Stockholm University

Of seagrass and society

Exploring contributions of tropical seagrass meadows to food security

Benjamin Jones

Doctoral Thesis in Marine Biology at Stockholm University, Sweden 2022

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Exploring contributions of tropical seagrass meadows to food security

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Abstract

Conserving biodiversity while simultaneously feeding a growing population is one of the grand challenges of the Anthropocene. Recently, global assessments have shone a light on the importance of the marine environment for the supply of food (often termed blue food), as well as the diverse and many livelihood opportunities associated to it. Small-scale fisheries (SSF) are essential to this, in which the pursuit of fish and invertebrates are central. If we are to look to blue foods to tackle food insecurity, we need deeper understanding of how coastal habitats function at the nexus of biodiversity, people, and food. Simply put, we need to know how habitats contribute to the supply of food, both in terms of ecological functions and social-economic drivers. Seagrass meadows, diverse and abundant across the Indo-Pacific region, are one of numerous coastal ecosystems that provide food and livelihoods opportunities. Using these systems as a setting, this thesis aims to explore how seagrass meadows and their associated SSF contribute to food security. Comprised of five papers, this thesis relies on a mixed-methods approach to understand seagrass social-ecological systems. The papers range in their dependence on empirical data, their scale as well as the methods employed. **Paper I** used biodiversity ecosystem function theories to assess the influence of seagrass biota on the production of associated fish in the context of SSF in Tanzania. It highlighted that structural seagrass traits, rather than species richness, are key for driving the abundance and richness of species that are key for food. **Paper II** investigated the socio-economic drivers that influence seagrass use at the household level. It revealed that household use of seagrass meadows for food and income was higher than all other habitats, and that people use seagrass meadows because they are reliable. It also revealed that household income was key in shaping why people use seagrass meadows as fishing grounds, where both low- and high-income households were dependent on the habitat; low income as a safety-net and high income for high rewards. **Paper III** examined two key elements of food security, food quantity and quality, and revealed how seagrass meadows contribute to both in the context of micronutrients that are vital for human health. Data from across East Africa showed that seagrass meadows played a more important role than other habitats in providing micronutrient-rich fish species. **Paper IV** used local ecological knowledge to reveal perceived temporal change in fish and invertebrate abundance and size, but simultaneously identified potential contrasting cognitions that place human communities at risk. Finally, **Paper V** provided a synthesis of past studies that explored how certain sustainable development initiative result in unintended consequences that influence the supply of blue food. It revealed a number of unintended effects which place the people that use seagrass meadows at risk while at the same time lessening the positive effects of the sustainable development initiative itself. This thesis describes the dynamic interactions between biodiversity, people and food, and place seagrass meadows – habitats that exist globally – at the forefront of the blue food agenda. It highlights how seagrass meadows represent many of the qualities we hope for in a food system – a system that provides sufficient, safe, and nutritious food for multiple and diverse individuals across society.

Keywords: *Biodiversity, Blue food, Food security, Social-ecological systems, Small-scale fisheries, Seagrass meadows.*

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Cover photo: Fisher in *Enhalus acoroides* meadow, Bali, Indonesia. Benjamin Jones

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For mum

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Conserving biodiversity while simultaneously feeding a growing population is one of the grand challenges of the Anthropocene. Recently, global assessments have shone a light on the importance of the marine environment for the supply of food (often termed blue food), as well as the diverse and many livelihood opportunities associated to it. Small-scale fisheries (SSF) are essential to this, in which the pursuit of fish and invertebrates are central. If we are to look to blue foods to tackle food insecurity, we need deeper understanding of how coastal habitats function at the nexus of biodiversity, people, and food. Simply put, we need to know how habitats contribute to the supply of food, both in terms of ecological functions and social-economic drivers. Seagrass meadows, diverse and abundant across the Indo-Pacific region, are one of numerous coastal ecosystems that provide food and livelihoods opportunities. Using these systems as a setting, this thesis aims to explore how seagrass meadows and their associated SSF contribute to food security. Comprised of five papers, this thesis relies on a mixed-methods approach to understand seagrass social-ecological systems. The papers range in their dependence on empirical data, their scale as well as the methods employed. **Paper I** used biodiversity ecosystem function theories to assess the influence of seagrass biota on the production of associated fish in the context of SSF in Tanzania. It highlighted that structural seagrass traits, rather than species richness, are key for driving the abundance and richness of species that are key for food. **Paper II** investigated the socio-economic drivers that influence seagrass use at the household level. It revealed that household use of seagrass meadows for food and income was higher than all other habitats, and that people use seagrass meadows because they are reliable. It also revealed that household income was key in shaping why people use seagrass meadows as fishing grounds, where both low- and high-income households were dependent on the habitat; low income as a safety-net and high income for high rewards. **Paper III** examined two key elements of food security, food quantity and quality, and revealed how seagrass meadows contribute to both in the context of micronutrients that are vital for human health. Data from across East Africa showed that seagrass meadows played a more important role than other habitats in providing micronutrient-rich fish species. **Paper IV** used local ecological knowledge to reveal perceived temporal change in fish and invertebrate abundance and size, but simultaneously identified potential contrasting cognitions that place human communities at risk. Finally, **Paper**

V provided a synthesis of past studies that explored how certain sustainable development initiatives result in unintended consequences that influence the supply of blue food. It revealed a number of unintended effects which place the people that use seagrass meadows at risk while at the same time lessening the positive effects of the sustainable development initiative itself. This thesis describes the dynamic interactions between biodiversity, people and food, and place seagrass meadows – habitats that exist globally – at the forefront of the blue food agenda. It highlights how seagrass meadows represent many of the qualities we hope for in a food system – a system that provides sufficient, safe, and nutritious food for multiple and diverse individuals across society.

