

Decades of eelgrass meadow dynamics across the northeast Pacific support seascape-scale conservation

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Eelgrass meadows provide vital nearshore habitats and ecosystem services, but they have declined from human stressors and conservation efforts are now widespread. Dynamic ecosystems like eelgrass meadows naturally rearrange as disturbance and recruitment unfold across seascapes. However, some decisions that protect eelgrass only consider extant meadows, thus ignoring the potential for change. Here, we report decades of eelgrass dynamics observed across the northeast Pacific. Our observations support conservation expanded to the seascape scale, which includes potentially inhabitable areas along with extant meadows. We found that total seascape meadow area changed over time, and changes within seascapes were often asynchronous. Some meadows rearranged across seascapes over multiple kilometres and decades. Also, some seascapes compartmentalized meadow collapse, which enabled later recovery, or supported local recruitment that substantially increased total meadow area. These observations were consistent with hierarchical patch dynamics, which promote ecosystem persistence over larger space and time scales. Thus, to enable the dynamics that underpin eelgrass persistence, it is necessary to keep many eelgrass habitat options open across seascapes, rather than protect only extant meadows. Given that dynamic, hierarchical ecosystems are common along marine shorelines, this approach may be effective for both nearshore ecosystems in general and for eelgrass in particular.

Keywords: coast, disturbance, estuary, habitat mosaic, hierarchical patch dynamics, marine, nearshore, persistence.

Introduction

Seagrass meadows are vital ecosystems. Seagrasses are marine flowering plants that form meadows along shorelines, where they influence the physical environment, creating habitat for fish, invertebrates, and waterfowl and providing numerous ecosystem services (Orth *et al.*, 2006). For example, seagrasses sequester harmful bacteria as well as at least 10% of the ocean's organic carbon despite occupying only 0.2% of the ocean's area (Fourqurean *et al.*, 2012; Lamb *et al.*, 2017). Moreover, seagrasses support fisheries globally (Unsworth *et al.*, 2019a).

However, eelgrass (*Zostera* spp.) and other seagrasses have declined markedly, with estimates indicating that ~35% of historical habitats remain globally and that downward trends are evident across the world (Orth *et al.*, 2006; Lotze *et al.*, 2006; Dunic *et al.*, 2021). Indeed, many activities associated with coastal development destroy eelgrass habitats and pose

existential threats to meadows (Orth *et al.*, 2006). Consequently, efforts to sustain or recover eelgrass meadows are widespread (Unsworth *et al.*, 2019b).

Eelgrass conservation can be difficult because meadows shift over time. One common conservation approach is to establish zones that encompass eelgrass meadows where human stressors are not permitted. A second is to attempt restoration to offset loss of extant meadows in areas where human stressors cannot practically be avoided, such as dredged navigable waterways (Minns *et al.*, 2011; NMFS, 2014; Marine Planning Partnership Initiative, 2015; Murphy *et al.*, 2021). However, as meadow boundaries shift, protected zones may become outdated, especially when they are defined simply by the presence of meadows at a given time (Munsch *et al.*, 2023).

Furthermore, a focus on extant meadows misses the bigger picture that eelgrass meadows persist in dynamic form, and

Table 1. Definitions of terms relevant to hierarchical patch dynamics.

Term	Definition
Patch	A spatial unit nested among others across seascapes.
Seascape	“Complex ocean spaces, shaped by dynamic and interconnected patterns and processes operating across a range of spatial and temporal scales” (Pittman <i>et al.</i> , 2021).
Inhabited	A patch status when eelgrass is present.
Temporarily uninhabitable	A patch status when eelgrass is absent and cannot recruit.
Empty inhabitable	A patch status when eelgrass is absent but can recruit.

thus seascapes support many meadow configurations. Nevertheless, the idea that unoccupied habitats should be given value in management decisions can be controversial (USACE, 2010). This controversy may reflect a scale mismatch that can undermine protection efforts.

Conservation in general grapples with scale mismatches between biological processes vs. monitoring and decisions (e.g. Borgström *et al.*, 2006; Cumming *et al.*, 2006; Davis and Schindler, 2021). The former can emerge over landscapes and long periods, while the latter is often focused locally and over short, recent periods. Such scale mismatch can lead to decisions that overlook key emergent phenomena and the ecosystem components that support them (Levin, 1992; Hilborn *et al.*, 2003). To navigate this stumbling block, conservation strategies can be crafted with an eye toward the scales most relevant to desired biological outcomes (e.g. persistence and resilience) and an awareness of observation bias toward more recent and finer scales (Levin, 1992).

A concept of eelgrass meadows as hierarchical and persistent in dynamic form may inform more robust conservation strategies. Eelgrass meadows express hierarchical patch dynamics (Wu and Loucks, 1995; Duarte *et al.*, 2006), a concept that describes landscapes (or seascapes) as a collection of nested habitat patches that change phases separately. Patches cycle through inhabited, temporarily uninhabitable, and empty inhabitable phases as disturbance, recruitment, and growth unfold across seascapes (Table 1).

Disturbances to eelgrass meadows only partially overlap with seascapes, are locally filtered by heterogeneous seascapes, or cause asynchronous physical shifts in local environments (*sensu* Wu and Loucks, 1995; Stanford *et al.*, 2005). Therefore, the patches nested within seascapes also cycle through habitat phases asynchronously. This promotes biological persistence over large space and time scales because universal extirpation is unlikely and may be offset by recruitment elsewhere or in the future (*sensu* Hanski, 1998).

