

Identifying Gaps in the Performance of Coastal Ecosystem Management

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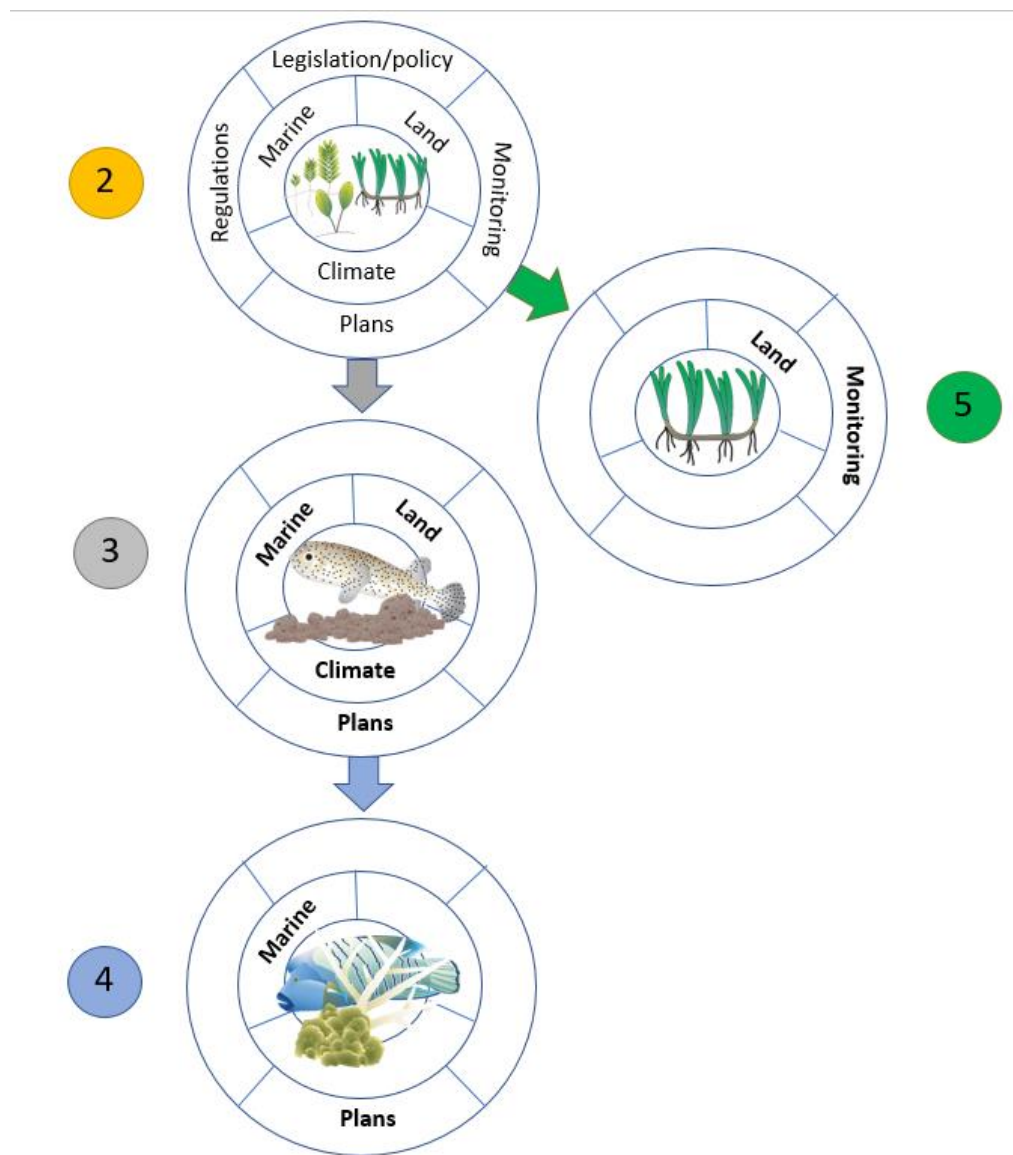
Abstract

Coastal ecosystems are crucial to sustain productive and functioning seascapes because they provide numerous ecosystem services. However, they are under threat and overburdened by multiple anthropogenic land-based and marine-based threats. Managing these threats is challenging because governance of the activities from which threats derive is often segregated and atomistic. Therefore, it is important to assess how management performs across the seascape to ensure adequate protection for coastal ecosystems from multiple threats. Assessing management performance, defined as the ability to meet management objectives, can help managers identify under-performing sites that may need extra management attention (e.g., enforcement, capacity building, or monitoring). Further, it can infer the recovery potential of targeted species or habitats to inform on biologically realistic performance targets. We use the systematic conservation planning framework to explore targeted questions about conservation planning, to identify management gaps and inform on global and regional management decisions. This work begins by asking a series of questions about why management is failing to protect one of the most neglected coastal ecosystems, seagrass. The underlying reason is that seagrass ecosystems are not recognised in legislation or policy and therefore their status and trends are not evaluated against any performance targets. This work has formed part of a global movement to improve the management of seagrass ecosystems, together with authorities charged with global governance of the environment. I then consider how performance targets take into account the social and environmental drivers of fish biomass and assess how this shapes fish recovery. I use this information to inform on management decisions in two case-studies: the northern region of New South Wales, Australia, and in two regional Marine Protected Areas (MPAs) in southern Raja Ampat, Indonesia. In the NSW case study, I identify coastal areas that are at greatest risk to cumulative threats and suggest how management performance could be improved to protect temperate reef fish. In the Indonesian case-study, I suggest that to effectively evaluate MPA performance, it is critical to link historical threats and environmental conditions with coral reef fish outcomes. I then return to seagrass ecosystems as a case study to refine performance targets for monitoring to enable better detection of ecosystem trends. This work, carried out in southern Moreton Bay, Queensland, indicated that metabolomics could allow ecosystem trends to be identified more consistently and with greater accuracy than current methods. In my final chapter, I discuss the implications of these findings and make

recommendations for key areas of further research. Each chapter of this thesis, although broad in design, has the same application to inform managers to make better decisions to protect coastal ecosystems. All chapters have an applied outcome and have utilised collaborators to make the information accessible to conservation managers.

Thesis in one sentence

This PhD thesis has analysed reasons underpinning why comprehensive management of coastal ecosystems is lacking by looking at how marine, land and climate threats are managed through legislation and policy, regulations, spatial plans and monitoring (Ch. 2), and uses three spatially managed seascapes as case studies to: identify marine, land and climate threats in temperate reef ecosystems (Ch. 3) and identify gaps to improve management performance of marine threats in coral reef ecosystems (Ch. 4), and identify a methodology to improve monitoring performance in seagrass ecosystems (Ch. 5). The numbers in the conceptual diagram below, represent the numbers of each data chapter.



Statement of Originality

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.



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Acknowledgement of co-authored papers

Included in this thesis is three published papers (Chapters 2, 4 and 5) and one paper currently under review at the time of submission (Chapter 3). My contribution to each co-authored paper is outlined at the front of the relevant chapter. The bibliographic details for these papers are:

Chapter 2: **Griffiths, L.L.**, Connolly, R.M., Brown, C.J., 2020. Critical gaps in seagrass protection reveal the need to address multiple pressures and cumulative impacts. *Ocean and Coastal Management* 183: 104946. <https://doi.org/10.1016/j.ocecoaman.2019.104946>

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Chapter 5: **Griffiths, L.L.**, Melvin, S.D., Connolly, R.M., Pearson, R.M., Brown, C.J., 2020. Metabolomic indicators for low-light stress in seagrass. *Ecological Indicators* 114: 106316. <https://doi.org/10.1016/j.ecolind.2020.106316>



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Related publications and presentations

Related publications and reports

Tulloch, V.J.D., Turschwell, M.P., Giffin, A.L., Halpern, B.S., Connolly, R., **Griffiths, L.**, Frazer, M., Brown, C.J., 2020. Linking threat maps with management to guide conservation investment. *Biological Conservation* 245: 108527.

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Fortes, M., **Griffiths, L.**, Collier, C., Mtwana Nordlund, L., de la Torre–Castro, M., Vanderkift, M., Ambo–Rappe, R., Grimsditch, G., Weatherdon, L., Lutz, S., Potouroglou, M. (2020) Part 2: Policy and Management Options *In* United Nations Environment Programme (2020). *Out of the blue: The value of seagrasses to the environment and to people*. UNEP, Nairobi.

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Presentations based on this thesis

Griffiths, L.L., Connolly, R.M., Brown, C.J. *Eye on Coastal Management: are seagrasses protected from multiple stressors?* Australian Marine Science Association South East Qld Branch, Marine and Freshwater Student Symposium **2018**, North Stradbroke Island, Brisbane, Australia.

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Chapter 1 Introduction

1.1 Coastal habitats and their importance

Coastal habitats are crucial to sustain healthy and functioning marine ecosystems (Barbier, 2013; Carrasquilla-Henao and Juanes, 2017; Jänes et al., 2020; Mtwana Nordlund et al., 2016; Sievers et al., 2019) and mitigate against climate change (Moomaw et al., 2018; Spalding et al., 2014), but are in a critical condition (Cloern et al., 2016; Collier et al., 2009; Tian et al., 2016). Located at the junction between the land and marine realms, coastal habitats including mangroves, seagrass, saltmarsh and coral reef, are overburdened by multiple anthropogenic land-based and marine-based threats (Cloern et al., 2016; Halpern et al., 2008). As a result of increasing pressure on ecosystems, fisheries catches are decreasing (Carrasquilla-Henao and Juanes, 2017; Liang and Pauly, 2017; Pauly and Zeller, 2016; Pinsky et al., 2011), the biodiversity of coastal species they support is declining (Butchart et al., 2010; Liu et al., 2016; McDonald et al., 2020; Sievers et al., 2019), the filtering capacity that sustains water quality is reducing (Lotze et al., 2006) and the important function they provide to mitigate against climate change impacts is compromised (Silliman et al., 2019; Tian et al., 2016). The combined or interactive effects of multiple threats from past, present and future activities, defined here as the cumulative impact, are also undermining ecosystem resilience (Ortiz et al., 2018). As coastal populations grow globally (Barragán and de Andrés, 2015; Bengtsson et al., 2006) and global environmental change becomes more prevalent (Halpern et al., 2019), strategies to effectively manage these habitats and ecosystems to prevent further degradation are of vital importance.

1.2 Planning for an integrated marine space

Management of coastal ecosystems is complex. The marine realm is dynamic and connected, and not aligned with jurisdictional boundaries (Álvarez-Romero et al., 2011; Garcia-Onetti et al., 2018). Landscapes and seascapes are also typically managed separately, governed under different legislation and policies, and by departments that are structured in silo (Elliott, 2014). Understanding how coastal ecosystems are managed is essential to move forward to develop more integrated systems of management, particularly for ecosystems at the centre of risk from numerous sectors (Cloern et al., 2016; Sale et al., 2014). For example, threats to ecosystems of the Great Barrier Reef are impacted by the activities from seven different sectors (commercial and recreational fishing, urban development, mining, agriculture,

tourism, and forestry) and governed by three divisions of management (local councils, state government and federal government). Ecosystem-based Management (EBM) or Integrated Coastal Zone Management (ICZM), a proposed directive of the EU (European Commission, 2013), provides a means to overcome sectoral constraints, however these concepts are still emerging and have yet to be integrated into management plans globally (Goble et al., 2017; Karabiyik, 2012; Queffelec et al., 2009). Instead, marine spatial planning has historically involved the use of Marine Protected Areas (MPAs) or Marine Parks (MP) to manage threats, which have often regulated single, marine-based threats only (Crain et al., 2009) such as spatial restrictions on fishing (e.g., no-take areas or cultural-take areas) or habitat based restrictions that target specific fishing methods (e.g., limits on trawling) or species.

Systematic Conservation Planning (SCP) emerged in the 1980s (Kirkpatrick, 1983) and was further refined in the 1990s (Margules and Pressey, 2000) as a tool to prevent the ad hoc, singular measure approach to conservation initiatives. The SCP concept systematically assesses the value of every part of the landscape and seascape in relation to its ability to represent ecological processes, identify threats, and, assign a level of priority. It has been widely up taken by conservation planners (Combes et al., 2021; Fernandes et al., 2005; Holness and Biggs, 2011; Kukkala and Moilanen, 2013), because it provides a framework to manage conflict between all marine users while protecting and conserving underlying ecosystems and their biodiversity (McIntosh et al., 2018). The SCP framework advances multi-scale planning processes (such as national parks, marine spatial planning, ICZM, EBM, etc.), through a suite of attributes including supporting key concepts of sustainability, setting quantitative targets in spatially explicit areas, minimising conflict and spatial overlap of competing uses by enabling trade-offs, considering cost-effectiveness, identifying high value features and enabling planning processes to be more evidence based (Zaucha and Gee, 2019). Eleven major stages are identified within the SCP framework (Figure 1.1) which build on earlier work by Margules and Pressey (2000). Stakeholders contribute in different ways throughout the process and there are several feedback mechanisms that enable management to be adaptive and inclusive of the all users in the marine space.

Systematic Conservation Planning Framework

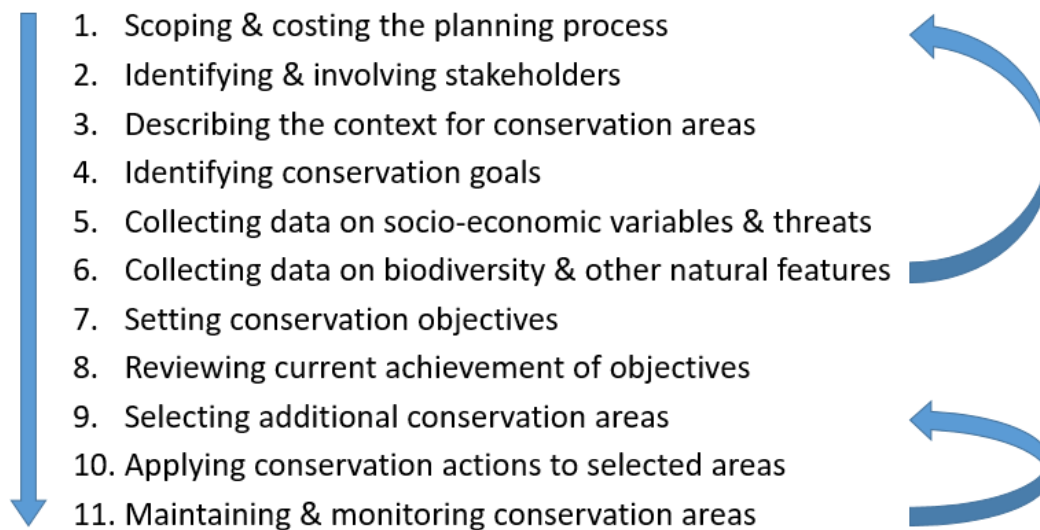


Figure 1.1 The systematic conservation planning framework represented by 11 main stages (adapted from Pressey and Bottril, 2009). Although represented in a linear sequence, feedback loops occur from later to earlier stages, including from stage 11 to 9 and from stage 6 to 1.

The SCP framework has strongly influenced global planning policies for governments, authorities on conservation (IUCN) and conservation organisations (World Wide Fund for nature (WWF), The Nature Conservancy (TNC), etc.) (IUCN and SSC Species Conservation Planning Sub-Committee, 2017; McIntosh et al., 2017). Global approaches to conservation planning have been compared using the SCP framework to assess effective conservation outcomes because of its strong influence (McIntosh et al., 2017). For example, the SCP process was used to compare and evaluate global approaches to conservation planning initiatives and outcomes (Pressey and Bottril, 2009). Comparison using the SCP framework also identified challenges and complexities for conservation planners; two main issues being the difficulty in managing the transition from planning to actions, and assessing the costs and benefits of conservation planning. We have used the SCP framework in a similar way; to explore targeted questions about conservation planning, to identify management gaps and inform on global and regional management decisions.

1.3 Examining management gaps

The logical sequence of the SCP framework provides a platform to examine the design, management and monitoring of coastal ecosystems and marine spatial areas. Evaluations of systematic conservation plans are currently lacking in global literature, particularly on implementation and outcomes (McIntosh et al., 2018). The lack of reporting on conservation planning effectiveness is a considerable barrier to adaptive management and is essential to perpetuate support for designation of marine space, given global marine conservation targets are yet to be fully achieved (Carr et al., 2020).

I have used the SCP framework as a guide to focus each chapter and identify gaps in the performance of coastal management using stage three, five, eight and 11 (Figure 1.2).

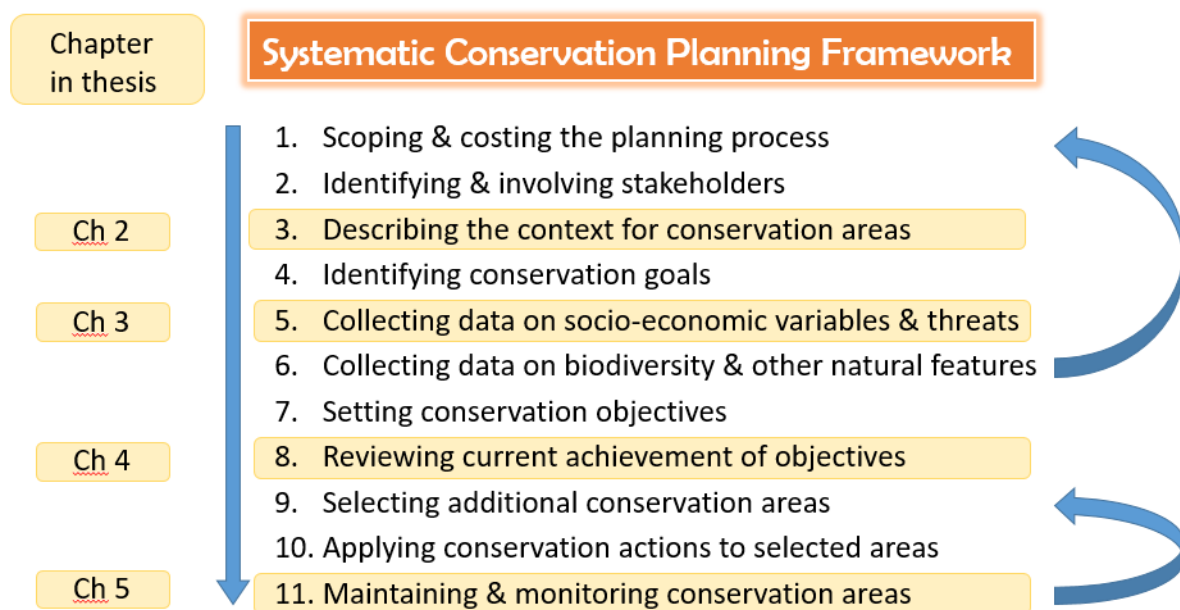


Figure 1.2 The stages of systematic conservation planning addressed in each chapter of the thesis.

1.3.1 Describing the context for conservation areas

Stage three is part of the SCP process that describes the social, economic and political setting for conservation planning, identifying the types of threats to natural features that can be mitigated by spatial planning and the broad constraints on, and opportunities for, conservation actions (Pressey and Bottril, 2009). This stage is important because it describes the foundations that shape constraints for conservation. We followed this stage by reviewing case studies to

assess how threats to seagrass ecosystems are managed through political (legislation, policy, and regulations) and social (spatial plans and monitoring) settings (chapter two).

The background and challenges involved with conservation planning as they relate to this stage are discussed in section 1.2.

1.3.2 Collecting data on threats

Stage five is part of the SCP process that compiles relevant spatially explicit biodiversity and use/threat data such as tenure, extractive uses, costs of, and constraints to, conservation, and often uses predictions about the expansion of threatening processes (Pressey and Bottril, 2009). This stage is fundamental to the process and shapes recommendations for conservation investment. We followed part of this stage by further developing a commonly used spatial method (cumulative threat maps) to assess threatening processes on focal species, using marine protected areas as a baseline (chapter three).

1.3.2.1 Background and challenges

Spatial methods, such as cumulative impact maps, are commonly used to highlight areas of conservation concern and help managers prioritise marine conservation efforts (Korpinen and Andersen, 2016). Cumulative impact maps have been widely used in the marine environment at global (Halpern et al., 2008, 2015) and regional scales (Coll et al., 2012; Korpinen et al., 2012; Maxwell et al., 2013; Singh et al., 2020; Trew et al., 2019) and to quantify threats to single species (Fuentes et al., 2020; Zhang and Vincent, 2019), functional groups (Fu et al., 2020; Giakoumi et al., 2015b) and ecosystems (Gao et al., 2021; Loiseau et al., 2021).

Cumulative impact maps typically consist of: (1) mapping the spatial distribution and strength of each anthropogenic threat (e.g. water quality); (2) mapping the location of the feature of interest (e.g. ecosystem, species, etc.); (3) applying a vulnerability weight to estimate impact to the feature of interest (creating a single impact score for each threat); and (4) summing across all threats to produce a cumulative impact score (Halpern et al., 2015, 2008). Cumulative impact maps are favoured by managers because they are easy to interpret when engaging with stakeholders and can identify areas requiring further conservation action or research. However, they are static in nature and do not usually account for temporal variation, treat threats as additive and therefore neglect threat interactions, and rely on expert opinion to interpret impact (Ban et al., 2010; Brown et al., 2014; Jones et al., 2018). Also threat maps alone inform only on the process (i.e., not the impact of the threat) rather than on

the biodiversity outcome from managing the process (Tulloch et al., 2016, 2015), which means they can be misleading if used to inform management priorities (Giakoumi et al., 2015a).

Ecosystem or ecological models can be used to quantify threats and can guide decision making by addressing the link between outcomes and actions, as well as overcome other limitations of cumulative impact maps (Dowling et al., 2016; Geary et al., 2020; Liu et al., 2021; Schmolke et al., 2010; Shin et al., 2018). These models mathematically represent a system at various scales (Liu et al., 2021) and there are numerous different approaches to ecosystem modeling at various levels of modelling complexity (Geary et al., 2020).

Ecosystem models can make predictions about alternative management interventions by modelling the counterfactual, i.e., explore what would have followed had a particular management action been different. Simulation models have been commonly used to investigate the impacts of threats on ecosystems (Fulton et al., 2015), particularly from fisheries (Dimarchopoulou et al., 2019; Romagnoni et al., 2015). Models have the advantages of being able to account for spatial and temporal variation, can incorporate dynamic processes and features, and can model the impact on the system based on different management actions and levels of threat (Fulton et al., 2015). However, simulation models require extensive ecological data, have high systems complexity (specific modelling skills), are often validated using inappropriately applied data-sets, and are not appropriate to apply at fine spatial scales typical of many small isolated MPAs (Chatzinikolaou, 2012; Fulton et al., 2015; Grützner, 1996; Jackson et al., 2000).

Statistical models could be integrated into threat impacts maps to overcome some of the limitations of cumulative impact maps (McClanahan et al., 2016; Tulloch et al., 2016). Statistical models quantify threats by fitting empirically-measured ecological responses (e.g. fish biomass) to threats (e.g. fishing), meaning that computational outputs are easier to interpret and analyses are not constrained by the requirement for extensive data sets. A statistical modelling approach to cumulative impact mapping could be based on the same principles as species distribution modelling (SDM), however treating threats as a covariate in the model and thus, threats are applied retrospectively to understand the spatial influences on the response variable (e.g. fish biomass or abundance). This alternative approach therefore uses indicator species or habitats as proxies for overall ecosystem impacts (Tulloch et al., 2016). This is particularly useful if used in combination with other parameters that are influential to species

distributions, e.g., exposure, currents and proximity to coastal wetland (Sánchez-Carnero et al., 2016). Models can also consider the interactions between threats, incorporate multiple and cumulative threats and provide a better fit of the uncertainty ignored by simple ‘process’ or ‘habitat’ type models (Tulloch et al., 2016).

1.3.3 Reviewing current achievement of objectives

Stage eight is part of the SCP process that uses data to estimate the extent to which objectives have already been achieved in areas considered to be adequately managed for conservation (Pressey and Bottril, 2009). This stage considers how existing conservation actions implemented previously can be strengthened and complementary to areas prioritised through the SCP framework. I used this stage to identify if the objectives of a marine spatial plan in Indonesia were being achieved and to identify gaps in MPA performance for consideration in future regional planning initiatives (chapter four). I also incorporated part of this stage in chapter three, where I assessed the performance of no-take zones to protect focal species from cumulative impacts.

1.3.3.1 Background and challenges

Evaluating the impact of management, defined here as management performance, is the ability of actions to meet management objectives. However, there are a number of challenges that influence the outcome of management actions in the marine realm. For example, outcomes are affected by the spatial distribution of threats, because impacts can vary significantly over small spatial and temporal scales (Ban et al., 2012; Hargreaves-Allen et al., 2017) and they are confounded by their nature as threats often co-occur, e.g., higher recreational fishing in areas where pressure on water quality is greater (Baylis et al., 2016). Identifying how threats vary spatially, where they accumulate and how management is minimising impacts is crucial knowledge for natural resources practitioners because it allows them to adapt their efforts and target sectors responsible for the greatest impacts. For example, it can identify if poaching is the cause of poor performance (Brown et al., 2018) or if other non-managed or cumulative threats mask the effect of recovery inside spatially managed areas (Stevenson et al., 2020).

Statistical models can be used to assess management performance by making predictions about counterfactuals, e.g., how fish respond under different management scenarios and thereby link biodiversity outcomes with management actions (Tulloch et al., 2015). Although SDMs have been used for MPA design and planning (Marshall et al., 2014), they have not

been commonly applied to evaluate MPA performance in the face of cumulative impacts (Fulton et al., 2015; Pelletier et al., 2008).

Models that are capable of assessing management performance offer enormous potential to managers. First, they can be used to understand how fish respond under current and alternative management interventions when multiple and/or interacting threats are considered. Second, they allow managers to adjust their expectations by accounting for spatial or temporal variation not previously considered when setting management objectives. This also has the potential to facilitate discussions about how spatial planning tools could be used to govern activities from other sectors that impose threats and work towards achieving nested governance.

1.3.4 Maintaining and monitoring conservation areas

Stage eleven is part of the SCP process that ensures individual areas are managed to promote the long-term persistence of the values for which they were established (Pressey and Bottril, 2009). This stage involves explicit management objectives & monitoring to ensure that management actions are effective. We used the principles of this approach to develop a methodology to improve monitoring performance in a seagrass ecosystem (chapter five).

1.3.4.1 Background and challenges

The use of feedback loops like ecosystem monitoring is another important method to assess how management is performing. For example, monitoring can be used to ‘ground truth’ spatial plans and inform on management actions to avert loss (Lefcheck et al., 2018).

Empirical evidence of the state of ecosystem or species through time is also essential to inform ecological models to better understand and predict threats. However, attributing change in coastal ecosystems like coral reef and seagrass, is difficult to elucidate because they are complex ecosystems that are highly susceptible to chronic exposure from multiple threats. For example, coral loss is exacerbated by multiple threats of fishing, climate change and benthic degradation because of complex feed web associations that prevent coral recovery (Ruppert et al., 2013). Further, seagrass meadows can disappear between sampling events because morphological indicators, widely used to monitor seagrass, fail to detect chronic threats that operate on a physiological level (Connell et al., 2017).

Being able to detect states of stress prior to collapse of tipping points allows managers time to act (i.e., by setting lower light guidelines for dredging (Collier et al., 2016)) before there are large-scale responses, such as loss of meadows. Recently, there has been considerable

advancement in understanding seagrass physiology using Nuclear Magnetic Resonance (NMR) spectroscopy for untargeted metabolomics (Melvin et al., 2017; Zou et al., 2014). Metabolomics has revealed considerable differences between samples related to the level of environmental threats (such as low light), which are reflected in distinct metabolite profiles which are characteristics of specific stress responses (Melvin et al., 2017). Metabolomic approaches may therefore be able to provide an early warning indicator of stressed seagrass beds. This area of research requires greater attention, and it could play an important role in informing the modelling of multiple threats and assessing the performance of management actions (Kumar et al., 2016).

1.4 Objectives and overview of thesis

1.4.1 Thesis objectives

The thesis consists of six chapters: a General Introduction (Chapter 1) and Discussion (Chapter 6) and four results chapters (Chapters 2-5). The results chapters are in the form of manuscripts formatted to meet the requirements of the peer reviewed academic journals where they have been submitted/published. The thesis was prepared in accordance with Griffith University policy. As a result, there is some repetition among the results chapters in the reference lists.

The overall objective of this thesis is to better understand how threats impact coastal ecosystems and species, and identify how we can improve the management of coastal ecosystems by examining the performance of current management mechanisms. The ultimate goal is to help managers make better decisions to protect coastal ecosystems and inform on management priorities.

To answer specific questions about the effectiveness of management of coastal ecosystems, this thesis includes the following studies:

Chapter 2 – Critical gaps in seagrass protection reveal the need to address multiple pressures and cumulative impacts

In this literature review, seagrass are used as a case-study to explore why management is failing to adequately protect coastal ecosystems. I reviewed policies, legislation, plans and management frameworks aimed at protecting seagrass meadows in 20 high-threat regions to identify critical gaps in their protection by asking five key questions.

Chapter 3 – A data driven approach for cumulative impact assessment on marine protected areas.

In this study, I created a cumulative threat map across two marine parks in New South Wales and developed a new approach to estimate impact to biodiversity. I then evaluated the performance of management to protect fisheries targeted species from cumulative threats. I did this by building a cumulative threat map and identifying the greatest threats to temperate reef fish. I then applied a statistical model to understand cumulative impacts that are likely to have the greatest impact on fish abundance. We use coral reef fish as a proxy for coral reef ecosystems more generally. I then assessed the performance of no-take zones to protect targeted fish species from cumulative impacts across the two parks.

Chapter 4 – Linking historical fishing pressure to biodiversity outcomes to predict spatial variation in Marine Protected Area performance

In this study, I developed a statistical modelling approach to evaluate the performance of spatially managed areas. I did this by predicting how historical fishing pressure and biophysical conditions affect expected recovery of fish biomass. I test my approach using empirical data obtained from a highly biodiverse coral reef ecosystem in Raja Ampat, Indonesia across two MPAs.

Chapter 5 – Metabolomic indicators for low-light stress in seagrass

In this study, I focused on exploring monitoring methods to improve management performance for seagrass in southern Moreton Bay. This field experiment tested if seagrass exposed to stress (low light) showed response through changes in metabolites when compared to controls. I tested this as a precursor to understanding the sub-lethal stress in seagrass to indicate functional changes before more obvious morphological changes, commonly used to indicate stress, occur.

1.4.2 Summary

Stages of the SCP framework were used to focus each chapter to address a different aspect of the conservation planning process in order to improve regional decision making. The outcomes from the literature review also highlighted which stages of the SCP framework should be addressed in the subsequent chapters. In chapter 2, I found that spatially managed areas (management plans, MPAs, etc.) were supported by the most effective setting for

conservation action. Therefore chapter 3 I focussed on developing methods to assess threat inside MPAs. I then focussed chapter 3 and 4 on analysing the performance of spatially managed areas (MPA, MP) to meet planning objectives for temperate reef fish (chapter 3) and coral reef fish (chapter 4). In chapter 2, I also found that consideration of cumulative impacts was often neglected in coastal management regimes, so I built a cumulative threat map for the study area in chapter 3. In chapter 2, I identified that there was a lack of temporal monitoring data on seagrass trends, so I focussed my last chapter on testing a different approach to detecting trends in seagrass loss that has potential to identify subtle trends in seagrass state.

This thesis contributes to the knowledge base about the effectiveness of management actions and explores novel approaches to assess and monitor the impact of management performance. This thesis also contributes to policy-making, decision-making and legislation pertaining to the coastal ecosystems more broadly, both locally and globally.

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Chapter 2 Critical gaps in seagrass protection reveal the need to address multiple pressures and cumulative impacts

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Author Contributions

Conceptualisation of the study: LLG, CJB, RMC. Conducting the literature review: LLG. Formal analysis of the data: LLG, CJB. Writing – original draft preparation: LLG. Writing – review and editing: CJB and RMC.



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2.1 Abstract

Management is failing to adequately protect coastal ecosystems. Here we reviewed the policies, legislation, plans and management frameworks aimed at protecting seagrass meadows in 20 case-studies with the aim of identifying critical gaps in seagrass protection. The case-studies were chosen to represent a range of regions known to have high cumulative impacts or outstanding seagrass management. We asked five ‘key questions’ in our review to identify gaps in seagrass protection: 1) are seagrass habitats identified as an ecosystem of environmental significance, 2) what are their main threats, 3) does management consider cumulative impacts and 4) multiple pressures, and 5) are these habitats recovering? Seagrass protection was enacted inconsistently, through a range of legislative, policy and planning processes that only sought to mitigate some of the known pressures. Although the importance of preserving biodiversity and ecosystem services were acknowledged in over 80% of the case-studies, actionable plans to specifically address known pressures were lacking. Poor integration across jurisdictional realms and sectoral management approaches prevented the holistic strategy needed to address multiple pressures. We suggest a priority for enhancing protection of seagrass ecosystems is improving legislation, policies and planning frameworks to consider multiple pressures and cumulative impacts from marine and land-based activities. Management of seagrass ecosystems is likely to be indicative of trends in coastal management more generally, highlighting the urgent need to address multiple pressures and cumulative impacts in legislation and policies.

Keywords: integrated coastal zone management; management plan; seagrass conservation; DAPSIR framework; ecosystem-based management

2.2 Introduction

The world’s coastlines are experiencing unprecedented increases in human population, with 40% of the Earth’s human population residing within 100 km of the coast (Bengtsson et al., 2006). Coastal ecosystems are overburdened with human activities driven by coastal, industrial and port development, energy generation, agriculture, fisheries and aquaculture (Halpern et al., 2007). Further, the escalating threat of climate change will be one of the top threats to biodiversity by mid-century (IPBES, 2018). Human activities impose multiple pressures on coastal ecosystems by reducing water quality, biodiversity and habitat availability, and altering hydrological processes and food web dynamics. Inadequate management of multiple pressures can reduce the capacity to provide ecosystem services

such as fisheries (Cullen-Unsworth and Unsworth, 2018). The combined or interactive effects of multiple threats from past, present and future activities, defined here as the cumulative impact, are also undermining ecosystem resilience (Ortiz et al., 2018).

The lack of integration of coastal management approaches may be one of the fundamental reasons why coastal ecosystems remain largely unprotected from multiple pressures. Some important hurdles to the integration of management include crossing spatial jurisdictions (e.g. land, water catchments, wetlands and coastal marine environments); overcoming institutional segmentation that imposes sectoral management policies and; coordinating across international boundaries (Elliott, 2014). These hurdles can be overcome with conceptual frameworks such as Integrated Coastal Zone Management (ICZM) (Cicin-Sain and Belfiore, 2005), marine spatial planning (Qiu and Jones, 2013), and ecosystem-based management (McLeod and Leslie, 2009). Although significant development of these concepts have been made, particularly with policy in the European Union (EU) (Borja et al., 2016), there is still a need to translate policy objectives into specific ‘on ground’ targets and measures (Katsanevakis et al., 2011). For example, lack of institutional structures to support ICZM (Karabiyik, 2012) and human capacity constraints (Goble et al., 2017), impede the ability to translate policy into measurable objectives. It is currently unknown how commonly these concepts are applied globally to protect coastal ecosystems.

Seagrass ecosystems provide a useful case-study to explore the current state of management in coastal areas challenged by multiple pressures and cumulative impacts. Seagrass meadows are often at their most extensive in estuaries and bays where ports and cities co-occur.

Seagrasses also provide numerous ecosystem services (e.g. Campagne et al., 2015; Sievers et al., 2019). Further, they are considered ecosystem engineers and global biological sentinels of multiple anthropogenic pressures in coastal ecosystems (Orth et al., 2006). Their high global rates of decline (losses of 7% per year in the two decades from 1990 (Waycott et al., 2009)) means they are among the most threatened and vulnerable ecosystems on earth.

In this review, we analyse the frameworks underpinning the management of seagrass habitats. We explore how management tools (namely legislation, policies, and regulatory and planning tools, Table 1) contribute to protecting seagrass ecosystems in 20 regions subject to high cumulative impacts. We developed a methodology that could be applied by governments or non-government organizations in any region to rapidly assess the status of protection of coastal ecosystems. This review highlights gaps in management, and identifies priorities for

rapid integration of the science of cumulative impacts into policy and legislative frameworks. Doing so can enhance the protection of coastal ecosystems.

Table 2.1 Policy and Planning Terminology

Terminology	Definition
Environmental Legislation	Provides the fundamental legal support for the development of policies and plans
Environmental Policies	Provide statements of principle and commitment concerning environmental issues and help guide decision-making processes. They are part of a suite of tools used to manage threats and are often used in conjunction with other non-legally binding tools such as strategic vision statements, guidelines and best practise standards.
Regulatory Systems	Are used to implement legislation and provide decision-making systems to manage human use of the environment, e.g. Environmental Impact Assessment (EIA), Assessment of Environmental Effects (AEE), Strategic Impact Assessment (SIA) or Strategic Environmental Assessment (SEA) toolbox.
Management Plans	Herein, referred to as ‘Plans’, specify how legislation and policies will be implemented thereby providing direct actions on programs of work. This term encompasses any planning framework such as Marine Spatial Plans, Marine Protected Areas, zoning plans or management strategies over a designated marine/coastal area.
Governance structures	The institutional structure upon which management of a coastal/marine area is based.
Management Frameworks	The set of methodologies, procedures and measures that facilitate environmental management.

2.3 Methods

2.3.1 Scope of the Review

Our objectives were to: (1) review the different management tools used to prevent or mitigate threats to seagrass habitats; (2) evaluate how management plans, herein referred to as ‘Plans’, address multiple pressures over a broad spectrum of activities to support the conservation and protection of seagrass habitats; and (3) identify management frameworks that have supported the stability or recovery of seagrass habitats. Management tools include legislation, policy, regulatory systems and management plans (Table 2.1).

2.3.2 Selection of regions

We chose 20 regions for review to best represent the geographic distribution of seagrass, and the range of potential pressures and governance structures. Fifteen coastal regions were selected from locations where seagrass meadows (UNEP-WCMC and Short, 2018) intersected with hotspots of threat (threat clusters) from land-based pressures (Halpern et al., 2009). This threat ranking approach was chosen because it provided a method for prioritising areas most at risk from land-based impacts (based on watershed processes contributing to nutrient and pollution input and coastal human population size) which directly applied to seagrass threats. Three additional regions with governance structures known to value seagrass habitats and/or support seagrass conservation goals were also included to give a deeper understanding of how directed management of multiple pressures can be achieved. Two other regions were included to ensure coverage over the majority of global seagrass bioregions (Figure 2.1, Supplementary Table A.2).

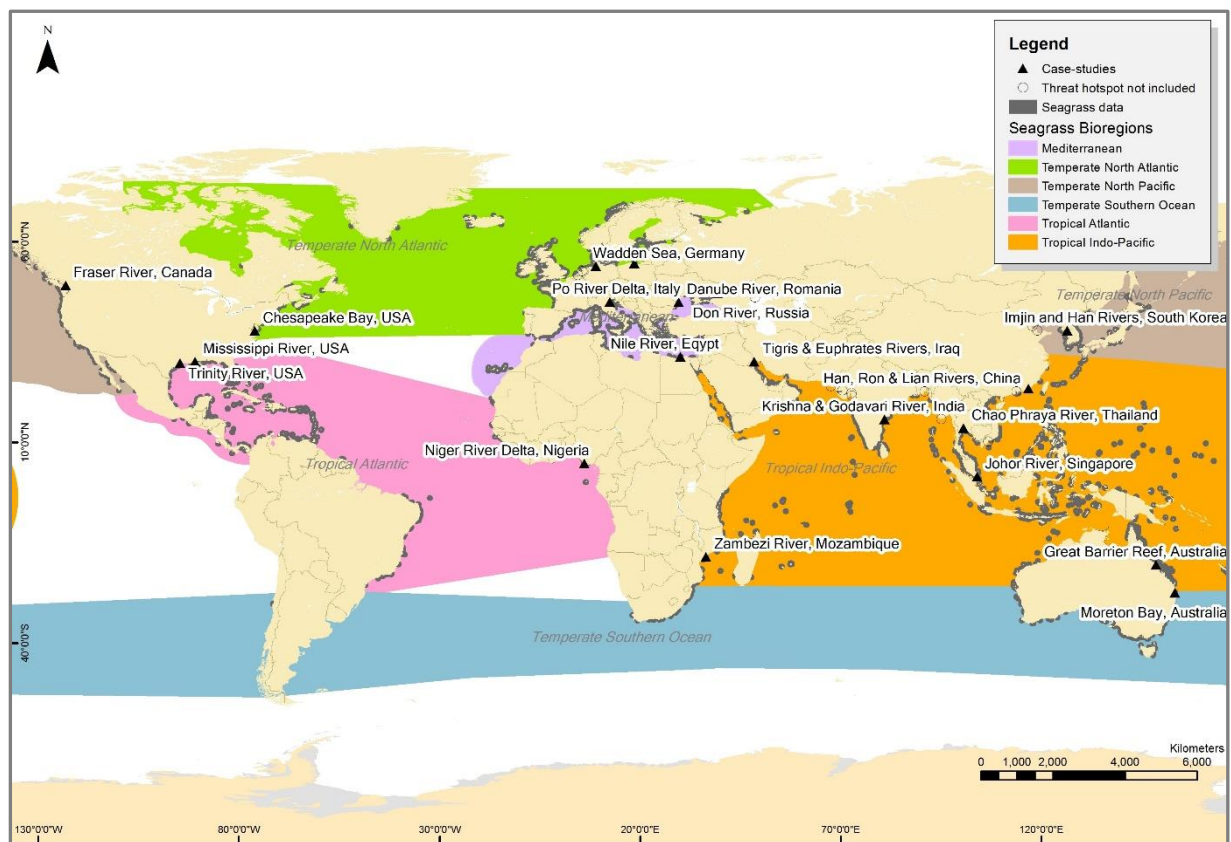


Figure 2.1 Location of selected sites for review overlaid with seagrass bioregions (Short et al., 2007) and global seagrass distribution as points and polygons (UNEP-WCMC & Short, 2018). “Threat hotspots not included” are Halpern et al., (2009) hotspot locations without a representative case study site in the present study.

2.3.3 Search Criteria

We evaluated how comprehensive seagrass protection was in each case-study by asking five questions of the grey and peer-reviewed literature (Table 2.2). We used two search strategies to assemble comprehensive information relevant to each question. Grey and peer-reviewed literature were searched using Google and Google Scholar with search terms including the region of interest, threat activity (energy generation, industrial development, port development, coastal urbanisation, invasive species, fisheries, water quality, climate change) and tools (coastal management, plan, work program, governance, policy, spatial planning). Grey literature is an important resource for management policies and plans (Adams et al., 2017; Corlett, 2011) and here included government documents or reports, legislation (acts, laws, regulations, decrees, subordinate legislation, etc.), non-governmental organization reports, intergovernmental organization reports (e.g. International Union Conservation Nature (IUCN)), political union reports (EU)), reports from environmental consultancies, and reports from private companies. To address the question “Are seagrass habitats stable or recovering?” (Q5, Table 2.2), only peer-reviewed literature was searched using Web of Science for studies of trends in seagrass status (areal coverage, diversity or productivity) in review regions. Peer-review literature provided the confidence that trends were measured to an international standard. Search terms included the region of interest as well as the following: seagrass (SAV, submerged, aquatic vegetation, eelgrass), rate of change (loss, change, recovery, stability, impact, decline, increase, gain) and area (cover, area, distribution, production, bed, diversity) and management (intervention, plan, restoration). In total we reviewed 658 documents across the 20 case-studies (Supplementary Table A.1).

