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

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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 seven bioregions with a global net loss of 5602 km^2 (19.1% of surveyed meadow area) occurring since 1880. 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 North Atlantic East, Temperate Southern Oceans and Tropical Indo-Pacific), with declining trends being the slowest and most consistent in the latter two bioregions. In some bioregions, trends have recently stabilised or reversed. 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.

KEYWORDS
attribution, coastal ecosystems, global change, meta-analysis, reconstruction, seagrass, time series

1 | 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.

2 | METHODS

2.1 | Study selection

We used Web of Science and Scopus to systematically search the peer-reviewed literature for studies that resampled seagrass meadow area over time. We updated the database of seagrass area time series in Waycott et al. (2009), by performing a search on 18 January 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 and 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 S1). 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, that is, *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 meadow area and were thus included.

2.2 | 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 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. two 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 (McClanahan et al., 2014), which precluded a meta-analysis of change in species composition.

2.3 | 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.

2.4 | 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

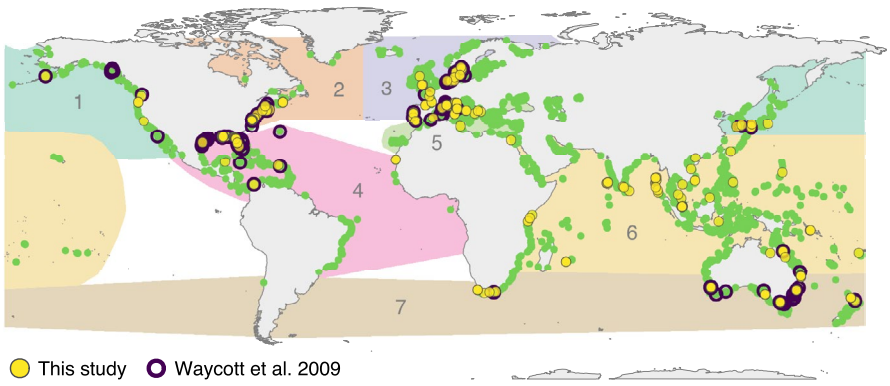

FIGURE 1 Global distribution of seagrass (green; data from UNEP-WCMC & Short, 2021), with sites (n = 219) from Waycott et al. (2009) and additional sites (n = 323) from this study. Included are the seagrass bioregions adapted from Short et al. (2007): 1. Temperate North Pacific, 2. Temperate North Atlantic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

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 GAMs 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:

$$\log_e(\text{area}_t) = \alpha + f(\text{year}_t) + f_{\text{site}_i}(\text{year}_t) + f(\text{site\_group}_i) + \varepsilon_t,\ \varepsilon_t \sim N(0, \sigma^2) \quad (1)$$

where $f(\text{year}_t)$ is the shared bioregional trend, $f_{\text{site\_}i}(\text{year}_t)$ is a site-specific trend that accounted for site-level deviations from the bioregional trend, and $f(\text{site\_group}_i)$ 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. There were sufficient data to fit GAMs in all bioregions, and include sites that had only been sampled at two time points, except for the Mediterranean. To fit the GAM for the Mediterranean we excluded 16 sites, which had only been sampled at two time points. Then, to reconstruct the time series of these 16 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 Supporting Information – Sensitivity Analysis. However, we believe it is important that we present the full dataset in Figure 2, which includes the less data-rich decades prior to the 1950s because omitting them severely shifts the baselines of the trends.

We then used the reconstructed time series to examine (1) bioregional trends in mean meadow 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 (Equation 2) and the fraction of meadow size relative to the maximum area ever observed at a site (Equation 3).

$$\text{annual rate of change}_{\text{decade}} = \frac{\ln\left(\frac{\text{area}_{\text{decade}_f}}{\text{area}_{\text{decade}_i}}\right)}{\text{year}_{\text{decade}_f} - \text{year}_{\text{decade}_i}} \quad (2)$$

$$\text{fraction of maximum observed}_{\text{decade}} = \frac{\text{area}_{\text{decade}_i}}{\text{maximum area observed in time series}} \quad (3)$$

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 area observed. We did the same with just the sites included in Waycott et al. (2009) to provide a visual comparison between our studies.