By implication, conservation that values not only extant meadows, but also empty areas that could become inhabited, would align with patch dynamics that unfold over time and enable persistence in nature. That is, conservation focused at the seascape scale, where persistence emerges, may enhance efforts to sustain eelgrass meadows.

Here we report decades of observed eelgrass meadow dynamics across the northeast Pacific and explain why these ob-

servations provide empirical support for seascape-scale conservation. That eelgrass meadows shift over time is known (e.g. Marba and Duarte, 1995; Duarte *et al.*, 2006). Building on this knowledge, our work (i) provides a rare, broad scale of observation that describes these shifts across multiple decades and sites that span 19° latitude; and (ii) interprets meadow shifts in the context of insights learned from dynamic, hierarchical systems that are relevant to conservation efforts generally.

The impetus for this study was to inform eelgrass conservation efforts along the US West Coast. There, government agencies are mandated to sustain *Essential Fish Habitats* like eelgrass, but have disagreed about whether there is habitat value in areas that lack eelgrass meadows but are near them (NMFS, 2007; USACE, 2010). Similarly, marine planning processes in Canada have created protection management zones based on the current-day presence of eelgrass and other habitats that could move (Marine Planning Partnership Initiative, 2015). Also, the Canadian Fisheries Act employs a “no net loss” policy that suggests eelgrass losses due to human stressors must be offset via restoration or mitigation (Minns *et al.*, 2011; Murphy *et al.*, 2021). These situations and approaches can be informed in part through research that shows how eelgrass habitats that are empty at present support meadow shifts over seascapes and years.

More broadly, dynamic, hierarchical ecosystems are common along marine shorelines (Boström *et al.*, 2011), as are the challenges of implementing conservation strategies that are robust to ecological change, particularly given the common but faulty assumption that ecosystems are stationary (Levin, 1992; Cumming *et al.*, 2006; Davis and Schindler, 2021). Indeed, important efforts to identify conservation areas along shorelines are unfortunately often limited to recent observations that may belie great potential for change (e.g. Tomlin *et al.*, 2021). Thus, our work may inform the interpretation of research and monitoring that is used to craft conservation strategies of ecosystems beyond eelgrass meadows.

Methods

To document eelgrass meadow changes over time, we gathered pre-existing surveys from across the northeast Pacific (Figure 1). Surveys were designed to map all eelgrass present across a given spatial domain, such as an estuary or a bay. This dataset included 71 surveys repeated within 12 seascapes, ranging from the 1930s to the 2020s (dates: Supplementary).

Survey methods differed across seascapes, but in most cases, the same methods were maintained for each seascape over time. Central British Columbia was surveyed simultaneously by unmanned aerial vehicles (UAVs) and towed underwater video; Morro Bay was surveyed by multispectral imaging using planes until 2017 and UAVs thereafter; Gibsons Harbour was surveyed by underwater camera; Padilla Bay and Elkhorn Slough were surveyed by aerial photography; Estero Americano and Estero de San Antonio were surveyed visually on the ground; and San Francisco Bay, Newport Bay, Mission Bay, and San Diego Bay were surveyed by sonar (further details: Merkel and Associates, 2013, 2014; Beaty and Sanford, 2019; Marine Taxonomic Services, 2020; Reshitnyk *et al.* (2020); Walter *et al.*, 2020; Beheshti *et al.*, 2022). Within San Francisco Bay, Richardson Bay was

