Predicting effects of environmental change on a migratory herbivore

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Abstract. Changes in climate, food abundance and disturbance from humans threaten the ability of species to successfully use stopover sites and migrate between non-breeding and breeding areas. To devise successful conservation strategies for migratory species we need to be able to predict how such changes will affect both individuals and populations. Such predictions should ideally be process-based, focusing on the mechanisms through which changes alter individual physiological state and behavior. In this study we use a process-based model to evaluate how Black Brant (*Branta bernicla nigricans*) foraging on common eelgrass (*Zostera marina*) at a stopover site (Humboldt Bay, USA), may be affected by changes in sea level, food abundance and disturbance. The model is individual-based, with empirically based parameters, and incorporates the immigration of birds into the site, tidal changes in availability of eelgrass, seasonal and depth-related changes in eelgrass biomass, foraging behavior and energetics of the birds, and their mass-dependent decisions to emigrate. The model is validated by comparing predictions to observations across a range of system properties including the time birds spent foraging, probability of birds emigrating, mean stopover duration, peak bird numbers, rates of mass gain and distribution of birds within the site: all 11 predictions were within 35% of the observed value, and 8 within 20%. The model predicted that the eelgrass within the site could potentially support up to five times as many birds as currently use the site. Future predictions indicated that the rate of mass gain and mean stopover duration were relatively insensitive to sea level rise over the next 100 years, primarily because eelgrass habitat could redistribute shoreward into intertidal mudflats within the site to compensate for higher sea levels. In contrast, the rate of mass gain and mean stopover duration were sensitive to changes in total eelgrass biomass and the percentage of time for which birds were disturbed. We discuss the consequences of these predictions for Black Brant conservation. A wide range of migratory species responses are expected in response to environmental change. Process-based models are potential tools to predict such responses and understand the mechanisms which underpin them.

Key words: climate change; foraging ecology; human disturbance; individual-based model; mechanistic modelling; migration; sea level rise.

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INTRODUCTION

Many species undertake regular seasonal migrations between breeding and non-breeding regions (Dingle and Drake 2007). However, few species can store the energy and nutrients required to undertake a long-distance migration in a single continuous event. Thus staging habitats are critical to the life cycles of many migratory animal populations (Drent et al. 2006). At such sites individuals must acquire sufficient body reserves of energy and nutrients to allow successful completion of the migration to the breeding grounds and subsequent reproduction. Individuals which depart the staging area with sub-optimal body reserves have a lower probability of completing their migration and lower reproductive success (Ebbinge and Spaans 1995, Prop et al. 2003). Therefore, any factor that limits the ability of migratory foragers to meet their energetic needs will have both individual- and population-level consequences (sensu Black et al. 2007).

Migration requires a large energy investment and its phenology must match closely with the timing of reproduction and food availability, making migratory species particularly sensitive to impacts of environmental change (Both and Visser 2001). Climate change may have multiple effects on animal use at staging sites. Changes in temperature can influence both the physiology and phenology of the migratory species and food resources (Bauer et al. 2008, Jensen et al. 2008). Increases in water depth resulting from sea level rise, may alter foraging habitats (Galbraith et al. 2002), and for those animals that forage on submerged food resources, increased water depth may decrease food availability (Clausen 2000, Moore and Black 2006a). Furthermore, human use of staging sites for leisure, agriculture, fisheries and industry, has been increasing in many regions in response to increasing human populations and economic development (van Eerden et al. 2005, Lotze et al. 2006). Such anthropogenic activities represent a source of disturbance to animals, which may suffer reduced foraging opportunities and increased costs associated with vigilance and escape behaviors (Ward et al. 1994, Madsen 1995, Stillman and Goss-Custard 2002).

In this paper we predict how future change in food abundance, sea level and human disturbance may affect a migratory wildfowl species, Black Brant (*Branta bernicla nigricans* Lawrence 1846), foraging on common eelgrass (*Zostera marina* L.) in a spring stopover site, Humboldt Bay, USA. Shallow coastal habitats dominated by eelgrass, are particularly vulnerable to the effects of environmental change (Shaughnessy et al. 2012) and are also globally important as staging and overwintering areas for a range of waterfowl species (e.g., Pérez-Arteaga et al. 2005). Our predictions are derived from an individual-based model (IBM), MORPH (Stillman 2008), parameterized and validated for the study system. MORPH makes no system- or species-specific assumptions and consequently has been used extensively to evaluate the responses of foraging animals to changes in their environment (e.g., Stillman 2008, Stillman and Goss-Custard 2010, Wood et al. 2012a, Stillman et al. 2015). The model predicts the physiological state, behavior and distribution of birds within the site, as each bird attempts to gain mass as quickly as possible by consuming eelgrass within reach of the water surface. IBMs have been previously used to successfully predict the interactions between waterfowl and their food supplies (e.g., Pettifor et al. 2000, Stillman and Goss-Custard 2010, Wood et al. 2012a, Stillman et al. 2015). We test the accuracy of the model and its sensitivity to variation in parameter values. We then use the model to predict the number of birds that could potentially be supported by the eelgrass within the bay, and the effect of changes in sea level, food abundance and human disturbance on the stopover duration and rate of mass gain of birds within the bay. We discuss the consequences of these predictions for Black Brant conservation, and consider how our approach could be more widely applied to other migratory species.

METHODS

Study system

Humboldt Bay (40°48′ N, 124°07′ W) is a 62.4-km^2 estuary in northern California, USA, which contains approximately 10.4 km^2 of eelgrass in discrete beds separated by channels (Moore et al. 2004) (Fig. 1). Black Brant (hereafter referred to as "brant") use the bay primarily during spring migration (Lee et al. 2007). Estimates of Hum-
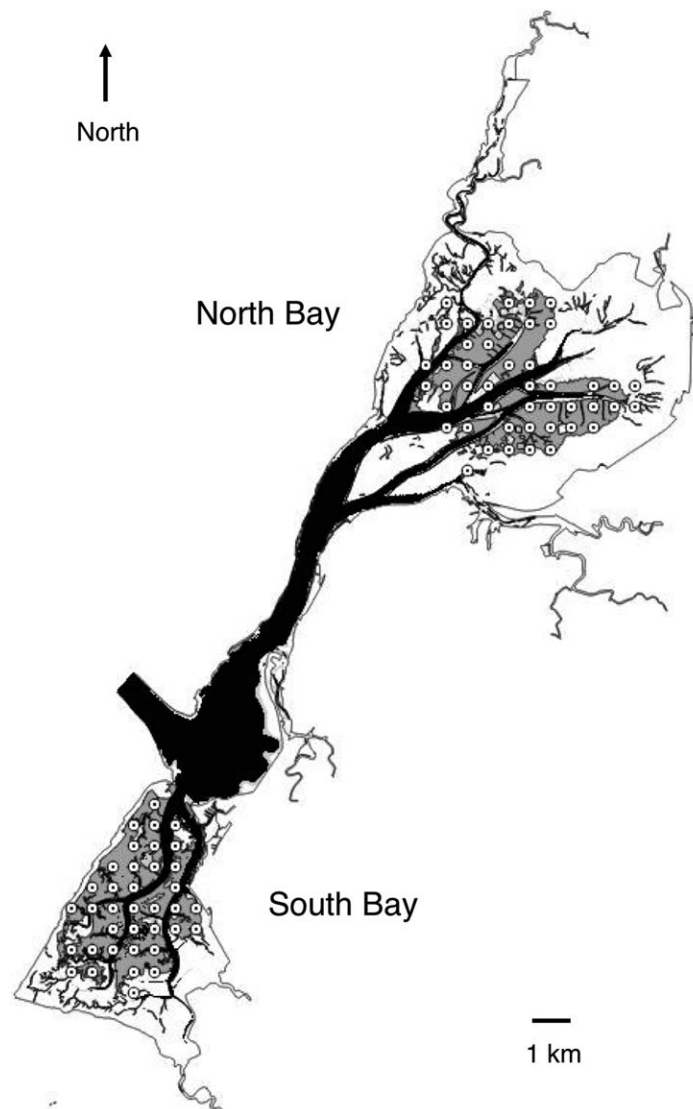
Fig. 1. Map of Humboldt Bay (north and south bays), California, showing the distribution of eelgrass (grey shading), sublittoral channels (black shading) and the distribution of 500×500 m cells used in the present-day version of the model (circles showing central locations).

boldt Bay brant use-days based on monthly counts (i.e., sum of the number of birds observed each month multiplied by number of days in month) ranged between 1 and 6 million prior to 1954. Thereafter, use-days declined to a low of 285,000 in 1985, coinciding with a winter, rather than autumn hunting season (Moore and Black 2006b). Use-days rebounded to over 1 million after resumption of an autumn-only hunt, which in recent years occurs on ~29 days in November–December. Using mark-recapture observations of individual tarsal-bands, Lee et al. (2007) calculated that up to 60,000 individual birds (58%) of the population staged at Humboldt Bay in 2001. Parameter values used to model the system are shown in Table 1.