Keywords: Biodiversity; Blue food; Food security; Social-ecological systems; Small-scale fisheries; Seagrass meadows

Contents

List of papers

Papers included within the thesis:

Paper I
Jones, B.L., Nordlund, L.M., Unsworth, R.K.F., Jiddawi, N.S. and Eklöf, J.S. (2021). Seagrass structural traits drive fish assemblages in small-scale fisheries. *Frontiers in Marine Science*, 8:640528.

Paper II
Jones, B.L.H, Unsworth, R.K.F., Nordlund, L.M., Eklöf, J.S., Ambo-Rappe, R., Carly, F., Jiddawi, N.S., La Nafie, Y.A., Udagedara, S. and Cullen-Unsworth, L.C. (2022). Dependence on seagrass fisheries governed by household income and adaptive capacity. *Ocean & Coastal Management,* 225.

Paper III
Jones, B.L.H, Lefcheck, J.S., Skoglund, S., Thunell, V., Bandeira, S.O., Jiddawi, N.S., Uku, J., Gullström, M. and Eklöf, J.S. Human micronutrient provision by seagrass fisheries outperform coral reefs in a malnourished region. *Submitted*.

Paper IV
Jones, B.L.H, Unsworth, R.K.F., Nordlund, L.M, Ambo-Rappe, R., La Nafie, Y.A., Lopez, M.R., Udagedara, S., and Cullen-Unsworth, L.C. (2022). Local ecological knowledge reveals change in seagrass social-ecological systems. *Oceans* 3(3)

Paper V
Jones, B.L.H., Cullen-Unsworth, L.C., de la Torre Castro, M., Nordlund, L.M., Unsworth, R.K.F. and Eklöf. J.S. (2022). Unintended consequences of sustainable development initiatives: risks and opportunities in seagrass social-ecological systems. *Ecology and Society,* 27(2).

Contributions to papers included within the thesis

For **Paper I**, I conceived the idea, designed the study, collected, and analysed the data, and wrote the first draft of the paper. For **Paper II** and **IV**, I conceived the idea, analysed the data, and wrote the first draft of the paper – while I did not collect the data, I was involved in training collaborators to collect the data. For **Paper III**, I conceived the idea, analysed the data, and wrote the majority of the paper – the data for this paper was originally collected for a different project with a different research question. For **Paper V**, I conceived the idea, performed the research, and wrote the first draft of the paper. Ultimately, all papers included within this thesis are the result of a collaborative effort.

Related publications not included in the thesis

Unsworth, R.K.F., Cullen-Unsworth, L.C., **Jones, B.L.H.**, & Lilley, R.J. (2022). The planetary role of seagrass conservation. *Science*, 377(6606): 609-613.

McKenzie, L., Nordlund, L.M., **Jones, B.L.**, Cullen-Unsworth, L.C., Roelfsema, C.M., & Unsworth, R.K.F. (2020). The global distribution of seagrass meadows. *Environmental Research Letters*, 15(7): 074041.

Jones, B.L., & Unsworth, R.K.F. (2020). The perverse fisheries consequences of mosquito net malaria prophylaxis in East Africa. *Ambio*, 49: 1257–1267.

Unsworth, R.K.F., McKenzie, L.J., Collier, C.J., Cullen-Unsworth, L.C., Duarte, C.M., Eklöf, J.S., Jarvis, J.C., **Jones, B.L.**, & Nordlund, L.M. (2019). Global challenges for seagrass conservation. *Ambio*, 48(8): 801-815.

Unsworth, R.K.F., Ambo-Rappe, R., **Jones, B.L.**, La Nafie, Y.A., Irawan, A., Hernawan, U.E., Moore, A.M. and Cullen-Unsworth, L.C. (2018). Indonesia's globally significant seagrass meadows are under widespread threat. *Science of the Total Environment*, 634: 279-286.

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Jones, B.L., Unsworth, R.K.F., Udagedara S. and Cullen-Unsworth, L.C. (2018). Conservation Concerns of Small-Scale Fisheries: By-Catch Impacts of a Shrimp and Finfish Fishery in a Sri Lankan Lagoon. *Frontiers in Marine Science* 5(52).

Additional publications, outside the scope of the thesis

Unsworth, R.K.F., Cullen-Unsworth, L.C., Hope, J.N., **Jones, B.L.H.**, Lilley, R.J., Nuuttila, H.K., Williams, B., Esteban, N.E. (2022). Effectiveness of Moorings Constructed from Rope in Reducing Impacts to Seagrass. *Oceans*

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Dalby, O., Sinha, I., Unsworth, R.K.F., McKenzie, L.J., **Jones, B.L.**, & Cullen-Unsworth, L.C. (2021). Citizen science-driven big data collection requires improved and inclusive societal engagement. *Frontiers in Marine Science*, 8, 432

Unsworth, R.K.F., Bertelli, C., Cullen-Unsworth, L.C., Esteban, N., Lilley, R. J., **Jones, B.L.,** Lowe, C., Nuuttila, H., & Rees, S. (2019). Sowing the seeds of seagrass recovery using hessian bags. *Frontiers in Ecology and Evolution*, 7, 311.

Contributing author to the following reports

United Nations Environment Programme (2020). Out of the blue: The value of seagrasses to the environment and to people. UNEP, Nairobi, Kenya.

Gamble C., Debney, A., Glover, A., Bertelli, C., Green, B., Hendy, I., Lilley, R., Nuuttila, H., Potouroglou, M., Ragazzola, F., Unsworth, R. and Preston, J, (eds) (2021). *Seagrass Restoration Handbook*. Zoological Society of London, UK., London, UK.

