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RESEARCH ARTICLE

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The vulnerability of World Heritage seagrass habitats to climate change

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Abstract

Seagrass is an important natural attribute of 28 World Heritage (WH) properties. These WH seagrass habitats provide a wide range of services to adjacent ecosystems and human communities, and are one of the largest natural carbon sinks on the planet. Climate change is considered the greatest and fastest-growing threat to natural WH properties and evidence of climate-related impacts on seagrass habitats has been growing. The main objective of this study was to assess the vulnerability of WH seagrass habitats to location-specific key climate stressors. Quantitative surveys of seagrass experts and site managers were used to assess exposure, sensitivity and adaptive capacity of WH seagrass habitats to climate stressors, following the Climate Vulnerability Index approach. Over half of WH seagrass habitats have high vulnerability to climate change, mainly from the long-term increase in sea-surface temperature and short-term marine heatwaves. Potential impacts from climate change and certainty scores associated with them were higher than reported by a similar survey-based study from 10 years prior, indicating a shift in stakeholder perspectives during the past decade. Additionally, seagrass experts' opinions on the cumulative impacts of climate and direct-anthropogenic stressors revealed that high temperature in combination with high suspended sediments, eutrophication and hypoxia is likely to provoke a synergistic cumulative (negative) impact ($p < .05$). A key component contributing to the high vulnerability assessments was the low adaptive capacity; however, discrepancies between adaptive capacity scores and qualitative responses suggest that managers of WH seagrass habitats might not be adequately equipped to respond to climate change impacts. This thematic assessment provides valuable information to help prioritize conservation actions, monitoring activities and research in WH seagrass habitats. It also demonstrates the utility of a systematic framework to evaluate the vulnerability of thematic groups of protected areas that share a specific attribute.

KEYWORDS
adaptive capacity, climate vulnerability, cumulative impact, environmental management, marine protected area, seagrass, UNESCO, World Heritage

1 | INTRODUCTION

World Heritage (WH) properties are internationally recognized for their outstanding universal value (OUV), with significance transcending national boundaries, and their permanent protection is of the highest importance for all humankind (UNESCO World Heritage Centre, 2008). For natural WH properties, the OUV is comprised of a combination of attributes (e.g., seagrass, rainforests) that together contribute to each property's outstanding natural beauty, significant geological processes, biological/ecological processes and/or exceptional biodiversity (UNESCO World Heritage Centre, 2008). To effectively manage WH properties, site managers need to identify key attributes contributing to the OUV, and strategies to protect them.

There are at least 28 WH properties where seagrass habitats are important attributes contributing to their OUV (hereafter called WH seagrass habitats; Losciale et al., 2022). WH seagrass habitats are one of the world's most important carbon sinks, storing at least 25% of the global seagrass blue carbon asset (UNESCO, 2020). Hence, the protection of WH seagrass habitats can include nature-based management approaches that help address climate change (Unsworth et al., 2022). WH seagrass habitats also play a significant role in climate change adaptation, through the provision of a wide range of ecosystem services. For example, they provide coastal protection from extreme weather events, through their ability to accumulate and stabilize sediments, and dampen wave action (Boudouresque et al., 2016; De Falco et al., 2017). They function as key nursery habitats for many fish and crustacean species, providing a sustainable source of food, which can ensure subsistence for many communities associated with these properties (Lee Long et al., 2000; Shenker, 2009; Unsworth et al., 2014). Additionally, seagrass habitats play an important role in maintaining WH properties' OUV, by helping to maintain other marine ecosystems' function (i.e., coral reefs, mangroves, and salt marshes), and collectively preserve biodiversity and biological processes (Guannel et al., 2016).

Climate change, the greatest and fastest-growing threat to natural WH properties (Osipova et al., 2020), is driving an increase in the intensity and frequency of extreme weather events, which are threatening seagrass habitats (Frölicher et al., 2018; Marbà & Duarte, 2010; McKenna et al., 2015; Strydom et al., 2020). On a global scale, the documented area of seagrass has declined by 19% since the start of the second industrial revolution, due to the cumulative impacts of direct-anthropogenic and climate stressors (Dunic et al., 2021). The negative impacts of destructive fishing practices and poor water quality, driven by pollution and coastal development, have been well-documented (de Los Santos et al., 2019; Turschwell et al., 2021) but how seagrasses respond to climate stressors is still unclear. Seagrass has received substantially less research effort compared with other coastal ecosystems (Unsworth et al., 2019) and the distribution of seagrass research has high geographical, species, and depth biases. Most studies have been conducted on intertidal seagrass meadows in Europe, the east coast of the USA, and Australia, leaving gaps in knowledge in many parts of the world (Dunic et al., 2021; Waycott et al., 2009).

Recent research showed that 40% of studies providing evidence of seagrass meadow extent trajectories inferred trends based on data from only two time points (Turschwell et al., 2021). Additionally, only 10% of the reviewed studies used inferential statistics to check associations between observed trends and causes (Dunic et al., 2021; Turschwell et al., 2021). Another factor affecting understanding of the impacts of climate change on seagrass is the lack of data about the cumulative impacts of direct-anthropogenic and climate stressors (Stockbridge et al., 2020). The few studies addressing the cumulative impacts of multiple stressors have been principally been undertaken in laboratory conditions and are biased towards a few species of the genera *Posidonia*, *Thalassia*, and *Zostera* (Stockbridge et al., 2020). Currently, the impacts of climate change on WH seagrass habitats are not adequately addressed within management plans nor reported to the WH Committee (Losciale et al., 2022). Hence, there is an urgent need to inform site managers about the vulnerability of WH seagrass habitats to climate change to prevent further seagrass loss, which could lead to an irreversible loss of OUV.

Vulnerability to climate change is a complex and multidimensional concept. The most-widely implemented vulnerability assessment framework is from the Intergovernmental Panel on Climate Change (IPCC, 2007). In this, vulnerability is determined as a function of exposure to a stressor, sensitivity of the system to that stressor and the capacity of the system to adapt (hereafter adaptive capacity) to the potential impacts of that stressor (IPCC, 2007). Multiple stressors can interact to influence the vulnerability of a natural system. As research and long-term monitoring activities within WH seagrass habitats are scarce, broad gaps exist in data about key variables of site-specific seagrass sensitivity—including meadow extent, species composition, meadow form, and habitat types (Kilminster et al., 2015). Moreover, tangible measures of adaptive capacity within WH seagrass habitats have not yet been investigated.

To overcome these limitations, analysis of experts' opinions is a systematic strategy to provide information to site managers and inspire collective action to improve the protection of WH seagrass habitats (Grech et al., 2012; Halpern et al., 2007). Interpretation of experts' opinions has been widely employed to evaluate the impact of anthropogenic activities on marine ecosystems on a global scale (Grech et al., 2012; Halpern et al., 2007; Halpern, McLeod, et al., 2008; Teck et al., 2010). Nevertheless, several studies have broadly addressed the vulnerability of multiple marine ecosystems, drawing results about seagrass vulnerability from only a small number of seagrass experts (Halpern et al., 2007; Teck et al., 2010). Additionally, the few studies specifically addressing seagrass vulnerability mainly focused on the impacts of anthropogenic activities, while lacking questions about climate change stressors (Grech et al., 2011; Holon et al., 2018). Finally, many studies have assumed only additive interactions among stressors, possibly underestimating seagrass vulnerability (Halpern, Walbridge, et al., 2008).

The overarching aim of this study is to provide a consistent approach to inform site managers and other stakeholders about the vulnerability of WH seagrass habitats to key climate stressors. A key objective of this study was to pilot the use of an existing vulnerability assessment for a specific natural attribute contributing to WH properties' OUV. The Climate Vulnerability Index (CVI; https://cvi-heritage.org/) is a rapid and systematic risk assessment tool, specifically developed to evaluate the vulnerability of individual WH properties (or other protected areas) to climate change (Day et al., 2020). The CVI is usually undertaken through a workshop of diverse stakeholders aiming to evaluate exposure, sensitivity, and adaptive capacity to assess OUV and economic-social-cultural vulnerability of individual WH properties (Day et al., 2019; Heron et al., 2021; Heron, Day, Cowell, et al., 2020; Heron, Day, Zijlstra, et al., 2020; Jon Day et al., 2022). However, due to the large number of WH properties and the urgent need for an understanding of and response to climate change, the comprehensive workshop approach cannot practically be undertaken for all properties individually. As outlined by Venkatachalam et al. (2022), a thematic approach can accelerate the understanding of climate change impacts upon areas with similar attributes rather than relying upon assessments of individual properties.

In this study, we pioneer the application of the CVI to a thematic group of WH properties, using the WH seagrass habitat thematic group defined by Losciale et al. (2022) as a case study. Losciale et al. (2022) defined the 'World Heritage seagrass habitats thematic group' as the WH properties that have the common attribute (seagrass habitat) contributing to their OUV. Additionally, the relative importance of this attribute towards the OUV was also assessed through an analysis of UNESCO documents and scientific literature.

This analysis combines seagrass scientists' and site managers' expert opinions on the major climate change and direct-anthropogenic stressors to seagrasses across six global bioregions (Short et al., 2007). The bioregional model proposed by Short et al. (2007) groups regions based on seagrass species distribution and diversity. Here, the assessment considers the variability in exposure and sensitivity of seagrasses across the six bioregions and applies the results to WH seagrass habitats within each region.

Through this analysis, we aim to

1. assess experts' opinions on the key climate stressors affecting seagrasses across bioregions,
2. assess experts' opinions on the cumulative impact of different stressors on seagrasses,
3. assess the site managers' level of adaptive capacity to deal with climate change impacts, and
4. identify gaps in knowledge regarding seagrass vulnerability to help guide future research.

The design of this study allows us to compare the results with the findings of Grech et al. (2012), to understand how experts' opinions may have changed in the past decade. This study provides valuable information to site managers about the vulnerability of their property in relation to other properties sharing the same attribute (in this case seagrass). Additionally, such a thematic vulnerability framework may also be applicable to other marine protected areas containing seagrass, or other thematic groups of protected areas sharing natural attributes where data are lacking (e.g., salt marshes, mangroves; Duarte et al., 2008).

