

**Drivers affecting seagrass meadows: An approach
for conservation and restoration in Mozambique**

Damboia Cossa

Doctoral Thesis



UNIVERSITY OF GOTHENBURG

Department of Marine Sciences

Faculty of Science

2024

Drivers affecting seagrass meadows: An approach for conservation and restoration in Mozambique

Copyright © Damboia Cossa 2024

ISBN 978-91-8069-895-2 (Print)

ISBN 978-91-8069-896-5 (PDF)

Available online at <http://hdl.handle.net/2077/83199>

Cover photo: Eduardo Infantes

Printed by Stema Specialtryck AB
Sweden, 2024

“Education is the most powerful weapon which you can use to change the world”

Nelson Mandela

To Kiomy, my dear family and friends

ABSTRACT

Seagrasses and other shallow-water vegetation are important coastal habitat because they provide many ecosystem services, including food, shelter and nursery areas of shellfish and finfish as well as marine endangered species such as dugongs and sea turtles. However, following a worldwide trend, seagrass meadows in Mozambique are experiencing a reduction in area due to a combination of natural disturbances and anthropogenic impacts. The aim of this thesis was to assess two relevant drivers affecting seagrass ecosystem services, while contributing to developing innovative management tools for conservation, restoration and sustainable use of this ecosystem in Maputo Bay, Mozambique. The thesis focuses on the impacts from both global (ocean acidification, OA) and local (fishing) stressors on marine invertebrates and dugongs. The thesis also aims to develop innovative methods for shallow-water monitoring using drones and machine learning as well as developing appropriate seagrass restoration techniques.

Paper I evaluates the biological response (growth rate and net calcification) of a marine calcifier (sea urchin), to different levels of variability of $p\text{CO}_2/\text{pH}$ imposed in the absence or presence of seagrass in the context of OA as a global stressor. The results showed that larvae growth rates significantly decreased with decreasing average pH in both absence and presence of seagrass. Moreover, larvae raised in presence of seagrass, maximized calcification during the day, and lowering their calcification during the night. These results have implications to better understand the mechanisms behind the sensitivity of organisms to OA in variable coastal ecosystems.

Paper II shows the influence of gillnet fishing activities as a local stressor on dugong feeding grounds. A drone survey revealed overlap between dugong foraging

areas and fishing grounds, increasing the risk of dugong entanglement when the gillnets are deployed at Inhaca Island, Mozambique. Thus, management initiatives to control gillnet fishing activity with involvement of the local community were highlighted to support future conservation efforts.

A survey on local ecological knowledge was used in **paper III** to assess community perceptions at Inhaca Island on both global and local stressors in seagrass meadows, while evaluating how fishing communities are adapting to face potential future changes of seagrass habitats and associated services. Results showed that the fishing community at Inhaca Island depends on fishing activities for their basic livelihood, and they perceived sedimentation associated with floods as the leading cause of seagrass changes, followed by destructive fishing practices. A decrease in coastal protection and loss of habitats (and associated invertebrates and fish) are perceived as the main threats to their livelihood and wellbeing.

Paper IV presents a field experiment to restore seagrass (*Halodule uninervis*), which is used as food by dugongs, with the aim to assess infauna biodiversity and colonization after planting. Two planting methods were tested, including a plug method and a single shoot method applied with two seagrass shoot densities. Results showed that the both methods influenced the transplants growth with consequences for the infauna abundance and composition.

The results of this thesis are discussed in an integrated approach to understand both global and local drivers of changes in seagrass meadows in Maputo Bay, Mozambique, while proposing an effective conservation and management strategies, which include the use of innovative technologies such as drones, involvement of local communities and restoration approaches to enhance the role of seagrass as an important coastal ecosystem.

Keywords: Coastal management | Coastal communities | Conservation | *Dugong dugon* | Gillnet fishing | Marine calcifiers | Ocean acidification | Restoration | Small-scale fisheries | Seagrass ecology |

SAMMANFATTNING PÅ SVENSKA

Sjögräs och annan undervattensvegetation utgör viktiga kusthabitat och bidrar till många ekosystemtjänster, inklusive mat, skydd och barnkammare för skaldjur och fiskar samt för hotade marina arter som dugonger och havssköldpaddor. I likhet med den globala trenden så har även utbredningen av sjögräs i Moçambique minskat på grund av en kombination av naturliga störningar och mänsklig aktivitet. Syftet med denna avhandling var att undersöka två relevanta faktorer som påverkar ekosystemtjänster från sjögräsängar och samtidigt bidra till att utveckla innovativa förvaltningsverktyg för bevarande, återställande och en hållbar användning av dessa viktiga ekosystem i Maputo-bukten, Moçambique. Denna avhandling fokuserar på effekterna av både globala (havsförsurning - OA) och lokala (fiske) stressfaktorer på marina ryggradslösa djur och dugonger. Avhandlingen syftar också till att utveckla innovativa metoder för miljöövervakning med hjälp av drönare och maskininlärning samt att utveckla lämpliga tekniker för återställande av sjögräs.

Artikel I utvärderar den biologiska responsen (tillväxthastighet och nettokalcifiering) hos en marin kalkifierare (sjöborre) under olika nivåer av $p\text{CO}_2/p\text{H}$ -variabilitet i frånvaro eller närvaro av sjögräs för att utvärdera effekten av OA som en global stressfaktor. Resultaten visade att tillväxten hos larver minskade signifikant med minskande pH både i frånvaro och närvaro av sjögräs. Larver som växt upp i närvaro av sjögräs maximerade kalkifieringen under dagen och minskade den under natten. Dessa resultat kan ha stor betydelse för att förstå mekanismer bakom organismers känslighet för havsförsurning i våra kustnära havsområden.

Artikel II visar påverkan av fiske med garn som en lokal stressfaktor på dugongers födosöksområden. En drönarundersökning visar på överlapp mellan

dugongers födosöksområden och fiskeområden, vilket ökar risken för att dugonger fastnar i fiskenät när dessa används vid Inhaca Island, Moçambique. Förvaltningsinitiativ för att kontrollera fiskeaktiviteten med garn föreslås därför att ske med lokalbefolkningens medverkan för att stödja framtida bevarandeinsatser.

En undersökning med fokus på lokal ekologisk kunskap (**artikel III**) gjordes för att bedöma samhällsuppfattningar hos den lokala befolkningen på Inhaca Island om både globala och lokala stressfaktorers påverkan på sjögräsängar, samtidigt som den även utvärderade hur fiskesamhällen anpassar sig för att möta potentiella framtida förändringar i sjögräsekosystemet och dess tillhörande ekosystemtjänster. Resultaten visade att fiskesamhället på Inhaca är beroende av fiskeaktiviteter för sin grundläggande försörjning, och de uppfattade sedimentation kopplad till översvämningar som den främsta orsaken till förändringar i sjögrässets utbredning, följt av ett destruktivt fiske. Ett minskat kustskydd och förlust av livsmiljöer (och associerade ryggradslösa djur och fiskar) uppfattas som de största hoten mot deras försörjning och välbefinnande.

Artikel IV presenterar ett fältexperiment för att återställa sjögräs (*Halodule uninervis*), som används som föda av dugonger, i syfte att bedöma biodiversitet och kolonisering av infauna efter plantering. Två planteringsmetoder testades, inklusive en pluggmetod och en enkelskottsmetod med två olika densiteter av sjögrässkott. Resultaten visade att metoden påverkade transplantatens tillväxt med konsekvenser för abundans och sammansättning av infauna.

Resultaten av denna avhandling diskuteras i form av ett integrerat tillvägagångssätt för att förstå både globala och lokala faktorer som påverkar förändringar i utbredning av sjögräsängar i Maputo-bukten, Moçambique, samtidigt som effektiva bevarande- och förvaltningsstrategier föreslås, vilket inkluderar

användning av innovativa teknologier såsom drönare, lokalbefolkningens medverkan och återställande metoder för att stärka sjögräsets roll som ett viktigt kustekosystem.

RESUMO

As ervas marinhas são um habitat costeiro importante, pois fornece muitos serviços ecossistêmicos, incluindo alimento, abrigo e áreas de berçário para mariscos e peixes, bem como para espécies marinhas ameaçadas, como dugongos e tartarugas marinhas. No entanto, seguindo uma tendência mundial, os tapetes de ervas marinhas em Moçambique estão a sofrer uma redução em sua área devido a uma combinação de distúrbios naturais e impactos antropogénicos. O objetivo desta tese foi avaliar dois fatores relevantes que afetam os serviços ecossistêmicos das ervas marinhas, contribuindo ao mesmo tempo para o desenvolvimento de ferramentas de gestão inovadoras para a conservação, restauração e uso sustentável deste ecossistema na Baía de Maputo, Moçambique. Esta tese foca nos impactos de stressores globais (acidificação dos oceanos - AO) e locais (pesca) em dois táxons marinhos chave, como invertebrados e dugongos. A tese também visa desenvolver métodos inovadores de monitoramento utilizando drones e aprendizagem de máquina, bem como desenvolver técnicas adequadas de restauração de ervas marinhas.

O **artigo I** avalia a resposta biológica (taxa de crescimento e calcificação líquida) de um calcificador marinho a diferentes níveis de variabilidade de $p\text{CO}_2/\text{pH}$, impostas na ausência ou presença de ervas marinhas no contexto da AO como um stressor global. Os resultados mostraram que a taxa de crescimento das larvas diminuiu significativamente com a diminuição do pH médio, tanto na ausência quanto na presença de ervas marinhas. Além disso, as larvas cultivadas na presença de ervas marinhas maximizaram a calcificação durante o dia e reduziram a calcificação durante a noite. Esses resultados têm implicações significativas para a compreensão do mecanismo por trás da sensibilidade dos organismos à AO em ecossistemas costeiros variáveis.

O **artigo II** mostra a influência das atividades de pesca com redes de emalhar como um stressor local nas áreas de alimentação dos dugongos. Uma pesquisa com drones revelou uma sobreposição entre as áreas de forrageamento dos dugongos e os locais de pesca, aumentando o risco de emalhamento dos dugongos quando as redes de pesca, particularmente redes de emalhe são usadas na Ilha de Inhaca, Moçambique. Assim, foram indicadas iniciativas de gestão para controlar a atividade de pesca com redes de emalhar, com a participação da comunidade local, para apoiar futuros esforços de conservação.

Uma pesquisa sobre o conhecimento ecológico local foi realizada no **artigo III** para avaliar as percepções da comunidade, na Ilha de Inhaca, sobre stressores globais e locais nos tapetes de ervas marinhas, ao mesmo tempo que se avalia como as comunidades pesqueiras se adaptam para enfrentar potenciais mudanças futuras no ecossistema de ervas marinhas e nos serviços associados. Os resultados mostraram que a comunidade pesqueira na Ilha da Inhaca depende das atividades de pesca para sua subsistência básica, e se apercebeu da sedimentação associada a inundações como a principal causa das mudanças nas ervas marinhas, seguida por práticas de pesca destrutivas. A diminuição da proteção costeira e a perda de habitats (de invertebrados e peixes) são percebidas como as principais ameaças à sua subsistência e bem-estar.

O **artigo IV** apresenta uma experiência de campo para restaurar ervas marinhas (*Halodule uninervis*), que são utilizadas como alimento por dugongos, e para avaliar a colonização da biodiversidade de macrofauna, após o plantio. Dois métodos de plantio foram testados: método de *plug* (rolha) e método de *single shot* (dedo) com duas densidades. Os resultados mostraram que ambos métodos influenciaram positivamente o crescimento dos transplantes, com consequências positivas para a abundância e composição da macrofauna.

Os resultados desta tese são discutidos em uma abordagem integrada para entender os fatores globais e locais que causam mudanças nos tapetes de ervas marinhas na Baía de Maputo, Moçambique, propondo ao mesmo tempo estratégias eficazes de conservação e gestão que incluem o uso de tecnologias inovadoras como drones, a participação das comunidades locais e métodos de restauração para fortalecer o papel das ervas marinhas como um importante ecossistema costeiro.

LIST OF PAPERS

The thesis is based on the following papers, which are referred to in text by roman numbers.

Paper I: Cossa D., Infantes E., Dupont S. 2024. Hidden cost of pH variability in seagrass beds on marine calcifiers under ocean acidification. *Science of the Total Environment* 915:170169.

Paper II: Cossa D., Cossa M., Timba I., Nhaca J., Macia A., Infantes E. 2023. Drones and machine-learning for monitoring dugong feeding grounds and gillnet fishing. *Marine Ecology Progress Series* 716:123-136.

Paper III: Cossa D., Silas M., Chemane, A., Mubai M., Gullström M., Infantes E. Community perceptions of seagrass and dugong status: Stressors and coping strategies at Inhaca Island, Mozambique. Manuscript.

Paper IV: Cossa D., Minda C., Nhaca J., Timba I., Chunguane Y., Vetina A., Riera R., Macia A., Gullström M., Infantes E. Restoring *Halodule uninervis*: Evaluating planting methods and biodiversity. *Under review in Restoration Ecology*, submitted June 2024, Ref: REC-24-295.

