Understanding the effect of multiple stressors using seagrass as a model system

by

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Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY
Spring 2023

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Abstract

Ecosystems around the world face an increasing frequency and intensity of human impacts, meaning that managing multiple co-occurring pressures is imperative. Unfortunately, our ability to predict ecosystem responses to multiple pressures is limited. Seagrasses are the foundation species of ecosystems that provide services such as carbon sequestration and improved water quality. Unfortunately, they are also heavily impacted by human activities. With an eye toward management, I use seagrass meadows as a model system to understand and predict the effects of multiple pressures across scales. First, I reconstructed area trends for 547 meadows. I found that one-fifth of the world's observed seagrass meadow area has been lost since the 1880s. However, losses were not consistent across time or space and only 10% of studies rigorously tested driver attributions, suggesting that local studies are important for informing relevant management actions. I then focused on one species, eelgrass (*Zostera marina*), to identify critical growth-related values that are pragmatic management targets and test whether these values change when pressures co-occur. I quantitatively reviewed studies of the effects of temperature and light on eelgrass performance. I found that two critical performance values, zero-growth rate and maximum growth rate, shifted across combinations of light and temperature values, suggesting that fixed thresholds are inappropriate targets. Finally, I used surveys of subtidal eelgrass meadows to examine the fine-scale (10s kms) variation in two metrics of eelgrass meadow health (shoot density and lesion prevalence) and relate this with variation in environmental conditions and human impacts. I found that environmental conditions were better predictors of eelgrass health than the human impacts considered (overwater structures and riparian modification), highlighting the importance of measuring conditions at the fine scale at which conservation and restoration efforts occur. As a whole, my research shows that although local context is important for seagrass management, there are generalisable patterns in how multiple stressors affect seagrass performance, which can be used to guide interventions.

Keywords: Global change; meta-analysis; cumulative impacts; dose-response; stressor interactions; threshold-based management

To my family. A curious spirit carefully observing the world around and looking for a better way. A beacon of patience, tenacity, and stoic support. An anchor that is always there to ground me, but also ready to lift and head out for the next adventure.

Acknowledgements

I want to acknowledge the Squamish, Musqueam, Tsleil-Waututh, and W̱SÁNEĆ on whose traditional territories I live and work. I hope to be an ally and have deep respect for this territory and the original stewards whose way of life was destroyed by colonisers.

To my family. You have supported all my science adventures since I was a kid. It's not a lot of parents who not only welcome their adult child home, but also her two lab mates that have come to help for a summer. Dad, you have been there all along from 'fishing for water', picking eelgrass from frosty wrack piles, crashing through salal bushes to quantify the value of wildlife trees, asking me what I saw every time I went diving, teaching me how to maintain, fix, and tow boats and trailers, waking up in the middle of the night with ideas on how to improve our tow camera frame. Matt – I wouldn't be the scientist I am without you. Thank you being there through it all, near and far.

Isa, thank you for giving me the freedom to take the time I needed and to follow my interests and take risks, yet you were always there when I needed.

My committee Nick and Mary – thank you for your guidance along the way, I am surprised by how much I still reflect on even small hallway chats, they have influenced me more than you know.

Grad school friends – bonds that are forged under this pressure really stick, I have been so lucky to have all your support and look forward to what is to come. Thank you to my academic fairy god mother Alison Haupt. Marc Hensel for all my WWMD moments. To the Base5-ers, the LoLers, The Goof Troop, and HoPers. Thank you for helping keep me sane and not constantly thinking about work. Milk Duck Knit Club – Thank you Jess for forcing me to join the sweater knitting crew and I look forward to many more retreats.

To my collaborators – I am so grateful to have crossed paths with you and I'm already coming up with ways to keep crossing paths. I have learned so much from you and look forward to working with you again!

To Maria Catanzaro and Nikki Wright, for providing me with a sense of community and keeping my feet and head in the water.

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Chapter 1. General Introduction

Ecosystems around the world continue to be transformed at an alarming rate as human activities increase in frequency, intensity, and spatial extent (Halpern et al., 2015; Williams et al., 2020). As these activities increase, ecosystems are increasingly threatened by multiple co-occurring pressures. This includes the presence of global pressures such as climate change, which cannot be managed locally and can interact with local pressures (e.g., deforestation, sedimentation) to further complicate management of ecosystems (Brown et al., 2013; Bruno & Valdivia, 2016). Unfortunately, our ability to predict ecological change in response to multiple pressures is limited. Moreover, ecosystems under stress can behave non-linearly: human impacts can force ecosystems over tipping points beyond which ecosystem structure and function are rapidly altered (Barbier et al., 2008; Koch et al., 2009).

Preservation of intact ecosystems is more affordable and practical than recovering degraded ones, particularly when the systems behave non-linearly (i.e., small changes in pressure level cause disproportionately large ecosystem responses) (Selkoe et al., 2015). One strategy that can improve management outcomes in cases where ecosystems behave non-linearly is threshold-based adaptive management (Kelly et al., 2015). This requires that a specific and manageable pressure be identified (e.g., fishing pressure) and that a critical level of that pressure linked to a desirable ecosystem state be quantified (Selkoe et al., 2015). Target pressure levels are then set to account for uncertainty and guide management actions that will maintain the pressure below this value (Carpenter et al., 2017; Selkoe et al., 2015). For example, land use changes in South Florida preceded the mass die-off of seagrass in the 1980s. Once the ultimate cause of seagrass mortality was identified as high salinity from run-off, direct and manageable freshwater thresholds below the salinity tolerance of seagrass were used to moderate water diversion (Foley et al., 2015). However, it is often difficult to attribute specific drivers to ecosystem change, particularly when multiple pressures co-occur. Furthermore, threshold-based approaches typically focus on only a single pressure, and it is unknown how multiple pressures affect critical threshold levels (Large et al., 2013).

Interactions between multiple pressures make predicting ecological change a challenge (Crain et al., 2008; Harley et al., 2017) and can have important management implications (Brown et al., 2013; Bruno & Valdivia, 2016). Despite the importance of identifying interactions between multiple drivers, we have yet to make accurate predictions or identify general patterns in the outcome of interaction impacts (Côté et al., 2016). Synergies were long thought to be the most common type of interaction, leading to a non-linear magnification of cumulative effects (e.g., Brook et al., 2008; Crain et al., 2008; Harvey et al., 2013), but more recent research has found that synergies are not the dominant interaction between drivers (Ban et al., 2014; Côté et al., 2016; Kroeker et al., 2013; Stockbridge et al., 2020). Instead, antagonistic interactions might be more common than synergies when organisms are exposed to natural or realistic levels of impacts (Lange & Marshall, 2017), while in seagrass ecosystems additive interactions are the most common (Stockbridge et al., 2020). Predicting interaction types is complicated because they depend on context, such as pressure type (Przeslawski et al., 2015), timing and intensity of pressures (Ostrowski et al., 2022; Wu et al., 2017), and level of biological organisation (Côté et al., 2016; Turschwell et al., 2022). Therefore, there is a need to translate small-scale experimental studies on multiple pressures up to the natural responses of species and communities which occur at the scale of a landscape.

Seagrass meadows are globally distributed in coastal areas and typically experience the effects of multiple stressors. These ecosystems provide valuable services such as nursery habitat, carbon sequestration, and improving water quality (Barbier et al., 2011; Mtwana Nordlund et al., 2016). Seagrasses themselves also serve as charismatic ‘umbrella’ species whose conservation indirectly also preserves a host of habitat-associated species. In Canada for example, eelgrass (*Zostera marina*) is designated as an Ecologically Significant Species, which enables federal level management for the protection of eelgrass meadows (DFO, 2009). However, seagrass meadows have suffered extensive losses globally (Waycott et al., 2009) because of multiple impacts, which include sediment loading (Cabaço et al., 2008), nutrient loading (Connell et al., 2017; Lefcheck et al., 2018), and disease (Bull et al., 2012; Short et al., 2011). They also show non-linear responses to stressors. Severe degradation or complete loss of a seagrass meadow disrupts negative feedbacks that facilitate seagrass persistence. This degradation can increase suspended sediment concentrations, which reduces light availability (Adams et al., 2016; van der Heide et al., 2007), can increase sediment anoxia (de Fouw et al., 2016), or can decrease sediment stability and prevent plants from anchoring themselves (Wicks et al., 2009). Once lost, recovery of seagrass meadows is often slow or impossible because of low rates of successful sexual reproduction, dispersal, and colonization (McGlathery et al., 2012; L. K. Reynolds et al., 2013). Furthermore, transplanting is expensive (Bayraktarov et al., 2015) and to date, successful recovery of highly degraded seagrass systems has been low (<37% success rate in Europe, van Katwijk et al., 2016). Restoration success is most probable with large-scale planting efforts (e.g., at least 1000 shoots or seeds; van Katwijk et al., 2016), which can be expensive and requires care to avoid damaging donor meadows (Borum et al., 2004; van Katwijk et al., 2016). Preservation of intact seagrass meadows is therefore essential.

In this thesis I use seagrass meadows as a model ecosystem to improve our ability to predict and understand the effects of multiple stressors. I use a combination of large-scale meta-analyses and fine-scale field surveys to understand how patterns of global change compare with the local scale at which management actions are often undertaken. Starting at the global scale, in Chapter 2, I reconstruct historical trends in seagrass meadow area extent in seven bioregions, using information from 547 meadows from around the world, to determine where, how, and why changes in seagrass meadow area have occurred. In Chapter 3, I focus on a single temperate species, eelgrass (*Zostera marina*), and demonstrate how management targets can shift when multiple stressors co-occur. I collate data from 20 studies to demonstrate an empirical modelling framework that can be used to synthesize data from a range of experiment types. I then dive into my own backyard in Chapter 4, where I examine the fine-scale effects of environmental conditions and human impacts on eelgrass health. Finally, in Chapter 5, I weave the insights obtained from these three chapters and reflect on what I found to be some of the key challenges in interpreting and translating multiple stressor effects into management applications.

Chapter 2.

Long-term declines and recovery of meadow area across the world's seagrass bioregions[1]

Abstract

As human impacts increase in coastal regions, there is concern that critical habitats that provide the foundation of entire ecosystems are in decline. Seagrass meadows face growing threats such as poor water quality and coastal development. To determine the status of seagrass meadows over time, we reconstructed time-series of meadow area from 175 studies that surveyed 547 sites around the world. We found an overall trajectory of decline in all 7 bioregions with a global net loss of 5602 km^2 (19.1% of surveyed meadow area) occurring since 1884. Declines have typically been non-linear, with rapid and historical losses observed in several bioregions. The greatest net losses of area occurred in four bioregions (Tropical Atlantic, Temperate Northern Atlantic East, Temperate Southern Oceans, and Tropical Indo-Pacific), with declining trends being the slowest and most consistent in the latter two bioregions. Losses, however, still outweigh gains. Despite consistent global declines, meadows show high variability in trajectories, within and across bioregions, highlighting the importance of local context. Studies identified 12 different drivers of meadow area change, with coastal development and water quality as the most commonly cited. Overall, however, attributions were primarily descriptive and only 10% of studies used inferential attributions. Although ours is the most comprehensive dataset to date, it still represents only one-tenth of known global seagrass extent, with conspicuous historical and geographic biases in sampling. It therefore remains unclear whether the bioregional patterns of change documented here reflect changes in the world's unmonitored seagrass meadows. The variability in seagrass meadow trajectories, and the attribution of change to numerous drivers, suggest we urgently need to improve understanding of the causes of seagrass meadow loss if we are to improve local-scale management.

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[1] A version of this chapter appears as Dunic JC, Brown CJ, Connolly RM, Turschwell MP, Côté IM. 2021. Long-term declines and recovery of meadow area across the world's seagrass bioregions. Global Change Biology. 27(17): 4096-4109. DOI: 10.1111/gcb.15684

Introduction

Marine ecosystems face an increasing number and intensity of human impacts (Halpern et al., 2019). In particular, nearshore ecosystems experience a disproportionately high level of disturbance (Halpern et al., 2015; Lotze, 2006) especially as human populations are rapidly increasing in coastal areas (Halpern et al., 2019). Land-use changes such as agriculture and road development, as well as sewage and other land-based pollutants, can reduce water quality by increasing sedimentation and nutrient loading in nearshore marine habitats. Meanwhile, coastal development such as port infrastructure, aquaculture, and dredging can directly destroy intertidal and subtidal habitats (Orth et al., 2006). These cumulative pressures need to be addressed in unison to prevent further loss of coastal habitats (Griffiths et al., 2020).

Seagrass meadows are an important nearshore coastal habitat that provides important ecosystem services such as nursery habitat (McDevitt-Irwin et al., 2016; Whitfield, 2017) improved water quality (Lamb et al., 2017; Orth et al., 2020), and carbon storage (Mtwana Nordlund et al., 2016). However, seagrasses are sensitive to multiple human activities taking place in the coastal zone that impact water quality through increased sedimentation and nutrient run-off, or cause direct habitat destruction (Grech et al., 2012; Holon et al., 2015; Lefcheck et al., 2017; Orth et al., 2006). Furthermore, seagrasses often live in embayments that can have long water residence times, which can magnify the impact of eutrophic and other unfavourable conditions (Bricker et al., 2008). As human impacts in coastal environments increase, there is a heightened concern that seagrasses will suffer global declines. More than a decade ago, seagrass meadow area was being lost at an estimated average global rate of 1.5% per year (Waycott et al., 2009). Importantly, this global loss figure belied substantial variation among sites in rates and directions of change, with 25% of sites increasing in area and 17% remaining stable over time (Waycott et al., 2009). Furthermore, for sites that were in decline the rate of loss was 7% per year and was accelerating (Waycott et al., 2009). Substantial monitoring efforts since then, provide a wealth of additional data that allow us to re-assess global patterns of seagrass change in the context of increasing human impacts. Recently, seagrass meadow trends in Europe have shown some stabilisation and recovery (de los Santos et al., 2019).

To improve the management of seagrass ecosystems, we must identify where and why seagrass meadows are declining. Despite the ubiquity of seagrass along the world's coastline, our understanding of the global status of seagrass meadows is limited, particularly in bioregions such as the Tropical Atlantic, Mediterranean, and Tropical Indo-Pacific (Unsworth et al., 2018). At the same time, management has fostered seagrass recovery over the long term. Notable examples of this include Chesapeake Bay (Virginia & Maryland, USA), Tampa Bay (Florida, USA), and the Wadden Sea (Denmark, Germany, and the Netherlands). In Chesapeake Bay, 40 years of policy implementation to control nutrient loading has led to improved water quality and increased abundance and cover of seagrass (Lefcheck et al., 2018; Orth et al., 2020). Similarly, in the Wadden Sea and Tampa Bay, seagrass meadow areas previously lost during times of high nutrient loading have recovered to pre-damage meadow area following years of management that limited nutrient inputs and wastewater run-off (Dolch et al., 2017; Sherwood et al., 2017; Tomasko et al., 2018). In addition to management actions, restoration projects have increased rapidly in scale and number since the 2000s (Saunders et al., 2020), which when coupled with management are an important component of restoring large areas of seagrass (Orth et al., 2020; Sinclair et al., 2021). However, while both the decline and recovery of seagrass at these locations can be attributed relatively unambiguously to specific causes (nutrient loading and run-off limitation measures, respectively), this is not the case for most other locations where changes in areal extent of seagrass habitat were previously noted (Waycott et al., 2009). Further, these examples of recovery may be the exceptions globally, because in many other places management of cumulative pressures is likely insufficient to prevent seagrass loss (Griffiths et al., 2020).

Here we assess the current status of seagrass ecosystems globally. We examined the peer-reviewed literature to identify studies documenting meadow area across multiple time periods, expanding the original meta-analysis by Waycott et al., (2009) with new studies from previously under-sampled regions. Our study thus expands the geographic scope of recent studies that have documented trends in parts of the USA (Lefcheck et al., 2017) and Europe (de los Santos et al., 2019). Our study also extends past analyses by using statistical time-series reconstruction techniques to account for gaps in data-series and geographic bias in sampling. We aimed specifically to (1) quantify trends in seagrass meadow area by major seagrass bioregions, (2) quantify variation in trends across individual meadows across bioregions, (3) identify the primary drivers that were cited by authors as potential drivers of change, and (4) identify the methods used for causal attribution to those drivers.

Methods

Study selection

We used Web of Science and Scopus to systematically search the peer-reviewed literature for studies that resampled seagrass area extent over time. We updated the database of seagrass area time-series in Waycott et al., (2009), by performing a search on January 18, 2018 using search terms modified from Waycott et al. (2009): "(seagrass* OR SAV OR submerged aquatic vegetation OR eelgrass*) AND (loss* OR change* OR recovery OR stability OR dynamic* OR impact* OR map* OR decline* OR increase* OR gain*) and (cover* OR area* OR distribution OR production OR bed*)". We restricted our search to the years 2006-2018 to avoid overlap with Waycott et al., (2009), whose last search year was 2006. We tested our search terms for the time period covered by Waycott et al., (2009) and found that our terms captured all of the studies found in Waycott et al., (2009) with the exception of Larkum & West (1990), which does not have a searchable abstract posted on any database. Our updated search for 2006-2018 returned 4808 records, which we filtered to 366 studies after reviewing titles, abstracts, and full text where necessary, to identify studies that met our three key selection criteria: (1) the study measured seagrass meadow area, (2) measurements were performed at the same sites over time, and (3) area was measured at a minimum of two time points over a period of at least one full year (Figure A1). Note that our keywords were in English, which means we predominantly captured literature written in English and this may overlook a portion of available published literature (Christie et al., 2020). Our search terms included 'submerged aquatic vegetation', but we only used studies that measured area of seagrass species. Two studies included freshwater species, i.e., *Potamogeton pectinatus* (Figueiredo da Silva et al., 2004) and *Lepilaena* sp. (Seddon et al., 2000), but did not provide species-specific cover data. Because freshwater species were noted as a minority of the community, we included these studies in the analysis. An additional nine studies provided no indication of the species but did indicate that they measured seagrass area extent and were thus included.

Data acquisition

We extracted variables that described areal extent over time, species, location, sampling methods, primary potential drivers of change as considered by authors, and the strength of attribution used to assess potential drivers of change of seagrass area. We also assigned each site to a seagrass bioregion according to Short et al., (2007) with the modification of the Temperate North Atlantic, which we separated into west and east (Figure 2.1). Time-series data on total areal extent were preferably extracted from data tables or, when this was not possible, from figures using WebPlotDigitizer 3.12 (Rohatgi, 2018). We also recorded whether study authors indicated an *a priori* reason for undertaking a study (e.g., 'because the seagrass bed had been declining'), to account for the potential non-random sampling of seagrass meadows when we performed our analysis of global change. When a range of years (e.g., 1994-1996) for a single measurement were listed, we chose the midpoint. Locations of all sites were recorded and were used to identify when a site or area (e.g., Chesapeake Bay) was surveyed across studies. To identify sites or areas that were sampled in more than one study, sites were tagged with an additional variable called 'site group' when the same sites or adjacent (e.g., < 5 km apart) were used or when sites in a study were nested within another study. Data from studies contained in Waycott et al. (2009) were included in our analysis and rechecked where possible to include additional ecological covariate and driver attribution data from these studies. When studies could not be accessed (i.e., 2 cases: (Blake & Ball, 2001; The Massachusetts Department of Environmental Protection 2006 Eelgrass map), we used the data reported in Waycott et al. (2009; Table S1) for the rates of change analysis. Only one study included data on relative abundance of seagrass species over time at a site (McKenzie et al., 2014), which precluded a meta-analysis of change in species composition.

Net change in seagrass area

To quantify the net change in seagrass meadow area in each bioregion and globally, we calculated and summed the observed change in meadow area from the first time point to the last time point in each time-series. We calculated the total area surveyed as the sum of the maximum observed area at each site. To avoid duplication of net area change that could occur, for example, when multiple studies were conducted in the same area, we selected the site that had the largest maximum area.

Bioregional trends and the status of seagrass meadows over time

To reconstruct time-series of seagrass meadow area at the site level and to estimate trends across bioregions, we fit hierarchical generalized additive models (GAMs) to all time-series (including the duplications removed from the net change analysis) from each bioregion using the 'mgcv' package in R (Wood, 2011). This method models the average trajectory of all meadows in a bioregion and allowed for trends to be non-linear. Thus, the bioregional trajectories estimated by the GAM were not as strongly influenced by change in single very large meadows as the net area analysis was. Meadow areas were ln-transformed prior to analysis. To handle zero values, we added 10% of the minimum, non-zero area detected at a site (zeros were rare, occurring in 4% of time points). We fit the following model to each bioregion independently:

$$log_e(area_t) = \alpha + f(year_t) + f_{site_i}(year_t) + f(site\_group_i) + \varepsilon_t, \qquad \varepsilon_t \sim N(0, \sigma^2) \tag{2.1}$$

where $f(year_t)$ is the shared bioregional trend, $f_{site\_i}(year_t)$ is a site-specific trend that accounted for site-level deviations from the bioregional trend, and $f(site\_group_i)$ is a random intercept term that accounted for similarities in mean area between the same, adjacent, or nested sites across studies. The method also reconstructs gaps in time-series by borrowing strength from the bioregional trend that is shared across sites within a bioregion. Smooths were fit using thin plate regression splines and using low-order penalized derivatives for the site-level smoothers (*m* = 1 in the 'mgcv' package) to reduce collinearity between the global smoother and site-level smoothers (Pedersen et al., 2019). The random effects and residual errors were assumed to be normally distributed with a mean of zero and a variance that was estimated from the data. We allowed the maximum number of basis functions, *k*, to vary by site, *i*, (*k* = number of years – 2; min = 2, max = 8), to handle the variation in the number of sampled time points and data density over time at each site. This improved site-level model fits. In all bioregions except for the Mediterranean, there were sufficient data to fit GAMs that included sites with two sampled time points. Therefore, to reconstruct the time-series of the 16 Mediterranean sites with only two time point sites so that they could be included in our analysis of seagrass status by decade, we performed linear imputation using the 'imputeTS' package in R (Moritz & Bartz-Beielstein, 2017). We also performed a sensitivity analysis to determine how the GAM reconstructions were affected by decades with fewer than five meadows surveyed (e.g., many of the earliest decades in our dataset). We found that in most bioregions there was no substantial change in the results and have included this analysis in Appendix A – Sensitivity Analysis. However, we believe it is important that we present the full dataset in Figure 2.2, which includes the less data-rich decades prior to the 1950’s because omitting them severely shifts the baselines of the trends.

We then used the reconstructed time-series to examine (1) bioregional trends in mean seagrass area over time, relative to the mean meadow area in the earliest year of each bioregion’s time-series, and (2) the status of seagrass meadows by decade and bioregion. We used two metrics to describe the status of each seagrass meadow in a given decade: the instantaneous annual rate of change (eqn (2.2)) and the fraction of meadow size relative to the maximum area ever observed at a site (eqn (2.3)).

$$annual\ rate\ of\ change_{decade} = \frac{ln\left(\frac{area_{decade_f}}{area_{decade_i}}\right)}{year_{decade_f} - year_{decade_i}} \tag{2.2}$$

$$fraction\ of\ maximum\ observed_{decade} = \frac{area_{decade_i}}{maximum\ area\ observed\ in\ time\ series} \tag{2.3}$$

To calculate these metrics, we used the initial, *i*, and final, *f*, year of a time-series within a decade, *decade* (e.g., ‘1990’: 1990 – 1999). If a time-series started or ended within the decade of interest, we used the first and/or last observed year (e.g., 1992 – 1995). To interpret the status of individual meadows, we plotted both metrics against one another to examine how annual rate of change (by decades and by bioregions) varied with meadow area as a fraction of maximum observed area. We do the same with just the sites included in Waycott et al., (2009) to provide a visual comparison between our studies.

Attributions to drivers

We identified the studies that attempted to attribute temporal trends in seagrass meadow area to specific drivers. To understand the strength of these driver attributions used in studies of temporal trends in seagrass meadow area, we categorized attributions in order of increasing strength from none, descriptive, visual, and inferential (Table 2.1). We identified the primary driver(s) considered in each of these studies, which we defined as the driver(s) tested with the strongest level of attribution or if attribution was only descriptive, the most discussed driver(s). Many studies identified multiple primary drivers. We then examined how the strength of attribution varied across drivers. Note that our purpose here was not to measure the specific effects or effect sizes of drivers.

Table 2.1 Categories of strength of attribution of change in seagrass area to specific drivers of change.

Attribution category	Description
None	Study did not attribute change to specific driver(s).
Descriptive	Attribution of change was mentioned only in the discussion and no driver data was presented, and/or attributions were made from anecdotal descriptions of the local context (e.g., increased human population over the time-series, assumed declines in water quality, etc.).
Visual	Environmental or driver (e.g., human population) data were graphically presented and compared visually with temporal trends in seagrass meadow area. Alternatively, direct image comparisons (e.g., before and after events such as a hurricane or building an aquaculture facility in a seagrass meadow) were provided.
Inferential	Inferential statistics were used to test for a relationship between a driver and temporal trends in seagrass meadow area. These included the use of before-after-control-impact designs, direct correlations between potential drivers and temporal trends in seagrass meadow area, or experiments testing the effect of drivers and coupled with temporal trends in seagrass meadow area.

Results

Data coverage

Our literature search, including studies from Waycott et al., (2009), resulted in 547 time-series of seagrass meadow area derived from 175 studies (Figure 2.1). The number of time-series has doubled in the 15 years since Waycott et al., (2009) (211 time-series from 70 studies, reported cut-off year 2006), with a considerable increase in the geographic scope of studies. In particular, data gaps in the Indo-Pacific region have begun to be addressed (Figure 2.1). Surprisingly, the new time-series added since Waycott et al., (2009) are not only the result of recent monitoring programs. Instead, many new studies within the last decade have identified sites in data-poor regions that had historical data, often in the form of aerial photography archives or ground surveys.

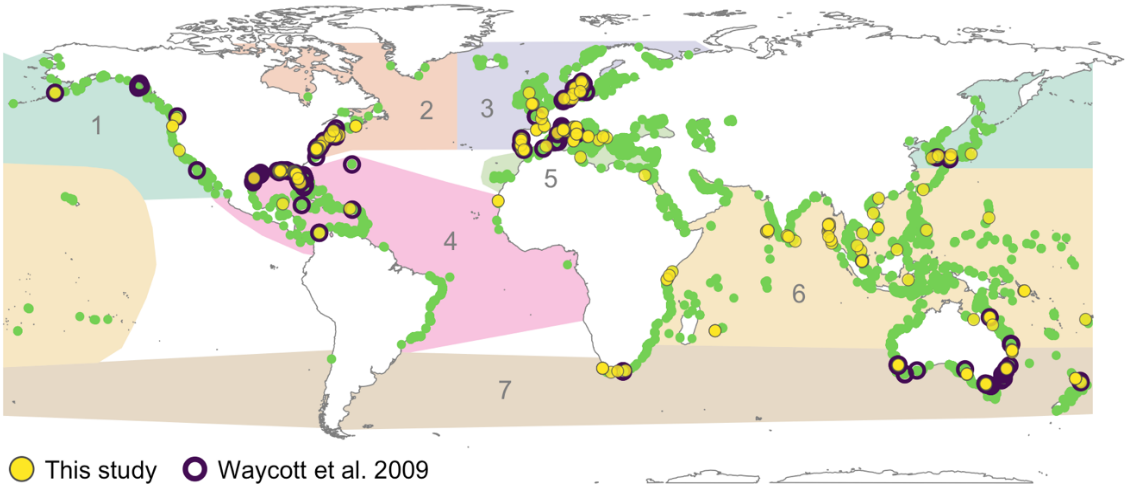

Figure 2.1 **Global distribution of seagrass (green; data from UNEP-WCMC & Short (2021), with sites (n = 219) from Waycott et al., (2009) and additional sites (n = 323) from this study. Included are the seagrass bioregions adapted from Short et al., (2007): 1. Temperate North Pacific, 2. Temperate North Atlantic West, 3. Temperate North Atlantic East, 4. Tropical Atlantic, 5. Mediterranean, 6. Tropical Indo-Pacific, 7. Temperate Southern Oceans.**

In our database, study durations ranged from 1 to 128 years (Figure A2), with 140 studies (70%) containing time-series of 10 years or more (Table A1). Studies with the longest durations were typically sampled using aerial photography. However, the oldest historical record was from ship surveys in 1891, resulting in a 128-year time-series in Limfjorden, Denmark (Krause-Jensen et al., 2012). Across studies, meadows were usually surveyed during peak growth season (i.e., spring-summer). Most sites ranged in maximum observed meadow area from 0.01 km^2 to 100 km^2.

In addition to geographic biases in the dataset, we made a coarse evaluation of sampling bias with respect to *a priori* expectations of change in meadow area as indicated by author's in the text. In our database, most studies (61%) had no indication of *a priori* expectations (Table A2). Of the 39% of studies that had statements about *a priori* expectations of trajectories of change, most were expectations of decline (29%).

Only 7% of studies had expectations of increase in meadow area over time, and 3% expected other (e.g., U-shaped) trajectories.

Global and bioregional trends in seagrass meadow area

Globally, 554 km^2 of seagrass has been recovered since 1900, which accounts for ~1.9% of the total area surveyed (Table 2.1). However, a net loss of 5602 km^2 of seagrass has occurred since 1884, which represents a 19.1% loss of the total area surveyed (i.e., 29 293 km^2; Figure A3).

Table 2.2 Net change, gains, and losses in total area of seagrass surveyed around the globe. Net change is expressed as a % of the maximum total area surveyed in each bioregion, as well as in absolute area (km^2).