2 | METHODS

2.1 | Survey development

Data were collected through two quantitative surveys using the software Survey Monkey with the Advantage plan. One survey targeted seagrass scientists, while the second survey targeted site managers of WH seagrass habitats. Online surveys were preferred over a focus group method due to the different locations and time zones of the participants (Dowler et al., 2006). The Advantage plan allowed us to embed skip logic and add matrices of dropdown menu questions within the survey, which reduced the completion time, aiding in a higher response rate (Bista & Saleh, 2017). Both surveys were provided to a selection of seagrass experts within our institution (James Cook University) and former site managers from the Great Barrier Reef Marine Park Authority to test them for clarity and completion time.

2.1.1 | Seagrass experts survey

Participating seagrass experts were provided with an information sheet and a consent form before starting the survey. The survey was designed to assess the exposure and sensitivity of seagrasses across bioregions to climate stressors and anthropogenic activities, and how the stressors may interact to produce a cumulative impact. First, participants were asked to select the bioregion (Short et al., 2007) where most of their research was conducted, their years of experience working with seagrass, and whether they had worked in any of the listed WH seagrass habitats. For the bioregion selected, participants were asked to assess six indicators (Table 2) for each of seven climate-related stressors and 12 anthropogenic activities (Table 1), formatted as a matrix. The selection of climate stressors and anthropogenic activities was adapted from Grech et al. (2012). Due to the increased evidence of seagrass mortality caused by marine heatwaves (Marbà & Duarte, 2010; Shields et al., 2019; Strydom et al., 2020) and droughts (De Fouw et al., 2016; El-Hacen et al., 2018), and the recent concern about the potential impacts of seaweed aquaculture (Hedberg et al., 2018; Short et al., 2011; Unsworth et al., 2018), those stressors/activities were also included. Halpern et al. (2007) identified two exposure (spatial scale and frequency) and three sensitivity (functional impact, resistance and recovery time) indicators to assess the vulnerability of ecosystems to different stressors. In this study, following the CVI framework, the 'trend' of the stressor was also added (Day et al., 2020). Participants were also asked to provide a measure of certainty for each of the exposure and sensitivity indicators provided. Certainty was measured on a Likert scale ranging from 1 (Low) to 4 (Very high; Table 2). Having completed the survey for their primary bioregion,

TABLE 1 Climate stressors and anthropogenic activities assessed in the study and associated coding terminology.

Climate stressors		Anthropogenic activities		Cumulative impact summary stressors	
Drought	DR	Agriculture run-off	AR	Eutrophication	EU
Marine heatwaves	MHW	Aquaculture impact	AQI	Increased irradiance	IR
Ocean acidification	OA	Coastal development	CD	High suspended sediments	HSS
Rainfall change	R	Dredging	DRG	High temperature	HT
Sea-level rise	SLR	Large commercial boat anchoring	LCBA	Hypoxia	HY
Sea-surface temperature increase	SST	Large commercial boat pollution	LCBP	Ocean acidification	OA
Storms/cyclones	S	Overfishing	OF	Salinity fluctuation	SF
		Seaweed aquaculture impacts	SWQ	Upwelling	UW
		Small recreational boat anchoring	SRBA		
		Small recreational boat pollution	SRBP		
		Trawling	TRA		
		Urban/industrial run-off	U/IR		

TABLE 2 Scoring system for the indicators of exposure ($n=3$), sensitivity ($n=3$), and certainty by seagrass experts.

	Exposure			Sensitivity			
Score	Spatial scale (km^2)	Frequency	Trend	Functional impact	Resistance	Recovery time (years)	Certainty
1	$x<1$	Never occurs	Decreasing	No Impact	High	No Impact	Low
2	$1\leq x<10$	Intermittent	Stable	Only spp. at geographic limit of distribution	Medium	$x\leq 1$	Medium
3	$10\leq x<100$	Occasional	Increasing	≤25% of spp.	Low	$1<x\leq 10$	High
4	$100\leq x<1000$	Frequent		25% $<x\leq$ 50% of spp.		$10<x\leq 100$	Very high
5	$1000\leq x<10{,}000$	Ongoing		50% $<x\leq$ 100% of spp.		$x>100$	
6	$x\geq 10{,}000$						

participants were given the choice to respond for other bioregions with which they were familiar.

The last survey section gathered experts' opinions on the cumulative impact of stressors affecting seagrass. Different climate-related stressors and anthropogenic activities can cause similar consequences for seagrasses; for example, coastal development, dredging, run-off, and an intense storm can all cause an increase in suspended sediments (Erftemeijer & Robin Lewis, 2006; Orth et al., 2006; Preen et al., 1995). Assessments of pairs of all listed stressors/activities would have required experts to respond for 171 possible pairs, significantly increasing the survey completion time. Instead, for this part of the survey, seagrass experts were asked to respond for combinations of eight summary stressors (Table 1). For each pairing of summary stressors, participants were asked to provide the interaction type (i.e., additive, synergistic or antagonistic) and the certainty of their response (Stockbridge et al., 2020).

2.1.2 | Site manager survey

The site manager survey aimed to assess the exposure of their WH property to anthropogenic activities and climate stressors, the level of adaptive capacity, and the relative importance of the seagrass habitat towards the OUV and the community associated with the property. The community was defined as those people who have an economic, social and/or cultural connection with the WH property (Day et al., 2020). First, participants were asked to specify the WH property they work with and their years of experience. These preliminary questions were provided to ensure that participants had the expertise to answer the survey. The exposure of each WH property to the 19 stressors/activities (Table 1) was assessed with the same method used in the experts' survey (see Section 2.1.1). To reduce complexity while adhering to the CVI methodology, the options for the spatial scale were given as percentages of the WH property affected by the stressors (Day et al., 2020). The OUV and community dependencies on the seagrass habitat were assessed through two multiple-choice questions (Table 3). For OUV dependency, participants were asked to select one of six responses describing the importance of seagrass as an attribute of OUV. For community dependency, participants selected as many of the four responses (indicating economic, social, cultural, and subsistence dependency on seagrass habitat) as was appropriate, and the

TABLE 3 Scoring system for the OUV and community dependency of World Heritage properties on their seagrass habitats.

OUV dependency		Community dependency	
Response	Dependency rank	Response	Dependency score (number of responses selected)
The seagrass habitat is the most important attribute towards the OUV of the property	Very high	The seagrass habitat is part or source of the *cultural* heritage of the local community	All 4 responses selected—Very high 3 responses selected—High 2 responses selected—Moderate 1 response selected—Low 0 responses selected—No dependency
The seagrass habitat is a fundamental value towards the OUV of the property	High		
The health of marine species included in the Statement of OUV depends on the integrity of the seagrass habitat (e.g., Dugongs, Manatees, Green turtles, Brant geese)	Moderate	The seagrass habitat is a source of "*social* capital" (e.g., manufacturing asset, aesthetic value, opportunity for leisure)	
The integrity of other marine habitats (e.g., coral reef, mangroves) included in the Statement of OUV depend on the integrity of the seagrass habitat	Low	The seagrass habitat is a direct source of food, critical for the community's *subsistence*	
The seagrass habitat is not important towards the OUV of the property	Potential	The seagrass habitat is an important source of *economic* income for the community	
No seagrass habitat is present in the property	None		

Note: Category names for community dependency are italicized in the description.
Abbreviation: OUV, outstanding universal value.

score for each participant was calculated based on the number of selected responses (Table 3).

Adaptive capacity was quantitatively assessed through consideration of available resources, scientific/technical support, and effectiveness to address climate change impacts, as outlined in the CVI framework (Day et al., 2020). In a separate email following the completion of the survey, site managers were asked to provide a pragmatic example of current or planned adaptive capacity. The last survey question assessed where each participant sourced the information provided in the survey (e.g., personal experience, scientific evidence). Upon request, the survey was translated from English into French to accommodate the responses of relevant managers.

2.2 | Recruitment

Seagrass experts' email addresses were collected during the development of the WH seagrass habitats thematic group (Losciale et al., 2022). Email addresses of site managers of WH seagrass habitats were sourced from the CVI existing network. Where email addresses were not available, Google Social Search engine was used to search for site managers' Twitter and LinkedIn accounts. In the invitation email, participants were informed about the aim of the survey, the average completion time, and were encouraged to share the survey with other seagrass experts/site managers within their network. To ensure that every participant received the invitation at an optimal time (e.g., 09:00 a.m. or 02:00 p.m.), the time zone of participants was assessed to schedule the invitation delivery. In case of lack of response, two follow-up reminders were sent after 2 weeks and 1 month, respectively. A final reminder was sent 2 weeks before the closure of the survey. The recruitment process was conducted from March 2021 to July 2021.

2.3 | Analysis

2.3.1 | Experts' opinion on global threats to seagrass

Data analysis was performed with the software RStudio V 2021.09.01 (R version 4.2.2). As shown in Table 2, the range of possible responses was different among the exposure and sensitivity indicators, hence, all scores were normalized to the range 1–5 so that each indicator (i.e., spatial scale, frequency, trend, etc.) had the same range of values and equal weighting.

Exposure of seagrass to each stressor in each bioregion was calculated by a weighted average of the mean scores of spatial scale, frequency, and trend, while sensitivity was calculated as the weighted average of the mean scores of functional impact, resistance, and recovery time. The weighting was based on certainty scores provided by respondents. The weighted average was performed with the function "weighted.mean()" from the package {stats}. The arguments were the normalized scores and the certainty scores spanning values from 1 (Low) to 4 (Very high).

The coefficient of variation (CV) among scores was used to assess consensus among seagrass experts. Differences in certainty scores across stressors, indicators and bioregions were also assessed. Differences in mean scores across bioregions and stressors were tested with a one-way ANOVA, while differences in mean scores between climate change and direct anthropogenic stressors were tested with a two-sample *t*-test. The homogeneity of variance was tested with the Levene Test, while the Shapiro–Wilk's Test was used to check for normality. Where normality was not apparent, the Kruskal–Wallis and the Wilcoxon rank sum tests were performed. The Tukey method was used to determine whether there was a difference between the means of exposure, sensitivity, and potential impact scores across all possible pairs of bioregion and stressors. Finally, the potential impact of 19 stressors in six seagrass bioregions was determined by combining weighted averaged exposure and sensitivity scores in a risk matrix approach (Figure 1).