Introduction

Biodiversity, people, and food

We live in a proposed epoch, the Anthropocene (Paul, 2002), that is subjugated by significant human activities impacting the Earth's geology and ecosystems. Humankind has transgressed several of the nine so-called planetary boundaries that encompass what Rockstrom et al. (2009a) call "a safe operating space for humanity", one of these being the current rate of biodiversity loss (Rockstrom et al., 2009b). Referred to by others as the "biodiversity crisis" (Western, 1992; Singh, 2002; Hoag, 2010), findings from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) show that humans are overwhelmingly responsible for the current rate of biodiversity loss (IPBES, 2019), driven by a host of factors including land-use change, exploitation, climate change, pollution and invasive species. The ongoing biodiversity crisis is simultaneously coupled with the grand challenge of feeding the world sustainably (FAO et al., 2021). With an ongoing climate emergency (Ripple et al., 2019) and increasing population, this challenge becomes even greater. Climate change has the potential to increase risk of food-insecurity both through direct effects (Rosenzweig and Parry, 1994; Baldos and Hertel, 2014; Hasegawa et al., 2021) and potentially through mitigation effects that could undermine efforts to eradicate poverty (Hasegawa et al., 2018; Soergel et al., 2021). Two of society's most pressing challenges then, are to improve food security[1] while simultaneously conserving biodiversity[2] (Tscharntke et al., 2012), both of which have been globally recognized in the United Nations Sustainable Development Goals (UN, 2015).

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[1] The most frequently cited definition of food security was diplomatically negotiated at the 1996 World Food Summit and refers broadly to "[…] a situation that exists when all people at all times have physical, social and economic access to sufficient, safe and nutritious food to meet dietary needs and food preferences for an active and healthy life" (FAO et al., 2021). This suggests then that food insecurity is the absence of one or more of these conditions. Food security is typically characterised using metrics that focus on availability, access, utilization, and stability, and can be assessed at the national, regional, household, or individual level (Jones et al., 2013).

[2] Under the Convention on Biological Convention on Biological Diversity (1992), biodiversity refers to the "variability among living organisms from all sources including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems."

In the last few decades, alarm over the consequences of biodiversity loss for people have stimulated the progression of biodiversity–ecosystem functioning (BEF) research (e.g., Tilman et al., 1996; Tilman et al., 1997; Cardinale et al., 2012; Tilman et al., 2014; Isbell et al., 2017; O'Connor et al., 2017). Such research has provided evidence that biodiversity has a positive, saturating influence on the rate of ecosystem functions (**Figure 1**). In general, the greater the variation in genes, species, or traits in a community the greater the likelihood of maintaining the provision of ecosystem services. Plants, or food crops, often require similar resources, such as nutrients, water, light and space, but occupy different niches (e.g., shallow vs deep rooted) or grow at different periods of the year. By increasing species richness, we can increase the likelihood that species will complement each other, rather that compete with each other for resources and ensure stable and resilient ecosystem functions (e.g., plant production). That said, others argue that newer diversity metrics, such as structural (trait) diversity, are better predictors of key ecosystem functions (LaRue et al., 2019).

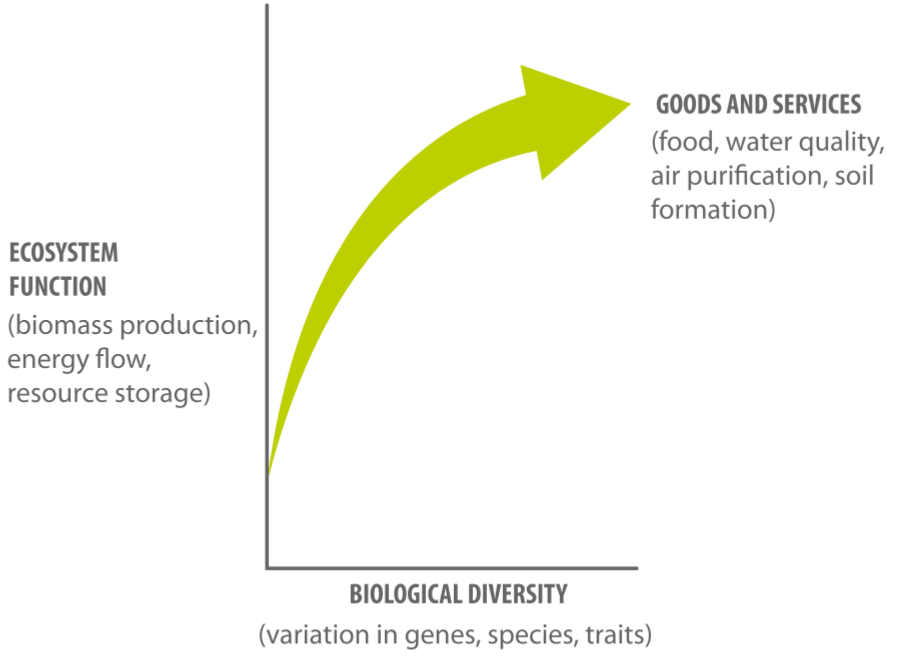

Figure 1. Biodiversity–ecosystem functioning (BEF) relationship.

