- Cai, W., et al. 2015. ENSO and greenhouse warming. *Nature Climate Change* 5:849–859.
- Camphuysen, C. J., et al. 2002. Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. *Biological Conservation* 106:303–317.
- Chen, I., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Clausen, K. K. 2013. Climate change impacts on coastal herbivorous waterbirds. PhD thesis. Aarhus University, Aarhus, Denmark.
- Clausen, P. 1994. Waterfowl as primary consumers in shallow water fiord areas. Dissertation. University of Aarhus/National Environmental Research Institute, Aarhus, Denmark.
- Clausen, P. 1997. Dark-Bellied Brent Geese *Branta b. bernicla* use of the White Sea. A progress report. Pages 174–183 in J. van Nugteren, editor. *Dark-Bellied Brent Goose Branta bernicla bernicla Flyway Management Plan*. Dutch Society for the Preservation of the Wadden Sea, The Netherlands.
- Clausen, P. 1998. Choosing between feeding on Zostera and Salt Marsh: factors affecting habitat use by Brent geese in spring. *Norsk Polarinstitutt Skrifter* 200:269–286.
- Clausen, P. 2000. Modelling water level Influence on habitat choice and Food Availability for Zostera Feeding Brent Geese *Branta bernicla* in Non-Tidal Areas. *Wildlife Biology* 6:75–87.
- Clausen, P., M. Frederiksen, S. M. Percival, G. Q. A. Anderson, and M. J. H. Denny. 2001. Seasonal and annual survival of East-Atlantic pale-bellied brent geese *Branta bernicla hrota* assessed by capture-recapture analysis. *Ardea* 89:101–112.
- Daniels, B. L. 2014. Activity budgets and daily energy expenditure of Black brant (*Branta bernicla nigricans*) during winter and spring along the Alaskan

- Peninsula. Thesis. Humboldt State University, Arcata, California, USA.
- Daniels, B. L., D. H. Ward, and J. M. Black. 2019. Activity budgets, daily energy expenditure and energetic model of Black Brant *Branta bernicla nigricans* during winter and spring along the Lower Alaska Peninsula. *Wildfowl* 69:134–159.
- Dau, C. P. 1992. The fall migration of Pacific Flyway Brent *Branta bernicla* in relation to climatic conditions. *Wildfowl* 43:80–95.
- Delacour, J. 1951. Preliminary note on the taxonomy of Canada Geese, *Branta canadensis*. *American Museum Novitates* 1537:1–10.
- Desmouts, D., H. Fritz, T. Cornulier, and R. Maheo. 2009. Rise in human activities on the mudflats and Brent Geese (*Branta bernicla*) wintering distribution in relation to *Zostera* spp. beds: a 30-year study. *Journal of Ornithology* 150:733–742.
- Dickman, A. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation* 13:458–466.
- Elkinton, E., L. Lo, and J. M. Black. 2013. Black brant *Branta bernicla nigricans* forage at both tides on Humboldt Bay, California, USA. *Wildfowl Special Issue* 3:90–103.
- Environmental Protection Agency (EPA). 2016. Climate Change Indicators: Weather and Climate. <https://www.epa.gov/climate-indicators/weather-climate>
- Ganter, B. 2000. Seagrass (*Zostera* spp.) as food for brent geese (*Branta bernicla*): an overview. *Helgoland Marine Research* 54:63–70.
- Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioral responses may not reflect the population consequences of human disturbance. *Biological Conservation* 97:265–268.
- Gudmundsson, G., S. Benvenuti, T. Alerstam, E. Papi, K. Lilliendahl, and S. Akesson. 1995. Examining the limits of flight and orientation performance: satellite tracking of Brent Geese migrating across the Greenland icecap. *Proceedings of the Royal Society London* 261:73–79.
- Harris, P. M., A. D. Neff, and S. W. Johnson. 2012. Changes in eelgrass habitat and faunal assemblages associated with coastal development in Juneau, Alaska. National Oceanic and Atmospheric Administration Technical Report, NMFS-AFSC-240.
- Hitch, A. T., and P. L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* 21:534–539.
- Hogrefe, K. R., D. H. Ward, T. F. Donnelly, and N. Dau. 2014. Establishing a Baseline for Regional Scale Monitoring of Eelgrass (*Zostera marina*) Habitat on the Lower Alaska Peninsula. *Remote Sensing* 6:12447.