2.5 | 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 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.

3 | RESULTS

3.1 | 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 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 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.

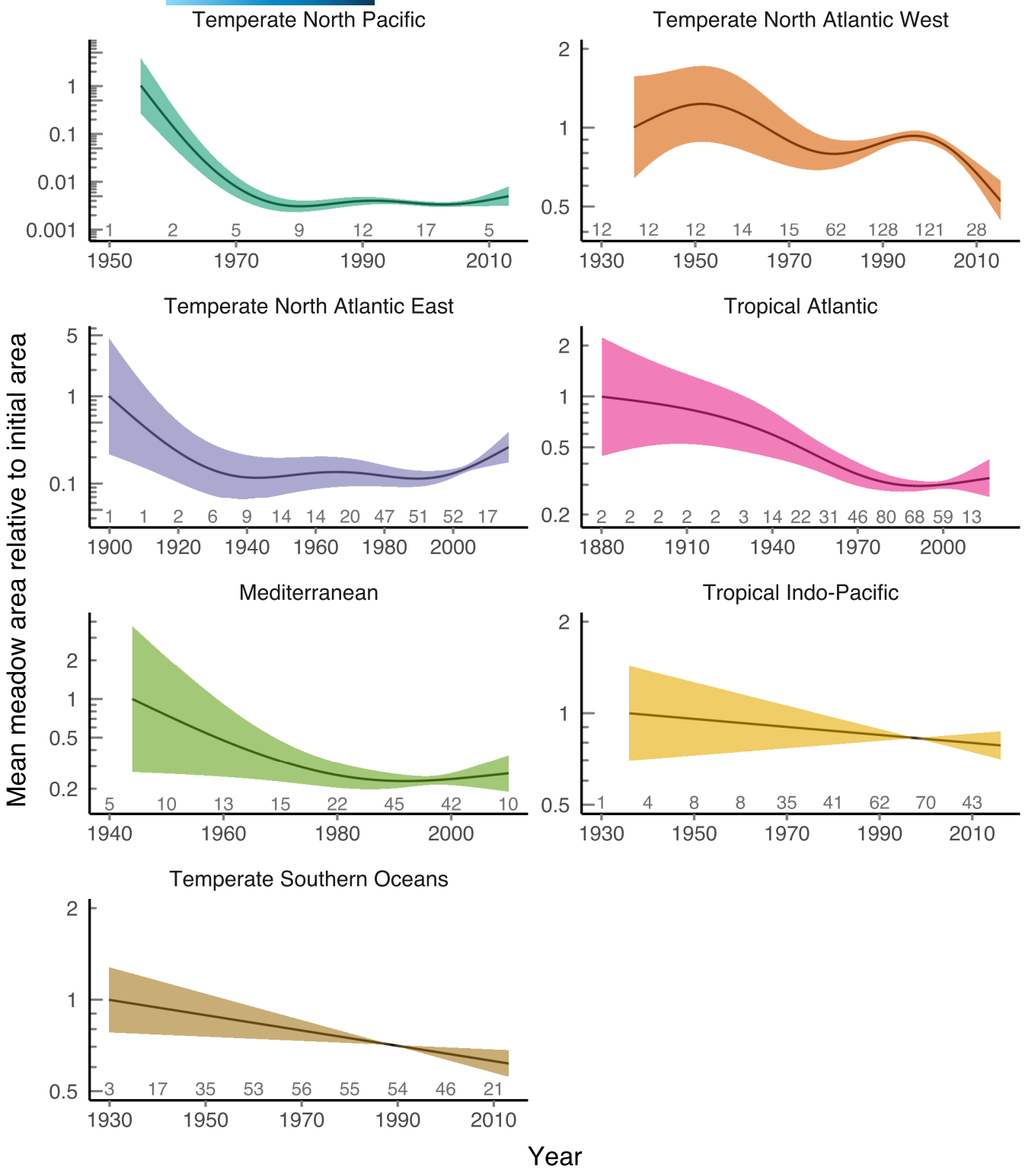

FIGURE 2 Bioregional trends in seagrass meadow area over time, estimated using bioregion-specific generalised additive models (GAMs). Mean meadow area is expressed as a proportion of the meadow area observed in the initial surveys, averaged across sites for each bioregion, and on a $\log_{10}$ scale, such that a change from 1 to 0.1 equals a 10-fold decrease in seagrass area over time. The shaded 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 [Colour figure can be viewed at wileyonlinelibrary.com]

In our database, study durations ranged from 1 to 127 years (Figure S2), with 140 studies (70%) containing time series of 10 years or more (Table S1). Studies with the longest durations were typically sampled using aerial photography. However, one historical record was from ship surveys in 1900, resulting in a 99-year time series in Limfjorden, Denmark (Krause-Jensen et al., 2012). Across studies, meadows were usually

TABLE 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 were 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 that were coupled with temporal trends in seagrass meadow area.

TABLE 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	−69.0	−420	17	−437	608	1900–2016
Tropical Atlantic	−32.3	−3301	183	−3485	10,218	1880–2013
Temperate Southern Oceans	−22.4	−326	121	−446	1455	1930–2013
Tropical Indo-Pacific	−16.2	−96	75	−171	592	1945–2016
Mediterranean	−9.9	−1477	25	−1502	14,958	1900–2012
