



SYMPOSIUM

Taking the Pulse of Resilience in Conserving Seagrass Meadows

Olivia J. Graham¹, Drew Harvell^{*}, Bart Christiaen[†], Jeff Gaeckle[‡], Lillian R. Aoki[§], Baylen Ratliff[§], Audrey Vinton^{*}, Brendan H. Rappazzo[¶] and Tina Whitman^{¶,||}

^{*}Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA.; [†]Washington State Department of Natural Resources, Olympia, WA 47027, USA; [‡]Department of Environmental Studies, University of Oregon, Eugene, OR 97403-1245, USA; [§]College of the Environment, University of Washington, Seattle, WA 98105, USA; [¶]Department of Computer Science, Cornell University, Ithaca, NY 14853, USA.; ^{||}Friends of the San Juans, Friday Harbor, WA 98250, USA

The first two authors contributed equally to this work.

From the symposium “The scale of resilience: mechanisms of recovery across biological systems” presented at the annual meeting of the Society for Integrative and Comparative Biology, in Seattle, Washington, USA from January 2-6, 2024.

¹E-mail: ojg5@cornell.edu

Synopsis Foundational habitats such as seagrasses and coral reefs are at severe risk globally from climate warming. Infectious disease associated with warming events is both a cause of decline and an indicator of stress in both habitats. Since new approaches are needed to detect refugia and design climate-smart networks of marine protected areas, we test the hypothesis that the health of eelgrass (*Zostera marina*) in temperate ecosystems can serve as a proxy indicative of higher resilience and help pinpoint refugia. Eelgrass meadows worldwide are at risk from environmental stressors, including climate warming and disease. Disease outbreaks of *Labyrinthula zosterae* are associated with recent, widespread declines in eelgrass meadows throughout the San Juan Islands, Washington, USA. Machine language learning, drone surveys, and molecular diagnostics reveal climate impacts on seagrass wasting disease prevalence (proportion of infected individuals) and severity (proportion of infected leaf area) from San Diego, California, to Alaska. Given that warmer temperatures favor many pathogens such as *L. zosterae*, we hypothesize that absent or low disease severity in meadows could indicate eelgrass resilience to climate and pathogenic stressors. Regional surveys showed the San Juan Islands as a hotspot for both high disease prevalence and severity, and surveys throughout the Northeast Pacific indicated higher prevalence and severity in intertidal, rather than subtidal, meadows. Further, among sites with eelgrass declines, losses were more pronounced at sites with shallower eelgrass meadows. We suggest that deeper meadows with the lowest disease severity will be refuges from future warming and pathogenic stressors in the Northeast Pacific. Disease monitoring may be a useful conservation approach for marine foundation species, as low or absent disease severity can pinpoint resilient refugia that should be prioritized for future conservation efforts. Even in declining or at-risk habitats, disease surveys can help identify meadows that may contain especially resilient individuals for future restoration efforts. Our approach of using disease as a pulse point for eelgrass resilience to multiple stressors could be applied to other habitats such as coral reefs to inform conservation and management decisions.

Introduction

Around the world, there is increasing urgency for improved conservation efforts to safeguard our planet and biota against climate change. Climate stress is eroding our highest biodiversity foundational habitats such as coral reefs and seagrasses (Ramírez et al. 2017; Smale et al. 2019; Wernberg et al. 2024). Pathogens fueled by warming temperatures further strain organisms, pushing them—in some cases—to the brink of

endangerment (Harvell et al. 2019; Gravem et al. 2021). Amid mounting pressure from heat waves and pathogens, implementing timely strategies to enhance resilience of marine foundation species is crucial. One approach is to increase marine protected areas (MPAs). For example, the United Nations established a global target to protect 30% of global ocean waters and land area by 2030 (Convention on Biological Diversity 2022), and new regional programs such as Unlocking Blue

Advance Access publication July 25, 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

Pacific Prosperity are creating opportunities to implement wider coastal protections ([Unlocking Blue Pacific Prosperity](#)). In the Washington state, the recent Senate Bill 5619 requires the implementation of a conservation plan to protect and restore 10,000 acres (~4050 ha) of kelp and eelgrass (*Zostera marina*), a temperate seagrass, throughout the state by 2040 (SB 5619, 2022). Ideally, large swaths of the coast could be protected and managed to bolster resiliency, but, practically, specific eelgrass meadows and kelp beds need to be strategically identified and prioritized for conservation to reach this target. In this time of simultaneous opportunity and shifting ocean stress, a clear priority is learning how to identify climate-resilient sites for conservation and management in a rapidly changing ocean ([Tittensor et al. 2019](#); [Wilson et al. 2020](#); [Grorud-Colvert et al. 2021](#); [Doxa et al. 2022](#)).

New approaches to design “climate-smart” networks of marine reserves include identifying climate refugia ([Arafeh-Dalmau et al. 2023](#)). An essential first step in identifying priority conservation areas is developing reliable, early measures of resilience. We suggest that evaluating the health of resident biota, particularly foundation species, can be an effective, integrative approach to assess coastal resilience.

Particularly important biota are foundation species such as corals and seagrasses, which have experienced dramatic declines in the last decade and are at severe risk globally from climate warming ([Ramírez et al. 2017](#); [Smale et al. 2019](#); [Wernberg et al. 2024](#)). Sea surface temperatures set record highs in 2023 ([Cheng et al. 2024](#)), and marine heat waves are projected to increase in frequency and intensity ([Oliver et al. 2019](#)). Direct and indirect effects of climate change and heat waves pose significant threats to marine foundation species ([Smale et al. 2019](#); [Smith et al. 2023](#); [Wernberg et al. 2024](#)). Direct heat stress can kill corals (reviewed in [Wernberg et al. 2024](#)) and seagrasses. For example, 1300 km² of seagrass meadows collapsed in Shark Bay, Western Australia, following the 2011 marine heat wave ([Serrano et al. 2021](#)). Thermal stressors impact individual species and erode community and ecosystem functions. The Shark Bay seagrass die-off resulted in the decline of many seagrass-associated species, ranging from sea snakes to dugongs, and compromised the meadow’s ecosystem services ([Serrano et al. 2021](#)). Thus, warming ocean temperatures can have cascading ecological effects, particularly when foundation species are at risk.

Ocean warming can also heighten disease risk ([Burge et al. 2014](#); [Harvell 2019](#); [Harvell et al. 2019](#); [Tracy et al. 2019](#); [Groner et al. 2021](#); [Aoki et al. 2022](#)), and the combination of warming and disease accelerates species declines ([Aoki et al. 2023](#); [Wernberg et al. 2024](#)). Surveyed seagrass meadows have lost an estimated 19% globally

since the 1880s ([Dunic et al. 2021](#)), due to warming, anthropogenic stressors, and pathogens, including the protist *Labyrinthula zosterae*, the causative agent of seagrass wasting disease. Historic disease outbreaks decimated eelgrass along the Atlantic Coasts of the United States and Europe ([Renn 1936](#)) and continue today, especially in the Northeast Pacific. In particular, high disease severity coincides with warmer sea surface temperatures ([Groner et al. 2021](#); [Aoki et al. 2023](#)) and widespread eelgrass declines ([Christiaen et al. 2022](#)) in the San Juan Islands, Washington, USA ([Fig. 1A–C](#)). Declining eelgrass may be less resilient to increasingly intense and frequent marine heat waves and pathogenic stressors such as *L. zosterae*. Monitoring this ecologically significant pathogen across broad spatiotemporal gradients necessitates creative, interdisciplinary approaches such as machine language learning and drone surveys.