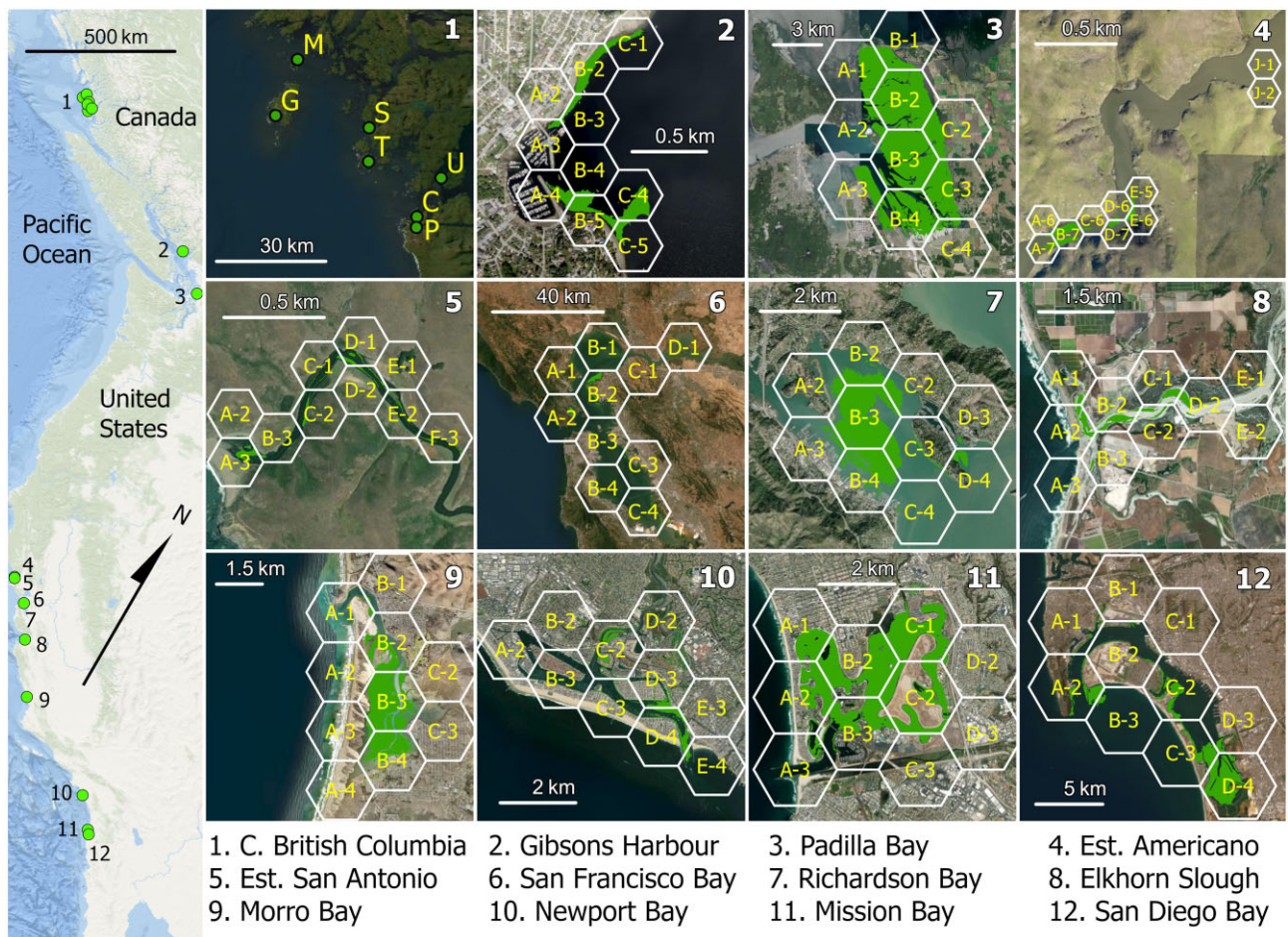


Figure 1. Locations of seascapes and delineation of seascape components (hexagons). In panels 2–12, green indicates places where eelgrass was present during any survey. In panel 1 (Central British Columbia), component names are the first initials of actual location names (Supplementary).

also surveyed by sonar in 2019; we present this additional survey separately, along with the previous survey of this site.

Early seagrass maps of Elkhorn Slough were multi-year composites generated by the original data analysts, who intended to minimize observation error attributable to interpreting aerial images (groupings: 1931 and 1937; 1956, 1966, and 1976; 1980, 1987, and 1992; 2000, 2003, and 2005; 2007, 2008, and 2009). For this time series, the year values that we presented were composites' averages. Based on the original survey reports, seagrass in all sites was presumably *Z. marina*, except in Padilla Bay, which also included *Z. japonica*. In studies that used sonar to map eelgrass, a subset of observations was ground-truthed to ensure a confident classification of meadow presence and absence (Supplementary Table S2 in Munsch *et al.*, 2023).

To document the existence of patch dynamics, we split seascapes into cells that we called “components”, which enabled us to describe changes in meadow area (component sizes: Table 2). We used ten cells per seascape simply because ten represented a tractable number of components to describe and visualize. One exception to this design was in Central British Columbia, where we treated seven smaller, proximate locations as separate components of the seascape.

Table 2. The area of seascape components 2–12 (Figure 1), estimated to be 2 significant figures.

Seascape	Component area (km ²)
Gibsons Harbour	0.10
Padilla Bay	12.0
Estero Americano	0.00061
Estero de San Antonio	0.00083
San Francisco Bay	58
Richardson Bay	2.2
Elkhorn Slough	1.0
Morro Bay	3.3
Newport Bay	2.1
Mission Bay	3.2
San Diego Bay	21

One caveat of this arbitrary cell definition was that eelgrass patches defined by biological and physical traits remained beyond the scope of this study. A second was that the different component sizes and survey periods prevented direct comparison among seascapes. Indeed, variation tends to decrease in larger systems (Moore *et al.*, 2015). However, this approach was sufficient for our primary objectives: to document the widespread existence of (i) asynchronous local-level changes in meadow area and (ii) seascape-level meadow expansions, contractions, and range shifts.