Bioregion	Net change (%)	Net change (km^2)	Gain (km^2)	Loss (km^2)	Maximum total area surveyed (km^2)	Time span
Temperate North Atlantic East	-76.5	-420	17	-437	548	1900 - 2016
Tropical Atlantic	-65.0	-3,301	183	-3,485	5,083	1937 - 2016
Temperate Southern Oceans	-27.2	-326	121	-446	1,195	1930 - 2013
Tropical Indo-Pacific	-16.4	-96	75	-171	583	1945 - 2016
Mediterranean	-9.9	-1,477	25	-1,502	14,953	1922 - 2012
Temperate North Pacific	0.6	6	75	-69	971	1955 - 2013
Temperate North Atlantic West	2.6	11	57	-46	440	1960 - 2015
Global	-19.1	-5,602	554	-6,156	29,293	1880 - 2016

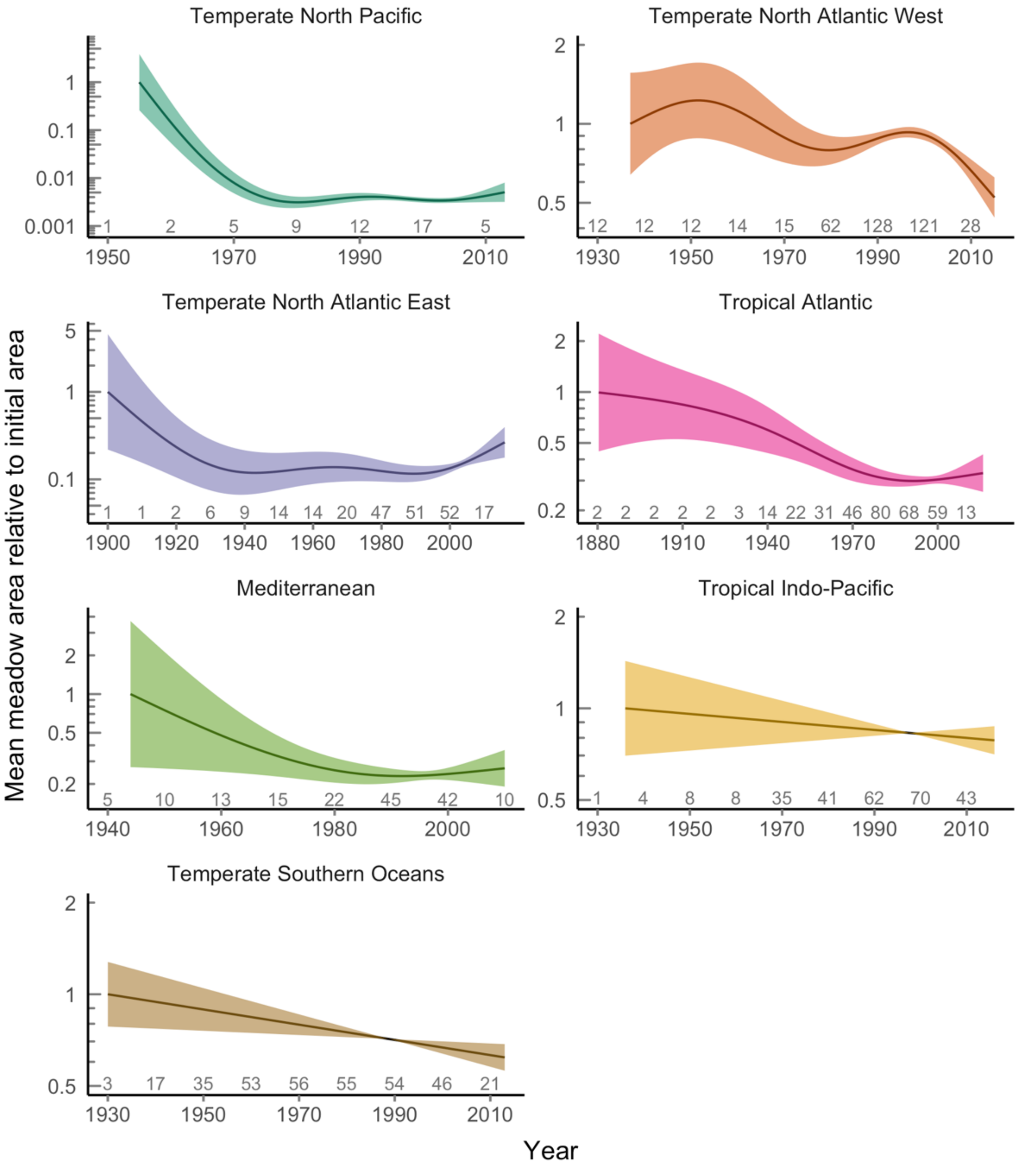

Figure 2.2 **Bioregional trends in seagrass meadow area over time, estimated using bioregion-specific generalised additive models (GAM). Mean meadow area is expressed as a proportion of the meadow area observed in the initial surveys, averaged across sites for each bioregion, and on a log10 scale, such that a change from 1 to 0.1 equals a 10-fold decrease in seagrass area over time. The shaded 95% confidence intervals reflect the simultaneous confidence intervals derived from the GAM fit to meadow area trends of all study sites within each bioregion. Note that the y-axis varies across bioregions. The number of meadows sampled in each decade are shown in grey along the x-axis. The bioregional trend in the Mediterranean does not include 16 sites that contained only two sampled time points.**

Seagrass meadows in all bioregions have experienced declines in meadow area (Figure 2.2, Figure A4). Most of the bioregions exhibited non-linear trajectories, with the exception of the Tropical Indo-Pacific and the Temperate Southern Oceans (Figure 2.2). As might be expected when site identities change throughout long-term time-series, some of the non-linearities are caused by sampling. For example, the fastest declines relative to the earliest measured baselines were observed in Temperate North Pacific and the Temperate Northern Atlantic East, with a 1000-fold loss of meadow area from the 1950s to the 1970s and a 10-fold loss from the early 1900s to 1940s, respectively (Figure 2.2). However, these rapid early declines were inferred from fewer than six sites (see number of sites labelled on the x-axis Figure 2.2). In general, by the 1940s more sites and total seagrass area were sampled across all bioregions (Figure 2.2, Figure A5). Large (~ 40-80%) declining trends were estimated in the Tropical Atlantic and Mediterranean from the 1940s until they stabilized by the 1980s to present. Meanwhile, the rates of change in seagrass area in the Temperate Northern Atlantic West fluctuated from the 1940s to late 1990s, and since 2000 this region has experienced a 40% decline in area relative to the earliest surveys. Conversely, the Temperate Northern Atlantic East has seen a marked recovery since 2000, although the areal extent remains ~30% below that of the earliest surveys.

Overall, the Tropical Atlantic experienced the largest net loss of seagrass area, losing 3485 km^2 of seagrass. Most of this loss was driven by one meadow that lost 2700 km^2 of seagrass between 1984-1992 (Table 2.2). Meanwhile the Temperate Northern Atlantic East experienced the highest percent loss relative to the maximum total area surveyed in this bioregion (76.5%; Table 2.2). Most of this loss was driven by one observed loss of more than 100 km^2 prior to the 1930s. Meadows in both the Tropical Indo-Pacific and the Temperate Southern Oceans also declined markedly, by nearly 20% compared to the maximum total area surveyed in these bioregions (Table 2.2). In absolute terms, the greatest loss of seagrass meadows reported was in the Tropical Atlantic and Mediterranean bioregions (Table 2.2).

Status of individual seagrass meadows over time

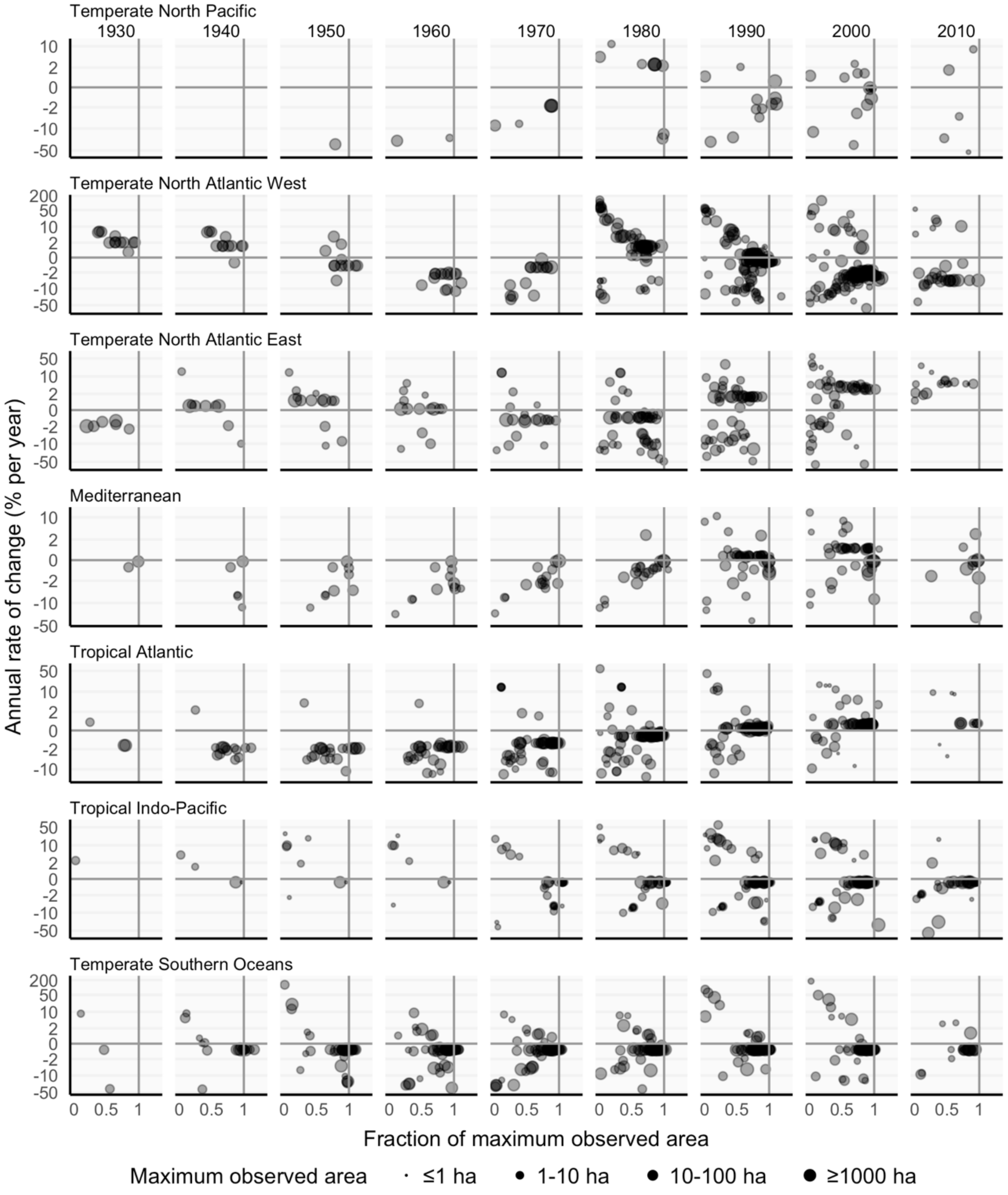

Figure 2.3 **Status of seagrass meadows over time and across bioregions. Each point represents the status of one seagrass meadow in a given decade, while point size represents the maximum area observed for that meadow. Meadows that have experienced more severe losses will be farther on the left of a panel; meadows near their maximum size will be on the right (near vertical line, x = 1); and stable/slowly changing meadows are near the horizontal line, *y* = 0. The x-axis indicates the size of a meadow at the beginning of a decade (e.g., 1990), as estimated using the bioregional GAMs, relative to the maximum area ever observed at that meadow. The y-axis is the instantaneous annual rate of change (%) in meadow area during a decade. Note that the y-axis varies in range across the bioregions and has been transformed using the signed pseudo logarithm (sigma = 0.5, base = 10) to improve visualisation of the high number of meadows with rates of change less than 10%. As values increase above 10, this axis approximates a $\log_{10}$ scale.**

Despite declines in seagrass meadow area across bioregions, changes in individual meadow area were highly variable (Figure 2.3, Figure A6). On average, annual rates of change were centred near zero (Figure 2.3, Figure A7) and most sites experienced annual rates of change of less than 2%. A greater number of meadows with positive rates of change were observed from the 1980s onwards in most bioregions, when new sampling methods (primarily remote sensing) were introduced. Many meadows in the Temperate North Atlantic East, Mediterranean and Tropical Atlantic bioregions shifted towards positive trends post 1990, explaining the recent increasing trends in those bioregions (Figure 2.2). However, overall meadow area over the past two decades has remained below 90% of maximum for most meadows.

High, positive annual rates of change (> 10%) were more common in meadows that had been reduced to less than half of their maximum area ever observed (Figure 2.3, Figure A8). Additionally, meadows larger than 1000 ha tended to have slower rates of change than smaller meadows (Figure A9), though there was no clear relationship between the coefficient of variation across time-series and the maximum observed area (Figure A10).

Attribution to drivers

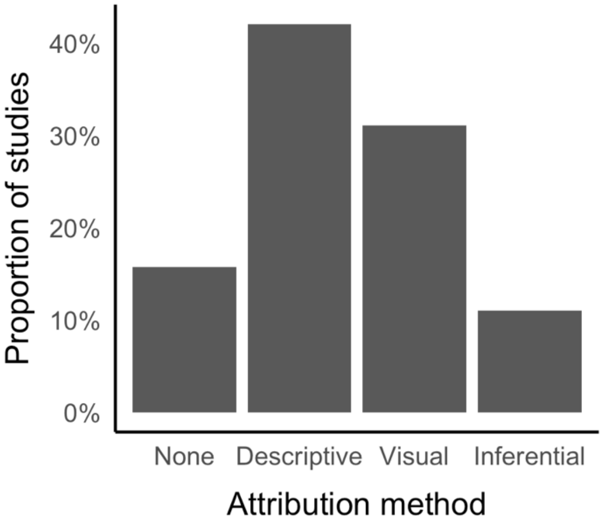

Figure 2.4 **Proportion of studies in each of the four categories of causal attribution method. The methods are described in Table 2.1 and are shown in order of strength of attribution.**

Attributions to potential drivers of change were primarily descriptive (> 40%; Figure 2.4), while ~15% of studies did not attempt to attribute patterns to a specific cause. The latter studies were often demonstrations of survey methods (e.g., satellite imaging techniques). Thirty percent of studies attributed change to a specific cause by visually examining concurrent trends in driver intensity and seagrass meadow characteristics (typically area) or by comparing imagery before and after events such as land appropriation. Meanwhile, only 10% of studies used inferential statistics to test the association of drivers on the trends observed in seagrass meadow area.

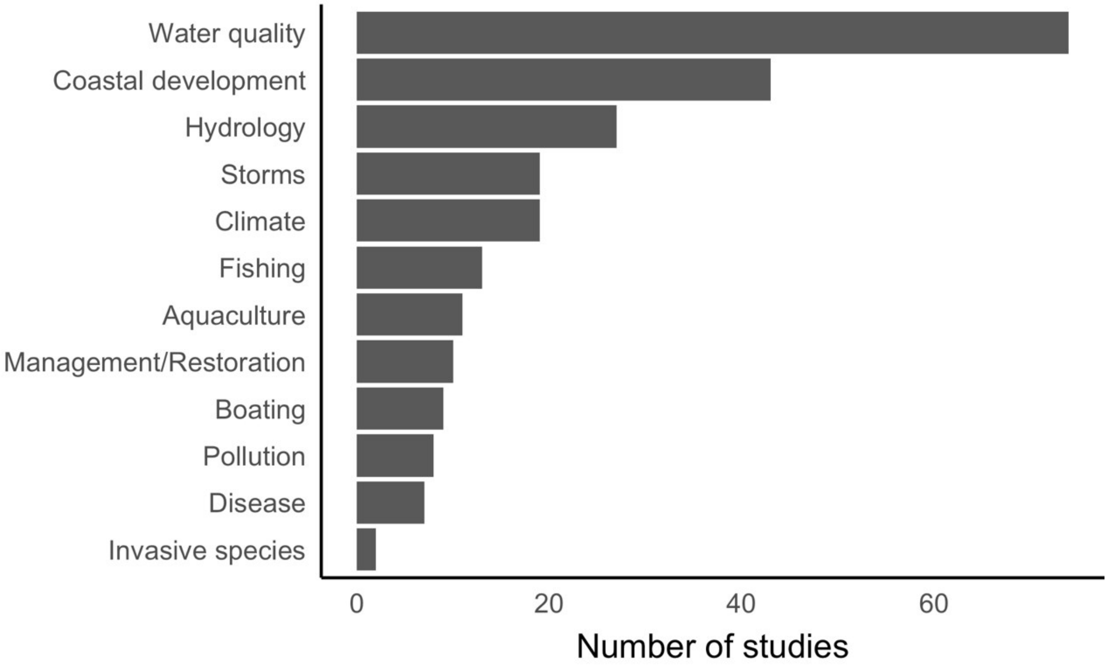

Figure 2.5 **Frequency of the primary drivers cited as potential drivers of change in seagrass meadow area. Examples of specific drivers considered in each driver category are detailed in Table A3.**

Poor water quality and coastal development were the most common primary drivers identified by study authors (Figure 2.5). Water quality was most often considered in study discussions or by visually comparing trends in water quality metrics with trends in seagrass meadow area over time (Figure A11). However, water quality was the driver most tested using inferential statistics. Meanwhile, coastal development was most often noted as a likely driver in study discussions (Figure A11). Coastal development was a broad category that included activities and environmental changes ranging from watershed land use change to port development (Table A3). Drivers such as hydrology, storms, or management/restoration, which were often discrete events, were more commonly considered visually or inferentially than other drivers. At nine locations, all in the USA, authors specified management or restoration events and their timing relative to the time-series of seagrass meadow area. All of these locations experienced net gains in seagrass area after the restoration or management actions taken (Figure A12) and at five of these nine sites, the interventions were related to water quality (Table A4).

Discussion

We reconstructed time-series of seagrass meadow area that span the last 70 to 130 years from seven bioregions and filled previous geographical data gaps (Waycott et al., 2009). Over this time period, human pressures to the world's marine ecosystems have increased in intensity and spatial extent (Halpern et al., 2019). Correspondingly we found that global declines in seagrass meadow area have been widespread and substantial over the last century. However, since the 2000s declining trends have stabilised or are now on recovery trajectories in some bioregions. These findings align with the recent reversal of declines documented at sites from across Europe (de los Santos et al., 2019). Despite reduced or reversed trajectories of loss, the absolute area lost still outweighs gains in all but two bioregions. Annual rates of change were typically less than 2% year^{-1}, but there was high variability in rates at individual sites, indicating that local context is important to understanding seagrass dynamics. Interestingly, the attribution to causes of seagrass area change is rarely inferential, which makes the identification of local contextual drivers difficult.

The global picture: bioregional trends

Trajectories of change in seagrass area are consistent across bioregions of the world; all bioregions show declines relative to the earliest recorded meadow areas. However, global losses have not all been linear over time, nor has the timing and rate of loss been uniform across bioregions. Some regions, such as the Temperate North Atlantic East, experienced rapid, early losses, while others like the Tropical Indo-Pacific and Temperate Southern Oceans exhibited slow, steady declines. The differences in trends across bioregions may reflect a variety of factors relating to differences in the spatial and temporal scales of disturbances affecting seagrass (O'Brien et al., 2018) and the ecologies of seagrass meadows (Kilminster et al., 2015; Marbá et al., 1996). For example, small-scale and acute disturbances are likely to be associated with faster rates of change (O'Brien et al., 2018), or differences in seagrass species diversity could make bioregions with higher species richness more resilient to change than bioregions characterised by monospecific meadows (Unsworth et al., 2015). Given the variety of disturbances observed and likely unobserved within the dataset, it is possible that the variation in disturbances outweighs meadow ecology effects when the data are aggregated.

Bioregional variation in seagrass area trends could also be due to sampling differences, including the duration and timing of data series and/or the number and identity of sites surveyed. For example, the early record in the Temperate Northern Atlantic East is largely influenced by the losses documented in Limfjorden starting at the turn of the 20th century, but it is likely representative of trends through much of the Temperate Northern Atlantic East given the widespread losses caused by wasting disease documented in the region (Godet et al., 2008; Krause-Jensen et al., 2012). The observed historical declines in several bioregions remind us to consider recent trends with some caution because their interpretation depends on the baseline used. For example, in a sensitivity analysis (Appendix A – Sensitivity Analysis) we found that the Temperate North Atlantic East showed increasing trajectories in meadow area when early sampling points were omitted. In contrast, it is less likely that the rapid decreasing trend in the Temperate North Pacific was representative of the bioregion from 1950s to the 1970s. The rapid decline observed in the reconstructions was driven by the loss of seagrass meadows in Japan (Aioi & Nakaoka, 2003; Hiratsuka et al., 2007) and Elkhorn Slough, a small meadow, on the west coast of the United States (Hughes et al., 2013) owing to multiple local causes.

In absolute terms, 19.1% of the 29 000 km^2 of seagrass meadow area that has been surveyed has been lost in the past 100+ years, although interestingly, the reconstructed bioregional trends over time did not always match patterns of net seagrass area change. The reason for the mismatch is that the bioregional trends represent the expected trajectory of change across all meadows regardless of meadow area, whereas the net loss statistic accounts for differences in meadow area. In some regions, like the Temperate Northern Atlantic East and the Tropical Atlantic, the loss of a single large meadow in each of these two bioregions (Limfjorden for the Temperate Northern Atlantic East, and Big Bend for the Tropical Atlantic) had a large influence on the net loss statistic, with Big Bend accounting for almost half of the absolute total area lost (2700 km^2). However, other bioregions (e.g., Temperate Southern Oceans, Tropical Indo-Pacific, and Mediterranean) also experienced large losses (~10-22%) over the last 70 to 90 years, which encompass multiple countries (e.g., Italy, Spain, and Tunisia for the Mediterranean; Telesca et al., 2015) and local causes, such as coastal modification

(Nayar et al., 2012), poor water quality (Petus et al., 2014) and direct physical damage from fishing (Harcourt et al., 2018), in each bioregion. Therefore, it is important to consider both the bioregional trajectories, particularly when there are regional drivers of change (e.g., disease, climate), and the associated net loss in a bioregion. For example, the Tropical Indo-Pacific and Temperate Southern Oceans had the slowest and most consistent trends in seagrass area loss over time, yet each have lost close to one-fifth of their total surveyed seagrass meadow area.

The apparent stability in some bioregions may be due to gaps in monitoring and limitations of analysing data from peer-reviewed studies. Unlike other bioregions that had similar total areas surveyed but experienced large losses, the Temperate Northern Atlantic West and Temperate North Pacific have shown little fluctuation in seagrass meadow area, with minimal gains and losses. Time-series from the Temperate Northern Atlantic West do not cover the period of wasting disease in the early decades of the 20th century, which is known to have caused the catastrophic losses observed in the Temperate North Atlantic East (Cotton, 1933; Milne & Milne, 1951). The minimal change observed in this bioregion might therefore be the result of a downward-shifted, post-disease baseline. Meanwhile, the Temperate North Pacific is likely one of the most data-deficient regions, relative to total abundance of seagrass (McKenzie et al., 2020). Similarly, the trends we estimated for the Indo-Pacific and Southern Oceans bioregions may be underestimates. It is possible that much seagrass was lost underneath port developments or through declines in water quality before meadows were even monitored. Historical ecological studies, such as with navigational charts (Bromberg & Bertness, 2005; McClanahan et al., 2014) could help fill this gap.

Sampling biases and data deficiencies pose a challenge when estimating global patterns of change (Gonzalez et al., 2016) prompting caution in the interpretation of reconstructed historical trends. Global syntheses, such as the present study, rely on data that do not represent random samples: sampled sites may be chosen for ease of access or to monitor the effects of specific disturbances or management actions; meadows could have disappeared before monitoring started; or published data can be subject to the ‘file-drawer’ problem (Csada et al., 1996; Rosenthal, 1979), meaning that sites with no change could be under-represented in our dataset. Including grey literature into future reviews is one way to help with the latter concern.

Although many geographical data gaps have been filled since Waycott et al. (2009), much of global seagrass extent has yet to be documented (McKenzie et al., 2020; Unsworth et al., 2018). In fact, the cumulative seagrass meadow area surveyed in this study represents just one-tenth (29 293 km^2) of recent estimates of global seagrass extent (266 562 km^2; McKenzie et al., 2020). It remains unclear whether the bioregional patterns of change documented here, and in previous global reviews, reflect changes in unmonitored seagrass meadows.

The local picture: site-level changes

The rates of change in seagrass area for individual meadows were generally in the order of 1–2% per year. At first glance, this suggests a great improvement in the status of seagrass over the 7% per annum decline reported by Waycott et al. (2009). However, we caution against making such a direct comparison. We analyzed new data and advanced on the linear interpolation method used in Waycott et al. (2009) by modelling non-linearity in seagrass trends and accounting for differences in trends across bioregions. Interpretation of the status plots of all sites in each dataset (Figure A13) suggests the 7% global decline estimate was strongly influenced by declining trends in the Temperate North Atlantic West: a trend that we also observe in our updated dataset, and which continues into the 2010s. Overall we find that observed declines have slowed in several bioregions that have suffered large historical declines (Temperate North Atlantic West) and those that have experienced substantial restoration efforts (Mediterranean, Tropical Atlantic).

Persistent declines of 1-2% per year are nevertheless of great concern for two reasons. First, consistent declines of this magnitude can still lead to substantial loss. Furthermore, this loss could be accelerated as meadow size decreases below a threshold size where recovery can be achieved naturally or through management (Moksnes et al., 2018; Olesen & Sand-Jensen, 1994; Orth et al., 2012). For example, large meadows are more likely to trap sediments in a positive feedback that improves water clarity (Adams et al., 2018; van der Heide et al., 2011) and dampens waves that are damaging to meadows (Uhrin & Turner, 2018). The fact that low rates of declines, although widespread, often affect large meadows (e.g., in the Tropical Indo-Pacific, Fig. 2.3) offers some reassurance because given the same rate of decline, large meadows will take longer to reach the point of no return than smaller meadows. Second, from a human perspective, declines of 1–2% might be imperceptible or attributed to natural variation. This sets the stage for the potential problem of shifting baselines (Duarte et al., 2009; Pauly, 1995), which could delay the recognition of declining trends and onset of management intervention.

Meadows that were small relative to their maximum observed area more commonly experienced large annual rates of change when compared to meadows that were close to their maximum ever observed area. There are several explanations for this pattern. First, it could be caused by sampling bias caused by higher variation in year-to-year estimates of meadow area when observing smaller meadows in turbid water. However, extreme rates of change associated with small relative size tended to occur more frequently when meadows increase in size than when they decline. This pattern suggests an ecological interpretation: seagrass meadow expansion is dominated by vegetative growth at meadow edges, and edge-to-area ratios, and thus the scope for large relative areal gains, are higher for small than for large meadows (Olesen & Sand-Jensen, 1994; Rasheed, 2004). It is also possible that the maximum observed size of a meadow approximates the maximum suitable habitat and so the potential for meadow expansion is low when meadows are near their maximum size. In contrast, loss processes are not strictly limited to the edges of meadows, and extreme rates of loss might depend on the type of local drivers, such that large proportional losses can occur regardless of meadow size.

Although the status of individual seagrass meadows generally paralleled bioregional trends in seagrass area, there was high variability in individual meadow rates of change, with many sites bucking the bioregional trends. This suggests that local context is important, particularly when regional-scale factors (e.g., wasting disease, storms) are not the primary driver of regional trends in seagrass area. Local factors that can be highly variable even within bioregion include the type, frequency, and intensity of human impacts.

Attributions to drivers of change

Given the observed declines in seagrass area, the high variability in individual meadow change, and large gaps in how meadows are currently managed, it is ever more important to understand what is driving change, so the gaps that contribute to ineffective seagrass management can be identified and filled (Griffiths et al., 2020). In our dataset, most studies attributed observed change in seagrass area to one or more drivers, but the strength of attribution was, in general, weak. Inferential tests provide the strongest attribution, because they are quantitative and repeatable (O'Connor et al., 2015), but only 10% of studies identified the causes of change using inferential tests. Admittedly, environmental data that coincide with seagrass meadow time-series are lacking in most places, which makes inferential attribution of changes in seagrass area to specific drivers difficult (Unsworth et al., 2018). Nevertheless, causal links between drivers such as water quality or coastal modification and the loss of seagrass meadows are well documented by many local studies (Breininger et al., 2017; Dolch et al., 2013; Lefcheck et al., 2017, 2018). In some locations water quality management strategies have promoted seagrass recovery (e.g., Cunha et al., 2013; Sherwood et al., 2017). For example, in Tampa Bay, implementation of water quality management strategies allowed seagrass meadow area to recover to a 1950's baseline, despite a population increase of ~3 million over that same time period (Sherwood et al., 2017). These unambiguous studies of coastal development and water quality on seagrass status might explain why these two drivers of change were the most frequently invoked by authors, even without local evidence, in the studies we reviewed, albeit with far weaker strength of attribution. However, causality is much less clear for most of the other drivers of change invoked in the studies considered here.

Weak attribution strength is a problem for two reasons. First it might artificially reinforce confidence in the importance and ubiquity of some drivers of change, such as water clarity and coastal development. Second it might lead to overlooking the effects of indirect or co-occurring multiple drivers of change. For example, while poor water clarity is undoubtedly a problem for many seagrass meadows, this widely acknowledged issue can sometimes be a consequence rather than a cause of seagrass loss (e.g., Hiratsuka et al., 2007; Kendrick et al., 2019; Krause-Jensen et al., 2012; Nowicki et al., 2017). For instance, despite concurrent coastal development/urbanization, water clarity in Lake Nakaumi, Japan, declined only after the loss of seagrass beds, which was likely initially driven by herbicides used to eradicate an invasive aquatic plant (Hiratsuka et al., 2007). Furthermore, multiple drivers generally co-occur spatially and temporally. Aquaculture development, destructive fishing, the introduction of non-native species, and boating are all more likely to take place adjacent to or near port development and urban centres. Moreover, all of these occur against a background of climate change, which further complicates any clear attribution to drivers, especially via non-inferential means.

Climate change was not a main driver of seagrass area change considered by many authors; however, its effects are expected to increase in the future. Marine ecosystems are expected to experience a higher frequency and intensity of extreme conditions such as heatwaves and increased storm frequency and intensity (Collins et al., 2022; Smale et al., 2019). While single extreme events have resulted in immediate and drastic loss of seagrass meadows (Kendrick et al., 2019; Oprandi et al., 2020), repeated occurrences and/or extreme and catastrophic events can reduce meadow resilience to multiple stressors (Kendrick et al., 2019; Krause-Jensen et al., 2021). Conversely, in some bioregions such as the Temperate North Pacific, poleward range shifts are expected to occur and may lead to gains outside of historical ranges (Wilson & Lotze, 2019). With the increase in high-quality global datasets on pressures and environmental change, future efforts can use high-resolution and hindcasted datasets to attribute drivers to trends in seagrass meadow area, identify vulnerable sites, and identify regions where monitoring of range shifts should be expanded.

In conclusion, the global outlook for seagrass meadows is that declines are continuing, but considerable nature and management driven variability in meadow area creates opportunities for recovery. The consistent, global patterns of loss are a concern and likely reflect the growing number and intensity of human impacts that threaten seagrass meadows. In some regions the loss over the past century has been rapid and large, and in others, there is a pattern of slower, less spectacular but more insidious loss. Because early data, especially from before the 1940s, are limited, seagrass meadows, like many other ecosystems, are likely subject to shifting baselines; we can therefore neither estimate nor even conceive the true extent of losses in some bioregions. Importantly, we need to improve our attribution of changes in seagrass area to specific human activities to understand the local context of trends in seagrass meadow area and to improve management. Certainty in attribution will continue to be challenging because of the ubiquitous presence of multiple stressors and confounding variables, and the often-unclear causal links between human activities and the consequent changes in environmental variables.

