



Northeast Pacific eelgrass dynamics: interannual expansion distances and meadow area variation over time

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ABSTRACT: Ecosystems constantly change, yet managers often lack information to move beyond static habitat assumptions. As human impacts and geographic information systems advance, it is important and feasible to quantify past habitat boundary shifts to inform management decisions (e.g. protective perimeters) robust to near-term habitat changes. This is the case in eelgrass (*Zostera* spp.), an ecosystem engineer that forms dynamic, often protected meadows. Practitioners protect areas to avoid human stress to eelgrass, but they can lack quantitative descriptions of the near-term potential for eelgrass meadows to shift into unprotected areas. Here, we quantified interannual eelgrass meadow boundary shifts within 23 sites spanning 9 decades and 19° latitude. Eelgrass meadow boundaries typically shifted into areas tens of meters away from previous meadow edges, but sometimes much farther. Also, eelgrass meadows often vacated and later recolonized the same areas. By implication, eelgrass protection efforts may be enhanced by considering that presently vacant areas may be inhabited in the future, especially near currently existing meadows. Additionally, eelgrass meadows changed less over time at sites less modified by people within temperate landscapes compared to sites located within human-dominated, warmer, and drought-prone landscapes with limited water turnover. We thus hypothesize that eelgrass meadows change more over time within landscapes exposed to greater stressor regimes because they more frequently or intensely cycle through disturbance and recovery phases. These results inform tactical decisions seeking to mitigate impacts of human activities to eelgrass and underscore the potential synergy of monitoring, research, and adaptive management approaches to protect dynamic habitats.

KEY WORDS: Coastal ecosystems · Ecosystem processes · Marine spatial planning · Recolonization · Seagrasses · Shifting habitat mosaics · *Zostera*

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1. INTRODUCTION

Habitats are dynamic. In the case of habitat-forming species, individuals continuously colonize and vacate patches, scaling up to habitat expansions, contractions, and shifts (sensu Levin 1992). Given that many biogenic habitats shift and advancing technologies enable us to observe these changes (Kerr & Ostrovsky 2003), researchers can synthesize information about past habitat boundaries to quantify the near-term potential for habitats to shift. Such analyses could inform protective perimeters that are robust to near-term habitat boundary shifts and inform a basic understanding of the magnitude and drivers of habitat boundary changes (e.g. Kareiva & Wennergren 1995, Alodos et al. 2004, WDNR 2014).

Eelgrass (*Zostera* spp.) management epitomizes the need to understand the potential for habitat boundaries to shift. Eelgrasses are habitat-forming marine angiosperms native to nearshore ecosystems across the globe. They provide many ecological services (e.g. carbon sequestration, Fourqurean et al. 2012), support culturally, economically, and ecologically significant species (e.g. Beck et al. 2001), and are important to coastal indigenous cultures (e.g. the origin of First Nations' names, Turner 2001). Despite this, human stressors have reduced eelgrass abundances globally (Lotze et al. 2006, Dunic et al. 2021). Consequently, eelgrass conservation efforts are now common, and human activities that stress eelgrass often draw management attention (e.g. NMFS 2014, WDNR 2014, Lefcheck et al. 2018).

One mode of protection involves attempts to delineate eelgrass meadows and decide which human actions should be permitted near them, but this is challenging because eelgrass meadow boundaries are dynamic. Indeed, numerous studies indicate that eelgrass meadow extent varies across time, often driven by natural and human-influenced environmental changes (e.g. Lyons et al. 2013, Dumbauld & McCoy 2015, Patrick & Weller 2015, Shelton et al. 2017, Nahirnick et al. 2020). What has yet to be determined and regionally synthesized, however, is the near-term (one to several years) potential for eelgrass meadows to expand away from occupied areas into unoccupied areas. Indeed, for the US west coast, we are aware of only one report that has attempted to address this gap, which found that the edges of an eelgrass meadow in Puget Sound (WA, USA) could expand 4 m annually (WDNR 2014). This information is particularly relevant to eelgrass management, as one of the primary regulatory agencies (the US Army Corps of Engineers [Corps]) typically does not re-

quire compensatory eelgrass mitigation unless there is evidence of direct impacts to existing vegetated areas coincident with the timing of project-associated surveys. For example, based upon comments from the Corps South Pacific Division during the development of the California Eelgrass Mitigation Policy, the Corps indicated that, only under rare exceptions where historical data are available for a given site, would they consider compensatory mitigation for suitable eelgrass habitat losses. In addition, they suggested that the definition of eelgrass habitat for management purposes be limited to the extent of vegetated cover where eelgrass is present and where gaps in coverage are <1 m between individual turion/shoot clusters¹. Overall, an extensive, regional analysis could enhance decisions seeking to craft protective boundaries around eelgrass meadows that will be robust to near-term meadow boundary shifts.

While eelgrass meadow boundaries are presumably influenced by environmental conditions globally, the amplitude of meadow dynamics may depend on natural attributes and human disturbances associated with particular landscapes. That is, eelgrass meadows may grow and shrink more dramatically in areas where disturbances are more intense or frequent. Eelgrass is sensitive to many aspects of the environment. Eelgrass requires anchorage in soft sediment, clean, clear, and cold water, appropriate salinities, and optimal sunlight; indeed, its depth distribution is naturally restricted by processes mediating desiccation in shallows and light attenuation at depth (Zimmerman et al. 1997, Orth et al. 2006, Nejrup & Pedersen 2008, Krumhansl et al. 2021). The potential for these environmental attributes to become stressful varies naturally across coastlines (e.g. climate regime, shoreform) and years (e.g. drought). Indeed, annual variation in eelgrass biomass within the northern hemisphere appears to vary more in warmer environments (Clausen et al. 2014). Environments are also influenced by human stressors, for instance by mobilizing sediment (e.g. boat anchors, propeller scour), increasing water turbidity (e.g. eutrophication, watershed sedimentation), and eliminating shallow water habitats (e.g. shoreline infrastructure). Eelgrass is

¹Attachment to December 15, 2010, letter from South Pacific Division, US Army Corps of Engineers, to Assistant Regional Administrator for Habitat Conservation, NOAA's National Marine Fisheries Service, Southwest Region: Comments of the South Pacific Division, US Army Corps of Engineers, on the Southwest Region of the National Marine Fisheries Service's 'Draft California Eelgrass Mitigation Policy' dated October 11, 2010

also sensitive to top-down cascades from predators (e.g. sea otters) historically extirpated by humans and direct disturbance from invasive species (Davis et al. 1998, Malyshev & Quijón 2011, Hughes et al. 2013, Matheson et al. 2016). Thus, the amount that eelgrass meadows change annually may vary substantially across coastlines, with some landscapes driving disturbance and recovery more than others.

Here, we quantified interannual changes in eelgrass meadow boundaries within 23 sites spanning 9 decades, 19° latitude, and multiple climate regimes of the Northeast Pacific from San Diego (USA) to central British Columbia (Canada). We assembled data sets that mapped the spatial extent of eelgrass and used them to quantify eelgrass meadow dynamics. The impetus for this study was to quantify the distances that boundary edges can expand. In this process, we noticed that natural and anthropogenic landscape context appeared to influence the magnitude of changes in eelgrass boundaries between years. Via post hoc analyses, we more formally documented that the landscapes across our study region contrasted markedly along a latitudinal gradient in their natural (ecoregion, sunlight, and temperature) and anthropogenic (human footprint) environments and that sites within landscapes characterized by more intense stressor regimes appeared to support more dynamic eelgrass meadows. Our goal was to present an analysis that quantified distances that meadow boundaries can move over time to inform efforts seeking to protect eelgrass into the near-term future, provide baseline information about eelgrass meadow dynamics, and compare dynamics among sites and their landscapes to potentially inform future research avenues.