Modelling time, space and environmental variables

The model divided time into discrete one-hour time steps, and ran for a 183-day period from 1 December to 31 May, reflecting the period of usage by migratory brant (Moore et al. 2004, Lee

Table 1. Parameter values used in the model.

Name	Value	Derivation
(a) Environmental parameters		
Time step length (hours)	1	Time interval to account for tidal cycle and individual forager behavior; standard time step length for estuarine bird models (e.g. Pettifor et al. 2000)
Duration of daylight (hours)	9 to 15	Range of hours of daylight over the December–May period, calculated using the United States Naval Observatory Astronomical Applications Department calculator (www.usno.nav.mil/data/docs/RS_OneDay.php) for 2012
Model length (days)	183	1 December to 31 May; the period of usage of Humboldt Bay by migratory brant (Moore et al. 2004, Lee et al. 2007)
Water level (m MLLW)	2.6 to −0.6	Hourly tidal water level data for North Bay Spit tide gage (tidesandcurrents.noaa.gov/geo.shtml?location=9418767) for December 2011 to December 2012
(b) Patch parameters		
Patch size (m^2)	$500 \times 500 = 250000$	Maximum area exploited by an individual in a single hour time step
No. patches	150	Total number of discrete 500×500 m areas occupied by eelgrass within Humboldt bay Shaughnessy et al. (2012)
Elevation (m MLLW)	0.3 to −2.1	
Eelgrass initial biomass (g DM m^{-2})	0 to 418	Range of values derived from surveys reported by Gilkerson (2008) multiplied by the proportion of biomass comprised by the three youngest leaves which the brant target (0.65; Moore 2002)
Eelgrass shoot length (m)	0.25 to 0.85	Range of values derived from Gilkerson (2008)
Eelgrass metabolizability (%)	46	*Zostera marina* leaves; Buchsbaum et al. (1986)
Eelgrass energy content (kJ g^{-1} DM)	16.8	*Zostera marina* leaves; Baldwin and Lovvorn (1994)
Eelgrass growth rate (g DM d^{-1})	$B_{t+1} = a\,[S_t + (dG_t\,10^4) - mS_t - H_t]$	Moore (2002), see text for derivation
Eelgrass floating biomass (% of total)	5	Estimated from information in Elkinton et al. (2013)
(c) Brant parameters		
Brant population size (no. ind.)	60000	Based mark-recapture estimates for 2001 (Lee et al. 2007)
Arrival date of first brant	1 January	Based on arrival dates given in Lee et al. (2007)
Brant mass on arrival (g)	1320	Derived from mean mass of adult female brant at San Quintin Bay, Mexico in January (1440 g; Mason et al. 2006) minus the cost of a non-stop flight to Humboldt Bay (120 g) following Calder (1974) in Vangilder et al. (1986)
Brant target mass on departure (g)	1580	Derived the mean mass of adult female brant at San Quintin Bay, Mexico prior to departure in late March (1580 g from Mason et al. [2006])
Brant target mass gain during stopover (g)	260	Departure mass − arrival mass
Brant lean mass (g)	964	Spaans et al. (2007) estimated the lean mass (i.e., with no energy stores) of dark-bellied brent geese *Branta bernicla bernicla* to be 73% of mass on arrival at breeding area. Thus for brant, 1320 g × 0.73 = 964 g
Brant energy density (kJ g^{-1})	34.3	Energy content of avian tissue, given in Kersten and Piersma (1987)
Brant energy store on arrival (kJ)	15984	(arrival mass − lean mass) × energy density
Brant target energy store on departure (kJ)	24902	(departure mass − lean mass) × energy density
Brant BMR (W)	5.77	Calculated from allometric equation derived by Bruinzeel et al. (1997); BMR $= 4.59 \times (M^{0.69})$, where M = mass (1.4 kg; Boyd 2005)
Brant energy expenditure whilst foraging (W)	9.81	$1.7 \times$ BMR; based on value given in Table 1 of Clausen et al. (2012)
Brant energy expenditure whilst resting (W)	9.23	$1.6 \times$ BMR; based on value given in Table 1 of Clausen et al. (2012)
Brant maximum feeding depth (m)	0.40	Clausen (2000), Moore and Black (2006a)

et al. 2007) (Table 1a). The model incorporated the diurnal cycle, incorporating annual variation in the times of sunrise and sunset in the bay (Table 1a). The model incorporated changes in water level derived from tidal curve predictions for the bay. Hourly tidal water level data for the North Bay Spit tide gage (available for download at: http://tidesandcurrents.noaa.gov/geo.shtml?location=9418767) was acquired for the period spanning December 2011 to December 2012 (Table 1a). We assumed that there was no tidal lag between North and South Bays. In reality, there is up to a 20-minute difference between parts of the bays, but thus was not incorporated into the model as it was relatively short compared to the 1-hour model time step.

Modelling eelgrass biomass and shoot length

The model contained the eelgrass food supply of brant in the North and South Bays of Humboldt Bay, representing the spatial arrangement of eelgrass as a grid of 500×500 m cells (Fig. 1). Each cell had a fixed elevation (which determined its depth through the tidal cycle), and contained a specific eelgrass biomass density and eelgrass shoot length (which combined with elevation determined whether the eelgrass was available to the geese). The elevation of each cell was calculated for its central coordinate from a digital elevation model (DEM) of Humboldt Bay using ArcGIS 10.1 (ESRI, Redlands, California, USA).

Eelgrass shoot length (meristem to tip of longest leaf) (m) and aboveground biomass density (g m^{-2}) were derived from quadrats sampled at low tide in December and January during the 2001/02 and 2002/03 seasons along 15 established transects representative of the major eelgrass beds within both North and South Humboldt Bay (S. Schlosser, *unpublished data*). Transects spanned the range of intertidal elevations within each eelgrass bed. Only intertidal eelgrass was sampled because the vast majority of eelgrass habitat and biomass in Humboldt Bay is distributed in the intertidal flats between approximately -0.6 and 0.3–0.4 m mean lower low water (MLLW; i.e., the annual mean of the lower low water heights of each tidal day) (Moore and Black 2006a). While eelgrass is capable of growing in deeper water, intertidal flats cover approximately 80% of the mean high tide area of Humboldt Bay. The area of Humboldt Bay lying between -0.6 m

and -2.1 m MLLW (eelgrass maximum depth in Humboldt Bay) is extremely limited in spatial extent and primarily consists of steep channel side slopes, which are not very suitable to eelgrass. The starting position of each transect was adjacent to a subtidal channel along the deep edge of a bed. Transects were oriented approximately perpendicular to the channels such that they ended at a higher intertidal elevation within the bed. Transects were divided into sections from 0 to 30 m (low), 30 to 60 m (mid), and 60 to 100 m (high) distance from the transect starting positions. The purpose of this approach was simply to collect samples at a range of elevations across the eelgrass beds. During each sampling period, 2 0.1-m^2 quadrats were randomly placed within each section so that a total of six quadrat samples was taken per transect.