Machine language learning ([Rappazzo et al. 2021](#); [Fig. 1D and E](#)) and drones ([Aoki et al. 2023](#); [Yang et al. 2023](#)) are valuable tools that enable rapid, accurate quantification of disease conditions and allow for larger-scale disease surveys. Disease surveys paired with an artificial intelligence program, drone mapping, and molecular diagnostics revealed increased *L. zosterae* risk at warming sites from San Diego, California, to Alaska ([Aoki et al. 2022, 2023](#)). At the same time, other surveys quantified lower disease in deeper eelgrass meadows, suggesting that they may provide valuable refugia from climate and disease stressors ([Jakobsson-Thor et al. 2018](#); [Graham et al. 2023](#); [Fig. 2](#)). This, coupled with recent declines in the San Juan Islands, underscores the need for further investigation of regional seagrass wasting disease risk and eelgrass decline, with a focus on thinking ahead to identifying signs of meadow resilience and locations of refugia from climate stress.

Several approaches to boosting coastal resilience include designing climate-smart MPAs and assisted evolution. Climate-smart MPAs help bolster biodiversity and support ecosystem resilience to climate change stressors, by increasing either organisms’ tolerance or ability to adapt ([Merwin et al. 2020](#)). Although they cannot protect against all climate stressors, well-designed MPA networks can mitigate damage by promoting resilience and including climate refugia. Recent studies show the value of MPAs in climate proofing or aiding recovery from thermal stress ([Arafeh-Dalmau et al. 2023](#); [Smith et al. 2022](#); [Ziegler et al. 2023](#)). For example, following a 2-year marine heat wave near California, fish trophic diversity increased faster in MPAs compared to reference sites ([Ziegler et al. 2023](#)). In Baja California Sur, Mexico, pink and green abalone recovered more rapidly in no-take reserves than non-reserves

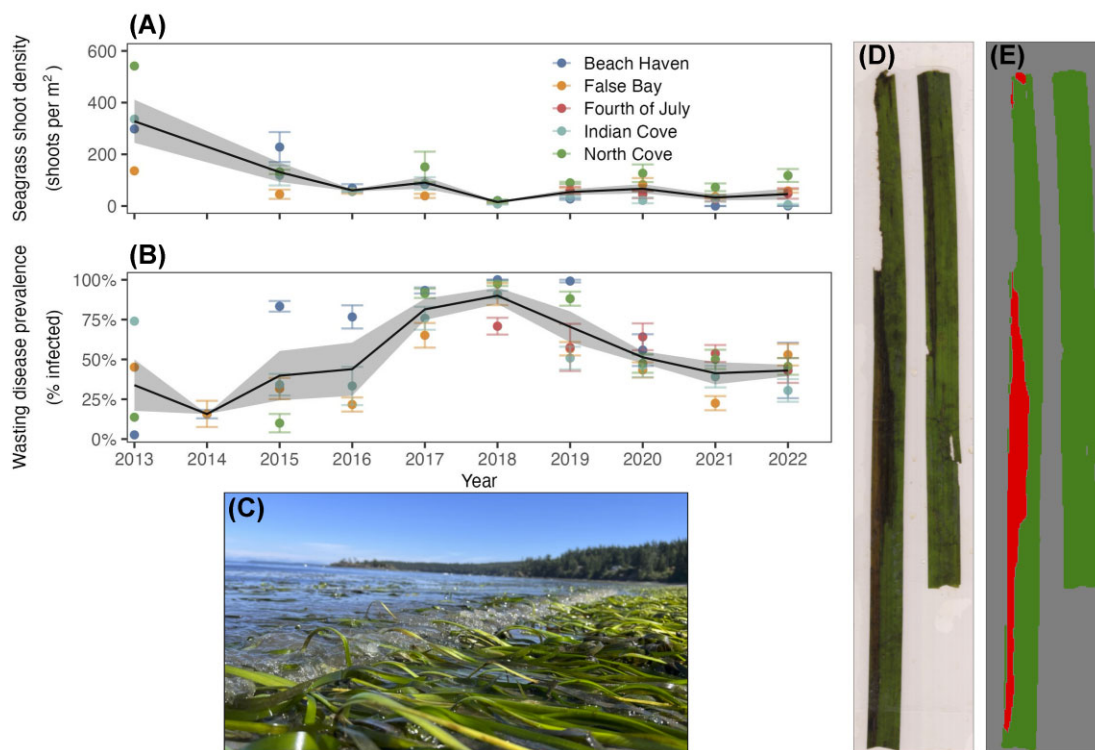


Fig. 1 A decade of health surveys of eelgrass meadows in the San Juan Islands, Washington, USA, indicate dramatic declines in eelgrass densities (A) coincident with high disease prevalence (B). The dark lines indicate regional means with 95% confidence intervals in lighter shading; points indicate site-level means with standard error bars. Eelgrass exposed to high temperatures at low tide is especially vulnerable to disease and climate stressors (C). High-resolution, scanned images of eelgrass leaves (D) allow for precise disease analyses via an artificial intelligence application (E).

following a mass mortality event (Smith et al. 2022). These studies underscore the value in establishing MPAs to expand the coverage of protections for our oceans and help future-proof marine environments from multiple stressors.

Health is a vital metric in future-proofing foundational ecosystems such as coral reefs and seagrass meadows. One hypothesis is that infectious disease can be quantified in one-time surveys to gauge future resilience. Monitoring foundation species such as eelgrass can be especially useful in evaluating coastal resilience, as they are widely considered sentinels of marine health (Purvaja et al. 2018). New tools such as drone imagery provide increasingly more efficient ways to scale up disease and health surveys (Yang et al. 2023). Disease monitoring is useful not only for identifying resilient meadows that should be prioritized for conservation efforts, but also for highlighting at-risk sites exposed to stressful environmental conditions. Understanding which sites are at the brink of stability is equally valuable, as the remaining individuals in these challenging environments could be especially resilient. These could then be used in conservation efforts such as assisted evolution, an approach that is proving to be increasingly valuable for future-proofing corals (Palumbi et al.

2014; Morikawa and Palumbi 2019; Colton et al. 2022) and potentially seagrasses (Pazzaglia et al. 2021) against warming temperatures. Here, we provide a case study of climate and disease impacts to eelgrass meadows in the Northeast Pacific, emphasize the need for predictive resilience mapping, and review new approaches to leveraging health surveys in seagrass meadows as a proxy for future resilience. We also draw connections to lessons learned from MPA development and assisted evolution for corals, another marine foundation species, and suggest approaches to integrating these into conservation efforts for seagrasses and other species.