2.3.4 Evaluation Criteria

To aid analysis of the literature we categorized the main threats to seagrass according to the Drivers-Activities-Pressures-State-Impact-Responses (DAPSIR) model (adapted from Elliott et al., (2017)). The division of threats into drivers and activities (Figure 2.2) enabled an understanding of if, and how, multiple threats and cumulative impacts were considered by management in each case-study region. Evidence of compliance and/or monitoring were identified as well as community led education and research programs.

Table 2.2 Key questions to decide what legislative, policy and planning actions are needed to adequately protect seagrass habitats

Question	Action
1 Are seagrass habitats explicitly identified as an ecosystem of environmental significance by legislation?	Review legislation to determine if seagrass is specifically protected and if so, how their values are considered (e.g. biodiversity, ecosystem services).
2 What are the main anthropogenic threats to seagrass and how are they managed?	Review grey and peer-reviewed literature to identify the main activities that threaten seagrass and determine which threats relate to the case-study area. Review legislation, policies, plans, guidelines and peer-reviewed literature to see if threats to seagrass are (A) specifically addressed and/or (B) protected indirectly through regulations that may benefit seagrass.
3 Have cumulative impact policies been developed?	Review cumulative impact policies and peer-reviewed literature governing the impact assessment toolbox and determine if they consider the cumulative effects of past, current and future activities.
4 Do Plans consider multiple pressures?	Construct an integrated DAPSIR for all activities identified in (2). Review Plans in detail to see if pressures to seagrass are specifically addressed with an action.
5 Are seagrass habitats stable or recovering?	Review peer-reviewed literature to determine if monitoring data exists for seagrass, particularly information addressing historic baselines and trends through time.

Drivers are the basic human needs of society; such as food provisioning (Supplementary Table A.3). **Activities** are the primary threats to seagrass and are often the level at which government policies and institutional structures are formed, e.g. fisheries are a threat to seagrass as fishing gear (nets, raking) are capable of directly damaging seagrass habitat (Supplementary Table A.4). **Pressures** are the mechanism through which activities (threats) have an effect, e.g. one of the pressures of fisheries is abrasion of the seabed (Supplementary Table A.5). **State change** was the change to the natural environment from unmanaged singular or multiple pressures, e.g. abrasion fragments meadows (Supplementary Table A.3). **Impact** is the social or economic consequence of state environmental change, e.g. loss in fishing productivity from fragmentation of seagrass habitat. **Responses** were the actions of management to prevent, detect or mitigate threat, restore lost habitat/species or adapt to

environmental change. For example, fragmented seagrass beds might be recovered through prohibition on use of benthic fishing gear in seagrass habitat (Figure 2.3).

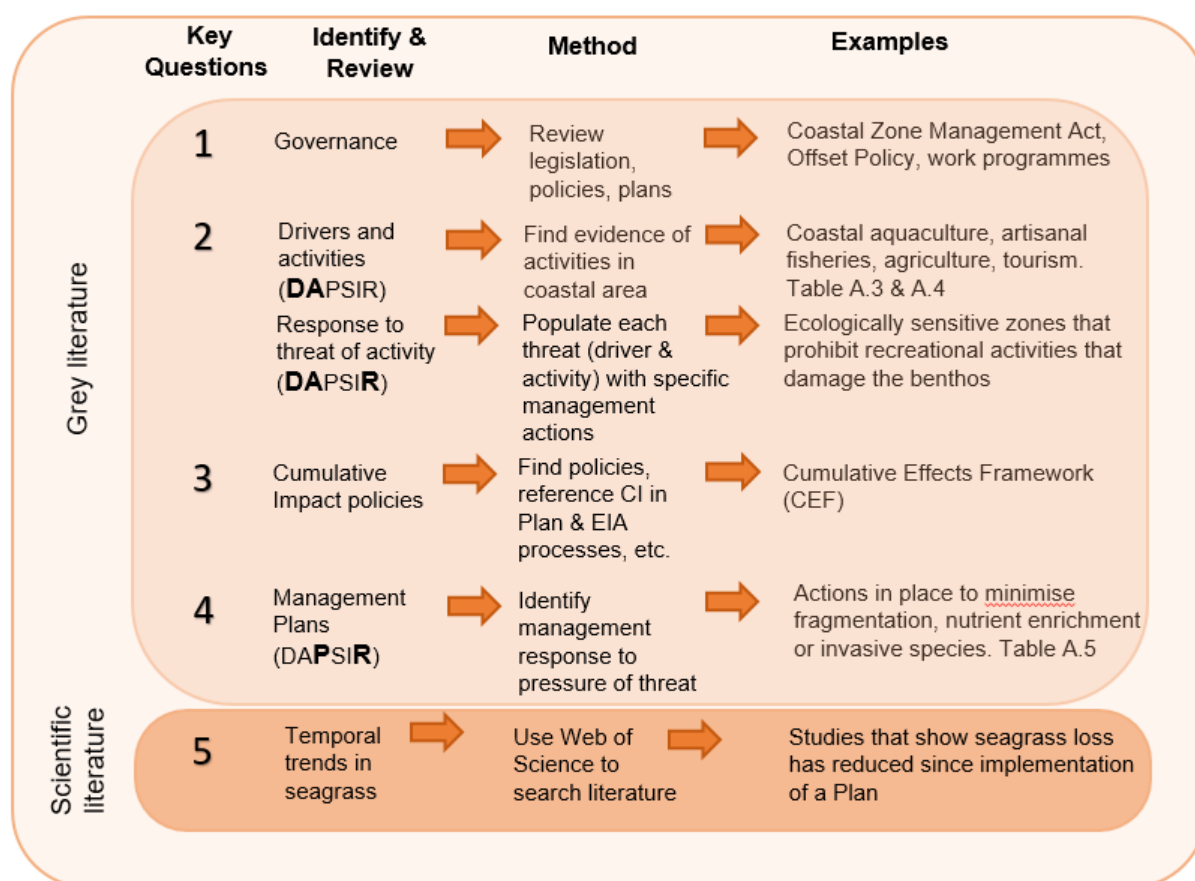


Figure 2.2 Methodology used in the review to answer the 5 key questions

The DAPSIR framework (and its predecessors) has been used as a tool for managers to understand the causes, consequences and responses to change in both the terrestrial and marine realm (Pinto et al., 2013). It has been widely applied to link science with management and policy, e.g. Thailand (Baldwin et al., 2016) and South Africa (Goble et al., 2017). Here we have used this tool to explore how management actions are currently implemented to address the pressures of human activities on seagrass. This process clearly identifies where gaps in regulatory, policy and planning frameworks exist.

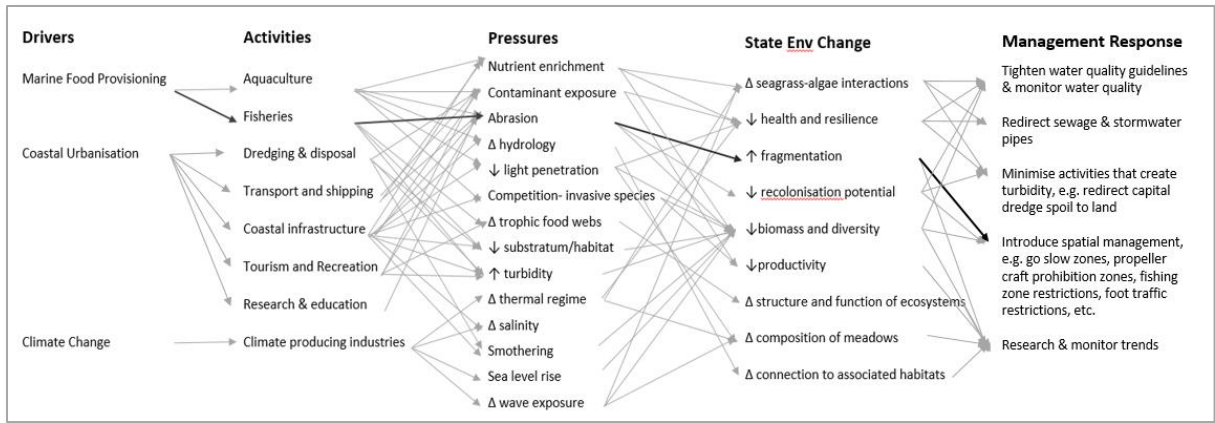


Figure 2.3 An example of the Driver-Activity-Pressure-State Change-Management Response relationships for seagrass for some of the activities identified through the review, highlighting a pathway from ‘marine food provisioning to environmental changes’. Adapted and expanded from Smith et al., (2016). See Supplementary Table A.3, A.4 and A.5 for further information.

2.3.5 Results of Key Questions

2.3.5.1 Are seagrass habitats explicitly identified as an ecosystem of environmental significance by legislation?

Seagrass habitats lacked protection through legislation, policies or spatial plans in half of the case-study regions, particularly for countries with a low human development index (HDI) (Supplementary Table A.6). These regions include the coastal seas adjacent to the Danube River (Romania), Chao Praya River (Thailand), Nile River (Egypt), Niger River (Nigeria), Krishna & Godavari Rivers (India), Zambezi River (Mozambique), Don River (Russia), Tigris and Euphrates Rivers (Iraq), Han, Ron and Lian Rivers (China), and Johor River (Singapore). Without legislative protection seagrass habitats in these areas remain at risk of decline, because there are no instruments to acknowledge their importance or minimize impact through regulatory systems (e.g. offset policies), planning processes (e.g. marine protected areas or zoning plans) or conservation agendas.

2.3.5.2 What are the main anthropogenic threats to seagrass and how are they currently managed?

Activities that impact on water quality through energy generation, industrial and port development, agriculture and coastal urbanisation were consistently identified as primary threats across all case-studies (acknowledging that we chose many case-study regions partly on the basis of a high cumulative threat index from land-based threats). Fisheries, coastal

infrastructure, recreation and tourism, and transport and shipping (invasive species) were also commonly identified. Major industrial development was identified only in some case-study regions such as in the state of Schleswig-Holstein (German Wadden Sea) and the city of Rostov-on-Don (Don River, Russia). Climate change was not recognised as a significant threat across the majority of case-studies, which may explain the lack of actions specifically targeting climate change (Figure 2.4). Government reports indicated that the main threats to coastal ecosystems are known in most case-study regions. However, measures to mitigate against threats to seagrass habitats specifically were only implemented in case-studies that directly identified the national or regional importance of seagrass habitats through legislation. For example in Nigeria, the former National Policy on the Environment (Federal Ministry of Environment, 2016) acknowledged the main threats facing coastal ecosystems and had policy statements to address threats. However, Nigeria lacked the legal framework to implement its policy, so coastal ecosystems remained at risk (Mmom and Chukwu-Okeah, 2011).

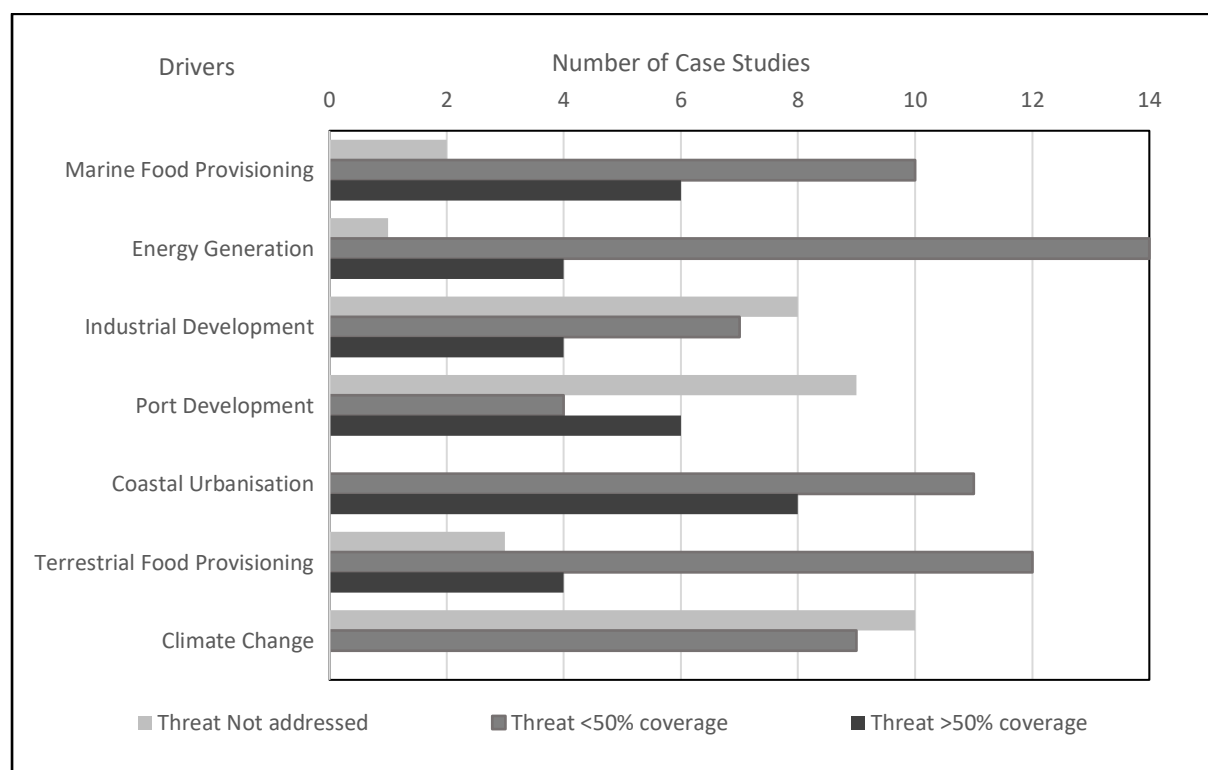


Figure 2.4 Summary of findings on seagrass threats from the 20 case-studies reviewed. Coverage refers to the percentage of threats within each driver targeted with a management action.

The main threats to seagrass were managed through a complex array of management tools, including legislation, policy, strategies, plans, work programs, public outreach practices, guidelines and best practice procedures. No single tool covered all threats. Threats were not equally addressed with management actions across all drivers (Figure 2.4) and within each case-study (Figure 2.5). Poor representation of threats was evident particularly for countries with a HDI rank of higher than 52, and not part of the EU (Supplementary Table A.6). The threat to water quality and from fisheries were addressed in the majority of case-studies regardless of economic status and HDI (Supplementary Table A.6). However, there was considerable variability in management of threats from other activities.

Water quality regulations are in place globally and primarily targeted at reducing nutrient, chemical and biological contaminants in waste-water. However, waste-water pollution still occurs in over 50% of the case-studies due to inadequate levels of treatment (generally only primary treatment), inadequate coverage, and/or aging infrastructure, as well as an inability to process seasonal overflows (Supplementary Table A.6). For example in the urban areas of Andhra Pradesh Province in India, only 15% of waste-water is treated through treatment plants (Ministry of Environment and Forests, 2013). Monitoring of wastewater was carried out across the majority of case-studies, however they varied from random checks to routine monitoring (Supplementary Table A.6). Very few countries treat storm water or tackle diffuse run-off. The state of Schleswig-Holstein (Germany), Singapore and Seoul Capital Area (Republic of Korea) are the only case-studies that have management policies in place to minimise run-off pollution (Supplementary Table A.6). Measures to manage non-point source pollution exist for some industries such as setting a minimal distance to coasts for agriculture and forestry (State of Louisiana, USA).

Spatial restrictions on bottom trawling in coastal areas have been implemented in 75% of case-studies on a permanent, seasonal and/or periodical basis to protect coastal habitats. However, seasonal or periodical restrictions are suspected to offer little protection for habitats. In some regions spatial restrictions were the main form of control on fishing activities (e.g. Alexandria Province, Egypt). Measures to reduce benthic impacts to coastal habitat from non-trawl related fishing activity such as intertidal dredging, raking or digging, were rare, particularly in areas not covered by a Plan. For example along the extensive tidal flats in the western Republic of Korea, there are limited provisions to mitigate the impact of harvesting bivalves within intertidal seagrass, despite the prevalence of this activity (Hahm et

al., 2014), and its effect on seagrass habitat (Park et al., 2011). However, implementation of regulations has occurred in some regions. For example, regulations protect some seagrass meadows in Venice Lagoon by restricting mechanical clam fishing to specified areas (Facca et al., 2014).

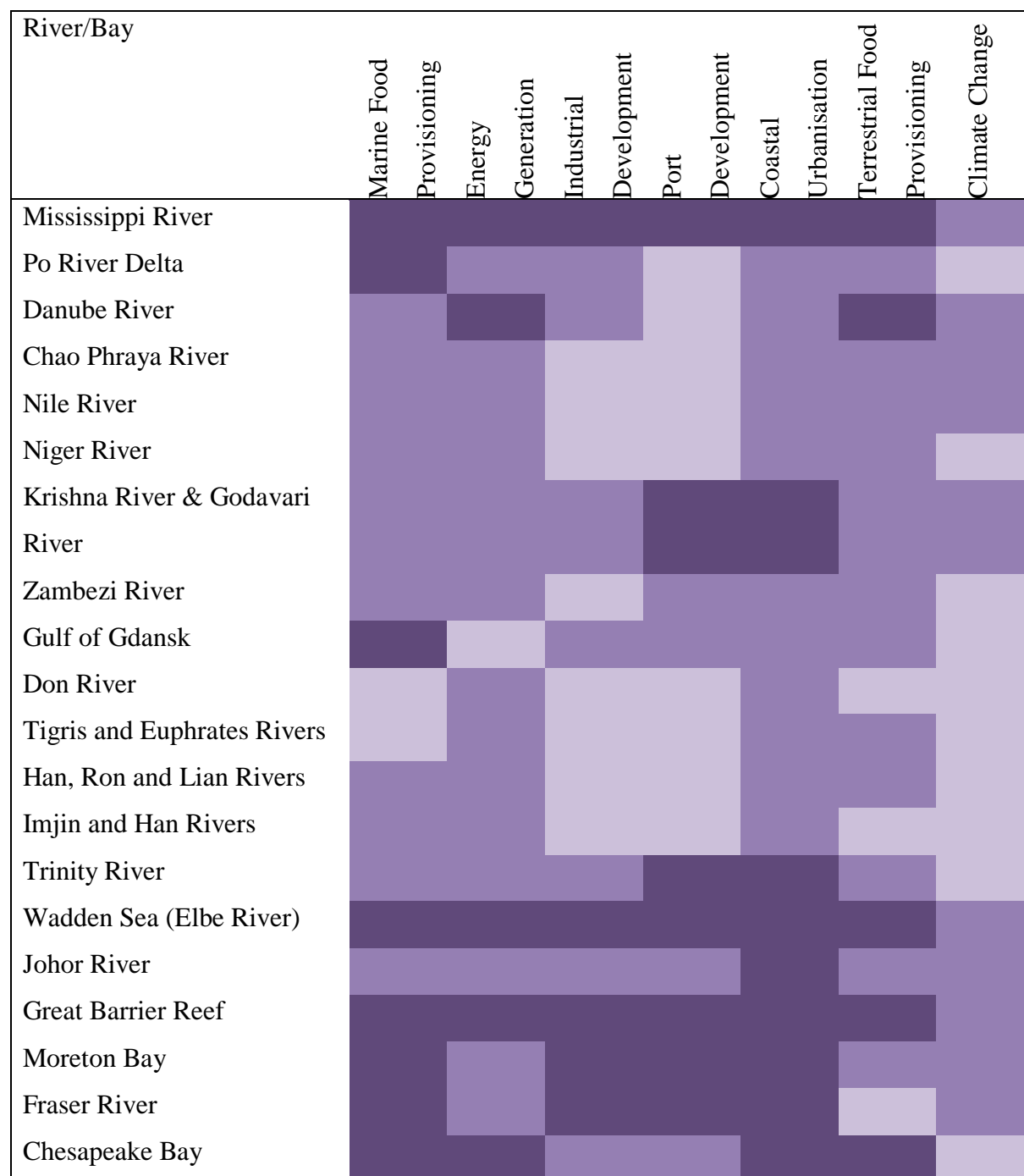


Figure 2.5 How comprehensively threats were addressed in each case study. Light purple indicates threat not addressed. Lilac indicates <50% of the threat was addressed and dark purple indicates >50% of the threats were addressed through all regulatory and policy avenues.

The main mechanisms for regulating coastal development were through permit approval processes. Requirements for an Environmental Impact Assessment (EIA) for coastal development activities in the coastal zone were in place at all case-studies except Iraq. This process can potentially play a pivotal role in protecting coastal ecosystems particularly against large-scale port development, coastal wind-farms or extraction industries. However, the EIA process minimises impact to seagrass only if meadows are protected specifically through legislation. For example, all marine plants are protected under fisheries legislation in Moreton Bay and the Great Barrier Reef, Australia, meaning that destruction, damage or disturbance of marine plants without approval is prohibited. Further, the EIA process is only effective if seagrass is valued for its ecosystem services. For example, none of the large state-led coastal land reclamations have been rejected in the Republic of Korea, despite protection for tidal flats (including seagrass) through legislation, largely because research on seagrass was limited to biodiversity and did not account for their functional roles (Lee et al., 2016).

Although 80% of case-studies have policies, adaptation strategies or action plans for climate change, only two regions, Great Barrier Reef (Great Barrier Reef Marine Park Authority, 2012) and German Wadden Sea (Common Wadden Sea Secretariat, 2010; Hofstede and Stock, 2016), specifically mention the value of an ecosystem based approach to climate change adaptation and mitigation. The absence of measures to mitigate the effects of rising sea level and sea temperature on coastal ecosystems indicates that climate change is not yet making the political agenda for seagrass protection, despite the threat it poses to seagrass (Kim et al., 2015). All case-study regions are signatories on the Paris Agreement (UNFCCC, 2015) except Russia and Iraq, and broad reductions in emissions should reduce the risk to seagrass habitats (Jordà et al., 2012).

The development of climate mitigation strategies specific to seagrass ecosystems is nascent. Some countries are working on ‘eco engineering’ alternatives to grey infrastructure that may allow seagrass habitats to migrate as the sea level rises. For example, options for mitigating coastal erosion in Thailand include restoring mangroves and planting bamboo fencing as ‘bioshields’ (Saengsupavanich, 2013). However, other regions prioritised historic and cultural protection over coastal habitat protection. For example, Venice (Italy) is building a system of storm surge mobile barriers at the lagoon inlets that will reduce seawater intrusion into Venice city during abnormal tides (above 1.1 MSL). The barriers are predicted to have

adverse consequences for coastal habitats under sea-level rise projections (Bellafiore et al., 2014).

The main mechanism through which countries minimised the risk of invasive species to seagrass habitats was through limiting activities that create vectors for invasive species, primarily through ballast water management. Seven countries had ratified or agreed to the International Convention for the Control and Management of Ships' Ballast Water and Sediments, which came into force in September 2017 (International Maritime Organisation, 2018). Countries of case-studies not signatory to this convention such as USA and Australia had their own ballast water regulations and guidelines in place minimising the risk of spread, (e.g. Department of Agriculture and Water Resources, 2017). Measures to mitigate the risk of biofouling were mainly limited to regional/national guidelines and International Maritime Organisation guidelines. With the exception of the EU, it was not clear that other case-studies had legislation or policies to address the threat of invasive species from mariculture and aquaria.

2.3.5.3 Does management consider cumulative impacts?

There was little protection for seagrass or any coastal resources from cumulative impacts in the majority of case-studies. Of the 20 review regions, cumulative impact policies were absent from 14 case-study regions (Supplementary Table A.6). This is concerning given that cumulative impact policies provide the main mechanism for decision-makers to consider multiple threats and cumulative effects through EIA, SIA, SEA, AEE or equivalent processes. The absence of cumulative impact policies means that only the footprint of the proposed activity requires assessment through these processes, rather than the impact on the receiving environment from the sum of all past, present and proposed future activities and land-based threats (Bidstrup et al., 2016; Willsteed et al., 2017). The six regions where cumulative impacts are accounted for include Moreton Bay and the Great Barrier Reef (Australia), Chesapeake Bay, Mississippi River and Trinity Bay (USA), and Fraser River (Canada). The USA provides the most comprehensive framework for considering cumulative impacts, which involves regulations, guidelines and handbooks to assist government practitioners.

The EU requires member states to consider the nature of cumulative effects compared to other existing projects through the EIA and SEA Directives, but lacks a specific policy helping to achieve this. The lack of policy supporting actions has hampered the ability of member states to thoroughly assess cumulative impacts, such as in the Veneto Region of Italy

(Ostoich and Wolf, 2017). Further, the documents that guide the assessment of cumulative effects are almost 20 years old (Walker and Johnston, 1999) and do not include the significant advancements made towards assessing cumulative impacts (Bidstrup et al., 2016; Brown et al., 2014).

2.3.5.4 Do Plans consider multiple pressures?

Plans can be an essential tool to address the interactions among multiple pressures and cumulative impacts, because they are capable of facilitating the integration across different sectors and jurisdictions (Portman, 2011). However, not all management plans achieve this. Only five of the 15 regions in the high cumulative impact zones had Plans in place and only two of these specifically addressed multiple pressures on seagrass (Table 2.3): the Trilateral Wadden Sea Plan (Common Wadden Sea Secretariat, 2010) (German component assessed only) and the Pilot Draft Plan for the Western Part of the Gulf of Gdansk, Poland (Zaucha, 2010).

Three of the five additional case-studies included in the review had spatial Plans protecting seagrass from multiple pressure (Australian Government, 2015; Chesapeake Bay Program, 2015a, 2015b, 2015c; Queensland Government, 2008). Three of these case-studies did not use the Plans in an integrated way to address multiple pressures on seagrass habitat (Table 2.3). For example, the Moreton Bay Zoning Plan only limits fishing and recreational use up to the mean high water spring tide and it lacks integration with the urban-land use plan. Therefore, there is no mechanism to manage the system holistically, because different sectors are responsible for water quality management and coastal development within the bay. Conversely, the Chesapeake Bay Program focused predominantly on improving water quality to reduce impacts to seagrass and other submerged aquatic habitats. The Australian Federal Government acknowledged the lack of cohesion in management to address threats to the Great Barrier Reef Marine Protected Area from a zoning plan alone and developed interrelated Plans that built on the original Zoning Plan (Queensland Government, 2004) to reduce pressures from marine and coastal activities (e.g. Australian Government, 2018, 2015). However overall, there was insufficient information within the Plans to ascertain how, and if, they controlled for cumulative impacts. No Plans referenced cumulative impact policies, despite such policies being available for some case-studies (Moreton Bay, the Great Barrier Reef, Chesapeake Bay, Mississippi River, Trinity Bay and Fraser River) suggesting that management plans are lagging behind policy recommendations on cumulative impacts.

Plans are particularly important to support implementation of legal instruments. For example, in India, seagrass is defined, as an ‘ecologically sensitive area’ in the Coastal Regulation Zone 2011 and states are required to develop a Coastal Zone Management Plan in order to protect these areas at the regional level. However, the timeframe for states to develop these plans continues to be delayed (Ministry of Environment Forest and Climate Change, 2017). Thus, in India there has been minimal protection for seagrass habitats, as national laws have not been translated into actionable outcomes at the regional level.

2.3.5.5 Are seagrass habitats stable or recovering in areas that address multiple pressures to seagrass?

The only evidence we identified from the peer-reviewed literature that attributed the stability or recovery of seagrass to the implementation of a Plan was from Chesapeake Bay and the German Wadden Sea (see references in Table 2.3). Chesapeake Bay’s Program focused on reducing nutrients and sediment in the surrounding catchment and includes ambitious restoration and monitoring goals. By 2015, the program had achieved an interim goal of restoring 36,500 ha of seagrass, although this was short of the project’s planned 90,000 ha by 2017 (Orth et al., 2017). The recovery of seagrass through improving water quality has been documented elsewhere (Sherwood et al., 2017). For example, Singapore managed to retain its seagrass diversity despite over 80% of its shoreline being modified (Lai et al., 2015), through applying stringent water quality standards and laws (Yaakub et al., 2014). This occurred despite the lack of a specific management plan for the coastal environment. The German Wadden Sea Plan employed a more holistic approach that spatially zones and manages most activities capable of exerting anthropogenic pressure on seagrass. In the German Wadden Sea, the potential for new sites to be colonised indicates the effectiveness of the current management regime (Folmer et al., 2016).

The other three case-studies with a Plan in place show variable seagrass trends. Annual environment report cards for Moreton Bay and the Great Barrier Reef indicate that some seagrass meadows are becoming more fragmented and declining in area, while other meadows remain stable (Coles et al., 2015; Maxwell et al., 2015). Seagrass is recovering in the western part of the Gulf of Gdansk (Węśławski et al., 2013), however the recovery occurred prior to development of the Plan from efforts to reduce eutrophication (Bostrom et al., 2003). Active seagrass restoration projects are also underway in the western part of the Gulf of Gdansk (Institute of Oceanology Polish Academy of Sciences, n.d.).

Table 2.3 Activities (relating to threats to seagrass) addressed through a management Plan in the five regions with management plans in place

Plan ^a	Activities addressed by a Plan ^b														Integrated with urban plan	% Pressures addressed	Seagrass stable or recovering (references)
	Fisheries & aquaculture	Energy generation	Extractive industries	Land-based industries	Port development -	Transport & shipping	Transport & shipping -	Coastal infrastructure -	Coastal infrastructure -	Coastal infrastructure -	Tourism & recreation	Military	Agriculture	Climate change	Zoning scheme		
WSP																79	Stable with habitat to recolonise (Folmer et al., 2016; Reise and Kohlus, 2008)
CB																29	Recovering (Lefcheck et al., 2018; Ruhl and Rybicki, 2010)
MB																37	Likely stable along the eastern banks (Roelfsema et al., 2009), losses along the western banks
GBR																68	Generalised declining trends (Coles et al., 2015)
PDP																45	Recovering (Bostrom et al., 2003) but prior to development of the Plan

^a WSP (Common Wadden Sea Secretariat, 2010), CB (Chesapeake Bay Program, 2015a), MB (Queensland Government, 2008), GBR (Australian Government, 2015), PDP (Zaucha, 2010).

^b Description of activities in Supplementary Table A.4. Shaded area indicates threat addressed through a Plan. Dark grey indicates not applicable as it is not identified as a major activity in the case-study region. White cells indicate that the activity is not considered within the Plan.

2.4 Discussion

We found that protection for seagrass is inadequate for the majority of case-studies in this review. Management frameworks are still dominated by sectoral management approaches and there remains poor integration across jurisdictional realms. The institutional structures that dominate the case-study regions prevent the holistic approach needed to address interactions among multiple pressures and cumulative impacts. There were several examples of Plans that addressed multiple threats, but none of these Plans addressed cumulative impacts. The data required to set regional thresholds for exceedance, such as identifying minimal light requirements for seagrass are being collected in some regions, such as the GBR (Chartrand et al., 2012). Yet the flexibility of management plans to cross jurisdictions and sectors to incorporate science into a cumulative impact framework which considers multiple threats (e.g., water quality and coastal development) is still in its infancy (Seitz et al., 2011; Therivel and Ross, 2007). Threat impact maps and dynamic quantitative modelling approaches may go some way towards assisting managers to develop these frameworks such as shown for the Great Barrier Reef (Anthony et al., 2013). These findings suggest that the translation of research on cumulative impacts and multiple pressures into management frameworks are a priority for improving protection of seagrass. This will require greater effort to translate science into policy, such as through transdisciplinary research or knowledge translation (Curran et al., 2011; Pohl, 2008).

The following priorities could fill management gaps, and speed development and implementation of Plans that address multiple pressures and cumulative impacts.

1. Seagrass habitats require more recognition of their value on a global scale (Cullen-Unsworth and Unsworth, 2018). In democratic societies, the recognition of value puts pressure on government to create policies for protection. The multitude and complexity of pressures faced by seagrass suggest seagrass require their own legislative and planning frameworks. Plans that implement zoning schemes and are integrated with urban or land-use plans provide the most effective method to manage multiple pressures and cumulative impacts. Importantly, such plans can also overcome sectoral and jurisdictional barriers. Management needs to be supported by research that considers the importance of functional roles and quantifies ecosystem services (Ruiz-Frau et al., 2017). Allowing local communities and stakeholders to have an active voice in planning and budgeting will also contribute to the success of

management activities (Chirenje et al., 2013). Public education and outreach documents, such as codes of practice, guidelines, vision statements, procedures and programs of work, are important tools to support environmental awareness and should be developed through public engagement in conjunction with planning and regulatory frameworks. For example, in the Gulf of Thailand buoys are used to mark the perimeter of valued seagrass beds in an effort to increase environmental awareness and minimise impact by coastal users (Department of Marine and Coastal Resources, 2016).

2. Monitoring of seagrass habitat requires a consistent approach across its range to detect inter-annual trends, because this will support both planning and approval processes and monitoring is essential to highlight the level of management intervention required (Ruiz-Frau et al., 2017). Monitoring information will also support the development for specific policy documents to manage multiple pressures and assess cumulative impacts. For example, the lack of information on seagrass distribution and diversity in China has hindered national conservation programs for seagrass (Zheng et al., 2013). Monitoring needs to extend into the subtidal sea, particularly for EU member states, to ascertain if protection gaps exist for subtidal seagrass habitat. Support to assist monitoring efforts of seagrass is gaining traction. For example, the United Nations Environment Program Northwest Pacific Action Plan (NOWPOP) Special Monitoring and Coastal Environmental Assessment Regional Activity Centre (CEARAC) is currently developing a tool for mapping seagrass distribution with satellite images using cloud computing technology in the NOWPOP regions (Russia, China, Republic of Korea and Japan) (NOWPOP-CEARAC, 2018).
3. More support is needed for countries with a medium to low HDI that are potentially suffering from extensive seagrass loss and lack adequate governance (Wonah, 2017), institutional knowledge and resources to effectively protect their coastal area (e.g. Nigeria). These losses are occurring despite the many avenues of support from the IUCN, United Nations and EU (Mmom and Chukwu-Okeah, 2011). The Memorandum of Understanding between the Republic of Korea and the Trilateral Wadden Sea Nations provides an example of how countries can transfer knowledge and provide support (Ministry of Land Transport and Maritime Affairs of the Republic of Korea and the Trilateral Cooperation on the Protection of the Wadden Sea, 2009), which could be replicated elsewhere.

4. Management Plans need to consider how local actions to protect seagrass can account for the impacts of climate change. The importance of choosing eco-engineering design to reinforce coastal stability needs to be part of climate change policies.
5. Cumulative impact policies need to be developed to enable consideration of multiple pressures and cumulative impacts through the EIA and similar processes. There are examples of Plans that address multiple pressures and cumulative impacts. These examples may guide management in regions that lag in addressing these issues. For instance, the German Wadden Sea Plan, effectively a Trilateral Wadden Sea Plan, provides the most comprehensive framework for the management of multiple pressures among 20 case-studies.

We comprehensively reviewed management literature in 20 regions, fifteen of which are exposed to the most threatening watershed processes. Seagrass ecosystems may also be highly threatened in regions unassociated with rivers, such as in regions with extensive coastal development (Holon et al., 2015). This review could be expanded in the future to cover more regions and consider hotspots of coastal development threat. In terms of coverage, we included some non-English language literature and case-studies from a range of seagrass bioregions and countries. The broad range of sites we reviewed means it is likely that we represented the current status of seagrass management globally. Future efforts could review more non-English language literature to improve our understanding of seagrass protection in certain hotspots of seagrass decline, which may also have low scientific capacity. In addition, the relative impacts of different threats to seagrasses varies by bioregion (Grech et al., 2012), thus future research should consider a greater number of bioregions to ask whether Plans reflect differences in the regional importance of threats. It is important that future reviews follow a comprehensive and detailed approach as we have, because many Plans intrinsically protect seagrass without specifically mentioning it as a valued habitat. There are other avenues to obtain information on existing management tools and policies in addition to a literature review process. Engagement with local agencies and experts that play a role in coastal management (e.g. Gill et al., 2017) could also be used to fill gaps in the literature.

The priorities we have proposed here are similar to regional findings about what is needed to enhance seagrass protection (Fortes, 2018; Kirkman and Kirkman, 2002). In South East Asia, a regional effort to increase awareness to conserve seagrass, monitor ecosystem changes, and

manage their services and users, is urgently needed to address seagrass conservation (Fortes, 2018). In India, utilising the existing legislative framework to develop and implement management practises that reduce the risk of threats would enhance protection for seagrass (Ramesh et al., 2018). Further, educating government bodies on the importance of seagrass ecosystems and how it relates to their role as environmental managers is also considered important to enhance protection (Ramesh et al., 2018).

The inefficiencies of Plans to effectively address multiple pressures and cumulative impacts on marine environments more broadly has been shown elsewhere (Halpern et al., 2008). For example, in a review of 8 global case-studies of regional Plans, less than 20% involved adequate stakeholder engagement, ecological monitoring, adaptive management or utilised a co-management approach (Arkema et al., 2006). Similarly, other reviews have identified an emphasis on strategic sectoral objectives and top-down approaches in marine Plans (Jones et al., 2016). The DAPSIR framework can help planners to integrate different sectors, for instance, a recent model of the impact of multiple pressures on food-webs in an estuary with shared governance suggested an intergovernmental masterplan is needed to prevent a significant loss of biomass (De Jonge and Schuckel, 2019).

Future work could pair our method for reviewing legislation, policies and Plans with monitoring data to measure the impact of management on seagrass distribution and cover. Promising signs of seagrass recovery have been found in regions that had long monitoring time-series, like Chesapeake Bay (Lefcheck et al., 2018). Furthermore, new management plans could be evaluated a-priori with quantitative models of cumulative impacts to seagrass habitats (e.g. De Jonge and Schuckel, 2019). However, it remains an important question as to whether more comprehensive management of multiple pressures and cumulative impacts translates into better outcomes for conservation of coastal habitats (Micheli et al., 2013). A key challenge to overcome in assessing conservation progress is the accurate assessment of counterfactuals, i.e., what would have happened if there was no management intervention (Baylis et al., 2016). Future work could apply the DAPSIR framework to identify management actions that are most effective at addressing specific drivers and pressures.

Unfortunately, the lack of data on seagrass trends in the case study regions made it difficult to evaluate if the existence of policies and Plans was actually making a difference to seagrass ecosystems at the local level. Thus, it is difficult to verify if the political will has a positive outcome for seagrass conservation for the majority of case studies. However, there are

examples where social will has made a difference to seagrass conservation. For example, Singapore protected one area of seagrass against a planned reclamation project due to effective outreach programmes which changed public opinion to value seagrass over development (Wee and Hale, 2008).

In identifying the disjunction between policy and practice and how this relates to management of multiple threats, our findings are consistent with Ruckelshaus et al., (2008) and Jones et al., (2016). The novelty of this review is in presenting the core issues specific to seagrass ecosystems that hinder the progression of conservation outcomes. Further this review offers, a unique perspective in regions that are less studied. Many of the Plans we reviewed were applied to coastal ecosystems generally, so it is likely our findings of significant gaps in the protection of seagrass also apply to other ecosystems. This remains to be tested, however. Efforts to improve the protection of coastal ecosystems more generally could benefit from the methodology we developed here: the five key questions we developed (Table 2.2) could be applied by governments or non-government organisations in any region to rapidly assess the status of protection of coastal ecosystems. Without legislation and policies to support actions that address multiple pressures and cumulative impacts, it is likely that the status of coastal ecosystems will continue to degrade.

2.5 Supporting Information

Supplementary information reference list (Supplementary Table A.1), Case studies included in the analysis (Supplementary Table A.2), DAPSIR for seagrass adapted from Smith et al., (2016) and Elliott et al., (2017) (Supplementary Table A.3), description of activities identified through the review (Supplementary Table A.4), examples of the pressure mechanisms identified in this review through which state changes were observed for seagrass ecosystems (Supplementary Table A.5) and a summary of case-studies included in this review (Supplementary Table A.6). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Chapter 3 A data driven approach for cumulative impact assessment on marine protected areas

This chapter includes a co-authored paper currently under review in Conservation Biology. This chapter is formatted to the journal that it is currently in review with. The bibliographic details of the co-authored paper, including all authors, is:

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Author Contributions

Conceptualisation of the study: LLG, CJB, JW, RC. Methodology: LLG, CJB, VJDT. Formal analysis of the data: LLG, CJB, CAB, MPT, MC. Data collection: LLG, JW, DH, HAM. Visualisation: LLG. Writing – original draft preparation: LLG. Writing – review and editing: CJB, CAB, MPT, MC, JW, DH, RC.

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3.1 Abstract

Coastal reef fish are subject to multiple threats from land- and marine-based activities. These threats are further exacerbated by climate change. However, most seascapes are not managed in a way that considers the impact of multiple threats, partly because we have a poor understanding of how these threats accumulate spatially and partly because we lack data on the impact of threats to species and ecosystems. Relationships between threats and species and ecosystems are potentially non-linear, and so current approaches to estimating the impact of threats may be misleading. We develop a data driven approach to deal with the effect of confounding variables when assessing cumulative impacts on temperate rocky reef fish and we apply it to the northern NSW near-shore environment (Northern Bioregion). We use data on water quality, commercial fishing, climate change, and indicators of recreational fishing and urbanisation to build a cumulative threat map to identify where the top 10% of threats co-occur. Using a statistical model of fish abundance for targeted fishery species (invertivores and carnivores), we quantified associations among cumulative threats and environmental covariates and predicted where cumulative impacts are likely to have the greatest impact on fish abundance. Lastly, we assessed the performance of no-take zones to protect near-shore targeted fish species from cumulative threats across two marine parks (Solitary Islands Marine Park and Port Stephen Great Lakes Marine Park). We found that the cumulative effects of fishing have a greater impact on fish abundance in comparison to the cumulative effects of water quality threats. We also found that cumulative impacts of fishing outside of no-take zones are impacting fish abundance inside no-take zones. However, the data driven approach resulted in some unexpected outcomes (such as an increase in fish abundance as water quality decreases) and therefore we discuss the strengths and weaknesses of this approach to cumulative impact assessment. Understanding the spatial influence of multiple threats is important because it enables managers to understand the potential complexity of management actions required to address them.

Keywords: cumulative impact maps, water quality, fishing, climate change, New South Wales.

3.2 Introduction

The coastal-marine environment supports rich biodiversity and provides numerous ecosystem services that support coastal communities, however, it is under increasing pressure from a

range of anthropogenic land-based and marine-based threats (Halpern et al 2019). Land-based activities introduce nutrients and pollutants into coastal waters that influence estuarine and marine coastal ecosystems (Brown et al., 2017; Lefébure et al., 2013; Smith et al., 1999). Marine-based activities, including fishing, have direct impacts on fish biomass and indirect effects on ecosystems through changes in food webs (Fu et al., 2020; Jennings and Polunin, 1997). Effective management is required to minimise and regulate the impact of these activities; however, they are commonly managed independently by different sectors and actors and often involve tools that target single activities, such as marine protected areas that limit fishing, but do not address the impacts of poor water quality (Álvarez-Romero et al., 2011; Elliott, 2014). The lack of integrated land-sea plans is one key reason coastal management has failed to address the cumulative impacts of multiple threats (Griffiths et al., 2020; Tulloch et al., 2021).

One of the reasons underpinning this lack of integration is the difficulty in predicting how threats translate into impacts on ecosystems. Mapping cumulative threats is important because it provides a mechanism to evaluate the footprint and intensity from land and marine based threats (Halpern et al., 2008). This information is useful for managers because it provides a tool to support and guide management decisions by enabling managers to adaptively target actions in spatially explicit areas of most concern (Giakoumi et al., 2015; Stelzenmuller et al., 2015; Tulloch et al., 2015). However, translating threats into impacts on species and ecosystems requires knowledge of their vulnerabilities to the threats. Typically we use expert knowledge or empirical knowledge to predict impacts from threats (Grech et al., 2012; Halpern et al., 2007; Turschwell et al., 2020). Expert elicitation is commonly used to weight the vulnerabilities of species and ecosystems to threats and thereby interpret the impact from cumulative threat maps (Loiseau et al., 2021; Stockbridge et al., 2021). However, this process is resource intensive (Grech et al., 2012; Halpern et al., 2007) and introduces ‘knowledge-based uncertainty’ which can affect the reliability of the results and its application to management (Jones et al., 2018). Impact maps typically also weight threats linearly or log-linearly by the vulnerabilities, so these impact maps assume a positive and monotonic relationship between increasing threats and increasing impacts.