Manuscripts co-authored during the PhD but not included in this thesis:

Infantes E., **Cossa D.**, Stankovic M., Panyawai J., Tuntiprapas P., Daochai C., Prathep A (2020). Dugong (*Dugong dugon*) reproductive behaviour in Koh Libong, Thailand: observations using drones. *Aquatic Mammals* 46:603–608. (17 citations).

Barcelona A., Colomer J., Serra T., **Cossa D.**, Infantes E (2023). The role epiphytes play in particle capture of seagrass canopies. *Marine Environmental Research* 192:106238.

Duvane J., **Cossa D.**, de Abreu D., Mafambissa M., Scarlet M P., Macia A., Dupont S (2024). Contrasting larval sensitivity to low pH in sea urchin inhabiting neighboring seagrass meadows. *African Journal of Marine Science*. Accepted.

Panyawai J., Stankovic M., Kaewutai K., Infantes E., **Cossa D.**, Prathep A (2024). UAVs aerial survey for seagrass and dugongs feeding trails: a case study from intertidal seagrass meadows in Mook Island and Libong Island, Trang, Thailand and Inhaca Island, Mozambique. *Under review in Remote sensing, submitted Aug 2024, Ref: remotesensing-3174032*.

TABLE OF CONTENT

BACKGROUND	1
Drivers of change	1
Seagrass meadows: benefits and threats.....	2
Drivers affecting seagrass	5
<i>Ocean acidification: Environmental variability and species response.....</i>	<i>5</i>
<i>Small-scale fisheries: Community reliance and their impact on biodiversity.....</i>	<i>7</i>
Seagrass restoration and management approaches: Toward solutions?	9
AIMS.....	11
METHODS.....	13
Study sites	13
Impact of ocean acidification and gillnet fishing.....	15
Local Ecological Knowledge (LEK)	16
Restoration methods: Management approach	18
MAIN RESULTS AND SYNTHESIS	19
Global and local drivers affecting seagrass ecosystem.....	19
Integrating local context	21
Implications for management and conservation of seagrass	23
KEY FINDINGS AND FUTURE PRESPECTIVES	27
MY CONTRIBUTIONS TO THE PAPERS.....	30
FINANCIAL SUPPORT	31
ACKNOWLEDGEMENTS.....	32
REFERENCES.....	35

BACKGROUND

Drivers of change

In nature, drivers are described as any natural and/or anthropogenic factors that directly and indirectly produce changes in an ecosystems and the services they provide (MEA 2005). Global drivers (e.g. ocean acidification and warming) are chronic, occurring gradually over extended periods of time, while local drivers (e.g. eutrophication, overfishing), can also be chronic but tend to change quickly over shorter, and more defined spatial and temporal scales (Ghedini et al. 2013; Arnberg et al. 2018). In a world facing global changes, marine ecosystems are increasingly threatened by global and local human impacts, in part as consequences of increasing human populations growth, and demanding for ocean space and resources (Halpern et al. 2015; He and Silliman 2019).

Ocean warming, ocean acidification, anoxia, sea level rise and extreme weather events are global-changes linked to increase in CO₂ concentration in the atmosphere, that have profound impact of marine biodiversity and ecosystem services (Gattuso et al. 2015; Smale et al. 2019; IPCC 2023). Furthermore, local drivers such as coastal development, fishing, nutrient inputs have also led to degradation or collapse of coastal ecosystems (He and Silliman 2019). For example, decreased water clarity due to eutrophication and warmer temperatures were pointed as the main drivers for eelgrass (*Zostera marina*) decline in Chesapeake Bay, USA, leading to profound ecological and economic consequences (Lefcheck et al. 2017).

Understanding how global and local drivers, alone or in combination, are affecting coastal ecosystems is crucial to safeguard essential ecosystem services, while supporting conservation and management strategies.

Seagrass meadows: benefits and threats

Seagrasses are a unique group of flowering plants that have adapted to survive submersed in the sea (Orth et al. 2006). They are distributed worldwide, occurring in coastal areas except in the Antarctic continent (Orth et al. 2006; Hemminga and Duarte 2000) . They can cover extensive areas often referred to as seagrass beds or seagrass meadows (Spalding et al. 2003). Seagrass consists of about 60 species belonging to 13 genera, and 5 families (Short and Coles 2001; Spalding et al. 2003). They occur mostly in areas dominated by soft substrates such as sandy or muddy sediments, which are easily penetrated by seagrass roots, but some species such as *Phyllospadix spp.*, *Posidonia oceanica* and *Thalassodendron spp.* can also be found on rocky substrates (Hemminga and Duarte 2000). Seagrass meadows are generally monospecific, particularly those in temperate zone. For example, the eelgrass *Zostera marina* is the dominant seagrass species in the northern hemisphere, while *Posidonia oceanica* is dominant in the Mediterranean Sea. In contrast, in tropical and subtropical meadows, particularly in the Indo-Pacific region may comprise up to a dozen species, encompassing the most diverse seagrass flora (Duarte et al. 2008).

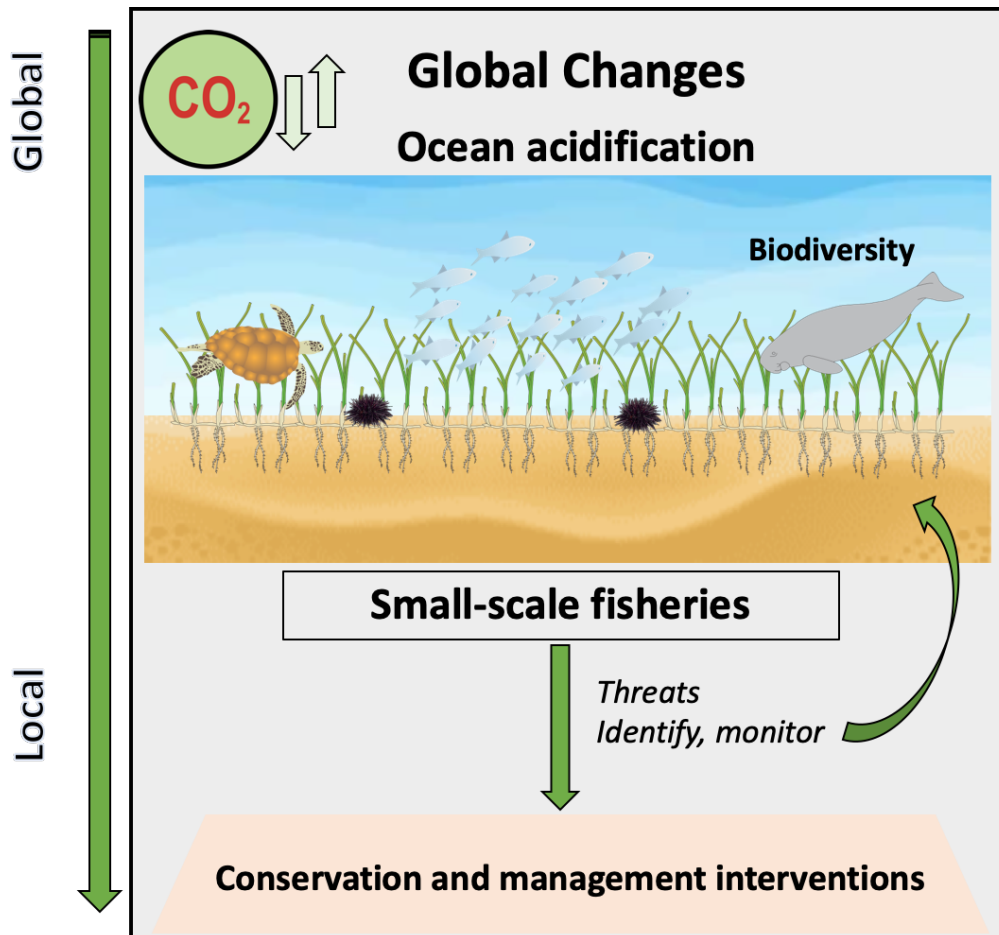
Seagrass beds are an important coastal ecosystem providing numerous ecosystem functions, including food, shelter and nursery areas for shellfish and finfish (de la Torre-Castro et al. 2014; Nordlund et al. 2016), as well as endangered marine species (such as dugongs, manatees and sea turtles) (Hughes et al. 2009). The ecological services provided by seagrass also include organic carbon production and export, nutrient cycling (Hemminga and Duarte 2000; Duarte et al. 2013b), sediment stabilization (Infantes et al. 2022a), improvement in water clarity (de los Santos et al. 2020), coastal protection by waves and storms (Barbier et al. 2008; Infantes et al. 2012) and trophic transfers to adjacent habitats (mangroves, coral reefs and others) in

tropical and temperate regions (Hemminga and Duarte 2000; Orth et al. 2006; Unsworth and Cullen 2010).

While seagrass provides vital ecosystem functions and services, it is among the most threatened ecosystem on earth. Seagrass losses have been attributed to a broad spectrum of natural and anthropogenic causes (Waycott et al. 2009). Natural disturbances include seagrass losses by geological events (e.g. coastal uplift and subsidence), meteorological events (e.g. heavy or prolonged rains, storms, hurricanes), and biological interactions (e.g. grazing, sediment bioturbation and disease) (Short and Wyllie-Echeverria 1996; Short and Neckles 1999; Alcoverro and Mariani 2002). Moreover, the increasing rate of global climate change is identified as a threat to seagrass ecosystem. Human-induced activities most affecting seagrass are those which alter water quality such as nutrient and sediment loading from runoff and sewage disposal, dredging and filling, pollution, coastal development, boating and fishing practices (Short and Wyllie-Echeverria 1996; Hughes et al. 2009; Waycott et al. 2009).

Due to these losses and the key roles that seagrass ecosystem provides, it is crucial to identify, monitor and understand the effect of threats/drivers affecting seagrass at global and local scale to enhance conservation and management efforts of this important coastal ecosystem (Box 1).

Box 1. General approach of global and local drivers addressed in present PhD thesis



This PhD aims to assess two drivers affecting seagrass meadows such as ocean acidification and small-scale fisheries. This was achieved by evaluating effect of increased concentration of CO₂ (as a global driver) and small-scale fisheries (as a local driver) on key marine taxa (marine calcifiers and dugongs), while integrating the local ecological knowledge (LEK) of seagrass-dependent coastal communities.

Drivers affecting seagrass

A large number of stressors impact seagrass meadows worldwide (e.g. global warming, ocean acidification, overfishing), affecting important ecological function and services. In this thesis, two main drivers were chosen: i) the **increasing concentration of CO₂** that leads to decrease of pH- a global process known as “ocean acidification (OA)”, which is projected to impact many marine species, particularly shell-building organisms; and ii) **small-scale fisheries**, which is a regional/local driver that has important implications for coastal ecosystems, wildlife and livelihoods.

Ocean acidification: Environmental variability and species response

The increasing ocean uptake of CO₂ (28% of anthropogenic CO₂ emissions since the 1750s) has changed carbonate chemistry cycle, resulting in reduction of pH via process known as ocean acidification (Gattuso et al. 2015). Projections shown that the ocean surface pH reduction is predicted to be ~0.3-0.5 units by year 2100, and ~0.8-1.4 units by year 2300 (Caldeira 2005). These will have profound impact on marine organisms and ecosystem functions, and as a consequence of combination of OA and other stressors (e.g. increased temperature), is expected that effects of OA may vary according to geographic region and latitudes (Figuerola et al. 2021). For example, marine calcifiers are negatively impacted through a reduction in survival, growth rate and calcification as a consequence of increased sea water temperature (Hughes et al. 2018), and ocean acidification (Cornwall et al. 2013; Figuerola et al. 2021). However, studies suggested that some marine species from short-lived phytoplankton to long-lived corals can develop mechanisms to cope with adverse environmental conditions (e.g. rapidly rising CO₂, heat waves), possessing physiological and/or phenotypical adaptations (see Boyd et al. 2016).

Variability of carbonate chemistry in coastal waters is considerably larger than in open water due to processes such as upwelling, freshwater input, eutrophication and biogeochemical (Gattuso et al. 2015). To be able to project how future ocean acidification will affect marine organisms or populations, it is necessary to consider the natural range of variability experienced in different environments (Vargas et al. 2017, 2022). Highly variable environment (e.g. coastal ecosystems) can put a given organism at the edge of their physiological tolerance making them highly sensitive to additional environmental challenges; while, local adaptation to environmental variability can lead to high level of phenotypic plasticity and the physiological ability to cope with more environmental changes (Wang et al. 2018; Strader et al. 2022). Organisms living in highly variable environments often develop a range of adaptations (e.g. change in development, behavior and allocation of resources) that allow them to maintain positive fitness (Reed et al. 2010).