Chapter 3. Management thresholds shift under the influence of multiple pressures: Eelgrass meadows as a case study[2]

Abstract

As human activities increase in intensity and extent, ecosystems face growing threats from multiple stressors. Successful management requires identifying measurable targets, which is challenging because of data limitations, non-linear ecosystem responses, and potentially shifting targets under multiple stressors. To identify critical management values and determine whether these values shift in the presence of multiple stressors, we use eelgrass (*Zostera marina*) meadows as a model system. We reviewed 20 studies that measured the effects of light and temperature on eelgrass performance, providing 109 unique study-site-treatment combinations. We modelled the interactive effect of temperature and light on eelgrass population growth rate (i.e., lateral shoot production rates) using a hierarchical generalised additive model and predicted population growth rates across a range of light levels and temperatures. We found that two critical performance metrics of population growth, zero-growth and maximum growth rates, shifted across a gradient of light and temperature, suggesting that fixed management targets linked to population growth rates might be unsuitable for managing meadows under multiple stressors. Our approach bridges the gap between data from laboratory and field studies and could be developed into an interactive management tool.

Introduction

Ecosystems are undergoing drastic change globally as human activities increase in frequency, intensity, and extent (Williams et al., 2020). Managing the impacts of human activities is critical for the preservation of ecosystem function and services. However, ecosystem responses to multiple stressors, which we define as environmental conditions that deviate from optimal life conditions and decrease organismal fitness, can be difficult to predict, in part because ecosystems can have non-linear responses to

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[2] A version of this chapter appears as Dunic JC and Côté IM. 2023. Management thresholds shift under the influence of multiple stressors: Eelgrass meadows as a case study. Conservation Letters. VOL(ISS): PAGES. DOI: 10.1111/conl.12938

increasing stressors (Hunsicker et al., 2016). Sometimes this change is reversible, but often reversal is costly because of self-reinforcing feedbacks and shifts to alternative stable states (Bayraktarov et al., 2015; Selkoe et al., 2015). Avoiding undesirable state change is therefore imperative.

One approach to managing ecosystems that demonstrate non-linear responses to increasing stressors is threshold-based management. This approach requires explicit stressor thresholds linked to a desired ecosystem state or population performance that can trigger management interventions (Cook et al., 2016). Once thresholds are identified, management can define a ‘safe-operating space’ to maintain stressors below certain levels (Selkoe et al., 2015). Management strategies that use a threshold approach are associated with better outcomes than strategies that neither identify nor target management actions in relation to stressor threshold values (Kelly et al., 2015). Harvest-based thresholds are commonly used to manage populations targeted by fisheries (Caddy & Mahon, 1995) and forestry (Päivinen et al., 2022). Threshold-focused management is also applied to natural ecosystems. For example, threshold-based management targeting stormwater regulations and residential fertilizer restrictions enabled the recovery of seagrass to pre-1950s areal extent in Tampa Bay, Florida, USA (Greening et al., 2014). However, identifying measurable management targets and useful metrics of successful ecosystem state is difficult because of lack of data and variability across populations and species (Johnson, 2013).

Another major impediment to quantifying management thresholds is the co-occurrence of multiple stressors, which is increasing in both terrestrial and marine environments (Bowler et al., 2020). Predicting how multiple stressors interact to affect management targets is challenging (Stockbridge et al., 2020). Temporal and spatial scales, level of biological organisation (e.g., physiological, population), and stressor type can all mediate multiple stressor interactions (Boyd et al., 2018; Turschwell et al., 2022). However, current applications of threshold-based management typically do not consider the effects of multiple co-occurring stressors, which may have harmful consequences. While the use of long-term fixed stressor thresholds is sometimes beneficial (e.g., Tampa Bay seagrass), it is associated with declines in fished Walleye (*Sander vitreus*) populations in the USA, which suggests that thresholds should be adapted to changes in environmental conditions (Embke et al., 2019). Even if management thresholds are identified for a single stressor, they could shift with additional stressors. Therefore, thresholds based on historical or current trends may not hold true under future conditions (S. Large et al., 2015).

Eelgrass (*Zostera marina*) is an ideal model organism to test how multiple co-occurring stressors might complicate threshold-based management. It is a well-studied, widespread species that is the foundation of coastal ecosystems subject to many human activities. Thus, eelgrass ecosystems face growing threats from multiple stressors. Management of eelgrass would benefit from the identification of stressor thresholds clearly linked to population performance because once lost, eelgrass can be difficult to recover (van der Heide et al., 2011). The effects of single stressors on various eelgrass responses have been previously reviewed (e.g., Lee, Park, & Kim, 2007); however, these data have not been combined using a predictive approach that allows the forecasting of eelgrass performance in response to common stressors like temperature, light, and, most importantly, their joint effect.

Here we develop an empirical, predictive approach that can help management by identifying critical stressor values linked to critical metrics of eelgrass population performance and predict how these threshold values change under multiple stressors. Using published data, we model the relationship of eelgrass (*Zostera marina*) lateral shoot production rates in response to light and temperature, two critical drivers of eelgrass productivity (Lee, Park, & Kim, 2007). Using eelgrass as a model system we (1) demonstrate how response surfaces can be used to empirically identify critical management targets in a foundation species, (2) test if stressor values linked to critical performance metrics vary in the context of multiple stressors, and (3) demonstrate a modelling approach that can incorporate species responses to multiple stressors from data obtained from a range of study types.

Methods

Data compilation

To find studies that tested the response of *Zostera marina* to light and temperature, we searched the published literature using Web of Science and Scopus on 9 January 2021. We used search terms that combined *Z. marina* identifiers: (eelgrass OR “*Zostera marina*” OR “*Z. marina*”) with keywords related to light and temperature.

Our goal was not to perform an exhaustive or systematic review but to obtain sufficient data to produce a proof of concept. Ultimately we selected 20 studies (n), which yielded a dataset of 109 unique study-site-treatment (k) combinations (Table B1). In studies where additional covariates were included, we used data from the control treatments.

Data extraction and variable standardisation

Population growth rate

We extracted four response metrics that could be standardised to a per-capita shoot production rate: shoot mortality, shoot survival, lateral shoot production, and shoot density. We converted proportional shoot survival to shoot mortality, which was then used as a negative shoot production value. Metrics were divided by initial shoot density if not already presented as per-capita rates. Once standardised, we converted these values into a rate by dividing by the number of days over which the response was measured if not already presented as a daily rate. When studies measured shoot density over time, we calculated the per-capita shoot production rate, *r*, as follows:

$$r = \frac{\frac{shoots_t - shoots_{t-1}}{shoots_{t-1}}}{t} \tag{3.1}$$

The authors, and thus we, did not differentiate between shoots produced via vegetative growth or seedling development. The contribution of sexual reproduction in eelgrass is highly variable but in established perennial meadows, it is often low (2 - 20%; (Lee, Park, Kim, et al., 2007; Xu et al., 2018) such that lateral shoot production can be the primary contributor to population growth. Therefore, for simplicity we refer to per-capita lateral shoot production as ‘population growth rate’.

Light

We used the daily light integral (DLI) to standardise light values across studies. The DLI measures the amount of photosynthetically active photons delivered per m^2 over a 24-h period, which is closely related to plant growth (eqn 3.2; Poorter et al., 2010)). If DLI was not provided, we calculated it by multiplying the mean photosynthetic photon flux density (PPFD) by the number of light hours. We used penetrating irradiance to calculate the DLI (n = 13, k = 64), which was provided for all field studies. When this was not available, as was the case only for laboratory studies in shallow mesocosms, we used surface irradiance instead (n = 7, k = 45).

$$Daily\ light\ integral = Irradiance\ (\mu mol\ s^{-1}m^{-2}) * Light\ (hours) \tag{3.2}$$

In outdoor mesocosms and field studies, where the number of light hours and PPFD varied over time (Table B2), studies presented light in one of two ways: a mean PPFD or DLI over the experiment duration, or a light time-series that corresponded to a shoot density or shoot production time-series (Figure B1). In the latter case, we calculated the average DLI between sampling points to improve the temporal link between the light data and measured response (Figure B1).

For cases (n = 4, k = 22) where neither the light hours nor DLI were provided, we used the ‘suncalc’ package (Thieurmel & Elmarhraoui, 2019) in R (R Core Team, 2022) to estimate the light hours at the study location so that we could calculate the DLI using the provided irradiance.

Temperature

We used the mean temperature value given, or the midpoint if only a range was provided. As with the light values, we calculated the mean temperature between response sampling points when a time-series of temperature data was provided (Figure B1).

Modelling the effect of temperature and light on population growth rate

To identify the eelgrass zero-growth isocline (population growth rate = 0) and to understand the effect of the interaction between temperature and light on this isocline, we fit an unweighted hierarchical generalized additive model (GAMM) to population growth rates, *r*, using the ‘mgcv’ R package (Wood, 2011). We used a GAMM to allow the shape of the relationships between population growth rate and the predictors to be data-driven instead of making *a priori* assumptions about the functional forms of the relationships. We fit the following model:

$$r = f(DLI_i, Temp_i) + f(study, site, treatment) + \epsilon_i \tag{3.3}$$

where $f(DLI_i, Temp_i)$ was fitted with a cubic regression spline and is the tensor product smooth of the DLI and temperature of a given data point, which allowed us to model two predictors that are on different scales (Wood et al., 2013). We included a random effect of unique study-site-treatment combinations, *f(study, site, treatment)*, to account for studies that contained data from more than one site and/or repeated measures of response values; ϵ_i is a Gaussian error term. We then used the fitted GAMM to identify the critical DLI and temperature values where $r = 0$ and $r = r_{max}$ and examine how these critical values change under different combinations of DLI and temperature.

Estimating critical values of light and temperature

To identify the critical DLI and temperature values where $r = 0$ and $r = r_{max}$ and examine how these critical values change under different combinations of DLI and temperature, we used predictions from the fitted, unweighted hierarchical generalised additive model (GAMM; eqn. 3.3). First, we extracted the mean expected eelgrass performance curves for DLI across a range of temperatures observed in the dataset and did the same for temperature performance curves across values of DLI. Next, we calculated the first derivative, $f'(x)$, of these mean functions using finite central differences. From the performance curves, we extracted the critical DLI and temperature values for: the minimum required light, $DLI_{r=0}$, where the light performance curve was increasing, $f'(x) > 0$, and where $r = 0$; the maximum tolerable temperature, $T_{r=0}$, where the thermal performance curve was decreasing, $f'(x) < 0$, and $r = 0$; and $DLI_{r=rmax}$ and $T_{r=rmax}$ where the slope of the mean fit was zero, $f'(x) = 0$ and $r = r_{max}$.

To estimate the uncertainty around the critical values, we used this same method on 1000 simulated draws from the posterior distribution of the fitted GAMM to create a posterior distribution of critical values and summarized these as the 2.5% and 97.5% quantiles of critical values. We chose to use a traditional 95% confidence interval, but this can be adjusted by choosing different quantiles. Simulated fits were drawn under the assumption that smoothness parameters are estimates and so the confidence intervals are marginalized across the random effect. For the $DLI_{r=rmax}$ and $T_{r=rmax}$, which were unduly influenced by high uncertainty at the tails of the predictor data ranges, we only estimated them for DLI < 26 mol m^{-2} day^{-1} and temperature > 8˚C.

Results

Description of dataset

Most of the 20 studies were indoor laboratory experiments (n = 15), but there were also outdoor mesocosms (n = 2), and field manipulations or observations (n = 3). Most studies had constant light and temperatures throughout the experiments (n = 18), but some studies included seasonal/temporally variable light and temperature data over the course of observations (n = 5). Vegetative adult shoots were the most tested life-stage (n = 19).

Response surface

Analysis of the combined effects of light and temperature on population growth rate showed that there are critical thresholds below which (for light) or above which (for temperature) shoot density should decline because growth rates become negative (i.e., shoots die). Population growth (i.e., positive growth rates) occurred with light levels above 3.75 mol m^{-2} day^{-1} and temperatures below 26.9˚C (Figure 3.1a). Maximum shoot production occurred at light levels 17.4 mol m^{-2} day^{-1} and temperatures of 19.4˚C (Figure 3.1a).

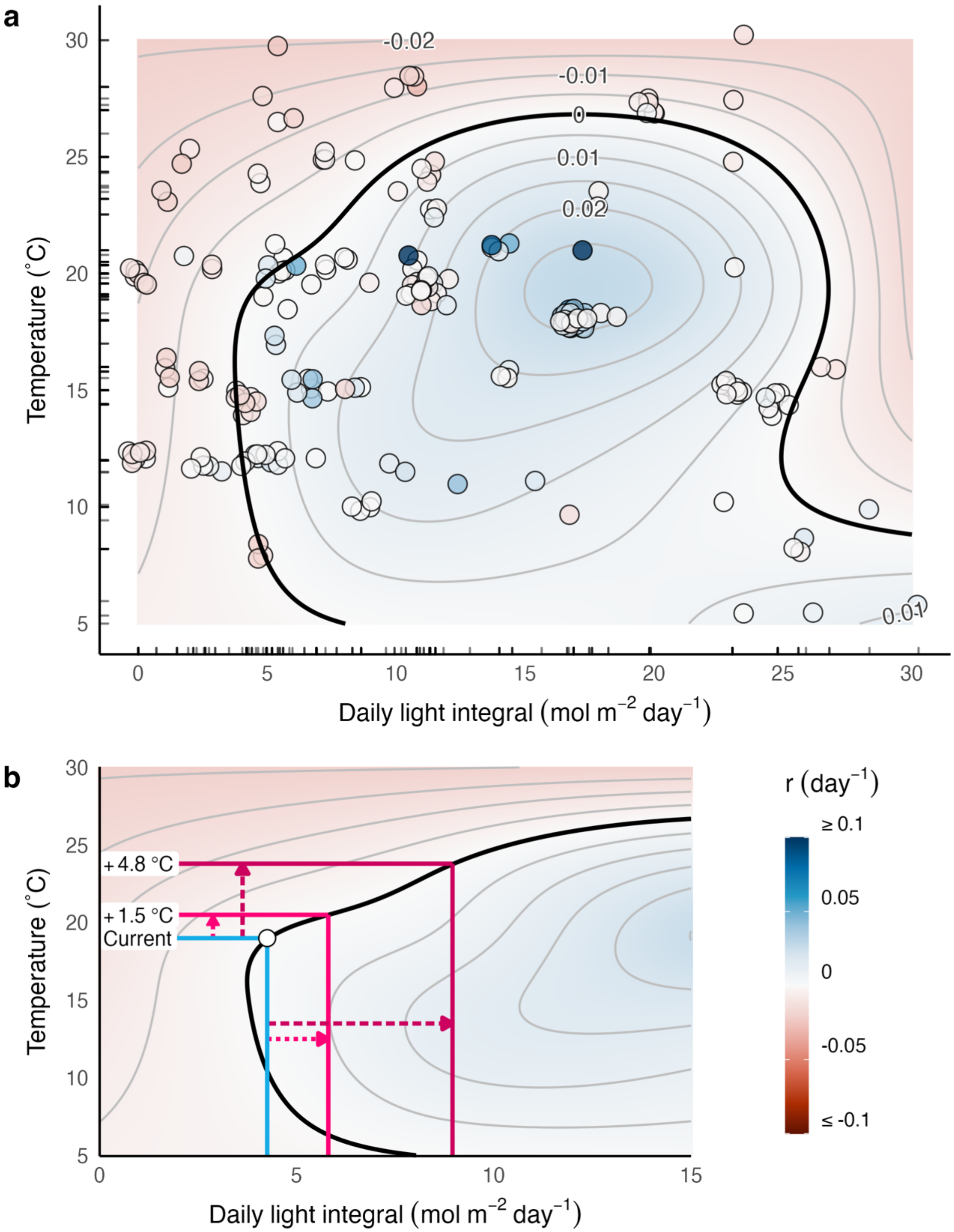
a
Temperature (°C)
30
25
20
15
10
5
-0.02
-0.01
0
0.01
0.02
0.01
0
5
10
15
20
25
30
Daily light integral (mol m^{-2} day^{-1})
b
Temperature (°C)
+4.8 °C
+1.5 °C
Current
0
5
10
15
Daily light integral (mol m^{-2} day^{-1})
r (day^{-1})
≥ 0.1
0.05
0
-0.05
≤ -0.1

Figure 3.1 Predicted response surface of population growth rate of eelgrass, *r*, (day^{-1}), in response to the combined effect of temperature and light availability (measured as daily light integral, DLI). (a) Response surface across all values of temperature and light. Shades of blue indicate combinations of temperature and light that allow lateral shoot growth while shades of red indicate conditions under which shoots die. The colour scale has been truncated at -0.1 and 0.1 to improve visualisation of the predicted values from a GAMM (i.e., three points > 0.1). Points are observed population growth rates (shoot density change or lateral shoot production rates) from unique study-site-treatments. Population growth rates are given for each contour line; the threshold for growth (contour *r = 0*) is highlighted in black. (b) Response surface for a subset of temperature and light values to show how the critical value of population growth rate, *r* = 0, varies with changing conditions. Population size at current light and temperature levels (white circle) cannot be maintained under warming scenarios unless accompanied by increases in light availability.

Shifting critical thresholds

The response surface can be used to predict how a given eelgrass meadow will respond to changes in light or temperature and to set management targets (Figure 3.1b). For example, a meadow that experiences a current-day average of 4.3 mol m^{-2} day^{-1} and a temperature of 19˚C can maintain shoot density (i.e., population growth rate is zero). However, with any increase in temperature, the minimum light required for persistence increases. With a 1.5˚C increase in temperature, light must increase by ~ 1.6 mol m^{-2} day^{-1} (37% increase), while with a warming of 4.8˚C light must increase by 4.7 mol m^{-2} day^{-1} (109% increase) for the same meadow to maintain its current shoot density (Figure 3.1b).

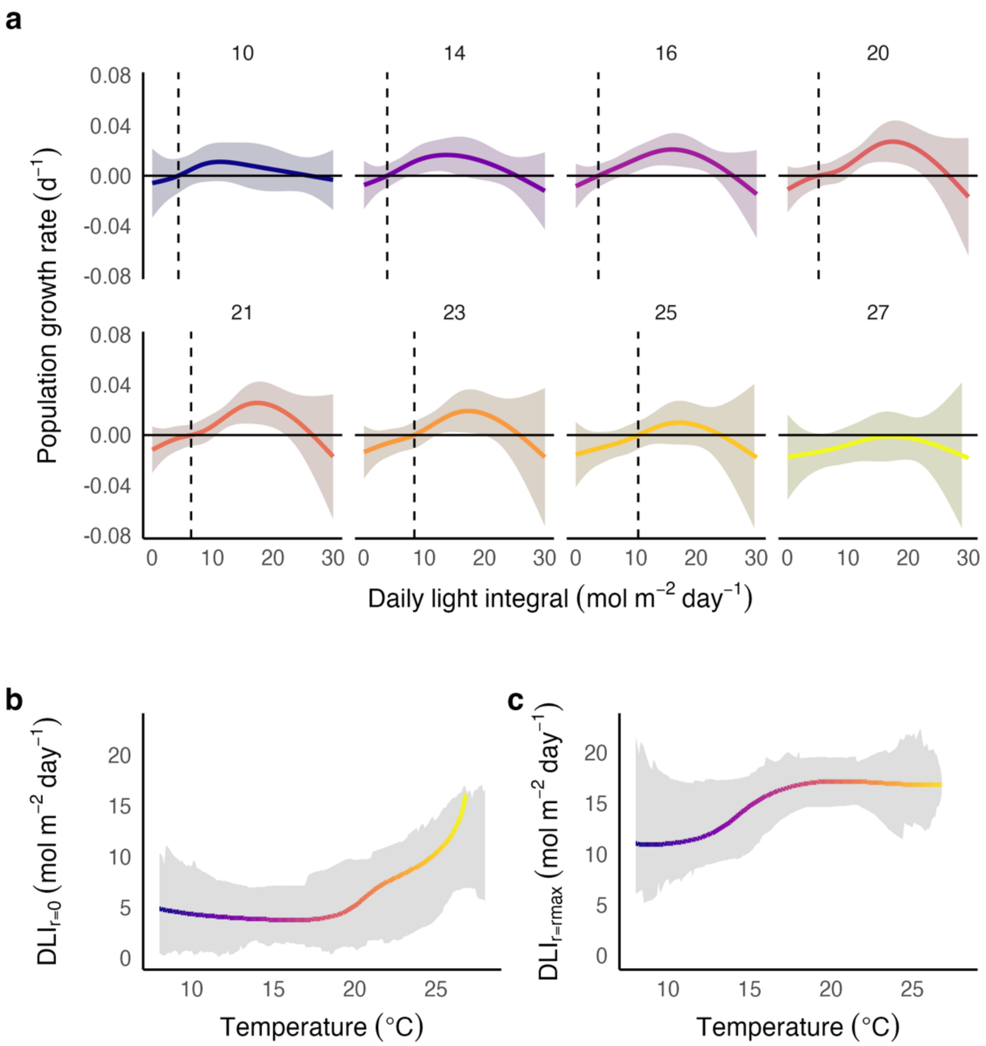

Figure 3.2 **Light performance curves of eelgrass, *Zostera marina*. (a) Predicted fits of population growth rate by eelgrass, r (day^{-1}), in relation to light levels at different temperatures, shown (in ˚C) above each panel. The vertical dashed lines denote the minimum daily light integral, $DLI_{r=0}$, at which population growth rate = 0 for a given temperature. The narrow temperature bins between 20 and 27˚C highlight the temperatures over which $DLI_{r=0}$ increases rapidly. The shaded areas are 95% simultaneous confidence intervals from model fits. (b) The relationship between $DLI_{r=0}$ and temperature and (c) between $DLI_{r=rmax}$ and temperature as estimated from mean GAMM fits. Uncertainty around the $DLI_{r=0}$ and $DLI_{r=rmax}$ estimates, in grey, indicates the 2.5% and 97.5% quantiles of $DLI_{r=0}$ and $DLI_{r=rmax}$ estimated from simulating 1000 draws of light performance curves across from the GAMM posterior distribution. To reduce the influence from high uncertainty at the tails of the predictor data ranges, we only estimated $DLI_{r=0}$ and $DLI_{r=rmax}$ for DLI < 26 mol m^{-2} day^{-1} and temperature > 8˚C. Colours in (b) and (c) correspond to the temperature bins in (a).**

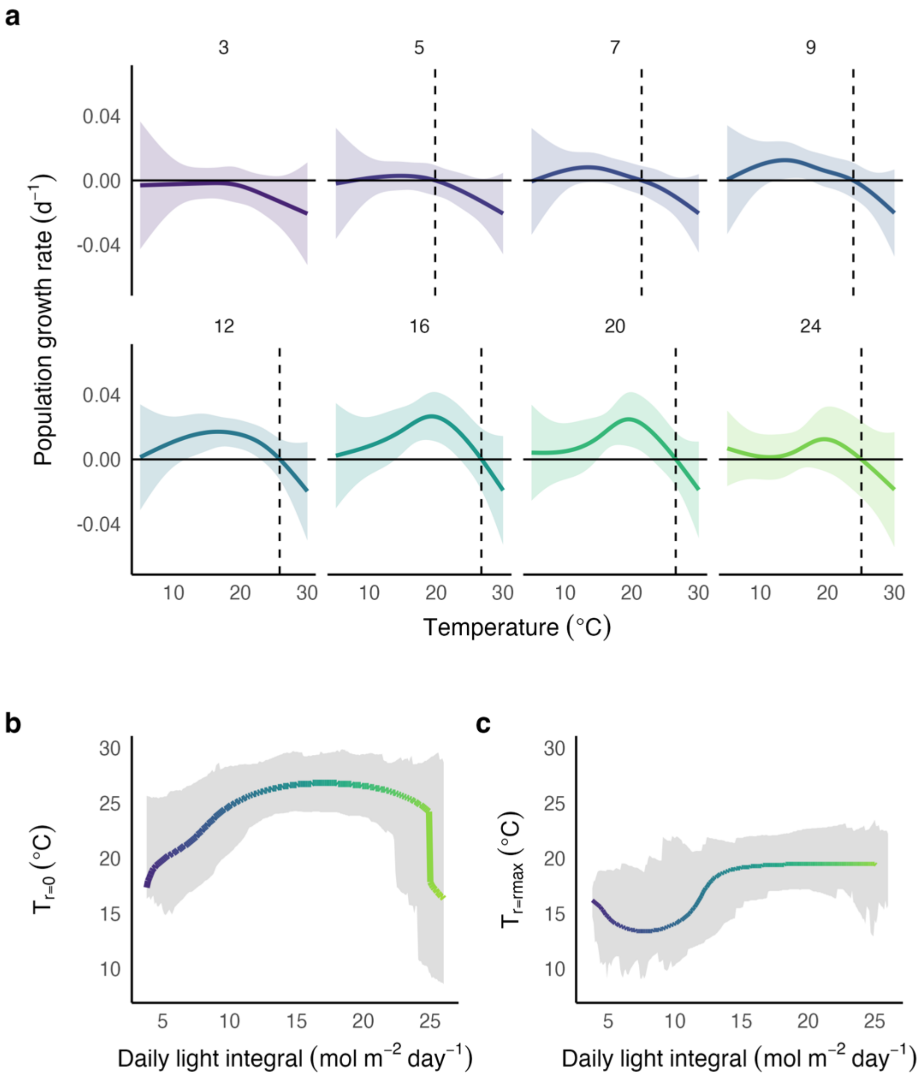

Figure 3.3 **Temperature performance curves of eelgrass, *Zostera marina*. (a) Predicted fits of population growth rate by eelgrass, r (day^{-1}), in relation to temperature at variable daily light integral (DLI) levels. The vertical dashed lines denote the critical thermal maximum, $T_{r=0}$, at which population growth rate, $r = 0$, for a given light level. The narrow light bins between 3 and 9 highlight the light values over which $T_{r=0}$ increases rapidly. The shaded areas are 95% simultaneous confidence intervals from model fits. (b) The relationship between $T_{r=0}$ and DLI and (c) $T_{r=rmax}$ and DLI, as estimated from mean GAMM fits. Uncertainty around the $T_{r=0}$ and $T_{r=rmax}$ estimates, in grey, indicates the 2.5% and 97.5% quantiles of $T_{r=0}$ and $T_{r=rmax}$ estimated from simulating 1000 draws of thermal performance curves across from the GAMM posterior distribution. To reduce the influence from high uncertainty at the tails of the predictor data ranges, we only estimated $T_{r=0}$ and $T_{r=rmax}$ for DLI < 26 mol m^{-2} day^{-1} and temperature > 8˚C. Colours in (b) and (c) correspond to the DLI bins in (a).**

The shape of light and temperature performance curves, as well as critical growth values, changed across the combinations of light and temperature that eelgrass meadows often experience (Figures 3.2, 3.3). Importantly, values of light and temperature associated with critical growth values (e.g., $r = 0$) changed non-linearly. For example, the minimum daily light integral, $DLI_{r=0}$, remained relatively constant at temperatures ranging from 5˚C to ~20˚C (with an absolute minimum of 3.8 mol m^{-2} day^{-1}) but increased rapidly as temperatures increased from 20˚C to 26˚C (Figure 3.2a,b). Similarly, the maximum temperature, $T_{r=0}$, that allows eelgrass persistence increased rapidly when light values were less than 10 mol m^{-2} day^{-1} but much more slowly beyond that point (Figure 3.3a,b). The daily light integral associated with maximum growth, $DLI_{r=rmax}$, increased with increasing temperature, but r_{max} decreased as temperature increased (Figures 2c, S2). Similarly, the pattern with maximum growth temperature, $T_{r=rmax}$, showed a region of rapid increase over light values between 12-18 mol m^{-2} day^{-1}, and no increase in r_{max} at temperatures beyond ~19˚C, (Figures 3.3c, B3).

Discussion

The responses of eelgrass to light and temperature are well documented, largely because these two factors are common proxies for two major stressors of eelgrass meadows: turbidity and warming. We combined light and temperature performance curves in a novel way to examine the validity of fixed management thresholds for eelgrass ecosystems. We found that critical eelgrass performance values, zero and maximum population growth rates, shifted across combinations of light and temperature values, suggesting that fixed stressor targets are inappropriate to guide the management of meadows under co-occurring stressors. Under predicted warming scenarios the minimum light required for meadows to persist increases rapidly, suggesting that strong management of a local stressor (light availability) could mitigate some of the negative effects of a global stressor (warming) on eelgrass population growth.

Eelgrass population responses to light and temperature

Three regions of interest emerge from the response surface. First, there were absolute limits for the minimum DLI and maximum tolerable temperature beyond which population loss occurs. For temperatures less than ~18˚C, the minimum DLI required for population maintenance (r = 0) was 3.8 mol m^{-2} day^{-1} (Figure 3.1a), suggesting that at these temperatures, light is a limiting resource. This value is comparable to field estimates of minimum DLI (e.g., 3 mol m^{-2} day^{-1} at 12-14˚C on the US Pacific coast, (R. M. Thom et al., 2008); 3.6-3.7 mol m^{-2} day^{-1} at 15-20˚C on the US Atlantic coast, (Dennison & Alberte, 1985)). Our model may, however, overestimate the $DLI_{r=0}$ at temperatures < 8˚C due to the low sample size (k = 3). Similarly, at temperatures > 27˚C, increases in DLI did not affect the zero-growth isocline (Figure 1a). Factors such as damage to plant tissue and photosynthetic pathways, and sediment condition could set an upper limit on the temperature that determines the zero-growth isocline. For instance, high temperatures can damage tissues and impair protein synthesis (Hammer et al., 2018); however, this typically occurs at temperatures beyond what is represented in our dataset (> 30-35˚C).

Second, maximum growth rate occurs at temperatures ~16-18˚C and irradiance between 15-20 mol m^{-2} day^{-1}. These optimal temperatures match those found across the range of eelgrass (Lee, Park, & Kim, 2007). Meanwhile the decrease in population growth rate at irradiances > 20 mol m^{-2} day^{-1} may reflect photoinhibition (P. J. Ralph et al., 2007). For example, in the congener *Zostera noltii*, photoinhibition begins at 20.4 mol m^{-2} day^{-1} (Peralta et al., 2002).

Third, above the absolute minimum light and below the absolute maximum temperature, the critical values of light, $DLI_{r=0}$, and temperature, $T_{r=0}$, shift as environmental conditions change. Between ~18˚C and 27˚C positive eelgrass growth rates were maintained only if DLI increased concurrently with temperature (Figure 3.2). Conversely, with declining DLI, eelgrass growth rates remain positive only with declines in temperature (Figure 3.3). If high temperature conditions and low light persist, populations will decline. In Chesapeake Bay, for instance, eelgrass cover declined, with the greatest losses occurring at the deep edge of meadows where light is most limited, concomitant with mean temperatures increasing from 24.9 to 26.4˚C and increasing pulses of extreme temperatures (> 28˚C; Lefcheck et al., 2017).

Underlying these general trends was a high variability in growth rates, indicating that there are other important covariates to consider. Genetic variation, initial condition, variability in stressors, and additional co-occurring stressors are factors that could be included with more data. For instance, eelgrass populations demonstrate high levels of genetic variation and phenotypic plasticity, which affect their capacity to withstand warmer temperatures (DuBois et al., 2022). In addition, as most data were from experiments with static environmental conditions or with predictors averaged over time, fluctuating or extreme stressors were not explicitly included. However, they could be, if environmental and growth data are provided at a fine enough temporal resolution. Our model could then be used to simulate eelgrass performance over time as a meadow 'moves' around the response surface seasonally or as light regimes are affected by activities like dredging or algal blooms. At any rate, how critical values shift across temperature–light combinations are likely qualitatively similar across populations and seagrass species, but critical values will differ.

