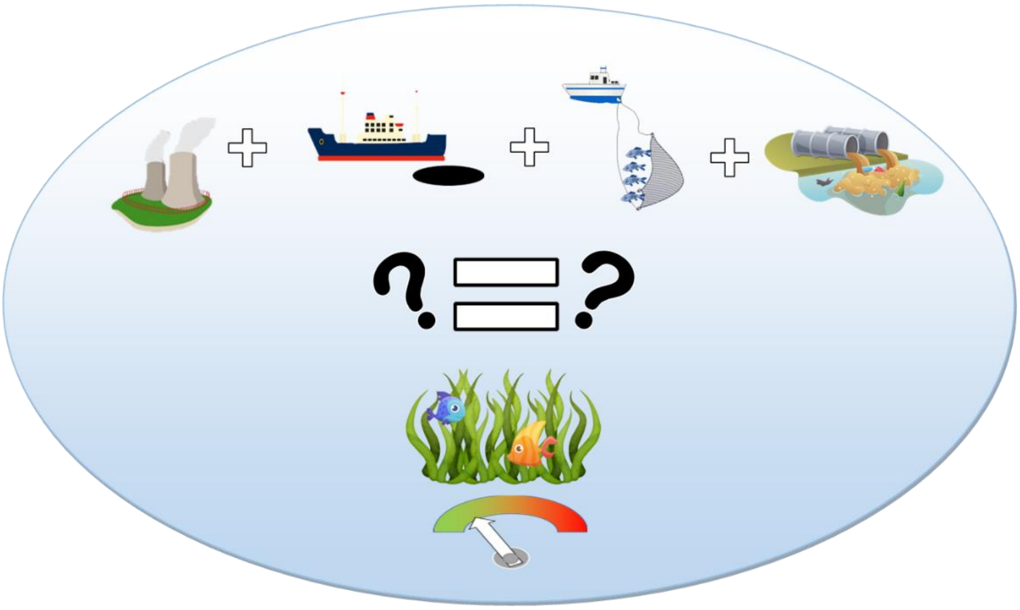
Evaluation of common assumptions in marine cumulative impact assessment models



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For Sophie,

You taught

me to fly

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Declaration

I, Jackson Stockbridge, certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

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Jackson Stockbridge

Date 31/05/2022

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Summary

The ecosystems of the world’s oceans provide services of great economic and environmental importance. However, increasing levels of human activity threaten to push marine ecosystems beyond thresholds they can recover from. Along with the loss of biodiversity and culturally significant areas, this will also compromise the ability of these ecosystems to provide essential services to coastal communities. Although studies have accurately quantified the impact of single human activities (stressors) on different marine ecosystems, the majority of the oceans are subjected to multiple concurrent stressors. Cumulative impact assessments aim to quantify the impact of multiple stressors on marine ecosystems, and inform management to help achieve sustainability goals. However, the complex nature and heterogeneity of the marine environment means that empirical data on ecosystem responses to many stressors are scarce, affecting our ability to ground-truth cumulative impact estimates.

Cumulative impact assessments are conducted using modelling methods that include assumptions. These methodological assumptions are needed to overcome problems related to data limitations, but they introduce uncertainty around cumulative impact estimates. Understanding and reporting this uncertainty can aid in risk analyses around management actions taken as a result of cumulative impact assessment outputs. In this thesis I evaluate the effect of different methodological assumptions on the uncertainty in outputs from cumulative impact assessments.

In the first study, I compare the output of a recent spatial cumulative impact assessment of Spencer Gulf, South Australia with observed data on seagrass condition. I use these datasets to test the assumption that the observable condition

of marine ecosystems (in this case seagrass) is related to cumulative impact assessment scores. Across three different approaches used to measure seagrass condition, two showed a small relationship with cumulative impact scores, and one showed no relationship. These results suggest that cumulative impact score, calculated using commonly-applied methods, may not accurately reflect the effect of multiple stressors on seagrasses.

The next two data chapters investigate the prevalence and effect of stressor interactions. Stressor interactions are not incorporated into the most commonly applied cumulative impact assessment methods. Rather, these methods assume that stressor impacts are additive (i.e., the individual impacts are summed to calculate the cumulative impact). Non-additive stressor interactions have the potential to produce cumulative impact estimates that are greater than, or less than, what we would expect from an additive model. Consequently, current methods are likely under- or over-estimating cumulative impacts. I conducted a meta-analysis of experimental multi-stressor studies on seagrasses to identify the prevalence of non-additive interactions. Whilst additive stressor interactions were most common, non-additive interactions occurred in 36 % of stressor combinations. The results of this chapter highlight a need to develop methods that can incorporate non-additive stressor effects, as not doing so may lead to misleading cumulative impact assessment outputs.

Following the findings of my second study, I developed a new modelling method for extending the existing methods for cumulative impact assessments to incorporate non-additive stressor interactions. To demonstrate the new method, I applied it to the case study of seagrasses in Spencer Gulf. I compared results from my new model that incorporated interactions to the ‘standard’ method that assumes only additive relationships between stressors. The outputs indicate that although including non-additive stressors is supported by experimental studies, it introduces greater uncertainty into the cumulative impact assessment outputs. Uncertainty maps, such as those generated here, assign higher values to grid cells with higher variance around the cumulative impact score. As such, these maps can be used to identify areas where there is greater risk associated with management decisions that are based on cumulative impact assessment results. The new method I have developed can be applied to any region to calculate spatial cumulative impact, assuming similar data availability, relevant to those areas.

Previous chapters of my thesis address uncertainty caused by assumptions that may sometimes be necessary, due to the lack of data on marine ecosystem stressor interactions. The final study of my thesis focuses on seagrass responses to individual stressors and offers insight into the assumption that ecosystems respond linearly to increasing (individual) stressor intensity. I modelled the relationships between nine individual stressors and seagrass condition to see how common linearity vs non-linear relationships were. I found that the relationship between a stressor and seagrass condition was rarely linear. This suggests that non-linear responses of ecosystems to stressors need to be incorporated into cumulative impact assessments.

Throughout this thesis, I have used a data-driven approach to test the impact of modelling assumptions in common marine spatial cumulative impact assessment methods. The body of research presented addresses key methodological and ecological knowledge gaps; demonstrates a new method for incorporating non-additive interactions between stressors into standard modelling approaches; and highlights that incorporating non-linear ecosystem responses should be a priority for future research in this area.

Publications and Contributions

Chapter 2: Evaluation of popular spatial cumulative impact assessment methods for marine systems

Authors: *Jackson Stockbridge, Alice R. Jones, Sam G. Gaylard, Matthew J. Nelson, Bronwyn M. Gillanders*
Status: Published in *Science of the Total Environment,* Vol. 780, Article no. 146401 (Stockbridge *et al.* 2021)

Chapter 3: A meta-analysis of multiple stressors on seagrasses in the context of marine spatial cumulative impacts assessment

Authors: *Jackson Stockbridge, Alice R. Jones & Bronwyn M. Gillanders*
Status: Published in *Scientific Reports,* Vol. 10, Article no. 11934 (Stockbridge *et al.* 2020)

Chapter 4: Incorporating non-additive stressor interactions into marine spatial cumulative impact assessments

Authors: *Jackson Stockbridge, Alice R. Jones, Christopher J. Brown, Mark J. Doubell & Bronwyn M. Gillanders*
Status: Written in style and format of manuscript – ready for submission

Chapter 5: Individual effects of multiple stressors on seagrass and the implications for marine cumulative impact assessments

Authors: *Jackson Stockbridge, Alice R. Jones & Bronwyn M. Gillanders*
Status: Written in style and format of a manuscript – not submitted

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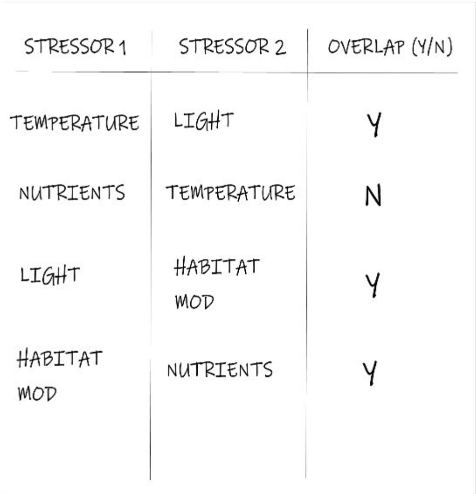
Chapter 1

General Introduction



STRESSOR 1	STRESSOR 2	OVERLAP (Y/N)
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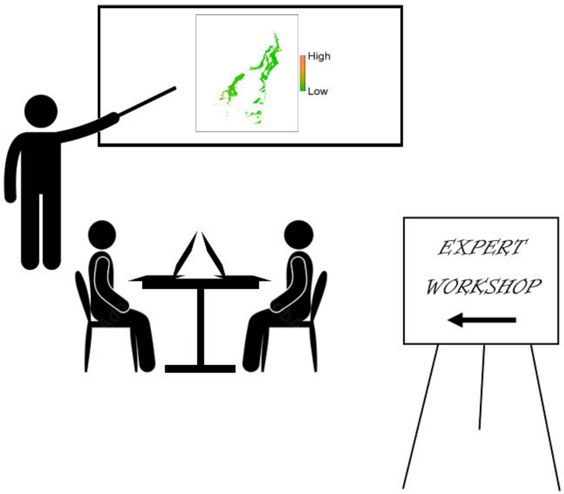
NUTRIENTS	TEMPERATURE	N
LIGHT	HABITAT MOD	Y
HABITAT MOD	NUTRIENTS	Y



1. General introduction

1.1. Human activities in the oceans and marine ecosystem services

The oceans provide resources and services that are essential to the survival and well-being of humans. The range of human uses of the oceans include food and livelihoods (Frawley *et al.* 2019; Jentoft 2019), for example the importance of the fisheries industry to Indonesian communities (Warren and Steenbergen 2021); and recreational and cultural significance, such as and the long-standing connection between the Australian coastline and around 150 First Nations clan groups (Evans *et al.* 2016). The benefits increase further when considering estuarine and coastal habitats, such as mangroves and seagrass, that protect the coast from erosion and provide water filtration (Campagne *et al.* 2014). Furthermore, these intertidal ecosystems mitigate the effects of climate change via carbon sequestration (Nellemann and Corcoran 2009), and store more carbon per unit area than most terrestrial vegetated ecosystems (Kennedy *et al.* 2010; McLeod *et al.* 2011).

Technological advancements mean that marine resource extraction is as efficient as ever, and previously unattainable resources are now accessible (Kark *et al.* 2015; Portman 2016). However, advances in technology and efficient resource extraction can be associated with habitat disturbance. For example, simple hand-operated fishing nets, have been replaced by ship-towed nets capable of modifying marine, benthic habitats (Kaiser *et al.* 2002). Furthermore, the multiple uses for the marine environment and their associated spatial footprint have increased over time. Examples include shipping channels, coastal development and offshore energy production, all of which have the potential impact the marine environment (Halpern *et* *al.* 2009; Zhang *et al.* 2017). As the global human population and demand for products and services from the oceans continues to grow, we are in danger of pushing ecosystems beyond thresholds where they can no longer sustain the communities that rely on them (Heinze *et al.* 2021).

The resources and services that the oceans provide fall under the umbrella term, ecosystem services, defined as any benefits that humans derive from nature (Sandifer and Sutton-Grier 2014). The listed benefits have developed over time, and recent definitions have classified different categories to include benefits relating to climate regulation, the conservation of key habitats, and the cultural and spiritual beliefs of Indigenous communities (Haines-Young and Potschin 2018). The importance of these categories being listed as ecosystem services should not be overlooked, as the valuation of ecosystem services is an important consideration of marine conservation and management (Börger *et al.* 2014; Buonocore *et al.* 2021). Marine management strategies and policies often focus around ensuring that ecosystem services are protected from the threat of increased human activity.

1.2. Human activity and stressor impact

Disturbance by human activity can negatively impact ocean ecosystems and reduce their capacity function and to provide ecosystem services (Halpern *et al.* 2015; Lu *et al.* 2018). Human activities that have the potential to negatively impact ecosystems are often referred to as ‘stressors’. Stressors impacting marine ecosystems include pollution from nutrient, heavy metal, chemical and oil inputs, as well as shipping, fishing, and climate change stressors such as ocean warming and acidification (Halpern *et al.* 2007).

As global populations increase, with many living within 100 km of the coast (Maul and Duedall 2019), there is the potential to increase both the number and intensity of marine stressors to meet a growing demand for ocean resources (Hodgson and Halpern 2018). For example, there has been a sharp increase in shipping activity through time and particularly since the development of global markets for products that rely heavily on ocean transport (Hulme 2009). Greater shipping intensity leads to multiple threats to marine ecosystems. These threats include a higher number of invasive organisms transported into marine areas via ballast water or attached to ship hulls (Hulme 2009), as well as disturbance to marine habitat due to the construction of shipping channels and ports (El Gohary and Hassan 2012).

When considered and tested in isolation, it is possible to accurately quantify the impact of a stressor on an aspect of an ecosystem (e.g. Bamber 1990; Anthony *et al.* 2007; Benham *et al.* 2019). For example, we can measure the change in biodiversity (measured by the number of distinct species) or abundance of individuals in relation to habitat modification (Fahrig 2003) The most repeatable results are achieved in controlled laboratory tests or mesocosms where individual stressors can be manipulated and measured precisely, enabling a determination of causation and avoiding the impact of confounding variables. However, this is often not representative of a real-world situation, as stressors rarely (if ever) act in isolation. As the number and intensity of stressors increases, the likelihood of overlap between stressors' increases, such that most ocean ecosystems are now exposed to impacts from multiple stressors.

1.3. Cumulative impacts and the development of assessment methods

Stressor overlap occurs when the impact from one stressor on an ecosystem fails to dissipate before a subsequent stressor starts to cause impacts. The effect of multiple, overlapping stressors is known as the 'cumulative impact'. An estimated 97% of the world's oceans are affected by cumulative impacts from human activities and climate change (Halpern *et al.* 2008). The field of research that aims to understand the consequences of cumulative impacts has grown significantly in the 21st century (Hodgson and Halpern 2018), and there have been many studies that have attempted to accurately quantify the cumulative impact of multiple stressors in marine areas (Cocklin *et al.* 1992; Halpern *et al.* 2008; Andersen *et al.* 2015; Lonsdale *et al.* 2020). Effective quantification of cumulative impacts helps to identify and protect vulnerable habitats and areas in need of management intervention, including restoration (Wintle 2008). Effective management of marine ecosystems helps to preserve the many ecosystem services that we rely on. As a result, robust cumulative impact assessments have the potential to contribute to the sustainable use of marine ecosystems, effective conservation actions and human well-being in communities that depend on the oceans (Halpern *et al.* 2007).

Multiple studies have advocated the integration of cumulative impacts assessments into policies targeted at achieving marine sustainability goals (Piet *et al.* 2015; Cormier *et al.* 2018). For example, Stelzenmüller *et al.* (2018) developed a risk-based management framework involving risk identification and evaluation, as well as potential solutions to problems these risks impose. However, the complexity of cumulative impact assessments means there is still work to do to evaluate the assessment outputs, and bridge the gap between scientifically driven approaches to cumulative impacts assessment, and their utility for coastal and ocean management.

The natural heterogeneity of the oceans means that accurate estimates of cumulative impacts are challenging to obtain (Halpern and Fujita 2013). Different ocean conditions can be observed over a range of a few millimetres, as well as between regions separated by 100’s of kilometres (Boyd *et al.* 2016). Stressor impacts can vary depending on the ocean conditions and the type of ecosystems present, as stressors impact distinct ecosystems differently (Breitburg and Riedel 2005). For example, under certain conditions, warming and CO_2 can negatively impact coral reefs (Carpenter *et al.* 2008), but can have positive effects on kelp forests at least up to a point (Connell and Russell 2010).

The presence of many stressor/ecosystem combinations causes complexity in cumulative impacts assessment. This complexity presents a challenging obstacle in achieving an important goal in the cumulative impacts field: the development of internationally coherent and meaningful assessment methods (Korpinen and Andersen 2016). Early cumulative impacts assessment methods were not quantitative or spatial, and included environmental checklists, which simply inventoried stressors in a given region (Cocklin *et al.* 1992). Later methods catalogued the number of stressors present and potential overlap with other stressors to estimate the likelihood of cumulative impacts occurring (Clark *et al.* 2002; Lawler *et al.* 2002). These early methods were specific to the region being assessed and not applicable to other areas due to the lack of clarity around how individual and stressor combinations were judged to impact ecosystems (Halpern and Fujita 2013).

Assessment methods continued to develop, resulting in quantitative, spatial and repeatable approaches that considered the cumulative impact of many stressors on multiple marine ecosystems (Halpern *et al.* 2008). However, these improved approaches initially had a global focus and still rely on expert judgement about the relevant stressors and their relative impacts on marine ecosystems (Halpern *et al.* 2007). This allowed the presence and spatial intensity of stressors to be combined with maps of the distribution of the marine ecosystems and/or species of interest. Further expert elicitation was used to assign standardised and spatially-resolved impact scores representing the effect of a stressor on specific ecosystems. In this method, the expert's impact scores were based on five ecological traits: (1) stressor spatial scale; (2) stressor frequency; (3) functional impact; (4) ecosystem resistance; (5) ecosystem recovery (Eq.1). The sum of these impact scores at any assessment location was considered the cumulative impact. Expert elicitation in cumulative impacts assessment means that any number of stressors can be considered, and is transferable to any study region where there are appropriate stressor data available with region/ecosystem specific experts.

(1) $$CI^s = \sum_{i=1}^{n} D_i \times \mu_{i,e}$$

Where CI^s is the cumulative impact score, D_i is a scaled 0-1 value based on the spatial intensity of stressor i, and $\mu_{i,e}$ is the expert elicited impact score (vulnerability weight) based on the vulnerability of ecosystem e to stressor i.

Probability models were adapted as a globally applicable method of cumulative impact assessment. Bayesian network models use probability distributions to predict relationships between multiple variables and a response, and have been utilised to predict cumulative impact in coastal ecosystems (e.g. Uusitalo *et al.* 2016; Bulmer *et al.* 2022). These models have a greater ability to handle missing data as probability distributions are more robust than a single, expert elicited score used by other cumulative impact models (Uusitalo 2007). However, these models have limited capability to deal with continuous data, as is often the case with environmental data.

This development in cumulative impacts assessment methods (from here on termed the ‘Halpern method’) was a significant advance in the field, and has formed the bedrock of hundreds of CIAs in different regions across the world (e.g. Halpern *et al.* 2009; Selkoe *et al.* 2009; Ban *et al.* 2010; Bevilacqua *et al.* 2018). However, there are several fundamental assumptions that are necessary, largely due to the limited availability of high spatial resolution and empirical data on stressor/ecosystem combinations and uncertainty around the magnitude, direction and variability in the impact of stressors on ecosystems (Halpern and Fujita 2013).

1.4. Assumptions of common marine cumulative impact assessment methods

Many of the challenges around any marine cumulative impact assessment approach are related to missing data, and the cost of collecting data at a small enough spatial scale to be considered robust and representative, whilst also achieving a reasonable spatial coverage. Coarsely resolved spatial data are often used to map cumulative impacts, and the heterogeneous nature of the oceans means that important stressor and ecosystem variation is missed at such low resolutions. Furthermore, cumulative impact assessment only captures a temporal snapshot of the marine environment, meaning variation in stressor intensity and, impact over time is missed. For example, seasonal coastal upwelling and downwelling events may alter the natural availability of nutrients in coastal waters. The impact of anthropogenic nutrient inputs could therefore differ depending on the time the impact was measured relative to an upwelling or downwelling event (Lapointe *et al.* 2004). Some of the main assumptions common to many cumulative impact assessment approaches are discussed below:

Stressor and habitat data within a grid cell

Due to the challenge of missing or low-resolution spatial data on both stressor presence/intensity and ecosystem distribution, assumptions must be made regarding the presence and intensity of stressors and ecosystems within each grid cell on a cumulative impact map. Stressor data are seldom available at a finer resolution than 1 km^2 (see Jones *et al.* 2018 for an exception), and as such, cumulative impact assessments assume a uniform distribution of stressors and that an ecosystem is either present or absent within a grid cell. However, marine spatial planning and conservation often make decisions based on planning units of less than 1 km^2 (Halpern and Fujita 2013). Consequently, management and planning strategies are being decided based on impact assessments that may be over or under-estimating impact, particularly in areas where patchy ecosystems exist (Halpern *et al.* 2007; Burke *et al.* 2011).

Expert scores of stressor impact are accurate

Calculating the impact of stressors on various ecosystems using empirical data would require a huge database comprised of multi-stressor experimental and in-field data. In the absence of such a database, expert-generated scores have been used, being developed to be as accurate and representative of stressor intensity as possible. However, expert elicitation introduces biases in the form of differing levels of expert knowledge and scientific understanding (Burgman 2016), and increases the uncertainty around impact assessments (hereafter referred to as “knowledge-based uncertainty”). Constraining the uncertainty around cumulative impacts estimates calculated using expert judgement would require a large number of experts to be surveyed, which is not always (if ever) possible. Therefore, in most cumulative impact assessment methods that use expert elicitation, it is assumed that the expert scores gained through expert elicitation are accurate. Jones *et al*. (2018) found that accounting for knowledge-based uncertainty in expert impact scores provided a clearer understanding of the confidence we can ascribe to cumulative impacts assessment results, and improved the transparency in their interpretation (Jones *et al.* 2018).

Response of ecosystems to cumulative impacts shows a linear response

One of the fundamental assumptions in cumulative impact assessments is that a change in cumulative impact score is truly representative of a corresponding change in ecosystem condition, and this relationship is usually assumed to be linear. Cumulative impact scores are assumed to reflect a linear change in ecosystem condition, such that an incremental increase in cumulative impact score results in an equivalent change in ecosystem condition (Halpern and Fujita 2013). This is extremely unlikely in a real-world scenario due to the presence of ecosystem thresholds, tipping points and unpredictable regime shifts (deYoung *et al.* 2008; Kraberg *et al.* 2011).

Stressor impact scores are additive

It is assumed that individual stressor impact scores (calculated based on stressor intensity combined with some estimate of effect size) can be summed to calculate a cumulative impact score. This is known as the additive model and is unrealistic due to the likely presence of non-additive interactions between stressors in marine ecosystems (Darling and Côté 2008; Stockbridge *et al.* 2020). Non-additive interactions can result in the real-world cumulative impact being far greater (synergies) or less than (antagonisms) what we would expect given an additive model. Despite evidence of the prevalence of non-additive interactions (Crain *et al.* 2008), the additive assumption is often considered necessary due to the lack of reliable data on stressor interactions, the variation in interactions between regions, and the potential for multi-way stressor interactions.

Aims and scope

The overarching aim of this thesis is to investigate and test some of the assumptions associated with the most commonly used marine spatial cumulative impact assessment method. I used seagrass as a model study system to do this due to their role in the broader marine environment as early indicators of environmental change (Orth *et al.* 2006). Assessments have used the condition of seagrasses to assess the status of coastal ecosystem health (e.g. McKenzie *et al.* 2012; Roca *et al.* 2016; IAN 2017). Furthermore, seagrasses are in decline in many regions (Dunic *et al.* 2021), and are one of the most vulnerable ecosystems to increasing cumulative impacts (Halpern *et al.* 2019).

The collective work contained within this thesis highlights some of the key knowledge gaps relevant to the development and improvement of marine cumulative impacts assessment methods and the potential impacts of the assumptions that underpin the most commonly-used approaches (Fig. 1.1). My work also contributes to the way we interpret spatial cumulative impact outputs, and demonstrates the importance of empirical data for the most robust results. Chapters 2, 3 and 5 use data collected from Spencer Gulf, South Australia; a large inverse estuary of significant environmental and economic importance to South Australia (Huveneers *et al.* 2013;

Gaylard 2014; Doubleday *et al.* 2017). Spencer Gulf represents an opportunity to evaluate cumulative impacts assessment methods following a recent assessment (Jones *et al.* 2018), the availability of spatial data on stressor intensity (Jones *et al.* 2018; Tanner *et al.* 2020), and the frequency of seagrass ecosystem condition field surveys (Gaylard *et al.* 2012).

The thesis is organised into six chapters. Chapter 1 is a general introduction with an overview of previous research. Chapters 2-5 are data chapters formatted as scientific manuscripts that are either published or ready to be submitted for peer review (Fig. 1.1). Finally, chapter 6 is a general discussion that consolidates the findings of this thesis. A brief overview of each chapter is given below:

Chapter 1: Introduction

Chapter 1 (this chapter) is a general introduction providing the background of previously published literature and context around the evolution and application of cumulative impact assessment methods for marine ecosystems.

Chapter 2: Evaluation of a popular spatial cumulative impact assessment method for marine systems: a seagrass case study

First, I looked at the relationship between ecosystem condition (for seagrasses) and cumulative impact assessment scores, calculated using methods that account for knowledge-based uncertainty (Jones *et al.* 2018). This allowed me to test the assumption that a change in the cumulative impact score at a location is reflected in a linear change in ecosystem condition. To achieve this, I compared survey data on seagrass condition with cumulative impact scores for spatially matched seagrass areas in Spencer Gulf. I found weak, negative relationships between two ecosystem condition indices and cumulative impact, and no relationship between cumulative impact and the third index.

This chapter was published in *Science of the Total Environment* (Stockbridge *et al.* 2021). https://doi.org/10.1016/j.scitotenv.2021.146401

Chapter 3: A meta-analysis of multiple stressors on seagrasses in the context of marine spatial cumulative impacts assessment

This chapter looks into the prevalence of non-additive stressor interactions to understand of how these may be affecting cumulative impacts assessments. We conducted a meta-analysis of studies that experimentally tested the individual and interactive effect of two or more stressors on seagrass. We aimed to establish if interactive effects were present or if stressor effects were additive. Whilst additive responses occurred most often, non-additive effects (both synergistic and antagonistic) were also common and difficult to predict.

This chapter was published in *Scientific Reports* (Stockbridge *et al.* 2020). https://doi.org/10.1038/s41598-020-68801-w

Chapter 4: Incorporating non-additive stressor interactions into marine spatial cumulative impact assessments

Chapter 4 uses the new evidence generated in Chapter 3 to develop a new approach for including interaction between stressors in models of cumulative impact. The results from this extension of the standard methods are then compared to those from the standard approach (that assumes additivity). Including non-additive interactions increased the uncertainty associated with cumulative impact score estimates, and highlights that additive cumulative impact assessment outputs need to be interpreted with caution.

This chapter has been submitted for review to *Journal of Applied Ecology*

Chapter 5: Individual effects of multiple stressors on seagrass and the implications for marine cumulative impact assessments

Finally, we modelled the individual effects of a number of different stressors and seagrass condition in Spencer Gulf. After evaluating the effect of non-additivity in cumulative impacts assessments (in chapter 4), here we look at the assumed linearity of the relationship between stressors and seagrass condition. The non-linear effects observed between stressors and condition highlight that these types of responses need to be considered in future cumulative impacts assessment methods.

Chapter 6: General discussion

Finally, I synthesise the results of each data chapter and discuss how they contribute to the aims and scope of the thesis. I suggest gaps in knowledge that should be prioritised for future research that aims to further our understanding of human impacts on marine ecosystems.

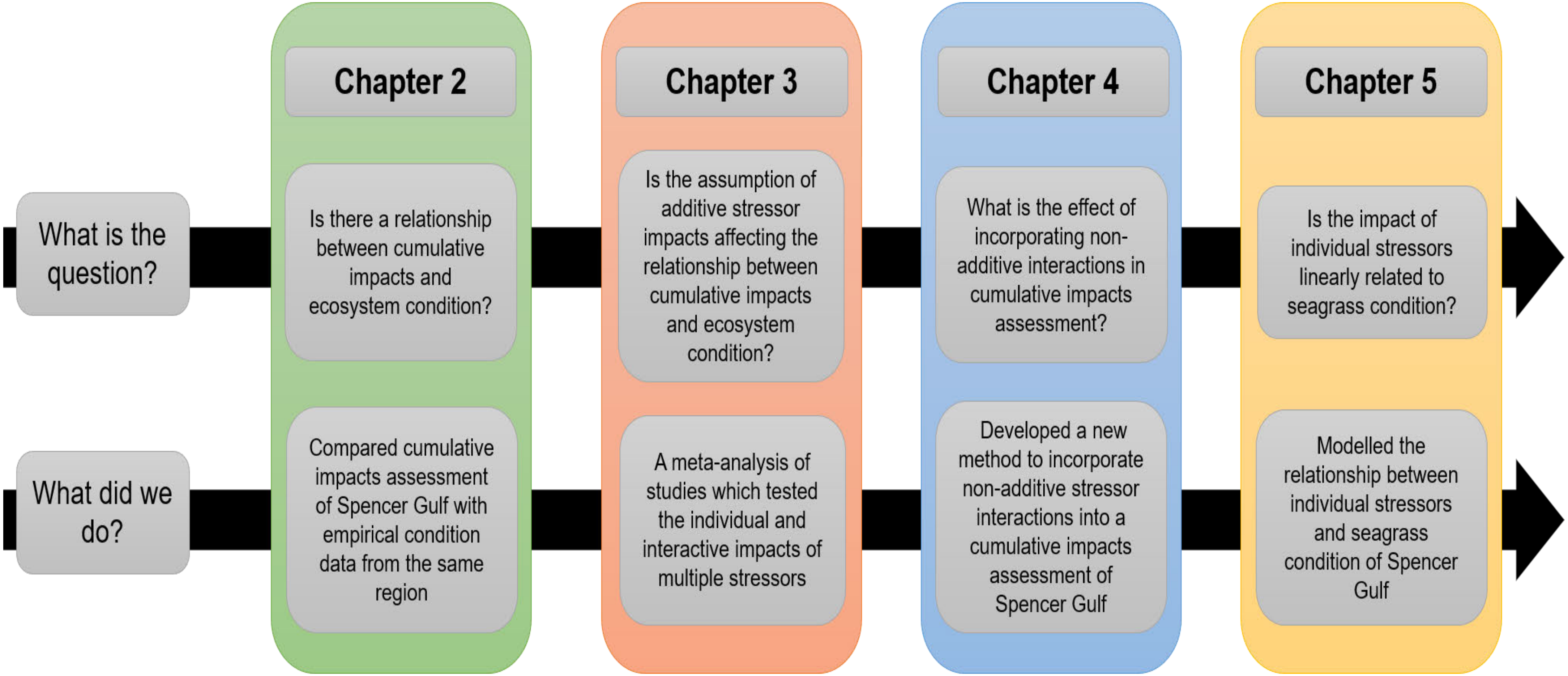


Figure 1.1. Schematic representing the questions I ask in this thesis, and what I did to answer these questions for each chapter.

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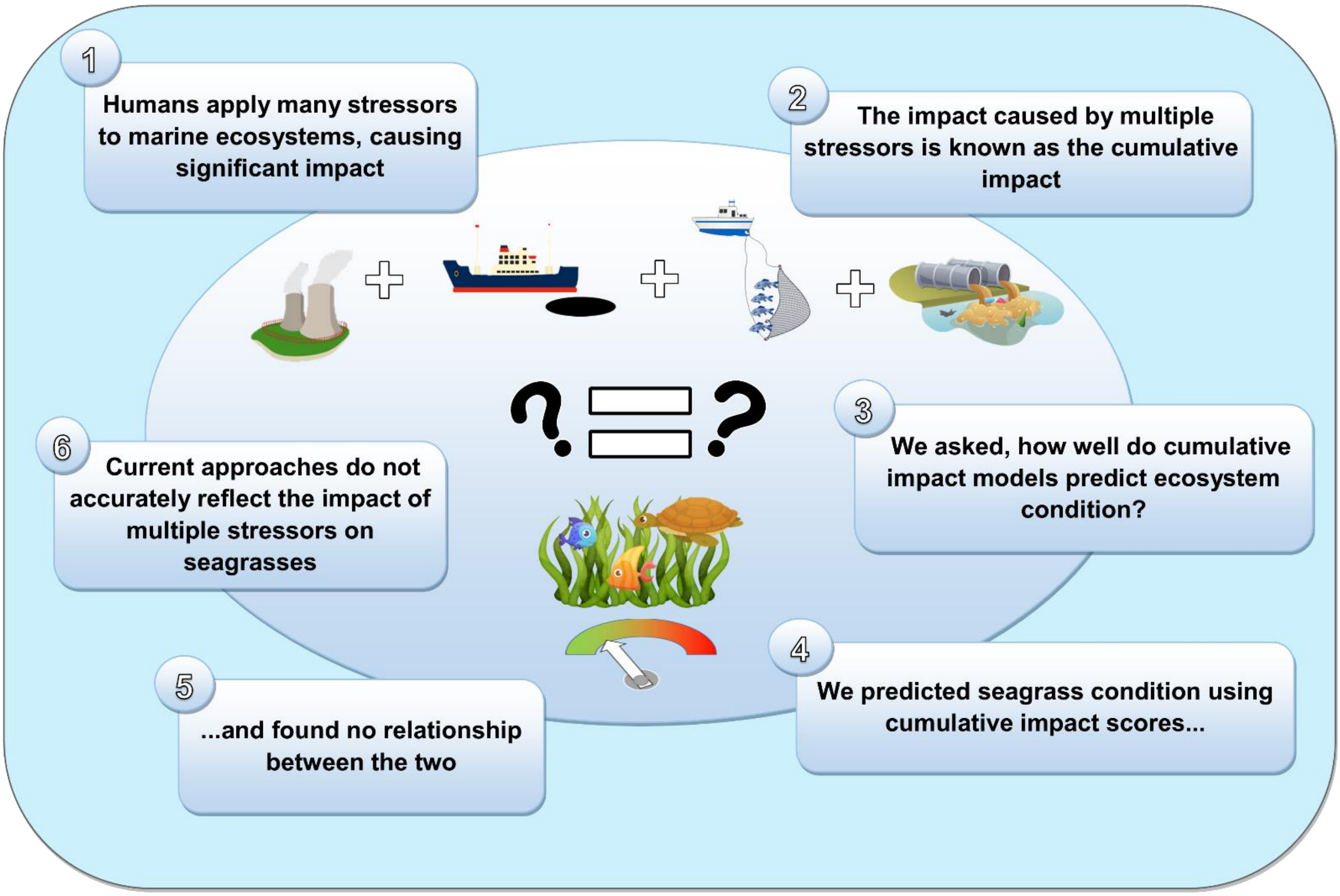
Chapter 2

Evaluation of a popular spatial cumulative impact assessment method for marine systems: A seagrass case study



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Principal Author

Name of Principal Author (Candidate)	Jackson Stockbridge		
Contribution to the Paper	Conceptualisation of the study, as well as: Data curation, formal analysis, investigation, methodology, visualisation, writing - original draft		
Overall percentage (%)	75		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contr bution to the publication is accurate (as detailed above);

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Subject: Authorship statement - Stockbridge et al 2021

Hi all,

Hope everyone is doing well. It's finally almost time for me to submit my thesis! I've attached a statement of authorship for our paper published in Science of the Total Environment that I need to ask you all to please sign and send back to me.

Sam, I know you are elsewhere on a boat and this might be tricky, I may be able to use a past email confirmation that acknowledges your agreement to be an author

All the best,

Jackson

Re: FW: Authorship statement - Stockbridge et al 2021 [SEC=OFFICIAL]

SG Sam Gaylard <sam.gaylard05@gmail.com>
To Nelson, Matt (EPA)
Cc Jackson Stockbridge
12/05/2022

CAUTION: External email. Only click on links or open attachments from trusted senders.

Hey Jackson wow time has flown and congratulations on the impending submission. Great work and you are making me feel inadequate and slack for not progressing mine.

Yes it might be a bit tricky at the moment as I have screwed my laptop up and have it in to some experts to try to fix it. So all correspondence is through my phone. That means signing things will be very tricky. If you can use a previous email from me that's great otherwise I can write you a new one but signing anything might be too hard probably until next week when I (hopefully) get my laptop back

Great work and hope the family is doing well

SG

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Evaluation of a popular spatial cumulative impact assessment method for marine systems: A seagrass case study

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HIGHLIGHTS

- Empirical data are rarely used to evaluate cumulative impact assessment (CIA) methods
- CIA methods assume a relationship between cumulative stress and ecosystem condition
- There is little to no relationship between CIA outputs and seagrass condition
- CIA methods may not be appropriate for assessing the effects of multiple stressors

GRAPHICAL ABSTRACT

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ABSTRACT

Human activities put stress on our oceans and with a growing global population, the impact is increasing. Stressors rarely act in isolation, with the majority of marine areas being impacted by multiple, concurrent stressors. Marine spatial cumulative impact assessments attempt to estimate the collective impact of multiple stressors on marine environments. However, this is difficult given how stressors interact with one another, and the variable response of ecosystems. As a result, assumptions and generalisations are required when attempting to model cumulative impacts. One fundamental assumption of the most commonly applied, semi quantitative cumulative impact assessment method is that a change in modelled cumulative impact is correlated with a change in ecosystem condition. However, this assumption has rarely been validated with empirical data. We tested this assumption using a case study of seagrass in a large, inverse estuary in South Australia (Spencer Gulf). We compared three different seagrass condition indices, based on survey data collected in the field, to scores from a spatial cumulative impact model for the study area. One condition index showed no relationship with cumulative impact, whilst the other two indices had very small, negative relationships with cumulative impact. These results suggest that one of the most commonly used methods for assessing cumulative impacts on marine systems is not robust enough to accurately reflect the effect of multiple stressors on seagrasses; possibly due to the number and generality of assumptions involved in the approach. Future methods should acknowledge the complex relationships between stressors, and the impact these relationships can have on ecosystems. This outcome highlights the need for greater evaluation of cumulative impact assessment outputs and the need for data driven approaches. Our results are a caution for marine scientists and resource managers who may rely on spatial cumulative impact assessment outputs for informing policy and decision making.

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1. Introduction

Coastal habitats are under threat from multiple human induced stressors (Halpern et al., 2008; Halpern and Fujita, 2013). A stressor is any human activity which causes an environmental or biotic factor of the ecosystem to exceed its natural variation (see glossary in Table 1; Crain et al., 2008). As the connection between land and sea, coastal areas are vulnerable to both terrestrial and ocean based stressors such as pollution, overfishing and physical degradation. It is therefore becoming more important to accurately quantify the effect of stressors on coastal habitats to manage them appropriately (Fontanini et al., 2018).

