

Predicted eelgrass response to sea level rise and its availability to foraging Black Brant in Pacific coast estuaries

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Abstract. Managers need to predict how animals will respond to habitat redistributions caused by climate change. Our objective was to model the effects of sea level rise on total eelgrass (*Zostera marina*) habitat area and on the amount of that area that is accessible to Brant geese (*Branta bernicla*), specialist grazers of eelgrass. Digital elevation models were developed for seven estuaries from Alaska, Washington, California (USA), and Mexico. Scenarios of future total eelgrass area were derived from combinations of estuarine specific sediment and tectonic rates (i.e., bottom change rate) with three rates of eustatic sea level rise (ESLR). Percentages of total eelgrass areas that were accessible to foraging Brant were determined for December when the birds overwinter at more southerly sites and in April as they move north to sites where they build body stores on their way to nesting areas in Alaska. The modeling showed that accessible eelgrass area could be lower than total area due to how daytime low-tide height, eelgrass shoot length, and the upper elevation of eelgrass determined Brant-reaching depth. Projections of future eelgrass area indicated that present-day ESLR (2.8 mm/yr) and bottom change rates should sustain the current pattern of estuarine use by Brant except in Morro Bay, where use should decrease because eelgrass is being ejected from this estuary by a positive bottom change rate. Higher ESLR rates (6.3 and 12.7 mm/yr) should result in less Brant use of estuaries at the northern and southern ends of the flyway, particularly during the winter, but more use of mid-latitude estuaries. The capacity of mid-latitude estuaries to function as Brant feeding refugia, or for these estuaries and Izembek Lagoon to provide drift rather than attached leaves, is eventually limited by the decrease in total eelgrass area, which is a result of a light extinction affect on the eelgrass, or the habitat being pushed out of the estuary by positive tectonic rates. Management responses are limited to the increase or decrease of sediment supply and the relocation of levees to allow for upslope migration of eelgrass habitat.

Key words: Brant geese; *Branta bernicla*; eelgrass; Pacific estuaries; sea level rise; sediment; tectonic change; *Zostera marina*.

INTRODUCTION

Sea level rise and other components of climate change, such as ocean acidification, increasing sea surface temperatures, and storm frequencies, could alter the distribution and productivity of coastal marine habitats and the animal populations they support (Short and Neckles 1999, Wang and Swail 2001, Behrenfeld et al. 2006, Orth et al. 2006, Doney et al. 2009). The occupation of habitats by animals is generally related to the relative ease of acquiring resources needed for survival and breeding, while avoiding disturbance, predation, and disease (Krebs and Davies 1993, Sutherland et al. 2002, Krebs 2009). In the face of uncertainty about global climate and sea level, managers are

increasingly in need of information to predict how animals will respond to changing habitats (Goss-Custard and Sutherland 1997, Root and Schneider 2002, Parmesan 2006). For example, managers of migratory flyways may need to determine how many geese particular habitats can support within a migratory range that may change over time (Sutherland 1996, Pettifor et al. 2000, Bauer et al. 2008, Jensen et al. 2008, Wisz et al. 2008).

Seagrasses, primarily eelgrass (*Zostera marina*) in the Northeast Pacific, are a habitat type on which migratory Brant geese (*Branta bernicla*) forage during their nine month nonbreeding period (Baldwin and Lovvorn 1994a, b, Reed et al. 1998, Ganter 2000). Brant are capital breeders relying on body stores acquired in more southerly wintering and spring staging locations to meet some, if not all, energy demands of egg-laying, incubation, and brood-rearing on arctic or subarctic breeding grounds (Drent and Daan 1980, Owen 1980,

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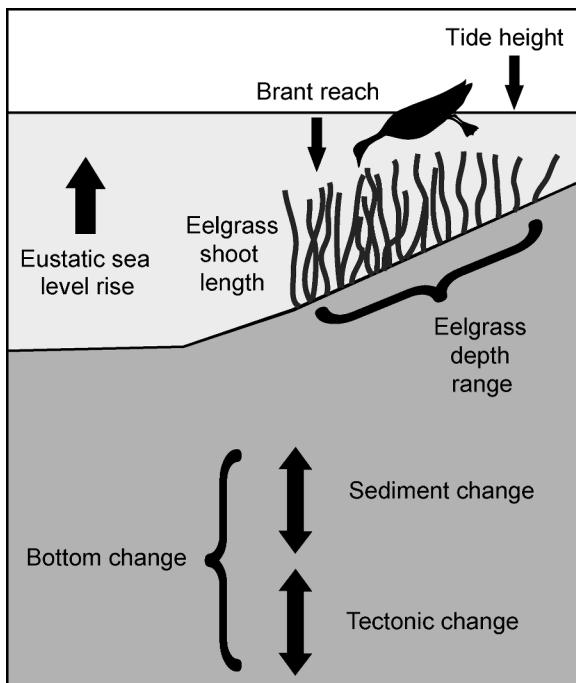


FIG. 1. The interaction between eustatic sea level rise (ESLR) and the change in elevation at the bottom of each estuary due to sediment and tectonic change, as well as the variables acting independently of the sea level rise process that affect access of Brant (*Branta bernicla*) to attached eelgrass leaves (*Zostera marina*).

Ankney 1984, Drent et al. 2006, 2007). The Brant goose in the eastern Pacific flyway is unique in that it still makes exclusive use of estuarine seagrasses as they move from wintering areas in Mexico (70% of population) to spring staging areas in coastal California, the Pacific northwest, and the Alaska Peninsula before moving to breeding areas in southwest Alaska (75% of population; Reed et al. 1998, Moore et al. 2004, Ward et al. 2005). Loss of eelgrass habitat during the nonbreeding season on the Pacific coast may severely impact Brant numbers and distribution, forcing them, as has already occurred on the eastern seaboard in the USA, and in Europe, to move to salt marsh habitat if available or inland to golf courses and agricultural pastures where competition occurs with livestock (Vickery et al. 1995, Ganter et al. 1998, Ward et al. 2005).

Since the amount and quality of eelgrass available to foraging Brant may be affected by changing sea level, the objective of this study was to prepare spatial models that describe potential changes in eelgrass abundance in seven west coast estuaries in Alaska, Washington, California (USA), and Mexico over 100 years so that estuarine and waterfowl managers may better anticipate potential changes in this plant–herbivore relationship. The persistence of marine habitats such as eelgrass beds depends, in part, on the balance between the vertical rates of eustatic (i.e., global) sea level rise (ESLR) vs. the

estuarine specific rates of sediment elevation change (i.e., based on sedimentation, compaction, and erosion) and tectonic elevation change (i.e., based on rates of interseismic uplift or subsidence). These two local processes (hereafter sediment change and tectonic change) combine to produce an overall rate of bottom elevation change (Fig. 1). An eelgrass ejection effect occurs when the rate of bottom change surpasses the ESLR rate and the eelgrass cannot survive the levels of desiccation and wave energy occurring at shallower depths into which it is being pushed (Fonseca and Bell 1998, Koch 2001, Boese et al. 2005). Different to the ejection effect, a light extinction effect on the eelgrass occurs when the rate of bottom change is slower than the ESLR rate and so eelgrass eventually does not receive enough light to maintain a positive carbon balance (Zimmerman et al. 1995, 2006, Short and Neckles 1999), and this effect is enhanced if bottom change is negative due to sediment compaction or tectonic subsidence. Light extinction in this context is, therefore, due to water depth and not water quality, although the latter could delay or accelerate this effect. The strength of the extinction effect on total eelgrass area is influenced by the amount of intertidal and upland area capable of accommodating a landward shift in eelgrass distribution. If this area is sufficient, then even though light levels decrease due to increasing depth, total eelgrass area may actually increase. Where expansion is constrained by natural and artificial shoreline barriers, then eelgrass area will decrease because there is less habitable upland space (Short and Neckles 1999).

The total size of an eelgrass bed upon which Brant may feed can therefore be changed by the balance between eustatic sea level rise and local bottom elevation change. Furthermore, due to how and when Brant feed, the eelgrass area available to the geese for grazing on attached leaves is potentially less than the total habitat area. As ebbing tides reach mid-intertidal elevations, Brant move from roost and gritting sites to eelgrass meadows where they reach down to remove attached leaves floating upright in the water column (Moore and Black 2006a). Variables that are independent of the sea level rise process and which affect access to these leaves include the reaching depth of the Brant, the height of the daytime tide height when the birds feed, eelgrass shoot length, and the upper vertical limit of eelgrass (Fig. 1).

These independent variables that determine Brant accessibility to eelgrass vary among estuaries spanning the Brant migratory range in the northeast Pacific. It is also the case that these estuaries demonstrate a wide variety of bottom change directions, rates, and upland slopes, and so the consequences of ESLR for total eelgrass habitat size will vary among estuaries. In contrast to the habitat survival models developed for salt marshes and mangrove swamps that incorporate interactions between vegetation and sediment (de Boer 2007, Koch et al. 2009, Kirwan and Guntenspergen 2010), the present cross-trophic model uses linear

TABLE 1. Brant goose (*Branta bernicla*) peak counts (sources given in footnotes) and eelgrass (*Zostera marina*) habitat area based on published studies (see Appendix for sources) and the total eelgrass area modeled in the present study for seven key Pacific flyway estuaries.

Estuary	No. Brant in winter	No. Brant in spring	Eelgrass habitat extent (ha) and year of estimate	Modeled total eelgrass habitat (ha)
Izembek Lagoon, Alaska, USA (IL)	26 443†	52 000‡	15 915 (1995)	21 784
Padilla Bay complex, Washington, USA (PBC)	6 002†	26 000§	4 342 (1996)	7 423
Willapa Bay, Washington, USA (WB)	2 250§	11 000§	3 427 (1997)	4 440
North Humboldt Bay, California, USA (NHB)	1 322‡	4 293¶	802 (2010)	1 254
South Humboldt Bay, California, USA (SHB)	5 049‡	20 958¶	788 (2006)	888
Morro Bay, California, USA (MB)	2 150†	3 100‡	40–174 (1994–2009)	373
Bahia San Quintin, Mexico (BSQ)	28 685#	38 000‡	1 949 (1999)	2 456

† Collins and Trost (2010).

