Effects of Marine Protected Areas on Tropical Seagrass Ecosystems

Elisa Alonso Aller

Academic dissertation for the Degree of Doctor of Philosophy in Marine Ecology at Stockholm University to be publicly defended on Tuesday 5 June 2018 at 09.30 in Vivi Täckholmssalen (Q-salen), NPQ-huset, Svante Arrhenius väg 20, Stockholm.

Abstract
Seagrass beds are highly productive coastal ecosystems that sustain a rich and diverse associated fauna and flora. Increasing anthropogenic pressures threaten seagrass ecosystems and have already led to major seagrass losses across the world. Marine Protected Areas (MPAs) have become one of the key strategies to manage coastal ecosystems and associated resources worldwide and have been often shown to successfully protect marine ecosystems. However, relatively few studies have assessed the effects of MPAs on seagrass ecosystems, and there are indications that MPAs may not be able to fully protect seagrasses, especially from disturbances originating outside their boundaries. Within this context, this thesis aimed to investigate the direct and indirect effects (those mediated by biotic interactions) of MPAs on tropical seagrasses, associated fish communities, and ecosystem processes.

The thesis consists of three parts. First, we used 10-years of seagrass monitoring data within a MPA to evaluate the temporal variability in seagrass cover and species composition in relation to changes in environmental conditions (**Paper I**). Second, we investigated the potential of MPAs to enhance the temporal stability of seagrass ecosystems using a 10-month field study. We surveyed seagrass-associated fish communities (**Paper II**) and estimated seagrass growth and herbivory rates (**Paper III**) during three different seasons within MPAs and unprotected sites. Finally, to evaluate the effects of MPAs and land-use on seagrass ecosystems we surveyed seagrass species and trait composition within government-managed MPAs, community-managed MPAs, and unprotected sites (**Paper IV**).

The seagrass bed monitored in **Paper I** showed a high temporal and spatial variability, with a temporal decline in cover and change in species composition, followed by a period of recovery. This pattern could not be associated with any of the climate and tidal variables considered, suggesting that potential drivers of decline may have originated outside MPA boundaries. The results from the seasonal field study showed that MPAs increased the temporal stability of seagrass-associated fish communities, particularly juvenile fish (**Paper II**), and strengthened a positive link between herbivorous fish, herbivory rates, and seagrass growth (**Paper III**), suggesting the presence of a positive feedback that promotes stability. Finally, MPAs affected seagrass species and trait composition (by selecting for more stress-sensitive species) but did not seem to be able to protect seagrasses from land-use effects, with seagrasses showing similar changes in species and trait composition within and outside MPAs (**Paper IV**). Considering these results, this thesis builds to a body of literature indicating that MPAs alone may not be sufficient to protect seagrass ecosystems and that improved management strategies may be necessary to preserve these important coastal habitats.

Keywords: *coastal ecosystems, seagrass, marine protected areas, management, conservation, fish, herbivory, Western Indian Ocean, East Africa, tropical.*

Department of Ecology, Environment and Plant Sciences

Stockholm University, 106 91 Stockholm

EFFECTS OF MARINE PROTECTED AREAS ON TROPICAL
SEAGRASS ECOSYSTEMS

Elisa Alonso Aller

Effects of Marine Protected Areas on Tropical Seagrass Ecosystems

Elisa Alonso Aller

Cover: Fish in a *Thalassodendron ciliatum* seagrass bed (Chumbe Island, Zanzibar, Tanzania)
All photos and illustrations by the author

*"In this great chain of causes
and effects, no single fact can
be considered in isolation."*

Alexander von Humboldt
(1769-1859)

Abstract

Seagrass beds are highly productive coastal ecosystems that sustain a rich and diverse associated fauna and flora. Increasing anthropogenic pressures threaten seagrass ecosystems and have already led to major seagrass losses across the world. Marine Protected Areas (MPAs) have become one of the key strategies to manage coastal ecosystems and associated resources worldwide and have often been shown to successfully protect marine ecosystems. However, relatively few studies have assessed the effects of MPAs on seagrass ecosystems and there are indications that MPAs may not be able to fully protect seagrasses, especially from disturbances originating outside their boundaries. Within this context, this thesis aimed to investigate the direct and indirect effects (those mediated by biotic interactions) of MPAs on tropical seagrasses, associated fish communities, and ecosystem processes.

The thesis consists of three parts. First, we used 10-years of seagrass monitoring data within a MPA to evaluate the temporal variability in seagrass cover and species composition in relation to changes in environmental conditions (**Paper I**). Second, we investigated the potential of MPAs to enhance the temporal stability of seagrass ecosystems using a 10-month field study. We surveyed seagrass-associated fish communities (**Paper II**) and estimated seagrass growth and herbivory rates (**Paper III**) during three different seasons within MPAs and unprotected sites. Finally, to evaluate the effects of MPAs and land-use on seagrass ecosystems, we surveyed seagrass species and trait composition within government-managed MPAs, community-managed MPAs, and unprotected sites (**Paper IV**).

The seagrass bed monitored in **Paper I** showed a high temporal and spatial variability, with a temporal decline in cover and change in species composition, followed by a period of recovery. This pattern could not be associated with any of the climate and tidal variables considered, suggesting that potential drivers of decline may have originated outside MPA boundaries. The results from the seasonal field study showed that MPAs increased the temporal stability of seagrass-associated fish communities, particularly juvenile fish (**Paper II**), and strengthened a positive link between herbivorous fish, herbivory rates, and seagrass growth (**Paper III**), suggesting the presence of a positive feedback that promotes stability. Finally, MPAs affected seagrass species and trait composition (by selecting for more stress-sensitive species) but did not seem to be able to protect seagrasses from land-use effects, with seagrasses showing similar changes in species and trait composition within and outside MPAs (**Paper IV**). Considering these results, this thesis builds to a body of literature indicating that MPAs alone may not be sufficient to protect seagrass ecosystems and that improved management strategies may be necessary to preserve these important coastal habitats.

List of papers

This thesis is based on the following papers, referred to in the text by their Roman numerals (I–IV):

I Alonso Aller E, Eklöf JS, Gullström M, Kloiber U, Linderholm HW, Nordlund LM. Monitoring of a protected multi-specific tropical seagrass meadow reveals a pattern of decline and recovery. *Manuscript*

II Alonso Aller E, Jiddawi NS, Eklöf JS (2017). Marine protected areas increase temporal stability of community structure, but not density or diversity, of tropical seagrass fish communities. PLOS ONE 12(8): e0183999. doi: 10.1371/journal.pone.0183999

III Alonso Aller E, Jiddawi NS, Eklöf JS. Fishing weakens a positive link between herbivore abundance and plant growth in tropical seagrass beds. *Manuscript*

IV Chirico ADA, Alonso Aller E, Eklöf JS. Additive effects of marine protected areas and land-use on inter- and intraspecific trait variability in tropical seagrass assemblages. *Manuscript*

Published **Paper II** is open access.

My **contributions** to the papers listed above: Paper I – data analyses and major part in writing. Paper II – planning and design, data collection, laboratory and data analyses, main responsibility in writing, corresponding author responsible of submitting the manuscript, dealing with reviewer feedback, and revising the manuscript. Paper III – planning and design, data collection, laboratory and data analyses, and main responsibility in writing. Paper IV – data analyses and major part in writing.

Contents

Introduction

Coastal marine ecosystems

Coastal marine ecosystems are of great importance, not only from an ecological perspective, but also in terms of their social and economic value, by providing, both directly and indirectly, functions and services beneficial for human populations, the so-called ecosystem services (Barbier et al. 2011). For instance, coastal marine ecosystems may provide shoreline protection (Spalding et al. 2014), maintain healthy and rich fish populations utilised by fisheries (Pauly and Zeller 2014), and provide opportunities for recreational activities (Brander et al. 2007). Humans have for long been heavily dependent on ecosystem services for their health, livelihoods, and survival (Daily 1997) and this dependence is likely to increase giving the present growth rate of human population (MEA 2005). Despite their importance, coastal ecosystems worldwide are under a constant impact from human activities and have already suffered from great deterioration in terms of biodiversity loss, habitat destruction, fishery declines, and poor water quality (Jackson et al. 2001; Lotze 2006). The effects of local anthropogenic pressures on coastal marine ecosystems may also be worsened in the context of climate change (Doney et al. 2012; IPCC 2013), threatening ecosystems' structure and function and ultimately their ability to provide goods and services (de Groot et al. 2012). Thus, there is a pressing need for effective management strategies to ensure the maintenance of coastal marine ecosystems and their associated services (Martínez et al. 2007).

Management and protection of coastal ecosystems

Strategies to manage coastal ecosystems and associated resources vary considerably and can include different forms of use restriction. For example, fishing activities may be regulated so that they only take place during certain times of the year (seasonal or temporal closures) (e.g. Nemeth et al. 2006), excluding certain locations (no-take zones) (e.g. McClanahan 2011), or by controlling which fishing gears are allowed in the area (gear restriction) (e.g. Kaiser et al. 2000). Over the last decades, no-take zones in the form of Marine Protected Areas (MPAs)

have become one of the key management strategies worldwide. Even though many different definitions of MPAs have emerged in the literature over the years, MPAs can generally be defined as marine areas where certain activities and uses are prohibited or restricted, although they may greatly vary in structure and conservation goals (Salm et al. 2000).

One of the mechanisms through which MPAs may positively influence ecosystems is by increasing biodiversity (McCann 2000; Worm et al. 2006). Species diversity is a key factor influencing ecosystem functioning and the resilience and resistance of ecosystems to changes in environmental conditions (Chapin et al. 2000), leading to increased ecosystem stability (McCann 2000). Increased diversity may enhance ecosystems' stability through different processes. Diverse communities are more likely to present a high response diversity, i.e. species that respond differently to a shared disturbance (Hooper et al. 2005; Bernhardt and Leslie 2013), leading to compensatory changes (negative-covariance effect) and an average stable community response (averaging effect) (McCann 2000). Moreover, a high species diversity also increases the chances that there is functional redundancy (different species that fulfill similar functions) between species that have important stabilizing roles in the ecosystem (insurance effect) (McCann 2000).

No-take MPAs have been shown to successfully protect marine ecosystems, sustain biodiversity, rebuild fish stocks, reduce impacts on critical habitat-forming species, and strengthen ecosystems' resilience to climate change (e.g. McClanahan et al. 2008; Lester et al. 2009; Roberts et al. 2017). However, several studies have also questioned the effectiveness of MPAs, especially regarding their potential to protect habitat-forming organisms such as corals and seagrasses. For example, MPAs have been shown to increase the vulnerability of coral reefs to bleaching events by changing coral community composition towards dominance of disturbance-sensitive species (Darling et al. 2010). As a result, MPAs may experience similar or even stronger declines in coral cover due to disturbance than unprotected reefs (Darling et al. 2010; Toth et al. 2014), with further negative consequences for the associated fish communities (Jones et al. 2004; Graham et al. 2007). MPAs may also not be sufficient to protect seagrass ecosystems from land-use impacts (Quiros et al. 2017) and sea urchin overgrazing events (Eklöf et al. 2009a). Moreover, MPAs do not seem to increase ecosystems' potential for recovery after disturbance (Graham et al. 2015).

The effectiveness of MPAs may depend on an array of factors. MPA size, age, and enforcement are some key factors controlling MPA effectiveness, with old, large, and well-enforced MPAs showing improved conservation outcomes (Edgar et al. 2014). MPAs implemented in areas that have been subjected to intense fishing may need a certain amount of time to show positive outcomes due to lag

effects in the recovery from the previous damaged state (McClanahan and Graham 2005; Claudet et al. 2008), and thus the effectiveness of MPAs will increase with their age, while large MPAs may increase the potential for self-recruitment and allow for mobile fish to remain within the MPA boundaries (Claudet et al. 2008). MPA effects may also be influenced by species interactions, e.g. trophic cascades, which could both strengthen or reduce MPA effectiveness (Pinnegar et al. 2000). For example, in the Caribbean, MPAs have been shown to indirectly enhance coral recruitment through increased macroalgal grazing by fish, which may increase the ecosystems ability to recover after disturbance (Mumby et al. 2007). On the other hand, protection from fishing in a MPA in Tasmania (Australia) indirectly led to a decrease in the abundance of abalone, one of the fisheries' target species in the region, due to an increase in lobster abundance (Barrett et al. 2009). At the same time, MPAs may not be capable of protecting ecosystems from impacts originating outside MPA boundaries (Allison et al. 1998), such as nutrients input, pollutants, and sediment runoff (Quiros et al. 2017), as well as climate change impacts (Graham et al. 2008). To gain a better understanding of the circumstances under which MPAs may or may not be effective in protecting coastal ecosystems, it is thus essential to evaluate their effectiveness in a wide range of ecosystems and geographical areas.

Seasonality of coastal ecosystems in tropical regions

Seasonality is known to be a key factor controlling coastal marine ecosystems in temperate regions, while in the tropics it has been often found that seasonality effects are minimal due to the relatively small variation in temperature across seasons (e.g. Blackburn et al. 1970; Steven and Glombitza 1972). However, many tropical regions experience strong seasonal changes in other climate variables, such as wind speed and direction and rainfall, due to the dominant effects of monsoons, a yearly weather cycle strongly affecting tropical coastal ecosystems. For instance, monsoon seasonality can strongly influence fish reproduction, recruitment, and distribution patterns (McClanahan 1988; Lugendo et al. 2007; Abesamis et al. 2015).

Climate change has been predicted to alter monsoonal seasonality, with monsoons expected to display a delayed onset and earlier recession, as well as intensified precipitation (Lee and Wang 2012; IPCC 2014; Mariotti et al. 2014). These changes are likely to affect coastal ecosystems (Przeslawski et al. 2008; Hoegh-Guldberg and Bruno 2010). For example, changes in the timing and intensity of monsoons may affect the reproduction, dispersal, and recruitment of organisms

such as corals and echinoderms (Przeslawski et al. 2008). Thus, there is a pertinent need to evaluate the effects of monsoon seasonality on coastal tropical ecosystems to improve management strategies in the face of climate change.

Even though MPAs have been shown to increase the stability of coastal ecosystems over long-term trends and in relation to disturbances (Babcock et al. 2010; Fraschetti et al. 2013; Mellin et al. 2016), few studies have assessed their ability to buffer seasonal effects. MPAs in temperate regions appear to be able to reduce the effects of seasonality on fish communities (Francour 1994; Seytre and Francour 2009). However, no such effects have yet been assessed in tropical regions.

Seagrass beds as model ecosystem

Seagrasses are marine angiosperms that form the basis for one of the most productive coastal ecosystems on Earth (Duarte and Chiscano 1999). Seagrass beds are coastal habitats that occupy inter- and subtidal environments in both temperate and tropical regions (Green and Short 2003). Even though most seagrass beds are monospecific (consisting of a single seagrass species), multi-specific seagrass beds (where several species co-occur) are also common, especially in tropical regions. Seagrass beds are known to be naturally dynamic, with seagrass cover and species composition varying both at seasonal and at inter-annual scales (Duarte et al. 2006).

The high importance of seagrasses lay in their role as ecosystem engineers. Ecosystem engineers are organisms that strongly modify the physical and geochemical conditions of their environment, controlling the availability of resources and creating or modifying habitats that facilitate the establishment of other species (Jones et al. 1994). Furthermore, ecosystem engineers can also modify the incoming and outgoing fluxes, forming and controlling connections that allow for other adjacent ecosystems to develop (Gillis et al. 2014; Barbier 2017). Owing to their role as ecosystem engineers, seagrasses are important ecosystem services providers (Duarte et al. 2013; Nordlund et al. 2016). For instance, seagrasses may be used as raw materials, as fertilizers, and for food, crafts, and in potions and rituals (Hemminga and Duarte 2000; de la Torre-Castro and Rönnbäck 2004; Lauer and Aswani 2010). Their structurally complex canopy plays a role in wave attenuation, protecting adjacent shores from erosion (Fonseca and Cahalan 1992; Duarte et al. 2013), and through their extensive rhizome and root systems, seagrasses stabilize sediments, preventing their re-suspension

(Björk et al. 2008), and increase sediment oxygenation, allowing for a more efficient recycling of nutrients (Björk et al. 2008). Seagrasses also improve water quality through nutrient uptake (Romero et al. 2006) and deposition of suspended particles, reducing water turbidity (Koch et al. 2006), and are considered important carbon sinks (Duarte et al. 2013; Tokoro et al. 2014). Additionally, seagrass beds support high rates of primary production both directly, through seagrass production, and indirectly, by providing substratum for epiphytic algae (Duffy 2006). They also sustain a high secondary productivity by hosting a diverse and abundant faunal community (Hemminga and Duarte 2000). Seagrass beds harbour a rich fish community (Gillanders 2006) that often presents higher abundance and diversity than neighbouring un-vegetated areas (Pollard 1984; Edgar et al. 1994). Seagrasses structural complexity is especially important for the associated fish assemblages, since it may increase food availability (Bell and Westoby 1986) and provide shelter from predation (Orth et al. 1984; Heck and Orth 2006). Due to the high productivity of seagrass ecosystems, combined with the fact that they are often located in sheltered and shallow coastal areas that are easily accessible to humans, seagrass beds are considered important fishing grounds in coastal areas across the world (Cullen-Unsworth et al. 2014; Nordlund et al. 2017).