The majority of experiments testing the effects of ocean acidification have been conducted using constant pH conditions and scenarios for the stable open ocean (Riebesell and Gattuso 2015). Although some recent studies have included the present natural variability in their experimental design (Dufault et al. 2012; Mangan et al. 2017; Johnson et al. 2019), there is still little information on the modulating role of the $p\text{CO}_2/\text{pH}$ natural variability on biological responses of species, particularly in coastal habitats.

Seagrass meadows are recognized as an important climate change mitigation ecosystem through their high-value ecosystem services such as coastal protection, erosion control and carbon sequestration (Short and Neckles 1999; Orth et al. 2006; Duarte et al. 2013b). They are an important CO_2 sink in the biosphere, with the excess of organic carbon produced buried into sediments (Duarte et al. 2005, 2013b). It is estimated that seagrass meadows globally can store between 4.2 and 8.4 Pg

(petagrams) of carbon in their biomass and sediment (Fourqurean et al. 2012), largely due to high net primary productivity (Fourqurean et al. 2012; Duarte 2017).

Seagrasses are also considered as possible refugia habitat for chemical changes associated with ocean acidification. Since the seawater pH increases during the daytime photosynthesis, this may periodically relieve marine organisms from the exposure to OA (Kapsenberg and Cyronak 2019), potentially enhancing their calcification rates (see Semesi et al. 2009). Further, seagrass productivity appeared to be higher under OA (Koch et al. 2013; Cox et al. 2015). Some seagrass species increase photosynthesis and growth under elevated ocean CO₂ and OA (Koch et al. 2013). This may favor the grazing rate of organisms due to increased shoot density and higher nutritional conditions of seagrass (higher nitrogen availability in conditions of increased CO₂) (see Scartazza et al. 2017). However, the idea that seagrass meadows can be a possible refugia habitat seems to be over simplistic. This ecosystem is characterized by a high variability in $p\text{CO}_2/\text{pH}$ due to the balance between the photosynthetic activity and respiration rate over the day/night cycle (Duarte et al. 2013a; Hendriks et al. 2014). Indeed, the concept that seagrass meadows can be a refugia against ocean acidification is based on the photosynthetic activity raising the pH during the day, but the increased variability and low pH during the night is often overlooked (Kapsenberg and Cyronak 2019) (**paper I**).

Small-scale fisheries: Community reliance and their impact on biodiversity

Seagrass meadows host a great abundance and diversity of fish and invertebrates (Gillanders 2006) as well as endangered species (such as dugongs, manatees and green turtles) (Hughes et al. 2009; Waycott et al. 2009). They are characterized by their structural complexity with large roots and rhizomes belowground and dense, highly structured leaf canopies aboveground. Seagrass

meadows form refuge and shelter, and provides food for marine species (Hughes et al. 2009). Seagrass habitat also supports fisheries through provision of nursery habitats, foraging areas and refuges for exploited species that are using to seagrass meadows at some stage of their life cycle (Gillanders 2006; Unsworth and Cullen 2010; Nordlund et al. 2018).

Coastal communities of many tropical and subtropical regions depend on seagrass fishery productivity for their income and food security (Nordlund and Gullström 2013; Nordlund et al. 2018) (**paper III**). A wide diversity of fishing gears such as gillnets, seine nets, collection by hand and spear guns, are used in seagrass habitats targeting a high diversity of taxa (Nordlund et al. 2018). In the Indo-Pacific region, invertebrate gleaning (collection of invertebrates or other animals from the substrate, usually by hand or with limited, simple gear) is commonly observed in the intertidal zone and support many coastal communities, although exploitation rates remain unquantified in some countries (Unsworth and Cullen 2010; Nordlund and Gullström 2013; Furkon et al. 2020; Chitará-Nhandimo et al. 2022). Fisheries are a significant threat to seagrass-associated species, leading to overexploitation or extinction (Orth et al. 2006; Hughes et al. 2009). For example, direct invertebrate exploitation on seagrass meadows can alter and reduce invertebrate biomass and diversity, which in turn can result in negative impacts on seagrass ecosystem, local economy and livelihood. (Nordlund et al. 2010; Nordlund and Gullström 2013; Chitará-Nhandimo et al. 2022).

The use of gillnets and seine nets directly on seagrass meadows have negative effects on both seagrass and associated fauna. For example, dugongs are vulnerable due to their dependence on seagrasses and are restricted to coastal habitats (Marsh et al. 1999), and entangling in mesh nets and traps set by fishers is considered as the main cause of mortality in many countries (Marsh et al. 1999, 2002; Ponnampalam et al. 2022). Direct entanglement of dugongs in gillnets has also been listed as a potential

cause for their decline in Mozambique, including also Inhaca Island (Guissamulo and Cockcroft 1997, Fernando et al. 2014). Although the number of incidental catches by fishermen is unofficially reported, these catches could pose a significant threat to the remaining population. Therefore, an appropriate monitoring approach to identify areas where fishing activity and seagrass-dependent species overlap, particularly endangered species, can support management and conservation initiatives for both seagrass and associated species (**paper II**).

Seagrass restoration and management approaches: Toward solutions?

Management strategies to mitigate local stressors can be used to increase resilience of marine ecosystems to global changes (see Scheffer et al. 2015; Green et al. 2017; Ramírez et al. 2018). Reducing local stressors will keep ecosystems within a “safe operating space (SOS)” in a future climate scenario. For example, improvement of water quality, reduction of industrial sewage, and fishery regulation are local actions to reduce seagrass damage (de los Santos et al. 2019), while also enhancing resilience of this ecosystem to global changes (Unsworth et al. 2018). These strategies should be integrated with ‘local ecological knowledge’ (LEK) that is seen as a participative involvement of the community to gathering information of ecological systems they depend on, in order to expand the understanding of the environment (Berkström et al. 2019; Jones et al. 2022). LEK is an important tool to obtain information about ecological systems on seagrass in developing countries where data and resources are lacking (Berkström et al. 2019). Understanding social-ecological systems has also significant implications for social and ecological resilience of the coupled ecosystem, and is crucial to withstanding local and global threats (Cullen-Unsworth et al. 2014). This is critically needed in order to identify and develop appropriate management

interventions, as well as coping measures that would contribute to sustainable use of resources by coastal communities (**paper III**).

Seagrass restoration is an additional management intervention that can offset the loss of seagrass ecosystem and associated ecosystem services (Van Katwijk et al. 2016). Restoring seagrass meadows can help to maintain biodiversity, support fisheries, and mitigate the impacts of climate change (e.g. through coastal protection). However, developing appropriate restoration techniques targeted to specific seagrass species is required to support long-term restoration programs. While a great effort has been placed in developing restoration methods for seagrass species, such as the temperate *Zostera marina* (e.g. Eriander et al. 2016) and the Mediterranean *Posidonia oceanica* (e.g. Alagna et al. 2019) restoration methods for tropical seagrass species and in particular in the Western Indian Ocean region requires more attention. Restoration methods for the tropical seagrass *Halodule uninervis* were explored in **paper IV**. This species is of key importance since it is an ecosystem building pioneer species and an important source of food for dugongs.

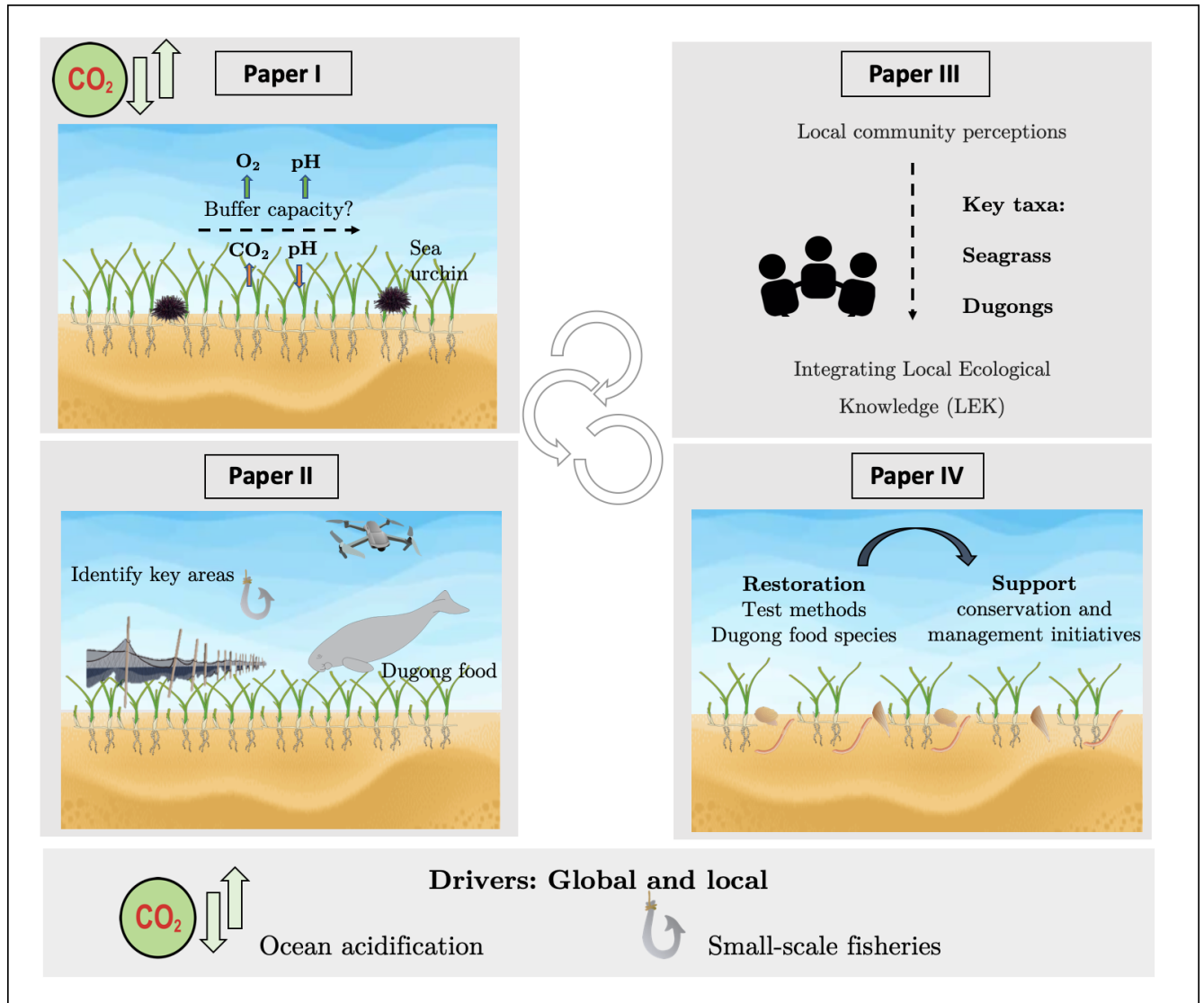
AIMS

The overall objective of the thesis is to understanding how a global driver such as the increased CO₂ concentration (ocean acidification), and a local driver such as small-scale fisheries, affect seagrass ecosystem while evaluating methods for appropriate conservation and management initiatives at Mozambique. This was achieved by studying key taxa (seagrass, sea urchins and dugongs) in both field and laboratory experiments (Box 2).

Specifically, the aims of each chapter in the thesis was:

- To evaluate the biological response (growth rate and net calcification) of a marine calcifier, to different level of variability of $p\text{CO}_2/\text{pH}$ imposed in the absence or presence of seagrass and under the context of ocean acidification **(paper I)**.
- To use an innovative cost-effective technique (drones) to identify dugong feeding hotspots based on their feeding trails while addressing the potential risk of small-scale gillnet fishing activities on their seagrass foraging habitats **(paper II)**.
- To assess local community perceptions of fisheries and climate drivers affecting seagrass and dugongs, while evaluating the community's adaptation strategies **(paper III)**.
- To develop restoration methods and assess potential changes in biodiversity after restoration to support conservation and management interventions **(paper IV)**.

Box 2: Conceptual framework of PhD



This PhD thesis looks at the effect of global and local drivers on seagrass meadows in order to safeguard the ecosystem services. Increased CO_2 is a global driver, while small-scale fisheries is described as regional/local driver, affecting marine ecosystems and organisms. In the present thesis, we evaluated how these two drivers can influence key marine taxa (seagrass, sea urchins and dugongs), while integrate the perceptions of coastal communities of fisheries and climate drivers affecting seagrass and dugongs to support appropriate conservation and management initiatives in Mozambique.

METHODS

To fulfill the aims, this PhD thesis comprises a variety of methodologies, which are described in the specific papers.

Study sites

Laboratory experiment was conducted at Kristineberg Centre for Marine Research and Innovation, Sweden to evaluate the biological responses of marine calcifiers to natural variability (photosynthesis and respiration) imposed by seagrass under ocean acidification scenarios (**paper I**). Sea urchin specimens were collected in the vicinity of Grundsund, along the Swedish west coast, and seagrass shoots in the bay of Bokevik in the Gullmars fjord.