2.3.2 | Cumulative impact

For each pair of summary stressors (Table 1), the cumulative impact was assessed based on the weighted counts of interaction type (i.e., additive, synergistic, or antagonistic) responses for each combination. The weighting was based on the provided certainty. A generalized log-linear model was used to determine whether the interaction between variables had an effect on the corresponding weighted frequencies, through (i) the stressor combination (e.g., eutrophication + high temperature) and (ii) the interaction type (i.e., additive, synergistic, or antagonistic). The model can be summarized as:

$$\text{Weighted frequencies} = \alpha(\text{stressor combination}) \times \beta(\text{interaction type}) + c.$$

Dispersion and residual tests for all regressions were performed with the R package 'DHARMa' (Hartig, 2022), with p values <.05 were considered significant.

2.3.3 | Vulnerability of WH seagrass habitats

For each WH property, the top three climate stressors (hereafter key climate stressors) based on exposure scores from site managers were used in the vulnerability assessment. The potential impact of each key climate stressor on each WH seagrass habitat was calculated using experts' sensitivity scores in the relevant bioregion. Then, the averaged potential impact from the key climate stressors and the adaptive capacity scores were used to determine the vulnerability of each WH seagrass habitat (Figure 2).

The OUV and community dependency on the seagrass habitat was assessed on a five-point scale ranging from "No dependency" to "Very high dependency". The potential impact from the top three direct-anthropogenic stressors was similarly calculated.

3 | RESULTS

3.1 | Response rate

Both surveys received an above-average response rate compared with similar studies and online surveys in general (Cook et al., 2000; Grech et al., 2012; Halpern et al., 2007). The response rate was 45% for the seagrass experts' survey and 49% for the site managers' survey.

3.1.1 | Seagrass experts

In total, 87 seagrass experts were contacted via email, of which 10 were not successfully delivered. Among the 77 experts who received the invitation, 64 opened the survey (83.1%) and 35 (45.5%) completed it. The distribution of responses across bioregions was variable; almost half of the responses came from the Tropical Indo-Pacific bioregion (Figure 3).

3.1.2 | Site managers

Of the 41 site managers' email addresses that were found, 37 invitations were successfully delivered. The survey was opened by 30 site managers (81%) and completed by 18 (49%). Site managers that completed the survey came from 13 WH seagrass habitats across five of the six seagrass bioregions (Temperate Pacific was not represented) (Figure 4). The French translation of the survey was used by site managers from the Banc D'Arguin and the Lagoons of New Caledonia. Exactly half of the responding site managers had more than 10 years of experience in their field, 45% (n = 8) had 1–10 years of experience, while only one (5%) had less than 1 year of experience. Around three-quarters of site managers' responses (n = 13) drew upon scientific evidence, whilst three site managers stated that the responses provided were sourced from consultation with

Exposure	Sensitivity				
	Very Low	Low	Moderate	High	Very High
Very Low	Low	Low	Low	Low	Low
Low	Low	Low	Moderate	Moderate	Moderate
Moderate	Low	Moderate	Moderate	High	High
High	Low	Moderate	High	High	Extreme

FIGURE 1 Risk matrix to assess the potential impact from exposure and sensitivity of each stressor (n = 19) across seagrass bioregion (n = 6). After Day et al. (2020).

Potential Impact	Adaptive Capacity			
	High	Moderate	Low	None
Low	Low	Low	Low	Low
Moderate	Low	Moderate	Moderate	Moderate
High	Moderate	Moderate	Moderate	High
Extreme	Moderate	Moderate	High	High

FIGURE 2 Climate Vulnerability Index risk matrix to assess the vulnerability of World Heritage seagrass habitats from the three selected key climate stressors. After Day et al. (2020).

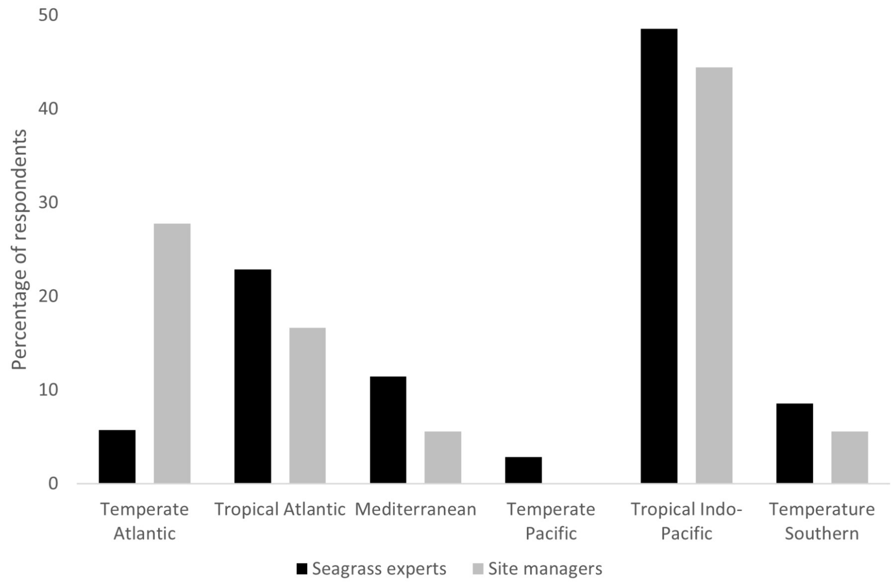

FIGURE 3 Distribution of seagrass experts' ($n=35$) and site managers' ($n=18$) responses across bioregions (defined by Short et al., 2007).

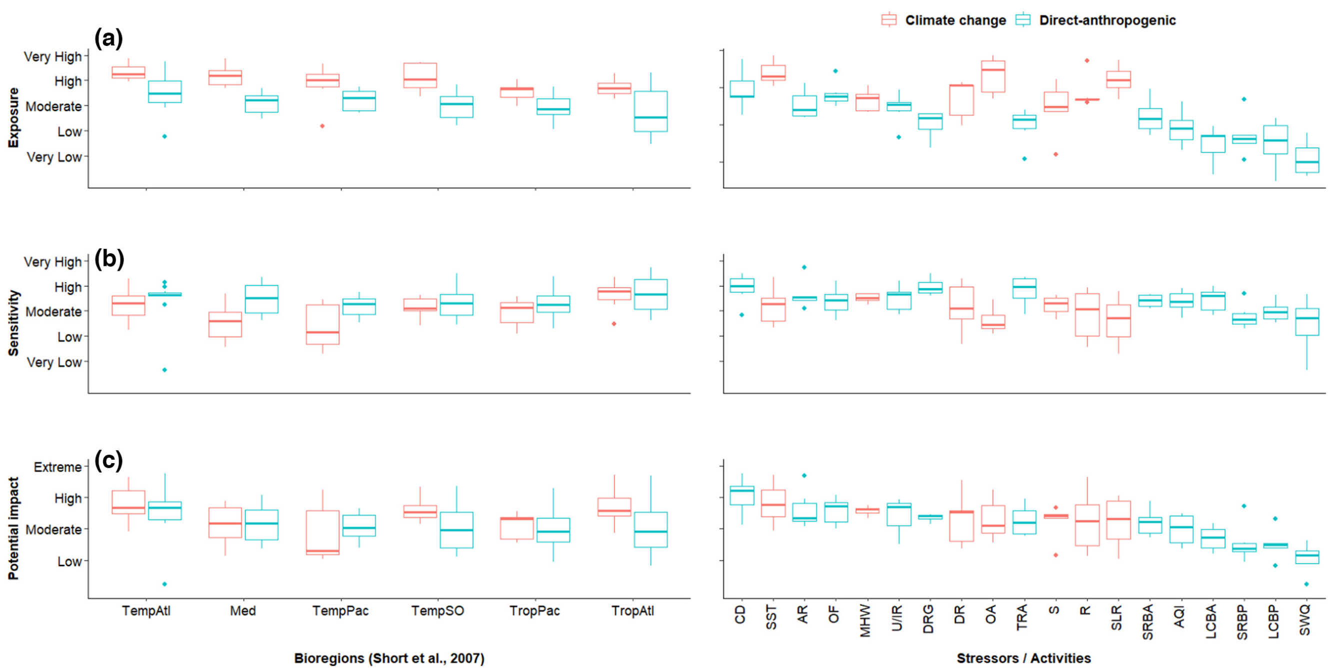

FIGURE 4 Boxplots of (a) exposure, (b) sensitivity, and potential impact (c) scores by seagrass experts across seagrass bioregions (left panels) and stressors (right panels), ordered by potential impact scores. *Bioregions*: Med, Mediterranean; TempAtl, Temperate Atlantic; TempPac, Temperate Pacific; TempSO, Temperate Southern Oceans; TropAtl, Tropical Atlantic; TropPac, Tropical Indo-Pacific. See Table 1 for the list of stressors and corresponding coding terminology.

previous managers and only two site managers drew solely upon personal experience.

3.2 | Potential impacts on seagrass across bioregions

Exposure to climate stressors was consistently higher than for direct-anthropogenic stressors when averaged within bioregions, and typically so when considering individual stressors averaged across all bioregions. The bioregion-average exposure scores across all climate stressors were high in all bioregions (Figure 4a, left). Exposure to sea-surface temperature increase, ocean acidification, and sea-level rise had the highest scores among climate change stressors across bioregions (Figure 4a, right).The exposure scores averaged across all stressors were significantly higher in the Temperate Atlantic compared with the Tropical Atlantic bioregion (Tukey multiple comparisons of means 95% family-wise confidence level, $p<.05$). The average exposure scores across all direct-anthropogenic activities were lower than for climate change stressors in each bioregion ($t = 6.7427$, $p < .05$) and mostly Moderate (Figure 4a, left). The top three direct-anthropogenic stressors by exposure across bioregions were coastal development, overfishing, and agriculture run-off, while large commercial boat anchoring was the only stressor with a low exposure score in all bioregions (Tukey multiple comparisons of means 95% family-wise confidence level, $p < .05$) (Figure 4a, right).