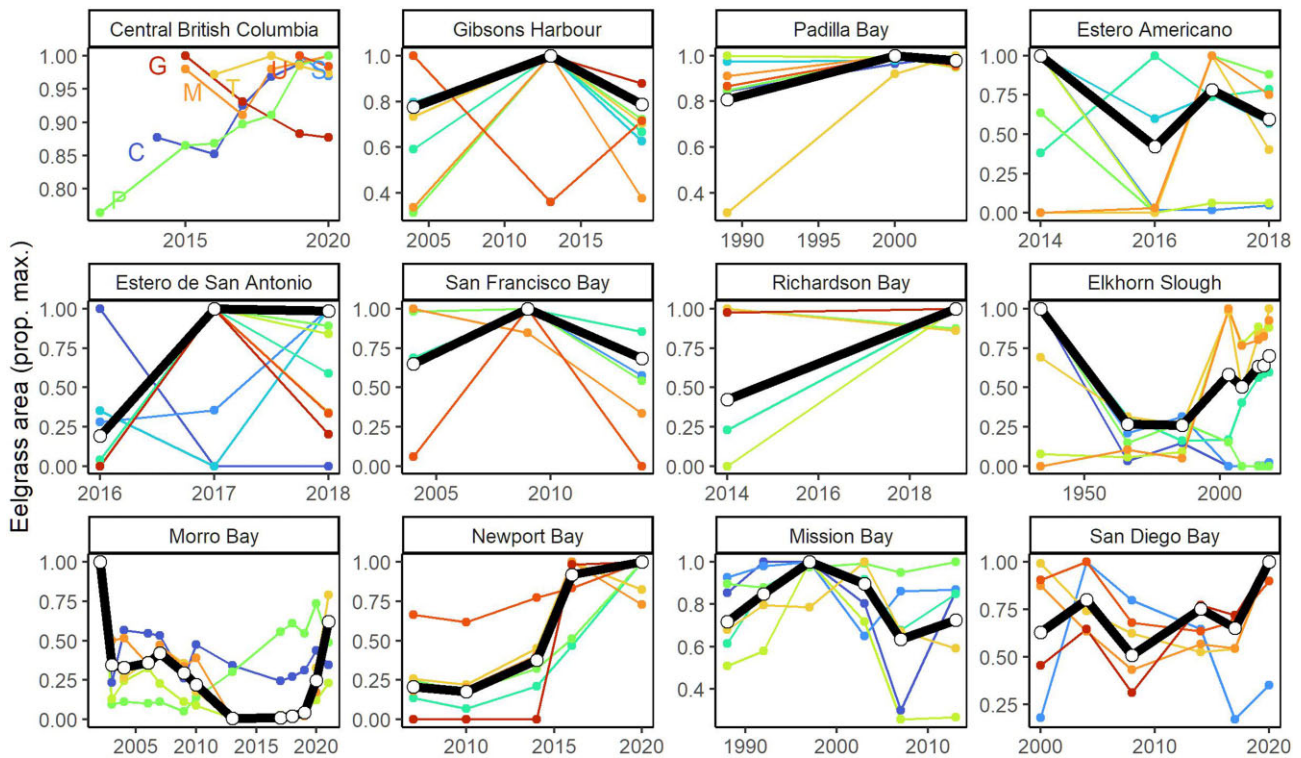


Figure 2. Time series of eelgrass area at the seascape (black and white) and component scale (each component is shown in a different colour). Dynamics are shown only for components that contributed at least 5% to seascape eelgrass area in at least one survey. Time series are standardized by dividing their maximum values (i.e. proportion of maximum) to place them on the same scale. See Figure 3, which assigns component time series to the same colours, for identification of components outside of Central British Columbia.

To assign spatial domains to components, we used the *Generate Tessellation* tool in ArcGIS to overlay ten grid cells over the spatial range of each seascape where eelgrass was observed in any survey. From these assigned cells, we quantified a time series of eelgrass area within each grid. Finally, to examine synchrony in eelgrass dynamics within seascapes, we quantified Pearson correlation coefficients between full-time series of eelgrass area for all pairs of seascape components.

Results

Eelgrass meadows across the northeast Pacific consistently changed at both seascape and component scales (Figures 2 and 3). Many seascapes supported both increases and decreases in meadow area over time. Also, components often transitioned between states of low and high meadow area, and these transitions included shifts between the highest and lowest observed eelgrass area in consecutive surveys.

Local collapse was relatively common, with local, abrupt shifts from high to low eelgrass area evident in some components of almost all seascapes. Conversely, localized recruitment sometimes markedly increased total eelgrass meadow area at the seascape scale, for example, in Richardson Bay. The relative contribution of seascape components to eelgrass area also changed at the seascape scale over time. Sometimes these shifts were striking, such as in Elkhorn Slough, Morro Bay, and Estero Americano. Within seascapes such as Central British Columbia, Elkhorn Slough, Morro

Bay, Richardson Bay, and San Diego Bay, close or adjacent components expressed similar changes in eelgrass area.

While eelgrass area dynamics tended to be coordinated at the component scale overall, in many cases, component-scale dynamics contrasted with dynamics at the seascape scale and with the dynamics of other components within the same seascape (Figure 4). In 14% of observations (unit of replication: seascape \times grid cell \times time step), eelgrass area was below the observed average for the component but above the observed average for the seascape; the opposite was true in 12% of observations. Additionally, in 13% of observations, eelgrass area decreased at the component level while increasing at the seascape level; the opposite was true in 11% of observations.

Additionally, dynamics between pairs of components within the same seascapes across their full time series were negatively correlated for 34% of component pairs (Figure 5). That is, eelgrass often tended to increase in one component while decreasing in another, or vice versa.

Some meadow dynamics amounted to remarkable expansions, contractions, and range shifts perceptible at the seascape scale (Figure 6). For example, eelgrass collapsed and recovered over two decades in Morro Bay, shifted ~ 2 km eastward over eight decades in Elkhorn Slough, and expanded ~ 1 km over 5 years in Richardson Bay. Notably, in Elkhorn Slough, a large meadow expanded in the main channel, and many smaller patches of eelgrass formed in tidal creeks. Additionally, during drought that increased salinity near the river delta in the northeast and increased