- Hupp, J. W., D. E. Safine, and R. M. Nielson. 2013. Response of cackling geese (*Branta hutchinsii taverneri*) to spatial and temporal variation in the production of crowberries on the Alaska Peninsula. *Polar Biology* 36:1243–1255.
- Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94:234–242.
- Jenssen, B. M., M. Ekker, and C. Bech. 1989. Thermoregulation in winter acclimatized common eiders (*Somateria mollissima*) in air and water. *Canadian Journal of Zoology* 67:669–673.
- Kirby, R. E., and H. H. III Obrecht. 1982. Recent changes in the North American distribution and abundance of wintering Atlantic Brant. *Journal of Field Ornithology* 53:333–341.
- Kirkwood, J. K. 1983. A limit to metabolizable energy intake in mammals and birds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 75:1–3.
- Klaassen, M. 1996. Metabolic constraints on long-distance migration in birds. *Journal of Experimental Biology* 199:57–64.
- Kramer, G. W., L. R. Rauen, and S. W. Harris. 1979. Populations, hunting, mortality, and habitat use of black brant at San Quintin Bay, Baja California, Mexico. Pages 242–254 in R. L. Jarvis and J. C. Bartonek, editors. *Management and biology of the Pacific Flyway geese: symposium*. Oregon State University Book Store, Corvallis, Oregon, USA.
- La Sorte, F. A., and F. R. III Thompson. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88:1803–1812.
- Lawrence, G. N. 1846. Description of a new species of Anser. *Annals of the Lyceum of Natural History of New York* 4:171–172.
- Leach, A. G., D. H. Ward, J. S. Sedinger, M. S. Lindberg, W. S. Boyd, J. W. Hupp, and R. J. Ritchie. 2017. Declining survival of black brant from subarctic and arctic breeding areas. *Journal of Wildlife Management* 81:1210–1218.
- Leach, A. G., D. H. Ward, J. S. Sedinger, T. V. Reicke, J. W. Hupp, and R. J. Ritchie. 2019. Spatial distribution of band recoveries of black brant. *Journal of Wildlife Management* 83:304–311.
- Lehikoinen, A., et al. 2013. Rapid climate driven shifts in wintering distribution of three common waterbird species. *Global Change Biology* 19:2071–2081.
- Lewis, T. L., D. H. Ward, J. S. Sedinger, A. Reed, and D. V. Derksen. 2013. Brant (*Branta bernicla*). Account 337. In P. G. Rodewald, editor. *The birds*

- of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Madsen, J. 1995. Impacts of disturbance on migratory waterfowl. *Ibis* 137:S67–S74.
- Mason, D. D., P. S. Barboza, and D. H. Ward. 2006. Nutritional condition of Pacific Black Brant wintering at the extremes of their range. *Condor* 108: 678–690.
- Mason, D. D., P. S. Barboza, and D. H. Ward. 2007. Mass dynamics of wintering Pacific Black Brant: Body, adipose tissue, organ, and muscle masses vary with location. *Canadian Journal of Zoology* 85:728–736.
- Merkel, K. 2015. San Francisco Bay eelgrass inventory October–November 2014. Report submitted to National Marine Fisheries Service.
- Merkel, K., and W. Gilkerson. 2017. Morro Bay comprehensive bay-wide eelgrass inventory. Report submitted to Morro Bay National Estuary Program.
- Mini, A. E., and J. M. Black. 2009. Expensive traditions: energy expenditure of Aleutian geese in traditional and recently colonized habitats. *Journal of Wildlife Management* 73:385–391.
- Moore, J. E. 2002. Distribution of spring staging black brant *Branta bernicla nigricans* in relation to feeding opportunities on south Humboldt Bay, California. Thesis. Humboldt State University, Arcata, California, USA.
- Moore, J. E., and J. M. Black. 2006. Historical changes in black brant *Branta bernicla nigricans* use on Humboldt Bay, California. *Wildlife Biology* 12:2.
- Moore, J. E., M. A. Colwell, R. L. Mathis, and J. M. Black. 2004. Staging of Pacific flyway Brant in relation to eelgrass abundance and site isolation, with special consideration of Humboldt Bay, California. *Biological Conservation* 115:475–486.
- Muñiz-Salazar, R., S. L. Talbot, G. K. Sage, D. H. Ward, and A. Cabello-Pasini. 2006. Genetic structure of eelgrass *Zostera marina* meadows in an embayment with restricted water flow. *Marine Ecology Series* 309:107–116.