When considered independently, the effects of individual stressors can be assessed and quantified in experimental settings, with some measurable level of precision (Benham et al., 2019). However, stressors rarely occur in isolation in real world settings outside of the laboratory, leading to a need to assess and predict the cumulative impact of multiple stressors (Halpern et al., 2008; Andersen et al., 2015; Kenny et al., 2018); though disentangling the relative impact of individual stressors and understanding their interactions remains a considerable challenge. The earliest ecological cumulative impact assessment (CIA) methods were qualitative. These included environmental checklists where stressors were inventoried but could not effectively quantify the impact of multiple stressors in combination and were not spatial (Cocklin et al., 1992). Later developments in CIA methods described the number of threats to an ecosystem and observed where overlap of these threats may occur (e.g. Lawler et al., 2002). These methods were not quantitative and lacked clarity on how stressors acted in combination to impact the ecosystem (Halpern and Fujita, 2013).

Halpern et al. (2008) developed a method for marine spatial CIA to quantify the combined impact of multiple stressors to an ecosystem, which has since been applied in hundreds of studies to spatially assess cumulative impacts on marine systems (Selkoe et al., 2009; Ban et al., 2010; Korpinen and Andersen, 2016; Andersen et al., 2017; Bevilacqua et al., 2018; Korpinen et al., 2020). The methods developed by Halpern et al. (2008) involves mapping the presence and intensity of stressors across a study region and combining this spatial information with maps of the distribution of the marine ecosystems and/or species of interest. Expert judgement is used to assign a vulnerability score for each ecosystem/species to each stressor it is exposed to; this creates a standardised and spatially resolved stressor impact score (see Eq. (1) below). The sum of these impact scores at each location in the assessment region is the cumulative impact score. The expert elicitation process means that any number of stressors can be considered, and the process is transferable to new regions where appropriate spatial data are available, albeit with different regional and ecosystem specific experts.

Despite this widely used method being a significant advance in spatial CIA for marine systems, several fundamental assumptions must be made (Halpern and Fujita, 2013). Here, we discuss two key assumptions:

(1) Vulnerability weights are sufficiently accurate

Table 1
Glossary of terms and definitions.

Terms	Definition
Stressor	Human activity which causes some abiotic or biotic factor of the ecosystem to exceed its natural variation (Crain et al., 2008)
Impact	A measurable change in a factor of the ecosystem due to a stressor
Cumulative impacts	A measurable change in a factor of the ecosystem due to the combined influence of multiple stressors
Vulnerability score	A score based on the vulnerability of an ecosystem to a combination of stressors (Halpern et al., 2008)
Expert bias	Inaccurate estimates given by experts due to the limitations on our knowledge of a fact and lack of data (Burgman, 2016)
Empirical data	Data collected through observations in the field

A lack of empirical data on stressor habitat combinations means we rely on expert judgement for vulnerability scores (e.g. Doubleday et al., 2017). These scores may be affected by potential biases or uncertainty about the ecosystems and processes involved, which are difficult to account for without surveying a very large number of experts or incorporating specific questions on each expert's certainty about their vulnerability scores (Jones et al., 2018).

(2) Cumulative impact scores reflect ecosystem condition

Calculated cumulative impact scores are assumed to relate inversely to ecosystem condition, such that an area with a lower cumulative impact score is expected to have a better ecosystem condition (and vice versa). Again, a lack of empirical data on how multiple stressors impact ecosystems (see above), combined with a lack of spatially resolved data on ecosystem condition at a relevant scale to use for evaluation, mean it is often not possible to assess how robust this assumption is.

Establishing a generalisable solution to assumption number 2 is almost impossible without considerable time and funding to collect finely resolved spatial data on ecosystem condition across each study site (Halpern and Fujita, 2013). Ideally, ecosystem condition data would be readily available to use for evaluating cumulative impact maps. However, empirical data rarely exist at such a scale to be comparable to these maps (and if they did, there would be little need for cumulative impact assessment models as they currently exist). Therefore, this assumption is relevant to many approaches to marine spatial CIA. That is, all approaches fundamentally assume that cumulative impact scores and ecosystem condition are related in some predictable, usually linear, way (Halpern et al., 2008; Brown et al., 2014; Teichert et al., 2016). However, a linear relationship with CIA scores is likely to be unrealistic, due to the many examples of tolerance thresholds and unpredictable ecosystem state shifts (Kraberg et al., 2011) as well as non additive stressor interactions (Stockbridge et al., 2020). In our study, the range of marine spatial cumulative impact scores calculated by Jones et al. (2018) for seagrass ecosystems in Spencer Gulf were compared with empirical data on seagrass ecosystem condition for the same region.

Seagrass habitats provide valuable ecosystem services, which contribute to the world's blue economy (Waycott et al., 2009). These ecosystem services include regulating our climate through carbon sequestration (Gaylard et al., 2020), supporting commercial fisheries (Watson et al., 1993), waste treatment, and protection from coastal erosion (Campagne et al., 2014). There is also higher biodiversity in areas with healthy seagrass cover (Reed and Hovel, 2006). Seagrass ecosystems are sensitive indicators of change to various marine environmental factors, such as pollution levels (Orth et al., 2006). As such, their condition is often indicative of the health of the broader marine environment. We aimed to use seagrass condition data to evaluate the common assumption in popular marine spatial CIA methods that ecosystem condition has an inverse linear relationship with cumulative impact scores (see assumption 2 above; Halpern and Fujita, 2013).

2. Materials and methods

2.1. Study area

Spencer Gulf is located in South Australia and covers approximately 30,000 km^2, making it Australia's largest estuary (Kampf, 2014). A seasonal density driven front at the mouth of the Gulf leads to reduced exchange of water with the open ocean. This, along with evaporation exceeding precipitation, means that Spencer Gulf is an inverse estuary, where salinity increases with distance from the ocean (Kämpf et al., 2010). Spencer Gulf produces more than 44,000 t of seafood annually (PIRSA, 2015), has an economically important and active shipping channel (Doubleday et al., 2017) and is home to many endemic species (Edyvane, 1999). Spencer Gulf is also home to some of the most extensive and diverse temperate seagrass meadows in Australia (Shepherd and Robertson, 1989), covering an area of 7423 km^2 (Jones et al., 2018).

2.2. Cumulative impact map generation

Cumulative impact maps were generated by Jones et al. (2018) using the framework developed by Halpern et al. (2008); Eq. (1)):

$$CI^s = \sum_{i=1}^{n} D_i \times \mu_{i,e} \tag{1}$$

Where CI^s is the cumulative impact score, D_i is a scaled 0–1 value based on the spatial intensity of stressor i, and $\mu_{i,e}$ is an expert elicited score (vulnerability weight) based on the vulnerability of ecosystem e to stressor i. These cumulative impact maps accounted for expert uncertainty (assumption 1 outlined in the Introduction) by asking surveyed experts for ranges of scores that reflected their confidence levels, which were used when calculating the impact of stressors on benthic marine ecosystems. The experts were asked to provide a worst case, most likely, and best case scenario score for each stressor–ecosystem combination, in an attempt to capture their uncertainty. Narrow score ranges indicated a higher level of confidence (or lower uncertainty) around impact scores than wider score ranges. By doing this, the authors were able to model the effect of expert uncertainty by generating multiple CIA maps (one for each scoring scenario) and assessing locations in the study region where there was consistency in CIA results across all expert scoring scenarios.

The regional-scale assessment by Jones et al. (2018) provides cumulative impact scores at a much finer spatial resolution than global marine cumulative impact maps (250 × 250 m, as opposed to 1 × 1 km in the global analyses of Halpern et al. (2008)), which is suitable for comparison to the empirical data on ecosystem condition that we collected (described in Section 2.2). The CIA assessment in Jones et al. (2018) considers the spatial and temporal exposure of seagrass across the study area to multiple stressors that are known to impact this specific habitat. The CIA accounted for the spatial overlap between seagrasses and footprint (and intensity) of stressors, combined with expert scores for the impact of each stressor on seagrasses. Experts provided detailed information on which stressors were likely to impact seagrasses and only those relevant were included in the assessment (others were given impact scores of 0; see Supplementary material in Doubleday et al., 2017). Across our study area 25 relevant stressors were known to overlap with seagrass habitats (min = 5, max = 20 and mean = 7.59 stressors at any one location; Doubleday et al., 2017; Jones et al., 2018). These stressors included five associated with habitat modification and coastal activities, four environmental variables, four fishing variables, four pollution variables, three invasive species variables, two aquaculture variables, two boating or shipping variables, and one associated with acid sulphate soils (Doubleday et al., 2017). The cumulative impact score for all seagrass areas in Spencer Gulf ranged from 6.22 to 22.99, with an average score of 13.99 (Jones et al., 2018).

2.3. Field data collection and processing

We collected video survey data from 31 seagrass sites (500 m × 500 m) in northern Spencer Gulf, within the area covered by the cumulative impact maps generated by Jones et al. (2018), Fig. 1; for a description of stressor types, see Supplementary material in Doubleday et al., 2017). At each of the survey sites, we undertook 10 towed underwater video transects with a minimum length of 50 m and used these data to assess benthic habitat (Fig. S1). For each transect, two cameras were towed 1 m above the seafloor at a 90° angle (i.e. looking straight down), with each video frame capturing an area of approximately 1 m^2. One camera collected standard definition images, each with time and GPS information encoded. The other camera collected high definition images that were used for reference if required. Videos were visually analysed after returning from the field using an Environment Protection Authority, South Australia (EPA) in-house video analysis software package that was linked to Microsoft Access, allowing annotated data on the habitat type and condition in each video frame to be saved directly to a database (and linked to position and time/date information from the video). The standard definition video frames were used to quantify seagrass percent cover and species composition in each ~1 m^2 field of view. This produced a dataset of seagrass cover and species composition of between 600 and 900 frames for each of the 31 surveys sites (Fig. S1; Fig. S2). This variation in the number of video frames per site occurred because the speed of the boat varied causing some videos to be slightly longer/shorter than others. Boat speed during video tows was typically 0.5–1 knot. The final seagrass condition dataset was quality checked by a second trained operator of the video analysis software package.

2.4. Seagrass condition indices

We conducted a literature search to create a database of published methods for quantitatively measuring seagrass condition from visual observation or image data (Fig. S1; Table S1 in supporting information). To be considered for inclusion, studies must have measured one or more seagrass metric (Table S1, 'Metric' column), and combined them into a single health or condition index (Table S1). When reviewing the literature, we found seven different published measures for calculating seagrass condition from observation data (Table S1). We used three of these condition indices in our study (Table S1), based on the parameters we could generate or measure using the video data from our 31 seagrass survey sites. These were:

(1) **Percent cover:** The percentage of seagrass cover in each video frame generated by our underwater videos (Gaylard et al., 2012).
(2) **Habitat structure index (HSI):** A score based on five different parameters: area of seagrass, patchiness, connectivity, percent cover, and species diversity (Irving et al., 2013).
(3) **Seagrass quality index (SQI):** A score based on three parameters: percent cover; shoot density; and species diversity (Neto et al., 2013). These are weighted and compared to a hypothetical site in perfect condition. Since we did not record shoot density, we removed this from our calculation and adjusted the weights accordingly (Supporting information, Eq. S1).

2.5. Statistical analysis

We modelled the relationship between seagrass condition based on the video data (for each of the three different indices) and spatially linked cumulative impact scores (from Jones et al., 2018) for the location of each video frame. To take account of the quantified expert uncertainty in the CIA scores (based on a range from the worst case to the best case scenario), we used a simulation-based approach. For each location where we had seagrass condition data (N = 24,394 video frames from 310 towed video transects at 31 sites), we extracted the three CIA scores (worst case, most likely and best case) from the corresponding grid cell in the map generated by Jones et al. (2018). We used these three values to parameterise a beta distribution and simulate a cumulative impact score to pair with the spatially matched video survey data (Fig. S1). Each cumulative impact score was the mean calculated from 1000 random samples from this beta distribution, which represented the plausible range of cumulative impact scores at each video frame location, from the worst case to the best case scenario (Fig. S1). This resulted in a simulated CIA score for each video frame location, which was paired with the seagrass condition index values calculated from the video survey data.

We then tested for a relationship between the simulated cumulative impact scores and each of the three seagrass condition indices using a generalised linear mixed model (GLMM) with a beta error distribution (Fig. S2). We rescaled all seagrass condition index scores to be between

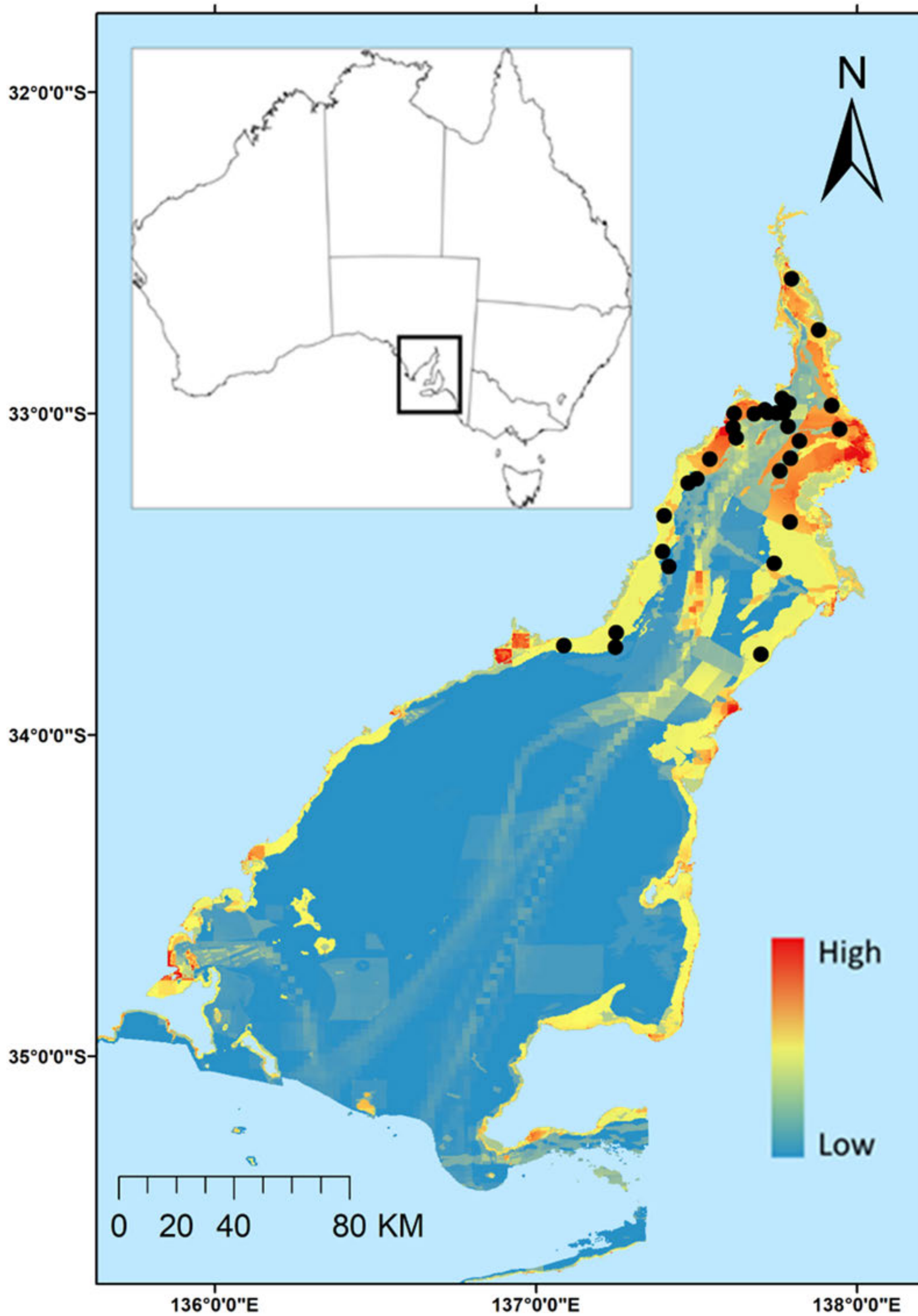

Fig. 1. Sites where seagrass condition data were collected (black points) overlaid on the cumulative impact map (most likely scenario) of Spencer Gulf, South Australia (34.3036° S, 136.9805° E; Jones et al., 2018). Colours indicate cumulative impact score. Inset map shows the location of Spencer Gulf within Australia.

0 and 1 so that they could be used in a beta distributed model. The models were built with the 'glmmTMB' package (*v0.2.3*; Mollie et al., 2017) in R 3.6.0 (R Core Team, 2019). We chose this approach because GLMMs are flexible enough to analyse non normal data using both random and fixed effects (Bolker et al., 2009). Both 'site' ($n = 31$) and 'transect' nested within 'site' ($n = 10$ per site) were included in the GLMM as random effects to control for the non independence of seagrass condition data within site and transects (Fig. S2).

To understand if the CIA scores were representative of the measured seagrass condition index score at each location in our study region, we looked at the slope coefficient of the fitted GLMMs (separate models were fitted for each of the three seagrass condition indices; Fig. S2). Each model had the simulated CIA scores as the predictor variable and seagrass condition index score as the response variable (with 'site' and 'transect' as nested random effects). We used a bootstrapping approach to generate 10,000 estimates of the model slope coefficient so that we could explore variance around this model parameter, which is related to uncertainty in the relationship between cumulative impact score and measured seagrass condition. This allowed us to assess the magnitude and direction of any relationship between CIA score and seagrass condition index scores (based on the mean slope coefficient) and the confidence in this relationship (based on the standard error to of the mean; Fig. S2). This entire process was repeated for each of the three seagrass condition indices, resulting in three mean and standard error estimates for the slope of the relationship; one for each of the three seagrass condition indices.

To further evaluate how well seagrass condition can be predicted by cumulative impact scores (i.e. evaluate the fit of the models), we assessed model prediction error using 10,000 bootstrapped predictions for seagrass condition index based on the cumulative impact score at the same location (Fig. S2). Each model predicted seagrass condition value was compared to the observed seagrass condition value from the video data and a difference value was calculated (Fig. S2). We calculated the median and median absolute deviation (MAD) of the differences be tween the observed and the model predicted seagrass condition index scores. These metrics are a measure of how well the models were able to predict seagrass condition at any given video frame location based on the spatially matched CIA score (i.e. the overall strength of the corre lation between CIA and condition index).

After calculating our model prediction error, we explored whether model predictive accuracy was consistent across the dataset, or whether systematic error was detectable, conditional on seagrass condition. We assessed this by sub setting the model predicted data into groups based on the quartiles of the observed seagrass condition scores. The seagrass condition groups were nominally, 'Poor' (<25th percentile of index values), 'Poor Moderate' (25th 50th percentile of index values), 'Moderate Good' (50th 75th percentile of index values) or 'Good' (>75th percentile of index values). This allowed us to examine whether there was any systematic inaccuracy in the modelled relationship be tween cumulative impact scores and seagrass condition index scores (i.e. was the cumulative impact score more or less strongly related to seagrass condition score in locations where the seagrass condition is poor, moderate or good?).

3. Results

The cumulative impact scores for each video frame location ranged from 0.004 to 0.654 (on a 0 1 scale), where a lower value represents a lower cumulative impact. Seagrass condition scores for the percent cover and HSI indices ranged from 0 to 100 (Fig. 2A; Fig. 2B), and for SQI ranged from 0 to 0.8 (Fig. 2C). We found no sig nificant relationship between cumulative impact and the HSI condi tion index (mean (SE) ≤ 0.01(<0.01); Fig. S3). Although we found a significant, negative relationship between cumulative impact and percent cover, the coefficient was very small (mean (SE) = −0.072 (0.01); Fig. S3). We found a similarly small but significant negative relationship for cumulative impact score and SQI (mean (SE) coeffi cient = −0.071 (0.01); Fig. S3). The coefficient values here represent the difference in the predicted value of seagrass condition (on the standardised beta scale), for each one unit difference in cumulative impact score. The size and direction of these coefficient values are il lustrated by the model predictions of seagrass condition based on CIA score (Fig. S2). When plotted, these show a slightly negative re lationship between CIA score and percent cover and SQI, but no rela tionship (a horizontal line at 0) between HSI and CIA score (Fig. S3).

The range of prediction error values was very wide for all three models of seagrass condition index as a function of cumulative impact score. For the model of seagrass percent cover, prediction error ranged from −100 to +100 (i.e. the full possible range of prediction errors) (Fig. S4). Model prediction error for seagrass condition ranged from −82.9 to +82.8 for HSI, and − 1 to +0.8 for SQI (Fig. S4). Median pre diction error was 30% (MAD = 4.8) for the percent cover model, 33.4% (MAD = 1.4) for the HSI model, and 23.4% (index score error = 0.2, MAD = 0.1) for the SQI model (Fig. 3).

The models of percent cover and SQI as a function of cumulative im pact score were better at predicting seagrass condition index score in areas where observed seagrass condition was 'Poor' (<25th percentile; Fig. S5). The opposite was true for the model of seagrass condition ac cording to the HSI index, which had lower prediction error in areas of better seagrass condition (Fig. S5).

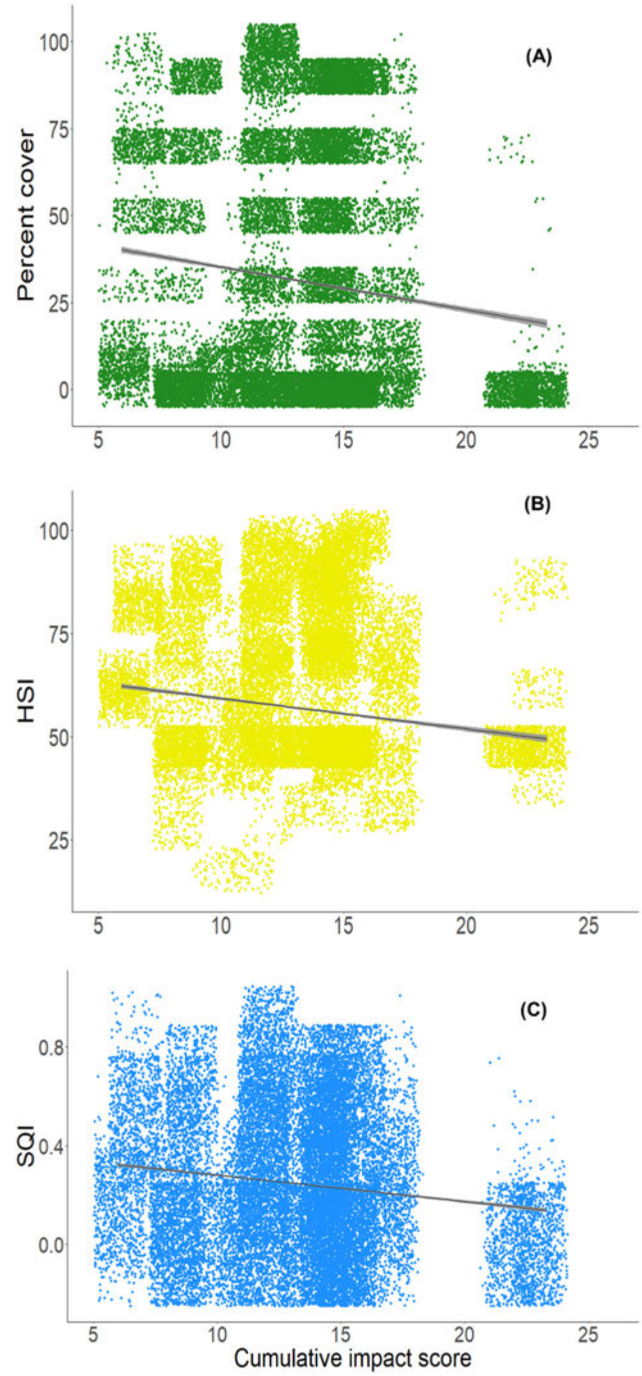

Fig. 2. Modelled relationship (line) with observed condition data (points) between seagrass condition indices and cumulative impact score. Grey shading shows 95% confidence intervals: (a) Percent cover (index ranges from 0 to 100), (b) Habitat structure index (HSI; index ranges from 0 to 100), (c) Seagrass quality index (SQI; index ranges from 0 to 1).

4. Discussion

Using seagrass ecosystems as a case study, we tested a fundamental assumption of many commonly used marine spatial cumulative impact assessment (CIA) methods (Halpern et al., 2008; Brown et al., 2014;

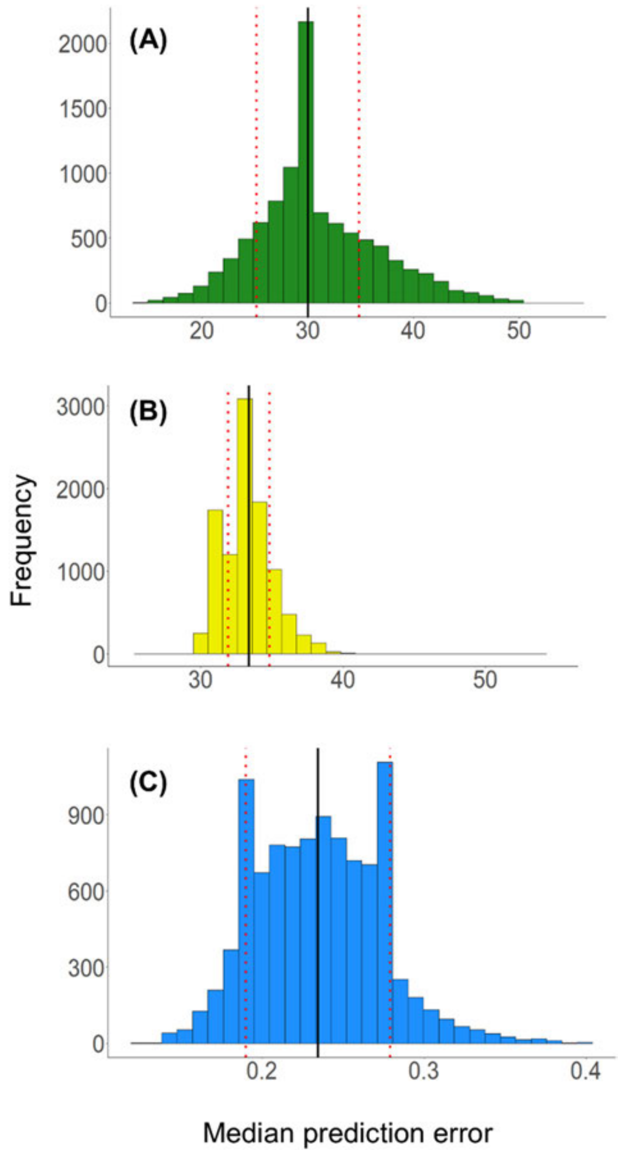

Fig. 3. Distribution of median prediction error from 10,000 GLMM model iterations when predicting seagrass condition index as a function of cumulative impact. (a) Percent cover (index ranges from 0 to 100); (b) Habitat structure index (HSI; index ranges from 0 to 100); (c) Seagrass quality index (SQI; index ranges from 0 to 1). Black vertical line on each plot shows the median and dashed red lines show the median absolute deviation as a measure of variance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Teichert et al., 2016), namely that cumulative impact score is representative of ecosystem condition. We did this by collecting empirical data on seagrass condition through video transects and comparing these to cumulative impact scores for the same locations generated in a previous study (Jones et al., 2018), which used the widely applied method proposed by Halpern et al. (2008). Our models of seagrass condition as a function of cumulative impact score found either no relationship or a weakly negative relationship between the two variables (Fig. 2), and had large median prediction errors of between 12 and 55% across our three seagrass condition indices (Fig. 3). There were differences in prediction error between the quartiles of our data ('Poor', 'Poor to moderate', 'Moderate to good', 'Good') but we found no consistent pattern of error across the dataset. Percent cover and SQI underestimated seagrass condition in the 'Poor' quartile, whereas HSI overestimated condition.

It could be argued that the lack of a predictable negative relationship between CIA scores and seagrass condition in our study was due to poorly performing seagrass condition indices, which do not adequately capture the true state of the ecosystem (as opposed to a poorly performing CIA method). We tested three different seagrass condition indices (suitable for use on the types of survey data we had) and did not find a strong relationship with CIA score for any of them. By calculating multiple different condition indices, we aimed to build confidence in our findings and illustrate that they are generalisable and robust to the choice of condition index. Multiple seagrass species from four different genera (*Posidonia, Zostera, Halophila,* and *Amphibolis*) are found in our study region (Gaylard et al., 2012); three of which are considered 'enduring', meaning that percent cover is a good indicator of their condition (Gaylard et al., 2012; Kilminster et al., 2015). As such, percent cover is considered an effective measure of seagrass condition by the South Australia EPA and is used in their monitoring (Gaylard et al., 2012). Wood and Lavery (2000) provide further support for using cover based seagrass metrics to indicate ecosystem condition. SQI differs from simple percent cover metrics in that it also incorporates species composition, whereas HSI considers further parameters such as area and patchiness (Fig. S1).

However, previous studies from other regions have used different metrics to measure seagrass condition, which have been shown to correlate with ecosystem condition (e.g. Romero et al., 2007; Gobert et al., 2009; Oliva et al., 2012; García Marín et al., 2013). Similar to the indices used here, these are based on abundance, but differ to ours in that they also consider chemical properties and other physical metrics such as leaf necrosis and shoot density (Fig. S1). The suitability of seagrass condition indicators in any given study area may also be influenced by habitat condition and the species being assessed (Marbà et al., 2013). In the absence of a large field and laboratory study to collect the data required for calculating different types of seagrass condition indices (such as those in Romero et al., 2007; Gobert et al., 2009; Oliva et al., 2012; García Marín et al., 2013), we used visually observable parameters that are widely available across our study region, accurate for the region's seagrass ecosystems, highly replicable, and cost and time efficient (Gaylard et al., 2013; Tanner et al., 2019). However, future research in Spencer Gulf and the surrounding areas should focus on empirically establishing the relationship between the seagrass condition indices used here and more direct physiological measures of seagrass health/condition (Romero et al., 2007; García Marín et al., 2013).

The key assumption that ecosystem condition is related to modelled cumulative impact scores in a predictable, negative way is critical to established CIA methodologies (Halpern and Fujita, 2013; Teichert et al., 2016). However, our findings show there is little to no relationship between cumulative impact scores and seagrass ecosystem health in our study area based on three different indices for measuring seagrass condition. This implies that the standard and frequently adopted marine spatial CIA approach may not adequately capture the true impacts of multiple stressors on seagrass ecosystems. The lack of correlation between CIA score and seagrass condition may be due to the methodological assumption that the impact from stressors and ecosystems are uniformly distributed (i.e. either entirely present or entirely absent) within a unit of assessment (e.g. a single map pixel) (Halpern and Fujita, 2013). The validity of this assumption will depend on the spatial resolution of the data used in the assessment, with finer scales supporting more accurate CIA results (de Vries et al., 2019), highlighting the need for finer scale marine CIAs (Andersen et al., 2015). Additionally, the complete presence or absence of an ecosystem or stressor within a map pixel is unlikely, as marine ecosystems are often heterogeneous and patchy (Irlandi, 1997) and marine spatial data are generally only available at a coarse scale (Halpern and Fujita, 2013). In addition, the intensity of stressors is likely to vary. For example, the concentration of pollutants at a specific location is dependent on several factors such as their residence time in the water column (Ranke, 2002), the level of freshwater flushing (Mecca et al., 2008) and the sorption rate to suspended sediment in a given area (Wicke et al., 2007). Future studies that comprehensively investigate direct relationships between spatial stressor data and seagrass condition may help to identify which, if any, of the spatial stressor datasets most influence seagrass condition.

Another common assumption of CIA method's is that an ecosystem will respond linearly to increases in stressor intensity (Ban et al., 2010; Halpern and Fujita, 2013). Given what we understand of ecosys tem tipping points and thresholds (Scheffer and Carpenter, 2003; May et al., 2008), a linear response is unlikely (Connell and Russell, 2010). Furthermore, threshold exceedance can be dependent on spatial and temporal factors, making predicting ecosystem responses even more challenging (Diaz and Rosenberg, 2008). Failing to understand the shape of relationships between stressor intensity and ecosystem tolerance, or to identify threshold exceedance may lead to under or overestimating cumulative impacts on ecosystems (Connell et al., 2017). Such ecosystem stressor dynamics almost certainly contribute to the poor relationship between cumulative impact scores and seagrass ecosystem condition found here.

The small to no correlation between CIA score and ecosystem condition that we found may also result from misidentifying stressor interactions in the cumulative impact assessment. (Stockbridge et al., 2020). The predominant marine spatial CIA methods assume an additive model, where the impact of one stressor can be summed to that of a second/third/nth stressor to calculate the cumulative im pact (Halpern and Fujita, 2013). Previous studies have shown vari able results when investigating the frequency of additive versus non additive interactions between marine stressors and there have been few attempts to understand the effects of misrepresentation of these relationships in CIA (Ihde and Townsend, 2017; Furlan et al., 2019). Although additive interactions appear to be most common (Côté et al., 2016; Stockbridge et al., 2020), a recent meta analysis concluded that the impact of over 45% of stressor interac tions on seagrasses were not additive (Stockbridge et al., 2020) and other earlier studies found an even higher frequency of non additive interactions (Crain et al., 2008; Darling and Côté, 2008). These studies highlight that some stressors can either exacerbate or mitigate the impact of one another, potentially leading to unex pected interactions (Taherzadeh et al., 2019). It stands to reason that assuming additivity when it is not the case can lead to inaccu rate cumulative impact scores. Furthermore, the inconsistency in the frequency of non additive interaction types across ecosystems of the same type lends support to the need for more localised empir ical data to enable appropriate relationships to be incorporated (Foden et al., 2011; Fluet Chouinard et al., 2020).

Inaccurate cumulative impact assessment may lead to the neglect of ecosystems in need of management intervention. Underestimating cumulative impacts may cause ecosystems to be pushed beyond ecolog ical tipping points before we have identified them as being at risk (Connell et al., 2017). Such regime shifts can be irreversible, preventing ecosystem recovery and impacting ecosystem service provision (Granek et al., 2010). This scenario may occur if, for example, a linear re sponse or additive stressor interactions are assumed but stressors are interacting synergistically. Whilst underestimating cumulative impact can have irreversible negative effects on an ecosystem and the services it provides, overestimating can also cause problems. Overestimating the potential damage to an ecosystem from cumulative impacts could pro voke unnecessary management intervention that is not cost efficient and uses limited resources that would be better applied to more vulner able areas. Furthermore, overestimating cumulative impacts is likely to occur in areas where one stressor is mitigating the effect of another (i.e. an antagonistic interaction). Removing a stressor in this situation could lead to decline in ecosystem condition. For example, suspended sedi ment caused by run off (stressor 1) may shade benthic habitat from the impact of UV radiation (stressor 2; Côté et al., 2016). Managing run off and thereby turbidity may actually cause the condition of the benthic habitat to worsen through greater exposure to UV radiation.

Future development of CIA methods should focus on more accu rately reflecting ecosystem condition by incorporating the relationships between stressors, and the effect of stressor interactions on ecosystem services. Our results highlight the need for more data driven ap proaches, (e.g. Kotta et al., 2020), and act as a cautionary tale for marine scientists and resource managers who may rely on similar spatial cumu lative impact assessment approaches for informing policy and decision making.

5. Conclusion

The main aim of marine spatial CIA is to detect the impact of multiple human activities on marine ecosystem condition (Halpern et al., 2008; Clark et al., 2016; Andersen et al., 2017; de Vries et al., 2019). However, we found only a weak, negative relationship after modelling seagrass condition against cumulative impact. Our findings suggest that the many assumptions associated with current methods can lead to a break down in the expected relationship between cumulative impact scores and observed ecosystem condition. The existence of cumulative impacts is not under question here, given what we know about the ef fects of human activities on marine ecosystems and species (IPCC, 2001; He and Silliman, 2019). However, it appears that the widely used approaches for detecting and mapping these impacts may be too general to provide accurate results and highlights the need for more ro bust and well validated spatial marine CIA methods.

CRediT authorship contribution statement

Jackson Stockbridge: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing original draft. **Alice R. Jones:** Conceptualization, Data curation, Formal analysis, Project administra tion, Supervision, Writing review & editing. **Sam G. Gaylard:** Concep tualization, Methodology, Writing review & editing. **Matthew J. Nelson:** Data curation, Methodology, Writing review & editing. **Bronwyn M. Gillanders:** Conceptualization, Formal analysis, Project ad ministration, Supervision, Writing review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influ ence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.146401.

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Appendix A. Supplementary data

Table S1. Different seagrass condition indices used in published research. Coloured squares indicate metrics that we also recorded (red = not recorded; green = recorded). 'Examples' column states which past study (or studies) have applied the index. 'Used/Not used/Adapted' column states if we applied the index completely ('Used'), did not use the index ('Not used'), or if we changed the index slightly to fit our data ('Adapted' – changes stated).