Fieldwork was carried out at Inhaca Island, southern Mozambique and included an assessment of the impact of gillnet fishing (local driver) on dugong feeding grounds through aerial survey (drones) (**paper II**), interviews with members of local fisheries communities to gathering perceptions on fisheries and climate drivers affecting seagrass and dugongs (**paper III**) and field experiment to test restoration methods and fauna colonization capacity (**paper IV**) to support appropriate management interventions (Fig. 1).

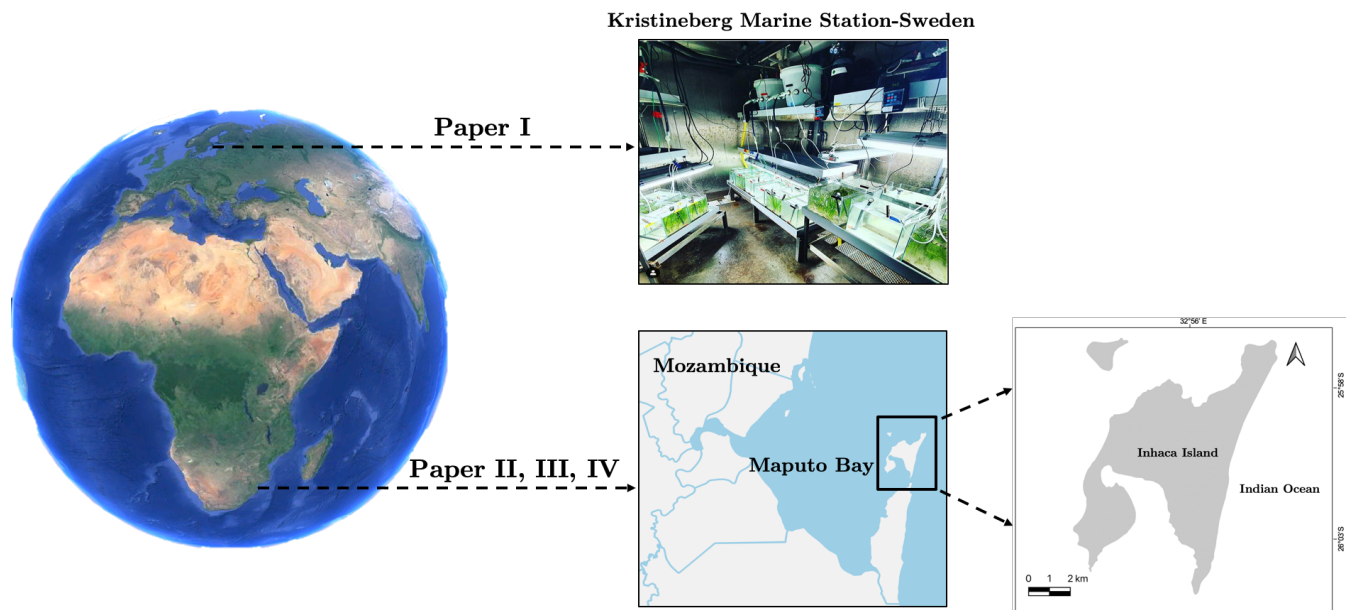


Figure 1. Map over the study sites, showing the laboratory set up at Kristineberg Marine Station, Sweden (**paper I**) and Inhaca Island located at Southern Mozambique (**paper II, III and IV**).

Inhaca Island, Maputo bay- Southern Mozambique

The studies in **paper II, III and IV** were conducted at Inhaca Island located the outer edge zone of Maputo Bay, Southern Mozambique (latitude: 25°58' - 26°05'S and longitude 32°55' - 33°00'E). At Inhaca, nine seagrass species are present: *Thalassia hemprichii*, *Halophila ovalis*, *Zostera capensis*, *Cymodocea rotundata*, *Cymodocea serrulata*, *Thalassodendron ciliatum*, *Thalassodendron leptocule*, *Syringodium isoetifolium* and *Halodule uninervis* (Bandeira et al. 2014), covering approx. 3943 ha. The tides are semidiurnal and the tidal amplitude ranges between 0.1 m and 3.9 m (de Boer and Longamane 1996). The water temperature varies within the extremes of 20–39°C, and salinity fluctuates within the range of 30–39 (mean 35) (Bandeira 2002).

Impact of ocean acidification and gillnet fishing

The biological response (growth and net calcification rates) of a marine calcifier to different levels of variability of pCO₂/pH imposed in the absence or presence of seagrass and under 4 pHs (nominal pHs = 7.4, 7.6, 7.9 and 8.2) were evaluated in the context of present natural variability and ocean acidification (**paper I**). The experiment was performed using the larvae of the sea urchin *Echinus esculentus* between August and September 2019, using a fully crossed design (4 nominal pHs x seagrass absence/presence = 8 treatments). Each treatment was replicated 3 times for a total of 24 experimental tanks. Body length (BL, in μm) and total length of all the skeletal rods (in μm) were measured using the software Image J. Relative mortality rate (RMR in day^{-1}) was calculated as coefficient of significant linear relation between relative density and time. The larvae growth rate ($\mu\text{m ln day}^{-1}$) was calculated using the coefficient of the significant logarithmic regressions between BL and time (Stumpp et al. 2011). Net calcification rate ($\mu\text{m h}^{-1}$) was estimated as the difference in total skeletal rod lengths between 2 consecutive sampling times (12 h) divided by 12. The statistical analyses were conducted using R. ANCOVA were used to test the effect of pH on growth rate and net calcification rate.

Gillnet fishing is a common small-scale fishing gear at Inhaca Island, where fishermen utilize permanently fixed fishing structures (stakes) to deploy temporary nets. To identify hotspots of dugong foraging and evaluate the influence of gillnet fishing activities on dugong feeding grounds, a drone survey was conducted monthly between June and December 2020 (**paper II**). Two locations, Saco West and Saco East in the south of Inhaca Island, were surveyed each time. All surveys were conducted during low spring tides over a period of ~ 2.5 h to cover the entire intertidal seagrass extent in each location. Aerial drone images were taken in nadir (looking straight downward), using Pix4Dcapture software, following regular transects in pre-

programmed flights at an altitude of 80 m, resulting in an image resolution of 2 cm pixel⁻¹. Collected images were imported into Pix4Dmapper desktop software to generate high-resolution aerial maps with corrected perspective, also known as orthomosaics (Infantes et al. 2022b). Dugong feeding trails and seagrass coverage were classified using an ML geo-spatial imagery platform, Picterra (<https://picterra.ch>). To develop the classifiers, detectors were trained to identify feeding trails and seagrass meadows by analyzing images using convolution neural networks (CNN), a deep-learning algorithm. To evaluate the influence of gillnet fishing, during each drone survey, the GPS position of gillnet structures was recorded using a Garmin GPSMap64s in both Saco West and Saco East. The number of stakes found within the surveyed areas was counted. The nearest distance of the gillnet fishing structures (stakes) to the dugong feeding areas was calculated per month at both sites using the ‘geopandas’ Python library (Jordahl et al. 2021).

Local Ecological Knowledge (LEK)

Local ecological knowledge is a well-recognized tool to complement scientific knowledge in order to gather information on ecological systems, resulting in better management outcomes (Berkström et al. 2019). In developing countries, where data are scarce and resources limited, local communities can provide valuable information to support appropriate conservation and management of seagrass ecosystem (e.g. de la Torre-Castro and Rönnbäck 2004; Berkström et al. 2019; Jones 2022; Wallner-Hahn and Dahlgren 2022). To gauge the perspective of local communities, semi-structured interviews were conducted between February and March 2023 (**paper III**). A total of 85 coastal fishers (randomly selected) participated in the household survey across three primary fishing communities in the Inhaca Island district, situated within Maputo Bay, Southern Mozambique: Inguane, Ribjene and Nhaquene. On the island, men

predominantly engage in fishing and cattle rearing, while women are involved in subsistence agriculture and the collection of invertebrates from seagrass meadows around the island (Nordlund and Gullström 2013). These communities rely heavily on fisheries for their livelihood, while simultaneously facing the impacts of various global and local stressors, such as sedimentation due to coastal flooding, coastal erosion and overfishing (Bandeira et al. 2021). The study aimed to gathering local community perceptions on key taxa, particularly seagrass and dugongs, by examining how local community responded to seagrass and dugong health status at the island, and regarding potential changes on seagrass ecosystems services and functions attributed to non-climate and climate drivers over the last decade (2013-2023). This was performed through interviews in a household survey contained both open-ended and closed questions. The survey was characterized by a mixture of ages of both genders, including 64 fishermen (coastal fishers) and 21 women gleaners (invertebrate collectors). The questionnaire used was adapted from a dugong and seagrasses UNEP/CMS standardized questionnaire (Pilcher et al. 2017). Additionally, the interviews captured the perceptions of the local community regarding their coping mechanisms in the face of climate changes. The questionnaire was translated into Portuguese and administrated in both Portuguese and the local language Xixanga/Xirhonga. The HHQ was taken positively among the fishing communities, and there was no rejection after permission was registered. Quantitative and qualitative approaches were used to analyse the data. Quantitative data was processed into descriptive statistics, i.e. percentages and means, used to summarise the demographic characteristics, status of seagrass and dugongs, as well as perceptions of drives and community's coping strategies. Qualitative information from the questionnaires were exposed to content analysis where the notes taken were translated into the smallest unit of meaningful information described by the respondents (Nyangoko et al. 2022) in relation their perceptions.

Restoration methods: Management approach

A seagrass restoration experiment of *Halodule uninervis* (dugong food) and fauna colonization capacity in planted plots were evaluated in order to support conservation and management interventions (**paper IV**). Two planting methods were tested at two locations in Inhaca Island: (1) the plug method where a group of shoots were transplanted within intact sediment using cores (Fonseca et al. 1998), and (2) the single shoot method, where single shoots were planted by pushing them individually into the sediment (Orth et al. 1999). To examine the potential impact of canopy sheltering and self-sustaining density interactions on plant survival, tests were conducted using two planting densities. High seagrass densities create conditions that facilitate further density increase through a positive feedbacks mechanism (Maxwell et al. 2017) potentially contributing to seagrass survival and growth. We tested two densities: low (~ 100 shoot m^2) and high (~ 300 shoots m^2). Each plug contained 10-25 shoots, with 4 plugs planted in the low-density treatment and 16 plugs in the high-density treatment. Fauna samples were collected using a PVC core ($\varnothing 11$ cm, length 15 cm) in the plots. One sediment sample was collected per plot ($n=3$ per treatment) and stored in plastic bags. Five cores were taken at the donor and sandy area, near the planting plots. In the laboratory, sediment samples were sieved through a 0.5 mm mesh, after which infauna was collected and preserved in 70 % ethanol and dyed in Bengal rose. Fauna was identified to species level, whenever possible, and counted using a stereomicroscope. A three-way analysis of variance (ANOVA) was performed to test for differences in shoot persistence and survival between the two methods (plug and single shoots) and the two densities (low and high) in both sites, and a permutational multivariate analyses of variances (PERMANOVA) was used to assess colonization capacity in restored sites.

MAIN RESULTS AND SYNTHESIS

Global and local drivers affecting seagrass ecosystem

Within seagrass ecosystems, responses to the exposure to global and local changes are expected to be taxa specific: seagrass, calcifiers, fish, marine mammals (e.g. Brown et al. 2014, 2013; Boyd et al. 2016; Marsh et al. 2017; Perry et al. 2019), and depending on local variability (e.g. Vargas et al. 2022). For example, it is well stated that calcifiers such as bivalves and sea urchins are sensitive to low pH during their early development (Stumpp et al. 2011; Dorey et al. 2013; Ventura et al. 2016). However, these studies have been performed under stable pH/pCO₂ scenarios, while the effect of fluctuating conditions such as experienced in variable ecosystems (i.e. seagrass) are still poorly resolved. **Paper I** revealed that sea urchin larvae exposed to both seagrass and ocean acidification shows differences in calcification mechanisms. Sea urchin larvae raised under constant environment (without seagrass), calcified at the same rate during the day and during the night, with a strong negative effect of low pH. In a fluctuating environment (with seagrass), the calcification rate peaked during the day when the pH was highest, showing no influence from decreasing pH, while it declined during the night, sometimes even resulting in dissolution at the lowest pH. These contrasting mechanisms had consequences for the growth and explained the observed slower growth rate in the presence of seagrass under near-future ocean acidification conditions. This suggests that living in variable environments like seagrass demands more energy than living in more stable ones supporting the hypothesis of Vargas et al. (2017, 2022). These results have significant implications for the design of experiments involving organisms in the coastal zones and for understanding their sensitivity to ocean acidification in variable coastal ecosystems, such as those found in seagrass.