Management implications

Interactions between multiple stressors can have implications for management actions, affecting conservation and restoration strategies (Brown et al., 2013; Spears et al., 2021). We showed that the eelgrass zero-growth isocline shifted rapidly between the absolute minimum value of light required for shoot production (3.8 mol m^{-2} day^{-1}) and the absolute the maximum temperature plants can tolerate (~27˚C). This suggests that below 27˚C, focusing management actions towards improving or maintaining water quality will be important in a warming world. However, where temperatures are close to, or expected to exceed 27˚C, improving water quality is unlikely to be enough and other actions, such as identifying refuges or assisting migration, should be prioritized.

Below the maximum temperature plants can tolerate, the amount of light needed to maintain eelgrass populations is temperature-dependent. If plants do not build sufficient carbohydrate reserves during peak growing seasons, they may not persist through seasonal periods of low light in the winter (Wong et al., 2020). Therefore, it is important that light (or turbidity) thresholds, especially during the growing period, be revisited in the context of warming. The water-quality and light-based thresholds that have been successfully applied to the conservation of seagrass ecosystems in Tampa Bay to reduce nutrient loading (Greening et al., 2014) and on the Great Barrier Reef to limit dredging (Chartrand et al., 2016) do not account for effects of temperature and might become ineffective under warming ocean conditions. Additionally, considering the duration and timing of combined stressors could improve management outcomes (Wong et al., 2020; Wu et al., 2017). For example, dredging times and locations can be limited to sites and seasons where temperatures are below 20˚C

Improved understanding of multiple stressor effects could also increase restoration success. For example, sites such as low-flow embayments, may be more likely in the future to reach temperatures that exceed eelgrass thermal limits and should be considered unsuitable for transplants. In cases where water quality management will be insufficient to enable population growth, a landscape approach to conserving eelgrass where refugia sites are identified may be a more prudent strategy (Morelli et al., 2016), as is currently done for coral reefs (Andrello et al., 2022) and terrestrial wildlife management (Choe et al., 2020).

Chapter 4. Fine-scale effects of environmental conditions and human impacts on eelgrass health

Abstract

Managing multiple stressors is necessary to protect nearshore coastal ecosystems from the cumulative effects of human activities. However, identifying relevant local-scale management actions is challenging, in part because of the contrasting scales at which human activities and impacts are measured and at which ecosystem condition is measured. A dearth of high-resolution environmental data has meant that most assessments of environmental conditions and/or human impacts are done at large spatial scales (e.g., > 100s kms), masking the small-scale variability that directly affects ecosystem condition. Here, we characterised fine-scale (10s kms) variation in environmental conditions, human impacts, and two metrics of eelgrass (*Zostera marina*) ‘health’ (shoot density and lesion prevalence), across 11 meadows in the Salish Sea, northeastern Pacific. To ascertain the link(s) between these predictors and eelgrass health, we used Akaike’s Information Criterion to compare generalised linear models. We found that environmental conditions, rather than human impacts, were better predictors of eelgrass shoot density and lesion prevalence. Two metrics of eelgrass meadow health varied widely at a fine-scale, with shoot densities varying 10-fold and lesion prevalence ranging from 0-75% across sites. Correspondingly, environmental conditions were much more variable than the two human impact metrics considered (overwater structures and riparian modification). Eelgrass shoot density was positively correlated with maximum annual water temperature, meanwhile lesion prevalence was negatively correlated with maximum water velocity. This study highlights the importance of linking variation in eelgrass meadow responses to environmental conditions and human impacts at the fine scale at which conservation and restoration efforts occur. It also provides important baseline data on conditions and pressures to aid in predictions for the future.

Introduction

Ecosystems around the globe are being altered by the cumulative effects of multiple stressors. The co-occurrence of, and interactions between, multiple pressures complicate the task of attributing ecosystem state change to specific drivers. This problem is magnified because the scales at which cumulative impacts are applied and measured often differ from the measurements used to evaluate ecosystem condition (Stockbridge et al., 2021). As a result, our ability to make predictions for the fine spatial scale at which local management and restoration is done is severely limited. One potential avenue to overcome this issue is to combine hypothesis-driven monitoring, where response metrics of interest (e.g., biodiversity, condition, performance) are sampled across a targeted gradient (e.g., of human impact) at a fine spatial scale, with remotely sensed data and scale up the relationship to improve cumulative effects assessment (Burton et al., 2014; Sparrow et al., 2020).

One marine ecosystem that exemplifies the scale mismatch between ecosystem condition and cumulative effect monitoring is eelgrass meadows. Globally, large extents of eelgrass meadows have been lost (Chapter 2) and are increasingly under threat from multiple human activities that reduce water clarity, cause physical damage, and cause warming sea temperatures (Grech et al., 2012; Lefcheck et al., 2018; Turschwell et al., 2021). Global syntheses are undoubtedly useful to generate large-scale pictures of change in seagrass ecosystems, but the environmental conditions examined as potential drivers of change are considered on similarly large scales (e.g., latitudinal gradients) that obliterate the small-scale variation (e.g., gradients over 10s of km) that is likely to influence seagrass condition locally. Moreover, only 10% of studies of seagrass meadows have inferentially tested attributions of changes in extent to specific drivers and pressures (Chapter 2). When multiple pressures act on a meadow and specific causes of change are uncertain, it can be difficult to assess the best local management actions.

In this study, we try to ascertain the link(s) between seagrass health and potential natural and human-made drivers of change at a small spatial scale. We measure ‘health’ using two distinct metrics. The first is shoot density, which is a commonly measured metric of habitat complexity that readily responds to environmental changes (McMahon et al., 2013) and is often used to assess seagrass restoration success (van Katwijk et al., 2016). Shoot density varies at the within-meadow scale, typically with lower shoot densities at deeper depths (Krause-Jensen et al., 2000; R. Thom et al., 2014), up to scales across latitudes, and can reflect differences in environmental factors such as nutrients (Schmidt et al., 2012; Touchette et al., 2003), light (McMahon et al., 2013), and temperature (Krumhansl et al., 2021). Meanwhile, high structural complexity (i.e., high shoot densities) can be mediate predator-prey relationships (Hovel et al., 2016; P. L. Reynolds et al., 2018) and can increase wave dampening and sediment accretion (Ondiviela et al., 2014).

The second metric is prevalence of disease. Wasting disease is a stressor of growing concern for seagrasses globally (Sullivan et al., 2013). In temperate seagrasses, wasting disease is caused by the slime mold *Labyrinthula zosterae*, which can result in necrotic lesions on leaf tissue and can compromise plant performance (P. Ralph & Short, 2002). The severity of infection (i.e., proportion of leaf area with lesions) is associated with decreased leaf growth rates and lower rhizome sugar content (Graham et al., 2021). Furthermore, stressors such as high temperatures (Aoki et al., 2022; Groner et al., 2021; Graham et al., 2023), high nutrients (Kaldy, 2014), and low salinity (Brakel et al., 2019) are likely to exacerbate disease prevalence and severity. In addition, disease can reduce the capacity of eelgrass to tolerate additional stressors such as light limitation (Jakobsson-Thor et al., 2020; P. Ralph & Short, 2002). Therefore, the combination of shoot density and disease prevalence are important metrics that can reflect the current ‘health’ of a meadow and help us anticipate responses to changing conditions.

Here, we focus specifically on eelgrass (*Zostera marina*) in the Salish Sea. Eelgrass is an important foundation species that provides valuable ecosystem services such as water quality improvement and nursery habitat for fishery species (Cote et al., 2013). It is also the most widely distributed and abundant species of seagrass in the Northern Hemisphere and is found through temperate to arctic latitudes (Short et al., 2007). The Salish Sea is an area of rapid human development and increasing human impacts, including global-scale threats such as ocean warming, sea-level rise, and ocean acidification (Khangaonkar et al., 2018). These increasing cumulative impacts are likely to negatively affect eelgrass ecosystems. While trends in eelgrass meadow extent have been variable throughout the Salish Sea, with some areas like Puget Sound observing stable meadow extents, recent monitoring suggests that more sites are declining than gaining eelgrass area (Nearshore Habitat Program, Washington State Department of Natural Resources, 2022). Meanwhile at other sites, long-term declines have been observed in bays associated with increasing human activities (Nahirnick et al., 2019). Therefore, it is critical to both establish a baseline of information about eelgrass meadows in this rapidly changing region and attempt to better understand the links between environmental conditions, human impacts and eelgrass condition to target management and ameliorate eelgrass health at a local scale.

Methods

Study site

The Saanich Peninsula is located on Southern Vancouver Island, Canada, in the Salish Sea (Figure 4.1). Eleven sites were selected along a 31-km span of coastline (Figure 4.1) with inter-site distances ranging from 500 m to ~5 km. The west and east coasts of the Saanich Peninsula represent contrasting sets of oceanographic conditions. On the west coast is Saanich inlet, a deep (~234 m) ~24 km long fjord with a shallow sill at the mouth which restricts water flow (Herlinveaux, 1962). On the more exposed east coast, conditions are more strongly influenced by strong tidal exchanges and oceanic conditions.

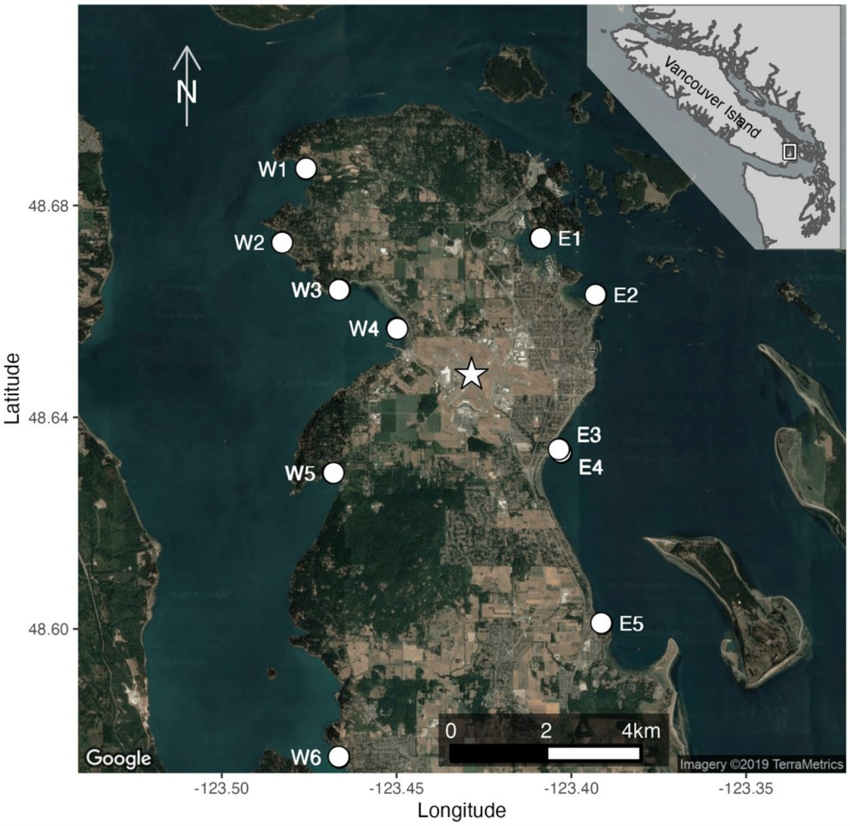

Figure 4.1 **Location of eelgrass study sites on the Saanich Peninsula (white box in inset map). The location of the Environment and Climate Change Canada weather station at Victoria International Airport is indicated by the star.**

Environmental data

To characterize the environmental conditions at each site we extracted water velocity, water temperature, and salinity data from the SalishSeaCast model (Soontiens et al., 2016; Soontiens & Allen, 2017) and wind data from the historical climate data from Environment and Climate Change Canada (Environment and Climate Change Canada, 2011) (Table 4.1). The SalishSeaCast model is a coupled biophysical model that allows high-resolution predictions of oceanographic, physical, and biological fields at hourly intervals and at a spatial resolution of ~500 m at 40 depths (between 0.5 m and 441.5 m) in the Salish Sea. Oceanographic processes, including 3-dimensional water flow, are modelled using the Nucleus for European Modelling of the Ocean (NEMO) architecture

(Soontiens et al., 2016; Soontiens & Allen, 2017) and biogeochemical fields such as temperature and salinity are predicted using the LiveOcean model (Fatland et al., 2016; MacCready et al., 2021; Olson et al., 2020). Cross-validation of the modelled temperature and salinity values shows that variation in temperature estimates increases as mean temperature increases and variation in salinity increases as mean salinity decreases; there is no bias in mean temperature and salinity estimates (MacCready et al., 2021). For each site, we extracted temperature and salinity from the SalishSeaCast model hourly from 1 January 2019 to 31 December 2019 and summarized these values into the maximum observed temperature, maximum daily temperature range, and the time at low salinity (proportion of time where salinity was below 25 PSU) (Table 4.1). We also extracted the hourly water velocities from the SalishSeaCast model for all days in August 2019 to calculate the maximum observed water velocity (Table 4.1). We used only one month because of computational limitations, but the water velocities obtained captured well the magnitude of current differences observed at the sites (JCD, personal observations).

To calculate the relative exposure index (Table 4.1) we used the package ‘windfetch’ (Seers, 2022) and the Global Self-consistent, Hierarchical, High-resolution Shoreline Database (Wessel & Smith, 1996) to estimate the fetch for each site, i.e., the distance over water that wind can travel unobstructed to reach a site (Figure C1). We combined the fetch data with historical windspeed data from the Environment and Climate Change Canada weather station at Victoria International Airport (Environment and Climate Change Canada, 2011), which is located on the Saanich Peninsula (Figure 4.1), accessed using the ‘weathercan’ R package (LaZerte & Albers, 2018).

Table 4.1 Descriptions of the environmental predictors used and their data sources.

Predictor	Description of summary value	Ecological relevance	Data sources
Temperature	Maximum annual temperature (˚C) from 2019-01-01 to 2019-12-31	Given that eelgrass is growing near its optimal temperature range at this location, high temperatures are more likely to impair eelgrass growth and performance in the long-term than low temperatures (e.g., Lee et al., 2007, Chapter 3).	SalishSeaCast, Dataset ID: ubcSSg3DTracerFields1hV19-05 (Temperature field)
	Maximum daily summer temperature range (˚C) from 2019-06-01 to 2019-08-31	Same as above. Temperature variability is a predictor of genetic structure in eelgrass (DuBois et al., 2022) and shoot density (Krumhansl et al., 2021)	SalishSeaCast, Dataset ID: ubcSSg3DTracerFields1hV19-05 (Temperature field)
Salinity	Proportion of the total hours where salinity was less than 25 PSU from 2019-01-01 to 2019-12-31	Salinity below 25 PSU is associated with lower prevalence and severity of eelgrass wasting disease (Jakobsson-Thor et al., 2018)	SalishSeaCast, Dataset ID: ubcSSg3DTracerFields1hV19-05 (Salinity field)
Water velocity	Maximum water speed (ms^{-1}) obtained by averaging the modelled u and v water velocity components from 0-5 m depth and then calculating the magnitude of the velocity: $\sqrt{\{\bar{u}^2 + \bar{v}^2\}}$ from 2019-08-01 to 2019-08-31	High water velocities can resuspend sediment and limit light availability to plants (e.g., Marin-Diaz et al., 2020; van der Heide et al., 2007). Longer water residence times may increase effects of nutrient loading (Bricker et al., 2008) or lead to higher extreme temperature exposures (e.g., Wong et al., 2013).	SalishSeaCast Dataset ID: ubcSSg3DuGridFields1hV19-05 (*u* component and velocity fields) SalishSeaCast Dataset ID: ubcSSg3DvGridFields1hV19-05 (*v* component & velocity fields)
Exposure	Relative exposure index (km^2h^{-1}) $REI = \sum_{i=1}^{36}\left(mean\ wind\ speed_{\{10i^{\circ}\}} \times frequency_{\{10i^{\circ}\}} \times fetch_{\{10i^{\circ}\}}\right)$ Over the period of 2019-01-01 to 2019-12-31	Strong winds and wave action can affect SAV distribution in deep waters and lakes (Koch, 2001). The creation of wind waves can suspend sediments and decrease light availability.	Historical weather station hourly wind speed and direction (Environment and Climate Change Canada, 2011)
Depth	Mean plot depth measured in the field and standardized to the mean lower low water depth using tide data taken from the “Tide Charts” app	Depth affects light availability and wave action (Koch, 2001).	Tide Charts (7th Gear, 2020)

Human impact values

To quantify human impacts at a scale relevant to the study design, we used the local-scale impact metrics described by Murphy et al. (2019) for coastal ecosystems in Canada. We obtained data for overwater structures, riparian land alteration, and water quality; at our sites there were no near-field or mid-field aquaculture activities and so these two metrics were excluded. We calculated the proportion of overwater structures (0 – 1) within 1 km of the centre of sites by digitizing overwater structures (docks and piers) as polygons using Google Earth imagery from 2016 (clearest image; Figure C2; *Google Earth Pro*, 2022). We then divided the water area within a 1-km radius of each site by the area of structures overwater, such that larger values represented more built-up seascapes. To estimate riparian land alteration (0 – 1), we used Google Earth imagery and site notes to classify land as ‘forest’ or ‘residential/commercial/industry’ 50 – 100 m adjacent to the shoreline within a 1-km radius of each site. We then calculated riparian land alteration as the proportion of unmodified (‘forest’) land over the total riparian area. As a proxy for water quality, we used data from the Canadian Shellfish Sanitation Program (Environment and Climate Change Canada, 2020), which monitors fecal coliform at coastal stations across the country. We used data averaged from 2009 – 2019 at the nearest station within 1 km of the sampling sites. Values were the mean ‘Most Probable Number’ (MPN; a statistically estimated cell count, Environment and Climate Change Canada, 2020) of fecal coliform cells per 100 mL. However, the number of sampling sites has decreased since 2005 such that there are recent (2009-2019) data for only six of our 11 sites. Therefore, we excluded these data from the site characterization and analysis but present a visualisation of the spatial distribution of the mean water quality for context (Figure C3).

Eelgrass response sampling

All eelgrass (*Zostera marina*) meadows were completely subtidal with the upper edge of meadows being at a minimum depth of 0 m mean lower low water (MLLW). Between 6 August and 9 August 2019, we counted shoot densities in four 75 cm x 75 cm quadrats at each of the 11 sites. Between 21 August and 21 September 2019, we took one eelgrass core that was 25 cm x 25 cm and up to 15 cm deep from 10 of the sites. The average depth of the eelgrass samples was ~2.2 m below LLW but ranged in depth from 1.0 m to 4.8 m below MLLW. From each core we counted the total number of shoots and noted how many individuals had putative wasting disease lesions.

Although we were unable to identify the causal agent of lesions, visual assessment and consultation with disease experts confirmed that the lesions we observed resembled lesions observed at other locations in the Salish Sea (Figure C4). The lesions did not appear near the base of the shoot nor were meristems rotted (indicative of sulphide toxicity; (Holmer & Bondgaard, 2001); they were also dark regions with distinct borders rather than non-pigmented and non-uniform, which indicate heat or desiccation stress (Boese et al., 2003). Since our study meadows were subtidal, the latter is unlikely.

Analysis

Site characterisation

We used a Principal Components Analysis (PCA) and Pearson correlation coefficients to characterize the variation in environmental conditions and human impacts across sites and to understand how these predictors covaried across our sites and varied between aspects of the peninsula (i.e., east vs west). The PCA allowed us to simplify the large (relative to our sample size) number of predictor variables into a linear combination (e.g., PC1) of these variables, such that we could include a summary metric of the suite of environmental and impact conditions at each site.

Identifying predictors of eelgrass responses

To determine which of the environmental or human impact metrics of interest were key predictors of the variation in our two response metrics (shoot density and disease prevalence, i.e., the proportion of shoots with lesions on blades) observed across our sites, we developed a set of 36 candidate models (Table C1). These candidate models included a null model that estimated the mean response only (i.e., intercept only), and tests of the individual predictors alone and in additive pairwise combinations. We also included models that used the first two principal components. To avoid overparameterization due to the low sample size, we limited candidate models to include a maximum of two predictors; interactions were not considered. We also excluded models that contained both maximum temperature and salinity because of the high correlation (Pearson's $r = 0.87$) between these two predictors. To identify the best predictive model from our set of candidate models, we used Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). We considered models that were within 2 AICc units of the top model to be equally supported (Burnham & Anderson, 2002).

To model shoot density at each site, we fit negative binomial generalised linear models (GLMs) to account for overdispersion in the variance of shoot densities. We visually inspected the residuals of all 36 candidate models (and compared these to Poisson GLMs, which showed that almost all models demonstrated overdispersion) to check model assumptions. To model disease prevalence at each site, we fit a logistic regression with the same 36 candidate model combinations.

Results

Site characterisation

The first principal component axis (PC1) of the PCA described 47.2% of the variability in the eight environmental predictors considered (Figure 4.2, Table 4.1). It describes a gradient of increasing open ocean influence, i.e., increasing water velocity, depth, and relative exposure, and decreasing maximum temperature, temperature variability, and low salinity. It is also associated with increasing riparian modification (Figures 4.1, 4.2). As expected, sites on the more sheltered west coast of the Saanich Peninsula were warmer, experienced more time at low salinities, generally had higher temperature variability within a day, and had lower wind exposure than sites on the east coast (Figures 4.2a, 4.3). Maximum annual temperature, salinity, and daily temperature variability were highly correlated with aspect (Figures 4.2b, 4.3, Figure C5) and so these environmental characteristics are likely to drive the differences between aspects.

The second principal component (PC2) explained 19.7% of the variation in conditions across sites. It represents mainly a gradient of increasing human impact, primarily increasing cover of overwater structures (Figure 4.2a). The ranges of the human impact predictors, i.e., proportion of overwater structures (values: 0 - 0.19) and proportion of modified riparian area (values 0.63 - 1), were limited. Almost all sites had highly or completely modified/urbanised riparian areas, except for site W5 (Figures 4.2a, 4.3 Figure C2). Similarly, most sites had a very low proportion of overwater structures except for site E1 and W6 (Figures 4.2a, 4.3 Figure C2).

Eelgrass meadow depths were similar across sites; however, deeper meadows were found on the east coast (Figure 4.3, Figure C6). In particular, E4 was exceptionally deep at 4.8 m MLLW, and it is the inclusion of depth that separates sites E3 and E4 in the PCA (Figure 4.2a).

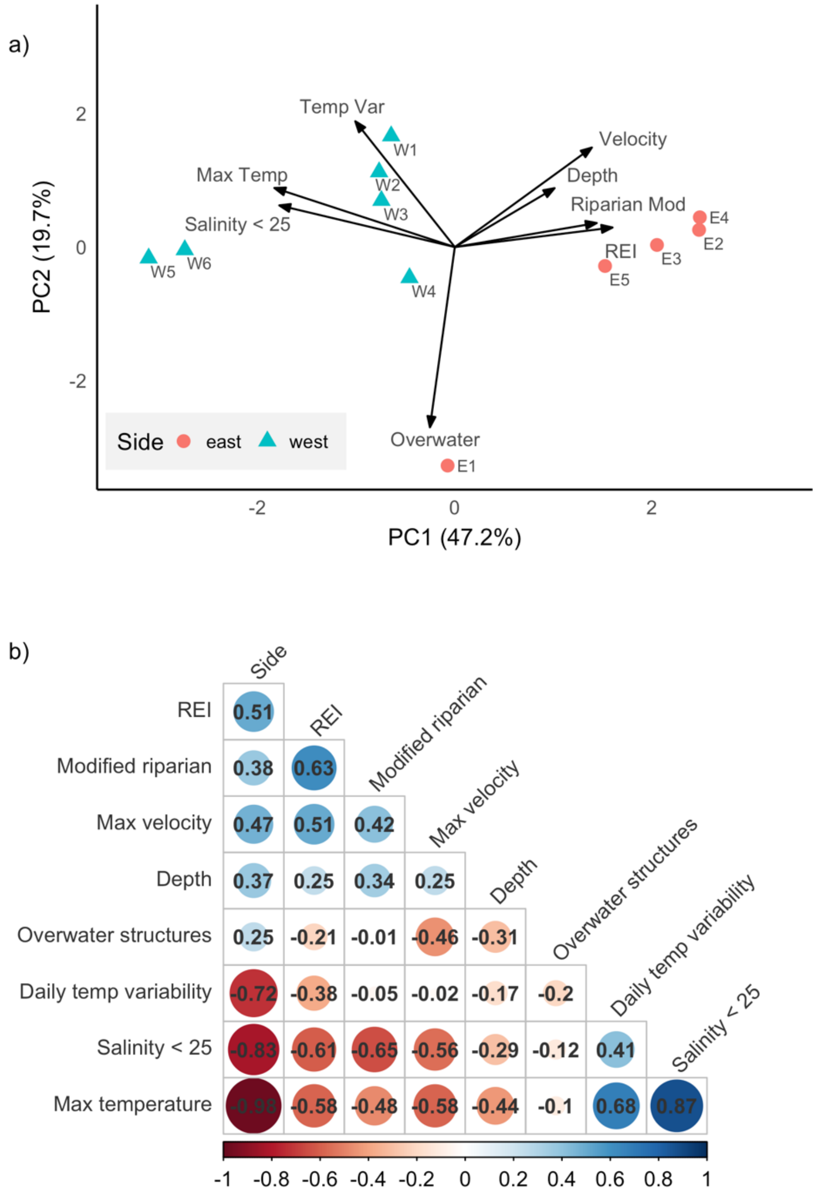

Figure 4.2 Characterisation of the environment and human impacts at 11 eelgrass meadow sites around the Saanich Peninsula. (a) Principal components of the environmental and human impacts at the 11 sites. Point shape and colour indicate on which coast of the Saanich Peninsula the sites are found. Loadings of the environmental variables are shown at the end of the arrows (see Table 4.1 for abbreviations). (b) Correlation of the environment characteristics and human impacts across the 11 sites; red indicates negative correlation, blue indicates positive correlation, and the values in the cells are the Pearson correlation coefficient. N = 11 in all cases.

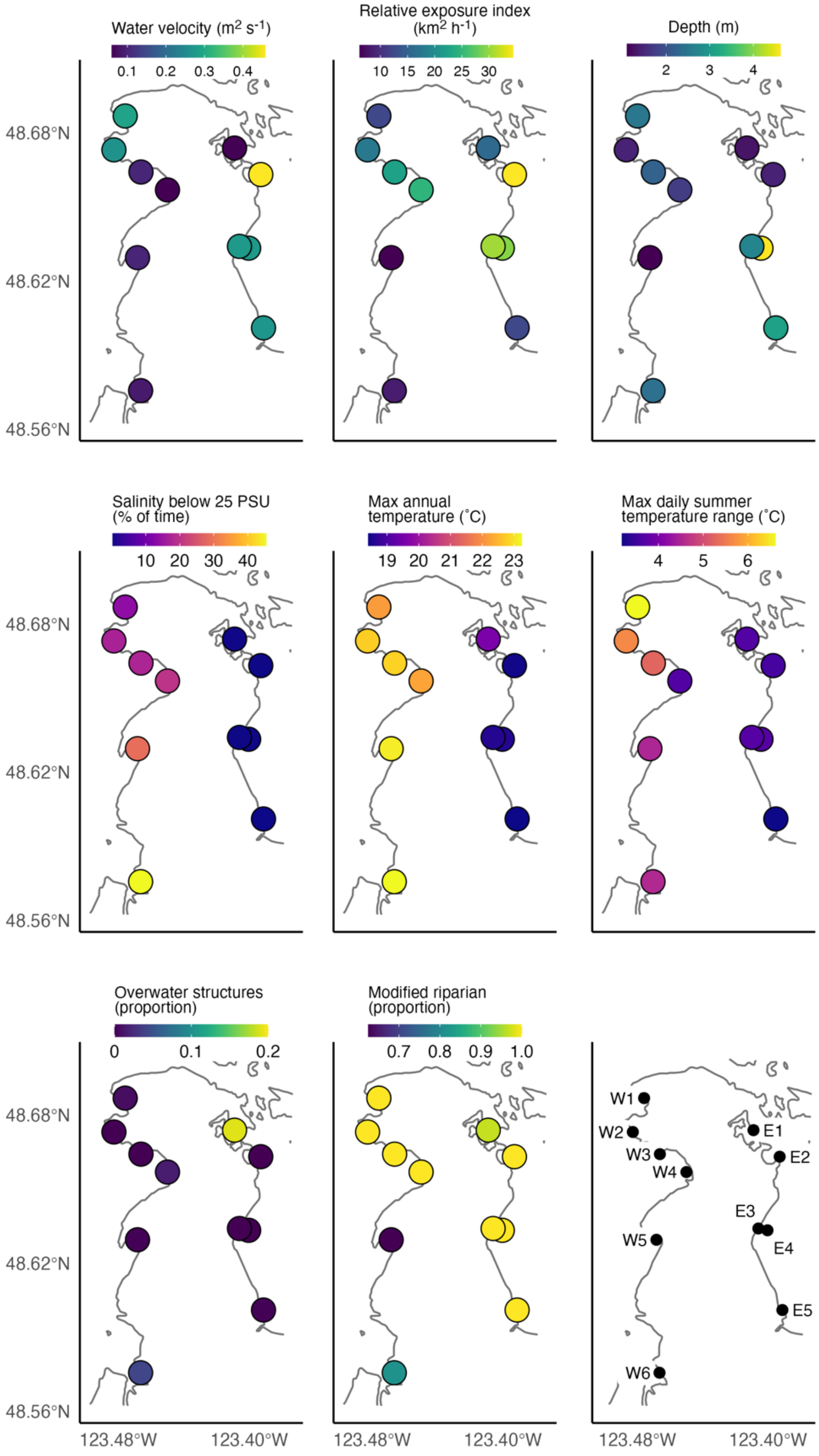

Figure 4.3 **Spatial variation in environmental characteristics and human impact associated variables across 11 eelgrass meadows around the Saanich Peninsula. Sites E3 and E4 have been jittered to improve visualisation of predictor values.**

Best predictors of eelgrass response metrics

Shoot density

Shoot density was consistently higher on the west than on the east aspect of the peninsula (Figure C7). Three candidate models predicting shoot density were equally well supported (Table 4.2) and all three of these models contained maximum annual temperature. The second-ranked model, which contained only maximum annual temperature, was equally likely to the top model (maximum temperature + overwater structures) (evidence ratio = 1; Table 4.2). Meanwhile, these top two models were 1.5 times more likely to be the best models than the third-ranked model (maximum temperature + maximum velocity) (Table 4.2).