Index developed	Metric		Method	Examples	Used/ Not used/ Adapted?	Ref
Habitat Structure Index (HSI)	Percent cover of seagrass		$\sqrt{A^2 + C^2 + P^2 + K^2 + S^2}$ * Scaler where *A* is a measure of Area; *C* is a measure of continuity or patchiness; *P* is a measure of proximity of seagrass patches to other patches; *K* represents percent cover; and *S* is species identity. The 'scaler' ensures the HSI lies between 0 and 100 and is calculated using a transect where *A, C, P, K* and *S* are set to the maximum possible value. For the full method of calculating the HSI, see Irving *et al.* (2013).	Irving *et al.* (2016)	Used	Irving *et al.* (2013)
	Species composition					
Conservation Index	Percent cover of live seagrass		$\frac{L}{L + D}$ where *L* is the percent cover of live seagrass and *D* is the percent cover of dead seagrass	Moreno *et al.* (2001)	Not used – we did not measure percent cover of dead seagrass	Sanchez Poveda *et al.* (1996)
	Percent cover of dead seagrass					

Seagrass Quality index (SQI)	Percent cover of seagrass		$$SQI = \left(\frac{T}{T\_ref}\right) * 0.2 + \left(\frac{E}{E_{ref}}\right) * 0.3 + \left(\frac{D}{D_{ref}}\right) * 0.5$$ where *T* is number of taxa; *E* is bed extent; *D* is shoot density; and *ref* is reference condition	Adapted by Wilkes *et al.* (2017) Neto *et al.* (2013)	Adapted – shoot density was removed from the equation and the weighting adjusted accordingly (0.2 → 0.4; 0.3 → 0.6).	Neto *et al.* (2013)
	Shoot density					
	Species composition					
Ecological Quality Ratio (EQR) based on the *Posidonia oceanica* Multi-variate Index (POMI)	Phosphorus content		$$\frac{(CI_x - CI_{worst})}{(CI_{optimal} - CI_{worst})}$$ Principal component analysis to combine all 14 metrics into a single score. The score of each site on the first axis (CI_x) is used as an estimate of the current status. Also established extreme conditions, with the 'optimal' condition ($CI_{optimal}$) being used as a reference site (where each metric is assigned the best possible score), and the 'worst' score (CI_{worst}) to represent the worst state for each site. For the full method of calculating EQR based on the POMI index, see Romero *et al.* (2007).	Bennett *et al.* (2011) Mascaro *et al.* (2012)	Not used – we only measured one of the required metrics	Romero *et al.* (2007)
	Nitrogen content					
	Sucrose content					
	$\delta^{15}N$ isotopic ratio in rhizomes					
	$\delta^{34}S$ isotopic ratio in rhizomes					
	Necrosis in leaves					
	Shoot leaf surface					
	Meadow cover					
	Shoot density					
	Plagiotropic rhizomes					
	Epiphyte nitrogen content					
	Copper concentration in rhizomes					
	Lead concentration in rhizomes					
	Zinc concentration in rhizomes					
Aquatic Ecosystem Condition Reports (AECR)	Percent cover of seagrass		Used percent cover to establish seagrass condition using a conceptual model	Used by the South Australia Environmental Protection Authority (EPA) Amran 2017	Used	Gaylard *et al.* (2012)

Benthic substrate ratio (BSR)/macroalgal evenness	Percent cover of seagrass		$$BSR = \frac{Percent\ cover\ of\ seagrass}{Macroalgae\ cover}$$ Macroalgal evenness was assessed using Margalef's D-statistic, calculated as follows: $$d = \frac{(S-1)}{\ln N}$$ Where S is the number of species and N is the total number of individuals	Houk *et al.* (2013)	Not used – we did not measure macroalgae cover	Houk *et al.* (2013)
	Macroalgae cover					
Report card	Seagrass meadow area		Scores were assigned to sites depending on how metrics deviated from baseline data. For example, an area with a >20% increase in seagrass cover from the baseline conditions was considered to be in very good condition.	Used to report on the status of seagrass in Gladstone harbour (Carter *et al.* 2017)	Not used – we do not have the required baseline data	Carter *et al.* (2017)
	Percent cover of seagrass					
	Species composition					
	Baseline data (past 10 years)					

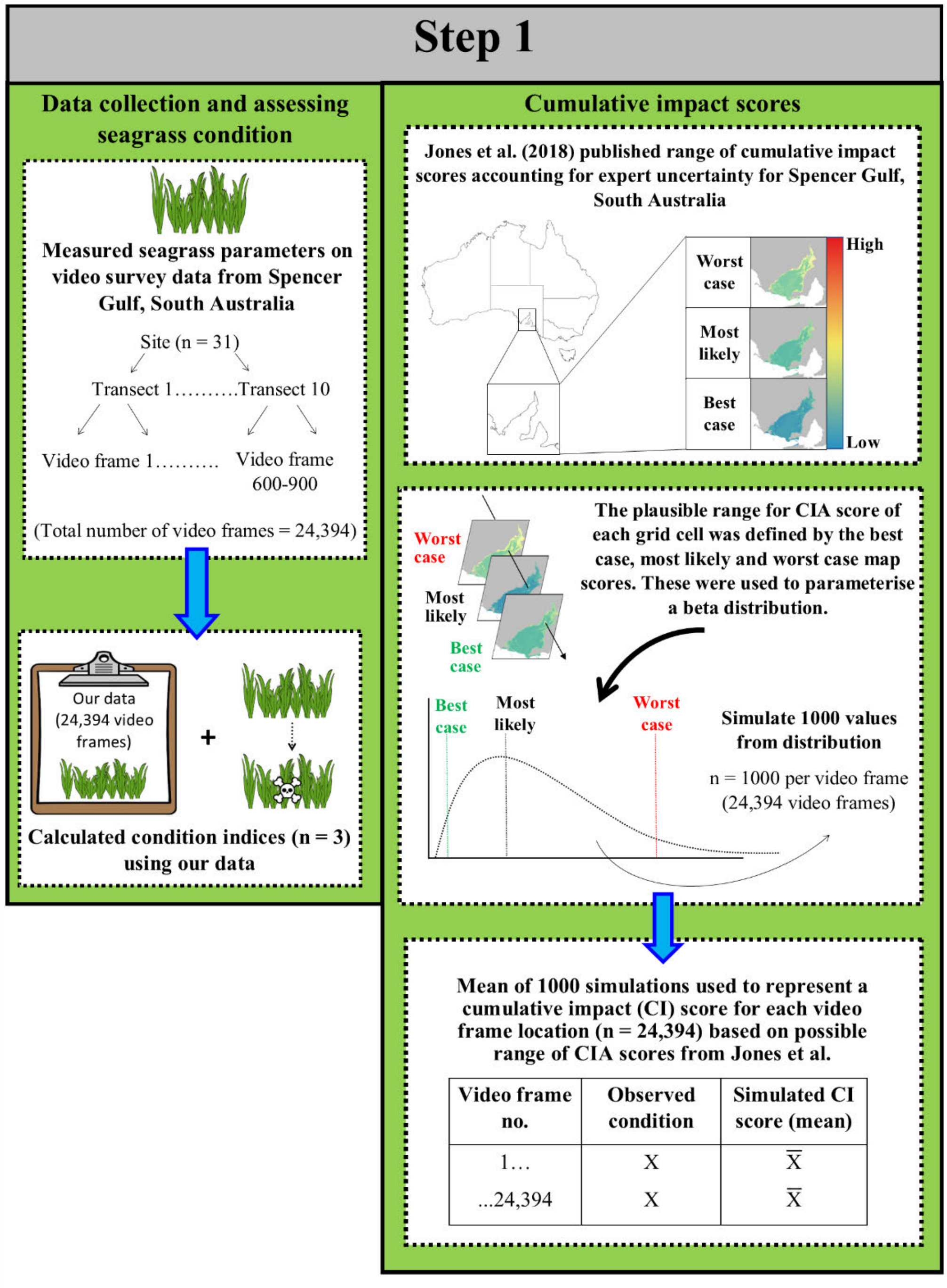


Figure S1. Methods for the collection, collation and processing of data for assessing the relationship between modelled cumulative impact (from Jones *et al.* 2018) and observed seagrass condition in northern Spencer Gulf, South Australia.

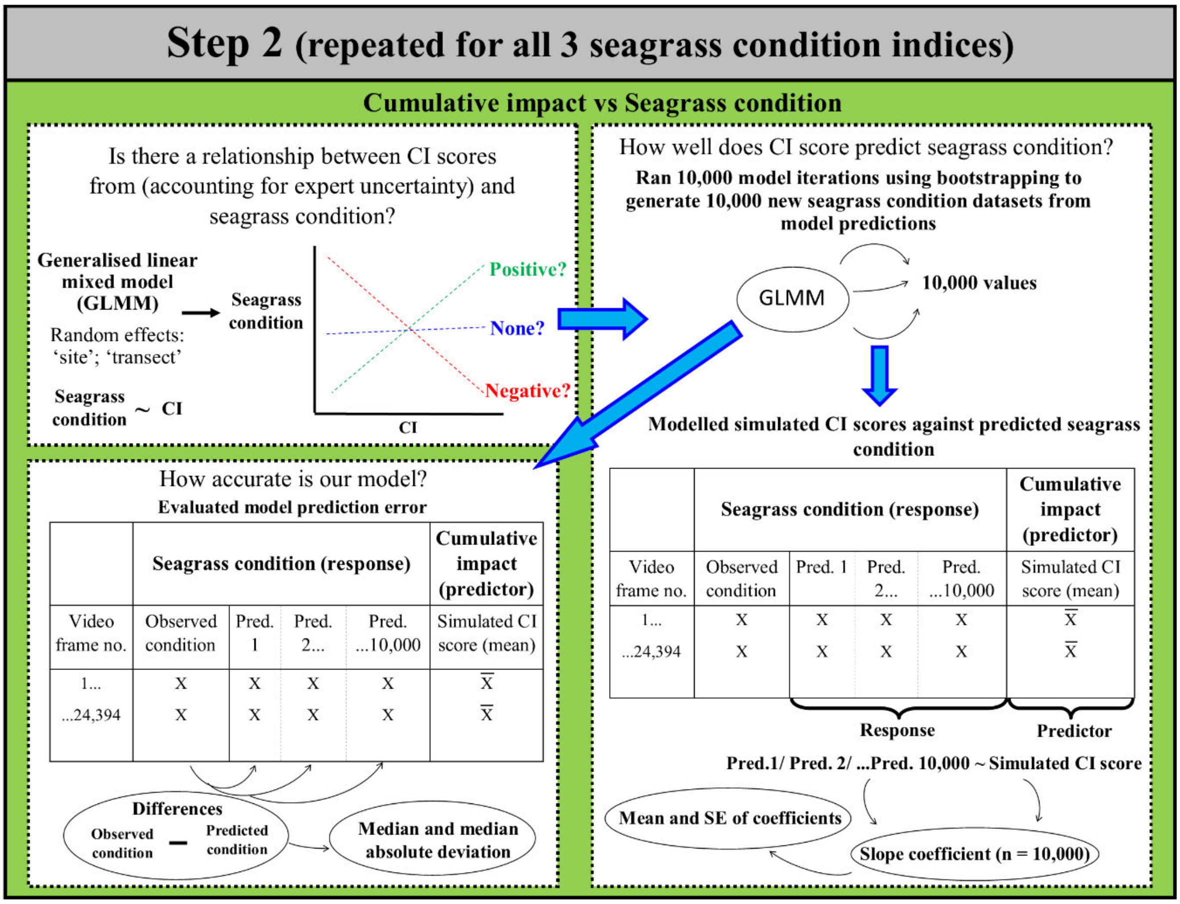


Figure S2. Methods for modelling the relationship between previously published cumulative impact scores (from Jones *et al.* 2018) and observed seagrass condition in northern Spencer Gulf, South Australia.

Eq. S1. Details of how Seagrass quality index (SQI) was adapted for our study

SQI is calculated using number of taxa, bed extent (percent cover) and shoot density (Neto *et al.* 2013).

$$SQI = \left(\frac{T}{T\_ref}\right) * 0.2 + \left(\frac{E}{E_{ref}}\right) * 0.3 + \left(\frac{D}{D_{ref}}\right) * 0.5$$

where *T* is number of taxa; *E* is bed extent; *D* is shoot density; and *ref* is reference condition

We did not measure shoot density in our dataset, so we eliminated this parameter from the calculation of SQI.

'*T*' is 4 because there are 4 species of seagrass observed in Spencer Gulf by the EPA.

'*E*' is 100%. Since shoot density is given a weighting of 0.5 in the standard SQI calculation, we split this weighting and applied it proportionately to the weighting for the remaining two factors. This ensured that the proportional weights of the remaining parameters were consistent with the original approach as the weight for taxa changed from 0.2 to 0.4, and the weight for extent changed from 0.3 to 0.6 (i.e. extent has a weighting 1.5 times that of taxa).

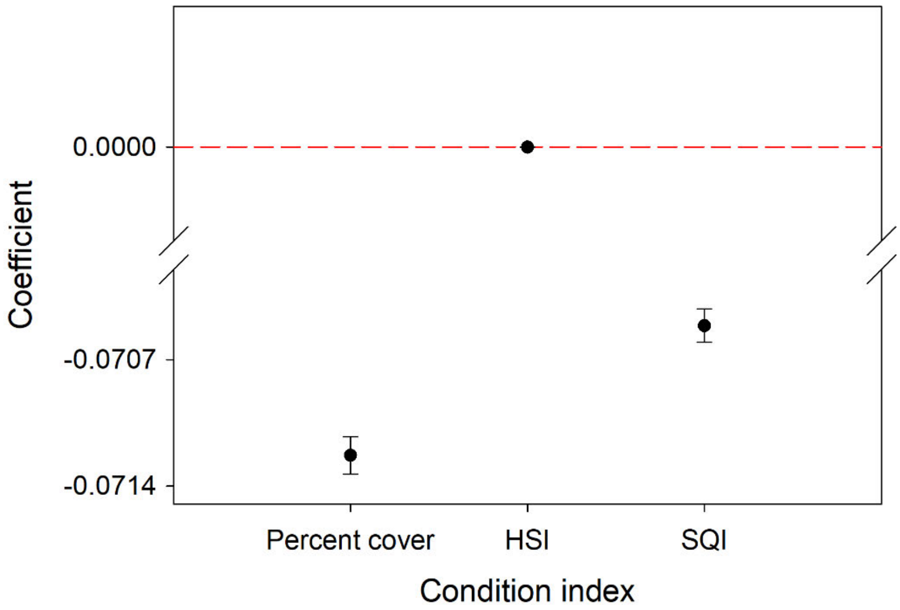


Figure S3. Mean (±SE) of the coefficient from 10,000 model simulations of seagrass condition (three different indices) as a function of cumulative impact. HSI = Habitat structure index; SQI = Seagrass quality index.

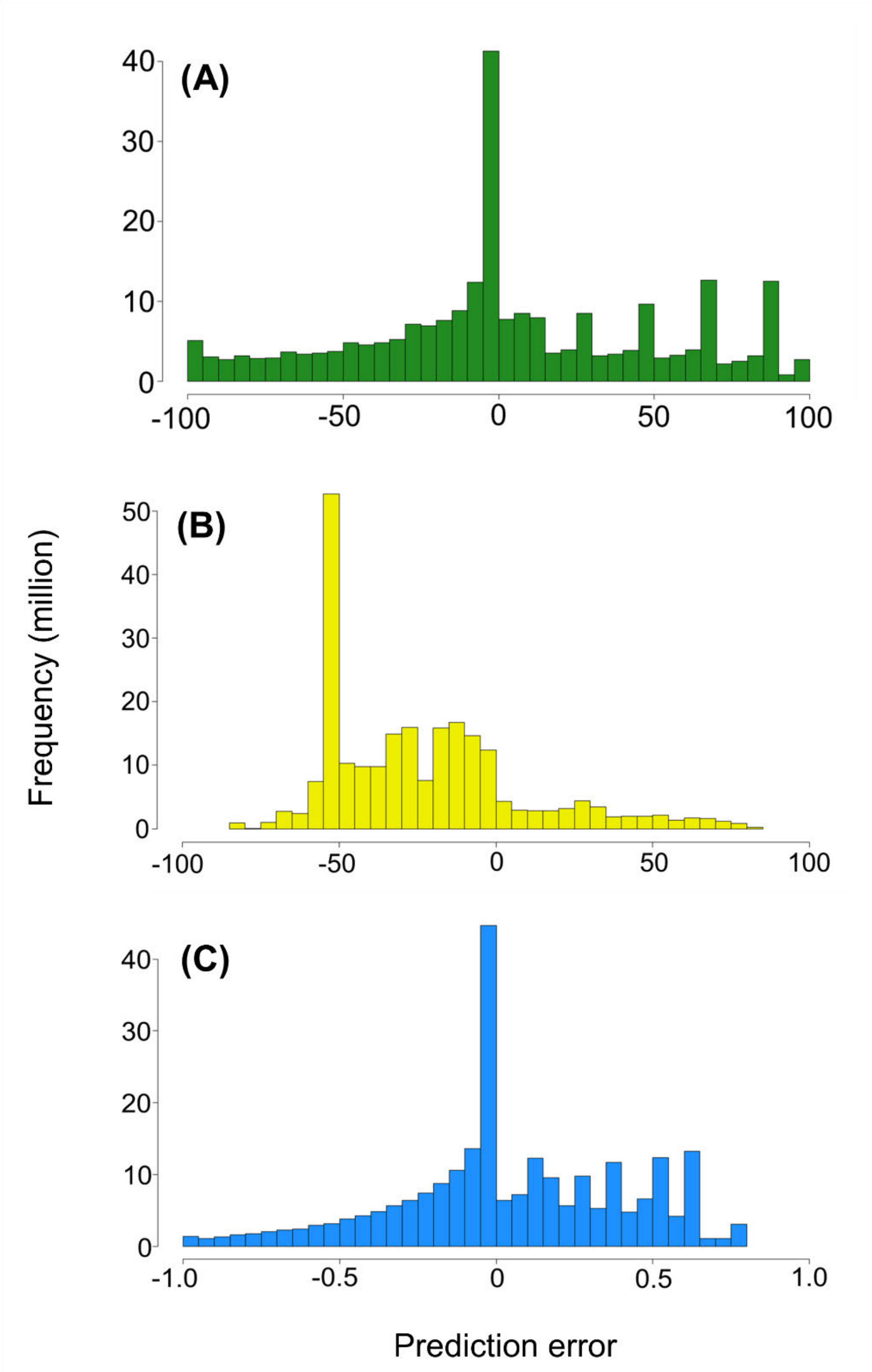
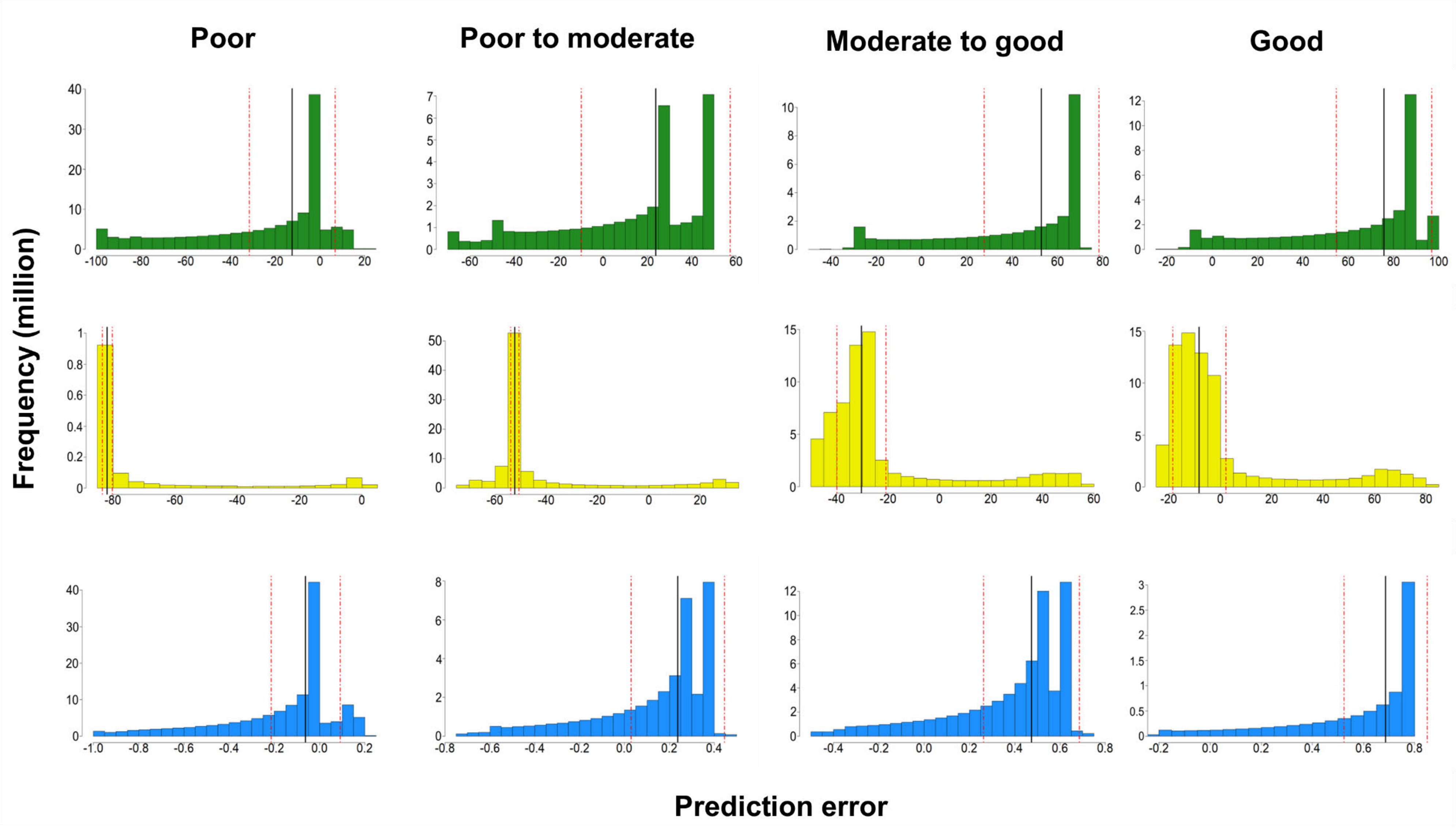


Figure S4. Model prediction error from 10,000 GLMM simulations of three seagrass condition indices. Prediction error calculated as observed seagrass condition index minus predicted seagrass condition index. (a) Percent cover (index ranges from 0-100); (b) Habitat structure index (HSI; index ranges from 0-100); (c) Seagrass quality index (SQI; index ranges from 0-1).



Poor
Poor to moderate
Moderate to good
Good
Frequency (million)
Prediction error

Figure S5. Prediction errors, median prediction error (black line) and the median absolute deviation of prediction error (red dashed lines) for the quartiles of the seagrass condition index data values. The first quartile corresponds to the lowest scores (poorest seagrass condition), the second quartile is poor to moderate seagrass condition, the third quartile is moderate to good seagrass condition and the fourth quartile are the highest condition index scores (good seagrass condition). Histograms colour indicates the seagrass condition index where green = percent cover, yellow = Habitat Structure Index (HSI), and blue = Seagrass Quality Index (SQI

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Chapter 3

A meta-analysis of multiple stressors on seagrasses in the context of marine spatial cumulative impacts assessment

Statement of Authorship

Title of Paper	A meta-analysis of multiple stressors on seagrasses in the context of marine spatial cumulative impacts assessment
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Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	19/05/2022

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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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A meta-analysis of multiple stressors on seagrasses in the context of marine spatial cumulative impacts assessment

Jackson Stockbridge, Alice R. Jones & Bronwyn M. Gillanders

Humans are placing more strain on the world's oceans than ever before. Furthermore, marine ecosystems are seldom subjected to single stressors, rather they are frequently exposed to multiple, concurrent stressors. When the combined effect of these stressors is calculated and mapped through cumulative impact assessments, it is often assumed that the effects are additive. However, there is increasing evidence that different combinations of stressors can have non-additive impacts, potentially leading to synergistic and unpredictable impacts on ecosystems. Accurately predicting how stressors interact is important in conservation, as removal of certain stressors could provide a greater benefit, or be more detrimental than would be predicted by an additive model. Here, we conduct a meta-analysis to assess the prevalence of additive, synergistic, and antagonistic stressor interaction effects using seagrasses as case study ecosystems. We found that additive interactions were the most commonly reported in seagrass studies. Synergistic and antagonistic interactions were also common, but there was no clear way of predicting where these non-additive interactions occurred. More studies which synthesise the results of stressor interactions are needed to be able to generalise interactions across ecosystem types, which can then be used to improve models for assessing cumulative impacts.

Humans rely on ocean ecosystem services and resources, and our growing population means demand for these services is rising[1,2]. Consequently, the threat of human impact on marine ecosystems and species is at an all-time high and continues to increase[1,3,4]. Impacts on marine ecosystems occur when they are under the influence of one or more stressors, often resulting from human activities. For example, overfishing is a stressor that may lead to fish population declines (see glossary of terms in Table 1).

There are many published studies that aim to understand the impact of stressors on marine ecosystems[5–8]. Recent meta-analyses have assessed interaction types between stressors in marine ecosystems, however many have only looked at specific stressor pairs, see Harvey et al.[9], Jackson[10] and Przeslavski et al.[11], or have focussed on limited biological responses (e.g. Strain et al.[12]). Broader meta-analyses looking at many stressor combinations were undertaken in the past (for example, Crain et al.[13]), but need to be updated due to the large number of studies that have been published since that time.

Accurately predicting and quantifying the impacts of stressors on marine environments is an important factor in establishing appropriate management and conservation strategies[14,15]. Inaccurate predictions of impact can potentially yield 'ecological surprises', which are unexpected changes in the natural environment[16]. Stressors rarely (if ever) occur in isolation, and the collective impact of multiple stressors is known as the cumulative impact (Table 1). It is important to know how stressors interact and how interactions affect the cumulative impact in order to inform management of marine ecosystems[17–19].

Predicting the cumulative impact of multiple stressors from single stressor studies is only possible if stressors act independently of one another. This allows us to use an additive model to calculate the cumulative impact[20], where we use the sum of the impact of individual stressors to indicate the combined overall impact. For example, if we have a quantified measure of change in biodiversity due to fishing, and the same measure of change, albeit at a different magnitude, due to pollution, we can sum these two measures of impact to estimate the cumulative impact of both stressors. However, this estimate will only be realistic if the stressors truly have independent effects

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Term	Definition
Stressor	A natural or anthropogenic pressure which causes a positive or negative quantifiable change in a response of the ecosystem[13]
Impact	The measurable effect of human activity on ecological condition[15]
Cumulative impacts	An estimate of the impact of multiple stressors[15]
Additive	An additive interaction type where the sum of the impact of individual stressors is used to calculate the cumulative impact[15]
Synergy	A non-additive interaction between stressors, where the cumulative impact is greater than the sum of the impact of individual stressors[14]. Above 0 indicates a positive synergy, below 0 indicates a negative synergy
Antagonistic	A non-additive interaction between stressors, where the cumulative impact is less than the sum of the impact of individual stressors[14]
Article	A published paper found through our literature searches
Study	A stressor combination on a seagrass response. A single article could have multiple studies if they tested multiple stressor combinations

Table 1. Glossary of terms and definitions.

on the biodiversity in the area. This assumption of additivity may not be appropriate. For example, synergies are common in marine ecosystems[21–23] and occur when the total impact from multiple stressors is greater than what we might expect from an additive model[14]. This leads to an underestimate of the cumulative impact if using an additive model[11], thereby increasing the chance of ecological surprises. Conversely, an antagonistic interaction occurs when the total impact of multiple stressors is less than what we expect based on an additive model[14]. For example, turbidity caused by run-off (stressor 1) could mitigate the effect of ultraviolet radiation (stressor 2) on benthic seagrass habitat by shading it[18]. Thus, the cumulative impact of turbidity and ultraviolet radiation may be less than what we would expect based on an assumption of additivity. Identifying interactions between multiple stressors is important to marine conservation and management as it presents an opportunity to achieve a larger benefit to an ecosystem by removing synergisms, whereas removing antagonisms may not be effective and could potentially worsen conditions. Conversely, where additive interactions are identified, stressors can be addressed individually without complex interactions needing to be considered[24].

Seagrass ecosystems are some of the most productive on earth and provide many valuable ecosystem services[25–27]. These services include carbon sequestration[28], supporting commercial fisheries[29], water filtration, and protection from coastal erosion[27,30]. It is estimated that the resources and services provided by seagrass ecosystems contribute over US$100 million per year to the world's blue economy[31].

Unfortunately, seagrass ecosystems and the services they provide are under increasing stress from human impacts[26,32–34]. The effects of coastal development, climate change, and ecological degradation threaten seagrass ecosystems the world over[35,36]. Habitat fragmentation occurs when seagrass cover is reduced due to the adverse effect of coastal development or because of boating activity, for example[32,37]. Ocean warming and acidification are two well-known impacts that result from climate change[38,39], which can increase herbivory pressure on seagrass[40] and negatively affect carbon reserves[41]. Other stressors caused by human activity include increased nutrients and pollutants from run-off[42] and invasive species presenting new challenges, such as increased competition or herbivory pressure[43]. To prevent further seagrass decline, we need to identify where and how often these stressors occur, if they interact, and the direction and magnitude of the impact[44].

Seagrass ecosystems provide a case study to test the assumption of additivity in marine spatial cumulative impact assessment methods. The status of seagrasses as biological sentinels and the close association of seagrass to densely populated coastlines make them good indicators of anthropogenic stressors[45]. Further, the ecosystem services seagrasses provide give them high value and importance in management, and conservation and restoration strategies.

This study aims to establish how different stressor combinations interact in seagrass ecosystems. We conducted a meta-analysis using data from published studies of two or more stressors on seagrasses and classified each combination as either additive, synergistic, or antagonistic. We attempt to identify generalisations of stressor interactions on seagrasses and to test the assumption of additive effects of multiple stressors in cumulative impact assessment methods.

Results

Across both searches, WoS returned 160 articles, and Scopus returned 165, for a total of 325 articles identified (Fig. 1). After duplicates were removed, we were left with 207 articles. Articles were removed if they were not relevant to this study, such as those looking at terrestrial or non-seagrass ecosystems (n = 116). Articles were also removed if the data required for calculating an effect size were not provided (n = 32). Some studies identified did not consider two or more stressors and so were omitted from our study (n = 26). In total, 201 stressor combinations from 41 studies taken from 33 articles were used for our meta-analysis.

The majority of studies were undertaken in a laboratory rather than a field setting (field = 7, lab = 34). Studies on temperate seagrass ecosystems were most common, followed by subtropical ecosystems (Fig. 2). Most studies used in this meta-analysis were undertaken in North-eastern America, Scandinavia and western Europe (Fig. 2). Published articles increased from 2006, however there have been peaks and troughs in publications through to the present day (Fig. 3a). *Zostera marina* and *Thalassia testudinum* were the most commonly studied species (Fig. 3b).

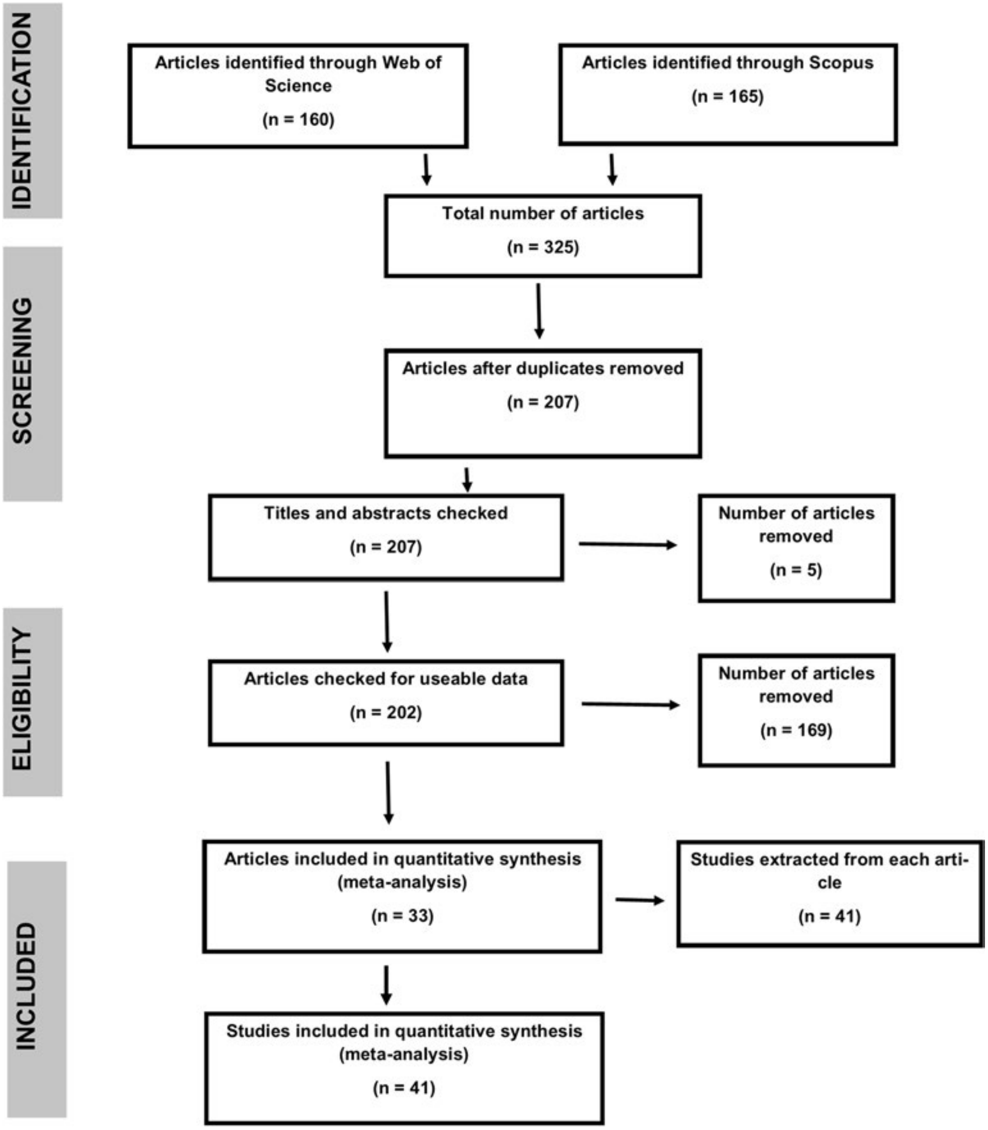

Figure 1. Article inclusions following a modified version of the PRISMA (Preferred Reporting Items for Systematic Review and Meta-Analysis) methodology[47].

Studies rarely tested more than two stressors and we did not find any that tested more than three (Fig. 3b). We found useable data for 35 unique stressor pairs in total (for a full breakdown, see Supplementary Table S2 online). Increased temperature and increased nutrient levels were the most commonly tested stressor pair (22), followed closely by increased temperature and increased competition (21), and increased temperature and hyposalinity (20; Fig. 4). Other commonly-tested stressor pairs were reduced light and increased temperature (19) and reduced light and increased nutrients (18; Fig. 4; Supplementary Table S2 online).

Of the 201 tested stressor combinations, 115 of the interactions were additive, and 86 were non-additive including 73 synergisms, and 13 antagonisms (see Supplementary Table S3 online). Positive synergies were identified in 47 studies, and negative synergies in 26 studies. Due to the high number of studies testing two stressors, our analysis was mostly focussed around these. However, when high nutrient levels were introduced to a test of increased temperature and reduced light, the interaction switched from additive to a negative synergy (Supplementary Table S3 online).

Discussion

In this study, we aimed to assess the validity of the assumption of additive stressor interactions which is used in many marine spatial cumulative impact assessment methods. Though additive interactions were most common in the seagrass studies we reviewed, synergies and antagonistic interactions were also frequently identified. This suggests that a blanket assumption of additivity in cumulative impact assessments is likely to over- or underestimate the impact of multiple stressors on seagrass ecosystems. Considering additivity is a general assumption in the cumulative impact assessment of many ecosystem types, more work evaluating the outputs of models which

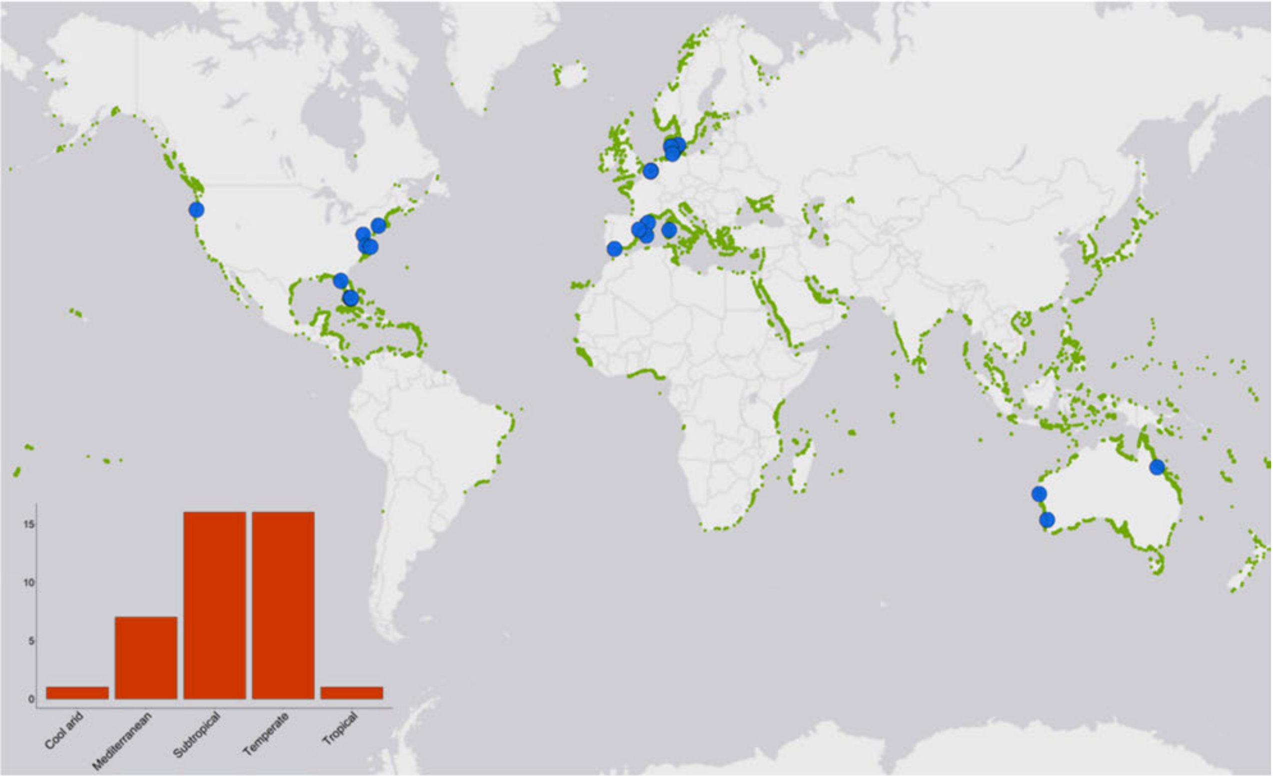

Figure 2. Map showing the location of studies used in our meta-analysis and the global distribution of seagrass[80]. Inset plot shows the count of studies depending on the broad climatic region where they were undertaken. Seagrass distribution data use layers 'WCMC_013_014_SeagrassesPt_v6' and 'WCMC_013_014_SeagrassesPy_v6', which can be accessed at https://gis.unep-wcmc.org/arcgis/rest/services/marine/WCMC_013_014_Seagrass_WMS/MapServer.

assume additivity is needed. Our results highlight the need for a better understanding of stressor interactions on various marine ecosystems to inform more realistic cumulative impact assessments verified with experimental data (for example Clark et al.[46]).

The most common interaction type we detected was an additive interaction (115 stressor interactions); however, there were some notable exceptions. When increased herbivory and habitat fragmentation were combined, many interactions were positively synergistic on the growth and biomass of seagrass (Supplementary Table S3 online). This suggests that when these stressors co-occur, growth and biomass of seagrass increases, which seems counter-intuitive since we expect both these stressors to have a detrimental impact on seagrass growth and biomass. However, it should be noted that this is based on a small number of studies ($n = 3$, with the fourth study reporting an additive interaction). There was a slightly higher number of both positive and negative synergistic interactions reported when increased herbivory was combined with high water nutrient levels, although additive interactions were also common. Exacerbation of stress by increased herbivory and high water nutrients can occur if the high nutrient content increases grazer population size[47], or improves the nutritional quality of seagrass to grazers[48,49]. Failure to account for these synergies in cumulative impact assessments will result in an underestimate of impact, potentially causing misidentification of ecosystem thresholds. Côté et al.[17] found that additive interactions were most common when increased herbivory and high water nutrients co-occurred in both terrestrial and marine ecosystems[18]. However, different studies that considered only the marine environment, report a mixture of antagonistic and synergistic interactions between increased herbivory and high water nutrients[50,51]. High nutrients is a particularly difficult stressor to predict as an increase in nutrients can have a positive impact up until a certain threshold, after which it can become toxic. This is an example of a non-linear response from an ecosystem to a stressor.