Threats to seagrass ecosystems

Seagrass beds are under increasing pressure from anthropogenic impacts that has already led to major seagrass losses worldwide (Waycott et al. 2009). Most of the current knowledge about seagrass temporal dynamics comes from temperate regions, where seagrasses have for long been included in annual monitoring programmes (e.g. Marbà and Duarte 1997; Ball et al. 2014; Shelton et al. 2016). In tropical regions, information about seagrass temporal patterns and variability is mostly available for Australia and the Caribbean (Rasheed and Unsworth 2011; Short et al. 2016), while developing regions, e.g. East Africa, often lack the resources to maintain long-term monitoring programmes. There is thus a need for improved seagrass monitoring in such areas to better understand seagrass temporal dynamics and response to environmental change.

Seagrasses are highly susceptible to local disturbances, both through physical destruction by e.g. fishing gear or boating activities (Walker et al. 1989; Daby 2003) and through cascading effects due to fisheries exploitation (McClanahan et al. 1994; Eklöf et al. 2008b). At the same time, distant disturbances can also have detrimental effects on seagrasses. For instance, nutrient and sediment in-

puts through runoff can pose a major threat to seagrasses through increased turbidity and nutrient loading (Terrados et al. 1998; Quiros et al. 2017). Moreover, there is an increasing understanding that climate change can have a strong negative impact on seagrasses. Even though seagrasses seem to be relatively resilient to moderate and gradual changes in environmental conditions, such as warming (Koch et al. 2013), extreme events such as heat waves, severe storms, and extreme low tides can have extensive detrimental effects (Preen et al. 1995; Björk et al. 1999; Campbell et al. 2006; Short et al. 2016).

Seagrass degradation and loss may have further consequences for ecosystem functioning and the provision of ecosystem services. For example, in the tropics, especially in the Indo-Pacific region, artisanal fisheries often target species that are highly dependent on seagrasses, such as herbivorous fish that feed on seagrasses and seagrass epiphytes (de la Torre-Castro et al. 2008; Hicks and McClanahan 2012).

Protection of seagrass ecosystems

Even though seagrasses are generally incorporated into management and conservation strategies in developed, rich countries (Kenworthy et al. 2006), they have often been ignored in developing regions (Unsworth and Cullen 2010), and in many cases may have only been included in management plans due to their proximity to the targeted ecosystems, e.g. coral reefs. When seagrass beds have been protected, MPAs appear to benefit seagrass-associated fish communities by increasing fish biomass, through changes in both fish abundance and size, and species richness (e.g. Valentine et al. 2008; Unsworth et al. 2010; Chirico et al. 2017). MPAs have been also shown to promote shifts in seagrass species composition towards more structurally complex, but sensitive, 'climax' species, potentially due to reduced grazing by sea urchins within MPAs (McClanahan et al. 1994; Alcoverro and Mariani 2004). However, MPAs may not be sufficient to protect seagrasses from more distant disturbances, with some studies suggesting that MPAs do not have the ability to protect seagrasses from land-use impacts (Freeman et al. 2008; Quiros et al. 2017). Therefore, there is a pertinent need to further assess the effects of MPAs on seagrasses in tropical coastal systems, particularly in relation to distant disturbances such as land-use and climate impacts.

Trait-based ecology

Traits are morphological, physiological, behavioural and phenological character-istics measurable at the individual level (Violle et al. 2007). In ecology, there has been an increased use of trait-based approaches to better understand the re-sponses of organisms, populations, and communities to environmental variabil-ity (Lavorel and Garnier 2002; Díaz et al. 2007). These approaches often evaluate the effects of environmental conditions on community-level traits, thus only as-sessing interspecific trait variability. However, most organisms show some plas-ticity in response to environmental conditions, and thus traits may show different attributes along environmental gradients (Violle et al. 2007). This plasticity can allow organisms to adapt to environmental changes, increasing their ability to tolerate stress, but at the same time it may influence and organism's effect on ecosystem processes (Miner et al. 2005). Thus, trait-based studies should simul-taneously account for both inter- and intraspecific trait variability to properly estimate the overall influence of environmental conditions on community-level trait composition (Violle et al. 2012). This is particularly important in the case of ecosystem engineer species such as seagrasses. Seagrasses display high pheno-typic plasticity, being able to modify morphological and physiological traits in response to local environmental conditions (Udy and Dennison 1997; Collier et al. 2008; La Nafie et al. 2013; Maxwell et al. 2013). Thus, phenotypic plasticity can determine their ability to persist in the face of environmental change (Lloret et al. 2012) as well as their influence on ecosystem structure and function.

Scope of the thesis

In light of this background, this thesis aims to investigate the direct and indirect (mediated by species interactions) effects of MPAs on tropical seagrasses, associated fish communities, and ecosystem processes (Figure 1). The four studies included in the thesis comprised different spatial and temporal scales (Figure 2).
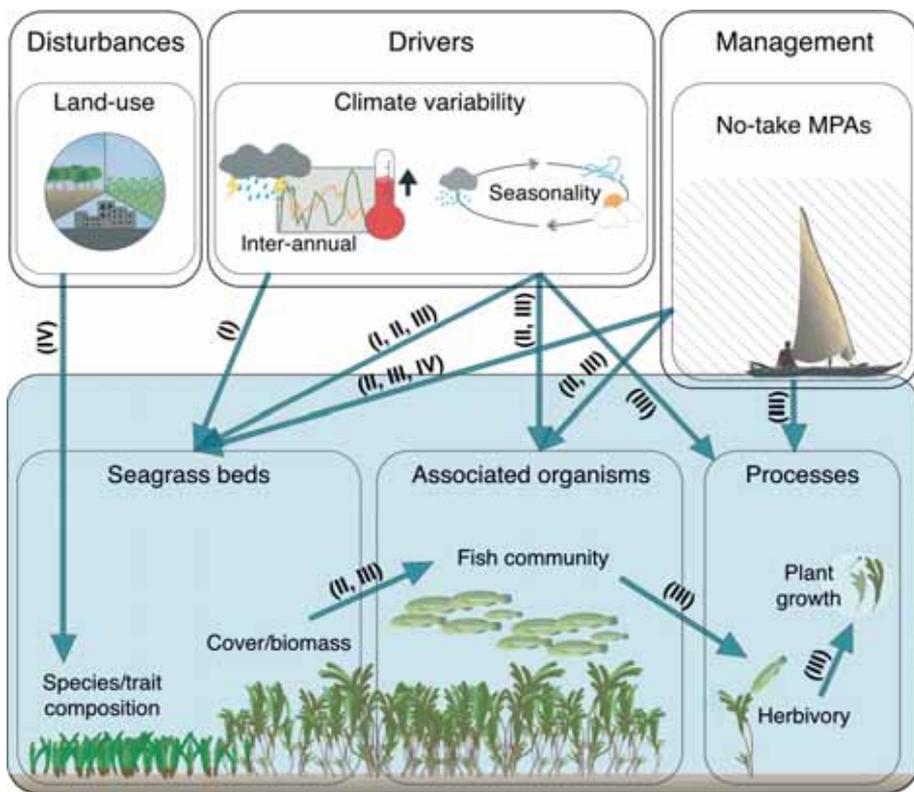

Figure 1 Conceptual framework of the thesis, highlighting the assessed relationships between disturbances, drivers, and MPAs, and some of the components of the seagrass ecosystem. The topics of each paper are highlighted using their roman numerals (I–VI)
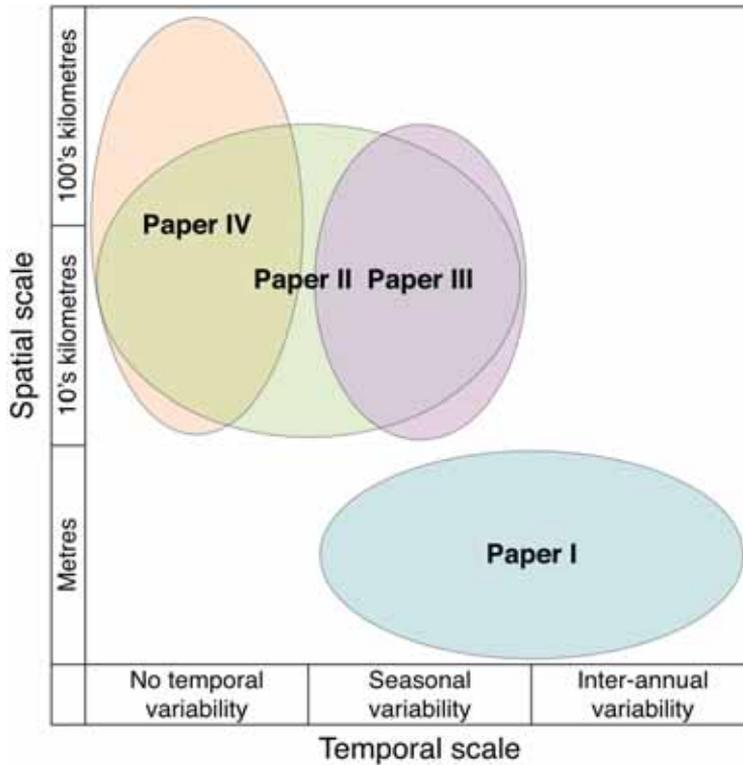
Figure 2 Conceptual figure highlighting the temporal and spatial scales addressed in each of the four papers (I–IV)

The thesis consists of three parts:

1. A temporal analysis of 10 years of seagrass monitoring data from a MPA to evaluate the seasonal and inter-annual variability in seagrass cover and species composition in relation to changes in environmental conditions (**Paper I**).

2. A 10-month field study investigating the direct and indirect effects of MPAs on seasonal variability of seagrass-associated fish communities (**Paper II**) and biotic interactions and ecosystem processes (**Papers II** and **III**).

3. A large-scale (along 200 km of coastline) field survey assessing the single and joint effects of MPAs and land-use on seagrass species and trait composition (**Paper IV**).

Methods

Study area

The work presented in this thesis was conducted in two different areas in East Africa (Western Indian Ocean (WIO) region): Unguja Island (Zanzibar, Tanzania) and the southern Kenyan coast (Figure 3). Coastal marine areas in this region are often comprised of a mosaic of coral reefs, mangrove forests, and seagrass and macroalgal beds. The climate is tropical (i.e. average temperatures above 18 °C year round) and strongly influenced by the monsoon cycle, characterized by two rainy seasons (March-May and October-December) and two dry seasons (January-February and April-September), with marked differences in temperature and rainfall (McClanahan 1988). Wind patterns also change with the monsoon, with stronger south-easterly winds dominating from April to September and weaker north-easterly winds from November to February (McClanahan 1988).
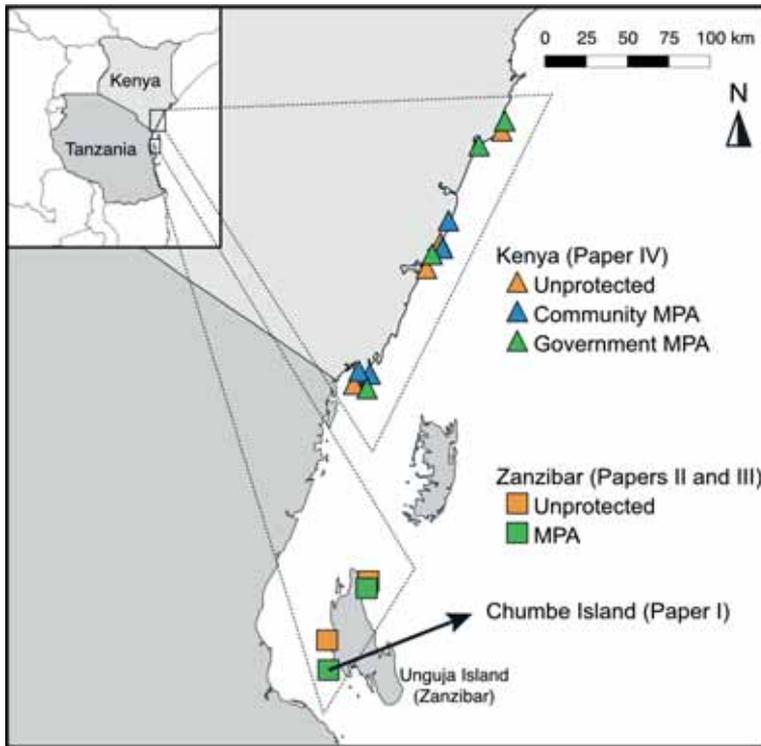
Figure 3 Map of the Kenyan and Tanzanian coasts and sampling locations

In the WIO region, fisheries are mostly small-scale and artisanal, taking place throughout the coastline in shallow water habitats, particularly in seagrass beds and coral reefs (UNEP 2001; Jiddawi and Öhman 2002; de la Torre-Castro and Rönnbäck 2004). The fisheries use a wide range of fishing gears and thus they are highly unselective, with almost any fish species being targeted and caught (Jiddawi and Öhman 2002; de la Torre-Castro and Rönnbäck 2004). Fishing activities are also dependant on the monsoon cycle, with fishing pressure being generally reduced from June to September due to strong winds and high waves (Jiddawi and Öhman 2002; Makame 2013).

The seagrass monitoring site from **Paper I** is located in Chumbe Island Coral Park (CHICOP), a 0.3 km² privately-run marine reserve that has been fully protected from extractive activities since 1994 (Kloiber 2013). Monitoring of the seagrass bed took place quarterly (4 times per year) between 2007 and 2016. The fieldwork for **Papers II** and **III** took place during three different seasons in 2014–2015 (November–December 2014, March–April 2015, and July–August 2015). Sampling was carried out at four sites around Unguja Island (Zanzibar, Tanzania): two no-take MPAs (Mnemba Island and Chumbe Island) and two control (unprotected) sites (Mnemba reef and Changuu Island). Mnemba Island

is a private resort where the sea area from the shore and 200 m out has been formally protected from fishing since 2002 (EcoAfrica 2005). The two MPAs included in the study are the only no-take zones in Unguja Island at present.

In **Paper IV**, a field survey was conducted along the southern Kenyan coast in October–December 2012. Three different types of sites were included in the survey: four old, government-managed no-take MPAs (Kisite, Malindi, Mombasa, and Watamu Marine National Parks), four recently stablished, community-managed no-take MPAs (Kanamai, Kibuyuni, Kuruwitu, and Wasini), and four unprotected (fished) sites (Chamjale, Kanamai, Mayungu, and Nyali).

Seagrass species

There are ca. 14 seagrass species described in the WIO region, accounting for more than 20% of the world seagrass species (Green and Short 2003). The seagrass bed in **Paper I** is a multi-specific meadow comprised of 6 species: *Cymodocea rotundata* Asch. & Schweinf, *Cymodocea serrulata* (R.Br.) Asch. & Magnus, *Halophila* spp., *Halodule* spp., *Syringodium isoetifolium* (Asch.) Dandy, and *Thalassia hemprichii* (Ehrenb.) Asch (Figure 4A).

In the second part of the thesis (**Papers II** and **III**) surveys were carried out in mono-specific *Thalassodendron ciliatum* (Forssk.) Hartog beds (Figure 4B). *T. ciliatum* is a canopy-forming seagrass species that consists of leaf clusters that grow from an erect branched or unbranched stem (Kuo and Hartog 2001). Even though it can be part of multi-specific seagrass beds, *T. ciliatum* often forms large mono-specific beds that harbour abundant and diverse fish communities (Gullström et al. 2006).