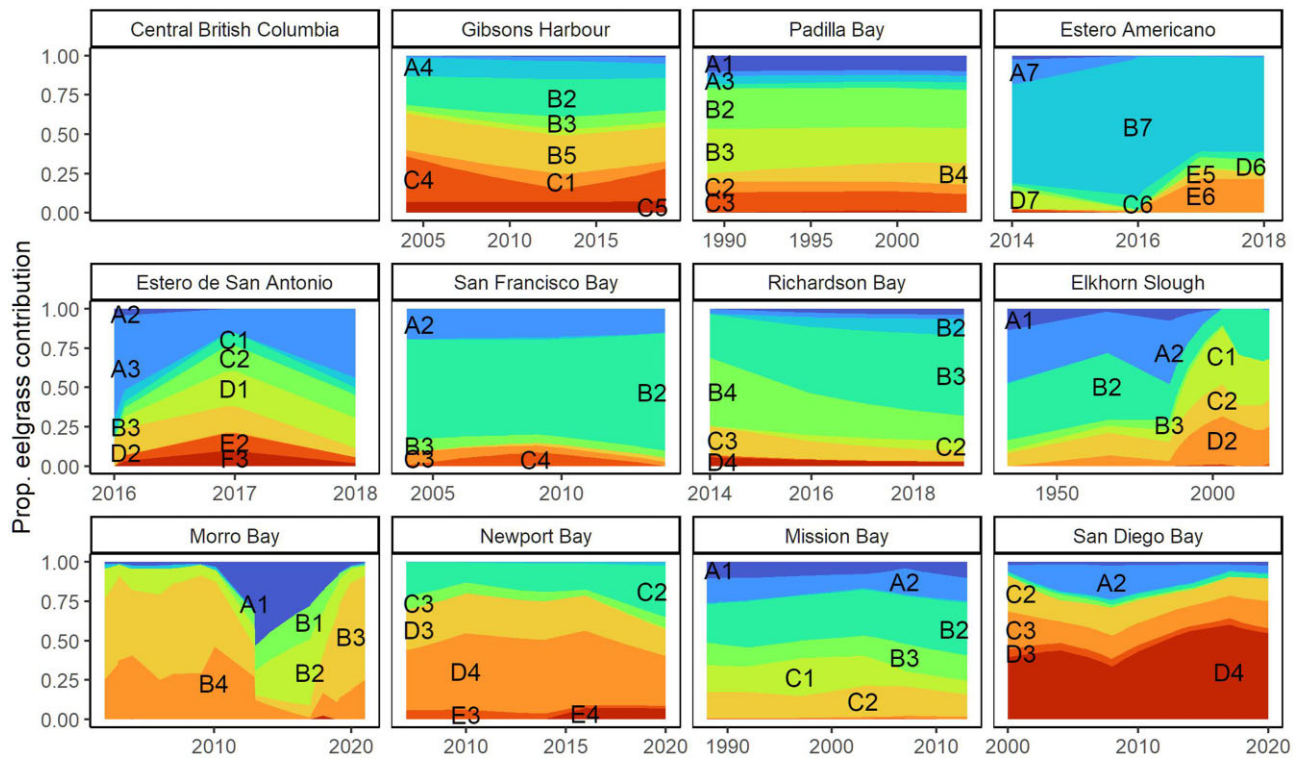


Figure 3. Time series showing proportional contribution of eelgrass area by components to total eelgrass area over seascapes. Central British Columbia is blank because not all components were surveyed every year. Text identifies components that contributed >5% of total seascape-level eelgrass in at least one survey.

turbidity in the south (Supplementary), eelgrass shifted ~20 km northeast, which included the formation of ~1 km meadows.

Discussion

Eelgrass meadows consistently shifted in size and location within seascapes that spanned 19° latitude and were observed over nine decades. A substantial portion of meadow changes within seascapes were asynchronous. Some meadows rearranged over multiple kilometres or over multiple decades. Seascapes compartmentalized meadow collapses to enable later recovery or supported local recruitment that substantially increased overall meadow area. These observations were consistent with patch dynamics, which promote persistence in many ecosystems over large space and time scales (Wu and Loucks, 1995).

By implication, in order to enable the dynamics that underpin eelgrass persistence, it will be necessary to keep many eelgrass habitat options open across seascapes, rather than only protect extant meadows (*sensu* Hanski, 1998). Indeed, areas that momentarily lack meadows can clearly have long-term habitat value for eelgrass. Moreover, considered in isolation, some surveys drastically underestimated the potential of their respective seascapes to support meadows over time.

Because of these dynamics, it is difficult to assign long-term eelgrass habitat value to locations based on extant meadows. Recent and local scales of observation that are typically available to inform decisions could be misaligned with previous and future eelgrass meadow shifts over seascapes and

decades (*sensu* Levin, 1992; Borgström *et al.*, 2006; Davis and Schindler, 2021). Put another way, if locations are excluded from conservation strategies because eelgrass is not present—or if their destruction is not offset by restoration elsewhere—then seascape-scale habitat capacity may erode over time as human stressors encroach upon empty inhabitable areas (*sensu* Hanski, 1998).

While this study was scoped to document patch dynamics, we considered other complementary concepts that can explain stability in dynamic, hierarchical systems and help identify appropriate scales for conservation. First, the concept of metapopulation dynamics, which describes locally unstable populations as networks connected across discrete habitat patches (Hanski, 1998). Metapopulations persist despite local instability because extirpations are staggered across time and reversed by recruitment from neighbouring patches (Hanski, 1998). Second, the portfolio concept describes diverse ecosystem components that are volatile but perform asynchronously, which dampens change at greater scales—scales that are often relevant to resource management (Schindler *et al.*, 2015). Third, the shifting habitat mosaic concept describes landscapes as heterogeneous environments that asynchronously change as environmental disturbances interact with geomorphic and biological processes (Stanford *et al.*, 2005). Habitat suitability shifts constantly, abruptly, and unevenly across landscapes, but biological stability emerges at the landscape scale because organisms also shift to exploit suitable habitats (Brennan *et al.* 2019,).