2. METHODS

2.1. Data assembly and preparation

We assembled pre-existing surveys that mapped the spatial extent of eelgrass meadows over multiple years within sites along the Northeast Pacific. We gathered a data set describing 23 sites (28, when sites are split as described below) from San Diego (USA) to Central British Columbia (Canada). Surveys were conducted between 1931 and 2020, with most taking place after 1990. The total number of surveys across all sites and years was 111 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m705p061_supp.pdf). Sites were located in embayment, lagoonal, and sound estuaries (Heady et al. 2014). Monitoring

programs used satellites, planes, unoccupied aerial systems, sonar, and direct visual observations to map eelgrass. Most proximate surveys repeated within sites occurred at intervals of less than 3 yr, but there were also longer gaps between some surveys (see Section 3). All sonar studies ground-truthed eelgrass presence to clarify portions of sites where sonograph output was ambiguous, and some studies employing remotely sensed observations ground-truthed eelgrass presence via direct visual observations (i.e. above-water viewing, underwater cameras, and diver surveys) to assess accuracy (i.e. correct classification of areas as having or lacking eelgrass) (Table S2).

Some data required pre-processing to make the data compatible and comparable within our spatial analysis approach. In one case (Nisqually River delta), we converted transect data describing point measurements of eelgrass presence and absence to produce a 2-dimensional polygon describing the spatial extent of eelgrass meadows (Fig. S1). In some cases, eelgrass was described at multiple levels of density, and we lumped all densities into 1 category of eelgrass presence to allow straightforward comparisons among years and because a designation of presence vs. absence would presumably be most relevant to eelgrass management efforts that delineate protected spaces. Within Padilla Bay, *Zostera japonica* was present in addition to *Z. marina* (all other sites were thought to be inhabited only by the latter, although in reality small amounts of other species could have been present). In Padilla Bay, we included both species in delineations of eelgrass meadow extent because this was preferable to the alternative of including only *Z. marina* and implying that areas occupied by *Z. japonica* were uninhabited. Within San Francisco Bay and Agua Hedionda Lagoon, monitoring efforts observed some regions in different years, and we split these regions into separate sites (Richardson Bay [within San Francisco Bay] and west, center, and east [within Agua Hedionda Lagoon]) so that comparisons between proximate years examined the same areas. We also excluded a section of Elkhorn Slough wherein eelgrass was transplanted in 2015 and 2016 (Beheshti et al. 2022), resulting in 2 time series: one of older dates examining the entire slough and another of more recent dates only examining unrestored areas. Our approach to gather disparate data sets acknowledges that, ideally, all observations would have followed the same protocols. Integrating existing data collected via different methods, while not perfect, allowed us to investigate previously unexplored patterns in eelgrass meadow dynamics over broad spatial and temporal scales along the Northeast Pacific.

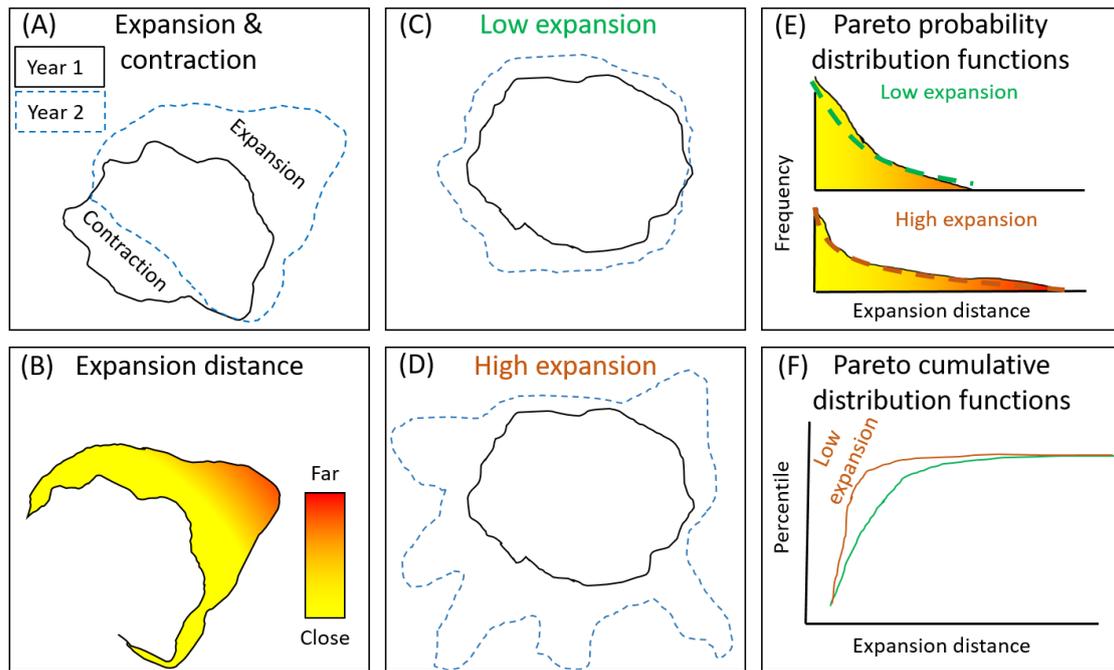


Fig. 1. Conceptualization of the analysis. (A) Given the extent of eelgrass measured in 2 years, expansion occurred where eelgrass was present in the second year, but not in the first. Contraction occurred where eelgrass was absent in the second year, but was present in the first. (B) Within expanded areas, we partitioned the area into 1×1 m cells and described expansion distances as the distances of eelgrass cells from the nearest eelgrass in the previous year. (C) Eelgrass could expand relatively close to its previous location. (D) Eelgrass could also expand relatively far from its previous location. (E) We modeled the distribution of expansion distances using Pareto distributions, which quantified the extent that eelgrass expansion was concentrated into distances close to the previous year's eelgrass locations. Expansion distances are shown with overlaid Pareto model probability distributions in dashed lines for 2 hypothetical eelgrass meadows that expanded relatively close (top) and far (bottom). (F) We visualized eelgrass expansion distances and models fit to Pareto distributions in terms of cumulative distributions so that expansion distances could be interpreted in terms of percentiles

2.2. Describing change in eelgrass meadow boundaries among years

We described eelgrass meadow dynamics in terms of area expansion, area contraction, area total absolute change, and expansion distances (Fig. 1). Of note, the impetus for this study was to quantify expansion distances, but this analysis led us to notice that variation in eelgrass meadow area over time differed among sites. To describe these differences quantitatively, we additionally calculated for each site the area of eelgrass expansion, area of eelgrass contraction, and absolute change in the area of eelgrass between time steps (term definitions are given in Table 1), while screening and attempting to correct for overt influences of the length of time between observations on eelgrass variation (most but not all temporally proximate

Table 1. Definitions of metrics used in this paper

Term	Definition
Expansion	Area (m^2) where eelgrass was present, but absent in the previous time step
Contraction	Area (m^2) where eelgrass was absent, but present in the previous time step
Absolute change	Difference in total eelgrass area (m^2) between 2 adjacent time steps, regardless of positive or negative
Expansion distance	Distance (m) of an expanded eelgrass cell from its nearest neighbor cell containing eelgrass in the previous time step. The distribution of expansion distances is defined by Pareto distribution shape parameters

observations were separated by less than 3 yr). We report metrics of expansion, contraction, and total absolute change in proportional terms, which we calculated by dividing their values by total eelgrass area in the previous time step.