In all models, shoot density increased with increasing maximum annual temperature, and temperature had a variable importance (VI) of 0.98, suggesting that it was the most important predictor tested compared to overwater structures (VI = 0.32) and maximum velocity (VI = 0.22). An increase in maximum temperature from 19˚C to 23˚C predicted a ~4.3-fold increase in shoot density, from 42 shoots to 180 shoots per m2 (Figure 4.4). For a given temperature, shoot density is expected to be lower as the proportion of overwater structures increases (Figure C8b) and is expected to increase with higher water velocities (Figure C8c). The effect of overwater structures as a predictor appears to be driven largely by site E1 (Figure C8b), which had the highest cover of overwater structures (value = 0.2, Figure 4.3).

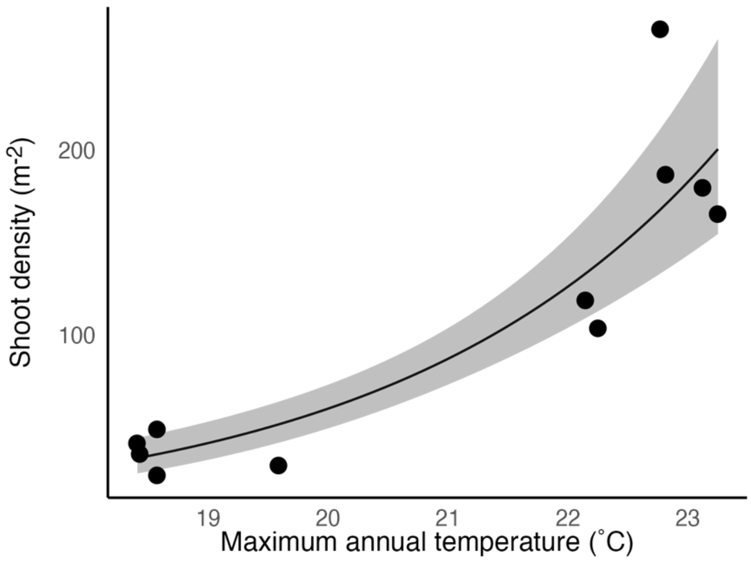

Figure 4.4 **Relationship between shoot density (m^{-2}) and maximum annual temperature (˚C), predicted by simplest top model in the AICc analysis (Table 4.2). Points are shoot densities observed at each of 11 sites (see Figure C7). The fitted model lines and 95% confidence intervals are shown.**

Table 4.2 **Shoot density model selection results using Akaike's Information Criterion for small samples sizes (AICc). Shown are the models that represent the minimal subset of models for which the cumulative weight (Cumul w_i) ≤ 0.95 (i.e., approximate 95% confidence that the best model considered is contained herein (Burnham & Anderson, 2002; Symonds & Moussalli, 2011), with the best-supported models in bold. All 36 candidate models are presented in Table C1. K is the number of parameters in each model; ∆AICc is the difference in AICc and the model with the minimum AICc; w_i is the interpreted as the probability that model *i* is the best model of the candidate set; LL is the log-likelihood of model *i*; and Dev is the percent deviance explained by the model.**

i	Shoot density model	K	AICc	ΔAICc	AICc wi	LL	Cumul wi	Dev (%)
1	**~ Overwater structures + Max temp**	**4**	**128.14**	**0.00**	**0.32**	**-56.74**	**0.32**	**91.44**
2	**~ Max temp**	**3**	**128.18**	**0.04**	**0.32**	**-59.38**	**0.64**	**86.08**
3	**~ Max velocity + Max temp**	**4**	**128.89**	**0.75**	**0.22**	**-57.11**	**0.86**	**90.83**
4	~ Daily temp var + Max temp	4	132.30	4.15	0.04	-58.81	0.90	87.45
5	~ Riparian mod + Max temp	4	132.89	4.75	0.03	-59.11	0.93	86.74

Lesion prevalence

Lesion prevalence varied from 0 to 80% (Figure C7). Four candidate models predicting lesion prevalence were equally well supported and all four of these models contained maximum water velocity (Table 4.3). The top two models (maximum velocity + time at low salinity; maximum velocity + maximum temperature) were equally likely (evidence ratio = 1) and were twice as likely to be the best models compared to the third-ranked model (maximum velocity) and fourth-ranked model (maximum velocity + depth) (Table 4.3). In all models, lesion prevalence decreased as maximum water velocity increased (Figure 4.5, Figure C9) and maximum velocity had a variable importance of 0.98, suggesting that it was the most important predictor tested compared to time at low salinity (VI = 0.24), maximum temperature (VI = 0.24), and depth (VI = 0.11). The combined variable importance of models containing time at low salinity and maximum temperature was only 0.48, reflecting the strong correlation between these two variables. An increase of maximum water velocity from 0.06 ms^{-1} to 0.46 ms^{-1} predicted a 58% reduction in lesion prevalence (Figure 4.5).

For a given maximum water velocity, lesion prevalence was predicted to decrease with more time spent at low salinity, increase at lower maximum temperatures, and increase with depth (Figure C9). These latter two results are contrary to expectations. However, the effect size of time spent at low salinity, maximum annual temperature, and depth were all small compared to the estimated effect of maximum velocity on lesion prevalence (Figure C9). For a maximum water velocity of 0.25 ms^{-1}, each of these three predictors was associated with an ~25% change in lesion prevalence.

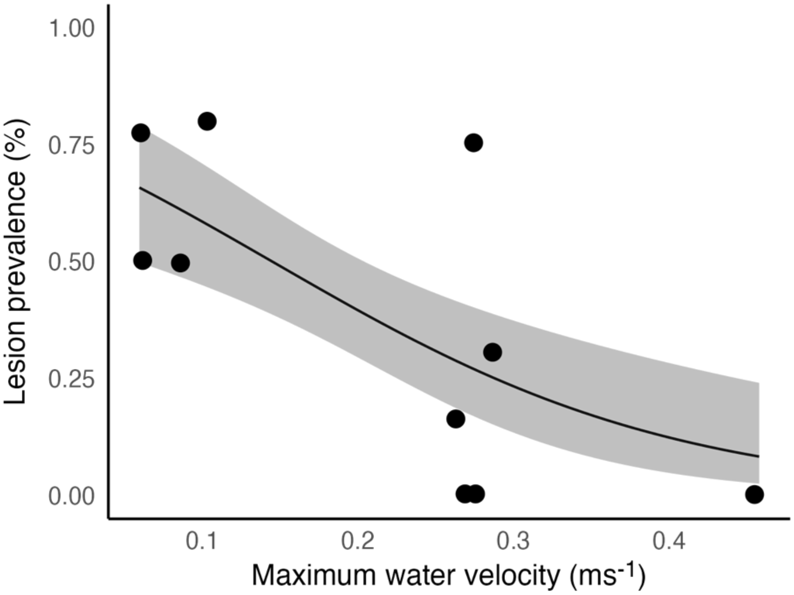

Figure 4.5 **Relationship between lesion prevalence (%) and maximum water velocity (ms^{-1}), predicted by the simplest top model in the AICc analysis (Table 4.3). Points are the lesion prevalence observed across 10 sites (see Figure C7). The fitted logistic regression model lines and 95% confidence intervals are shown.**

Table 4.3 Disease prevalence model selection results using Akaike's Information Criterion for small samples sizes (AICc). Shown are the models that represent the minimal subset of models for which the cumulative weight ≤ 0.95 (i.e., approximate 95% confidence that the best model considered is contained herein (Burnham & Anderson, 2002; Symonds & Moussalli, 2011), with the best-supported models in bold. All 36 candidate models are presented in Table C1. K is the number of parameters in each model; △AICc is the difference in AICc and the model with the minimum AICc; wi is the interpreted as the probability that model i is the best model of the candidate set; LL is the log-likelihood of model i; and Dev is the percent deviance explained by the model.

i	Disease prevalence model	K	AICc	ΔAICc	AICc wi	LL	Cumul wi	Dev (%)
1	**~ Max velocity + (Salinity < 25)**	**3**	**123.13**	**0.00**	**0.24**	**-58.44**	**0.24**	**14.10**
2	**~ Max velocity + Max temp**	**3**	**123.13**	**0.00**	**0.24**	**-58.44**	**0.48**	**14.09**
3	**~ Max velocity**	**2**	**124.45**	**1.32**	**0.12**	**-60.16**	**0.61**	**11.56**
4	**~ Depth + Max velocity**	**3**	**124.70**	**1.57**	**0.11**	**-59.23**	**0.72**	**12.94**
5	~ REI + Max velocity	3	125.28	2.15	0.08	-59.51	0.80	12.52
6	~ Riparian mod + Max velocity	3	125.54	2.41	0.07	-59.65	0.87	12.32
7	~ Max velocity + Daily temp var	3	126.06	2.92	0.06	-59.90	0.93	11.95

Discussion

Understanding the scale at which environmental and human activities affect eelgrass meadows can enable us to make predictions relevant to the scale of management. The contrasting oceanographic conditions around the Saanich Peninsula presented an opportunity to examine variation in eelgrass meadow condition at a fine geographic scale that can be used to inform conservation and restoration of eelgrass meadows in this region of the Salish Sea. Over a small distance, within tens of kilometres, we found substantial variation in environmental conditions and also high variation in shoot density and lesion prevalence, our two indicators of health. Of the environmental and human impact predictors tested, maximum annual water temperature was the best predictor of shoot density while maximum water velocity was the best predictor of lesion prevalence. The two human pressures considered, overwater structures and riparian alteration, had little effect on eelgrass health. These results, particularly the high variation in response metrics despite the small inter-site distances, suggest that it is important to incorporate studies that consider fine-scale variation to link seagrass condition to predictors such as environmental conditions and human impacts.

Predictors of eelgrass health

Shoot density

We found that, of the predictors tested, maximum annual water temperature was the best-supported predictor of eelgrass shoot density. Warmer temperature regimes (e.g., > 23˚C), which also had high short-term temperature variability, were also associated with higher density shoots in intertidal and subtidal meadows sampled across ~200 km in Nova Scotia, Canada (Krumhansl et al., 2021, Wong et al., *in prep*). Similar to our study, the Nova Scotian meadows did include some fine-scale comparisons of within-site sampling locations (e.g., sampling at different depths or in different substrates). In contrast, across latitudes throughout the Northern Hemisphere, there is no relationship between shoot density and mean summer temperature (Clausen et al., 2014). The conflicting results could arise for a number of reasons. Mean summer temperatures and maximum annual water temperatures might be poorly correlated, although this is not the case, at least in our dataset (Figure C5). Additionally, mean summer ocean temperatures estimated from satellite-derived, interpolated air temperatures might not accurately reflect meadow-scale in-water temperatures, as seen in Figure C5. In addition, the inclusion of both intertidal and subtidal meadows could mask effects that are specific to the latter.

Intertidal eelgrass meadows that experience high temperatures, assumed to lead to desiccation stress, can exhibit ‘facilitation-maximizing’ traits, which include smaller shoots and higher shoot densities (Boyé et al., 2022). It is unclear whether such a set of traits is also associated with high temperatures in fully subtidal meadows. It is possible that temperatures that approach thermal tolerances of subtidal eelgrass trigger an adaptive response for high shoot production. Alternatively, bays with warmer temperatures are often associated with oceanographic conditions that allow for better light penetration, particularly at shallow sites with limited water flow (Krumhansl et al., 2021) — conditions similar to the sites observed on the west coast of the Saanich Peninsula. Light, rather than temperature, may therefore be the factor controlling shoot density at these sites.

Overwater structures and maximum water velocity were two predictors that were also included in the top models tested. The effect of overwater structures was driven by a single site (E1), which is a meadow at the mouth of a bay that contains eight large marinas (Figure C2). Although there were no overwater structures within 400 m of the sampling site to create a direct shading effect, it is possible that the high proportion of overwater structures is associated with additional activities like dredging and boating traffic, which could be affecting shoot density. These are activities that could reduce light by altering sediment accumulation or causing sediment resuspension (Erftemeijer & Robin Lewis III, 2006).

For a given water temperature, the third-ranked model showed that high shoot densities were associated with higher water velocity. Shoot density was negatively correlated with water velocity across eelgrass meadows in Nova Scotia (Krumhansl et al., 2021); however, in our analysis water velocity was only an important predictor in combination with temperature. High water velocities can promote oxic conditions with improved gas diffusion at the leaf-water interface (Noisette et al., 2020) and can increase flushing rates to decrease eutrophic conditions (Lemley et al., 2015). Therefore, for a given temperature, higher water velocities may alleviate stressful conditions and increase shoot densities.

Light is in important covariate that we were unable to include in our analysis. Light can be correlated with other variables we measured like depth, velocity, overwater structures, and temperature, as alluded to above. Shoot density typically decreases with depth, likely due to low light levels (Lee, Park, & Kim, 2007; McMahon et al., 2013; R. M. Thom et al., 2008), because eelgrass compensates by producing longer, wider blades and reducing shoot density to minimize shading. However, in our analysis, depth was not an important predictor of shoot density: most sites on the east coast were at similar depths as those on the west coast yet had much lower shoot densities. Interestingly, photosynthetically active radiation (PAR) was not a top predictor of various measures of eelgrass productivity in a large-scale analysis of Nova Scotia meadows (Krumhansl et al., 2021).

Disease

Water temperature is an important predictor of wasting disease prevalence and severity that has been particularly well documented along the Pacific coast of North America (Aoki et al., 2022; Groner et al., 2021; Graham et al., 2023). However, in our analysis, water velocity was identified instead as the best predictor of lesion prevalence across our sites. High water velocities can affect the microclimate around eelgrass leaves and are associated with more favourable conditions by improving gas diffusion and reducing leaf tissue warming (Noisette et al., 2020). The high correlations between predictors and low sample size mean that it is difficult to tease out the causal links. Nevertheless, our results suggest that further consideration of water velocity in field studies of disease prevalence is warranted, particularly given the large effect size of water velocity relative to maximum annual temperature, time at low salinity, and depth.

Disease prevalence is lower in subtidal than intertidal meadows, possibly driven by lower temperatures (Graham et al., 2023). In intertidal meadows, positive temperature anomalies are associated with higher disease prevalence and severity (Aoki et al., 2022; Groner et al., 2021) and higher-resolution metrics of disease severity, such as total lesion area and proportion lesion area, tend to show a stronger signal of predictors like temperature compared to site-level disease prevalence (Aoki et al., 2022; Graham et al., 2023). Consequently, subtidal meadows, with less short-term variability in environmental conditions and cooler temperatures, have the potential to be refuges from disease (Graham et al., 2023). We observed the opposite effect of maximum annual temperature in our analysis – lower prevalence of lesions at higher maximum temperatures. Given the importance of positive temperature anomalies for disease prevalence, we might have expected maximum daily temperature variability to predict lesion prevalence, but this was not the case. Our counter-intuitive results might be due to limited sample size, or because cumulative temperature anomalies cause a specific physiological stress that maximum temperature or maximum temperature variability do not. Other factors that were not considered here but are possibly important include the eelgrass microbiome and controlling factors, light limitation, hydrogen sulphide stress, and genetic variability (DuBois et al., 2022; Jakobsson-Thor et al., 2020; Sullivan et al., 2013).

Conflicting scales of effects of environmental conditions and human impacts

At global and regional scales, human pressures, and hence their cumulative impacts, are associated with (or assumed to be linked to) declines in ecosystem condition (Turschwell et al., 2021; Williams et al., 2020). In contrast, recent analyses have shown that at small spatial scales, cumulative impact scores do not correlate with empirical measurements of seagrass ecosystem condition (e.g., Stockbridge et al., 2021). We also found that the two human impacts that we examined (i.e., overwater structures and riparian area modification) appeared to explain little variation in eelgrass meadow health compared to environmental conditions like temperature and water velocity. This is perhaps not surprising when we consider the magnitude of variation in environmental characteristics, human impacts, and eelgrass response observed at a fine scale. In the meadows we examined, the two metrics of meadow health varied substantially, with shoot densities varying 10-fold and lesion prevalence ranging from 0-75%. Meanwhile, the range of environmental conditions across these meadows varied much more than did the human impact metrics. Our results therefore highlight a conflict of scales in the study of cumulative impacts. Fine-scale variation in environmental and response metrics suggests that variation from meadow to meadow may be overlooked in analyses at larger scales. Conversely, variation in human impacts and cumulative effects might be variable enough only at scales much larger than we should collect specific stressor data and ecosystem condition information. The result is a lack of causal link between large-scale cumulative impacts and ecosystem responses, which limits the applicability of large-scale cumulative impact scores as predictors of small-scale ecosystem condition (Stockbridge et al., 2021).

Our results do not mean that human impacts have no effect on eelgrass meadows around the Saanich Peninsula. Water quality and light availability are two important drivers of eelgrass productivity and health that we could not include due to data limitations. Activities that pose the greatest threat to seagrass meadows include coastal development, dredging, and agriculture (Grech et al., 2012), all of which decrease water quality and clarity. Thus, human activity as a proxy for expected negative effects can be an important heuristic, particularly when data on environmental conditions are limited. For example, eelgrass meadows elsewhere in the Salish Sea have contracted in areal extent since 1930, a phenomenon that is associated with increasing coastal development and boating activity in and around these meadows (Nahirnick et al., 2019). Understanding of the drivers of fine-scale variation in eelgrass meadows will, however, require improvements in nearshore coastal environmental data collection to provide baselines against which change can be measured.

Chapter 5. General Discussion

Eighteen years ago, I was blasting music from a little silver radio as I planted eelgrass in aquaria in my parents' basement. Bright growlights glinted off the water and there I was, squealing whenever I peeled eelgrass blades apart to discover thin red worms that made a little nest between the blades. The project never panned out, but the original plan had been to cover one aquarium with green cellophane to mimic an algal bloom and compare eelgrass growth with an aquarium that had full light. The motivation for the project came from Nikki Wright, who took me on a tour of *SṈIDȻEŁ (*pronounced *sngeet-kwith*; Tod Inlet in English) and explained some of the local impacts (e.g., boats pumping and dumping in the low flow embayment, nutrient run-off from a nearby display garden). SṈIDȻEŁ was—*is*—a special place, and Nikki is part of a community working to restore the inlet and the eelgrass meadow that was once found there.

I share this story because this thesis was *a lot* of synthesis; data points—*meadows*—from around the world all plunked onto a single plot. Synthesis is powerful. It allows us to make decisions based on the data at hand and to make generalisations that help us predict how changing conditions could affect ecosystem responses into the future (Chapter 3). There is, however, a balancing act between global averages (Chapter 2) and fine-scale variation (Chapter 4) that should be considered, particularly when global averages belie high variability. However, using empirical models to understand the effects of multiple stressors will improve our ability to reconcile these differences across scales and to be explicit about the conditions/context that can affect predicted outcomes. Identifying these general trends can allow us to take management actions when information is lacking, but also helps us identify knowledge gaps to prioritise future research and quantify uncertainty.

A balancing act

Global summaries can gloss over a lot of details, but they are an important starting point. They help us identify large-scale trends, likely driven by large-scale changing factors like increasing sea surface temperatures; inform high-level (e.g., international) policy and mandates, which support conservation and restoration actions even at the local scale; and help us to identify knowledge gaps. In writing Chapter 2, I wrestled with how to present a global status update. Trends in seagrass meadow extent were highly variable across bioregions and were non-linear. How do you present the information, knowing that a single number can be taken out of context, especially when trends are variable over across regions and non-linear? Little to no change between two time points can miss changes while an average of little to no change can obscure high underlying variability (e.g., Dornelas et al., 2014).

A key take-home value from Chapter 2 was that almost 20% of the world's observed seagrass meadow area has been lost: a useful number for grabbing the attention of global policy makers and helping keep seagrasses on the map in terms of being an important ecosystem in need of protection. Additionally, using a bioregional breakdown helped to discuss more regional context and to focus on the context occurring in the background that could be driving trends. In a follow-up analysis based on the data I compiled, we showed that declining trajectories of meadow area are associated with bottom fishing and poor water quality. Importantly, using an empirical modelling approach to reconstruct seagrass meadow trends allowed us to make generalisations and determine where meadows might be at risk of decline across the globe, including places lacking long-term data (Turschwell et al., 2021).

In the end, however, even using the bioregional models/summaries felt like the importance of local context was downplayed. Figure 2.3 in Chapter 2 (status of all meadows over time) is complex, possibly overly complex. But for me, it was important that the reader see an overview of the trends at every meadow. I wanted it to serve as a reminder that global trend be damned, what might be happening in your backyard could be completely different and, at the end of the day, that is what you will care about as a manager or community member.

Every meadow is special, or is it?

Although local context matters, because this is the scale at which management is often performed (e.g., a single meadow or network of meadows), there are two reasons why we should be careful to avoid thinking any given meadow is 'too' special. First, global pressures act on local sites but are not under the control of local managers. Furthermore, it is important to identify the effects of these global-scale pressures as they may overwhelm the effects of or interact with local stressors. Second, if each site is 'too' special, we can fall into the trap of thinking that there is no common ground to make generalisations that will apply across sites. Waiting for more data is not a prudent strategy for habitats at high risk of loss/destruction. Chapter 3 highlights the value of leveraging the wealth of data that has been gathered at meadows throughout the range of eelgrass. Empirically based, predictive modelling approaches can help managers make decisions, even in data-limited situations.

One of the most exciting things about Chapter 3 is the potential represented by the response surface; it focuses discussion and can help prioritise research that answers specific management questions. We can take this figure beyond a static image, and imagine an interactive tool that managers can use, where they either add their local meadow conditions, or slide a dial changing one of the stressors and watching how critical values change. Interactions are likely to be highly site-specific, being determined by the combination of specific pressures, their relative magnitudes, timing, dominance patterns, and are likely to vary even within a habitat (e.g., the deep edge of a meadow compared to the shallow edge of a meadow). Until I used a model to visualize the response surface (Figure 3.1), I could recount what individual studies found, but it was difficult to talk to local managers and colleagues about how I thought light and temperature changes might would specifically affect other meadows.

Factors like local adaptation will mean that different meadows may have different critical threshold values (e.g., higher maximum temperature limits) but the general trend of shifting thresholds is likely robust. This means that it is a useful tool for managers when data are limited. For example, managers could avoid activities that limit light (e.g., dredging), in a poorly flushed embayment that experiences high temperatures. Although management decisions should not be delayed until we have perfect information, it is important to prioritise future data collection to inform adaptive management strategies. It can be challenging to identify appropriate management actions in an ecosystem that demonstrates highly variable responses to environmental conditions (e.g., Chapter 4). Initially, the high variability in meadow characteristics at a fine-scale, as seen in Chapter 4, can seem insurmountable. When I was diving in those meadows, I couldn’t get over how a meadow just one bay over could seem so different. The response surface in Chapter 3 provides us with a framework/anchor to add data to, such as the data collected in Chapter 4.

Advancing multiple stressor research

Given the ubiquity of non-linear ecosystem responses (Hunsicker et al., 2016) and prevalence of pressure interactions (Côté et al., 2016; Crain et al., 2008), shifting thresholds are likely to occur and have implications for management targets across many populations and ecosystems. Meanwhile, there is a growing awareness of the importance of considering harvest thresholds as climate change increases environmental stochasticity and warms habitats (Cameron et al., 2016; Gamelon et al., 2019; Shelton & Mangel, 2011; Souther & McGraw, 2014). Therefore, it will be important to address questions like: How do threshold shifts vary based on the nature of the pressures? Can we predict where and when shifts will be more extreme? How do we link expectations across scales of biological organization?

When a stressor isn't stressful

Attempts to identify patterns in the multiple stressor literature have not yielded any clear pattern in when and why we observe different interaction types between stressors (Côté et al., 2016; Crain et al., 2008; Przeslawski et al., 2015; Stockbridge et al., 2020). However, the approach used so far, has been a vote-counting style of interaction type which limits the inferences that can be made from comparing these studies. For example, many studies (physiological up to community levels) compare the difference in effect of a driver or stressor between ambient conditions that are currently observed in the field, with either 'high' or 'low' treatments (e.g., Breitburg et al., 1999; Lange & Marshall, 2017; Strain et al., 2014). Similarly, researchers may choose to use stressor levels that are predicted to occur with increasing human impacts. For example, researchers may design an experiment using a 2-3 ˚C warming scenario with 0.5 unit reduction in pH as these values are projected by the Intergovernmental Panel on Climate Change (Kroeker et al., 2013; Pachauri et al., 2015). This is a useful strategy to limit the range of stressors that is tractable for an experiment. But when we compare interaction types across studies in a vote-counting style are we lose important context about the levels of other 'stressors'.

As seen in Chapter 3, 'stressful' conditions (i.e., conditions under which fitness of an organism declines) are dependent on current conditions of other 'stressors'. I initially wrote Chapter 3 with the word 'pressure' in place of 'stressor' because I was hesitant that the word stressor implied something that caused stress. Ultimately, I think that research that hopes to management, ‘pressure’ or ‘driver’ is more apt (i.e., following a Driver-Pressure-State-Impact-Response, (DPSIR) or Driver-Activities-Pressure-State-Impact-Response- DAPSI(W)R(M) framework; Elliott et al., 2017), but I kept ‘stressor’ to be consistent with the current literature. Moving forward, we should shift the focus of multiple stressor syntheses from categorising stressor interaction types and instead aspire to create driver-response curves. This will improve our predictive capacity and will be important for managing across a landscape that is likely to experience a gradient of drivers/stressors.

The trouble with attribution

Attributing drivers of change is challenging but is an important step to guiding management actions to avoid undesirable ecological states/impacts. Without a doubt, coastal development and poor water clarity are important factors that cause declines in seagrasses around the world (Chapter 2). Yet, only 10% of studies rigorously attribute pressures to observed changes in seagrass meadow area, whereas most attributions were descriptive (Chapter 2). Importantly, there is a suite of additional pressures such as storms, damage from boating propellors, grubbing, trawling, changing climate, and aquaculture that affect seagrasses. These often co-occur meaning we don’t always know how much is from a single pressure rather than the combination of many. Furthermore, blanket barring of ‘coastal development’ is not a realistic management strategy in most cases. Instead, by improving attributions of pressures to undesirable ecological states/impacts, we are more likely to be able to define and advocate for specific actions (e.g., ensuring that riparian areas are maintained, using sediment traps to reduce run-off from development).

This does not preclude action before activities or pressures have been attributed to changes in ecosystem responses. For example, we know that more specifically, activities and pressures associated with coastal development, such as dredging and sedimentation, are threats to seagrass (Chapter 2). If a meadow is in a low flushed embayment and already experiences high summer temperatures, proactive management actions, based on current knowledge, would suggest reducing activities like dredging and boat mooring, and restoring riparian areas to maintain or improve water clarity (Chapter 3). However, for a given site, observations may deviate from modelled predictions (e.g., Chapter 3) or follow-up monitoring may identify other factors affecting meadows more than any of the human activities considered (e.g., Chapter 4). Such results would then allow management actions to be revised.

Concluding thoughts

The pace at which ecosystems around the world are threatened and changing is overwhelming. Management of even local-scale threats is challenging, let alone with global threats like climate change. But I am hopeful. I spent a lot of time asking questions and listening to anyone who was willing to share. There is a lot of passion and will towards protecting our coastal ecosystems, especially in the Salish Sea. There is also a desire to share our knowledge and stories. To me, synthesis is a celebration of local-scale research—an anthology of what is happening in meadows around the world (in the sea or on land!). I hope that in this thesis I have shown that despite the complexity of ecosystem management, there are generalisable patterns in how multiple pressures/stressors affect ecosystem responses that can guide interventions. I look forward to seeing the development of more tools that will help us translate small-scale experimental studies on multiple pressures up to the natural response of species and communities at the scale of landscapes.

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Appendix A.

Supporting Information for Chapter 2

Supplementary Tables and Figures

Table A1. **Frequency of time-series with short, moderate, and long time-series. The proportion of total time-series and studies (%) is show next to the count in parentheses.**

Duration (years)	Number of time-series (proportion %)	Number of studies (proportion %)
≤ 10	157 (29)	60 (30)
10 - 40	271 (50)	89 (44)
> 40	119 (22)	51 (26)

Table A2. **Distribution of a priori expectations of studies, as indicated by authors, across bioregions. Categories of 'none', 'decrease', 'increase', and 'other' were made from author statements in the introduction of studies. The category 'other' captured U-shaped trajectories of declines then recovery.**

Bioregion	A priori category			
	None	Decrease	Increase	Other
Temperate North Pacific	10	4	1	1
Temperate North Atlantic West	9	7	2	0
Temperate North Atlantic East	20	9	3	1
Tropical Atlantic	15	9	5	2
Mediterranean	15	4	1	0
Tropical Indo-Pacific	17	9	1	0
Temperate Southern Oceans	24	9	0	1
All regions	110	51	13	5

Table A3. **Examples of the types of activities and environmental states assigned to the driver categories used in Figure 2.5.**

Driver	Examples
Aquaculture	Oyster farming, fish farming
Boating	Mooring, propellor scarring
Climate	Precipitation, temperature, drought, warming, above average wet seasons, El Niño, ice cover
Coastal development	Land appropriation, shoreline armouring, coastline construction, land use change (e.g., logging, agriculture), dredging, port construction, urbanisation
Disease	Wasting disease (e.g., *Labyrinthula zosterae*)
Fishing	Bait grubbing, bivalve trawling, recreational bivalve harvesting
Hydrology	Coastal erosion, flood, sea level, sediment deposition patterns (e.g., sand banks), water velocity
Invasive species	*Syringodium isoetifolium* (seagrass)
Management/restoration	Removal of dikes/coastal armouring, storm water run off regulations, relocation of wastewater outfalls
Pollution	Herbicides, oil spills, land based pollution (non-nutrient)
Storms	Hurricanes/typhoons, flooding, storm swell, wind velocity
Water quality	Algae blooms, chlorophyll, depth, nutrients (nitrogen, phosphorous), oxygen, ocean acidification, salinity, sedimentation, turbidity, water quality metrics

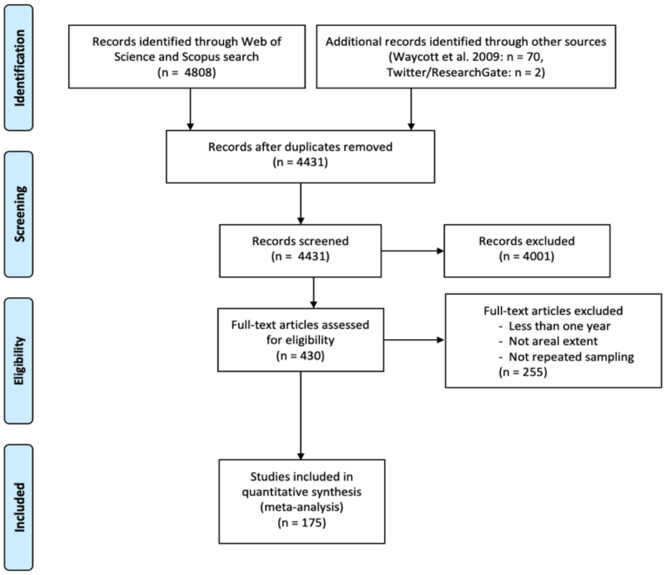


Figure A1. **PRISMA flow diagram documenting the study selection criteria and process.**

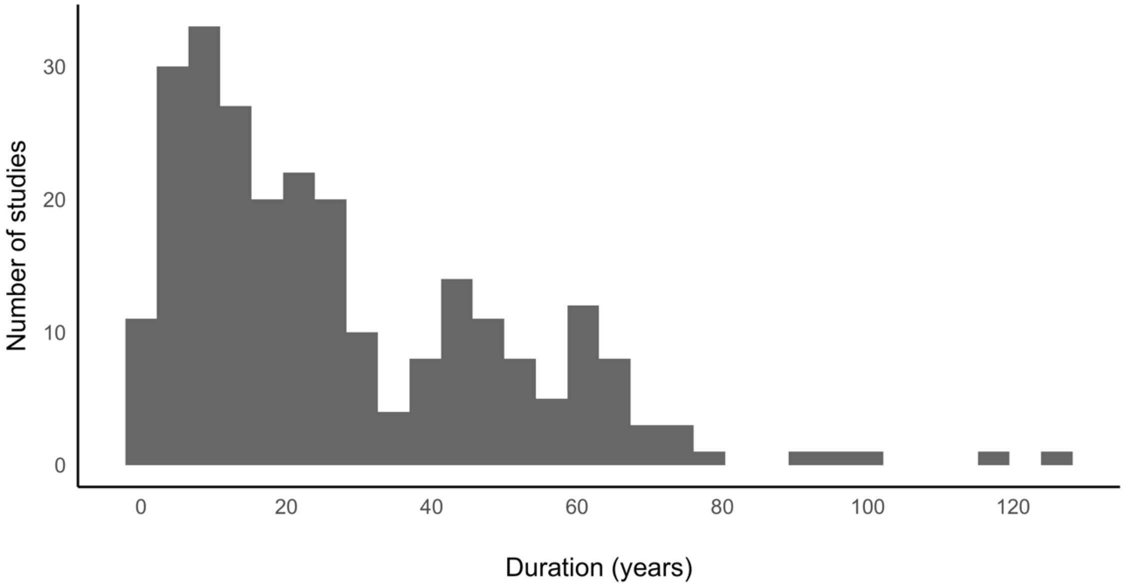


Figure A2. Distribution of study durations. Study durations ranged from one to 128 years.