- Nolet, B. A., A. Kölzsch, M. Elderenbosch, and A. J. van Noordwijk. 2016. Scaring waterfowl as a management tool: How much more do geese forage after disturbance? *Journal of Applied Ecology* 53:1413–1421.
- Nudds, R. L., and D. M. Bryant. 2000. The energetic cost of short flights in birds. *Journal of Experimental Biology* 203:1561–1572.
- Petrich, C., A. C. Tivy, and D. H. Ward. 2014. Reconstruction of historic sea ice conditions in a sub-Arctic lagoon. *Cold Regions Science and Technology* 98:55–62.
- Prop, J., and C. Deerenberg. 1991. Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87:19–28.
- Purcell, J., and A. Brodin. 2007. Factors influencing route choice by avian migrants: a dynamic programming model of Pacific Brant migration. *Journal of Theoretical Biology* 249:804–816.
- Reed, A., R. Stehn, and D. Ward. 1989. Autumn use of Izembek Lagoon, Alaska, by Brant from different breeding areas. *Journal of Wildlife Management* 53:720–725.
- Riddington, R., M. Hassall, S. J. Lane, P. A. Turner, and R. Walters. 1996. The impact of disturbance on the behavior and energy budgets of Brent Geese *Branta b. bernicla*. *Bird Study* 43:269–279.
- Root, T. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69:330–339.
- Rudolf, V. H. W. 2019. The role of seasonal timing and phenological shifts for species coexistence. *Ecology Letters* 22:1324–1338.
- Ruesink, J. L., J. S. Hong, L. M. Wisehart, S. D. Hacker, B. R. Dumbauld, M. Hessing-Lewis, and A. C. Trimble. 2010. Congener comparison of native (*Zostera marina*) and introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific Northwest estuary. *Biological Invasions* 12:1773–1789.
- Schamber, J. L., J. S. Sedinger, and D. H. Ward. 2012. Carry-over effects of winter location contribute to variation in timing of nest initiation and clutch size in Black Brant (*Branta bernicla nigricans*). *Auk: Ornithological Advances* 129:205–210.
- Sedinger, J. S., C. J. Lensink, D. H. Ward, R. M. Anthony, M. L. Wege, and G. V. Byrd. 1993. Current status and recent dynamics of the black Brant breeding population. *Wildfowl* 44:49–59.
- Sedinger, J. S., and C. A. Nicolai. 2011. Recent trends in first-year survival for black Brant breeding in southwestern Alaska. *Condor* 113:511–517.
- Sedinger, J. S., D. H. Ward, C. A. Nicolai, and B. Conant. 2011. Carryover effects associated with winter location affect fitness, social status, and population dynamics in a long-distance migrant. *American Naturalist* 178:E110–E123.
- Sedinger, J. S., D. H. Ward, J. L. Chamber, W. I. Butler, W. D. Eldridge, B. Conant, J. F. Voelzer, N. D. Chelgren, and M. P. Herzog. 2006. Effects of El Niño on distribution and reproductive performance of Black Brant. *Ecology* 87:151–159.
- Stillman, R. A. 2008. MORPH: an individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling* 216:265–276.
- Stillman, R. A., K. A. Wood, W. Gilkerson, E. Elkinton, J. M. Black, D. H. Ward, and M. Petrie. 2015. Predicting effects of environmental change on a migratory herbivore. *Ecosphere* 6:114.

- Stock, M. 1993. Studies on the effects of disturbances on staging Brent geese: a progress report. *Wader Study Group Bulletin* 68:29–35.
- Suter, W., and M. R. Van Eerden. 1992. Simultaneous mass starvation of wintering diving ducks in Switzerland and the Netherlands: A wrong decision in the right strategy? *Ardea* 80:229–242.
- Swanson, D. L. 2010. Seasonal metabolic variation in birds: Functional and mechanistic correlates. *Current Ornithology Volume 17, Current Ornithology*. Springer-Verlag, New York, New York, USA.
- Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: Competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B* 279:2072–2080.
- Van Hemert, C. R., P. L. Flint, M. S. Udevitz, J. C. Koch, T. C. Atwood, K. L. Oakley, and J. M. Pearce. 2015. Forecasting wildlife response to rapid warming in the Alaskan Arctic. *BioScience* 65:718–728.
- Viaroli, P., P. Lasserre, and P. Camprostrini. 2007. Lagoons and coastal wetlands in the global change context: impact and management issues. Springer, Dordrecht, The Netherlands.