Sensitivity scores were generally lower for climate stressors than for direct-anthropogenic stressors. The bioregion-average sensitivity scores were moderate in all bioregions except for the Tropical Atlantic (high) (Figure 4b, left). The sensitivity of seagrass to individual climate stressors was mostly moderate, except for marine heatwaves which had a high sensitivity score across all bioregions (Figure 4b, right). The average sensitivity scores across all direct-anthropogenic stressors were Moderate across all bioregions except for the Tropical Atlantic (high), and they were higher than the average sensitivity scores across climate stressors (Figure 4b, left). The Wilcoxon rank test showed that the sensitivity score averaged across all stressors was significantly higher in the Tropical Atlantic than the Temperate Pacific bioregion (Kruskal–Wallis chi-squared = 13.766, $p < .05$). Coastal development, trawling and dredging were the top three stressors by sensitivity, while the seaweed aquaculture score was the lowest (low). Agriculture run-off in Tropical Atlantic was the only stressor with a very high sensitivity score (Table 4).

Potential impact, derived from the exposure and sensitivity scores, was typically higher for climate stressors than for direct-anthropogenic stressors when averaged for each bioregion. The bioregion-average potential impact from climate stressors was high for all bioregions except for the Temperate Pacific (Moderate) (Figure 4c, left). Sea-surface temperature increase and marine heatwaves were the key climate stressors in four and three bioregions, respectively (Figure 5). Coastal development, overfishing, and urban/industrial runoff had the highest potential impact scores among direct-anthropogenic stressors, when averaged across all bioregions, while seaweed aquaculture and boat pollution (both large commercial and small recreational) had the lowest scores (Figure 4c, right).

Certainty scores averaged across indicators (listed in Table 2) and stressors were medium for all bioregions, except for Temperate Pacific (high). When averaged across bioregions, high certainty was apparent for marine heatwaves and sea-surface temperature increase, with moderate or low certainty for the other stressor indicators. The CV among exposure scores across climate stressors were

TABLE 4 Seagrass experts' scores for exposure and sensitivity (with their coefficients of variance, CV%), and potential impact of 19 stressors across seagrass bioregions (Mod = moderate).

		Temperate Pacific				Tropical Indo-Pacific				Temperate Southern Oceans
	Stressor	Exp (CV%)	Sens (CV%)	Pot imp	Rank	Exp (CV%)	Sens (CV%)	Pot imp	Rank	Exp (CV%)
Climate change	DR	4.06 (6)	1.69 (84)	Mod	13	2.98 (42)	2.69 (40)	Mod	15	4.06 (25)
	MHW	4.06 (25)	3.26 (38)	High	11	3.39 (11)	3.69 (23)	High	6	3.72 (30)
	OA	4.67 (12)	3.47 (39)	High	1	3.70 (32)	2.10 (21)	Mod	16	4.72 (10)
	R	3.67 (16)	1.69 (84)	Mod	14	3.71 (29)	3.13 (38)	High	7	3.59 (37)
	S	2.19 (12)	2.64 (35)	Mod	15	3.35 (24)	3.56 (20)	High	5	3.37 (18)
	SLR	3.97 (26)	1.31 (23)	Mod	16	3.67 (31)	2.38 (10)	Mod	13	4.72 (10)
	SST	4.31 (16)	3.44 (19)	High	2	4.04 (18)	3.15 (12)	High	3	4.68 (12)
Direct-anthropogenic	AQI	3.61 (35)	3.42 (42)	High	4	2.85 (49)	3.30 (22)	Mod	11	2.53 (44)
	AR	3.47 (48)	3.42 (42)	High	6	3.21 (22)	3.58 (30)	High	8	3.19 (12)
	CD	3.74 (30)	2.85 (45)	High	7	3.76 (35)	4.37 (15)	High	1	3.74 (40)
	DRG	-	-	-	-	3.04 (30)	4.01 (25)	High	4	3.29 (30)
	LCBA	2.72 (43)	3.50 (52)	Mod	9	2.11 (58)	2.85 (12)	Mod	18	2.71 (54)
	LCBP	3.00 (40)	2.56 (42)	Mod	11	2.26 (37)	3.18 (20)	Mod	17	2.21 (24)
	OF	3.61 (48)	3.67 (31)	High	3	3.50 (41)	2.97 (10)	High	9	3.85 (17)
	SRBA	2.72 (43)	3.17 (55)	Mod	10	2.85 (60)	3.10 (20)	Mod	12	3.05 (51)
	SRBP	2.72 (43)	2.56 (42)	Mod	12	2.07 (56)	2.31 (13)	Low	19	2.56 (36)
	SWQ	4.17 (20)	-	-	-	2.79 (46)	2.92 (15)	Mod	14	2.25 (71)
	TRA	3.28 (43)	3.75 (37)	High	5	2.84 (44)	3.42 (24)	Mod	10	3.11 (34)
	U/IR	3.33 (50)	2.89 (46)	Mod	8	3.59 (35)	3.69 (12)	High	2	3.61 (35)

Note: Stressors are grouped into climate change and direct-anthropogenic, arranged in alphabetical order for each group. Rank is based on potential impact scores across all stressors for each bioregion. Dashes indicate insufficient responses to enable calculation.

typically lower than the CV among the corresponding sensitivity scores (Table 4).

3.3 | Cumulative impact of climate and direct-anthropogenic stressors

Experts' opinions on cumulative impact showed a high degree of synergism. All pair combinations between high temperature, high suspended sediments, hypoxia and eutrophication had a statistically higher probability ($p < .05$, generalized log-linear model) to have synergistic rather than either additive or antagonistic interaction (Figure 6). Additionally, the 'synergistic' interaction type accounted for more than 50% of weighted responses for all the combinations between salinity fluctuation, eutrophication, and high temperature; however, combinations among these involving salinity fluctuations were not statistically significant (at a .05 level). The probability of the cumulative impact of increased irradiance and high suspended sediments to be antagonistic was statistically significant ($p < .05$; Figure 6). Most seagrass experts (>50%) also reported that increased irradiance and upwelling have an antagonistic effect on hypoxia and high temperature, though these effects were not statistically significant ($p > .05$).

3.4 | The vulnerability of WH seagrass habitats to climate change

Sea-surface temperature increase was the most common key climate stressor (i.e., top-three), identified in 11 out of 13 WH seagrass habitats represented by site managers' responses (Table 5). Only two key climate stressors were selected for the Belize Barrier Reef Reserve System. The potential impact on seagrass from key climate stressors was mostly high. Exceptions to this were: Low potential impact from rainfall change in Ibiza; moderate potential impact from ocean acidification in two WH seagrass habitats of the Temperate Southern Ocean (Ningaloo Coast and Shark Bay), and sea-surface temperature increase in Ibiza and Lagoons of New Caledonia; extreme potential impact from sea-level rise in Everglades National Park (Table 5).

Averaging potential impact scores from the key climate stressors for each property, we found that all but one of the assessed WH

			Temperate Atlantic				Tropical Atlantic				Mediterranean			
Sens (CV%)	Pot imp	Rank	Exp (CV%)	Sens (CV%)	Pot imp	Rank	Exp (CV%)	Sens (CV%)	Pot imp	Rank	Exp (CV%)	Sens (CV%)	Pot imp	Rank
3.11 (33)	High	7	4.06 (25)	3.26 (38)	High	11	3.39 (11)	3.69 (23)	High	8	3.72 (30)	3.68 (13)	High	4
3.68 (13)	High	6	4.13 (16)	4.28 (21)	High	3	3.26 (13)	3.94 (6)	High	7	3.77 (23)	-	-	-
2.42 (40)	High	10	4.26 (25)	2.25 (45)	Mod	18	3.75 (40)	2.49 (53)	Mod	13	4.86 (5)	2.96 (13)	High	3
2.99 (18)	High	13	4.71 (5)	3.86 (26)	High	2	3.68 (10)	3.94 (2)	High	6	3.69 (25)	1.56 (33)	Mod	16
3.64 (23)	High	9	3.96 (13)	3.37 (18)	High	10	3.59 (21)	3.24 (7)	High	10	4.21 (9)	2.89 (18)	High	7
3.06 (14)	High	3	4.36 (11)	3.31 (20)	High	6	4.03 (3)	3.79 (22)	High	4	4.45 (11)	1.85 (7)	Mod	12
3.55 (17)	High	2	4.86 (5)	2.41 (45)	High	14	4.28 (10)	4.34 (12)	High	1	4.18 (23)	2.33 (34)	Mod	11
2.71 (30)	Mod	17	2.93 (43)	3.78 28	High	16	2.32 (102)	3.11 (6)	Mod	16	3.19 (28)	3.88 (23)	High	6
3.48 (16)	High	11	4.11 (15)	3.58 (15)	High	4	3.88 (26)	4.73 (10)	High	2	3.33 (50)	3.11 (6)	High	9
4.50 (11)	High	1	4.75 (5)	3.94 (6)	High	1	4.31 (21)	3.67 (12)	High	3	3.25 (36)	4.06 (8)	High	5
3.75 (11)	High	8	3.29 (19)	3.61 16	High	13	2.38 (57)	4.50 (19)	High	11	-	-	-	-
2.89 (7)	Mod	15	2.95 (17)	3.70 14	High	17	1.67 (93)	4.00 (25)	Mod	17	2.69 (26)	3.75 (37)	High	10
3.15 (15)	Mod	16	3.18 (13)	3.63 15	High	15	1.48 (62)	2.78 (25)	Low	19	2.90 (25)	2.64 (21)	Mod	13
3.63 (27)	High	4	4.43 (6)	3.24 (47)	High	7	3.81 (21)	2.64 (21)	High	12	3.68 (40)	4.19 (25)	High	1
3.54 (21)	High	12	3.96 (28)	3.65 (24)	High	5	3.27 (49)	3.67 (31)	High	9	3.48 (32)	3.30 (20)	High	8
2.44 (21)	Mod	18	3.67 (28)	3.69 (18)	High	9	2.67 (45)	2.94 (14)	Mod	15	2.47 (27)	2.78 (25)	Mod	15
2.50 (35)	Mod	19	1.77 (77)	0.67 87	Low	19	1.62 (96)	3.67 (31)	Mod	18	3.78 (28)	-	-	-
2.86 (25)	Mod	14	3.17 (25)	4.14 17	High	12	2.09 (37)	4.33 (13)	Mod	14	3.40 (28)	4.33 (13)	High	2
3.78 (9)	High	5	3.93 (18)	3.63 (15)	High	8	3.49 (21)	4.20 (5)	High	5	2.66 (370)	2.86 (19)	Mod	14