‡ Moore et al. (2004).

§ Wilson and Atkinson (1995).

¶ Calculation based on 83% of complete count in SHB and 19% in NHB (Moore and Black 2006b).

Mallek et al. (2010).

bottom change rates to assess eelgrass habitat survival and its accessibility to Brant because the sediment trapping capability of eelgrass should be less than for marsh plants and mangrove trees. Our model is a first approximation of how sea level rise could affect total eelgrass area and food availability for the Brant at the scale of each estuary and the entire flyway.

METHODS

Study species and study sites

Brant geese are thought to have coevolved with coastal seagrasses, primarily eelgrass, on which they feed (Owen 1980, Ganter 2000, Moore et al. 2004). Once on the breeding grounds, these geese switch from a seagrass diet to emerging saltmarsh plants (e.g., sedges, grasses, and arrowgrass *Triglochin* spp.) a few centimeters above sea level (Person et al. 1998, 2003, Person and Ruess 2003). After breeding and the molt at the end of summer, most Brant congregate at Izembek Lagoon, the main staging site on the lower Alaska Peninsula, USA, returning to an eelgrass-rich diet, before migrating to Mexico (Reed et al. 1989b, Dau 1992). Brant geese in this flyway are managed as two separate populations, currently numbering $141\,749 \pm 40\,29$ (mean \pm SE) dark-feathered, Black Brant (*B. b. nigricans*) and $10\,495 \pm 3013$ light-colored, Western High Arctic Brant (three-year averages; Collins and Trost 2010). The latter variety has not received subspecies designation (Boyd et al. 1988, Reed et al. 1989a, Shields 1990). We chose seven key estuaries where eelgrass habitat had been mapped, including Izembek Lagoon Alaska (hereafter, referred to as IL; $55^{\circ}19'05''$ N, $162^{\circ}50'40''$ W); the Padilla Bay complex, Washington, USA (PBC; $48^{\circ}32'12''$ N, $122^{\circ}31'49''$ W); Willapa Bay, Washington, USA (WB; $46^{\circ}32'22''$ N, $123^{\circ}59'19''$ W); the North and South sections of Humboldt Bay, California, USA (NHB; $40^{\circ}49'57''$ N, $124^{\circ}07'48''$ W, SHB; $40^{\circ}43'01''$ N, $124^{\circ}14'15''$ W); Morro Bay, California, USA (MB; $35^{\circ}20'20''$ N, $120^{\circ}50'48''$ W); and Bahia San Quintin, Mexico (BSQ; $30^{\circ}25'10''$ N, $115^{\circ}58'24''$ W). The Padilla Bay complex (PBC) consisted of Padilla Bay and the

two adjacent bays, Fidalgo and Samish. The relative use of all these estuaries by Brant as indicated by field surveys, eelgrass area based on existing imagery, and the total amount of eelgrass area we modeled is provided in Table 1.

Digital elevation models

New digital elevation models (DEMs) were developed for IL, PBC, and BSQ using ArcGIS 9.2 software Z(ESRI 1999–2006). Source data used to develop DEMs and model input scenarios are given in the Appendix. DEMs for IL, PBC, and BSQ were generated from depth survey data and aerial imagery using inverse distance weighted (IDW) interpolation. The DEM of IL was produced by taking field measurements of depth relative to mean lower low water (MLLW), in conjunction with 1:36 000-scale aerial imagery from Ward et al. (1997) delineating eelgrass and other major habitat types across the lagoon. Shuttle Radar Topography Mission digital elevation data for surrounding upland terrain was fused with lagoon bathymetry data to complete the DEM. National Land Cover Data was then used in conjunction with the DEM to identify low-lying terrain that was both susceptible to future inundation and capable of supporting eelgrass based on inferred substrate suitability; land cover classes that were considered potentially suitable to eelgrass included “Barren Land” (intertidal mudflats), as well as several classes of woody and herbaceous vegetative cover indicative of underlying unconsolidated substrate. The DEM for PBC was derived from historic hydrographic survey data (Appendix). Since the easternmost portion of the intertidal mudflats in Samish Bay lacked sounding data, depths were estimated by visual interpretation of the extent of mudflat and salt marsh vegetation identified from imagery (Appendix). For BSQ, imagery classified from digital multispectral videography (Ward et al. 2004) was used in conjunction with depth data referenced to local MLLW (Ward et al. 2003, Ward 2006) to generate a DEM. Information describing the depth range occupied by regional salt marsh species

TABLE 2. Model inputs for present-day (†) and alternative sea level rise scenarios and the eelgrass parameters necessary to model the distribution of this habitat.

Characteristic	Estuary [tectonic change, sediment change] and ESLR (mm/yr)	
	IL	PBC
A) Sea level rise scenario		
Low bottom change and low ESLR	[0, 0] 2.8†	[1.5, -3] 2.8†
Low bottom change and moderate ESLR	[0, 0] 6.3	[1.5, -3] 6.3
Low bottom change and high ESLR	[0, 0] 12.7	[1.5, -3] 12.7
High bottom change and low ESLR	[0, 2] 2.8	[1.5, 0] 2.8
High bottom change and moderate ESLR	[0, 2] 6.3	[1.5, 0] 6.3
High bottom change and high ESLR	[0, 2] 12.7	[1.5, 0] 12.7
B) Eelgrass inputs		
Eelgrass depth range (m MLLW): low, high	-1.6, 0.9	-3, 0.5
Eelgrass shoot length (m): Dec, Apr	0.15, 0.35	0.25, 0.75
Maximum depth of eelgrass available to Brant during Dec (m MLLW)	0.19	1.12
Maximum depth of eelgrass available to Brant during Apr (m MLLW)	-0.77	-1.66

Notes: There are three rates (mm/yr) for each scenario and estuary: tectonic change, sediment change, and eustatic sea level rise (ESLR). Bottom change is the combination of tectonic and sediment change. Sediment change values were added to the range of tectonic values for NHB and SHB. Maximum depths of eelgrass available to Brant depend on eelgrass vertical range limits, eelgrass shoot length, and daytime low-tide height. MLLW stands for mean lower low water. See see *Methods: Digital elevation models* and the Appendix for input sources, and Table 1 for estuary abbreviations and locations.

(MacDonald 1969, Zedler 1982) was used to estimate marsh elevations above the upper limit of eelgrass in order to extend the BSQ DEM to areas where explicit depth data were lacking and where eelgrass would be expected to migrate in response to rising sea level.

Existing DEMs were adapted for NHB, SHB, WB, and MB. For both NHB and SHB, the Humboldt Bay Fusion DEM (Appendix) was used as the foundation for modeling. Gilkerson (2008) modified the DEM by referencing it to local mean MLLW and by supplementing areas of intertidal channels with depth soundings from a digitized nautical chart (Appendix) prior to model development. In WB, a DEM referenced to MLLW (Appendix) was used as a foundation for modeling. A DEM of MB was generated from the Port San Luis DEM (Appendix). The latter DEM was clipped to limit the extent of the model area for MB and adjusted from a vertical reference of mean high water to MLLW in meters, using tidal data (Appendix). Recent imagery depicting salt marsh extent (Appendix) was used in conjunction with elevation estimates of regional salt marsh species (Zedler 1982) in order to update the MB DEM where depth data were insufficient and where eelgrass would be expected to migrate in response to rising sea level.

Future bathymetries for each estuary were modeled in 25-year increments for the next 100 years by adjusting each DEM for ESLR, tectonic, and sediment change. We chose three alternative scenarios representing low, moderate, and high ESLR rates for model input (Table 2). The low ESLR rate scenario (2.8 mm/yr) was from the current estimated ESLR rate for the Pacific Ocean basin based on satellite altimetry (Appendix), the moderate ESLR rate scenario (6.3 mm/yr) was derived from the mean rate estimated for the period 2090–2099 for IPCC AR4 scenario A1FI (Meehl et al. 2007), and

the high ESLR rate scenario (12.7 mm/yr) was based on a study linking global sea level rise to projections of global mean surface temperature (Rahmstorf 2007). Sea level rise can potentially increase the tidal prism and potentially change the tidal range in an estuary (Short and Neckles 1999). This factor was not included in our model because existing data was insufficient for projecting potential future changes in tidal circulation.

Tectonic, volcanic, and isostatic rebound processes influence local sea level in many coastal areas from Alaska to Northern California (Verdonck 2006, Freymueller et al. 2008, Burgette et al. 2009). For estuaries associated within the Cascadia subduction zone (e.g., PBC, WB, NHB, SHB), subduction of plates leads to a cycle of interseismic strain accumulation and subsequent coseismic strain release manifest as great earthquakes with a recurrence interval of 220–520 years (Goldfinger et al. 2008). The large amount of subsidence resulting from this type of earthquake is not modeled in this study. However, recently refined rates of interseismic vertical land movement (i.e., tectonic change) derived from leveling surveys and tidal gauging records provide us with estimates of vertical land movement rates, ranging from ~4 mm/yr to -3 mm/yr for most of this region (Table 2; Flück et al. 1997, Verdonck 2006, Burgette et al. 2009). For IL, MB, and BSQ, interseismic uplift rates were negligible for the timescale of our model (Lettis and Hall 1994, Orme 1999, Merritts and Bull 1989; J. T. Freymueller, *personal communication*) and set at zero (Table 2). For NHB and SHB, where the intra-estuarine gradient in interseismic uplift rate was projected to be steep, we developed a raster surface representing interseismic uplift rate 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.