An alternative approach to assessing impacts is to use statistical models to fit empirically-measured ecological responses to threats (Stockbridge et al., 2021). The vulnerability of an ecological response to a threat then becomes a function (potentially non-linear) rather than a

single weight. Empirical assessment is useful in that it is not subject to expert biases, and may suggest a non-monotonic or decreasing relationship between a threat and its impacts on the ecosystem. However, empirical data can have greater cost to acquire than expert elicited vulnerabilities and so has not been as widely explored as an option for assessing cumulative impacts (Halpern et al., 2008; Johannes, 1998; Teck et al., 2010). Estimating vulnerabilities from data is also challenging because cumulative threats are confounded by their nature (hence being cumulative) so it may be difficult to statistically separate the effect of one threat from another. Therefore, there is a need to further develop cumulative impact mapping approaches that draw directly on empirical measurements of ecological responses.

The Northern Region of New South Wales (NSW) from Port Stephens to Tweed Heads, provides an ideal setting to explore the empirical approach to cumulative impact assessment. The region has a coastal zone that is scattered with no-take zones inside Marine Parks, which have been the subject of ongoing monitoring of fish abundance since 2010 (Harasti et al., 2018a; Knott et al., 2021; Malcolm et al., 2016). The landscape is also moderately urbanised, with gradients of human threats inshore-to-offshore and north-to-south. Key threats include reduced water quality, and the marine environment is an important recreational and commercial fishing area (NSW Government, 2018). The area is also actively managed with routine ecosystem health monitoring, marine park management plans, recreational fishing bag and size limits and commercial fisheries reporting. Thus, the area is rich with spatial and temporal data on threats and biodiversity.

In this study, we develop a cumulative threat map to predict how different threats impact reef fish abundance and then make predictions about the impact of cumulative threats on fish abundance through a no-take zone lens. Specifically we aim to: i) build a cumulative threat map based on indicators of water quality, fishing and climate change; (ii) build a predictive model of fish abundance from the threat data and other environmental covariates; (iii) apply predictive modelling to predict cumulative human impacts on fish abundance, and; (iv) assess the performance of no-take zones to protect near-shore targeted fish species from cumulative impacts. The approach we propose addresses both the issues of non-linearity in the vulnerability of ecosystems to threats and confounding of cumulative impacts. This information provides an exploratory analysis of cumulative impact assessment in the coastal-marine environment. It also identifies further research needs that will improve the

understanding of cumulative impacts in northern NSW and inform future management priorities.

3.3 Methods

3.3.1 Northern Region of NSW

We used the Northern Region of NSW as a case study (Figure 3.1). The Northern Region extends from Tweed Heads (Queensland) to Port Stephens (NSW) and encompasses approximately 700 km of coastline. The region contains rich sub-tropical and temperate marine biodiversity and a diverse range of habitats including coral reefs, mangroves, seagrass, saltmarsh, inter-tidal and sub-tidal rocky reefs and estuaries. The area is also valued for its relatively intact natural landscapes and numerous National Parks and Nature Reserves that border the coast. However, the region is also experiencing urban growth as people migrate from capital cities to regional centres (Department of Premier and Cabinet, 2018). The majority of the population in NSW lives within 50 km of the coast (Clark and Johnston, 2016) and the region includes, or is adjacent to, Australia's largest non-capital cities being Newcastle and the Gold Coast (population density of 896 and 476 persons/km², respectively; Australian Bureau of Statistics, 2021; Haward et al., 2013). Recreational fishing is popular in the region with the North Coast accounting for approximately 30% of funds spent by anglers in NSW (McIlgorm and Pepperell, 2014). Significant commercial fisheries are also widespread over the region, based on ocean trawl, trap, line and haul methods (Department of Primary Industries, 2017). Elevated threats to marine species identified for this region are related to fishing (commercial and recreational fishing), intensification of human land-uses (elevated urban stormwater discharge, foreshore development, and estuarine modification), and climate change (elevated sea surface temperatures (SST), and altered nutrients, current and weather patterns) (Fletcher and Fisk, 2017).

The region includes three multiple use NSW marine parks: Cape Byron Marine Park (CBMP), Solitary Islands Marine Park (SIMP) and Port Stephens-Great Lakes Marine Park (PSGLMP). The SIMP was established in 1998 with zoning and rules applied in 2002 and is approximately 710 km². Part of the SIMP was a marine reserve prior to formal establishment (since 1991). A federally managed jurisdiction (Australian Marine Park) joins the park out to the 50 m depth contour. The PSGLMP is 980 km² and was established and zoned in 2005 and 2007, respectively. The commonwealth managed Hunter Marine Park adjoins the PSGLMP and extends from the state water boundary to off the continental shelf. The CBMP is the

smallest of park systems in the region (220 km²) and is not the subject of this study because comparative fish monitoring data was not available. All of the State marine parks extend out to a distance of three nautical miles which is the seaward limit of the NSW Marine Estate (NSW Government, 2018). A range of fisheries restrictions are utilised in the Marine Parks including Sanctuary Zones (no-take), Habitat Protection Zones (limits imposed on some commercial fishing, aquaculture and collecting activities) and general use zones (limits on some netting and longlining activities). We restricted our analysis to the study region out to a distance of 50 km as it was an area of moderate impacts to the marine environment over a range of threats and has been a focal area for long-term monitoring data of fish abundance (Knott et al., 2021; Malcolm et al., 2018).

3.3.2 Threats

We identified ten anthropogenic threats (stressors) (Table 3.1) of relevance to the Northern Region marine environment (Fletcher and Fisk, 2017) and for which data was available throughout the study area (detailed description in Supplementary Table A.7). The threats represent the common dimensions of human-derived threats for coastal marine species: pollution, fishing, coastal development and climate change.

Data on threats were obtained from the NSW government, Australian Ocean Data Network (AODN), the Australian Bureau of Statistics (ABS) and other sources (Supplementary Table A.7). Water quality indicators consisted of nutrient (chlorophyll-*a*) and turbidity data (Scanes et al., 2007). Nutrient and turbidity data was derived from routine water quality monitoring of NSW estuaries and recorded as the mean total Nitrogen (N) and turbidity (NTU) value, respectively, from the site/s located closest to the river/estuary mouth from 2007 to 2020 (Department of Planning Industry and the Environment, 2020). Nutrient data (mean chlorophyll-*a* concentration) was also obtained from daily surface multi-spectral measurements of sunlight collected from satellites from 2006-2020 (Integrated Marine Observing System, 2014a). Both chlorophyll-*a* and turbidity provide effective measures of water quality (Scanes et al., 2007). We also considered estuarine modification and condition ranking data (OzEstuaries, 2003) in addition to the water quality parameters, however, the data was not comprehensive across the study region and was confounded with measured water quality parameters.

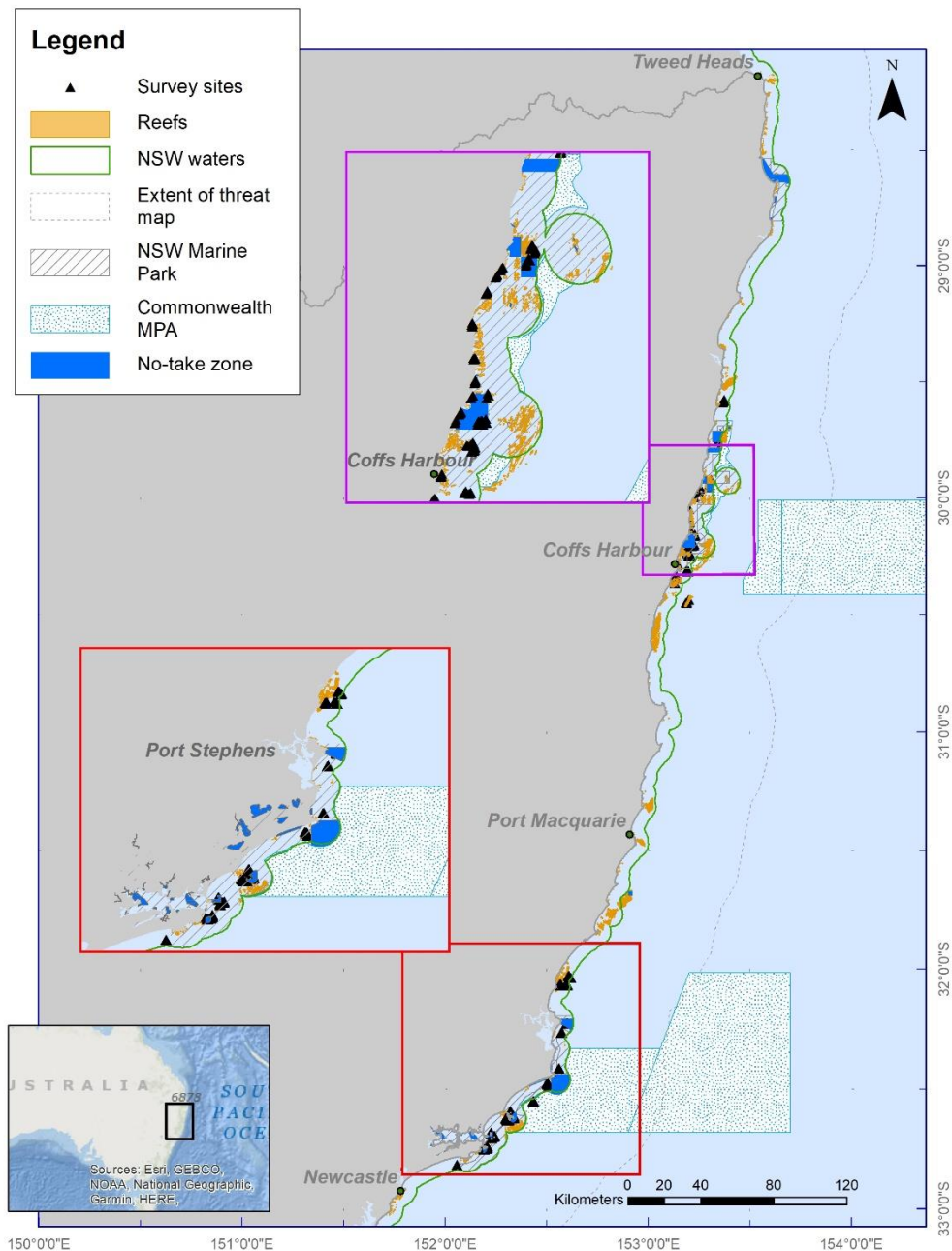


Figure 3.1 Map of Northern Bioregion of New South Wales, Australia showing the study area. Map produced using ArcGIS, ArcMap version 10.3 software. Reef polygons and BRUV survey locations provided by NSW DPI (2013). Protected area zones sourced from Department of Agriculture Water and the Environment (2020). Source of the ocean base map: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors.

Climate change threats consisted of SST anomalies (i.e. the number of years where current SST is greater than historic SST) obtained from single-sensor NOAA polar-orbiting multi-satellite data (Integrated Marine Observing System, 2014b). We also considered ocean

acidification (OA) from the AODN as an additional climate change measure, but there was very little difference in OA concentration within the study area for differences to be detectable. Commercial fishing catch per unit effort data was obtained from the NSW Department of Primary Industries (DPI). Recreational fishing pressure was based on the linear distance to boat ramps (Transport Roads and Maritime Services, 2021), weighted by an indicator of boat-ramp usage (single vs multi-lane ramps). Indicators of population pressure followed the method of Ostwald et al. (2021) and utilised population and housing data from the 2016 Census (Australian Bureau of Statistics, 2021). All threat layers were reprojected to the same base raster with a consistent resolution (500 x 500 m) and projection (UTM zone 56S WGS84). Analyses were performed with the R program (R Development Core Team, 2018), using the raster (Hijmans et al., 2021) and sf packages (Pebesma, 2018).

Table 3.1 Summary of the anthropogenic threats used in the Northern Region, NSW threat map.

Category	Measure	Description	Original Resolution	Date	Source
Pollution	Nutrients - ocean	Ocean chlorophyll- <i>a</i> concentrations from satellite data from the MODIS sensor.	0.02 degrees	2006-2020	IMOS (2014a)
	Nutrients - estuary	Total nitrogen (N) concentrations from routine water quality monitoring in all estuaries throughout NSW	modelled 0.5 km ²	2007-2020	NSW DPIE (2020)
	Turbidity - estuary	Turbidity measurements from routine water quality monitoring in all estuaries throughout NSW	modelled 0.5 km ²	2007-2020	NSW DPIE (2020)
Fishing	Commercial – demersal	Trap, bottom trawl (prawns) and bottom line catch per unit effort from commercial fishing logbook data. Three threat layers included.	0.01 degrees	2009-2020	NSW DPI
	Commercial - midwater	Midwater line catch per unit effort from commercial fishing logbook data	0.01 degrees	2009-2020	NSW DPI
	Recreational	Estimated by distance to boat ramp based on a proxy for regional boat ramp usage	modelled 0.5 km ²	2020	TRMS (2021)
Climate Change	Sea surface temperature (SST) anomaly	Frequency of SST above the historical mean from daily SST satellite derived data	0.01 degrees	1992-2020	IMOS (2014b)
Urbanisation	Population pressure	Estimated by population density	modelled 0.5 km ²	2020	ABS (2021)

3.3.3 Fish monitoring data

Fish abundance data was collected using stereo baited remote underwater video (stereo-BRUV) at shallow reefs (<50 m) over randomly selected, spatially independent sites between 2010-2018 (Harasti et al., 2018b; Knott et al., 2021; Malcolm et al., 2018; Williams et al., 2018). Shallow rocky reef habitat had been previously identified using acoustic bathymetry maps (Jordan et al., 2010), or maritime chart information or depth sounders in the absence of acoustic maps (Malcolm et al 2018). Sites included Sanctuary Zones, Habitat Protected Zones and locations outside the marine park; herein referred to as ‘no-take’, ‘partial protection’ and ‘outside’, respectively. However, only no-take and outside sites were considered in the analysis. Four replicate stereo-BRUVs were deployed per site for a period of 30 minutes and baited with approximately one kilogram of pilchards (*Sardinops sp.*) at the end of a PVC pole to attract targeted temperate reef fish species. Video imagery was post-processed and a relative abundance score was assigned (maxN) as the maximum number of fish in any one frame for each species to the lowest taxonomic level possible (Langlois et al., 2020). The BRUV data was interrogated for trends across categories (functional group, effect of MP, etc.). The data was grouped into two functional groups: invertivores and carnivores (Supplementary Table A.8). Invertivores accounted for the majority of fish (n = 3,616) and included 12 species (algae/invertebrate consumer, invertebrate carnivore and zooplanktivores feeding guilds). Carnivores (n = 2,840) included 31 species (scavenger, piscivore, and generalist carnivore feeding guilds).

3.3.4 Hotspots of cumulative threats

We combined the layers of threats to identify hotspots of cumulative threat. Hotspots were defined as grid cells that were in the top 10% of all grid cells for more than one threat. The cumulative threat score was the count of the number of threats that cell was in the top 10% for each grid. Thus, the hotspot index H_i could take only integer values, between 0 and 10 threats and was defined:

$$H_i = \sum_j^{10} (T_{i,j} \geq T_j^{90\%}) \quad (1)$$

Where $T_{i,j}$ is the value for threat j in grid cell i and $T_j^{90\%}$ is the upper 10% quantile for the threat j . We see this approach as a precursor to a full cumulative impact assessment that does

not require vulnerability weights and thus is agnostic about the ecosystem's vulnerability to the threats.

We additionally calculated spearman's pairwise correlations among threats. A high positive pairwise correlation between two threats means those threats co-occur more often than by chance. A strong negative correlation means the two threats disassociate more often than by chance. Thus, strong positive correlations suggest combinations of threats that would benefit from a co-management approach, whereas strong negative correlations suggest threats that can be managed independently of each other.

3.3.5 Model of fish abundance

The abundance of temperate rocky reef fish was modelled for two functional groups (carnivores and invertivores) of fisheries targeted species (Knott et al., 2021) captured by stereo-BRUV. Fishery targeted species includes 57 species from 31 families. Fish abundance was compared in two areas subject to different management: (i) no-take and (ii) outside (sites located outside MPs).

We used biophysical covariates and threats to quantify associations among environmental gradients, threats and the abundance of fish across two MPs (SIMP and PSGLMP). The biophysical covariates tested were based on two *a priori* hypotheses for biophysical drivers of fish abundance. First, fish abundance is greater when reef habitats are ecologically connected to adjacent coastal wetlands (Olds et al., 2012), so we used distance from reef survey sites to mangrove, seagrass and saltmarsh habitats (NSW Department of Primary Industries, 2013). Second, we included depth as a covariate as the BRUV data was collected across shallow (<20 m) and intermediate reefs (>25 m) and depth has a strong effect on fish abundance (Malcolm et al., 2018). Year was also included in the model as a random effect, where we expected to observe recovery of abundance inside MPs over time and stable or declining trends outside of no-take MPs.

For each fish functional group, we fitted a model of threats and biophysical variables with covariates as additive effects. Modelling was undertaken in R (R Development Core Team, 2018) by fitting a negative binomial generalised additive model with log link functions (GAM, mgcv package, Wood et al. (2020)) using restricted maximum likelihood estimation (REML). We applied a negative binomial family because other more simple models were over-dispersed (Wood et al., 2016). We used the REML approach so we could interpret effect

sizes and predictions of fish abundance. The GAM framework allowed us to include non-linear effects for the continuous variables, which we modelled with thin plate regression splines (Wood, 2017). Concurvity was investigated to ensure that the remaining predictors were not strongly related (Wood, 2017). The majority of covariates had concurvity values within acceptable limits, apart from the effect of site variation (Supplementary Table A.9). The assumptions of homoscedasticity of variance and approximate normal distribution of the deviance of residuals were verified visually, revealing no major issues (Wood, 2017). Plots with confidence intervals were also used to visualise strength of effect on fish abundance for each covariate (visreg package, Breheny and Burchett (2020)). Highly confounded variables were removed from the final model (total nitrogen, commercial trawl fishing and distance to mangroves).

All threats used in the threat map were included as covariates. Some threats were partially confounded, so cubic shrinkage splines (Wood and Scheipl, 2020) were used to accommodate confounded covariates. Site was included as a random intercept in all models to allow for spatial co-variation in the data that was not explained by the predictor variables. All layers were checked against each other using a correlation matrix (ggally package in R, Schloerke (2021)) and layers that showed high collinearity were removed. The final model included three biophysical variables (depth, and proximity to seagrass and saltmarsh), six threats (SST anomalies, urbanisation, nutrients (chlorophyll-*a*), turbidity, recreational fishing pressure and commercial fishing (trap and line fishing)), protection status, year and site.

3.3.6 Cumulative impact map for reef fish

We created cumulative impact maps for fish abundance using the fitted models of invertivore and carnivore abundance. Maps were made for the cumulative impacts of all threats, all fishing threats and all water quality threats. To create these maps, we first predicted fish abundance across the entire region based on predictions using: (1) status-quo conditions, (2) status-quo conditions with no water quality threats (by setting water quality threats to zero), (3) status-quo conditions with no fishing threats (by setting all fishing related threats to zero) and (4) status-quo conditions with no threats (by setting all threats to zero). Water quality threats included chlorophyll-*a* (satellite data), turbidity (estuary monitoring data) and urbanisation (population pressure). Fishing threats included recreational fishing pressure (weighted boat ramp distance) and commercial fishing pressure (trap and line fishing CPUE). We then defined cumulative impacts at a grid cell to reef fish C_i as:

$$C_i = \hat{A}_{i,0} - \hat{A}_{i,T}$$

Where $\hat{A}_{i,0}$ is predicted fish abundance at a grid cell i with no threats and $\hat{A}_{i,T}$ is predicted fish abundance with either: all threats, no water quality threats or no fishing threats. Thus, the cumulative impact index represents the loss of fish abundance that could be attributed to the threat from water quality and/or fishing. By predicting cumulative impacts in these three categories, we could avoid issues associated with making predictions when there is confounding among similar types of threats.

Cumulative impact maps were created for both reef fish functional groups. Predictions were made using the ‘terra’ package in R (Hijmans et al., 2021). Covariates that were not spatially comprehensive over the study region were excluded from analysis (site and year). Predicted values were set to the observed maximum value for that variable to overcome issues with extrapolation of non-linear models.

3.3.7 Performance of Marine Parks to protect reef fish

For each fish functional group, we determined whether fish abundance improved inside no-take zones from the model of threats and biophysical variables by examining models’ coefficients for the no-take zone effects. We assessed the expected benefit of no-take zones in terms of non-fishing threats and non-water quality threats. We did this by taking the mean of all grid cells within each no-take zone for (1) the cumulative threat map that lacked fishing related threats, and (2) the cumulative threat map that lacked water quality threats, for each functional group.

3.4 Results

3.4.1 Hotspots of cumulative threats

We found cumulative threats operating throughout the NSW and commonwealth waters, with a greater concentration of threats within State Waters (Figure 3.2). We found the highest number of threats operating in the coastal regions of Ballina, between Nambucca Heads and Scotts Head and in areas between Laurieton and Forster beyond the limit of NSW jurisdiction. Offshore waters further than 20 km contained the least number of cumulative threats, including areas with no threats. A maximum of eight threats impacted any grid cell throughout the region. Individual maps of each threat are shown in Supplementary Figure A.1. The map of threats ranked by the top 5% of grid cells showed similar spatial patterns,

except that hotspots were clustered closer to the coast than in the top 10% map (Supplementary Figure A.2).

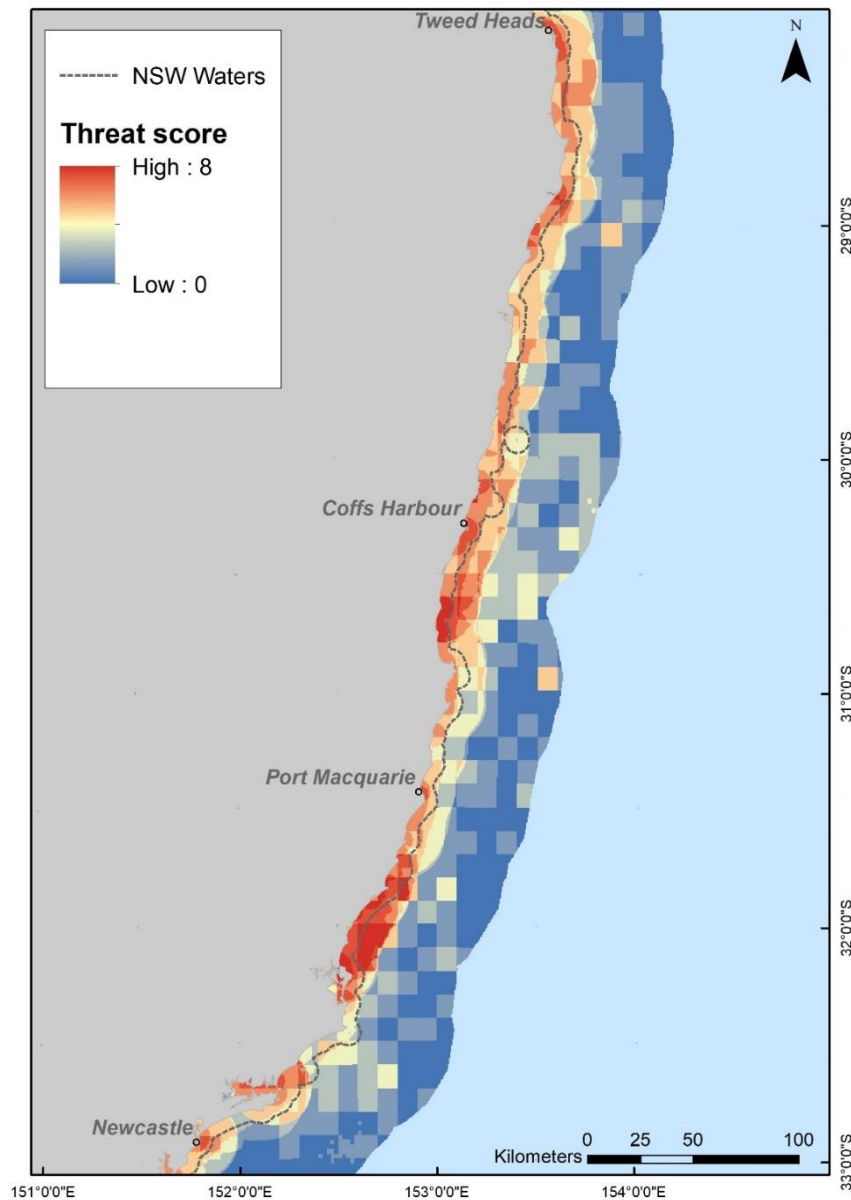


Figure 3.2 Map of hotspots of cumulative threat, where threat scores (H_i) are defined as the count of threats in the top 10% of all values for each grid. Refer to Table 3.1 for the list of threats layers included. Map produced using ArcGIS, ArcMap version 10.3 software.

A comparison of correlations between different threat layers (Figure 3.3) indicated that some threats were highly correlated, including water quality variables (turbidity and total N) being most positively correlated. Indicators associated with urban areas were also positively

correlated (population pressure, recreational fishing pressure and water quality). Threats that are highly correlated are likely to have cumulative effects.

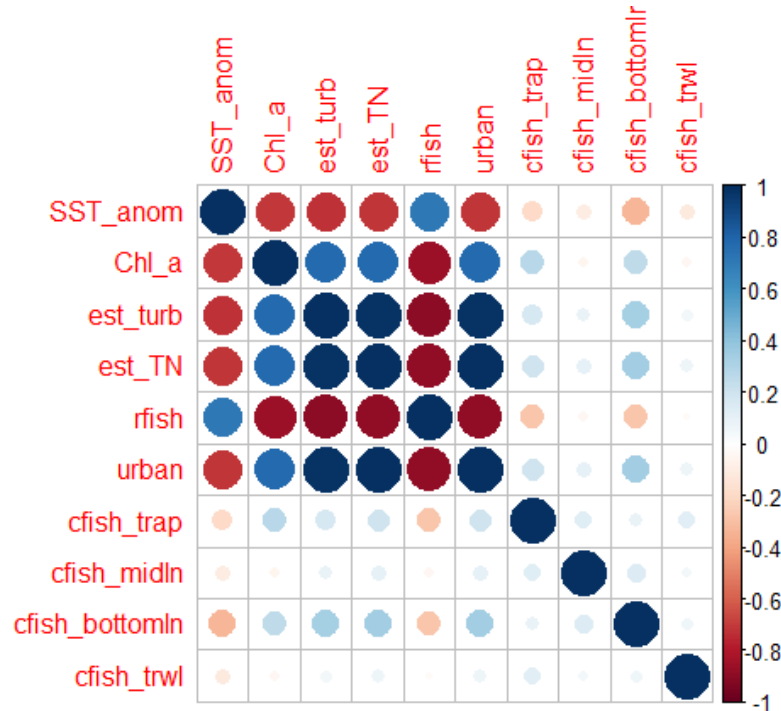


Figure 3.3 Spearman's correlations between layers used in the map of hotspots of cumulative threats. Zero value indicates no correlation and high positive or low negative value (large circles) indicates high correlation.

3.4.2 Model of fish abundance

There were a total of 16,181 counts of fish captured by BRUV (9,632 and 6,549 counts of invertivores and carnivores, respectively). These functional feeding categories accounted for the majority of all species captured by BRUV, with herbivores having only 329 counts of fish across all sites. There was a greater diversity of carnivores (31 species generalist carnivores and piscivores) than invertivores (13 species of consumers and algae-invertivores). There were 952 observations for each functional group overall.

The correlation matrix for all covariates considered for the model showed correlation values greater than 0.5 between some threats and biophysical covariates (Supplementary Figure A.3). For example, proximity to mangroves was correlated with recreational fishing pressure (correlation value of 0.663) and commercial line mid-water fishing (correlation value of

0.654). Overall, correlations were greatest between the same types of threat indicator. For example, water quality indicators (turbidity and total nitrogen) had a correlation value of 0.96 and commercial fishing indicators (trawling and mid-water line fishing) had a correlation value of 0.68. The plots were very similar for carnivore and invertivores, hence only the matrix for carnivores is shown in the appendix (Supplementary Figure A.3). The model explained 50% of the variation (deviance) in fish abundance for both functional groups.

The effect of no-take zones had a strong positive influence on carnivores (times increase inside no-take zones of mean \pm S.E. of 1.37-1.55) and weaker, but significant, influence on invertivores (times increase inside no-take zones of mean \pm S.E. of 1.06-1.20). The effect of no-take zones was supported by the raw data which showed a higher mean abundance of fish in no-take zones in both MP (PSGLMP: mean count of 12.4 ± 5.3 in no-take zones cf. 9.5 ± 5.0 in outside areas, and SIMP: mean count of 9.2 ± 3.4 cf. 6.1 ± 3.5 , respectively). Carnivorous fish abundance declined as SST anomalies increased and when closer to centres of urbanisation, and increased when closer to vegetated habitats. Carnivorous fish abundance also was higher with elevated recreational and commercial fishing pressure, which indicates that some relationships are confounded. This is supported by correlation metrics between many variables in the model (Supplementary Figure A.3) indicating that the individual effects of threats and biophysical variables cannot be considered in isolation. Similar confounding was shown in the model of invertivores, because all significant threats had a positive influence on fish abundance. In addition, the effects of water quality covariates are not confounded with fishing pressure covariates, or the climate change covariate. Therefore, the cumulative effects of all fishing related threats or all water quality related threats can be predicted separately.

3.4.3 Cumulative impact map for reef fish

Fish abundance increased when fishing threats were removed (Figure 3.4a, 3.5a). Invertivores were predicted to have a stronger response (increase per grid cell of maxN up to 196 fish) in comparison to carnivores (increase per grid cell of maxN by up to 97 fish). The cumulative effect of fishing pressure on invertivores was spread consistently along the majority of the coastline, particularly within the 40 km contour which was the maximum extent of recreational fishing pressure used in the model (i.e. the majority of recreational fishing pressure is likely to occur within this extent (National Marine Safety Committee, 2009)) (Figure 3.4a). The cumulative effect of fishing pressure on carnivores was patchily

distributed with increases predicted for state and commonwealth waters east of Kempsey and Mullumbimby, and in commonwealth waters adjacent to Coffs Harbour, and north of Port Stephens and Yamba (Figure 3.4a).

There was little cumulative impact from water quality threats on reef fish abundance (Figure 3.4b, 3.5b). Fish abundance increased as water quality threats increased, indicating that fish respond non-linearly to indicators of water quality. Regions include Port Stephen for both functions groups, and in Coffs Harbour and south of Tweed Heads for invertivores. Fishing threats masked the overall cumulative impact on carnivorous and invertivorous fish (Figure 3.4c, 3.5c).

3.4.4 Marine Park performance for reef fish

The effect of removing all fishing threats (recreational and commercial fishing) had a greater benefit for invertivores inside no-take zones compared to carnivores inside no-take zones. For example, there was an increase in maxN for invertivores by 387% compared to carnivores by 213%, inside no-take zones. The difference between the functional group responses to no-fishing was driven by the effect on invertivores in PSGLMP, where an increase in maxN of 978% was predicted, compared to an increase of 178% for carnivores. The increase in maxN was similar between carnivores and invertivores in SIMP (349% and 326%, respectively).

Removing all water quality threats (turbidity, population pressure indicator and chlorophyll-*a*) had different effects on the maxN of functional groups inside no-take zones. For example, the maxN of carnivores increased by 51% inside no-take zones, but invertivore maxN decreased by 56%. When comparing the effect between no-take zones, a different pattern was observed. Both carnivores and invertivores maxN decreased inside no-take zones in SIMP when water quality threats were removed by 12% and 28%, respectively. However, carnivores' maxN increased, and invertivore maxN decreased inside PSGLMP, each by 103%.

3.5 Discussion

Effective management requires knowledge about the spatial distribution of threats as well as the impact of threats to species and ecosystems (Halpern et al., 2008). This enables managers to coordinate cross-jurisdictional actions to address the drivers of threats (Crowder et al., 2006; Griffiths et al., 2020). We offer an exploratory analysis of the spatial distribution of threats and impacts to temperate rocky reef fish along the north coast of NSW. Our analysis

highlighted threat hotspots of potential concern that require further investigation. We also demonstrated that data driven approaches to cumulative impact assessment reveal some interesting non-linear relationships between threat and impact, particularly the finding that fish abundance was higher in areas with putatively higher water quality threat. This information can help the NSW government to focus on areas of future research that will assist them to prioritise and coordinate future management actions to fulfil objectives of the NSW Marine Estate Management Strategy (MEMS) (NSW Government, 2018).

The cumulative threat map shows that the greatest threats occur along the coastline, within NSW state waters (3 nm). High coastal impacts are widely recognised within Australia and globally and driven by catchment related processes (Halpern et al., 2008; Halpern et al., 2019; Loiseau et al., 2021; Ostwald et al., 2021). There are nine coastal river catchments within the North Bioregion, which include two major rivers (Clarence and Hunter) and 133 sources of input into coastal waters (estuaries, rivers, inlets, creeks, and partially connected lagoons and lakes) (Department of Planning Industry and the Environment, 2020). Fifty percent of the sources are considered modified or extensively modified, while only 10% are in pristine condition (OzEstuaries, 2003). The level of coastal modification is likely explained by the long history of agricultural use in the region (Townsend, 2020), despite a low-medium population density of most coastal communities (mean population density of 400 people per one kilometre grid cell; Australian Bureau of Statistics (2021)). Areas of high cumulative impact are likely driven by water quality threats in combination with other threats. For example, the threat hotspot surrounding Coffs Harbour was driven by water quality (turbidity and total nitrogen) and demersal line fishing, while the threat hotspot surrounding Taree was driven by a combination of threats (chlorophyll-*a* and commercial trawling recognised as two of them).

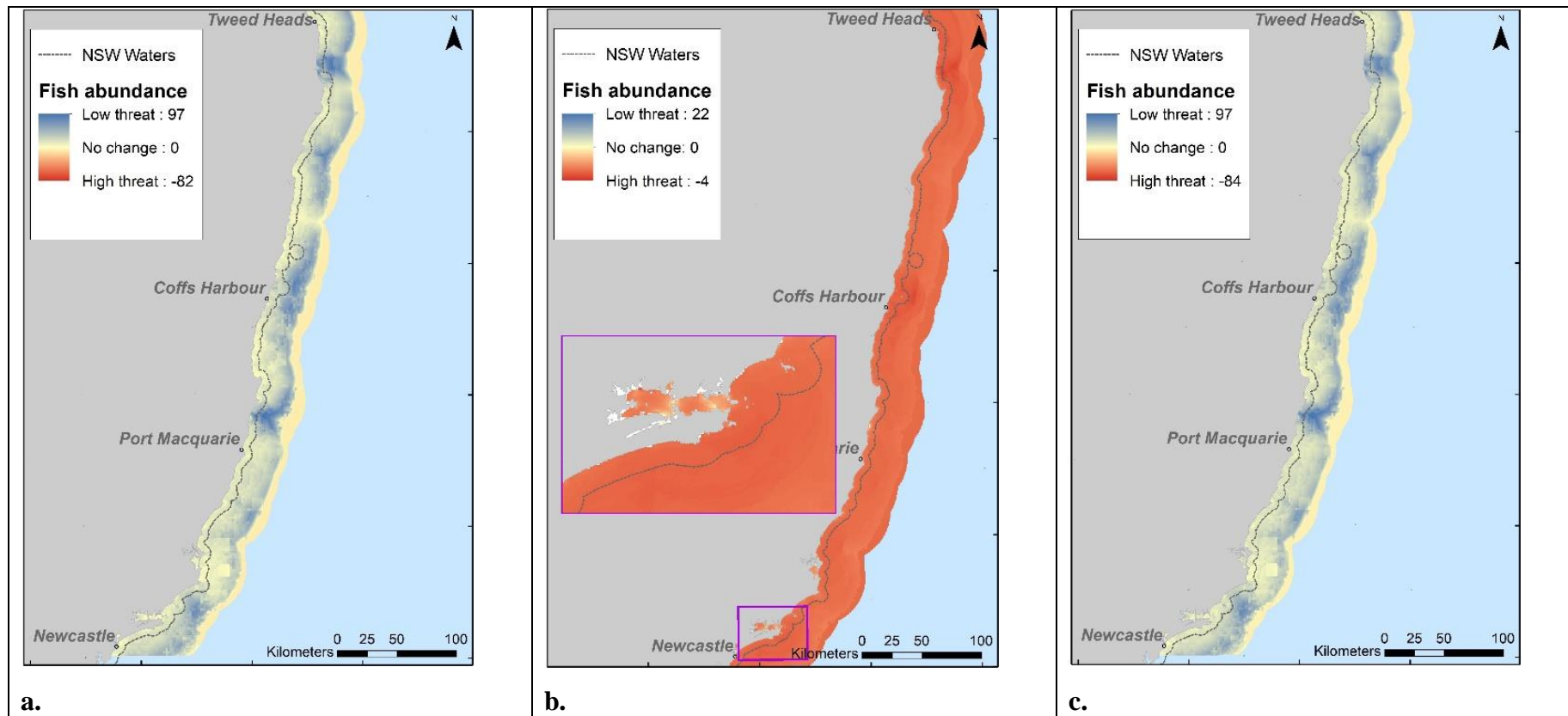


Figure 3.4 The cumulative effect on carnivorous maxN from the removal of fishing threats (a), water quality threats (b), and both water quality and fishing threats (c). Positive maxN values indicate a high cumulative impact from the threat, while negative fish abundance values indicate an increase in abundance with the threat. Maps produced using ArcGIS, ArcMap version 10.3 software.

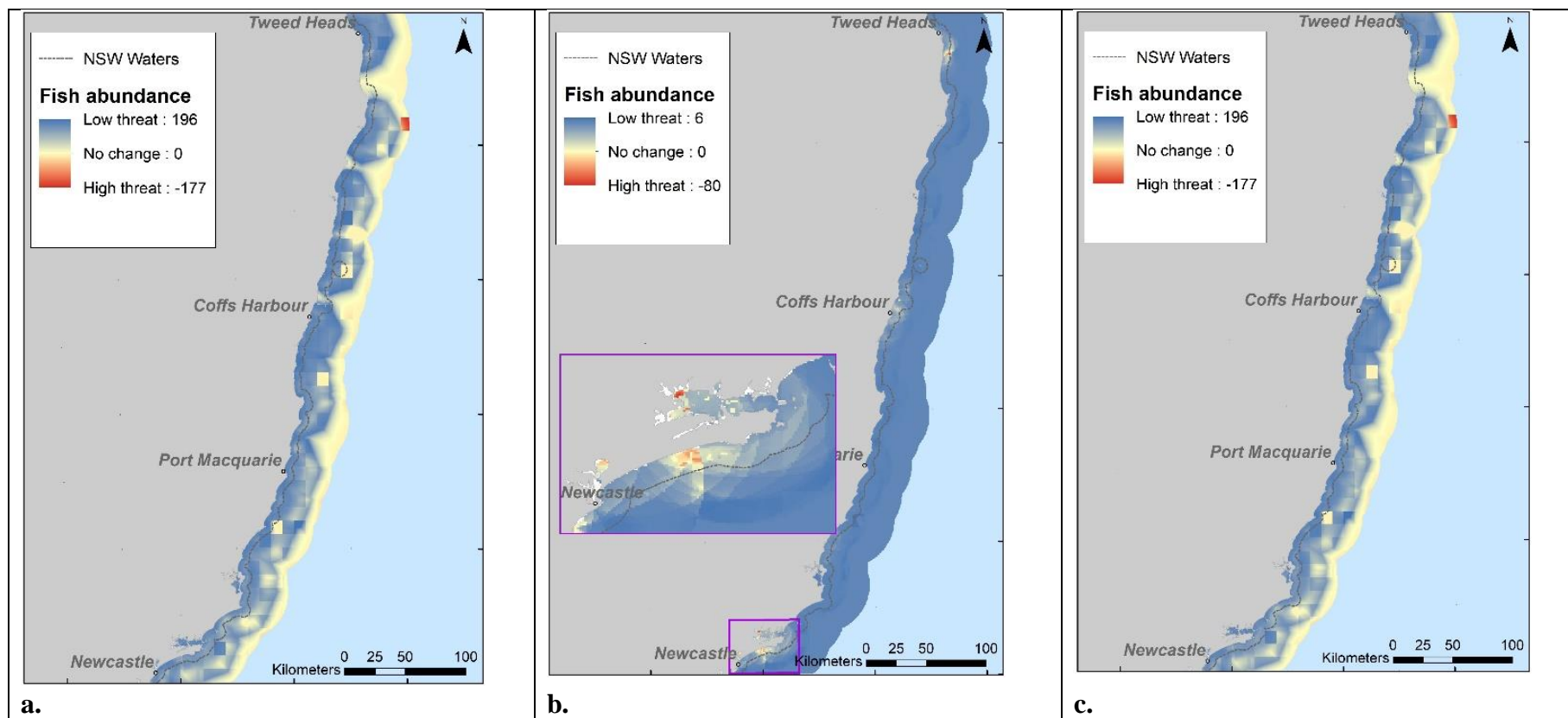


Figure 3.5 The cumulative effect invertivorous maxN from the removal of fishing threats (a), water quality threats (b), and both water quality and fishing threats (c). Positive maxN values indicate a high cumulative impact from the threat, while negative fish abundance values indicate an increase in abundance with the threat. Maps produced using ArcGIS, ArcMap version 10.3 software.

When looking at threats individually, majority of threats operate on small spatially defined scales, with the exception of recreational fishing which is fairly homogenous along the coast, with only few notable gaps. The climate change threat (SST variance) doesn't affect the near-shore environment (within 25 km from the coast) which is supported elsewhere (Dunstan et al., 2018). Commercial fishing effort is highly variable dependant on the type of method, with very patchy high use areas within state waters and more concentrated effort within commonwealth waters. Areas of localised hotspots for nutrients (up to 100 ug/L of) and turbidity (up to 15 NTU) occur within and adjacent to the Clarence River, which is the largest estuary in the region and one of the largest rivers in mainland Australia (NSW Department of Primary Industries, 2006).

We predicted the removal of cumulative impacts from fishing to benefit invertivores more than carnivores. There are three potential explanations for the difference in response between functional groups. First, there is likely to be a level of preferential selection of the 31 targeted carnivorous species by fishers, despite all species being targeted by fishers (Malcolm et al., 2018). This requires further analysis at the species level to determine if the same pattern is evident for highly selected carnivores, such as *Chrysophrys auratus* (Pink snapper) and *Seriola lalandi* (Yellowtail kingfish). Second, complex predator-prey and competitive relationships have been shown to be a stronger driver of community structure compared to fishing intensity (Boaden & King 2015). Therefore, the absence of a strong increase in carnivores when fishing is removed could be related to compensatory response mechanisms operating between predators and prey, or between competitors (Hunsicker et al., 2011; Mitchell and Harborne, 2020). Third, there were approx. 30% more BRUV captures of invertivores in comparison to carnivores, suggesting that we had greater statistical power to detect impacts on invertivores than carnivores.