We found that positive synergies were most common when hypersalinity was combined with phytol stimulation in seagrass. Phytol is a compound that inhibits photosynthesis by degrading chloroplasts[52]. This contrasts to findings by Crain et al.[13], who reported a higher number of antagonistic interactions between these stressors. Our results show that antagonistic interactions were most common when hypersalinity was paired with hypoxic conditions, which may well be one stressor mitigating another, or could be because the negative effect of one is so large that the second stressor seemingly has no effect[13,19]. Identifying where antagonistic interactions occur is important as the removal of one stressor may make little difference to ecosystem health or may even increase the impact of the other stressor. When photosynthesis-inhibiting toxins were added to hypersalinity and hypoxia, the interaction switched from antagonistic to a positive synergy on seagrass growth. This outcome was only detected in one study[53] and may not be a general response, as hypersalinity has been reported to inhibit photosynthesis

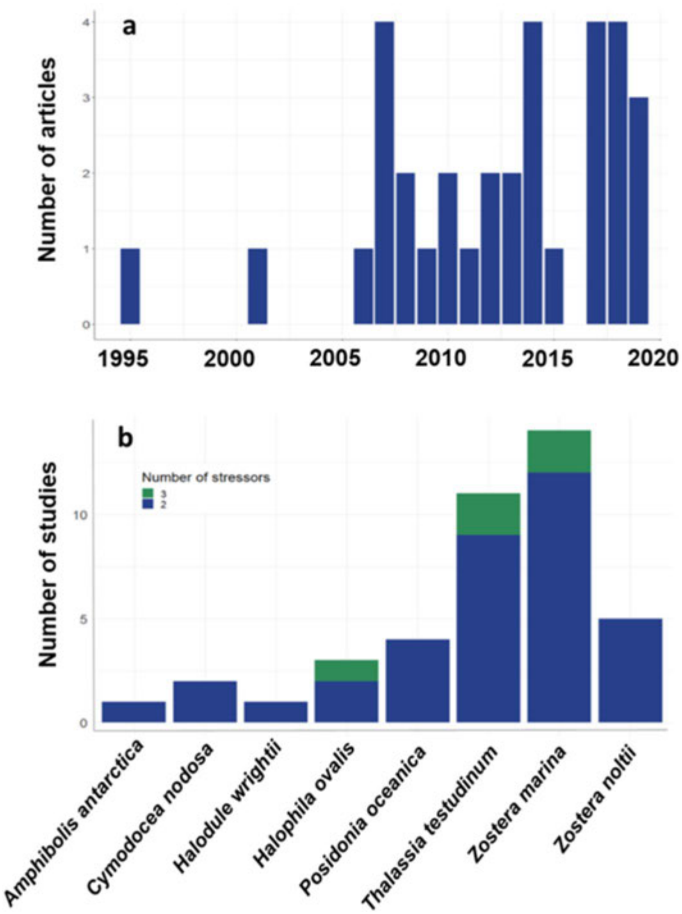

Figure 3. (**a**) Number of published articles over time, based on a search of published studies in Web of Science and Scopus. Search terms were all derivatives of the words 'synergy', 'antagonistic' and 'additive' and 'seagrass'. (**b**) The frequency of multi-stressor experiments on each species of seagrass across all studies included in our meta-analysis.

in some seagrass species such as *Thalassia testudinum*[54]. Therefore, there is little reason to expect that adding further photosynthesis-inhibiting toxins would increase the growth of seagrass[55–57].

Reduced light and high water nutrient levels yielded a mixture of interaction types, which is consistent with results from Crain et al.[13]. However, it should be noted that Crain et al.[13] looked at a range of marine ecosystems, not just seagrasses. We found that synergies were the most common interaction when increased temperature was combined with either reduced light or increased competition, although additive effects also occurred (in 28% of studies). These results are supported by previous meta-analyses, which also report a mixture of interactions between increased temperature and reduced light[13], with antagonistic interactions occurring frequently[17]. Interactions between increased temperature and increased competition have been reported as additive in previous literature[58]. Increased temperature and hyposalinity was one of the most well-studied stressor combinations in our dataset, and we found a mixture of all three interaction types, with additive being the most common. This is consistent with other meta-analyses which also found that these stressors interacted differently depending on response or location[13,17,58]. Increased temperature and hyposalinity seems to be a difficult stressor combination to predict the effects of, with contrasting reports from various reviews and meta-analyses on different marine ecosystems. For example, Côté et al.[17] found additive interactions between these stressors to be most common, whereas Darling and Côté[18] found no additive interactions between these two stressors. However, it should be noted that Côté et al.[17] focused on a broader range of ecosystems, including terrestrial, whereas Darling and Côté[18] focused only on marine ecosystems. New research published in the 8 years between these studies may have also contributed to the differing results.

The most consistent result between our study and previous meta-analyses was the variation in interaction types detected across studies[11,13,17,18], though none of these meta-analyses were specific to seagrass. Variation can be caused by a plethora of factors, which makes predicting all interactions extremely challenging without a large number of studies at regional scales[18]. Interactions between stressors can differ depending on the life history stage of the response organism[11], though this was not explored in our study. Target species/ecosystems can also be a factor in differing interaction types[9], for example, stressors that influence a species' range may depend on the species being studied. Only one study in our meta-analysis compared the effect of a stressor combination

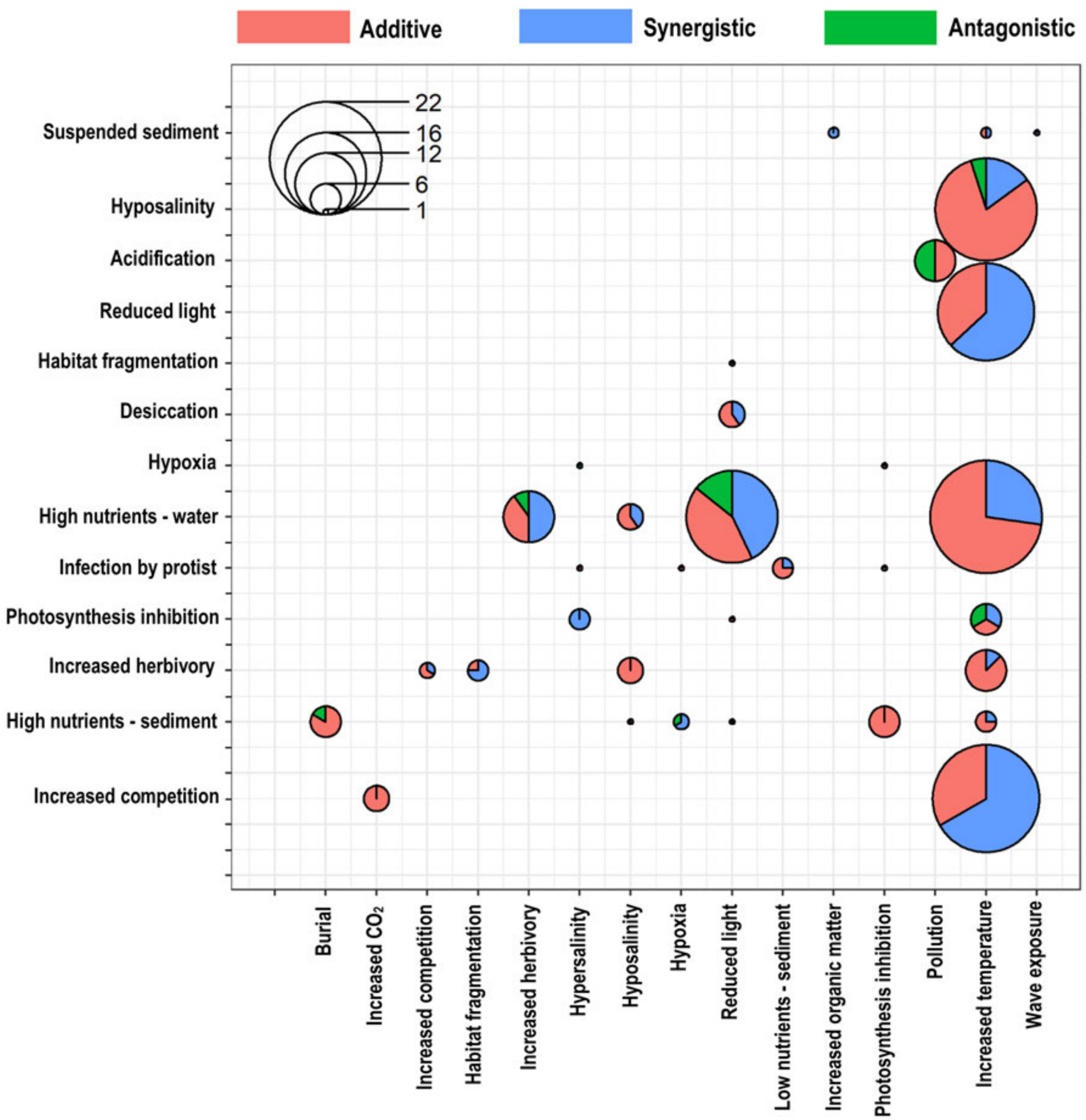

Figure 4. Plot to show the interaction type and number of tested stressor pairs. Points are sized according to the number of tested stressor pairs (i.e. larger points represent a higher number of tested pairs) and partitioned depending on the interaction type identified in each pair.

on two different species of seagrass[59]. Koch et al.[59] reported a mixture of interaction types between increased temperature and photosynthesis inhibition. Other studies that have tested stressor combinations across different species of macroalgae have reported a mixture of interaction types[60,61]. Though these studies were not on seagrass, the results suggest that further research across different species are needed if we are to make generalisations of stressor interaction types on all seagrass ecosystems. Depending on the seagrass genus being studied, we would expect different levels of resilience to stress and rates of recovery following disturbance. Resilience and recovery of seagrass would depend on the biology of that specific genus, including whether they are enduring and slow growing (*Posidonia*), or a transitory and fast-growing genus (*Halophila*)[62].

Since we distinguish additive from non-additive interaction classification based on whether confidence intervals include 0, we looked at if non-additive interactions were more frequently detected in studies with a larger sample size. We looked at studies which used a sample size of greater than 10 and did not find a larger proportion of non-additive interactions. However, it should be noted that the majority of studies (81%) had a sample size of < 5.

The mixture of interaction types detected for the same stressor combinations across different studies suggests a need for location-specific cumulative impact assessment. Previous research on a freshwater ecosystem has highlighted the benefit of cumulative impact assessment methods which consider local stressor effects on specific ecosystem components present at the study location[63]. These results, and our work here, supports the idea that we cannot generalise how stressors interact across different ecosystems and regions.

Stressor combinations can interact differently depending on the latitude and climate of the study location[50]. The southern hemisphere is not well-represented here, with only 4 studies in our dataset (Fig. 2). Research by Burkepile and Hay[50] found that the interactive effects of nutrient enrichment and increased herbivory on algae were opposite depending on if the algae was a temperate or tropical species. As with studies across different species, generalisations of stressor interactions across regions becomes more challenging when such variable results are found.

Variation in interaction types reflects the complexity and unpredictability of marine systems[64,65]. Complexity can be caused by a plethora of factors including ontogeny, spatial or temporal factors, as well as the pathways within trophic systems. These factors, and the complexity they cause, make it difficult to make generalities of stressor interactions across regions, organisms, species or life histories. Stressor interactions in many cumulative impact assessment methods are assumed to be additive[20], and though the potential weakness of this assumption has been acknowledged for some time[64], an additive model is still the most common when calculating cumulative impacts[66].

Korpinen and Andersen[67] reviewed 40 cumulative impact studies and found that 35 (88%) of the assessments assumed additive interactions. At present, the additive model is still the default for cumulative impact assessment methods despite the mounting evidence against it, though it should be noted that there are some published studies which do not assume additivity (for example Coll et al.[68] and Griffith et al.[69]). This highlights the need for an evidence base on the appropriate use of stressor interaction types. Our data add to this evidence base, which can support a more nuanced approach to modelling marine spatial cumulative impacts that goes beyond the assumption of additivity and in doing so generates more realistic predictions of cumulative impacts for use in marine management[70]. Results presented here, and from previous reviews and meta-analyses[2,13], suggest that cumulative impact methods based on the additive model should be interpreted with caution and their caveats clearly outlined. Whilst additive interactions are the most prevalent, non-additive interaction types are also common, suggesting that these should potentially be considered when calculating cumulative impacts. Prioritising experimental studies that test the combined effect of multiple stressors on different ecosystems and species (such as Clark et al.[46] and Andersen et al.[71]) would help to fill gaps in the knowledge presented here.

Without more accurate predictions of stressor interactions, calculating reliable cumulative impact scores is challenging using existing modelling methods[72,73]. Marine ecosystems are complex environments with myriad factors seemingly altering stressor interactions from one ecosystem to another[9,18] Future research could use the results from meta-analyses such as this one to re-calculate cumulative impact scores based on different and appropriate types of interactions between specific stressors, giving us a measure of impact, which can then be related to empirical condition data. Doing so could help us to understand how stressors are impacting marine ecosystems, and where removing stressors will provide the greatest benefit and help inform management of human-induced stressors and estimates of cumulative impacts.

Methods

Data collection. We conducted a literature search using the Web of Science (WoS) and Scopus search tools. Our search focused on seagrass ecosystems around the world. The initial literature search was undertaken on 10 October 2018. We searched the titles, abstracts and keywords of articles using the search terms: (synerg* OR antag* OR *additiv*) AND 'seagrass', where the asterisks represent all derivatives of the words 'synergy', 'antagonistic', and 'additive'. These terms allowed us to cover all types of interactions (synergistic; antagonistic; non-additive/additive). We followed the preferred reporting items for systematic review and meta-analysis (PRISMA) protocol[74] (Fig. 1).

A second search was undertaken on 11 June 2019 with the same search terms to update the results. Duplicates were removed following both searches. Titles and abstracts were checked for relevance to our study, and the articles then checked for useable data. Useable data here refers to the mean and variance of a control and treatment, including each stressor in isolation and the same stressors in combination.

To be included, each study needed to investigate the individual effect of two or more stressors, as well as their interactive effect (i.e. stressor 1; stressor 2; stressor 1 × 2). Articles which tested three or more stressors were treated as multiple, separate studies:

1. Stressor A vs. stressor B;
2. Stressor A vs. stressor C;
3. Stressor B vs. stressor C;
4. Stressor A vs. stressor B vs. stressor C.

Articles were subdivided into separate studies if the researchers tested different stressor combinations in the same paper (Table 1; Fig. 1). For example, if an article tested the effects of increased temperature and salinity on seagrass growth, and then increased temperature and nutrients on seagrass biomass, the article would be subdivided and treated as two studies as there were two response variables. Articles were also subdivided into separate studies if the researchers tested more than one level of the same stressor. For example, Kahn and Durako[75] tested high and low nutrients against high and low salinity. Therefore, this article was treated as four separate studies:

1. High nutrients vs. high salinity;
2. Low nutrients vs. high salinity;
3. High nutrients vs. low salinity;
4. Low nutrients vs. low salinity.

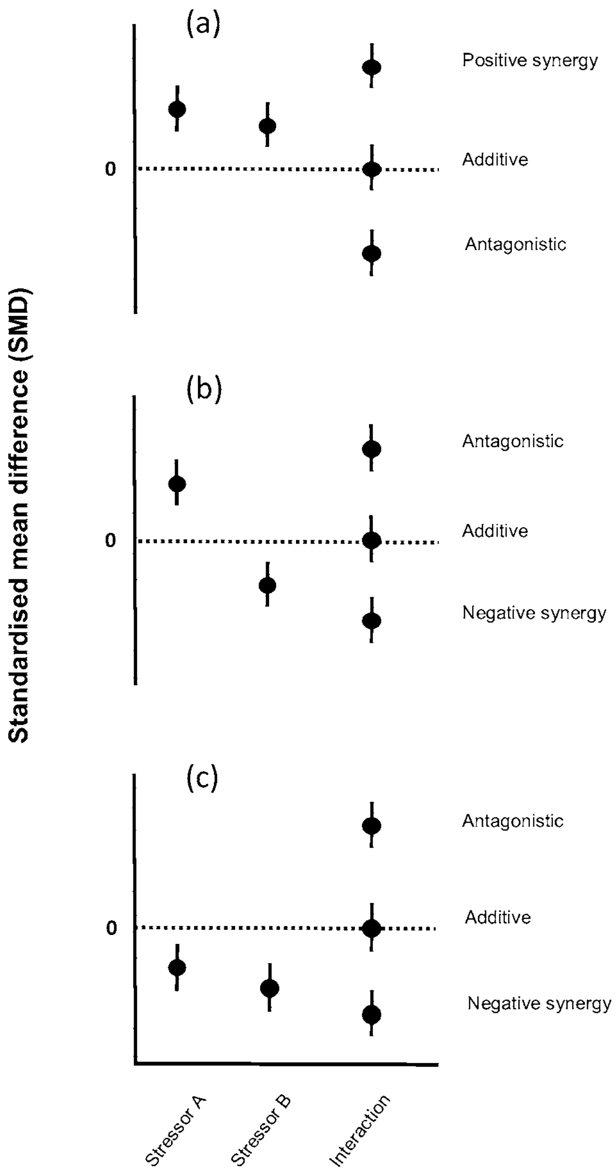

Figure 5. Conceptual schematic of interaction types, where the effect size of individual stressors (**A**,**B**) and the interaction are shown. Deviation from the additive model (Y = 0) represents a significant interaction. (**A**) Two positive individual effect sizes; (**B**) One positive, one negative individual effect sizes; (**C**) Two negative effect sizes[45] (adapted from Crain et al. [13]).

If stressors were tested at multiple levels we only used the highest and lowest values[76]. Seagrass responses to each stressor pair were grouped into categories of impact for clearer interpretation and analysis. These categories were 'Biodiversity', 'Biomass', 'Chemistry', "Epiphytes', 'Growth', 'Mortality', and 'Survival'. 'Biodiversity' here refers to the number of organisms associated with seagrass.

Effect size calculation. We used the standardised mean difference (SMD), also known as Hedge's *d*[13], and 95% confidence intervals to determine the effect size. We calculated the effect size for stressors acting in isolation, as well as the interactive effect between stressor combinations. For full details on how SMD was calculated see Supplementary Equation S1 online.

SMD uses the pooled sampling variance and a correction term to calculate and standardise the difference between the control and experimental means[77,78]. SMD has frequently been used as an effect size for factorial meta-analyses in ecology[13,76,78], and uses an additive model, where deviation from this model signifies a non-additive interaction. The additive model is best suited for interpreting data from manipulative experiments[18,19].

Interaction classification. Three interaction types were classified here based on comparing the effect sizes of single and multi-stressor experiments (Table 1). Previous published studies have defined more interactions[18], however we decided to use the main three as these are the most commonly and consistently defined. We followed the same definitions set out in Crain et al.[13] and used by Lange et al.[76], and we stated the direction (positive or negative) of the interaction when a synergy occurred.

We used the interaction effect size (based on SMD) and the 95% confidence interval of this to determine interaction type. The interaction was considered additive if the 95% confidence intervals of the effect size included 0, signifying that the interaction is not significantly different from the sum of individual stressors[13,79] (Fig. 5). When the individual effect sizes for all stressors were positive, an interaction effect size less than zero was classified as antagonistic, and an interaction effect size greater than zero was classified as synergistic (Fig. 5). When the individual effect sizes for all stressors were negative, interaction type was interpreted in the opposite manner (> 0 was antagonistic and < 0 was synergistic. For a visualisation of all effect size definitions, see Fig. 5).

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Author contributions
All authors conceived the project idea and designed the data analysis. J.S. collected the data, undertook the data analysis, wrote the manuscript and prepared the figures and tables. B.M.G. and A.R.J. reviewed the manuscript, figures and tables. B.M.G. and A.R.J. provided advice and guidance throughout the study.

Competing interests
The authors declare no competing interests.

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Supplementary material

TITLE: **A meta-analysis of multiple stressors on seagrasses in the context of marine spatial cumulative impacts assessment**

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Supplementary Equation S1. Calculations of standardised mean difference (SMD) as an effect size

SMD, or Hedge's *d*, was calculated as:

For stressor *A*:

$$d_A = \frac{(Y_A - Y_{ct})}{s} J(m)$$

For stressor *B*:

$$d_B = \frac{(Y_B - Y_{ct})}{s} J(m)$$

For interaction (*AB*):

$$d_{AB} = \frac{(Y_{AB} - Y_B) - (Y_A - Y_{ct})}{2s} J(m)$$

Where Y_{ct}, Y_A, Y_B and Y_{AB} are the mean responses of the control, stressor *A*, stressor *B* and the interactive effect of *A* and *B*, respectively. *S* is the pooled sampling variance and *J(m)* is a correction factor for small sample bias [1]. *J(m)* is calculated as:

$$J(m) = 1 - \frac{3}{4(N_{AB} + N_A + N_B + N_{ct} - 4) - 1}$$

Pooled sampling variance was calculated as:

$$S = \sqrt{\frac{(N_{AB} - 1)(\sigma_{AB}^2) + (N_A - 1)(\sigma_A^2) + (N_B - 1)(\sigma_B^2) + (N_{ct} - 1)(\sigma_{ct}^2)}{N_{AB} + N_A + N_B + N_{ct} - 4}}$$

Where *N* is the sample size and σ the standard deviation of each treatment.

Supplementary Table S2. Summary information of studies included in this meta-analysis including each stressor combination tested.

Study no.	Location	Climate	Species	Latitude	Longitude	Number of stressors	Response variable	Stressor 1	Stressor 2	Stressor 3	Reference
1	Portugal	Temperate	*Zostera noltii*	40.616	-8.738	2	Survival	Pollution	Acidification	-	2
1	Portugal	Temperate	*Zostera noltii*	40.616	-8.738	2	Biomass	Pollution	Acidification	-	2
1	Portugal	Temperate	*Zostera noltii*	40.616	-8.738	2	Growth	Pollution	Acidification	-	2
2	Mallorca	Mediterranean	*Posidonia oceanica*	39.35276	2.73665	2	Biomass	Temperature	Competition	-	3
2	Mallorca	Mediterranean	*Posidonia oceanica*	39.35276	2.73665	2	Mortality	Temperature	Competition	-	3
2	Mallorca	Mediterranean	*Posidonia oceanica*	39.35276	2.73665	2	Chemistry	Temperature	Competition	-	3
2	Mallorca	Mediterranean	*Posidonia oceanica*	39.35276	2.73665	2	Growth	Temperature	Competition	-	3
3	Alfacs Bay, NW Med	Mediterranean	*Cymodocea nodosa*	40.60495	0.68331	2	Chemistry	Temperature	Nutrient enrichment - water	-	4
3	Alfacs Bay, NW Med	Mediterranean	*Cymodocea nodosa*	40.60495	0.68331	2	Growth	Temperature	Nutrient enrichment - water	-	4
3	Alfacs Bay, NW Med	Mediterranean	*Cymodocea nodosa*	40.60495	0.68331	2	Mortality	Temperature	Nutrient enrichment - water	-	4
4	Alfacs Bay, NW Med	Mediterranean	*Cymodocea nodosa*	40.60495	0.68331	2	Chemistry	Temperature	Nutrient enrichment - sediment	-	4

Study no.	Location	Climate	Species	Latitude	Longitude	Number of stressors	Response variable	Stressor 1	Stressor 2	Stressor 3	Reference
4	Alfacs Bay, NW Med	Mediterranean	*Cymodocea nodosa*	40.60495	0.68331	2	Growth	Temperature	Nutrient enrichment - sediment	-	4
4	Alfacs Bay, NW Med	Mediterranean	*Cymodocea nodosa*	40.60495	0.68331	2	Mortality	Temperature	Nutrient enrichment - sediment	-	4
5	Denmark	Temperate	*Zostera marina*	55.7	11.78333	3	Growth	Temperature	Low light	Nutrient enrichment - water	5
5	Denmark	Temperate	*Zostera marina*	55.7	11.78333	3	Biomass	Temperature	Low light	Nutrient enrichment - water	5
5	Denmark	Temperate	*Zostera marina*	55.7	11.78333	3	Mortality	Temperature	Low light	Nutrient enrichment - water	5
5	Denmark	Temperate	*Zostera marina*	55.7	11.78333	3	Chemistry	Temperature	Low light	Nutrient enrichment - water	5
6	Sardinia	Mediterranean	*Posidonia oceanica*	40.56694	9.13472	2	Epiphytes	Burial	Nutrient enrichment - sediment	-	6
6	Sardinia	Mediterranean	*Posidonia oceanica*	40.56694	9.13472	2	Biomass	Burial	Nutrient enrichment - sediment	-	6
6	Sardinia	Mediterranean	*Posidonia oceanica*	40.56694	9.13472	2	Mortality	Burial	Nutrient enrichment - sediment	-	6
6	Sardinia	Mediterranean	*Posidonia oceanica*	40.56694	9.13472	2	Growth	Burial	Nutrient enrichment - sediment	-	6
7	Netherlands	Temperate	*Zostera noltii*	51.52778	3.94361	2	Biomass	Low light	Desiccation	-	7

Study no.	Location	Climate	Species	Latitude	Longitude	Number of stressors	Response variable	Stressor 1	Stressor 2	Stressor 3	Reference
7	Netherlands	Temperate	*Zostera noltii*	51.52778	3.94361	2	Growth	Low light	Desiccation	-	7
8	New York	Subtropical	*Zostera marina*	41.41667	-72.83333	2	Growth	CO2	Competition	-	8
8	New York	Subtropical	*Zostera marina*	41.41667	-72.83333	2	Chemistry	CO2	Competition	-	8
9	Queensland, Australia	Tropical	*Halophila ovalis*	-19.19111	146.85083	2	Growth	Temperature	Photosynthesis inhibition	-	9
10	Germany	Temperate	*Zostera marina*	54.65	10.3	2	Growth	Nutrient limitation - sediment	Infection	-	10
10	Germany	Temperate	*Zostera marina*	54.65	10.3	2	Biomass	Nutrient limitation - sediment	Infection	-	10
11	Florida	Subtropical	*Thalassia testudinum*	29.33333	-83.38333	2	Growth	Hypersalinity	Infection	-	11
12	Florida	Subtropical	*Thalassia testudinum*	29.33333	-83.38333	2	Growth	Temperature	Infection	-	11
13	Florida	Subtropical	*Thalassia testudinum*	29.33333	-83.38333	2	Growth	Photosynthesis inhibition	Infection	-	11
14	Florida	Subtropical	*Thalassia testudinum*	29.33333	-83.38333	2	Growth	Hypoxia	Infection	-	11
15	Denmark	Temperate	*Zostera marina*	55.48611	9.75556	2	Mortality	Light	Habitat modification	-	12
16	Denmark	Temperate	*Zostera marina*	55.71222	11.79306	2	Growth	Hyposalinity	Nutrient enrichment - water	-	13
16	Denmark	Temperate	*Zostera marina*	55.71222	11.79306	2	Biomass	Hyposalinity	Nutrient enrichment - water	-	13
16	Denmark	Temperate	*Zostera marina*	55.71222	11.79306	2	Mortality	Hyposalinity	Nutrient enrichment - water	-	13

Study no.	Location	Climate	Species	Latitude	Longitude	Number of stressors	Response variable	Stressor 1	Stressor 2	Stressor 3	Reference
17	Denmark	Temperate	*Zostera marina*	55.71222	11.79306	2	Mortality	Temperature	Hyposalinity	-	14
17	Denmark	Temperate	*Zostera marina*	55.71222	11.79306	2	Growth	Temperature	Hyposalinity	-	14
17	Denmark	Temperate	*Zostera marina*	55.71222	11.79306	2	Biomass	Temperature	Hyposalinity	-	14
18	Oregon, USA	Cool arid	*Zostera marina*	44.60639	-124.07472	2	Growth	Temperature	Nutrient enrichment - water	-	15
19	Netherlands	Temperate	*Zostera noltii*	51.65	4.01667	2	Biomass	Organic matter	Suspended sediment	-	16
19	Netherlands	Temperate	*Zostera noltii*	51.65	4.01667	2	Epiphytes	Organic matter	Suspended sediment	-	16
20	Shark Bay, WA	Temperate	*Amphibolis antarctica*	-25.93333	113.54222	2	Biomass	Temperature	Suspended sediment	-	17
21	Denmark	Temperate	*Zostera marina*	55.79456	11.77713	2	Growth	Low light	Nutrient enrichment - sediment	-	18
21	Denmark	Temperate	*Zostera marina*	55.79456	11.77713	2	Mortality	Low light	Nutrient enrichment - sediment	-	18
21	Denmark	Temperate	*Zostera marina*	55.79456	11.77713	2	Biomass	Low light	Nutrient enrichment - sediment	-	18
21	Denmark	Temperate	*Zostera marina*	55.79456	11.77713	2	Survival	Low light	Nutrient enrichment - sediment	-	18
22	Spain	Mediterranean	*Posidonia oceanica*	41.68417	2.81861	2	Biomass	Habitat modification	Herbivory	-	19

Study no.	Location	Climate	Species	Latitude	Longitude	Number of stressors	Response variable	Stressor 1	Stressor 2	Stressor 3	Reference
22	Spain	Mediterranean	*Posidonia oceanica*	41.68417	2.81861	2	Growth	Habitat modification	Herbivory	-	19
22	Spain	Mediterranean	*Posidonia oceanica*	41.68417	2.81861	2	Chemistry	Habitat modification	Herbivory	-	19
23	Netherlands	Temperate	*Zostera noltii*	51.56639	3.94906	2	Biomass	Wave exposure	Suspended sediment	-	20
24	Perth, WA	Temperate	*Halophila ovalis*	-32.00716	115.79298	3	Mortality	Temperature	Competition	Herbivory	21
24	Perth, WA	Temperate	*Halophila ovalis*	-32.00716	115.79298	3	Biomass	Temperature	Competition	Herbivory	21
25	Perth, WA	Temperate	*Halophila ovalis*	-31.98333	115.81667	2	Growth	Temperature	Competition	-	22
25	Perth, WA	Temperate	*Halophila ovalis*	-31.98333	115.81667	2	Biomass	Temperature	Competition	-	22
26	Virginia, USA	Subtropical	*Zostera marina*	39.52583	-77.05806	3	Epiphytes	Temperature	Hyposalinity	Herbivory	23
26	Virginia, USA	Subtropical	*Zostera marina*	39.52583	-77.05806	3	Biomass	Temperature	Hyposalinity	Herbivory	23
26	Virginia, USA	Subtropical	*Zostera marina*	39.52583	-77.05806	3	Growth	Temperature	Hyposalinity	Herbivory	23
26	Virginia, USA	Subtropical	*Zostera marina*	39.52583	-77.05806	3	Biodiversity	Temperature	Hyposalinity	Herbivory	23
27	Denmark	Temperate	*Zostera marina*	55.5	9.66667	2	Survival	Temperature	Competition	-	24
28	Denmark	Temperate	*Zostera marina*	55.51588	9.67549	2	Growth	Hypoxia	Nutrient enrichment - sediment	-	25
28	Denmark	Temperate	*Zostera marina*	55.51588	9.67549	2	Survival	Hypoxia	Nutrient enrichment - sediment	-	25

Study no.	Location	Climate	Species	Latitude	Longitude	Number of stressors	Response variable	Stressor 1	Stressor 2	Stressor 3	Reference
29	Germany	Temperate	*Zostera marina*	54.35	10.15	2	Epiphytes	Nutrient enrichment - water	Herbivory	-	26
29	Germany	Temperate	*Zostera marina*	54.35	10.15	2	Growth	Nutrient enrichment - water	Herbivory	-	26
29	Germany	Temperate	*Zostera marina*	54.35	10.15	2	Chemistry	Nutrient enrichment - water	Herbivory	-	26
30	Spain	Mediterranean	*Zostera noltii*	36.5	-6.16667	2	Growth	Low light	Nutrient enrichment - water	-	27
31	Spain	Mediterranean	*Posidonia oceanica*	42.04217	3.21434	2	Biomass	Nutrient enrichment - sediment	Photosynthesis inhibition	-	28
31	Spain	Mediterranean	*Posidonia oceanica*	42.04217	3.21434	2	Mortality	Nutrient enrichment - sediment	Photosynthesis inhibition	-	28
31	Spain	Mediterranean	*Posidonia oceanica*	42.04217	3.21434	2	Chemistry	Nutrient enrichment - sediment	Photosynthesis inhibition	-	28
32	Florida	Subtropical	*Thalassia testudinum*	25.04639	-80.75306	3	Growth	Photosynthesis inhibition	Hypersalinity	Hypoxia	29
32	Florida	Subtropical	*Thalassia testudinum*	25.04639	-80.75306	3	Survival	Photosynthesis inhibition	Hypersalinity	Hypoxia	29
33	Florida	Subtropical	*Thalassia testudinum*	24.92222	-80.7925	2	Growth	Temperature	Photosynthesis inhibition	-	30
33	Florida	Subtropical	*Thalassia testudinum*	24.92222	-80.7925	2	Biomass	Temperature	Photosynthesis inhibition	-	30
34	Florida	Subtropical	*Halodule wrightii*	25.22806	-80.79361	2	Growth	Temperature	Photosynthesis inhibition	-	30

Study no.	Location	Climate	Species	Latitude	Longitude	Number of stressors	Response variable	Stressor 1	Stressor 2	Stressor 3	Reference
34	Florida	Subtropical	*Halodule wrightii*	25.22806	-80.79361	2	Biomass	Temperature	Photosynthesis inhibition	-	30
35	Virginia, USA	Subtropical	*Zostera marina*	37.21667	-76.38333	2	Epiphytes	Nutrient enrichment - water	Herbivory	-	31
35	Virginia, USA	Subtropical	*Zostera marina*	37.21667	-76.38333	2	Biomass	Nutrient enrichment - water	Herbivory	-	31
35	Virginia, USA	Subtropical	*Zostera marina*	37.21667	-76.38333	2	Mortality	Nutrient enrichment - water	Herbivory	-	31
35	Virginia, USA	Subtropical	*Zostera marina*	37.21667	-76.38333	2	Biodiversity	Nutrient enrichment - water	Herbivory	-	31
36	Florida	Subtropical	*Thalassia testudinum*	25.0325	-80.50194	2	Growth	Nutrient limitation - water	Hyposalinity	-	32
37	Florida	Subtropical	*Thalassia testudinum*	25.0325	-80.50194	2	Growth	Nutrient enrichment - water	Hyposalinity	-	32
38	Florida	Subtropical	*Thalassia testudinum*	25.0325	-80.50194	2	Growth	Nutrient limitation - water	Hypersalinity	-	32
39	Florida	Subtropical	*Thalassia testudinum*	25.0325	-80.50194	2	Growth	Nutrient enrichment - water	Hypersalinity	-	32
40	Florida	Subtropical	*Thalassia testudinum*	25.125	-80.45083	3	Growth	Temperature	Hypersalinity	Photosynthesis inhibition	33
40	Florida	Subtropical	*Thalassia testudinum*	25.125	-80.45083	3	Biomass	Temperature	Hypersalinity	Photosynthesis inhibition	33
41	Virginia, USA	Subtropical	*Zostera marina*	37	-75	2	Growth	Low light	Photosynthesis inhibition	-	34

Supplementary Table S3. Summary of individual, combined and interaction type of each stressor and stressor combinations. When the individual effect sizes for all stressors were positive, an interaction effect size less than zero was classified as antagonistic, and if the interaction was more than 0 it was classified as synergistic (Fig. 5). For a visualisation of all effect size definitions, see Fig. 5.