Production-oriented perspectives have advanced our understanding of the role that biodiversity plays in food systems; enhancing biological diversity may provide benefits to food systems through enhanced production driving ecosystem functioning (Minns et al., 2001; Snapp et al., 2010; Samnegård et al., 2019). However, our quest for food is one of the major drivers of global biodiversity loss, identified in the landmark Millennium Ecosystem Assessment (MEA, 2005) and more recently in the IPBES Global Assessment Report (IPBES, 2019). Food security and biodiversity then are interlinked (Mehrabi et al., 2018), especially given conversion of natural ecosystems to meet future demands for food are expected to exacerbate threats to biodiversity (Williams et al., 2021), and strictly enforced biodiversity protection scenarios are projected to increase human diet- and weight-related mortalities (Henry et al., 2022). Moreover, production-oriented perspectives are heavily skewed towards terrestrial food systems (e.g., plant crops).

While there is merit in focusing on increasing aggregate levels of production to meet the rising demand for food (Renard and Tilman, 2019), production-oriented perspectives fail to address the multiple and often reinforcing causes of food insecurity (Koning et al., 2008). It is not a lack of food *per se* that drives food insecurity; humanity already produces enough food to feed 10 billion (Holt-Giménez et al., 2012). Hunger and food insecurity is caused by inequality and poverty, not scarcity. Recent investigations into household food insecurity during the COVID-19 pandemic revealed that access to cash safety nets mattered more than access to food, and that drivers such as gender, education and poverty were barriers to food security (Dasgupta and Robinson, 2022); these broad barriers were not just unique to low- and middle-income countries (Fitzpatrick et al., 2021). While there has been frequent discussion and alarm over the vulnerabilities of the global food systems, the COVID-19 pandemic highlighted how pressing these vulnerabilities are and has strengthened the need to increase the resilience of food systems or transform them entirely (Ruben et al., 2021; Swinnen et al., 2021). Nearly 700 million people go hungry, with 250 million potentially on the brink of starvation. Charting a course to nutritious, sustainable, and just food systems demands that we engage with all aspects of their functioning (IPBES, 2022), and requires that we also look to the aquatic environment as a source of food.

Blue food agenda

Aquatic foods are an important component of many food systems yet have received little attention in the food policy discourse. More recently, however, a landmark Blue Food Assessment[3] has brought together more than 100 scientists to advance understanding of the role blue foods play in global food systems and to inform new policies and practices that recognise the role of blue foods (**Figure 2**). To date, the assessment has produced a new framework

[3] The Blue Food Assessment is a joint initiative bringing together over 100 scientists from more than 25 institutions around the world: https://bluefood.earth

that can be used to understand the diversity of small-scale actors, revealing that small-scale fisheries (SSF) are dynamic and made up of multiple and diverse actors (Short et al., 2021). The assessment has also revealed that blue foods, on average, have higher nutritional benefits than most terrestrial foods (Golden et al., 2021), which are simultaneously coupled with lower environmental footprints (Gephart et al., 2021). In their assessment of nutrition, Golden et al. (2021) highlight that the consumption of blue foods can tackle malnutrition as well as support nutritional equality, especially focusing on women.

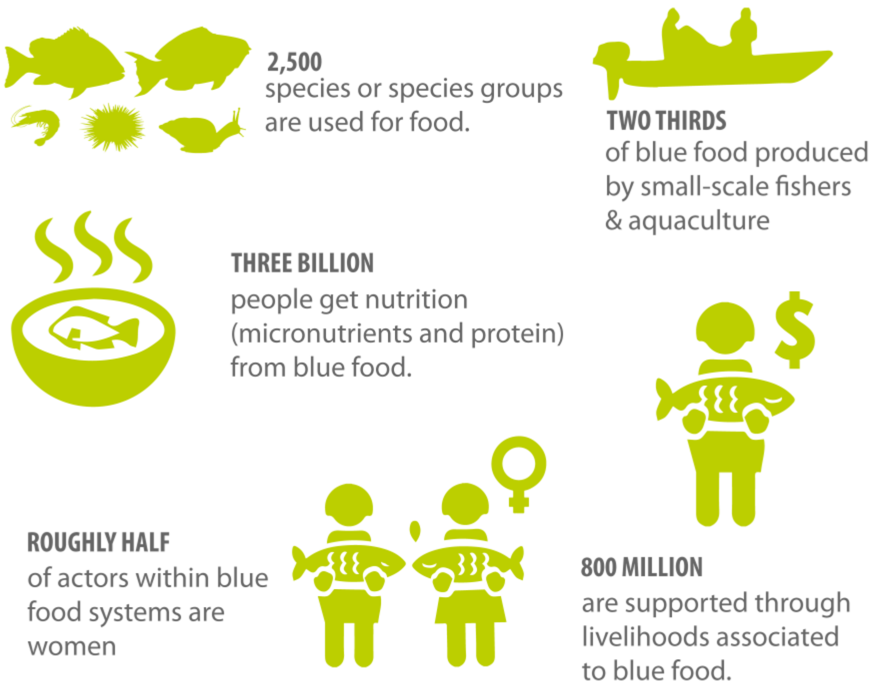

Figure 2. Key findings from the Blue Food Assessment (https://bluefood.earth).

Roughly three billion people rely on blue food, and Naylor et al. (2021) project a near doubling of demand by 2050. This growth in demand and consumption have occurred where blue foods have become more affordable and accessible, increasing opportunities for those in poverty. However, such growth will no doubt have environmental and social implications (Gephart et al., 2021; Naylor et al., 2021) and is also shaped by climate risks (Tigchelaar et al., 2021). Tigchelaar et al. (2021) revealed that tropical capture fisheries are particularly at risk from climate change. Coupled with new understanding of where demand for blue food is highest (Naylor et al., 2021), countries in

Africa and across the Indo-Pacific region are particularly exposed to high climate hazards (Tigchelaar et al., 2021).