TABLE 2. Extended.

Estuary [tectonic change, sediment change] and ESLR (mm/yr)				
WB	NHB	SHB	MB	BSQ
[1.5, 0] 2.8†	[0.7 to 3.1, 1] 2.8†	[-0.5 to 1.7, 1] 2.8†	[0, 3] 2.8	[0, 3] 2.8
[1.5, 0] 6.3	[0.7 to 3.1, 1] 6.3	[-0.5 to 1.7, 1] 6.3	[0, 3] 6.3	[0, 3] 6.3
[1.5, 0] 12.7	[0.7 to 3.1, 1] 12.7	[-0.5 to 1.7, 1] 12.7	[0, 3] 12.7	[0, 3] 12.7
[1.5, 2] 2.8	[0.7 to 3.1, 3] 2.8	[-0.5 to 1.7, 3] 2.8	[0, 6] 2.8†	[0, 6] 2.8†
[1.5, 2] 6.3	[0.7 to 3.1, 3] 6.3	[-0.5 to 1.7, 3] 6.3	[0, 6] 6.3	[0, 6] 6.3
[1.5, 2] 12.7	[0.7 to 3.1, 3] 12.7	[-0.5 to 1.7, 3] 12.7	[0, 6] 12.7	[0, 6] 12.7
-1.5, 0	-1.3, 0.3	-2.1, 0.4	-1.5, 0.4	-2.9, 0.5
0.4, 0.9	0.65, 0.8	0.6, 0.6	0.6, 0.6	0.4, 0.4
-0.52	-1.23	-1.18	-1.27	-1.07
-1.6	-1.44	-1.24	-1.15	-0.82

Local sea level is also affected by the rate of vertical movement of the sediment surface (i.e., sediment change) in an estuary, which is influenced by sediment supply and quality, tidal elevation, tidal asymmetry, compaction, erosion, and vegetation (Thom 1992, Callaway et al. 1996, Kirwan and Murray 2007, Peralta et al. 2008, Moore et al. 2009, Kairis and Rybczyk 2010). Maintenance of sediment surface elevation with respect to sea level at the estuary scale requires an adequate sediment supply to offset elevation loss associated with erosion, compaction, and ESLR (Cahoon 1997). Because of the desirability of including a sediment change rate that could be used as a management target, two sediment change rates were used for each estuary (Table 2). Estimations of relevant sedimentation rates were based on sediment elevation table (SET) table studies or, preferably, approaches that captured long-term sediment accretion that would include episodic sediment additions (e.g., floods) and compaction. The latter approaches included dated sediment cores or, when those were lacking, we compared historic sounding data to recent bathymetry or sediment change rates from similar estuaries in a region (Appendix). Rates were applied uniformly across each estuary.

The choice of three ESLR rates to be applied across all seven estuaries, one tectonic change value for each estuary except for SHB and NHB, and two sediment change values for each estuary allowed us to model six scenarios (one present-day, and five alternative) for each estuary (Table 2). The scenario names were shortened by making them reflect the two variables that ultimately determined the distance between the bottom and the water surface: the bottom change and ESLR rates. The designation of which of the six-model scenario represented present-day sea level rise conditions was based on the current estimated rates of ESLR and bottom change.

Determining total eelgrass habitat area

Present-day vertical depth ranges of eelgrass in each estuary (Table 2), as well as substrate suitability, were

used in conjunction with DEMs to delineate eelgrass habitat footprints. Areas of estuaries exposed to open ocean swell, where the wave environment would likely preclude eelgrass establishment, were masked and excluded from our models. Substrate suitability was determined from intertidal habitat and land cover imagery and nautical chart datasets (Appendix). These data sets were overlaid with DEMs of each estuary to restrict model footprints to areas considered capable of supporting eelgrass both currently, as well as in the future, under assumptions of increased relative sea level up to existing levees and natural barriers. We assumed that both the tidal range and depth distribution of eelgrass remain constant relative to mean sea level through time in each estuary. Starting dates for model initiation in each estuary (Table 2) were based on the year of publication or development of the DEM used to support modeling.

Eelgrass depth range inputs are variable both within and among bays (Table 2). For estuaries where site-specific data were available and depicted significant variation (e.g., IL, WB, NHB, SHB, and MB), we used IDW interpolation to model variation in either eelgrass maximum depths, upper limits, or both. In estuaries where a single value representing the upper or lower eelgrass elevation limit was reported, these values were used to identify the portions of the model DEMs where elevations would be suitable to eelgrass. For each modeled estuary, classified aerial imagery (Appendix) was used to infer substrate suitability on the basis of land cover categories to identify areas capable of supporting eelgrass; categories depicting developed areas were excluded from the analysis, whereas those depicting wetlands or unconsolidated sediments were deemed capable of supporting eelgrass.

For WB, upper and lower eelgrass elevations used to model total eelgrass habitat were 0 m and -1.5 m MLLW, respectively (Thom et al. 2003). An analysis mask was created to exclude the bay entrance from the model where waves and currents would be unfavorable

to eelgrass growth. In NHB, upper and lower eelgrass elevations were ~ 0.3 m and -1.3 m MLLW, respectively (Gilkerson 2008). For SHB, the depth range of eelgrass was 0.4 m to -2.1 m MLLW (Gilkerson 2008). For both NHB and SHB, upper eelgrass elevation limits were determined by overlaying eelgrass imagery (Judd 2006; NOAA Digital Coast Benthic Cover Data: California–Humboldt Bay and Eel River Estuary, *available online*)⁷ with Humboldt Bay DEMs. The upper and lower eelgrass elevations used to determine the extent of potential eelgrass habitat in MB were 0.2 m and -1.6 m MLLW, respectively (R. Thom and A. Borde, *unpublished report*).

In IL, the eelgrass depth range used for total eelgrass habitat was 0.9 to -1.6 m (Ward et al. 1997, 2009). An analysis mask was created to exclude areas near the Bering Sea where ocean swell would preclude the establishment of eelgrass despite the otherwise suitable elevation and substrate. Upper and lower eelgrass elevations reported for PBC (0.5 m and -3.0 m MLLW; Thom 1990, Bulthuis 1995) were used for this complex. For BSQ, the eelgrass depth range applied to the model was 0.5 to -2.9 m MLLW (Ward et al. 2003, Ward 2006).

The choice of upper and lower elevation limits for eelgrass may have a large effect on the size of the modeled eelgrass footprint. Upper eelgrass limits can be particularly difficult to delineate, even at one site within an estuary, depending upon whether or not the focus is on the upper limit of continuous vs. patchy eelgrass, and because both upper limits vary across sites within an estuary in a given year (Thom et al. 2003, Gilkerson 2008, Ruesink et al. 2010). We used more conservative upper elevation limits that come closer to describing the average upper edge of continuous eelgrass in each estuary because the majority of Brant feeding activity occurs where eelgrass growth is continuous. When the literature reported a wide range of upper limits, as in the case of WB (0.0 – 0.6 m MLLW; Thom et al. 2003, Ruesink et al. 2010), the lower of these two values was used because it resulted in a present-day eelgrass footprint that was more similar to historic and recent estimates of WB eelgrass area (Borde et al. 2003, Ruesink et al. 2006).

Determining Brant accessibility to eelgrass

We assume that Brant foraging would be restricted to daylight conditions when the birds rely on visual cues to locate optimal foraging areas (Moore and Black 2006a). Feeding during moonlit nights (Madsen 1988, Lane and Hassall 1996) has not been quantified at our study sites. Sunrise and sunset times were determined for each estuary during December and April staging periods to identify the low tides occurring during daylight hours by using the U.S. Naval Observatory's day length calcula-

tor (Appendix). Brant can reach 0.4 m into the water column (Clausen 2000), but some overlap is required with plant height for a bird to obtain younger leaves, which are shorter and more desirable than older leaves (Moore and Black 2006a). Most feeding occurs within ~ 0.15 m of the water surface (Moore and Black 2006a). The current proportion of eelgrass area accessible (i.e., reachable) to Brant that could begin to forage 0.15 m below the water surface was based on, for each estuary, published estimates (Appendix) of eelgrass shoot lengths, the upper and lower eelgrass depth limits (Table 1), and daylight low-tide heights relative to MLLW. This was done in each estuary during both winter (December) and spring (April) staging periods. We then applied the same methodology to model the proportion of future eelgrass habitat expected to be available to Brant for each scenario.

RESULTS

Total eelgrass area

Model estimates of future total eelgrass area using present-day sea level rise conditions fell into two general groups: estuaries that increased eelgrass area across the 100 years (IL, PBC, WB, SHB) and those where area decreased immediately or after 50 years (NHB, MB, BSQ). For the first group, the present-day scenario of low ESLR and low bottom change resulted in a steady expansion of eelgrass area, especially for IL and PBC (Fig. 2). The 100-year area increases for the four estuaries in this group ranged from 6% to 12% (Table 3). Total eelgrass area in the second group (NHB, MB, BSQ) declined from the present-day scenario, though estimates varied among the three estuaries (Fig. 2). The range of bottom change values for NHB that were generated by the tectonic output from the Flück et al. (1997) model, in combination with a low ESLR rate, resulted in -30% loss of eelgrass area after 100 years (Fig. 2, Table 3). In MB and BSQ, the present-day high bottom change and low ESLR scenario resulted in either an immediate (MB) or delayed (BSQ) loss of eelgrass area (Fig. 2). The -64% loss in area in MB, based on present-day inputs, was greater than the losses for any of the other six estuaries (Table 3). All the present-day scenarios in this group of three estuaries had faster bottom change rates than ESLR rates (Fig. 1).