We described eelgrass expansion distances using Pareto distributions (Arnold 2015). Pareto distributions are interdisciplinary (e.g. economics, weather) tools used to describe the extent to which a large portion of observations is concentrated within a small range of possible values (e.g. tree dispersal distances, Svenning & Skov 2007). Here, we used Pareto distributions to quantify eelgrass expansion distances whereby the majority of newly colonized areas tended to be close to places occupied by eelgrass in the previous time step, but the degree to which eelgrass boundary shifts were concentrated close to previously occupied areas varied among observations within a small range of possible values, resulting in a skewed distribution. The Pareto probability density function and cumulative probability function are parameterized as:

$$f(x) = \frac{\alpha x_m^\alpha}{x^{\alpha+1}} \quad (1)$$

and

$$F(x) = 1 - \left(\frac{x_m}{x}\right)^\alpha \quad (2)$$

respectively, where x is the nearest-neighbor distance, x_m is the minimum possible distance of the nearest neighbor, and α is a shape parameter. Higher α values indicate that eelgrass meadow expansion was highly concentrated within short distances of areas previously occupied by eelgrass, whereas lower alpha values indicated eelgrass meadows more frequently expanded farther away. Because the minimum value of eelgrass meadow expansion distance was always 1 m (i.e. $x_m = 1$), the shapes of expansion distance distributions among observations were distinguished only by differing estimates of α . For each proximately observed pair of years within sites, we calculated expansion distances by partitioning the expanded eelgrass area polygons into 1×1 m cells, which was a spatial resolution reasonably scaled to observation precision and computationally feasible for later analyses, and calculated the cells' distances from the nearest eelgrass location in the previous time step (often 1 or 2 yr prior, but sometimes more).

We used linear models to quantify interannual eelgrass meadow dynamics among sites. Our goal was to produce 1 estimate for each of the 4 dynamism metrics per site, while screening and accounting for detectable effects of time between observations. The models' response variables (Y) were proportional absolute change, proportional expansion, proportional contraction, or the Pareto α . The explanatory variables were a site-specific intercept (β_s) and the log-transformed number of years (X_1) between observations:

$$Y = \beta_s + \log(X_1)\beta_1 \quad (3)$$

The purpose of the latter parameter (β_1) was to screen and attempt to correct for the possibility that changes in eelgrass area would increase with more time between observations, but with diminishing returns, as represented by the log-transformation. Final models included the time gap parameter if their Akaike information criterion corrected for small sample sizes (AICc) was lower than their counterpart model omitting the parameter. Notably, if the year term was not included in final models, site effects from linear models were essentially the same as site-specific averages. We treated sites as fixed rather than random effects because we were interested in examining differences among sites and did not want site estimates to shrink toward their grand mean estimates (McElreath 2020). We log transformed the response variables of expansion, absolute change, and α , and logit-transformed the response variable of contraction so that the distributions of these variables approached normality. The latter transformation also placed contraction values on an unbound scale.

We used output from these models to characterize eelgrass area variation across sites. Using final models, we made one prediction for each site and dynamism metric and presented these in histograms. We also plotted metrics faceted by time between observations to facilitate comparisons among sites while holding the number of intervening years constant. Also, we input the 4 site-specific estimates of eelgrass dynamism (i.e. β_s) for each site into a principal components analysis (PCA) (row data: sites; column data: β_s estimates of expansion, contraction, absolute change, and Pareto α) to understand relationships among these variables and generate an integrative, site-specific index of eelgrass dynamism.

Additionally, we report a metric of recolonization, i.e. instances when eelgrass in an area was present, absent, then present again. For time series with 3 or more observations, we calculated the proportion of newly expanded eelgrass that occupied locations previously occupied.

2.3. Post hoc comparison of variation in seagrass meadow boundaries across landscape attributes

To explore how the magnitude of changes to eelgrass meadow boundaries varied among sites in different landscapes, we gathered pre-existing data sets describing the environment across the region enclosing our study sites. We then compared the principal component values calculated above describing eelgrass dynamism to these environmental attributes.

The environmental attributes were (1) areas of similar climate and biota, termed ecoregions (source and methods: Omernik & Griffith 2014), (2) mean direct normal irradiation from 1994 to 2019 as a proxy for light intensity (source and methods: ESMAP 2019), (3) mean monthly August air temperature from 1950 to 2000 as a proxy for potential heat stress (source and methods: UC Berkeley Museum of Vertebrate Zoology 2011), (4) a human footprint index describing built environments, human population density, nighttime lights, crop and pasture lands, roads and railways, and navigable waterways as of 2009 as a proxy for human stressors (source and methods: Venter et al. 2018). Because the human footprint index, temperature, and sunlight intensity at local scales decreased with increasing latitude (Fig. S2), as did sea surface temperature at a coast-wide scale (NOAA 2023), we elected to formally use only the human footprint index as an explanatory variable while showing its correlation with latitude, but discussed the potential effects of all putative environmental drivers collectively. Of note, high-resolution data describing water temperature, depth, and turbidity, which would more precisely describe environments experienced by eelgrass, were not available. Overall, the purpose of examining environmental variables at the sites was to acknowledge that eelgrass inhabiting sites under less anthropogenic stress probably also experienced lower temperatures and sunlight intensity.

Our analyses included linear models wherein the response variable was the first principal component scores calculated above and the explanatory variable was the mean human footprint index within 25 km of a site. We chose 25 km buffers arbitrarily as an attempt to capture the landscape context surrounding sites. We acknowledge that relevant spatial scales are subjective depending on context (Levin 1992) while noting that this metric captured obvious (e.g. via satellite imagery) differences between sites that were relatively unmodified and remote in the north and sites near human-developed areas elsewhere, along with salient latitudinal gradients in temperature and sunlight intensity.

2.4. Additional details

We repeated the analysis twice over 2 data sets to address tradeoffs between data inclusiveness—hence replication across time and space—and presumed quality. The first analysis included all data. The second analysis was restricted to one group of data (hereafter, tier one; designations in Table S1)

that included temporally proximate observations of a site where horizontal data (i.e. excluding the Nisqually River data because we interpolated polygon shapes from point data along linear transects) were collected for the entirety of a given site using the same methods during one continuous effort within the same season(s) (winter: December–February; spring/summer: March–August; summer/fall: June–November). For example, all surveys of Choked Pass occurred in July and August using unoccupied aerial systems, so we designated these data as tier one observations. The purpose of performing 2 analyses was to provide one analysis with less replication across time and space but presumably informed by more precise comparisons between proximate years within sites, and another analysis with presumably less precise comparisons but greater replication across time and space. Notably, this approach split tier one data for Morro Bay into 2 time series, each using consistent methods. We followed the convention of presenting figures using all data in the main text and tier one data in the Supplement. We performed the analysis in R version 4.2.1 (R Core Team 2022).