Small-scale fisheries

Small-scale fisheries (SSF) are central to blue food production, accounting for *more than half* of total global fisheries production. More than 90% of the 120 million people engaged in capture fisheries are supported by SSF (Berkes, 2001; Peckham et al., 2007; IPBES, 2022). In emerging economies, the sector involves as many as 200 million people (Béné et al., 2007). Whilst there is increasing recognition of the need for improved management of these fisheries, there remains limited context-specific understanding of their social-ecological complexity, despite increasing focus from researchers and practitioners alike (Kittinger et al., 2013). This lack of understanding can lead to unintended and perverse consequences, such as economic damage to fisheries leading to mistrust in scientific institutions and management authorities (Degnbol and McCay, 2007).

Nearly all of the world's fishers (~97%) live near the coast in low income and emerging economies (Béné et al., 2007), and due to migration, development and globalization, this number is increasing (Curran et al., 2002; Small and Nicholls, 2003; Cinner et al., 2011). As such, SSF are central to socio-economic well-being (Teh and Sumaila, 2013) and play a fundamental role in generating wealth, alleviating poverty and providing food security (Allison and Ellis, 2001; Béné et al., 2007). These developments in understanding have been central in placing SSF within the context of the poverty agenda (Béné, 2004). However, the sector is poorly planned and controlled, inadequately supported, overlooked and often ignored by most levels of government relative to other food sectors such as agriculture (Teh and Pauly, 2018). As a result, SSF are characteristically overfished and overexploited, confounded by lack of management, bullying, bribery, open access, poor fishing practices, an absence of data (Pauly, 1997b; Teh et al., 2011) and fisheries policies that favour large-scale fisheries (Pauly, 1997a). Even in the shadow of large-scale fisheries, the economic weight, number of dependents and effects on biodiversity have led to realisations that SSF are undoubtedly "too big to ignore" (Chuenpagdee, 2011; Jentoft and Chuenpagdee, 2015; Pauly and Zeller, 2016; TBTI, 2022).

SSF are defined by a number of physical and social traits, with an overall theme of being low investment in terms of monetary value (Teh et al., 2011). Characteristically, SSF involve the use of low-tech fishing gear, with fishers operating from small, traditional craft with fairly labour-intensive fishing methods. The small-scale fishery archetype is centralised around fisher*men*, either operating individually or in small teams. Often undocumented fisher*women* are also key to SSF (Nordlund and Gullstrom, 2013; Kleiber et al., 2014), either at the processing and sales end or as collectors (e.g., gleaning). In general, SSF operate from small vessels or from the shore, and involve simple fishing gears such as traps, handlines, spearguns and variations in nets (Ruddle, 1996). While such fisheries have existed for 1000's of years, only in the last 30 years has research begun to unravel the complex nature of SSF when compared with large-scale industrial fisheries (Polunin et al., 1996), which in contrast use more advanced gears, technologically developed to target single species or groups of fish and invertebrates (Granzotto et al., 2004).

Augmenting the lack of research in SSF is the fact that there is no real definition of what SSF are. What we consider being "small-scale" in one location could be considered "large-scale" in another (Smith, 1979; Berkes and Kislalioglu, 1989; Kurien, 1996; Pomeroy, 2016). As a result, terms such as "traditional", "subsistence", "artisanal" and "small-scale" are used interchangeably and often coupled with inshore, local, or coastal to describe fisheries in the tropics (Kurien, 1996; Allison and Ellis, 2001; Berkes, 2001; Johnson, 2006). Yet, the recent drive in research focus on SSF has mainly occurred due to scrutiny of large-scale industrial fisheries (Carvalho et al., 2011). Moreover, the notion that SSF are likely the best option for fisheries sustainability, yet can have far reaching effects on fish and invertebrate stocks on a global level if not managed successfully (Polunin et al., 1996), is now central to development. This has been coupled with an understanding of their important, and often substantial social significance, cultural diversity and economic importance, especially in reference to poverty and food-security (Allison and Ellis, 2001; Berkes, 2001; Béné, 2004; Ellis and Freeman, 2004; Granzotto et al., 2004; Blount, 2005; Sadovy, 2005; Zeller et al., 2006). SSF are undoubtedly one of the frontiers in which social-ecological systems (SES) research has taken centre stage, with much attention focusing on highlighting the importance of transdisciplinary approaches to management and governance (Ferrol-Schulte et al., 2013).

Despite increasing research and new approaches to management and governance, a rising global population and ecosystem degradation have resulted in small-scale fishery catches declining dramatically (McClanahan et al., 2009). For example, SSF in the Philippines have been deteriorating since the 1970s (Muallil et al., 2014), despite increased management. As a result, focus now lies on improving policies and goals for sustaining SSF, not least through the Sustainable Development Goals and the new poverty agenda (Béné, 2004). The adoption of such measures seeks to shift focus away from increasing catches and employment while sustaining fish stocks by maximum sustainable yield approaches, towards a more interdisciplinary approach that improves both ecological status and human well-being. Despite this, the social-ecological complexity of SSF, which include the dimensions of poverty, management, and *mismanagement*, make this growing field even harder to disentangle.