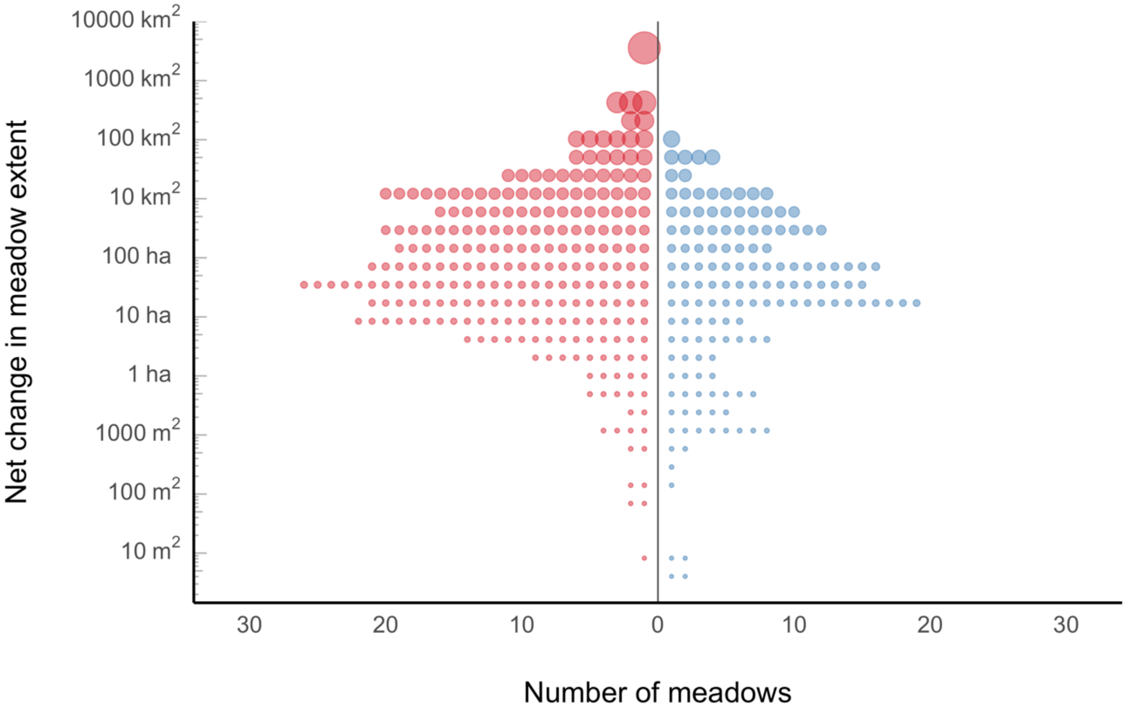


Figure A3. **Global size distribution of net losses (red, left) and net gains (blue, right). Net change in meadow extent (y-axis) is $\log_{10}$-scaled and number of meadows is on the x-axis. Each point represents the net change in a meadow over its entire time series ($\text{area}_{\text{final}} - \text{area}_{\text{initial}}$). To demonstrate the difference in magnitude of net change between small and large extents, point size corresponds to net change in area in a near-linear fashion.**

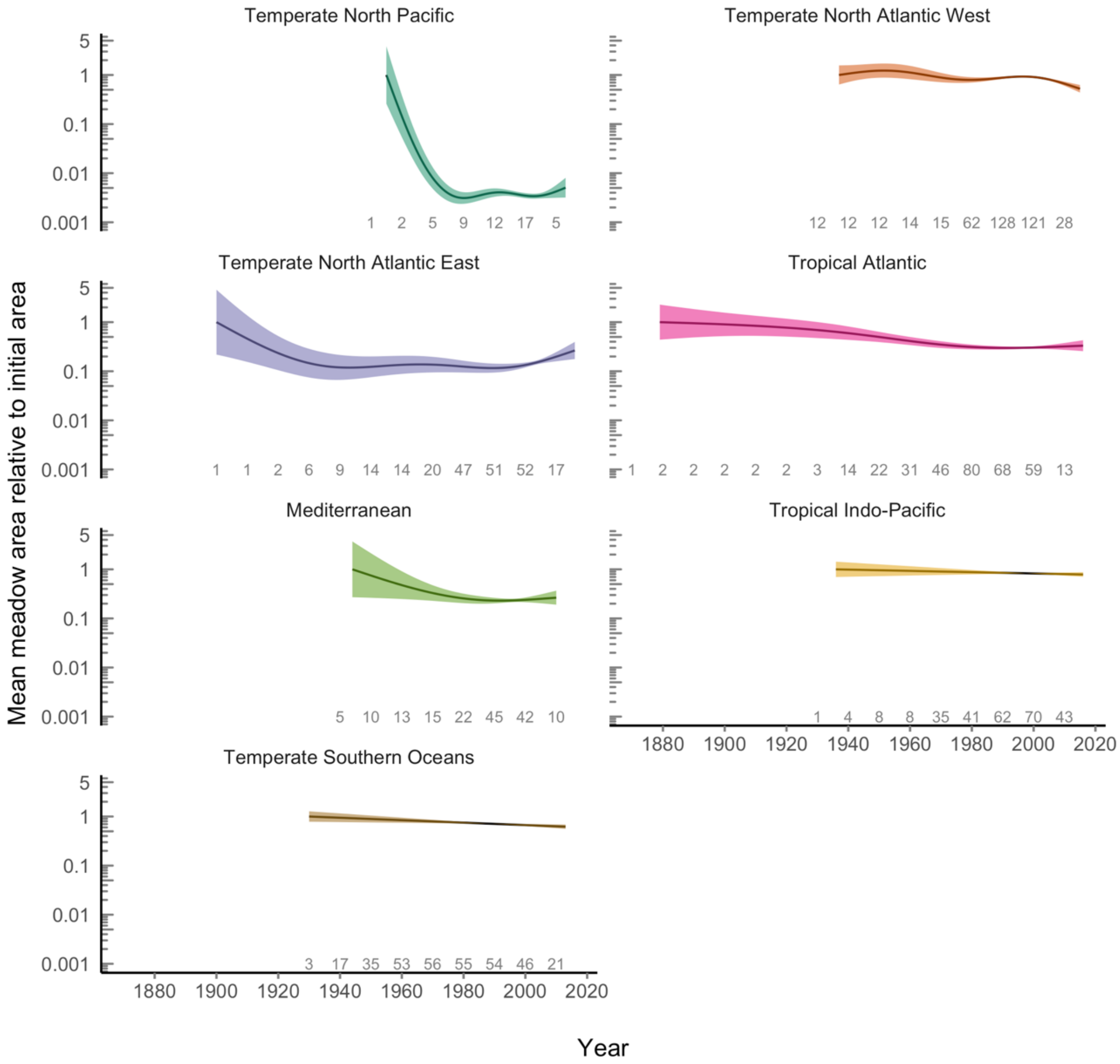


Figure A4. **Bioregional trends in seagrass areal extent over time, estimated using bioregion specific generalised additive models. The shaded areas represent 95% confidence intervals of the GAM fits. The same data are presented as in Figure 2 but axes are fixed across bioregions to highlight differences in magnitude of trends in seagrass areal extent and the length of time-series. Mean proportion of change is scaled to the initial values estimated for each bioregion and on a log10 scale, such that a change from 1 to 0.1 equals a 10-fold decrease in seagrass area over time.**

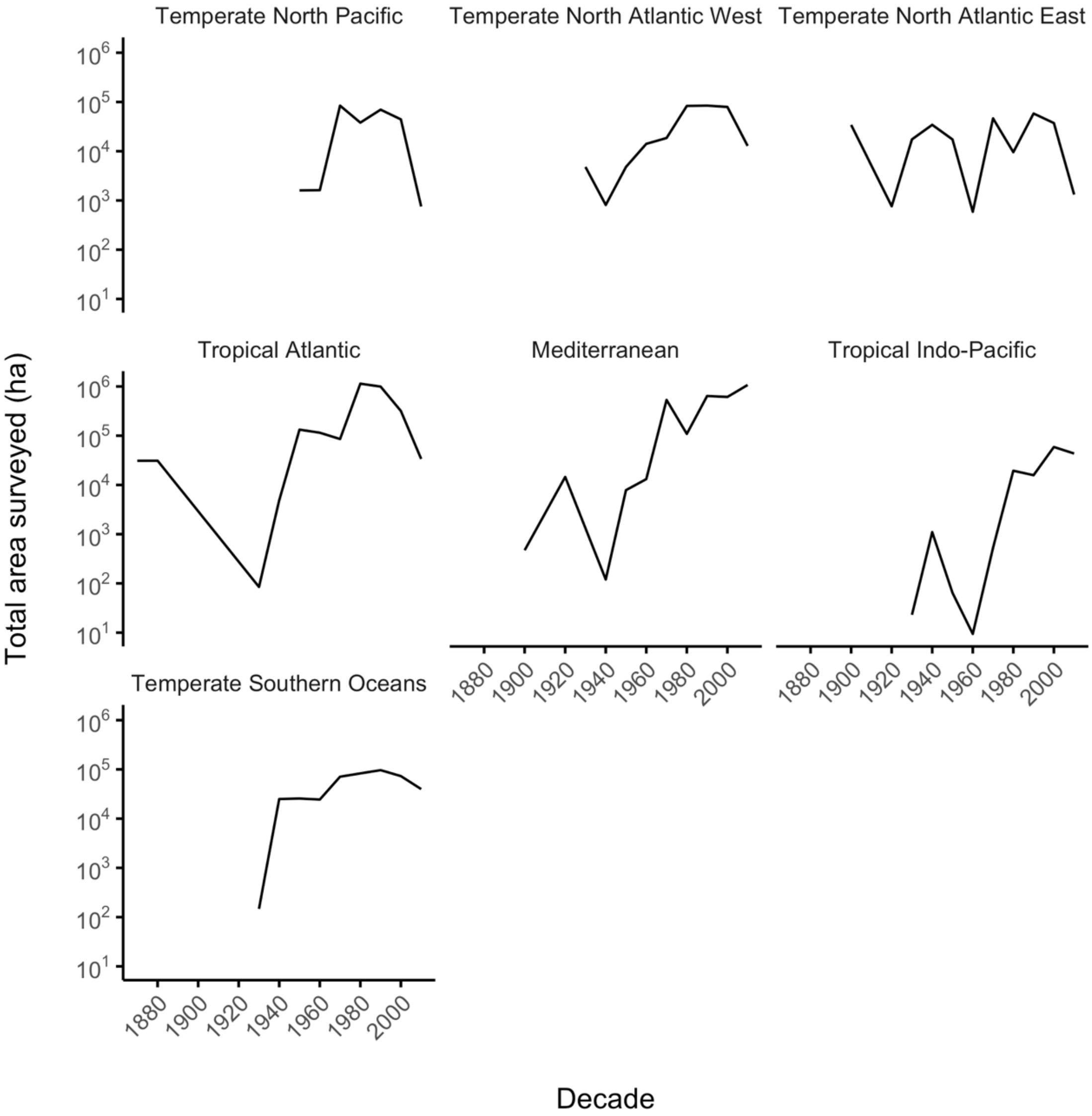


Figure A5. **Total area of seagrass surveyed over time. Total area surveyed in each decade was calculated using the observed maximum areal extent for all sites sampled in a given decade.**

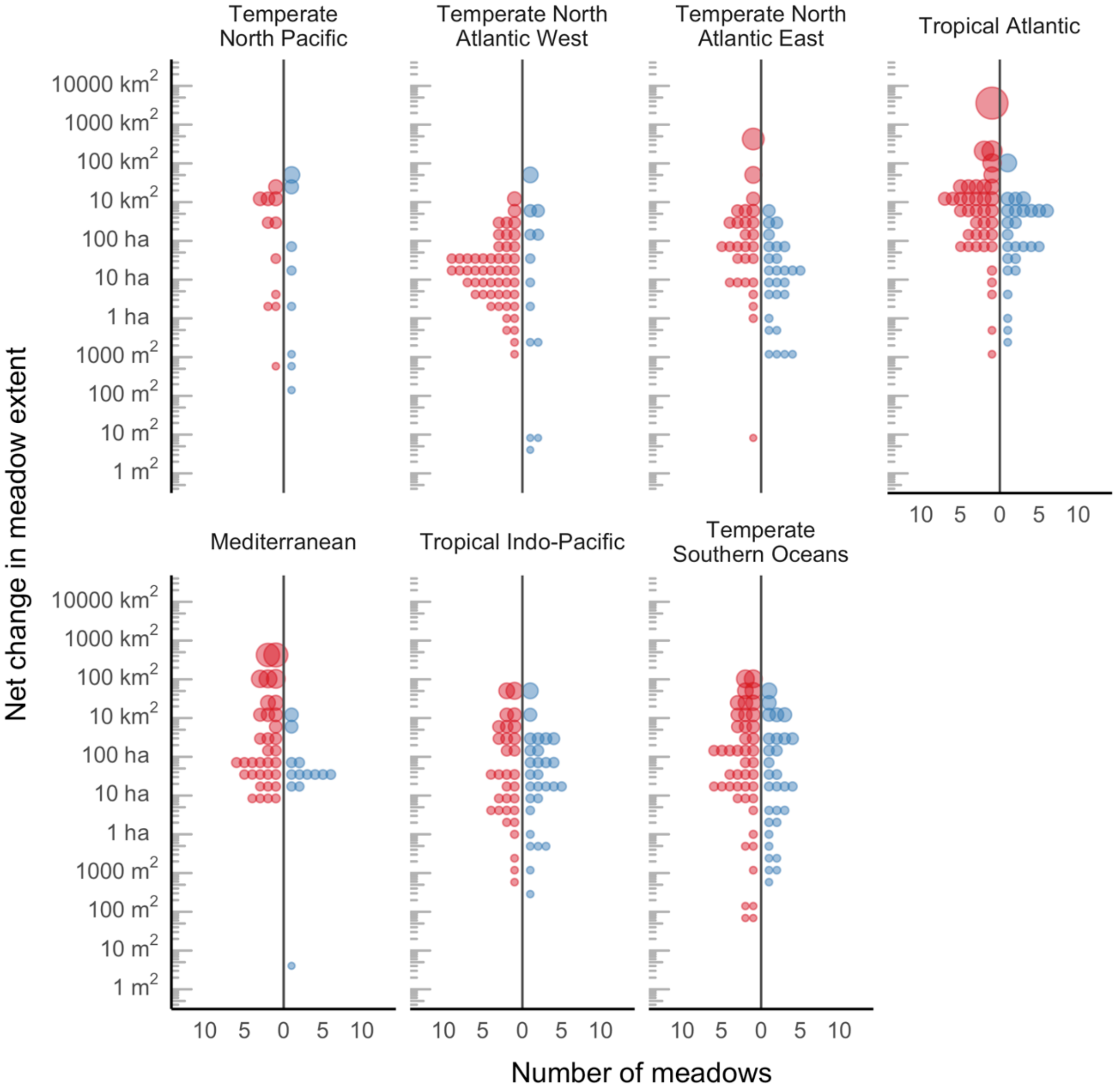


Figure A6. **Size distribution of net losses (red, left) and net gains (blue, right) across bioregions. Net change in meadow area (y-axis) is $\log_{10}$-scaled and number of meadows is on the x-axis. Each point represents the net change in a meadow over its entire time series ($\text{area}_{\text{final}} - \text{area}_{\text{initial}}$). To demonstrate the difference in magnitude of net change between small and large areas, point size corresponds to net change in area in a near-linear fashion.**

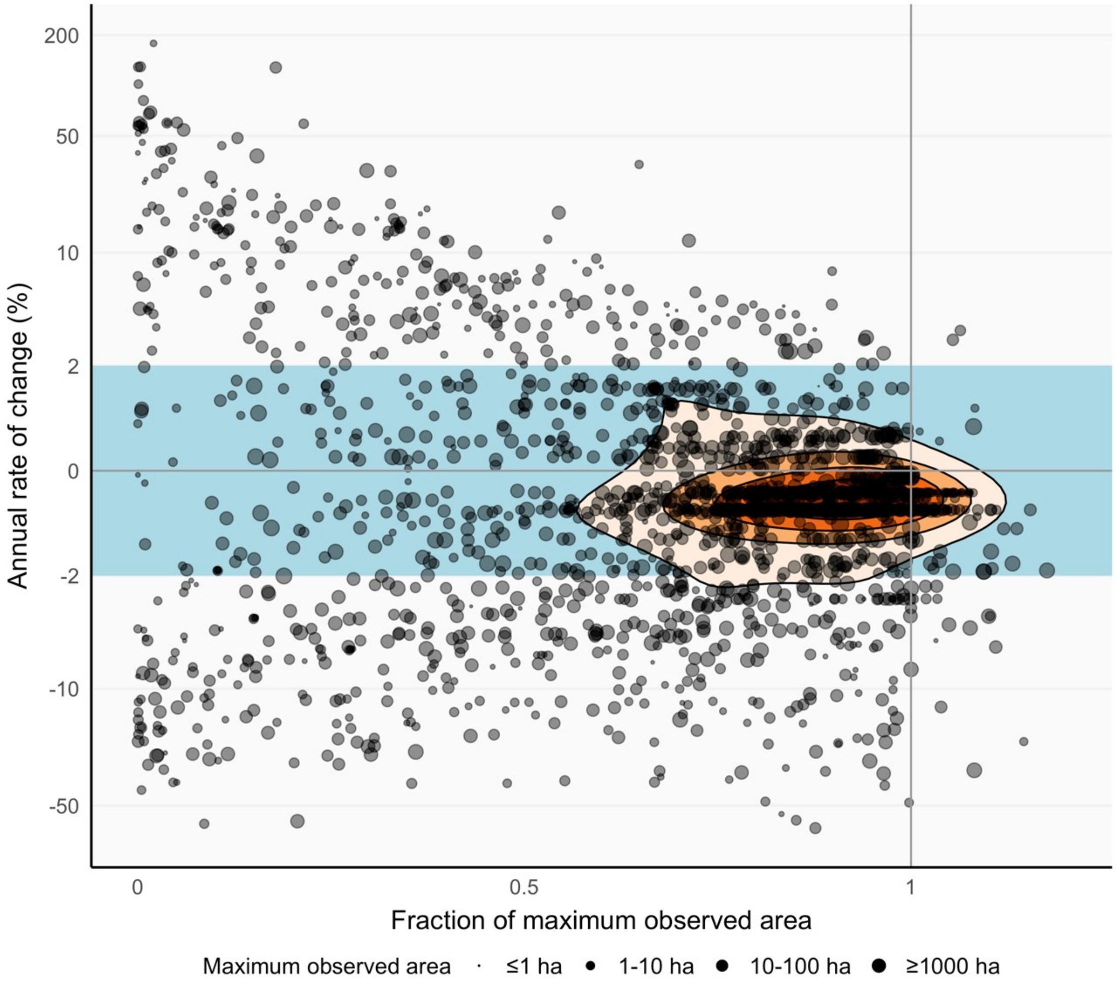


Figure A7. **Status of all seagrass meadows in all decades. Each point represents one seagrass meadow in a decade and point size represents the maximum area ever observed for that meadow. The x-axis indicates the size of a meadow at the beginning of a decade (e.g., 1990), as estimated using the bioregional GAMs, relative to the maximum area ever observed at that meadow. The y-axis is the instantaneous annual rate of change (%) in meadow area during a decade. This axis has been transformed using the signed pseudo logarithm (sigma = 0.5, base = 10) to improve visualisation of the high number of meadows with rates of change less than 10%. As values increase above 10, this axis approximates a $\log_{10}$ scale.**

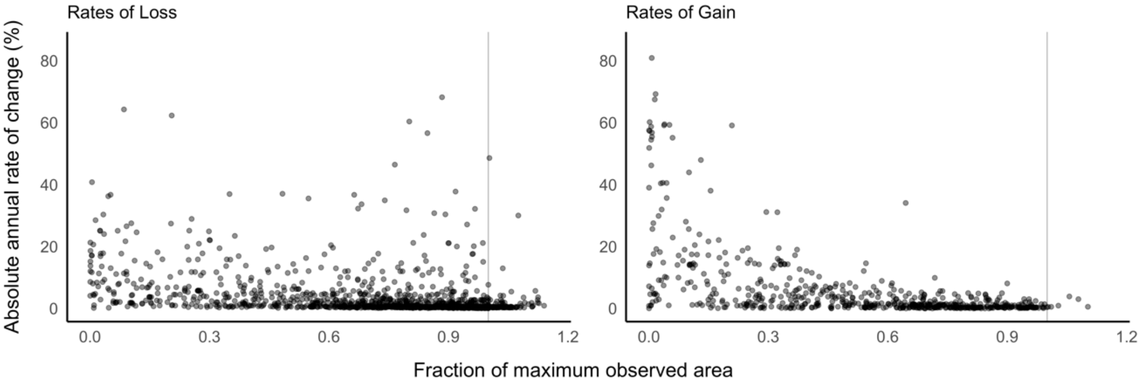


Figure A8. Comparison of the relationship between the absolute annual rate of change (%) and fraction of maximum ever observed area between meadows that experienced losses and those that experienced gains. Each point represents one seagrass meadow in a decade and point size represents.

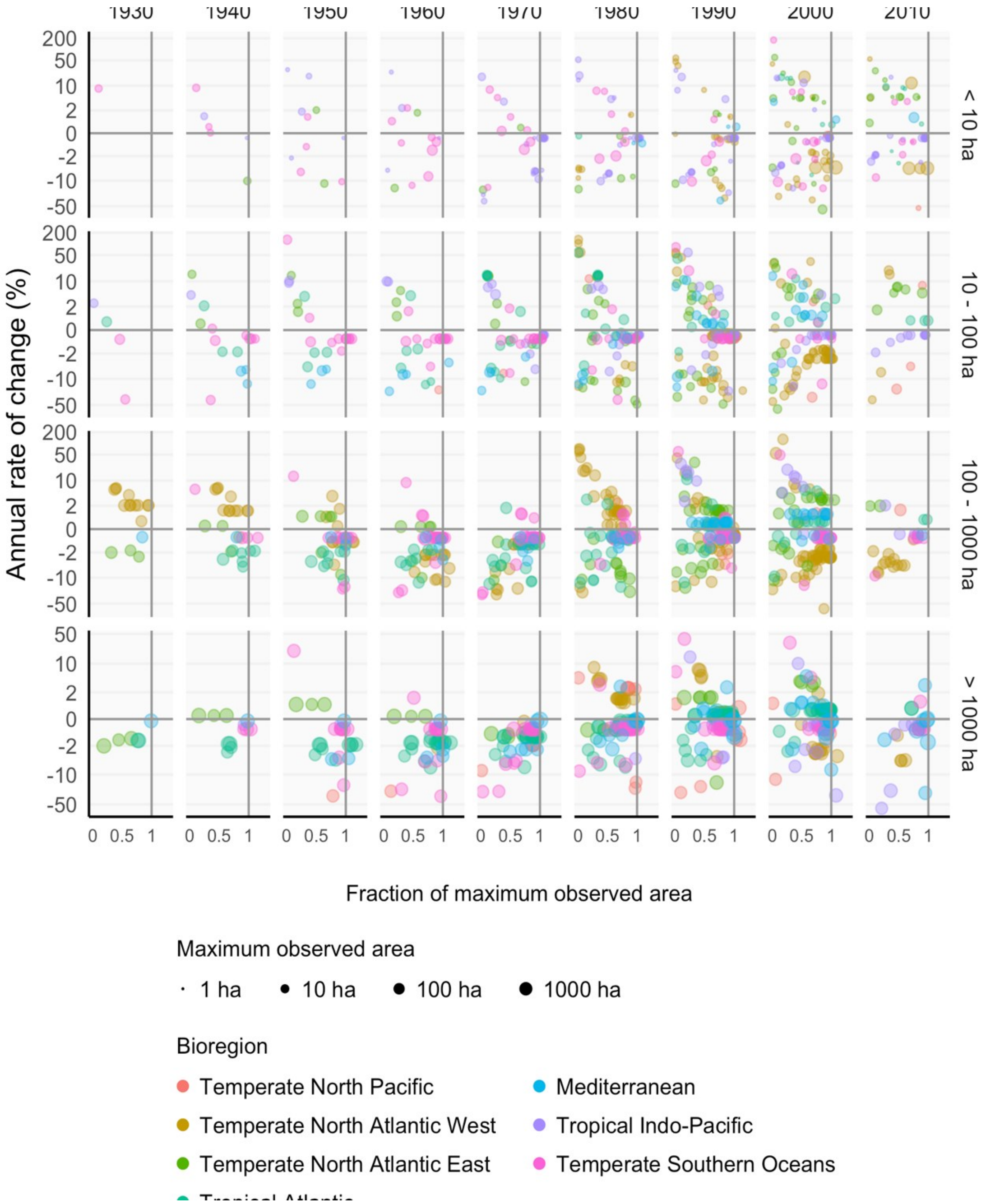


Figure A9. **Status of seagrass meadows split into four size bins of maximum observed meadow size (< 10 ha, 10 – 100 ha, 100 – 1000 ha, > 1000 ha). Each dot represents one seagrass meadow, with size representing the maximum areal extent observed at that meadow over its entire time series and colour indicating the bioregion. The x-axis indicates the size of a meadow in a decade, as estimated using the bioregional GAMs, relative to the maximum size ever observed in the time series of that meadow. Rate of change (%) in meadow areal extent, shown on the y-axis, has been transformed using the signed pseudo logarithm (sigma = 0.5, base = 10)**

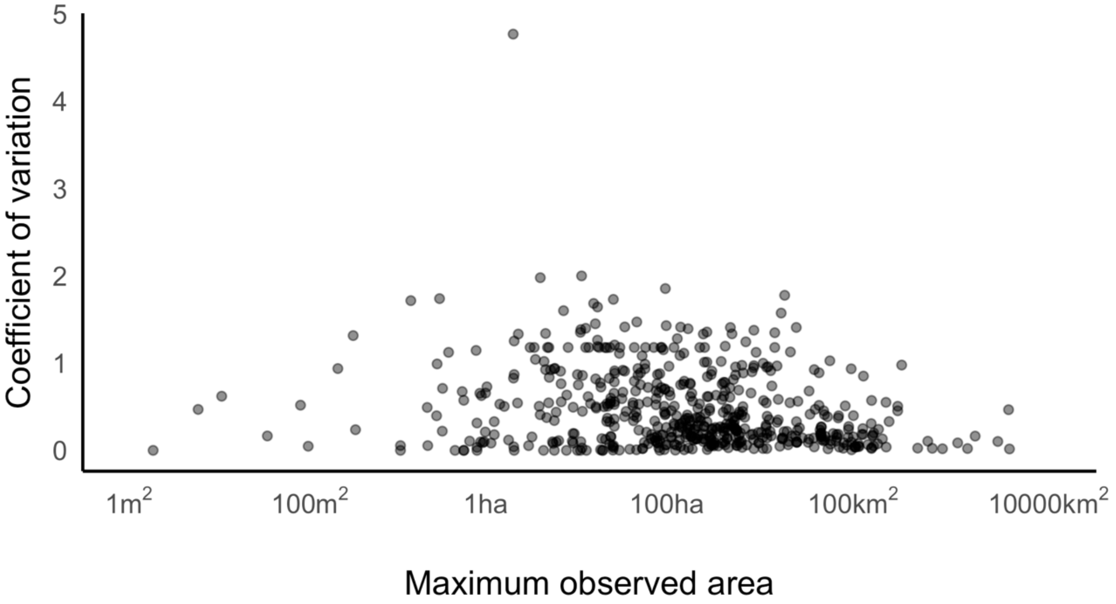


Figure A10. **Relationship between coefficient of variation of each meadow extent time-series and the maximum observed meadow size. The coefficient of variation was calculated for each meadow as the standard deviation of observed meadow sizes divided by the mean observed meadow size.**