Methods

Snorkel surveys and disease analyses

To assess the value of eelgrass health as a proxy for meadow resilience to disease and thermal stressors, we surveyed 11 subtidal eelgrass meadows throughout the San Juan Islands in June and July 2023. We selected sites with a history of long-term monitoring to evaluate 20-year changes in meadow extent and disease assessments. For each survey, we recorded the start time and end time and measured the starting depth from the surface using a transect tape with a weighted end; this enabled us

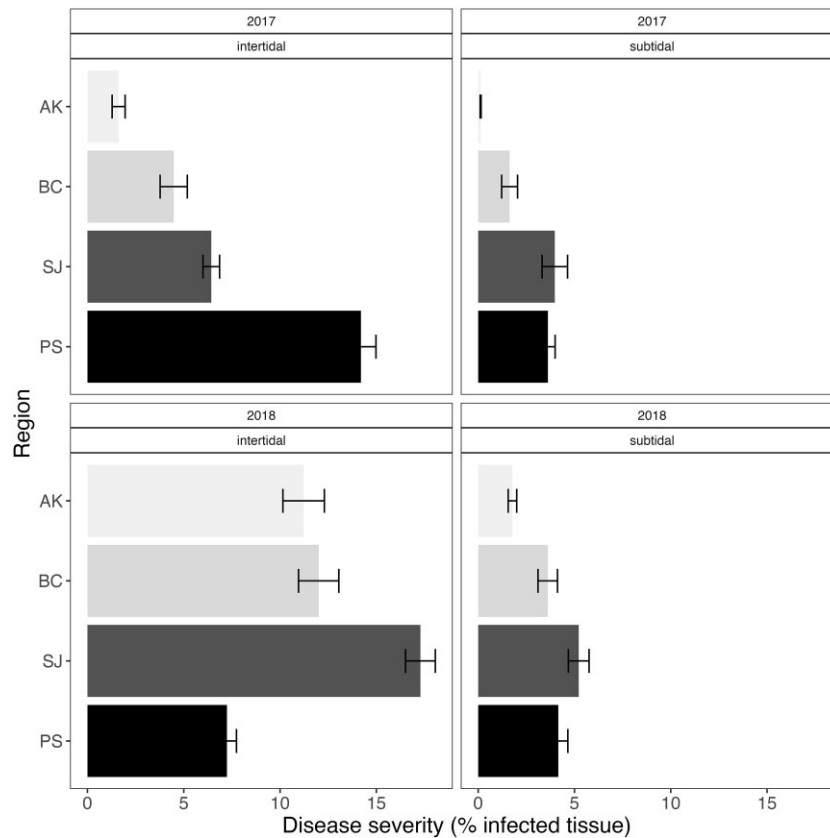


Fig. 2 Seagrass wasting disease surveys spanning 8° of latitude revealed that disease severity was three times less in deeper, subtidal eelgrass meadows than in shallower, intertidal meadows (Wilcoxon signed-rank test, $p < 0.001$, $n = 5761$ eelgrass leaves; adapted from [Graham et al. 2023](#)). Region abbreviations are as follows: AK, Alaska; BC, British Columbia, Canada; SJ, San Juan Islands, Washington; PS, Puget Sound, Washington.

to adjust the depth measurements for each site to meters relative to mean lower low water. For each survey, we collected 20–25 shoots per meadow, collecting one shoot approximately every 3 m, swimming parallel to shore to sample at a consistent depth. Given the range of meadow sizes and extent, we sampled the middle of each meadow to avoid edge effects, taking 10 big “kicks” from an edge before beginning collections. Following each survey, we stored shoots and seawater in Ziplock bags on ice until lab processing within 1–4 h.

Because disease can vary by leaf age ([Groner et al. 2014](#)), we standardized the age of the leaf used for disease analyses. In the lab, we removed the second-rank leaf at the top of the sheath, gently removed epiphytes using flexible rulers, arranged leaves on transparencies, and scanned them using a Cannon CanoScan LiDE 220 scanner at 600 dpi resolution to capture precise images. Subsequently, we ran all images through the Eelgrass Lesion Image Segmentation Analyzer (EeLISA), an artificial intelligence application that rapidly and accurately measures the area of diseased and healthy tissue on eelgrass leaves ([Rappazzo et al. 2021](#); [Aoki et al. 2022, 2023](#); [Graham et al. 2023](#)). We performed all data

organization, analysis, and visualization in R ([R Core Team 2023](#)).

We leveraged fine-scale disease severity (proportion of leaf area covered in lesions) as a key indicator for eelgrass health ([Aoki et al. 2022](#); [Graham et al. 2023](#)). To see whether there were statistically significant differences in mean disease severity between sites, we ran a Kruskal–Wallis test using the “kruskal.test” function, which is part of the *stats* package (version 3.6.2) in base R. As data were not normally distributed, we used a non-parametric test.

Eelgrass 20-year change surveys and data analyses

Given the recent, widespread declines in eelgrass in the San Juan Islands, we re-surveyed eelgrass meadows throughout the San Juans to identify changes in meadow extent over 20 years. At 21 embayments, we collected towed underwater video footage along 10 or more randomly selected transects, oriented perpendicular to shore, using a camera mounted on a tow-fish that we towed approximately 1 m above the sediment surface. At most embayments, we first surveyed

Table 1 Seagrass wasting disease severity and depth at meadows throughout the San Juan Islands, Washington, USA, surveyed in summer 2023.

Site name	n	Site depth (m)	Mean disease severity \pm SE (% leaf area infected)
Salmon Banks	25	-5.43	0.08 \pm 0.072
Fourth of July	22	-2.77	0.70 \pm 0.45
Mosquito Pass	21	-2.74	0.40 \pm 0.25
North Cove	25	-2.55	0.82 \pm 0.54
North Shore	22	-2.33	1.49 \pm 0.81
False Bay	22	-1.89	0
Beach Haven	24	-1.85	0
Mud Bay	22	-1.85	0.82 \pm 0.34
Indian Cove	24	-1.81	2.25 \pm 1.13
Fisherman's Bay	23	-1.72	5.38 \pm 1.96
Hunter Bay	21	-1.66	1.07 \pm 0.71

in 2003/2004 and subsequently re-surveyed in summer 2023 using the same set of transects. We analyzed the video footage to identify eelgrass presence or absence at 1 s intervals, associated each observation with GPS and depth data, and calculated the length of the vegetated portion of transects in ArcGIS, a geographic information system software. To assess whether meadows changed over time, we compared the vegetated length along repeat transects at each site using paired *t*-tests via the “t.test” function in base R. If data were not normally distributed, we used a Wilcoxon signed-rank test instead. We visualized the shallow and deep edges of meadows at each site with boxplots of the depths of all eelgrass observations per site during the initial survey.

Results

Disease surveys

Disease severity varied among the 11 initial sites (Kruskal–Wallis test, χ^2 (10, $n = 251$) = 60.12, $p < 0.001$; Table 1). Site-level mean disease severity ranged from 0% at Beach Haven, Orcas Island, and False Bay, San Juan Island to $5.38 \pm 1.96\%$ SE at Indian Cove, Shaw Island. Initial analyses indicate that deeper meadows had reduced disease—particularly those below -2 m mean lower low water—compared to shallower meadows (Table 1).

Eelgrass 20-year change analysis surveys

Sites with eelgrass declines outnumbered sites with increases 3 to 1 in the San Juan Islands (Table 2). Most sites with eelgrass declines were shallow. Losses occurred throughout the bed but were often most pronounced in shallow areas near the head of the bay. At some

locations, such as Westcott Bay and Blind Bay, eelgrass completely disappeared from the shallower head of the embayment. We observed the opposite pattern at sites with increases in eelgrass cover. Here, eelgrass tended to grow at deeper depths and gains were mostly found in the subtidal (Fig. 3).