3. RESULTS

3.1. Describing change in eelgrass meadow boundaries among years

As expected, eelgrass meadows changed between time steps at all sites (Figs. 2 & 3; Figs. S3–S5). Eelgrass meadow contraction and expansion distances (i.e. Pareto alphas) in the full data set were detectably influenced by the length of the time gaps between observations (median time gap between surveys: 2.25 yr [all data], 1 yr [tier one]); estimates of these metrics that we report here are from models that included the number of years between observations as a covariate and are predicted from these models assuming observations were made between a time period of 1 yr (Table 2; Fig. S6). Eelgrass meadow boundaries typically expanded away from meadow fringes on the order of single to low tens of meters, but in some cases eelgrass meadow boundaries shifted into areas much farther away (Fig. 3; Fig. S4). After attempting to account, as appropriate, for variable time gaps (see Section 2), there was considerable variation among sites in the amount that eelgrass meadows changed annually (Fig. 3; Fig. S4). Changes were typically around 10–30% of total meadow size, but in many instances changes were much greater.

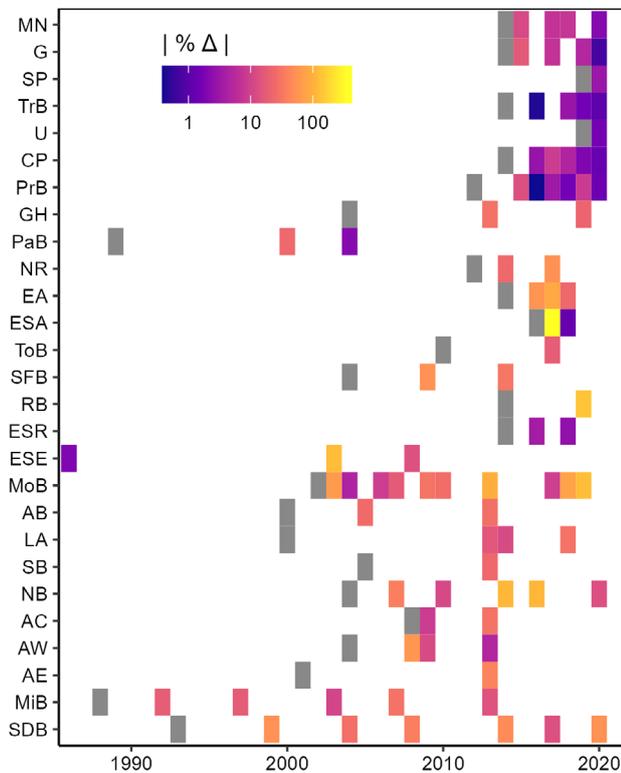


Fig. 2. Time series of absolute (i.e. positive or negative) percent change in eelgrass across all sites. Note that the absolute percent change color ramp is log transformed so that outliers do not dominate the value range. The first tiles in each time series are gray because there are no earlier time steps to inform calculations of change. Two early observations from Elkhorn Slough (composites of 1931 and 1937 and 1956, 1966, and 1976) are omitted to improve visibility of the remaining observations. Sites: McMullin North (MN), Goose (G), Superstition Point (SP), Triquet Bay (TrB), Underhill (U), Choked Pass (CP), Pruth Bay (PrB), Gibsons Harbour (GH), Padilla Bay (PaB), Nisqually River Delta (NR), Estero Americano (EA), Estero de San Antonio (ESA), Tomales Bay (ToB), San Francisco Bay (SFB), Richardson Bay (RB), Elkhorn Slough (recent and early: ESR and ESE), Morro Bay (MoB), Alamitos Bay (AB), Los Angeles and Long Beach Harbor (LA), Seal Beach (SB), Newport Bay (NB), Agua Hedionda Lagoon (West, Center, and East: AW, AC, and AE), Mission Bay (MiB), and San Diego Bay (SDB)

Examining these patterns collectively further suggested that year-to-year changes in eelgrass meadows varied among sites. PCAs indicated that most variation (82 and 86%, all data and tier one data, respectively) among sites was captured by one principal component describing year-to-year expansion, contraction, absolute change, and expansion distances. That is, sites tended to support greater eelgrass area expansion, eelgrass area contraction, absolute change, and eelgrass area expansion distances (note: higher Pareto α values indicate lower expansion distances) (Fig. 4; Fig. S7). Vector loadings

on the PCAs indicated that differences in eelgrass dynamism among sites were especially driven by differences in the amount that eelgrass meadows contracted (Fig. 4; Fig. S7). Sites with eelgrass meadows that varied less over time (according to their PC1 values) included those within the Central Coast of British Columbia (Choked Pass, Goose, McMullin North, Pruth Bay, Superstition Point, Triquet Bay, and Underhill), Padilla Bay (WA), the central portion of Agua Hedionda Lagoon (CA), Elkhorn Slough (CA) (in recent years), and Tomales Bay (CA). Sites with comparatively dynamic meadows included the remaining California estuaries, the Nisqually River delta, and Gibsons Harbour (BC).

Eelgrass often recolonized areas that were occupied by meadows in previous years (Fig. 5; Fig. S8). That is, among sites that we observed at least 3 times (21/27 [all data] and 11/17 [tier one]), eelgrass meadows within various areas of these sites were frequently present, then absent, then present again. As time series grew longer, documented incidence of recolonization typically increased and in many cases included the majority of areas where eelgrass expanded to in a given year. Notably, incidence of expansion constituting recolonization was especially high in Morro Bay as its bay-wide eelgrass population was collapsing.

3.2. Post hoc comparison of variation in seagrass meadow boundaries across landscape attributes

From the above analyses emerged a pattern that eelgrass meadows located in the less human-modified Central Coastal British Columbia sites changed relatively little. Indeed, variation in eelgrass meadow area over time increased significantly with increasing human footprint in the landscapes surrounding sites ($p = 0.043$ [all data], 0.007 [tier one]) (Fig. 4; Fig. S7). Notably, there was substantial error around these linear model predictions, particularly involving some sites with intermediate human footprint indexes and relatively variable eelgrass. Additionally, human footprint indexes of different sites were collinear with latitude (Pearson correlation coefficient: -0.86 [all data], -0.84 [tier one]), itself a proxy for the collinear attributes of ecoregion, sunlight intensity, and air and sea surface temperature (Fig. S2, NOAA 2023). That is, relatively unmodified sites were also within landscapes characterized by a marine temperate rainforest rather than Mediterranean ecoregion, lower temperatures, and less sunlight intensity, and their eelgrass meadows varied