Meadow dynamics observed in other studies and ours appear to be explained at least in part by these conceptual models. Among many others, Rozenfeld *et al.* (2008) identified

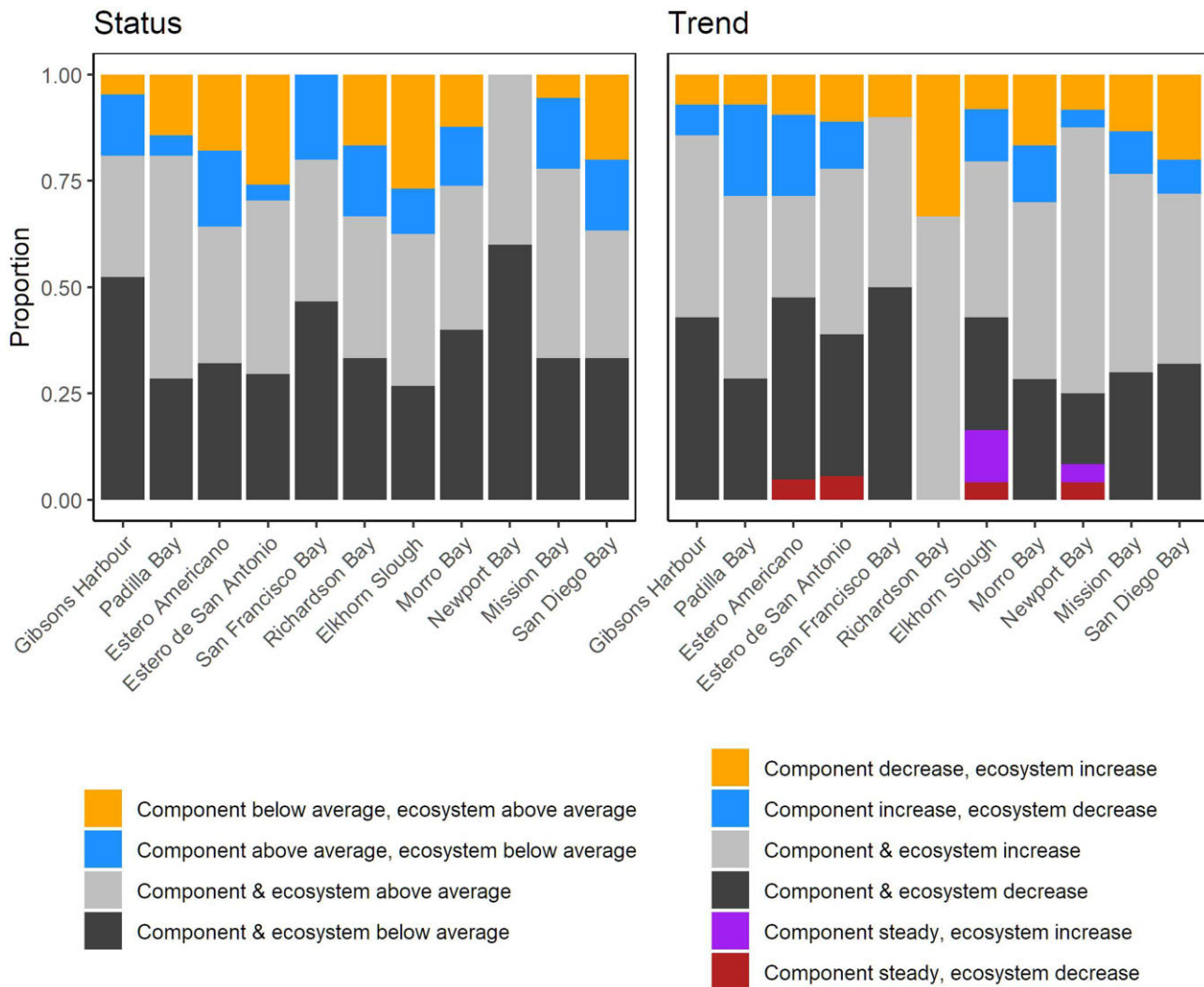


Figure 4. Synchrony of eelgrass area dynamics within seascapes. Relative frequency of component- vs. seascape-scale patterns is shown. *Status* refers to the amount of eelgrass area in a given time step relative to the long-term average of the seascape or component. *Trend* refers to change in eelgrass area between consecutive time steps. Columns show observations for each seascape combined across years.

metapopulation dynamics in eelgrass meadows. From our observations, the collapse and recovery in Morro Bay were perhaps most consistent with the metapopulation model: eelgrass was nearly extirpated, but remnant populations near the bay mouth may have contributed to later recruitment that eventually led to recovery.

Portfolio effects are also evident if underrecognized in eelgrass meadows (Shelton *et al.*, 2017). Perhaps the clearest example of the portfolio effect in our observations was the diversity of trajectories in eelgrass meadow area across Central British Columbia. Additionally, within seascapes like San Diego Bay, the dynamics of meadows exposed to vs. sheltered from direct oceanic inputs were often asynchronous and arguably represent separate eelgrass portfolio components.

Finally, although we are unaware of eelgrass studies that characterized meadow performance in the context of shifting habitat mosaics, this concept appears to apply. For example, Marba and Duarte (1995) and Yamakita *et al.* (2011) found that environmental disturbances drive subaqueous dune and sandbar migrations that shift seagrass habitat suitability over

seascapes and years. Indeed, Yamakita *et al.* (2011) noted that local asynchronies in seagrass area contributed to larger-scale stability. In our findings, drought shifted appropriate eelgrass habitat by as much as 20 km toward the river delta in San Francisco Bay. Future observations in San Francisco Bay may show that meadow ranges shift back to areas away from the delta during wet years. This would suggest that the drought-prone climate of this region drives a shifting mosaic of eelgrass habitat.

These four conceptual models—hierarchical patch dynamics, metapopulation dynamics, portfolio effects, and shifting habitat mosaics—provide insights that may inform eelgrass conservation strategies. First, they all recognize that ecosystems are not stationary and imply that regardless of present status, the protection of many habitat options across seascapes would ensure that natural shifts in biological performance do not undermine conservation schemes (*sensu* Hilborn *et al.*, 2003). Indeed, Hanski (1998) concluded that managers “should absorb the key message of classic metapopulation dynamics: currently unoccupied habitat fragments may be critical for long-term persistence”.