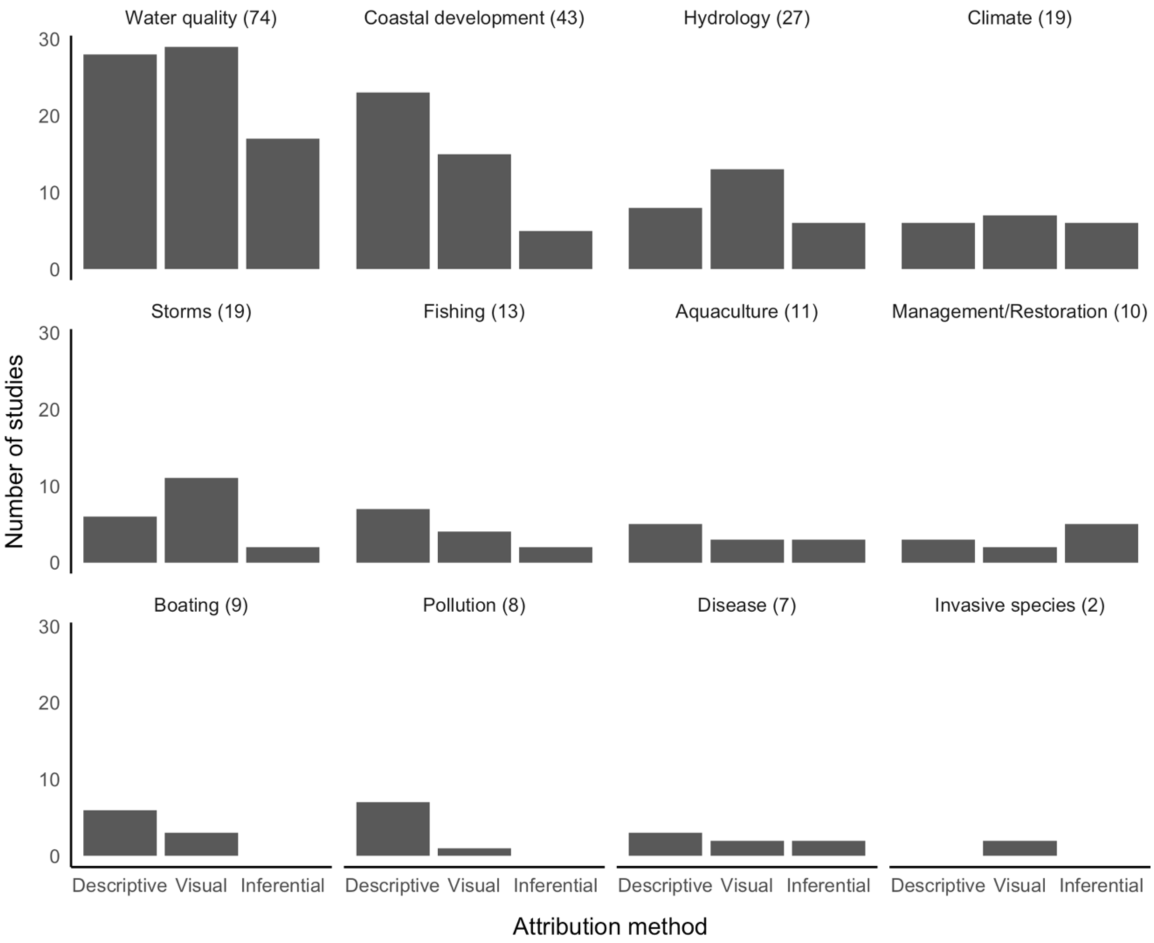


Figure A11. **Frequency of the consideration of potential drivers of change in seagrass meadow area and attribution method used in these considerations. Examples of specific drivers considered in each driver category are detailed in Table A3.**

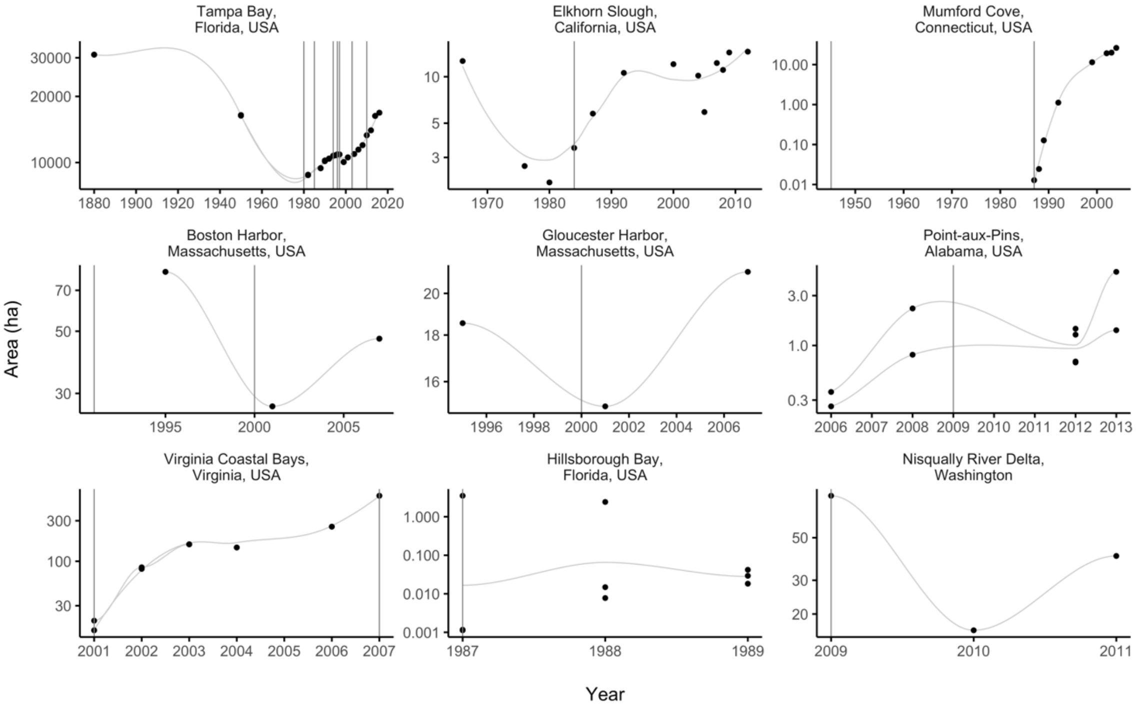


Figure A12. **Management actions. After management or restoration actions (grey lines), most sites experienced an increase in areal extent over time. Management and restoration actions are described in Table A4.**

Table A4. Management and restoration actions taken in Figure A12.

Study id	Location	Site name	Event	Year
11[*]	Tampa Bay, Florida, USA	Tampa Bay	Advanced wastewater treatment begins	1980
11[*]	Tampa Bay, Florida, USA	Tampa Bay	Stormwater regulations enacted	1985
11[*]	Tampa Bay, Florida, USA	Tampa Bay	El Nino heavy rains	1994
11[*]	Tampa Bay, Florida, USA	Tampa Bay	Advanced wastewater treatment begins	1996
11[*]	Tampa Bay, Florida, USA	Tampa Bay	Extreme El Nino event	1997
11[*]	Tampa Bay, Florida, USA	Tampa Bay	Air emissions reduced	2003
11[*]	Tampa Bay, Florida, USA	Tampa Bay	Residential fertilizer restrictions enacted	2010
207	Gloucester Harbor, Massachusetts, USA	Gloucester Harbor	Outfall relocation	2000
207	Boston Harbor, Massachusetts, USA	Boston Harbor	Sewage sludge sent to landfills	1991
207	Boston Harbor, Massachusetts, USA	Boston Harbor	Wastewater upgrades begin	1991
207	Boston Harbor, Massachusetts, USA	Boston Harbor	Wastewater outfall relocated offshore	2000
218	Mumford Cove, Connecticut, USA	Mumford Cove	Waste water treatment facility	1945
218	Mumford Cove, Connecticut, USA	Mumford Cove	Waste water treatment outfall diverted	1987
242	Virginia Coastal Bays, Virginia, USA	Virginia Coastal Bays	Seeding	2001
242	Virginia Coastal Bays, Virginia, USA	Virginia Coastal Bays	Seeding	2007
W1	Virginia Coastal Bays, Virginia, USA	Southern Delmarva Coastal Bays	Seeding	2001
142	Elkhorn Slough, California, USA	Elkhorn Slough	Sea otter recolonisation	1984
W8	Hillsborough Bay, Florida, USA	Hillsborough Bay - test plantings	Shoot plantings	1987
41	Point-aux-Pins, Alabama, USA	Pairs 1 & 2	Oyster reef construction	2009
41	Point-aux-Pins, Alabama, USA	Pairs 3 & 4	Oyster reef construction	2009
14	Nisqually River Delta, Washington	Nisqually River Delta	Dikes removed	2009

*Event data from study 87.

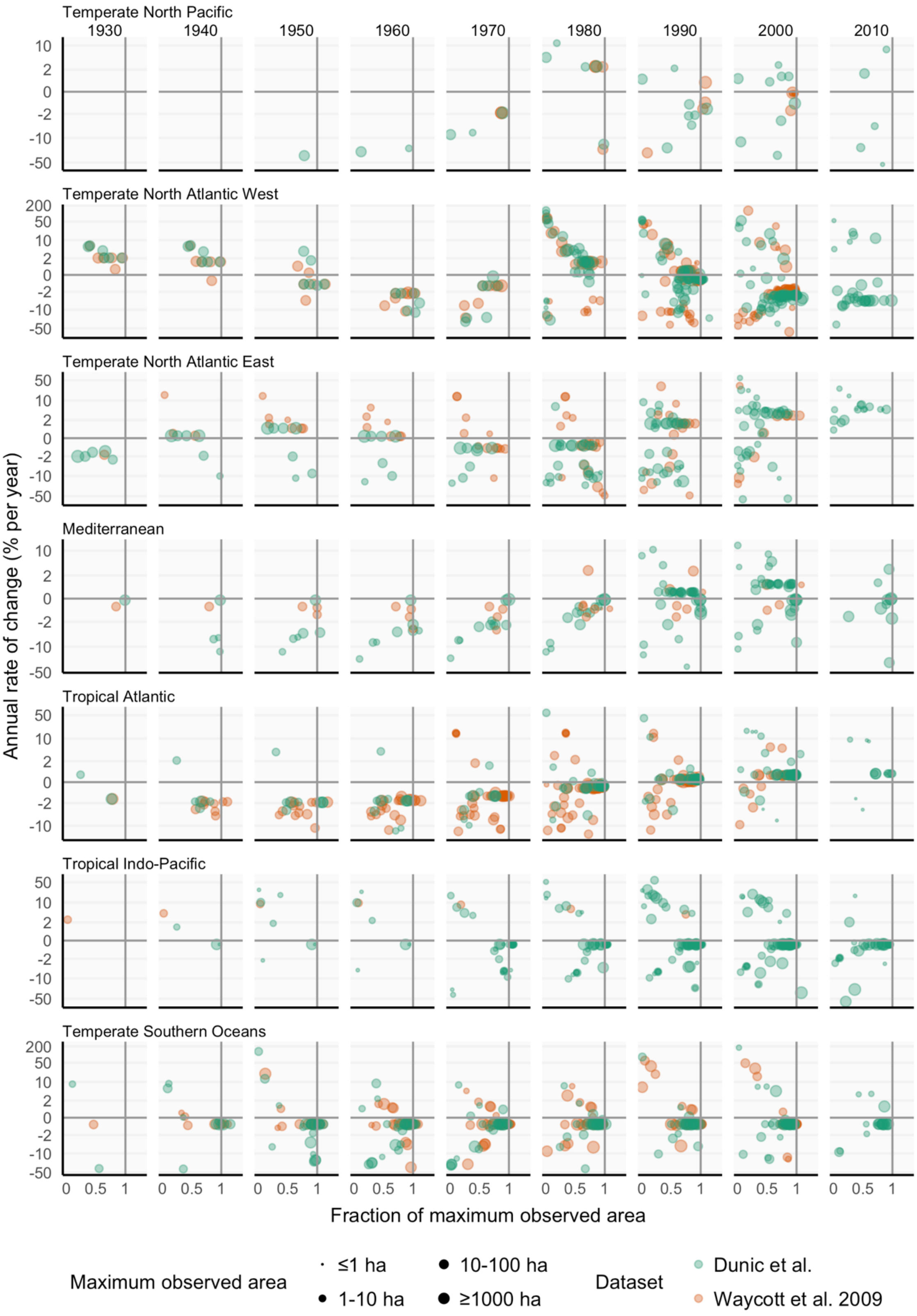

Temperate North Pacific
1930
1940
1950
1960
1970
1980
1990
2000
2010
Temperate North Atlantic West
Temperate North Atlantic East
Mediterranean
Tropical Atlantic
Tropical Indo-Pacific
Temperate Southern Oceans
200
50
10
2
0
-2
-10
-50
0
0.5
1
Annual rate of change (% per year)
Fraction of maximum observed area
Maximum observed area
≤1 ha
1-10 ha
10-100 ha
≥1000 ha
Dataset
Dunic et al.
Waycott et al. 2009

Figure A13. **Status of seagrass meadows over time and across bioregions comparing the sites found in this study (green) and sites first included in Waycott et al. (2009; orange). Each point represents the status of one seagrass meadow in a given decade, while and point size represents the maximum area ever observed for that meadow. Meadows that have experienced more severe losses will be farther on the left of a panel; meadows near their maximum size will be on the right (near vertical line, x = 1); and stable/slowly changing meadows are near the horizontal line, y = 0. The x-axis indicates the size of a meadow at the beginning of a decade (e.g., 1990), as estimated using the bioregional GAMs, relative to the maximum area ever observed at that meadow. The y-axis is the instantaneous annual rate of change (%) in meadow area during a decade. Note that the y-axis varies in range across the bioregions and has been transformed using the signed pseudo logarithm (sigma = 0.5, base = 10) to improve visualisation of the high number of meadows with rates of change less than 10%. As values increase above 10, this axis approximates a log10 scale.**

Sensitivity Analysis

To perform a sensitivity analysis and test the effect of decades with fewer than five meadows, we re-fit the GAMs for datasets beginning in decades with the number of meadows >= 5. Three bioregions show notable differences (Figure A14: Temperate North Pacific, Temperate North Atlantic East, and Tropical Indo-Pacific). However, these despite these differences the complete dataset is generally a better representative of trends and minimizes the effect of shifting baselines.

(1) The rapid loss in the Temperate North Pacific is no longer present. This is unsurprising as this was driven by one study. The trend from 1980 onward is essentially unchanged and matches what has recently been observed in the TNP (e.g., Shelton et al., 2017). The influence of only a few meadows surveyed pre-1980 is however already addressed in the discussion.

(2) The Temperate North Atlantic East now shows an increasing trend in recent decades. However, this reflects a shifted baseline and the overall trend is quite similar to when early time-series were included. When early studies are omitted, the reconstruction gives the appearance of meadow expansions (e.g., potentially range expansions) in the TNAE, but given the well-documented history of wasting disease causing catastrophic losses, it is most likely that meadows are continuing to recover from large, historical losses.

(3) Rapid increases were observed in the Tropical Indo-Pacific. When the early studies are omitted, the initial trend shows a rapid increase. However, this is the result of rapid gains in a set of small meadows (Figure A15. Cuvillier et al. 2017). These meadows were all less than one hectare at their maximum size. The raw data (Figure A16) indicate that the GAM reconstructions capture the overall trend in the Tropical Indo-Pacific bioregion.

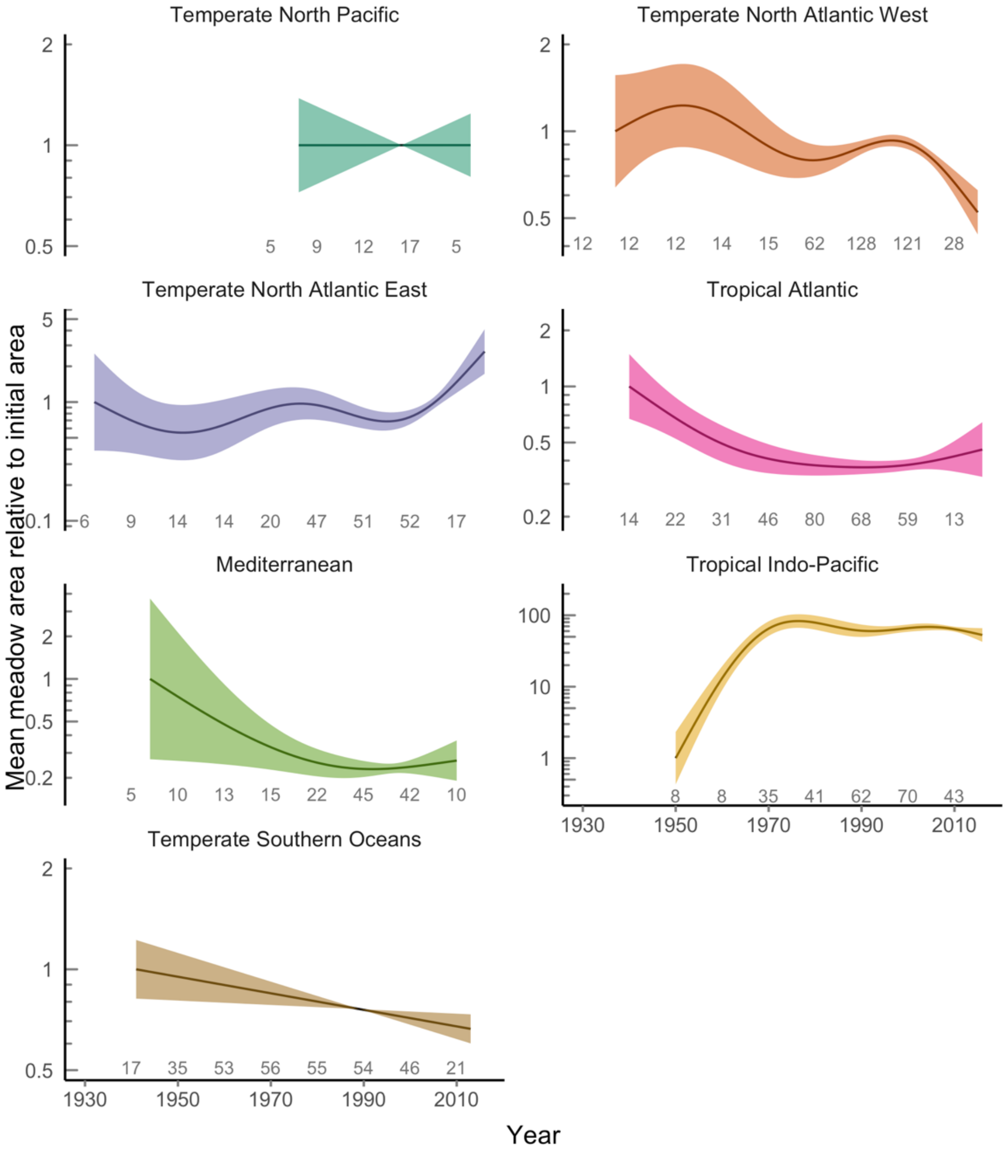


Figure A14. **Bioregional trends in seagrass meadow area over time, estimated using bioregion-specific generalised additive models when decades with fewer than five meadows were excluded. Mean meadow area is expressed as a proportion of the meadow area observed in the initial surveys, averaged across sites for each bioregion, and on a $\log_{10}$ scale, such that a change from 1 to 0.1 equals a 10-fold decrease in seagrass area over time. The shaded areas represent 95% confidence intervals of the GAM fits. Note that the y-axis varies across bioregions. The number of meadows sampled in each decade are shown in grey at the bottom of each panel. The bioregional trend in the Mediterranean does not include 16 sites that contained only two sampled time points.**

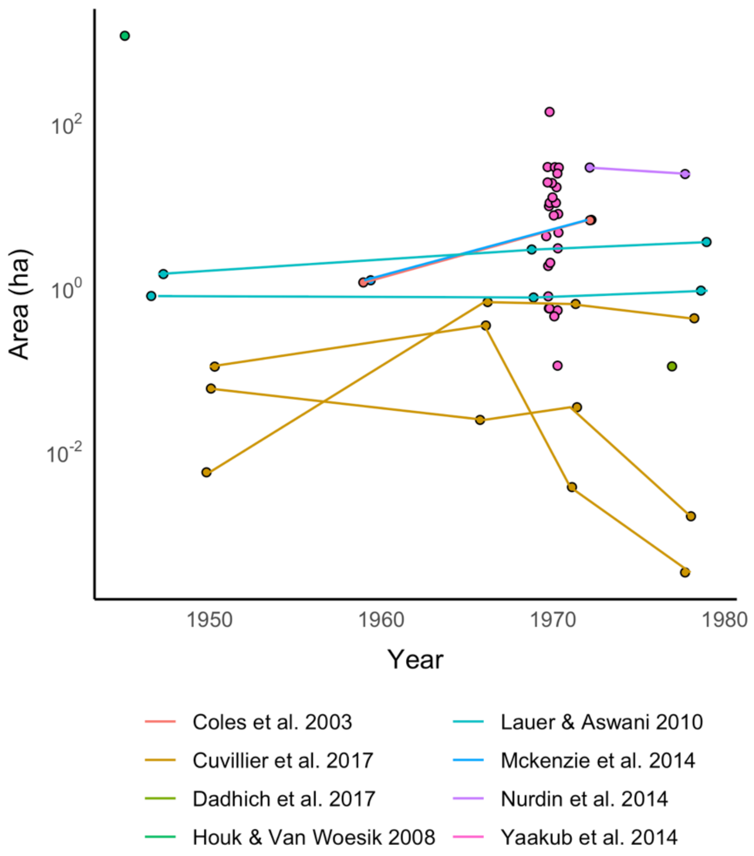


Figure A15. Meadow time-series from a subset of studies in the Tropical Indo-Pacific, to identify the meadows driving the rapidly increasing trend observed in the sensitivity analysis that used decades containing at least 5 meadows and generalized additive models to model trends in seagrass area over time for the Tropical Indo-Pacific (Figure A1). Point and line colours indicate different studies. Some lines are omitted because only samples taken in 1980 or prior are shown here.

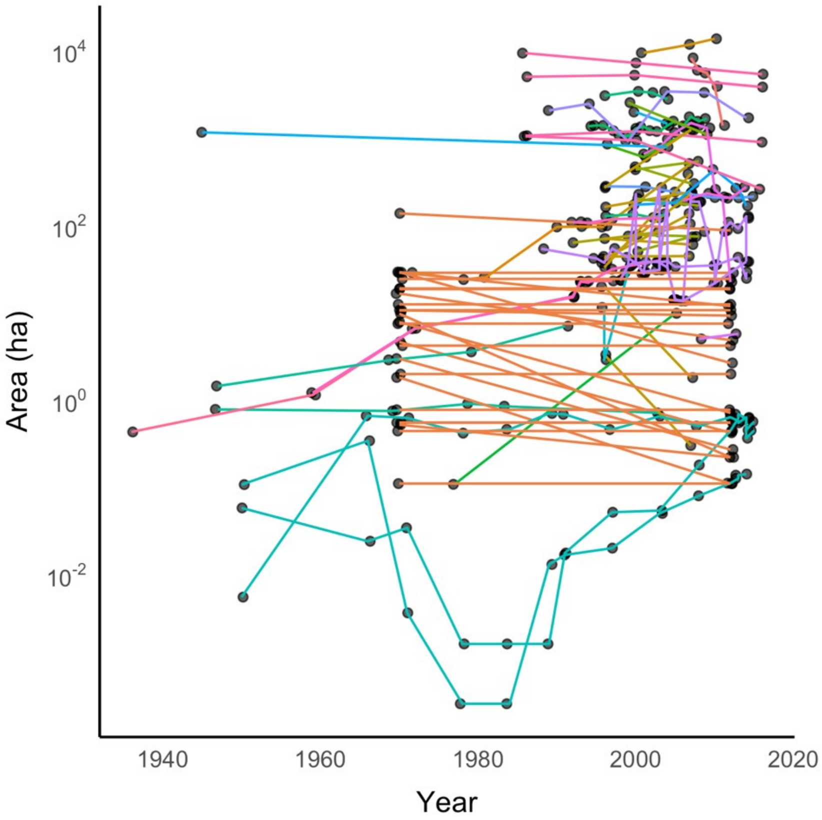


Figure A16. **Meadow time-series from all studies in the Tropical Indo-Pacific. Line colours indicate different studies.**

Supplementary References

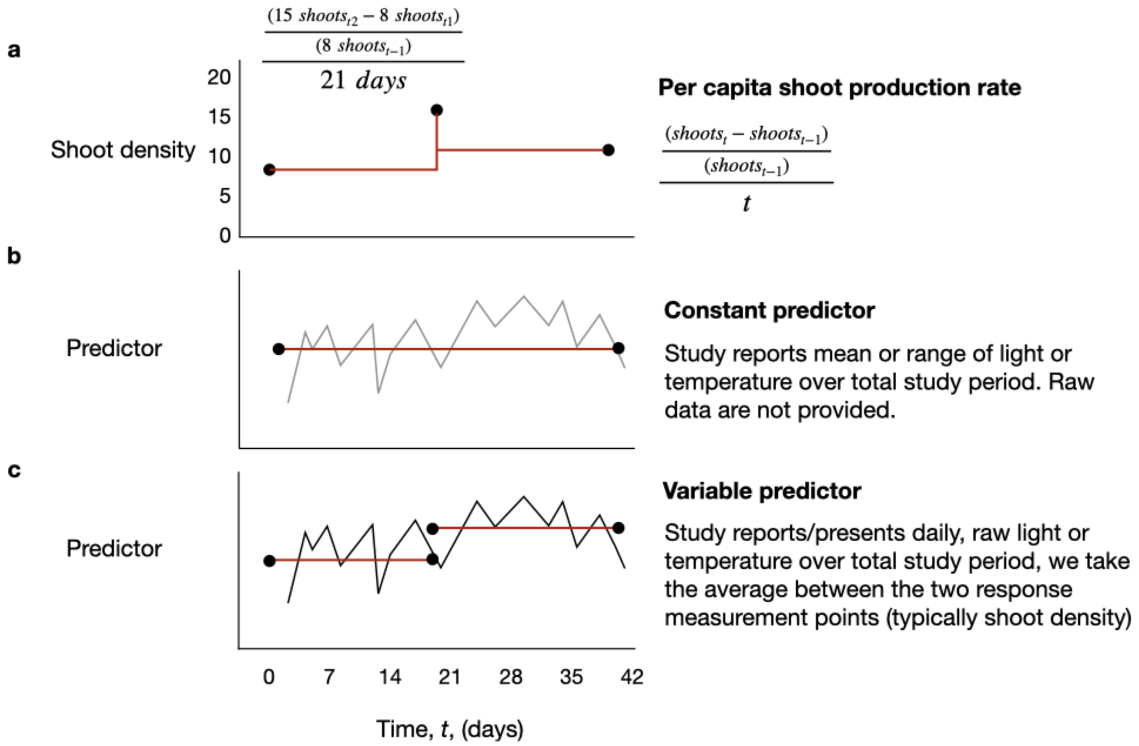
Cuvillier, A., Villeneuve, N., Cordier, E., Kolasinski, J., Maurel, L., Farnier, N., & Frouin, P. (2017). Causes of seasonal and decadal variability in a tropical seagrass seascape (Reunion Island, south western Indian Ocean). *Estuarine, Coastal and Shelf Science*, *184*, 90–101. https://doi.org/10.1016/j.ecss.2016.10.046

Shelton, A. O., Francis, T. B., Feist, B. E., Williams, G. D., Lindquist, A., & Levin, P. S. (2017). Forty years of seagrass population stability and resilience in an urbanizing estuary. *Journal of Ecology*, *105*(2), 458–470. https://doi.org/10.1111/1365-2745.12682

Appendix B.

Supporting Information for Chapter 3

Supplementary Tables and Figures



Per capita shoot production rate

$$\frac{\frac{(shoots_t - shoots_{t-1})}{(shoots_{t-1})}}{t}$$

Constant predictor

Study reports mean or range of light or temperature over total study period. Raw data are not provided.