Finally, in **Paper IV** we surveyed both mono- and multi-specific meadows, comprising a total of ten species: *C. rotundata*, *C. serrulata*, *Enhalus acoroides* (L.f.) Royle, *Halophila ovalis* (R.Br.) Hook.f., *Halophila stipulacea* (Forssk.) Asch., *Halodule uninervis* (Forssk.) Asch., *Halodule wrightii* Asch., *S. isoetifolium*, *T. ciliatum*, and *T. hemprichii*.
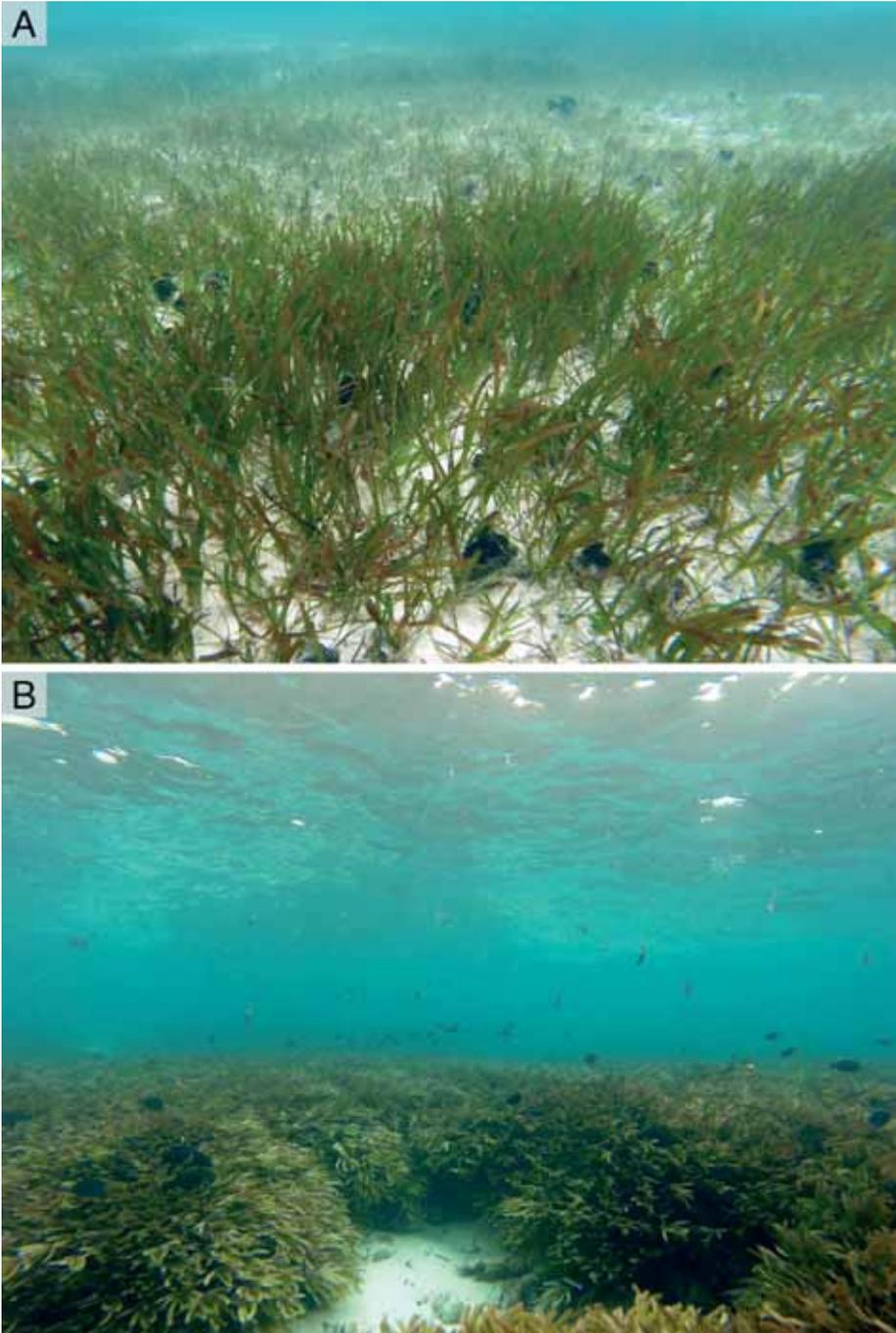
Figure 4 A) A multi-specific seagrass bed (Chumbe Island) and B) a mono-specific *Thalassodendron ciliatum* seagrass bed (Mnemba reef)

Field surveys and assays

Seagrass surveys

The method used to quantify seagrass abundance and species composition will depend on the question of concern. For instance, to quantify seagrass presence along a gradient, e.g. depth or salinity, a stratified sampling method should be used, while in absence of such gradients, a random sampling approach would be more appropriate (Duarte and Kirkman 2001). Seagrass abundance is best characterized based on biomass (above- and below-ground). Biomass samples are collected by extracting all plant material (shoots, roots, and rhizomes) using standardized quadrats or corers. Samples are then taken to the laboratory where above- and below-ground plant material is dried separately at 60 °C until reaching a stable weight (Duarte and Kirkman 2001). In cases where the assessment of seagrass biomass may not be possible due to its destructive nature (e.g. within MPAs), seagrass abundance can be visually estimated as per cent aerial cover within standardized quadrats (Duarte and Kirkman 2001). Seagrass abundance can also be estimated in terms of shoot density and canopy height. Shoot density can be quantified by counting the number of seagrass shoots rooted within a standardized area. In the case of seagrass species whose stems may be branched, the number of leaf clusters should also be counted (Duarte and Kirkman 2001). Canopy height can be measured directly on shoots collected for biomass samples or by measuring the distance from the sediment to the top of the canopy, ignoring the tallest 20% to avoid canopy height overestimation (Duarte and Kirkman 2001).

In **Paper I**, we used seagrass cover data collected as part of a long-term monitoring program initiated by SeagrassNet (a global seagrass monitoring network) in collaboration with Chumbe Island Coral Park (CHICOP). The monitoring program uses a stratified sampling method where seagrass abundance and species composition are characterised at permanent quadrats (0.5×0.5 m) along three transects placed parallel to the shore at three different distances from shore (Short et al. 2006b). Due to the conservation status of the monitoring site, only visual estimations of seagrass cover, shoot density, and canopy height are carried out.

Papers II and **III** focused on monospecific *T. ciliatum* seagrass beds, and thus a randomized sampling approach was used. In **Paper II**, seagrass aerial cover was estimated along the same random transects used in the fish surveys (see below) using 0.25 m² quadrats placed at 5 m intervals along each transect. Within each quadrat, we visually estimated the bottom per cent cover of seagrass and

other sessile organisms (e.g. corals, macroalgae) no the nearest 10%. This resulted in six subsamples per transect, which were averaged to obtain one value per transect. In **Paper III**, seagrasses were characterized in terms of shoot density, canopy height, and above-ground biomass of seagrass and associated epiphytes. Biomass samples were taken at random stations within each site and shoot density was estimated within 0.25×0.25 m quadrats at each station.

In **Paper IV** one of the questions of interest was the effect of distance to shore on seagrass species and trait composition. Therefore, here we used a stratified sampling approach. At each site, seagrass surveys were conducted at three different zones: shallow, middle, and reef. The shallow zone was in the intertidal area, 10 m seaward from the closest point to the shoreline where the first rooted seagrass plant was, or could have been, observed. The reef zone was placed in the coral reef flat and was usually dominated by hard corals interspersed with seagrass and macroalgae. The middle zone was placed in the lagoon at an equal distance from the shallow and the reef zones. Within each zone, samples were taken at 50 m intervals along a transect parallel to the shoreline. Seagrass samples were collected using 10 cm diameter steel corers (to a sediment depth of 20 cm). in an area representative of the seagrass species composition within a 5 m radius. Seagrass composition was then characterized based on five morphological traits (number of leaves per shoot, leaf length and width, and above- and below-ground biomass) which were measured in the laboratory for each species present.

Fish surveys

Extractive methods, such as the use of nets or trawls, can prove useful to assess fish abundance and species composition in coastal ecosystems, especially since these methods do not depend on underwater visibility and can be used at any time of the day (e.g. day-night surveys). However, such methods may not be suitable to survey fish communities within MPAs were extractive activities are not allowed. Alternatively, there are several non-destructive methods that can be used. Underwater visual census (UVC) is one of the most widely used methods to assess fish densities, especially in tropical regions where visibility is usually favourable. UVC can be used in many different habitats, it is a fast, non-destructive, and inexpensive method, and produces data that can be easily comparable with many other studies (Hill and Wilkinson 2004). Despite its advantages, UVC precision and accuracy depend on many factors. For example, fish abundance estimations can be affected by census duration (St John et al. 1990), method, e.g. point-counts vs. belt transects (Thresher and Gunn 1986; Watson and Quinn 1997) or SCUBA diving vs. snorkelling (Dearden et al. 2009), and speed (Lincoln

Smith 1988), as well as transect width (Cheal and Thompson 1997). Estimations of fish abundance and size may also differ among observers (Thompson and Mapstone 1997) and errors can arise in the estimation of fish sizes (Bell et al. 1985; St John et al. 1990). Moreover, fish behaviour can affect their detectability, with cryptic and nocturnal species being underestimated or even missed (Brock 1982; Willis 2001), while large predatory species are often overestimated (Ward-Paige et al. 2010), and presence of divers can also affect fish behaviour by either frightening or attracting them (Kulbicki 1998). Nevertheless, UVC is one of the most well-accepted and practical methods for non-destructive estimations of fish abundance (Cheal and Thompson 1997; MacNeil et al. 2008), and have been used in a wide range of studies in coral reefs (Campbell and Pardede 2006; McClanahan et al. 2009; Pittman and Brown 2011) and seagrass ecosystems (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002; Campbell et al. 2011).

During the last decade, there has been an advancement in the development of fish census methods using video systems, such as remote underwater video systems, which can be baited or un-baited, diver operated video systems, and towed underwater cameras. These methods have generally been shown to overcome some of the biases associated with UVC, such as issues associated with diver presence (Fox and Bellwood 2008) and accuracy of fish size estimations (Harvey et al. 2001; Holmes et al. 2013; Goetze et al. 2015). At the same time, video systems may not be as accurate as UVC in detecting some species, and fish density (individuals per unit area), size distribution, and species richness can be underestimated in certain circumstances (Watson et al. 2005; Lowry et al. 2012; Tessier et al. 2013). Therefore, it is recommended that a combination of methods is used to accurately assess fish density and diversity (Watson et al. 2005; Colton and Swearer 2010; Lowry et al. 2012). However, compared to UVC, underwater video systems are costly and time consuming (Holmes et al. 2013) and thus their use depends on time and funding availability.

Fish surveys in **Paper II** (data also used in **Paper III**) were carried out through UVC by means of snorkelling. Despite its inherent biases, we used this method due to its rapid and inexpensive qualities and to make the collected data comparable to most of the research carried out in the region. To avoid observer bias, all UVCs were carried out by the same snorkeler (E Alonso Aller). Moreover, census method, duration, and speed were standardized throughout the study, and fish identification and size estimation were practiced prior to the study and again before each field season. UVCs were conducted using replicated 25×4 m belt transects which were randomly placed and located > 5 m apart and parallel to the shoreline. After deployment of a 25 m transect line, we allocated a period of 5–10 min to reduce fish disturbance. To account for differences in fish behaviour, the transects were swam through twice, first counting and identifying all

mobile, large fish, and the second time the less mobile, small fish. Swimming speed was kept constant (~0.1 m/s) to standardize search time per transect. All fish observed within or crossing the transect were identified to the lowest taxonomic level possible, usually species, counted, and their total body length was estimated to the nearest 5 cm. All fish surveys were carried out during high neap tide (± 3 h), when water movement was minimal.

Herbivory assays

There are different methods available that can be used for the estimation of herbivory rates of seagrasses by herbivorous fish in field conditions. Herbivory can be indirectly estimated based on the presence of fish bite marks in collected leaves by comparing the maximum leaf length reached on intact leaves versus leaves with fish bite marks (Cebrián and Duarte 1998). While this method is simple and cost-efficient, it presents some disadvantages. Indirect measurements of herbivory only provide information on cumulative grazing, i.e. over the species leaf life-span (Cebrián and Duarte 1998), making it unsuitable for seasonal studies on seagrass species with long leaf lifespans, such as *T. ciliatum* (Kamermans et al. 2001), and it can underestimate rates of consumption (Cebrián and Duarte 1998; Heck and Valentine 2006). Other indirect measurements of herbivory, such as counting the number of bite marks in collected leaves, have also been used in seagrass studies (e.g. Alcoverro and Mariani 2004), however this method may also underestimate herbivory rates (Zieman et al. 1984; Cebrián and Duarte 1998).

Alternatively, herbivory rates can be directly measured by using tethering techniques. Tethering involves the deployment of intact leaves in the field during a certain period of time. By measuring leaf length or area before and after deployment, herbivory rates can be estimated as the difference between the two measurements (Hay 1981). Even though tethering techniques could potentially lead to over- or underestimation of consumption rates (McGuinness 1997; Kirsch et al. 2002), tests of potential tether artefacts have shown that tethering does not lead to strong bias in the estimation of consumption rates (Kirsch et al. 2002). Thus, tethering assays are considered to be a reliable method to compare relative consumption rates over space and time (Heck and Valentine 2006) and they have been frequently used to assess herbivory rates in both seagrass and coral reef areas (Hay 1981; McClanahan et al. 1994; Kirsch et al. 2002; Prado et al. 2007).

To estimate herbivory rates in **Paper III**, we used a modified tethering technique. Most studies deploy the tethers attached to a rope or line (McClanahan et

al. 1994; Kirsch et al. 2002). In our study, since herbivory rates were to be estimated on *T. ciliatum* leaves, the tethers were directly attached to the stems of live *T. ciliatum* shoots to ensure that the tethers displayed a natural position and movement in the water column. Tethers were deployed for ~24h at a time during three consecutive days. The tethered leaves were photographed before and after deployment and the area of each leaf was measured from the photographs using image software. Herbivory rates were then calculated as leaf area lost (leaf area before - leaf area after) per day. To avoid overestimation of herbivory rates, samples where all leaves in a tether completely disappeared were removed from analyses, since they could have detached from the tethers for other reasons than grazing. Additionally, we recorded the number of bite marks present on randomly collected seagrass leaves.

Seagrass growth assays

Leaf production in seagrasses is commonly measured *in situ* using different leaf marking methods depending on the growth form of the seagrass species of interest – leaf-replacing vs. non-leaf-replacing forms (Short and Duarte 2001). In **Paper III** the focus species was *T. ciliatum*, a seagrass species with a leaf-replacing growth form, i.e. leaf tissue is continuously produced within a leaf cluster (Short and Duarte 2001). For species with this growth form, the hole punch method is recommended, and it has been widely used in the literature to measure production rates in several seagrass species (e.g. Zieman 1974; Dennison 1990; Cebrián et al. 1998; Uku and Björk 2005; Eklöf et al. 2008a). To measure leaf production, all leaves within a cluster are marked by punching a hole in the lower part of the outer leaf sheath. As the leaves grow, the marking scar will move, while the scars will stay in place in the sheath area. After a period of time, the marked shoots are collected and cut at the height of the original marking in the sheath area. Any leaf material below the marking scars is newly produced material. Leaf production rates can then be calculated as the area of newly produced material divided by the time interval.

Assessing the effectiveness of MPAs

Before-After vs. MPA-reference assessment

When assessing the effectiveness of MPAs, ideally, one should compare the present conditions with baseline data (collected prior to protection) in both the protected area and in reference areas (a Multiple Before/After Control/Impact design or MBACI) to be able to directly evaluate any potential effects of protection in ecosystem status (Underwood 1991; 1993). However, in most cases, and particularly in developing regions, the availability of baseline information (before the MPA was implemented) is scarce. A common approach used to assess MPA effectiveness in absence of baseline information is to compare the ecosystem status within the MPA to the status in a reference site (Watson et al. 2005; Micheli et al. 2012; Fraschetti et al. 2013). To avoid the influence of confounding factors, reference sites should be carefully selected so that environmental conditions are as similar as possible to the conditions within the MPA. In some cases, partially confounding factors can be included as statistical covariates. Here, we investigated the effects of MPAs on seagrass ecosystems in the WIO region, an area generally characterized by a lack of baseline information, especially regarding seagrasses (Waycott et al. 2009). We therefore used the MPA vs. reference site approach. In **Papers II** and **III**, a reference site was selected for each MPA, while in **Paper IV**, since two types of MPAs were included, the same number of sites were surveyed for each category (government-managed MPA, community-managed MPA, and unprotected). In **Paper IV**, we also applied a space-for-time replacement approach by sampling MPAs of different ages (time since protection) to be able to evaluate how time since protection affects MPA effectiveness (McClanahan and Graham 2005; Sala et al. 2012; Guidetti et al. 2014).

Drawing general conclusions about MPA effects

To be able to draw general conclusions, that not only assess the effects of a single MPA, the effectiveness of MPAs should be evaluated in several locations so that site-specific effects will not be confounded with MPA effects. However, this may not always be possible. In **Papers II** and **III**, two MPAs and two reference sites were evaluated. Even though these studies were originally planned to also include MPAs and reference sites along the Kenyan coast, the security situation in coastal Kenya during the start of the study prevented us from sampling repeatedly in

these locations. Moreover, due to the seasonal character of the studies and the dependence on specific tides, it was logistically problematic to include more locations. Despite the low site replication, both **Papers II** and **III** showed significant effects from MPAs, and thus, increased replication could have potentially only strengthened the results. In **Paper IV**, four sites of each category (government-managed MPAs, community-managed MPAs, and unprotected) were assessed, and thus there was a good level of replication at each management category level.

Piecewise path analyses

In ecological studies, researchers have traditionally used statistical methods that evaluate the effect of one or more factors on a single response variable, e.g. ANOVA or linear models. While these methods provide important information, they are not able to detect indirect effects (e.g. factor A influences factor B through changes in a third factor C). Given the complex nature of ecosystems, where interactions between species or between species and the environment do not occur in isolation, statistical methods that can identify such indirect effects are essential to improve our understanding of ecosystems (Wootton 2002).

Structural equation modelling (SEM) is a statistical method that aims to make a connection between empirical data and theoretical ideas (Grace et al. 2010). SEM combines multiple predictor and response variables into a single causal network where any variable may act as both predictor and response, allowing for the quantification of both direct and indirect effects (Grace 2006; Grace et al. 2010). SEM is usually represented by path diagrams, where the observed variables are connected through directional arrows (pathways) that indicate their relationship and represent hypothesised causal relationships between a set of variables (Bollen and Pearl 2013).

In the past, SEM has been mostly used in other fields of science, particularly in economy, social science, and psychology. However, SEM presents certain advantages that make it especially useful to study complex ecological systems. For instance, it allows to assess direct and indirect effects (Grace 2006; Lefcheck 2015) and to test causal implications of ecological interactions (Grace 2006; Shipley 2009), and can include latent variables (hypothesized variables with no direct measurements) to represent theoretical entities (Grace et al. 2010). Therefore, SEM has been increasingly used in ecological studies during the last decade (e.g. Alsterberg et al. 2013; Duffy et al. 2015; Lefcheck et al. 2018).