Discussion

Key findings from long-term eelgrass monitoring

From 10 years of surveying seagrass wasting disease dynamics in the San Juan Islands, Washington, and 20-year change analyses of eelgrass meadows, we found the following:

- (1) High disease prevalence was associated with warming ocean temperatures along the Pacific Coast, USA (Groner et al. 2021; Aoki et al. 2022; Graham et al. 2023).
- (2) A 10-year survey showed region-wide declines in eelgrass shoot density (average 14.05% loss across all sites) and increases in seagrass wasting disease prevalence (average 9.17% increase across all sites), with a 56.14% increased peak in prevalence in 2018 (Fig. 1).
- (3) Mean disease severity was three times lower in deeper, subtidal meadows compared to shallower, intertidal meadows at the same site (Graham et al. 2023; Fig. 2).
- (4) At 21 embayments in the San Juan Islands, 13 sites with intertidal and shallow subtidal eelgrass declined, while 4 sites with deeper eelgrass beds were stable and 4 increased over 20 years (Fig. 3).
- (5) Drone mapping in some locations detected seagrass wasting disease (Aoki et al. 2023; Yang et al. 2023).

We advance the hypothesis that health is one useful proxy for eelgrass resilience and is a valuable tool for assessing resilient and at-risk meadows for future preservation. We suggest disease surveys can help pinpoint specific meadows that are more resilient to climate and pathogenic stressors and that can be prioritized for future conservation efforts, directly supporting the statewide effort to protect 10,000 acres (~ 4050 ha) of the Washington state eelgrass and kelp in the next 16 years (SB 5619, 2022). Our study supports the emerging hypothesis that some deeper eelgrass meadows are refugia against climate and disease stressors, as we found reduced disease at deeper sites, consistent with previous studies (Jakobsson-Thor et al. 2018; Graham et al. 2023). Through subsequent

Table 2 Pairwise comparisons of vegetated length (with eelgrass) along repeat transects at 21 embayments, sampled over an ~ 20-year monitoring interval.

Embayment	Interval	Test	# transects	Test statistic	p-value	Trend	
Barlow Bay	2003–2023	Paired t-test	11	$t = -4.52$	<0.001	Decline	
Blind Bay	2003–2023	Wilcoxon	38	$W = 0$	<0.001	Decline	
Fisherman Bay	2003–2023	Paired t-test	23	$t = -2.07$	0.050	Decline	
Garrison Bay	2003–2023	Wilcoxon	13	$W = 0$	0.006	Decline	
Hunter Bay	2002–2023	Paired t-test	14	$t = -3.72$	0.003	Decline	
Picnic Cove	2004–2023	Wilcoxon	13	$W = 0$	<0.001	Decline	
Prevost Harbor	2003–2023	Paired t-test	10	$t = -3.59$	0.006	Decline	
Reef Net Bay	2006–2023	Wilcoxon	14	$W = 30$	0.173	Potential decline*	
Secret Harbor	2010–2023	Wilcoxon	11	$W = 0$	<0.001	Decline	
Shallow Bay	2003–2023	Paired t-test	12	$t = -4.4$	<0.001	Decline	
Shoal Bay	2003–2023	Wilcoxon	17	$W = 0$	<0.001	Decline	
Swifts Bay	2004–2023	Paired t-test	23	$t = -5.41$	<0.001	Decline	
Westcott Bay	2000–2023	Complete loss (~15 ha) between 2000 and 2003, no recovery in 2023					Decline
Mitchell Bay	2003–2023	Wilcoxon	13	$W = 65$	0.005	Increase	
Nelson Bay	2003–2023	Wilcoxon	14	$W = 61$	0.092	Potential increase**	
Salmon Bank	2003–2023	Wilcoxon	13	$W = 69$	0.021	Increase	
Thatcher Bay	2003–2023	Paired t-test	14	$t = 3.51$	0.004	Increase	
Eagle Harbor	2017–2023	Wilcoxon	12	$W = 52$	0.100	No trend	
False Bay	2004–2023	Paired t-test	8	$t = 0.65$	0.534	No trend	
Fossil Bay	2004–2023	Paired t-test	10	$t = -0.18$	0.859	No trend	
Mud Bay	2003–2023	Wilcoxon	19	$W = 58$	0.623	No trend	

*Analysis of additional samples, taken in different years, suggests substantial decline in an area not covered by the simple random sample of transects repeated in 2006 and 2023

**Significant at $\alpha = 0.1$

Data were tested using either paired t-tests or Wilcoxon signed-rank tests (in the case of non-normality). At one location (Westcott Bay), most eelgrass had already disappeared at the time of the initial survey in 2003. Earlier survey data collected by the Washington State Department of Natural Resources indicate a loss of ~15 ha between 2000 and 2003.

analyses, we aim to examine the relationship between meadow stability and disease risk. Our results align with recent analyses of a 12-year restoration project in Virginia, wherein depth was a critical predictor of both eelgrass restoration success and resilience following marine heat wave disturbance; eelgrass at intermediate depths, ranging from -0.8 to -1.5 m below mean sea level, survived longer following restoration compared to shallower or deeper sites (Aoki et al. 2020). The same likely applies to eelgrass climate and disease refugia, which presumably exist at intermediate depths. Naturally, there is not a “one-size-fits-all” approach to marine conservation and climate resiliency, so our suggested approach of using disease as an indicator for eelgrass resilience may not be appropriate for all meadows globally. However, it can be a valuable tool in some regions, such as the Northeast Pacific, that have high disease levels and dramatic eelgrass declines coinciding with warming ocean temperatures.

Future-proofing foundational habitats (Jackson et al. 2014; Wood et al. 2019) for climate resilience is the management challenge of our time. As climate stress continues to intensify, pinpointing predictors of future resilience to protect valuable habitats should be a first line of attack, as conserving habitats is faster and less risky and costly than restoring damaged habitats (Arico 2024). New, climate-smart restoration methods can then serve as useful, secondary approaches. Indeed, understanding drivers of eelgrass health can help inform restoration approaches and meet—or exceed—habitat target goals and improve species models under future climate change scenarios (Ward and Beheshti 2023). A central tenet of restoration ecology is that the damaging stressor(s) must be removed before restoration can be successful (Hobbs and Harris 2001), and this is not possible as climate stress intensifies. Recent analyses of 82 eelgrass restoration projects spanning the West Coast, USA, indicated that 32.3–59.6% of restoration plots were unsuccessful, depending on how suc-