For each quadrat sample, representative shoot length was calculated by taking the average length of all non-flowering shoots within the quadrat. Eelgrass wet biomass was determined after rinsing eelgrass shoots in freshwater to remove sediment and debris, draining on 0.5-cm mesh, and drying on cloth towels to remove residual moisture. To calculate dry weight biomass (g DM m^{-2}), wet weight values determined for each quadrat were multiplied by a factor of 0.1 (S. Schlosser, *personal communication*). The elevation (m MLLW) of each quadrat sample was derived at the midpoint of each transect section from the DEM of Humboldt Bay. A second-order polynomial function was used to relate aboveground biomass to elevation, as biomass was observed to peak near the center of the eelgrass elevation distribution. For North Bay and South Bay, respectively, biomass (B; g DM m^{-2}) was calculated as:

$$B = 31.30 - 21.28H - 33.83H^2 \quad (1)$$

$$B = 47.61 - 41.92H - 31.13H^2 \quad (2)$$

where H = elevation (m MLLW). A linear expression was used to express shoot length in terms of elevation (Ruesink et al. 2010). For North Bay and South Bay, respectively, shoot length (L; m) was calculated as:

$$L = 0.590 - 0.423H \quad (3)$$

$$L = 0.349 - 0.095H \quad (4)$$

Eqs. 1–4 were used to predict eelgrass winter biomass and shoot length, within the eelgrass elevation range (0.3 to −1.3 m MLLW in North Bay and 0.4 to −2.1 m MLLW in South Bay; Shaughnessy et al. 2012), in each model 500 × 500 m cell based on the elevation at the center of the cell.

Changes in eelgrass biomass through time, independent of depletion by the birds, were predicted by adapting the equation used by Moore (2002):

$$B_{t+1} = B_t + G_t - mB_t \qquad (5)$$

where B_{t+1} = biomass within patch at start of time step $t+1$ (g DM m^{-2}), B_t = biomass in patch at end of time step t (g DM m^{-2}), G_t = increase in biomass due to growth in time step t (g DM m^{-2}) and m = proportion of biomass lost due to senescence within a time step. Moore (2002) calculated that 10% of biomass was lost due to senescence per week, and so m was set to 0.000595 (=0.1/7 days/24 hours) per one-hour time step. Moore (2002) estimated eelgrass daily growth rates (g m^{-2}) under ideal conditions (G^*_{daily}) using data collected by Bixler (1982) in South Bay:

$$G^*_{daily} = 0.4597e^{0.0122d} \qquad (6)$$

where d = day number (1 = 1 December). These data were collected at the optimal elevation for eelgrass growth (i.e., −0.3m MLLW) and so lower growth rates would be expected at different elevations. Following Moore (2002), we used data collected by Keller and Harris (1966) to relate eelgrass growth rate to elevation. These data showed that maximum eelgrass growth rate occurred below shore levels of −0.3 MLLW and lower growth rates occurred at higher elevations. The proportional growth rate of eelgrass (p) was predicted from:

$$p = \begin{cases} 1 & \text{if } H \leq -0.3 \\ e^{-3.398(H+0.3)} & \text{if } H > -0.3 \end{cases} \qquad (7)$$

where H = elevation (m MLLW) (rearranged from equations in Moore [2002]). The biomass growth per time step was calculated by multiplying Eqs. 6 and 7, and dividing 0.4597 by 24 (=0.0192) to convert from growth per day to growth per one-hour time step:

$$G_t = \begin{cases} 0.0192e^{0.0122d} & \text{if } H \leq -0.3 \\ 0.0192e^{0.0122d}e^{-3.398(H+0.3)} & \text{if } H > -0.3. \end{cases} \qquad (8)$$

Substituting $m = 0.000595$ and G_t into Eq. 5 gives the equation used to predict time step changes of eelgrass biomass excluding depletion by the birds:

$$B_{t+1} = \begin{cases} B_t + 0.262e^{0.0122d} - 0.000595B_t & \text{if } H \leq -0.3 \\ B_t + 0.262e^{0.0122d}e^{-3.398(H+0.3)} \\ \quad -0.000595B_t & \text{if } H > -0.3. \end{cases} \qquad (9)$$

Growth in eelgrass shoot length was modeled from data collected in winter (December and January) and summer (July) 2000 by Moore (2002) as follows: mean lengths of the first to third youngest leaves (i.e., those selected by the geese) were 20.1, 38.8 and 44.5 cm in winter and 31.1, 57.8 and 55.6 cm in summer, meaning that on average shoot length was 1.43 times greater in summer than in winter. Eelgrass shoot length until 31 January was predicted from Eqs. 3 and 4 for North and South Bays, respectively, after which it increased linearly daily until it was 1.43 times greater on 31 May (see above and Moore [2002]; Table 1b).

In addition to feeding on eelgrass rooted to the substrate, brant also consume eelgrass that becomes displaced and floats to the water surface as the tide rises above eelgrass beds (Moore 2002, Elkinton et al. 2013). The amount of dislodged eelgrass on the water surface varies with wave action and dropped leaves while birds forage (Elkinton et al. 2013). We assumed the biomass of 'drift' eelgrass to be 5% of the rooted biomass in each modeled patch. Within a time step birds either consumed rooted eelgrass biomass when it could be reached from the water surface, and floating eelgrass biomass if no rooted biomass was available.

Modelling brant migration, energetics and behavior

The total brant population size passing through the bay was assumed to be 60,000 birds, the mean estimate for 2000 and 2001 (Lee et al. 2007). At the start of a simulation all birds were assumed to be on, or migrating from, San Quintin Bay, Mexico, the major brant wintering site south of Humboldt Bay (Ward et al. 2005). Each bird within the population was given a date on which it arrived in the bay. We assumed that birds arrived at a constant rate between 1

January and 30 April, based on information in Lee et al. (2007), and so each bird had an arrival date drawn at random from a uniform distribution between these dates. Each bird was given an arrival energy store related to the date on which it arrived, derived from the body mass of birds at San Quintin ($M_{JanSanQuintin}$ = 1,440 g up to 15 January [day 46] and increasing at 2 g per day afterwards until 31 March; Mason et al. 2006) and the cost of flying to Humboldt Bay ($M_{migrate}$ = 120 g; calculated based on flight costs following Calder [1974]). The arrival energy store size of the birds (E_{arrive}) was derived from their fat store size (arrival body mass − lean body mass [M_{lean} = 964 g]) multiplied by the energy content of fat (E_{fat} = 34.3 kJ g^{-1}; Kersten and Piersma 1987).

$$
E_{arrive} =
\begin{cases}
E_{fat}(M_{\text{JanSanQuintin}} - M_{migrate} \\
\qquad -M_{lean}) & \text{if } D_{\text{arrive}} \leq 46 \\
E_{fat}\Big(M_{\text{JanSanQuintin}} + 2 \\
\qquad \cdot(D_{arrive} - 46) \\
\qquad -M_{migrate} - M_{lean}\Big) & \text{if } D_{\text{arrive}} > 46.
\end{cases}
\tag{10}
$$

Model birds emigrated north from the bay when they reached a threshold energy store size. No data were available to estimate this parameter from Humboldt Bay, and so instead it was estimated from the late-April departure masses of birds migrating north from San Quintin Bay (M_{depart} = 1576 g; Mason et al. 2006). This assumed that the birds were gaining enough mass for onward migration and were not also building up reserves for breeding (Schamber et al. 2012). The departure energy store (E_{depart}) was calculated as departure mass minus lean body mass multiplied by the energy content of fat.

$$
E_{depart} = E_{fat}(M_{depart} - M_{lean}). \tag{11}
$$

Energy expenditure and energy assimilation

The energy expenditure of model birds was calculated from basal metabolic rate (BMR) and their behavior. BMR was calculated from body mass using an allometric equation (Bruinzeel et al. 1997).