Furthermore, local threats such as overfishing, use of destructive fishing gears, eutrophication have seen to increase the sensitivity of marine ecosystems to global change threats, suggesting that local management actions are needed to improve resilience of these ecosystems (see Halpern et al. 2007; Brown et al. 2014; Ramírez et al. 2018; Gissi et al. 2021). This is crucial since seagrass have been highly affected by local threats worldwide (Waycott et al. 2009), putting on risk their associated fauna. For instance, at Inhaca Island, marine calcifiers are recognized as important seagrass associated fauna for a local community, while at same time are threatening by harvesting activities (Chitará-Nhandimo et al. 2022). Moreover, other local threat is presented in results of **paper II** where a clear overlap between dugong foraging areas and fishing grounds were observed, suggesting an increasing risk of dugong entanglement when gillnets are deployed. Dugongs recently re-classified by the IUCN as Critically Endangered in Eastern Africa (Trotzük et al. 2022), are seagrass dependent, which are their main food source. However, if we look into food availability perspective, we might expected that future ocean acidification might be beneficial for dugongs, since evidence suggest that seagrass may benefit from a high CO₂ conditions (Zimmerman 2021), even though this relationship might not be straightforward and should take into account interaction of increased CO₂ with other factors such as temperature (Marsh et al. 2017). Nonetheless, looking at local scale, addressing the potential risk of dugong mortality from entanglement need to be prioritized, as fishing constitutes one of their major threat (Marsh et al. 2002). Therefore, establishing effective management initiatives to control fishing activity in the area is crucial for sustaining the small dugong population without disrupting their feeding habitat, while also protect resources such as marine calcifiers important for subsistence and livelihood of the local communities. These results also reinforce the importance of identify and understanding global and local drivers affecting seagrass ecosystem looking into local context, while also highlight the importance of minimize local threats, that would help

to compensate the possible effects of future global scenarios (such as ocean acidification).

Integrating local context

More than 60% of the human population in Mozambique live along coastal areas and rely on coastal natural resources for their livelihoods (Vicente and Bandeira 2014). Seagrass meadows are one of the most important habitats and a relatively easily accessible coastal ecosystem. Coastal invertebrate fisheries (achieved mainly by women and children) use seagrass habitats as important fishing ground for their basic livelihood. For example, a recent survey showed that about 7.7 and 7.6 tons of invertebrates (mostly molluscs) were collected in seagrass meadows in the peak catch weeks (spring low tides) in Maputo Bay and Inhambane Bay, southern Mozambique, respectively (Chitará-Nhandimo et al. 2022). These harvesting activities performed in seagrass meadows are made with low technology, self-employed people targeting a wide variety of invertebrate species. Moreover, seagrass meadows at Inhaca Island sustain a diversity of fish and are important for fishery productivity (Gullström and Dahlberg 2004). Results of **paper III** reinforce that seagrass is important for the local community at Inhaca Island and that the locals are generally aware of seagrass threats and impacts for their wellbeing. The fishery communities at the Island perceived decreased coastal protection and loss of habitats (for invertebrates and fish) as the most affected seagrass ecosystem services due to climate change and variability in the last 10 years (2013-2023) (**paper III**). The use of destructive fishing gears was also noticeable a threat to seagrass, primarily beach seine and gillnets, which might also pose a risk to dugongs' foraging activity (**papers II-III**). Previous studies in the western Indian Ocean region have also reported impacts of climate and non-climate stressors on seagrass ecosystem services (SES). Decrease of coastal protection due to

coastal flooding (e.g. Amone-Mabuto et al. 2023), decline of fish and invertebrate catches due to the use of destructive fishing gears and/or overfishing (e.g. Nordlund and Gullström 2013; Chitará-Nhandimo et al. 2022; Jones et al. 2022; Wallner-Hahn and Dahlgren 2022; Rakotonjanahary et al. 2024), and habitat degradation due to sea urchin overgrazing (e.g. Wallner-Hahn and Dahlgren 2022; Rakotonjanahary et al. 2024) are examples of where SES have been affected with consequences on food security and wellbeing of coastal people.

Ocean acidification was an unknown risk, and therefore not recognized by the fishery communities at Inhaca Island, in part due to their lack of knowledge, but results of **paper I** suggests that growth and calcification of marine calcifiers (sea urchins) inhabiting seagrass habitat might be compromised under OA conditions. These threats on seagrass ecosystems at the Island are even more alarming since local communities showed limited coping strategies to deal with local and global changes impacts (**paper III**). **Papers III-IV** discussed some actions to safeguard seagrass ecosystem functions and services at the Island (see *management implication section below*). First, involvement of the local community through appropriate education and awareness programs about seagrass conservation, while encouraging alternative livelihoods initiatives such as eco-tourism at the Island (**paper III**), is highlighted. Secondly, developing of seagrass restoration methods is highlighted because this can be seen as a potential reversal of seagrass decline due to anthropogenic activities, and also a way to safeguarding key seagrass ecosystem services (e.g dugongs food), as support for management interventions (**paper IV**)

Implications for management and conservation of seagrass

The results of **paper II** revealed that use of destructive fishing activities pose risk to seagrass dependent fauna (i.e. dugongs) at Inhaca Island, while the results of **paper III** reinforce the dependence of communities on fishing activities, reflected on limited strategies to cope with the impacts of global change. Inhaca is part of Maputo National Park, officially declared in 2021 for protection, conservation and sustainable use of biological diversity. However, only 5% of the marine area inside the park are fully protected, and most of the seagrass areas are in the category of *marine areas of controlled use* where subsistence fishing is allowed, although with some restrictions (e.g. beach seine and gillnets are not allowed in some sites) (ANAC 2021).

In Mozambique, steps towards developing policies and legislation for the protection and management of natural resources are notable. Indeed, the policy framework comprises important instruments for protection of marine and coastal habitats, such as The Decree 89/2017 regulating the law on protection, conservation and sustainable use of biodiversity, Environmental Act 20/97, and the Fisheries Act 22/2013. However, the enforcement of the laws is still deficient and to date there is no specific seagrass management plan. Therefore, there are challenges to protect coastal ecosystems, safeguard benefits of local communities, while also withstanding global change.

The present thesis discusses some management interventions of seagrass ecosystem, while also being aligned with global agendas such as the ongoing sustainable development goals (SDG), particularly SDG 14, *Life below water*, designed to conserve and sustainably use marine resources for sustainable development. Specifically, results of **papers II-IV** highlight three management initiatives:

1. Drone and AI-driven seagrass monitoring for conservation in Mozambique and the WIO region

The adoption of innovative technologies such as drones to support monitoring and mapping of seagrass, associated fauna and threats (fishing activities) would be highly beneficial. Drones are an emerging cost-effective technology which provide accurate and large data sets in a short period compared to traditional survey methods, and thus can be applied in a range of marine science surveys (e.g. Duffy et al. 2018; Torres et al. 2018; Infantes et al. 2020; Yamato et al. 2021). Moreover, the combined use of drones with machine learning methods has expanded in different scientific areas and is gaining interest in long-term monitoring programs. Here, drones and machine learning proved to be an effective tool for identifying dugong feeding hotspots and mapping seagrass at meadow scale (**paper II**), which can contribute to conservation strategy of the species. Effective mapping and monitoring of seagrass are still challenging in many places (Nordlund et al. 2024; Unsworth et al. 2019), and even more critical in developing countries due to lack of resources. Therefore, the results of the thesis are crucial to support management of seagrass meadows in Mozambique, and in the Western Indian Ocean (WIO) region.

2. Integrating Local Ecological Knowledge for sustainable marine resource management in Mozambique

The integration of local ecology knowledge (LEK) to support natural resource management will be highly beneficial. Results of **paper II** highlight the establishment of effective management initiatives to control gillnet fishing activity in the area for sustaining the small dugong population without disrupting their

feeding habitat. Although not directly assessed in the present thesis, sustainable harvesting activities should also be prioritized to safeguarding the invertebrate communities of seagrass meadows, important for the local fishery community (**paper III**). Effective management interventions can be achieved by integration of local community knowledge, and have also been reported in other western Indian Ocean studies (e.g. de la Torre-Castro et al. 2014; Berkström et al. 2019; Chitará-Nhandimo et al. 2022; Jones et al. 2022). Developing appropriate education and awareness programs targeting seagrass conservation, and promoting Locally Managed Marine Areas (LMMAs) (Chitará-Nhandimo et al. 2022), to support sustainable resources uses, for example, through establishing community-managed no-take zones might be one of the initiatives. Alternative livelihood initiatives such as eco-tourism at the Island should also be effectively promoted. Most of the tourism activity at the Island are associated to South African cruise ships, which are run in a specific periods, and with involvement of a small local group of operators, which means that the local community is not engaged in tourism. Fishing is thus still the mainly reported option for their livelihood (**paper III**).

3. Restoration strategies for seagrass ecosystems: Enhancing biodiversity and climate resilience in Mozambique

Effective restoration approaches for seagrass ecosystems are also crucial to support management interventions (**paper IV**). Ecosystem restoration is supported by the UN Decade 2021-2030 that aims to prevent, halt and reverse the degradation of ecosystems. Developing restoration methods aimed for large-scale planting are key to conserve seagrass ecosystems in Mozambique. Restoring seagrass meadows can contribute to maintaining (or recovering) biodiversity, supporting fisheries, and mitigating the impacts of climate change (e.g. through coastal protection) (Box 3).

Box 3: Seagrass restoration methods

The first restoration experiments of seagrass took place in Europe in 1939. However, since the 1960s, restoration experiments have increasingly grown worldwide using different seagrass species (Fonseca 1998; Paling et al. 2009). Seagrass restoration is an important tool to offset the loss of habitat ecosystem biodiversity and ecosystem services (van Katwijk et al. 2016). In the Indo Pacific region, where seagrass meadows are important fishery areas, and seagrass losses might have negative consequences for food security (Unsworth and Cullen 2010), thus, restoration programs may contribute to seagrass recover while safeguarding important ecosystem services (e.g. recovering of biodiversity, coastal protection).

Developing appropriate restoration methods is essential for sustaining successful long-term restoration programs (Van Katwijk et al. 2016; Tan et al. 2023; Nordlund et al. 2024). Use of plug method, i.e. when plants are transplanted rooted in their original sediment; single shoots, i.e. when individual leaf washed free of sediments are transplanted with/without anchoring method, and seagrass seeds or seedlings (Phillips 1990), have been widely attempted with varying degrees of success at temperate, sub-tropical (e.g. Orth et al. 2010, 2012; Eriander et al. 2016; Infantes et al. 2016; Tan et al. 2023), and tropical regions (e.g. Uku et al. 2022; Wegoro et al. 2022). Results of **paper IV** demonstrates the feasibility of restoring the pioneer narrow leaf *Halodule uninervis* at Inhaca Island using both plug and single shoot methods, with high-density planting as the most efficient results (Fig. 2). Results also indicate a rapid fauna colonization on the planted sites. These findings are particularly significant because restoration efforts focused on *H. uninervis* could benefit dugong populations by recovering their feeding grounds if they are lost. However, while restoration approaches prove valuable in managing coastal areas, conserving existing seagrass should remain the primary focus.

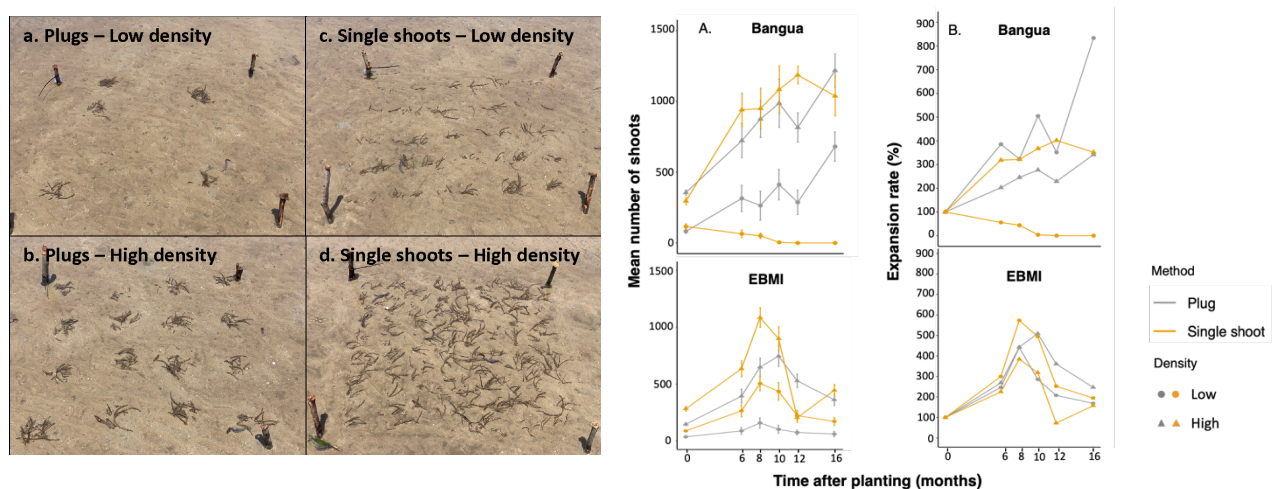


Figure 2. Left panel: Initial planting configurations in the seagrass restoration experiment using sediment plugs (a, b) and single shoots (c, d), at low and high seagrass shoot densities. **Right panel: A.** Average number of seagrass shoots per m², and **B.** Expansion rate/ survival (%) of seagrass shoots after planting using both the plug and single shoot methods during the experimental period. Two initial planting densities were used (low: 100 shoot m², and high: 300 shoot m²) at the two study sites, i.e. Bangua and EBMI.