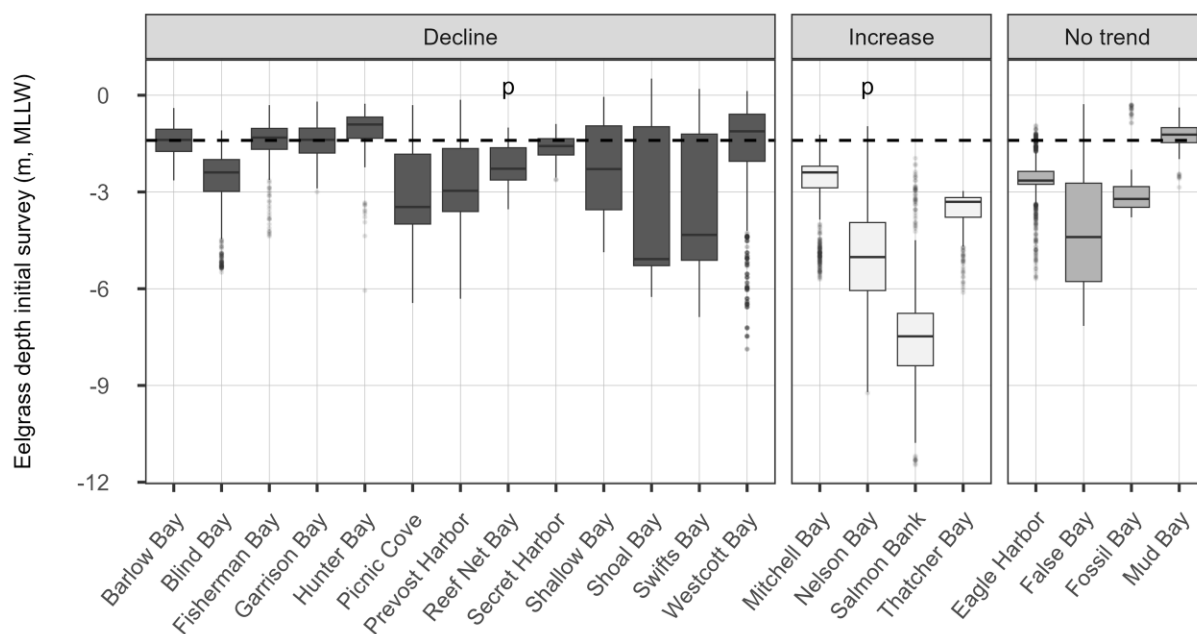


Fig. 3 Boxplot of eelgrass depth observations during the initial survey of a 20-year change analysis at 21 embayments in the San Juan Islands, Washington, USA. Colors indicate how eelgrass beds changed over time. The dotted line is the extreme low tide line in the Puget Sound area of the Washington state (-1.4 m, mean lower low water). Sites with a p indicate lower confidence in a potential trend. Sites with intertidal and shallow subtidal eelgrass often experienced declines, while sites with deeper eelgrass beds were mostly stable or increasing.

cess was defined (Ward and Beheshti 2023). As such, it can be much more valuable and effective to proactively protect stable, healthy habitats such as eelgrass rather than solely relying on restoration to revive degraded habitats.

Designing climate-smart MPAs is a powerful approach for conserving resilient marine habitats. Ongoing monitoring programs can provide valuable insights into the health and stability of marine species, such as the Washington State Department of Natural Resources' Submerged Vegetation Monitoring Program (Christiaen et al. 2022), which tracks the status and trends of seagrasses statewide. Integrating health metrics into similar monitoring programs can provide another valuable indicator for resilience and highlight key sites for conservation and/or restoration activities such as assisted evolution. Of course, when developing creative, timely methods for marine conservation, it is imperative to share and learn from successful conservation approaches for other marine foundation species. While climate-smart conservation approaches such as identifying climate refugia and assisted evolution are still relatively new in the seagrass world (Pazzaglia et al. 2021), they are more advanced for coral reefs due to corals' more narrow thermal tolerances and three decades of catastrophic declines from ocean warming. As such, coral research can inform potential future-proofing approaches to help secure the survival of seagrasses and other marine foundation species. For example, while

climate forecasting shows coral reefs that are vulnerable to future heat and disease stress (Maynard et al. 2015), it also indicates locations with a history of heat stress that have been valuable areas for natural selection for future heat resilience (Drury 2020; Fox et al. 2021). Just as disease surveys highlight deeper, healthier eelgrass meadows as priority conservation sites in the Northeast Pacific (Graham et al. 2023), so too do these climate projections show key coral reefs for targeted, proactive coastal management approaches, including breeding for thermal tolerance or preservation as refugia. Recent efforts in coral conservation include the search for "super corals" (Palumbi et al. 2014; Morikawa and Palumbi 2019; Colton et al. 2022), heat-resistant genotypes that may exist as remnant populations in heat-stressed areas.

One approach to future-proofing coral reefs is to assist evolution of heat or disease tolerance. Multiple groups worldwide are working to select for heat-resistant corals, including Steve Palumbi and his team, who seek out coral reefs that are unusually heat resistant and harbor unusual genetic strains (Palumbi et al. 2014; Morikawa and Palumbi 2019; Cornwell et al. 2021; Walker et al. 2022). Working in Palau, their team visually evaluates coral bleaching and mortality following short-term heat stress (Cornwell et al. 2021; Walker et al. 2022) and aims to identify "super reefs" that have experienced and survived unusual warming and could be prioritized for future conservation efforts. For example, reciprocal coral transplants showed that those

from warmer areas had enhanced thermal resilience compared to corals from cooler regions (Palumbi et al. 2014). Further, after the 2015 heat wave in American Samoa, nursery coral stock from heat tolerant parents demonstrated two to three times less bleaching than corals from less heat tolerant parents (Morikawa and Palumbi 2019). They named this approach of raising thermally resilient coral genotypes “conservation engineering” (Morikawa and Palumbi 2019). Various approaches to conservation engineering are underway in many habitats worldwide (Ibáñez et al. 2013; Havens et al. 2015; Pazzaglia et al. 2021). What stands out in these examples is the use of proxies in initial design to expedite the time needed to select optimal genotypes. For example, researchers and community groups in Fiji work closely to design small, locally managed protected areas that are refuges for heat tolerant corals, their photosymbionts, and diverse reef–fish assemblages (Clements et al. 2012). As our oceans face mounting stressors, we must apply these types of creative conservation approaches to other marine foundation species.

A key component of climate-smart resilience and future-proofing ecosystems is the ability of plants and animals to evolve in response to stressors. Resilient habitats are either protected from localized stressors or inhabited by genotypes that can withstand the stress. We suggest that successful coastal management strategies for foundation species such as eelgrass will involve (1) pinpointing habitats that are resilient to climate stress and (2) identifying or engineering resilient genotypes. Our focus in this paper is to show an approach to rapidly identifying eelgrass meadows that are resilient to climate and disease stressors. However, it is key to understand that successfully managing regional foundation species will likely involve preserving a portfolio of both stressed and resilient sites to assist evolution of resistance to heat and pathogenic stressors. While an unhealthy site may not likely thrive in the future, it may harbor unusual heat- or disease-resistant genotypes. In this way, one way forward to climate-smart management is to maintain a portfolio of “good and bad” sites that encompass a variety of environmental conditions to maintain genetic variants (Fox et al. 2021; Colton et al. 2022).

Although we emphasize the value of identifying and conserving resilient sites as a first line of attack, future-proofing seagrasses will also involve managing for thermal tolerance (Serrano et al. 2021). New work is underway to test approaches to engineering heat resistance in seagrasses. In the first report of stress memory in seagrasses, plants that were exposed to an initial, simulated heat wave had significantly higher photosynthetic capacity, leaf growth, and chlorophyll *a* content when exposed to a second simulated heat wave,

compared to plants that had not experienced the initial heat wave (Nguyen et al. 2020). Further, recent experiments with the Mediterranean seagrass *Posidonia oceanica* demonstrated that seedlings primed to a simulated warming event performed better than unprimed controls, reflected by improved physiology and growth rates and high expression of genes associated with stress, photosynthesis, and epigenetics (Pazzaglia et al. 2022). Experiments with eelgrass exposed to a simulated heat wave revealed that previous heat treatments altered plant morphology and growth across multiple generations and years (DuBois et al. 2020) and that cold-water adapted plants could not recover (Franssen et al. 2011). Recent mesocosm experiments also demonstrated that eelgrass exposed to elevated seawater temperatures (+5.6°C) for 1–2 years had compromised shoot production rates and elevated disease prevalence and severity in the summer, indicating that warming ocean temperatures could impact long-term eelgrass declines in Puget Sound, Washington, USA (Breiter et al. 2024). Collectively, this work suggests that the thermal conditions in which plants live influence their heat tolerance; exposing seagrasses to increased thermal stress could prime them for future warming conditions or they could be bred for thermal resilience (Pazzaglia et al. 2021).