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Pollution	Acidification	-	Biomass	1.92	0	-	1.02	0.38	1.67	Antagonistic	-	2
Pollution	Acidification	-	Biomass	1.91	-0.443	-	1.95	1.21	2.68	Antagonistic	-	2
Light	High nutrients - water	-	Biomass	1.2	0.265	-	1.47	-0.332	3.28	Additive	-	5
Temperature	High nutrients - water	Light	Biomass	0.822	0.265	1.2	1.34	-0.43	3.11	Additive	-	5
Temperature	Light	-	Biomass	0.822	1.2	-	1.89	-0.0336	3.82	Additive	-	5
Temperature	High nutrients - water	-	Biomass	0.822	0.265	-	1.31	-0.452	3.08	Additive	-	5
Burial	High nutrients - sediment	-	Biomass	0.125	-0.417	-	0.616	-0.329	1.56	Additive	-	6
Burial	High nutrients - sediment	-	Biomass	0.451	-0.344	-	0.741	-0.214	1.7	Additive	-	6
Burial	High nutrients - sediment	-	Biomass	-0.461	-0.00376	-	-0.266	-1.19	0.662	Additive	-	6
Light	Desiccation	-	Biomass	0.587	1.08	-	1.08	-0.247	2.41	Additive	-	7
Light	Desiccation	-	Biomass	0.74	0.639	0.801		-0.488	2.09	Additive	-	7
Light	Desiccation	-	Biomass	0.62	1.31	-	1.42	0.0312	2.8	Synergistic	Positive	7
Light	Desiccation	-	Biomass	-0.437	0.644	-	-0.4	-1.65	0.852	Additive	-	7
Low nutrients - sediment	Infection	-	Biomass	1.64	1.39	-	2.58	0.413	4.74	Additive	-	10
Hyposalinity	High nutrients - water	-	Biomass	1.39	-1.67	-	-0.277	-1.89	1.33	Additive	-	13

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individual effect B	Individual effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Hyposalinity	Temperature	-	Biomass	0.3	0.0907	-	1.54	-0.285	3.36	Additive	-	14
Hyposalinity	Temperature	-	Biomass	-0.678	0.489	-	1.04	-0.669	2.74	Additive	-	14
Organic matter	Suspended sediment	-	Biomass	8.78	4.05	-	4.35	2.08	6.63	Synergistic	Positive	16
Temperature	Suspended sediment	-	Biomass	-0.893	1.03	-	0.147	-0.432	0.725	Additive	-	17
Temperature	Suspended sediment	-	Biomass	1.29	0.227	-	1.46	0.81	2.11	Synergistic	Positive	17
Light	High nutrients - water	-	Biomass	-0.571	-0.619	-	-2.64	-4.83	-0.453	Synergistic	Negative	18
Light	High nutrients - sediment	-	Biomass	0.296	0.28	-	4.79	1.64	7.94	Synergistic	Positive	18
Habitat modification	Herbivory	-	Biomass	0.8	1.16	-	2.46	1.3	3.62	Synergistic	Positive	19
Habitat modification	Herbivory	-	Biomass	0.746	-0.0897	-	-0.448	-1.34	0.439	Additive	-	19
Wave exposure	Suspended sediment	-	Biomass	0.95	1.08	-	1.25	0.371	2.12	Synergistic	Positive	20
Competition	Herbivory	-	Biomass	0.02	-0.0177	-	-0.602	-2.24	1.03	Additive	-	21
Temperature	Competition	Herbivory	Biomass	0	0.02	-0.0177	0.0436	-1.56	1.64	Additive	-	21
Temperature	Competition	-	Biomass	0	0.02	-	1.46	-0.342	3.26	Additive	-	21
Temperature	Herbivory	-	Biomass	0	-0.0177	-	0.748	-0.907	2.4	Additive	-	21
Temperature	Competition	-	Biomass	0.632	5.37	-	5.42	2.74	8.11	Synergistic	Positive	22
Temperature	Competition	-	Biomass	1.01	6.83	-	2.93	1.15	4.72	Synergistic	Positive	22
Temperature	Competition	-	Biomass	2.35	4.76	-	5.84	3	8.69	Synergistic	Positive	22
Hyposalinity	Herbivory	-	Biomass	0.697	0.606	-	0.483	-1.14	2.11	Additive	-	23
Temperature	Hyposalinity	Herbivory	Biomass	0.702	0.697	0.606	0.343	-1.27	1.95	Additive	-	23
Temperature	Hyposalinity	-	Biomass	0.702	0.697	-	0.435	-1.18	2.05	Additive	-	23

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Temperature	Herbivory	-	Biomass	0.702	0.606	-	0.676	-0.969	2.32	Additive	-	23
Hyposalinity	Herbivory	-	Biomass	-0.242	-0.0175	-	0.171	-1.43	1.77	Additive	-	23
Temperature	Hyposalinity	Herbivory	Biomass	-0.0938	-0.242	-0.0175	0.0831	-1.52	1.68	Additive	-	23
Temperature	Hyposalinity	-	Biomass	-0.0938	-0.242	-	0.495	-1.13	2.12	Additive	-	23
Temperature	Herbivory	-	Biomass	-0.0938	-0.0175	-	0.572	-1.06	2.2	Additive	-	23
Photosynthesis inhibition	High nutrients – sediment	-	Biomass	2.05	NA	-	1.86	-0.0528	3.78	Additive	-	28
Photosynthesis inhibition	High nutrients - sediment	-	Biomass	0.601	NA	-	0.96	-0.73	2.65	Additive	-	28
Photosynthesis inhibition	High nutrients - sediment	-	Biomass	0.895	NA	-	-0.0412	-1.64	1.56	Additive	-	28
Herbivory	High nutrients - water	-	Biomass	4.24	2.15	-	1.76	0.304	3.23	Synergistic	Positive	31
Hyposalinity	Herbivory	-	Biodiversity	0.254	0.761	-	1.09	-0.625	2.81	Additive	-	23
Temperature	Hyposalinity	Herbivory	Biodiversity	0.334	0.254	0.761	0.775	-0.884	2.43	Additive	-	23
Temperature	Hyposalinity	-	Biodiversity	0.334	0.254	-	-0.249	-1.86	1.36	Additive	-	23
Temperature	Herbivory	-	Biodiversity	0.334	0.761	-	0.988	-0.707	2.68	Additive	-	23
Herbivory	High nutrients - water	-	Biodiversity	-0.292	-1.5	-	-0.0386	-1.28	1.2	Additive	-	31
Herbivory	High nutrients - water	-	Biodiversity	0.593	1.73	-	1.8	0.33	3.27	Synergistic	Positive	31
Herbivory	High nutrients - water	-	Biodiversity	0.456	1.1	-	0.957	-0.352	2.27	Additive	-	31
Herbivory	High nutrients - water	-	Biodiversity	-0.501	0.915	-	1.02	-0.297	2.34	Additive	-	31
Temperature	Competition	-	Chemistry	-1.21	-0.506	-	-0.704	-2.13	0.724	Additive	-	3
Temperature	Competition	-	Chemistry	-4.6	0.157	-	-2.38	-4.2	-0.571	Synergistic	Negative	3

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Temperature	Competition	-	Chemistry	-0.862	0	-	-0.824	-2.27	0.62	Additive	-	3
Temperature	Competition	-	Chemistry	-1.33	-1.27	-	0.434	-0.968	1.84	Additive	-	3
Temperature	Competition	-	Chemistry	-3.62	-0.424	-	-3.17	-5.25	-1.09	Synergistic	Negative	3
Temperature	High nutrients - water	-	Chemistry	-3.54	-1.65	-	-1.18	-2.91	0.557	Additive	-	4
Temperature	High nutrients - water	-	Chemistry	-0.531	-1.98	-	-1.28	-3.04	0.474	Additive	-	4
Temperature	High nutrients – water	-	Chemistry	-0.958	-1.05	-	-1.72	-0.359	0.155	Additive	-	4
Temperature	High nutrients - sediment	-	Chemistry	-0.718	0.105	-	-1.79	-3.68	0.105	Additive	-	4
Temperature	High nutrients - sediment	-	Chemistry	0.868	0.964	-	-0.695	-2.34	0.953	Additive	-	4
Temperature	High nutrients - sediment	-	Chemistry	1	-0.767	-	-1.3	-3.06	0.463	Additive	-	4
Light	High nutrients - water	-	Chemistry	8.24	8.06	-	9.5	3.89	15.1	Synergistic	Positive	5
Temperature	Light	High nutrients - water	Chemistry	4.55	8.24	8.06	9.41	3.85	15	Synergistic	Positive	5
Temperature	Light	-	Chemistry	4.55	8.24	-	8.65	3.5	13.8	Synergistic	Positive	5
Temperature	High nutrients - water	-	Chemistry	4.55	8.06	-	8.66	3.5	13.8	Synergistic	Positive	5
Light	High nutrients - water	-	Chemistry	2.23	3.1	-	3.12	0.739	5.51	Synergistic	Positive	5
Temperature	Light	High nutrients - water	Chemistry	1.85	2.23	3.1	2.89	0.6	5.17	Synergistic	Positive	5
Temperature	Light	-	Chemistry	1.85	2.23	-	2.43	0.322	4.54	Synergistic	Positive	5
Temperature	High nutrients - water	-	Chemistry	1.85	3.1	-	3.38	0.884	5.87	Synergistic	Positive	5

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Light	High nutrients - water	-	Chemistry	-1.43	-5.14	-	-8.61	-13.7	-3.48	Synergistic	Negative	5
Temperature	Light	High nutrients - water	Chemistry	-0.634	-1.43	-5.14	-3.98	-6.74	-1.22	Synergistic	Negative	5
Temperature	Light	-	Chemistry	-0.634	-1.43	-	-1.7	-3.57	0.167	Additive	-	5
Temperature	High nutrients - water	-	Chemistry	-0.634	-5.14	-	-3.52	-6.08	-0.966	Synergistic	Negative	5
Light	High nutrients – water	-	Chemistry	-2.29	-2.24	-	-2.79	-5.04	-0.544	Synergistic	Negative	5
Temperature	Light	High nutrients - water	Chemistry	-0.712	-2.29	-2.24	-1.23	-2.98	0.512	Additive	-	5
Temperature	Light	-	Chemistry	-0.712	-2.29	-	-1.45	-3.25	0.35	Additive	-	5
Temperature	High nutrients - water	-	Chemistry	-0.712	-2.24	-	-0.579	-2.21	1.05	Additive	-	5
CO2	Competition	-	Chemistry	-1.31	-0.412	-	-1.13	-2.85	0.593	Additive	-	8
CO2	Competition	-	Chemistry	0.461	0.921	-	0.921	-0.762	2.6	Additive	-	8
Habitat modification	Herbivory	-	Chemistry	1.74	0.194	-	1.79	0.756	2.83	Synergistic	Positive	19
Herbivory	High nutrients - water	-	Chemistry	-0.175	3.21	-	2.26	0.213	4.31	Antagonistic	-	26
Photosynthesis inhibition	High nutrients - sediment	-	Chemistry	0.0269	NA	-	-0.349	-1.96	1.26	Additive	-	28
Photosynthesis inhibition	High nutrients - sediment	-	Chemistry	0.287	NA	-	0.0048	-1.6	1.61	Additive	-	28
Photosynthesis inhibition	High nutrients - sediment	-	Chemistry	0.772	NA	-	1.17	-0.56	2.9	Additive	-	28
Burial	High nutrients - sediment	-	Epiphytes	0.426	0.148	-	-1.7	-2.78	-0.621	Antagonistic	-	6
Organic matter	Suspended sediment	-	Epiphytes	-4.6	-5.31	-	-5.16	-7.74	-2.58	Synergistic	Positive	16
Hyposalinity	Herbivory	-	Epiphytes	0.694	0.694	-	0.685	-0.962	2.33	Additive	-	23

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individual effect B	Individual effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Temperature	Hyposalinity	Herbivory	Epiphytes	0.404	0.626	0.694	0.614	-1.02	2.25	Additive	-	23
Temperature	Hyposalinity	-	Epiphytes	0.404	0.626	-	0.812	-0.853	2.48	Additive	-	23
Temperature	Herbivory	-	Epiphytes	0.404	0.694	-	0.682	-0.964	2.33	Additive	-	23
Hypoxia	High nutrients - sediment	-	Epiphytes	0	-1.05	-	-5.83	-9.49	-2.16	Synergistic	Negative	25
Herbivory	High nutrients - water	-	Epiphytes	4.25	-21.5	-	-14.3	-22.5	-6.05	Synergistic	Negative	26
Herbivory	High nutrients - water	-	Epiphytes	-1.47	0.639	-	-1.03	-2.35	0.291	Synergistic	Negative	31
Pollution	Acidification	-	Growth	0.895	0.356	-	0.447	-0.165	1.06	Additive	-	2
Pollution	Acidification	-	Growth	2.37	-0.103	-	1.44	0.76	2.12	Antagonistic	-	2
Pollution	Acidification	-	Growth	1.26	-0.0427	-	0.683	0.0606	1.31	Antagonistic	-	2
Pollution	Acidification	-	Growth	1.75	0.72	-	-1.17	-2.39	0.0556	Additive	-	2
Pollution	Acidification	-	Growth	2.9	0	-	0.362	-0.779	1.5	Additive	-	2
Temperature	Competition	-	Growth	-0.631	-0.721	-	-0.239	-1.63	1.15	Additive	-	3
Temperature	High nutrients - water	-	Growth	2.89	-0.509	-	3.02	0.676	5.36	Synergistic	Positive	4
Temperature	High nutrients - water	-	Growth	2.07	0.128	-	1.89	-0.0371	3.81	Additive	-	4
Temperature	High nutrients - sediment	-	Growth	0.439	-1.04	-	1.51	-0.305	3.32	Additive	-	4
Temperature	High nutrients - sediment	-	Growth	9.71	2.08	-	6.15	2.32	9.98	Synergistic	Positive	4
Temperature	High nutrients - sediment	-	Growth	-0.755	-0.195	-	1.38	-0.403	3.16	Additive	-	4
Light	High nutrients - water	-	Growth	1.66	1.01	-	3.09	0.719	5.46	Synergistic	Positive	5

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Temperature	Light	High nutrients - water	Growth	2.63	1.66	1.01	7.01	2.73	11.3	Synergistic	Positive	5
Temperature	Light	-	Growth	2.63	1.66	-	5.55	2.03	9.07	Synergistic	Positive	5
Temperature	High nutrients - water	-	Growth	2.63	1.01	-	4.95	1.72	8.17	Synergistic	Positive	5
Light	High nutrients - water	-	Growth	2.32	1.44	-	1.25	-0.497	3	Additive	-	5
Temperature	Light	High nutrients - water	Growth	1.44	2.32	1.44	3.41	0.902	5.91	Synergistic	Positive	5
Temperature	Light	-	Growth	1.44	2.32	-	3.25	0.815	5.69	Synergistic	Positive	5
Temperature	High nutrients - water	-	Growth	1.44	1.44	-	0.649	-0.993	2.29	Additive	-	5
Light	High nutrients – water	-	Growth	2.81	1.18	-	2.02	0.0512	3.98	Synergistic	Positive	5
Temperature	Light	High nutrients - water	Growth	1.99	2.81	1.18	4.81	1.65	7.96	Synergistic	Positive	5
Temperature	Light	-	Growth	1.99	2.81	-	2.68	0.476	4.89	Synergistic	Positive	5
Temperature	High nutrients - water	-	Growth	1.99	1.18	-	1.39	-0.394	3.17	Additive	-	5
Light	High nutrients - water	-	Growth	1.2	-0.37	-	0.206	-1.4	1.81	Additive	-	5
Temperature	Light	High nutrients - water	Growth	-0.0375	1.2	-0.37	1.4	-0.387	3.18	Additive	-	5
Temperature	Light	-	Growth	-0.0375	1.2	-	0.881	-0.795	2.56	Additive	-	5
Temperature	High nutrients - water	-	Growth	-0.0375	-0.37	-	0.667	-0.977	2.31	Additive	-	5
Burial	High nutrients - sediment	-	Growth	0.116	-0.772	-	-0.964	-1.94	0.012	Additive	-	6

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individual effect B	Individual effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Light	Desiccation	-	Growth	0.606	1.01	-	1.53	0.122	2.94	Synergistic	Positive	7
CO2	Competition	-	Growth	-0.736	0.106	-	-0.417	-2.03	1.2	Additive	-	8
CO2	Competition	-	Growth	-0.854	-0.0678	-	-0.679	-2.33	0.966	Additive	-	8
CO2	Competition	-	Growth	-1.37	0.361	-	0.181	-1.42	1.78	Additive	-	8
Temperature	Photosynthesis inhibition	-	Growth	-1.74	-8.87	-	-8.24	11.1	-5.39	Synergistic	Negative	9
Low nutrients - sediment	Infection	-	Growth	1.5	0.0986	-	2.11	0.111	4.1	Synergistic	Positive	10
Low nutrients - sediment	Infection	-	Growth	0.767	1.52	-	1.65	-0.203	3.5	Additive	-	10
Low nutrients - sediment	Infection	-	Growth	-0.563	-0.439	-	-0.436	-2.06	1.18	Additive	-	10
Hypersalinity	Infection	-	Growth	-3.57	1.08	-	0.744	-0.538	2.03	Additive	-	11
Temperature	Infection	-	Growth	-0.642	0.713	-	0.707	-0.57	1.99	Additive	-	11
Photosynthesis inhibition	Infection	-	Growth	0.128	0.53	-	0.754	-0.529	2.04	Additive	-	11
Hypoxia	Infection	-	Growth	-0.336	0.675	-	0.692	-0.584	1.97	Additive	-	11
Hyposalinity	High nutrients - water	-	Growth	-0.793	-2.28	-	-0.985	-2.68	0.71	Additive	-	13
Hyposalinity	High nutrients - water	-	Growth	-0.369	0.109	-	0.00819	-1.59	1.61	Additive	-	13
Hyposalinity	High nutrients - water	-	Growth	1.89	-6.14	-	-2.21	-4.24	-0.179	Synergistic	Negative	13
Hyposalinity	High nutrients - water	-	Growth	1.37	-1.79	-	-2.09	-4.08	-0.0983	Synergistic	Negative	13
Hyposalinity	Temperature	-	Growth	2.25	-0.293	-	5.34	1.92	8.77	Antagonistic	-	14
Hyposalinity	Temperature	-	Growth	0.857	0.0932	-	5.93	2.21	9.65	Synergistic	Positive	14
Hyposalinity	Temperature	-	Growth	0.391	-0.23	-	1.73	-0.146	3.61	Additive	-	14
Hyposalinity	Temperature	-	Growth	-0.696	0.354	-	1.79	-0.106	3.68	Additive	-	14

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Temperature	High nutrients - water	-	Growth	-0.844	-0.54	-	-0.925	-2.61	0.759	Additive	-	15
Temperature	High nutrients - water	-	Growth	-0.642	-0.216	-	-1.24	-2.98	0.509	Additive	-	15
Light	High nutrients - water	-	Growth	-1.38	-0.859	-	-0.639	-2.28	1	Additive	-	14
Light	High nutrients - water	-	Growth	-0.327	-0.378	-	1.81	-0.0885	3.71	Additive	-	14
Light	High nutrients - water	-	Growth	-1.65	-2.27	-	0.618	-1.02	2.26	Additive	-	14
Light	High nutrients - water	-	Growth	0.739	-0.077	-	4.92	1.71	8.13	Antagonistic	-	14
Habitat modification	Herbivory	-	Growth	1.71	1.25	-	2.33	1.19	3.46	Synergistic	Positive	19
Temperature	Competition	-	Growth	0.417	4.07	-	3.32	1.41	5.24	Synergistic	Positive	22
Temperature	Competition	-	Growth	0.874	4.78	-	5.29	2.66	7.92	Synergistic	Positive	22
Temperature	Competition	-	Growth	2.07	4.03	-	3.69	1.65	5.73	Synergistic	Positive	22
Temperature	Competition	-	Growth	1.63	2.23	-	1.12	1.72	5.87	Synergistic	Positive	22
Hyposalinity	Herbivory	-	Growth	0.679	0.628	-	0.348	-1.26	1.96	Additive	-	23
Temperature	Hyposalinity	Herbivory	Growth	0.792	0.679	0.628	-0.0127	-1.61	1.59	Additive	-	23
Temperature	Hyposalinity	-	Growth	0.792	0.679	-	0.474	-1.15	2.1	Additive	-	23
Temperature	Herbivory	-	Growth	0.792	0.628	-	0.371	-1.24	1.98	Additive	-	23
Hypoxia	High nutrients - sediment	-	Growth	0.738	2.91	-	6.99	2.72	11.3	Synergistic	Positive	25
Herbivory	High nutrients - water	-	Growth	-9.93	1.46	-	-2.93	-5.23	-0.626	Synergistic	Negative	26
Light	High nutrients - water	-	Growth	14.1	-6.32	-	4.24	1.36	7.13	Antagonistic	-	27
Hypersalinity	Photosynthesis inhibition	Hypoxia	Growth	1.82	1.16	-0.547	3.01	0.984	5.03	Synergistic	Positive	29

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Hypersalinity	Photosynthesis inhibition	-	Growth	1.82	1.16	-	2.4	0.581	4.22	Synergistic	Positive	29
Hypersalinity	Hypoxia	-	Growth	1.82	-0.547	-	4.37	1.82	6.92	Antagonistic	-	29
Photosynthesis inhibition	Hypoxia	-	Growth	1.16	-0.547	-	-0.134	-1.52	1.25	Additive	-	29
Hypersalinity	Photosynthesis inhibition	-	Growth	5.83	2.56	-	6.25	2.89	9.62	Synergistic	Positive	29
Temperature	Photosynthesis inhibition	-	Growth	3.06	1.72	-	3.39	1.23	5.56	Synergistic	Positive	30
Temperature	Photosynthesis inhibition	-	Growth	-0.449	-0.96	-	1.47	0.0908	3.03	Additive	-	30
Temperature	Photosynthesis inhibition	-	Growth	3.13	-0.147	-	2.34	0.541	4.14	Antagonistic	-	30
Temperature	Photosynthesis inhibition	-	Growth	-0.385	0.767	-	8.62	4.18	13.1	Antagonistic	-	30
Temperature	Photosynthesis inhibition	-	Growth	0.445	1.92	-	0.631	-0.789	2.05	Additive	-	30
Light	Photosynthesis inhibition	-	Growth	0.147	0.0179	-	0.184	-1.43	1.78	Additive	-	34
Temperature	Competition	-	Mortality	-8.61	-0.699	-	-4.55	-7.18	-1.93	Synergistic	Negative	3
Temperature	High nutrients - water	-	Mortality	-0.661	-0.604	-	-1.71	-3.58	0.161	Additive	-	4
Temperature	High nutrients - sediment	-	Mortality	-5.02	-0.491	-	-2.33	-4.41	-0.259	Synergistic	Negative	4
Light	High nutrients - water	-	Mortality	-0.543		-	-1.25	-3	0.499	Additive	-	5
Temperature	Light	High nutrients - water	Mortality	-0.547	-0.543	-	-2.68	-4.88	-0.474	Synergistic	Negative	5
Temperature	Light	-	Mortality	-0.547	-0.543	-	-0.805	-2.47	0.859	Additive	-	5

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individual effect B	Individual effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Temperature	High nutrients - water	-	Mortality	-0.547		-	-0.965	-2.66	0.726	Additive	-	5
Burial	High nutrients - sediment	-	Mortality	-1.15	-0.849	-	-0.869	-1.84	0.0975	Additive	-	6
Light	Habitat modification	-	Mortality	-1.79	0.0202	-	-10.3	-14.6	-6.04	Synergistic	Negative	12
Hyposalinity	High nutrients - water	-	Mortality	-1.2	-0.98	-	-0.741	-2.39	0.914	Additive	-	13
Hyposalinity	Temperature	-	Mortality	-0.0739	-0.387	-	-2.21	-4.24	0.18	Synergistic	Negative	14
Hyposalinity	Temperature	-	Mortality	-0.000242	-0.0694	-	-0.44	-2.06	1.18	Additive	-	14
Hyposalinity	Temperature	-	Mortality	-0.0212	-0.675	-	-2.78	-5.2	-0.535	Synergistic	Negative	14
Hyposalinity	Temperature	-	Mortality	-0.358	-0.61	-	-1.08	-2.8	0.632	Additive	-	14
Light	High nutrients - water	-	Mortality	0.624	-2.3	-	-4.14	-6.97	-1.3	Synergistic	Negative	14
Competition	Herbivory	-	Mortality	-5.02	-0.332	-	-2.73	-4.95	-0.505	Synergistic	Negative	21
Temperature	Competition	Herbivory	Mortality	-1.42	-5.02	-0.332	-3.32	-5.79	-0.854	Synergistic	Negative	21
Temperature	Competition	-	Mortality	-1.42	-5.02	-	-2.95	-5.26	-0.637	Synergistic	Negative	21
Temperature	Herbivory	-	Mortality	-1.42	-0.332	-	-2.34	-4.41	-0.261	Synergistic	Negative	21
Competition	Herbivory	-	Mortality	-1.42	0.236	-	-1.52	-3.33	0.298	Additive	-	21
Temperature	Competition	Herbivory	Mortality	-0.733	-1.42	0.236	-1.67	-3.52	0.191	Additive	-	21
Temperature	Competition	-	Mortality	-0.733	-1.42	-	-1.96	-3.9	-0.00982	Synergistic	Negative	21
Temperature	Herbivory	-	Mortality	-0.733	0.236	-	-1.38	-3.16	0.403	Additive	-	21
Herbivory	High nutrients - water	-	Mortality	-1.54	-1.21	-	-1.22	-2.56	0.134	Additive	-	31
Pollution	Acidification	-	Survival	0	-0.291	-	0	-1.13	1.13	Additive	-	2
Light	High nutrients - water	-	Survival	-0.651	0.519	-	0.0698	-1.53	1.67	Additive	-	14
Temperature	Competition	-	Survival	1.86	0.595	-	5.47	1.99	8.95	Synergistic	Positive	24

Stressor A	Stressor B	Stressor C	Response variable	Individual effect A	Individua l effect B	Individua l effect C	Interaction effect	Interaction lower CI	Interaction upper CI	Interaction type	Direction (if synergistic)	Reference
Hypoxia	High nutrients - sediment	-	Survival	-0.048	1.63	-	2.64	0.449	4.82	Antagonistic	-	25
Hypersalinity	Photosynthesis inhibition	-	Survival	2.99	1.22	-	3.34	1.2	5.49	Synergistic	Positive	29

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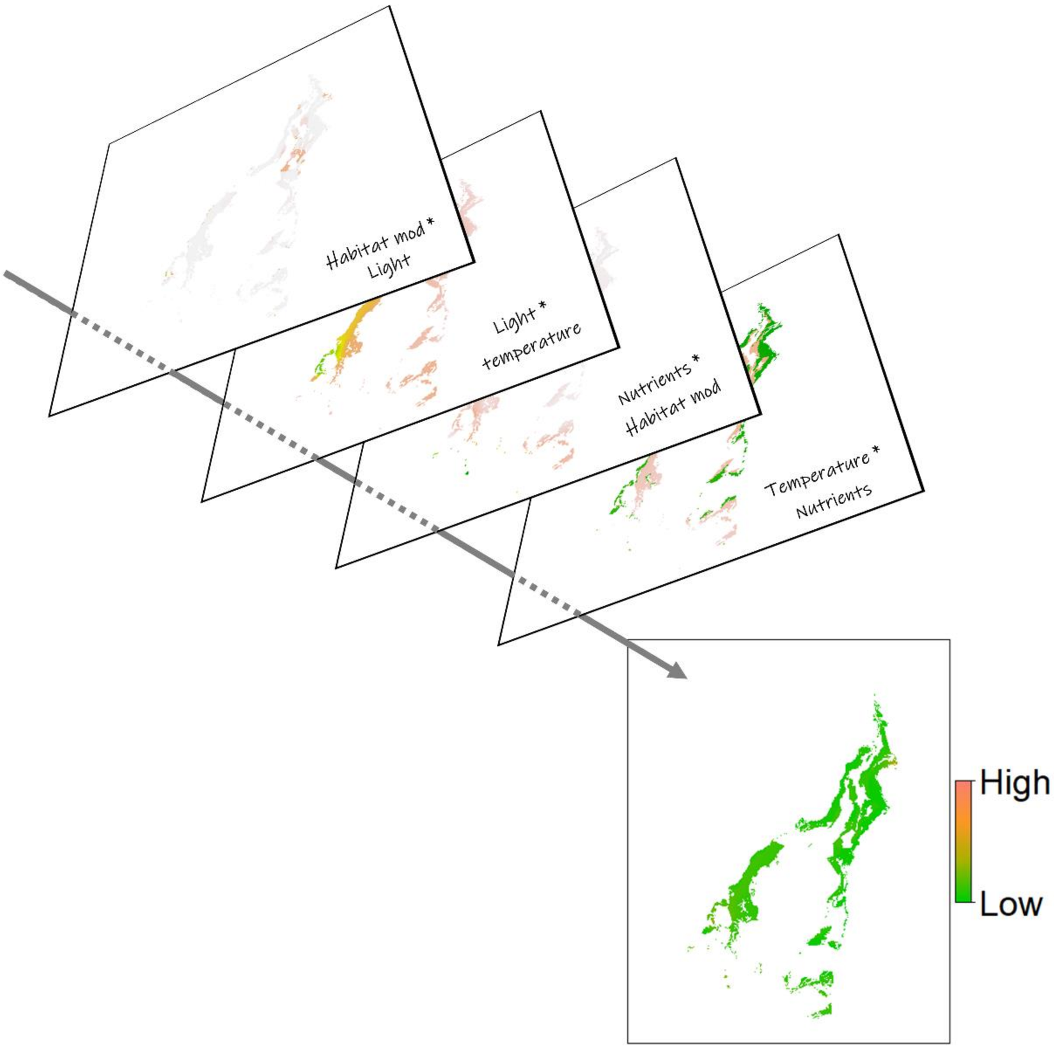
Chapter 4

Incorporating non-additive stressor interactions into marine spatial cumulative impact assessments



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Principal Author

Name of Principal Author (Candidate)	Jackson Stockbridge		
Contribution to the Paper	Conceptualisation, data curation, formal analysis, investigation, methodology, visualisation, writing - original draft		
Overall percentage (%)	75		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contr bution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Title

Incorporating stressor interactions into marine spatial cumulative impact assessments

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Abstract

1. Human induced stressors are impacting the oceans and reducing the biodiversity of their ecosystems. The many stressors affecting marine environments do not act in isolation. However, their cumulative impact is difficult to predict, despite representing a much more likely real-world scenario. Most of the available methods for quantifying cumulative impacts on marine ecosystems sum the impact of individual stressors to estimate cumulative impact. We demonstrate that cumulative effects from non-additive stressors can be accounted for in commonly used cumulative impact assessment methods.
2. We incorporated synergistic and antagonistic stressor interactions into a widely-used additive model for marine spatial cumulative impact assessment. We combined experimental data on the impact of multiple stressors with spatial data on stressor intensity to test whether stressor interactions impact seagrasses in a case study region in South Australia. The results from an additive spatial cumulative impact assessment model were compared with results from the model incorporating interactions. We propagated uncertainty from the experimental effect estimates to the cumulative impact maps to illustrate how including interactions affects uncertainty in the cumulative impact estimates.
3. Cumulative effects from the interaction model were more variable than those produced by the additive model. Five of the 15 interacting stressors that we tested produced impacts that significantly deviated from those predicted by an additive model. Areas of our study region that showed the largest

discrepancies between the additive and interactive outputs were associated with higher uncertainty.

4. *Synthesis and application:* Current marine cumulative impact assessment methods often rely on models that assume additive stressor impacts. Our study demonstrates that the inclusion of stressor interactions changes the pattern and intensity of modelled spatial cumulative impact. Our results indicate that additive models have the potential to both underestimate and overestimate cumulative impact. This highlights the importance of including stressor interactions in cumulative impact assessments. Appropriate inclusion of interacting stressor data may have implications for the identification of key stressors and the subsequent spatial planning and management of marine ecosystems and biodiversity.

Keywords: Antagonistic stressors; anthropogenic threats; human threats; multiple stressors; non-additive; synergistic threats; uncertainty analysis.

Introduction

Human activities (hereafter referred to as ‘stressors’; see glossary of terms in Table 1) are reducing ocean resources and impacting the biodiversity of its ecosystems (Costello et al., 2010). Stressors on marine and coastal ecosystems include overfishing, nutrient loading, pollution discharges and coastal development (Hodgson, 1999, Hughes et al., 2003, Tian et al., 2018). The impact of a stressor can be calculated to provide an estimate of the effect on an ecosystem and/or a service it provides. These estimates can be reasonably accurate when considering the impact of an individual stressor (Benham et al., 2019). However, marine ecosystem-based management faces the challenge of multiple, overlapping stressors, and as such it is important to be able to accurately estimate the cumulative impact to inform ecosystem management (Levin et al., 2009).

Early methods for assessing cumulative impacts were simple, non-spatial environmental checklists (Cocklin et al., 1992). These were later improved by incorporating spatial information on stressors and their overlap within defined assessment regions (e.g. Lawler *et al.* 2002). In recent years, these methods have been further refined by the development of standardised spatial cumulative impact assessment methods (e.g., Halpern et al., 2008), which have been applied in hundreds of studies of marine ecosystems (e.g. Selkoe et al., 2009, Ban et al., 2010, Jones et al., 2018). Some studies have successfully built upon these methods to further our understanding of cumulative impact in marine ecosystems by identifying and addressing sources of uncertainty (e.g. Jones et al., 2018, Stockbridge et al., 2021, Stock and Micheli, 2016).

Despite their wide application, the complexity of marine ecosystems means the most commonly used cumulative impact assessment methods have limitations due to the necessary assumptions in the methods (Halpern and Fujita, 2013). These assumptions make the methods more generalisable and repeatable, enabling application across multiple regions and ecosystems. However, they may also lead to misleading or inaccurate cumulative impact assessments (Stock and Micheli, 2016). For example, a recent study suggests that the most commonly-used assessment approach may not accurately reflect ecosystem health (Stockbridge et al., 2021), with methodological assumptions likely contributing to this misrepresentation. Some previous studies have attempted to highlight and address the impacts of these assumptions. For example, by incorporating interactions between two stressors

(Brown et al., 2014) and addressing knowledge-based uncertainty in expert elicited scores for the impact of stressors on ecosystems (Jones et al., 2018).

One of the fundamental assumptions in the most commonly-used marine cumulative impact assessment method is that the impact of multiple stressors can be predicted by an additive model. The additive model assumes that the individual impact of a single stressor can be summed with the individual impact of other concurrent stressor(s) to predict the cumulative impact (Halpern et al., 2008). However, the additive model represents an unrealistic scenario within marine environments, where complexity and heterogeneity are likely to result in varying and interacting effects (hereby referred to as ‘interactions’; Breitburg et al., 1998). Incorporating interactions into cumulative impact assessment methods is frequently suggested as an important and challenging missing link for more effective ecosystem management and policy-making (Halpern and Fujita, 2013, Brown et al., 2014, Darling and Côté, 2008). Interactions between stressors have been identified under experimental conditions (e.g. Salo and Pedersen, 2014, Ontoria et al., 2019), in field studies (e.g. Ceccherelli et al., 2018), and in reviews and meta-analyses (e.g. Crain et al., 2008, Stockbridge et al., 2020). Based on these studies some stressors can either act in synergy with (exacerbate), or act antagonistically with (mitigate) others. Identifying where real-world non-additive stressors occur is a gap in knowledge to which marine ecosystem management is particularly vulnerable (Halpern and Fujita, 2013).

We developed a new, globally applicable method for cumulative impact assessment methods. We have undertaken a data-informed assessment of the value of including interactive effects in cumulative impact assessments. We aim to identify potential generalities that could be included in assessments of other regions that have similar data availability. Using a case study of seagrasses in Spencer Gulf, South Australia, we combined spatial data on stressor intensity (from Jones et al., 2018) with empirical data on stressor effect sizes and interactions from a recent meta-analysis (Stockbridge et al., 2020). Seagrass habitats provide valuable ecosystem services such as climate regulation (Gaylard et al., 2020), supporting commercial fisheries (Watson et al., 1993), and coastal protection (Campagne et al., 2014). However, seagrasses are impacted by multiple environmental and anthropogenic stressors (Grech et al., 2011), and are in decline in many regions (Turschwell et al., 2021). Seagrass sensitivity to change in conditions means their health is often indicative of that of the broader marine environment and they are a useful case-study to test cumulative impact assessment methods. Our novel cumulative impact assessment modelling provides a method for including interactions between stressors (i.e. non-additive effects) and the difference this makes to assessment outputs compared to the additive model approach developed by Halpern *et al.* (2008).

Methods

Study area

Our research used a case study in Spencer Gulf, South Australia (Fig. 1), which is Australia's largest estuary covering approximately 30,000 km^2 (Kämpf, 2014). Spencer Gulf is characterised by a reduced exchange of water with the open ocean, and evaporation exceeding precipitation, resulting in inverse estuarine conditions (i.e. salinity higher than seawater; Kämpf et al., 2010). Spencer Gulf is also home to some of the most extensive and diverse temperate seagrass meadows in Australia (Larkum et al., 2018).

Due to its substantial environmental and economic importance, as well as proposed port and shipping infrastructure developments associated with mining, recent studies have used Spencer Gulf as a case study to test cumulative impact assessment methods that aim to reduce uncertainty (Doubleday et al., 2017, Jones et al., 2018, Stockbridge et al., 2021). Spencer Gulf represents a unique opportunity to evaluate cumulative impact assessment methods due to the availability of empirical data and modelled datasets for the region (Tanner et al., 2020, Gaylard et al., 2013, Stockbridge et al., 2021).

Stressor impact scores

We used published stressor impact scores based on experimental data (n = 41 studies) from a meta-analysis of both individual and interactive stressors on seagrasses (Stockbridge et al., 2020). We updated the literature search from that paper using the same search terms and databases; the updated search was undertaken in May 2021. Search terms used were all derivatives of the words 'synergy', 'antagonistic' and 'additive' (synerg* OR antag* OR *additiv*) AND 'seagrass' (for more details, see Stockbridge et al., 2020). Additional studies (n = 7) resulted in a total of 48 studies and 576 experimental results that could be incorporated by recalculating relevant stressor meta-analysis scores using the same methods, as described below.

Scores from Stockbridge *et al.* (2020) were based on the impact on seagrasses from individual stressors tested in isolation, as well as the combined impact of co-occurring stressors. Individual and interactive effect sizes were calculated using the standardised mean difference (SMD; Table 1), also referred to as *Hedge's d,* according to methods for factorial meta-analysis (Crain et al., 2008, Gurevitch et al., 2000). SMD uses the pooled sampling variance to quantify the difference between means of experimental and control groups, then standardises these values to ensure comparability between studies (Hedges and Olkin, 1985). SMD values for 'mortality' and 'epiphytes' were inverted, due to the detrimental effects of epiphytes on seagrass (Brush and Nixon, 2002), to ensure that the appropriate stressor effects were reflected in the SMD (i.e. a negative experimental result, such as increased mortality, produced a negative SMD value; Nakagawa et al., 2015).

SMD values of all studies were weighted using the inverse of their sample variance (Gurevitch et al., 2000). Inverting the sample variance gives more weight to a study with a larger sample size and smaller standard error. The mean of the weighted SMD values was used to generate pooled effect sizes for all studies relating to the same stressor or stressor pairs. We used the pooled SMD mean and 95% confidence intervals of individual stressors and each stressor combination to parameterise a normal distribution. For each stressor and stressor combination, we used 1000 random samples from the normal distribution to determine a distribution that is representative of a range of stressor impact scores (Table 1; Fig. S1 in Supplementary material).

Mapping stressor intensity and seagrass

We used spatial data layers representing the relative intensity of stressors corresponding to those assessed in the Stockbridge *et al.* meta-analysis (2020). Where appropriate, spatial data layers from Jones et al. (2018) were used. Data layers were excluded if there were no corresponding effect sizes (from Stockbridge et al., 2020) or if more recent spatial data were available. For example, the point source nutrient layer from Jones *et al.* (2018) was excluded in favour of modelled annual time-averaged concentration of ammonium and nitrate, since these data were modelled over a longer time scale and had better spatial coverage (Middleton et al., 2013; Table S1). In some cases, spatial data were combined to create a single layer where this provided more representative estimates of stressor intensity (Table S1).

Data were provided either as raster layers or as spatial points. Spatial points were then rasterised, and missing grid cell values were interpolated using the mean of a matrix of neighbouring grid cells and a "moving window" (focal) approach. Grid cell values in the data layers representing pH and O_2 were inverted to represent the stressors "Acidification" and "Hypoxia" respectively (i.e. acknowledging that hypoxia is indicated by the inverse of available oxygen), and to ensure that all stressor layers were consistent in terms of higher values indicating higher stress.

The raw units for stressor intensity layers varied, so they were all scaled to between 0 and 1 based on the minimum and maximum values of each stressor. When multiple data layers represented a stressor (e.g. ammonium and nitrate concentrations represent "Pollution: nutrients"), the scaled individual data layers were summed and then re-scaled to generate the final stressor layer.

Since the effect sizes from Stockbridge *et al.* (2020) are based on seagrass studies, this analysis only focussed on areas where seagrass is the dominant benthic habitat in Spencer Gulf (Fig. 1). The areas of seagrass habitat were identified using a benthic habitat map (raster) from Jones *et al.* (2018) and cover approximately 5,512 km^2 (Edyvane, 1999). All non-seagrass cells in this raster were given a value of NA to exclude them from the study's area of interest. All spatial layers provided by Jones *et al.* (2018) are available at https://doi.org/10.6084/m9.figshare.5047786.v1). Raster generation was undertaken using the ‘terra’ (Hijmans RJ, 2022) and ‘raster’ (Hijmans, 2022) packages in R 4.2.1 (R Core Team, 2022).