Alternative scenarios where at least one model component, ESLR or bottom change, was not a present-day condition usually resulted in the fastest rates of total eelgrass area increase or decrease. Low bottom change and high ESLR produced the fastest rates of habitat expansion up to 75 years after which the first group of four estuaries (IL, PBC, WB, SHB) either declined or leveled in eelgrass area (Fig. 2). The bottom change rate was much slower than the ESLR rate for this alternative scenario. The scenario producing the lowest area projections in this group of four estuaries was the combination of high bottom change and low

⁷ <http://www.csc.noaa.gov/digitalcoast/data/benthiccover/download>

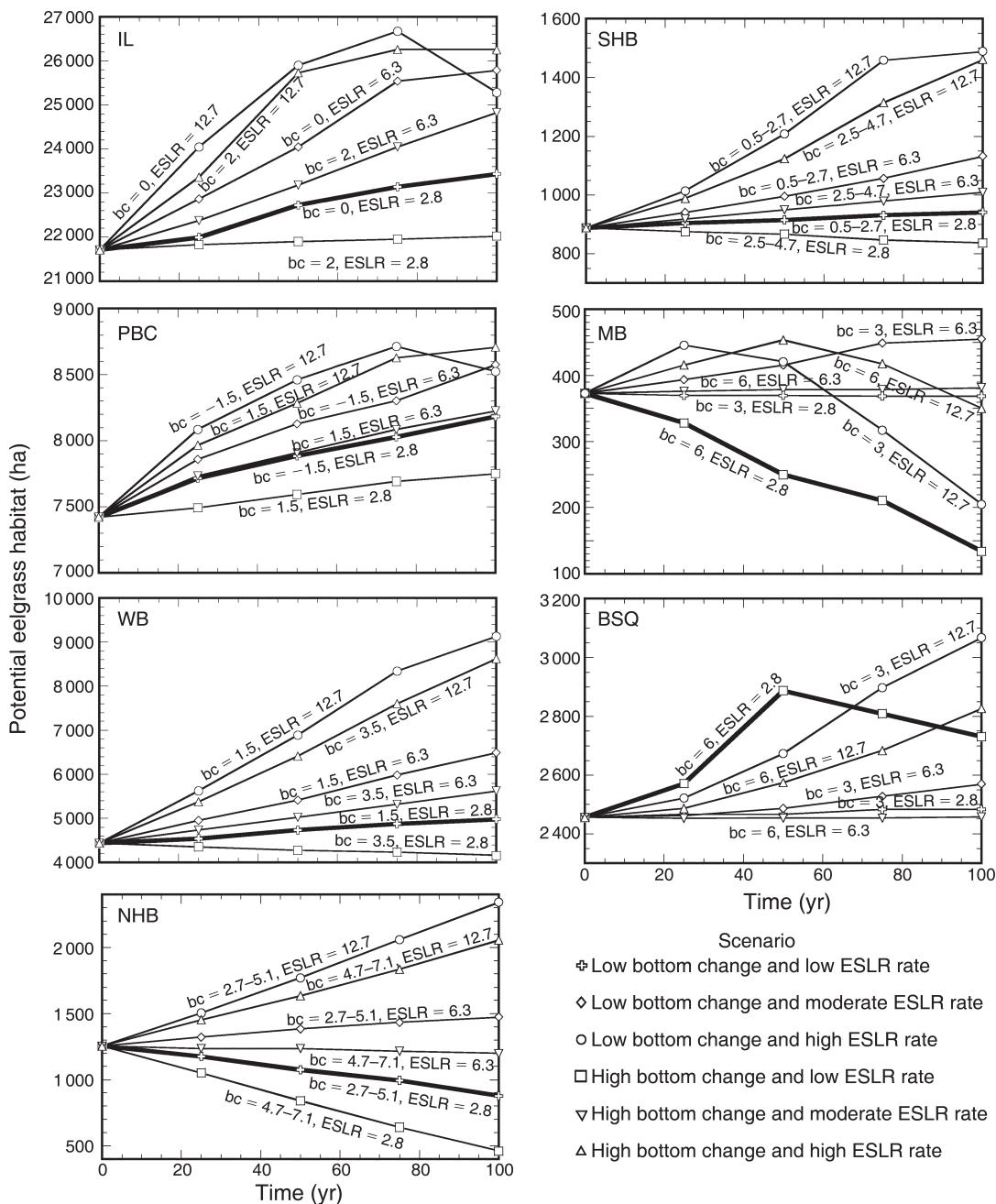


FIG. 2. Present-day (thick line) and alternative projections (thin lines) of potential total eelgrass area over 100 years in each estuary. Bottom change (bc; in mm/yr) equals tectonic change plus sediment change, and ESLR represents eustatic sea level rise (in mm/yr). See Table 2 for the specific tectonic and sediment rates that determine bc. Estuaries are: Izembek Lagoon Alaska, USA (IL); the Padilla Bay complex, Washington, USA (PBC); Willapa Bay, Washington, USA (WB); North Humboldt Bay, California, USA (NHB); South Humboldt Bay, California, USA (SHB); Morro Bay, California, USA (MB); and Bahia San Quintin, Mexico (BSQ).

ESLR. While it resulted in a 4% increase for PBC, the projected area changes for IL, WB, and SHB were 1%, -6%, and -6%, respectively (Fig. 2, Table 3). In the second group of estuaries (NHB, MB, BSQ) the fastest, most sustained expansion rate for eelgrass area resulted from the alternative scenario of low bottom change and high ESLR for NHB and BSQ, which increased by 87%

and 25%, respectively, whereas low bottom change combined with moderate ESLR produced the most sustained expansion for MB (22%; Fig. 2, Table 3). The greatest loss in area for NHB (-63%) and BSQ (0%) resulted from, respectively, the scenarios of high bottom change and low ESLR, and high bottom change and moderate ESLR (Fig. 2, Table 3).

TABLE 3. Modeled percentage change in eelgrass habitat area over 100 years for each present-day (in boldface type) and alternative sea level rise scenarios for each estuary.

Estuary and scenario	Percentage change in eelgrass		
	Total	December	April
Izembek Lagoon (IL)			
Low bottom change and low ESLR	8	-37	5
Low bottom change and moderate ESLR	19	-75	6
Low bottom change and high ESLR	16	-98	-45
High bottom change and low ESLR	1	-11	1
High bottom change and moderate ESLR	14	-60	9
High bottom change and high ESLR	21	-86	-22
Padilla Bay complex (PBC)			
Low bottom change and low ESLR	10	0	5
Low bottom change and moderate ESLR	16	0	4
Low bottom change and high ESLR	15	0	-16
High bottom change and low ESLR	4	0	4
High bottom change and moderate ESLR	11	0	4
High bottom change and high ESLR	17	0	-3
Willapa Bay (WB)			
Low bottom change and low ESLR	12	3	12
Low bottom change and moderate ESLR	46	14	46
Low bottom change and high ESLR	106	74	106
High bottom change and low ESLR	-6	-7	-6
High bottom change and moderate ESLR	27	6	27
High bottom change and high ESLR	94	76	94
North Humboldt Bay (NHB)			
Low bottom change and low ESLR	-30	-30	-30
Low bottom change and moderate ESLR	18	18	18
Low bottom change and high ESLR	87	87	87
High bottom change and low ESLR	-63	-63	-63
High bottom change and moderate ESLR	-5	-5	-5
High bottom change and high ESLR	64	64	64
South Humboldt Bay (SHB)			
Low bottom change and low ESLR	6	6	6
Low bottom change and moderate ESLR	27	28	28
Low bottom change and high ESLR	68	69	69
High bottom change and low ESLR	-6	-7	-7
High bottom change and moderate ESLR	14	14	14
High bottom change and high ESLR	64	66	65
Morro Bay (MB)			
Low bottom change and low ESLR	-1	-2	-2
Low bottom change and moderate ESLR	22	22	22
Low bottom change and high ESLR	-45	-45	-45
High bottom change and low ESLR	-64	-64	-64
High bottom change and moderate ESLR	2	2	2
High bottom change and high ESLR	-6	-6	-6
Bahia San Quintin (BSQ)			
Low bottom change and low ESLR	1	0	1
Low bottom change and moderate ESLR	5	-9	-17
Low bottom change and high ESLR	25	-24	-31
High bottom change and low ESLR	11	-5	2
High bottom change and moderate ESLR	0	1	-1
High bottom change and high ESLR	15	-20	-23

Notes: Total eelgrass refers to the entire eelgrass habitat, whereas the December and April values describe only the percentage change in the eelgrass area that is accessible to Brant during each month. See Table 1 for estuary locations.