A front line of attack in climate-smart conservation is developing metrics of resilience that can aid rapid, wide-scale assessments to predict future success. While the sensitivity of corals to bleach when heat stressed is an extremely useful metric of condition, other foundation taxa such as seagrasses do not reliably bleach, and other measures of stress and resilience are needed. We suggest the use of selected disease syndromes of seagrasses such as eelgrass that are known to vary with heat stress as indicators and initial proxies for heat- and disease-resistant genotypes and locations. Identification of presumptive resilient meadows and genotypes is only the beginning, but proxies for resilience can shorten the time needed to future-proof marine habitats. As such, we suggest that eelgrass disease can be a useful indicator for meadow resilience.

These collective examples provide an option for a way forward in future-proofing our coastal ecosystems for resilience. Managers can detect and incorporate resilient sites or refugia into MPA networks to help marine organisms survive in rapidly changing environments. At the same time, impacted sites can naturally select for rare, heat- or disease-tolerant individuals that could be used in assisted evolution approaches, including restoration focused on resilient genotypes. To effectively safeguard these valuable marine ecosystems against climate and disease stressors, we suggest an approach that not only protects and conserves a port-

folio of habitats that are connected (Harrison et al. 2020; Gignoux-Wolfsohn et al. 2024) and at risk from long-term loss from anthropogenic stressors (e.g., overfishing, pollution), but also assists evolution to enhance species resilience. More broadly, conservation initiatives such as MPAs, management, and restoration of habitats such as eelgrass need to be strategically implemented in targeted areas and expanded to increase impacts (Langhammer et al. 2024).

Author contributions

OJG, DH, and LRA helped conduct the 10-year disease surveys; LRA made Fig. 1(A) and (B). OJG, BR, AV, and TW conducted the 2023 subtidal snorkel surveys; OG made Fig. 2 and Table 1; BR created the video abstract. BC and JG conducted the 20-year change analysis and made Fig. 3 and Table 2. BHR developed the EeLISA that we used for disease analyses and created Fig. 1(D) and (E). DH envisioned this paper; OJG and DH drafted the manuscript with input and suggestions from all coauthors.

Acknowledgments

We would like to thank our terrific research assistants who helped with the summer 2023 surveys: Jess Newley, Katherine Dietzman, Holly Durham-Guckian, Nickie Davis, Greg Lange, Kari Koski, Sharon Massey, Yuki Wilmerding, Hayley Turner, and Lauren Johnson. We also thank Steve Palumbi and all the participants for organizing and co-leading with DH the graduate discussion group on Climate Proofing MPAs at Hopkins Marine Station. We also appreciate the thoughtful feedback from Dr. Andrea Liebl, Dr. Ione Hunt von Herbing, and two anonymous reviewers. Finally, we would like to thank Dr. Emily Le Sage, Cori Richards-Zawacki, Jamie Voyles, and Cherie Briggs for organizing the research symposium, “The scale of resilience: mechanisms of recovery across biological systems,” at the 2024 Society for Integrative and Comparative Biology (SICB) meeting. This paper is part of the special issue associated with this symposium.

Funding

This work was supported by grants to Friends of the San Juans [SeaDoc Society, grant UC Davis A23-3414-S002; US Fish and Wildlife Service, grant F19AC00363; WA State Salmon Recovery Funding Board, grant RCO-22-1423] and NSF Bio-Oce grant #2109607 to DH (co-PIs Maya Groner, Colleen Burge, and Eileen Hofmann).

Supplementary data

Supplementary data available at ICB online.

Conflict of interest

The authors do not have any conflicts of interest to declare.

Data availability

Data underlying this article will be shared on reasonable request to the corresponding author.

References

- Aoki LR, McGlathery KJ, Wiberg PL, Al-Haj A. 2020. Depth affects seagrass restoration success and resilience to marine heat wave disturbance. *Estuaries Coasts* 43:316–28. <https://doi.org/10.1007/s12237-019-00685-0>
- Aoki LR, Rappazzo B, Beatty DS, Domke LK, Eckert GL, Eisenlord ME, Graham OJ, Harper L, Hawthorne T, Hessing-Lewis M et al. 2022. Disease surveillance by artificial intelligence links eelgrass wasting disease to ocean warming across latitudes. *Limnol Oceanogr* 67:1577–89. <https://doi.org/10.1002/lno.12152>
- Aoki LR, Yang B, Graham O, Gomes C, Rappazzo B, Hawthorne T, Duffy E, Harvell D. 2023. UAV high-resolution imaging and disease surveys combine to quantify climate-related decline in seagrass meadows. In *Frontiers in Ocean Observing: Emerging Technologies* Emerging Technologies for Understanding and Managing a Changing Ocean Kappel E.S., Cullen V., Costello M.J., Galgani L., Gordó-Vilaseca C., Govindarajan A., Kouhi S., Lavin C., McCartin L., Müller J.D., Pirenne B., Tanhua T., Zhao Q., Zhao S. eds, *Oceanography* 36(Supplement 1), <https://doi.org/10.5670/oceanog.2023.s1.12>
- Aráfeh-Dalmau N, Munguia-Vega A, Micheli F, Vilalta-Navas A, Villaseñor-Derbez JC, Précoma-De La Mora M, Schoeman DS, Medellín-Ortiz A, Cavanaugh KC, Sosa-Nishizaki O et al. 2023. Integrating climate adaptation and transboundary management: guidelines for designing climate-smart marine protected areas. *One Earth* 6:1523–41. <https://doi.org/10.1016/j.oneear.2023.10.002>
- Arico S. 2024. Seagrass science in an international cooperation and policy context: a game-changer opportunity not to miss. In: *World Seagrass Conference, Naples, Italy*. <https://www.isbw15.it/plenary-speakers>. Accessed on July 8, 2024.
- Unlocking Blue Pacific Prosperity. Pacific Community. <https://www.spc.int/ubpp>. Accessed on July 31, 2023.
- Breiter AL, Sokoloski CT, Yang S, Gaeckle JL. 2024. Effect of prolonged seawater warming on *Zostera marina* ecotypes of the northeast Pacific. *J Exp Mar Biol Ecol* 578:152036. <https://doi.org/10.1016/j.jembe.2024.152036>
- Burge CA, Mark Eakin C, Friedman CS, Froelich B, Hershberger PK, Hofmann EE, Petes LE, Prager KC, Weil E, Willis BL et al. 2014. Climate change influences on marine infectious diseases: implications for management and society. *Annu Rev Mar Sci* 6:249–77. <https://doi.org/10.1146/annurev-marine-010213-135029>
- Cheng L, Abraham J, Trenberth KE, Boyer T, Mann ME, Zhu J, Wang F, Yu F, Locarnini R, Fasullo J et al. 2024. New record ocean temperatures and related climate indicators in 2023. *Adv Atmos Sci* 41:1068–82. <https://doi.org/10.1007/s00376-024-3378-5>