Path analysis is a variant of SEM that only uses observed data (with no latent variables). Traditionally, path analyses are estimated using a maximum likelihood approach on the observed variance-covariance matrix. However, this method presents certain limitations that restricts its use in certain conditions: it assumes that all observations are independent and that all variables are normally distributed (Grace 2006). To overcome some of these limitations, a piecewise estimation approach can be applied. PiecewiseSEM transforms the path diagram to a series of equations that are solved and evaluated individually (Lefcheck 2015). Since each equation is evaluated separately, different error distributions can be applied to each equation (Shipley 2009; Lefcheck 2015). Moreover, piecewiseSEM can account for hierarchical sampling designs, by including random factors, as well as for temporal autocorrelation, by including autocorrelation structures (Lefcheck 2015).

SEM and path analyses are useful tools for studying complex ecological interactions; however, care should be taken when specifying and interpreting the models. Piecewise SEM cannot resolve the directionality of pathways, i.e. whether factor A influences factor B or B influences A, and also cannot disentangle cyclic (feedback) relationships (Shipley 2009; Lefcheck 2015). Therefore, previous knowledge of the system is essential to be able to properly hypothesize causal relationships. Even though SEM has been often criticized for establishing causal relationships from correlations (Freedman 2004), in practice, causality is not directly derived from the models. Instead, SEM tests carefully specified models based on hypothesized causal relationships that are derived from previous research, scientific knowledge and logical arguments (Bollen and Pearl 2013). Thus, the validity of the causal relations relies on the validity of the theoretical causal hypotheses.

Main results and discussion

Seagrass temporal variability

Seagrass beds are known to be naturally dynamic in terms of cover, species composition, and distribution at both seasonal and inter-annual scales (Duarte et al. 2006). However, most research on seagrass temporal dynamics has focused on temperate mono-specific seagrass beds (e.g. Bernard et al. 2007; Shelton et al. 2016), while in the tropics, especially in developing regions, the knowledge about seagrass variability and species-specific responses is more limited.

In **Paper I**, we used ten years of monitoring data (2007–2016) to investigate the temporal dynamics within a multi-specific tropical seagrass bed. Despite some differences between the three transects, seagrass cover showed a general pattern of gradual decline, followed by a period of recovery. The length and range of the period of decline increased with distance to shore, so that the farthest transect experienced the longest and strongest period of decline, with up to 50% loss in seagrass cover. After reaching a minimum, seagrass cover increased in all three transects, although not yet reaching the levels of seagrass cover observed in 2007. Inter-annual changes in seagrass cover also varied between quarter of the year, e.g. seagrass decline was strongest during the first quarter of the year, leading to changes in seasonality patterns. We also observed some species-specific responses, suggesting some degree of response diversity within the assemblage. For instance, *S. isoetifolium* seemed to strongly decline in all transects where it was present, while the cover of other species such as *C. serrulata* increased instead. Species-specific changes also displayed some patterns of replacement between species, where increases in cover of a certain species were observed after another species had declined, e.g. between *C. rotundata* and *T. hemprichii*.

Seagrass cover not only varied over time and between transects. Distance along the transect (i.e. position of each quadrat on a transect) was a strong predictor of seagrass cover, indicating that seagrass cover is highly variable in time and at small spatial scales.

Seagrass species composition also displayed a pattern of disturbance and recovery that varied between transects (Figure 5). Seagrass species composition seemed to gradually deviate from the original species composition (observed in 2007). After a period of departure, there was a switch in the direction of year-to-

year changes in seagrass species composition, moving back towards the original composition. In the transect closest to shore, there seemed to be a short period of departure, rapidly returning to the original composition and stabilising. In the other two transects however, the period of departure was longer, and the changes were greater. By 2016, the species composition of the middle and farthest transects had not yet returned to the original composition.
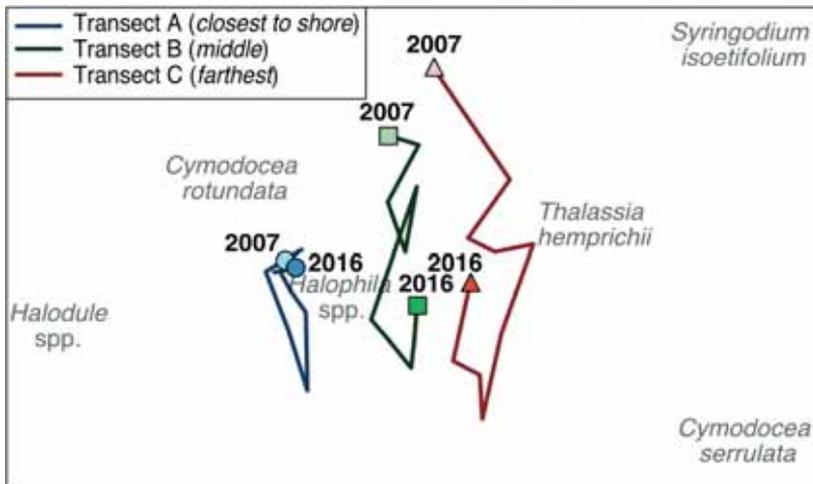
Figure 5 Year-to-year changes in seagrass species composition per transect

Causes of seagrass temporal variability

Seagrass beds are under increasing pressure from human disturbances (Waycott et al. 2009), ranging from local physical disturbance to global climate change effects. Even though seagrasses seem to be able to tolerate gradual changes in climatic conditions to a certain extent, extreme events such as heat waves or severe storms may pose a major threat (Preen et al. 1995; Campbell et al. 2006; Short et al. 2016).

In **Paper I**, we investigated factors that could potentially explain the observed pattern of decline and recovery in seagrass cover. Since the monitoring site is located in a well-enforced MPA, local physical disturbances within the MPA are unlikely to occur. Thus, we focused on the potential influence on 11 climate and tidal exposure variables that were chosen based on the literature. Out of these, five variables seemed to influence seagrass cover. Seagrass cover positively correlated with cloud cover and height of the diurnal low tide, and negatively with minimum air temperature, number of sunspots, and storms (Fig. 5 in **Paper I**).

Both cloud cover and increased tidal height may reduce seagrass exposure to direct sun during low tide events, reducing the risk of burning and desiccation (Björk et al. 1999). Increased temperature negatively influenced seagrass cover. Even though moderate increases in temperature may benefit seagrasses (Koch et al. 2013), extreme temperatures can have a strong adverse impact (Campbell et al. 2006; Koch et al. 2013). In field conditions, however, previous studies show contradictory effects of increased temperature on seagrasses (e.g. Freeman et al. 2008; Rasheed and Unsworth 2011; López-Calderón et al. 2013). Seagrass cover was also negatively correlated with the number of sunspots. Only one previous study has shown a similar effect (Marques et al. 2015), although other studies also observed an influence of solar radiation on seagrass cover (Unsworth et al. 2012). Finally, storms may negatively influence seagrasses through increases in water turbidity and sediment and water movement. Our results showed a negative correlation between the occurrence of storms and seagrass cover, in agreement with previous studies (Short et al. 2006a; Rasheed et al. 2014). Despite the significant influence of the above-mentioned climate and tidal variables, they explained very little of the seagrass cover temporal variability, indicating that other unmeasured variables may be more responsible for the observed pattern of decline and recovery.

Effects of MPAs on seagrass beds

This thesis also investigated the direct and indirect effects of MPAs on seagrasses, associated fish communities, and ecosystem processes in relation to monsoon seasonality (**Papers II** and **III**) and land-use (**Paper IV**).

Effects on seagrass-associated fish communities

Fish density and diversity

Overall, MPAs did not increase fish abundance or diversity in seagrass beds (**Paper II**), contrasting with other studies in the WIO region that show a general positive effect of protection on fish communities (McClanahan et al. 2009; McClanahan 2011; Tyler et al. 2011). This difference could potentially be explained by differences in focus habitat, differences in focus species, or due to relatively low site replication. First, while most studies have assessed the effects

of protection on coral reef communities (e.g. McClanahan 2011), our study focused on seagrass-associated fish. Compared to coral reefs, fish communities in seagrass beds are generally less diverse and often comprised of more mobile (less sedentary) species (Gillanders 2006), two qualities that could reduce the effectiveness of MPAs. Second, previous studies in the region have generally evaluated the effects of protection on a subset of fish species, often species that are targeted by fisheries (e.g. McClanahan et al. 2009). Even though MPAs have the potential to protect all species present in within the area, it is only logical that fishery target species will be benefitted the most. In our study, the whole fish community was taken into consideration, and thus the positive effects of protection on target species could have been underestimated. Finally, as discussed in the methods section, the study presented a relatively low level of site replication. Thus, any strong differences between individual sites was more heavily weighted in the overall results.

Fish community temporal stability

Paper II investigated the potential of MPAs to increase seasonal stability of seagrass-associated fish communities. The stabilising effect of MPAs seemed to differ between fish age classes. Juvenile and adult fish were more seasonally stable within MPAs than in the reference sites, both in terms of density and species composition, while subadult fish communities were less affected by MPAs. When considering the overall fish community, there were no effects of MPAs or seasonality, potentially due to differential responses between age classes leading to an overall stability. More importantly, MPAs seemed to stabilise fish communities through a combination of direct and indirect effects. Our results showed that seagrass cover was more seasonally stable within MPAs, indirectly increasing the stability of fish communities (Figure 6). Fish communities in seagrass beds are known to be influenced by seagrass cover (Gullström et al. 2008; Alonso Aller et al. 2014), and thus any seasonal changes in seagrass cover are likely to affect the associated fish communities. This is especially important for juvenile fish, since they depend on the seagrass canopy for protection from predation (Orth et al. 1984), and may explain why we observed a stronger effect of MPAs on juvenile fish communities.

An important functional group of fish in tropical seagrass beds are herbivorous fish that feed on seagrasses (from now 'herbivorous fish'). Even though only a few species of fish feed directly on seagrasses, they are highly important from both an ecological and a socio-economic perspective (de la Torre-Castro et al. 2008; Gullström et al. 2011). In **Paper III**, we showed that, even though herbivorous fish density varied seasonally, this variability was weaker within than outside MPAs (Fig. 4 in **Paper III**).
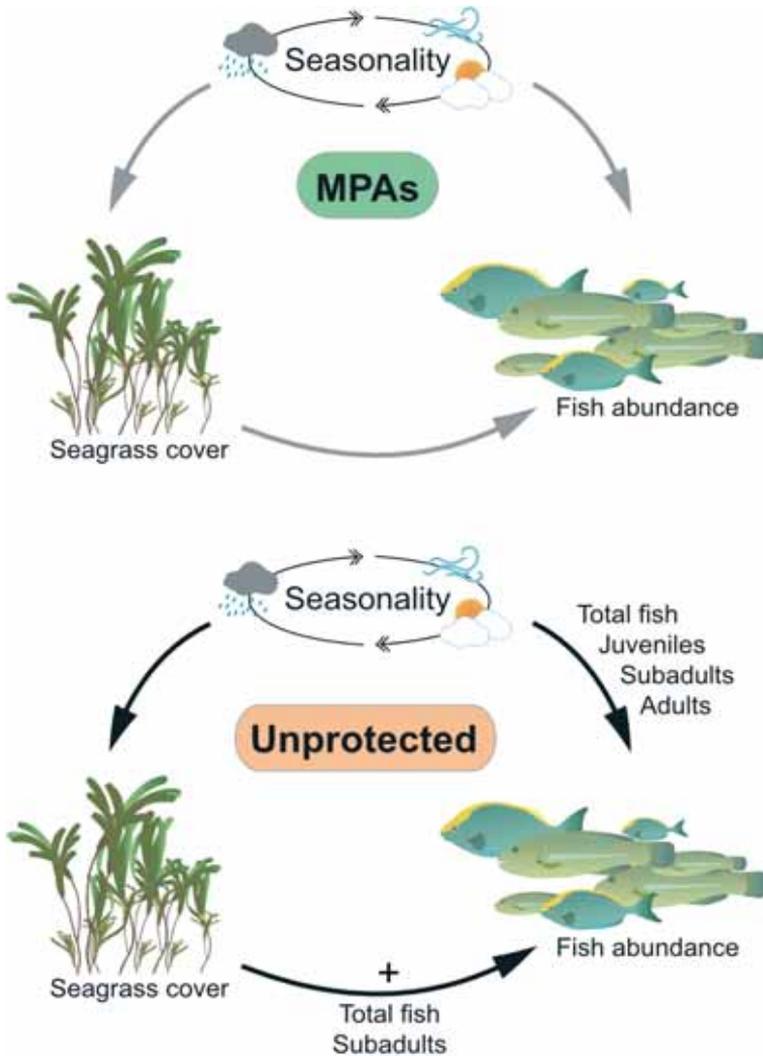
Figure 6 Direct and indirect (habitat-mediated) effects of seasonality on fish densities in MPAs and unprotected seagrass beds. Grey arrows are non-significant effects

Effects on ecosystem processes

Herbivory is a key ecosystem process structuring tropical seagrass ecosystems and the services they generate (Scott et al. 2018). While intense herbivory events may cause declines, or even losses, in seagrass biomass (McGlathery 1995; Eklöf

et al. 2008b), moderate levels of herbivory can promote seagrass growth (Valentine et al. 1997; Vergés et al. 2008) through 'overcompensation', a mechanism by which plants compensate for the loss of tissue by using stored resources to increase growth (McNaughton 1983; Valentine et al. 1997). The link between herbivores, herbivory, and seagrass growth depends on multiple factors that can in turn be influenced by human activities (Fig. 1 **Paper III**). For instance, some of the main seagrass herbivores (e.g. *Leptoscarus vaigiensis* and *Siganus sutor*) in the WIO region are target species of high economic value in artisanal fisheries (Jiddawi and Öhman 2002; de la Torre-Castro et al. 2014). Thus, reductions in herbivorous fish abundance due to fishing will affect herbivory rates and could ultimately affect seagrass growth. Herbivorous fish abundance may also vary with changes in seagrass biomass (Gullström et al. 2008; Alonso Aller et al. 2014), which can also vary seasonally (Erftemeijer and Herman 1994). Herbivory rates also depend on herbivore type, e.g. fish vs. sea urchin (McClanahan et al. 1994), which are in turn affected by fishing pressure (Alcoverro and Mariani 2004; Prado et al. 2008) and nutrient load (Tewfik et al. 2007). Seagrass growth can also vary seasonally (Uku and Björk 2005) and with changes in the light environment (Eklöf et al. 2009b). Moreover, both herbivory and growth may depend on the presence and abundance of seagrass epiphytes (Montague et al. 1995; Brodersen et al. 2015), which is also influenced by seasonality (Uku and Björk 2001).

Considering these potential interactions, in **Paper III** we investigated the direct and indirect effects of seasonality on seagrass herbivory and growth rates in MPAs and unprotected areas. We found clear differences between MPAs and the reference sites (Figure 7). Within MPAs, seasonally high herbivorous fish densities increased herbivory rates, which in turn positively influenced seagrass growth. However, this indirect effect of herbivore abundance on growth rates was not apparent in the unprotected reference sites. Moreover, the effects of seasonality on herbivorous fish and epiphyte abundance were stronger in the reference sites, suggesting that MPAs may also have a role stabilising key ecosystem processes such as herbivory.
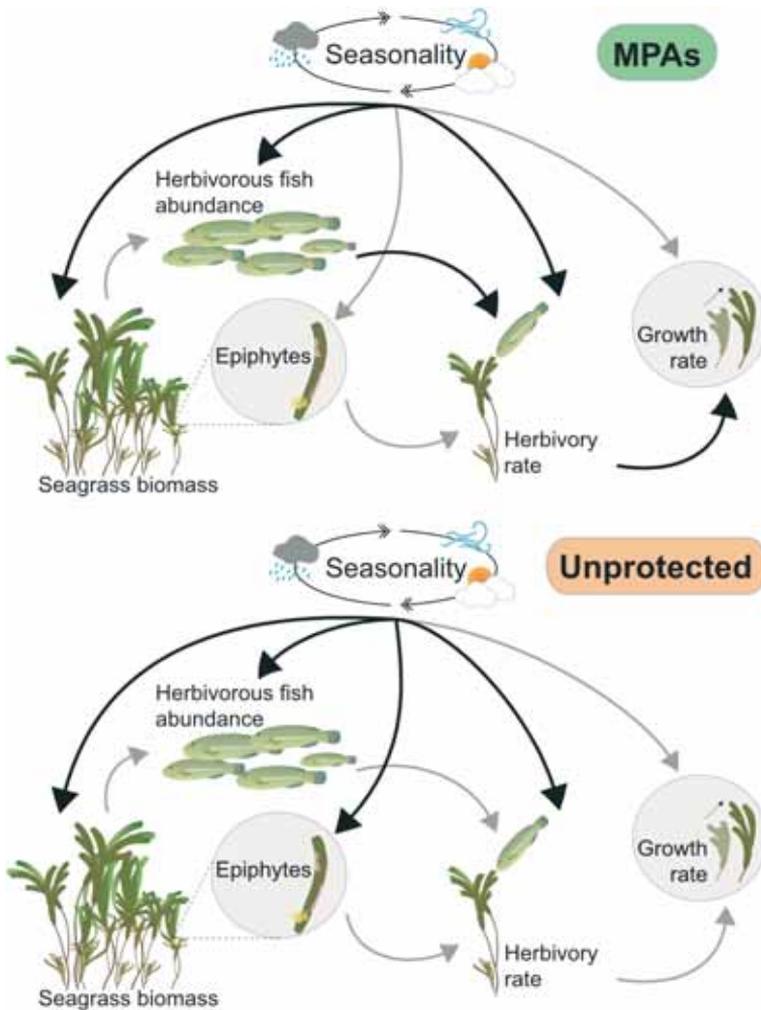
Figure 7 Direct and indirect effects of seasonality on herbivory and growth rates in MPAs and unprotected seagrass beds. Grey arrows are non-significant effects

Effects of MPAs and land-use on seagrasses

Even though MPAs seem to protect seagrasses from certain local disturbances such as intense grazing by sea urchins (McClanahan et al. 1994; Alcoverro and Mariani 2004), their potential to prevent the effects from more diffuse and spatially distant disturbances is unclear. Disturbances originating from intense land-use, such as increased nutrient- or sediment-rich runoff, can strongly influence

seagrasses in terms of cover and species composition (Terrados et al. 1998; Rivera-Guzmán et al. 2014), and recent studies have argued that MPAs may not be able to protect seagrasses from such disturbances (Eklöf et al. 2009a; Quiros et al. 2017). Moreover, seagrasses present a high phenotypic plasticity, i.e. they can change their morphological or physiological traits in response to changes in environmental conditions (Short and Wyllie-Echeverria 1996; Peralta et al. 2005; Cabaço et al. 2009). Therefore, disturbances originating from land-use may affect seagrass community trait composition not only through changes in species composition, but also through changes in individual plant traits.