KEY FINDINGS AND FUTURE PRESPECTIVES

Conclusion

The results of this thesis contribute to the understanding of the impact of both global and local drivers of changes in seagrass meadows in Mozambique, while proposing effective conservation and management strategies, to enhance the role of seagrass as an important coastal ecosystem. The findings show that both ocean acidification and small-scale fisheries (i.e use of destructive fishing gear) threaten seagrass and their associated fauna, and thus management interventions are urgently needed. Since mitigation measures to withstanding global changes impacts, such as future acidification is challenging, the results highlight the need of local management actions in order to increase resilience of the seagrass ecosystem. Results also highlight the importance of integration of local communities' knowledge and scientific knowledge, while also showing the importance of appropriate restoration approaches to safeguarding key ecosystem services, and support seagrass management and restoration in Mozambique.

- **Paper I** demonstrated that seagrass may not act as refuge under ocean acidification for marine calcifiers as extreme low pH during the night may be more detrimental than the relief of high pH during the day. This study also reinforces that living in variable environments such as seagrass requires more energy than living in a more stable one. Larvae exposed to seagrass and ocean acidification showed slower growth rate as compared to those exposed to ocean acidification in absence of seagrass, and a clear difference in calcification mechanisms in sea urchin larvae raised in constant or fluctuating conditions

(presence of seagrass) were observed. This study focused on physiological mechanisms used by calcifiers. Future studies are needed to integrate ecological processes since in the field, hydrodynamic conditions and other environmental parameters lead to more complex and dynamic variability in the seawater physico-chemical conditions. Furthermore, understanding the combined effect of ocean acidification with local stressors (e.g. fishing) in a multi-stressor perspective would be complex but highly needed to support the management interventions of seagrass at Mozambique, since marine calcifiers are crucial for food security.

- **Paper II** showed that use of gillnet fishing might pose a risk to a small dugong population at Inhaca Island since a clear overlap of dugong foraging areas and gillnet fishing ground were observed. Therefore, this study highlighted the establishment of effective management strategies to monitor and control the use of gillnets, thereby avoiding the accidental bycatch of dugongs. This should be achieved through active participation of local communities including compliance with fishing regulations. Moreover, results in **paper III** showed that small-scale fisheries are crucial for local communities at Inhaca Island, and that they have limited livelihood alternatives. Therefore, the development of seagrass management plan with involvement of local stakeholders (i.e. local authorities, community members, academia), will be highly beneficial for the improvement of sustainable use of seagrass ecosystem in the area.
- Finally, **papers II, III and IV** highlight the importance of adoption of effective management interventions. **Paper II** proved that the use of drones and machine learning is effective to detect dugong feeding grounds through indirect surveying of indicators of feeding activity, and thus can be applied as

important monitoring tool in intertidal seagrass meadows. **Paper III** showed the integration of local community knowledge and scientific knowledge to understand global and local threats is crucial for appropriate management decisions. Finally, **paper IV** showed that the use of restoration methods are crucial to support long-term restoration programs, while also safeguard important seagrass ecosystem services (i.e enhancing dugong food, and biodiversity).

MY CONTRIBUTIONS TO THE PAPERS

Paper I: Hidden cost of pH variability in seagrass beds on marine calcifiers under ocean acidification.

DC, SD and EI conceived the ideas and designed the experiment; DC, SD and EI collected the data; SD and DC analysed the data; DC and SD led the writing of the manuscript.

Paper II: Drones and machine-learning for monitoring dugong feeding grounds and gillnet fishing.

DC, EI and AM conceived the ideas and designed methodology; DC, MC, IT and JN collected the data; DC analysed the data; DC and EI led the writing of the manuscript.

Paper III: Climate change and small-scale fisheries in seagrass meadows: A social survey at Maputo Bay, Mozambique.

DC, EI, and MG conceived the ideas; DC, EI, MG, MS, MM designed the methodology; DC, EI, and AC collected the data; DC, AC, and MS analysed the data; DC led the writing of the manuscript.

Paper IV: Restoring narrowleaf seagrass (*Halodule uninervis*): Impact on biodiversity and dugong habitat.

DC, EI and AM conceived the ideas and designed methodology; DC, MC, JN, IT, YC, and AV collected the data; DC, EI, MG, analysed the data; DC and EI led the writing of the manuscript.

FINANCIAL SUPPORT

This thesis was funded by the Swedish Cooperation Agency (SIDA) through the bilateral program with Eduardo Mondlane University (Mozambique).

ACKNOWLEDGEMENTS

As I conclude this cycle, which I refer as ‘the most challenging, powerful and incredible journey of my last 5 years’, I express my deepest gratitude to God for allowing me to stay steadfast throughout this journey, and to all awesome people who contributed to this outcome. I owe you all!

First, I would like to thank my supervisor, **Eduardo Infantes**, who has been more than a mentor throughout this journey. With you, I learned to pay attention to detail, to be consistent, and to persist. You were always present, while providing me with all the necessary tools to be independent. So, I will always be grateful. I remember your first trip to Mozambique, where we sat in front of the beach at Inhaca Marine Station with a notebook, discussing science and talking about seagrasses. From that moment, I realized this was a path of no return; I had to match your 'pace'. So, thank you for the trust, friendship, laughter, and all the support during the ups and downs. I hope to continue collaborating with you in the future (and ensuring you get the Mozambican *Piri Piri* ☺). My gratitude also extends to your family.

I express my gratitude to **Sam Dupont**, my co-supervisor, for whom I greatly esteem, and who immediately embraced the idea of a 'crazy' experiment on ocean acidification and seagrass. I will definitely carry this experience with me for life (it was intense work but very productive and fun). Thank you for the partnership, the teachings, and all the opportunities throughout this journey. I would also like to say thanks to you and Floor for the fun moments we shared. **Adriano Macia**, *meu Prof.*, thank you for this opportunity. This would not have been possible without your support, so I am grateful for believing in me from the beginning of this journey. Thank you also for the support at my home institution; it was crucial for maintaining my focus during my stay in Sweden. I would also like to thank **Matz Berggren**, who, with great kindness and efficiency, provided essential support to ensure the progress of this project.

Martin Gullström, thank you for being there for me. I met you before starting this journey, during a field campaign at Inhaca, and I am grateful that we have continued working together. Thank you for all your support, partnership, and advice.

Thank you **Helle Ploug**, my examiner for your availability whenever I needed your help.

I would like to thank all the wonderful people in the administration, especially **Liliana, Sheila, Therese, and Monica**, for taking care of all the paperwork over the years. Thank you for all support.

My gratitude extends especially to **Daniela de Abreu** for friendship, advice, and for taking care of the courses (it's done Dani); to **Salomão Bandeira, Almeida Guissamulo, Aidate Mussagy, Angelina Martins, Perpétua Scarlet, Eunice Ribeiro, Telma Magaia, Ivan Nerantzoulis** and all my colleagues from the Department of Biological Sciences of Eduardo Mondlane University for all support throughout this journey. A special thanks goes to **Jossias Duvane and Mizeque Mafambissa**, *meus companheiros de batalha*. Thank you for all your support and friendship. I also extend my thanks to **Erica Tovela, Irina de Sousa, Vilma Machava, Sónia Guilundo, Mariamo Machado, Hugo Mabilana and Manuela Amone**, colleagues and PhD friends, for sharing in the ups and downs of the journey (we did our best ☺).

A special thanks to my collaborators, **Minda Cossa, Yudmila Chunguane, Ilário Timba, Jeremias Nhaca, Alice Chemane**, for all support during fieldwork and for the enjoyable moments we shared at Inhaca Island. I also extend my thanks to **Mito, Castigo, Graça, Sergio Fuca** and all the staff at Inhaca Marine Biological Station for your support during my fieldwork. I am grateful to **Marlino Mubai and Mathew Silas** for your assistance with the social survey, and to **Alvaro Vetina** for your support during lab work.

Aina, Carrie, and Elena, my dear friends who made my stays in Sweden unforgettable, thank you so much. You are very special to me, and I am grateful for all your support. **Carl Kristensson** (my *Swedish father*), thank you for all the support and fun moments. I also want to thank **Alba, Leon, Roland, Bengt, Jessica, Andrea, Petra** and all my colleagues at Kristineberg Marine Station, and Gothenburg University as well as the friends I made during my stay in Sweden. I appreciate all of your support.

Aos meus amigos que estiveram sempre ao meu lado, apoiando-me incondicionalmente: às *virtuosas* (**Katya, Dulce, Denise e Heloísa** e suas famílias), aos meus *bebiologos* (**Pipocas, Denise, Vera e Vanda** e suas famílias), **Alima, Simplício e Benelsa**, ao *DCB* *boa cena* (são muitos ☺) e todos que tornaram esta caminhada especial e garantiram o meu “stop stress”, muito obrigada por tudooo!

Ao **Márcio**, a **Noémia**, **Félix** e toda família Madussa, o meu muito obrigada.

Timothy Dykman, my mentor and friend, your memory continues to inspire and guide me.

A minha família amada: meus pais, **Francisco Cossa** (meu Mr. Cossa), **Judite Mandua** (minha estrela guia, minha luz, onde quer que estejas, sei que olhas por mim), **Salomé Pinto** (minha Miss). Aos meus irmãos, **Misete, Esaú, Segone, Eric, Dorcas, Vania, Miranda** e aos meus amados sobrinhos. Às minhas tias, **Filipa, Ana, Yoya, Olguita, Alda, Lucinha, Aldinha, Tucha** e toda família **Cossa e Mandua**. Muito obrigada pelo suporte, compreensão, carinho e amor. Love you all☺

Kiomy, minha filha, a minha força vem de ti; tudo isto é por ti. A mamã ama-te incondicionalmente!♥

REFERENCES

- Administração Nacional das Áreas de Conservação (ANAC). (2021). *Management plan of Maputo National Park for the Period 2022 - 2032*.
- Alagna, A., D'Anna, G., Musco, L., Vega Fernández, T., Gresta, M., Pierozzi, N., Badalamenti, F. (2019). Taking advantage of seagrass recovery potential to develop novel and effective meadow rehabilitation methods. *Marine Pollution Bulletin* 149, 110578.
- Alcoverro, T., Mariani, S. (2002). Effects of sea urchin grazing on seagrass (*Thalassodendron ciliatum*) beds of a Kenyan lagoon. *Marine Ecology Progress Series* 226, 255–263.
- Amone-Mabuto, M., Mubai, M., Bandeira, S., Shalli, M.S., Adams, J.B., Lugendo, B.R., Hollander, J. (2023). Coastal community's perceptions on the role of seagrass ecosystems for coastal protection and implications for management. *Ocean & coastal management* 244, 106811.
- Arnberg, M., Calosi, P., Spicer, J.I., Taban, I.C., Bamber, S.D., Westerlund, S., Vingen, S., Baussant, T., Bechmann, R.K., Dupont, S., (2018). Effects of oil and global environmental drivers on two keystone marine invertebrates. *Scientific Reports* 8, 17380.
- Bandeira, S.O. (2002). Diversity and distribution of seagrasses around Inhaca Island, southern Mozambique. *South African Journal of Botany* 68, 91–198.
- Bandeira, S., Gullström, M., Balidy, H., Samussone, D., Cossa, D. (2014). Seagrass meadows in Maputo Bay. In: The Maputo Bay ecosystem (eds. Bandeira, S.O, Paula, J.P.M.). Western Indian Ocean Marine Science Association (WIOMSA), Zanzibar Town. pp. 147–169.

- Bandeira, S., Amone-Mabuto, M., Chitará-Nhandimo, S., Scarlet, M.P., Rafael, J. (2021). Impact of cyclones and floods on seagrass habitats. In: *Cyclones in Southern Africa: Volume 3: Implications for the Sustainable development goals*. Sustainable development goals series (eds. Nhamo, G., Chikodzi, D.). Springer International Publishing, Cham. pp. 279–288.
- Barbier, E.B., Koch, E.W., Silliman, B.R., Hacker, S.D., Wolanski, E., Primavera, J., Granek, E.F., Polasky, S., Aswani, S., Cramer, L.A., Stoms, D.M., Kennedy, C.J., Bael, D., Kappel, C.V., Perillo, G.M.E., Reed, D.J. (2008). Coastal ecosystem-based management with nonlinear ecological functions and values. *Science* 319, 321–323.
- Berkström, C., Papadopoulos, M., Jiddawi, N.S., Nordlund, L.M. (2019). Fishers' local ecological knowledge (LEK) on connectivity and seascape management. *Frontiers in Marine Science* 6, 130.
- Boyd, P.W., Cornwall, C.E., Davison, A., Doney, S.C., Fourquez, M., Hurd, C.L., Lima, I.D., McMin, A. (2016). Biological responses to environmental heterogeneity under future ocean conditions. *Global Change Biology* 22, 2633–2650.
- Brown, C.J., Saunders, M.I., Possingham, H.P., Richardson, A.J. (2013). Managing for interactions between local and global stressors of ecosystems. *PLOS ONE* 8, e65765.
- Brown, C.J., Saunders, M.I., Possingham, H.P., Richardson, A.J. (2014). Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Diversity and Distributions* 20, 538–546.
- Caldeira, K. (2005). Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research* 110, C09S04.