- Christiaan B, Ferrier L, Dowty P, Gaeckle J, Berry H. 2022. Puget sound seagrass monitoring report, monitoring year 2018–2020. Olympia (WA): Washington State Department of Natural Resources. https://www.dnr.wa.gov/publications/aqr_nrs_h_svm_monitoring_report_2018_2020_data.pdf. Accessed on July 8, 2024.
- Clements C, Bonito V, Grober-Dunsmore R, Sobey M. 2012. Effects of small, Fijian community-based marine protected areas on exploited reef fishes. *Mar Ecol Prog Ser* 449:233–43. <https://doi.org/10.3354/meps09554>
- Colton MA, McManus LC, Schindler DE, Mumby PJ, Palumbi SR, Webster MM, Essington TE, Fox HE, Forrest DL, Schill SR et al. 2022. Coral conservation in a warming world must harness evolutionary adaptation. *Nat Ecol Evol* 6:1405–7. <http://doi.org/10.1038/s41559-022-01854-4>
- Convention on Biological Diversity. 2022 December 19, Montreal, Canada, 1–15. Accessed on July 8, 2024. <https://www.cb.d.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf>
- Cornwell B, Armstrong K, Walker NS, Lippert M, Nestor V, Golbuu Y, Palumbi SR. 2021. Widespread variation in heat tolerance and symbiont load are associated with growth trade-offs in the coral *Acropora hyacinthus* in Palau. *eLife* 10:e64790. <https://doi.org/10.7554/eLife.64790>
- Doxa A, Almpandou V, Katsanevakis S, Queirós AM, Kaschner K, Garilao C, Kesner-Reyes K, Mazaris AD. 2022. 4D marine conservation networks: combining 3D prioritization of present and future biodiversity with climatic refugia. *Glob Chang Biol* 28:4577–88. <https://doi.org/10.1111/gcb.16268>
- Drury C. 2020. Resilience in reef-building corals: the ecological and evolutionary importance of the host response to thermal stress. *Mol Ecol* 29:448–65. <https://doi.org/10.1111/mec.15337>
- Dubois K, Williams SL, Stachowicz JJ. 2020. Previous exposure mediates the response of eelgrass to future warming via clonal transgenerational plasticity. *Ecology* 101:e03169. <https://doi.org/10.1002/ecy.3169>
- 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. *Glob Chang Biol* 27:4096–109. <https://doi.org/10.1111/gcb.15684>
- Fox MD, Cohen AL, Rotjan RD, Mangubhai S, Sandin SA, Smith JE, Thorrold SR, Dissly L, Mollica NR, Obura D. 2021. Increasing coral reef resilience through successive marine heatwaves. *Geophys Res Lett* 48:e2021GL094128. <https://doi.org/10.1029/2021GL094128>
- Franssen SU, Gu J, Bergmann N, Winters G, Klostermeier UC, Rosenstiel P, Bornberg-Bauer E, Reusch TBH. 2011. Transcriptomic resilience to global warming in the seagrass *Zostera marina*, a marine foundation species. *Proc Natl Acad Sci USA* 108:19276–81. <https://doi.org/10.1073/pnas.1107680108>
- Gignoux-Wolfsohn SA, Dunn DC, Cleary J, Halpin PN, Anderson CR, Bax NJ, Canonico G, Chaniotis P, Deland S, Diorio M et al. 2024. New framework reveals gaps in US ocean biodiversity protection. *One Earth* 7:31–43. <https://doi.org/10.1016/j.oneear.2023.12.014>
- Graham OJ, Stephens T, Rappazzo B, Klohmann C, Dayal S, Adamczyk EM, Olson A, Hessing-Lewis M, Eisenlord M, Yang B et al. 2023. Deeper habitats and cooler temperatures moderate a climate-driven seagrass disease. *Phil Trans R Soc B* 378:20220016. <https://doi.org/10.1098/rstb.2022.0016>
- Gravem S, Heady W, Saccomanno V, Alvstad K, Gehman A, Frierson T, Hamilton S. 2021. *Pycnopodia helianthoides*. In: IUCN red list of threatened species. https://rodrigoebas.com/wp-content/uploads/2023/06/2021_01_iucn_pycno.pdf. Accessed on July 8, 2024.
- Groner M, Burge C, Couch C, Kim C, Siegmund G, Singhal S, Smoot S, Jarrell A, Gaydos J, Harvell C et al. 2014. Host demography influences the prevalence and severity of eelgrass wasting disease. *Dis Aquat Org* 108:165–75. <https://doi.org/10.3354/dao02709>
- Groner M, Eisenlord M, Yoshioka R, Fiorenza E, Dawkins P, Graham O, Winningham M, Vompe A, Rivlin N, Yang B et al. 2021. Warming sea surface temperatures fuel summer epidemics of eelgrass wasting disease. *Mar Ecol Prog Ser* 679:47–58. <https://doi.org/10.3354/meps13902>
- Grorud-Colvert K, Sullivan-Stack J, Roberts C, Constant V, Horta E Costa B, Pike EP, Kingston N, Laffoley D, Sala E, Claudet J et al. 2021. The MPA guide: a framework to achieve global goals for the ocean. *Science* 373:eabf0861. <https://doi.org/10.1126/science.abf0861>
- Harrison HB, Bode M, Williamson DH, Berumen ML, Jones GP. 2020. A connectivity portfolio effect stabilizes marine reserve performance. *Proc Natl Acad Sci USA* 117:25595–600. <https://doi.org/10.1073/pnas.1920580117>
- Harvell CD, Montecino-Latorre D, Caldwell JM, Burt JM, Bosley K, Keller A, Heron SF, Salomon AK, Lee L, Pontier O et al. 2019. Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). *Sci Adv* 5:eaa07042. <https://doi.org/10.1126/sciadv.aau7042>
- Harvell D. 2019. Ocean outbreak: confronting the rising tide of marine disease. Oakland, California, USA. University of California Press.
- Havens K, Vitt P, Still S, Kramer AT, Fant JB, Schatz K. 2015. Seed sourcing for restoration in an era of climate change. *Nat Areas J* 35:122–33. <https://doi.org/10.3375/043.035.0116>
- Hobbs RJ, Harris JA. 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restor Ecol* 9:239–46. <https://doi.org/10.1046/j.1526-100x.2001.009002239.x>
- Ibáñez I, Gornish ES, Buckley L, Debinski DM, Hellmann J, Helmut B, Hillerislambers J, Latimer AM, Miller-Rushing AJ, Uriarte M. 2013. Moving forward in global-change ecology: capitalizing on natural variability. *Ecol Evol* 3:170–81. <https://doi.org/10.1002/ece3.433>
- Jackson EL, Davies AJ, Howell KL, Kershaw PJ, Hall-Spencer JM. 2014. Future-proofing marine protected area networks for cold water coral reefs. *ICES J Mar Sci* 71:2621–9. <https://doi.org/10.1093/icesjms/fsu099>
- Jakobsson-Thor S, Toth G, Brakel J, Bockelmann A, Pavia H. 2018. Seagrass wasting disease varies with salinity and depth in natural *Zostera marina* populations. *Mar Ecol Prog Ser* 587:105–15. <https://doi.org/10.3354/meps12406>
- Langhammer PF, Bull JW, Bicknell JE, Oakley JL, Brown MH, Bruford MW, Butchart SHM, Carr JA, Church D, Cooney R et al. 2024. The positive impact of conservation action. *Science* 384:453–458.
- Maynard J, Van Hooidonk R, Eakin CM, Puotinen M, Garren M, Williams G, Heron SF, Lamb J, Weil E, Willis B et al. 2015. Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence.