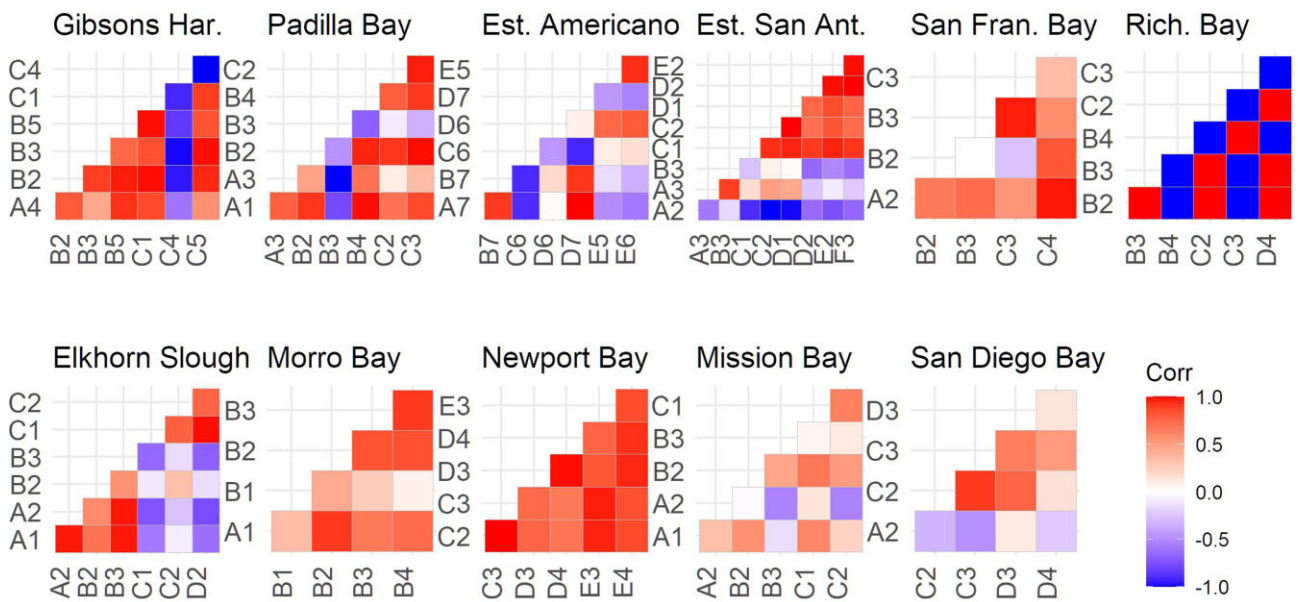


Figure 5. Pairwise Pearson correlation coefficients describing synchrony in eelgrass area between components. Values are only reported for components that contributed >5% of total seascape eelgrass in at least one survey.

Second, the idea that seascapes are collections of diverse habitat components that function together to create desirable outcomes. Seascape components exposed to different environments and disturbance regimes may support asynchronous biological performance, manifesting stability at greater scales (*sensu* Schindler *et al.*, 2010; Harrison *et al.*, 2020). Additionally, even though appropriate habitat conditions shift unevenly across seascapes, eelgrass meadows will take advantage of new opportunities as they arise (*sensu* Brennan *et al.*, 2019). Overall, to allow eelgrass to spread risk and exploit opportunities in constantly shifting environments requires keeping many habitat options open regardless of the meadow configurations supported by seascapes at a given point in time.

Where the protection of entire seascapes is not feasible, conservation that is quasi-robust to meadow shifts may still be implemented. For example, buffer zones may be delineated around extant meadows to protect potential recruitment, which tends to happen within several metres of extant meadows on an annual basis (Munsch *et al.*, 2023). Conversely, deep-water areas, rocky intertidal zones, or other areas that will plainly not be used by eelgrass for the foreseeable future may be considered permanently uninhabitable patches that could inform delineation of protection boundaries around potentially uninhabitable areas. Lastly, management of human activities that are temporarily permitted or mobile (e.g. aquaculture and boat anchoring) could involve protocols that monitor eelgrass and relocate or modify activities if meadows become too close.

The conservation ideas presented here may be relevant to other nearshore systems. Along shore are many biogenic species that create dynamic ecosystems like coral reefs, kelp forests, mangrove forests, and oyster reefs that rely on temporarily uninhabited areas to persist over the long term (Hughes and Connell, 1999; Seavey *et al.*, 2011; Krumhansl *et al.*, 2016; McClenachan *et al.*, 2021). Additionally, the nurs-

ery value (*sensu* Beck *et al.*, 2001) and spawning habitat use of nearshore seascape components varies asynchronously over time (Harrison *et al.*, 2020; Tomlin *et al.*, 2021), which can stabilize recruitment at the seascape scale (Harrison *et al.*, 2020). Ecological change, hierarchically organized biological systems, and the emergence of stability with scale are fundamental to the natural world (Levin, 1992); thus, the idea to scale protections to the seascape rather than limit protections to extant habitats or presently productive components in order to conserve emergent phenomena (e.g. persistence, reliability, and stability) may apply to marine nearshore ecosystems generally.