- Chitará-Nhandimo, S., Chissico, A., Mubai, M.E., Cabral, A. de S., Guissamulo, A.,
Bandeira, S. (2022). Seagrass invertebrate fisheries, their value chains and the
role of LMMAs in sustainability of the coastal communities—Case of southern
Mozambique. *Diversity* 14, 170.
- Cornwall, C.E., Hepburn, C.D., McGraw, C.M., Currie, K.I., Pilditch, C.A., Hunter,
K.A., Boyd, P.W., Hurd, C.L. (2013). Diurnal fluctuations in seawater pH
influence the response of a calcifying macroalga to ocean acidification.
Proceedings of the Royal Society B 280, 20132201.
- Cox, T.E., Schenone, S., Delille, J., Díaz-Castañeda, V., Alliouane, S., Gattuso, J.,
Gazeau, F. (2015). Effects of ocean acidification on *Posidonia oceanica*
epiphytic community and shoot productivity. *Journal of Ecology* 103, 1594–
1609.
- Cullen-Unsworth, L.C., Nordlund, L.M., Paddock, J., Baker, S., McKenzie, L.J.,
Unsworth, R.K.F. (2014). Seagrass meadows globally as a coupled social–
ecological system: Implications for human wellbeing. *Marine Pollution Bulletin*
83, 387–397.
- de Boer, L. W.F., Longamane, F. (1996). The exploration of intertidal food resources
in Inhaca bay, Mozambique, by shorebirds and humans. *Biological
Conservation* 78: 295-303
- de la Torre-Castro, M., Rönnbäck, P. (2004). Links between humans and seagrasses—
an example from tropical East Africa. *Ocean & coastal management* 47, 361–
387.
- de la Torre-Castro, M., Di Carlo, G., Jiddawi, N.S. (2014). Seagrass importance for a
small-scale fishery in the tropics: The need for seascape management. *Marine
Pollution Bulletin* 83, 398–407.
- de los Santos, C.B., Krause-Jensen, D., Alcoverro, T., Marbà, N., Duarte, C.M., Van
Katwijk, M.M., Pérez, M., Romero, J., Sánchez-Lizaso, J.L., Roca, G.,
Jankowska, E., Pérez-Lloréns, J.L., Fournier, J., Montefalcone, M., Pergent, G.,

- Ruiz, J.M., Cabaço, S., Cook, K., Wilkes, R.J., Moy, F.E., Trayter, G.M.-R., Arañó, X.S., De Jong, D.J., Fernández-Torquemada, Y., Auby, I., Vergara, J.J., Santos, R. (2019). Recent trend reversal for declining European seagrass meadows. *Nature Communications* 10, 3356.
- de los Santos, C.B., Olivé, I., Moreira, M., Silva, A., Freitas, C., Araújo Luna, R., Quental-Ferreira, H., Martins, M., Costa, M.M., Silva, J., Cunha, M.E., Soares, F., Pousão-Ferreira, P., Santos, R. (2020). Seagrass meadows improve inflowing water quality in aquaculture ponds. *Aquaculture* 528, 735502.
- Dorey, N., Lançon, P., Thorndyke, M., Dupont, S. (2013). Assessing physiological tipping point of sea urchin larvae exposed to a broad range of pH. *Global Change Biology* n/a-n/a.
- Duarte, C.M., Middelburg, J.J., Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2, 1-8.
- Duarte, C.M., Dennison, W.C., Orth, R.J.W., Carruthers, T.J.B. (2008). The charisma of coastal ecosystems: Addressing the imbalance. *Estuaries and Coasts: J CERF* 31, 233–238.
- Duarte, C.M., Hendriks, I.E., Moore, T.S., Olsen, Y.S., Steckbauer, A., Ramajo, L., Carstensen, J., Trotter, J.A., McCulloch, M. (2013a). Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. *Estuaries and Coasts* 36, 221–236.
- Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., Marbà, N. (2013b). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Clim Change* 3, 961–968.
- Duarte, C.M. (2017). Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. *Biogeosciences* 14, 301–310.

- Dufault, A.M., Cumbo, V.R., Fan, T.-Y., Edmunds, P.J. (2012). Effects of diurnally oscillating p CO₂ on the calcification and survival of coral recruits. *Proceedings of the Royal Society B* 279, 2951–2958.
- Duffy, J.P., Pratt, L., Anderson, K., Land, P.E., Shutler, J.D. (2018). Spatial assessment of intertidal seagrass meadows using optical imaging systems and a lightweight drone. *Estuarine Coastal Shelf Science* 200:169–180
- Eriander, L., Infantes, E., Olofsson, M., Olsen, J.L., Moksnes, P.-O. (2016). Assessing methods for restoration of eelgrass (*Zostera marina* L.) in a cold temperate region. *Journal of Experimental Marine Biology and Ecology* 479, 76–88.
- Fernando, S., Bandeira, S., Guissamulo, A. (2014). Seagrass grazing by dugongs: Can habitat conservation help protect the dugongs? In: The Maputo Bay ecosystem (eds. Bandeira, S.O, Paula, J.P.M.). Western Indian Ocean Marine Science Association (WIOMSA), Zanzibar Town. pp. 223–227.
- Figuerola, B., Hancock, A.M., Bax, N., Cummings, V.J., Downey, R., Griffiths, H.J., Smith, J., Stark, J.S. (2021). A review and meta-Analysis of potential impacts of ocean acidification on marine calcifiers from the Southern Ocean. *Frontiers in Marine Science* 8, 584445.
- Fonseca, M.S., Kenworthy, W.J., Thayer, G.W. (1998). Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. *NOOA Coastal Ocean Program, Decision Analysis Series No. 12*.
- Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M.A., Apostolaki, E.T., Kendrick, G.A., Krause-Jensen, D., McGlathery, K.J., Serrano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5, 505–509.
- Furkon, Nessa, N., Ambo-Rappe, R., Cullen-Unsworth, L.C., Unsworth, R.K.F. (2020). Social-ecological drivers and dynamics of seagrass gleaning fisheries. *Ambio* 49, 1271–1281.

- Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W.W.L., Howes, E.L., Joos, F., Allemand, D., Bopp, L., Cooley, S.R., Eakin, C.M., Hoegh-Guldberg, O., Kelly, R.P., Pörtner, H.-O., Rogers, A.D., Baxter, J.M., Laffoley, D., Osborn, D., Rankovic, A., Rochette, J., Sumaila, U.R., Treyer, S., Turley, C. (2015). Contrasting futures for ocean and society from different anthropogenic CO₂ emissions scenarios. *Science* 349, aac4722.
- Ghedini, G., Russell, B., Connell, S. (2013). Managing local coastal stressors to reduce the ecological effects of ocean acidification and warming. *Water* 5, 1653–1661.
- Gillanders, B.M. (2006). Seagrasses, fish, and fisheries. In: Seagrass biology, ecology and conservation (eds. Larkum, A.W.D., Orth, R.J., Duarte, C.M.). Springer. pp 503-536.
- Gissi, E., Manea, E., Mazaris, A.D., Fraschetti, S., Almpnidou, V., Bevilacqua, S., Coll, M., Guarnieri, G., Lloret-Lloret, E., Pascual, M., Petza, D., Rilov, G., Schonwald, M., Stelzenmüller, V., Katsanevakis, S. (2021). A review of the combined effects of climate change and other local human stressors on the marine environment. *Science of the Total Environment* 755, 142564.
- Green, A.J., Alcorlo, P., Peeters, E.T., Morris, E.P., Espinar, J.L., Bravo-Utrera, M.A., Bustamante, J., Díaz-Delgado, R., Koelmans, A.A., Mateo, R., Mooij, W.M., Rodríguez-Rodríguez, M., Van Nes, E.H., Scheffer, M. (2017). Creating a safe operating space for wetlands in a changing climate. *Frontiers in Ecology and the Environment* 15, 99–107.
- Guissamulo, A.T., Cockcroft, V.G. (1997). Dolphin and dugong occurrence and distribution and fisheries interactions in Maputo and Bazaruto Bays, Mozambique. Scientific Committee Report SC/49/SM24. International Whaling Commission, London.

- Gullström, M., Dahlberg, M. (2004). Fish community structure of seagrass meadows around Inhaca Island, Southern Mozambique. Minor field study. Sweden, Uppsala University.
- Halpern, B.S., Selkoe, K.A., Micheli, F., Kappel, C.V. (2007). Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conservation Biology* 21, 1301–1315.
- Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J.S., Rockwood, R.C., Selig, E.R., Selkoe, K.A., Walbridge, S. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications* 6, 7615.
- He, Q., Silliman, B.R. (2019). Climate change, human impacts, and coastal ecosystems in the anthropocene. *Current Biology* 29, R1021–R1035.
- Hemminga, M.A., Duarte, C.M.C. (2000). Seagrass ecology. Cambridge University Press, Cambridge.
- Hendriks, I.E., Olsen, Y.S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T.S., Howard, J., Duarte, C.M. (2014). Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences* 11, 333–346.
- Hughes, A.R., Williams, S.L., Duarte, C.M., Heck, K.L., Waycott, M. (2009). Associations of concern: declining seagrasses and threatened dependent species. *Frontiers in Ecology and the Environment* 7, 242–246.
- Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Liu, G., McWilliam, M.J., Pears, R.J., Pratchett, M.S., Skirving, W.J., Stella, J.S., Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature* 556, 492–496.
- Infantes, E., Orfila, A., Simarro, G., Terrados, J., Luhar, M., Nepf, H. (2012). Effect of a seagrass (*Posidonia oceanica*) meadow on wave propagation. *Marine Ecology Progress Series* 456, 63–72.

- Infantes, E., Eriander, L., Moksnes, P. (2016). Eelgrass (*Zostera marina*) restoration on the west coast of Sweden using seeds. *Marine Ecology Progress Series* 546, 31–45.
- Infantes, E., Cossa, D., Stankovic, M., Panyawai, J., Tuntiprapas, P., Daochai, C., Prathep, A. (2020). Dugong (*Dugong dugon*) Reproductive Behaviour in Koh Libong, Thailand: Observations Using Drones. *Aquatic Mammals* 46, 603–608.
- Infantes, E., Hoeks, S., Adams, M., Van Der Heide, T., Van Katwijk, M., Bouma, T. (2022a). Seagrass roots strongly reduce cliff erosion rates in sandy sediments. *Marine Ecology Progress Series* 700, 1–12.
- Infantes, E., Carroll, D., Silva, W.T.A.F., Härkönen, T., Edwards, S.V., Harding, K.C. (2022b). An automated work-flow for pinniped surveys: A new tool for monitoring population dynamics. *Frontiers in Ecology and Evolution* 10, 905309.
- Intergovernmental Panel On Climate Change (IPCC). (2023). Climate change 2022 – impacts, adaptation and vulnerability: Working group II contribution to the sixth assessment report of the intergovernmental panel on climate change, 1st ed. Cambridge University Press.
- Johnson, M.D., Rodriguez Bravo, L.M., O’Connor, S.E., Varley, N.F., Altieri, A.H. (2019). pH variability exacerbates effects of ocean acidification on a caribbean crustose coralline alga. *Frontiers in Marine Science* 6, 150.
- Jones, B.L.H., Unsworth, R.K.F., Nordlund, L.M., Ambo-Rappe, R., La Nafie, Y.A., Lopez, M.R., Udagedara, S., Cullen-Unsworth, L.C. (2022). Local ecological knowledge reveals change in seagrass social–ecological systems. *Oceans* 3, 419–430.
- Jordahl, K., Bossche, J.V.D., Fleischmann, M., McBride, J. and others. (2021). geopandas/geopandas: v0.9.0. <https://zenodo.org/record/4569086>

- Kapsenberg, L., Cyronak, T. (2019). Ocean acidification refugia in variable environments. *Global Change Biology* 25, 3201–3214.
- Koch, M., Bowes, G., Ross, C., Zhang, X.-H. (2013). Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology* 19, 103–132.
- Lefcheck, J.S., Wilcox, D.J., Murphy, R.R., Marion, S.R., Orth, R.J. (2017). Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. *Global Change Biology* 23, 3474–3483.
- Mangan, S., Urbina, M.A., Findlay, H.S., Wilson, R.W., Lewis, C. (2017). Fluctuating seawater pH/ p CO₂ regimes are more energetically expensive than static pH/ p CO₂ levels in the mussel *Mytilus edulis*. *Proceedings of the Royal Society B* 284, 20171642.
- Marsh, H., Eros, C., Corkeron, P., Breen, B. (1999). A conservation strategy for dugongs: implications of Australian research. *Marine and Freshwater Research* 50, 979-90.
- Marsh, H., Penrose, H., Eros, C., Hugues, J. (2002). The Dugong (*Dugong dugon*) status reports and action plans for countries and territories in its Range. Final Report, United Nations Environment Programme, Nairobi, Kenya.
- Marsh, H., Arraut, E.M., Diagne, L.K., Edwards, H., Marmontel, M. (2017). Impact of climate change and loss of habitat on sirenians. In: Marine mammal welfare, animal welfare (ed. Butterworth, A.). Springer international publishing, Cham, pp. 333–357.
- Maxwell, P.S., Eklof, J.S., van Katwijk, M.M., O'Brien, K.R., de la Torre-Castro, M., Boström, C., Bouma, T.J., Krause-Jensen, D., Unsworth, R.K., van Tussenbroek, B.I., van der Heide, T. (2017). The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems - a review. *Biological Reviews* 92, 1521-1538.