- Nature Clim Change 5:688–94. <https://doi.org/10.1038/nclimate2625>
- Merwin A, Cooley S, McBee J, Taraska G, Zivian A, Robbins C. 2020. “Climate-Smart” marine protected areas for mitigation and adaptation policy. Ocean Conservancy. https://oceanconservancy.org/wp-content/uploads/2020/07/Climate-Smart-MPAs-Brief_FINAL_7_1_update.pdf. Accessed on July 8, 2024.
- Morikawa MK, Palumbi SR. 2019. Using naturally occurring climate resilient corals to construct bleaching-resistant nurseries. *Proc Natl Acad Sci USA* 116:10586–91. <https://doi.org/10.1073/pnas.1721415116>
- Nguyen HM, Kim M, Ralph PJ, Marín-Guirao L, Pernice M, Procaccini G. 2020. Stress memory in seagrasses: first insight into the effects of thermal priming and the role of epigenetic modifications. *Front Plant Sci* 11:494. <https://doi.org/10.3389/fpls.2020.00494>
- Oliver ECJ, Burrows MT, Donat MG, Sen Gupta A, Alexander LV, Perkins-Kirkpatrick SE, Benthuyse JA, Hobday AJ, Holbrook NJ, Moore PJ et al. 2019. Projected marine heatwaves in the 21st century and the potential for ecological impact. *Front Mar Sci* 6:734. <https://doi.org/10.3389/fmars.2019.00734>
- Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA. 2014. Mechanisms of reef coral resistance to future climate change. *Science* 344:895–8. <https://doi.org/10.1126/science.1251336>
- Pazzaglia J, Badalamenti F, Bernardeau-Esteller J, Ruiz JM, Giacalone VM, Procaccini G, Marín-Guirao L. 2022. Thermal-priming increases heat-stress tolerance in seedlings of the Mediterranean seagrass *P. oceanica*. *Mar Pollut Bull* 174:113164. <https://doi.org/10.1016/j.marpolbul.2021.113164>
- Pazzaglia J, Nguyen HM, Santillán-Sarmiento A, Ruocco M, Dattolo E, Marín-Guirao L, Procaccini G. 2021. The genetic component of seagrass restoration: what we know and the way forwards. *Water* 13:829. <https://doi.org/10.3390/w13060829>
- Purvaja R, Robin RS, Ganguly D, Hariharan G, Singh G, Raghuraman R, Ramesh R. 2018. Seagrass meadows as proxy for assessment of ecosystem health. *Ocean Coast Manag* 159:34–45. <https://doi.org/10.1016/j.ocecoaman.2017.11.026>
- R Core Team. 2023. R: a language and environment for statistical computing. <https://www.R-project.org>. Accessed on May 2, 2024.
- Ramírez F, Afán I, Davis LS, Chiaradia A. 2017. Climate impacts on global hot spots of marine biodiversity. *Sci Adv* 3:e1601198. <https://doi.org/10.1126/sciadv.1601198>
- Rappazzo BH, Eisenlord ME, Graham OJ, Aoki LR, Dawkins PD, Harvell D, Gomes C. 2021. EeLISA: combating global warming through the rapid analysis of eelgrass wasting disease. *Proc AAAI Conf Artif Intell* 35:15156–65.
- Renn CE. 1936. The wasting disease of *Zostera marina*: a phyto-logical investigation of the diseased plant. *Biol Bull* 70:148–58.
- Serrano O, Aria-Ortiz A, Duarte C, Kendrick G, Lavery P. 2021. Impact of marine heatwaves on seagrass ecosystems. In: Canadell J, Jackson R, editors. *Ecosystem collapse and climate change*. Cham: Springer. p. 345–64.
- Smale DA, Wernberg T, Oliver ECJ, Thomsen M, Harvey BP, Straub SC, Burrows MT, Alexander LV, Benthuyse JA, Donat MG et al. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat Clim Chang* 9:306–12. <https://doi.org/10.1038/s41558-019-0412-1>
- Smith A, Aguilar JD, Boch C, De Leo G, Hernández-Velasco A, Houck S, Martinez R, Monismith S, Torre J, Woodson CB et al. 2022. Rapid recovery of depleted abalone in Isla Natividad, Baja California, Mexico. *Ecosphere* 13:e4002. <https://doi.org/10.1002/ecs2.4002>
- Smith KE, Burrows MT, Hobday AJ, King NG, Moore PJ, Sen Gupta A, Thomsen MS, Wernberg T, Smale DA. 2023. Biological Impacts of Marine Heatwaves. *Annu Rev Mar Sci* 15: 119–45. <https://doi.org/10.1146/annurev-marine-032122-121437>
- Tittensor DP, Beger M, Boerder K, Boyce DG, Cavanagh RD, Cosandey-Godin A, Crespo GO, Dunn DC, Ghiffary W, Grant SM et al. 2019. Integrating climate adaptation and biodiversity conservation in the global ocean. *Sci Adv* 5:eaay9969. <https://doi.org/10.1126/sciadv.aay9969>
- Tracy AM, Pielmeier ML, Yoshioka RM, Heron SF, Harvell CD. 2019. Increases and decreases in marine disease reports in an era of global change. *Proc Biol Sci* 286:20191718. <https://doi.org/10.1098/rspb.2019.1718>
- Walker NS, Cornwell BH, Nestor V, Armstrong KC, Golbuu Y, Palumbi SR. 2022. Persistence of phenotypic responses to short-term heat stress in the tabletop coral *Acropora hyacinthus*. *PLoS One* 17:e0269206. <https://doi.org/10.1371/journal.pone.0269206>
- Ward M, Beheshti K. 2023. Lessons learned from over thirty years of eelgrass restoration on the US West Coast. *Ecosphere* 14:e4642. <https://doi.org/10.1002/ecs2.4642>
- Wernberg T, Thomsen MS, Baum JK, Bishop MJ, Bruno JF, Coleman MA, Filbee-Dexter K, Gagnon K, He Q, Murdiyars D et al. 2024. Impacts of climate change on marine foundation species. *Annu Rev Mar Sci* 16:247–82. <https://doi.org/10.1146/annurev-marine-042023-093037>
- Wilson KL, Tittensor DP, Worm B, Lotze HK. 2020. Incorporating climate change adaptation into marine protected area planning. *Glob Chang Biol* 26:3251–67. <https://doi.org/10.1111/gcb.15094>
- Wood G, Marzinelli EM, Coleman MA, Campbell AH, Santini NS, Kajlich L, Verdura J, Wodak J, Steinberg PD, Vergés A. 2019. Restoring subtidal marine macrophytes in the Anthropocene: trajectories and future-proofing. *Mar Freshwater Res* 70:936. <https://doi.org/10.1071/MF18226>
- Yang B, Hawthorne TL, Aoki L, Beatty DS, Copeland T, Domke LK, Eckert GL, Gomes CP, Graham OJ, Harvell CD et al. 2023. Low-altitude UAV imaging accurately quantifies eelgrass wasting disease from Alaska to California. *Geophys Res Lett* 50:e2022GL101985. <https://doi.org/10.1029/2022GL101985>
- Ziegler SL, Johnson JM, Brooks RO, Johnston EM, Mohay JL, Ruttenberg BI, Starr RM, Waltz GT, Wendt DE, Hamilton SL. 2023. Marine protected areas, marine heatwaves, and the resilience of nearshore fish communities. *Sci Rep* 13:1405. <https://doi.org/10.1038/s41598-023-28507-1>