$$
E_{BMR} = 4.59 M_{brant}^{0.69} \tag{12}
$$

where E_{BMR} = basal metabolic rate (J s^{-1}) and M_{brant} = average body mass of a brant (=1.4 kg; Boyd 2005). The energy expenditure of different behaviors were calculated from the following multipliers of BMR (Clausen et al. 2012): feeding on rooted or floating eelgrass (E_{feed}) = 1.7 BMR; resting on a patch and not feeding (E_{rest}) = 1.6 BMR. The energy expenditure (E_{expend}) within a patch was calculated from the proportion of time spent feeding (p_{feed}).

$$
E_{expend} = p_{feed}E_{feed} + (1 - p_{feed})E_{rest}. \tag{13}
$$

Rooted eelgrass was assumed to be available to the geese when it was either on the surface or within reach from the surface. The water depth over each patch during each time step was calculated as the difference between water level and the elevation of the patch, both measured relative to MLLW. The availability (A; 1 = available to geese; 0 = not available to geese) of rooted eelgrass was calculated from

$$
A =
\begin{cases}
1 & \text{if } W - H + L \leq F_{\max} \\
0 & \text{if } W - H + L > F_{\max}
\end{cases}
\tag{14}
$$

where W = water level (m MLLW), H = patch elevation (m MLLW), L = eelgrass shoot length (m) and F_{max} = maximum foraging depth of a goose (m) (=0.4; Clausen 2000). Floating eelgrass was assumed to always be available to the birds.

The birds assimilated energy by consuming rooted or floating eelgrass. In both cases it was assumed that the rate of consuming eelgrass was related to the biomass of eelgrass using the following functional response derived for a closely related sub-species Brent Goose (*Branta bernicla bernicla* L.) consuming related eelgrass species (*Z. noltii* Hornem. and *Z. angustifolia* (Hornem.) Reichb.) (Pettifor et al. 2000). (We consider the consequences of this assumption in the discussion.)

$$
C = 0.01028(1 - e^{-0.1050B})\Big(1.0373(1 - e^{-0.0184B})\Big)
\tag{15}
$$

where C = rate of consuming eelgrass (g DM s^{-1}) and B = rooted and floating eelgrass biomass (g DM m^{-2}). The left hand term of the equation calculates the grams of eelgrass consumed per second while the bird's bill is in contact with the food, and the right hand term calculates the proportion of time the bird has its bill in contact

with the food (Pettifor et al. 2000). No suitable data were available to describe the functional response of brant feeding on *Z. marina* but observations were available across a narrow range of biomass densities, from 339 focal feeding observations in South Bay between January and April 2011. Observations of at least 180 s were made of actively foraging geese. Feeding was recorded as the number and length (five size classes estimated relative to the size of the bird, bill and neck) of eelgrass leaves consumed per bite. To determine grams associated with each bite size during 'bed feeding' and 'drift feeding', eelgrass was collected from beds and from drifting mats. The lengths (cm) of randomly selected subsamples of 50 'green' leaves (10 within each size class) from bed samples and all green leaves from drift samples were measured, the latter due to the relatively small number of drift leaves. Samples were dried at 60°C for 72 hrs and total sample weight (g DM) and individual leaf weights (g DM) measured, to determine the average dry mass of each bite size for both bed and drift samples. Intake rate was determined from the sum of intake derived from each bite size class. These data were compared to the predictions of Eq. 15 to assess the accuracy with which this equation explains the functional response (Fig. 2). Eq. 15 consistently overestimated the intake rates observed within the Bay, and so Eq. 15 was calibrated (by multiplying by 0.6) to pass through the center of the observed intake rates (Fig. 2). This calibrated equation was used to predict intake rate from the biomass of rooted or floating eelgrass.

The model incorporated within species competition due to resource depletion. Other sources of competition, such as prey stealing or competitor avoidance, were not included as they were not considered important in this particular system. They can be incorporated though, and have been in other models (Stillman and Goss-Custard 2010).

The rate at which geese assimilated energy from the food (E_{assim}) was calculated from the rate at which eelgrass was consumed (C; g s^{-1}; Eq. 15), the energy content of eelgrass ($E_{eelgrass}$; KJ g^{-1}; 16.8; Baldwin and Lovvorn 1994) and the efficiency of assimilating eelgrass (a; 0.46; Buchsbaum et al. 1986).
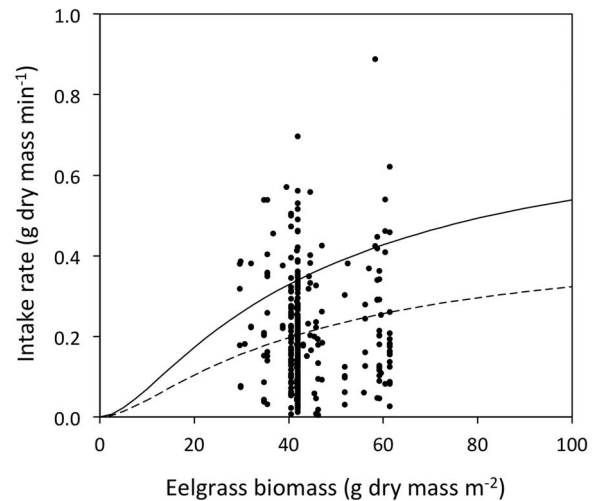

Fig. 2. The calibrated functional response curve (dashed line) for brant feeding on eelgrass, relative to the curve reported by Pettifor et al. (2000) (solid line) and the observed data reported in this study (filled circles and short).

$$E_{assim} = aE_{eelgrass}C. \qquad (16)$$

The maximum daily energy consumption of the birds (E_{max}; KJ day^{-1}) was limited based on the following allometric equation (Kirkwood 1983).

$$E_{max} = 1713M_{brant}^{0.72}. \qquad (17)$$

Birds attempted to gain mass as quickly as possible given the constraints of the time for which eelgrass beds were available, the biomass of eelgrass and the maximum amount of energy that was consumed per day. Birds that could not meet their daily energy requirements from foraging depleted their fat energy stores. Birds emigrated successfully if their energy store reached the threshold energy target for departure (24,902 J), but died of starvation if their energy store size was reduced to zero.

During each time step model birds decided which patch to occupy and whether to consume rooted or drifting eelgrass. Birds could only consume rooted eelgrass from patches in which eelgrass could be reached from the surface, whereas floating eelgrass could be consumed from any patch. Birds calculated their energy assimilation rate from consuming either rooted eelgrass from patches in which it was reachable,

Table 2. Comparisons of the mean (± SE) model predictions and observed values for 11 properties of our study system. Accuracy was calculated as (predicted/observed) × 100.

Test	Predicted value	Observed value	Accuracy (%)	Reference for observed value
Time devoted to foraging (%)	49.3 ± 0.1	37	132	Elkinton et al. (2013)
Survival probability	1.0 ± 0.0	1.0	100	Ward et al. (1997)
Emigration probability	1.0 ± 0.0	1.0	100	Ward et al. (1997)
Carrying capacity (no. bird use-days)	1392000 ± 109654	1600000	87	Moore and Black (2006b)
Mean stopover duration (days)	23 ± 2	17	135	Mean January to April duration reported by Lee et al. (2007)
Proportion of bird days in South Bay	0.74 ± 0.01	0.83	89	Moore et al. (2004)
Peak count (no. birds)	32800	24500	134	Moore and Black (2006b)
Timing of peak count (days after 1 December)	100 ± 1	111	90	Lee et al. (2007)
Mean rate of mass gain (g d^{-1})	18.1 ± 1.2	15.3	118	260 g/17 days; stopover mass gain (Table 1c)/stopover duration (Lee et al. 2007)
North Bay eelgrass biomass during February (g DM m^{-2})	26.2 ± 0.1	28.0 ± 2.0	94	Tennant (2006)
South Bay eelgrass biomass during February (g DM m^{-2})	32.4 ± 0.2	39.0 ± 5.0	83	Tennant (2006)

or floating eelgrass from all patches. In the real system, birds do not feed constantly, but instead concentrate feeding at the most profitable times (i.e., when eelgrass is available; Moore and Black 2006a). Model birds were assumed to feed during the most profitable time steps. This was calculated by comparing the energy assimilation rate available from each patch (from either rooted or floating eelgrass) with that average achieved over the previous 24 hours (i.e., the 24 previous time steps). If this average assimilation rate could be exceeded or equaled during a given time step (i.e., it was a profitable time to feed), a bird consumed eelgrass from the patch on which energy assimilation rate was maximized (i.e., the most profitable patch). If this assimilation rate could not be equaled or exceeded (i.e., it was not a profitable time to feed), birds did not feed during a time step, but moved to the patch with the highest eelgrass biomass. This rule meant that birds tended to feed during times when rooted eelgrass was available because a higher energy assimilation rate could be achieved from rooted eelgrass. The rule did not include the cost of moving between patches.