In **Paper IV**, we evaluated the single and interactive effects of MPAs and land-use on seagrass species and trait composition. We considered land-use effects at two different scales – site and river basin scales – to account for both local and distant disturbances. Both MPAs and land-use variables influenced seagrass species and trait composition (Figure 8). Seagrass species composition was influenced by MPAs and land-use variables at both the local and the river basin scales. MPAs seemed to promote a change in dominant species within seagrass beds, from *E. acoroides* and/or *T. hemprichii* in the unprotected reference sites, to *T. hemprichii* in the recently-established, community-managed MPAs, and *T. ciliatum* in the old, government-managed MPAs. A similar shift in species dominance between MPAs and unprotected areas have been previously described in the region (McClanahan et al. 1994; Alcoverro and Mariani 2004). Seagrass trait composition was mostly explained by species composition, but MPAs and land-use at the river basin scale also had a significant effect. Thus, land-use and MPAs seem to influence seagrass trait composition both directly, through phenotypic plasticity, and indirectly, through changes in species composition. Among the seagrass traits considered, land-use and management mostly influenced seagrass above-ground biomass and leaf length and width. MPAs promoted seagrass with wider leaves and higher above-ground biomass. Regarding land-use, a higher proportion of agricultural land seemed to promote seagrasses with longer, narrower leaves, and lower above-ground biomass. Variability in these traits, particularly leaf length and above-ground biomass, seemed to be strongly influenced by phenotypic plasticity (Fig. 3 in **Paper IV**). Seagrass trait composition was also influenced by distance to shore, particularly through phenotypic plasticity, by promoting seagrasses with shorter leaves and higher below-ground biomass.

We also assessed a potential interaction between MPAs and land-use effects on seagrasses, under the assumption that the presence of MPAs may buffer the effects of land-use. MPAs did not seem to buffer the effects of land-use on either species or trait composition, with land-use showing a similar effect on seagrasses both in the old, government-managed MPAs and in the unprotected reference sites. However, seagrass beds in the community-managed MPAs did not show

any influence from land-use neither at the site nor at the river basin scales. This lack of influence of land-use in the community-managed MPAs could potentially be explained by their location, often in rural areas with low population density that do not attract as much tourism as the old government-managed MPAs. However, all land-use variables presented a lower variability the community-managed MPAs than across unprotected sites and government-managed MPAs, and thus our data may not be ideal to test this interaction.
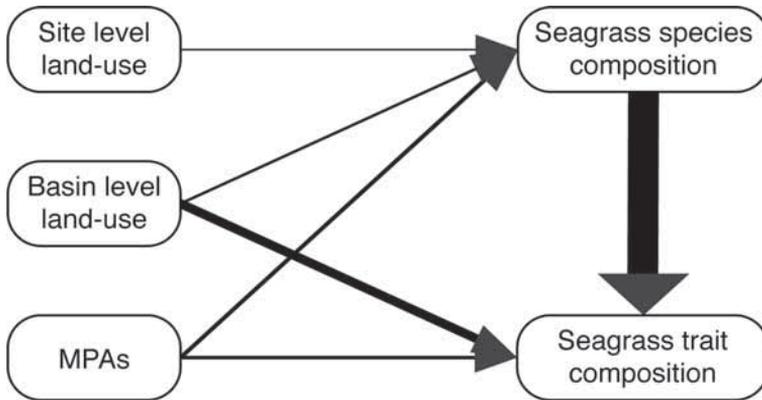

Figure 8 Semi-conceptual model illustrating the direct and indirect effects of MPAs and land-use on seagrass trait composition

Synthesis

Temporal dynamics in seagrass ecosystems

This thesis investigated the spatial and temporal (seasonal and inter-annual) variability of seagrass beds, highlighting the highly dynamic nature of these ecosystems.

Seagrass beds are characterised by a high temporal variability, with seagrass cover and species composition varying between years and seasons (**Paper I**). More importantly, these changes may further influence ecological interactions and ecosystem processes. Changes in seagrass cover, biomass, and species composition can influence the density and diversity of associated organisms (e.g. Adams 1976; Vonk et al. 2010). This thesis demonstrates that seagrass-associated fish communities vary seasonally in terms of abundance and species composition, and that this effect is caused by a combination of direct and indirect (habitat-mediated) effects (**Paper II**). Seasonality can directly affect fish communities in terms of reproduction and recruitment, and/or migration patterns (Pollard 1984; McClanahan 1988; Abesamis et al. 2015). At the same time, seasonality seems to also indirectly affect fish communities through changes in seagrass cover and biomass, which influence habitat quality. Increased seagrass cover and biomass have a positive influence on fish density (Gullström et al. 2008; Alonso Aller et al. 2014) through increasing protection from predators (Orth et al. 1984; Heck and Orth 2006) and food availability (Bell and Westoby 1986). Changes in seagrass cover and biomass can also influence fish species composition. For example, seagrass beds with higher seagrass biomass often present a higher proportion of herbivorous fish (Alonso Aller et al. 2014). By altering the presence and abundance of key functional groups, such as herbivores, seasonality can indirectly influence important ecosystem processes, e.g. herbivory (**Paper III**).

Seagrasses also display a high spatial variability at a wide range of spatial scales, and in response to disturbances such as land-use, both in terms of species and trait composition. Previous studies have shown that impacts from land-use, such as increased sediment-rich runoff, can affect seagrass beds in terms of cover and species composition (Terrados et al. 1998; Quiros et al. 2017), by selecting for the most resistant species. At the same time, seagrasses have been shown to pre-

sent a high phenotypic plasticity, by altering their morphological and physiological traits in response to disturbances such as light reductions or nutrient enrichment (Udy and Dennison 1997; Collier et al. 2012; La Nafie et al. 2013). This thesis demonstrates that land-use can induce changes in seagrass species and trait composition (**Paper IV**). On the one hand, phenotypic plasticity can enhance seagrasses ability to resist changes in environmental condition (Maxwell et al. 2013; McDonald et al. 2016), which is of especial importance given their role as ecosystem engineers. On the other hand, by modifying seagrass species and trait composition, land-use impacts can have indirect effects on associated organisms and ecosystem processes. Our results suggest that higher proportion of agricultural land at the river basin level can influence seagrasses by reducing aboveground biomass both through shifts towards species with lower biomass and through phenotypic plasticity. Seagrass biomass has been shown to strongly influence associated fish communities by enhancing fish abundance and increasing proportion of herbivorous fish (e.g. Alonso Aller et al. 2014), which in turn can influence key trophic interactions (**Paper III**). Similar indirect effects could also be expected to be driven by changes in seagrass cover and species composition at longer time scales, such as the ones observed in **Paper I**.

Temporal and spatial changes in seagrasses and associated fauna can further influence key ecosystem processes through biotic interactions like trophic cascades (**Paper III**). We found that seasonality can influence fish density both directly and indirectly through changes in seagrass cover (**Paper II**). Seasonally higher herbivorous fish density can increase herbivory rates (McClanahan et al. 1994). At the same time, herbivory at moderate levels may promote seagrass growth (Valentine et al. 1997; Vergés et al. 2008), which in theory could generate a positive feedback that promotes ecosystem stability. This thesis shows evidence of a positive interaction between herbivorous fish, herbivory rates, and seagrass growth (**Paper III**). However, this interaction may be weakened, or even broken, under anthropogenic disturbance like removal of herbivores through fishing.

The temporal and spatial variability of seagrass beds can also be influenced by seagrass species diversity. Increased species diversity often implies a higher response diversity (that different co-occurring species respond in different ways to a shared stressor) due to different environmental tolerances or to reduced competition (McCann 2000; Elmqvist et al. 2003; Worm et al. 2006), increasing the resilience of ecosystems to environmental change (Hooper et al. 2005; Bernhardt and Leslie 2013). In tropical regions, seagrass beds are often multi-specific, with several seagrass species co-occurring within a single bed. Given their higher diversity, multi-specific seagrass beds may also show a high response diversity (Elmqvist et al. 2003), potentially increasing their resistance to environmental stress. **Paper I** demonstrates that, within multi-specific seagrass beds, individual

species may respond differently to disturbances. Even though seagrass cover showed a general pattern of decline followed by recovery over the 10-year period, some species declined more than others, while other species increased following the decline of another species, causing a pattern of replacement. These could be caused by a combination of high response diversity between species (Campbell et al. 2006) and competition for e.g. space or light, thus promoting growth of less competitive, opportunistic species. Similarly, response diversity can also affect the stability of seagrass-associated fish communities. In **Paper II**, different fish age classes were influenced by seasonality; however, there was no effect on overall fish density, potentially due to the different responses of each age class. Similar stabilising effects of diversity have been shown for fish communities elsewhere (e.g. Worm et al. 2006; Duffy et al. 2016).

Protection of seagrass ecosystems

This thesis also evaluated the potential of MPAs to protect seagrass beds from fishing, seasonal climate variability, and land-use effects.

MPAs can increase stability of ecosystems in response to long-term changes and point disturbances (Babcock et al. 2010; Bates et al. 2014; Mellin et al. 2016). However, so far, few studies have assessed the stabilising effect of MPAs in seagrass ecosystems and in relation to seasonal variability (but see Francour 1994; Harmelin et al. 1995; Seytre and Francour 2009). This thesis evaluated the potential of MPAs to buffer the effects of seasonal variability on seagrass-associated fish communities and ecosystem processes. Regarding fish communities, stabilising effects of MPAs differed between fish groups. MPAs increased seasonal stability of juvenile and adult fish, while subadult fish were less influenced (**Paper II**). The effects of MPAs on fish temporal stability seemed to be both direct and indirect, mediated by reduced variability in seagrass cover. MPAs also increased seasonal stability of herbivorous fish (**Paper III**). Herbivorous fish are a key functional group that influence important ecosystem processes such as herbivory, which in turn may influence seagrass growth (e.g. Vergés et al. 2008), promoting a positive feedback that enhances ecosystem stability. In seagrass beds within MPAs, there was a positive link between herbivore abundance, herbivory, and seagrass growth rates. However, this link was not observed in the unprotected sites, where seasonality seemed to be the main factor influencing herbivory (**Paper III**). These results show evidence that MPAs can potentially increase seasonal stability of ecosystems to a certain extent, and that they can help to maintain, or facilitate the recovery of key ecosystem processes and interactions.

Even though MPAs may be able to protect ecosystems from local disturbances, their potential to buffer distant and large-scale disturbances has been questioned (e.g. Eklöf et al. 2009a; Darling et al. 2010; Quiros et al. 2017). In **Paper IV**, we assessed the potential for MPAs to buffer impacts from land-use. MPAs seemed to protect seagrasses to a certain extent. For instance, there was a shift in species composition from seagrass beds dominated by *E. acoroides* and/or *T. hemprichii* in unprotected sites to dominance of climax species such as *T. ciliatum* in the old, large MPAs. However, land-use effects on species and trait composition were apparent in both MPAs and unprotected sites, indicating that MPAs may not be able to buffer the impacts from land-use on seagrass beds.

Finally, in **Paper I**, seagrass cover showed a considerable inter-annual variability, including periods of strong declines (up to 50%). Even though the temporal variability of seagrass cover and potential effects of climate variables was only assessed at one site, this site is a strongly-enforced MPA, where extractive activities, as well as mooring, are not allowed. Although the causes of decline are not clear, given the protection status of the area, it is likely that disturbances originating outside the MPA borders may have been involved (see also **Paper IV**), suggesting that MPAs may not be sufficient to protect seagrass beds from disturbances originating outside of MPA borders.

Implications for management

Overall, MPAs seem to be able to protect seagrasses and seagrass ecosystems only to a certain extent. Most MPAs focus on reducing or fully stopping fishing activities in the area, as well as reducing local physical disturbances. Thus, positive effects of protection are more likely to appear in relation to fish communities, and indirectly in ecological interactions and processes in which fish may be involved. However, seagrasses can be strongly influenced by stressors originating outside MPA boundaries, such as effects of land-use or climate variability. In such cases, MPAs may not be sufficient to protect seagrass ecosystems, particularly given the role of seagrasses as ecosystem engineers. A recent study demonstrated that management of watersheds can lead to reductions in nutrient loads, and in turn enhance the recovery of degraded submerged aquatic vegetation along large spatial scales (Lefcheck et al. 2018). Thus, to ensure the maintenance of these key coastal ecosystems and the services they provide, management strategies should be improved to manage resource use in both the marine and the adjacent terrestrial environments.

Future perspectives

This thesis demonstrates that even though MPAs may prove useful to protect seagrass-associated fish communities and enhance ecosystem processes to a certain extent, they may not be effective to prevent the impact from disturbances originating outside their borders, e.g. land-use.

In **Paper I,** we showed that seagrasses present a high temporal and spatial variability, even within a well-enforced MPA. Seagrass cover gradually declined over a period of 4–7 years, followed by a steady increase. Changes in local climate and tidal conditions could only explain a minimal part of the variability in seagrass cover, indicating that other variables not measured in the study may be responsible. This suggests that seagrass monitoring programmes should consider in advance potential drivers of seagrass change, both at the local and regional scales, and include measurements of such drivers as part of the monitoring. For example, changes in sediment transport and accumulation can strongly influence seagrasses (e.g. Cabaço et al. 2008), and could be easily measured, e.g. by using sediment traps.

MPAs increased temporal stability of juvenile, and to a certain extent adult, fish assemblages (**Paper II**) and the results suggest that this effect may also be apparent for certain fish functional groups, e.g. herbivorous fish (**Paper III**). Changes in individual functional groups may lead to changes in overall functional diversity, with further consequences for ecosystem function and stability (Tilman 1997; Duffy et al. 2016). Thus, further studies should investigate the effects of MPAs on the temporal stability of individual functional groups and functional diversity based on multiple fish traits.

The results in this thesis also show that MPAs strengthen the link between herbivores, herbivory rates, and seagrass growth (**Paper III**), suggesting the presence of a positive feedback that promotes stability. However, the mechanisms behind this MPA effect are not yet clear. For instance, a stronger link between herbivore abundance and herbivory rates could be caused by a generally higher abundance of herbivorous fish. However, while MPAs had higher herbivorous fish abundance than the reference sites, this difference was not significant. A replication of this study including more MPAs and reference sites could potentially increase the statistical power and thus allow us to confirm this hypothesis.

Studies including field experiments, e.g. by using exclusion cages, or by simulating herbivory through clipping, could also provide further insight into the mechanisms behind these results.

While this thesis provides new information regarding the potential of MPAs to increase the seasonal stability of seagrass ecosystems, the results are based on a one-year seasonal study. Ideally, similar studies should be carried out over longer time periods (> 1 year) to account for potential differences between years and to be able to draw more general conclusions.

Finally, regarding the potential of MPAs to protect seagrass beds from land-use disturbances, our results demonstrate that seagrasses seem to be influenced by land-use regardless of protection, even though MPAs also affect seagrasses (**Paper IV**). Seagrasses are known to be temporally dynamic in terms of species composition (Duarte et al. 2006) and previous studies have shown that they may alter their morphology in response to modified environmental conditions over short time scales (Collier et al. 2012). Our results suggest that land-use impacts were mainly caused by presence of agriculture, which may lead to increased nutrient- and sediment-rich runoff. Since runoff may greatly vary seasonally (McClanahan 1988), further studies should investigate the potential seasonality of the observed effects of land-use on seagrass species and trait composition. Moreover, effects of land-use and MPAs on seagrass physiological traits (e.g. growth rates) could also prove valuable by provide insight into the mechanism through which seagrasses may be able to persist changes in environmental conditions.