December and April accessible eelgrass

The year-zero amount of accessible eelgrass area (hereafter called "starting amount") during December in IL, PBC, WB, and BSQ was, respectively, -44.9%, -100%, -28%, and -21.3% less than the year-zero total amount of area in each of these estuaries (Figs. 2 and 3, Table 3). The amount of December eelgrass area

projected under current day sea level rise conditions either showed modest changes (i.e., 6% to -5% for SHB, WB, BSQ) or large losses after 100 years (i.e., -30% to -100% for NHB, IL, MB, PBC; Fig. 3, Table 3). Although daytime tides are lower and eelgrass leaves are longer in April, the starting amount of April eelgrass in IL, PBC, and BSQ was, respectively, -5.1%, -13.9%,

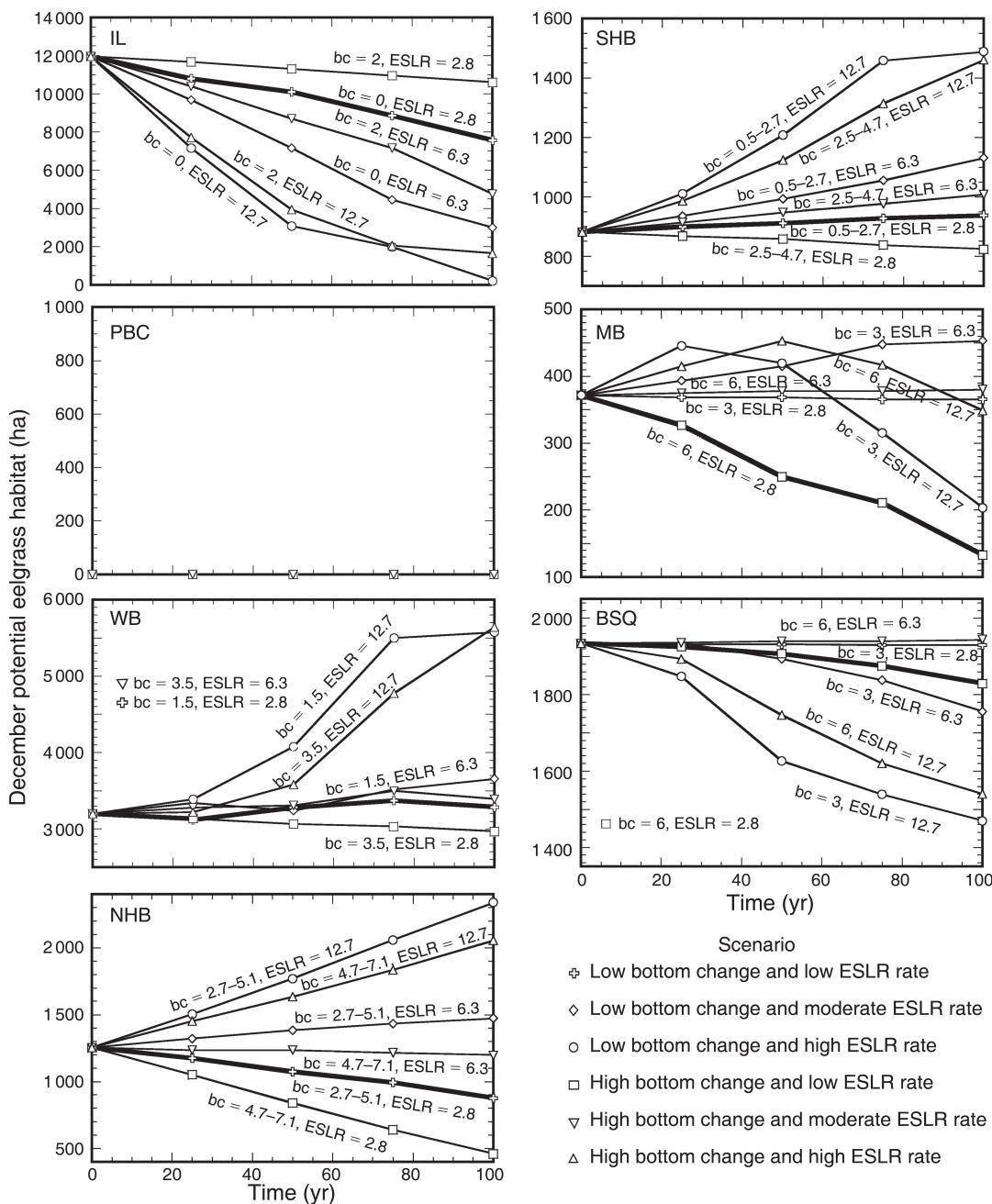


FIG. 3. Present-day (thick line) and alternative projections (thin lines) of potential Brant-accessible eelgrass area during December over 100 years in each estuary. Bottom change (bc; in mm/yr) equals tectonic change plus sediment change, and ESLR represents eustatic sea level rise (in mm/yr). See Table 2 for the specific tectonic and sediment rates that determine bc, as well as the eelgrass parameters and values determining Brant accessibility, and Fig. 2 for estuary abbreviations.

and -32.9% less than the year-zero amount of total eelgrass area in each of these estuaries. However, these drops in starting area in April were less than the December starting drops (Figs. 2 and 4). The pattern of present-day December projections were similar to those of April for WB, NHB, SHB, MB, and BSQ, but differed between the two months for IL and PBC (Figs. 3 and 4). During April in both IL and PBC, the present-

day scenario of low bottom change with low ESLR resulted in 5% more accessible eelgrass after 100 years (Fig. 4, Table 3).

Alternative scenarios of sea level rise, in either December or April, usually resulted in more and less eelgrass than present-day conditions modeled for these months. None of these alternative scenarios made December attached eelgrass more available to Brant in

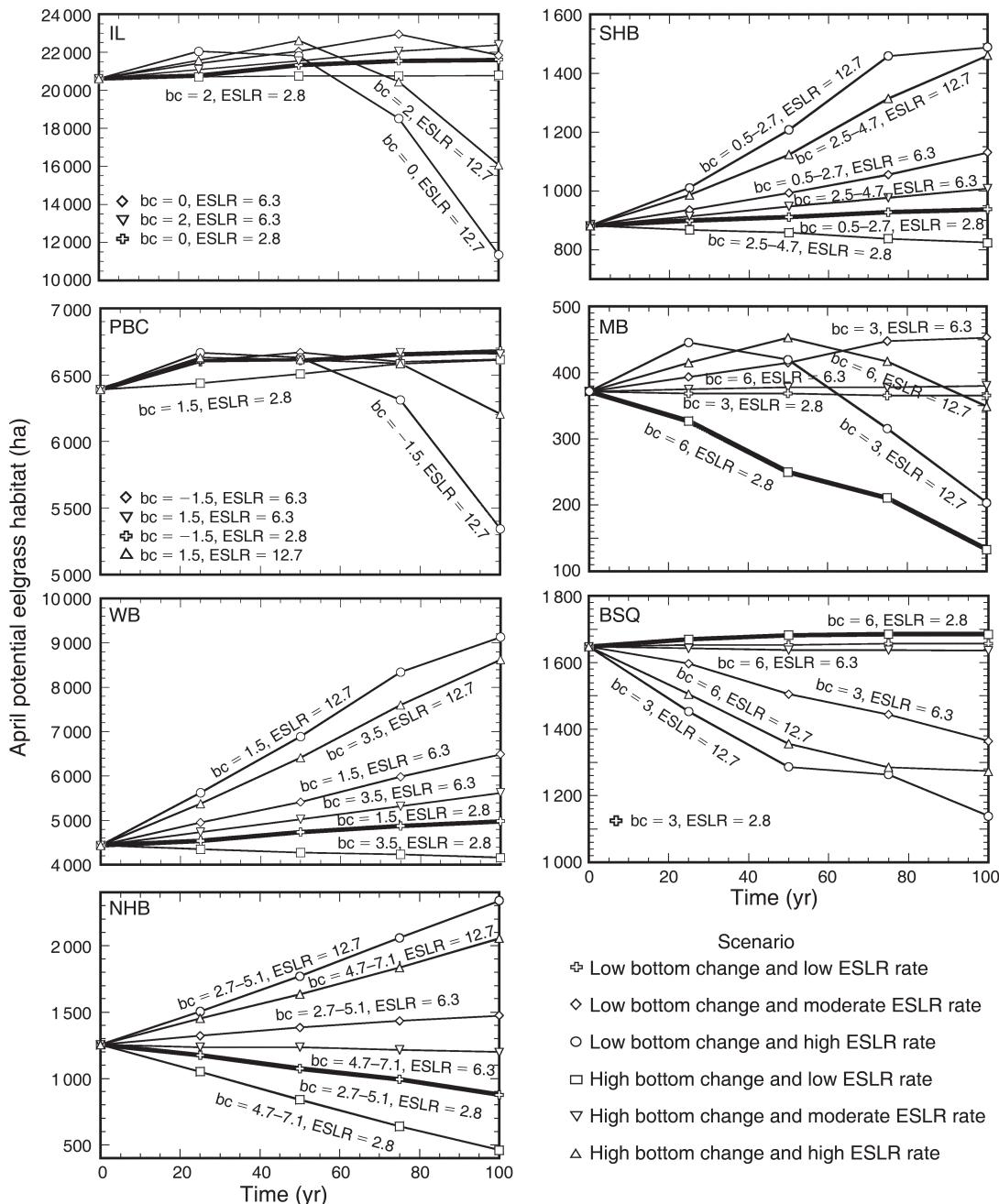


FIG. 4. Present-day (thick line) and alternative projections (thin lines) of potential Brant-accessible eelgrass area during April over 100 years in each estuary. See Table 2 for the specific tectonic and sediment rates that determine bc, as well as the eelgrass parameters and values determining Brant accessibility, and Fig. 2 for estuary abbreviations.

PBC, and the combination of high bottom change with low ESLR resulted in a -11% decline in area for IL (Figs. 2 and 3, Table 3). The remaining five estuaries have at least one alternative scenario that resulted in more December eelgrass area for Brant. Low bottom change with high ESLR produced accessible area increases of 74%, 87%, and 69% for WB, NHB, and SHB, respectively, and in MB, low bottom change with

moderate ESLR resulted in a 22% expansion of December eelgrass (Fig. 3, Table 3). Except for MB, where present-day sea level rise conditions produced the lowest amount of December eelgrass in this estuary, it was also an alternative scenario that resulted in the most loss of eelgrass area for the remaining estuaries. Low bottom change with high ESLR projected the greatest 100-year December losses for IL (-98%) and BSQ

(−24%), and high bottom change with low ESLR resulted in the largest declines for WB (−7%), NHB (−63%), and SHB (−7%; Fig. 3, Table 3). The scenario that produced the most and least accessible eelgrass area in December for WB, NHB, SHB, MB, and BSQ also resulted in the most and least April area for these estuaries. During April, the most rapid expansion rate in PBC was also the present-day projection, whereas in IL, the alternative scenario of high bottom change and moderate ESLR produced 9% more accessible eelgrass in April. The alternative combination of low bottom change and high ESLR produced the most loss of April accessible areas for IL (−45%) and PBC (−16%; Fig. 4, Table 3).