Fisheries and poverty

Poverty is characteristically presented as being endemic to SSF; fishers have been perceived as the 'poorest of the poor' (Bailey and Jentoft, 1990). This is viewed by some as consequence of the open access nature of SSF, where any member of society has the opportunity to harvest marine resources, even without fishing gear or transport. This nature of *open* access leads to biological and economic overexploitation of resources, reduced benefits from assets such as ownership of fishing grounds and rights (e.g. reduced economic rent) and systemic impoverishment of actors (Gordon, 1954; Pauly, 1990; Pauly, 2005); in sum "the tragedy of the commons" (Hardin, 1968). This view of poverty and fisheries has resulted in a 'paradigmatic trap' where ultimately, poverty is perceived to be characteristic of such SSF. Literature on this Malthusian narrative of SSF (**Box 1**) overweighs the fact that in reality, those in poverty may be more adaptive to other livelihoods (Daw et al., 2012) and that there exist several pathways for SSF to alleviate poverty and provide food security (Béné, 2003). Moreover, the narrative of the commons, especially for fisheries, has been critiqued by many, including Ostrom's pioneering work showing that communities are capable of avoiding the tragedy of the commons without requiring top-down regulation (Ostrom, 1990; 2010), e.g. fisheries can be sustainable systems were poverty is not present. The view of poverty-stricken fisheries negates that fact that for centuries, isolated communities across the globe have respected a delicate balance with the ocean — taking fish only from certain areas, of certain sizes and with specific methods to maintain a healthy ecosystem and supply of fish for present and future. But with added human pressures such as competition both through smaller fishing areas and larger populations, such traditional views of fisheries may be lost to history (Hanh and Boonstra, 2018).

Generally, SSF are not wealth generating, even though there are exceptions to this such as those engaged in the trade of live fish (Sadovy et al., 2003; Fabinyi et al., 2012), and specifically for traders where local markets have expanded for export (Crona et al., 2015). While SSF do not generate significant wealth, fishers are not the poorest in society, at least in terms of income. Instead, the concept of poverty within fisheries can be related to different measures of wellbeing. For example, in Mozambique, fishing households have sufficient income security and education needs to escape poverty but lack sufficient capacity to meet other needs including shelter, sanitation, and food security (Chaigneau et al., 2019). Moreover, looking at SSF from the perspective of fishers, it is evident that fishers value the activity for more than just economic gains. Studies show that fishers value the work over the income they gain, as fishing gives them a sense of identity (Bavinck et al., 2012; Cinner, 2014), but such an attitude makes fishers vulnerable.

Box 1. **Malthusian overfishing defined**

In tropical emerging economies, those that engage in fisheries are generally poor or lack other suitable employment. Therefore, once you engage in fishing (e.g., putting all your eggs in one basket) it is difficult to leave even when the resources decline.

Those that engage in small-scale fisheries generally increase over time, due to internal recruitment (e.g., male children will typically follow their fathers and become fishermen) and through external recruitment (e.g., people entering the fishery from other sectors such as farming or migration from inland areas). For external recruits, coupled with lack of other employment options, fishing becomes "the occupation of last resort". Thus, *Malthusian overfishing*, originally proposed by Pauly (1988), generally occurs when these external recruits lack the alternative forms of support and employment that traditional fishers have (e.g., seasonal work or a small holding). When catches decline, these fishers are faced with no other solution than to invest in increasingly destructive fishing techniques to maintain income, ultimately resulting in resource collapse. The seriousness of these techniques generally increases over time and may involve:

- Fishers first investing in fishing techniques and gears that are either illegal or prohibited in some way, such as mosquito nets.
- Fishers moving to fish in areas that are prohibited, such as MPA's or in fishing grounds owned by another community.
- Fishers using gears that destroy the fishing habitat itself, such as trawling
- Fishers using destructive methods that endanger the fishers themselves, such as dynamite and cyanide fishing.

Small-scale and artisanal fisheries are dynamic (Finkbeiner, 2015). They can be influenced by constantly changing markets, governance, and climatic drivers. These present both social and ecological challenges, as well as new opportunities for fishers, more so for fishers that depend solely on such fisheries for livelihood and subsistence. Managing such fisheries is intrinsically difficult when considering these constantly fluctuating drivers (Mahon et al., 2008), and even more so with limited understanding of how fishers shift focus to account for such drivers. Yet, adaptive capacity in small-scale and artisanal fisheries to such changing conditions allows participants to overcome economic hardship (e.g. poor sales) and environmental change (e.g. habitat degradation, monsoons) by shifting focus to other, more accessible fishing locations, collection methods, or target species (Selgrath et al., 2018; Silas et al., 2020). In addition to adaptive capacity within fishing itself, fisher households with a broad set of alternative livelihoods have reduced vulnerability to risks faced by fisheries (Allison and Ellis, 2001; Cinner et al., 2009a; Daw et al., 2012; Cinner et al., 2015; Cinner et al., 2018a). Fishers may engage in multiple alternative livelihoods such as farming, the sale of groceries and other household items, aquaculture (e.g. seaweed farming) and more to income (Silas et al., 2020). Those fishers that have alternative livelihoods, which are generally older fishers, are quicker to exit a declining fishery (Cinner et al., 2015). Those that do not, are generally stuck in a poverty trap and will stop fishing only when stocks are in serious decline (Cinner et al., 2009a; Cinner et al., 2009b; Daw et al., 2012); a feedback mechanism most likely exacerbating fish stock decline and potentially contributing to poverty traps.

In 2020, some 58.5 million people were engaged in full- or part-time work in fisheries and aquaculture (FAO, 2022). Yet, estimates for the actual number of people that are supported by SSF range from 100 to some 800 million, suggesting that large numbers of people, and many in poverty, depend on income from fisheries. While SSF help to alleviate poverty at the household level, they do not reduce poverty *per se*, but instead prevent further poverty (Teh et al., 2011). Evidence suggests that in the majority of SSF in low income and emerging economies the activities do not generate high economic returns (Panayotou, 1980; Bailey and Jentoft, 1990). Instead, for households engaged in such activities, they provide resilience and prevent individuals from falling into deeper deprivation (Teh et al., 2011; Quiros et al., 2018). The above is defined by the open access argument of SSF. When access to capital (e.g. finance) and production schemes (e.g. land) are restricted, the marine environment, being free and open, provides the poorest members of society with the means to collect resources needed to sustain livelihoods or gain employment (Panayotou, 1980; Bailey and Jentoft, 1990). As such, SSF are a safety-net (Machena and Kwaramba, 1997; Béné, 2003) or even the "bank in the water" (Béné et al., 2009).