Sammanfattning (Svenska)

Sjögräsängar är mycket produktiva kustekosystem som upprätthåller en hög biologisk mångfald av associerad fauna och flora. Ökande mänsklig påverkan i form av t ex övergödning, fiske och klimatförändringar hotar sjögräsekosystem och har redan lett till stora förluster av sjögräs världen över. Marint områdesskydd (t ex marina reservat eller fiskefredade zoner) har blivit en av nyckelstrategierna för att förvalta kustekosystem och deras associerade resurser världen över och har ofta visats vara framgångsrika i att skydda och stärka fiskpopulationer. Relativt få studier har däremot utvärderat effekterna av marina skyddsområden på sjögräsekosystem, och det finns indikationer på att skyddade områden möjligen inte till fullo lyckas skydda sjögräs, särskilt inte från störningar som uppkommer utanför reservatsgränser (som t ex övergödning från jordbruk och urbana miljöer via landavrinning). Mot denna bakgrund syftar denna avhandling till att undersöka direkta och indirekta effekter (genererade av biologiska interaktioner) av marina skyddsområden för tropiska sjögräsängar, associerade organismer (särskilt fiskar) och ekosystemsprocesser (såsom herbivori).

Avhandlingen består av tre delar; först använde vi en 10 år lång tidsserie av sjögräsdata från ett skyddat område för att utvärdera temporala förändringar i sjögrästäckning och artsammansättning i relation till förändringar i miljöförhållanden (**Studie I**). Därefter undersökte vi potentialen hos skyddade områden att förbättra stabiliteten hos sjögräsekosystem över tid med hjälp av en 10 månaders fältstudie. Vi kartlade sjögräsassocierade fisksamhällen (**Studie II**) och uppskattade sjögrästillväxt och betningshastighet (**Studie III**) under tre olika säsonger, både inom skyddade och oskyddade (fiskade) områden. Slutligen, för att utvärdera de simultana effekterna av skyddade områden och markanvändning på sjögräsekosystem, undersökte vi sammansättningen av sjögräsarter och egenskaper inom myndighetskontrollerade marina nationalparker, lokalt förvaltade fiskefrednings-områden och oskyddade områden (**Studie IV**).

Den undersökta sjögräsängen i **Studie I** visade en hög tidsmässig och rumslig variation, med en minskning i täckningsgrad och förändring i artsammansättning över tid, följd av en period av återhämtning. De observerade förändringarna kunde inte starkt kopplas till någon av de klimateller tidvattenvariabler som undersöktes, vilket tyder på att potentiella orsaker till nedgången kan ha uppkommit utanför det skyddade områdets gränser. Resultaten från den säsongsbaserade fältstudien visade att skyddade områden ökade stabiliteten hos sjögräsassocierade fisksamhällen över tid, särskilt för juvenil fisk (**Studie II**). Studien visade också på en positiv koppling mellan betande fisk, betestryck och tillväxt hos sjögräs (**Studie III**), vilket tyder på marina skyddsområden skulle kunna ha en positiv återkoppling som främjar ekosystemens stabilitet. Slutligen föreföll skyddade områden påverka artsammansättning men också egenskaper hos sjögräs (genom att gynna stresskänsligare arter), men föreföll inte lyckas skydda sjögräset från effekter av landanvändning, där sjögräset visade liknande förändringar i art- och egenskapskomposition såväl inom som utanför skyddade områden (**Studie IV**). Baserat på ovan nämnda resultat bidrar avhandlingen till en växande litteratur som indikerar att skyddade områden allena troligtvis inte är tillräckliga för att skydda sjögräsekosystem, och att förbättrade förvaltningsstrategier kan vara nödvändiga för att bevara dessa viktiga kusthabitat.

Resumen (Español)

Las praderas marinas son ecosistemas altamente productivos que sostienen una rica y diversa fauna y flora. El incremento de las presiones de origen antropogénico amenaza estos ecosistemas y ya ha dado lugar a grandes pérdidas de pastos marinos en todo el mundo. Las Áreas Marinas Protegidas (AMP) se han convertido en una de las estrategias clave para la gestión de los ecosistemas y recursos costeros. A pesar de que su éxito en la protección de ecosistemas marinos se ha demostrado a menudo, relativamente pocos estudios han evaluado los efectos de las AMP sobre las praderas marinas y hay indicios de que pueden no ser capaces de proteger completamente las hierbas marinas, especialmente de perturbaciones que se originen fuera de sus límites. En este contexto, esta tesis tiene como objetivo investigar los efectos directos e indirectos (aquellos mediados por interacciones bióticas) de las AMP sobre las praderas marinas tropicales, las comunidades de peces asociadas y los procesos de ecosistema.

La tesis consta de tres partes. Primero, utilizamos 10 años de datos de monitoreo de pastos marinos dentro de una AMP para evaluar la variabilidad temporal en la cobertura y la composición de especies de pastos marinos en relación con cambios en las condiciones ambientales (**Artículo I**). En segundo lugar, investigamos el potencial de las AMP para mejorar la estabilidad temporal de los ecosistemas de pastos marinos mediante un estudio de campo de 10 meses donde examinamos las comunidades de peces asociadas a pastos marinos (**Artículo II**) y estimamos las tasas de crecimiento y herbivoría de pastos marinos (**Artículo III**) durante tres estaciones diferentes en AMP y sitios no protegidos. Finalmente, para evaluar los efectos de las AMP y el uso de suelo en los ecosistemas de pastos marinos, examinamos la composición de especies y rasgos de pastos marinos en AMP administradas por el gobierno, AMP administradas por la comunidad y sitios no protegidos (**Artículo IV**).

La pradera marina monitoreada en el **Artículo I** mostró una alta variabilidad temporal y espacial, con un declive en la cobertura y cambios en la composición de especies, seguido por un periodo de recuperación. Este patrón no pudo asociarse con ninguna de las variables climáticas y de mareas consideradas, lo que sugiere que los posibles factores que causaron el declive pueden haberse originado fuera de los límites de la AMP. Los resultados del estudio de campo mostraron que las AMP aumentaron la estabilidad temporal de las comunidades de peces asociadas a los pastos marinos, particularmente de peces juveniles (**Artículo II**), y fortalecieron un vínculo positivo entre peces herbívoros, tasas de herbivoría y tasas de crecimiento de pastos marinos (**Artículo III**), sugiriendo la presencia de una retroalimentación positiva que promueve la estabilidad. Finalmente, las AMP afectaron la composición de especies y rasgos de los pastos marinos (seleccionando especies más sensibles al estrés) pero no parece que fueran capaces de proteger las hierbas marinas de los efectos del uso de suelo, con pastos marinos mostrando cambios similares en la composición de especies y rasgos dentro y fuera de las AMP (**Artículo IV**). Teniendo en cuenta estos resultados, esta tesis construye sobre una creciente literatura que indica que las AMP por sí solas pueden no ser suficientes para proteger los ecosistemas de pastos marinos y que puede ser necesario mejorar las estrategias de gestión para preservar estos importantes hábitats costeros.

Acknowledgements

I would like to take this opportunity to thank everyone who made this thesis possible. This thesis could not have come into existence without the support, inspiration, and friendship of so many people that have crossed my path during my PhD.

First and foremost, I would like to thank my supervisor Johan Eklöf. Thank you for not only giving me the opportunity to work with you, but also for the continued support and guidance. I also would like to thank my co-supervisors Martin Gullström, Charlotte Berkström, and although only briefly, Nils Kautsky, for their assistance and encouragement. I would also like to express my gratitude towards Kristoffer Hylander and Francisco Nascimento for the careful revision and scientific input they had on my thesis.

This work was made with the contribution of many collaborators. A special thanks to Lina Nordlund and Angelica Chirico, for constructive collaborations and for making the first and fourth papers possible. Thanks to Hans Linderholm for providing data and scientific input into the first paper. I sincerely thank Narriman Jiddawi and all the staff at the Institute of Marine Science (IMS) in Zanzibar for valuable assistance during my time there. Thank you to my one and only master student, Emily Ramqvist, to my local field assistants, Khamis Rabii and Said Shaib, and all boat operators in Zanzibar for indispensable help during the long days in the field. Thanks also to the staff and administration at Mnemba Island and at Chumbe Island Coral Park, especially Ulli Kloiber, for logistic assistance while in the field. I also wish to thank Christiaan Vermeulen for assistance in the lab and Erik Öhrner for assistance with GIS analyses.

My gratitude also goes to all of you at DEEP and particularly to my closest colleagues and friends, past and present: Peter B, Jennie S, Lina R, Isa K, Jens N, Alfred B, and Chiara D. A special thanks to Anni (who surely deserves a whole paragraph, but I will just skip it now and thank you in person) and to Stina T, Serena D, Elina K, and Maria E, for all the great times, and for making the not so great times better.

Finally, I would like to thank my family. Gracias a mis padres, por el continuo apoyo y ánimo a seguir adelante. Me disteis todas las oportunidades en la vida y me convertisteis en la persona que soy. Gracias por todo.

References

Abesamis RA, Jadloc CRL, Russ GR (2015) Varying annual patterns of reproduction in four species of coral reef fish in a monsoonal environment. Mar Biol 162:1993–2006. doi: 10.1007/s00227-015-2725-6

Adams SM (1976) The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. J Exp Mar Biol Ecol 22:269–291.

Alcoverro T, Mariani S (2004) Patterns of fish and sea urchin grazing on tropical Indo-Pacific seagrass beds. Ecography 27:361–365. doi: 10.1111/j.0906-7590.2004.03736.x

Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecol Appl 8:S79–S92. doi: 10.1890/1051-0761(1998)8[S79:MRANBN]2.0.CO

Alonso Aller E, Gullström M, Eveleens Maarse FKJ, Gren M, Nordlund LM, Jiddawi N, Eklöf JS (2014) Single and joint effects of regional- and local-scale variables on tropical seagrass fish assemblages. Mar Biol 161:2395–2405. doi: 10.1007/s00227-014-2514-7

Alsterberg C, Eklöf JS, Gamfeldt L, Havenhand JN, Sundbäck K (2013) Consumers mediate the effects of experimental ocean acidification and warming on primary producers. PNAS 110:8603–8608. doi: 10.1073/pnas.1303797110

Babcock RC, Shears NT, Alcala AC, Barrett NS, Edgar GJ, Lafferty KD, McClanahan TR, Russ GR (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. PNAS 107:18256–18261. doi: 10.1073/pnas.0908012107

Ball D, Soto-Berelov M, Young P (2014) Historical seagrass mapping in Port Phillip Bay, Australia. J Coast Conserv. doi: 10.1007/s11852-014-0314-3

Barbier EB (2017) Marine ecosystem services. Curr Biol 27:R507–R510. doi: 10.1016/j.cub.2017.03.020

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193.

Barrett NS, Buxton CD, Edgar GJ (2009) Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. J Exp Mar Biol Ecol 370:104–119. doi: 10.1016/j.jembe.2008.12.005

Bates AE, Barrett NS, Stuart-Smith RD, Holbrook NJ, Thompson PA, Edgar GJ (2014) Resilience and signatures of tropicalization in protected reef fish communities. Nat Clim Chang 4:62–67. doi: 10.1038/nclimate2062

Bell JD, Craik GJS, Pollard DA, Russell BD (1985) Estimating length frequency distributions of large reef fish underwater. Coral Reefs 4:41–44. doi: 10.1007/BF00302203

Bell JD, Westoby M (1986) Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. J Exp Mar Biol Ecol 104:249–274.

Bernard G, Boudouresque CF, Picon P (2007) Long term changes in *Zostera* meadows in the Berre lagoon (Provence, Mediterranean Sea). Estuar Coast Shelf Sci 73:617–629. doi: 10.1016/j.ecss.2007.03.003

Bernhardt JR, Leslie HM (2013) Resilience to climate change in coastal marine ecosystems. Ann Rev Mar Sci 5:371–392. doi: 10.1146/annurev-marine-121211-172411

Björk M, Short F, McLeod E, Beer S (2008) Managing seagrasses for resilience to climate change. IUCN, Gland, Switzerland

Björk M, Uku J, Weil A, Beer S (1999) Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. Mar Ecol Prog Ser 191:121–126.

Blackburn M, Laurs RM, Owen RW, Zeitzschel B (1970) Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical pacific. Mar Biol 7:14–31. doi: 10.1007/BF00346804

Bollen KA, Pearl J (2013) Eight myths about causality and structural equation models. In: Handbook of causal analysis for social research. Springer Netherlands, Dordrecht, pp 301–328

Brander LM, van Beukering P, Cesar HSJ (2007) The recreational value of coral reefs: A meta-analysis. Ecol Econ 63:209–218. doi: 10.1016/j.ecolecon.2006.11.002

Brock RE (1982) A critique of the visual census method for assessing coral reef fish Populations. Bull Mar Sci 32:269–276(8).

Brodersen KE, Lichtenberg M, Paz L-C, Kühl M (2015) Epiphyte-cover on seagrass (*Zostera marina* L.) leaves impedes plant performance and radial O_2 loss from the below-ground tissue. Front Mar Sci 2:217–11. doi: 10.3389/fmars.2015.00058

Cabaço S, Machás R, Santos R (2009) Individual and population plasticity of the seagrass *Zostera noltii* along a vertical intertidal gradient. Estuar Coast Shelf Sci 82:301–308. doi: 10.1016/j.ecss.2009.01.020

Cabaço S, Santos R, Duarte CM (2008) The impact of sediment burial and erosion on seagrasses: A review. Estuar Coast Shelf Sci 79:354–366. doi: 10.1016/j.ecss.2008.04.021

Campbell SJ, Kartawijaya T, Sabarini EK (2011) Connectivity in reef fish assemblages between seagrass and coral reef habitats. Aquat Biol 13:65–77. doi: 10.3354/ab00352

Campbell SJ, McKenzie LJ, Kerville SP (2006) Photosynthetic responses of seven tropical seagrasses to elevated seawater temperature. J Exp Mar Biol Ecol 330:455–468. doi: 10.1016/j.jembe.2005.09.017

Campbell SJ, Pardede ST (2006) Reef fish structure and cascading effects in response to artisanal fishing pressure. Fish Res 79:75–83.

Cebrián J, Duarte CM (1998) Patterns in leaf herbivory on seagrasses. Aquat Bot 60:67–82. doi: 10.1016/S0304-3770(97)00070-3

Cebrián J, Duarte CM, R Agawin NS, Merino M (1998) Leaf growth response to simulated herbivory: a comparison among seagrass species. J Exp Mar Biol Ecol 220:67–81. doi: 10.1016/S0022-0981(97)00084-1

Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S (2000) Consequences of changing biodiversity. Nature 405:234–242. doi: 10.1038/35012241

Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: Implications of transect width and species selection. Mar Ecol Prog Ser 158:241–248. doi: 10.3354/meps158241

Chirico AAD, McClanahan TR, Eklöf JS (2017) Community- and government-managed marine protected areas increase fish size, biomass and potential value. PLoS One 12:e0182342–19. doi: 10.1371/journal.pone.0182342

Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, García-Charton JA, Pérez-Ruzafa Á, Badalamenti F, Bayle-Sempere J, Brito A, Bulleri F, Culioli J-M, Dimech M, Falcón JM, Guala I, Milazzo M, Sánchez-Meca J, Somerfield PJ, Stobart B, Vandeperre F, Valle C, Planes S (2008) Marine reserves: size and age do matter. Ecol Lett 11:481–489. doi: 10.1111/j.1461-0248.2008.01166.x

Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. Estuar Coast Shelf Sci 55:309–321. doi: 10.1006/ecss.2001.0907

Collier CJ, Lavery PS, Ralph PJ, Masini RJ (2008) Physiological characteristics of the seagrass *Posidonia sinuosa* along a depth-related gradient of light availability. Mar Ecol Prog Ser 353:65–79. doi: 10.3354/meps07171

Collier CJ, Waycott M, Ospina AG (2012) Responses of four Indo-West Pacific seagrass species to shading. Mar Pollut Bull 65:342–354. doi: 10.1016/j.marpolbul.2011.06.017

Colton MA, Swearer SE (2010) A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. Mar Ecol Prog Ser 400:19–36. doi: 10.3354/meps08377

Cullen-Unsworth LC, Nordlund LM, Paddock J, Baker S, McKenzie LJ, Unsworth RKF (2014) Seagrass meadows globally as a coupled social–ecological system: Implications for human wellbeing. Mar Pollut Bull 83:387–397. doi: 10.1016/j.marpolbul.2013.06.001

Daby D (2003) Effects of seagrass bed removal for tourism purposes in a Mauritian bay. Environ Poll 125:313–324. doi: 10.1016/S0269-7491(03)00125-8

Daily G (ed) (1997) Nature's services: societal dependence on natural ecosystems. Island Press

Darling ES, McClanahan TR, Côté IM (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. Conserv Lett 3:122–130. doi: 10.1111/j.1755-263X.2009.00089.x

de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, Hussain S, Kumar P, McVittie A, Portela R, Rodriguez LC, Brink ten P, van Beukering P (2012) Global estimates of the value of ecosystems and their services in monetary units. Ecosyst Serv 1:50–61. doi: 10.1016/j.ecoser.2012.07.005

de la Torre-Castro de M, Di Carlo G, Jiddawi NS (2014) Seagrass importance for a small-scale fishery in the tropics: The need for seascape management. Mar Pollut Bull 83:398–407. doi: 10.1016/j.marpolbul.2014.03.034

de la Torre-Castro de M, Eklöf JS, Rönnbäck P, Björk M (2008) Seagrass importance in food provisioning services: fish stomach content as a link between seagrass meadows and local fisheries. West Indian Ocean J Mar Sci 7:95–110.