Overall, fish numbers were predicted to be greater as water quality decreased for both functional groups. This finding could be an artefact of other more important variables acting on fish abundance that were not included in the current study. Alternatively, it could suggest that fish benefit from low levels of increased nutrients, an effect which has been observed for *C. auratus* in this region (Rees et al., 2021). The relationship between water quality threats and fish responses are complex and do not always act linearly (Meador and Frey, 2018). Further, temperate rocky reef fish have a wide exposure gradient to water quality threats as they can range from within 100 m up to distances of >5 km from the mouth of estuaries and outlet sources. Therefore, coastal reef fish are unlikely to be exposed to acute concentrations

observed in lakes and semi-enclosed watersheds because of the dispersion into the coastal environment (Meador and Frey, 2018; Parker et al., 2016; Uriarte and Borja, 2009).

We measured the performance of no-take zones as the predicted increase in fish abundance inside the no-take zones if fishing was removed from areas around the no-take zones. We analysed performance in this way to represent poaching and the effect of fishing around the edge of no-take zones which can be significant hindrance to abundance improvement inside no-take zones (Harasti et al., 2019; Ohayon et al., 2021). We are therefore assessing the expected benefit inside MP by removing the threat of fishing from areas adjacent to no-take zones. Our predictions indicated that no-take zones supported a higher abundance of carnivore and invertivore groups when compared to outside areas (up to 1.5 and 1.3 times, respectively), which is consistent with previous findings (Harasti et al., 2018a; Knott et al., 2021; Malcolm et al., 2018). This indicates that the cumulative impacts of fishing outside of no-take zones are impacting fish abundance inside no-take zones. It also suggests that illegal fishing could be occurring within no-take zones, which has been identified previously within PSGLMP (Davis and Harasti, 2020; Harasti et al., 2019). Strong differences between functional group responses was also predicted between SIMP and PSGLMP, indicating that complex, site-level influences and predator-prey relationships are driving the model predictions (Knott et al., 2021; Malcolm et al., 2018).

Here we have identified the vulnerability of targeted fishery species to threats and predicted how fish numbers respond if cumulative threats were removed. Most threat impact map methods are based on impacts at the ecosystem level (Halpern et al., 2008; Micheli et al., 2013; Ortiz et al., 2018; Stockbridge et al., 2021) while here we have interpreted impact at the functional group level for reef fish taxa (Maxwell et al., 2013; Ostwald et al., 2021; Zhang and Vincent, 2019). An objective of the MEMS is to determine the risk of threats to benefits of marine environment usage, and fishing is recognised an important benefit to the community of NSW (NSW Department of Primary Industries, 2018). Therefore this threat impact map approach will be most useful when used in conjunction with other objectives set out in the MEMS (Tulloch et al., 2015). Our hotspot approach also identifies the number of threats active in the seascape and therefore indicates the complexity of management (co-management approach) to address threats. For example, several moderate threats are harder to manage than one high impact threat (Griffiths et al., 2020). More importantly, this approach could help to motivate cross-jurisdictional discussion about how impacts to the marine environment can be addressed more holistically (Hayes et al., 2021).

The caveats in the current study limit interpretation of the results and require further investigation to improve the understanding of cumulative impacts on reef fish in the North Bioregion. The patterns of fish response to cumulative impacts are a test of a method that is entirely driven by the data used to define vulnerability weights, rather than assuming all threats are negative as is common practise (Halpern et al., 2008; Korpinen and Andersen, 2016). Therefore there are some unexpected and unexplained outcomes in the prediction maps, such as the positive response (or lack of response) of fish abundance to high threat (Figure 3.4b, 3.5b). This suggests that defining the vulnerability value using a combination of expert opinion and data could link threats to impacts in more meaningful ways. We also considered only additive effects in the model of threat impact when they could have been interactive (Brown et al., 2014; Cote et al., 2016; Crain et al., 2008; Stock and Micheli, 2016). Including covariate interactions would help to explain other non-linear outcomes between threats (Brown et al., 2014), but in this case we were limited by sufficient power to model interactions. Dispersion parameters for the water quality threats were also applied consistently across the seascape, as is common practise with cumulative threat maps (Halpern et al., 2008; Halpern et al., 2015). However, the effect of hydrodynamic variation (currents, wind and waves) is likely to influence dispersion at the watershed level. Although we considered the effect of catchment size, we did not include other parameters, such as flow volume and rate, currents, exposure, etc., known to be important influences of dispersion (Deignan-Schmidt et al., 2021; Tseng, 2002; Yu et al., 2016). The omission of these influences in the cumulative threat map may change the footprint and distribution of water quality impact.

Statistical analysis quantifies the associations between threat and fish abundance, but better spatially resolved data, using measured data rather than proxies and including other mechanisms (covariates) not modelled here, would greatly benefit interpretation of the findings. For example, commercial fishing data was only available at a one-degree grid cell, while all other threats were more resolved. Although the use of proxies is common practise for large scale threat maps (Halpern et al., 2008; Ostwald et al., 2021), spatially explicit measured data (e.g. for recreational fishing (Keramidas et al., 2018; Lynch et al., 2020; Taylor et al., 2018)) would provide a clearer link between threat and impact. Other variables to consider in future cumulative impacts for the region include other drivers of fish abundance and distribution (e.g. seafloor rugosity (Burgos et al., 2017; Emslie et al., 2014; Rees et al., 2021), exposure and currents (Fulton and Bellwood, 2004; Williams and Bax,

2001), food-web dynamics (Fu et al., 2020; Lefébure et al., 2013), habitat type and condition (Fulton et al., 2016; Quaas et al., 2019), and larval and recruitment variability (Planes et al., 2009)). Socio-cultural, economic, and political factors also influence the performance of MP (Glew et al., 2012; Noble et al., 2021, 2020) such as community support, enforcement and degree of remoteness (Edgar et al., 2014). The inclusion of social variables in the models of MP performance could help to explain the differences observed between functional groups and MPs, and better inform management actions.

The approach we propose addresses two limitations common in cumulative impact assessment. First, our method overcomes issues of non-linearity in the vulnerability of ecosystems to threats, by modelling the spatial gradient in fish abundance in response to threats. This approach has the advantage over the expert elicitation approach because it doesn't require identifying the vulnerabilities of each threat in a pre-conceived way but rather, allows the data to drive the patterns in fish abundance. This is important because we assume all threats are negative when in some cases they could have benefits. For example, the abundance (maxN) of invertivores were predicted to decrease when water quality threats were removed by up to 56%. This suggests that additional nutrients may be beneficial to invertivores which is not surprising given the invertivore group included algal-invertebrate consumers (Supplementary Table A.9). The influence of water quality on fish abundance has been shown elsewhere (Meador and Frey, 2018; Rees et al., 2021). Second, the approach offers a clearer path for management action because it quantifies correlations between threats and partitions out the numbers of threat rather than the values of threats. In this way, the number of actors/stakeholders responsible for managing the threat, and amount/level of management action required to address threats are identified.

We have developed a data-driven approach using existing fisheries, water quality and climate change data to predict the impact of cumulative threats to fishery targeted temperate rocky reef fish. Cumulative threats have not been mapped in NSW previously, although fishing is considered to be one of the greatest threats to reef fish. However, this work is exploratory and offers an alternative to assessing cumulative impacts that does not rely on expert elicitation. Further research is needed to assess the impacts on rocky reef fish from cumulative threats before investing conservation resources to mitigate the threats, particularly in regards to water quality. However, the data iterates the importance of no-take zones to buffer reef fish from threats and suggests where conservation action could improve the performance of these zones.

3.6 Supporting Information

Supplementary table of indicators used in the cumulative threat map (Supplementary Table A.7), frequency of fishery-targeted carnivorous and invertivorous species (Supplementary Table A.8), pairwise concurrency values between all variables used in the GAM model (Supplementary Table A.9), threat maps for individual threats (Supplementary Figure A.1), map of hotspots of cumulative threat (Supplementary Figure A.2), and correlation matrix for all covariates used in the model of carnivore abundance (Supplementary Figure A.3).

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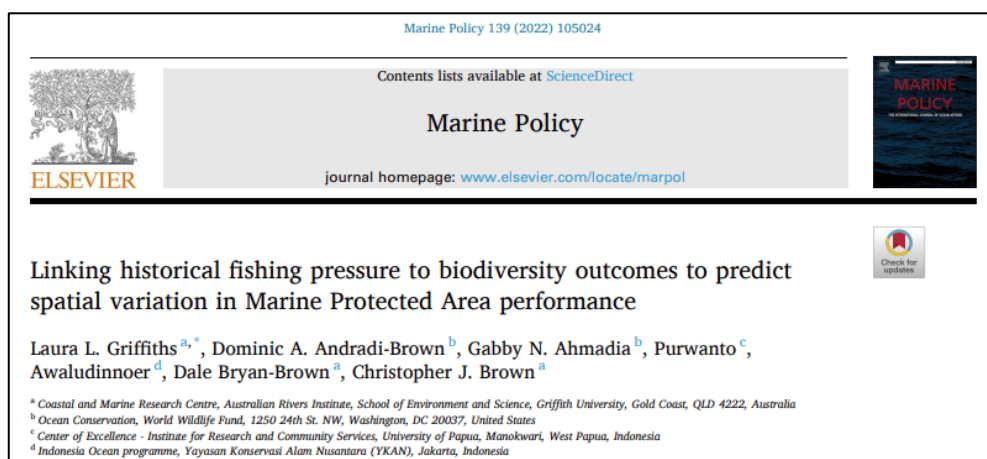
Chapter 4 Linking historical fishing pressure to biodiversity outcomes to predict spatial variation in Marine Protected Area performance

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Author Contributions

Conceptualisation of the study: LLG, CJB, DAB, GAB. Methodology: LLG, CJB. Formal analysis of the data: LLG, CJB, DBB. Visualisation: LLG. Writing – original draft preparation: LLG. Writing – review and editing: CJB, DAB, GA, P, A.



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4.1 Abstract

Marine Protected Areas (MPAs) often have dual goals of protecting biodiversity and increasing sustainability of fisheries. To understand how MPAs are performing at these goals, evaluation of fish biomass outcomes against management targets is needed. However, the evaluation of performance should consider multiple biophysical and social drivers that vary over the seascape to inform spatially explicit targets for fish biomass. Including spatial variation when evaluating MPA performance is particularly important for MPA networks because it enables managers to set more realistic expectations for MPA outcomes and adapt management across individual areas. Here we develop a modelling approach to predict how fishing pressure and biophysical conditions affect expected recovery of fish biomass. We apply the approach to model herbivore and predator biomass at 57 sites for two MPAs in Raja Ampat, Indonesia. We then use this model to predict biomass recovery towards reference sites indicative of low-fishing pressure. We found that historical fishing pressure, wave exposure and proximity to coastal habitats were all important determinants of pre-MPA fish biomass. Our predictions therefore, indicated the implemented MPA no-take zones should have some of the highest reef fish biomass based on both their location within the MPA, and the removal of fishing pressure. We also identify sites that may be underperforming and warrant further management, for instance, further investigation of poaching as a cause of poor recovery trends. We suggest that evaluation of MPA performance needs to consider the link to historical fishing pressure and biophysical conditions with biodiversity outcomes.

Keywords: MPA performance, fish biomass, Raja Ampat, predictive models, GAM.

4.2 Introduction

Marine Protected Areas (MPAs) are a crucial tool for achieving fisheries and ecosystem conservation goals globally (Secretariat of the Convention on Biological Diversity, 2010). Conservation objectives for biodiversity inside MPAs include rebuilding fish biomass (Lester et al., 2009), restoring habitats (Hays et al., 2020) and/or restoring ecosystem functions (Cheng et al., 2019; Halpern et al., 2009). Fisheries objectives similarly include rebuilding or maintaining fish biomass and additionally include export of fish larvae or migration of adults to fished areas (Fogarty and Botsford, 2007). Thus, high fish biomass is a key performance objective of MPAs. However, recovery or preservation of fish in MPAs compared to outside areas does not always meet expectations in all places (Edgar et al., 2014; Gill et al., 2017) or on expected timescales (Kaplan et al., 2019) because other important determinants can drive

spatial variability in fish biomass, such as biophysical gradients (Fidler et al., 2021; Nickols et al., 2019), insufficient capacity for MPA management (Gill et al 2017) or poaching (Brown et al., 2018b). It is important to set achievable conservation targets for MPA performance, so managers can decide if management needs to be adapted to improve performance on a specific objective. If MPA targets are not realistic, the MPA may be perceived to be ineffective or poorly performing, such as when the expectation for recovery of fish is not met because the MPA was implemented in an area with low historical fishing pressure (Kaplan et al., 2019). Poor performance can have detrimental consequences for the social acceptance needed to make MPAs effective, especially considering the trade-offs required by local communities and those accountable for regional MPA planning (Dehens and Fanning, 2018). Therefore, we need to understand the spatial variation of fish biomass prior to MPA implementation to set achievable performance targets for recovery and preservation of fish biomass in MPAs.

A number of essential design and management features have been identified for effective MPA's (Edgar et al., 2014; Giakoumi et al., 2018; Nickols et al., 2019). Design features include large size (>100 km²), declaring areas no-take (NTZ) for fishing, location selection to maximize isolation (Edgar et al., 2014) and high fishing exploitation pre-MPA (Nickols et al., 2019). Management features include sufficient enforcement (Brown et al., 2018b), stakeholder participation (Giakoumi et al., 2018) and resource capacity (Gill et al., 2017), and biologically and socially realistic expectations for recovery timeframes (generally >10 years) (Edgar et al., 2014; Kaplan et al., 2019). Biophysical features also play an important role in driving recovery; MPA success is affected by connectivity to adjacent habitats (Olds et al., 2012; Ortodossi et al., 2019), recruitment variability, adult movement, population stochasticity and trophic interactions (Nickols et al., 2019; White et al., 2011). One of the features particularly lacking when evaluating MPA performance is the level of previously harvested populations (Nickols et al., 2019). Data on fishing pressure prior to MPA zoning is particularly hard to obtain for established reserves, because monitoring efforts commonly begin once an MPA has been created (García-Rubies et al., 2013; Horta e Costa et al., 2020). Although baselines are now commonly available for newly created reserves, the lack of accurate fishing pressure information pre-MPA implementation for established reserves makes it difficult for managers to evaluate the MPA's performance at recovering fish biomass. Performance objectives focused on maintaining biodiversity and sustaining fisheries

would equally benefit from understanding spatial influences of fishing pressure and allow improved interpretation of MPA performance across a network of MPAs (Sangil et al., 2013).

Statistical methods that make predictions of spatial variation in fish biomass could help to improve evaluations of the performance of MPAs (Guisan and Zimmermann, 2000; Pittman et al., 2007; Trifonova et al., 2015). Species distribution models (SDM), in particular, are commonly used to support ecosystem-based management by identifying critical species-habitat associations (Ahmadi et al., 2015; Galaiduk et al., 2018; Young and Carr, 2015). However, in theory they could also be applied to predict the spatial effects of adaptive management on fish biomass by incorporating species-habitat-threat associations. The inclusion of pre-MPA threats, such as historical fishing pressure, into species-habitat models would enable MPA performance to be quantified against realistic expectations to see if MPAs are reaching their objectives

In this study, we develop a spatial model of fish biomass using measured pre-MPA fishing pressure data and biophysical variables to understand important drivers of fish biomass and how they can affect MPA performance in terms of meeting conservation objectives for fish biomass. Specifically, we aim to: i) verify the relationship between measured fishing pressure prior to MPA implementation and another known proxy for fishing pressure, namely distance to settlement; (ii) predict fishing pressure across the seascape and relate it to other biophysical parameters to build a predictive model of fish biomass; (iii) apply predictive modelling to predict fish biomass that MPA outcomes can be compared to, and; (iv) compare our predicted model of fish biomass to empirical data. This information will indicate where MPAs are not fulfilling their potential and facilitate the setting of more realistic expectations of MPA performance.

We test our approach and focus our discussion in two MPAs that are part of an MPA network, the Bird's Head Seascape (BHS), in West Papua, Indonesia. In Indonesia, MPAs are typically designed for both biodiversity conservation and fisheries management, and as such, include fished zones with fisheries management regulations additional to non-MPA areas, as well as NTZ for biodiversity conservation and spawning stock enhancement. This integration of fisheries management with MPA zoning decisions is essential for MPAs to provide benefits to fisheries (Greenstreet et al., 2009; Hilborn, 2018). The BHS contains some of the richest diversity of reef fish and coral species worldwide (Veron et al., 2009) and protects over 22.5 million hectares of seascape (Glew et al., 2015) (Figure 4.1). Birds Head Seascape

MPAs employ a range of management strategies to balance human well-being (food security, livelihoods and economic sustainability) alongside biodiversity conservation (Purwanto et al., 2021; Setyawan et al., 2022). The performance of MPAs in Indonesia are evaluated against a range of specific ecological, cultural and social objectives, which include the objective of increasing or maintaining the status quo fish biomass (Directorate for Conservation of Area and Fish Species, 2012). The collaborative governance of the MPA network, with government, civil society, and local community involvement (Glew et al., 2015), has enabled substantial ecological and social monitoring programs (Ahmadia et al., 2016; Purwanto et al., 2021). Empirical data on both fishing effort and ecosystems prior to MPA zoning provides a unique opportunity to understand how MPA performance outcomes vary with regard to measured fishing pressure pre-MPA. Differing levels of pre-MPA impact within the MPAs are not currently incorporated into routine analysis of monitoring data, which shows considerable variability in fish biomass recovery throughout the differing MPAs of the BHS network (Ahmadia et al., 2016; Fidler et al., 2021). By incorporating measured fishing pressure pre-MPA, temporal and spatially relevant predictions can be made about the contribution of MPAs to maintain biodiversity and support fish stocks in the BHS.

4.3 Methods

4.3.1 Study Regions

The two focal areas of this study; South East Misool MPA (Taman Wisata Perairan (TWP) Raja Ampat - Misool Timur Selatan) referred to here as Misool MPA (343,200 ha, zoned November 2012) and Kofiau and Boo Islands MPA (TWP Raja Ampat - Kepulauan Kofiau dan Boo), referred to here as Kofiau MPA (170,000 ha, zoned October 2011) form part of the TWP Raja Ampat MPA in the BHS MPA network (Figure 4.1; Purwanto et al. 2021). The two MPAs are classified as a Marine Recreation Park designated for the protection of biodiversity and eco-tourism and were the subject of pre-MPA fishing pressure surveys (three-five years prior to zonation) (Brown et al., 2018b). Although not discussed in this study, MPAs also benefit tourism (Purwanto et al., 2021; Setyawan et al., 2022). Further information on the fisheries community surrounding Misool MPA and Kofiau MPA are available in the Supplementary Data – community overview.

4.3.2 Fish Biomass and Fishing Surveys

Fish biomass was estimated from underwater visual census (UVC) using the belt transect method performed by scuba divers (Ahmadia et al., 2013; Fidler et al., 2021). At each site,

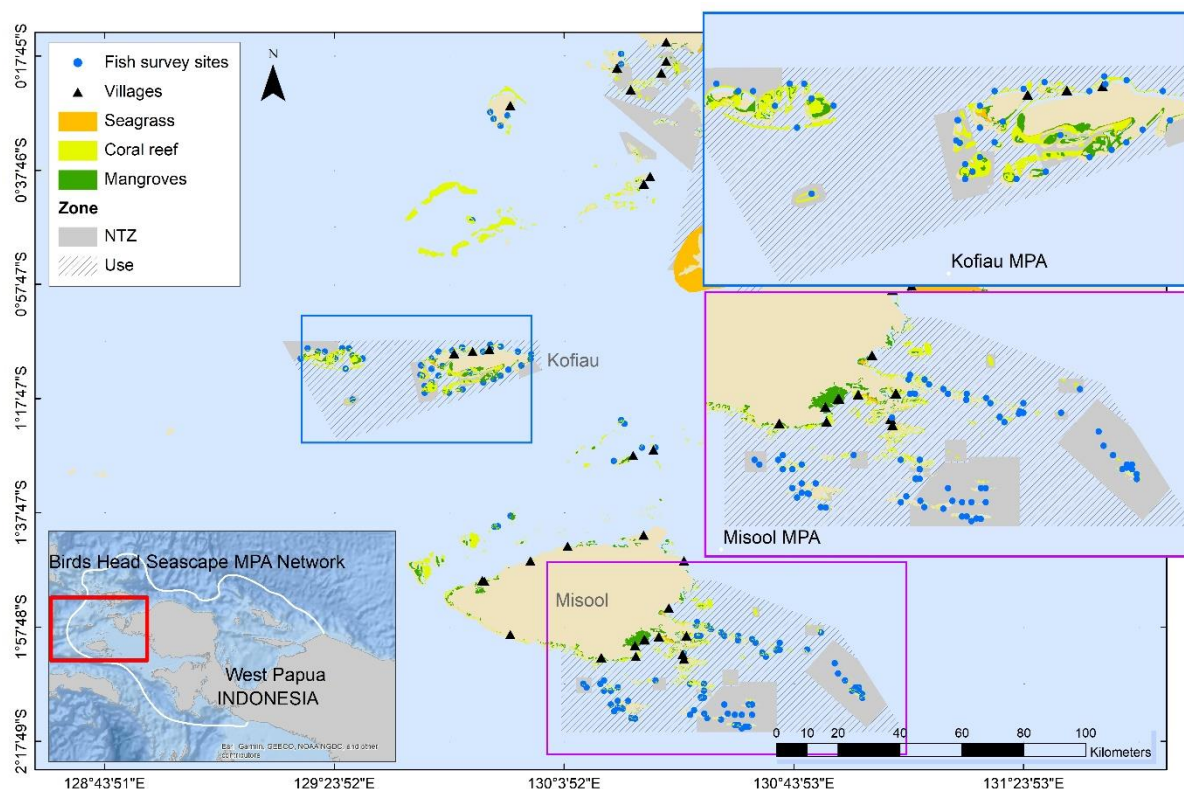


Figure 4.1 Map of Kofiau and Boo Islands MPA and South East Misool MPA. Both MPAs are legally defined as part of TWP Raja Ampat MPA (Purwanto et al., 2021). Map produced using ArcGIS, ArcMap version 10.3 software. Habitat polygon data sourced from Giri et al. (2011) (mangroves), UNEP_WCMC and Short (2018) (seagrass) and UNEP-WCMC et al. (2018) (coral reef). Fish survey locations, patrol routes and zones are provided by Ahmadia et al. (2015). Only MPA zones that have official zonation as of 2016 are displayed. Source of the ocean base map: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors.

two divers counted individuals on five transects of variable width according to the size class of fish: $\geq 10\text{cm}$ and $\leq 35\text{ cm}$ (5 m wide and 50 m long), and $\geq 35\text{ cm}$ (20 m wide and 50 m long). All individuals were recorded to their species level and to the nearest cm (fish $\geq 35\text{ cm}$) or in 5 cm length classes (fish $\geq 10\text{cm}$ and $\leq 35\text{ cm}$). Length and abundance data were standardised and converted to biomass (Ahmadia et al., 2013). A total of 799 and 675 surveys were included in the dataset for Kofiau and Misool, respectively. The surveys were conducted from 2009 to 2016 and distributed across 57 unique sites with: 170 in NTZ, 524 in use zones and 105 in control zones for Kofiau and; 225 in NTZ, 395 in use zones and 55 in control zones for Misool. Not every site had replicated surveys through time and control sites were only available for years 2012 and 2015. There were more use zones compared to other zone types because monitoring began prior to the official zonation of MPA sites, therefore

several NTZ were use zones during baseline monitoring of fish. Further information on the methods are available in the Supplementary Data – methods.

4.3.3 Modelling Approach

We developed a multi-stepped modelling approach to test the effects of pre-MPA fishing pressure and biophysical covariates on fish biomass, and then used this model to predict the spatial effect of NTZ on fish biomass (Figure 4.2).

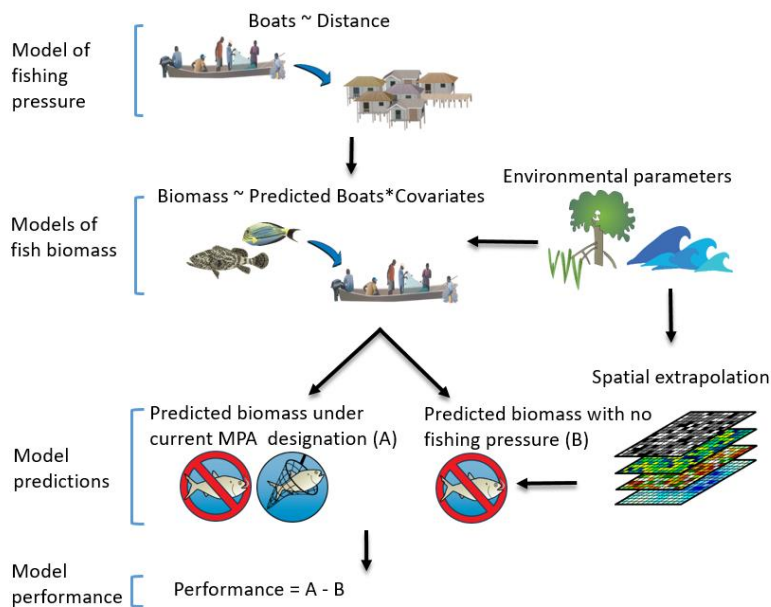


Figure 4.2 Flow diagram of the methodology used to predict the spatial effect of management on fish biomass. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols).

4.3.2.1 Model of fishing pressure

We fit a model of measured pre-MPA fishing pressure to test the hypothesis that fishing boat numbers would be greater nearer to settlements. Distance to settlement is important because it is a proxy for fishing pressure on coral reefs (Brewer et al., 2012; Cinner et al., 2013). Distance to settlement was calculated in two ways; direct linear distance and shortest distance via water. However, there was little difference observed between the two maps of distance, so the direct linear distance measure was used in the final model. A generalised additive model (GAM, (gamm4) (Wood and Scheipl, 2020)) with random effects (Wood, 2017) was applied to model number of boats as a function of distance. The model was then used to predict the number of

boats operating pre-MPA implementation at every coral reef pixel (22,500 m²). Boat density in areas lacking survey data (e.g. North Misool) were predicted from the fitted model and distance to settlement raster.

4.3.2.2 *Models of fish biomass*

Fish biomass as modelled for two functional groups; herbivores (Acanthuridae, Scaridae and Siganidae) and predators (Lutjanidae, Haemulidae and Serranidae). Predators are indicators of fishing pressure (Ahmadia et al., 2015) and export markets (Campbell et al., 2018).

Herbivores are indicators of reef resilience (Ahmadia et al., 2016; Glew et al., 2015) and local fishing pressure (Wawan pers.comm, 18 February 2020). Pelagic predators (Scombridae and Carangidae) were also included initially as they form an important export market to Sorong (Wawan pers.comm, 18/02/2020), however there were insufficient biomass data to consider these families separately. Fish biomass was compared in three areas subject to different management: (i) NTZ, (ii) use zones located inside MPAs, and (iii) control sites located outside MPAs (see Supplementary Table A.10 for a list of explanatory variables used). Use zones are zoned into multiple different types of managed areas, such as ‘sustainable fishing zones’ and traditional ‘sasi’ zones (Purwanto et al., 2021). Sustainable fishing zones exclude large fishing vessels (>10 GT) and prohibit destructive fishing gears (McLeod and Leslie, 2009; Muawanah et al., 2020). Sasi zones are intermittent closures of harvesting for specific species (mostly invertebrates) or complete bans for all species lasting months to years (Kementerian Kelautan dan Perikanan, 2020; McLeod and Leslie, 2009). We were unable to consider sasi zones separate from sustainable use zones because sasi zones were not monitored across a sufficient number of sites for analysis. No-take zones, referred to as ‘core zones’ or ‘tourism use zones’ locally, exclude all extractive uses permanently but can permit other non-extractive uses such as tourism (Ford et al., 2020). Control zones (for monitoring) were located outside of the MPA.

We used the predicted fishing pressure layer and biophysical covariates to quantify the drivers of fish biomass across the two MPAs. The biophysical covariates tested were based on two a priori hypotheses for biophysical drivers of fish biomass. First, fish biomass is greater when reef habitats are ecologically connected to adjacent coastal wetlands (Olds et al., 2012), so we compared distance from reef survey sites to mangrove (Giri et al., 2011) and seagrass (UNEP-WCMC and Short, 2018) habitats in separate models (Supplementary Data - methods). We then chose to use only the habitat that had the lowest Akaike Information

Criterion (AIC) (Burnham and Anderson, 2004). Distance to seagrass habitats however, was confounded with fishing pressure in Misool MPA, so we only used distance to mangroves in the modelling for Misool. Second, reefs with moderate exposure to wind and waves can have higher fish abundance, size and/or richness for some trophic groups, because currents can carry suspended food items and attract planktivores and larger carnivores that are adapted to withstand greater flow velocities (Eggertsen et al., 2016; Friedlander et al., 2003; Sartori et al., 2021; Schmiing et al., 2013), so we included wave exposure as a covariate. Two indicators were used to represent wave exposure, wave height (m) and wave period (sec). Wave exposure data was created in ARC GIS using the fetch and waves 2012 models (Supplementary Data - methods). The dataset was dominated by semi-exposed and exposed sites (> 96%). Wave exposure indicators were tested separately in each model and the indicator with the lowest AIC was chosen in the final model. Year was also included in the model, where we expected to observe recovery of biomass inside MPAs over time and stable or declining trends outside of no-take MPAs. Site was included as a random effect in all models to allow for spatial co-variation in the data that was not explained by the predictor variables.

For each fish functional group we fitted the most complex ‘full model’. The full model included all covariates as additive effects, interactions between covariates and type of zone and an interaction between years. The fishing pressure covariate represented the pre-MPA state and the year by zone interaction allowed for different rates of recovery in different zone types. The model thus partitioned the effects of historical fishing pressure, MPA zone and time since MPA implementation on fish biomass. We then simplified the full model using the AIC, stopping when removal of any term caused an increase in the AIC. We termed this model the ‘optimal’ model. When two models had similar AIC values we proceeded with the most complex one, but we confirmed in all cases that predictions did not differ substantially among models with comparable AIC values.

Following AIC model selection, we fit the optimal model with the restricted maximum likelihood (REML) approach, so we could interpret effect sizes and predictions of fish biomass. Plots with confidence intervals were also used to visualise strength of effect on fish biomass for each covariate and modelled interactions.

Modelling was undertaken in R (R Development Core Team, 2018) using a generalised additive mixed model (GAMM, mgcv package, Wood, 2019) and maximum likelihood

estimation (MLE). The GAMM framework was chosen because it allowed us to include non-linear effects for the continuous variables, which we modelled with thin plate regression splines (Wood, 2017). We verified all model fits, by first confirming there was no spatial autocorrelation in model residuals with semi-variograms (sgeostat package, Majure and Gebhardt, 2016). The assumptions of homogeneity of variance and normal distribution of residuals by all covariates were verified visually (Wood, 2017).

4.3.2.3 Model Predictions for MPA performance

The optimal GAMM was used to: 1) predict the spatial variability in fish biomass for each functional group under current MPA zone designations (contemporary biomass) and, predict biomass for a reference condition with no fishing, and 2) determine if the MPA has performed to meet its objectives for fish biomass. We predicted MPA performance for reefs in each grid cell as:

$$\text{MPA performance} = \text{Predicted contemporary biomass} - \text{Predicted biomass with no fishing} \quad (1)$$

The prediction for pre-fishing biomass was the biomass predicted by the GAMM, but setting all grid cells to low-fishing reference sites (reference condition). Biomass within the MPA was predicted by the GAMM with all grid cells set to their current MPA designation. Here, MPA performance is defined as the difference between model predictions for biomass in 2015 (Misool MPA) and 2016 (Kofiau MPA) (contemporary biomass, the most recent year of data) compared to biomass predicted with no historical fishing. The performance measure thus reflects the average predicted difference between the reference conditions and the local recovery averaged over all sites. These predictions smooth out noise across individual surveys, and allowed us to predict performance across the entire seascape (including at reefs with no survey data).

We also measured observed outcomes as a difference from the average expected outcome for a site with a given set of environmental conditions and MPA zoning. This measure relies on observed data, so can only be calculated at the survey sites. It was defined:

$$\text{Outcome} = \text{Observed biomass} - \text{predicted contemporary biomass} \quad (2)$$

This comparison enables comparison of expected performance against actual observed outcomes and is relevant when managers are interested in the performance of individual sites.

Predictions for each fish functional group were made with the optimised models and rasters of the biophysical covariates and extent of the MPAs set at resolution of 150 m² (Table 4.1). We predicted biomass conditional on the random effect set at the mean for all sites. Fish biomass was extrapolated to all coral reefs where reef survey data were missing for both herbivore and predator functional groups. Biomass predictions were corrected for retransformation biomass (Duan, 1983) and converted to kg/150m² (the size of each pixel on our grid).

4.4 Results

4.4.1 Model of fishing pressure

The fitted model predicted greater numbers of boats closer to settlements (Figure 4.3a, b). In Misool, an exponential decline in boat numbers was observed out to 40 km (Figure 4.3a, straight line on a log-scale indicates exponential effect). In Kofiau, there was a more rapid non-linear decline in the number of fishing boats further from shore (Figure 4.3b). At distances greater than 10 km, there was no clear effect of distance and numbers of fishing boats in Kofiau. In both case studies, the majority of boats (~80%) had no motor or only a small outboard motor. However, there was almost twice as many boats without a motor in the Kofiau MPA (62%) compared to Misool MPA (33%), which may explain the more rapid decline in boats in Kofiau when compared to Misool.

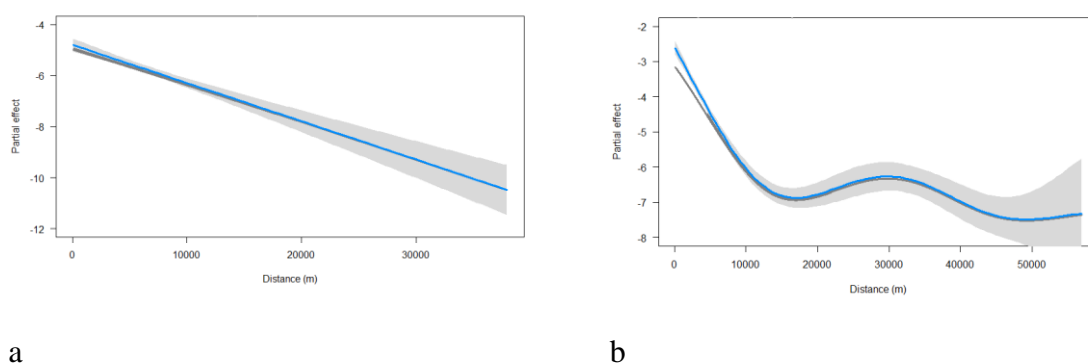


Figure 4.3 Partial effect of distance (m) on the number of fishing boats for Misool (a) and Kofiau (b). Blue solid show the estimated smooth effect (\pm standard errors in grey band).

4.4.2 Models of fish biomass

4.4.2.1 Misool Case Study

In the Misool MPA the model of herbivore biomass with the lowest AIC was the model with an interaction between fishing pressure and zone type, and additive effects of year, wave exposure and distance to mangroves (AIC = 2488.8, Table 4.1). The optimal model for predatory reef fish had all variables as additive effects (AIC = 2287.6, Table 4.1). These optimal models explained 31.9% and 34.1% of the variation in herbivore and predator biomass, respectively.

Predator biomass had a negative relationship with pre-MPA fishing pressure (Supplementary Figure A.5 (i)), while the same effect was only found at NTZ for herbivorous reef fish (Supplementary Figure A.4 (i)). Predator biomass decreased slowly through time in all zones (Supplementary Figure A.5 (ii)), while an increase in herbivore biomass was found from 2009 to 2011 before it trended downwards (Supplementary Figure A.4 (ii)). A weak positive, linear effect of exposure was found for fish biomass (Supplementary Figures A.4 (iii), A.5 (iii)). There was little effect of proximity of mangroves on fish biomass, though it was included in the optimal model (Table 4.1, Supplementary Figures A.4 (iv), A.5 (iv)). Mean herbivore and predator biomass was four times greater in NTZ than control zones and two times greater compared to use zones. Herbivore biomass was also greater than predator biomass in NTZs (1.5x), while mean herbivore biomass was more similar in both control and use zones when compared to predator biomass.

4.4.2.2 Kofiau Case Study

In the Kofiau MPA, the optimal models for herbivores and predators included an additive effect of distance to seagrass and three-way interactions among pre-MPA fishing pressure, year and zone type (Table 4.2). These optimal models explained 33.5% and 38.2% of the variation in herbivore and predator biomass (logged) respectively. Seagrass habitats were not confounded with settlements in Kofiau and were used in the final model because the model with proximity to seagrass had a slightly lower AIC than the model with proximity to mangroves. Wave period was also chosen as a better indicator of exposure than wave height.

Fish biomass had a negative relationship with pre-MPA fishing pressure at use zones only (Supplementary Figures A.6 (i), A.7 (i)). Herbivore biomass decreased slowly through time at both control zones and use zones although an increase was found from 2013 to 2016

Table 4.1 Comparison of the GAMMs for predictions for Misool MPA, including all tested models for herbivorous and predatory reef fish biomass. Asterix denotes optimal model.

Model effects	AIC	
	Herbivores	Predators
Pre-MPA fishing pressure * year * type of zone + distance to mangroves + wave period + random site	2497.5	2290.0
Pre-MPA fishing pressure * type of zone + year + distance to mangroves + wave period + random site	2488.8*	2290.4
Pre-MPA fishing pressure + year + type of zone + distance to mangroves + wave period + random site	2498.0	2287.6*
Year * type of zone + Historical fishing pressure + distance to mangroves + wave period + random site	2503.4	2288.4
Pre-MPA fishing pressure * type of zone + year + wave period + random site	2488.8	2290.4
Pre-MPA fishing pressure * type of zone + year + random site	2494.7	2291.5
Pre-MPA fishing pressure + year + type of zone + wave period + random site	NA	2287.6
Pre-MPA fishing pressure + year + type of zone + random site	NA	2289.9

Table 4.2 Comparison of the GAMMs for predictions for Kofiau MPA, including all tested models for herbivorous and predatory reef fish biomass. Asterisk denotes optimal model.

Model effects	AIC	
	Herbivores	Predators
Pre-MPA fishing pressure * year * type of zone + distance to seagrass + wave period + random site	2650.8	2649.6*
Pre-MPA fishing pressure * type of zone + year + distance to seagrass + wave period + random site	2667.5	2657.0
Pre-MPA fishing pressure * year + type of zone + distance to seagrass + wave period + random site	2650.3	2655.5
Year * type of zone + Historical fishing pressure + distance to seagrass + wave period + random site	2657.2	2658.4
Pre-MPA fishing pressure * year * type of zone + wave period + random site	2651.1	2649.6
Pre-MPA fishing pressure * year * type of zone + distance to seagrass + random site	2649.4*	2649.6
Pre-MPA fishing pressure * year + type of zone + wave period + random site	2650.4	NA
Pre-MPA fishing pressure * year + type of zone + distance to seagrass + random site	2650.0	NA

(Supplementary Figure A.6 (ii)). Predator biomass remained stable through time at control and NTZ, while a slight increase was found at use zones (Supplementary Figure A.7 (ii)). A weak positive, linear effect of exposure was found for predator fish biomass (Supplementary Figure A.7 (iii)), while a weak effect of distance to seagrass habitat was found for herbivore biomass (Supplementary Figure A.6 (iii)). Mean herbivore and predator biomass were similar in NTZ (133.5 kg/ha and 131.4 kg/ha, respectively), while herbivore biomass was 3.3 times

greater than predator fish biomass in control zones and 1.3 times greater than predator fish biomass in use zones.

4.4.3 Model Predictions for MPA Performance

Higher regional biomass estimates were predicted for the Kofiau MPA when compared to the Misool MPA (herbivores 1,753,188 kg and predators 1,932,991 kg in Kofiau MPA c.f. to herbivores 577,763 kg and predators 639,700 kg in Misool MPA). There were 2.4 times more reef pixels in Misool MPA than Kofiau MPA. Spatial predictions of contemporary fish biomass for the Misool MPA predicted the highest biomass in the NTZ of the MPA, particularly in the offshore reefs bordering the north-eastern perimeter of the MPA (up to 291.5 kg/ha and 224.8 kg/ha for herbivorous and predatory reef fish respectively, Supplementary Figures A.8, A.9). Reefs located outside of Misool MPA, particularly along the northern shorelines of mainland Misool, were expected to have the lowest biomass for both herbivores and predators (<17.8 kg/ha) in Misool. Spatial predictions for Kofiau MPA predicted the highest biomass for key herbivorous reef fish within the NTZ of the MPA (up to 186.7 kg/ha Supplementary Figure A.10). In comparison, the highest biomass for key predatory reef fish in Kofiau MPA was located in the Boo Islands (up to 333.3 kg/ha, Supplementary Figure A.11).

Predictions of MPA performance indicated that key predatory reef fish were close to the no fishing reference condition in the outer reefs of Misool MPA and in the outer reefs and NTZ of Kofiau MPA (Figure 4.5, 4.7). Differences between biomass under reference conditions and contemporary biomass were as much as 131.1 kg/ha (295 kg/22,500 m²) in the reefs adjacent to settlements in the Kofiau MPA for predatory reef fish (use zones). In comparison, differences of up to 128.9 kg/ha (290 kg/22,500 m²) were predicted for predatory reef fish along the inshore reefs in Misool MPA.

Performance for herbivore fish differ to predatory reef fish in both regions. In the Kofiau MPA, key herbivorous fish were predicted to have approached baseline levels within all the NTZs (Figure 4.6). Differences between reference condition biomass and contemporary biomass for herbivores in Kofiau MPA were greatest in the use zones adjacent to settlements by as much as 111.1 kg/ha (250 kg/22,500 m², Figure 4.6). In Misool MPA, biomass was not expected to reach reference conditions for herbivores under current management regulations, as differences of between 45 kg/ha to 180kg/ha were predicted across the inshore and

offshore reefs (Fig 4.4). The lowest predicted recovery of biomass towards reference conditions were in the reefs outside of Kofiau and Misool MPA.