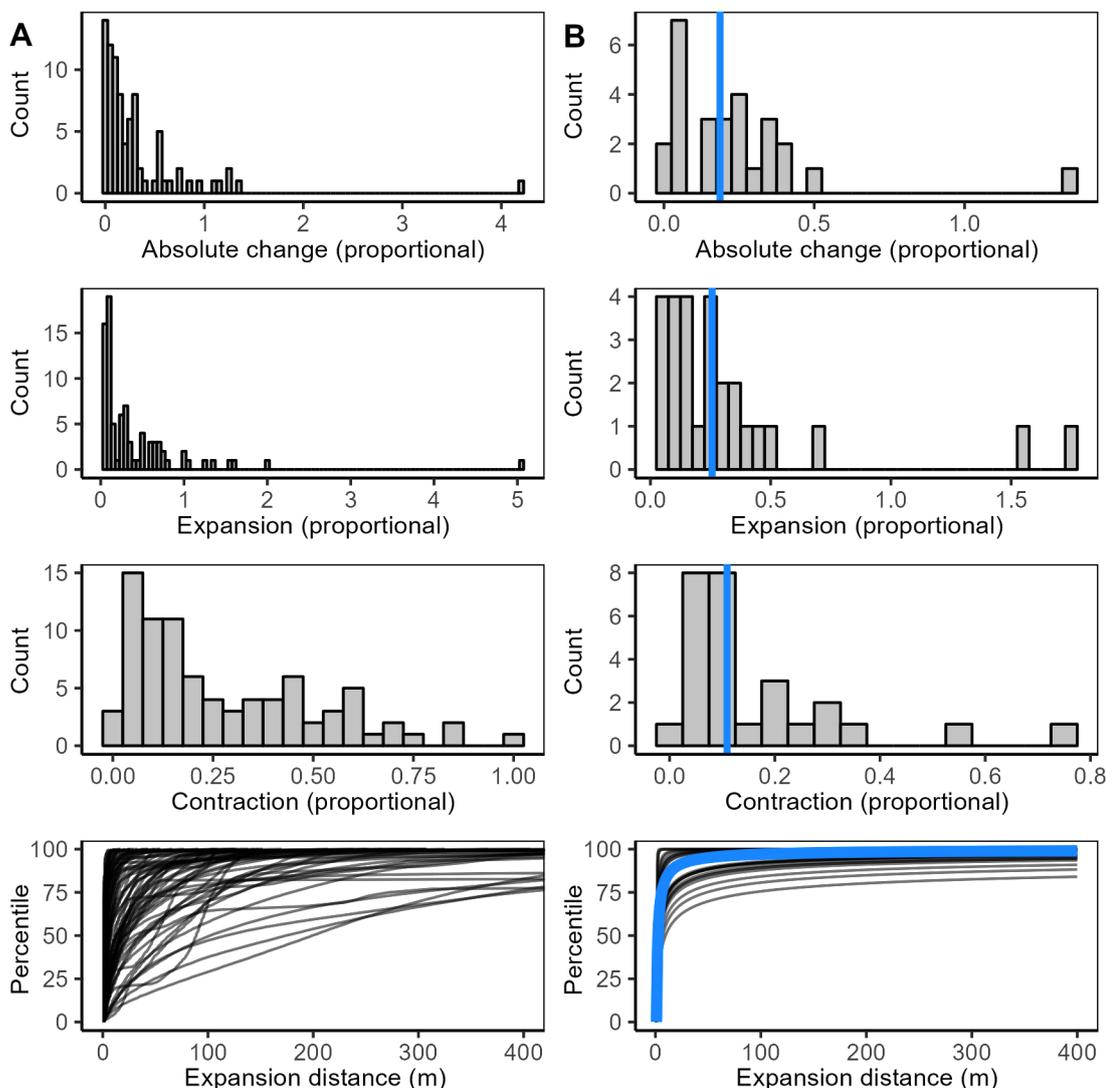


Fig. 3. Change in meadow area over time as described by 4 dynamism metrics. The top 3 rows show frequency histograms. The bottom row shows cumulative distributions. (A) All empirical observations, including multiple observations per site. (B) Dynamism metrics predicted by models accounting as appropriate for time interval between observations (Eq. 3 and Table 2), providing one prediction per site. Contraction and expansion distance models detected increased changes with increased time between observations and model predictions assume 1 yr between observations. Blue lines indicate median model predictions across all sites

Table 2. Inclusion of time gap parameters in models describing eelgrass dynamics. For each comparison (row), we fit 2 candidate models: one including and one omitting a time gap parameter. We chose to include a time gap parameter in final models if Akaike’s information criterion corrected for small sample size (AICc) of the candidate model including this parameter was lower than its counterpart model omitting the parameter. The term $\Delta AICc$ describes the absolute difference in AICc between final models and their rejected counterparts

Data	Response	Time gap parameter (β_1) included	$\Delta AICc$
All	Expansion (proportional)	No	3.57
	Contraction (proportional)	Yes	7.38
	Absolute change (proportional)	No	3.29
	Pareto α	Yes	1.36
Tier one	Expansion (proportional)	No	0.27
	Contraction (proportional)	No	4.48
	Absolute change (proportional)	No	0.47
	Pareto α	No	3.74

comparatively less over time. This pattern was evident via visual inspection of these metrics in tier one data compared among sites while holding the number of years between observations constant (Fig. S9), suggesting it was not an artifact of variable amounts of time between observations.

To illustrate dynamics epitomizing this contrast, Richardson Bay (CA), which lies in a highly modified landscape known to stress eelgrass (Lesberg 2021), and Choked Pass (BC), which lies in a relatively unmodified landscape, were both observed in 2014 and 2019. During this time, eelgrass meadows in Richardson Bay expanded substantially and contracted slightly, whereas eelgrass meadow extent in Choked Pass was nearly static (Fig. 6).