de la Torre-Castro de M, Rönnbäck P (2004) Links between humans and seagrasses—an example from tropical East Africa. Ocean Coast Manag 47:361–387. doi: 10.1016/j.ocecoaman.2004.07.005

Dearden P, Theberge M, Yasué M (2009) Using underwater cameras to assess the effects of snorkeler and SCUBA diver presence on coral reef fish abundance, family richness, and species composition. Environ Monit Assess 163:531–538. doi: 10.1007/s10661-009-0855-3

Dennison WC (1990) Leaf production. In: Phillips RC, McRoy CP (eds) Seagrass research methods. UNESCO, Paris, pp 77–79

Díaz S, Lavorel S, de Bello F, Quétier F, Grigulis K, Robson TM (2007) Incorporating plant functional diversity effects in ecosystem service assessments. PNAS 104:20684–20689. doi: 10.1073/pnas.0704716104

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N, Polovina J, Rabalais NN, Sydeman WJ, Talley LD (2012) Climate change impacts on marine ecosystems. Ann Rev Mar Sci 4:11–37. doi: 10.1146/annurev-marine-041911-111611

Duarte CM, Chiscano CL (1999) Seagrass biomass and production: a reassessment. Aquat Bot 65:159–174. doi: 10.1016/S0304-3770(99)00038-8

Duarte CM, Fourqurean JW, Krause-Jensen D, Olesen B (2006) Dynamics of seagrass stability and change. In: Larkum AWD, Orth RJ, Duarte CM (eds) Physiological and morphological responses of the seagrass Zostera capricorni Aschers, to light intensity. Springer, The Netherlands, pp 271–294

Duarte CM, Kirkman H (2001) Methods for the measurement of seagrass abundance and depth distribution. In: Short FT, Coles RG (eds) Global seagrass research methods. Elsevier, Amsterdam, pp 141–153

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N (2013) The role of coastal plant communities for climate change mitigation and adaptation. Nat Clim Chang 3:961–968. doi: 10.1038/nclimate1970

Duffy JE (2006) Biodiversity and the functioning of seagrass ecosystems. Mar Ecol Prog Ser 311:233–250. doi: 10.3354/meps311233

Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ (2016) Biodiversity enhances reef fish biomass and resistance to climate change. PNAS 113:6230–6235. doi: 10.1073/pnas.1524465113

Duffy JE, Reynolds PL, Boström C, Coyer JA, Cusson M, Donadi S, Douglass JG, Eklöf JS, Engelen AH, Eriksson BK, Fredriksen S, Gamfeldt L, Gustafsson C, Hoarau G, Hori M, Hovel K, Iken K, Lefcheck JS, Moksnes PO, Nakaoka M, O'Connor MI, Olsen JL, Richardson JP, Ruesink JL, Sotka EE, Thormar J, Whalen MA, Stachowicz JJ (2015) Biodiversity mediates top-down control in eelgrass ecosystems: a global comparative-experimental approach. Ecol Lett. doi: 10.1111/ele.12448

EcoAfrica (2005) Mnemba Island and Chwaka Bay Conservation Areas: a preliminary situational assessment. Department of Fisheries and Marine Resources, Ministry of Agriculture, Natural Resources, Environment and Cooperatives, Revolutionary Government of Zanzibar

Edgar GJ, Shaw C, Watson GF, Hammond LS (1994) Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. J Exp Mar Biol Ecol 176:201–226.

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro MA, Bernard ATF, Berkhout J, Buxton CD, Campbell SJ, Cooper AT, Davey M, Edgar SC, Försterra G, Galván DE, Irigoyen AJ, Kushner DJ, Moura R,

Parnell PE, Shears NT, Soler G, Strain EMA, Thomson RJ (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature. doi: 10.1038/nature13022

Eklöf JS, Fröcklin S, Lindvall A, Stadlinger N, Kimathi A, Uku JN, McClanahan TR (2009a) How effective are MPAs? Predation control and "spill-in effects" in seagrass–coral reef lagoons under contrasting fishery management. Mar Ecol Prog Ser 384:83–96. doi: 10.3354/meps08024

Eklöf JS, Gullström M, Björk M, Asplund ME, Hammar L, Dahlgren A, Öhman MC (2008a) The importance of grazing intensity and frequency for physiological responses of the tropical seagrass *Thalassia hemprichii*. Aquat Bot 89:337–340. doi: 10.1016/j.aquabot.2008.03.009

Eklöf JS, de la Torre-Castro de M, Gullström M, Uku J, Muthiga N, Lyimo T, Bandeira SO (2008b) Sea urchin overgrazing of seagrasses: A review of current knowledge on causes, consequences, and management. Estuar Coast Shelf Sci 79:569–580. doi: 10.1016/j.ecss.2008.05.005

Eklöf JS, McMahon K, Lavery PS (2009b) Effects of multiple disturbances in seagrass meadows: shading decreases resilience to grazing. Mar Freshw Res 60:1317–1327. doi: 10.1071/MF09008

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Front Ecol Environ 1:488–494. doi: 10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2

Erftemeijer PLA, Herman PMJ (1994) Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. Oecologia 99:45–59. doi: 10.1007/BF00317082

Fonseca MS, Cahalan JA (1992) A preliminary evaluation of wave attenuation by four species of seagrass. Estuar Coast Shelf Sci 35:565–576.

Fox RJ, Bellwood DR (2008) Remote video bioassays reveal the potential feeding impact of the rabbitfish *Siganus canaliculatus* (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. Coral Reefs 27:605–615. doi: 10.1007/s00338-008-0359-6

Francour P (1994) Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). Oceanol Acta 17:309–317.

Fraschetti S, Guarnieri G, Bevilacqua S, Terlizzi A, Boero F (2013) Protection enhances community and habitat stability: evidence from a Mediterranean Marine Protected Area. PLoS One 8:e81838–13. doi: 10.1371/journal.pone.0081838

Freedman DA (2004) Graphical models for causation, and the identification problem. Eval Rev 28:267–293. doi: 10.1177/0193841X04266432

Freeman AS, Short FT, Isnain I, Razak FA, Coles RG (2008) Seagrass on the edge: Land-use practices threaten coastal seagrass communities in Sabah, Malaysia. Biol Conserv 141:2993–3005. doi: 10.1016/j.biocon.2008.09.018

Gillanders BM (2006) Seagrasses, fish, and fisheries. In: Larkum AWD, Orth RJ, Duarte CM (eds) Physiological and morphological responses of the seagrass Zostera capricorni Aschers, to light intensity. Springer, The Netherlands, pp 503–536

Gillis LG, Bouma TJ, Jones CG, van Katwijk MM, Nagelkerken I, Jeuken CJL, Herman PMJ, Ziegler AD (2014) Potential for landscape-scale positive interactions among

tropical marine ecosystems. Mar Ecol Prog Ser 503:289–303. doi: 10.3354/meps10716

Goetze JS, Jupiter SD, Langlois TJ, Wilson SK, Harvey ES, Bond T, Naisilisili W (2015) Diver operated video most accurately detects the impacts of fishing within periodically harvested closures. J Exp Mar Biol Ecol 462:74–82. doi: 10.1016/j.jembe.2014.10.004

Grace JB (2006) Structural Equation Modeling and Natural Systems. Cambridge University Press, Cambridge, UK

Grace JB, Anderson TM, Olff H, Scheiner SM (2010) On the specification of structural equation models for ecological systems. Ecol Monogr 80:67–87. doi: 10.1890/09-0464.1

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97. doi: 10.1038/nature14140

Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y, Bigot L, Galzin R, Ohman MC, Garpe KC, Edwards AJ, Sheppard CRC (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS One 3:e3039. doi: 10.1371/journal.pone.0003039

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conserv Biol 21:1291–1300. doi: 10.1111/j.1523-1739.2007.00754.x

Green EP, Short FT (2003) World Atlas of Seagrasses. University of California Press, Berkeley, USA

Guidetti P, Baiata P, Ballesteros E, Di Franco A, Hereu B, Macpherson E, Micheli F, Pais A, Panzalis P, Rosenberg AA, Zabala M, Sala E (2014) Large-scale assessment of Mediterranean marine protected areas effects on fish assemblages. PLoS One 9:e91841. doi: 10.1371/journal.pone.0091841

Gullström M, Berkström C, Öhman MC, Bodin M, Dahlberg M (2011) Scale-dependent patterns of variability of a grazing parrotfish (*Leptoscarus vaigiensis*) in a tropical seagrass-dominated seascape. Mar Biol 158:1483–1495. doi: 10.1007/s00227-011-1665-z

Gullström M, Bodin M, Nilsson PG, Öhman MC (2008) Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. Mar Ecol Prog Ser 363:241–255. doi: 10.3354/meps07427

Gullström M, Lundén B, Bodin M, Kangwe J, Öhman MC, Mtolera MSP, Björk M (2006) Assessment of changes in the seagrass-dominated submerged vegetation of tropical Chwaka Bay (Zanzibar) using satellite remote sensing. Estuar Coast Shelf Sci 67:399–408. doi: 10.1016/j.ecss.2005.11.020

Harmelin J-G, Bachet F, Garcia F (1995) Mediterranean marine reserves: fish indices as tests of protection efficiency. Mar Ecol 16:233–250. doi: 10.1111/j.1439-0485.1995.tb00408.x

Harvey E, Fletcher D, Shortis M (2001) A comparison of the precision and accuracy of estimates of reef-fish lengths determined visually by divers with estimates produced by a stereo-video system. Fish Bull 99:63–71.

Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: Herbivory and algal distribution. Aquat Bot 11:97–109. doi: 10.1016/0304-3770(81)90051-6

Heck KL Jr, Orth RJ (2006) Predation in seagrass beds. In: Larkum AWD, Orth RJ, Duarte CM (eds) Physiological and morphological responses of the seagrass Zostera capricorni Aschers, to light intensity. Springer, The Netherlands, pp 537–550

Heck KL Jr, Valentine JF (2006) Plant–herbivore interactions in seagrass meadows. J Exp Mar Biol Ecol 330:420–436. doi: 10.1016/j.jembe.2005.12.044

Hemminga MA, Duarte CM (2000) Fauna associated with seagrass systems. In: Seagrass Ecology. Cambridge University Press, Cambridge, pp 199–247

Hicks CC, McClanahan TR (2012) Assessing gear modifications needed to optimize yields in a heavily exploited, multi-species, seagrass and coral reef fishery. PLoS One 7:e36022. doi: 10.1371/journal.pone.0036022

Hill J, Wilkinson C (2004) Methods for ecological monitoring of coral reefs - A Resource for managers. Australian Institute of Marine Science, Townsville, Australia

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328:1523–1528. doi: 10.1126/science.1189930

Holmes TH, Wilson SK, Travers MJ, Langlois TJ, Evans RD, Moore GI, Douglas RA, Shedrawi G, Harvey ES, Hickey K (2013) A comparison of visual- and stereo-video based fish community assessment methods in tropical and temperate marine waters of Western Australia. Limnol Oceangr Methods 11:337–350. doi: 10.4319/lom.2013.11.337

Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiveristy on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75:3–35. doi: 10.1890/04-0922

IPCC (2013) Summary for Policymakers. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate Change 2013: The physical science basis. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp 1–30

IPCC (2014) Summary for policymakers. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (eds) Climate Change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA, pp 1–32

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637. doi: 10.1126/science.1059199

Jiddawi NS, Öhman MC (2002) Marine fisheries in Tanzania. Ambio 31:518–527. doi: 10.1579/0044-7447-31.7.518

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. doi: 10.2307/3545850

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. PNAS 101:8251–8253. doi: 10.1073/pnas.0401277101

Kaiser MJ, Spence FE, Hart PJB (2000) Fishing-Gear restrictions and conservation of benthic habitat complexity. Conserv Biol 14:1512–1525. doi: 10.1046/j.1523-1739.2000.99264.x

Kamermans P, Hemminga MA, Marbà N, Mateo MA, Mtolera M, Stapel J (2001) Leaf production, shoot demography, and flowering of *Thalassodendron ciliatum* along the east African coast. Aquat Bot 70:243–258. doi: 10.1016/S0304-3770(01)00156-5

Kenworthy WJ, Wyllie-Echeverria S, Coles RG, Pergent G, Pergent-Martini C (2006) Seagrass conservation biology: an interdisciplinary science for protection of the seagrass biome. In: Larkum AWD, Orth RJ, Duarte CM (eds) Physiological and morphological responses of the seagrass Zostera capricorni Aschers, to light intensity. Springer, The Netherlands, pp 595–623

Kirsch KD, Valentine JF, Heck KL Jr (2002) Parrotfish grazing on turtlegrass *Thalassia testudinum*: evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. Mar Ecol Prog Ser 227:71–85.

Kloiber U (2013) Chumbe Island Coral Park – Conservation and education, Status Report 2013. Zanzibar, Tanzania

Koch EW, Ackerman JD, Verduin J, van Keulen M (2006) Fluid dynamics in seagrass ecology – from molecules to ecosystems. In: Larkum AWD, Orth RJ, Duarte CM (eds) Physiological and morphological responses of the seagrass Zostera capricorni Aschers, to light intensity. Springer, The Netherlands, pp 193–225

Koch M, Bowes G, Ross C, Zhang XH (2013) Climate change and ocean acidification effects on seagrasses and marine macroalgae. Glob Chang Biol 19:103–132. doi: 10.1111/j.1365-2486.2012.02791.x

Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. J Exp Mar Biol Ecol 222:11–30. doi: 10.1016/S0022-0981(97)00133-0

Kuo J, Hartog den C (2001) Seagrass taxonomy and identification key. In: Short FT, Coles RG (eds) Global seagrass research methods. Elsevier, pp 31–58

La Nafie YA, de los Santos CB, Brun FG, Mashoreng S, van Katwijk MM, Bouma TJ (2013) Biomechanical response of two fast-growing tropical seagrass species subjected to in situ shading and sediment fertilization. J Exp Mar Biol Ecol 446:186–193. doi: 10.1016/j.jembe.2013.05.020

Lauer M, Aswani S (2010) Indigenous knowledge and long-term ecological change: detection, interpretation, and responses to changing ecological conditions in Pacific island communities. Environ Manage 45:985–997. doi: 10.1007/s00267-010-9471-9

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545–556. doi: 10.1046/j.1365-2435.2002.00664.x

Lee J-Y, Wang B (2012) Future change of global monsoon in the CMIP5. Clim Dyn 42:101–119. doi: 10.1007/s00382-012-1564-0

Lefcheck JS (2015) piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods Ecol Evol 573–579. doi: 10.1111/2041-210X.12512

Lefcheck JS, Orth RJ, Dennison WC, Wilcox DJ, Murphy RR, Keisman J, Gurbisz C, Hannam M, Landry JB, Moore KA, Patrick CJ, Testa J, Weller DE, Batiuk RA (2018) Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. PNAS 37:201715798–5. doi: 10.1073/pnas.1715798115

Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46. doi: 10.3354/meps08029

Lincoln Smith MP (1988) Effects of observer swimming speed on sample counts of temperate rocky reef fish assemblages. Mar Ecol Prog Ser 43:223–231. doi: 10.2307/24825774

Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F (2012) Extreme climatic events and vegetation: the role of stabilizing processes. Glob Chang Biol 18:797–805. doi: 10.1111/j.1365-2486.2011.02624.x

Lotze HK (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809. doi: 10.1126/science.1128035

Lowry M, Folpp H, Gregson M, Suthers I (2012) Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries. J Exp Mar Biol Ecol 416-417:243–253. doi: 10.1016/j.jembe.2012.01.013

López-Calderón JM, Guzmán HM, Jácome GE, Barnes PAG (2013) Decadal increase in seagrass biomass and temperature at the CARICOMP site in Bocas del Toro, Panama. Rev Biol Trop 61:1–12. doi: 10.15517/rbt.v61i4.12854

Lugendo BR, de Groene A, Cornelissen I, Pronker A, Nagelkerken I, van der Velde G, Mgaya YD (2007) Spatial and temporal variation in fish community structure of a marine embayment in Zanzibar, Tanzania. Hydrobiologia 586:1–16. doi: 10.1007/s10750-006-0398-3

MacNeil MA, Tyler EHM, Fonnesbeck CJ, Rushton SP, Polunin NVC, Conroy MJ (2008) Accounting for detectability in reef-fish biodiversity estimates. Mar Ecol Prog Ser 367:249–260. doi: 10.3354/meps07580

Makame MO (2013) Vulnerability and adaptation of Zanzibar east coast communities to climate variability and change and other interacting stressors. Rhodes University

Marbà N, Duarte CM (1997) Interannual changes in seagrass (*Posidonia oceanica*) growth and environmental change in the Spanish Mediterranean littoral zone. Limnol Oceanogr 42:800–810. doi: 10.4319/lo.1997.42.5.0800

Mariotti L, Diallo I, Coppola E, Giorgi F (2014) Seasonal and intraseasonal changes of African monsoon climates in 21st century CORDEX projections. Clim Change 125:53–65. doi: 10.1007/s10584-014-1097-0

Marques LV, Short FT, Creed JC (2015) Sunspots drive seagrasses. Biol Rhythm Res 46:63–68. doi: 10.1080/09291016.2014.948300

Martínez ML, Intralawan A, Vázquez G, Pérez-Maqueo O, Sutton P, Landgrave R (2007) The coasts of our world: Ecological, economic and social importance. Ecol Econ 63:254–272. doi: 10.1016/j.ecolecon.2006.10.022

Maxwell PS, Pitt KA, Burfeind DD, Olds AD, Babcock RC, Connolly RM (2013) Phenotypic plasticity promotes persistence following severe events: physiological and morphological responses of seagrass to flooding. J Ecol 102:54–64. doi: 10.1111/1365-2745.12167

McCann KS (2000) The diversity-stability debate. Nature 405:228–233. doi: 10.1038/35012234

McClanahan TR (1988) Seasonality in East Africa's coastal waters. Mar Ecol Prog Ser 44:191.