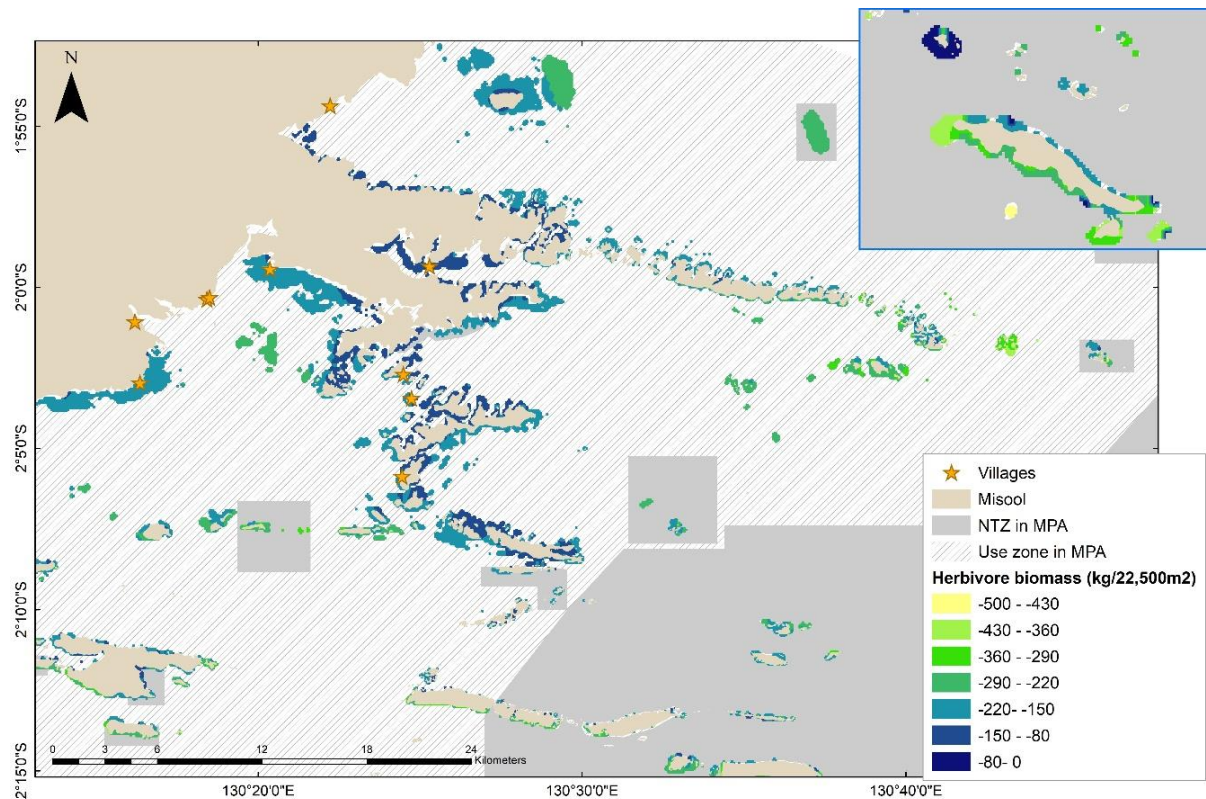


Figure 4.4 Predicted recovery of herbivorous fish in 2015 towards biomass in reference conditions. Map is at a resolution of 30 m² and shows the Misool MPA. Zero values indicate that biomass was predicted to be the same as at reference conditions, whereas negatives values indicate that biomass predicted in 2016 was below reference conditions. Inset shows the island of Daram which is not shown in the main map to improve visual inspection.

Comparison of reef fish survey data to predicted biomass indicated variation in observed outcomes compared to the predicted average (Supplementary Figure A.12). Marine Protected Areas (NTZ and use zones) were observed to be over-performing between 2 to 3 times relative to the average predicted biomass in both MPAs and functional groups (Supplementary Figure A.12). The site where observations were well below the model predictions (suggesting MPA under-performance) was Daram in 2011 and 2013, which is the most remote reef in the Misool MPA. Sites surrounding Warakaket, the most southern islands in the Misool MPA, also had much lower herbivore biomass in 2015 than predicted. Under-prediction of observed biomass was more common for herbivores in comparison to predators in Misool MPA. In Kofiau MPA, residuals were smaller across all years, particularly for predators. Only one site had much lower biomass than predicted (up to six times for herbivores), which was Wamei in 2016, a site naturally high in fish biomass and of interest to

managers. In the same year, Wambong, a site in close proximity to Wamei but located in a NTZ, had greater biomass than predicted by the model (by up to four times).

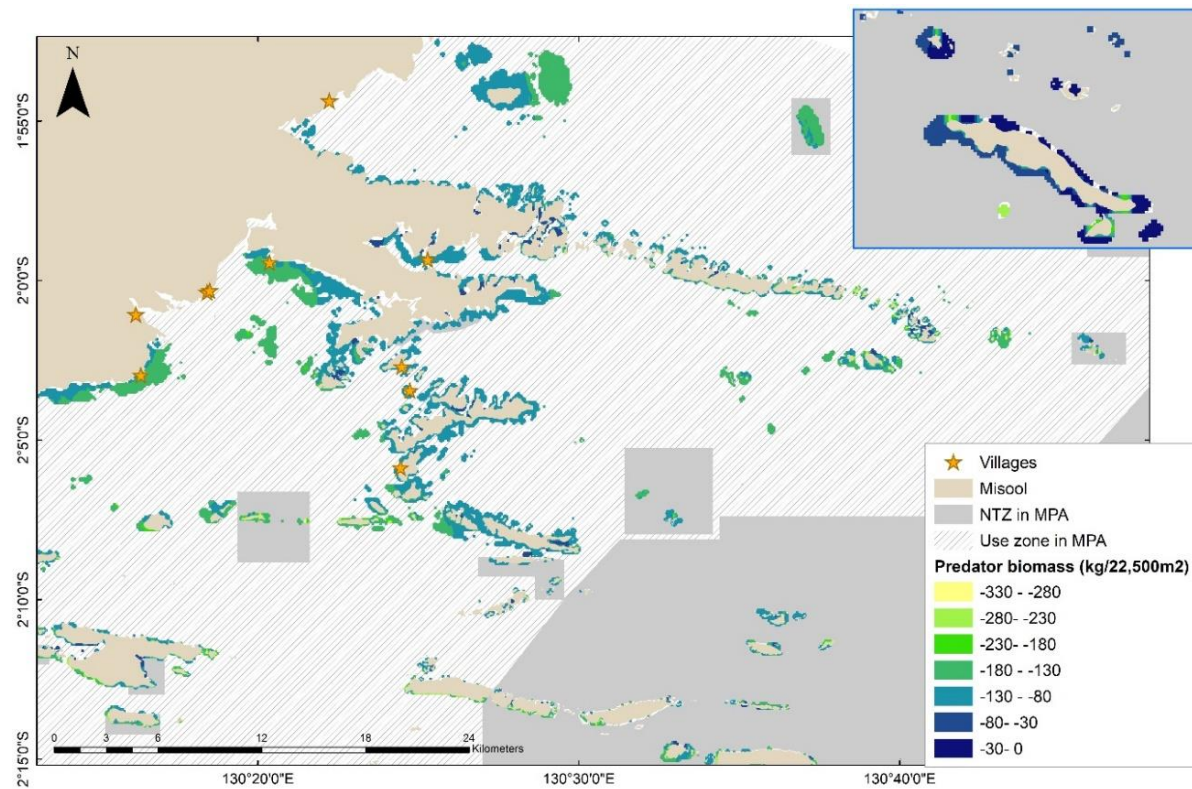


Figure 4.5 Predicted recovery of fished predatory fish in 2015 towards biomass at reference conditions. Map is at a resolution of 30 m² and shows the Misool MPA. Zero values indicate that biomass was predicted to be the same as at reference conditions, whereas negatives values indicate that biomass predicted in 2016 was below reference conditions. Inset shows the island of Daram which is not shown in the main map to improve visual inspection.

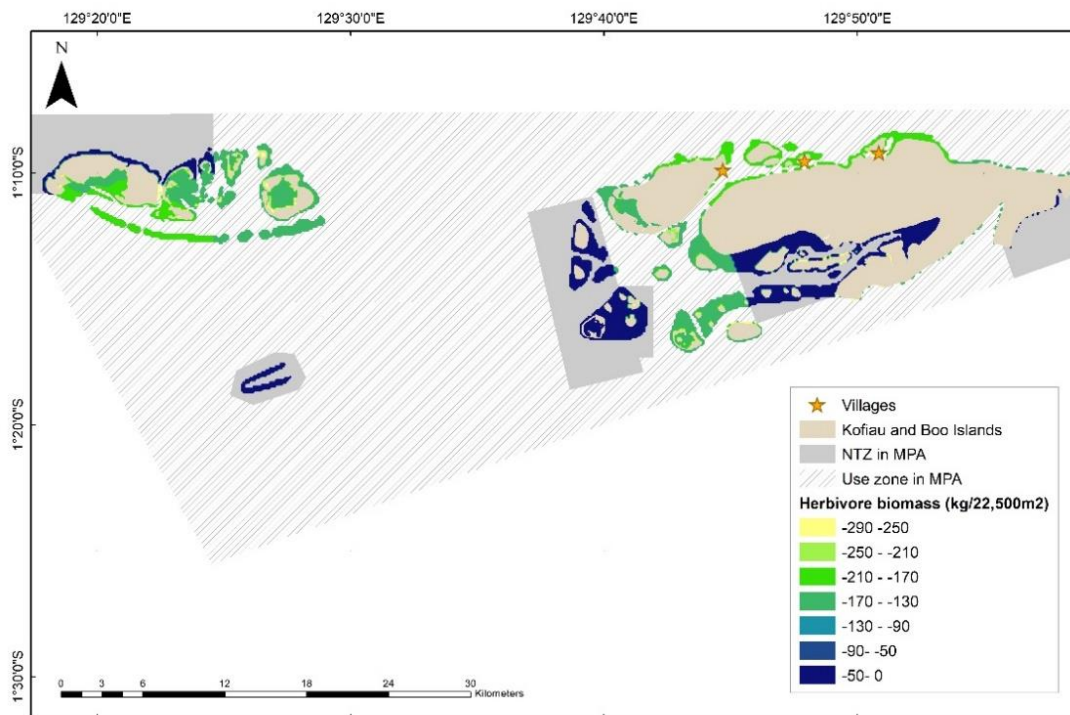


Figure 4.6 Predicted recovery of herbivorous fish in 2016 towards biomass at reference conditions. Map is at a resolution of 30 m² and shows the Kofiau MPA. Zero values indicate that biomass was predicted to be the same as at reference conditions, whereas negatives values indicate that biomass predicted in 2016 was below reference conditions.

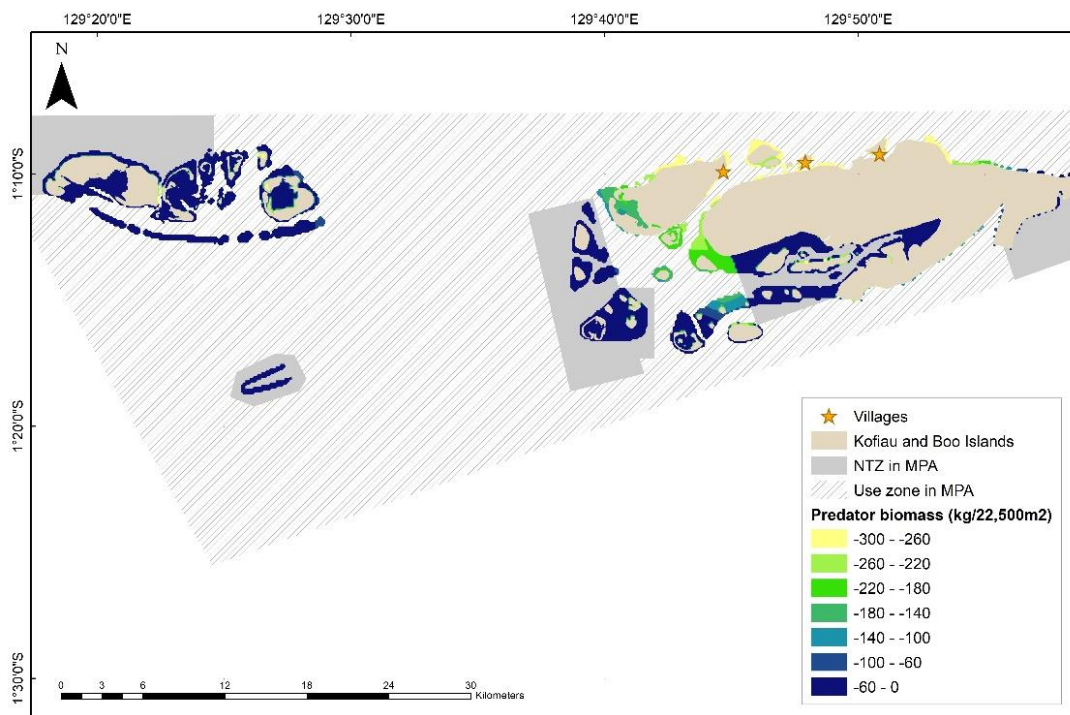


Figure 4.7 Predicted recovery of predatory fish in 2016 towards biomass in reference conditions. Map is at a resolution of 30 m² and shows the Kofiau MPA. Zero values indicate that biomass was predicted to be the same as at reference conditions, whereas negatives values indicate that biomass predicted in 2016 was below reference conditions.

4.5 Discussion

4.5.1 Summary

The evaluation of MPA performance would benefit from understanding how conservation targets for fish biomass are impacted by spatial differences in pre-MPA threats and biophysical conditions. Doing so would allow conservation managers to make better decisions on actions needed to adaptively manage threats. This study identified social and biophysical drivers that influence fish biomass distribution, and utilised realistic conservation targets of fish biomass, to predict how two MPAs within the TWP Raja Ampat MPA network were performing. We found that MPA performance varied spatially and was affected by the type of management action, trophic group (or species) of interest and differences in fishing vessels used across the two MPAs. Overall, high coral reef fish biomass was predicted across the seascape in all MPA zones, comparable to fish biomass in other Indonesian MPAs (Campbell et al., 2020; McClanahan et al., 2016). We therefore predicted modest recovery of fish biomass, which implies that the overall objectives of the MPA are being achieved. We suggest achievable performance objectives for the MPAs future would be framed as the maintenance of the fish biomass existing in 2015 in Misool and 2016 in Kofiau.

No-take zones showed the greatest performance for predatory reef fish because biomass was predicted to have reached, or be close to, the reference state in both regions within five years of implementation. The biomass of predatory fish at reefs outside of MPAs was far below a no-fishing reference condition. The performance of NTZs for protecting herbivores differed depending on region. No-take zones performed well for protecting herbivores in the Kofiau MPA. In the Misool MPA, herbivore biomass was not higher in NTZs compared to use zones, suggesting that Kofiau had recovered better, had greater compliance with regulations in the use zones to protect fish or that it might be a more important fish refuge than Misool. Regional differences in MPA performance could also be caused by spatial bias in the placement of NTZs towards sites that had historically high herbivore biomass or socio-economic differences that affect compliance with MPA regulations (Campbell et al., 2012). Misool has greater access to external markets via ferries (see Supplementary Data – community overview), so there are greater incentives for poaching and illegal fishing practices are known to occur inside the Misool MPA (Purwanto et al., 2021; Varkey et al., 2010). A poaching problem is also suggested by a number of sites in NTZs of the Misool MPA having lower herbivore biomass than expected. Poor compliance has been reported elsewhere in Indonesia. For example, compliance with spatial restrictions in a government-

controlled MPA in Indonesia (Karimunjawa National Park) were weak, despite high community awareness of fishing restrictions, which resulted in a >50% reduction in reef fish biomass inside a NTZ over a four-year period (Campbell et al., 2012).

4.5.2 Performance of MPAs

Overall, the recovery of fish towards pre-fishing biomass baselines in southern Raja Ampat MPAs suggests that MPAs are performing well at protecting fish biomass. We suggest this performance is a consequence of two factors. First, we predicted the recovery of reef fish was closer to the reference condition inside MPAs than compared to outside MPAs. For example, our indicator for herbivore biomass was closer to the reference condition inside Misool's MPA than outside the MPA. Second, biomass trends were consistent through time inside NTZs and use zones, but declining outside the MPA, consistent with regional studies of fish trends in Raja Ampat (Fidler et al., 2021). Fish biomass has not recovered equally in both regions however; there was a stronger effect of the NTZs in the Kofiau MPA when compared to Misool MPA. Enforcement of some of Kofiau's MPAs could be more effective, because, for instance, the Wambong NTZ is located close to a patrol post. In Misool, several NTZs (Daram, Warakaket and Kalig) had slower than expected biomass recovery trends and are remote from patrol posts.

Our findings of performance were consistent with the expectation that reef fish biomass is higher further from settlements and in more exposed sites (Harborne et al., 2018), inside NTZs (Sangil et al., 2013), and closer to coastal wetlands (Mumby et al., 2004). The order of importance for these covariates differs for each trophic level and region. The effect of distance from settlements was greatest for reefs within 5-6 km of settlements in Kofiau MPA, while the effect of distance was linear out to 40 km from settlements in Misool MPA. The RUM data supported spatial limitations on travel; the majority of vessels in Kofiau MPA manually paddled or sailed (62%) in comparison to half the number of fishing vessels with no motor in Misool MPA (33%). The exposure model also supported limitations on travel; calmer waters within 40 km of settlements in Misool MPA in comparison to near-shore sheltered waters (within ~7 km) from settlements in Kofiau MPA followed by stretches of unimpeded fetch up to 20 km between Kofiau and Boo Islands. Limitations on the spatial dispersal of fishing effort has been shown in Pacific Island nations (Adams et al., 2011). Fish biomass has been shown to reduce along the exposure gradient, contrary to this study (Friedlander et al., 2003; Shepherd et al., 2010). Covariates of distance to habitat had a small

but significant influence on reef fish and likely explained the spatial nuances shown in the model prediction maps.

4.5.3 Caveats and future research

There are several caveats that limit interpretation of the results and require further investigation to improve the assessment of MPA performance. We estimated the reference condition for unfished biomass from low fishing pressures sites, which are likely an underestimate of the unfished biomass. Fish stocks in southern Raja Ampat may have already undergone a decline by an order of magnitude between 1970 to 2006 (Ainsworth et al., 2008). We also have not accounted for fishing effort from non-local fishers that target reefs remote from communities. Earlier studies have inferred a limited effect of foreign vessels on reef fish biomass, but further research is needed (Brown et al., 2018b). The effect of non-local fishers could explain why lower fish abundances have been observed further from settlements in other areas of Raja Ampat Regency (Andradi-Brown et al., 2021; Fidler et al., 2021). Despite these caveats, our predictions for mean biomass at reference conditions for the six fish families considered in this study (256 kg/ha and 368 kg/ha in Misool MPA and in Kofiau MPA, respectively) are within the range of global scale reef fish biomass in the absence of fishing (MacNeil et al., 2015).

Future modelling in this region should consider incorporating additional covariates that are known to be important predictors of reef fish biomass. For example, benthic habitat can also influence fish biomass (e.g. Brown et al., 2018a; Komyakova et al., 2013) and recovery trends in MPAs (Fidler et al., 2021). While we had benthic composition data at survey sites, we could not use this data in the models because it was not spatially comprehensive. Higher resolved wind data which was used as input in the wave exposure model, would also reduce spatial and temporal variation, as the wind data had not been validated for Indonesia and was modelled from a wind measurement station located in Papua New Guinea (Technical University of Denmark, 2018). Socio-cultural, economic, and political factors also influence the performance of MPA (Glew et al., 2012; Maire et al., 2016), such as community support, enforcement and degree of remoteness. Further, distance to markets (where middlemen buy fish from locals) could be a better indicator of fishing pressure than distance to settlements. We utilised settlements here, because markets are dispersed within settlements, which made it difficult to separate statistically the effects of markets from the effects of settlement location. The inclusion of more specific social variables in the models of MPA performance could help

to explain why individual MPAs are performing worse than average, and better inform management actions.

4.5.4 Management Implications

We found that managers need to consider the historical fishing pressure when setting realistic expectations of outcomes. There are expectations that MPAs in Indonesia, particularly NTZ, increase fish biomass, even if recovery is not a prescribed objective (Ford et al., 2020) and fish biomass recovery is often used to advocate for MPAs (Marshall and Morris, 2019). In Indonesia, conservation managers that utilise NTZ in a patchwork of other MPA management measures, expect fish biomass to be improved or at least maintained (Purwanto et al., 2021). The placement of MPAs however, is often a trade-off between environmental gains and economic/social costs (Mills et al., 2010; Schratzberger et al., 2019; Watson et al., 2014), resulting in stronger fisheries restrictions, such as NTZs, established in areas of low-fishing interest or accessibility (Devillers et al., 2015). No-take zones cannot be expected to increase fish biomass in places that historically have low-fishing pressure (Nickols et al., 2019), such as some of the outer islands of the Misool MPA.

We developed a spatial modelling approach for setting expectations for fish biomass in MPAs that are consistent with biophysical gradients (wave exposure and proximity to habitats) and gradients in historical fishing pressure. This method helps to set clearer expectations for MPA performance and we recommend incorporating these variables when designing a monitoring program to capture the effect of this variation. It is important that expectations of MPA performance are clear so that the benefits can be clearly demonstrated. Evidence of the benefits of MPA using more realistic targets is important to: 1) ensure continued support for the MPA, particularly when community engagement is a main form of compliance, (2) support well-informed adaptive management, 3) provide evidence to funders about the impact of their investment and, 4) provide regionally relevant evidence to gain support for MPAs as a viable management tool going into the future.

4.6 Supporting Information

Supplementary data on the community (Supplementary Data – community overview), methods (Supplementary Data - Methods), the range of explanatory variables filtered from reef fish survey data (Supplementary Table A.10), plots of expected herbivore biomass (Supplementary Figure A.4) and predator biomass (Supplementary Figure A.5) as estimated by the most parsimonious model for Misool MPA, plots of expected herbivore biomass

(Supplementary Figure A.6) and predator biomass (Supplementary Figure A.7) as estimated by the most parsimonious model for Kofiau MPA, predicted herbivore biomass (Supplementary Figure A.8) and predator biomass (Supplementary Figure A.9) in Misool MPA, predicted herbivore biomass (Supplementary Figure A.10) and predator biomass (Supplementary Figure A.11) in Kofiau MPA, and yearly comparison between the observed and predicted MPA performance (Supplementary Figure A.12).

4.7 Acknowledgements

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Chapter 5 Metabolomic indicators for low-light stress in seagrass

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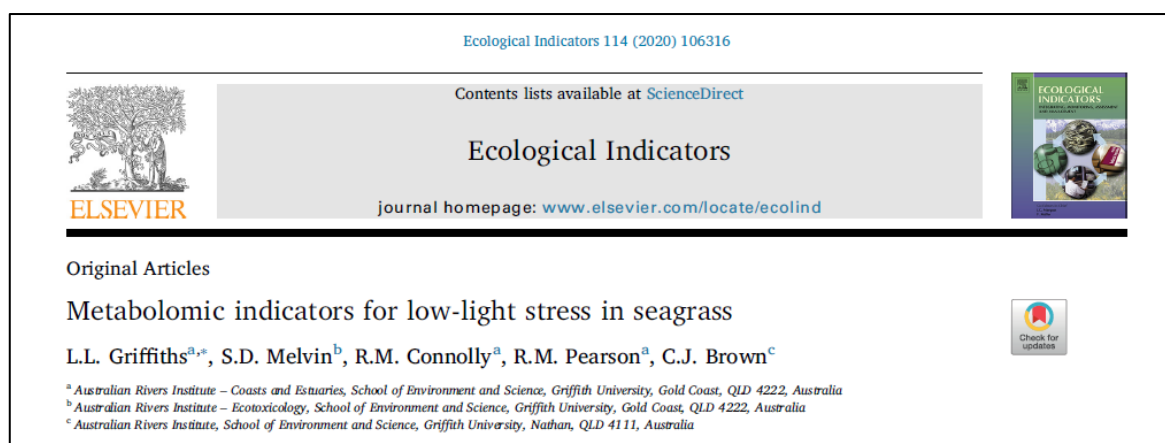
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Author Contributions

Conceptualisation of the study: RMC. Methodology: LLG, CJB, RMP. Formal analysis of the data: LLG, CJB, SDM. Writing – original draft preparation: LLG. Validation: SDM. Writing – review and editing: CJB, RMC, RMP, SDM.

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5.1 Abstract

Monitoring of seagrass meadows is essential to inform adaptive management and address widespread declines in seagrass ecosystems. Effective monitoring techniques require sensitive indicators that are capable of detecting sub-lethal stressors and differentiating stress responses from background environmental variation. Here we explore untargeted metabolomics as a means to measure multi-parameter molecular responses of seagrass to low-light stress. We subjected *Zostera muelleri* to reduced light scenarios (<10% natural light) in a six-week field experiment. Biomass loss was quantified over time and leaf samples were analysed by Nuclear Magnetic Resonance (NMR) spectroscopy to explore the effect of low-light exposure on metabolic activity. We identified several potential bioindicators of low-light stress: a reduction of soluble sugars and their derivatives, glucose, fructose, sucrose and myo-inositol, N-methylnicotinamide, organic acids and various phenolic compounds, and an increase in some amino acids. These signals were evident even amongst a noisy background of environmental variation and are consistent with inhibition of photosynthesis. Metabolite profiles showed a more consistent response to low-light stress than to biomass loss. These results suggest that metabolomics measurements may be useful bio-indicators of low-light stress in seagrass and that molecular indicators could inform on management of seagrass ecosystems.

Keywords: *Zostera muelleri*; low-light stress; metabolomics; bioindicator; seagrass; biomass.

5.2 Introduction

Seagrass ecosystems play a critical role in mitigating against climate change and provide essential habitat to fisheries, marine megafauna and protected species (Mtwana Nordlund et al., 2016; Sievers et al., 2019), however they are facing a widespread decline due to human impacts (Waycott et al., 2009). Turbidity has been identified as one of the most significant threats to seagrass, since the associated reduction in light inhibits growth (Collier et al., 2016). Extensive seagrass meadows are often found in estuaries and bays where ports and cities co-occur, so they are frequently exposed to poor water quality from capital dredging works and turbid river plumes associated with urban and agricultural development (Saunders et al., 2017). Prolonged periods of reduced light can result in complete loss of a meadow (Lavery et al., 2009). Monitoring of seagrass meadows, including their responses to human stressors (threats), is required to inform on management actions to avert loss (Griffiths et al., 2020).

Recognising when meadows are stressed, or more susceptible to stress, can be difficult using traditional approaches for routine monitoring. Growth-condition metrics such as species composition, above ground biomass and spatial coverage are commonly used to indicate seagrass health (Collier et al., 2016; Moore et al., 2000) although a range of other metrics are also widely used (Chartrand et al., 2016; Petus et al., 2014; Vonk et al., 2015). Condition metrics detect change in seagrass biomass over time, however at times their efficacy is limited by substantial variation within sites and among seasons (Hossain et al., 2010). Further, they offer little insight into sub-lethal stresses that may be occurring at a physiological and molecular level, and which may precede morphological responses between routine sampling events. The development of sensitive alternative methodologies capable of revealing environmental perturbations at the molecular level are becoming essential for monitoring ecosystem health (Rotini et al., 2013), including for seagrass ecosystems (Macreadie et al., 2014). However, among the many methods previously used to measure light stress in seagrass, several of those reflecting physiological processes, such as respiration rate and concentrations of nitrogen, phosphorous and carbon (among others), do not respond consistently to light reduction and as such are not recommended as bioindicators (McMahon et al., 2013). Endpoints that integrate multi-parameter molecular responses to stress show great potential for addressing this shortcoming (Kumar et al., 2016).

Metabolomics has become a significant contributor to the identification of stress in plants (Shulaev et al., 2008). Metabolomics can identify by-products of stress metabolism and molecules that are part of the acclimation response of plants (Hong et al., 2016), so measurements of metabolites could indicate stress in seagrass meadows (Hasler-Sheetal et al., 2015). Physiological responses to stress may include elevated levels of amino acids or a reduction in sugars important in the signaling of cells under stress (Kumar et al., 2016). Liquid- and Gas-Chromatography paired with Mass Spectrometry (LC/GC-MS) and Nuclear Magnetic Resonance (NMR) spectroscopy are powerful tools for metabolomics analysis, each offering different strengths and weaknesses (Emwas, 2015; Pan and Raftery, 2007). NMR offers a particularly rapid and repeatable platform for untargeted metabolomics, including the ability to identify and quantify minor differences in a wide range of biologically relevant amino acids, carbohydrates, nucleotides and other metabolites (Melvin et al., 2017; Zou et al., 2014). The method has been used to obtain comprehensive metabolite profiles for the Northern Hemisphere seagrass species, *Zostera marina* (Hasler-Sheetal et al., 2015; Mochida et al., 2019). The untargeted nature of metabolomics is what makes it particularly

relevant to ecological studies, because it reflects all interactions between and within species, and with their environment, rather than targeting specific biochemical pathways. This approach is referred to as eco-metabolomics and provides mechanistic evidence for biochemical processes that are relevant at ecological scales by detecting changes in metabolite concentrations (Peters et al., 2018). The results of early research has revealed considerable differences in profiles of metabolites between samples collected from an aquatic environment with variable levels of natural environmental stress (i.e., low-light, high temperature and anoxic conditions (Kumar et al., 2016; Zidorn, 2016). Thus, untargeted metabolomics is ideal to further test the adaptation strategies of seagrass to low-light stress. If stress responses can be identified in metabolomic measurements, then they may also have potential to be used as an early warning indicator of seagrass stress.

Here we utilised a common monitoring technique to measure the loss of biomass from light stressed *Z. muelleri*, a Southern Hemisphere seagrass. The morphology of stressed seagrass was compared to its metabolic state which was measured using NMR-based metabolomics. We subjected seagrass to a continuous period of low-light *in situ*. Loss of above-ground biomass was quantified over time and metabolites were extracted from leaf samples after 6 weeks and analysed by NMR. Two important questions were asked: 1) how does biomass loss in stressed seagrass compare to metabolic activity? And 2) are differences in metabolite profiles between seagrass subjected to low-light stress and those exposed to natural light conditions detectable? The overall aim of this paper is to explore the use of non-targeted metabolomics for characterising low-light stress on seagrass.

5.3 Materials and Methods

5.3.1 Experimental set-up in the field

We subjected shallow subtidal (<3 m) beds of the seagrass *Z.muelleri* to reduced light conditions using shading structures for a continual six week period during the summer of 2018/2019 in southern Moreton Bay, Queensland. Shading structures (1 m²) were erected over five replicate patches of dense *Z.muelleri* (~ 3 m apart) along the subtidal fringe of large meadow. Shading material was a mesh canopy that reduced light penetration to subtidal seagrass well below natural levels, tethered at each corner to a plastic stake. We installed vertical isolation borders 10 cm inside the edges of the treatment plots to a depth of 25 cm in the sediment to sever the roots and prevent the transfer of nutrients and carbohydrates from unshaded and shaded areas via rhizomes (Chartrand et al. 2016). Unshaded control plots that

received natural light intensities were also prepared both with and without vertical isolation borders (two replicates of each). Light loggers (4 x Odyssey photosynthetically active radiation (PAR), and 5 x HOBO models) were placed in control and shaded plots to measure light levels throughout the period. Odyssey loggers were installed with automatic wipers. The shade cloth and HOBO light loggers were also manually cleaned every 2 days throughout the experiment to ensure relative differences in light penetration between treatments remained consistent, and to minimise sedimentation and biofouling. We quantified biomass inside a 25 cm² sub-quadrat installed within each 80 cm² plot. Shoot density (every shoot) and leaf-length (from five randomly selected leaves) were counted and measured, respectively, inside each sub-quadrat every 2 weeks throughout the experiment. A regression model was developed to quantify total biomass based on shoot density and leaf length (Eq. 1). This model was based on data collected from 6 seagrass cores (25 cm × 25 cm squares) from randomised locations adjacent to experimental plots prior to installation of the shade structures.

$$\text{Eq.1 Above ground biomass} = (0.213 * \text{shoot count}) + (0.148 * \text{average leaf length}) - 3.233$$

The standard error of the biomass estimate was ± 1.36g, or ~9% of the average starting biomass in each plot.

5.3.2 Sampling for metabolomics

We randomly collected between 7-20 single leaves of approximately 5cm in length from each 80 cm shaded (treatment, n=5) and unshaded (controls, n=4) plot after a continual shading period of 39 days. Each leaf was manually cleaned of epiphytes whilst submerged and immediately placed inside plastic vials and snap frozen in a liquid nitrogen dry shipper (Taylor Wharton™). We took care to remove the 2nd or 3rd youngest leaf closest to the sheath, avoiding the youngest leaf to ensure samples were standardised, since leaf age can influence metabolite composition and concentration (Agostini et al., 1998; Hasler-Sheetal et al., 2015). Samples were stored at -80°C in the laboratory until subsequent extraction of metabolites.

5.3.3 Sample extraction and processing for NMR spectroscopy

Samples were extracted and processed according to previously established methods (Melvin et al., 2017). In summary, after freeze-drying the samples, a modified Bligh-Dyer extraction (Bligh and Dyer, 1959) was performed to separate polar metabolites from lipids and cellular debris. Extracted metabolites were dried and re-suspended in 200µL phosphate buffer made

with deuterium oxide (D₂O), which contained 0.05% sodium-3-(tri-methylsilyl)-2,2,3,3-tetraduteriopropionate (TSP) as an internal standard (¹H δ 0.00, ¹³C δ 0.0). The dry weight of each leaf in each sample was measured.

Samples were loaded into 3 mm NMR tubes and analysed using an 800 MHz Bruker® Avance III HDX spectrometer equipped with Triple (TCI) Resonance 5 mm Cryoprobe with Z-gradient and automatic tuning and matching. The general methodology has been described elsewhere (Melvin et al., 2018a, 2018b). Briefly, spectra were acquired at 298 K with D₂O used for field locking. The zg30 pulse program was used for proton (¹H) spectra, with 128 scans, 1.0 s relaxation delay, 6.80 μs pulse width and spectral width of 16 kHz (¹H δ -3.02-16.02). Peaks were post processed with MestReNova v8.1.4 (Mestrelab Research S.L., Spain). Post-processing included manual phase-correction, ablative baseline adjustment and normalisation of the spectra to the TSP standard (¹H δ 0.00). Individual spectral features were then manually integrated and the data was exported and normalised to individual sample weight prior to statistical analysis (Melvin et al., 2018a, 2018b). An edited ¹H-¹³C Heteronuclear Single Quantum Coherence (HSQC) spectra was also acquired for one representative sample with 210 scans, 128 experiments, 0.8 s relaxation delay, 6.80 μs pulse width and spectral widths of 12.8 kHz (¹H δ -3.23-12.82) and 33.1 kHz (¹³C δ -9.40-155.2). Metabolites were tentatively assigned using Chenomx NMR suite 8.5 software (ChenomxInc., Edmonton, Canada), and assignments were further validated by comparison of HSQC spectra with freely available reference spectra (e.g., Human Metabolome Database; HMDB).

5.3.4 Multivariate statistical analysis

Data were grouped by the following treatments for multivariate analysis: 1) shaded plots with vertical isolation borders (shaded, treatment), 2) unshaded plots with vertical isolation borders (unshaded and bordered, treatment) and, 3) unshaded plots without vertical isolation borders (unshaded, control). We normalised the data to account for sample mass, and then scaled the data using the pareto scale function ('RFmarkerDetector' package in the R program (Palla and Armano, 2016). Pareto scaling is common in metabolomics studies, because it reduces the influence of extreme outliers (Emwas et al., 2018). We used Principle Component Analysis (PCA) ('pca3d' package in the R program) initially to explore correlations between treatment and control groups (Weiner, 2017). Linear regression was used to explore differences between groups based on mass of whole dried leaves.

We conducted multivariate regression with the Bayesian Ordination and Regression AnaLysis model ('boral' package in the R program) with explanatory (light effect and optimal peak in metabolite activity) and two latent variables (Hui, 2016). The boral model is suitable for metabolomics data because it models correlations between different metabolites measured across the same set of samples. We included as a fixed effect the two treatment groups and random effects as two latent variables. The latent variables model correlations between metabolites from unexplained sources of variation (Hui, 2016). The effect size of the treatment relative to the control was taken to be the median difference (\pm 95% highest posterior density intervals) in each metabolite's scaled value between control and treatment plots. We then quantified the signal-to-noise ratio in terms of each metabolite's ability to detect a change in low-light relative to background variation in that metabolite. The signal-to-noise ratio was quantified as the per cent of the variance attributed to the treatment effect relative to the sum of the treatment effect and the variance attributed to the latent variables.

We then tested whether changes in the metabolite concentrations were more consistent with light loss or biomass loss. To do this test, we compared the fit of two boral models: (1) a model with biomass percent loss at 39 days as a fixed effect against (2) a model with light intensity as a fixed effect. We did not include treatment type in either model, because this would be confounded with biomass/light. We compared these two models for their WAIC statistic (Vehtari et al., 2017), where the model with the lowest WAIC is most consistent with the differences in the metabolites. To aid interpretation of these patterns, we plotted metabolic activity, treatment (light) exposure and biomass loss for the metabolites with the greatest effect sizes. We also plotted an ordination from a principal components analysis of the weight normalised and pareto-transformed metabolomics data.

5.4 Results

5.4.1 Light measurements and biomass loss

The average total daily light penetration measured from the light loggers was $0.7 \text{ mol m}^{-2} \text{ d}^{-1}$ in shaded plots compared to $8.2 \text{ mol m}^{-2} \text{ d}^{-1}$ in unshaded plots over the experiment duration. The average PAR was $52.8 \text{ } \mu\text{mol m}^{-2} \text{ min}^{-1}$ at the time of collection for metabolomics in the shaded plots compared to $273.7 \text{ } \mu\text{mol m}^{-2} \text{ min}^{-1}$ in the unshaded plots (averaged over 2-hour collection period). The water temperature was 27°C across all plots.

A loss of biomass was observed over time in seagrass exposed to light stress through manipulative shading. In unshaded control plots, biomass on average declined slightly (13 %) over the 6-week period. Shaded plots lost on average 82% of biomass (Figure 5.1). Biomass loss in shaded plots was consistent with an average reduction of leaf length of 3.2 cm in shaded plots compared to an average increase of 3.1 cm in the unshaded plots. Loss of biomass in shaded plots was supported by a reduced leaf condition: individual leaves that were randomly sampled and dried for the metabolomics measurements had a lower weight in the shaded plot (10.6 mg) than leaves from the unshaded plots (14.7 mg, $p < 0.001$, $r^2 = 0.21$).

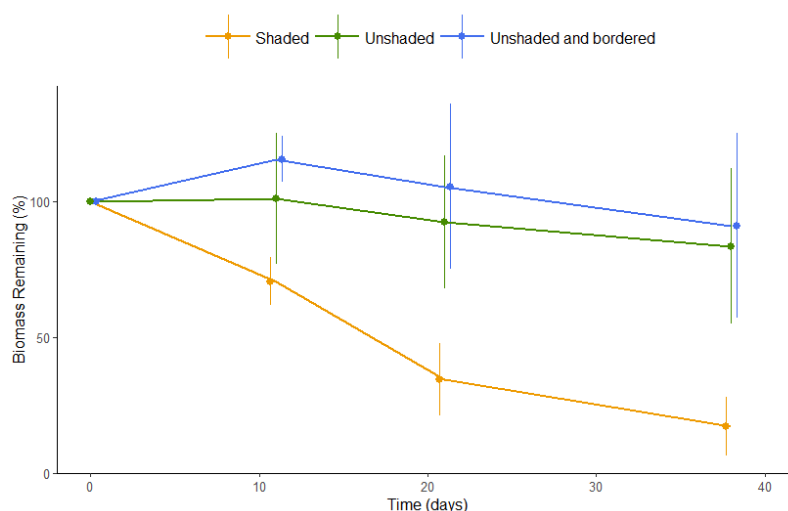


Figure 5.1 Seagrass biomass change during the shading experiment (mean, SE), as change from initial biomass 38 days after shade structures were erected. Treatment groups are shaded plots with vertical isolation borders (Shaded), unshaded plots with vertical isolation borders (unshaded and bordered) and unshaded plots without any treatment (Unshaded). Metabolomics samples were collected 39 days after shade structures were erected.

5.4.2 Metabolite differences

A total of 84 peaks were integrated from the ^1H spectra, corresponding to 33 distinct metabolites and 10 unidentified features (Figure 5.2). Numbers were assigned to identify individual peaks from the same metabolite (i.e. Fructose-1). Differences between the three treatment groups were clearly visible in a plot of the principal components (Figure 5.3). Further analysis with the Bayesian hierarchical models found that shaded plots had a high probability of lower glucose and fructose, some phenolics (and spectral regions where phenolics overlapped with other chemical features), sucrose (and regions where sucrose overlaps with other features), malic acid, N-methylnicotinamide, asparagine, myo-inositol and cinnamic acid (Figure 5.4a, Supplementary Figure A.13). Shaded plots had higher levels

of trigonelline and several amino acids (gamma aminobutyric acid, proline, betaine and glutamine), however, increases of trigonelline and the amino acids appear to be related to the effect of severing rhizomes from vertical isolation borders rather than shade stress (Figure 5.4b). Glutamine was an exception and remained elevated in the shaded plots.

The combined variance explained by shading for all metabolites was 3.5% (signal to noise ratio), indicating that there was considerable leaf to leaf variation among plots. However, variation explained by shading for individual metabolites was higher; as much as 93% for N-methylnicotinamide, between 16-30% for glucose, 10% for fructose and several phenolic compounds and the remainder of metabolites generally less than 10% (Supplementary Figure A.13). Overall high residual variation (Supplementary Figure A.14) suggested there was considerable variation in metabolites within and between plots for reasons other than the effect of shading.

Changes in light intensity were more consistent with changes in the metabolite profile than changes in biomass, according to the WAIC statistic (WAIC = 6448 for the light model versus 7006 for the biomass model). The assertion that shading, rather than biomass loss, was the predominant cause of metabolic variation was supported by visual interpretation of metabolite changes. For instance, peaks for glucose and fructose were elevated in unshaded plots, even when those unshaded plots had similar amounts of biomass loss as shaded plots (Figure 5.5).

5.5 Discussion

Here we demonstrated that light-stress triggers distinguishable changes in metabolite profiles of the seagrass *Z. muelleri*, indicating that metabolomics may be a useful and sensitive tool for identifying stressed meadows. We also observed a loss of biomass from reduced light, consistent with findings from other studies (Collier et al., 2016; Silva et al., 2013). Several metabolites changed in a way that is consistent with plant responses to light stress (Hasler-Sheetal et al., 2016). Considerable background variation between and within treatment plots was also observed, with low variance explained by the treatment relative to residual variance (Table 5.1), which is not unexpected for complex field ecosystems. However, some of the responses to low-light were identified as being a result of isolating the treatment plots, which prevents plants from receiving nutrients via rhizomes in adjacent unshaded areas. For example, amino acids such as trigonelline and gamma-aminobutyric acid showed no difference between the effects of isolation (Figure 5.4b) in comparison to the effect of

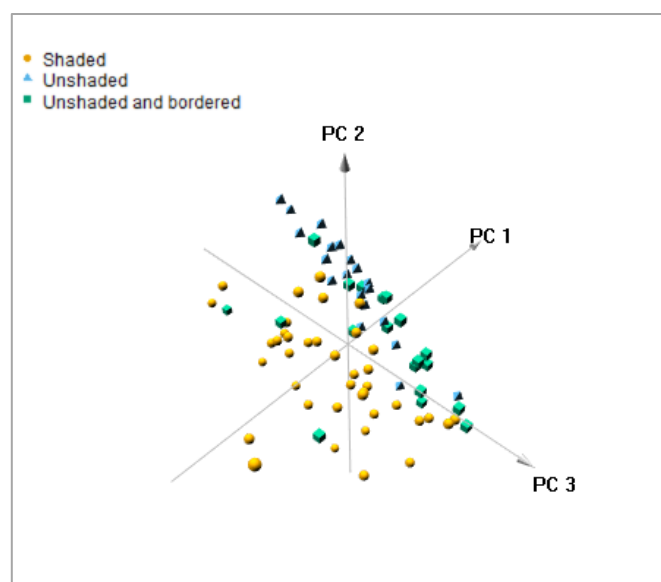


Figure 5.3 PCA plot of metabolites showing separation between shaded and unshaded plots.