Calculating cumulative impacts

We calculated cumulative impact using the commonly applied additive model (Halpern et al., 2008), as well as a model that incorporated stressor interactions (Fig. S1). The additive model includes only the SMD values for stressors tested in isolation. To incorporate stressor interactions, we used a version of the additive model adapted from Brown et al. (2014), hereby referred to as the interaction model. The interaction model includes the SMD values for stressors tested in isolation, as well as the SMD values for the stressors tested in the presence of another stressor. Since few studies have tested the interactive effects of three or more concurrent stressors on seagrass (see Moreno-Marin et al., 2018, Koch and Erskine, 2001 for exceptions), only two-way interactions were considered in our interaction model. We used the additive and interaction models to conduct two cumulative impact assessments of Spencer Gulf. For each assessment, we calculated the cumulative impact of multiple stressors at each grid cell, and combined all layers into a single 250 m x 250 m raster (Eq. 1; Folt et al., 1999).

$$(1) \qquad C_k = \sum_{i=1}^{n} a_i S_{j,k} + \sum_{i,j=1}^{n} a_{ij} S_{j,k} S_{i,k}$$

The first summation (**red**) *indicates additive model*; the second summation (**black**) *indicates interaction term (Folt et al., 1999)*

Where C_k is the cumulative impact at each grid cell, a_i is the i^{th} of 1000 iterations of the SMD score for stressor i, and S_j is the spatial intensity for stressor i and there are *n* stressors. When two stressors were present in the same grid cell (i.e. S_j > 0), $a_{ij}S_{j,k}S_{i,k}$ is the SMD score (a_{ij}) combined with the spatial intensity of both stressors ($S_{j,k}S_{i,k}$). Each cell's cumulative impact score (C_k) was represented by a distribution generated with the 1000 random independent draws of the additive and interactive effects (a_{ij}) from normal distributions defined by their SMD parameters (Fig. S1). We generated uncertainty estimates of our cumulative impact scores for each grid cell by calculating the variance across the 1000 iterations for both the additive and interaction models (Fig. S1). Note that the uncertainty could be estimated directly by multiplying the variances by the stressor intensities, however we used a simulation-based approach so that the method can generalize to any distribution of a_i values.

To determine the significance of an interaction (i.e. an interaction that significantly deviates from additive, and is non-additive), we calculated the 0.025 and 0.975 quantiles of each grid cell across the 1000 cumulative impact score raster layers. Significant stressor interactions occurred at grid cells where the quantiles did not contain zero. We then calculated the proportion of variance that was attributed to the interactive effect, as a proportion of the total variance in the cumulative impact including additive effects.

We used the two most commonly accepted terms to define stressor interactions; synergistic and antagonistic (Folt et al., 1999; Table 1). These definitions have been applied in numerous cumulative impact studies and reviews (e.g. Crain et al., 2008, Darling and Côté, 2008, Brown et al., 2013). We acknowledge that the terms related to stressor interactions vary in the literature, and there are studies that have expanded on these definitions to include more types of interactions (e.g. Côté et al., 2016, Piggott et al., 2015). However, for the purposes of this study, we adopted the terms 'synergistic' and 'antagonistic' to be consistent with the majority of the literature. Eq. 1 results in a higher CI^s value than the additive model when stressors interact synergistically (Eq. 2), and a lower CI^s value when they interact antagonistically (Table 1; Eq. 3). Where a stressor was not present in a grid cell (i.e. stressor intensity = 0), the grid cell impact scores were 0 for both an individual stressor and any stressor combinations including the stressor.

(2) $$\textit{Synergistic}: \quad C_k = \sum_{i=1}^{n} a_i S_{j,k} \quad < \quad \sum_{i,j=1}^{n} a_{ij} S_{j,k} S_{i,k}$$

(3) $$\textit{Antagonistic}: \quad C_k = \sum_{i=1}^{n} a_i S_{j,k} \quad > \quad \sum_{i,j=1}^{n} a_{ij} S_{j,k} S_{i,k}$$

The first summation (**red**) *indicates additive model*; the second summation (**black**) *indicates interaction term (Folt et al., 1999)*

Results

We calculated stressor impact scores for nine individual stressors and 15 stressor combinations in total (Table S2). In the meta-analysis (Stockbridge *et al.,* (2020), nine of these stressor combinations were found to be 'additive', and five as 'interacting' (Table S3).

The additive model underestimated cumulative impacts when compared to the interaction model (Fig. 2). Cumulative impact scores from the additive model ranged from -1.69 to 4.63 compared to a range of -10.78 to 19.85 from the interaction model. The median (and median absolute deviation, MAD) cumulative impact of all stressors across all seagrass areas from the additive model was 0.63 (MAD = 0.69), compared to 1.01 (MAD = 1.73) from the interaction model (Fig. 2). Despite the differences between the additive and non-additive outputs, significant, interactions (i.e., grid cells where 0.025 and 0.975 quantiles of the 1000 interactive cumulative impact did not include zero) were present in only 0.069 % of the seagrass grid cells. The interaction model indicated that the majority of seagrass areas in Spencer Gulf were subject to higher cumulative impacts - a consequence of synergistic stressor interactions (Fig. 3). However, there were some areas where antagonistic interactions led the interactive model to have lower scores than the additive model (Fig. 3). Five stressor interactions were significantly non-additive when their impact was assessed independently (Fig. 4). For example, increased temperature significantly interacted with hypoxia, reduced light and heavy metal pollution (Fig. 4).

Variance around the cumulative impact estimates increased with the inclusion of stressor interactions (Fig. 5). The proportion of variance in the estimates varied throughout the seagrass area in Spencer Gulf, with heavily impacted areas, such as the industrial hubs at Port Pirie and Whyalla, being associated with higher uncertainty (Fig. 2; Fig. 5).

Discussion

Previous studies on the cumulative impact of multiple stressors on marine ecosystems warn of the prevalence of stressor interactions (Darling and Côté, 2008, Salo and Pedersen, 2014, Ceccherelli et al., 2018), and highlight the need for caution when omitting these interactions from cumulative impact assessment (Halpern and Fujita, 2013, Côté et al., 2016, Brown et al., 2013). Our study demonstrates a modelling method for extending the commonly-used additive model to include interactions, with stressor impact scores based on empirical data rather than expert elicitation. The results show the difference in cumulative impact assessment output when interactions are incorporated, compared to the additive model that assumes independent impacts of all stressors. Additive models do not capture the variability and range of cumulative impact scores that are produced by the interaction model.

There are a number of different assumptions associated with additivity and linearity in cumulative impact assessment methods and these can be conflated in the literature. For example, the assumption of a negative linear relationship between ecosystem condition and cumulative impact score (addressed by Stockbridge et al., 2021) can be conflated with the assumption that an ecosystem will respond linearly to changes in the intensity of an individual stressor, as opposed to having a threshold or tipping point response (Halpern and Fujita, 2013). Further confusion is introduced if ‘non-additive’ and ‘non-linear’ are used interchangeably when discussing stressor interactions. Interactions can be linear or non-linear, depending on how changes in the spatial intensity of the stressor(s) affect each other and the response of the underlying ecosystem. For example, as the spatial intensity of water quality and temperature stressors increase, their interactive impact can generate non-linear effects in seagrass ecosystems as they are pushed past a tipping point (Lefcheck et al., 2017). Although our model enables the inclusion of interactions between stressors, it does not capture non-linear relationships between stressors (whether individual or interacting) and ecosystem responses (Duncan and Kefford, 2021). Addressing gaps in knowledge associated with linearity in future assessments would help inform where non-linear responses to stressors and stressor interactions may push an ecosystem beyond its stress tolerance threshold. However, accurate predictions of ecosystem thresholds that can be generalised across regions would require far more empirical data than are currently available.

Our model incorporates the effect of individual and pairwise stressor interactions using experimental data from studies on seagrasses (Stockbridge et al., 2020), removing the need for expert elicitation. Cumulative impact assessments often rely on expert knowledge to generate impact scores, which can be an effective method of data collection when empirical data are scarce and there is an urgency to make conservation decisions (Sutherland, 2006, Kuhnert et al., 2010). Previous studies have advanced the expert elicitation process by quantifying and minimising uncertainty (Martin et al., 2012, Jones et al., 2018, e.g. Cooke and Goossens, 2004), however, reservations remain around biases associated with differing expert scores and subjective influences (Slovic, 1987, Halpern and Fujita, 2013). The model we use reduces our reliance on expert elicitation and uses empirical data to generate cumulative impact estimates, which improves reliability (Duncan and Kefford, 2021). In addition, by moving beyond expert elicitation for estimating stressor impact scores, our modelling approach allows us to incorporate two-way stressor interactions into cumulative impact assessment. Furthermore, this model is flexible enough to include 3-way, or higher order, interaction terms, if data on the impacts of such interactions are available. By using the meta-analysis SMD scores we ensure that so that stressor interactions from different experimental studies are comparable. The advantage of using the SMD is that we can standardise scores across disparate studies, however individual study context can be lost by doing this.

Interactions rarely led to significant differences in the cumulative impact scores within our study area (except in 0.069 % of grid cells). This is likely affected by the accumulating variance introduced by including more stressor pairs, as each stressor pair score has an associated variance. Therefore, cumulative impact maps of our study area have limited usefulness when confidently determining how stressor interactions affect the overall cumulative impact score. However, it is likely that output from our model used here would vary depending on the assessment region, number of included stressor pairs, and availability of more precise estimations of interactive effects. Cumulative impact maps may provide a broad overview of human impact on marine ecosystems and indicate where impact hotspots are likely to occur due to synergistic stressor interactions. Furthermore, cumulative impact maps may identify potential marine refuges in areas where antagonistic interactions are reducing the impact of stressors.

We found only a small proportion of our study area (0.07 % of grid cells) had significantly different cumulative impact scores between the interactive and additive models. The non-significant differences between the two model's output across much of the study area is likely driven by propagation of uncertainty in the interaction model, as there is error associated with each stressor pair's interaction effect score. Since the effect scores used in our model were derived from meta-analysis SMD scores, uncertainty is introduced by the varying number of studies that tested each stressor and stressor pair (Stockbridge et al., 2020). For example, there was only one test on the effects of habitat modification and reduced light (higher variance), compared to 44 tests on the effects of increased temperature and hypoxia (lower variance; Table S2). There are more data available from studies that tested single stressors in isolation than interacting stressor pairs. This means that SMD scores for single stressors tended to have lower variance compared to the scores for interacting stressor pairs. Consequently, the stressor interaction SMD values calculated here are based on data with higher variance, which is reflected in the higher uncertainty associated with the inclusion of interactive effects in the cumulative impact model. More experimental and field studies on the impacts of multiple interacting stressors are required to increase the data for cumulative impact assessments and help to identify generalities and reduce uncertainty (Côté et al., 2016). Ultimately, the development of models that can concurrently account for all interactions between all stressors present, rather than simple pairwise stressor interactions, would be an important improvement. This would enhance our understanding of, and ability to model cumulative impacts that account for stressor interactions. However, the empirical data needed to robustly parameterise such models (e.g. experimental studies that quantify the individual and interacting effects of many stressors on specific ecosystems) are lacking. As methods for marine spatial cumulative impact assessment continue to develop there is a need to undertake and present uncertainty analyses associated with these estimates (Stock and Micheli, 2016, Jones et al., 2018, Jansen et al., 2022), as we have done here. This is especially important if there is potential for aggregation of uncertainty from different sources (Stock and Micheli, 2016). Priority areas for management action can be identified as those deemed to be heavily impacted based on robust cumulative impact estimates (Stock et al., 2018).

Our additive and interactive model outputs show similar spatial patterns in predicted cumulative impacts, although the score ranges are greater when interactions are included. This result suggests that our ability to identify refuges (‘cold spots’) or areas of particularly high cumulative stressor impact (‘hot spots’) is not notably affected by including interactions in the model, at least for our study region. However, although relying on the additive model may lead to under- or over-estimation of risk magnitude as the interaction model generated scores that were outside of the range of those generated by the additive model (both higher and lower). Ecosystems that are impacted by stressor interactions are more likely to be misrepresented by the additive impact model outputs. We found that the cumulative impact was often greater than additive, rather than lower than additive, and that synergistic (exacerbating) stressor interactions were more common than antagonistic (mitigating) interactions. The presence of synergistic interactions could mean that ecosystems are more vulnerable than indicated by the additive model, potentially shifting management priorities to target areas where impact has previously been underestimated. For example, the output from our interaction model shows higher scores for areas closely associated with potentially harmful human impacts, such as heavy industry at Whyalla and Port Pirie. Therefore, when synergistic stressors are prevalent, additive models should be considered a ‘best-case’ scenario, and managing based on this model could lead to poor management of vulnerable ecosystems or areas. For our study area’s seagrasses, the interaction model would enable conservative management since the output represents a ‘worst-case’ scenario. By identifying where synergistic interactions occur, our maps could help prevent accelerated seagrass degradation and biodiversity loss (Large et al., 2015).

The similarity in spatial patterns between two models’ cumulative impact outputs could be interpreted as there being limited benefits to the interaction model over the additive model. However, the interaction model output and its deviation from the additive model output will vary depending on the study region, the number of stressor pairs included in the assessment, and the availability and precision of interactive stressor effect scores. When digging deeper into the outputs of the interaction model, we found that there were significant interactive effects when the impact of stressor pairs was calculated independently of other stressor pairs. This ability to map specific pairs of interactive stressors, as well as looking at the complete cumulative impacts map, enables deeper interrogation of interactive stressor effects. These pairwise interaction maps can inform more targeted strategies to mitigate impact from specific stressor interactions.

Areas impacted by synergistic stressors present an opportunity for management to receive a greater return on conservation effort if the correct stressors are targeted. The removal or alleviation of a synergistic stressor would benefit an ecosystem more than if the same effort were spent on an additive stressor (Brown et al., 2013). For example, we found that temperature significantly interacted with three other seagrass stressors (hypoxia, reduced light, and metal pollution). Having this knowledge allows managers to address the causes of higher water temperature and understand where the greatest outcomes could be realised, based on the stressor pair interaction maps. Furthermore, confident predictions of the effects of synergistic stressors may encourage greater consideration of the regulation of these stressors and help avoid ecosystem state shifts. Antagonistic stressors present a different kind of challenge to those of synergistic stressors. The idea that the removal of one stressor could potentially make conditions worse for marine ecosystems would seem counterintuitive (Côté et al., 2016). However, effort and resources spent on the alleviation of antagonistic stressors may cause little difference or worsen ecosystem condition (Brown et al., 2013). Therefore, it is equally important to try to identify antagonistic and synergistic stressors (Côté et al., 2016).

Conclusion

The unpredictability of stressor interactions has led to current marine ecosystem management approaches often being based on cumulative impact assessment methods that assume stressors do not interact. Furthermore, the heterogeneity of global ecosystems represents a significant challenge in the standardisation of cumulative impact assessment methods (Côté et al., 2016, Darling and Côté, 2008, Crain et al., 2008). Standardised methods that incorporate interactions are essential for future cumulative impact assessments to realistically represent the impact of human activities on marine ecosystems. In doing this, we will support improved management (Brown et al., 2014) and help to avoid the severe impacts that may lead to ecosystem degradation and state shifts (Kraberg et al., 2011). However, empirical data on the presence and impact of stressor interactions on marine ecosystems are scarce, and consequently, the additive model is the default option for marine spatial cumulative impact assessments. Our results suggest that the additive impact model may not produce reliable estimates of the cumulative impact of multiple stressors and should be interpreted with caution. The inclusion of interactions into cumulative impact models is likely a more realistic approach, but may increase the uncertainty around the estimates of cumulative impact. Further research and empirical data on multi-stressor impacts is needed to reduce this uncertainty and produce more robust estimates for the cumulative impacts of multiple stressors on marine ecosystems.

Author contributions

B.M.G, A.R.J and J.S conceived the project. A.R.J and M.J.D collated the data. J.S, A.R.J, C.J.B and B.M.G designed the analysis, J.S, A.R.J and C.J.B conducted the analysis. J.S wrote the manuscript and prepared figures and tables. All authors reviewed the manuscript, figures and tables. B.M.G, A.R.J, C.J.B and M.J.D provided advice and guidance throughout the study.

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Figures and tables

Table 1. Glossary of terms and definitions

Terms	Definition
Stressor	Human activity that causes a component of an ecosystem to exceed its natural variation (Crain et al., 2008).
Impact	A measurable change in a factor of an ecosystem due to a stressor. 'Stressor impact' is often used interchangeably in the literature with 'stressor effect'.
Cumulative impact	A measurable change in a factor of the ecosystem due to the combined impact of multiple stressors.
SMD	Standardised mean difference. A value to quantify the difference in effect of an experimental group versus a control group (Sedgwick and Marston, 2013). The effect value is standardised and weighted by the inverse of the sampling variance to make it comparable across studies.
Stressor impact scores	A score to quantify the effect of a stressor tested in isolation, or a stressor pair.
Additive model	The most commonly used cumulative impact model. Individual stressor impacts are summed to calculate the cumulative impact.
Interaction model	The cumulative impact model used to incorporate stressor interactions in this study. This model is an extension of the additive model commonly used in cumulative impact assessments (e.g. Halpern et al., 2008) but is able to include interacting impacts of pairs of stressors (Brown *et al.* 2014).
Synergistic	In the context of stressor interactions, a synergistic interaction between two co-occurring stressors results in a cumulative impact that is greater than predicted by the sum of the individual stressors (i.e. the additive model).
Antagonistic	In the context of stressor interactions, an antagonistic interaction between two co-occurring stressors results in a cumulative impact that is less than predicted by the sum of the individual stressors (i.e. the additive model).

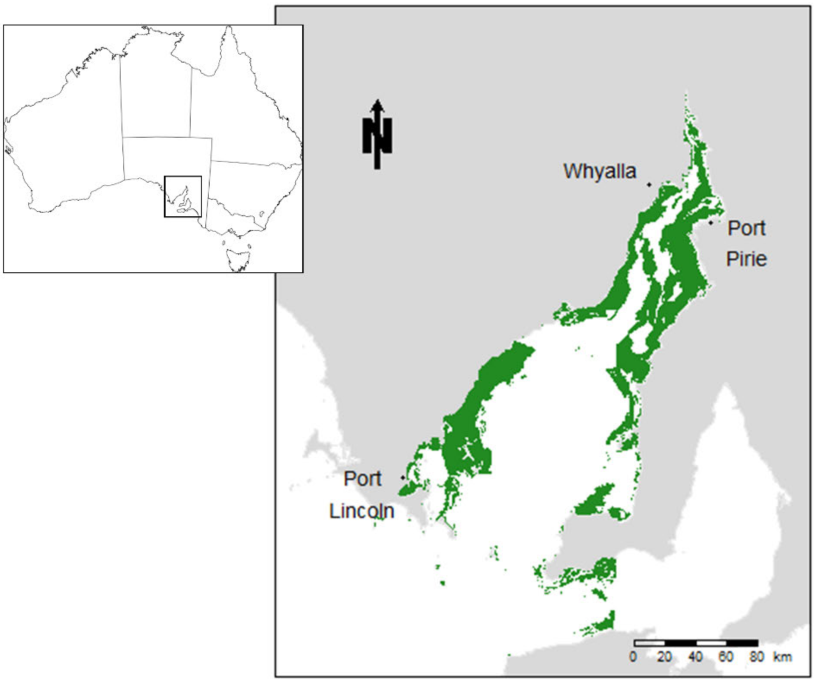

Fig. 1. Seagrass distribution (green areas) of our study area, Spencer Gulf, South Australia (general location indicated on an overview map of Australia).

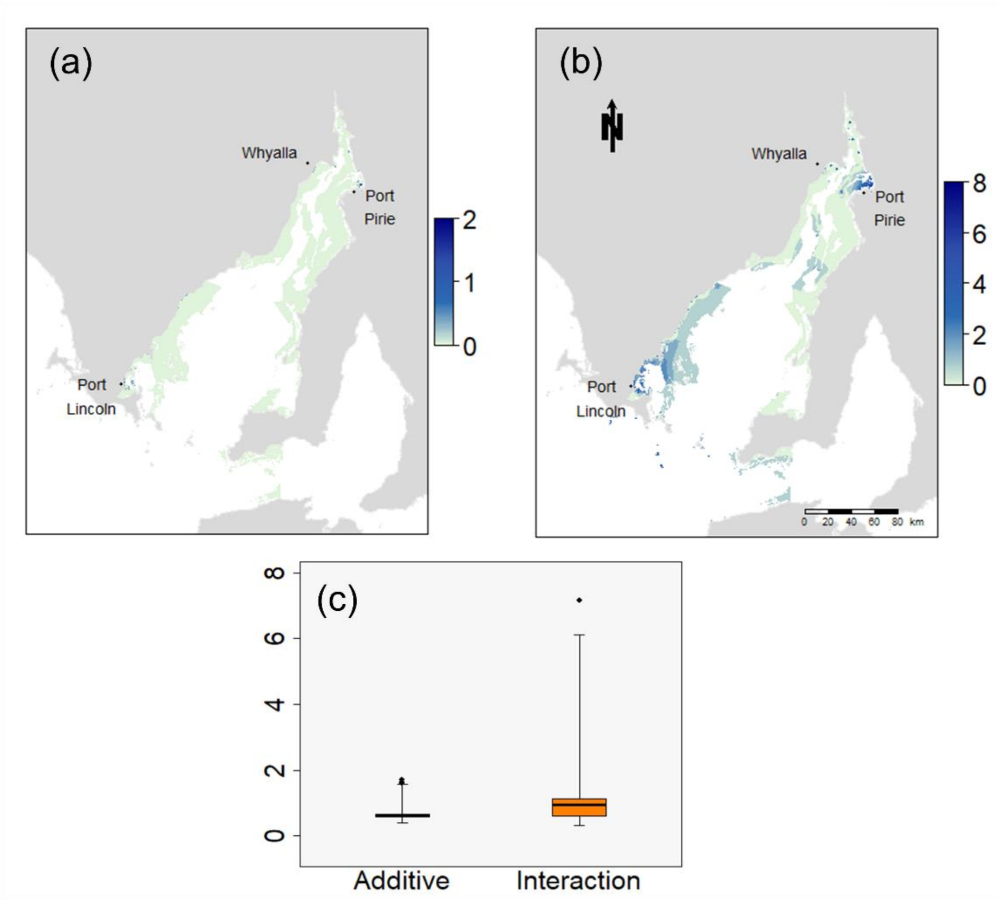

Fig. 2. Estimated cumulative impact of multiple stressors on known seagrass distribution (c). Cumulative impact maps generated using (a) the additive model and (b) the interaction model. Plot and maps show the median of 1000 randomly simulated impact scores. Note greater range of values in (b) than (a).

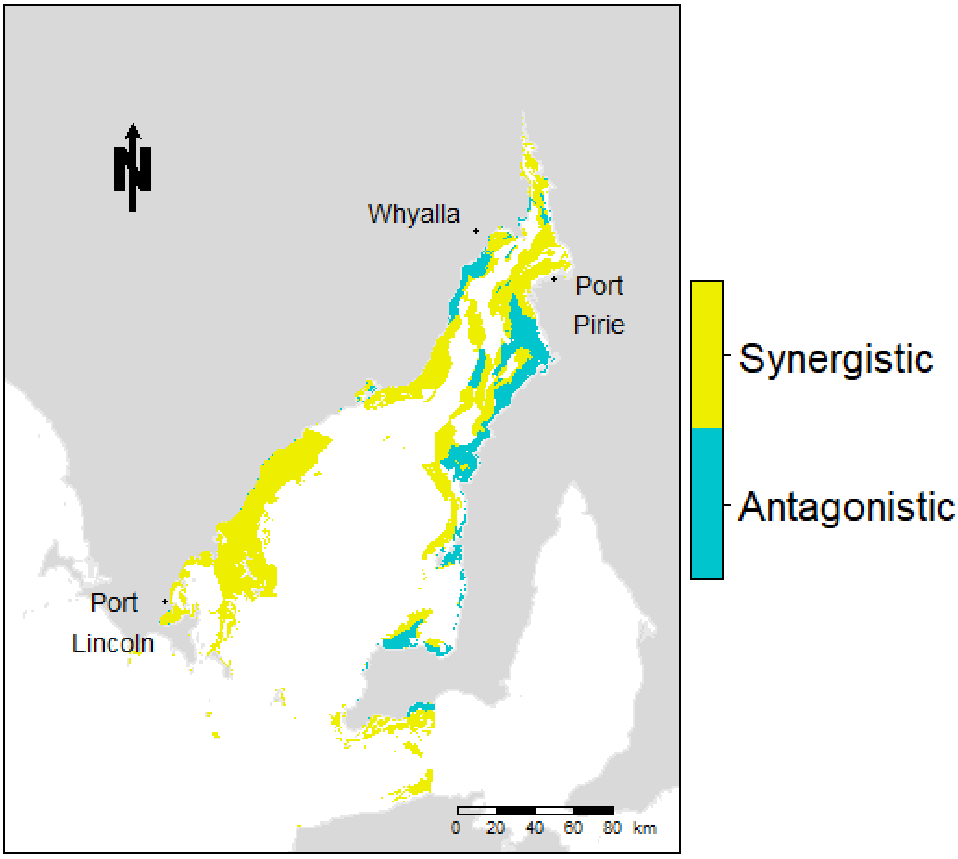

Fig. 3. Map of areas impacted by synergistic (yellow) and antagonistic (blue) stressor interactions (although these interactions may not be deemed to be significantly different to the additive model, refer to text).

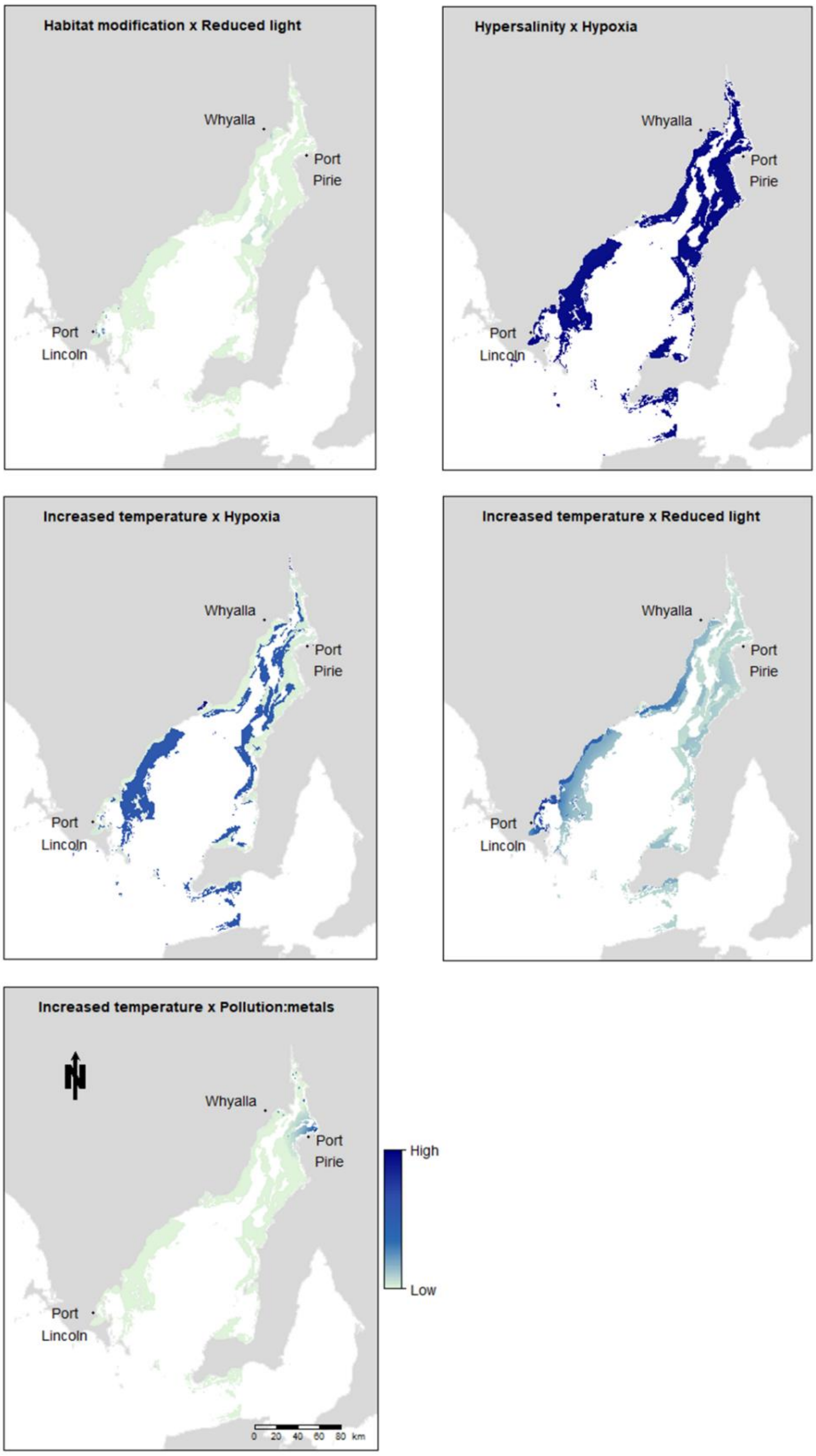

Fig. 4. Maps of impact scores from stressor pairs where the interaction was significantly non-additive (i.e., grid cells where 0.025 and 0.975 quantiles of the 1000 interactive cumulative impact did not include zero, where zero represents an additive model).

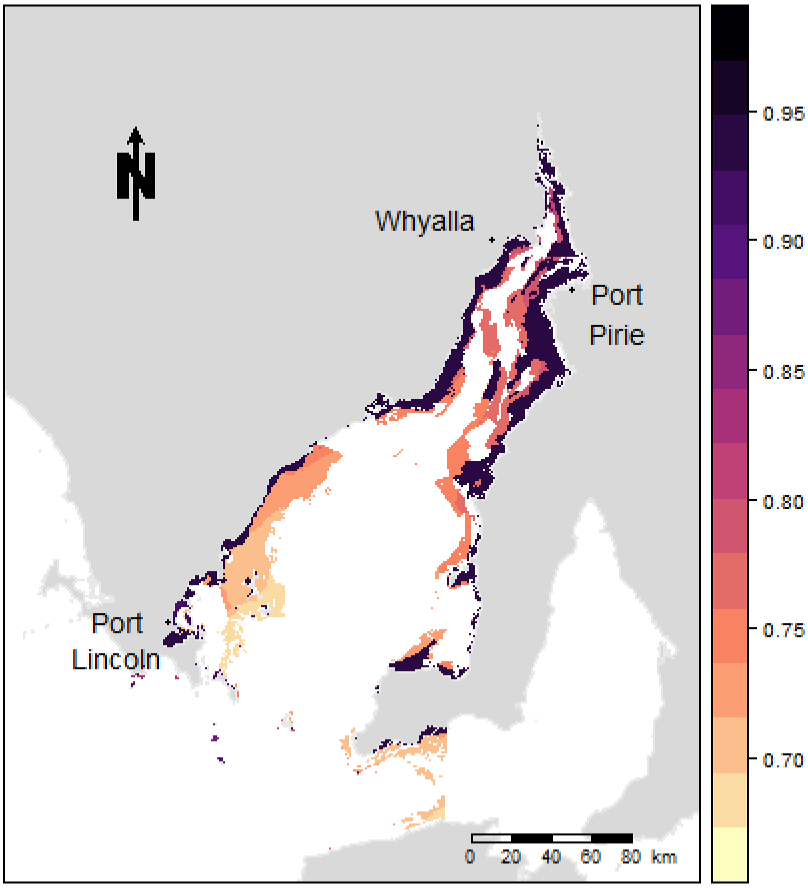

Fig. 5. Map of the proportion of total variance in the cumulative impact scores that is explained by the interactive stressors.

Supplementary Table S1: Table of stressor layers used for the cumulative impact maps of Spencer Gulf, South Australia. A brief description of the data used to generate the layer is listed, as well as details of how stressor layers were determined from the available spatial data. Stressor data layers marked with an * were contributed by Jones *et al.* (2018) and are available to download at https://figshare.com/s/8953f66d9a91f069ba01. Stressor data layers marked with an ** were provided as spatial points and rasterised. PIRSA = Department of Primary Industry and Regions South Australia; SARDI = South Australian Research and Development Institute. Table adapted from Jones *et al.* (2018).

Stressor	Data layer	Source	Rationale
Acidification	Bathymetry - Spencer Gulf *	Increasing depth from the coast was used as a proxy for decreasing pH Data were inverted such that high depth values indicated more acidic conditions	pH is more variable in shallower, coastal areas (Middelboe and Hansen 2007; Kerrison *et al.* 2011) In Spencer Gulf, pH varied with depth. Higher values occurred closest to the coast, and decreased in deeper waters (Tanner *et al.* 2019)
Habitat modification	Commercial fishing: prawn trawling * Coastal habitat modification (e.g. land reclamation, native vegetation removal, shoreline hardening) * Marine habitat modification: jetties * Marine habitat modification: marinas * Marine habitat modification: ports *	Spatial data provided by PIRSA. Intensity was based on the annual average trawl distance per fishing area Data from the Department for the Environment Spatial data provided by DEWNR. Intensity scores were weighted depending on distance from each grid cell to the feature, as well as the size of the feature	Fishing and trawling can affect sediment dynamics of marine habitats (Turner *et al.* 1999) The breaking apart of habitat leads to changes in biotic and abiotic habitat features (Fahrig 2003) Harbour breakwaters and other structures can alter the wave field (Tsoukala *et al.* 2015)
Hypersalinity	Maximum salinity **	Spencer Gulf regional ocean model outputs provided by SARDI (Tanner *et al.* 2020)	Maximum salinity of Spencer Gulf modelled over 4 years
Hyposalinity	Minimum salinity ** Climate change: extreme rain *	Due to the lack of fine-scale spatial data on the variation of climate change related impacts in Spencer Gulf, all grid cells were given a value of 1	Minimum salinity of Spencer Gulf modelled over 4 years Extreme rainfall events cause flood pulses which lower salinity levels in estuaries (Alosairi *et al.* 2019)
Hypoxia	Minimum dissolved oxygen concentration **	Spatial data provided by SARDI (Tanner *et al.* 2020) Data were inverted such that low oxygen values indicated lower oxygen conditions	Low-oxygen conditions lowers photosynthetic efficiency and can cause seagrass die-off events (Pulido and Borum 2010). Sulfide production is increased in low-oxygen conditions via anaerobic respiration (Goodman *et al.* 1995). Sulfide is a phytotoxin that inh bits photosynthesis (Koch and Erskine 2001)
Increased temperature	Climate change: hot weather (<10 m depth areas only) * Maximum temperature ** Point source thermal pollution *	Due to the lack of fine-scale spatial data on the variation of climate change related impacts in Spencer Gulf, all grid cells were given a value of 1 Spatial data provided by SARDI (Tanner *et al.* 2020)	Increased heatwave frequency leads to ocean warming (Ishii and Kimoto 2009; Cheung and Frölicher 2020) Maximum temperature of Spencer Gulf modelled over 4 years Power plants are a major source of thermal pollution (Dai *et al.* 2012)
Pollution: heavy metals	Heavy metal contamination *	Data from Gaylard (2014). Intensity was based on the volume of input and weighed by the distance from pollution source	Heavy metals are pollutants which can cause leaf necrosis and reduce growth of seagrasses (Llagostera *et al.* 2016)
Pollution: nutrients	Time-averaged ammonium concentration ** Time-averaged nitrate concentration **	Spatial data provided by SARDI (Tanner *et al.* 2020). Concentrations are based on inputs from wastewater treatment plants, finfish aquaculture and Whyalla steelworks	Excessive nutrient loading can lead to harmful algae blooms and eutrophication-related diseases in coastal ecosystems (Smith and Schindler 2009)
Reduced light	Aquaculture: finfish (presence or absence data only) * Aquaculture: oysters *	Spatial data provided by PIRSA (Wiltshire *et al.* 2010). Presence (1) or absence (0) of an aquaculture operation in a grid cell	Shading decreases light levels, reducing seagrass growth and structure (Bulmer *et al.* 2012; Skinner *et al.* 2014)
	Time-averaged large fraction carbon detritus concentration ** Time-averaged small fraction carbon detritus concentration ** Time-averaged zooplankton concentration ** Time-averaged phytoplankton concentration **	Spencer Gulf regional ocean model outputs provided by SARDI (Tanner *et al.* 2020)	Seagrass growth is inhibited under low-light conditions caused by high turbidity (Moore *et al.* 1997; Newell and Koch 2004). Food web interactions between zooplankton, phytoplankton, and organic matter, such as detritus particles, promote turbidity in marine ecosystems (Roman *et al.* 2001)

Table S2. Mean stressor standardised mean difference (SMD) scores and 95% confidence intervals used to parameterise a normal distribution, and the number of experimental results combined to calculate SMD scores.

Stressor(s)	**No of exp tests**	**SMD score**	**SMD score lower ci**	**SMD score upper ci**
Acidification	8	0.01	-0.27	0.29
Habitat modification	5	-0.99	-1.88	-0.11
Hypersalinity	9	-0.60	-1.88	0.68
Hyposalinity	38	-0.40	-0.67	-0.13
Hypoxia	31	0.23	-0.50	0.94
Increased temperature	122	0.003	-0.22	0.23
Pollution: metals	15	-0.87	-1.35	-0.39
Pollution: nutrients	62	-0.02	-0.36	0.32
Reduced light	30	-0.57	-1.08	-0.05
Acidification & Hyposalinity	1	-0.40	-2.04	1.24
Habitat modification & Reduced light	1	-10.32	-15.42	-5.22
Hypersalinity & Hypoxia	43	-1.08	-1.54	-0.61
Increased temperature & Hypersalinity	2	-1.22	-7.46	5.03
Increased temperature & Hyposalinity	39	-0.45	-0.69	-0.21
Increased temperature & Hypoxia	44	2.31	1.06	3.55
Increased temperature & Pollution: metals	1	-5.24	-10.26	-0.22
Increased temperature & Pollution: nutrients	40	0.21	-0.33	0.75
Increased temperature & Reduced light	12	-0.82	-1.77	0.13
Pollution: metals & Acidification	14	-0.51	-0.95	-0.07
Pollution: nutrients & Hypersalinity	2	-1.50	-6.26	3.27
Pollution: nutrients & Hyposalinity	24	-0.27	-0.82	0.28
Reduced light & Hyposalinity	1	-1.19	-3.12	0.74
Reduced light & Hypoxia	4	0.00	-0.08	0.08
Reduced light & Pollution: nutrients	28	-0.75	-1.61	0.11

Table S3. Stressor combinations and interaction type (additive, synergistic or antagonistic).