Model validation and sensitivity analysis

The arrival dates of birds were drawn from a uniform random distribution, and so predictions varied between replicate simulations based on the same parameter values. Therefore, five replicate simulations were run for each combination of parameter values. Mean predictions and associated standard deviations are presented.

The model was tested by comparing its predictions to the following observed field data; proportion of daylight hours spent foraging, mean stopover duration within the bay, proportion of birds surviving between January and May, proportion of birds emigrating between January and May, number of bird use days, peak number of birds within the bay, date of peak number of birds in the bay, mean rate of mass gain, proportion of birds within North and South Bays and mean eelgrass biomass at the end of the study period (Table 2).

The individual parameter perturbation method was used to assess the sensitivity of the model predictions to adjustments in parameter values. We assess the amount of change that occurs in stopover duration (days) and daily mass gain (g day^{-1}) after each model input parameter was increased and decreased sequentially by 10% relative to the originally assigned parameter value. 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 brant population size

We first assessed, under current environmental conditions, the capacity of Humboldt Bay to meet

the stopover needs of brant for a range of population sizes. Accordingly, we varied brant population size between 25,000 and 400,000 individuals, increasing the population size by 25,000 in each set of simulations. The range of population sizes tested exceeds the historical range reported for both Humboldt Bay (25,000–150,000) and the entire Pacific Flyway (10,0000–200,000) in order to allow us to examine site capacity for future population sizes which may be considerably greater than those that currently use Humboldt Bay (Moore and Black 2006b). For each simulation we recorded the number of individuals that were predicted to emigrate successfully from the site.

Scenario II: Changes in sea level

To model the predicted future biomass of eelgrass we used published information describing projected eustatic sea level rise, vertical tectonic land level change, and long-term sediment accretion rate data (Shaughnessy et al. 2012). Steric, dynamic ocean, and ice sheet sea level data for San Francisco and Newport were used to develop estimates of eustatic sea level rise of 13.8 cm by 2030, 29.8 cm in 2050, and 89.9 cm by 2100 relative to the year 2000 for Humboldt Bay (which is located approximately half way between Newport and San Francisco) (National Research Council [NRC] 2012). Following guidance from the U.S. Army Corps of Engineers (USACE 2011), a second order polynomial was fit to the NRC (2012) sea level rise estimates for 2030, 2050, and 2100 to generate the following eustatic sea level rise curve:

$$y = 0.006x^2 + 0.286x - 0.069$$

where y is equal to the eustatic sea level rise rate at year x.

Sediment accretion was modeled as a function of tidal inundation frequency (Temmerman et al. 2003) and location, using long-term accretion rate data derived from gouge-coring with inundation frequency data obtained from the North Bay Spit tide gage. Radio-carbon-dated gouge cores with survey control tied to local benchmarks provided elevation-specific long-term accretion rates (1.3–2.4 mm yr^{-1}) for both North and South Bay (Valentine 1992). Tidal inundation frequency was calculated as a function of elevation using five years of water level observations from 2007 to 2012 at the North Bay Spit tide gage. Historic minimum and maximum water levels from the period (1982–2012) were used to establish maximum and minimum inundation frequencies, respectively, for curve fitting. A sigmoidal curve was fit to the data to describe inundation frequency as a function of tidal elevation. Sediment accretion rates derived from gouge cores calibrated to diurnal tide level (1.1 m MLLW), were then integrated with the tidal inundation function to model sediment accretion rates across both North and South Bays. To account for the capacity of salt marsh to facilitate deposition and enhance sediment accretion (Peralta et al. 2008) relative to unvegetated mudflat and eelgrass habitat, we applied an accretion rate of 3.6 mm yr^{-1} (Thom 1992, Pritchard 2004) to areas of the DEM where salt marsh was distributed (assumed present between ~1.7 and 2.6 m MLLW; Eicher 1987).

Interseismic tectonic vertical land level changes associated with the Cascadia subduction zone also influence relative sea level observations in Humboldt Bay (Burgette et al. 2009). To account for the influence of tectonic land level changes on local sea level projections, a raster surface representing interseismic uplift rate was developed from a three-dimensional dislocation model of the Cascadia subduction zone optimized to fit recent deformation geodetic data (Flück et al. 1997) using IDW interpolation.

The sea level rise scenario model was implemented in one year time steps, incorporating the eustatic sea level rise rate, tectonic vertical land level change rate, and sediment accretion rate model components to project future depth/elevation changes to the Humboldt Bay DEM. Expressions describing eelgrass shoot length and biomass as a function of depth under present-day conditions, were then integrated with sea level rise scenario output DEMs at 25-year time steps for 100 years to model future projections of eelgrass biomass and shoot length for both North and South Humboldt Bay.

Scenario III: changes in food abundance

To examine the effects of changes in the biomass of eelgrass, we ran simulations in which the initial eelgrass biomass of each patch was sequentially varied in 10% increments between −50% and +10% of its original value. This range

reflects the commonly reported changes in seagrass abundance within temperate sites (e.g., Waycott et al. 2009).

Scenario IV: changes in human disturbance

To examine the effects of increased human disturbance to brant, we varied the proportion of time that the geese spent disturbed in 10% increments between 0% and 50% of the total time. This range reflects the levels of disturbance commonly reported for coastal bird populations (e.g., Madsen 1995, Stillman and Goss-Custard 2002). Birds were only able to feed during the time in which they were not disturbed.

RESULTS

Model validation and sensitivity

We compared the default model predictions of 11 properties of the study system with observed values for those properties (Table 2). The suite of 11 model predictions were all within ±35% of the observed value, 8 of which were within ±20%, indicating close agreement between model predictions and observed values across a suite of system properties.