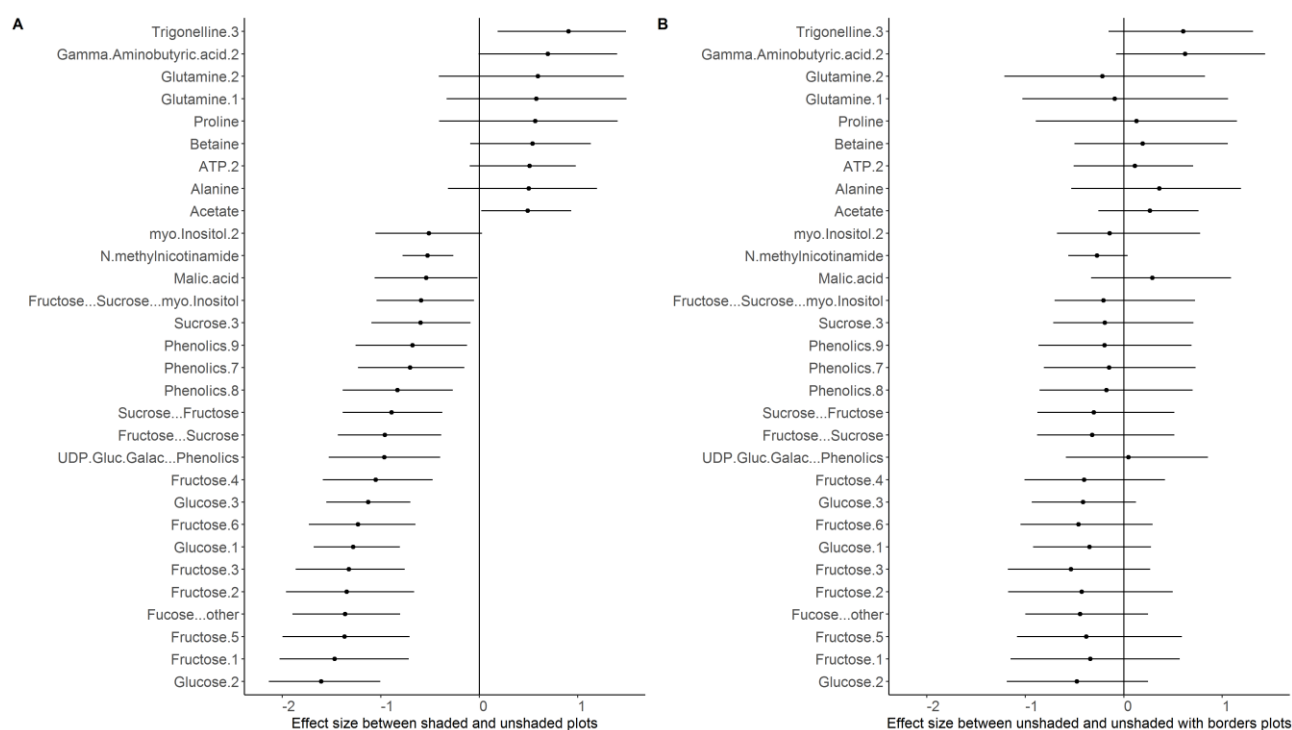


Figure 5.4 Differences in the median effect sizes (black dots) with errors (95% highest posterior density intervals) for the highest 30 metabolic peaks of *Z.muelleri* showing the greatest response to shade stress. Plot A (left) shows differences between shaded (treatment) and unshaded (control) plots while Plot B (right) shows differences between unshaded (control) plots and unshaded plots with vertical isolation borders (treatment). A value above or below zero indicates an increase or decrease, respectively, in concentration of the treatment in comparison to the control. Bars indicate there is 95% probability of falling between the upper and lower limits.

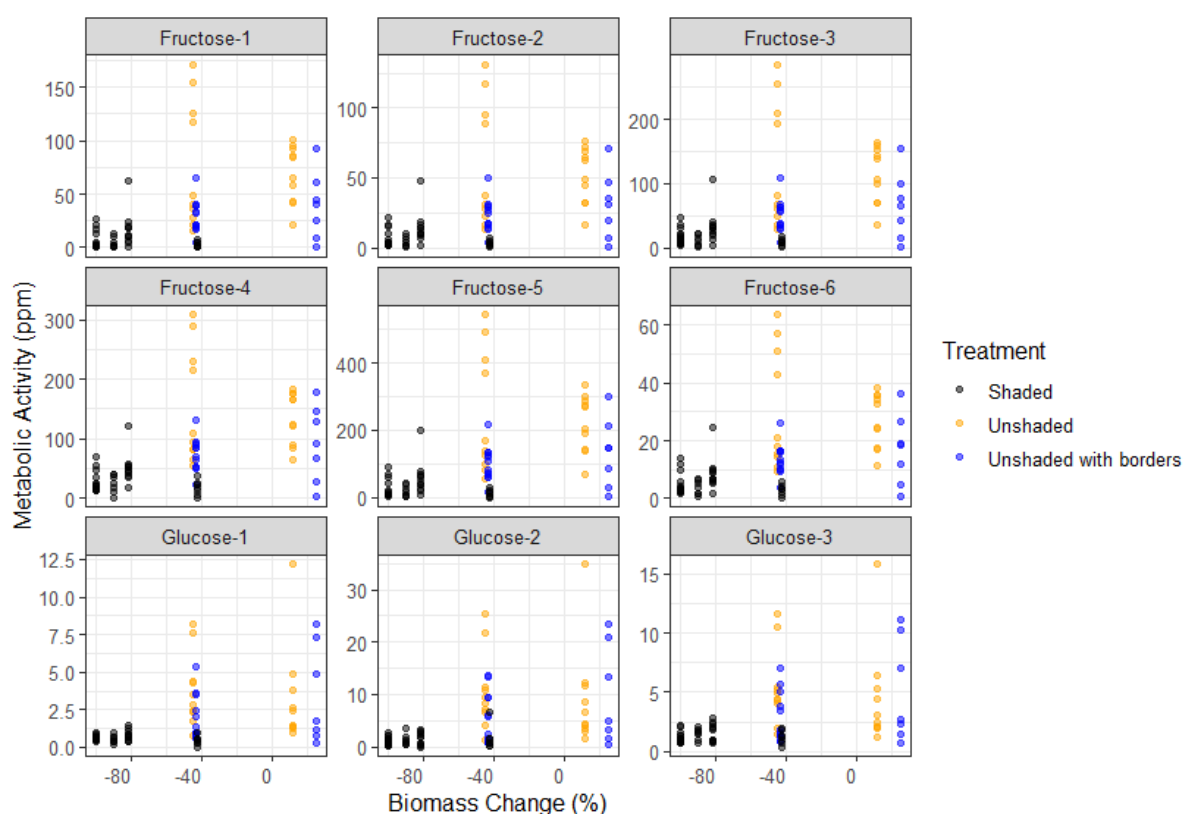


Figure 5.5 Individual glucose and fructose metabolites showing biomass change and metabolic activity (spectra intensity measured as ^1H chemical shift in ppm) for each plot within each treatment group. Biomass change is the percent change over the 38 day experimental period from initial biomass measurements. Treatment groups include shaded plots with vertical isolation borders (Shaded), unshaded plots with vertical isolation borders (Unshaded with borders) and unshaded plots without any treatment (Unshaded). Numbers are assigned to metabolites to identify individual peaks in activity. Plot of individual sucrose metabolites is shown in Figure Supplementary Figure A.15.

shade and isolation (Figure 5.4a). Other metabolites that showed a strong response to reduced light became lost in the noise of background variation, as was the case for fructose. We suggest that N-methylnicotinamide, glucose, fructose and malic acid have the most potential to be useful indicators of low-light stress in *Z.muelleri*, because these metabolites had the strongest effect to shading relative to background variation.

5.5.1 Metabolome analysis

Carbohydrates were predicted to show the greatest response to low-light. Low-light reduces carbohydrates in seagrass (sucrose, fructose and glucose) due to lower rates of photosynthesis (Hasler-Sheetal et al., 2016; M. Kumar et al., 2017). We found a reduction in all soluble carbohydrates in shaded seagrass (Table 5.1). The reduced abundance of carbohydrates is

consistent with the morphological changes we observed of slower growth, smaller shoots, and higher mortality. The sensitivity of soluble sugars to reduced light was supported by the elevated concentrations of glucose, fructose and sucrose in the unshaded plots despite a loss of biomass in this treatment group (Figure 5.5 and Supplementary Figure A.15, Table 5.1).

Glucose had the strongest response to shading (-10) and clearest (30% variance explained by shading) response to low-light and, as such, we suggest it is the best carbohydrate indicator of light stress (Table 5.1). It is unclear why levels of glucose showed a stronger response to low-light than levels of sucrose. Previous metabolomics studies with *Z. marina* have identified sucrose as having the largest magnitude of response to low-light (Mochida et al., 2019). In healthy plants, glucose levels are lower than other carbohydrates (Figure 5.5), particularly in leaves compared to other parts of the plant, because glucose is readily converted into starch (Silva et al., 2013). Fructose showed a strong signal in response to low-light but was more readily influenced by other unknown environmental factors. The production of fructose is highly sensitive to multiple environmental stresses (threats) (Mochida et al., 2019) so the fructose response to shading may be masked by its response to other threats.

N-methylnicotinamide showed the clearest response to low-light, with the treatment effect explaining 93% of the variance in this metabolite, and therefore it may be a good indicator of low-light stress (Table 5.1). N-methylnicotinamide is a co-enzyme in plant growth and may play a vital role in pathways controlling adaptation to environmental stresses, such as through the redox shuffle and retaining nicotinamide adenine dinucleotide phosphate (NADP) and NADPH homeostasis (Chai et al., 2005). The major NADPH generating source in darkness is the oxidative pentose phosphate pathway (OPPP) coupled with the central carbon metabolism in chloroplasts. This system maintains the redox potential necessary to protect the plant against oxidative stress (Kruger and Von Schaewen, 2003). Thus, it is possible that the reduction of N-methylnicotinamide from low-light is related to the physiological mechanisms aimed at preventing oxidative stress, although it is unclear why stressed plants have less of this compound. The OPPP pathway also utilises glucose and fructose rather than sucrose, which may explain the greater reduction in glucose and fructose compared to sucrose (Kruger and Von Schaewen, 2003).

Malic acid shows potential as an indicator of light stress. The reduced capacity of seagrass to fix carbon in low-light is a likely explanation for the reduced abundance of malic acid observed in light stressed plants. Current research suggests that seagrass are C3-C4

intermediate plants because some species have been identified to have CO₂ concentrating mechanisms (Larkum et al., 2017), but seagrasses lack many of the physiological characteristics consistent with C4 plants (Kim et al., 2018). The observed reduction in malic acid in plants exposed to low-light stress supports the theory that seagrass share some of the biochemical features characteristic of C4 plants. The reduction of malic acid and enzymes responsible for its synthesis in stressed seagrass has been shown elsewhere (unpublished data in Larkum et al., 2017; Moreno-Marín et al., 2018).

Some metabolites responded differently to previous studies in response to low-light stress, including phenolics and myo-inositol. For example, recent studies have shown that total phenols increased when subjected to low-light stress (up to 75% reduction in light) in *Z. marina* and *Cymodocea nodosa* (Silva et al., 2013), whereas we observed a decline in total phenols. This decline could be an artefact of the duration of stress exposure required before phenolic concentrations decline, because Silva et al. (2013) sampled after 3 weeks compared with approximately 6 weeks in this study. This hypothesis is supported by an observed reduction in secondary metabolites proportional to the degree of light reduction observed over longer timeframes (Toniolo et al., 2018). Alternatively, it could also be related to the sampling season, because reduced concentrations of phenolic compounds in seagrass have been observed in summer, in comparison to winter samples (Agostini et al., 1998). Similarly, an increase of myo-inositol in *Z. marina* was shown when subjected to darkness (Mochida et al., 2019), in contrast to the results of this study. More research is needed to better understand the significance of these responses and whether there are species specific differences.

5.5.2 Reliable indicators of light stress

Robust indicators should have a consistent response to stressors that can be distinguished from background variation (McMahon et al., 2013; Roca et al., 2016). In this study, individual metabolites responded more consistently to shading than to biomass loss (as indicated by the WAIC, also Figures 5.5 & Supplementary Figure A.15). Biomass loss rates varied across control and treatment plots, with some control plots also losing considerable biomass. This biomass loss may be explained by this study occurring when *Z. muelleri* is approaching the summer period of natural senescence. This suggests that condition metrics such as biomass would be more suitable as a later warning indicator of functional change in contrast to early detection methods like metabolomics that has the potential to measure stress responses within a plant before external symptoms manifest.

Metabolomics could support existing indicators of low-light stress by providing biologically meaningful responses to light deprivation (de Kock et al., 2020). Metabolite responses to low-light in this study were consistent with inhibition of photosynthesis through a disruption to carbon fixation and energy metabolism (Table 5.1). Thus it served as a biological measure of sufficient light. Indicators of low-light stress allow managers to obtain an accurate indication of local conditions, which is particularly relevant for monitoring impacts in dredge operations and around ports, to facilitate prompt adaptive management (Chartrand et al., 2012; Griffiths et al., 2020; Statton et al., 2018). Light dependant thresholds and photosynthetic indicators, such as saturating irradiance for photosynthesis (E_K) and maximum electron transport rate (ETR_{max}) (Collier et al., 2009; Dattolo et al., 2014) are comonly used to monitor light conditions. However, biomass and below-ground productivity has been shown to be affected by light quality as well as light quantity in some seagrass species (Strydom et al., 2018).

A high level of metabolite specificity was achieved in the study, given the high magnetic strength of the NMR (800MHz) and cryoprobe, and through confirmation of metabolite identification using the HSQC pulse experiment. Metabolomics using NMR spectroscopy also fills other criteria for bioindicator adequacy such as ease of collection, quick processing of samples and ease of interpretation of responses (McMahon et al., 2013). In addition, only small volumes of the sample are required for processing which reduces the impact of destructive techniques involved with biomass collections such as trampling (Rotini et al., 2013). Further, the method we have described here has the capacity to cover both polar and non-polar metabolites (Rivas-Ubach et al., 2013). Thus, it is able to identify metabolites involved in primary metabolism such as sugars, amino acids and small organic acids as well as secondary metabolites that can play a key role in an organism's response to environmental change such as phenolics. Further, this study utilises established protocols making data processing and metabolite identification for *Z.muelleri* more streamlined (Melvin et al., 2018b, 2017).

Table 5.1 Metabolites that responded most notably to low-light stress in *Z. muelleri* and their usefulness as a bioindicator.

Metabolite	Functional role	Response of metabolite to light reduction	Consistent with literature?	Effect size [^]	Variance explained by shading (%)	Useful as an indicator?	References
N-methylnicotinamide	A metabolite of niacin which synthesizes nicotinamide adenine dinucleotide (NAD) through a salvage pathway.	Possible response to reduced carbon fixation due to its role in maintaining redox potential to prevent oxidative stress.	Unknown	–5	93.3	Yes	Berglund et al., 2017; Chai et al., 2005; Matsui et al., 2007
Glucose	Signalling and regulatory molecule that controls growth and developmental programs, gene and protein expression, cell-cycle progression and primary and secondary metabolism in plants.	Response to suppressed photosynthesis, which suppresses glucose production	Yes	–10	29.9	Yes	Sheen, 2014
Fructose	An important signalling molecule in plant development and stress response	Response to suppressed photosynthesis, which suppresses fructose production	Yes	–10	9.3	Yes	Cho and Yoo, 2011
Malic acid	A dicarboxylic acid particularly important in C4 or CAM plants, which convert CO ₂ into carboxylic acids and reduces the rate of photorespiration.	Response to lower rates of carbon fixation from the downregulation of enzyme (carbonic anhydrase) responsible for converting CO ₂ to carboxyl acids in <i>Z.muelleri</i> exposed to 90% light reduction.	Yes	–5	7.0	Yes	Unpub. data in Larkum et al., 2017; Moreno-Marín et al., 2018; Ubierna et al., 2013
Phenolics	Are essential as defence mechanisms to protect against stress and	Could be a secondary response from reduction in photosynthesis and	Yes	–5	5.0	Maybe	Bryant et al., 1983; Caretto et al., 2015; Fajer et

Metabolite	Functional role	Response of metabolite to light reduction	Consistent with literature?	Effect size [^]	Variance explained by shading (%)	Useful as an indicator?	References
	constituent of secondary metabolites implicated in plant allelopathy in seagrass by either beneficially or adversely effecting neighbouring plants through the release of chemicals	limited carbohydrates available for production of energy demanding plant defence metabolites. Alternatively, it could be a growth promoting response that benefits the rest of the meadow 'neighbours' to release the individual plant from competitive growth when energy reserves are low.					al., 1992; Li et al., 2010; Zapata et al., 1979
Asparagine	A major nitrogen storage amino acid that accumulates during periods of low rates of protein synthesis.	Response as a nitrogen carrier to remobilise and salvage nitrogen during light suppression and senescence.	Yes	+2	5.0	Maybe	Forde and Lea, 2007; Kim et al., 2018; Lea et al., 2007; Lin and Wu, 2004; Ubierna et al., 2013
Glutamine	An abundant free amino acid synthesised from ammonia and it is a major amino donor for synthesis of amino acids and other nitrogen-containing compounds	Response to insufficient energy available for its synthesis.	Mixed	+5	3.6	No	Hasler-Sheetal et al., 2016; R. Kumar et al., 2017; Mochida et al., 2019; Moreno-Marín et al., 2018
Cinnamic acid	A monocarboxylic acid that plays a role in stress response.	Response to stress to prevent significant growth against bacterial and fungal species	Yes	+2	3.4	No	de Kock et al., 2020; Subhashini et al., 2013

Metabolite	Functional role	Response of metabolite to light reduction	Consistent with literature?	Effect size [^]	Variance explained by shading (%)	Useful as an indicator?	References
Sucrose	The primary storage carbohydrate in seagrass which forms up to 90% of the total soluble carbohydrate pool.	Response to suppressed photosynthesis which suppresses sucrose production and remobilises sucrose from stored carbohydrates.	Yes	−2	2.4	No	Touchette and Burkholder, 2000
Myo-inositol	A sugar-like carbohydrate biosynthesised from glucose and it is central to the growth and development of plants and participates in the plant's stress response	Myo-inositol is rapidly metabolized, so this may be a response to reduced availability of carbohydrates for biosynthesis.	No	−5	2.3	No	Loewus and Murthy, 2000

[^] Effect size range from -10 (strong negative) to 10 (strong positive)

5.5.3 Limitations and future research directions

There are several caveats that limit interpretation of the results and the limitations of this study warrant further investigation to understand the other causes of variation in *Z.muelleri* metabolites. First, we were unable to identify ten of the individual metabolite features from their peaks in activity because reference spectra were unavailable. Therefore, we may have missed part of the plant's stress response. Further work identifying metabolites and developing standards for this species are needed.

Second, the various phenolic components were not readily distinguishable, which limits interpretation of the functional role of phenolics in the response to light stress. This relates to our use of D₂O to optimise comparison of primary metabolites against reference spectra, which was a trade-off since D₂O is not an ideal solvent for plant phenolics. Further work characterising individual phenolics may help to associate discrete stressors with specific biochemical responses.

Third, our parameters were limited to biomass and light intensity, however other ecological parameters would have helped to associate changes in metabolites with changes in ecosystem function (Jesch et al., 2018). For example, metabolite profiles have been shown to be affected by sediment structure (Holmer and Hasler-Sheetal, 2014), temperature (Kaldy, 2014), leaf herbivory (Arnold et al., 2008), prevalence of competitors (Dumay et al., 2004) and taxonomic relationships (Gillan et al., 1984). These abiotic effects can vary over small spatial scales. For example, different metabolic profiles have been shown for the same plant over small temporal and spatial scales for *Arabidopsis* and *Silene* plants (Dötterl et al., 2012; Stitt et al., 2007). Future research of light stress on the metabolome would therefore benefit from laboratory or mesocosm studies to limit the amount of environmental variation confounding interpretation of results (e.g. Bertelli and Unsworth, 2018). Fully or partially controlled environments would allow those metabolites involved specifically in the light stress response to be identified, so that field testing could focus on detecting change in those metabolites.

Fourth, samples for metabolite analyses could also be extracted at the onset of shade stress and at regular intervals throughout the shading experiment to understand temporal changes in the biochemical response to shading. This would help to understand the role of secondary metabolites (particularly phenolics) and to monitor sub-lethal responses to

low-light stress. It is particularly important to identify metabolites that play a specific role in the plant's response to light deprivation. The metabolites identified in this study, such as glucose and fructose, have broad functions, and so may be more subject to environmental noise from other non-light stressors. Metabolomic sampling at the onset of shading may help to identify specific light-response metabolites. It is also needed to test how the method performs as an early-warning indicator. For instance, depletion of sugars in leaves may not be apparent early in the shade response, because the plant can translocate stored sugars from rhizomes to leaves (Mackay et al 2007).

Fifth, it would be helpful to look at the effect of varying light levels. We initially attempted to create a gradient of light levels in the treatments, but were unsuccessful in retaining the variable light penetrations due to constant covering of the shade cloth with sediment and biofouling. Further, the study should be expanded to other seagrass species as tolerance to light has shown to vary between species (Silva et al., 2013).

Finally, while the relative change in the abundance of different metabolites were used to indicate the effect of low-light stress on seagrass, absolute values for the metabolites were not quantified. Future studies could therefore utilise other methods capable of quantifying values more specifically, such as LC-MS (Kim et al. 2015). This would be particularly important if discrete quantities of metabolites were a central goal of the study.

The method developed here could be complementary to support other research on stress responses in seagrass. For example, metabolomics coupled with other omics technologies, such as genomics (Bruno et al., 2010) or proteomics (M. Kumar et al., 2017), can identify the functional role of metabolites in stress responses (Toniolo et al., 2018). Genomics in particular, could be useful to map how genotypes shape local scale variation to stresses (Salo et al., 2015). Metabolomics would also complement more traditional approaches such as biomass measurements. Multi-variable measurements will provide an integrated view of the functional status of seagrass as it responds to light stress. For example, metabolite analysis could support intermittent measurements of biomass loss from light stress experiments to determine if biochemical tipping points can be detected prior to loss in biomass. The complement of molecular interpretation combined with other physiological or morphometric analysis are put forward as

strategies to evaluate the impact of human stressors on the ecosystem and to monitor environmental changes (Toniolo et al., 2018).

This study used experimental manipulations of seagrass meadows in the field to determine if metabolomic indicators could be identified for the response of *Z.muelleri* to prolonged low-light. Clear separation in metabolite profiles and strong signals from identifiable metabolites in comparison to traditional monitoring methods, suggest that metabolomics have potential as an indicator of low-light stress in seagrass. We suggest support for more research on metabolomics as a potential bioindicator for early impact assessment monitoring and to assess its contribution to the list of alternative indicators for low-light stress in seagrass meadows (McMahon et al., 2013).

5.6 Supporting Information

Supplementary figure of differences in the median effect sizes with errors of all metabolite activities of *Z.muelleri* exposed to shade stress (Supplementary Figure A.13), degree of correlation between metabolites on latent variable 1 and 2 (Supplementary Figure A.14), and plot of individual sugar metabolites showing biomass change and metabolic activity for each plot within each treatment group (Supplementary Figure A.15).

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Chapter 6 Discussion

6.1 Introduction

In the face of global climate change (Cracknell and Varotsos, 2021; McNutt, 2013) and global fisheries collapses (Hollowed et al., 2013; Plagányi, 2019), the protection of coastal ecosystems are essential to support government commitments towards achieving zero net target carbon emissions (Macreadie et al., 2019; Sanderman et al., 2018) and sustain livelihoods (Barnett and Adger, 2007; Jänes et al., 2020; McNamara and des Combes, 2015). Understanding gaps in the performance of coastal ecosystem management (i.e., conservation progress to meet objectives) is therefore crucial to facilitate better protection from anthropogenic change. However, the performance of management actions is rarely measured at spatially and temporally relevant scales that inform on their ability to deliver objectives and protect coastal ecosystems (Giakoumi et al., 2018; Kemp et al., 2012; Sangil et al., 2013; Tulloch et al., 2015). There are a number of reasons for this, including a lack of capacity (Gill et al., 2017) and clear objectives, mismatch between objectives and the unit of measurement for monitoring (Agardy et al., 2016; Cheal et al., 2008; Kaplan et al., 2019; Wilson et al., 2009) and inadequate systems of accounting for, or measuring performance (Buonocore et al., 2019; Kemp et al., 2012). Further, performance measurements often exclude how species and ecosystems respond to threats other than the direct threat that is being managed (e.g., fishing) (Jameson et al., 2002; McClanahan, 2011; Pomeroy et al., 2005).

The overall aim of this thesis was to understand some of the gaps in the performance of management, to improve protection for coastal ecosystems, help managers make more informed decisions and inform on management priorities. To achieve this aim, I targeted specific stages in the systematic conservation planning (SCP) framework as a guide to focus each chapter. I first reviewed the literature (Chapter 2) to understand the context for effective conservation outcomes. Spatial plans were the main tools that enabled effective conservation outcomes for coastal habitats and considered multiple threats. Therefore, I analysed the effectiveness of spatial plans to protect coastal species in chapter 3 and 4. I developed a spatial analysis method that was driven by data to quantify threats and cumulative impacts and make predictions about whether management is effective at mitigating against these threats for temperate reef fish in

New South Wales (Chapter 3). I used a similar statistical approach to assess the performance of management to protect coral reef fish in Raja Ampat, Indonesia, from fishing threats, however this time I considered historical influences in the spatial variability (Chapter 4). I also assessed how fish would respond given different spatial planning scenarios (Chapter 4). In my last data chapter, I tested a method to improve the monitoring efficacy of seagrass to a common threat (low-light stress) through field experiments to help inform on feedback loops in the SCP framework (Chapter 5). This final chapter provides a synthesis of the key findings from each of the main chapters and considers implications for management, limitations of the thesis' studies and areas for future research.

The urgency to more adequately protect coastal ecosystems means it is important we find ways to rapidly translate science into management actions. One way we can speed up the translation of science into management is to ensure that researchers partner with management agencies (Cook et al., 2013). Consequently, each chapter in this thesis was developed as a partnership with management or policy agencies, to help it have impact beyond the contribution to academic research. Chapter 2 was used as a foundation for a chapter in a United National Environment Programme (UNEP) report (Fortes et al., 2020). The global synthesis report is designed to improve understanding of the value of seagrass to people and provide recommendations to policy makers on the importance and actions needed to protect them globally. **Chapter 3** was a collaborative project with the Department of Primary Industries, Fisheries Division in the state of NSW, Australia. The outcomes of this chapter are designed to inform the development and review of management plans for marine parks in NSW which are currently underway, and to fill research gaps outlined in the Marine Estate Management Strategy (MEMS). **Chapter 4** was a collaborative project with The Nature Conservancy (TNC) and the World Wide Fund for Nature (WWF) who actively work with regulators in Indonesia and who have access to global funding conservation schemes. This work has helped scientists and authorities to put monitoring trends in context and identify places that could benefit from increased management and protection, e.g., from poaching. **Chapter 5** was funded by the Great Barrier Reef Marine Park Authority through the Reef Guardian Research Grant. The grant was approved because it contributed towards the agency's science for management priorities and their Reef 2050 Long Term Plan.

6.2 Synthesis of findings

Assessing the effectiveness of management performance can disentangle spatial and temporal inconsistencies in monitoring data and strengthen the understanding of feedback loops between management action and ecological outcomes. This information is essential to help guide SCP and contribute towards understanding the links between ecological and socio-economic outcomes. Key findings of this thesis are: 1) spatial planning tools are the only mechanism that allows for the regulation of activities from multiple threats, however they often focus on regulating marine-based threats only and exclude threats from land-based activities (chapter 2), 2) cumulative threats did not always translate into higher impact and fishing threats are the most significant threat for temperate rocky reef fish (chapter 3), 3) assessing management performance can highlight spatial inconsistencies of threats and conservation outcomes, and reveal areas requiring greater management action (e.g., to reduce poaching) (chapter 4), , and 4) the seagrass metabolome responds to low-light stress in a consistent, quantifiable way and shows promise for further evaluation as a bioindicator (chapter 5).

6.3 Implications for management

There are a number of findings from this thesis that are relevant for managers to consider at stage three, five, eight and 11 of the SCP framework (Figure 6.1). Conservation outcomes cannot be achieved without a supportive political and social setting. For example, we found that inadequate protection for seagrass habitats was largely because of low or absent recognition in legislation and policy. Seagrass habitats, and potentially coastal ecosystems in general, need to be better valued for the services they provide (Cullen-Unsworth and Unsworth, 2018). Policy and regulatory documents that guide how to incorporate the impact of multiple and cumulative threats from all threatening activities' into strategic decision making need to be developed to address all threats (Grech et al., 2016; Lonsdale et al., 2020). Further, spatial management plans need to explicitly link objectives with achievable monitoring outcomes that considers the unique spatial features, historic and current threatening processes, and socio-economic conditions of the region (Facca et al., 2014; Giakoumi et al., 2018; Katsanevakis et al., 2011; Nickols et al., 2019). These objectives should be performance tested and refined through the modelling of counterfactuals (Baylis et al., 2016; Stevenson et al., 2021). The species-threat distribution modelling approach that I have developed could provide spatially explicit predictions about whether objectives are

achievable, particularly if this is coupled with biophysical and socio-economic data. Future regional conservation planning initiatives should build on the strengths of current measures, by considering the underlining cause of spatial disparity and how that could subtract from meeting conservation objectives. Spatial management plans should also be linked to a monitoring framework that considers enforcement and restoration. We need better ways to monitor seagrass trends and implement actions to avert loss ahead of time (Hossain et al., 2010; McMahon et al., 2013). I found that metabolomics offers potential for use as a molecular indicator of low-light stress in seagrass and should be further tested under chronic low-light conditions, and with other stressors, to assess its suitability in routine analysis.

6.4 Limitations and future research directions

There are a number of limitations in the thesis that future research should focus on (Table 6.1). My literature review looked at seagrass habitats as a case study for coastal ecosystems, however other coastal ecosystems could have different needs to improve protection (Table 6.2 (i)). For example, mangroves and coral reef receive far more recognition of their value in providing ecosystem services such as supporting fisheries (Cinner et al., 2009) and enhancing coastline protection (Giffin et al., 2021; World Bank, 2016) (World Bank Group 2016). Therefore, the focus on management gaps for mangroves could be in the need to strengthen regulatory action to prevent loss to agriculture and aquaculture (Buelow et al., in review) rather than strengthen legislation and policy. The literature review would have also greatly benefited from looking more closely at countries with a low to medium Human Development Index (HDI) to understand the reasons underpinning inadequate coastal protection of seagrass (Table 6.1(ii)). Another major limitation is the omission of non-English grey documents through web-based searchers. For example, policy documents on seagrass conservation in countries such as Egypt may exist, however this information may not appear in internet searchers because they are in Arabic. This form of omission introduces bias and can lead to incorrect assumptions about countries commitments to conservation (Chowdhury et al., 2022; Khelifa et al., 2022).

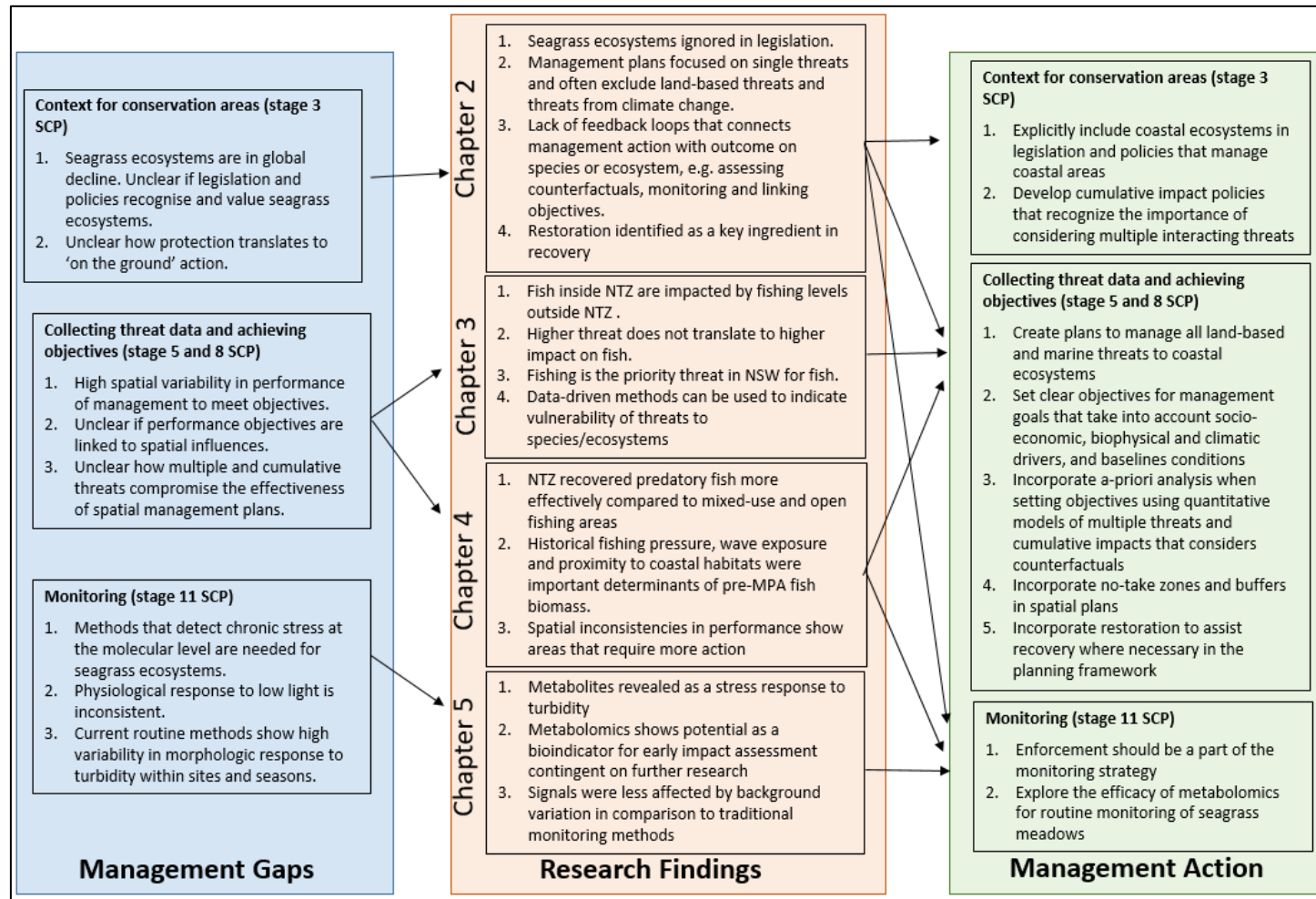


Figure 6.1 Summary of the management gaps, research findings and actions required by management in context of the SCP framework. Arrows indicate a link between the reasons for research (management gaps), findings (research findings) and implications of research findings (management actions).

Predictions of management performance are based on simplifications of real-world systems, and therefore can only be as precise as the data they are based on (Morales-Barbero and Vega-Álvarez, 2019; Morán-Ordóñez et al., 2017). Not all threat data were spatially and temporally consistent with monitoring data (Table 6.2 (iv)). For example, commercial fishing data had a spatial resolution of 0.1 degree (approximately 11 km) while Baited Remote Underwater Video (BRUV) monitoring data was resolved down to 0.050 km. Further, some threat layers were averaged over a time period (e.g., water quality threats) while other threats were estimated from a single time period (e.g., urbanisation was based on the population as at 2020). Incorporating more resolved and consistent data would capture threat-species relationships more accurately (Halpern and Fujita, 2013).

I only considered the effect of no-take zones (NTZ) when assessing management performance. However, there is growing movement away from single parameter NTZ to multi-parameter spatial zoning plans that incorporate mixed-use zones because of greater stakeholder support, less resistance from fishing industries, and they adhere to the principles of SCP (Margules and Pressey, 2000; Himes, 2007; Mangi and Austen, 2008; Rodríguez-Rodríguez et al., 2015). Further, there is increasing evidence that shows the benefits of mixed-use zones in comparison to open access areas (Sciberras et al., 2013) (Table 6.2 (v)), despite the strong evidence of the benefit of including NTZ in spatial plans (Edgar et al., 2014; Costello and Ballantine, 2015). Therefore, identifying the performance of multi-use zones across the seascape to protect fish in the two study regions (Raja Ampat and NSW) would provide evidence to guide management decisions and facilitate more constructive stakeholder engagement. For example, in the NSW MEMS, future spatial plans specifically state that only multi-use zones that benefit stakeholders and the environment will be considered in future spatial plans (NSW Government, 2018). Investigating threats across the entire management region would also considerably support management to achieve policy objectives (Table 6.2 (vi)).

Table 6.1 Future research directions

	Future research need	How the research need arose	Outcome
i.	Understand the gaps in management performance to protect other coastal ecosystems (e.g., mangroves, saltmarsh, coral reefs)	Chapter 2 focussed on seagrass but other coastal ecosystems could have different management gaps	Determine priority next steps for advancing recognition of ecosystems in policy and their management
ii.	Take an in depth look at the evolution of coastal ecosystem protection in countries with a HDI of low or medium	Chapter 2 identified ecosystem losses in countries with a low/medium HDI (medium or less) but the reasons underpinning this are unclear	Provide valuable information to support better protection for other low/medium countries who are facing significant ecosystem losses
iii.	Resolving reference conditions for non-linear threats	Chapter 3 identified that not all threats act in a positive linear way, but we do not know what reference level constitutes a healthy state for non-linear responses	More precise recommendations to managers on thresholds for threats that require action
iv.	Include more spatially resolved and accurate information on fishing threats	Chapter 3 used current fishing but at lower resolution than other threat layers and Chapter 4 used historical fishing to predict future fishing effort.	Improved interpretation of fishing threats that are current and match the spatial resolution of management action
v.	Include different levels of fishing restrictions when assessing management performance	Chapter 3 and 4 considered only two layers of management, no-fishing and fishing, however there are many levels of restrictions to link to performance	Understanding the benefit of other management restrictions to fish would allow managers to be more flexible in their strategies and could support better stakeholder engagement
vi.	Investigate threats and management performance across the whole managed seascape	Chapter 3 and 4 identified threats within management subregions but it would be worthwhile to assess how more populated regions (with greater threats) compare to this study with low-medium threats	This would enable managers of obtain a region-wide perspective about threats and management actions to use in future strategies and plans
vii.	Include hydrodynamic influences in the model of threats and performance	Chapter 3 and 4 used surrogates for wave exposure and dispersion of pollutants but currents, winds and tides can have an important influence on these variables	Improved interpretation of threats that impact water quality and thus have a better ability to inform on management performance

	Future research need	How the research need arose	Outcome
viii.	Link species surrogates with other performance metrics	Chapter 3 and 4 used fish biomass and fish abundance as performance metrics, however other metrics are more relevant at the habitat or ecosystem level	This type of approach would facilitate reporting on broader ecosystem objectives, such as ecological integrity of the ecosystem
ix.	Investigate chronic low-light stress in seagrass and other threatening processes	Chapter 5 identified metabolites involved in acute stress response, however we now need to understand if the same metabolites respond under chronic stress to low-light and other stressors (e.g., grazing pressure)	Managers would have a better understanding of chronic stress signals from threats and how it relates to the state of seagrass meadows (i.e., morphology)
x.	Investigate metabolomic indicators for chronic stress in other seagrass species and in other regions	Chapter 5 identified metabolite response in <i>Zostera muelleri</i> , but it would be useful to understand if other common seagrass species respond to stress in a similar way and at different sites	Managers could understand chronic stress signals more holistically in conspecific seagrass meadows under a range of conditions
xi.	Assess the efficacy of incorporating metabolomics as part of the broader routine monitoring program by identifying thresholds	Chapter 5 identified that metabolomics has potential to be further tested for consideration in monitoring programs (contingent on the previous outcome) but now we need to understand if metabolite thresholds could be applied to routine monitoring	Provide a clearer link between management action and outcome for seagrass. Facilitate adaptive management to better protect seagrass meadows by reducing the impact of threatening processes from managed activities (e.g., dredging)
xii.	Investigate feedback mechanisms operating between management objectives and performance indicators to better monitor species/ habitat/ ecosystem trends	Chapter 2, 3, 4 and 5 identified approaches to understand management's ability to protect coastal species and ecosystems, however rarely are monitoring objectives aligned with management action and response	Clearer understanding of management actions and outcomes for ecosystems to better inform adaptive management

Hydrodynamic influences (currents, wind and waves) have a significant effect on the dispersion of pollutants (Deignan-Schmidt et al., 2021; Tseng, 2002; Yu et al., 2016). The omission of all or some of these influences in the model predictions in chapter 3 and 4 could change the footprint and intensity of water quality threats and their impacts on species (Table 6.1(vii)). Managers of the marine environment would greatly benefit from understanding the

impact of other threats managed by different sectors to facilitate cross-jurisdictional discussions to reduce impact on the coastal environment.

The method we developed (a map of cumulative impacts based on threats and a species distribution model) has a number of pros and cons compared to the traditional approach for mapping cumulative impacts (Halpern et al., 2008, 2015) (Table 6.2). Two major differences between these two methods include the use of proxies for ecosystem status (in this case fish numbers/biomass) and the ability of the new method to model non-linear responses of species to threats (Table 6.1 (viii, iii)). I used proxies to model cumulative impacts on the ecosystem in chapter 3 and 4, which is advantageous over the traditional approach because it does not rely on eliciting ecosystem responses from experts (Jones et al., 2018). However, the drawback when using this method with proxies to assess performance is that it fails to incorporate broad species or habitat metrics to represent ecosystem level effects (Table 6.1(vii)). Habitat and ecosystem indicators such as species richness or diversity, habitat type and condition, benthic cover, or ecosystem services could be used in place of fish abundance and would enable a more holistic understanding of the effect of management actions on outcomes at the ecosystem level (Fulton et al., 2016; Quaas et al., 2019). The SDM cumulative impact map approach is also entirely data driven, meaning that the data drives the direction of threat impact, whether positive or negative (Table 6.1 (viii)). For example, poor water quality was associated with higher abundance of fish, a correlation which has been observed previously in the region (Meador and Frey, 2018). Therefore, it remains to be known at what level the reference condition of water quality is considered beneficial versus detrimental to temperate fish, and therefore, how managers should respond to poor water quality.

The strength of molecular indicators as a routine biomonitoring method is to detect chronic stress early in seagrass to prevent imminent mortality (Macreadie et al., 2014). However, the contribution I made towards this goal only provided the first tier and looked at acute exposure to low-light stress in only one seagrass species and in one region. The method needs to be further tested with other threats (Table 6.1 (ix)) and other seagrass species and regions (Table 6.1 (x)) before it can be evaluated for its effectiveness as a monitoring option. Despite advancement in the field of molecular research on seagrass (Franssen et al., 2011; Mazzuca et al., 2013; Ransbotyn and Reusch, 2006), routine monitoring methods are still yet to utilise molecular approaches as indicators of environmental stress for seagrass (Davey et al., 2016; Duffy et al., 2019; Jordà et al., 2012; Roca et al., 2016). Therefore, there is a real need to

further develop this method for seagrass in Australia (Table 6.1 (xi)), given its widespread distribution (Mckenzie et al., 2020), importance as a fish habitat area (Bertelli and Unsworth, 2014), and its contribution towards government commitments regarding its carbon sequestration capacity (Macreadie et al. 2015), particularly in the state government of Queensland, which was the first state to make a pledge to be carbon neutral by 2050 (Department of Environment and Heritage Protection, 2021). Further, this method could complement temporal mapping of seagrass condition to indicate chronic stress, particularly if used in combination with routine morphological monitoring methods.