Temperate North Pacific	0.6	6	75	−69	971	1955–2013
Temperate North Atlantic West	2.3	11	57	−46	492	1960–2015
Global	−19.1	−5602	554	−6156	29,293	1880–2016

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 the authors in the text. In our database, most studies (61%) had no indication of a priori expectations (Table S2). 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 trajectories (e.g. U-shaped).

3.2 | 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). However, a net loss of 5602 km^2 of seagrass has occurred since 1880, which represents a 19.1% loss of the total area surveyed (i.e. 29,293 km^2; Figure S3).

Seagrass meadows in all bioregions have experienced declines in meadow area (Figure 2; Figure S4). Most of the bioregions exhibited non-linear trajectories, with the exception of the Tropical Indo-Pacific and the Temperate Southern Oceans (Figure 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 the Temperate North Pacific and the Temperate North 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). However, these rapid early declines were inferred from fewer than six sites (see number of sites labelled on the *x*-axis Figure 2). In general, by the 1940s more sites and total seagrass area were sampled across all bioregions (Figure 2; Figure S5). 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 North 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 North Atlantic East has seen a marked recovery since 2000, although the areal extent remains ~70% 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 and 1992 (Table 2). Meanwhile the Temperate North Atlantic East experienced the highest percent loss relative to the maximum total area surveyed in this bioregion (69%; Table 2). Most of this