- Millennium Ecosystem Assessment (Program) (MEA). (2005). Ecosystems and human well-being: synthesis. Island Press, Washington, DC.
- Nordlund, L., Erlandsson, J., de La Torre-Castro, M., Jiddawi, N. (2010). Changes in an East African social-ecological seagrass system: invertebrate harvesting affecting species composition and local livelihood. *Aquatic Living Resources* 23, 399–416.
- Nordlund, L.M., Gullström, M. (2013). Biodiversity loss in seagrass meadows due to local invertebrate fisheries and harbour activities. *Estuarine, Coastal and Shelf Science* 135, 231–240.
- Nordlund, L.M., Koch, E.W., Barbier, E.B., Creed, J.C. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLOS ONE* 11(10), e0163091.
- Nordlund, L.M., Unsworth, R.K.F., Gullström, M., Cullen-Unsworth, L.C. (2018). Global significance of seagrass fishery activity. *Fish and Fisheries* 19, 399–412.
- Nordlund, L.M., Unsworth, R.K.F., Wallner-Hahn, S., Ratnarajah, L., Beca-Carretero, P., Boikova, E., Bull, J.C., Chefaoui, R.M., de los Santos, C.B., Gagnon, K., Garmendia, J.M., Gizzi, F., Govers, L.L., Gustafsson, C., Hineva, E., Infantes, E., Canning-Clode, J., Jahnke, M., Kleitou, P., Kennedy, H., Klayn, S., Moller, T., Monteiro, J., Piñeiro-Juncal, N., Ponis, E., Papathanasiou, V., Poursanidis, D., Pieraccini, R., Serrano, O., Sousa, Ana.I., Schäfer, S., Rossi, F., Storey, D.S., Van Katwijk, M.M., Wall, D., Ward, E.A., Wilkes, R. (2024). One hundred priority questions for advancing seagrass conservation in Europe. *Plants People Planet* 3.10486.
- Nyangoko, B.P., Berg, H., Mangora, M.M., Shalli, M.S., Gullström, M. (2022). Community perceptions of climate change and ecosystem-based adaptation in the mangrove ecosystem of the Rufiji Delta, Tanzania. *Climate and Development* 14, 896–908.

- Orth, R.J., Harwell, M.C., Fishman, J.R. (1999). A rapid and simple method for transplanting eelgrass using single, unanchored shoots. *Aquatic Botany* 64, 77-85.
- Orth, R.J., Marion, S.R., Moore, K.A., Wilcox, D.J. (2010). Eelgrass (*Zostera marina* L.) in the Chesapeake Bay region of Mid-Atlantic Coast of the USA: Challenges in conservation and restoration. *Estuaries Coasts* 33:139–150.
- Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L. (2006). A global crisis for seagrass ecosystems. *BioScience* 56, 987.
- Orth, R., Moore, K., Marion, S., Wilcox, D., Parrish, D. (2012). Seed addition facilitates eelgrass recovery in a coastal bay system. *Marine Ecology Progress Series* 448:177–195.
- Paling, E.I., Fonseca, M., van Katwijk, M.M., van Keulen, M. (2009). Seagrass restoration. In: Coastal wetlands: An integrated ecosystem approach (eds. Perillo, G., Wolanski, E., Cahoon, D., Brinson, M.). Elsevier, Amsterdam. pp. 687-713.
- Perry, D., Staveley, T., Deyanova, D., Baden, S., Dupont, S., Hernroth, B., Wood, H., Björk, M., Gullström, M. (2019). Global environmental changes negatively impact temperate seagrass ecosystems. *Ecosphere* 10, e02986.
- Phillips, R.C. (1990). Transplant methods. In: Seagrass research methods (eds. Phillips, R.C., McRoy, C.P.). Paris: UNESCO. pp.51-55
- Pilcher, N.J., Adulyanukosol, K., Das, H., Davis, P., Hines, E., Kwan, D., Marsh, H., Ponnampalam, L., Reynolds, J. (2017). A low-cost solution for documenting distribution and abundance of endangered marine fauna and impacts from fisheries. *PLOS ONE* 12, e0190021.
- Ponnampalam, L.S., Keith-Diagne, L., Marmontel, M., Marshall, C.D., Reep, R.L., Powell, J., Marsh, H. (2022). Historical and current interactions with humans.

- In: Ethology and behavioral ecology of Sirenia (ed. Marsh, H.). Springer, Cham. pp. 299–349.
- Rakotonjanahary, F., Rakotomahazo, C., Nirinamamiko, J., Razakarisoa, T., Todinanahary, G., Lavitra, T., Lepoint, G., Vanderklift, M., Ranivoarivelo, L. (2024). Use and management of seagrass ecosystems in southwestern Madagascar. *African Journal of Marine Science* 46, 77–89.
- Ramírez, F., Coll, M., Navarro, J., Bustamante, J., Green, A.J. (2018). Spatial congruence between multiple stressors in the Mediterranean sea may reduce its resilience to climate impacts. *Scientific Reports* 8, 14871.
- Reed, T.E., Waples, R.S., Schindler, D.E., Hard, J.J., Kinnison, M.T. (2010). Phenotypic plasticity and population viability: the importance of environmental predictability. *Proceedings of the Royal Society B* 277, 3391–3400.
- Riebesell, U., Gattuso, J.-P. (2015). Lessons learned from ocean acidification research. *Nature Climate Change* 5, 12–14.
- Scartazza, A., Moscatello, S., Gavrichkova, O., Buia, M.C., Lauteri, M., Battistelli, A., Lorenti, M., Garrard, S.L., Calfapietra, C., Brugnoli, E. (2017). Carbon and nitrogen allocation strategy in *Posidonia oceanica* is altered by seawater acidification. *Science of the Total Environment* 607–608, 954–964.
- Scheffer, M., Barrett, S., Carpenter, S.R., Folke, C., Green, A.J., Holmgren, M., Hughes, T.P., Kosten, S., Van De Leemput, I.A., Nepstad, D.C., Van Nes, E.H., Peeters, E.T.H.M., Walker, B. (2015). Creating a safe operating space for iconic ecosystems. *Science* 347, 1317–1319.
- Semesi, I., Beer, S., Björk, M. (2009). Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. *Marine Ecology Progress Series* 382, 41–47.
- Short, F.T., Neckles, H.A. (1999). The effects of global climate change on seagrasses. *Aquatic Botany* 63, 169–196.

- Short, F.T., Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23, 17–27.
- Short, F.T., Coles, R.G. (2001). Global seagrass research methods. Elsevier. New York.
- Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows, M.T., Alexander, L.V., Benthuyzen, J.A., Donat, M.G., Feng, M., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Sen Gupta, A., Payne, B.L., Moore, P.J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change* 9, 306–312.
- Spalding, M., Taylor, M., Ravilious, C., Short, F., Green, E. (2003). The distribution and status of seagrasses. In: World atlas of seagrasses (eds. Green, E.P., Short, F.). University California Press. pp. 5-26.
- Strader, M.E., Wolak, M.E., Simon, O.M., Hofmann, G.E. (2022). Genetic variation underlies plastic responses to global change drivers in the purple sea urchin, *Strongylocentrotus purpuratus*. *Proceedings of the Royal Society B* 289, 20221249.
- Stumpp, M., Wren, J., Melzner, F., Thorndyke, M.C., Dupont, S.T. (2011). CO₂ induced seawater acidification impacts sea urchin larval development I: Elevated metabolic rates decrease scope for growth and induce developmental delay. *Comparative Biochemistry and Physiology Part A* 60, 331–340.
- Tan, Y.M., Coleman, R.A., Biro, P.A., Dalby, O., Jackson, E.L., Govers, L.L., Heusinkveld, J.H.T., Macreadie, P.I., Flindt, M.R., Dewhurst, J., Sherman, C.D.H. (2023). Developing seed and shoot-based restoration approaches for the seagrass, *Zostera muelleri*. *Restoration Ecology* 31: e13902.
- Torres, L.G., Nieukirk, S.L., Lemos, L., Chandler, T.E. (2018). Drone up! Quantifying whale behavior from a new perspective improves observational capacity. *Frontiers in Marine Science* 5, 319.

- Trotzduk, E., Allen, K., Cockcroft, V., Findlay, K. and others. (2022). *Dugong dugon* (Eastern Africa subpopulation). The IUCN Red List of Threatened Species 2022:e.T218582764 A218589142 <https://www.iucnredlist.org/species/218582764/218589142>.
- Uku, J., Daudi, L., Muthama, C., Alati, V., Kimathi, A., Ndirangu, S. (2022). Seagrass restoration trials in tropical seagrass meadows of Kenya. *Western Indian Ocean Journal of Marine Science* 20, 69–79.
- Unsworth, R.K.F., Cullen, L.C. (2010). Recognising the necessity for Indo-Pacific seagrass conservation. *Conservation Letters* 3, 63–73.
- Unsworth, R.K.F., McKenzie, L.J., Nordlund, L.M., Cullen-Unsworth, L.C. (2018). A changing climate for seagrass conservation? *Current Biology* 28, R1229–R1232.
- Unsworth, R.K.F., McKenzie, L.J., Collier, C.J., Cullen-Unsworth, L.C., Duarte, C.M., Eklöf, J.S., Jarvis, J.C., Jones, B.L., Nordlund, L.M. (2019). Global challenges for seagrass conservation. *Ambio* 48, 801–815.
- Van Katwijk, M.M., Thorhaug, A., Marbà, N., Orth, R.J., Duarte, C.M., Kendrick, G.A., Althuizen, I.H.J., Balestri, E., Bernard, G., Cambridge, M.L., Cunha, A., Durance, C., Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K., Meinesz, A., Nakaoka, M., O'Brien, K.R., Paling, E.I., Pickerell, C., Ransijn, A.M.A., Verduin, J.J. (2016). Global analysis of seagrass restoration: the importance of large-scale planting. *Journal of Applied Ecology* 53, 567–578.
- Vargas, C.A., Lagos, N.A., Lardies, M.A., Duarte, C., Manríquez, P.H., Aguilera, V.M., Broitman, B., Widdicombe, S., Dupont, S. (2017). Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity. *Nature Ecology & Evolution* 1, 0084.
- Vargas, C.A., Cuevas, L.A., Broitman, B.R., San Martín, V.A., Lagos, N.A., Gaitán-Espitia, J.D., Dupont, S. (2022). Upper environmental pCO₂ drives sensitivity

- to ocean acidification in marine invertebrates. *Nature Climate Change* 12, 200-207.
- Ventura, A., Schulz, S., Dupont, S. (2016). Maintained larval growth in mussel larvae exposed to acidified under-saturated seawater. *Scientific Reports* 6, 23728.
- Vicente, E.I., Bandeira, S.O. (2014). Socio-economic aspects of gastrop and bivalve harvest from seagrass beds- comparison between urban (disturbed) and rural (undisturbed) areas. In: The Maputo Bay ecosystem (eds. Bandeira, S.O., Paula, J.P.M.) Western Indian Ocean Marine Science Association (WIOMSA), Zanzibar Town. pp. 329-334.
- Wallner-Hahn, S., Dahlgren, M. (2022). Linking seagrass ecosystem services to food security: The example of southwestern Madagascar's small-scale fisheries. *Ecosystem Services* 53, 101381.
- Wang, J., Russell, B.D., Ding, M.-W., Dong, Y.-W. (2018). Ocean acidification increases the sensitivity of and variability in physiological responses of an intertidal limpet to thermal stress. *Biogeosciences* 15, 2803–2817.
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences USA* 106(30), 12377–12381.
- Yamato, C., Ichikawa, K., Arai, N., Tanaka, K., Nishiyama, T., Kittiwattanawong, K. (2021). Deep neural networks based automated extraction of dugong feeding trails from UAV images in the intertidal seagrass beds. *PLOS ONE* 16: e0255586
- Zimmerman, R.C. (2021). Scaling up: Predicting the impacts of climate change on seagrass ecosystems. *Estuaries and Coasts* 44, 558–576.