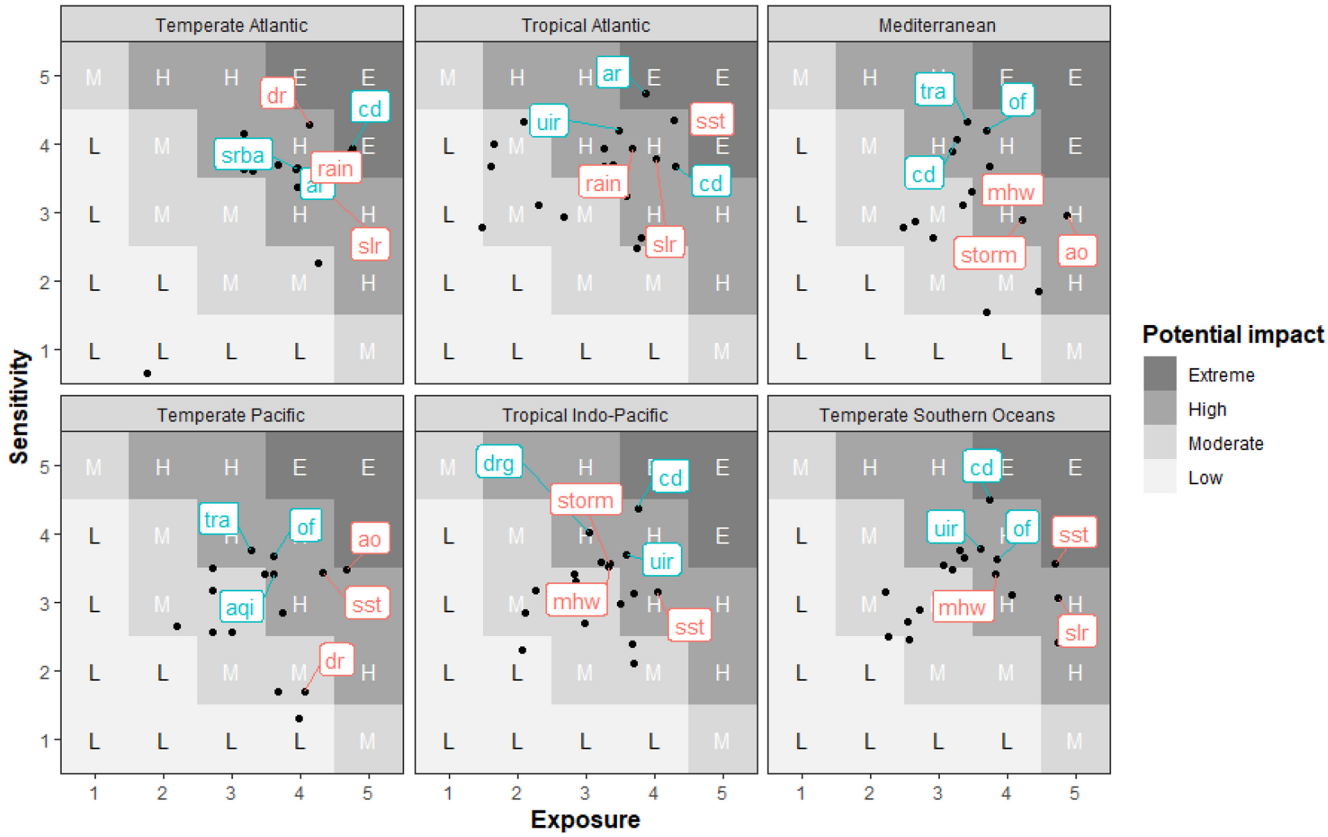

FIGURE 5 Risk matrix of potential impacts from 19 stressors to seagrass habitats across bioregions. Labels show the top three climate change (red) and direct-anthropogenic (blue) stressors in each bioregion based on potential impact scores. See Table 1 for the list of stressors and codes.

seagrass habitats have high potential impact from their key climate stressors. The exception was Ibiza, for which the potential impact was moderate (Table 6).

Adaptive capacity lowered the climate vulnerability from the level of potential impact in 46% of the properties. Adaptive capacity was low for seven assessed WH seagrass habitats; three properties each had moderate or high adaptive capacity (Table 6). As a result, more than 50% of WH seagrass habitats were assessed as having high vulnerability to climate change (Table 6).

Five site managers also provided qualitative examples of pragmatic adaptive capacity measures. Interestingly, site managers whose responses scored High in adaptive capacity ($n=2$), only mentioned management strategies which aim to limit direct-anthropogenic impacts, such as "protect the seagrass ecosystem by limiting the activities in the seagrass areas" or "have patrol boats to stop the anchoring in the seagrass in summer". In contrast, managers whose responses scored low or moderate in adaptive capacity ($n=3$) provided more examples of adaptive measures such as, "long-term monitoring projects using UVC and BRUVS," "drone mapping projects." and "educate the community where about the value of seagrass through signage and other forms of community information (e.g., monthly updates, community householders etc.)". Moreover, climate change adaptation strategies, such as "temperature loggers in place throughout the park in sensitive areas to monitor for change" and "assessment of seagrass habitat contributions to carbon sequestration" were only mentioned by site managers whose responses scored low in adaptive capacity.

More than 60% of assessed WH properties scored a High or Very high OUV dependency on their seagrass habitats; however, only 23% ($n=3$) scored High or Very high regarding community dependency. Interestingly, responses for two properties indicated no community dependency even though the OUV dependency was moderate (Wadden Sea and Tubbataha Reef) (Table 7).

4 | DISCUSSION

4.1 | High potential impact of climate change on WH seagrass habitats

Through a combination of seagrass experts' and site managers' opinions, this study assessed that more than 50% of WH seagrass habitats are at high vulnerability from climate change impacts, with long-term increases in sea-surface temperature and short-term marine heatwaves being the greatest threats. Additionally, most WH seagrass habitats are at high risk from synergistic cumulative impacts from high temperatures and poor water quality driven by anthropogenic activities that are occurring within these sites.

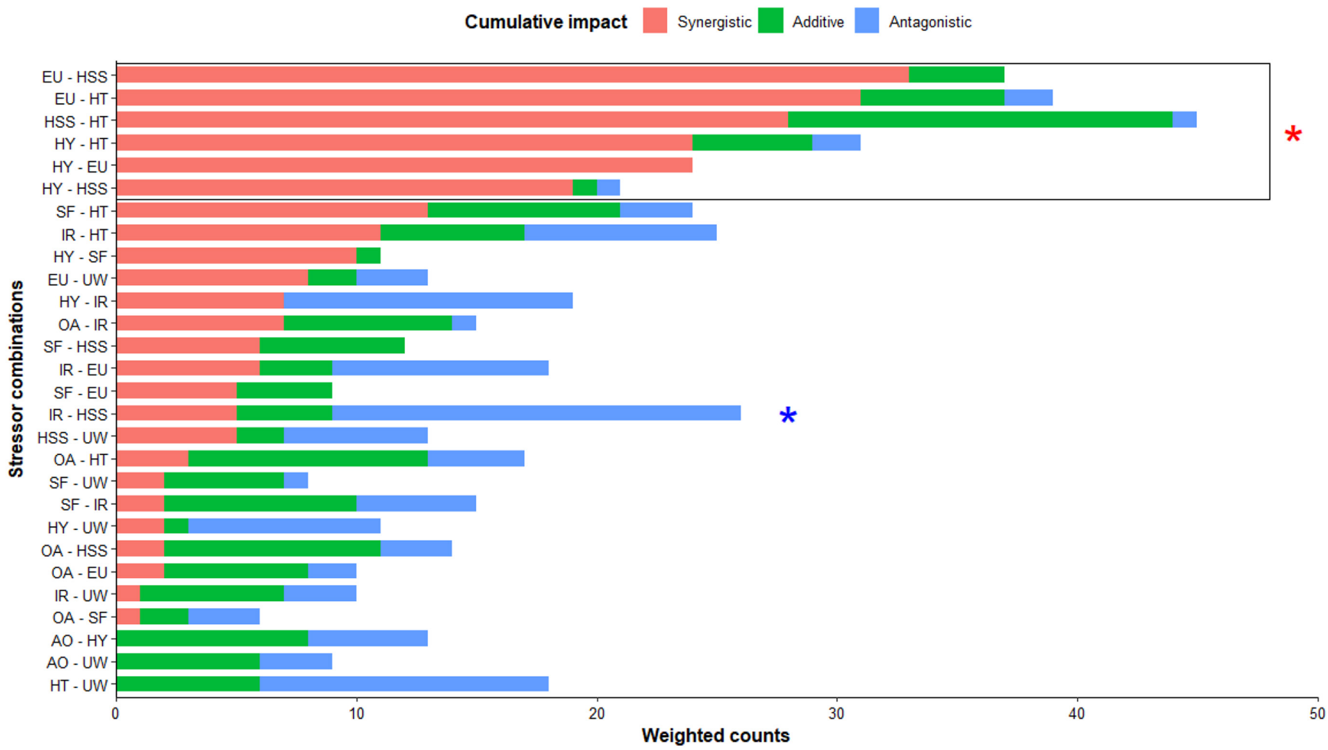

FIGURE 6 Seagrass expert responses on the cumulative impact of 29 stressors combinations. Bars represent the frequency of response for each category weighted by certainty scores. The bars grouped in the box show all stressors combinations where the probability of a *synergistic* cumulative impact was significantly higher ($p < .05$) than in other categories (red star). The blue star shows the only stressor combination where the probability of an *antagonistic* cumulative impact was higher ($p < .05$) than other categories (generalized log-linear model). See Table 1 for the list of stressors and codes.