SSF also exist as a safety-net for households that are vulnerable in the face of economic or social shocks (e.g. those which were not previously poor or engaged in fisheries) (Fauzi and Anna, 2010). For example, if farm crops fail or the local economy deteriorates, the open access nature of the marine environment provides alternative sources of income and employment (as well as food). This reliance on fisheries for household income relates not only to direct benefits, but also indirect aspects such as upstream and downstream activities. These aspects add gender to the mix, given that women are significant participants in these related activities (Fauzi and Anna, 2010). For example, if the male head of a household dies, a mother still has potential to provide for her family either by working in the fisheries sector or collecting resources herself through gleaning (Kleiber et al., 2015).

The open-access nature of SSF lies at the heart of the safety-net function; open and free access to marine resources allows any members of society to engage with the SSF sector either briefly or continuingly (Bailey and Jentoft, 1990; Béné, 2003; Quiros et al., 2018). From a poverty and human well-being stance, this open access is central to the provisioning service that SSF provide. Generally, those that exist below and fringe the poverty line lack access to adequate, safe, and nutritious food. Lack of access to food products and malnutrition more broadly, have negative impacts on livelihood and education success (Underwood, 2000), and therefore has a greater impact to individuals and communities that are already vulnerable. Therefore, having adequate access to food is a precursor to alleviate poverty, but also to increase well-being, and remains high on the sustainable development agenda (Haddad et al., 2016).

Fisheries and food security

SSF contribute to food security in multiple ways. But a key process, and one of the most direct contributions, is associated to household consumption of catch. This pertains to their "safety-net" function, in that communities have multiple options to collect food resources from marine environments. Much like the poverty safety-net, open access can be pivotal in providing communities with opportunities to collect marine resources for household consumption, especially for households engaged in full-time, seasonal, or occasional fishing activities.

Globally, fish and fisheries are a crucial element in reducing food insecurity due to the nutritional content they provide, even in small amounts (Kawarazuka and Bene, 2011). In the absence of a nutritionally balanced diet (Ruel, 2003), foods products derived from animals are generally considered to be important sources of micronutrients, and as a result, are promoted to combat micronutrient deficiencies (Kawarazuka and Béné, 2010). Yet for poor households, and for those that fringe the poverty line, it is not always possible to regularly consume animal derived food products due to high costs, limited availability, and in some cases cultural or religious reasons. However, marine products in most cases are affordable (or free to those that can collect it) and almost always available. Moreover, aside for a couple of cultural beliefs and taboo's, most cultures permit the eating of marine products, especially fish. As a result, sustainable development initiatives have been implemented across Africa and Asia to increase fish consumption (Kawarazuka and Bene, 2011). For example, in Somalia many communities historically had a taboo against the consumption of fish and would refrain from integrating with the few communities that did, but the government in collaboration with FAO initiated a "Fish is Good for You" campaign to reduce hunger[4].

Nutritionally, marine food products are better than other staple foods consumed in emerging economies, such as rice, wheat, maize, and cassava. Fish in particular are an important source protein, essential fatty acids and micronutrients. Hicks et al. (2019) showed that many fish caught in small scale fisheries in low income and emerging economies have the potential nutrients to meet dietary requirements for all children under 5-year-olds that live within coastal communities. Small fish species in particular, which are generally eaten whole, contain large amounts of vital micronutrients such as calcium, iron, zinc, and vitamin A (Kawarazuka and Bene, 2011). Consuming such fish therefore has the potential to contribute significantly to curbing malnutrition in many low income and emerging economies (Hicks et al., 2019). Sustainable development interventions that have been initiated to tackle nutrient deficiencies promote the consumption of fish instead of supplements for this very reason (Gibson et al., 2000; Tontisirin et al., 2002; Roos et al., 2003), but also the sale of fish. Fish are a highlight traded commodity and increase household cash-income, allowing those at the lower end of the income scale to purchase other food products, including staple foods. This income generation is a central element of the food security benefit of SSF that is now well established and central to many sustainable development initiatives (Béné et al., 2009; Kawarazuka and Béné, 2010; Barnes-Mauthe et al., 2013).

Knowledge gaps

The pursuit of marine fauna – mainly fish and invertebrates – is central to SSF; whether as a source of subsistence or for monetary value, fauna lie at the heart of how humans value and use the marine environment for blue food. Marine and coastal habitats are vital for the production of fish and invertebrate fauna and such habitats can be comprised of both fauna and flora (e.g., coral reefs) or simply flora alone (e.g., seagrass meadows, kelp forests). If we are to look to the aquatic environment to tackle food insecurity, while simultaneously combating biodiversity loss, we need to take a deep dive into understanding how marine and coastal habitats function within this space. Below, I first present some key questions and link these to coastal habitats in the following section.

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[4] The UN's Food and Agriculture Organization (FAO) and the World Food Programme (WFP) joined forces with Somali authorities to encourage Somalis to eat more fish as a way to fight hunger. The countries per capita fish consumption was 2.4 kg per year, despite having a 3,300km stretch of coastline.