Variable predictor

Study reports/presents daily, raw light or temperature over total study period, we take the average between the two response measurement points (typically shoot density)

Figure B1. **Example of the ways in which data were extracted when (a) shoot density time-series were provided, (b) a single value of the predictors (temperature and/or light) was provided over the duration of all response measurements, and (c) raw data time-series were provided for predictors. The data were then summarised over the time-scale corresponding to the duration over which responses were measured. In all cases rates of per-capita shoot production were standardised to per day.**

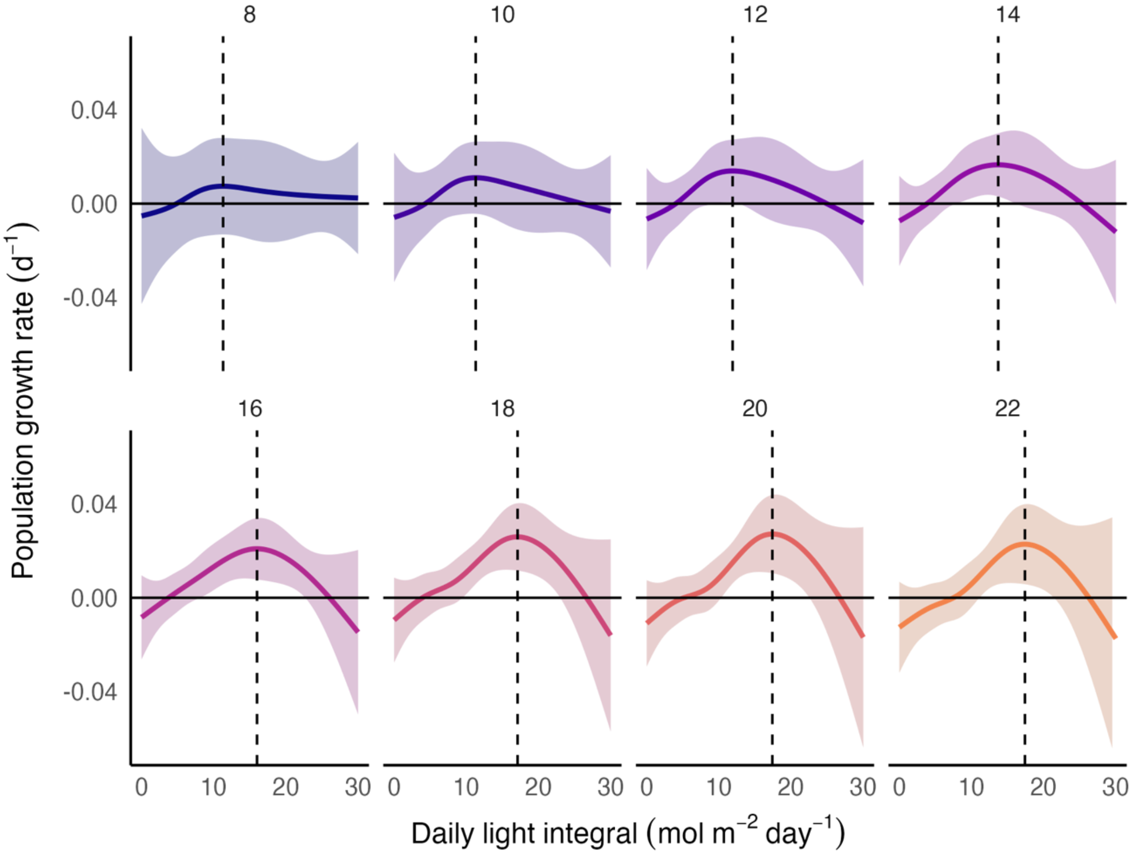


Figure B2. **Predicted fits of population growth rate by eelgrass, *r* (day^{-1}), in relation to light at different temperatures, shown (in ˚C) above each panel. The vertical dashed lines denote the daily light integral, *DLI*$_{r=rmax}$, at which population growth is maximal for a given temperature. The narrow temperature bins between 25 and 30˚C highlight the temperatures over which *DLI*$_{r=rmax}$ increases rapidly. The shaded areas are 95% simultaneous confidence intervals from model fits. Colours corresponds to temperature bins.**

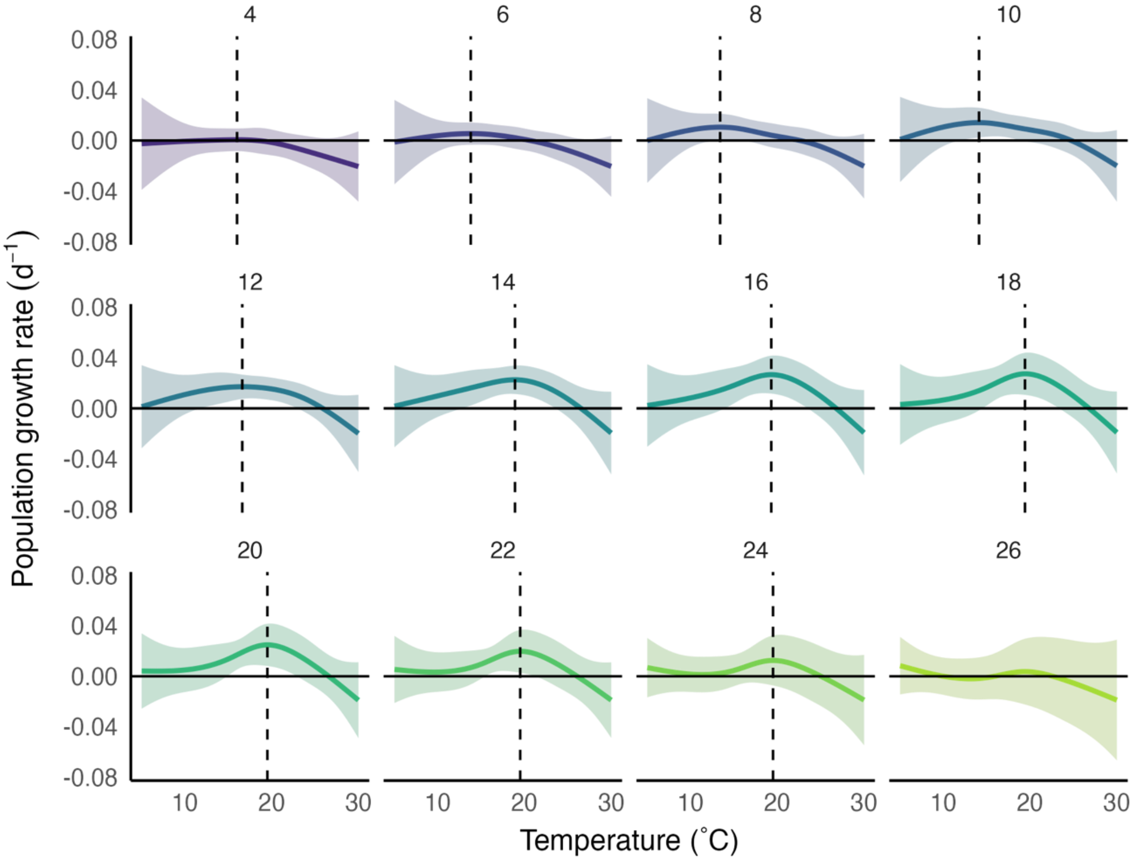


Figure B3. **Predicted fits of population growth rate by eelgrass, *r* (day^{-1}), in relation to temperature at different light levels, shown (in mol m^{-2} day^{-1}) above each panel. The vertical dashed lines denote the temperature, $T_{r=rmax}$, at which population growth is maximal for a given light level. The narrow light bins between 10 and 15 mol m^{-2} day^{-1} highlight the light bins over which $T_{r=rmax}$ increases rapidly. The shaded areas are 95% simultaneous confidence intervals from model fits. Colours corresponds to light level bins.**

Table B1. **Data sources from which data were extracted for the analysis. IDs correspond with IDs used in the supplemental code and data associated with this manuscript.**

ID	Source
15	Moreno-Marín, F., Brun, F. G., & Pedersen, M. F. (2018). Additive response to multiple environmental stressors in the seagrass *Zostera marina* L. *Limnology and Oceanography*, *63*(4), 1528–1544. https://doi.org/10.1002/lno.10789
24	Eriander, L. (2017). Light requirements for successful restoration of eelgrass (*Zostera marina* L.) in a high latitude environment – Acclimatization, growth and carbohydrate storage. *Journal of Experimental Marine Biology and Ecology*, *496*, 37–48. https://doi.org/10.1016/j.jembe.2017.07.010
47	Castorani, M. C. N., Glud, R. N., Hasler-Sheetal, H., & Holmer, M. (2015). Light indirectly mediates bivalve habitat modification and impacts on seagrass. *Journal of Experimental Marine Biology and Ecology*, 472, 41–53. https://doi.org/10.1016/j.jembe.2015.07.001
57	Kim, Y. K., Kim, S. H., & Lee, K.-S. (2015). Seasonal growth responses of the seagrass *Zostera marina* under severely diminished light conditions. *Estuaries and Coasts*, *38*(2), 558–568. https://doi.org/10.1007/s12237-014-9833-2
78	Villazán, B., Pedersen, M., Brun, F., & Vergara, J. (2013). Elevated ammonium concentrations and low light form a dangerous synergy for eelgrass *Zostera marina*. *Marine Ecology Progress Series*, *493*, 141–154. https://doi.org/10.3354/meps10517
97	Höffle, H., Thomsen, M. S., & Holmer, M. (2011). High mortality of *Zostera marina* under high temperature regimes but minor effects of the invasive macroalgae *Gracilaria vermiculophylla*. *Estuarine, Coastal and Shelf Science*, *92*(1), 35–46. https://doi.org/10.1016/j.ecss.2010.12.017
103	Martínez-Lüscher, J., & Holmer, M. (2010). Potential effects of the invasive species *Gracilaria vermiculophylla* on *Zostera marina* metabolism and survival. *Marine Environmental Research*, *69*(5), 345–349. https://doi.org/10.1016/j.marenvres.2009.12.009
107	Ochieng, C. A., Short, F. T., & Walker, D. I. (2010). Photosynthetic and morphological responses of eelgrass (*Zostera marina* L.) to a gradient of light conditions. *Journal of Experimental Marine Biology and Ecology*, *382*(2), 117–124. https://doi.org/10.1016/j.jembe.2009.11.007
116	Biber, P. D., Kenworthy, W. J., & Paerl, H. W. (2009). Experimental analysis of the response and recovery of *Zostera marina* (L.) and *Halodule wrightii* (Ascher.) to repeated light-limitation stress. *Journal of Experimental Marine Biology and Ecology*, *369*(2), 110–117. https://doi.org/10.1016/j.jembe.2008.10.031
123	Vinther, H. F., & Holmer, M. (2008). Experimental test of biodeposition and ammonium excretion from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance. *Journal of Experimental Marine Biology and Ecology*, *364*(2), 72–79. https://doi.org/10.1016/j.jembe.2008.07.003
127	Nejrup, L. B., & Pedersen, M. F. (2008). Effects of salinity and water temperature on the ecological performance of *Zostera marina*. *Aquatic Botany*, *88*(3), 239–246. https://doi.org/10.1016/j.aquabot.2007.10.006
152	Lee, K.-S., Park, S. R., & Kim, J.-B. (2005). Production dynamics of the eelgrass, *Zostera marina* in two bay systems on the south coast of the Korean peninsula. *Marine Biology*, *147*(5), 1091–1108. https://doi.org/10.1007/s00227-005-0011-8
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Appendix C.

Supporting Information for Chapter 4

Supplementary Tables and Figures

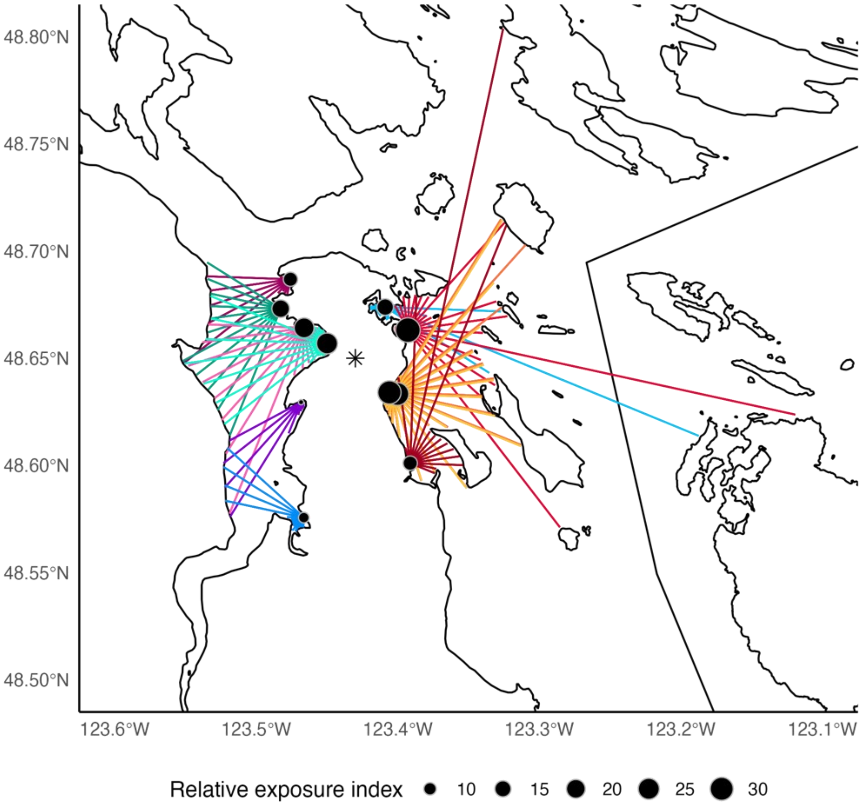

Figure C1. Relative exposure index calculated for 11 eelgrass meadow sites around the Saanich Peninsula. Sites E3 and E4 have been jittered to improve visualisation. Lines indicate the unobstructed overwater distance calculated using 'windfetch' (Seers 2022) and point size indicates the relative exposure index (Table 4.1).

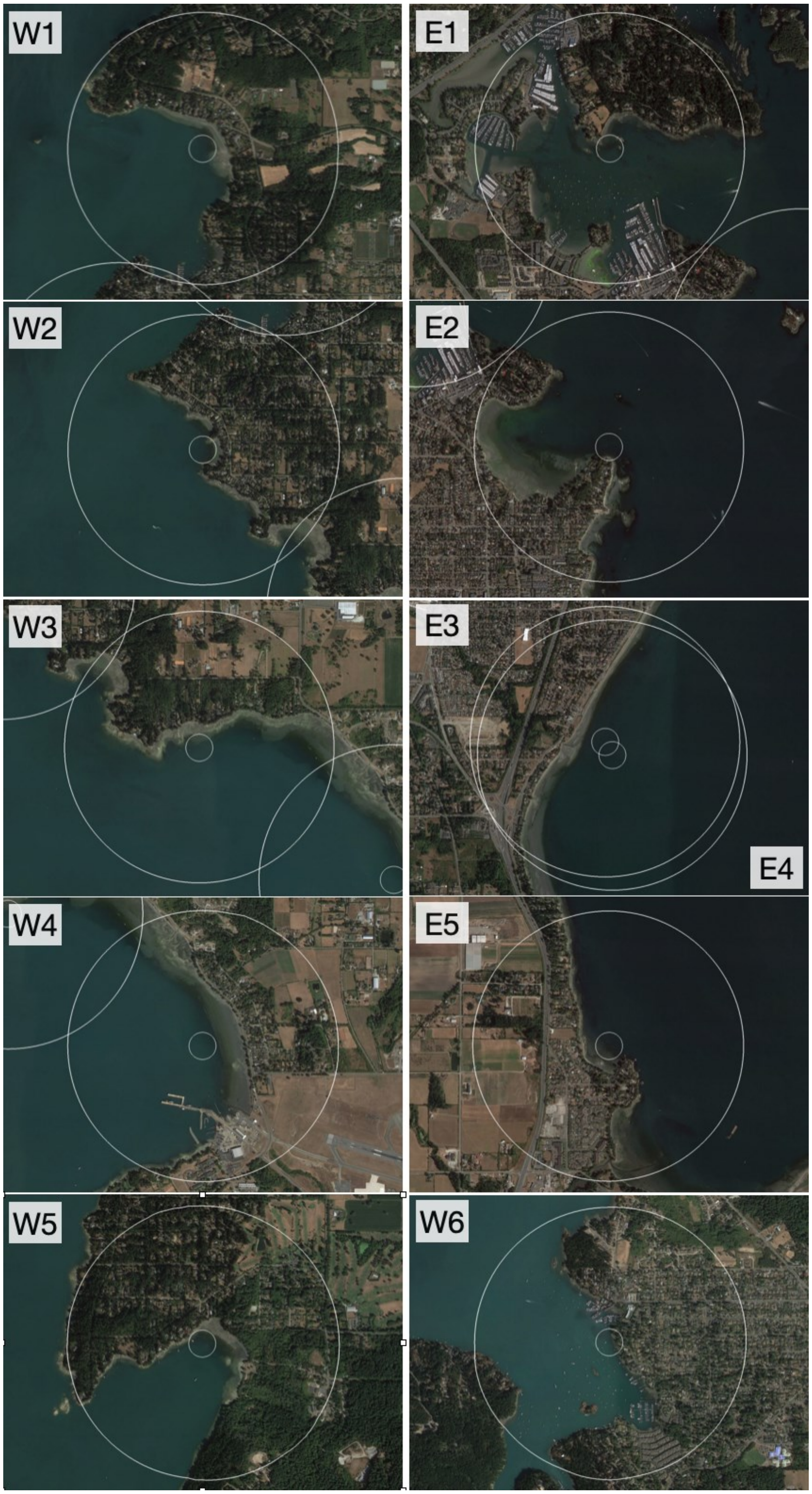

Figure C2. Mosaic of Google Earth sites with 1 km buffer circle around each eelgrass meadow site (small inner circle).

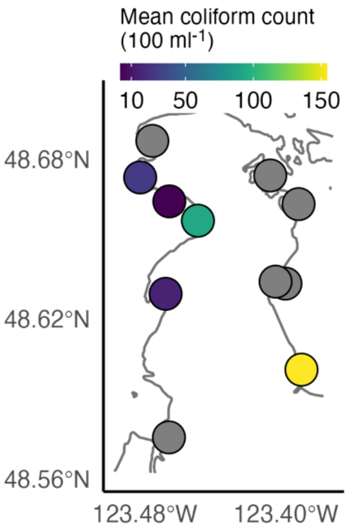

Figure C3. **Spatial variation in mean coliform counts (cells per 100 mL) across 11 eelgrass meadow sites around the Saanich Peninsula; grey points indicate no data. Mean values were calculated using Canadian Shellfish Sanitation Program data averaged from 2009 – 2019 at the nearest station within 1 km of the sampling sites.**

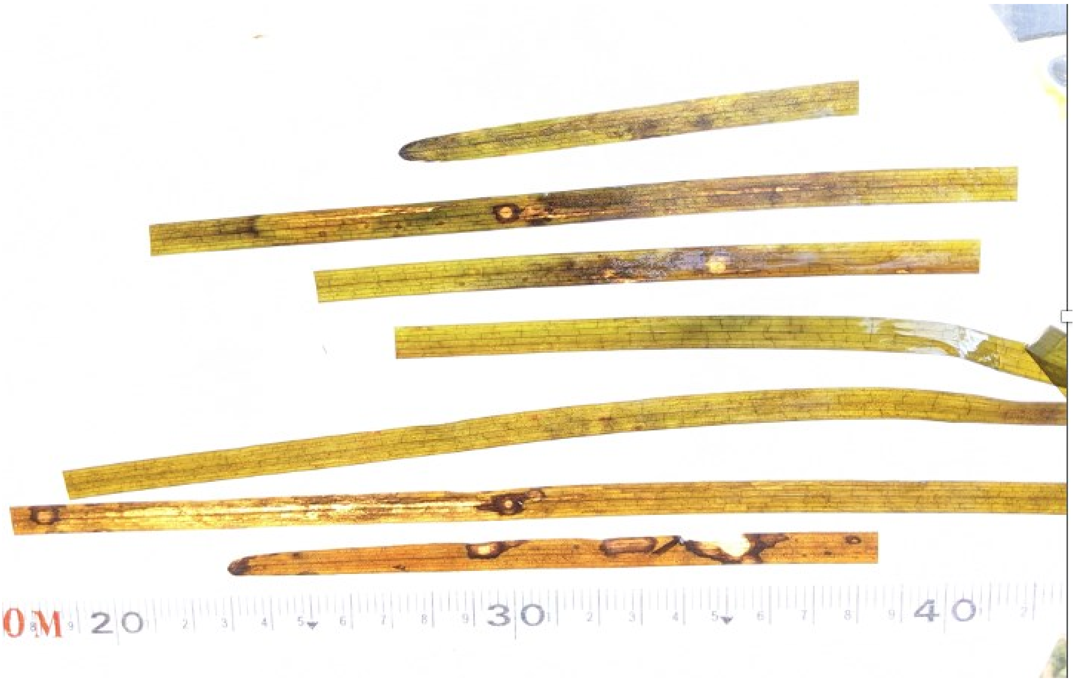

Figure C4. **Example of lesions found on a shoot from site W3.**

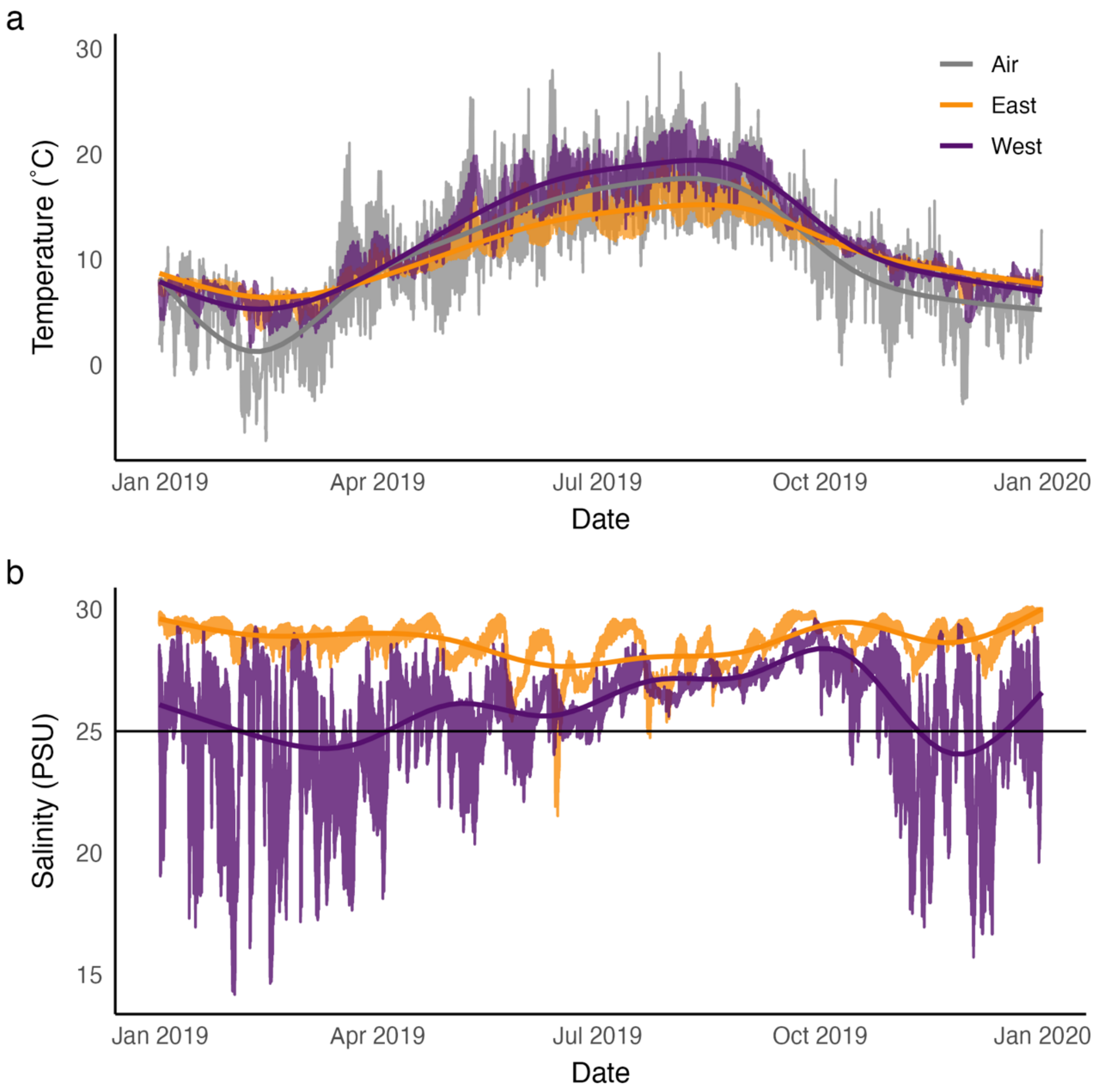

Figure C5. **Comparison of the (a) temperature and (b) salinity time-series of all sites combined along each aspect of the Saanich Peninsula. Data for lines in orange and purple were taken extracted from the SalishSeaCast model (Soontiens et al. 2016, Soontiens and Allen 2016) from 1 January to 31 December 2019. The grey data shown in (a) is the hourly air temperature measured at Victoria International Airport, extracted from the Environment and Climate Change Canada historical climate data (ECCC 2011). Smooth lines show the mean trend, as calculated using a generalised additive model smoother. The black horizontal line in (b) shows the 25 PSU threshold used as the cut-off for the 'time at low salinity' used in the analysis of environmental predictors.**

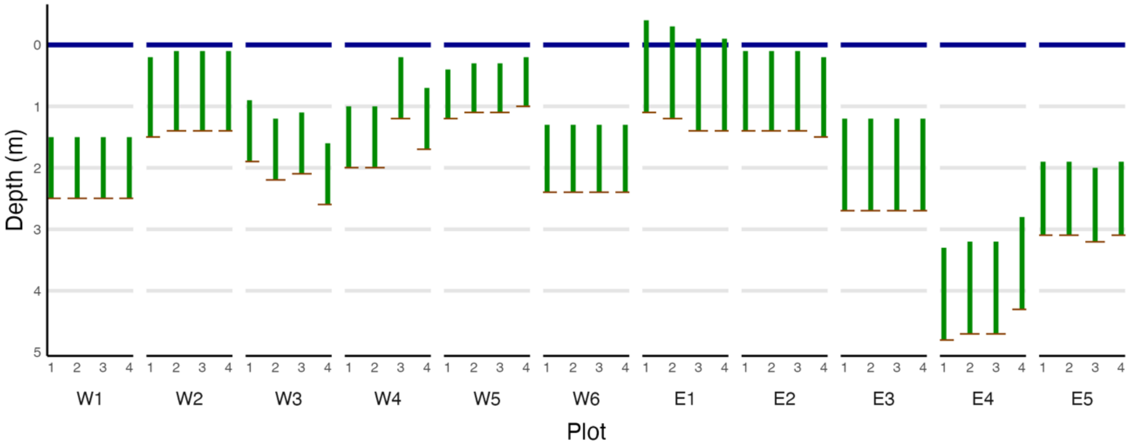

Figure C6. Schematic of plot depths (brown lines) and position of eelgrass canopy in the water (green bars) standardized to MLLW = 0 (blue lines).

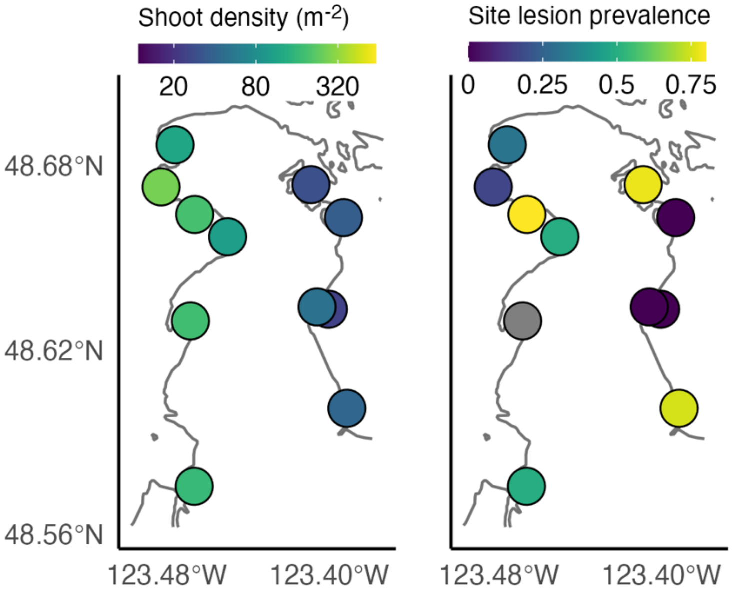

Figure C7. Spatial variation in eelgrass response metrics across 11 meadows around the Saanich Peninsula. Sites E3 and E4 have been jittered to improve visualisation. Note the logarithmic colour scale for shoot density.

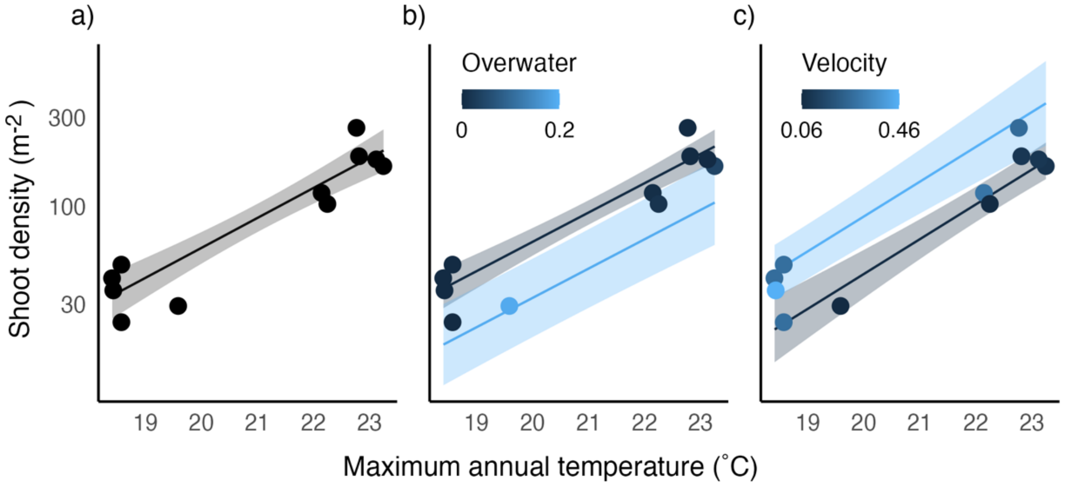

Figure C8. **Relationship between shoot density (m^{-2}) and maximum annual temperature (˚C), predicted by the top three models in the AICc analysis (Table 2). The fitted model lines and 95% confidence intervals are shown for (a) the relationship between shoot density and maximum temperature, (b) the same relationship for the minimum (dark blue) and maximum (light blue) proportion of structures overwater observed in the dataset, and (c) the same relationship for the minimum (dark blue) and maximum (light blue) maximum water velocity observed in the dataset. Points are the shoot densities observed at each of 11 sites (see Figure C7). Colours of the points in (b) indicate the proportion of structures overwater at each site or (c) maximum velocity (see Figure 4.2). Note the log scale of the y-axis.**

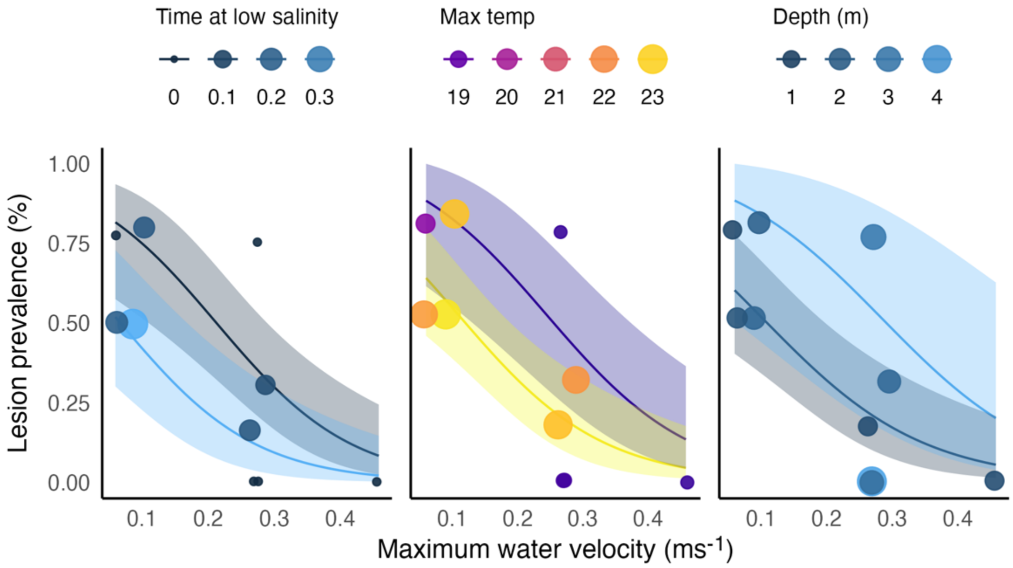

Figure C9. **Relationship between lesion prevalence (%) and maximum water velocity (ms^{-1}), predicted by the top 1, 2, and 4 models in the AICc analysis (Table 4.2). The fitted model lines and 95% confidence intervals are shown for the relationship between lesion prevalence and maximum water velocity at the (a) minimum (small, dark blue) and maximum (large, light blue) time at low salinity observed in the dataset, (b) minimum (small, yellow) and maximum (large, purple) maximum annual temperature (˚C) observed in the dataset, and (c) minimum (small, dark blue) and maximum (large, light blue) depth observed in the dataset. Points are the lesion prevalence (%) observed at each of 10 sites (see Figure C7).**

Table C1. Candidate models evaluated in the AICc analysis.

ID	Model
1	~ Intercept
2	~ Max temp
3	~ (Salinity < 25)
4	~ Daily temp var
5	~ Max velocity
6	~ REI
7	~ Overwater structures
8	~ Riparian mod
9	~ Depth
10	~ Daily temp var + Max temp
11	~ Max velocity + Max temp
12	~ REI + Max temp
13	~ Overwater structures + Max temp
14	~ Riparian mod + Max temp
15	~ Depth + Max temp

ID	Model
16	~ Daily temp var + (Salinity < 25)
17	~ Max velocity + (Salinity < 25)
18	~ REI + (Salinity < 25)
19	~ Overwater structures + (Salinity < 25)
20	~ Riparian mod + (Salinity < 25)
21	~ Depth + (Salinity < 25)
22	~ Max velocity + Daily temp var
23	~ REI + Daily temp var
24	~ Overwater structures + Daily temp var
25	~ Riparian mod + Daily temp var
26	~ Depth + Daily temp var
27	~ REI + Max velocity
28	~ Overwater structures + Max velocity
29	~ Riparian mod + Max velocity
30	~ Depth + Max velocity
31	~ Riparian mod + Overwater structures
32	~ Depth + Overwater structures
33	~ Depth + Riparian mod
34	~ PC1
35	~ PC2
36	~ PC1 + PC2