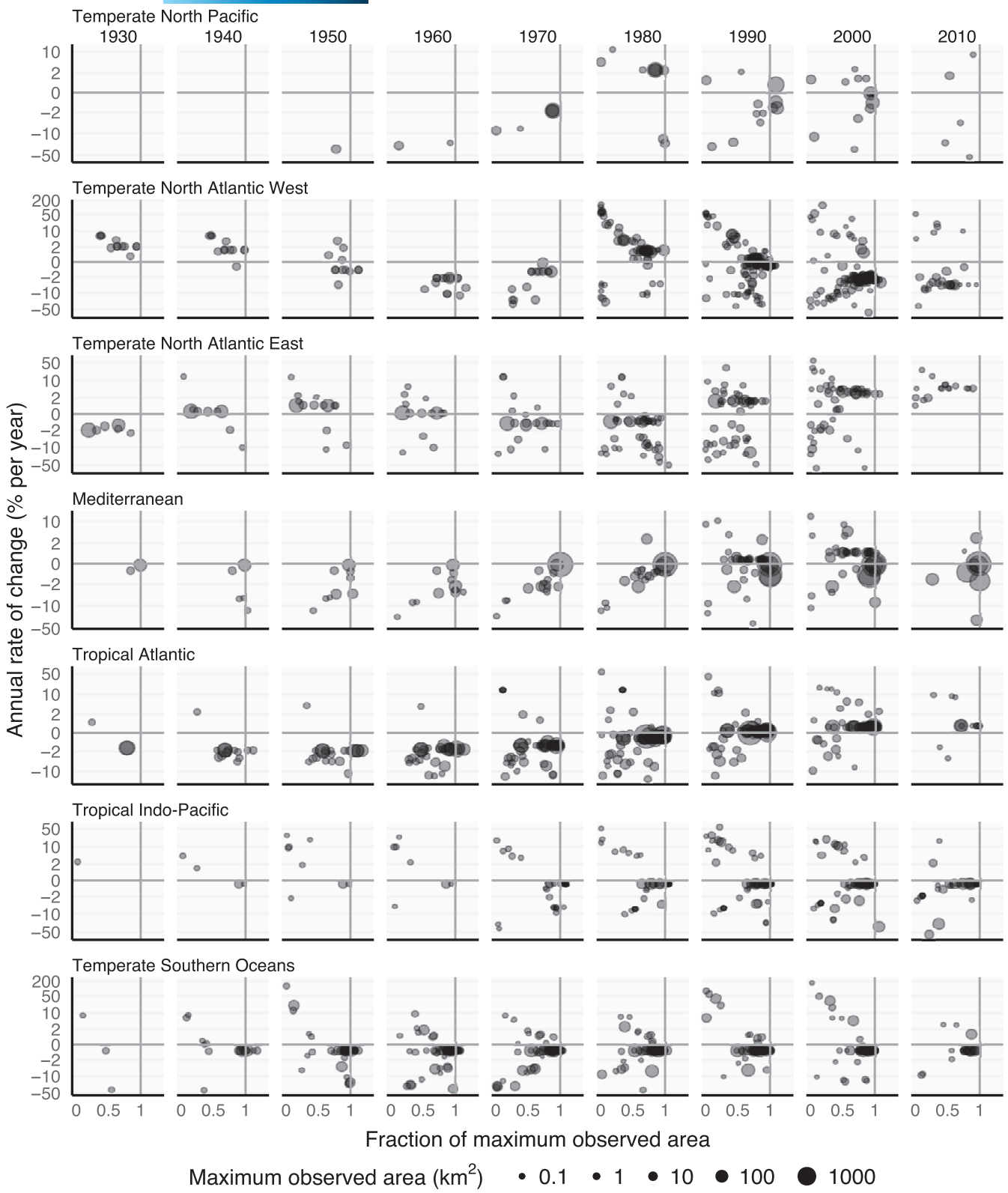

FIGURE 3 Status of seagrass meadows over time and across bioregions. Each point represents the status of one seagrass meadow in a given decade, while point size represents the maximum area observed for that meadow. Meadows that have experienced more severe losses will be farther on the left of a panel; 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

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). In absolute terms, the greatest loss of seagrass meadows reported was in the Tropical Atlantic and Mediterranean bioregions (Table 2).

3.3 | Status of individual seagrass meadows over time

Despite declines in seagrass meadow area across bioregions, changes in individual meadow area were highly variable (Figure 3; Figure S6). On average, annual rates of change were centred near zero (Figure 3; Figure S7) 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). 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 3; Figure S8). Additionally, meadows larger than 1000 ha tended to have slower rates of change than smaller meadows (Figure S9), though there was no clear relationship between the coefficient of variation across time series and the maximum observed area (Figure S10).