Table 6.2 Comparison between the traditional cumulative impact map approach and the threat impact map approach developed in this thesis

	Traditional cumulative impact approach (Halpern et al., 2008, 2015).	Cumulative impact modelling based on SDM approach
(a)	Quantitatively maps threats and their cumulative impacts	Quantitatively maps threats and species response to threats
(b)	Requires experts with knowledge on the vulnerabilities of species and habitats to threats	Does not require knowledge on vulnerabilities, they are modelled from data
(c)	Uses experts to elicit impacts to species, habitats or ecosystems so impact is estimated qualitatively across broad scales	Uses surrogates to model habitat and ecosystem impacts so impact is inferred based on species responses
(d)	Introduces knowledge-based uncertainty	Entirely data-driven
(e)	Threat impacts to ecosystem are linear	Threat impacts on the indicators can be linear or non-linear
(f)	Threats combine in an additive way only	Threats can interact and have antagonistic or synergistic responses
(g)	Requires spatially resolved data on threats	Requires spatially resolved data on threats and empirical data on indicators, such as species abundance

I looked at assessing the performance of management based on established objectives, however it would be equally relevant to understand how feedback mechanisms operate between management objectives and monitoring outcomes within the SCP framework (Table 6.1 (xii)). Understanding the systems and processes in place to facilitate change in management because of monitoring outcomes is not straightforward. For example, thresholds are in place for species and habitats under state environmental regulations (e.g., Environmental Protection Act (EPA)), to inhibit dredging when light thresholds are exceeded (Collier et al., 2016). But how this translates to species, habitat and ecosystem wide effects

when the threats stem from different sectors or activities that are unrelated to the management plan, remains to be determined. For example, is there a chain of action when turbidity thresholds are exceeded from another source (such as flooding, or increased maritime traffic) that still inhibit activities that contribute to increasing turbidity? A clearer understanding of how management actions are triggered by all activities within the spatial area should be clearly defined.

There are a number of other limitations in this thesis in addition to those mentioned above that are incorporated in the caveats section in each chapter. Overall, each chapter would have benefitted from incorporating socio-cultural, economic and political factors that can have significant impact on the ability of management to effectively regulate their seascapes (Bennett and Dearden, 2014; Gallacher et al., 2016). For example, employing social science strategies to incorporate expert opinion about how, and if, multiple and cumulative threats and their impacts are managed in a regional context (chapter 1), or incorporating the effect of social willingness to adhere to regulations and how this can impact recovery and protection (chapter 3 and 4). I did not include social implications because the data was unavailable. This area of research should be prioritised in the future.

6.5 Conclusion

Significant progress has been made towards developing methods that affectively measure management performance (Picone et al., 2020). These methods incorporate diverse approaches and use a range of tools to measure success with varying levels of data input (Geary et al., 2020). Here I have contributed to this field by developing ways to understand management performance by building on established methods to assess the impacts of multiple threats to coastal species and habitats within the SCP framework. Whether more comprehensive management of multiple pressures translates into better outcomes for conservation of coastal habitats remains to be tested (Micheli et al., 2013). However, coastal managers would benefit from understanding the outcomes of their management actions. This thesis has identified a number of research areas that would contribute towards linking management action with outcome and increase the understanding of variability in management performance.

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Appendix

Supporting information from Chapter 2

Supplementary Table A.1 Is a spreadsheet containing references from all of the data sources I reviewed for my case studies. The supporting information is available through the open access [publication](#), or find a link to the document [here](#).

Supplementary Table A.2 Case studies included in the analysis

Bioregion	Case-study	Region, Country	Cumulative threat rank (Halpern et al., 2009)	Reason included for sites not identified in Halpern et al., (2009)
Tropical	Mississippi River	Louisiana, USA	1	NA
Atlantic	Niger River	Bayelsa State, Nigeria	17	NA
	Trinity River	Texas, USA	27	NA
Tropical Indo-Pacific	Chao Phraya River	Samut Prakan Province, Thailand	9	NA
	Krishna & Godavari River	Andhra Pradesh, India	18 & 20	NA
	Zambezi River	Zambezi, Republic of Mozambique	19	NA
	Tigris and Euphrates Rivers	Al-Basrah, Iraq	25	NA
	Han, Ron and Lian Rivers,	Guangdong Province, China	29	NA
	Johor River	Singapore	NA	Community supports seagrass conservation
	Great Barrier Reef	Queensland, Australia	NA	Seagrass habitat valued
	Moreton Bay	Queensland, Australia	NA	Seagrass habitat valued
Mediterranean	Nile River	Alexandria Governorates, Egypt	11	NA
	Venice Lagoon & Po River Delta	Veneto region, Italy	5	NA
	Danube River	Tulcea County, Romania	8	NA
	Don River	Rostov-on-Don, Russian Federation	23	NA
Temperate	Gulf of Gdansk	Gdańsk Pomerania, Poland	22	NA
North Atlantic	Wadden Sea (Elbe River)	Schleswig-Holstein, Germany	30	NA
	Chesapeake Bay	Maryland and Virginia, USA	NA	Government supports seagrass conservation goals
Temperate North Pacific	Imjin and Han Rivers	Seoul Capital Area, Republic of Korea	26	NA
	Fraser River	British Columbia, Canada	NA	Coverage over bioregions

Supplementary Table A.3 DAPSIR for seagrass adapted from Elliot et al., (2017) and Smith et al., (2016).

Drivers	Activities	Pressures	State Environmental Change
Marine Food Provisioning	Production of Living Resources - Aquaculture	Nutrient enrichment	Change in seagrass-algae interactions
		Contaminant exposure	Change in health and resilience potential
		Abrasion	Fragmentation and biomass reduction
		Changes to hydrology	Barriers to recolonisation
		Changes to light penetration	Loss of biomass from chronic light reduction
	Extraction of living resources	Invasive species introduction	Reduction in productivity and change seagrass species composition
		Benthic damage & abrasion	Fragmentation and biomass reduction
		Change to trophic food webs	Change in structure and function of associated ecosystems
		Substratum loss (habitat loss)	Reduced biomass and effect recolonisation
		Increased turbidity	Loss of biomass from chronic light reduction
Energy Generation	Renewable energy generation	Removal of seagrass - direct harvesting	Loss of biomass
		Substratum loss	Effect recolonisation potential
		Changes to hydrology	Barriers to recolonisation
		Changes to light penetration (shading)	Loss of biomass from chronic light reduction; reduce resilience potential
		Increased turbidity (construction)	Loss of biomass from chronic light reduction
	Non-renewable energy generation	Abrasion (construction)	Fragmentation and biomass reduction
		Abrasion	Fragmentation and biomass reduction
		Substratum loss	Reduced biomass and effect recolonisation
		Contaminant exposure	Change in health and resilience potential
		Change to thermal regime	Change in seagrass-algae interactions
Industrial Development	Extraction of non-living resources	Substratum loss and supply	Effect recolonisation potential
		Contaminant exposure	Change in health and resilience potential
		Changes to hydrology	Barriers to recolonisation
		Changes to salinity (reduced flow)	Alter the composition of seagrass species and change seagrass-algae interactions
	Land based industry	Nutrient enrichment	Change in seagrass-algae interactions
		Change to thermal regime	Change in seagrass-algae interactions
		Increased turbidity	Loss of biomass from chronic light reduction
		Contaminant exposure	Change in health and resilience potential
		Smothering	Reduction in diversity and biomass
Port Development	Navigational dredging	Substratum loss	Reduced biomass and effect recolonisation
		Contaminant exposure	Change in health and resilience potential

Drivers	Activities	Pressures	State Environmental Change
Coastal Urbanisation	Transport and shipping	Nutrient enrichment	Change in seagrass-algae interactions
		Invasive species introduction	Reduction in productivity and change seagrass species composition
	Coastal infrastructure	Abrasion	Fragmentation and biomass reduction
		Smothering	Reduction in diversity and biomass
		Invasive species introduction	Reduction in the productivity and change seagrass species composition
		Changes to light penetration (shading)	Loss of biomass from chronic light reduction
		Increased turbidity	Loss of biomass from chronic light reduction
		Contaminant exposure	Change in health and resilience potential
		Changes to salinity (reduced flow)	Alter the composition of seagrass species and change seagrass-algae interactions
		Nutrient enrichment	Change in seagrass-algae interactions
		Substratum loss	Reduced biomass and effect recolonisation
Terrestrial Food and Material Provisioning	Tourism and Recreation	Abrasion	Fragmentation and biomass reduction
		Food web changes	Change in structure and function of associated species ecosystems
		Increased turbidity	Loss of biomass from chronic light reduction
		Contaminant exposure	Change in health and resilience potential
	Military	Contaminant exposure	Change in health and resilience potential
		Substratum loss	Reduced biomass and effect recolonisation
	Research & education	Abrasion	Fragmentation and biomass reduction
	Agriculture	Nutrient enrichment	Change in seagrass-algae interactions
		Increased turbidity	Loss of biomass from chronic light reduction
Climate Change	Air emitting industries & over population	Contaminant exposure	Change in health and resilience potential
		Thermal change	Change in seagrass-algae interactions
		Salinity change	Alter the composition of seagrass species and change seagrass-algae interactions
		Sea level rise	Reduction in diversity and biomass
		Changes in wave exposure	Reduction in diversity and biomass and alter the composition of seagrass species and change seagrass-algae interactions

Supplementary Table A.4 Description of activities identified through the review

Activity	Description of activity
Production of living resources	Aquaculture (including mariculture)
Extraction of living resources	Benthic trawling (scallop dredging, prawns trawling, etc), hydraulic trawling (suction) eg clams, bait digging, anchor damage, seaweed harvesting, shellfish hand collecting, potting
Renewable energy generation	Wind farm construction and operation (including cable laying)
Non-renewable energy generation	Exploration and construction of land based or coastal oil and gas facilities and subsequent decommissioning
Extraction of non-living resources	Construction of land based, coastal power stations or cooling plants
	Sand and gravel extraction
	River water abstraction - industry (desalination plants, etc.), agriculture (irrigation), drinking
	Sediment diversion from river
Land-based industry	Industrial effluent treatment and discharge
	Desalination effluent, sewage and thermal discharge
Navigational dredging	Capital and maintenance dredging, removal of substratum, dredged material disposal
Transport and Shipping	Mooring, anchoring, beaching, launching, ship waste, risk of pollution (collision), invasive species risk
Coastal infrastructure	Construction of ports and marinas
	Land claim projects (airports, housing estates, industry, tourism, etc.) - draining wetlands or estuaries and coastal reclamations
	Construction of culverted lagoons, estuaries, wetlands
	Construction of urban dwellings and land based facilities adjacent to coast
	Construction of urban effluent treatment plants and stormwater drainage facilities
	Construction of infrastructure in the coastal environment (jetties, wharves, pipelines, coastal defence structure, etc.)
Tourism and recreation	Angling and potting
	Boating, yachting, diving and water sports
	Public use of beach (trampling)
	Construction of tourist facilities on foreshore
	Litter and debris production
Military	Warfare
	Munitions testing and disposal areas operation
Research and education	Marine research, engaging in field education and training activities on seabed
Agriculture	Agriculture waste production, coastal forestry and farming, operating land/waterfront drainage
Air emitting industries	Production of greenhouse gas from expanding industries and agriculture
	Construction of coastal defence structures (groynes, sea walls, dikes, etc.) and cementing or fixing river/coastal banks

Supplementary Table A.5 Examples of the pressure mechanisms identified in this review through which state changes were observed for seagrass ecosystems (Smith et al., 2016)

Main pressures identified for seagrass	Pressure Mechanism on State Changes	References*
Nutrient enrichment	Eutrophication - chronic eutrophication can lead to increase in algae and epiphytic cover within seagrass meadows, reducing light availability and impeding its capacity to produce viable seed bank, leaving meadow vulnerable to episodic events and in poor health.	(Holmer et al., 2016; van Katwijk et al., 2010)
Contaminant exposure	Herbicides have been shown to affect photosynthesis. Heavy metals have also affected seagrass with variable response. Unknown how other contaminants impact seagrass.	(Flores et al., 2013; Llagostera I et al., 2016; Negri et al., 2015)
Abrasion	Direct interaction with seagrass from infrastructure causing physical damage to plant.	(Nordlund and Gullström, 2013)
Changes to hydrology	Hydrology can potentially affect reproduction pathways and connection to other habitats.	nd
Changes to light penetration	Light availability can have significant impact on seagrass growth and reproduction. Reduced light penetration can also be advantageous to seagrass located in high temperatures during climatic episodes of elevated temperature.	(Collier et al., 2016; McMahon et al., 2011; Ruiz and Romero, 2001)
Invasive species introduction	Intraspecific competition within native and introduced seagrass species and interspecific competition between seagrass and invasive species (shellfish, bivalves, polychaetes, etc.).	(Thomsen et al., 2012)
Change to trophic food webs	Reduced herbivory pressure leading to dominance and smothering by algae.	(Heck and Valentine, 2006)
Substratum loss (habitat loss)	Removal of seagrass habitat and substrate.	(Burgin and Hardiman, 2011)
Increased turbidity	Stress from chronic light reduction and reduced resilience to environmental change.	(Fraser et al., 2017)
Removal of seagrass - direct harvesting	Direct removal of seagrass potentially puts pressure on adjacent meadows to perform ecosystem services.	nd
Change to thermal regime	Change in biochemistry of seawater - changes in temperature can have significant impacts on seagrass especially those on edge of range.	(Nejrup and Pedersen, 2008)
Changes to salinity (reduced flow)	Affects the physio-chemical state change.	(Nejrup and Pedersen, 2008; Ruíz et al., 2009)

Main pressures identified for seagrass	Pressure Mechanism on State Changes	References*
Smothering	Physical interaction with seagrass by filling in existing meadows with sediment and/or structures.	(Newell et al., 1998)
Sea level rise	Changes natural boundaries of seagrass range.	(Valle et al., 2014)
Changes in wave exposure	Physical removal of seagrass and damage. Potentially alters the composition on seagrass meadows by supporting species with greater tolerance to higher wave energy.	nd

* nd = no data

Supplementary Table A.6 Summary of case-studies included in the review

River/Bay	EU Member State	HDI ^b	Seagrass habitats protected through legislation or policies	Seagrass habitat protected spatially	Management Plan	Coastal area of Plan	Seagrass given active protection through plan	Waste-water pollution issues	Stormwater treatment	Water Quality Monitoring and compliance	Cumulative Impact Policies developed	Climate Change Policies
Mississippi River	N	VH	Essential Fish Habitat	N	Comprehensive Master Plan for a Sustainable Coast ^c	Coastal nearshore zone	N	N	N	Y	Y	Y
Po River Delta, Venice Lagoon	Y	VH	N	Natura 2000 Site	N	NA	NA	Y	N	Y	N	Y
Danube River	Y	VH	N	N	Master Plan for Danube Delta ^d	Out to 20m contour	N	Y	N	Y	N	Y
Chao Phraya River	N	H	N	N	N	N	NA	Y	N	Y	N	Y
Nile River	Y	M	N	N	N	NA	NA	Y	N	Y	N	Y
Niger River Delta	N	L	N	N	N	NA	NA	Y	N	N	N	Y
Krishna River & Godavari River	N	M	N	N	N	NA	NA	Y	N	N	N	Y
Zambezi River	N	L	N	N	N	NA	NA	Y	N	Y	N	N
Gulf of Gdansk	Y	VH	N	Natura 2000 Site	Pilot Draft Plan for the West Part of Gulf of Gdansk 2010 ^e	West Part of Gulf of Gdansk	Y	Y	N	Y	N	Y
Don River	N	VH	N	N	N	NA	NA	Y	N	unknown	N	Y
Tigris and Euphrates Rivers	N	M	N	N	N	NA	NA	Y	N	N	N	N
Han, Ron and Lian Rivers	N	H	N	N	N	NA	NA	Y	N	Y	N	N

River/Bay	EU Member State	HDI ^b	Seagrass habitats protected through legislation or policies	Seagrass habitat protected spatially	Management Plan	Coastal area of Plan	Seagrass given active protection through plan	Waste-water pollution issues	Stormwater treatment	Water Quality Monitoring and compliance	Cumulative Impact Policies developed	Climate Change Policies
Imjin and Han Rivers	N	VH	Nationally threatened species	N	N	NA	NA	N	Y	Y	N	Y
Trinity River	N	VH	Essential Fish Habitat	N	Galveston Bay Estuary Program ^f	Galveston Bay	N	N	N	Y	N	N
Wadden Sea	Y	VH	N	Natura 2000 Site	Trilateral Wadden Sea Plan ^g	German Wadden Sea	Y	N	Y	Y	N	Y
Johor River	N	VH	N	N	Singapore Integrated Urban Coastal Management ^h	EEZ	N	N	Y	Y	N	Y
Great Barrier Reef	N	VH	Fish Habitat Area	Marine Protected Area	Reef 2050 Long Term Sustainability Plan ⁱ	Entire GBR complex in Coral Sea	Y	N	N	Y	Y	Y
Moreton Bay	N	VH	Fish Habitat Area	Marine Protected Area	Moreton Bay (Marine Park) Zoning Plan ^j	Moreton Bay	Y	N	N	Y	Y	Y
Fraser River	N	VH	Ecologically and Biologically Significant (EBSA) species	N	N	NA	NA	N	N	Y	Y	Y

River/Bay	EU Member State	HDI ^b	Seagrass habitats protected through legislation or policies	Seagrass habitat protected spatially	Management Plan	Coastal area of Plan	Seagrass given active protection through plan	Waste-water pollution issues	Stormwater treatment	Water Quality Monitoring and compliance	Cumulative Impact Policies developed	Climate Change Policies
Chesapeake Bay	N	VH	Essential Fish Habitat	Y	Y	Chesapeake Bay catchment	Y	N	N	Y	Y	N

^a GDP (Gross Domestic Product) is the total market value of all final goods and services produced in 2018, adjusted for differences in prices in different countries.

The list is made up of 192 countries, 1 having the highest GDP (<http://statisticstimes.com/economy/countries-by-projected-gdp.php>)

^b HDI (Human Development Index) is a summary measure of average achievement in key dimensions of human development: a long and healthy life, being knowledgeable and have a decent standard of living. The HDI is the geometric mean of normalized indices for each of the three dimensions. VH = very high (country ranks 1-51), H = high (ranks 52-105), M= medium (ranks 106-147), L= low (ranks 148-188). <http://hdr.undp.org/en/composite/HDI>

Y= yes, N = no, NA = not applicable

^c Coastal Protection and Restoration Authority of Louisiana (2017)

^d Swedish Environmental Research Institute (2006)

^e Zaucha, (2010)

^f Galveston Bay Estuary Program (2018)

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^h The Technical Committee on the Coastal and Marine Environment (2013)

ⁱ Australian Government (2015)

^j Queensland Government (2008)

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Supporting information from Chapter 3

Supplementary Table A.7 Indicators used in the cumulative threat map.

Threat Theme	Threat data	Data source	Date	Accessed	Metadata description and electronic source
Water Quality	Chlorophyll <i>-a</i> (nutrients) - ocean	IMOS - SRS - MODIS - 01 day - Chlorophyll-a concentration (OC3 model)	2006-2020	18/11/2020	Satellite data from MODIS sensor that takes daily multi-spectral measurements of sunlight reflected within the ocean surface layer and used to infer the concentration of chlorophyll- <i>a</i> (Chl- <i>a</i>) using the OC3 model method, most typically due to phytoplankton, present in the water. The mean value from 2006-2020 was used in the threat map at 0.02 degrees. The data is available at https://catalogue-imos.aodn.org.au:443/geonetwork/srv/api/records/27cc65c0-d453-4ba3-a0d6-55e4449fee8c
	Total nitrogen and turbidity river/estuary discharge	NSW Government, Department of Planning, Industry and Environment (DPIE)	2007-2020	20/10/2020	Publically available data on estuary water quality collected by the Estuaries and Catchments Team of the Environment, Energy and Science Group in DPIE using a standard monitoring protocol was used to derive water quality conditions (https://datasets.seed.nsw.gov.au/dataset/nsw-estuary-water-quality-data-compilation-2007-2020). This dataset was analysed across all estuaries and two key parameters were used as indicators based on spatial and temporal comprehensiveness: these included total Nitrogen (N) concentration (µg/L) and turbidity (NTU). The mean value from monitoring sites located closest to the mouth of the river/estuary was calculated for each estuary from data collected between 2007 and 2020. Total N and turbidity were assigned a weighting, which was the variable unit (a concentration) times the watershed area (as a proxy for total end-of-system flows) for each estuary. Weightings thus represented total relative contribution to coastal water quality. For each estuary, water quality dispersion layers were calculated using an exponential decay with distance from estuary mouth. The dispersion coefficient was set to -0.5. Watershed area data is from the OzCoasts website (http://www.ozcoasts.gov.au/search_data/estuary_search.jsp).

Threat Theme	Threat data	Data source	Date	Accessed	Metadata description and electronic source
Fishing	Recreational fishing pressure	NSW Government, Transport Roads and Maritime Services	2021	20/10/2020	Distance to boat ramps were used as a proxy for recreational fishing pressure (Stuart-Smith et al., 2008). Boat ramp locations sourced from Roads and Maritime Services, NSW (https://www.rms.nsw.gov.au/maritime/using-waterways/boat-ramps-map/boat-ramps) were classified into two use categories: low (single lane ramps) and high (multi-lane ramps). The linear distance to boat ramp for each use category was calculated out to a limit of 40 km and represented two levels of recreational fishing pressure. Single lanes were indicative of local boat ramp usage (low-level fishing activity) while multiple lane ramps were indicative of regional boat ramp usage (higher fishing pressure) (NSW Department of Transport Roads and Maritime Services, 2015). A buffer of 40 km represents the approximate limit of travel for recreational fishers within one day (J Williams, NSW DPI, pers. comm 24 April 2021).
	Commercial fishing pressure – demersal and midwater	NSW Department of Primary Industries (DPI) Commercial Fisheries Catch and Effort Logbooks,	2009-2020	31/05/2021	De-sensitised gridded commercial trap, line (bottom and midwater) and trawl fishing catch per unit of effort (CPUE) data from catch and effort logbooks within the Northern Region of NSW was provided on request by DPI at 0.1 degrees. Catch effort data for each fishing event per day of active fishing activity was used to indicate commercial fishing pressure; cumulative hours for the trawl fishery, total number of hooks multiplied by the total number of drops for the line fishery, and the total number of traps pulled for the trap fishery. Location data for CPUE was reported in a gridded fisheries logbook format (https://www.dpi.nsw.gov.au/_data/assets/pdf_file/0008/753146/New-South-Wales-Department-of-Primary-Industries-Commercial-Fisheries-Catch-and-Effort-Logbook.pdf). Therefore the data was converted to a spatial base raster consistent with this study using the raster (Hijmans et al., 2021) and tidyverse (Wickham et al., 2019) package in R (R Development Core Team, 2018). The mean CPUE at each location from 2009-2020 represented commercial fishing effort for each fishery: inshore trawling (prawns), line (bottom) fishery, line (midwater) fishery, and the trap fishery.

Threat Theme	Threat data	Data source	Date	Accessed	Metadata description and electronic source
Climate Change	Elevated sea surface temperature (SST)	IMOS, CSIRO Marine and Atmospheric Research (CMAR), BOM	2006-2020	20/11/2020	Publically available satellite data of SST at 20cm depth from the SST Atlas of Australian Regional Seas (SSTAARS) was downloaded from the Australian Ocean Data Network (AODN) Portal (https://portal.aodn.org.au/), provided through the Integrated Marine Observing System (IMOS). Metadata accessed here - https://catalogue-imos.aodn.org.au:443/geonetwork/srv/api/records/79c8eea2-4e86-4553-8237-4728e27abe10 . Daily SST (night-only measurements) were converted to mean yearly values from 1992-2020 at 0.02 degree resolution. The number of years that current SST (2003 - 2020) was greater than historical SST (1992 to 2002) was used to indicate elevated SST (SST anomalies) for the threat map.
Coastal development	Population pressure	Australian Bureau of Statistics (ABS)	2019-2020	9/06/2021	Population data from the Australian Population Grid 2020 was used to represent coastal development from population pressure (https://www.abs.gov.au/statistics/people/population/regional-population/latest-release). The population grid uses 2016 Census of Population and Housing data (number of residential dwellings and population) to estimate residential population (ERP) using 1 km ² grid cells across Australia (SA1). Each SA1 grid has a population of between 200 and 800 people with an average population size of approximately 400 people. Data was transformed by summing grid cells >1, 000 people and creating a buffer of 20 km around a population centre to account for pollution and habitat degradation from human use (Ostwald et al., 2021). Buffers were weighted by population, by summing the population in each buffer, transforming the numbers using the square root and normalising to 1 (Ostwald et al., 2021).

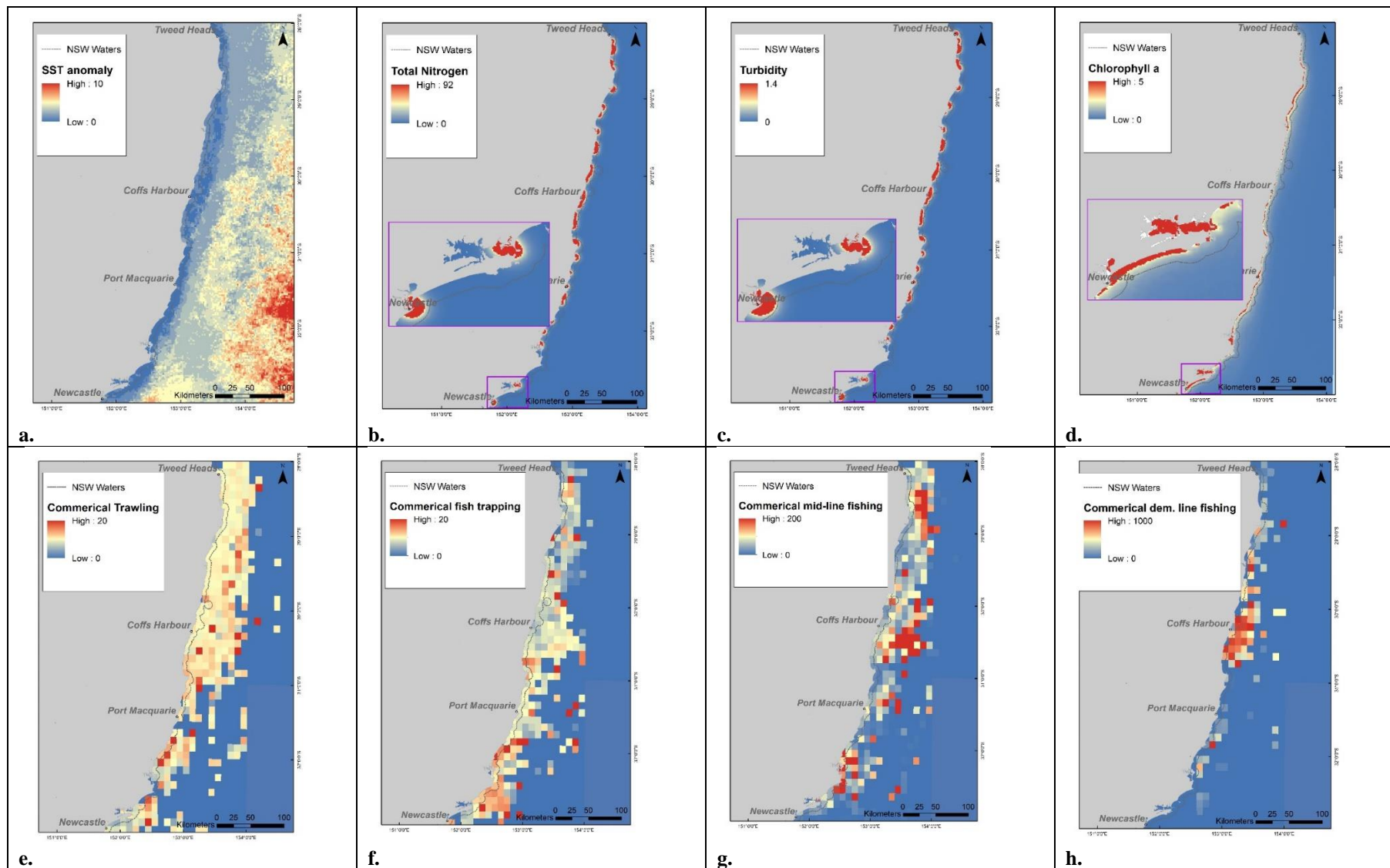
Supplementary Table A.8 Frequency of fishery-targeted carnivorous and invertivorous species included in the study

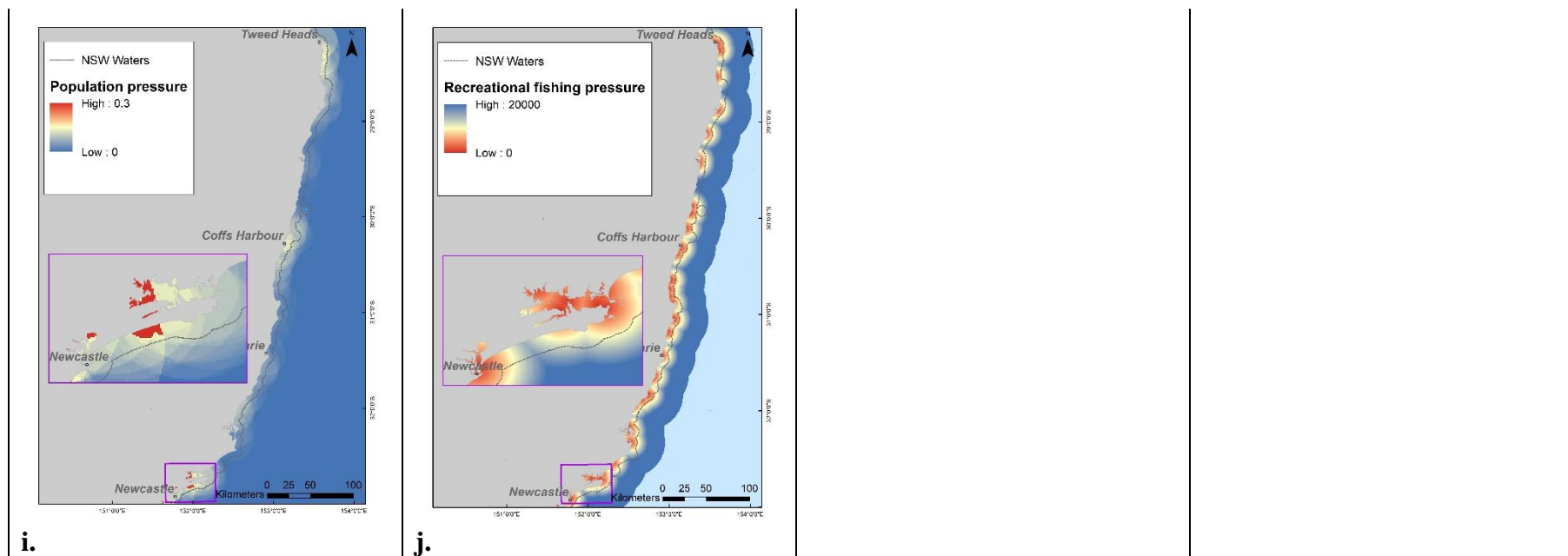
Functional Group	Species	Common Name	Frequency
Carnivore	<i>Atractoscion aequidens</i>	Teraglin	11
	<i>Bodianus frenchii</i>	Foxfish	95
	<i>Caranx sexfasciatus</i>	Bigeye trevally	4
	<i>Caranx sp.</i>	Trevally	3
	<i>Carcharhinus limbatus</i>	Common blacktip shark	1
	<i>Carcharhinus obscurus</i>	Dusky whaler	1
	<i>Centroberyx affinis</i>	Redfish	21
	<i>Chrysophry auratus</i>		19
	<i>Epinephelus sp.</i>	Grouper/rockcod	1
	<i>Epinephelus undulatostratus</i>	Maori rockcod	32
	<i>Glaucosoma scapulare</i>	Pearch pearl	88
	<i>Latridopsis forsteri</i>	Bastard trumpeter	8
	<i>Lutjanus adetii</i>	Hussar	6
	<i>Lutjanus russellii</i>	Moses snapper	29
	<i>Mustelus antarcticus</i>	Gummy shark	3
	<i>Nelusetta ayraud</i>	Ocean leatherjacket	116
	<i>Nemadactylus douglasii</i>	Blue morwong	601
	<i>Chrysophrys auratus</i>	Pink snapper	865
	<i>Platycephalus caeruleopunctatus</i>	Eastern bluespot flathead	23
	<i>Platycephalus fuscus</i>	Dusky flathead	2
	<i>Platycephalus longispinis</i>	Longspined flathead	4
	<i>Platycephalus sp.</i>	Flathead	1
	<i>Pomatomus saltatrix</i>	Tailor	4
	<i>Sarda australis</i>	Australian bonito	34
	<i>Scomber australasicus</i>	Blue mackerel	1

Functional Group	Species	Common Name	Frequency
	<i>Scorpaena cardinalis</i>	Eastern red scorpionfish	738
	<i>Seriola dumerili</i>	Amberjack	15
	<i>Seriola hippos</i>	Samsonfish	18
	<i>Seriola lalandi</i>	Yellowtail kingfish	59
	<i>Seriola rivoliana</i>	Amberjack	33
	<i>Thyrsites atun</i>	Barracouta	4
Invertivore	<i>Acanthopagrus australis</i>	Silver bream	124
	<i>Bodianus perditio</i>	Foxfish	26
	<i>Bodianus unimaculatus</i>	Eastern pigfish	36
	<i>Cheilodactylus fuscus</i>	Red morwong	377
	<i>Choerodon venustus</i>	Venus tuskfish	161
	<i>Girella elevata</i>	Rock blackfish	27
	<i>Girella tricuspidata</i>	Luderick	23
	<i>Notolabrus gymnogenis</i>	Crimsonband wrasse	922
	<i>Ophthalmolepis lineolata</i>	Southern maori wrasse	941
	<i>Pseudocaranx georgianus</i>	Silver trevally	443
	<i>Rhabdosargus sarba</i>	Tarwhine	312
	<i>Upeneichthys lineatus</i>	Bluestriped goatfish	224

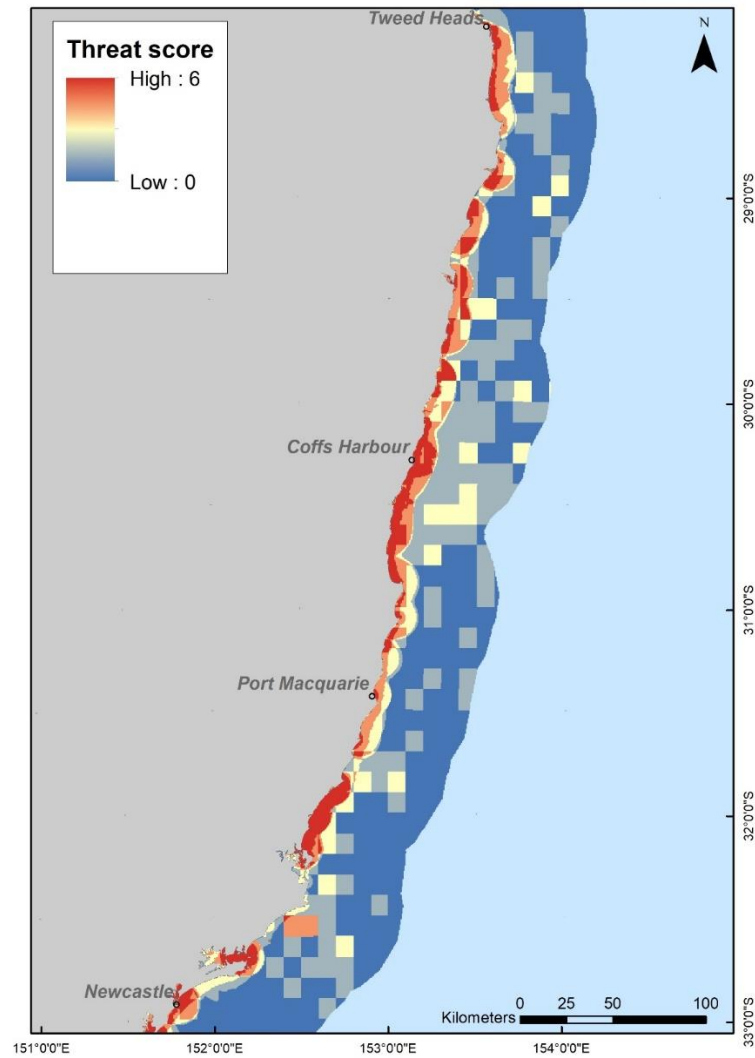
Supplementary Table A.9 Pairwise concurrency values between all variables used in the GAM model of carnivorous fish abundance

	Depth	SST anomaly	Proximity to seagrass	Proximity to saltmarsh	Chlorophyll <i>-a</i>	Turbidity	Recreational fishing	Urban	Commercial Trapping	Commercial line fishing	Commercial demersal line fishing	Year	Site
Depth	1	0.12	0.1	0.11	0.18	0.08	0.13	0.13	0.13	0.12	0.09	0.02	0.04
SST anomaly	0.02	1	0.07	0.07	0.02	0.01	0.03	0.03	0.1	0.06	0.06	0.01	0.01
Proximity to seagrass	0.2	0.28	1	0.32	0.2	0.19	0.29	0.27	0.27	0.23	0.21	0.01	0.04
Proximity to saltmarsh	0.12	0.39	0.31	1	0.31	0.23	0.26	0.45	0.36	0.37	0.31	0.01	0.04
Chlorophyll- <i>a</i>	0.14	0.11	0.13	0.2	1	0.14	0.19	0.25	0.17	0.22	0.2	0.01	0.04
Turbidity	0.15	0.29	0.21	0.2	0.23	1	0.28	0.35	0.36	0.42	0.18	0.02	0.03
Recreational fishing	0.15	0.14	0.29	0.28	0.25	0.1	1	0.33	0.32	0.24	0.25	0	0.04
Urban	0.1	0.1	0.23	0.45	0.32	0.07	0.3	1	0.41	0.41	0.42	0.01	0.04
Commercial trapping	0.16	0.61	0.3	0.36	0.28	0.11	0.31	0.37	1	0.39	0.38	0.03	0.04
Commercial line fishing	0.16	0.42	0.26	0.31	0.29	0.22	0.27	0.44	0.48	1	0.51	0.01	0.04
Commercial Demersal line fishing	0.09	0.37	0.24	0.31	0.1	0.24	0.24	0.31	0.24	0.45	1	0.02	0.03
Year	0.01	0.04	0.01	0.01	0.01	0	0	0.01	0.01	0.02	0.03	1	0.01
Site	0.92	1	1	1	1	1	1	1	1	1	1	0.29	1

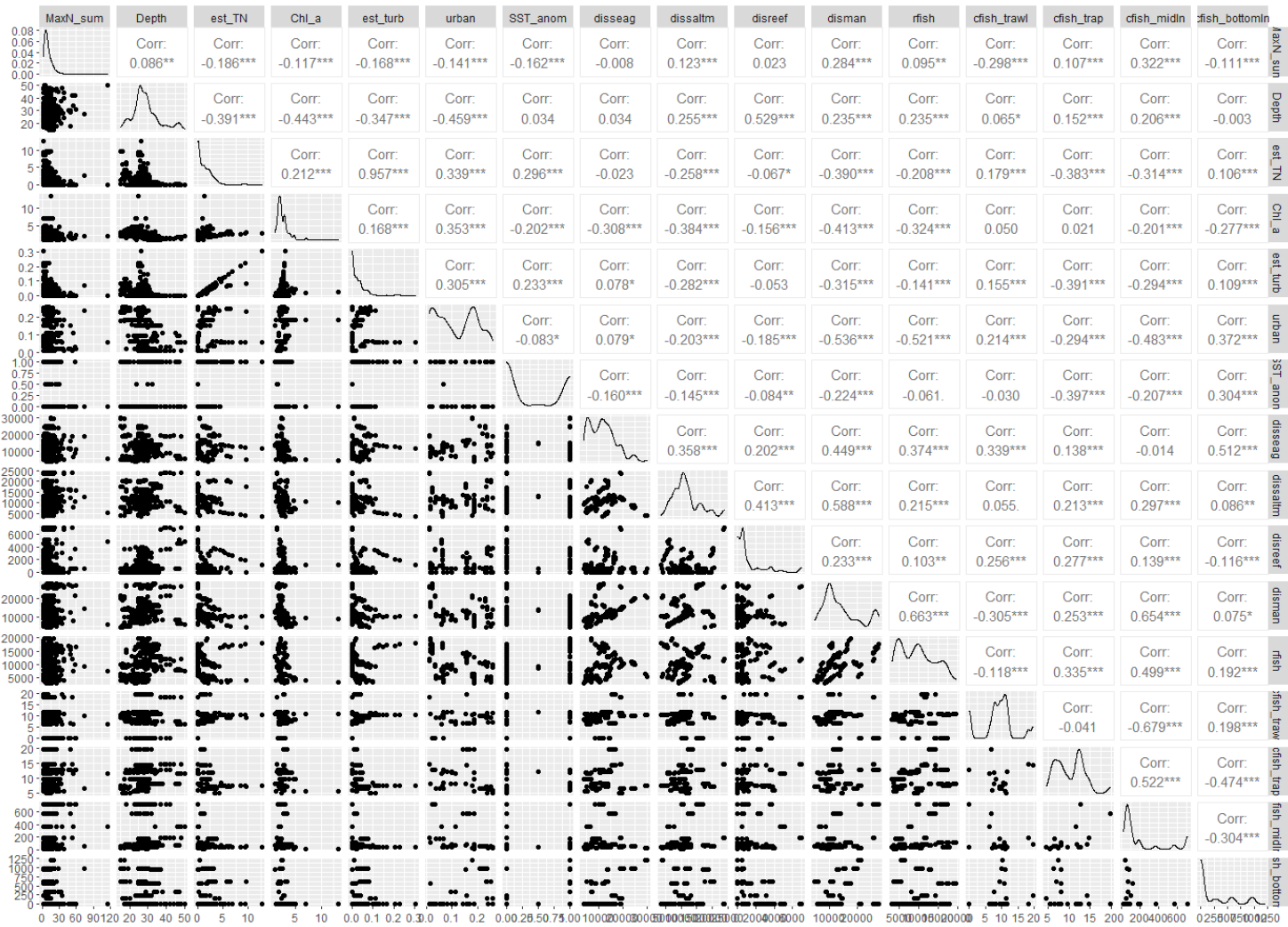




Supplementary Figure A.1 Threat maps for individual threats. Note that recreational fishing threats were measured as distance from boat ramps, therefore the colour scale is reversed (so red indicates areas with low distances that have high threat). Also note that the scales have been adjusted to enable visual inspection of the threat gradient (i.e. maximum values have been reduced in the maps).



Supplementary Figure A.2 Map of hotspots of cumulative threat, where threat scores (H_i) are defined as the count of threats in the top 5% of all values for each grid. Map produced using ArcGIS, ArcMap version 10.3 software.



Supplementary Figure A.3 Correlation matrix for all covariates used in the model of carnivore abundance.

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Supporting information from Chapter 4

Supplementary Data – community overview

Fisheries provide communities living within and adjacent to these MPAs with their main form of dietary protein (~70% of people in the BHS) and income (9% and 16% of people for Kofiau and Misool, respectively) (Ahmadia et al., 2016; Glew et al., 2015). The mining of coral for construction purposes also occurs within Raja Ampat (Ahmadia et al., 2016). The larger of the two regions, Misool, sustains a greater population (10,163 cf. 2,714 in Kofiau) and number of settlements (16 cf. three in Kofiau) in comparison to Kofiau (BPS-Statistics of Raja Ampat Regency, 2017). However, the islands have a lower population density in comparison to other sub-regions within the BHS (BPS-Statistics of Raja Ampat Regency, 2017). The Misool MPA was subject to greater fishing pressure compared to Kofiau MPA during the period of data collection because in Misool distributors buy fresh fish from local fishers and transport it by ferry to fish markets in Sorong. At the time of the data collection the export market in Kofiau was for dried fish only and transport to Sorong was limited. The MPAs of the BHS are monitored and enforced through government programmes, however illegal fishing practises are still observed (Ahmadia et al., 2016).