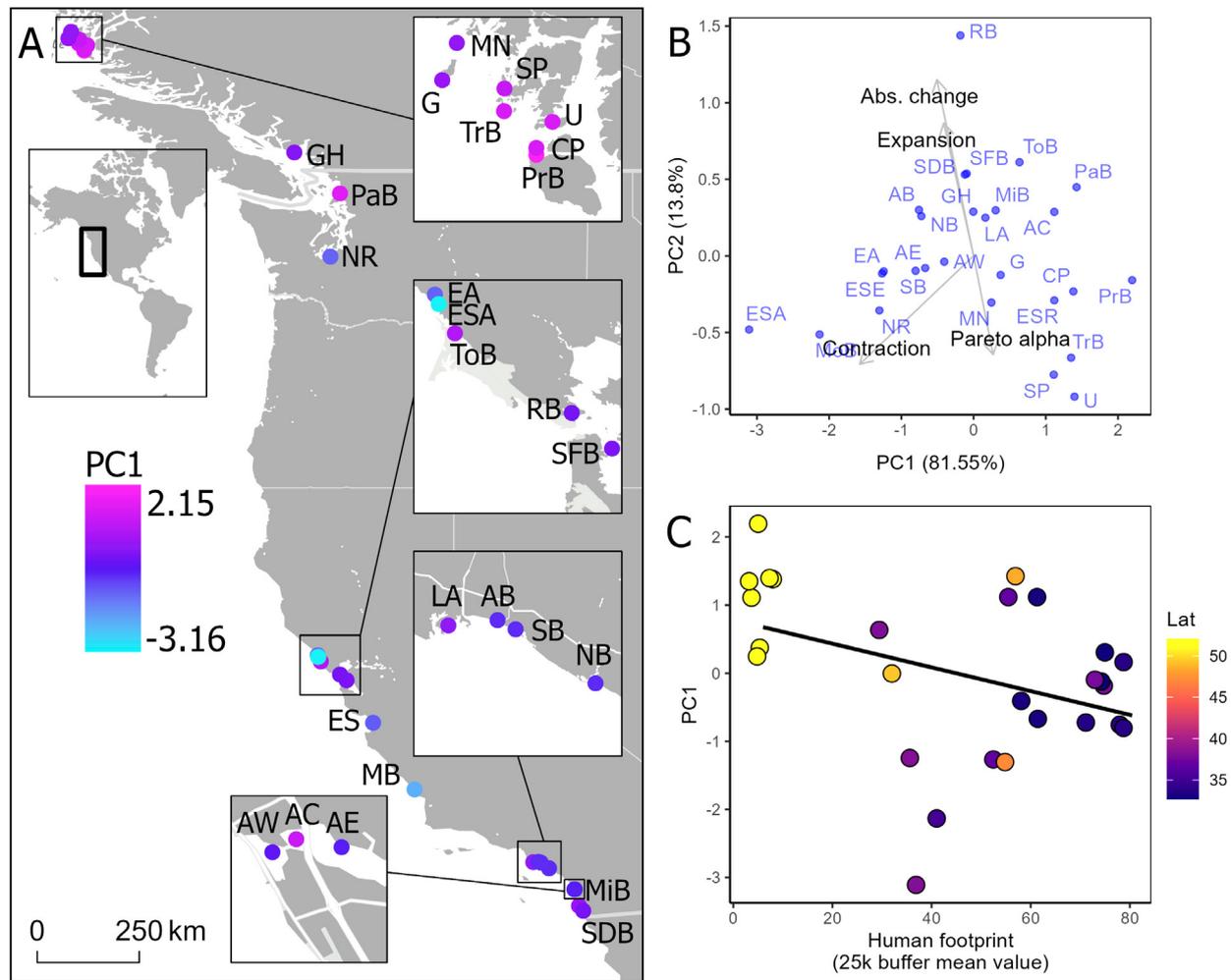


Fig. 4. Principal components analysis (PCA) comparing eelgrass dynamism metrics among sites and to a human footprint index. Site abbreviations are the same as in Fig. 2. (A) Study sites colored according to their first principal component scores. (B) PCA plot showing vectors indicating loadings of eelgrass dynamism metrics on the first 2 principal components and the first 2 principal component scores of the sites. (C) First principal component scores of the sites, describing eelgrass dynamism compared to an index of human footprint within 25 km of sites, with points colored according to latitude. Line shows linear model fit to points

4. DISCUSSION

We assembled eelgrass surveys repeated within sites across the Northeast Pacific to quantify the potential for meadow boundaries to shift over time. Noticing that eelgrass meadows appeared to change more over time at some sites than others, we quantified additional metrics describing meadow dynamics and compared them to environmental attributes of the landscapes at the sites. Eelgrass meadow boundaries expanded, contracted, changed in total extent, and shifted at all sites. Typically, changes in total meadow extent were 10–30% of total meadow size, and expansions were on the order of tens of meters, but sometimes changes and expansion distances

were much greater. Indeed, between some years of observation, the majority of total eelgrass present could be lost or gained, a phenomenon that has also been reported in the Western Atlantic across decades of observation (Bartenfelder et al. 2022). Eelgrass meadows tended to expand along their fringes and often recolonized areas where they used to be present; the latter was documented more often by longer time series. The magnitude of these dynamics varied considerably and cohesively (i.e. metrics quantifying dynamics varied together) among sites. This range in eelgrass meadow dynamism across sites appeared to be related to natural attributes and anthropogenic stressors, which we discuss below. Understanding the potential for the boundaries of eelgrass meadows

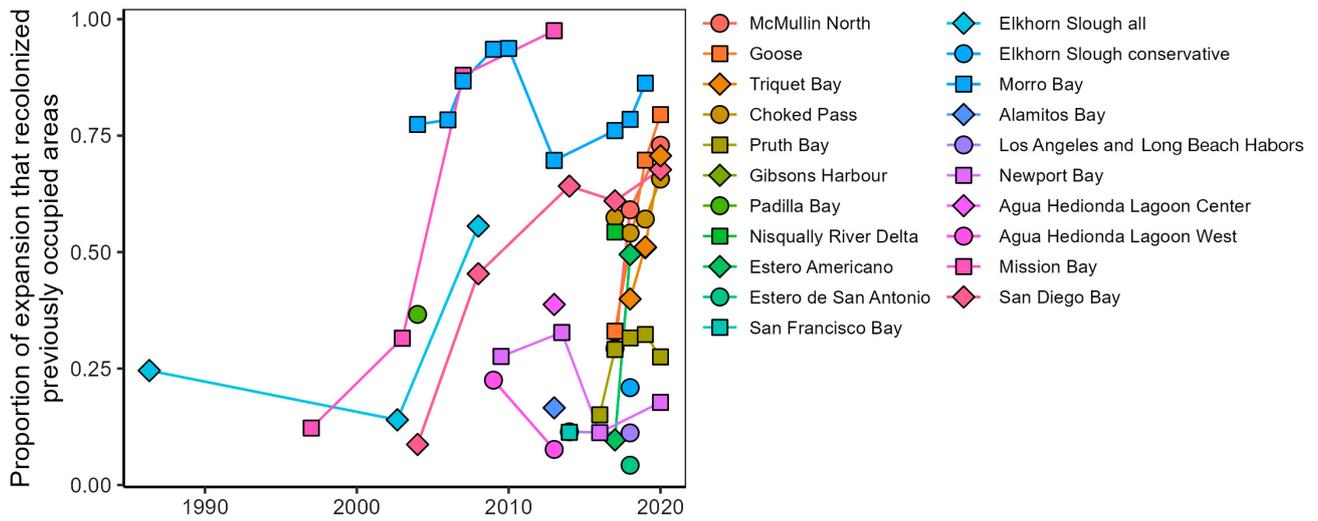


Fig. 5. Proportion of eelgrass observed within sites during singular years that recolonized areas occupied by eelgrass in previous years, separated by data set