This study showed that seagrass experts are increasingly concerned that climate change is one of the greatest threats to seagrass habitats globally (Jordà et al., 2012; Salinas et al., 2020; Strydom et al., 2020). The design of this study complemented that of Grech et al. (2012), allowing us to assess how seagrass experts' opinions have changed in the last decade. In Grech et al. (2012), the increase in sea-surface temperature was ranked within the top three stressors only in the Temperate Pacific bioregion, based on the opinions of five experts. Additionally, their vulnerability scores for climate change stressors had the highest variability among all stressors, indicating a lack of consensus among the scientific community. It is worth noting that the high variability across vulnerability scores to climate stressors could have been due to the natural variability and complexity of seagrass sensitivity, which is driven by several biotic and abiotic factors including habitat type, meadow form, and genetic diversity (Kilminster et al., 2015). Hence, experts from different locations might have provided different vulnerability scores based on their personal experience with specific meadows. In contrast, we found that seagrass experts now consider sea-surface temperature increase among the top three stressors in four of the six bioregions: Tropical Atlantic, Temperate Pacific, Tropical Indo-Pacific and Temperate Southern Oceans. Furthermore, the certainty associated with sea-surface temperature increase and marine heatwaves scores within bioregions were the highest among all stressors.

The consensus among experts about the potential impact of climate change on seagrass has also grown. While in Grech et al. (2012) the highest variation (CV) was found in climate change stressors, in this study the CV among exposure and sensitivity of seagrass scores to climate change was lower than for anthropogenic activities (see Table 4). This result is in line with the growing evidence that more-frequent and intense extreme temperature events, driven by climate change (Frölicher et al., 2018), are becoming a major threat to seagrass globally (Kendrick et al., 2019; Marbà & Duarte, 2010; Strydom et al., 2020). In the last two decades, there has been an increase in studies documenting seagrass mortalities attributed to the impact of extreme temperature events. Currently, the largest seagrass mortality events both globally (Strydom et al., 2020) and regionally (Kendrick et al., 2019; Seddon et al., 2000) have been attributed to extreme water temperatures. Seagrass diebacks, due to high temperatures have been documented in various regions, including Spencer Gulf, South Australia in 1993 (Seddon et al., 2000), the Mediterranean in 2003 and 2006 (Marbà & Duarte, 2010), the Chesapeake Bay in 2010 and 2015 (Shields et al., 2019), and Shark Bay in 2011 (Strydom et al., 2020).

Nevertheless, extreme temperature events are not the only climate change stressors threatening WH seagrass habitats. In the Tropical Indo-Pacific bioregion, storms (including tropical cyclones) had the second-highest potential impact score among climate stressors, and was the third ranked climate stressor for the Mediterranean (Figure 5; Table 4). Tropical seagrass species, which

TABLE 5 Exposure, sensitivity, and potential impact of the selected key climate stressors for each WH seagrass habitat.

Bioregion	World Heritage seagrass habitat	Key climate stressors	Exposure	Sensitivity	Potential impact
Temperate Atlantic	High Coast/Kvarken Archipelago	Sea-level rise	Very high	Moderate	High
		Sea-surface temperature increase	Very high	Low	High
		Rainfall change	High	High	High
	Wadden Sea	Sea-level rise	High	Moderate	High
Tropical Atlantic		Sea-surface temperature increase	High	Low	High
		Rainfall change	High	High	High
	Belize Barrier Reef Reserve System	Sea-surface temperature increase	Moderate	High	High
		Storm intensity and frequency	Low	Moderate	Moderate
		NA	NA	NA	NA
	Banc d'Arguin National Park	Droughts	High	High	High
		Rainfall change	High	High	High
		Marine heatwaves	Low	High	Moderate
	Everglades National Park	Sea-level rise	Very high	High	Extreme
		Sea-surface temperature increase	Very high	High	High
		Ocean acidification	Very high	Low	High
Mediterranean	Ibiza, Biodiversity and Culture	Marine heatwaves	Moderate	High	High
		Rainfall change	Moderate	Low	Low
		Sea-surface temperature increase	Moderate	Low	Moderate
Tropical Indo-Pacific	Aldabra Atoll	Sea-surface temperature increase	High	Moderate	High
		Droughts	High	Moderate	High
		Marine heatwaves	High	High	High
	Great Barrier Reef	Ocean acidification	Very high	Low	High
		Sea-level rise	Very high	Low	High
		Sea-surface temperature increase	Very high	Moderate	High
	Lagoons of New Caledonia[a]	Sea-level rise	Very high	Low	High
		Storm intensity and frequency	Moderate	High	High
		Sea-surface temperature increase	Moderate	Moderate	Moderate
	Ningaloo Coast	Sea-surface temperature increase	Very high	Moderate	High
		Sea-level rise	High	Low	High
		Ocean acidification	High	Low	Moderate
	Tubbataha Reefs Natural Park	Sea-surface temperature increase	High	Moderate	High
		Droughts	High	Moderate	High
		Marne heatwaves	High	High	High
Temperate Southern Oceans	Lord Howe Island Group	Ocean acidification	High	Low	High
		Droughts	High	Moderate	High
		Rainfall change	High	Moderate	High
	Shark Bay, Western Australia	Marine heatwaves	Very high	Moderate	High
		Sea-surface temperature increase	High	High	High
		Ocean acidification	High	Low	Moderate

Note: Exposure scores were calculated from site managers' responses, while sensitivity scores were sourced from seagrass experts' responses for the relevant bioregion. No WH properties from the Temperate Pacific bioregion were analyzed. A map of the WH seagrass habitats is available from Losciale et al. (2022). Colour shade indicate CVI colours.

Abbreviation: WH, World Heritage.

[a]Full name: Lagoons of New Caledonia: Reef Diversity and Associated Ecosystems.

are usually more tolerant to extreme temperature events, might be more vulnerable to storms and associated floods (Rasheed et al., 2014) whose frequency and intensity are predicted to increase, with climate change (Harley et al., 2006). Intense storms impact seagrass directly, by physically uprooting and burying the plants, and indirectly through reduced light penetration in the

TABLE 6 Vulnerability of the assessed World Heritage seagrass habitats to three (property-specific) key climate stressors.

World Heritage seagrass habitat	Potential impact	Adaptive capacity	Seagrass vulnerability
Shark Bay, Western Australia	High	Low	High
Great Barrier Reef	High	Low	High
Belize Barrier Reef Reserve System	High	Low	High
Lagoons of New Caledonia	High	Low	High
Wadden Sea	High	Low	High
Ningaloo Coast	High	Low	High
High Coast/Kvarken Archipelago	High	Low	High
Lord Howe Island Group	High	Moderate	Moderate
Banc d' Arguin National Park	High	Moderate	Moderate
Aldabra Atoll	High	Moderate	Moderate
Tubbataha Reefs Natural Park	High	High	Moderate
Everglades National Park	High	High	Moderate
Ibiza, Biodiversity and Culture	Moderate	High	Low

Note: Potential impact scores are the average of the three scores from Table 1. WH seagrass habitats are ordered based on seagrass vulnerability, then adaptive capacity, from the most to the least vulnerable.

Abbreviation: WH, World Heritage.

TABLE 7 OUV and community dependency of the assessed World Heritage seagrass habitats.

World Heritage seagrass habitat	OUV dependency	Community dependency
Ibiza, Biodiversity and Culture	Very high	Very high
Shark Bay, Western Australia	Very high	Moderate
Great Barrier Reef	High	Very high
Everglades National Park	High	High
Banc d' Arguin National Park	High	Moderate
Belize Barrier Reef Reserve System	High	Moderate
Aldabra Atoll	High	Low
Lagoons of New Caledonia	High	Low
Tubbataha Reefs Natural Park	Moderate	No dependency
Wadden Sea	Moderate	No dependency
Ningaloo Coast	Moderate	NA
Lord Howe Island Group	Low	Low
High Coast/Kvarken Archipelago	Low	No dependency

Note: WH seagrass habitats are ordered based on OUV dependency, then community dependency, from the highest to the least value.

Abbreviations: OUV, outstanding universal value; WH, World Heritage.

water column due to the high volume of suspended sediments (Preen et al., 1995; Rasheed et al., 2014). The projected increase in the frequency of intense events might reduce the chance of seagrass recovery, mainly in shallow water (Rasheed et al., 2014). In the last two decades, severe cyclones have had significant impacts on three WH seagrass habitats (GBR, Shark Bay, and Ningaloo), resulting in die-offs and substantial declines in seagrass populations (McKenzie et al., 2019; van Keulen, 2019).

Sea-level rise was identified by experts as a key climate stressor for the Atlantic bioregions (tropical and temperate) and Temperate Southern Oceans (Figure 5; Table 4). The potential impact from sea-level rise on seagrass is still not fully clear and it can depend on several variables. For instance, the increase in depth will reduce habitat availability in deeper areas (Davis et al., 2016), while potentially forming new suitable habitats in shallow areas (Albert et al., 2017; Valle et al., 2014). It is worth noting that rates of seagrass colonization of newly available substrates are highly uncertain due to several factors including the instability of bare sediments and the lack of seed banks in bare sediments areas (Saunders et al., 2013). Management strategies, such as planned coastal retreat and water quality improvement, have demonstrated the potential to offset the impacts of sea-level rise (Saunders et al., 2013). However, WH seagrass habitats adjacent to high developed coastal areas or locations with steep topography, might not be able to expand their distribution (Harley et al., 2006).