Stressor combination	Additive or interacting
Acidification & Hyposalinity	Additive
Habitat modification & Reduced light	Interacting
Hypersalinity & Hypoxia	Interacting
Increased temperature & Hypersalinity	Additive
Increased temperature & Hyposalinity	Additive
Increased temperature & Hypoxia	Interacting
Increased temperature & Pollution: metals	Interacting
Increased temperature & Pollution: nutrients	Additive
Increased temperature & Reduced light	Interacting
Pollution: metals & Acidification	Additive
Pollution: nutrients & Hypersalinity	Additive
Pollution: nutrients & Hyposalinity	Additive
Reduced light & Hyposalinity	Additive
Reduced light & Hypoxia	Additive
Reduced light & Pollution: nutrients	Additive

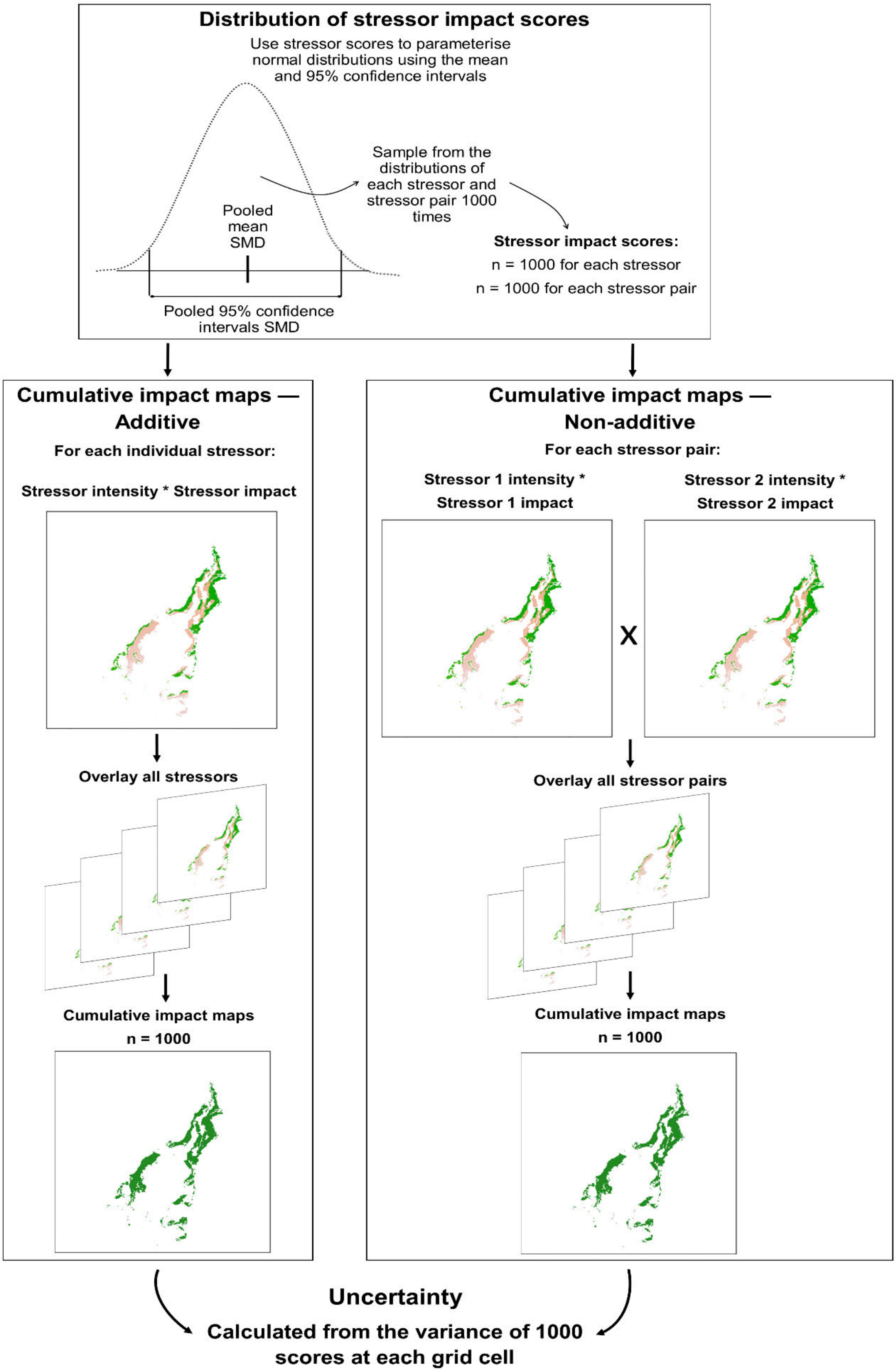

Fig. S1. Schematic representation of the additive and non-additive cumulative impact map calculations.

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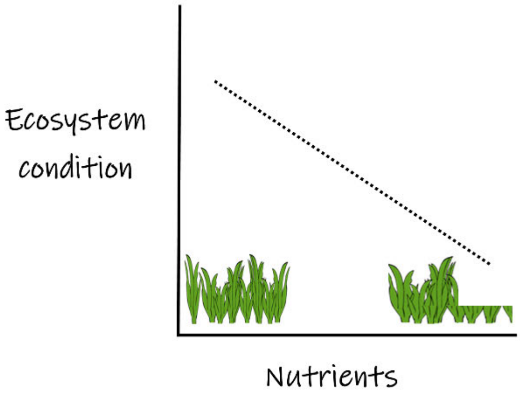
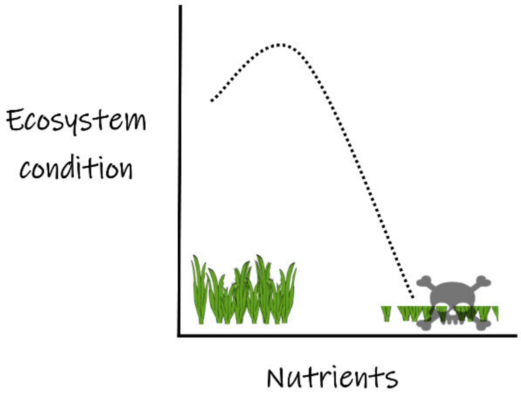
Chapter 5

Individual effects of stressors on seagrass and the implications for marine cumulative impact assessments





Statement of Authorship

Title of Paper	Individual effects of stressors on seagrass and the implications for marine cumulative impact assessments
Publication Status	☐ Published ☐ Accepted for Publication ☐ Submitted for Publication ☑ Unpublished and Unsubmitted w ork w ritten in manuscript style
Publication Details	This is a co-authored paper that has been prepared for submission

Principal Author

Name of Principal Author (Candidate)	Jackson Stockbridge		
Contr bution to the Paper	Conceptualisation, data curation, formal analysis, investigation, methodology, visualisation, writing - original draft		
Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Non-linear effects of individual stressors on seagrass and the implications for marine cumulative impact assessments

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Abstract

Seagrasses have a global distribution and form important habitats for many marine species. These key marine ecosystems also offer environmental and economic benefits through the provision of many ecosystem services. However, seagrasses and the services they provide are threatened by the impacts of multiple human-induced stressors. Due to the scarcity of empirical data on ecosystem responses to stressors, assessment methods that aim to accurately quantify human impact requires the assumption that the relationship between ecosystem condition and stressors is linear. We combined seagrass condition data obtained from field surveys with co-located data on the intensity of up to eight different potential stressors. We modelled the separate effect that each stressor had on three seagrass condition indices using generalised additive models. Hypersalinity, oxygen, temperature and turbidity consistently impacted seagrasses based on all three seagrass condition indices. Disturbance from aquaculture and coastal population density were not good predictors of seagrass condition based on any of the three condition indices. We found that none of the stressors were linearly correlated to seagrass condition, highlighting the prevalence of non-linearity in how seagrass condition responds to stressor impacts. This result has implications for cumulative impact assessment methods that assume a linear relationship between stressor intensity and ecosystem condition. We advocate that studies aiming to quantify the impact of multiple stressors need to incorporate non-linear relationships into modelling methods to produce more accurate estimates of human-induced impacts.

Introduction

Seagrass meadows cover an estimated global area of 300,000 to 600,000 km^2 and form key habitats in coastal regions (Green and Short 2003; Duarte *et al.* 2010). Considered some of the most productive ecosystems in the world (Waycott *et al.* 2009), seagrass meadows provide important functions, such as nutrient cycling, to other marine ecosystems (Hemminga and Duarte 2000). Seagrasses contribute to human well-being by providing ecosystem services such as protecting shores from coastal erosion and regulating the climate via carbon sequestration (McLeod *et al.* 2011; Campagne *et al.* 2014; Gaylard *et al.* 2020). Furthermore, there are economic benefits from seagrass ecosystem services (Worm *et al.* 2006; Waycott *et al.* 2009; Barbier *et al.* 2011; Costanza *et al.* 2014), including seagrass-supported commercial fisheries (Watson *et al.* 1993). Despite the numerous benefits, seagrass ecosystems are experiencing global decline, largely due to increasing human activity (Waycott *et al.* 2009; Lu *et al.* 2018; Turschwell *et al.* 2021). Coastal regions are densely populated, and as the population grows the demand for ocean resources increases (Reid *et al.* 2005). Humans apply stressors that can directly or indirectly impact seagrass ecosystems (Orth *et al.* 2006; Clark and Johnston 2016). Stressors that directly impact seagrasses include benthic trawling (Pasqualini *et al.* 1999), nutrient loading from agriculture (Nixon 1995), waste water discharges (Coggan *et al.* 2019), heavy metal pollution (Al-Najjar *et al.* 2021) and coastal development (Ostrowski *et al.* 2021). Indirect stressors on seagrasses can occur because of human induced climate change and include ocean warming and acidification (Lefcheck *et al.* 2017; He and Silliman 2019). Stressors can trigger an instant change in a characteristic of an ecosystem (Crain *et al.* 2008), or the impacts may be seen over time. For example, eutrophication promotes the growth of algae and epiphytes on seagrass leaves, reducing light and productivity over time within the ecosystem (Orth *et al.* 2006).

Previous studies have attempted to quantify how an increase or decrease in stressor intensity will impact seagrass (e.g. Marbà and Duarte 2010; Govers *et al.* 2014; Statton *et al.* 2018). Single stressor studies can provide accurate estimates of individual stressor impact on seagrass ecosystems. However, the majority of seagrass ecosystems worldwide are subjected to multiple stressors, meaning multi-stressor studies are required to provide estimates more representative of a real-world scenario (e.g. Andersen *et al.* 2015; Halpern *et al.* 2015; Jones *et al.* 2018). Cumulative impact assessment methods have been developed to quantify and map the impact of multiple stressors on marine ecosystems (Halpern *et al.* 2007). Since the publication of these methods, there has been a sharp increase in regional applications of such cumulative impact assessment approaches (e.g. Selkoe *et al.* 2009; Ban *et al.* 2010; Bevilacqua *et al.* 2018; Jones *et al.* 2018; Lange *et al.* 2018). However, despite being applied in hundreds of assessments of marine areas, there remain several key sources of uncertainty associated with these modelling methods (Halpern and Fujita 2013). Recent studies have furthered our understanding of the level of confidence we can ascribe to marine spatial cumulative impact assessment results by addressing different sources of uncertainty (Stock and Micheli 2016; Gissi *et al.* 2017; Jones *et al.* 2018; Stockbridge *et al.* 2021: Chapter 2). These include the uncertainty associated with quantifying the vulnerability of an ecosystem to different stressors (Jones *et al.* 2018), and the uncertainty around how an ecosystem responds to changing cumulative impacts (Stockbridge *et al.* 2021: Chapter 2). However, few studies have evaluated the uncertainty associated with how ecosystems respond to stressors using empirical data.

Some fundamental assumptions associated with commonly used cumulative impact assessment methods are necessary due to the scarcity of empirical data on ecosystem responses (Johannes 1998). These assumptions include accurate impact scores, additive stressor impacts, and a linear response of ecosystems to impact (for a comprehensive list of assumptions, see Halpern and Fujita 2013). The validity of assumptions associated with accurate impact scores and stressor interactions have been investigated (e.g. see Stockbridge *et al.* 2020: Chapter 3) for evidence of non-additive interactions between stressors), however, few studies have used a data-driven approach to test the assumption of linearity.

We investigated how individual stressors relate to seagrass ecosystem condition in a region previously assessed for cumulative impacts (Jones *et al.* 2018). We combined field survey data on seagrass condition with spatially-matched data on eight different potential stressors present within Spencer Gulf, South Australia (Fig. 1). We aim to establish if and how the presence and intensity of each stressor individually relates to seagrass condition scores and the implications of these relationships for cumulative impact assessment approaches and marine ecosystem management.

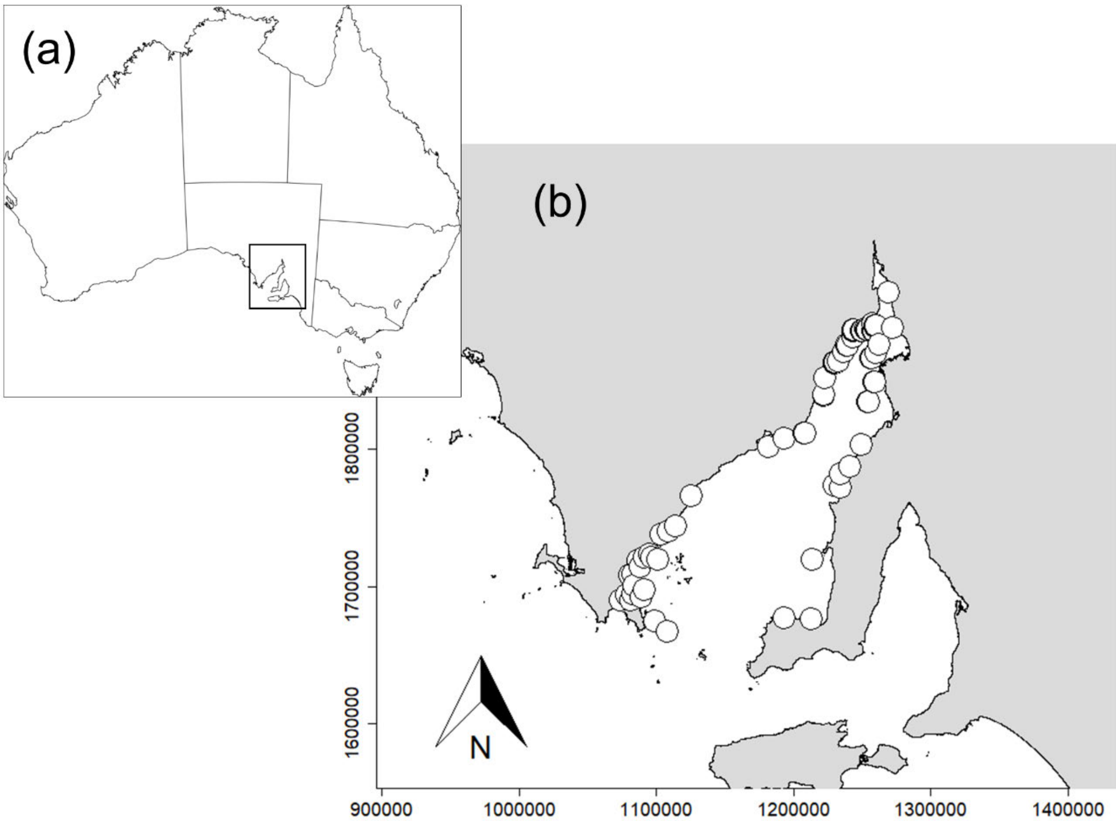

Figure 1. (a) Map of Australia with Spencer Gulf region indicated. (b) Seagrass survey sites around Spencer Gulf displayed as points (n = 115).

Methods

Spencer Gulf covers an area of approximately 30,000 km^2 and is an inverse estuary; characterised by evaporation exceeding precipitation, leading to conditions where salinity is often higher than seawater (Kämpf *et al.* 2010). There is a high diversity of temperate seagrasses present within Spencer Gulf, which are surveyed regularly for condition (Gaylard *et al.* 2013; Stockbridge *et al.* 2021). Spencer Gulf is subjected to a high number of human-induced stressors due to its environmental and economic importance. For example, Spencer Gulf is an active shipping region (Doubleday *et al.* 2017), a hotspot for ecotourism (Huveneers *et al.* 2013), and it contains multiple industrial hubs especially in the northern region (Gaylard 2014). Recent studies have assessed the cumulative impact of multiple stressors on Spencer Gulf (Doubleday *et al.* 2017; Jones *et al.* 2018; Stockbridge *et al.* 2021). For this study, stressors were selected based on the availability of spatial data on processes that are influenced by human activities and have the potential to impact seagrasses. Stressors included habitat disturbance due to aquaculture operations, coastal population density, nutrient pollution, turbidity, oxygen, salinity, temperature, and the number of stressors present within each grid cell. For a list of stressor data sources, see Table S1 in supplementary information.

The stressor intensity data used here were from spatially-resolved stressor data recently included in two spatial cumulative impact assessments of Spencer Gulf; one using additive stressor impacts (Jones *et al.* 2018), and one incorporating non-additive stressor impacts (Chapter 4 of this thesis). Stressor intensity represents the intensity level of a stressor within a 250 x 250 m grid cell with a 0 to 1 continuous score, where 0 indicates the stressor is absent and 1 represents highest intensity (Jones *et al.* 2018). Some stressor layers were combined to provide more robust estimates of intensity (Fig. S1; Table S1). Stressors were excluded if the spatial coverage of the stressor did not contain any seagrass survey sites.

Seagrasses were surveyed at 79 500 x 500 m sites using towed underwater video. Within each site, 10 transects with a minimum length of 50 m were surveyed. Boat speed was 0.5 – 1 knot whilst seagrasses were being surveyed. A custom-made housing was used to position a geo-referenced 450-line analogue video camera (Scielex/Kongsberg) 1 m above the seafloor, capturing an area of 1 m^2 per frame along the 50m transect. Video data were analysed using an Environmental Protection Authority, South Australia, in-house video analysis software package

(Gaylard *et al.* 2013). This software allowed us to record the GPS, as well as seagrass cover and species diversity for each video frame (representing a 1 m^2 area of Spencer Gulf). We used the mean seagrass cover and species diversity of all 1 m^2 frames within a transect to calculate three different condition indices: percent cover (Gaylard *et al.* 2012), habitat structure index (HSI; Irving *et al.* 2013), and seagrass quality index (SQI; Neto *et al.* 2013). Seagrass condition has been summarised using these indices in multiple studies across different regions, for example, percent cover in Foster *et al.* (2017), HSI in Irving *et al.* (2016), and SQI in Hernawan *et al.* (2021). All seagrass condition indices were calculated at grid cells where the appropriate seagrass metrics were measured (see Table S1 in Stockbridge *et al.* 2021: Chapter 2, for details on how each index was calculated). Briefly, the percent cover approach to seagrass condition requires a simple assessment of the area of each 1 m^2 video frame covered by seagrass, with no additional metrics measured. HSI and SQI incorporate additional parameters such as species diversity and habitat patchiness.

Transects with seagrass condition index scores were spatially linked to grid cells containing stressor intensity scores at a resolution of 250 x 250 m. There were a higher number of total grid cells where percent cover could be scored (n = 115) compared to HSI (n = 84) and SQI (n = 86); as the latter two indices incorporate additional metrics that could not always be scored from every video survey location. To generate index values that were representative of each 250 x 250 m grid cell, we used the mean condition score of all transects within the same grid cell. Potential seagrass stressors were excluded if their spatial extent did not overlap with surveyed seagrass condition sites.

We modelled the relationship between the spatially-matched individual stressor impact scores (n = 8) and seagrass condition using generalised additive models (GAMs) with a beta distribution in R (Wood 2011). Beta distributions are versatile enough to provide good descriptions of a range of data types and distributions (Ng *et al.* 2018). GAMs can be used to analyse non-normally distributed response data, which do not meet the assumptions of traditional linear models (i.e. they can allow for non-linear correlations between the response and predictor variables). These models do this by fitting smooth functions to describe the contribution of a predictor to the response, allowing the relationship to be “wiggly” rather than a straight line. GAMs will not apply a smoothing function if the relationship between the predictor and response is linear, instead a linear relationship will be fit. To test the effect of individual stressors on seagrass condition, interactive terms between stressors were excluded from all models. The GAM then tests the effect on seagrass condition of varying the intensity of one stressor with all other stressors held constant at their respective means. A separate model was built for each of the three seagrass condition indices. Percent cover and HSI scores (both usually expressed on a 0 – 100 scale) were rescaled to between 0 and 1 to be compatible with a beta distributed model structure. SQI is measured at a scale of 0 to 1, meaning no transformation was necessary. A candidate set of models was created for each seagrass condition index, testing multiple different combinations of stressor variables. The candidate model sets for each condition index were compared and ranked using two processes. We used Akaike’s Information Criterion (AIC) to rank models, and also compared all models using k-fold cross validation and calculating the mean absolute error between model predictions and observed values. The final model for each seagrass condition index was selected based on both the AIC rank and mean error scores.

Results

All candidate models of stressor impacts on seagrass condition were compared to a null model containing no predictor variables (i.e. an intercept only model; Table S2). The null model was the lowest ranked model in the candidate model sets for all seagrass condition indices. The differences in AIC between the top-ranked and lowest-ranked (null) model was 57.63 for percent cover, 86.26 for HSI, and 85.07 for SQI (Table S2). The mean prediction error values for the top-ranked models were 21.8 % for percent cover, 9 % for HSI, and 11.2 % for SQI (Fig. 2; Table S2).

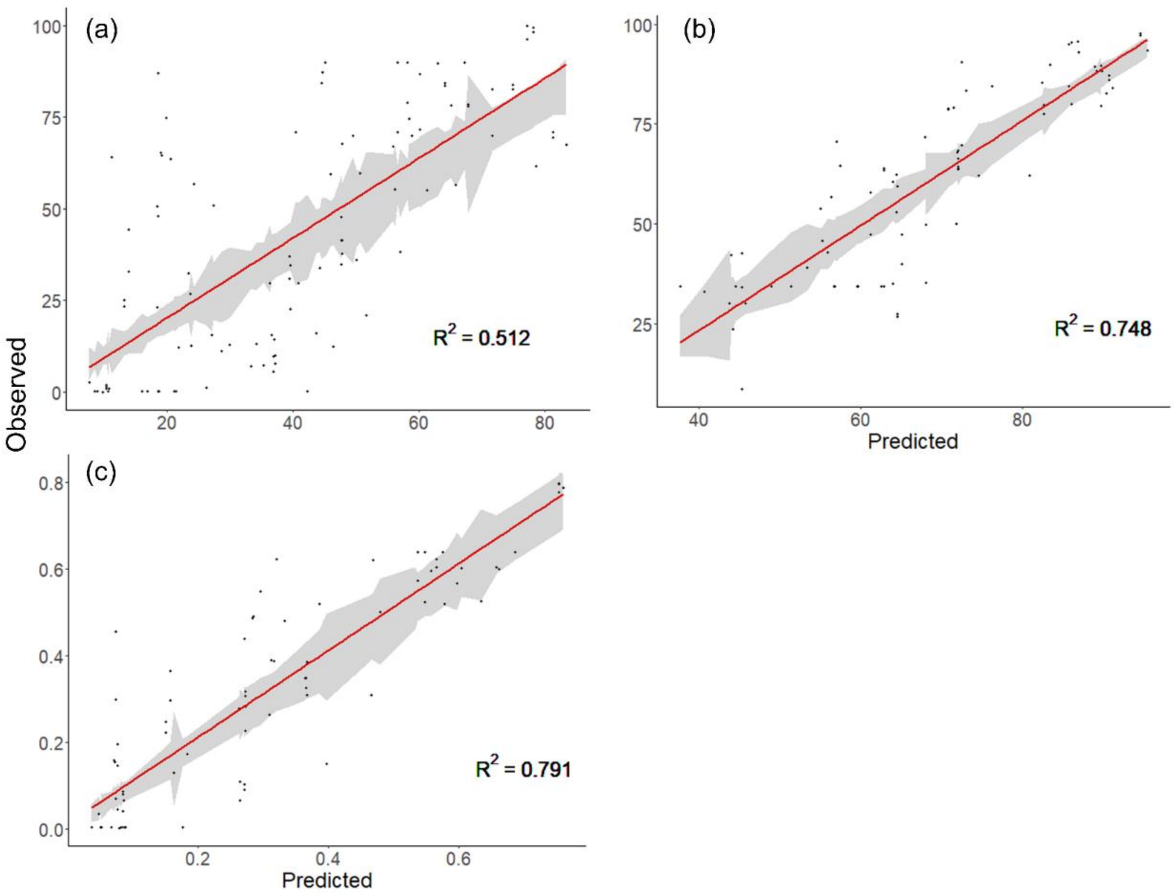

Figure 2. Model predicted (red line) vs observed values (with R^2) of seagrass condition (points) for (a) percent cover, (b) habitat structure index (HSI), and (c) seagrass quality index (SQI). Standard error of model predictions is shown by grey shading. Predictions were generated from the top-ranked GAM for each seagrass condition index. Points that fall on the line represent where model predictions = observed values. Points above and below the line indicate where seagrass condition is over-or-underestimated by the model, respectively.

The top-ranked model for percent cover based on lowest AIC score and mean prediction error contained seven predictors (aquaculture, number of stressors present, hypersalinity, nutrient pollution, oxygen, temperature, and turbidity). However only hypersalinity, oxygen, temperature and turbidity were significant ($p = <0.05$; Table 1; Fig. 3). The top-ranked models for HSI and SQI both contained eight predictors (aquaculture, number of stressors present, hypersalinity, nutrient pollution, oxygen, population density, temperature, and turbidity). Both these models found six of these predictors to be significant. These were hypersalinity, number of stressors present, nutrient pollution, oxygen, temperature, and turbidity (Table 1; Fig. 4 and 5).

Table 1. Results from GAM models of potential stressors as predictors of seagrass condition index scores. Stressor inclusion in the top-ranked model (based on AIC and prediction error) is indicated as present (✔) or absent (✖). Green cells indicate significant stressors ($p < 0.05$) and grey cells indicate non-significant stressors that were still included in the best models (see Table S2 for model comparison).

	In top model?		
Stressor	**%**	**HSI**	**SQI**
Oxygen	✔	✔	✔
Increased temperature	✔	✔	✔
Nutrient pollution	✔	✔	✔
Turbidity	✔	✔	✔
Hypersalinity	✔	✔	✔
Aquaculture disturbance *	✔	✔	✔
Coastal population density	✖	✔	✔
Stressors present	✔	✔	✔

* *Aquaculture disturbance = physical disturbance from aquaculture operations*

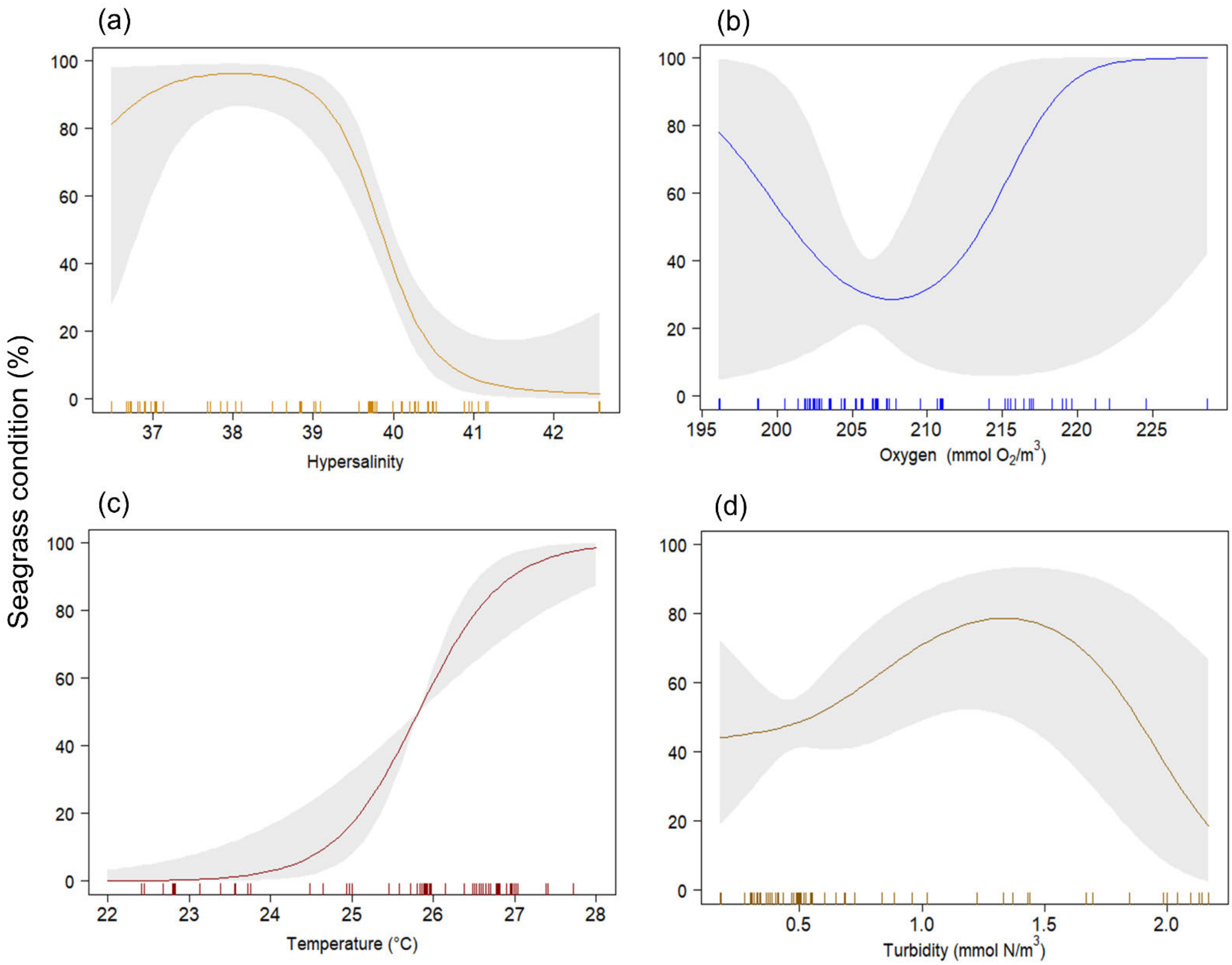

Figure 3. Plots of the modelled relationships between seagrass percent cover and stressors from the top ranked GAM. Only stressors that were significant ($p < 0.05$) are shown; (a) hypersalinity, (b) oxygen, (c) temperature, and (d) turbidity. Rugplot lines along the x-axis represent the data values of the stressor.

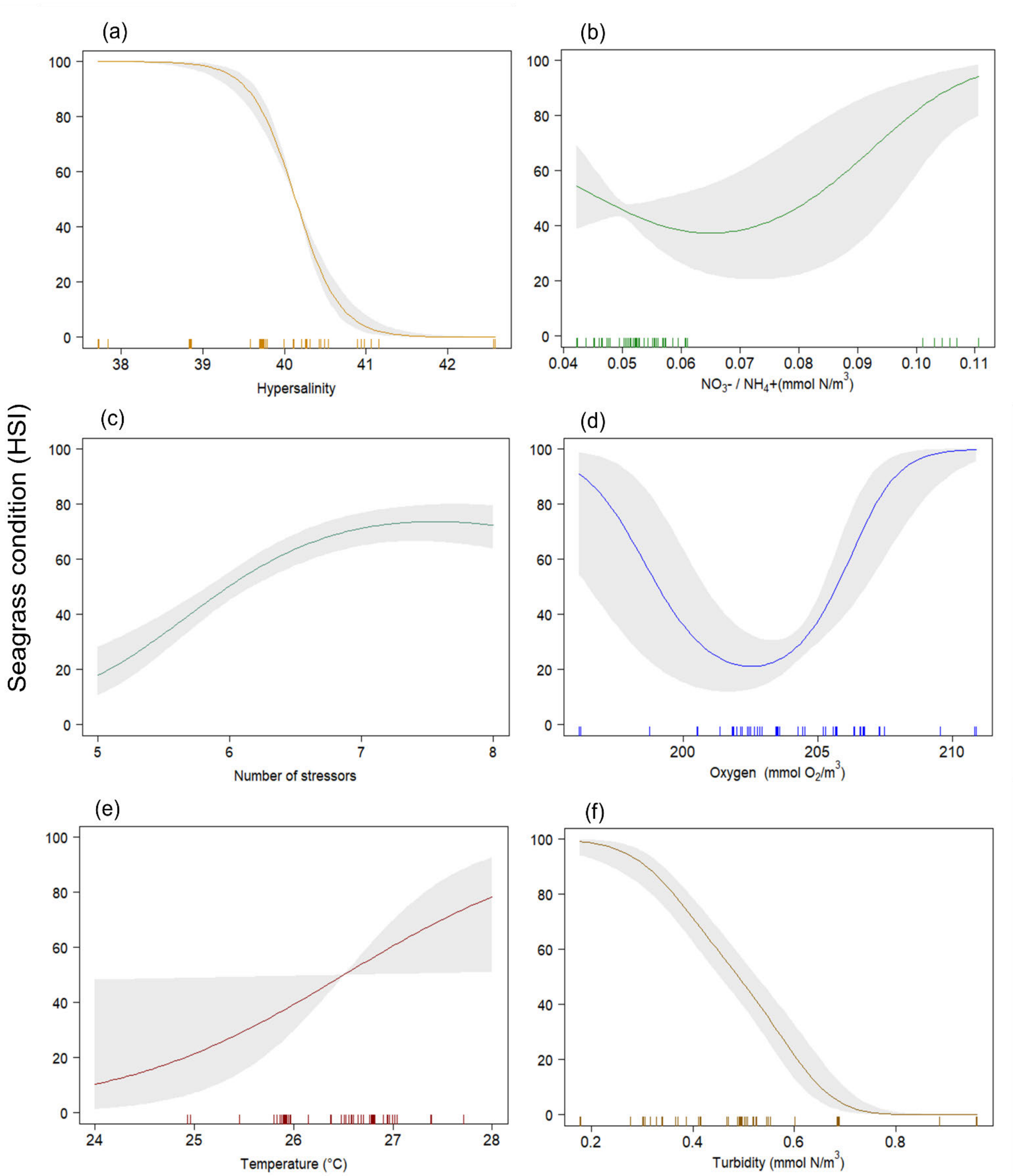

Figure 4. Plots of the modelled relationships between habitat structure index (HSI) and stressors from the top ranked GAM. Only stressors that were significant ($p < 0.05$) are shown; (a) hypersalinity, (b) nutrient pollution, (c) number of stressors, (d) oxygen, (e) temperature, and (f) turbidity. Rugplot lines along the x-axis represent the data values of the stressor.

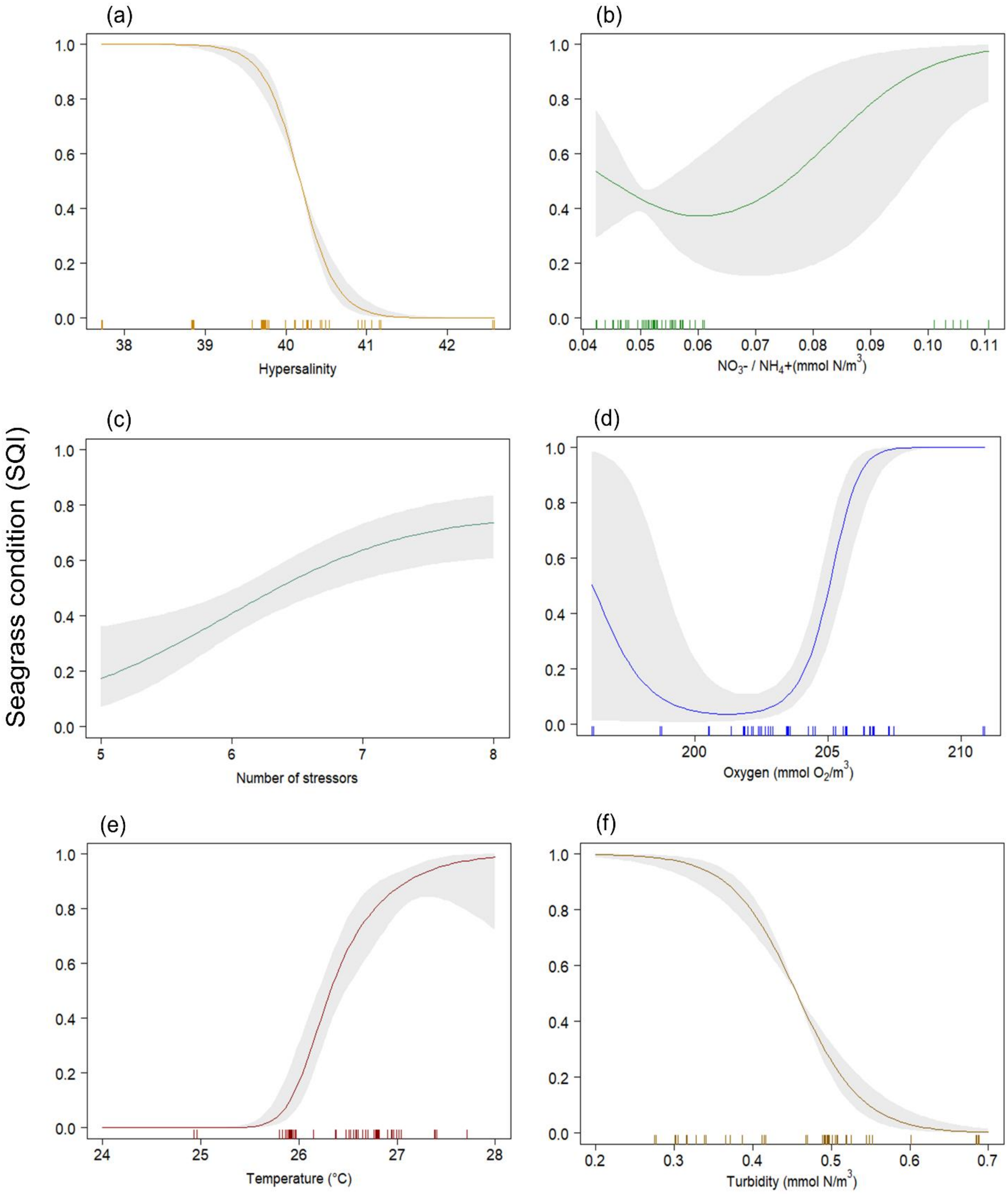

Figure 5. Plots of the modelled relationships between seagrass quality index (SQI) and stressors from the top ranked GAM. Only stressors that were significant ($p < 0.05$) are shown; (a) hypersalinity, (b) nutrient pollution, (c) number of stressors, (d) oxygen, (e) temperature, and (f) turbidity. Rugplot lines along the x-axis represent the data values of the stressor.