3.4 | Attribution to drivers

Attributions to potential drivers of change were primarily descriptive (>40%; Figure 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.

Poor water quality and coastal development were the most common primary drivers identified by study authors (Figure 5) and were typically considered in study discussions. However, water quality was more likely than other drivers to be visually compared with trends in seagrass meadow area over time (Figure S11) or tested using inferential statistics. Coastal development was a broad category that included activities and environmental changes ranging from watershed land use change to port development (Table S3). 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 S12) and at five of these nine sites, the interventions were related to water quality (Supporting information - Supplementary Figures: Table S3).

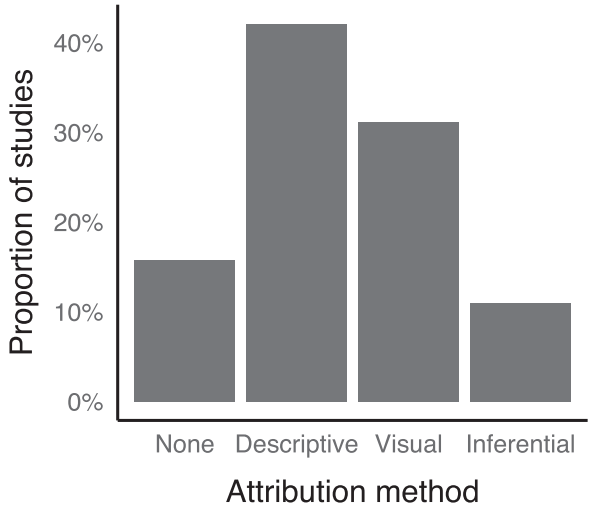

FIGURE 4 Proportion of studies in each of the four categories of causal attribution method. The methods are described in Table 1 and are shown in order of strength of attribution

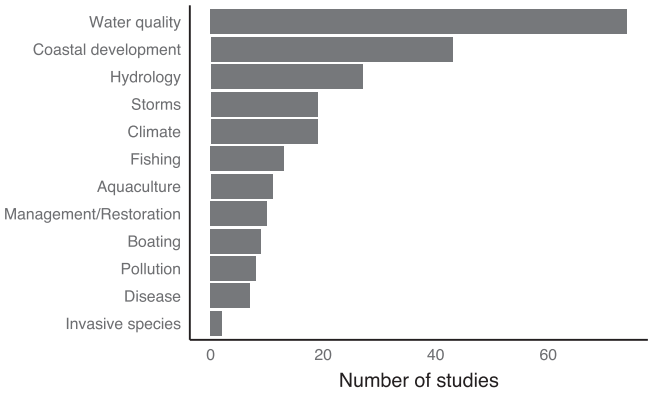

FIGURE 5 Frequency of the primary drivers cited as potential drivers of change in seagrass meadow area. Examples of specific drivers considered in each driver category are detailed in Table S3

4 | 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 on 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.

4.1 | 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 length and timing of data series and/or the number and identity of sites surveyed. For example, the early record in the Temperate North 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 North 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 (Supporting Information – 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 the 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 North Atlantic East and the Tropical Atlantic, the loss of a single large meadow in each of these two bioregions (Limfjorden for the Temperate North 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 North Atlantic West and Temperate North Pacific have shown little fluctuation in seagrass meadow area, with minimal gains and losses. Time series from the Temperate North 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 Temperate 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.

4.2 | 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 analysed 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. In addition, the 7% decline reported by Waycott pertained only to declining meadows, not to all meadows as is the case for our figures of decline. Interpretation of the status plots of all sites in each dataset (Figure S13) 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, Figure 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 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 decrease. 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.

4.3 | 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 1950s baseline, despite a human 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 quality 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 quality 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., 2019; 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 et al., 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.

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DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available on Github at http://doi.org/10.5281/zenodo.4743275.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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