Interestingly, ocean acidification was among the three key climate stressors in the Mediterranean and Temperate Pacific bioregions (Figure 5; Table 4). In both bioregions, the potential impact scores were driven by Very high exposure and Moderate sensitivity scores. Ocean acidification has been shown to either benefit or negatively impact seagrass habitats and currently, it is difficult to determine seagrass vulnerability to ocean acidification (Garrard & Beaumont, 2014; Pacella et al., 2018; Zunino et al., 2019). Seagrasses, unlike other marine plants, are not carbon saturated, thus, an increase in dissolved CO_2 and a consequent lower water pH might increase seagrass photosynthesis and productivity (Björk et al., 2008; Collier et al., 2018; Gattuso & Buddemeier, 2000; Palacios & Zimmerman, 2007; Zimmerman et al., 1997). Long-term changes in pH can affect seagrass's ability to buffer natural pH fluctuations. This can lead to indirect impacts on seagrass ecosystems, including altered epiphytic communities and reduced production of phenolic compounds that deter grazers (Pacella et al., 2018; Zunino et al., 2019). These indirect effects may increase grazing pressure, causing a reduction of aboveground biomass, habitat complexity, and potentially limit carbon sequestration (Zunino et al., 2019).

While the effects of climate change on seagrasses are identified by experts as among the greatest threats, it is widely recognized that seagrass mortality is rarely driven solely by the impact of climate stressors but rather by the cumulative impacts of multiple stressors (Griffiths et al., 2020; Kendrick et al., 2019).

4.2 | High risk from the cumulative impact of high temperatures with reduced light and oxygen availability

Our results indicate that seagrass experts agree that the impact of high temperatures, reduced light availability and hypoxia can have a synergistic (negative) cumulative impact on seagrass. We found that coastal development, land-based run-off (both agricultural and urban/industrial), and overfishing are among the direct-anthropogenic activities of most concern to seagrass experts. This is not surprising since, while evidence of the impact of climate change on seagrass is relatively recent, poor water quality (due to eutrophication and pollution) and extractive and destructive activities (such as demersal fishing, dredging and coastal development) have been long identified as major direct-anthropogenic threats to seagrass (Dunic et al., 2021; Moksnes et al., 2008; Turschwell et al., 2021). One of the major impacts of these activities is the rapid increase in turbidity and nutrients in the water column, which reduces light and oxygen availability.

Cumulative impact studies, aiming at detecting “hotspots” of seagrass vulnerability, are growing in number; however, the majority of these assume additive interaction between stressors (Grech et al., 2012; Halpern, McLeod, et al., 2008; Holon et al., 2015; Stockbridge et al., 2020). The current understanding of cumulative impacts on seagrass is poor, based mostly on laboratory studies and biased towards a few temperate and subtropical species (Stockbridge et al., 2020). Nevertheless, it is known that heat stress causes an increase in respiration, photosynthetic enzyme breakdown and non-photochemical quenching, leading to an overall reduction in photosynthetic yield (Campbell et al., 2006; Duarte et al., 2018; Koch et al., 2013). During extreme temperature events, a reduction in light availability, due to climate change stressors (such as storms and sea-level rise) and direct-anthropogenic activities, will further impair seagrass photosynthetic yield and reduce their chance to colonize deeper cooler waters (Arnold et al., 2017). Prolonged shading can significantly impair the carbon storage ability of seagrass (Dahl et al., 2016). In addition, high nutrients in the water column, which could be a consequence of the aforementioned stressors, also enhance epiphyte growth on seagrasses, limiting the available leaf surface area to absorb light (Duarte et al., 2018).

Our results indicate that additive impact assessments might have underestimated seagrass vulnerability to the cumulative impacts of reduction in water quality and climate change-driven extreme temperature events (Grech et al., 2011; Halpern, McLeod, et al., 2008; Holon et al., 2015). Therefore, we recommend that site managers of WH seagrass habitats consider the cumulative impact of climate change and direct-anthropogenic stressors during the planning and implementation of conservation measures (Halpern, Walbridge, et al., 2008; Stockbridge et al., 2020).

The analysis of site managers' exposure scores (see Figure A1) showed that localized direct-anthropogenic stressors, such as small recreational boat anchoring and pollution, were among the top three direct-anthropogenic stressors in 10 out of 13 WH seagrass habitats. Anchoring seasonally impacts seagrass at the population level by altering the structure and reducing its ecological role (Montefalcone et al., 2008). The adoption of mooring technologies, together with increased education and law enforcement, can reduce the impact of recreational boating, as demonstrated in Ibiza and Everglades (BOIB, 2018; Hallac et al., 2012). However, most of the documented decline of WH seagrass habitats due to anthropogenic activities has been attributed to changes in water quality due to anthropogenic hydrological modifications, coastal development, and eutrophication (Cortés et al., 2019; Cyrus et al., 2010; Dolch et al., 2017; Durako, 2002; Páez-Osuna et al., 2017). Hence, we suggest that site managers should also focus on large-scale stressors, also noting that these can originate from outside of WH property boundaries to impact WH seagrass habitats.

4.3 | A need to develop the capacity to adapt to climate change impacts on WH seagrass habitats

A key factor contributing to the vulnerability of WH seagrass habitats is the level of adaptive capacity. Our results showed that all WH seagrass habitats assessed as having high vulnerability to climate change, scored low in adaptive capacity. Qualitative examples provided by site managers suggest that, in some cases, adaptive capacity might be overestimated or not fully understood. The only example given by site managers who scored high in adaptive capacity to climate change impacts was the limitation of anthropogenic activities (mainly anchoring) that directly damage the seagrass habitats. In contrast, responses from managers who scored low in adaptive capacity were more comprehensive. These include the implementation of mapping projects; monitoring of seagrass conditions and temperature fluctuations; public education; and assessment of seagrass carbon stock. This incongruence between quantitative results and qualitative descriptions provides some evidence that there is a need to better inform managers about tangible adaptive capacity measures, and their feasibility, when undertaking climate vulnerability assessments. However, this also speaks to an opportunity for knowledge sharing across seagrass manager networks regarding adaptation strategies.

In the context of WH seagrass habitats, it is possible to identify key adaptive measures that could reduce vulnerability. The ongoing increase in water temperatures will likely cause a shift in seagrass species distribution, with some species increasing their range while others face the risk of extinction (Jordà et al., 2012; Lopez-Calderon et al., 2010). In several regions, colonizing species like *Ruppia maritima* and *Halophila stipulacea* are already displacing dominant species, such as *Zostera marina* and *Posidonia oceanica* (Lopez-Calderon et al., 2010; Wesselmann et al., 2020). Research on the future distribution and diversity of WH seagrass habitats is needed to allow site managers to develop plans and policies that consider the likely future composition of WH seagrass habitats (Unsworth et al., 2019).

Monitoring WH seagrass habitats, including species composition, should focus on detecting early signs of increased sensitivity. Seagrass sensitivity can vary between WH seagrass habitats due to differences in historical exposure, differences in human pressures due to geographic location (Halpern, Walbridge, et al., 2008), species composition (Campbell et al., 2006), local adaptation (Duarte et al., 2018), thermal priming (Nguyen et al., 2020), and meadow form (Kilminster et al., 2015). It is of note that these factors can be inter-related (e.g., historical exposure can influence species composition and local adaptation).

There is some evidence indicating that WH properties in temperate bioregions of the northern hemisphere might be more vulnerable to climate change. Exposure scores by seagrass experts across all stressors were higher in temperate bioregions of the northern hemisphere than elsewhere. Globally, the highest direct human impact on marine ecosystems is occurring in northern Europe, North America, and the South and East China Seas (Halpern, McLeod, et al., 2008). Additionally, most of the documented seagrass loss linked to climate change has occurred in temperate bioregions of the northern hemisphere. Except for the pan-tropic marine heatwave of 2016–2017 (Hughes et al., 2017), the majority of documented marine heatwaves impacting seagrass have occurred in temperate regions—Europe, North America and South Australia (Hobday et al., 2018).

The species composition and the meadow form of WH seagrass habitats are also important characteristics that can affect their vulnerability. Persistent (e.g., *P. oceanica*) seagrass species that form enduring meadows suffered the greatest decline when affected by extreme temperature events (Marbà & Duarte, 2010; Shields et al., 2019; Strydom et al., 2020). These species have generally higher physiological resistance to disturbance than colonizing or opportunistic species, which are often dominant in tropical transitory meadows (Kilminster et al., 2015). However, if mortality occurs, recovery times in enduring meadows are longer due to a lack of seed banks, slow shoot turnover and a long time to reach sexual maturity. Moreover, shallow seagrass meadows and species at their limit of distribution are the most vulnerable to extreme temperature events (Björk et al., 2008).

With a better understanding of seagrass sensitivity, reducing non-climate related anthropogenic impacts in vulnerable 'hotspots' and during seasons of high risk from extreme temperatures will also reduce the chance of cumulative impacts. Measures of genetic diversity (Duarte et al., 2018), reproductive effort through seed bank density and viability (Rasheed et al., 2014) and connectivity (Björk et al., 2008) can provide early warning of reduced resilience and allow time to increase protection. Implementing restoration of heat-tolerant seagrass species, raising awareness about the importance and vulnerability of WH seagrass habitats, and promoting environmental education are potential strategies to reduce seagrass vulnerability in the short term (Duarte et al., 2008; Perry, 2015; van Katwijk et al., 2016). However, to prevent irreversible changes in natural systems, including WH seagrass habitats, a global effort to reduce greenhouse gas emissions and limit warming below 2°C from pre-industrial levels is essential (IPCC, 2021).

Among the projected benefits of a thematic analysis is that the lessons from individual WH properties can help to inform other thematically similar properties, especially in terms of relevant climate stressors, vulnerability, and adaptation responses. Day et al. (2020) discussed how pre-existing vulnerability assessments might provide benefits to others with similar values but less expertise or access to resources. Losciale et al. (2022) outlined the benefits of thematic approaches including contextual understanding of climate impacts, networking opportunities within the thematic group, and shared strategies for adaptive management (UNESCO World Heritage Committee, 2020).