Supplementary Data – methods

All explanatory variables were at a 150 m resolution (2.25 ha per cell) and at a grid boundary that encompassed each MPA and their respective control sites (outside of MPAs) and projected in WGS84 geographic coordinate system. All statistical analysis was performed using 'R' software version 3.4.3 (2017-11-30) developed by 'The R Foundation for Statistical Computing' using the mgcv package (Wood and Scheipl, 2020)

Villages in Kofiau and each of the four districts in Misool were identified and assigned spatial coordinates from government websites (www.nomor.net.) and google earth (earth.google.com/web). Two 150 m grids of distance to the nearest village, a) direct linear distance and b) shortest distance via water, for each region were produced using the Raster package in R (Hijmans et al., 2020). Villages were buffered to 500 m to ensure each village intersected with water cells for the raster that calculated distance around land.

RUM interview questions included the origin village of the fishers and vessel, its current activity, location of fishing effort, and details on fish catch. Only boats that were actively fishing and from the district of Raja Ampat were included in this analysis. Local fishing boats accounted for the majority of fishing effort in both regions (711 cf. 111 for Kofiau

MPA and 1627 cf. 1035 for Misool MPA). Rasters of historical fishing pressure (number of predicted boats) and number of days on patrol were created from the RUM data. A spatial data frame of counts of fishing events was produced for each gridded reef cell (2.25 ha per cell) for each region. The number of patrol days were standardised to a per day usage to account for the variation in monitoring intensity. Grid cells that were within the observation distance of the surveys (5.9 km from the survey route, which is the line-of-sight standing at sea level) were given a zero value when no boats were observed.

Wave exposure data was created in ARC GIS using the fetch and waves 2012 models (Rohweder et al., 2012). Input rasters for the models included bathymetry (Weatherall et al., 2015), shoreline (Wessel and Smith, 1996), wind direction (in 10 degree bins) and speed (MPH) for a 12 month period (Technical University of Denmark 2018) at a spatial resolution of 0.029 degrees (~3km). The output adf files from ARC GIS were rasterised in R (Hijmans et al., 2020) which placed a weighting on each cell based on the number of days wind was blowing in a direction. Rasters of wave height (m); the vertical distance between the trough of a wave and the following crest in meters and wave period (sec); spectral peak in wave energy in seconds, were created and used as indicators of wave exposure.

Habitat data was obtained for mangroves (30 m resolution, Giri et al., 2011), seagrass (UNEP-WCMC and Short, 2018) and coral reef (UNEP-WCMC et al., 2018). Habitat data, shoreline data (1:120,000,000 scale, Wessel and Smith, 1996) and MPA polygons were extrapolated onto 150 m boundary grids for each region.

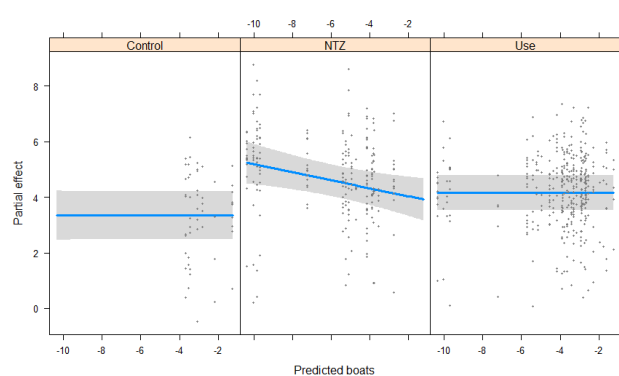
Fish biomass data (Ahmadia et al., 2015; Fidler et al., 2021) consisted of information on species, abundance and size of fish. Fish were identified down to genus if not species level. Data on fish biomass were geographically referenced and assessed by UVC using SCUBA following the protocol by Ahmadia et al., (2013). Survey sites were located in NTZ and Use zones within Kofiau Area and Misool Area as well as control sites using a stratified haphazard selection. Data was controlled for confounding covariation between paired MPA and control sites as extensive planning took place prior to implementation of the monitoring program (Ahmadia et al., 2015). Fish were assigned into two functional groups; herbivores (Acanthuridae, Scaridae and Siganidae) and predators (Lutjanidae, Haemulidae and Serranidae). Predators are indicators of fishing pressure (Glew et al., 2015) and commercial export markets (Campbell et al., 2018). Herbivores are indicators of reef resilience (Glew et al., 2015) and local market pressure (Wawan pers.comm,

18/02/2020). Pelagic predators (Scombridae and Carangidae) were also included initially as they form an important export market to Sorong (Wawan pers.comm, 18/02/2020), however there were insufficient biomass data to consider these families separately. Biomass values were calculated from fish size estimates following the method in Ahmadia et al. (2013) and standardized using a log transformation to obtain comparable density measures (number of individuals per 100 m²). The final data frame consisted of 20 explanatory variables. Data were filtered to minimise variation (depths, reef type, and exposure) and rows were removed where data was lacking (Supplementary Table A).

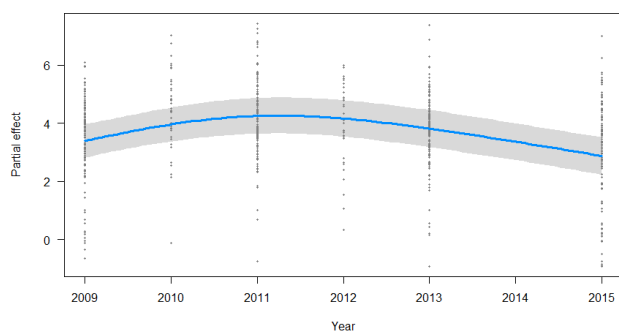
Maps throughout this paper were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and were used herein under license. Copyright © Esri.

Supplementary Table A.10 The range of explanatory variables filtered from reef fish survey data used in this analysis.

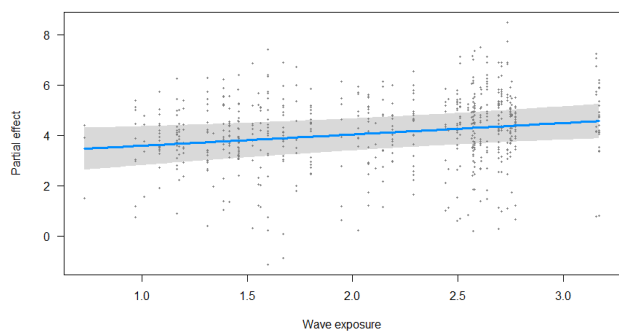
Explanatory variables	Misool Area	Kofiau Area
Sample size (n)	675	789
Number of transects per site (n)	4-5	4-5
Year	2009-2015	2009-2016
Depth (m)	9-10	8-10
Exposure	semi-exposed, exposed	semi-exposed, exposed
Reef aspect	South, North and East-West	South, North and East-West
Reef type	Fringing	Fringing



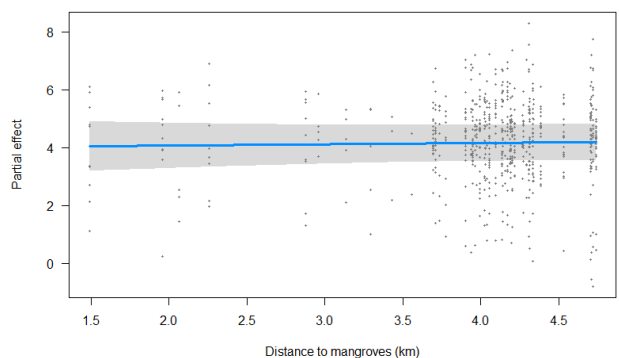
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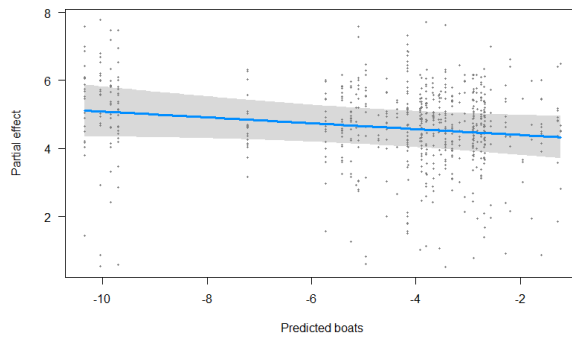
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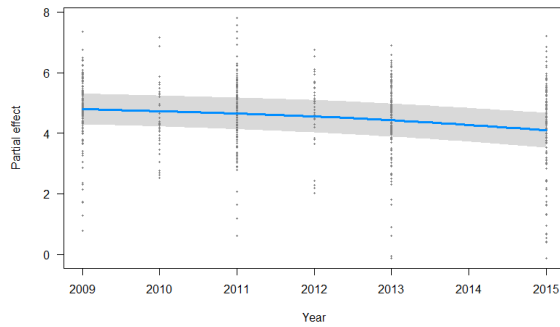
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Supplementary Figure A.4 Plots of expected herbivore biomass as estimated by the most parsimonious model for Misool MPA. The effect of historical fishing pressure on biomass for each management zone (i). The effect of time (year) on biomass (ii). The effect of wave exposure on biomass (iii). The effect of proximity to mangroves (iv). Blue lines shows the estimated smooth effect of the predicted biomass including the model intercept. The grey band shows the 95% confidence interval for the predicted biomass value. The grey dots show the partial residuals.

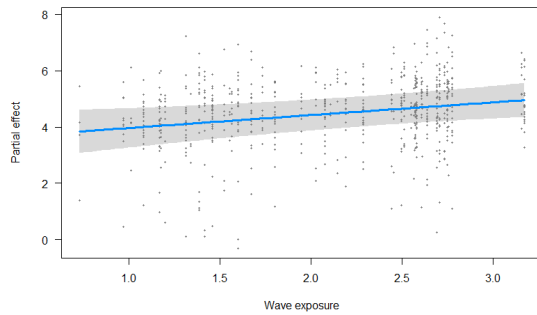
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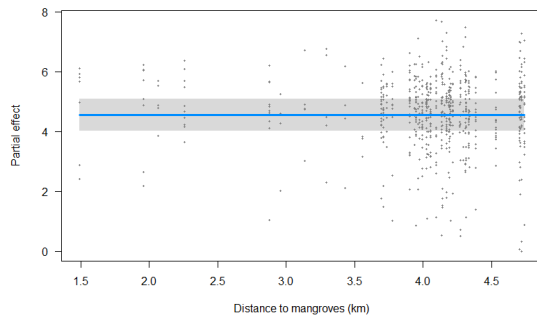
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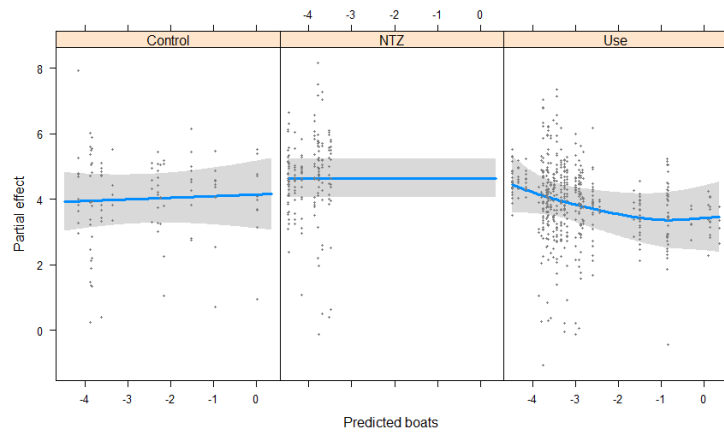
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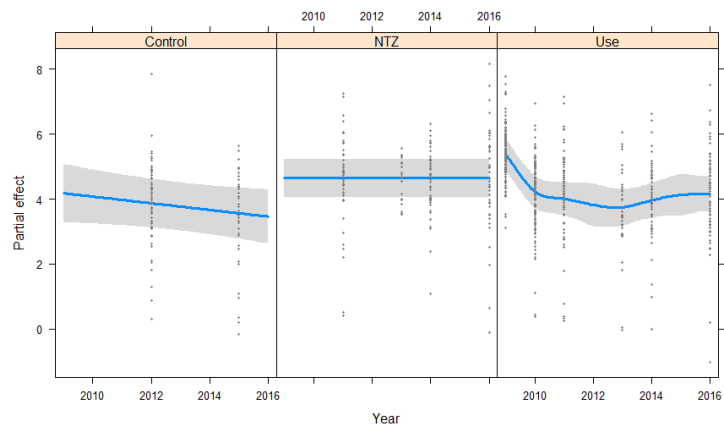
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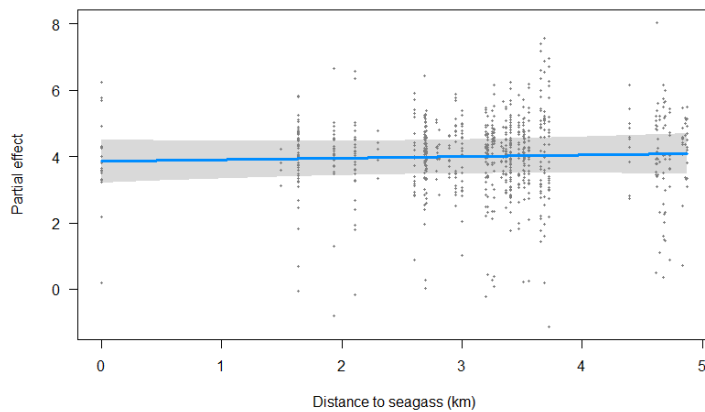
Supplementary Figure A.5 Plots of expected predator biomass as estimated by the most parsimonious model for Misool MPA. The effect of historical fishing pressure on biomass for each management zone (i). The effect of time (year) on biomass (ii). The effect of wave exposure on biomass (iii). The effect of proximity to mangroves on biomass (iv). Blue lines shows the estimated smooth effect of the predicted biomass including the model intercept. The grey band shows the 95% confidence interval for the predicted biomass value. The grey dots show the partial residuals.



i

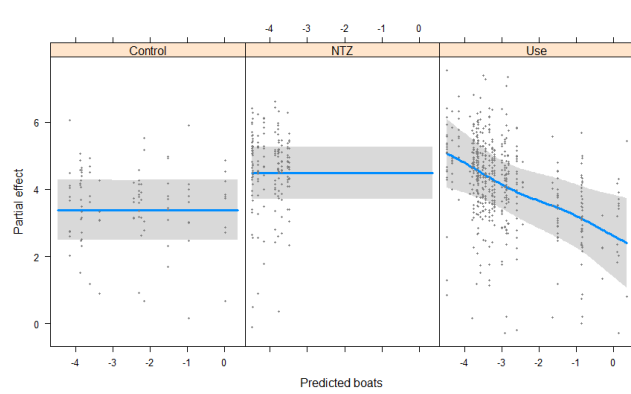


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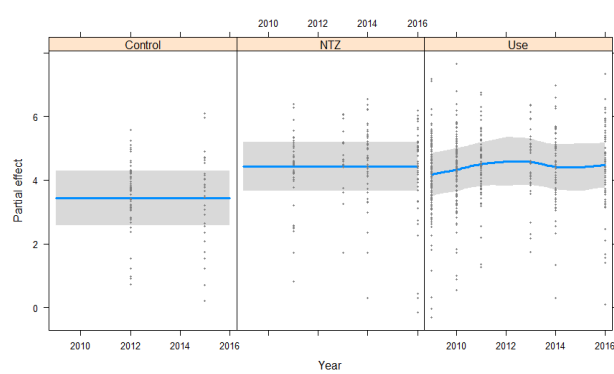


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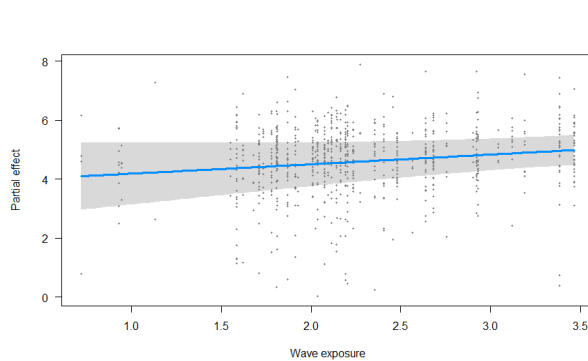
Supplementary Figure A.6 Plots of expected herbivore biomass as estimated by the most parsimonious model for Kofiau MPA. The effect of historical fishing pressure on biomass for each management zone (i). The effect of time (year) on biomass for each management zone (ii). The effect of distance to seagrass on biomass (iii). Blue lines shows the estimated smooth effect of the predicted biomass including the model intercept. The grey band shows the 95% confidence interval for the predicted biomass value. The grey dots show the partial residuals.



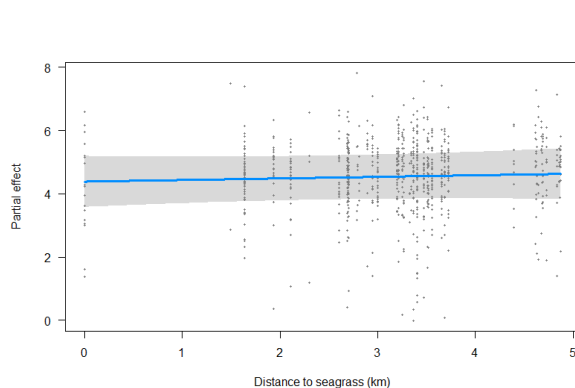
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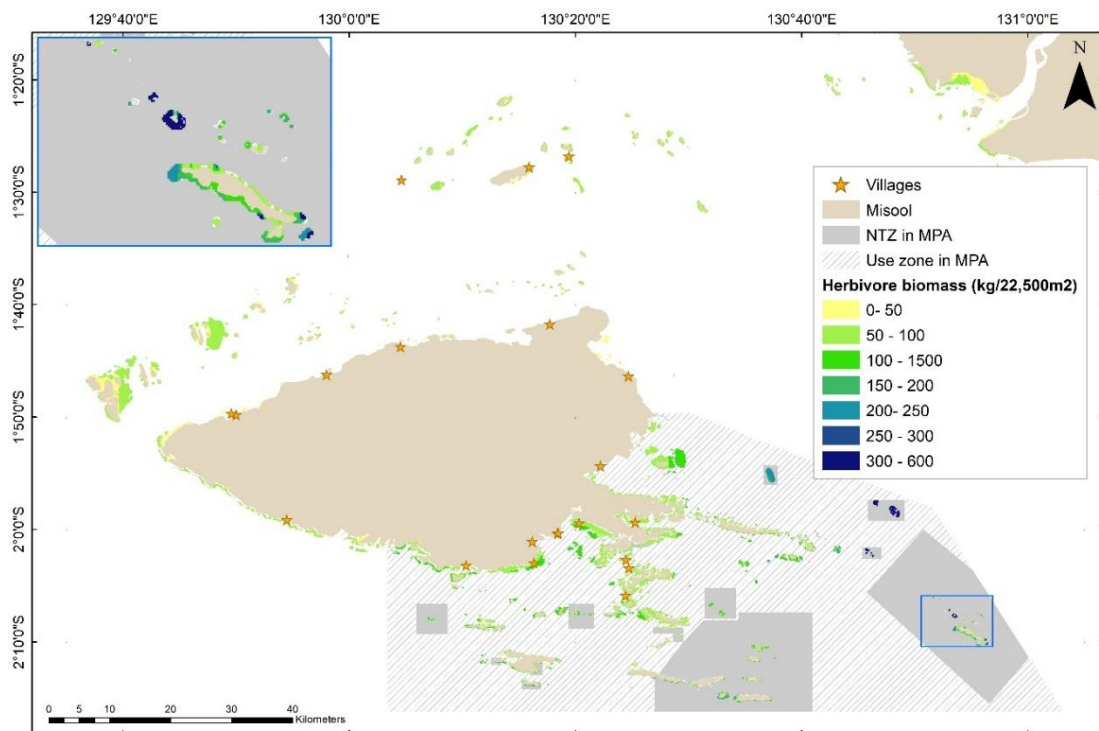


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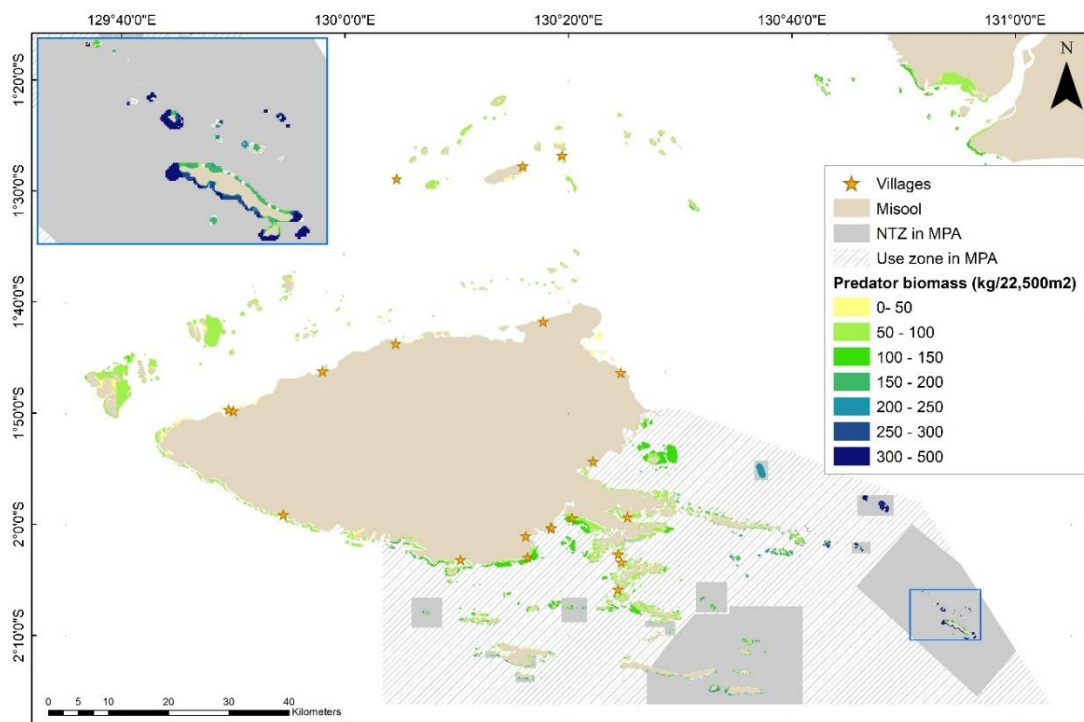


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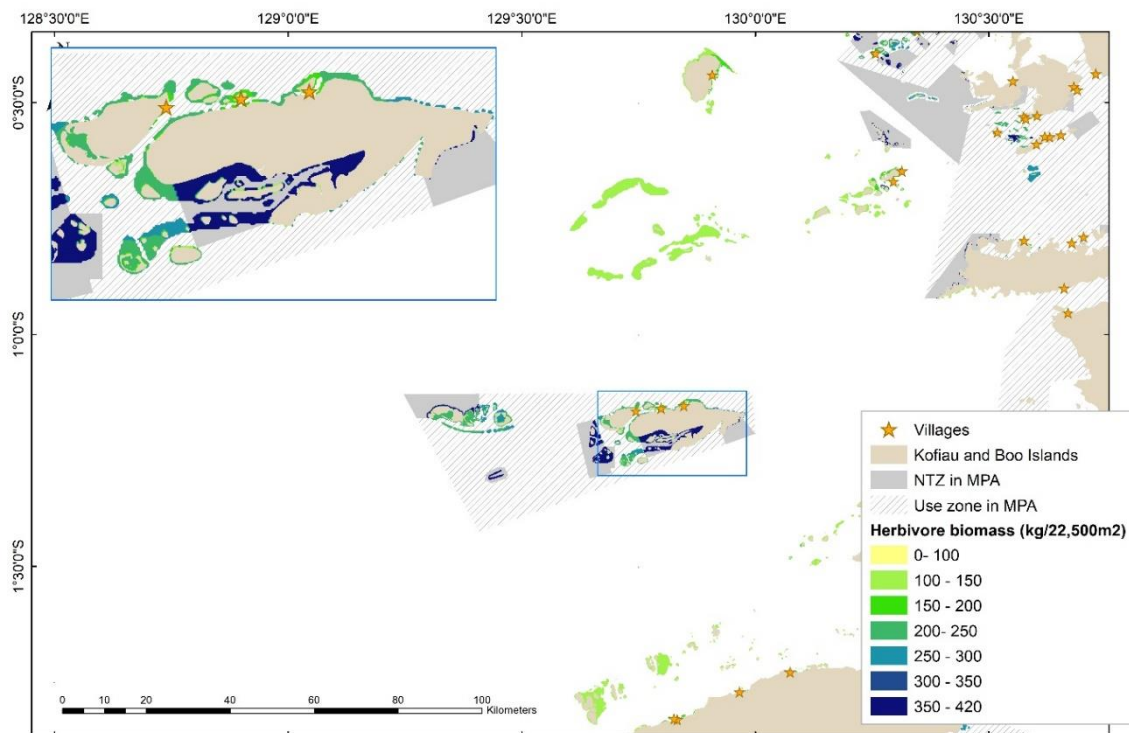
Supplementary Figure A.7 Plots of expected predator biomass as estimated by the most parsimonious model for Kofiau MPA. The effect of historical fishing pressure on biomass for each management zone (i). The effect of time (year) on biomass for each management zone (ii). The effect of wave exposure on biomass (iii). The effect of proximity to seagrass in biomass (iv). Blue lines shows the estimated smooth effect of the predicted biomass including the model intercept. The grey band shows the 95% confidence interval for the predicted biomass value. The grey dots show the partial residuals.



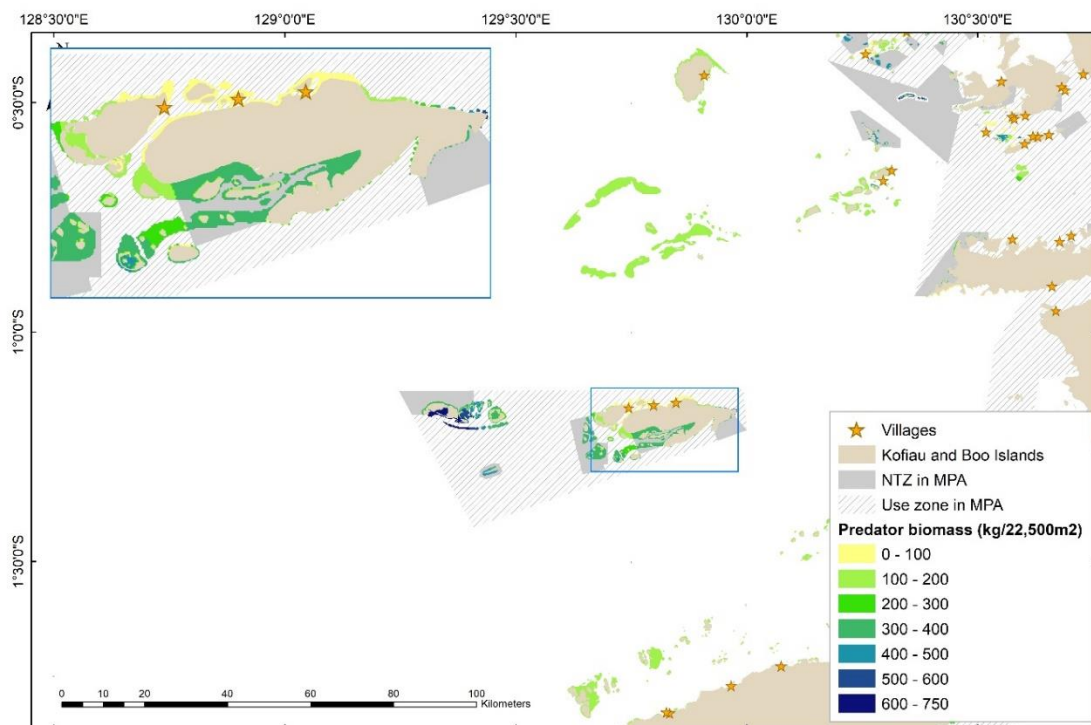
Supplementary Figure A.8 Predicted herbivore biomass (kg/150m²) with current management designation. Map is at a resolution of 30 m² and shows the Misool MPA.



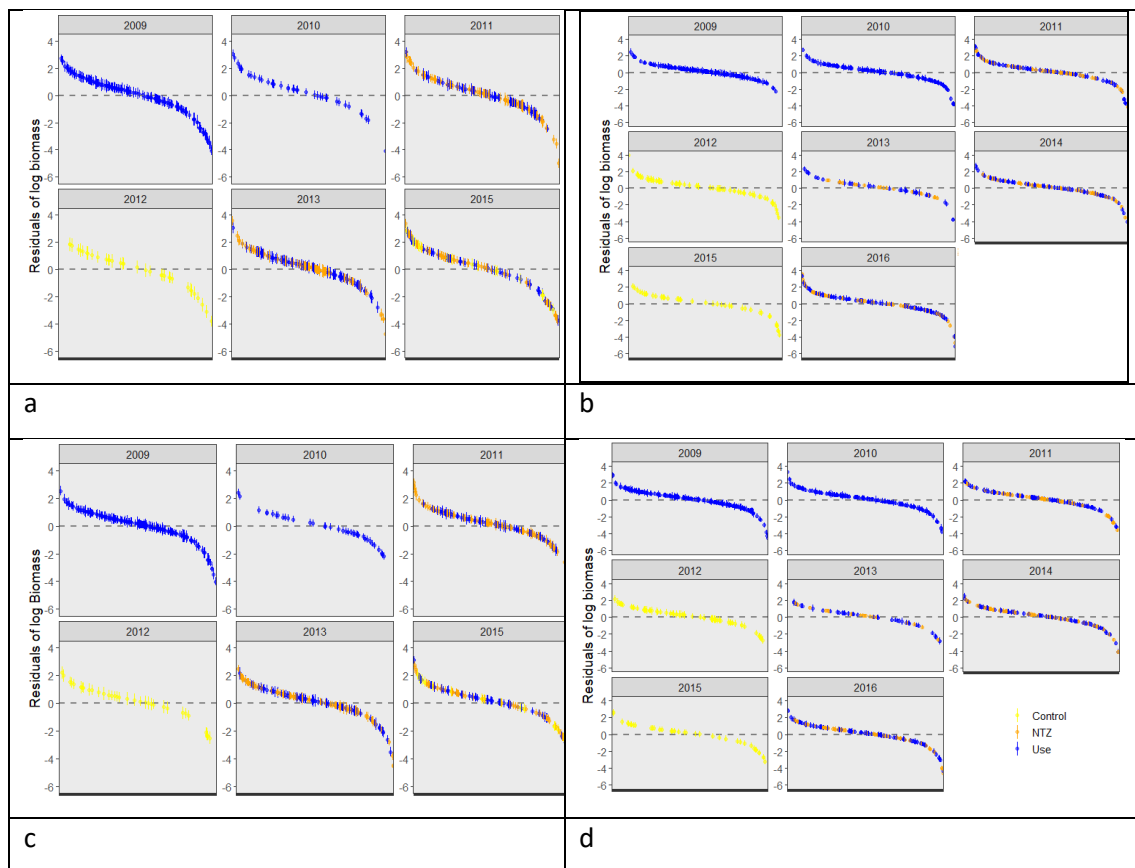
Supplementary Figure A.9 Predicted predator biomass (kg/150m²) with current management designation. Map is at a resolution of 30 m² and shows the Misool MPA.



Supplementary Figure A.10 Predicted herbivore biomass (kg/150m²) with current management designation. Map is at a resolution of 30 m² and shows the Kofiau MPA.



Supplementary Figure A.11 Predicted predator biomass (kg/150m²) with current management designation. Map is at a resolution of 30 m² and shows the Kofiau MPA.



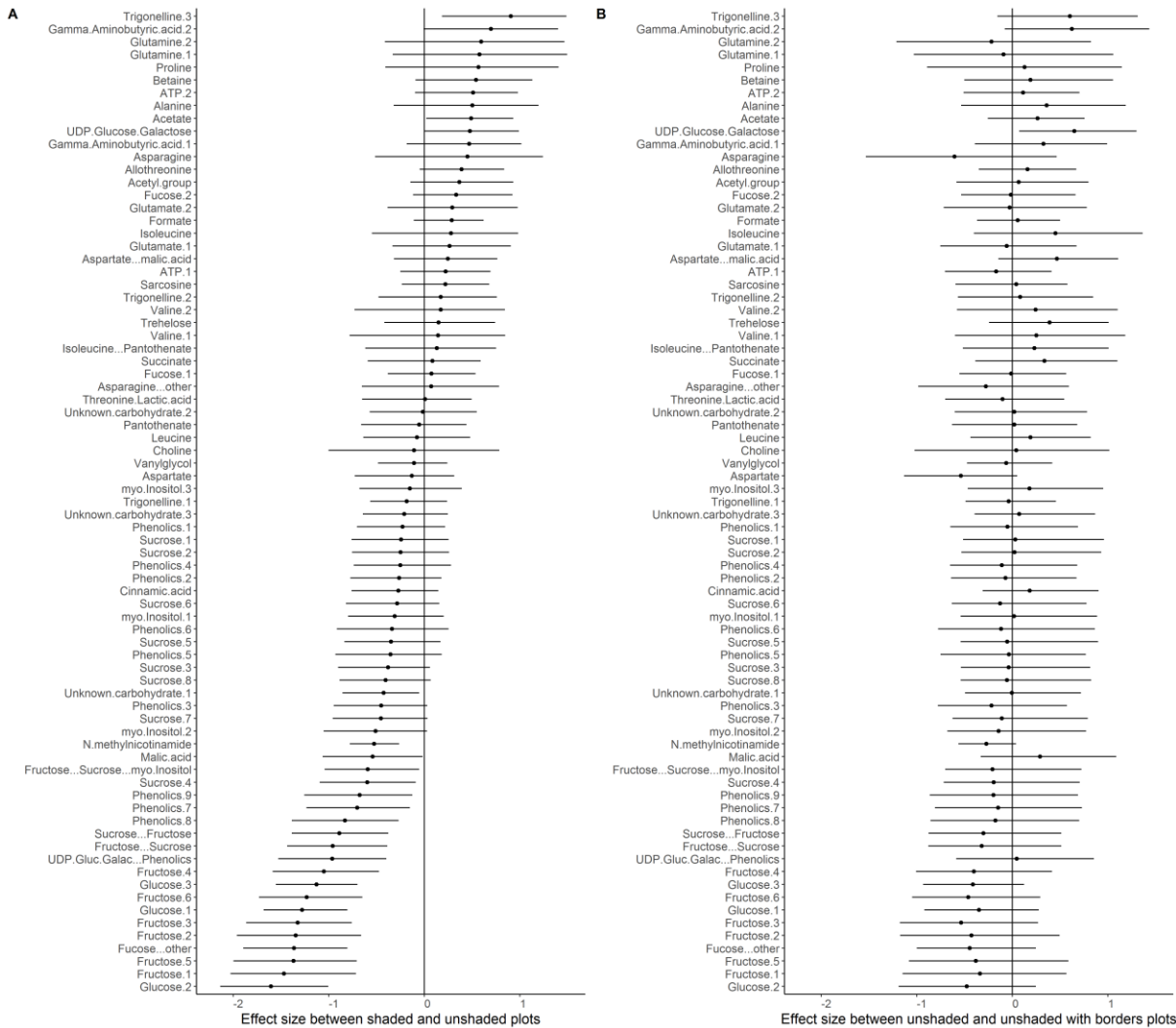
Supplementary Figure A.12 Yearly comparison between the observed and predicted MPA performance, showing residuals of logged biomass and SE at each reef survey site for herbivores in Misool (a), herbivores in Kofiau (b), predators in Misool (c) and predators in Kofiau (d). Residuals within each zone are itemised by colour: no-take zones (orange), use (blue) and control (outside of MPAs, yellow).

Additional references for chapter 3 supporting information

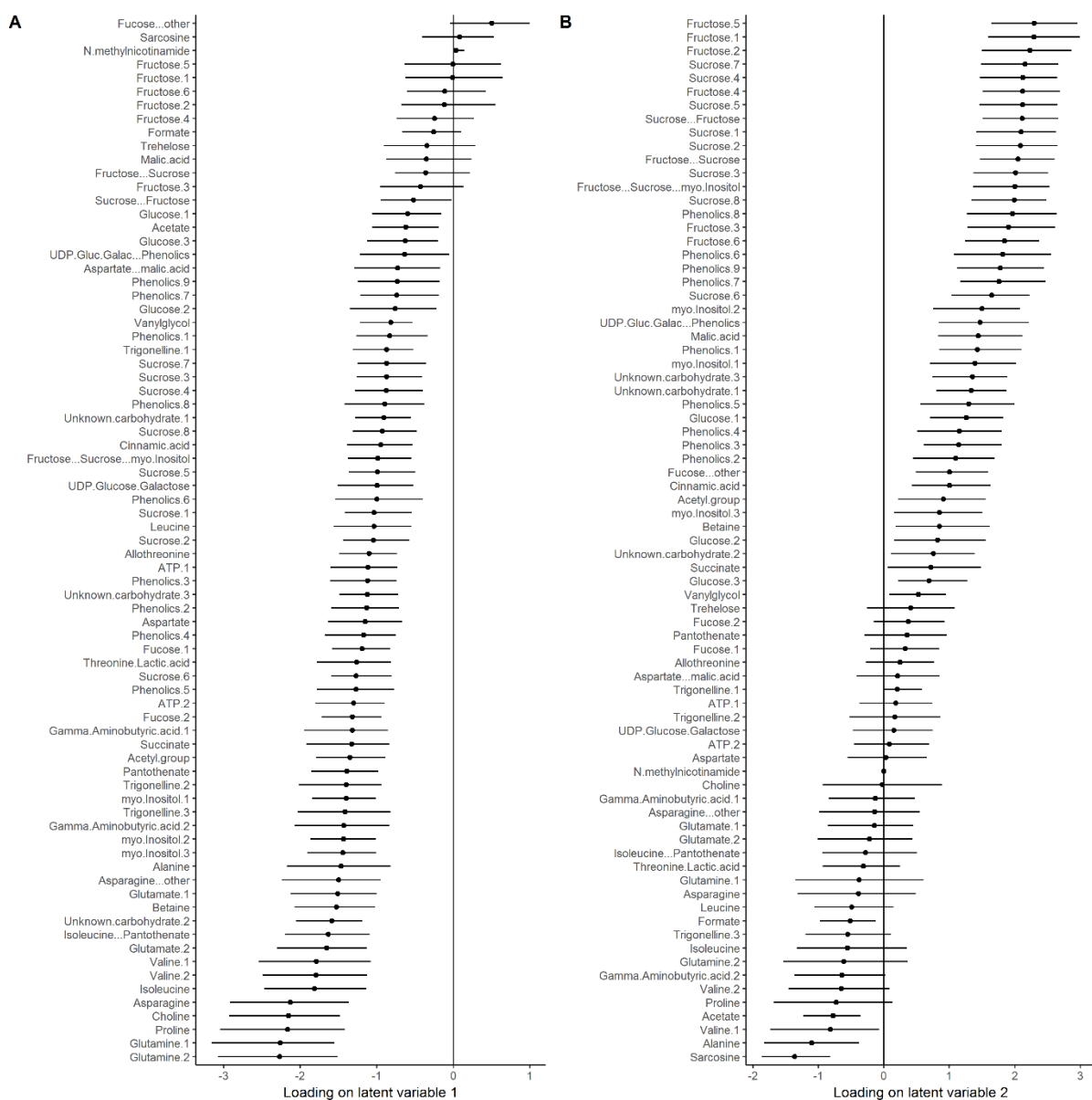
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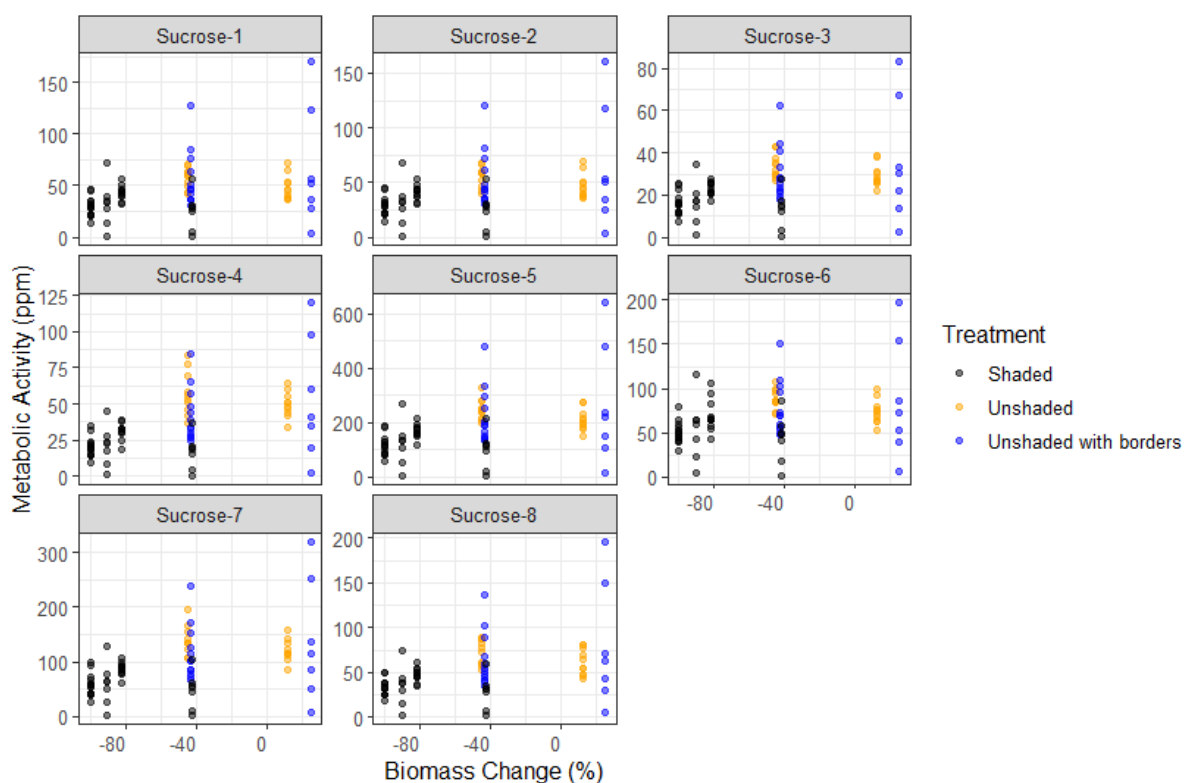
Supporting information from Chapter 5



Supplementary Figure A.13 Differences in the median effect sizes (black dots) with errors (hpd intervals) of all metabolite activities of *Z.muelleri* exposed to shade stress. Plot A (left) shows differences between shaded and unshaded plots while Plot B (right) shows differences between unshaded plots and unshaded plots with vertical isolation borders as a treatment. Bars indicate there is 95% probability of falling between the upper and lower limits.



Supplementary Figure A.14 Degree of correlation between metabolites on latent variable 1 (A) and 2 (B). The plots show differences in the median effect sizes (black dots) with errors (hpd intervals) of metabolites of *Z.muelleri* exposed to shade stress. Bars indicate there is 95% probability of falling between the upper and lower limits.



Supplementary Figure A.15 Plot of individual sugar metabolites showing biomass change and metabolic activity (spectra intensity measured as ^1H chemical shift in ppm) for each plot within each treatment group. Biomass change is the percent change over the 38 day experimental period from initial biomass measurements. Treatment groups include shaded plots with vertical isolation borders (Shaded), unshaded plots with vertical isolation borders (Unshaded with borders) and unshaded plots without any treatment (Unshaded). Numbers are assigned to metabolites to identify individual peaks in activity.