DISCUSSION

This study models the link between sea level rise processes and subsequent changes in eelgrass habitat area and how those changes affect the amount of winter and spring feeding area that would be within the reach of foraging Brant. In this cross-trophic model, both ESLR and local vertical land movement (i.e., bottom change) affected the distribution of eelgrass. In order to understand the links between sea level rise and potential herbivore response, we consider (1) how present-day and alternative scenarios of ESLR and bottom change could affect total eelgrass habitat area in an estuary or group of estuaries; (2) how these present-day and alternative changes alter Brant accessibility to eelgrass leaves during December and April; (3) and what the large-scale flyway pattern of food availability becomes and how the birds' distribution may change according to each ESLR rate.

Total eelgrass area

The estuaries form three groups with respect to the present-day bottom change conditions they experience. IL, PBC, and WB are relatively sediment starved with sediment change rates from −3.0 mm/yr to 2.0 mm/yr, primarily due to a low sediment supply and autocompaction. Sediment supply has been limited by the effects of dams that trap sediments, levees that restrict flood sediments from historic channels, and in the case of PBC, the Skagit River was diverted from the estuary into a more southern part of Puget Sound (Simenstad et al. 1992, Borde et al. 2003, Kairis and Rybczyk 2010). The IL watershed is completely vegetated, lacks logging and grazing, and has a watershed that is small relative to estuary size (T. Babbitts, *personal communication*). The present-day scenario in each of these estuaries projected an increase of total eelgrass area even though, due to a relatively low sediment supply, the local bottom change rates were less than the ESLR rate of 2.8 mm/yr (Fig. 2). Total eelgrass area increased because there was upslope mudflats and marsh areas into which eelgrass could migrate. Also, upland barriers in PBC, WB, and IL had not been encountered by 100 years because the ESLR rate is low (2.8 mm/yr). When the barriers are encountered, then total eelgrass will decrease due to

the extinction of light by deepening water. This present-day scenario may be the best case for managers because, geography permitting, it gives them time to potentially reposition upland barriers before the extinction effect occurs. This kind of management action is also motivated by the upward migration of mudflat and salt marsh habitats that would be displaced before the loss of seagrass habitats (Galbraith et al. 2005).

NHB and SHB also have a relatively low present-day rate of sediment change, but bottom change was more affected by tectonics. We estimated a sediment change rate of 3.0 mm/yr for Humboldt Bay based on a comparison of recent and historic bathymetry data, but we used 1.0 mm/yr for the present-day rate because suspended sediment loads in the region are declining due to lower river flows and the recovery of local watersheds from the aggressive clear-cut logging during the middle of the 20th century (Klein and Anderson 2012). NHB and SHB have the largest gradient in interseismic land level change rates of all modeled Cascadia subduction zone estuaries (Verdonck 2006, Burgette et al. 2009). The Flück et al. (1997) model, therefore, generated tectonic rates that were often greater than the sediment change rate of 1.0 mm/yr. The consequences of these present-day bottom change rates on total eelgrass area yielded contrasting results between the two adjacent estuaries. Whereas eelgrass at NHB was lost due to the ejection effect, it increased slightly at SHB despite the potential for a depth-induced extinction effect. Eelgrass habitat in NHB is more vulnerable to ejection than SHB because the maximum depth of eelgrass in NHB is shallower than in SHB. This is a consequence of the water presumably being more turbid in NHB due to it receiving more streams and, because it has longer wind fetches, it also has the potential for greater re-suspension of sediments (Gilkerson 2008). The combination of light attenuation due to poor water quality and modeled upward tectonic movement therefore continued to shrink the NHB eelgrass niche. The present-day scenario for SHB produced a slow expansion in total eelgrass area. Bottom change almost kept pace with ESLR on the eastern half of the bay, but did not on the western half. The tectonic rates for SHB were lower than for NHB, ranging from −0.5 mm/yr in the southwest corner to 1.7 mm/yr on the east side of SHB (Table 2). However, since maximum depths of eelgrass in SHB are deeper due to the better water quality, and a lot of upland mudflat was available, then SHB eelgrass area expanded for 100 years.

BSQ and MB formed the third group of estuaries where present-day rates of sediment change, ranging from 3.0 to 6.0 mm/yr, are high due primarily to anthropogenically accelerated erosion in contributing watersheds (Josselyn et al. 1989, Ward et al. 2003). The latter rates have probably been at this high level since land disturbance associated with expanded agriculture accelerated in the 1980s in BSQ (Ward et al. 2003). Accelerated erosion and corresponding sedimentation

began as early as the 1880s when land was cleared for grazing and agriculture in MB (Josselyn et al. 1989). Using current-day sediment change rates that were more than double the ESLR rate of 2.8 mm/yr, the eelgrass was steadily ejected. At BSQ, sedimentation-induced ejection also occurred but the effect was not as sudden. Eelgrass at BSQ increased during the first 50 years because the high bottom change rate converted deep, previously unsuitable parts of the estuary to shallower depths, and ESLR allowed eelgrass to temporarily expand upslope. Of all the scenarios modeled, the steepest rates of total eelgrass area loss in MB and BSQ occurred using present-day conditions, indicating that for these estuaries local sedimentation processes are a more immediate threat to eelgrass habitat than ESLR.

Alternative scenarios of bottom change and ESLR resulted in projections of total eelgrass area that were often more and less than the present-day scenario. A combination of low bottom change and high sea level rise (12.7 mm/yr) yielded the largest expanse of eelgrass in all the estuaries except MB. For the other six estuaries, there was ample room for eelgrass to expand upslope into mudflat and salt marsh habitat. For example, it took 75 years for the light extinction effect to reduce eelgrass area when the habitat hit bluffs around IL and dikes and hardened structures at PBC and SHB. Light extinction was avoided in WB, NHB, and BSQ for two reasons. At WB, the bottom change rate was positive, which keeps the lower portion of the WB eelgrass habitat closer to the water surface. These estuaries also have extensive low-slope mudflats and marshes above their current upper limits of eelgrass, which means that eelgrass has relatively more mid- and high-intertidal habitat to occupy in the future. The alternative scenario producing the most expansion of eelgrass in MB was the combination of a low bottom change rate (3.0 mm/yr) that converted deep parts of the estuary to more suitable depths and the moderate ESLR rate (6.3 mm/yr), which allowed eelgrass to expand up into present-day mudflat area.

The biggest projected loss of total eelgrass area in WB, NHB, SHB, MB, and BSQ was the alternative scenario of high positive bottom change and low ESLR, although this scenario was also the present-day condition for MB. Area loss due to ejection occurred from the combination of sediment and tectonic change in WB, NHB, and SHB, but primarily sediment in MB and BSQ. There were no alternative scenarios that resulted in immediate eelgrass loss from IL and PBC because a higher sediment change rate allowed bottom change to almost keep pace with ESLR.

Brant-accessible eelgrass

The present model demonstrated that Brant access to attached eelgrass was affected by sea level rise as well as variables independent of this process. The independent variables of daytime tide heights, which were strongly influenced by season, as well as eelgrass shoot lengths

and upper elevation limits combined to reduce the starting accessible amounts (i.e., year zero) of eelgrass in IL, PBC, WB, and, to a lesser degree, BSQ. This became apparent by comparing the starting amounts of eelgrass area in December and April in each estuary to their total amounts of eelgrass area at year zero. In these four estuaries, the starting areas for both months, but particularly in December, were a smaller portion of the total eelgrass area available, with PBC being the extreme example. In this estuary, due to the exceptional height of the December daytime low tides and the short winter shoot lengths (0.25 m), Brant would only be able to reach down to 1.12 m MLLW, which is well above the upper eelgrass limit of 0.5 m MLLW. Consequently, neither the current-day nor the five alternative scenarios yielded any available eelgrass for Brant during December. Presumably, current-day Brant are making substantial use of drift eelgrass, as well as the non-native *Zostera japonica* Ascherson and Graebner and ulvoid green algae that grow in the higher intertidal zone of this estuary (Baldwin and Lovvorn 1994a, b; M. Axelson, personal communication). The much lower daytime low tides during April in PBC with the longer shoots (0.75 m) in that estuary permit Brant to access depths down to -1.66 m MLLW, well below the upper limit of eelgrass at 0.5 m MLLW. At IL, the upper elevation of eelgrass was comparatively high (0.9 m MLLW), the December shoots were shorter (0.15 m) than for any other estuary, and the daytime low tides were relatively high. There was almost 45% more starting eelgrass available in April than December in IL due to the lower tides and longer shoots in the spring. Starting amounts of accessible area in BSQ are less than year-zero total eelgrass area because more of the eelgrass occurs in deep water that is beyond the Brant's reach. BSQ tides also affect starting accessible amounts, but with a seasonal pattern of daytime heights that is the opposite from those in northern estuaries. Lower daytime tidal heights in December resulted in more accessible eelgrass for Brant during the time of year when they are overwintering. Higher daytime tides in April produced less accessibility at the time of year when Brant are leaving this estuary.

Beyond the starting amount of accessible eelgrass, the patterns of the different 100-year trajectories for December and April accessible eelgrass in WB, NHB, SHB, and MB were similar to that described for total eelgrass areas in these estuaries. Thus, interpretations of the sea level rise conditions that influence accessibility by Brant in December and April are the same as those already given for total eelgrass area in these estuaries. This is not the case in IL, PBC, and BSQ, where the present-day trajectory patterns for December and April accessibility did not resemble those for total eelgrass area.