Furthermore, the results of this assessment in combination with the dependency scores from Losciale et al. (2022) are useful to provide a preliminary indication of overall OUV vulnerability for individual sites. For instance, in places where seagrass dependence was Very high (Shark Bay) or High (Aldabra Atoll), the seagrass vulnerability was reflected in the property-specific CVI outcome (Table 8; Heron et al., 2021; Heron, Day, Cowell, et al., 2020). Additionally, the High seagrass vulnerability for Wadden Sea likely contributed to the High overall CVI outcome through the Moderate seagrass dependence (Heron, Day, Zijlstra, et al., 2020; Losciale et al., 2022). In contrast, the Low dependence on seagrass in High Coast/Kvarken Archipelago is consistent with the lack of direct translation of High

TABLE 8 Comparison between OUV vulnerability assessments from property-specific CVI assessments, OUV seagrass dependence (Losciale et al., 2022), and seagrass vulnerability assessment from this study.

WH property	CVI OUV vulnerability[a]	Seagrass dependence (Losciale et al., 2022)	Potential impact	Adaptive capacity	Seagrass vulnerability
Shark Bay, Western Australia	High	Very high	High	Low	High
Aldabra Atoll	Moderate	High	High	Moderate	Moderate
Wadden Sea	High	Moderate	High	Low	High
High Coast/Kvarken Archipelago	Moderate	-	High	Low	High

Abbreviations: CVI, Climate Vulnerability Index; OUV, outstanding universal value; WH, World Heritage.

[a]References in order from top to bottom: Heron et al. (2021), Heron et al. (2022), Heron, Day, Cowell, et al. (2020), and Heron, Day, Zijlstra, et al. (2020).

seagrass vulnerability to the overall CVI outcome. This demonstrates that a thematic assessment can align with the assessment from a detailed CVI workshop, especially when a single attribute such as seagrass is such a dominant feature of the property (while recognizing that the broader CVI workshop assesses OUV for the entire property, rather than a single attribute).

4.4 | Limitations

This thematic assessment provided an overview to site managers about the vulnerability of WH seagrass habitats to climate change through a rapid, low-cost, and repeatable methodology. It is worth noting that these results came from a relatively small sample size, with a high proportion of experts in tropical bioregions. This overrepresentation is consistent with previous studies, pointing to a possible lack of seagrass experts in some regions, such as the Temperate Pacific (Grech et al., 2012). However, it is worth noting that the primary researchers of both Grech et al. (2012) and our study were based in Australia (Tropical Indo-Pacific bioregion) and that this may have been influential in the success of contacting and receiving responses from seagrass experts based in the same region. While seagrass experts' contacts were mostly available, recruitment of site managers was a rather more arduous task, due to the lack of available contact details. Hence, we propose the development of an accessible database of contacts for site managers of protected areas to enable managers to develop topic-based networks and for use by researchers. Another obstruction to reaching site managers was the importance of providing the materials in their locally-preferred language. While these materials were initially developed in English, which was appropriate for most of the relevant WH properties, the French translation of the survey allowed us to gather opinions from site managers who may have been less comfortable responding, or proving less compherensive information, in English (i.e., Banc D'Arguin and Lagoons of New Caledonia). Future studies involving site managers, whether for seagrass or other thematic attributes, should consider having the survey translated into multiple languages to increase the chance of a higher response rate. Due to the global scope of the study, travel restrictions imposed by the global pandemic (limiting conference/meeting participation), and time differences among participants, the online survey was the preferred methodology and proved successful.

In this study, the impact of overgrazing by megaherbivores (i.e., dugongs and green turtles) was not assessed. However, recent research has shown that megaherbivore grazing can significantly reduce seagrass meadow complexity and structure by decreasing aboveground biomass and shoot height (Scott et al., 2020, 2021). A reduction in meadow structure can have an effect on ecosystem services such as carbon storage, sediment accumulation, and nursey habitat (Scott et al., 2018). If grazing rates exceed seagrass productivity, meadow collapse can occur (Fourqurean et al., 2019). This can be due to a reduced top-down control on megaherbivores, for example, in areas where predators are depleted or where turtle conservation is successful (Fourqurean et al., 2019; Kelkar et al., 2013). Moreover, overgrazing can also have cascading impacts such as sediment erosion and sedimentary organic carbon loss. However, a recent review showed that this topic remains understudied, and more research is required to understand the impact of grazing on carbon cycling and sediment erosion (Dahl et al., 2021). Hence, site managers of WH seagrass habitats in tropical and subtropical regions should also consider the potential impact of megaherbivore grazing when interpreting monitoring data and producing impact assessments; future seagrass vulnerability assessments should also consider this emerging pressure.

The strengths of the thematic methodology presented here were the ease of analysis, repeatability of the study, and comparability of outcomes with previous studies. However, the results suggest that topics such as exposure, sensitivity and, most of all, adaptive capacity may have been understood differently by different respondents. This indicates the value of face-to-face engagement that enables discussion in clarifying definitions and undertaking assessments. Hence, we recommend that future thematic vulnerability assessments should include more extensive preparatory material and be run as workshops or focus groups, to allow participants to better develop final assessments after discussions (Day et al., 2020; Dowler et al., 2006).

5 | CONCLUSIONS

World Heritage seagrass habitats have high vulnerability to the impacts of climate change, mainly from the increase in intensity and frequency of extreme temperature events (Frölicher et al., 2018). While seagrass experts are increasingly concerned about the cumulative impacts of anthropogenic activities and climate change, site managers are not well equipped to effectively deal with these impacts. The concept of adaptive capacity is poorly understood by site managers, possibly leading to management strategies that less effectively address the impacts of climate change. This assessment for seagrass demonstrates the effectiveness of the thematic vulnerability methodology, developed here, in providing useful information to WH property managers about the vulnerability of a specific attribute of OUV of their property, which can be used to develop and improve adaptation strategies and to prioritize the application of property-specific climate vulnerability assessments.

In summary, based on this thematic analysis, five recommendations for potential adaption strategies arise:

1. Inspire increased collaboration between seagrass experts and site managers to develop ambitious and coordinated strategies to protect and restore WH seagrass habitats.
2. Increase the understanding of property-specific seagrass habitats and their sensitivity by the implementation of systematic mapping and monitoring activities. Species composition, meadow form, and habitat types, which are still unknown in most WH properties, should be more systematically assessed (see Kilminster et al., 2015).
3. Choose a few representative monitoring locations and establish a clearly defined baseline as a benchmark (while acknowledging it is likely to already be a disturbed baseline) to inform the development of improved monitoring activities and provide a reference to measure changes in environmental, and anthropogenic impacts on seagrass status over time.
4. Increase protection through the identification and limiting of anthropogenic activities that can lead to synergistic cumulative impacts.
5. Increase adaptive capacity through raising community awareness and encouraging citizen science input into the above mapping and monitoring activities.

AUTHOR CONTRIBUTIONS

Riccardo Losciale: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; software; visualization; writing – original draft; writing – review and editing. **Jon C. Day:** Conceptualization; funding acquisition; methodology; validation; writing – original draft; writing – review and editing. **Michael A. Rasheed:** Methodology; writing – review and editing. **Scott F. Heron:** Conceptualization; funding acquisition; methodology; project administration; supervision; validation; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at http://doi.org/10.5281/zenodo.10360034.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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APPENDIX A

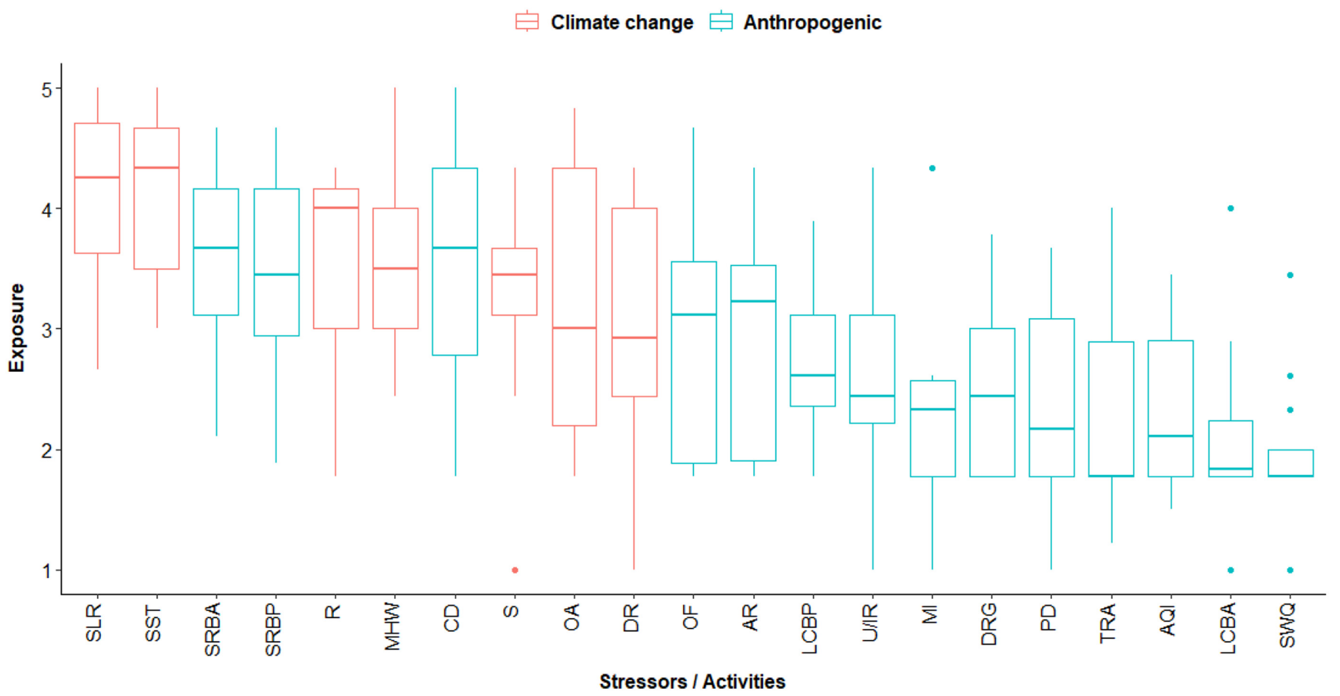

FIGURE A1 Boxplot of exposure scores derived from the site managers' survey.