Our model predictions of stopover duration (Fig. 3a) and rate of mass gain (Fig. 3b) exhibited sensitivity to changes in all eight of the key parameters tested. In particular, both properties were sensitive to changes in eelgrass energy content and metabolizability. For example, mean (± SD) stopover duration was predicted to increase from 23.2 ± 4.1 days to 38.2 ± 4.2 days and 36.6 ± 3.4 days in response to 10% decreases in eelgrass energy content and metabolizability, respectively. Similarly, decreases of 10% in eelgrass energy content and metabolizability reduced the mean (± SD) rate of mass gain from 18.1 ± 2.6 g d^{-1} to 10.3 ± 1.5 g d^{-1} and 10.7 ± 2.2 g d^{-1}, respectively. However, mass gain exhibited the greatest sensitivity to changes in departure mass, with a 10% decrease in departure mass predicted to result in a decrease in the mean (± SD) rate of mass gain to 11.6 ± 1.4 g d^{-1}. This happened because the rate of mass gain increased through time as the biomass of eelgrass increased; a decrease in departure mass meant that birds left the bay earlier, and hence when the rate of mass gain was lower.
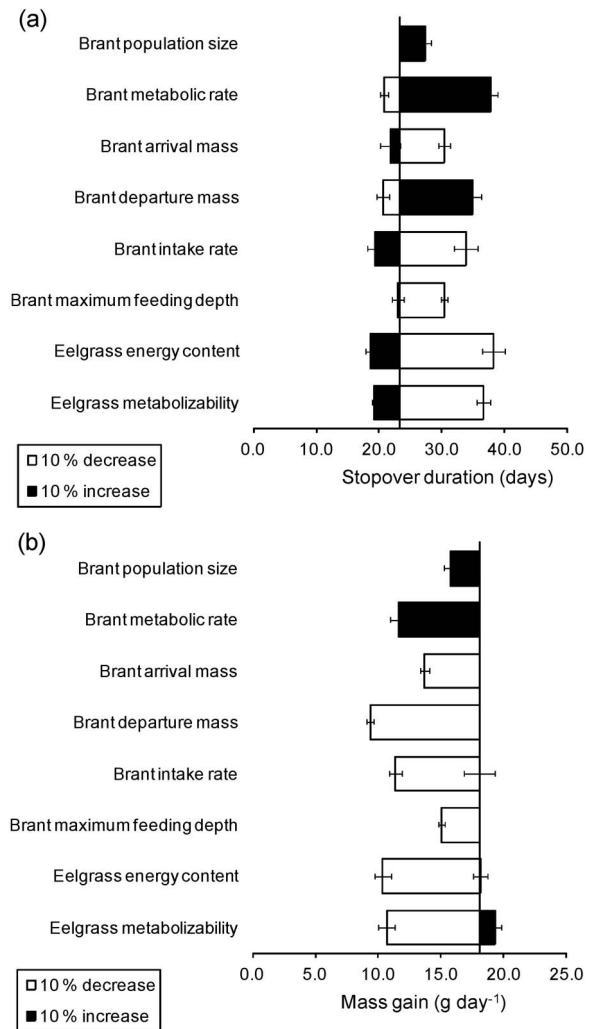

Fig. 3. The effects of ±10% changes in key parameters on model predictions of (a) stopover duration and (b) rate of mass gain. Black bars show predictions when a parameter value was increased and open bars show predictions when a parameter value was decreased. Bars are shown relative to the final model predictions with regard to stopover duration (23 d) and daily mass gain (18.1 g d^{-1}).

Depletion of eelgrass

To predict the amount of depletion caused by the brant population we ran simulations either including 60,000 birds or no birds. We then compared the mean biomass of eelgrass on 31 May predicted by these simulations. The final mean biomass density across both bays was 76.5 g DM m^{-2} (SE between 5 replicate simulations =
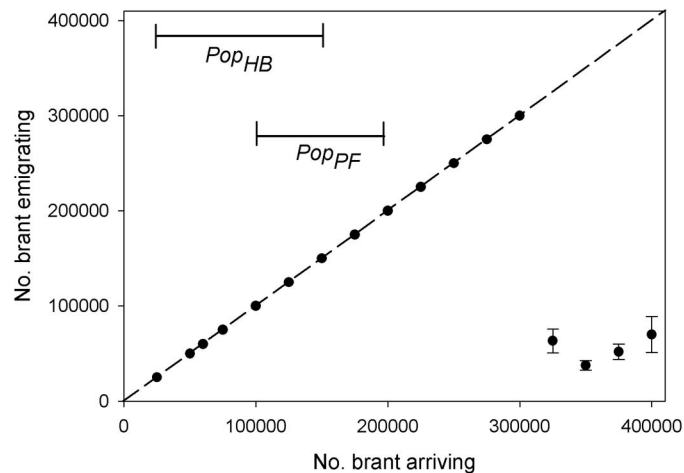
Fig. 4. The mean (±SD) predicted number of brant that emigrated successfully from Humboldt Bay compared with the number that arrived. The dashed line indicates a 1:1 relationship (i.e., all arrivals emigrate successfully). The historical ranges in both the Humboldt Bay population (Pop_{HB}: 25000–150000) and total Pacific Flyway population (Pop_{PF}: 100000–200000) are indicated, based on the data presented by Moore and Black (2006b).

0.0) in the absence of birds and 75.4 g DM m^{-2} (SE = 0.02) in the presence of birds. The birds therefore depleted less than 2% of the eelgrass biomass.

Scenario I: changes in brant population size

For population sizes of ≤300,000 brant, our model predicted that 100 % of individuals would emigrate successfully from the site (Fig. 4). However, for population sizes between 325,000 and 400,000 individuals, model predictions indicated that ≤20% of individuals would emigrate successfully, with the remainder failing to gain sufficient body mass to depart the site and potentially starving. This happened because of the cumulative depletion of eelgrass by the birds; with population sizes over 300,000, eelgrass was depleted to the extent that relatively few birds could gain enough mass to emigrate. As examples, the mean (±SD) numbers of brant predicted to emigrate for population sizes of 325,000 and 400,000 birds were 63,440 ± 12,476 and 70,000 ± 18,847 individuals, respectively (Fig. 4). The bay was therefore predicted to potentially be able to support many more birds than currently, consistent with the prediction that 60,000 birds depleted less than 2% of the eelgrass biomass.

Scenario II: changes in sea level

Predicted increases in sea level rise over the period 2012 to 2112 had no effect on the percentage of individuals successfully emigrating from Humboldt Bay with 100 % emigration in all simulations (Fig. 5a). Similarly, stopover duration and mass gain changed little over the projection period. The mean (±SD) stopover duration decreased by about 3.5 days between 2012 (23.2 ± 4.1 days) and 2112 (19.8 ± 1.1 days; Fig. 5b), while mean rate of mass gain during staging increased about 3 g day^{-1} between 2012 (18.1 ± 2.6 g day^{-1}) and 2112 (20.9 ± 1.1 g day^{-1}; Fig. 5c).

Scenario III: changes in food abundance

Effects were evident on the percentage of brant successfully emigrating after a ≥40% decline in eelgrass abundance, but were apparent on stopover duration and rate of mass gain after a ≥10% decline in eelgrass abundance (Fig. 6a). Stopover duration was predicted to increase as eelgrass abundance declined with mean stopover duration decreasing from 18.0 (± 1.9) days at +10% eelgrass biomass to 67.0 (±6.3) days at −30% eelgrass biomass (Fig. 6b). Correspondingly, mean rate of mass gain declined as eelgrass abundance decreased, declining from 20.4 (±0.2) g day^{-1} at +10% eelgrass biomass to 3.8 (±1.8) g day^{-1} at −30% eelgrass biomass (Fig. 6c).

Scenario IV: changes in human disturbance
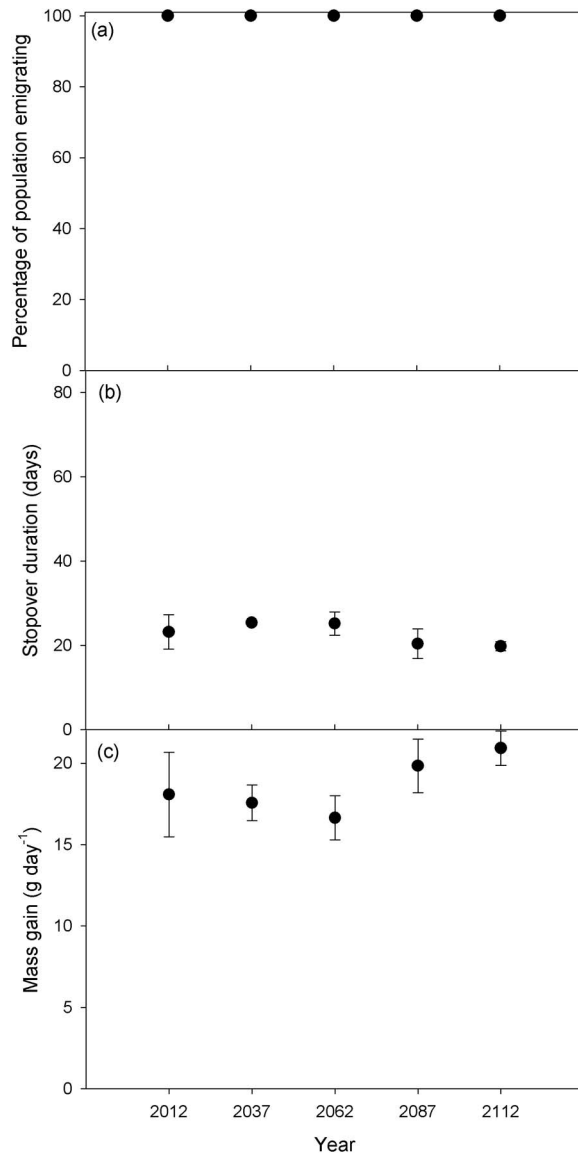
The percentage of brant emigrating successful-

Fig. 5. Predicted mean (±SD) changes in (a) percentage of individuals emigrating successfully from Humboldt Bay, (b) stopover duration, and (c) rate of mass gain, in response to changes in sea level between 2012 and 2112.