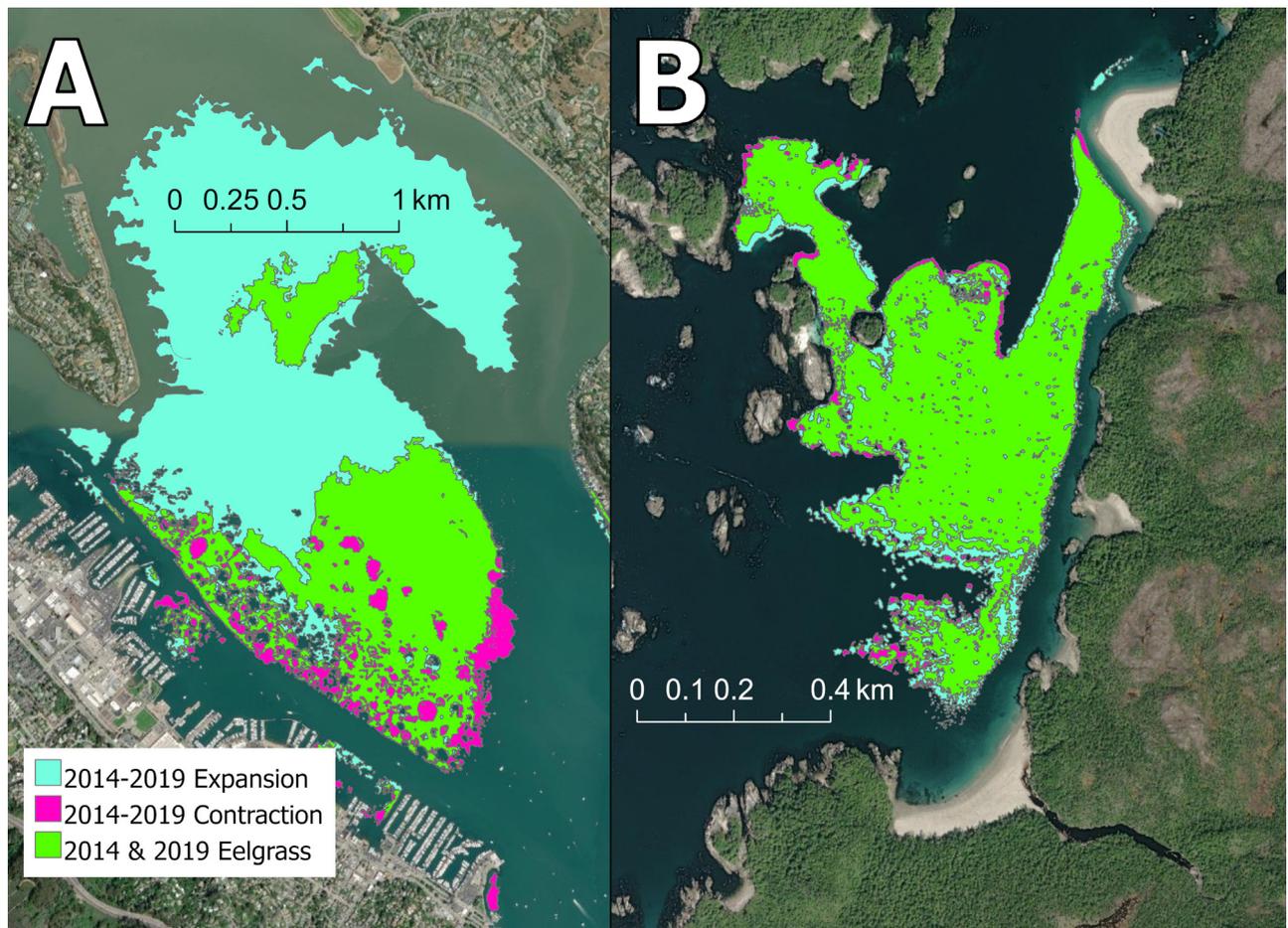


Fig. 6. Greater eelgrass dynamism between 2014 and 2019 in (A) Richardson Bay, CA, compared to (B) Choked Pass, BC. Richardson Bay is exposed to stressors including eutrophication, runoff, heat stress, drought, sedimentation, and scour, whereas these natural and human stressors are less intense at Choked Pass

and other biogenic habitats to shift over time can inform tactical management seeking to avoid short-term conflicts between point stressors and protected species (WDNR 2014). It can also inform strategic conservation seeking to protect long-term ecosystem function by acknowledging that presently unoccupied areas may prove to be important eelgrass habitats over long time horizons, especially as changes such as rising sea levels shift optimum habitat locations (Lyons et al. 2013, S. H. Munsch et al. unpubl.).

Shifting eelgrass meadows underscore the need to craft management approaches compatible with naturally dynamic ecosystems. Tactically, practitioners may couple an understanding of the potential for meadow boundaries to rearrange with monitoring that provides near-real-time information on meadow locations to make adaptive decisions seeking to avoid near-term conflicts between human stressors and dynamic habitats. Key to this approach is protecting areas that are presently unoccupied because they may be occupied in the future (Lyons et al. 2013). Strategically, it is important to acknowledge that ecosystems constantly change and support asynchronous fine-scale dynamics that have been shown to promote large-scale stability (Hilborn et al. 2003, Brennan et al. 2019). In the case of eelgrass, diverse (e.g. depth, freshwater and oceanic connectivity) and temporarily unoccupied habitats are likely to support seagrass resilience over long timelines (Fonseca et al. 1998, Lyons et al. 2013, Shelton et al. 2017). Indeed, eelgrass area varied less at the site scale than at the scale of sections within sites because these sections supported asynchronous eelgrass meadow area dynamics, probably supported by spatially heterogeneous ecosystem environments and ongoing viability of habitats even when vacant (S. H. Munsch et al. unpubl.). Additionally, practitioners seeking to buffer eelgrass from stressful human activities may consider the greater potential for eelgrass meadow boundaries to shift among years in systems experiencing greater anthropogenic and natural stressor regimes. Furthermore, because eelgrass presence is used to indicate ecosystem status (e.g. Puget Sound Partnership 2022), site-scale variance in eelgrass extent may indicate ecosystem status in a way that is not captured by snapshot information or abundance metrics (*sensu* Kareiva & Wennergren 1995). Overall, tactically protecting areas that may soon be colonized while strategically maintaining a diversity of temporarily unoccupied habitats to enable long-term shifts in eelgrass presence may facilitate the coexistence of a dynamic, keystone species and human activities.

There are many attributes that could influence eelgrass meadow dynamics across the Northeast Pacific. Eelgrass meadows within this region occur across a range of latitudes, climates, shoreforms, and anthropogenic influences. Sites are generally warmer and receive more intense sunlight at lower latitudes. Moreover, in contrast to higher latitudes, California's Mediterranean climate provides little to no summertime precipitation and exceptionally variable precipitation among years (Dettinger 2011), creating episodic estuarine physical environments and sediment delivery (Largier 2010, Walter et al. 2020). Indeed, drought-prone Australian landscapes support similarly episodic estuarine physical environments that dramatically impact eelgrass presence even within relatively unmodified systems (Scanes et al. 2020). Notably, these factors potentially link changing climates and future eelgrass meadow dynamism. Additionally, the geomorphology of the California estuaries included in this study naturally (e.g. barrier embayments) and/or artificially (e.g. breakwaters) tend to constrain fresh and saltwater exchange through small bay and lagoon mouths, which can lead to high water residence times for many of these systems, particularly during periods of low freshwater inflow (Heady et al. 2014). Another important factor may be that the relatively complex shorelines of British Columbia tend to create more low-exposure, protected shallow environments, as was the case in the northerly, less-modified sites except Choked Pass. Plausibly, sites that are less exposed to wave energy or similar mechanical stressors such as currents may support eelgrass meadows that change less over time. Notably, eelgrass in Choked Pass, which is exposed to storms, large waves, and currents, did not appear to vary more over time than its neighboring, less exposed sites, and it may be worth considering that its comparatively low anthropogenic footprint overridingly contributed to its lower variation in eelgrass area. Furthermore, land development is common across the USA and southern British Columbia but is especially intense along estuaries of the Southern California Bight (Greene et al. 2015, Sobocinski 2021). Similarly, agriculture is common along the coasts of the USA and British Columbia, but especially high along and upstream of estuaries of central California (Greene et al. 2015, Sobocinski 2021). Eutrophication is also more common in Californian estuaries than at higher latitudes (Greene et al. 2015). Additionally, multiple stressors can act synergistically to affect eelgrass. Heat stress exacerbates effects of low light on photosynthesis (Krumhansl et al. 2021) and diminishes disease resistance (Graham et al. 2021). The effects of

runoff, eutrophication, sedimentation, and heat stress may be exacerbated by water withdrawals, drought, or landform changes that decrease estuarine water turnover (Walter et al. 2018). Overall, sites varied in natural (e.g. light, hydroclimate, temperature) factors and human-caused (e.g. anchor scour, dredging, nutrient input) or influenced (e.g. water turnover) stressors relevant to eelgrass.

Eelgrass meadows appeared to change less over time in landscapes with less natural constraints and human stressors. In general, eelgrass meadows within sites along the central coast of British Columbia changed least over time. These sites uniquely occurred within relatively unmodified landscapes (Venter et al. 2018), at higher latitudes where excessive heat and light were presumably least frequent (*sensu* Krumhansl et al. 2021), and outside of California's episodic hydroclimate, greater eutrophication stress, and increased urbanization (Greene et al. 2015). Other locations inhabited by eelgrass meadows that changed comparatively less over time included Padilla Bay, Elkhorn Slough (in recent years), Tomales Bay, and the central portion of Agua Hedionda Lagoon. While hardly pristine, the former 3 sites are in some ways less impacted by human development than other sites. Padilla Bay and Elkhorn Slough lie within modified but unurbanized landscapes, and nearly all of Padilla Bay and much of Elkhorn Slough are protected by the NOAA National Estuarine Research Reserve system (<https://coast.noaa.gov/nerrs/>), with the latter also owned and managed by the California Department of Fish and Wildlife. Tomales Bay also lies within a relatively unurbanized landscape. Additionally, Padilla Bay, Elkhorn Slough, and Tomales Bay were directly connected to the California Current summer upwelling that transports cooler waters to nearshore environments and moderates summer warming (García-Reyes & Largier 2012). Interestingly, original surveyors (Merkel & Associates 2014) noted that the west and east portions of Agua Hedionda Lagoon experienced direct human (dredging) and climatic (sediment delivery and suspension by waves) disturbance regimes, respectively, and we found that eelgrass meadows within the central portion changed least over time. A potential nuance to these patterns may be that dredging near the mouth may have increased delivery of cool upwelled waters to the central section of the lagoon during warm summer months, providing a thermal refuge.