- Visser, M. E., A. C. Perdeck, J. H. van Balen, and C. Both. 2009. Climate change leads to decreasing bird migration distances. *Global Change Biology* 15:1859–1865.
- Ward, D. H., and C. A. Amundson. 2019. Monitoring annual trends in the abundance of eelgrass (*Zostera marina*) at Izembek National Wildlife Refuge in 2018. U.S. Geological Survey Open-File Report 2019–1042.
- Ward, D. H., C. L. Amundson, R. A. Stehn, and C. P. Dau. 2018. Long-term trends in fall age ratios of black brant. *Journal of Wildlife Management* 82:362–373.
- Ward, D. H., C. P. Dau, T. L. Tibbitts, J. S. Sedinger, B. A. Anderson, and J. E. Hines. 2009. Change in abundance of Pacific brant wintering in Alaska: evidence of a climate warming effect? *Arctic* 62:301–311.
- Ward, D. H., C. J. Markon, and D. C. Douglas. 1997. Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. *Aquatic Botany* 58:229–240.
- Ward, D. H., A. Morton, T. L. Tibbitts, D. C. Douglas, and E. Carrera-González. 2003. Long-term change in eelgrass distribution at Bahía San Quintín, Baja California, Mexico, using satellite imagery. *Estuaries* 26:1529–1539.
- Ward, D. H., A. Reed, J. S. Sedinger, J. M. Black, K. V. Derksen, and P. M. Castelli. 2005. North American Brant: effects of changes in habitat and climate on population dynamics. *Global Change Biology* 11:869–880.
- Ward, D. H., and R. A. Stehn. 1989. Response of Brant and other geese to aircraft disturbance at Izembek lagoon, Alaska. Final Report No. 14–12–0001–30332 to Minerals Management Service, U.S. Fish and Wildlife Service, Anchorage, Alaska, USA.
- Ward, D. H., R. A. Stehn, and D. V. Derksen. 1994. Response of staging brant to disturbance at the Izembek Lagoon, Alaska. *Wildlife Society Bulletin* 22:220–228.
- Waycott, M., et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106:12377–12381.
- Wilson, H. M. 2017a. Aerial survey of wintering Pacific brant and other species at the Izembek Lagoon Complex and the Sanak Islands, Alaska, 2017. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Anchorage, Alaska, USA. https://www.fws.gov/r7/mbsp/mbm/waterfowl/surveys/pdf/2017_Winter_Izembek_Brant.pdf
- Wilson, H. M. 2017b. Fall Izembek Brant Survey 2016. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Anchorage, Alaska, USA https://www.fws.gov/r7/mbsp/mbm/waterfowl/surveys/pdf/2016_Winter_Izembek_Brant.pdf
- Wilson, H. M. 2017c. Aerial survey of emperor geese and other waterbirds in southwestern Alaska, Spring 2016. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Anchorage, Alaska, USA. https://www.fws.gov/r7/mbsp/mbm/waterfowl/surveys/pdf/2016_EMGO_Spring_Survey.pdf
- Wilson, H. M. 2019. Fall Izembek Brant Aerial Survey, Alaska, 2018. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Anchorage, Alaska, USA. https://www.fws.gov/r7/mbsp/mbm/waterfowl/surveys/pdf/2018_Fall_Izembek_Brant.pdf
- Wilson, H. M., and C. P. Dau. 2016. Aerial survey of wintering Pacific brant and other species at the Izembek Lagoon Complex and the Sanak Islands, Alaska, January 2016. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Anchorage, Alaska, USA. https://www.fws.gov/r7/mbsp/mbm/waterfowl/surveys/pdf/2016_Winter_Izembek_Brant.pdf
- Wilson, H. M., and W. W. Larned. 2020. Alaska Winter Brant Survey 2020. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Anchorage, Alaska, USA.

- Wood, K. A., R. A. Stillman, D. Wheeler, S. Groves, C. Hambly, J. R. Speakman, F. Daunt, and M. T. O'Hare. 2013. Go with the flow: Water velocity regulates herbivore foraging decisions in river catchments. *Oikos* 122:1720–1729.
- Zimmer, C., M. Boos, O. Petit, and J. Robin. 2010. Body mass variations in disturbed mallards *Anas platyrhynchos* fit to the mass-dependent starvation-predation risk trade-off. *Journal of Avian Biology* 41:637–644.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3405/full>