Fig. 6. Predicted mean (±SD) changes in (a) percentage of individuals emigrating successfully from Humboldt Bay, (b) stopover duration, and (c) rate of mass gain, in response to changes in eelgrass abundance.

ly from Humboldt Bay was predicted to show a non-linear response to increased disturbance. The mean (± SD) percentage of brant emigrating began to decline when time lost to disturbance exceeded 30%, reaching 30.7% (±4.4%) of individuals when 50% of time was lost to disturbance (Fig. 7a). Stopover duration was predicted to increase as disturbance increased, reaching 62.6
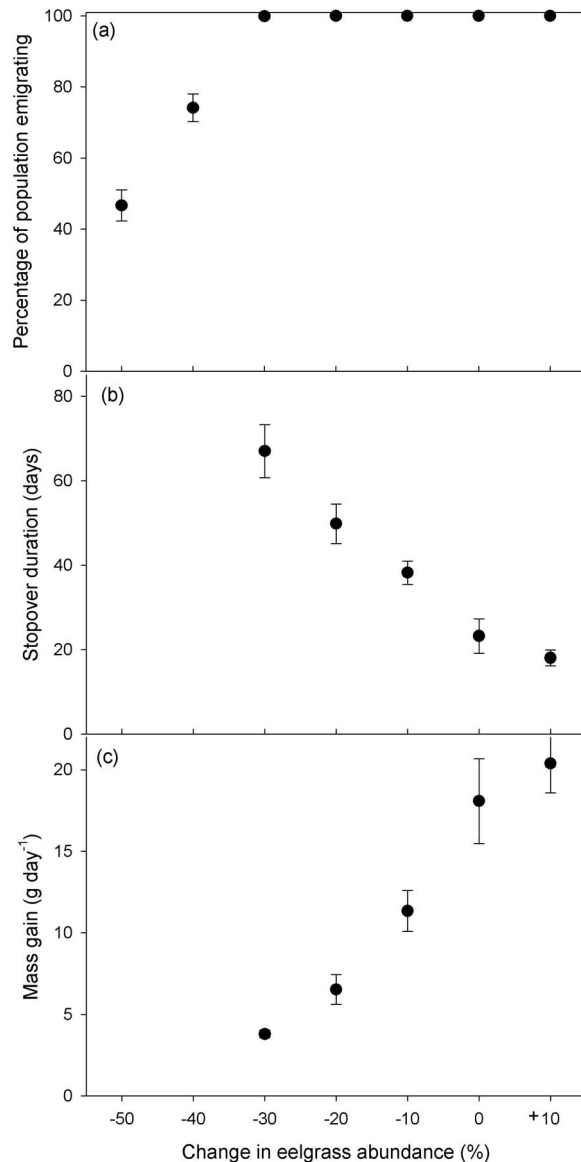
(± 1.8) days when 30% of time was lost to disturbance (Fig. 7b). Again, mean (± SD) rate of mass gain declined as disturbance increased, reaching 4.2 (± 0.2) g day^{-1} when 30% of time was lost to disturbance (Fig. 7c).
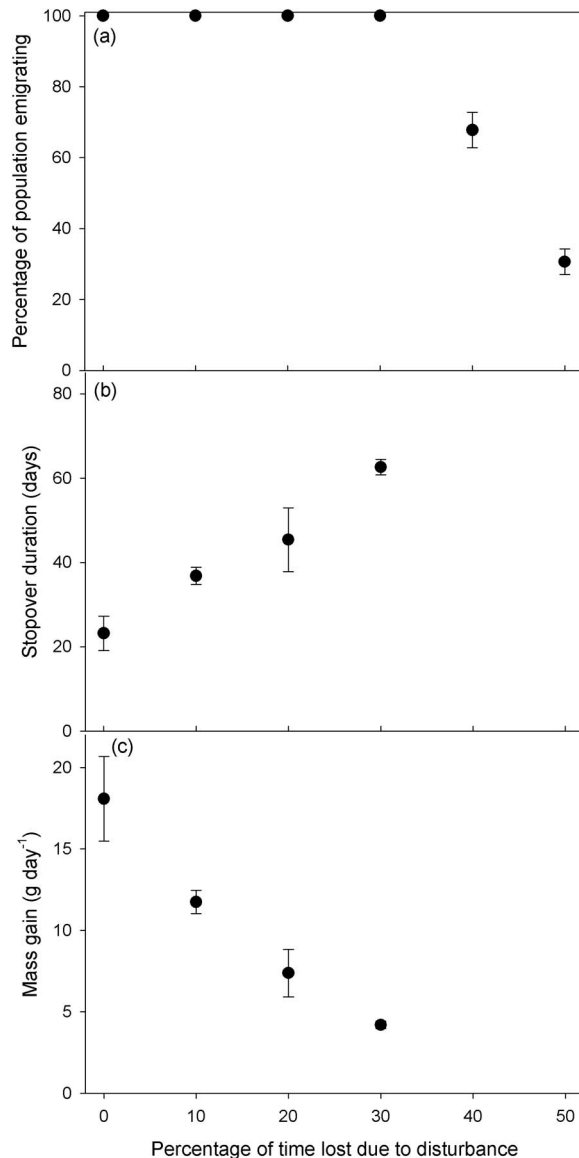
Fig. 7. Predicted mean (±SD) changes in (a) percentage of individuals emigrating successfully from Humboldt Bay, (b) stopover duration, and (c) rate of mass gain, in response to changes in disturbance within Humboldt Bay.

Discussion

Migratory species can be particularly sensitive to changes in their environment that affect their ability to acquire the resources needed to complete their migration and subsequent life cycle phases. Better understanding of the poten-

tial threats to migration can improve the conservation of these species. In this paper, we used a process-based model for a migratory species on a stopover site, validated against a range of observations from the real system, to assess the likely effects of four scenarios on the ability of the species to migrate through the stopover site.

Our model predicted that stopover duration and rate of mass gain of the birds were relatively insensitive to sea level rise. This happened because there were relatively small changes in the total biomass and extent of eelgrass due to sea level rise, and the total area of eelgrass was predicted to increase between 50 and 100 years into the future. The future distribution and biomass of eelgrass under the sea level rise scenarios were predicted from present-day relationships between biomass and elevation, assuming that eelgrass would be able to colonize areas higher on the shore in response to sea level rise (Shaughnessy et al. 2012). This was considered a realistic assumption given that there are at present no barriers (e.g., deep water or unfavorable sediment) that could prevent such movement. Substantial low-gradient intertidal mudflats capable of supporting eelgrass under various sea level rise scenarios in North and to a lesser degree, South Humboldt Bay provide for the potential shoreward migration of eelgrass habitat (Shaughnessy et al. 2012). The shoreward boundary of eelgrass would be anticipated to expand much more rapidly than the seaward boundary would contract. While it is conceivable that the channel network within the bay might expand somewhat as a consequence of sea level rise and an increase in hydraulic forces associated with more water moving in and out of the bay, these changes are unlikely to allow the shoreward migration of the steeper subtidal elevation profile to keep pace with that of the lower gradient intertidal elevation profile.