In contrast, sites inhabited by more dynamic eelgrass meadows tended to occur within landscapes that may naturally create more extreme or variable physical environments for eelgrass and be more

stressed by human activities. Studies examining these systems individually have argued that the stressors such as those previously discussed contribute to such dynamism. For example, shoreform modifications that reduced water exchange with the ocean, and land-use change and dredging that increased sedimentation are hypothesized to have contributed to eelgrass collapse in Morro Bay (Walter et al. 2018, 2020 and references therein). Additionally, vessel scour contributes to dynamics in Richardson Bay (Kelly et al. 2019) and presumably at most urbanized sites. Red tides are hypothesized to disturb eelgrass in California estuaries (Merkel & Associates 2014), and industrial activity (e.g. log booming) and vessel mooring are hypothesized to contribute to dynamics in Gibsons Harbour (BC) (Beaty & Sanford 2019). Furthermore, sedimentation and salinity gradients driven by episodic precipitation and drought are hypothesized to influence San Francisco's eelgrass meadow range (Merkel & Associates 2015), highlighting the potential impacts of hydroclimate on eelgrass meadow shifts, especially within the volatile precipitation climate of California. Overall, eelgrass meadows appeared to change less over time in systems experiencing less intense regimes of natural and human stressors.

These patterns suggest a hypothesis that variation in eelgrass meadow boundaries over time can depend on natural and anthropogenic landscape context. Related to this hypothesis, practitioners have anecdotally noted a contrast between eelgrass meadows that vary comparatively little over time in relatively unimpacted Drakes Estero and dynamic eelgrass in nearby, highly impacted San Francisco Bay (Beheshti & Ward 2021). While we are unaware of other studies that have specifically examined dynamism in meadow boundaries, previous work across North America, Europe, and Asia found that eelgrass biomass varied more over time in warmer environments (Clausen et al. 2014). Work in the Southern Gulf Islands of British Columbia noted that eelgrass declined from 1934 to 2016 as shoreline activities and development increased (Nahirnick et al. 2020), and there is a sizeable literature documenting natural constraints and human stressors on eelgrass abundance (e.g. Zimmerman et al. 1997, Orth et al. 2006, Patrick et al. 2014, Krumhansl et al. 2021). Indeed, Krumhansl et al. (2021) found that productivity was greater in cooler, well-flushed sites and that higher temperatures exacerbated effects of low-light conditions. As argued by Clausen et al. (2014), greater temporal variation in seagrass biomass in warmer waters may be driven by reduced respiration rates at lower

temperatures enabling more biomass to persist during winter and less severe warm temperature events during the summer that cause mortality. Nejrup & Pedersen (2008) showed experimentally that especially cold waters and warm waters slow growth by limiting photosynthetic rates and increasing respiration, respectively, and that shoot mortality increased sharply in waters over 20°C. Our results are somewhat consistent with these findings, as dynamism tended to be greater at sites where instances of such stressors (e.g. warm regional conditions, low water turnover) were liable to occur. In addition to being influenced by stressful events directly, increased dynamism may reflect endogenous responses of eelgrasses to invest more in dispersive, annual forms via sexual reproduction rather than perennial forms within areas of greater stressor regimes (Blok et al. 2018 and references therein). Indeed, Phillips et al. (1983) found that incidence of sexual reproduction was especially high in low-latitude eelgrass populations along the Northeast Pacific that routinely experience stressful heat events. Furthermore, Marín-Guirao et al. (2019) showed experimentally that heat stress caused flowering in another species of seagrass and argued that flowering could reflect an adaptive response to disperse offspring via sexual reproduction away from stressful environments. Following our opportunistic, post hoc, hypothesis-generating perspective, future studies could attempt to investigate the role of natural and artificial stressor regimes on eelgrass meadow boundary dynamics by employing more deliberate sampling regimes designed to develop generalizable estimates of the potential for meadows to shift depending on landscape context.

Limitations should be considered in the interpretation of this study. First, there is human bias in delineating edges of eelgrass meadows, which are actually aggregations of individual eelgrass shoots. Next, time series of the different study sites varied in length and sampling frequency. Longer, more frequent sampling would have enabled us to more precisely quantify interannual variation, particularly within the context of long-term trends, and more fundamentally increased sample size. Our candidate models included a covariate that attempted to correct for variation in the length of time between observations, but there is no statistical approach that can substitute for high-resolution observations. Indeed, it is important to consider that eelgrass meadow area may have varied substantially and included both increases and decreases between observations, especially when these time gaps were long. An additional concern is that short, recent time series may overlook

the historical context of more recent dynamics. For example, perhaps the recent, substantial expansion of eelgrass in Richardson Bay only took place after human or natural disturbances extirpated these meadows in the first place, followed by temporarily suitable conditions that enabled recovery. Furthermore, given almost 2 centuries of modification to this landscape, it is highly likely that eelgrass area has declined substantially compared to its pre-industrial state (Lesberg 2021). Indeed, longer time series would have allowed us to characterize eelgrass trajectories and variation over time with more confidence. Perhaps one of the more important avenues for future research that could be addressed using longer, high temporal resolution time series would be to assess the role of increasing water temperatures and increasingly frequent marine heatwaves (Oliver et al. 2018) on eelgrass meadow disturbance and recovery. Eelgrass in warmer, shallower systems may be more sensitive to thermal stress (Magel et al. 2022), implying that responses of eelgrass meadows to warming oceans will vary across landscapes. Additionally, high-resolution, long-term monitoring may be necessary to accurately link marine heatwaves to impacts on eelgrass meadows, especially if eelgrass die-offs take place slowly and over long periods following heat stress events (Strydom et al. 2020).

In conclusion, eelgrass meadow boundaries across the Northeast Pacific were universally dynamic. Dynamism varied among sites, and landscapes with greater natural and human stressors appeared to support eelgrass meadow boundaries that changed more over time. The quantitative information presented here may guide short-term (~1–5 yr) interventions seeking to prevent co-occurrence of eelgrass and stressful human activities, and suggests the importance of including presently unoccupied habitats in crafting long-term conservation strategies to protect productivity at scales relevant to people and the ecosystems they benefit from. Metrics similar to those presented here can be extended to other habitat-forming species (e.g. canopy-forming seaweeds, Blanfuné et al. 2019), and may become increasingly feasible to monitor with technologies that facilitate data collection (e.g. unoccupied aerial systems) and processing (e.g. GIS and machine learning algorithms). Monitoring such dynamics is also important against the backdrop of global changes such as increasing heatwaves (Oliver et al. 2018) and sea level rise (Pontee 2013) that are likely to shift eelgrass boundaries, and in the context of other habitat-forming species boundaries and their associated stressors.

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