The present-day scenario in IL of low bottom change and sea level rise produced an increase in total eelgrass area, but a decrease in availability to Brant in December. This decrease occurred due to the combina-

tion of the high winter low tides with an ESLR rate that effectively lifted Brant away from the eelgrass. Being a sediment-starved estuary, the bottom change rates for IL were too low to compensate for increasing sea level. In April, the much lower daytime low tides and longer shoots ameliorate the eelgrass accessibility problem for Brant created by low sediment supply. In PBC, the same present-day scenario of low bottom change and low ESLR was overwhelmed by the exceptionally high tides during December. However, as was the case in IL, this present-day scenario in April allowed for a slight increase in Brant-accessible eelgrass area despite the negative sediment change rate (-3.0 mm/yr) because eelgrass had ample upslope area into which it could migrate, at least for the next 100 years. In BSQ, much of the initial 50-year increase in total eelgrass occurred in deep water and so remains out of reach of the Brant. Present-day December and April trajectories in BSQ, therefore, do not resemble the present-day total eelgrass projection. December accessibility gradually declined across the 100 years because the DEM between -1.07 m MLLW (December-reaching depth) and -0.82 m MLLW (April-reaching depth) contracted by 105 ha due to the high present-day bottom change rate of 6.0 mm/yr. April accessibility remained level because area losses due to the ejection effect were offset by the gain of 36 ha above -0.82 m MLLW.

Alternative scenarios usually resulted in the greatest gains and losses of accessible eelgrass. For example, for Brant in IL during December, the combination of high bottom change with low ESLR yielded the most eelgrass because the eelgrass remained closer to the Brant than any other scenario. During April in IL and PBC, the current conditions experienced by Brant were also the best case scenario for them, although in IL the combination of high bottom change with moderate ESLR provided geese with slightly more eelgrass over time. Since these two estuaries are relatively sediment starved, low bottom change with high ESLR resulted in large losses of direct feeding area during both December and April due to the extinction effect. In BSQ, the alternative scenario that would be the best case for overwintering Brant and management was the combination of low bottom change and low ESLR, which projected consistent accessibility for the next 100 years.

In IL, the amount of eelgrass area accessible during December was predicted to decline over time for present-day and alternative scenarios. Historically, the reduction at this time of year would not have been immediately relevant to the Brant because IL would have been covered in ice and most of the Brant would be overwintering in Mexico (Dau 1992). However, ice cover in the Arctic, and in IL in particular, is currently diminishing and an increasing number of Brant are now overwintering there (Ward et al. 2009), and so the December accessibility of eelgrass is becoming more relevant to the population. It is not clear if ice cover loss would offset the modeled declines in accessible eelgrass

area during December. Upslope expansion of eelgrass and winter leaf lengthening may not occur if the bottom scouring and leaf cropping effect of ice that is likely setting the upper limit of eelgrass now (McRoy 1969) was replaced by disturbance from winter storm waves. A loss of ice and a potential increase of aquatic light also may not result in a large increase in eelgrass productivity if that light is attenuated by sediments suspended by the same winter waves.

The Brant's flyway perspective

How ESLR potentially interacts with estuarine specific land movement rates to affect total eelgrass area and Brant-accessible area, and how other factors (e.g., eelgrass elevation limits, shoot lengths, daytime low-tide height) also affect accessibility, is necessary for identifying which variables affecting Brant food are actionable by managers. In large part, however, Brant use of an estuary depends on the availability of food it presents regardless of why that availability varies. This assertion is based on the considerable attention given by waterfowl biologists to how wild geese respond to their food supply (e.g., Owen 1980, Prop and Loonen 1989, Prop and Deerenberg 1991, Black et al. 2007). Evidence that Brant track eelgrass along temporal and spatial scales is provided from several multi-year studies (Clausen 1998, 2000, Clausen and Percival 1998, Ganter 2000, Ward et al. 2005). In the Dungeness area of the Juan de Fuca Strait, Washington, USA, 12 years of monitoring demonstrated that a 31% decline in eelgrass area coincided with a 63% drop in Brant use (i.e., Brant numbers \times days present; Wilson and Atkinson 1995). A similar correlation was described over a shorter span of years at MB (Moore et al. 2004). Response to food supply within estuaries was documented at Humboldt Bay by mapping the location of foraging flocks and, as predicted by optimality theory, Brant spent more time foraging on eelgrass meadows highest in protein, calcium, and biomass than sites offering a less profitable bite (Moore and Black 2006a). The most compelling evidence that Brant respond to eelgrass on a migratory flyway scale comes from the strong positive correlation between bird numbers from maximum annual counts and the size of total eelgrass area (ha) at the 11 most heavily visited estuaries from the southern to northern ends of the Pacific Flyway (Moore et al. 2004). The seven bays in our study followed the same pattern with the two most heavily used estuaries, IL and BSQ, ranging from 26 443–52 000 birds, two of the primary migratory staging sites, PBC and SHB, supporting between 5490 and 26 000 birds, and three lesser but consistently used sites, WB, NHB and MB, which attract 1322–11 000 birds (Table 1).

Given the close relationship between Brant distribution and eelgrass area, how could the current distribution of Brant in overwintering and migratory sites change according to our modeled amounts of accessible,

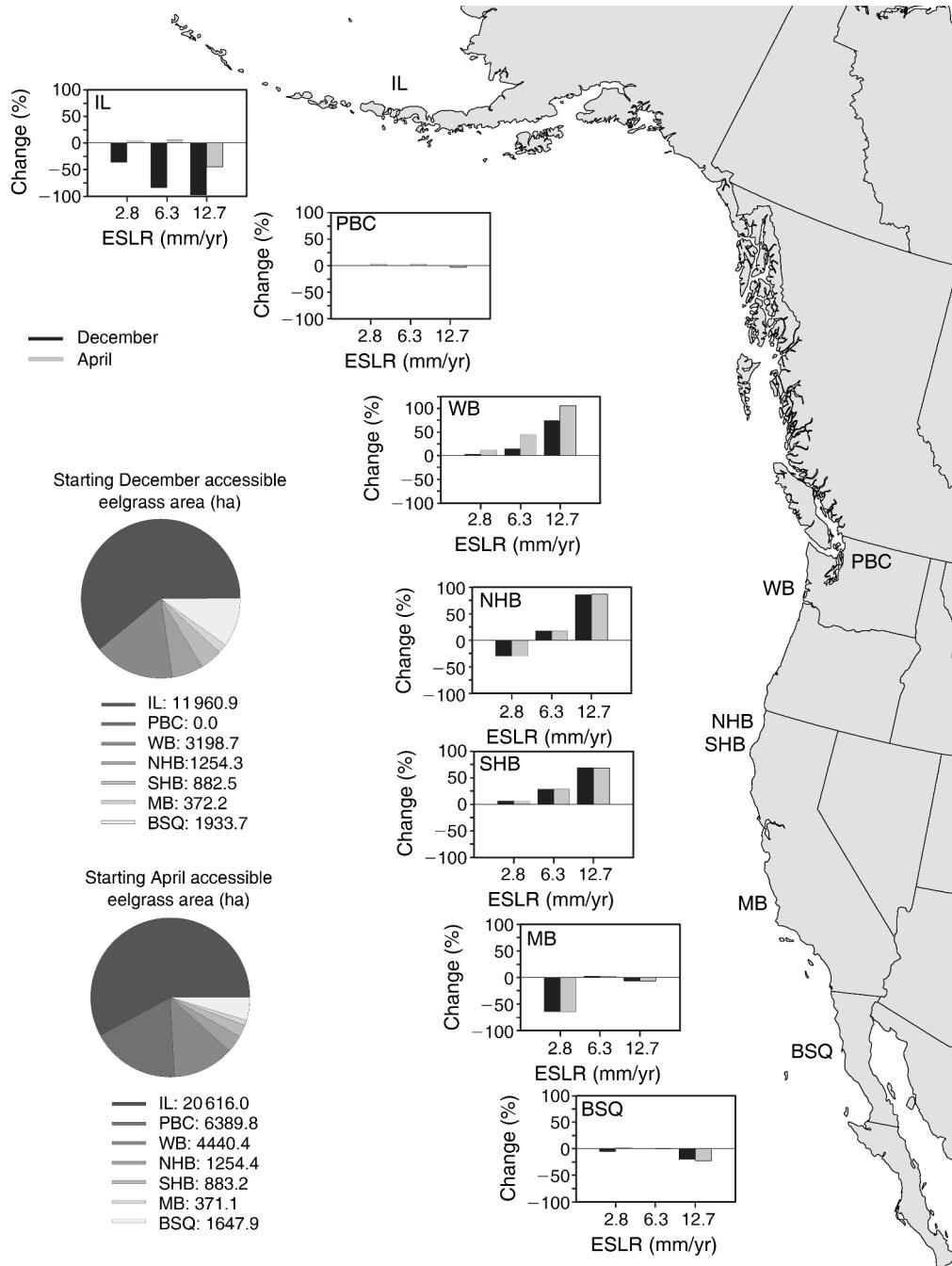


FIG. 5. The flyway perspective of eelgrass area available to Brant during each season, showing the starting amount of accessible area (ha) in each pie chart and, in the bar plots, the percentage of change in this starting area after 100 years. There are three pairs of percentage area changes for each estuary: present-day ESLR rate (2.8 mm/yr) with the present-day bottom change rate, moderate ESLR (6.3 mm/yr) with the present-day bottom change rate, and high ESLR (12.7 mm/yr) with the present-day bottom change rate (see Table 2 for specific rates). See Fig. 2 for estuary abbreviations.

attached eelgrass? Fig. 5 depicts the starting absolute amounts of accessible eelgrass area and the future 100-year percent changes in eelgrass area in the seven focal estuaries. The amount of December accessible eelgrass indicates how attractive, from a food perspective, a particular estuary will be for overwintering, whereas the

April amounts will service Brant during northward migration and for pre-breeding fattening.