Predicted stopover duration and rate of mass gain were sensitive to changes in the total biomass of eelgrass. Any future reduction in total biomass of eelgrass within the site could adversely affect the successful migration of birds through the site. The current ongoing global declines in eelgrass populations (Waycott et al. 2009) therefore represent a substantial threat to the birds, compounded by lack of alternative food resources, in contrast with many other

waterfowl species, which exploit terrestrial food resources (e.g., Clausen et al. 2012, Wood et al. 2013). *Zostera japonica* is an invasive species of eelgrass which has the potential to compete with the native eelgrass (*Zostera marina*) on which the brant currently feed, and hence is another factor that could potentially decrease the biomass of the brant food supply. *Zostera japonica* is present in the Eel River estuary immediately south of Humboldt Bay and there are active efforts currently underway to monitor and eradicate it. It has been found in very low abundance in a few isolated locations around Humboldt Bay. Ongoing monitoring and eradication efforts seem to be keeping it from spreading. Its abundance is currently so low in Humboldt Bay that it does not at present provide a substantial threat to the overall biomass of native eelgrass. That said, it is likely to be continuously reintroduced by migratory waterfowl and will require ongoing management/vigilance to keep it from invading Humboldt Bay in the future.

The model predicted that the birds were sensitive to the time lost due to potential disturbance. The birds had a limited ability to compensate for lost time as access to their most profitable food resource (rooted eelgrass) was constrained by tidal cycle (Clausen 2000, Moore and Black 2006*a*). In order to meet their needs for energy and nutrients, herbivorous birds such as geese need to consume large quantities of vegetation (low nutritional quality) and thus devote large proportions of time feeding. Thus geese are sensitive to fluctuations in food availability and are frequently time limited, either by short day lengths or tidal cycles (e.g., Black et al. 2007). Disturbed birds may alter their behavior to meet their food requirements, for example by increasing foraging effort, altering when they feed in the day, shifting to a new food source, or moving to a new location along the flyway (Béchet et al. 2004, Mini and Black 2009). Due to tidal constraints which limit foraging opportunity, brant will have a limited capacity to increase their foraging effort. Inland feeding on terrestrial food resources by the Pacific Flyway brant population migrating through Humboldt Bay has only rarely been reported (see Moore et al. 2004). The last option, of moving to alternative staging area in the eastern Pacific Flyway is possible but the nearest alternative site to

Humboldt Bay is 400 km to south (Bedga Bay, California) and 500 km to the north (Coos Bay, Oregon). Moore and Black (2006*b*) document large variation in brant-use days at Humboldt Bay during periods of hunting within the bay. Current levels of disturbance at Humboldt Bay include a 22-day hunting season in November, and negligible amounts of fishing and clamming activities. The majority of brant use the southern portion of Humboldt Bay, which is within the jurisdiction of the U.S. Fish and Wildlife Service and Humboldt Bay National Wildlife Refuge. Our study suggests that when disturbance levels cause a >30% loss in feeding time, mass gain will decrease and stopover time increase for some geese, reducing their ability to continue migrating northward. Thus, our results suggest that geese are most sensitive to disturbance at low tide when the birds have access to their most profitable food.

Our model was based on current understanding of brant behavior and ecology, and eelgrass biology, but the process of building the model emphasized the need for a better estimation of some parameters. In particular, more data are required to better understand how the rate at which brant consume eelgrass declines as eelgrass biomass decreases towards zero. No field data were available to estimate this relationship within the study system and so we used an equation derived from another brant subspecies consuming a different species of eelgrass. The sensitivity analysis showed that the predictions of the model were sensitive to consumption rate, and the rate at which consumption rate declines at low food biomass will influence the total number of birds that can be supported within the site. Other studies of brant and wildfowl have shown that the general shape of the functional response is similar to that used in our model. Charman (1979) showed that the rate at which European brent geese consumed eelgrass increases as the percentage cover of eelgrass increased, approaching an asymptote at high eelgrass abundance. Wood et al. (2013) showed a similar shape of functional response in Mute Swan (*Cygnus olor* Gmelin) consuming an aquatic plant (*Ranunculus penicillatus* ssp. *pseudofluitans* (Webster)). The shape of the relationship used in our model was based on that expected from the mechanics of goose foraging behavior (Pettifor et

al. 2000). Although further information is required, we based our model on the latest understanding of the shape of the functional response in such wildfowl foraging systems.

Daily ration models (e.g., Charman 1979) are simpler than individual-based models, and typically predict the number of bird days that can be supported by a given food resource, from the food requirements of the birds and the amount of food. They do not include details such as the time for which feeding areas are available, or the rate at which food can be consumed by animals. There are two apparently counter-intuitive predictions of the individual-based model that highlight the difficultly of applying a daily ration approach to brant in Humboldt Bay. First, the model predicted that up to 300,000 birds could be supported by the eelgrass food resource in the bay, many more than the current population of 60,000 birds passing through the bay (Fig. 4). This is analogous to the type of prediction that would be derived from a daily ration model, and implies that there is a great surplus of eelgrass food in the bay. Second, the model predicted that the number of birds supported by the bay and their rates of mass gain were sensitive to 10–30% reductions in the biomass of eelgrass (Fig. 6), which implies that the amount of eelgrass in the bay is only just sufficient to support the current population. The apparent inconsistency can be explained by the time the eelgrass is available to the birds, and the effect of biomass density on their feeding rate. In a tidal habitat birds only have a limited time to feed on rooted eelgrass, and so their rate of mass gain depends on the rate at which they can consume this eelgrass, which itself depends on eelgrass biomass. Hence, a reduction in biomass reduces the rate at which birds can feed and gain enough mass for onward migration, even though the total biomass of eelgrass is much greater than the amount actually consumed by the birds. It is the rate at which birds can consume the food, rather than the total amount of food that is important, and daily ration models do not take account of these rates.

Our model was developed at Humboldt Bay because long-term data existed on brant and eelgrass that could be used to test a number of predictions and assess their likely reliability in future scenario predictions. Moving forward it will be important to develop such models in sites for which less data are available (e.g., other staging sites in the flyway). Individual-based models of shorebirds went through this evolution about a decade ago (Stillman and Goss-Custard 2010). Early models were based on one species, the Eurasian Oystercatcher (*Haematopus ostralegus*), within an intensively studied system, the Exe Estuary, UK. Steps allowing these models to be applied more rapidly to other shorebird species and systems included developing a reusable individual-based model, applicable to many systems rather than one (i.e., the MORPH model used in this paper), and predicting the foraging behavior of the birds from general principles rather than observing birds in each new study site (Stillman and Goss-Custard 2010). For example, Goss-Custard et al. (2006) showed how differences in the functional responses of shorebird species could be understood in terms of differences in bird and prey species size. Similarly, Wood et al. (2012b) conducted a meta-analysis of herbivorous waterfowl and found that maximum intake rate scaled with waterfowl body size. These approaches could potentially be used to understand the functional responses of herbivorous wildfowl species such as brant, explaining between species differences in terms of differences in bird species size, foraging mode (e.g., walking, swimming, upending) and vegetation structure.

Our predictions were for a single staging site, but have consequences for the flyway population of the birds. Approximately 75% of the Pacific Flyway population of brant winters in Mexico, and nearly 60% of those birds rely on Humboldt Bay as a spring staging site. Any factors that reduce the number of birds that can emigrate northwards from the bay, or increase the time taken to do so, will have consequences for survival and reproduction and hence overall population size (sensu Moore et al. 2004). We identified declines in eelgrass biomass and increases in disturbance as such factors. Our simulations also suggested that Humboldt Bay could potentially support more birds than it does currently assuming that current eelgrass biomass was unchanged.

In this paper we have demonstrated how a process-based model can be developed and validated for a migratory wildfowl species, and

used to quantify possible threats posed by future changes in sea level, food abundance and disturbance. A wide range of migratory species responses are expected in conjunction with environmental change, and such process-based models offer powerful tools to predict such responses and understand the mechanisms which underpin them.

ACKNOWLEDGMENTS

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