To conclude, management decisions that ultimately seek sustainable eelgrass meadows often focus on extant meadows, yet meadows shift across seascapes and over decades or longer. Extant meadows represent a snapshot of continuous reconfiguration, and short-term monitoring can belie considerable potential for seascapes to support different meadow arrangements. Because patches cycle through occupied and unoccupied phases, unoccupied habitats have long-term value to eelgrass that can be overlooked when focusing on extant meadows. If expanded to the seascape scale, which includes occupied and unoccupied habitat, efforts to conserve eelgrass would be robust to meadow shifts and protect collective dynamics that promote persistence in nature.

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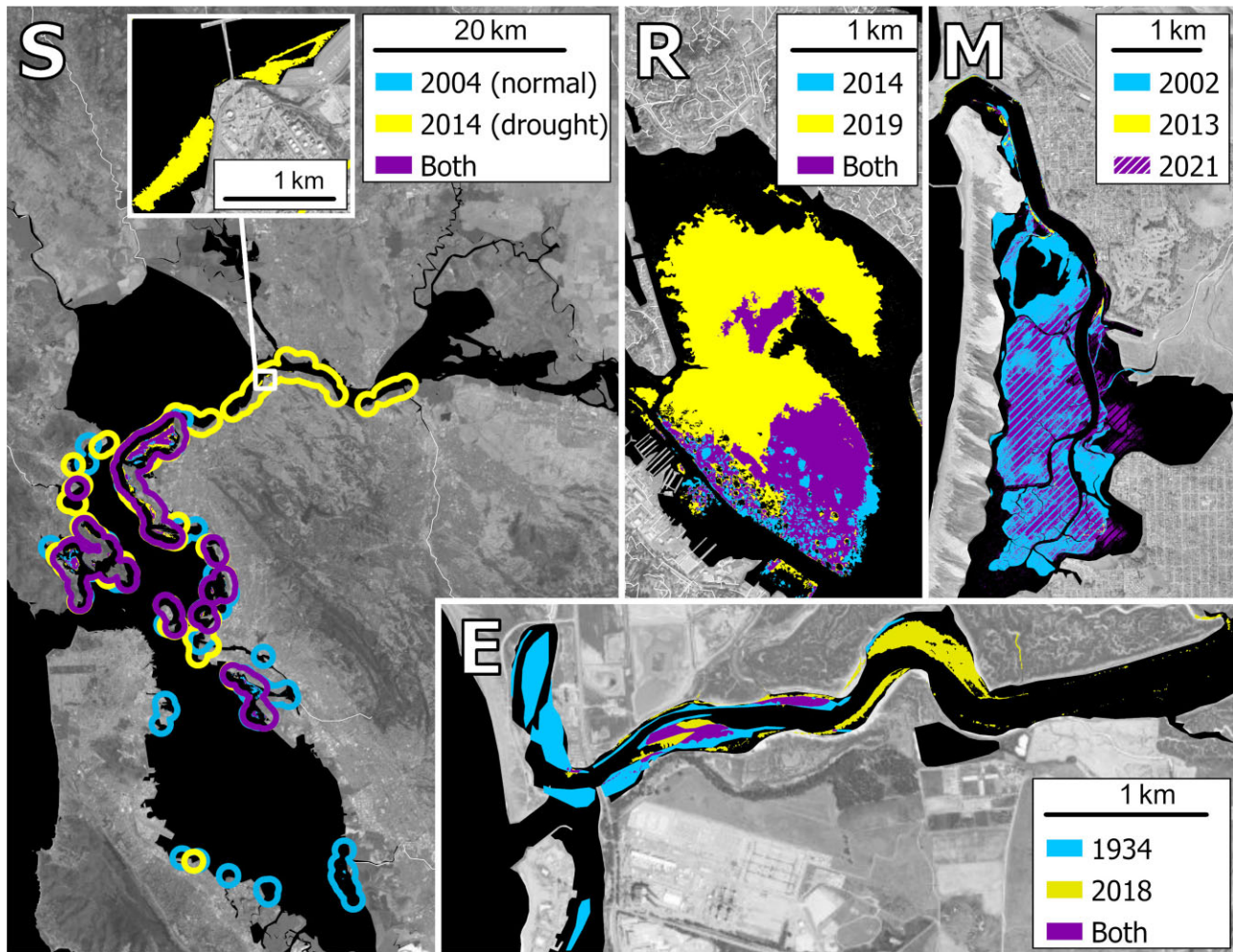


Figure 6. Examples of large eelgrass meadow changes in San Francisco Bay (S), Richardson Bay (R), Morro Bay (M), and Elkhorn Slough (E). In the San Francisco Bay panel, lines show buffers 1 km around eelgrass to improve meadow visibility at the bay's comparatively large seascape scale. In the Morro Bay panel, remnant meadows during the collapse in 2013 are visualized on top of other years and observations during recovery in 2021 are shown using hash marks to allow meadow locations to be visualized across three surveys (eelgrass in 2021 was present in hash marks' interstitial spaces).

Data availability

Eelgrass surveys from San Francisco Bay, Richardson Bay, Morro Bay (partial time series), Newport Bay, Mission Bay, and San Diego Bay are available at <https://www.ecoatlas.org/>. Surveys from Central British Columbia are available in Reshtnyk *et al.* (2020). Other data remain property of their original owners but are available upon reasonable request.

Supplementary data

Supplementary material is available at the *ICES/JMS* online version of the manuscript.

Author contributions

SHM: conceptualization, formal analysis, investigation, writing—original draft, writing—review and editing, and visualization. RKW, LR, JKO, MHL, CAE, KMB, and FLB: methodology, data curation, and writing—review and editing. BLS, PMK, and WBC: writing—review and editing, supervi-

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Conflict of interest

None declared.

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