The number of stressors selected in the top models and the number significantly impacting seagrass condition differed depending on the index used to measure seagrass condition. However, there was some agreement between the models about which stressors were, or were not, important when predicting seagrass condition (Table 1). Out of the 24 potential seagrass stressor and condition relationships tested by our three models (eight stressors in each of three models), 16 had statistically significant correlations in the GAM models across all three condition indices ($p < 0.05$; Table 1). Significant impacts from coastal population density and physical disturbance from aquaculture operations were not detected using any seagrass condition index, however these variables were retained in some of the top models, based on the model ranking and evaluation procedures (e.g. population density for HSI and SQI, and disturbance from aquaculture in all three models; Table 1 and Table S2).

All of the stressors that significantly impacted seagrass condition showed non-linear relationships (Fig. 3, 4 and 5). There was a decline in seagrass condition when salinity levels reached ~40 ppt according to all indices (Figs. 3a, 4a & 5a). Oxygen had a u-shaped relationship with seagrass that was consistent across all indices (Figs. 3b, 4d & 5d), with lowest condition scores at moderate oxygen levels. Temperature positively impacted seagrass, however, there are wider 95% confidence intervals around the smooth terms from the percent cover and HSI models at high and low temperature values (Figs. 2c & 3e). Nutrient pollution was not significantly correlated to seagrass percent cover and was negatively related to HSI and SQI. This relationship turned positive when nutrient levels reached 0.06 mmol N/m^3, however there are wide confidence intervals around this relationship at values greater than 0.06 (Fig. 4b & 5b).

Discussion

We investigated the relationship between eight potential stressors and seagrass condition, measured using three different condition indices. We found variability between the stressors that significantly impacted seagrass condition when assessed using the different condition indices. However, the best models for all seagrass condition indices included some common predictors (hypersalinity, oxygen and temperature; Table 1). Importantly, the relationships between stressors and seagrass condition were all non-linear (Fig. 3, 4, and 5).

We used multiple condition metrics to test the generalisability of our findings, assuming that agreement across models (i.e. different condition metrics) would indicate more reliable results. The best model for seagrass condition based on the percent cover index contained four significant predictor variables (hypersalinity, oxygen, temperature and turbidity). All three of these predictors were also selected by the best models for HSI and SQI, although they also included further environmental predictors (Table 1). The model of percent cover had relatively large prediction error (22 %) compared to the models for HSI and SQI (9 % and 11 % respectively). The differences between the predictor variables selected by each model, and their predictive performance may be due to differences in the way that the condition indices are calculated, and their adequacy at capturing seagrass condition.

Percent cover is a simple measure of the area covered by seagrass of any species in a given video frame (Gaylard *et al.* 2013). This simple, area-based metric is easy and quick to measure, but has some drawbacks as it does not account for seagrass species diversity or structural parameters. SQI describes seagrass condition using percent cover and an additional measure of species diversity (Neto *et al.* 2013). It may also include shoot density if this is measurable from the data, but was not included in this case (for details, see Table S1 in Stockbridge *et al.* 2021). HSI included the parameters in SQI, as well as additional variables related to survey area and habitat structure (Irving *et al.* 2013). It is reasonable to assume that the additional metrics incorporated into both SQI and HSI may provide more robust measures of seagrass condition at the cost of simplicity. This was supported by our model evaluation scores for these two indices, with far lower prediction error than the model based on percent cover. Therefore, from this point forward, we have focused the discussion on the models of seagrass condition measured by HSI and SQI.

The models based on HSI and SQI both found six common environmental variables to have a significant effect on seagrass condition. These were hypersalinity, number of stressors present, nutrient pollution, oxygen level, temperature and turbidity. The best models for these indices also included two further non-significant stressor variables: physical disturbance from aquaculture and coastal population density (Table 1). Although these variables had non-significant relationships with seagrass condition, their inclusion in the best models for both HSI and SQI indicates that they helped to improve model predictive ability.

Hypersalinity and temperature were significant stressors in the top-ranked models. High salinity levels (beyond ~ 40 ppt) had a strongly negative, but non-linear effect on seagrass condition (Fig. 3a, 4a and 5a). This finding is supported by previous studies on one of the dominant seagrass species within Spencer Gulf (*Posidonia oceanica*), which found that salinity levels of 39 ppt reduced growth and shoot density (Sanchez-Lizaso *et al.* 2008; Ruíz *et al.* 2009). Our models found that temperature had a positive effect on seagrass condition (Fig. 4e and 5e), at least up to the maximum temperature recorded in our study, which was 28°C. Previous studies have shown that light efficiency and photosynthetic activity in seagrass (*Zostera marina* in Denmark) improved when temperatures were elevated up to 27°C (Hansen *et al.* 2022). Positive relationships between stressors and seagrass condition can also occur in situations where stressors interact antagonistically, meaning that the combined impact of two stressors is less than their additive effect. Antagonistic stressor interactions can mitigate the impact of multiple stressors, and can even produce surprising ecological benefits (Côté *et al.* 2016). Our models found that the direction of correlation between seagrass condition and oxygen changed depending on oxygen concentration, resulting in a u-shaped curve where lower and higher values were associated with better seagrass condition than moderate values. This relationship is difficult to explain and does not corroborate past research (Buapet *et al.* 2013), however, it was consistent across models, and has relatively narrow confidence intervals for HSI, and for SQI at the majority of oxygen levels (Fig. 4d and 5d). Our models found that HSI and SQI had a negative, non-linear relationship with turbidity, where condition declines steeply after a moderate value of turbidity is reached (0.3 mmol N/m^3; Fig. 4f & 5f). This non-linear relationship between turbidity and seagrass condition scores indicates a tolerance for low levels of turbidity-related stress until a certain level is reached. Turbidity reduces photosynthetic activity of seagrass by inhibiting the amount of light available (Amri *et al.* 2021; Tang and Hadibarata 2022). Our results support the presence of a threshold or tipping point effect of turbidity on seagrass condition.

The concept of ecological thresholds is well established across all ecosystems (Holling 1973; May 1977). Small increases in an environmental stressor pushes an ecosystem beyond a threshold and elicits a dramatic change in ecosystem state. An example of a state shift occurred in Florida Bay, where an oligotrophic seagrass-dominated ecosystem changed to a turbid system dominated by phytoplankton (Groffman *et al.* 2006). There are a number of examples that demonstrate the vulnerability of seagrasses to being pushed beyond thresholds in response to increased stress (e.g. McGlathery *et al.* 2013; Mayol *et al.* 2022), with temperate seagrasses known to be vulnerable to state shifts under eutrophic conditions (Connell *et al.* 2017).

The HSI and SQI models found a negative relationship between nitrogenous nutrients and seagrass condition, which turned positive after a moderate nutrient level is reached (0.06 mmol N/m^3; Fig. 4b & 5b). A key impact of increased nutrient levels on seagrass is the growth of epiphytes on leaves. This overgrowth can decrease the amount of light reaching the leaves and reduce condition (Orth et al. 2006), meaning temperate seagrasses are vulnerable to state shifts under eutrophic conditions (Connell *et al.* 2017). Therefore, we would expect to see a negative relationship between nutrient pollution and seagrass condition, with a sharp decline in condition once a tipping point was reached. However, none of the indices we used to measure seagrass condition include epiphyte cover as a parameter, which may lead to an inaccurate representation of the actual relationship between nutrient concentration and seagrass condition. The index used by the Environment Protection Authority South Australia (Gaylard *et al.* 2012) excludes epiphytes as they are considered a warning sign of seagrass stress, rather than an indication of current condition.

The difficulty in finding clear biological explanations for some of the apparent relationships between seagrass condition and environmental stressors may, in part, be due to interactions between stressors (Stockbridge *et al.* 2020: Chapter 3). If the cumulative impact of all stressors equalled the sum of the individual stressors' impacts, we would expect a linear relationship between seagrass condition index scores and the count of stressors present. However, count of stressors was non-linearly related to HSI and SQI (Fig. 4c and 5c). This supports the idea that interactions between stressors are present (Crain *et al.* 2008; Stockbridge *et al.* 2020: Chapter 3) and may be influencing the modelled relationships between individual stressors and seagrass condition in unpredictable ways. For example, a study on temperate seagrasses identified a synergistic interaction when elevated temperature increased metabolic activity, which could not be met when light reduction caused by turbidity inhibited photosynthesis (Fraser *et al.* 2014). Another study found that a low amount of epiphyte growth on seagrasses can mitigate the effect of nutrient pollution by preventing ammonium from reaching levels that are toxic to seagrasses (Moreno-Marín *et al.* 2016). We did not include an investigation of the effect of stressor interactions in our models due to sample size constraints.

Despite these caveats, our analysis detected clear non-linearities in the relationships between stressors and seagrass condition. Examining the relationships between habitat condition and stressor intensity allows us to examine the assumption of linearity that is common to many spatial cumulative impact assessment approaches (Halpern and Fujita 2013). Previous studies support our findings of non-linear relationships between stressors and ecosystem condition (deYoung *et al.* 2008), although these can be very difficult to detect due to spatio-temporal variability (Diaz and Rosenberg 2008). Incorporating non-linear relationships into cumulative impact assessments will be critical to avoid pushing ecosystems beyond ecological thresholds and to retain ecological function and associated ecosystem services (Connell *et al.* 2017).

Marine ecosystems are inherently complex, and improved methods of modelling human impacts can help achieve conservation and management goals (Halpern *et al.* 2006). By better understanding how ecosystem condition responds to stressors, and identifying thresholds and potential tipping points, we can improve decision making for the sustainable use of marine environments (Halpern *et al.* 2006). Quantifying stressor impact remains one of the greatest challenges to effective ecosystem-based management (Halpern *et al.* 2007; Pressey *et al.* 2007; Halpern *et al.* 2008). Empirical data are rarely available for ground-truthing impact assessments (Andersen *et al.* 2015; Stockbridge *et al.* 2021). Our results improve understanding around the dominance of non-linear relationships between seagrass condition and stressor intensity. We propose that not accounting for these non-linear relationships in cumulative impact assessments introduces further uncertainty, and increases the risk associated with management decisions based on assessment outputs. To enable further assessment, or testing of the linearity assumption, we advocate for the collection and accessibility of experimental data on ecosystem responses to stressors, regular surveys to collect empirical data to validate assessment outputs, and the incorporation of non-linear relationships into cumulative impact assessment methods.

Acknowledgements

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collaboration between a broad range of industry investors, the University of Adelaide, South Australian Research and Development Institute (SARDI) – a division of Primary Industries and Regions SA and Flinders University. The program aims to reduce costs, aid development and answer environmental challenges for one of South Australia's leading economic development zones.

Supplementary information

Section S1: Methods used to calculate our three seagrass condition indices

All three seagrass condition indices were calculated using video transects to record seagrass percent cover and species diversity. Seagrass quality index (SQI) sums the weighted values of percent cover and species diversity at the survey site relative to the same metrics at a reference site. Habitat structure index (HSI) uses percent cover and species diversity to calculate and combine five different metrics into one condition index. Some metrics require measurements taken at the quadrat level. We define a quadrat as each 1 m^2 area along a 50 m transect. HSI is calculated using the combination of these metrics relative to a hypothetical 'perfect' site (i.e. where all values are at their maximum):

$$\sqrt{A^2 + C^2 + P^2 + K^2 + S^2} * Scaler$$

Where:

- *Area* (A) – the sum of the proportion of each 1 m^2 quadrat within our 50 m transects covered by seagrass.
- *Continuity/patchiness* (C) – the number of quadrats where no seagrass cover is present.
- *Proximity* (P) – distance(s) between patches within a transect (i.e. distance between a quadrat with no seagrass to the nearest quadrat with seagrass present).
- *Percent cover* (K) – average percent cover of seagrass across all quadrats within a transect.

- *Species diversity (S)* – average number of species across all quadrats within a transect.

The $'scaler'$ ensures the HSI lies between 0 and 100 and is calculated using a transect where A, C, P, K and S are set to the maximum possible value. For the full method of calculating the HSI, see Irving *et al.* (2013).

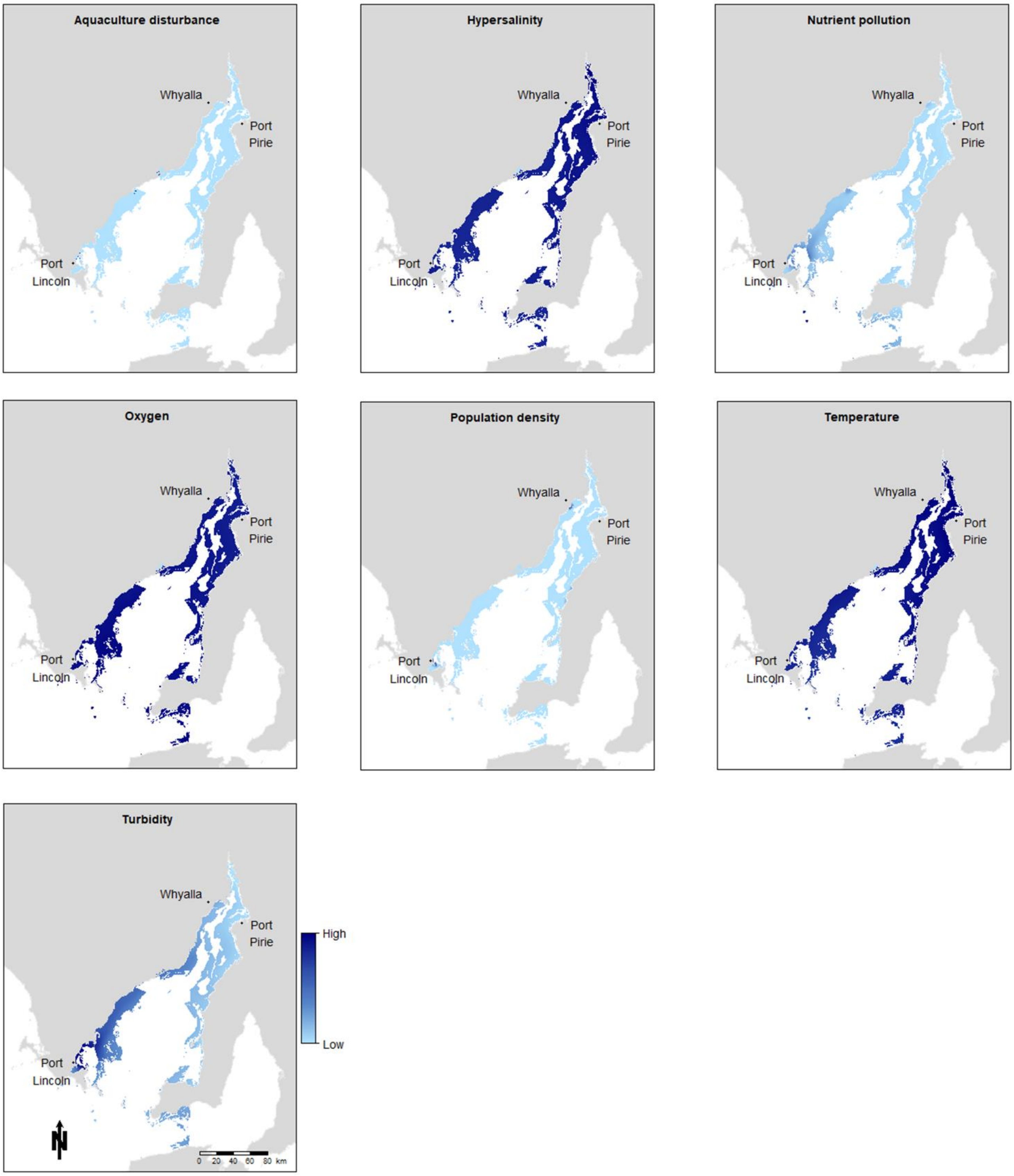

Fig. S1. Spatial intensity of each stressor modelled against seagrass condition.

Table S1. Table of stressors tested against seagrass condition of Spencer Gulf, South Australia. The minimum and maximum values of each stressor are based on the pooled range of a stressor across all three condition indices. Data source is listed, as well as units of stressors and relevant layers were determined from the available spatial data. Stressor data marked with an * were obtained from Jones *et al.* (2018) and are available to download at https://figshare.com/s/8953f66d9a91f069ba01. PIRSA = Department of Primary Industry and Regions South Australia; SARDI = South Australian Research and Development Institute.

Stressor	Units	Min	Max	Data	Details
AC: disturbance *	Presence/ absence	0	1	Spatial data provided by PIRSA (Wiltshire *et al.* 2010)	Presence (1) or absence (0) of an aquaculture operation in a grid cell. Physical disturbance to seagrass habitat by the presence of absence of aquaculture operations. For example, the presence of sea cages, intertidal structures and fishing lines
Hypersalinity	ppt	36.48	42.58	Spatial data provided by SARDI (Tanner *et al.* 2020)	Maximum salinity modelled over 4 years
No. of stressors	Count	0	8	Various	Count of grid cells with a value > 0 across all stressors
Nutrient pollution	mmol N/m³	0.04	0.24	Spatial data provided by SARDI (Tanner *et al.* 2020)	Time- averaged concentration of nitrate (NO_3-) and ammonium (NH_4+)
Oxygen	mmol O_2/m³	196.15	228.67	Spatial data provided by SARDI (Tanner *et al.* 2020)	Minimum dissolved oxygen concentration modelled over 4 years
Population density	Count	0	3138.87	Spatial population data from Halpern *et al.* (2008)	Population density used as a proxy for coastal activities. Based on modelled data of the number of people living within 10 km of the coast. Data were updated from the 2013 analysis
Temperature	°C	20.12	27.71	Spatial data provided by SARDI (Tanner *et al.* 2020)	Maximum temperature modelled over 4 years
Turbidity	mmol N/m³	0.18	2.17	Spatial data provided by SARDI (Tanner *et al.* 2020)	Time-averaged concentration of: - Large fraction carbon detritus - Small fraction carbon detritus - Zooplankton - Phytoplankton

Table S2. Model comparison table with different metrics used to select the top-ranked model (shown in blue cells and in bold). Each model evaluates the relationship between a seagrass condition index (scaled to between 0 and 1) and a different combination of stressors using a beta distributed generalised additive model. Results from the top-ranked model are presented in the main text. RMSE = Root mean squared error; MAE = Mean absolute error. RMSE and MAE are scaled to between 0 to 1 to be comparable to the scale of our response.

Model name	Condition index	AC disturbance	Hypersalinity	Increased temperature	Oxygen	Pollution: nutrients	Population density	Turbidity	No. of stressors	AIC	Deviance explained (%)	R^2	RMSE	MAE
M1. NULL	Cover									-41.84	1.31	NA	0.32	0.29
M1.1	Cover								✓	-40.98	2.6	0.11	0.32	0.29
M1.2	Cover	✓	✓	✓	✓	✓	✓	✓	✓	-97.37	62.8	0.45	0.26	0.22
M1.3	Cover	✓	✓	✓		✓	✓	✓	✓	-94.83	61.1	0.41	0.27	0.22
M1.4	Cover	✓	✓	✓	✓		✓	✓	✓	-94.4	60.6	0.42	0.26	0.23
M1.5	**Cover**	**✓**	**✓**	**✓**	**✓**	**✓**		**✓**	**✓**	**-99.47**	**62.9**	**0.49**	**0.25**	**0.21**
M2. NULL	HSI									-52.94	0.1	NA	0.18	0.16
M2.1	HSI								✓	-51.68	1.11	0.13	0.18	0.16
M2.2	**HSI**	**✓**	**✓**	**✓**	**✓**	**✓**	**✓**	**✓**	**✓**	**-139.2**	**78.6**	**0.63**	**0.12**	**0.09**
M2.3	HSI		✓	✓	✓	✓	✓	✓	✓	-137.92	77.6	0.68	0.11	0.09
M2.4	HSI	✓	✓			✓		✓	✓	-107.02	65.1	0.61	0.12	0.09
M2.5	HSI	✓	✓			✓	✓	✓	✓	-105.16	65.1	0.56	0.13	0.09
M3. NULL	SQI									-46.22	1.49	NA	0.24	0.21
M3.1	SQI								✓	-44.64	2.08	0.12	0.25	0.22
M3.2	**SQI**	**✓**	**✓**	**✓**	**✓**	**✓**	**✓**	**✓**	**✓**	**-131.29**	**82**	**0.66**	**0.15**	**0.11**
M3.3	SQI		✓	✓	✓	✓	✓	✓	✓	-127.07	79.4	0.70	0.14	0.11
M3.4	SQI		✓	✓	✓	✓		✓	✓	-128.57	79.4	0.69	0.14	0.11

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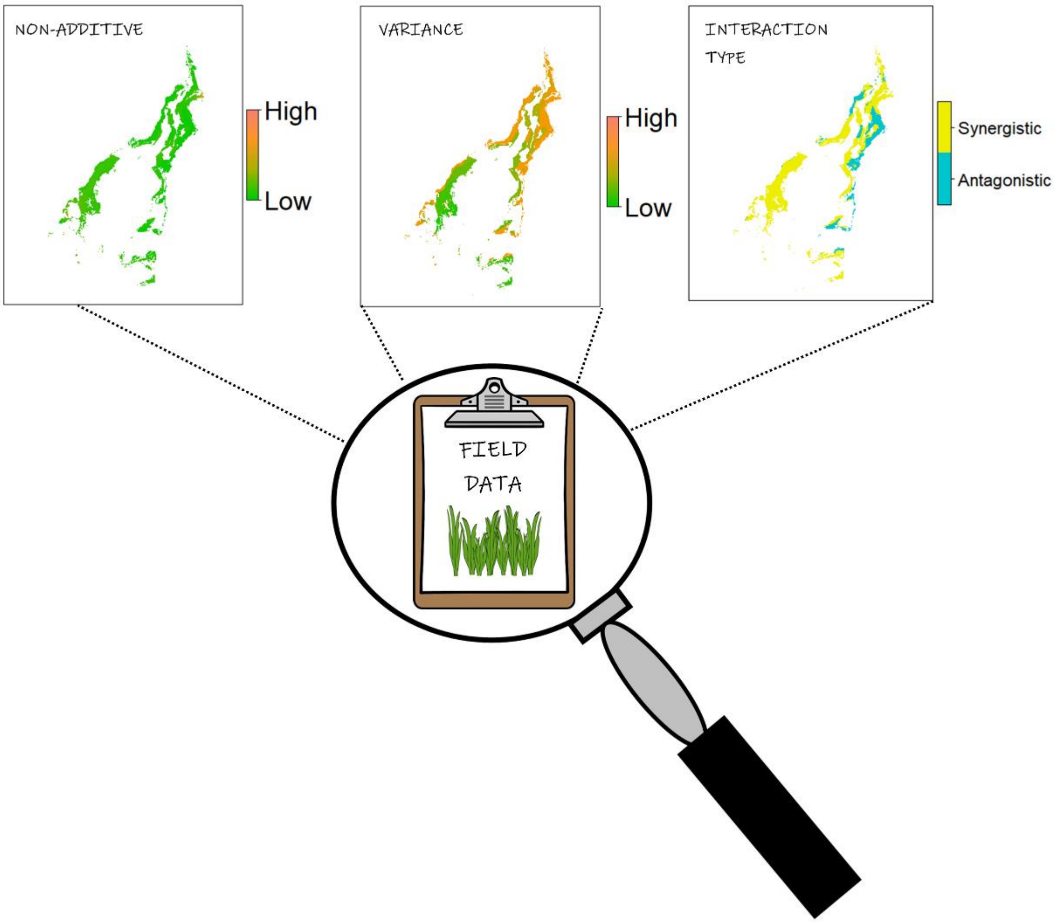
Chapter 6

General Discussion



6. General discussion

6.1 Aims, significance and knowledge gaps

Marine spatial cumulative impact assessments are a useful tool for effective ecosystem-based management and marine spatial planning (Halpern *et al.* 2008a; McLeod and Leslie 2009). However, the complexity of the marine environment combined with common data limitations means that several assumptions are required to ensure that assessment methods are generalisable between regions and ecosystems (Halpern and Fujita 2013). Some of these assumptions contradict well-established ecological concepts such as non-additive ecosystem responses to the presence of multiple interacting stressors, and ecosystem thresholds (Groffman *et al.* 2006; Darling and Côté 2008). As a consequence of the assumptions required, there is uncertainty associated with marine spatial cumulative impact assessment outputs (Stock and Micheli 2016). Empirical data on ecosystem responses to stressors are required to address uncertainty in assessment outputs and minimise the implications of assumptions (Halpern *et al.* 2007; Claudet and Fraschetti 2010). However, these data are often scarce (Johannes 1998), making it difficult to predict the effect of stressor interactions or ground-truth cumulative impact assessments to test their reliability and understand the uncertainty associated with them (Halpern *et al.* 2008b; Halpern and Fujita 2013; Andersen *et al.* 2015). For this thesis, I aimed to test the assumptions of cumulative impact assessment methods that stem from limited data on how ecosystems respond to multiple stressors (Fig. 6.1).

Since the development of standardised spatial cumulative impact assessment methods for marine environments (Halpern *et al.* 2008b), there has been an exponential increase in these semi-quantitative assessments (Hodgson *et al.* 2019). Using spatial methods to quantify and map the distribution of human impact provides several benefits over the categorical methods used in past assessments (e.g. Cocklin *et al.* 1992; Clark *et al.* 2002; Lawler *et al.* 2002). For example, quantitative spatial methods use higher resolution data to provide a more informative assessment of how impacts vary between ecosystems and regions (Halpern *et al.* 2008b). Despite the significant progress in cumulative impacts research and the increase in assessments across different regions (e.g. Selkoe *et al.* 2009; Foden *et al.* 2011; Korpinen *et al.* 2012) and ecosystems (e.g. Allan *et al.* 2013; Lange *et al.* 2018), the methods still require further development and validation (Halpern *et al.* 2008b).

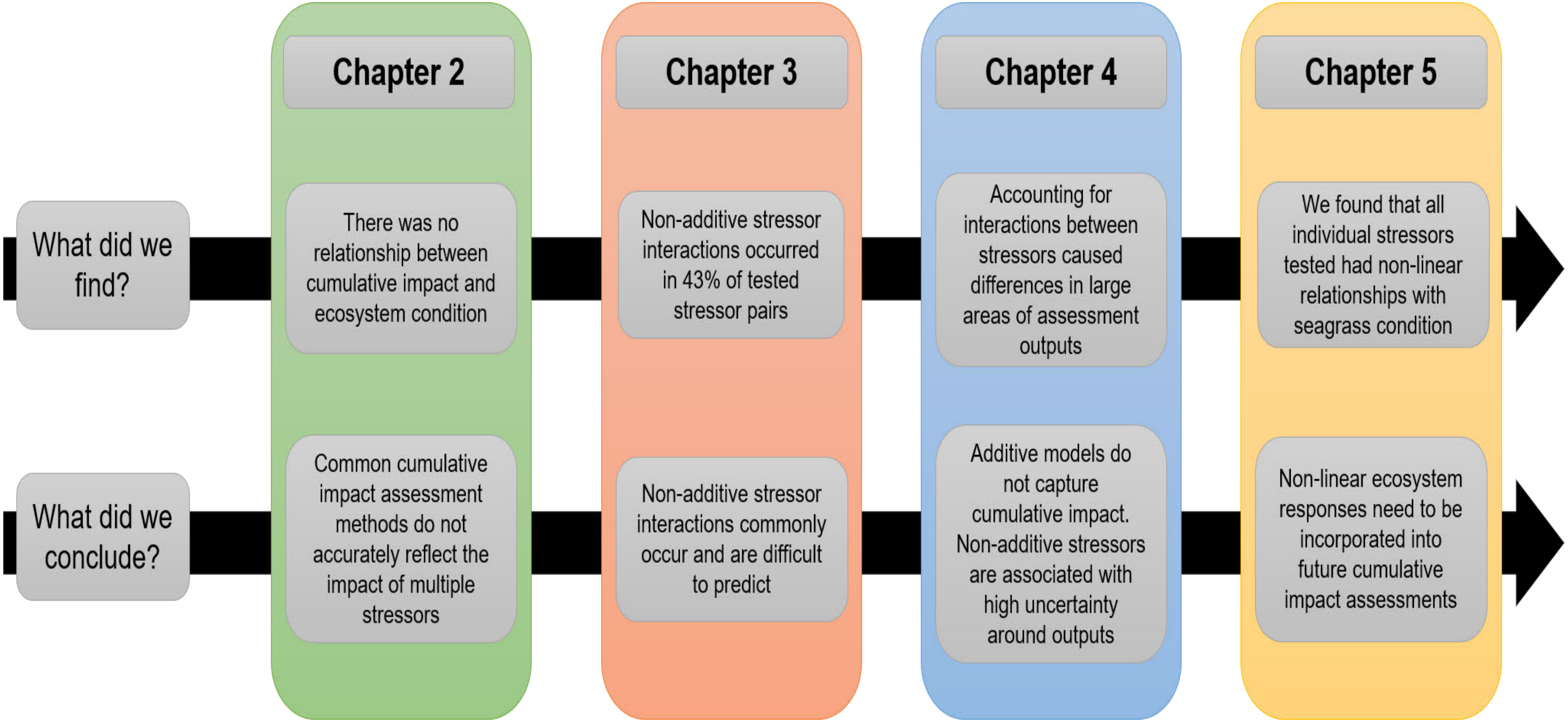


Figure 6.1. Schematic representing the key findings of each chapter

6.2 Evaluation of current cumulative impact assessments

For the first data chapter of my thesis (Chapter 2), I had a rare opportunity to use empirical data to ground-truth a recent cumulative impact assessment of Spencer Gulf and found that there was no relationship between cumulative impact score and seagrass condition. This enabled me to address a significant gap in cumulative impacts research, as few studies have tested cumulative impact assessment outputs against field-collected data, and those that have, found mixed results (Andersen *et al.* 2015; Clark *et al.* 2016). My results indicate that current cumulative impacts assessment methods do not accurately reflect seagrass condition (Fig. 6.1), and this result may be applicable to a broader range of ecosystems. More studies similar to mine would provide further insight into the performance of cumulative impact assessment methods when applied across a range of marine environments. Uncertainty and inaccuracy are introduced by the assumption that ecosystems respond linearly to cumulative impacts as this approach cannot incorporate threshold effects or tipping points. The purpose of conducting cumulative impact assessments is to capture the direct effect of human impacts on ecosystem condition, and then communicate this relationship to marine resource managers to inform strategies and achieve sustainability goals (Cormier and Elliott 2017; Hodgson *et al.* 2019). However, if assessments are not accurately capturing ecosystem condition, then management decisions will be based on misleading results. I concluded that the commonly used marine spatial cumulative impact assessment method does not accurately reflect the impact of multiple stressors (Fig. 6.1) and that more robust and well-validated methods are required.

6.3 Incorporating non-additive stressor interactions

The lack of relationship between cumulative impact and ecosystem condition (found in Chapter 2) is likely a culmination of the uncertainty introduced by the assumptions of the commonly used cumulative impact assessment methods. These assumptions have been well-documented and discussed in the literature (Halpern and Fujita 2013). My second data chapter (Chapter 3) investigated the effect of the additivity assumption. This assumption suggests that cumulative impact can be modelled as the sum of the individual stressor impacts. I investigated this by looking at how pairs of stressors combine to impact seagrass using a meta-analysis based on published studies. My study updated the meta-analysis undertaken by Darling and Côté (2008) and supports their findings that around one-third of tested stressor pairs interacted synergistically. Synergistic stressor interactions result in ecological surprises that amplify ecosystem impacts (Chapin Iii *et al.* 2000; Sala *et al.* 2000). The outcomes of this chapter and previous synthesised findings on stressor interactions (e.g. Crain *et al.* 2008; Darling and Côté 2008) help identify generalities to infer stressor interactions in future assessments (Côté *et al.* 2016).

Non-additive interactions are rarely accounted for in cumulative impact assessments. However, the presence of these interactions is not disputed, and their exclusion is often flagged as a caveat (e.g. Halpern *et al.* 2008b; Selkoe *et al.* 2009; Ban *et al.* 2010). Experimental data on ecosystem responses to multiple stressors are scarce (Johannes 1998), and studies that have included non-additive interactions have been restricted to a maximum of three stressors (e.g. Brown *et al.* 2013; Brown *et al.* 2014). The meta-analysis in Chapter 3 produced effect sizes for individual stressors and stressor pairs that were based on experimental data. I then used these data in Chapter 4 to develop a novel, data-driven method that incorporates non-additive stressor interactions into marine cumulative impact assessment by extending one of the most commonly-used additive modelling approaches (Halpern *et al.* 2008b) Using this new approach, I compared the cumulative impact estimates from a non-additive (interaction) model against those from the commonly-used additive model. The considerable differences in these maps have significant implications for cumulative impacts research and are evidence that stressor interactions are likely causing us to under-or-over estimate human impact.

Inaccurate cumulative impact estimates could lead to detrimental effects on marine ecosystems by misleading ecosystem-based management decisions. The interaction model outputs from Chapter 4 highlighted areas where synergistic stressors were producing a greater-than-additive impact. Using the additive model to inform management in these areas would be misleading, may cause poor management of key stressors, and lead to an overestimate of ecosystem resilience (Folke *et al.* 2004). Conversely, we showed areas where antagonistic stressor interactions were causing a cumulative impact that was lower than we would expect from the additive model. Management actions targeting these areas based on the additive approach may lead to the removal of stressors that are likely to make little difference to ecosystem condition, and could even have a negative effect on ecosystems by removing a mitigating stressor (Brown *et al.* 2013).

The outcomes of Chapter 4 quantified the uncertainty that is introduced to cumulative impact assessments as a result of including non-additive stressor interactions. Our study is one of the first to use empirical data to quantify the risk around management decisions that are based on additive cumulative impact assessment results. Not only should this act as a caution when interpreting additive outputs, but it also emphasises the importance of calculating and presenting uncertainty analyses when conducting these assessments. Uncertainty maps help inform the reliability of cumulative impact assessments, and outline the risk associated with management decisions that are based on the outputs (Stock and Micheli 2016; Gissi *et al.* 2017; Jansen *et al.* 2022).

6.4 Non-linear ecosystem responses to stressors

Chapter 5 of my thesis investigated the assumption, common to many cumulative impact assessment methods, that ecosystem condition has a negative linear relationship with stressor intensity. On the contrary, I found that none of the eight stressors tested were linearly related to seagrass condition (Fig. 6.1). Many previous studies on multiple stressors have not included a sufficient number of intensity levels to detect non-linear relationships (Griffen *et al.* 2016). By using field-collected seagrass data, this chapter contributes to the accumulation of empirical data that can be used to support more robust estimates of ecosystem responses to stressors (Boyd *et al.* 2018), and infers relationships between ecosystem responses and stressor intensity levels.

The results from this chapter have important implications for cumulative impact assessments because of the pervasive assumption of linear relationships between stressors and ecosystem condition. In addition, there is evidence that stressor intensity levels can affect interactions between multiple stressors (i.e., as stressor intensity increases, synergistic interactions are more likely; Crain *et al.* 2008). It is important that the linear impact assumption in cumulative impact assessment methods is addressed, because stressors that elicit non-linear responses from ecosystems have the potential to cause ecological surprises that are not predicted by assuming linearity (Griffen *et al.* 2016; Carrier-Belleau *et al.* 2021). If an ecosystem condition moves beyond a threshold, or tipping point, it could no longer be able to provide key ecosystem functions and services (Luisetti *et al.* 2010). Therefore, being able to predict the intensity levels at which a stressor pushes ecosystem condition beyond its tipping point would be a valuable tool for preserving ecosystem services. Additionally, synthesis of data, such as those collected for this chapter, will help to identify where ecosystem responses to stressors are most likely to be non-linear, which could infer relationships in future assessments.

6.5 Future directions

Having established that non-linear relationships between stressors and ecosystem condition are common, determining the effect of the assumption of linear relationships on cumulative impact assessment outputs is a natural next step. I propose an extension of the non-additive model, developed in Chapter 4, to include non-linear relationships between ecosystem condition and stressor impacts. This could provide a novel way of incorporating non-linear responses into cumulative impact assessment methods, whilst also accounting for non-additive stressor interactions. However, this approach would require a large amount of data specific to the region where these data are collected, which may reduce the generalisability of the results. Additionally, future cumulative impact assessments should continue to address sources of uncertainty to produce outputs that clearly state the confidence level that can be ascribed to the results (e.g. Jones *et al.* 2018). This can be achieved by following a risk-based approach. Risk-based approaches predict when an increase in stressor intensity levels will cause the risk of significant cumulative impact to exceed an accepted level (Stelzenmüller *et al.* 2018).

Whether by addressing some of the underlying assumptions, or better communicating uncertainty in outputs, or both, developing standardised frameworks to address and communicate different sources of error and uncertainty (such as method assumptions) will produce more reliable cumulative impact assessments. Calculating the proportion of variance explained by non-linear stressors relative to the total variance in cumulative impact scores (see Chapter 4) can establish the uncertainty introduced by the linearity assumption. This, along with the uncertainty associated with non-additive stressor interactions presented in this thesis, can contribute to future, informative risk-based assessments. Furthermore, future studies that investigate cumulative impact assessment method assumptions using field-collected data should aim to identify generalities in ecosystem responses to stressor combinations that can infer impact in future assessments.

Process-based models that include different stressor intensity levels are considered another approach to predict the impact of multiple stressors under future environmental conditions (Cuddington *et al.* 2013; Griffen *et al.* 2016). This approach requires investigation of stressor impact on ecosystems across a stressor intensity range (e.g., Chapter 5). Process-based models could be used to estimate how ecosystems may respond to the increased effects of climate change (Frölicher *et al.* 2018), and changing cumulative impact intensity (Halpern *et al.* 2019). However, these models require a considerable amount of data on both ecosystem condition and how stressors (and combinations of stressors) impact condition. Studies that include empirical data collection should make these data freely available to add to existing spatial data (e.g. Nicholls and Cazenave 2010; Walbridge 2013), which remains a priority if we are to promote more data-driven approaches to cumulative impact assessments (Halpern and Fujita 2013).

6.6 Concluding remarks

Marine spatial cumulative impact assessment methods help us to quantify how human activity is affecting the oceans. The work I conducted for this thesis progresses the field of cumulative impacts research by:

- Contributing to the database of empirical data that can be used to validate assessment results.
- Addressing knowledge gaps regarding the uncertainty associated with unknown stressor interactions, and assuming a linear relationship between ecosystem condition and stressor intensity.
- Developing a novel and generalisable method to incorporate non-additive interactions into cumulative impact assessment methods.

The complexity of the marine environment and the resulting variability present in marine environmental data means that capturing the true impact of multiple stressors is challenging. Furthermore, validating assessments on a global scale requires a vast, accessible database of empirical ecosystem condition data and accurate information on the presence and intensity of stressors. Importantly, robust, and clear uncertainty information provides a greater understanding of the level of confidence in the outputs of cumulative impact assessments, which aids in the appropriate interpretation of results. More realistic cumulative impact assessments will lead to better decision making, which will ultimately help preserve the marine environment and its valuable ecosystem services.

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