McClanahan TR (2011) Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs – Maldives vs. Kenya. Aquat Conserv Mar Freshw Ecosyst 21:186–198. doi: 10.1002/aqc.1172

McClanahan TR, Graham NAJ (2005) Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Mar Ecol Prog Ser 294:241–248. doi: 10.3354/meps294241

McClanahan TR, Hicks CC, Darling ES (2008) Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. Ecol Appl 18:1516–1529. doi: 10.1890/07-0876.1

McClanahan TR, Muthiga NA, Maina J, Kamukuru AT, Yahya SAS (2009) Changes in northern Tanzania coral reefs during a period of increased fisheries management and climatic disturbance. Aquat Conserv Mar Freshw Ecosyst 19:758–771. doi: 10.1002/aqc.1020

McClanahan TR, Nugues M, Mwachireya S (1994) Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. J Exp Mar Biol Ecol 184:237–254.

McDonald AM, Prado P, Heck KL Jr, Fourqurean JW, Frankovich TA, Dunton KH, Cebrián J (2016) Seagrass growth, reproductive, and morphological plasticity across environmental gradients over a large spatial scale. Aquat Bot 134:87–96. doi: 10.1016/j.aquabot.2016.07.007

McGlathery KJ (1995) Nutrient and grazing influences on a subtropical seagrass community. Mar Ecol Prog Ser 122:239–252. doi: 10.3354/meps122239

McGuinness KA (1997) Tests for artefacts in some methods used to study herbivory and predation in mangrove forests. Mar Ecol Prog Ser 153:37–44. doi: 10.3354/meps153037

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329. doi: 10.2307/3544305

MEA (2005) Ecosystems and human well-being: synthesis. Island Press, Washington, DC

Mellin C, MacNeil MA, Cheal AJ, Emslie MJ, Caley M (2016) Marine protected areas increase resilience among coral reef communities. Ecol Lett 19:629–637. doi: 10.1111/ele.12598

Micheli F, Saenz-Arroyo A, Greenley A, Vazquez L, Espinoza Montes JA, Rossetto M, De Leo GA (2012) Evidence that marine reserves enhance resilience to climatic impacts. PLoS One. doi: 10.1371/journal.pone.0040832

Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences of phenotypic plasticity. Trends Ecol Evol 20:685–692. doi: 10.1016/j.tree.2005.08.002

Montague JR, Carballo JL, Valdes LM, Chacken M (1995) Analyses of decay and parrot fish grazing along attached blades of turtle grass (*Thalassia testudinum*) from tow sites in Biscayne Bay. Florida Scientist 58:206–215.

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG (2007) Trophic cascade facilitates coral recruitment in a marine reserve. PNAS 104:8362–8367. doi: 10.1073/pnas.0702602104

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, Hartog den C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf Sci 51:31–44. doi: 10.1006/ecss.2000.0617

Nemeth RS, Herzlieb S, Blondeau J (2006) Comparison of two seasonal closures for protecting red hind spawning aggregations in the US Virgin Islands. Okinawa, Japan, pp 1306–1313

Nordlund LM, Koch EW, Barbier EB, Creed JC (2016) Seagrass ecosystem services and their variability across genera and geographical regions. PLoS One 11:e0163091–23. doi: 10.1371/journal.pone.0163091

Nordlund LM, Unsworth RKF, Gullström M, Cullen-Unsworth LC (2017) Global significance of seagrass fishery activity. Fish Fish 11:12. doi: 10.1111/faf.12259

Orth RJ, Heck KL Jr, van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7:339. doi: 10.2307/1351618

Pauly D, Zeller D (2014) Accurate catches and the sustainability of coral reef fisheries. Curr Opin Environ Sustain 7:44–51. doi: 10.1016/j.cosust.2013.11.027

Peralta G, Brun FG, Hernández I, Vergara JJ, Pérez-Lloréns JL (2005) Morphometric variations as acclimation mechanisms in *Zostera noltii* beds. Estuar Coast Shelf Sci 64:347–356. doi: 10.1016/j.ecss.2005.02.027

Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, Hereu B, Milazzo M, Zabala M, D'Anna G, Pipitone C (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ Conserv 27:179–200. doi: 10.1017/s0376892900000205

Pittman SJ, Brown KA (2011) Multi-scale approach for predicting fish species distributions across coral reef seascapes. PLoS One 6:e20583. doi: 10.1371/journal.pone.0020583

Pollard DA (1984) A review of ecological studies on seagrass—fish communities, with particular reference to recent studies in Australia. Aquat Bot 18:3–42. doi: 10.1016/0304-3770(84)90079-2

Prado P, Farina S, Tomas F, Romero J, Alcoverro T (2008) Marine protection and meadow size alter fish herbivory in seagrass ecosystems. Mar Ecol Prog Ser 371:11–21. doi: 10.3354/meps07662

Prado P, Tomas F, Alcoverro T, Romero J (2007) Extensive direct measurements of Posidonia oceanica defoliation confirm the importance of herbivory in temperate seagrass meadows. Mar Ecol Prog Ser 340:63–71. doi: 10.3354/meps340063

Preen AR, Lee Long WJ, Coles RG (1995) Flood and cyclone related loss, and partial recovery, of more than 1000 km^2 of seagrass in Hervey Bay, Queensland, Australia. Aquat Bot 52:3–17.

Przeslawski R, Ahyong S, Byrne M, Wörheide G, Hutchings P (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. Glob Chang Biol 14:2773–2795. doi: 10.1111/j.1365-2486.2008.01693.x

Quiros TEAL, Croll D, Tershy B, Fortes MD, Raimondi P (2017) Land use is a better predictor of tropical seagrass condition than marine protection. Biol Conserv 209:454–463. doi: 10.1016/j.biocon.2017.03.011

Rasheed MA, McKenna SA, Carter AB, Coles RG (2014) Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia. Mar Pollut Bull 83:491–499. doi: 10.1016/j.marpolbul.2014.02.013

Rasheed MA, Unsworth RKF (2011) Long-term climate-associated dynamics of a tropical seagrass meadow: implications for the future. Mar Ecol Prog Ser 422:93–103. doi: 10.3354/meps08925

Rivera-Guzmán NE, Moreno-Casasola P, Ibarra-Obando SE, Sosa VJ, Herrera-Silveira J (2014) Long term state of coastal lagoons in Veracruz, Mexico: Effects of land use changes in watersheds on seagrasses habitats. Ocean Coast Manag 87:30–39. doi: 10.1016/j.ocecoaman.2013.10.007

Roberts CM, O'Leary BC, McCauley DJ, Cury PM, Duarte CM, Lubchenco J, Pauly D, Saenz-Arroyo A, Sumaila UR, Wilson RW, Worm B, Castilla JC (2017) Marine reserves can mitigate and promote adaptation to climate change. PNAS 114:6167–6175. doi: 10.1073/pnas.1701262114

Romero J, Lee K-S, Pérez M, Mateo MA, Alcoverro T (2006) Nutrient dynamics in seagrass ecosystems. In: Larkum AWD, Orth RJ, Duarte CM (eds) Physiological and morphological responses of the seagrass Zostera capricorni Aschers, to light intensity. Springer, The Netherlands, pp 227–254

Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F, Foley D, Fraschetti S, Friedlander A, Garrabou J, Güçlüsoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, Macpherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F, Zabala M (2012) The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. PLoS One 7:e32742. doi: 10.1371/journal.pone.0032742

Salm RV, Clark JR, Siirila E (2000) Marine and coastal protected areas. A guide for planners and managers, 3rd edn. IUCN, Washington DC

Scott AL, York PH, Duncan C, Macreadie PI, Connolly RM, Ellis MT, Jarvis JC, Jinks KI, Marsh H, Rasheed MA (2018) The role of herbivory in structuring tropical seagrass ecosystem service delivery. Front Plant Sci 9:361–10. doi: 10.3389/fpls.2018.00127

Seytre C, Francour P (2009) The Cap Roux MPA (Saint-Raphaël, French Mediterranean): changes in fish assemblages within four years of protection. ICES J Mar Sci 66:180–187. doi: 10.1093/icesjms/fsn196

Shelton AO, Francis TB, Feist BE, Williams GD, Lindquist A, Levin PS (2016) Forty years of seagrass population stability and resilience in an urbanizing estuary. J Ecol 105:458–470. doi: 10.1111/1365-2745.12682

Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368. doi: 10.1890/08-1034.1

Short FT, Duarte CM (2001) Methods for the measurement of seagrass growth and production. In: Short FT, Coles RG (eds) Global seagrass research methods. Elsevier, pp 155–182

Short FT, Koch EW, Creed JC, Magalhães KM, Fernandez E, Gaeckle JL (2006a) SeagrassNet monitoring across the Americas: case studies of seagrass decline. Mar Ecol 27:277–289. doi: 10.1111/j.1439-0485.2006.00095.x

Short FT, Kosten S, Morgan PA, Malone S, Moore GE (2016) Impacts of climate change on submerged and emergent wetland plants. Aquat Bot 135:3–17. doi: 10.1016/j.aquabot.2016.06.006

Short FT, McKenzie LJ, Coles RG, Vidler KP, Gaeckle JL (2006b) SeagrassNet Manual for Scientific Monitoring of Seagrass Habitat, Worldwide edition. University of New Hampshire Publications

Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. Environ Conserv 23:17–27. doi: 10.1017/S0376892900038212

Spalding MD, Ruffo S, Lacambra C, Meliane I, Hale LZ, Shepard CC, Beck MW (2014) The role of ecosystems in coastal protection: Adapting to climate change and coastal hazards. Ocean Coast Manag 90:50–57. doi: 10.1016/j.ocecoaman.2013.09.007

St John J, Russ GR, Gladstone W (1990) Accuracy and bias of visual estimates of numbers, size structure and biomass of a coral reef fish. Mar Ecol Prog Ser 64:253–262. doi: 10.2307/24844575

Steven DM, Glombitza R (1972) Oscillatory variation of a phytoplankton population in a tropical ocean. Nature 237:105–107. doi: 10.1038/237105a0

Terrados J, Duarte CM, Fortes MD, Borum J, Agawin NSR, Bach S, Thampanya U, Kamp-Nielsen L, Kenworthy WJ, Geertz-Hansen O, Vermaat J (1998) Changes in community structure and biomass of seagrass communities along gradients of siltation in SE Asia. Estuar Coast Shelf Sci 46:757–768. doi: 10.1006/ecss.1997.0304

Tessier A, Pastor J, Francour P, Saragoni G, Crec'hriou R, Lenfant P (2013) Video transects as a complement to underwater visual census to study reserve effect on fish assemblages. Aquat Biol 18:229–241. doi: 10.3354/ab00506

Tewfik A, Rasmussen JB, McCann KS (2007) Simplification of seagrass food webs across a gradient of nutrient enrichment. Can J Fish Aquat Sci 64:956–967. doi: 10.1139/f07-071

Thompson AA, Mapstone BD (1997) Observer effects and training in underwater visual surveys of reef fishes. Mar Ecol Prog Ser 154:53–63. doi: 10.3354/meps154053

Thresher RE, Gunn JS (1986) Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). Environ Biol Fishes 17:93–116. doi: 10.1007/BF00001740

Tilman D (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302. doi: 10.1126/science.277.5330.1300

Tokoro T, Hosokawa S, Miyoshi E, Tada K, Watanabe K, Montani S, Kayanne H, Kuwae T (2014) Net uptake of atmospheric CO_2 by coastal submerged aquatic vegetation. Glob Chang Biol 20:1873–1884. doi: 10.1111/gcb.12543

Toth LT, van Woesik R, Murdoch TJT, Smith SR, Ogden JC, Precht WF, Aronson RB (2014) Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. Coral Reefs. doi: 10.1007/s00338-014-1158-x

Tyler EHM, Manica A, Jiddawi N, Speight MR (2011) A role for partially protected areas on coral reefs: maintaining fish diversity? Aquat Conserv Mar Freshw Ecosyst 21:231–238. doi: 10.1002/aqc.1182

Udy JW, Dennison WC (1997) Growth and physiological responses of three seagrass species to elevated sediment nutrients in Moreton Bay, Australia. J Exp Mar Biol Ecol 217:253–277. doi: 10.1016/S0022-0981(97)00060-9

Uku J, Björk M (2001) The distribution of epiphytic algae on three Kenyan seagrass species. S Afr J Bot 67:475–482. doi: 10.4314/sajb.v67i3.20465

Uku J, Björk M (2005) Productivity aspects of three tropical seagrass species in areas of different nutrient levels in Kenya. Estuar Coast Shelf Sci 63:407–420. doi: 10.1016/j.ecss.2004.12.007

Underwood AJ (1991) The logic of ecological experiments: a case history from studies of the distribution of macro-algae on rocky intertidal shores. J Mar Biol Ass UK 71:841–866. doi: 10.1017/S0025315400053509

Underwood AJ (1993) The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Austral Ecol 18:99–116. doi: 10.1111/j.1442-9993.1993.tb00437.x

UNEP (2001) Eastern Africa atlas of coastal resources – Tanzania. United Nations Environment Programme, Nairobi

Unsworth RKF, Cullen LC (2010) Recognising the necessity for Indo-Pacific seagrass conservation. Conserv Lett 3:63–73. doi: 10.1111/j.1755-263X.2010.00101.x

Unsworth RKF, Cullen LC, Pretty JN, Smith DJ, Bell JJ (2010) Economic and subsistence values of the standing stocks of seagrass fisheries: Potential benefits of no-fishing marine protected area management. Ocean Coast Manag 53:218–224. doi: 10.1016/j.ocecoaman.2010.04.002

Unsworth RKF, Rasheed MA, Chartrand KM, Roelofs AJ (2012) Solar radiation and tidal exposure as environmental drivers of *Enhalus acoroides* dominated seagrass meadows. PLoS One 7:e34133–8. doi: 10.1371/journal.pone.0034133

Valentine JF, Heck KL Jr, Blackmon D, Goecker ME, Christian J, Kroutil RM, Peterson BJ, Vanderklift MA, Kirsch KD, Beck M (2008) Exploited species impacts on trophic linkages along reef-seagrass interfaces in the Florida Keys. Ecol Appl 18:1501–1515. doi: 10.1890/07-1720.1

Valentine JF, Heck KL, Busby J Jr, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. Oecologia 112:193–200. doi: 10.1007/s004420050300

Vergés A, Pérez M, Alcoverro T, Romero J (2008) Compensation and resistance to herbivory in seagrasses: induced responses to simulated consumption by fish. Oecologia 155:751–760. doi: 10.1007/s00442-007-0943-4

Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J (2012) The return of the variance: intraspecific variability in community ecology. Trends Ecol Evol 27:245–253. doi: 10.1016/j.tree.2011.11.014

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882–892. doi: 10.1111/j.0030-1299.2007.15559.x

Vonk JA, Christianen MJA, Stapel J (2010) Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia. Mar Biol Res 6:282–291. doi: 10.1080/17451000903233789

Walker DI, Lukatelich RJ, Bastyan G, McComb AJ (1989) Effect of boat moorings on seagrass beds near Perth, Western Australia. Aquat Bot 36:69–77. doi: 10.1016/0304-3770(89)90092-2

Ward-Paige C, Mills Flemming J, Lotze HK (2010) Overestimating fish counts by non-instantaneous visual censuses: consequences for population and community descriptions. PLoS One 5:e11722. doi: 10.1371/journal.pone.0011722

Watson DL, Harvey ES, Anderson MJ, Kendrick GA (2005) A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. Mar Biol 148:415–425. doi: 10.1007/s00227-005-0090-6

Watson RA, Quinn TJ II (1997) Performance of transect and point count underwater visual census methods. Ecol Monogr 104:103–112. doi: 10.1016/S0304-3800(97)00117-8

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL Jr, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. PNAS 106:12377–12381. doi: 10.1073/pnas.0905620106

Willis TJ (2001) Visual census methods underestimate density and diversity of cryptic reef fishes. J Fish Biol 59:1408–1411. doi: 10.1111/j.1095-8649.2001.tb00202.x

Wootton JT (2002) Indirect effects in complex ecosystems: recent progress and future challenges. J Sea Res 48:157–172. doi: 10.1016/S1385-1101(02)00149-1

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790. doi: 10.1126/science.1132294

Zieman JC (1974) Methods for the study of the growth and production of turtle grass, *Thalassia testudinum* König. Aquaculture 4:139–143. doi: 10.1016/0044-8486(74)90029-5

Zieman JC, Iverson RL, Ogden JC (1984) Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. Mar Ecol Prog Ser 15:151–158. doi: 10.3354/meps015151