If present-day ESLR (2.8 mm/yr) and bottom change rates hold for the next 100 years, then estuarine usage by the Brant should not change appreciably (Fig. 5). The one exception is MB, where, especially during the

greater winter use of this estuary, there was a 64% loss of accessible area. Due to the lack of alternative food choices within MB and in adjacent agricultural fields (Roser 2011) the Brant with a migratory tradition to stop at MB may face energetic deficits unless they adjust and make more use of BSQ or mid-latitude estuaries (*sensu* Mini and Black 2009). Although individually marked Brant show high rates of fidelity to wintering areas (including BSQ and MB), some geese move among wintering sites and a portion permanently emigrate to other sites (Lindberg et al. 2007).

Scenarios of higher ESLR rates (6.3 and 12.7 mm/yr) in combination with present-day bottom change would result in contractions of estuarine use by Brant at both ends of the flyway and potential increases in use of mid-latitude estuaries (Fig. 5). In BSQ, while accessibility is unchanged by an ESLR rate of 6.3 mm/yr, the scenario of 12.7 mm/yr results in a -20% and -23% decline in accessible area during December and April, respectively. These changes will likely result in a northward shift in Brant from BSQ similar to what occurs during years when El Niño conditions temporarily increase sea level (Sedinger et al. 2006, 2011).

At the northern end of the flyway in IL, our model shows that the two higher ESLR scenarios should decrease winter, but not spring use of this estuary. We modeled a 45% loss of spring accessible eelgrass but, given that there is still more than 10 000 ha of accessible spring eelgrass, Brant use of IL is not expected to decline at this time of year. In contrast, both of the higher ESLR scenarios result in greater losses of winter accessible eelgrass in IL (Fig. 5, Table 3). These losses could be temporarily offset by feeding on drift leaves because the pool of drift leaves would increase for the first 75 years as total eelgrass habitat area increased in IL (Fig. 2), but beyond that time, the drift leaf supply should decrease as more of the eelgrass habitat is lost due to the light extinction effect (Fig. 2). The higher ESLR rates should eventually push Brant out of IL south to overwinter in mid-latitude estuaries. The current pattern of increasing winter use of IL by Brant (Ward et al. 2009) due to one aspect of climate change, warming, could therefore reverse to decreasing winter use of IL because of a different component of climate change, sea level rise.

The southern and northern contractions of estuarine use that could result from these higher ESLR scenarios (6.3 mm/yr and 12.7 mm/yr) would both result in a greater use of mid-latitude estuaries by Brant, especially during the winter. SHB, NHB, and WB had increases in accessible area since the eelgrass moved upslope, and while accessible area was unchanged for PBC, it also may accommodate more Brant because of its large amount of accessible area. However, accessibility even in these estuaries must eventually diminish due to upland barriers (SHB after 75 years; Figs. 3 and 4). Continued mid-latitude accessibility of winter eelgrass for Brant

will, therefore, be affected by decisions about the repositioning of dikes, levees, and sediment supply rates.

Model limitations and considerations

Our modeling approach often used one bottom change rate within a particular scenario and estuary. NHB and SHB were the exceptions because a range of bottom change rates were used due to the steep spatial gradient in interseismic tectonic rates in and around Humboldt Bay. However, for Humboldt Bay and the other five estuaries, once a particular bottom change rate or range of rates was identified, it remained the same for each 100-year projection. This linear approach to the future is, conceptually, less desirable than a “nonlinear” approach that allows future bottom change rates to vary based upon interactions between physical and biological features of the habitat. The nonlinear approach has been emphasized when modeling salt marsh and mangrove habitat survival (e.g., Koch et al. 2009, Kirwan and Guntenspergen 2010) because of the capacity of the types of vegetation in these habitats to increase sedimentation rates, thereby allowing those areas of the habitat to keep pace with sea level rise, provided that the suspended sediment supply and tidal amplitude is adequate.

This particular nonlinear interaction between sediments and plants should not be as important to eelgrass habitat survival as it is for salt marsh and mangrove habitats. Relative to bare mudflat, eelgrass does trap sediment because its shoots do attenuate flow (Fonseca and Kenworthy 1987, de Boer 2007, Koch et al. 2009), but since eelgrass shoots bend over under high flow (Peralta et al. 2008), their capacity to trap sediments should be lower than for the stiffer *Spartina* in the high marsh or mangrove trees. A further difference between high marsh habitats and the lower intertidal to subtidal eelgrass beds includes the exposure of the latter habitat to longer intervals of high energy tidal and wind waves. This combination of flexible plants and water movement means that sediments around and even within eelgrass beds should re-suspend more easily than in salt marshes. In sediment starved estuaries, therefore, eelgrass habitat survival should be affected as much by how much upslope area is available for bed migration as it is by its capacity to trap sediments and keep pace with ESLR.

Our comparison of multiple estuaries also emphasized that models investigating the relationship between sea level rise and habitat survival need to diversify beyond focusing on whether or not sediment accretion will allow a habitat to persist. In MB and BSQ, rather than potentially saving the habitats, accretion rates are so high that habitats could be ejected (filled in) before they can be drowned by ESLR. In Humboldt Bay, the irony of better sediment management is that habitat survival is now more dependent on the spatially variable and rapid interseismic tectonic rates than it is on sediment delivery. Even in sediment-starved estuaries, other nonlinear interactions (e.g., tectonics and sediment accretion,

estuarine geomorphology and water currents, tributary discharge and sediment delivery) could be at least as important to eelgrass survival as the potential for eelgrass plants to trap sediment.

Further understanding of Humboldt Bay tectonics is necessary in order to identify management options for habitat survival. In contrast to SHB, where the model of Flück et al. (1997) generated a range of positive and negative interseismic tectonic values, the same model described only positive uplift values for NHB. These are inconsistent with tidal gauging data at the North Spit (NOAA Tide Predictions, *available online*)⁸ suggesting that at least the west side of NHB is subsiding. If the tidal data is accurate and an updated version of the Flück model indicated that all of SHB and NHB is subsiding, then the total eelgrass footprint in NHB would still be projected to decrease, but the reason for that decline would be light extinction rather than a combination of extinction and ejection effects as is presently modeled.

CONCLUSIONS

The present model demonstrated that factors operating relatively independently of sea level rise, primarily the height of daytime low tides, the upper elevation of eelgrass, and eelgrass shoot lengths, can reduce the area of accessible eelgrass for Brant below the total eelgrass available in an estuary. This should be particularly true when Brant use northern estuaries. When the interactions between local and global sea level rise processes were modeled to project the total and accessible eelgrass area over the next 100 years, present-day ESLR and bottom change rates should sustain the current estuarine pattern of Brant overwintering and migrating with the caveat that even with an ESLR rate of 2.8 mm/yr, the eelgrass in SHB, WB, PBC, and IL will eventually decline due to the extinction effect as beds bump into upland barriers. The ejection effect, due primarily to tectonic uplift in NHB and sedimentation in MB and BSQ, is more of an immediate threat to eelgrass and Brant in these estuaries than ESLR. These present-day ESLR conditions should not result in a large inter-estuarine redistribution of Brant because the eelgrass footprint (ha) does not change greatly over the next 100 years and several of the mid-latitude estuaries contain alternative food choices. Higher ESLR rates (6.3 and 12.7 mm/yr) should eventually result in less Brant use of southern and northern estuaries, particularly during the winter. In IL, the warming trend that is increasing winter use of this estuary by Brant (Ward et al. 2009) could therefore be reversed by a different aspect of climate change, sea level rise that will deprive Brant of sufficient food. These same higher ESLR rates should increase Brant usage of mid-latitude estuaries.

ESLR therefore presents different kinds of large challenges to eelgrass beds and Brant along the Pacific Flyway with only a limited set of management actions from which to choose. IL is an example of an estuary where, in the event of higher ESLR rates, nothing practical or supportable could be done to increase the rate of sedimentation in order to allow bottom change to keep pace with ESLR. Other northern sediment-starved estuaries face a sediment management paradox. The traditional focus has been on the improvement of water quality which, in the NE Pacific, is often directed at the reduction of suspended sediments since they attenuate light, fill navigation channels, and may be vectors for nutrients, pollutants, and pathogens (Hansen et al. 2002, Lewis 2005, Ralph et al. 2006). In estuaries such as PBC and WB that have been artificially starved of sediments, the longer term consequence of this policy is that present locations of marine habitats will not be able to move vertically and potentially keep pace with ESLR. If upland barriers were removed, then this problem is partially solved because eelgrass habitat can move upslope. However, locations that are too deep for eelgrass would remain that way in the absence of an adequate sediment supply. The sediment challenge in the southern estuaries of BSQ and MB is quite different where, if the present-day ESLR rate of 2.8 mm/yr persists, then the eelgrass habitats and the overwintering Brant they support will only avoid ejection if the sediment input rate is decreased. Finally, NHB and SHB are an example of an estuary (Humboldt Bay) where the bottom change rate is affected by both tectonics and sedimentation. The tectonic model of Flück et al. (1997) yielded such a high range of uplift values for NHB that, with an ESLR rate of 2.8 mm/yr, Brant-accessible eelgrass declined immediately, whereas the more moderate uplift and subsidence rates in SHB and the existence of lower mudflats allowed accessible eelgrass area to expand.

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⁸ http://tidesandcurrents.noaa.gov/tide_predictions.shtml

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SUPPLEMENTAL MATERIAL

Appendix

Data sources used for digital elevation models (DEM), sediment and tectonic vertical movement rates, eelgrass habitat distributions, and eelgrass elevation limits and shoot lengths (*Ecological Archives* A022-93-A1).