Firstly, are the same characteristics that drive terrestrial food production (e.g., plant identity and diversity) applicable to the aquatic environment, or do other characteristics matter more (e.g., habitat structure), since capture fisheries rely on wild populations? Secondly, are all marine and coastal habitats equal when placed in the context of poverty and food security, or do some matter more for certain demographics or for the supply of nutrients – and if so, why? Thirdly, we know that SSF are dynamic and engage multiple actors, but how do these actors view aquatic food systems and how they change? Lastly, aquatic food systems are exposed to multiple external factors, not least through actions that aim to meet multiple goals at once (e.g., conserving biodiversity), but how do these goals influence the supply and production of foods?

Knowledge relating to the importance of SSF is mounting, yet the principal tenets of why such fisheries are deteriorating and the elements that need management can only be understood by taking a systems approach that spans both the social and ecological space. In order to address some of the knowledge gaps identified above, the focus of this thesis was to investigate SSF associated to seagrass meadows using a SES framework across the Indo-Pacific region. Thus, this thesis aims to answer the overreaching question: *How do seagrass meadows and their associated small-scale fisheries contribute to food security and poverty alleviation?*

Seagrass meadows as a model system

Seagrasses – a unique group of flowering plants – have evolved to live a life fully submerged in marine environments (Olsen et al., 2016). Like terrestrial plants, their reproduction can be facilitated by a range of pollinators (Van Tussenbroek et al., 2016) and seed dispersers (Tol et al., 2017), and symbiotic nitrogen-fixing bacteria have allowed the plants to occupy nitrogen poor environments (Mohr et al., 2021). Globally distributed (McKenzie et al., 2020) and comprised of roughly 72 species, they bioengineer their own environment with a positive feedback to facilitate the creation of dense beds or meadows in shallow, coastal environments (Maxwell et al., 2017). Seagrass meadows are one habitat that form a crucial component of the tropical seascape and cover huge inter- and subtidal areas of the Indo-Pacific region, where species diversity is greatest (Short et al., 2007). Here, they are simultaneously being degraded by a host of factors including eutrophication, sedimentation, physical destruction, and overfishing (Kirkman and Kirkman, 2002; Coles et al., 2011; Unsworth et al., 2018). As a key habitat for a diverse array of fish and invertebrate species (Unsworth et al., 2014), seagrass meadows provide a suitable fishing ground and represent a model system allowing us to understand how coastal habitats function at the nexus of biodiversity, people and food.

Firstly, seagrass meadows are considered a nursery habitat for marine organisms (Mumby, 2006; Campbell et al., 2011; Nagelkerken et al., 2013) and harbour diverse and abundant populations of fish (Unsworth et al., 2014). We know that these fish assemblages are influenced by seagrass structure (Heck and Orth, 1980a), by seagrass canopy complexity (Bell and Westoby, 1986b; Bell and Westoby, 1986a; Nakamura and Sano, 2004) and by seagrass landscapes (Salita et al., 2003). Structural simplification is, in part, a causal factor in the loss of biodiversity. As a result, terrestrial biodiversity conservation is underpinned by conserving specific habitat qualities and characteristics – greater habitat complexity results in greater species diversity. In general, habitats with heterogeneous structures are better for conserving biodiversity (Getzin et al., 2008; Lam et al., 2014), as faunal diversity is positively correlated with habitat heterogeneity. Similarly, preserving specific and unique biological legacies enhance habitat quality, biodiversity and ecosystem function (Pharo and Lindenmayer, 2009). However, different taxa respond to habitat heterogeneity over a range of spatial scales (Tews et al., 2004), and the aspects of habitat composition and complexity that are key for positive relationships remain relatively unclear for coastal habitats such as seagrass. Therefore, an emerging gap here is that very few studies have tried to assess how gradients of seagrass diversity influence fish abundance. Linking back to our understanding of how aggregate levels of production are influenced by plant diversity in terrestrial systems, relatively 'hyper-diverse' seagrass meadows within the Indo-Pacific region offer a suitable setting in which to explore these theories within an aquatic setting.

Seagrass fisheries are of fundamental importance to those in poverty because they are shallow and close to shore (Nordlund et al., 2018). In cases, they are therefore much more accessible and favourable than coral reefs (Unsworth et al., 2014), potentially to the fishers in society whom cannot afford expensive fishing gear and either operate on foot (e.g. gleaning) or in small canoes (Nordlund et al., 2011; de la Torre-Castro et al., 2014). Fishers that utilise seagrass may be the poorest in society due to their strong dependence on the habitat for food security and livelihoods (Cullen-Unsworth et al., 2014; de la Torre-Castro et al., 2014; Unsworth et al., 2014; Nordlund et al., 2018; Quiros et al., 2018) – but are these fishers poor because they use seagrass meadows, or do they use seagrass meadows because they are poor? The few attempts the have delved into this topic have been highly localised, making it difficult to make broad scale generalisations about their role for people of varying demographics.

We know that fish contain micronutrients that are essential to human health such as calcium, iron, selenium, and zinc, and as a result SSF have the potential to supply nutritious food to respond to the global challenge of food insecurity (Hicks et al., 2019; Hicks et al., 2021). Emerging research from the Western Indian Ocean has highlighted the importance of coral reef fishes as sources of essential dietary nutrients (Robinson et al., 2022), but the role of seagrass associated fish is understudied and unknown. Given that smaller fish often contain higher concentrations of micronutrients (Kawarazuka and Bene, 2011), it may be that seagrass meadows, despite lower total fish biomass, supply comparable, or even higher nutrition than other habitats.

Fishing in seagrass meadows is highly adaptive; their characteristics, being shallow, with reduced solid structures for snagging and soft sediments, make using numerous different gear types possible. Seagrass fishers can utilise their hands, traps, fyke nets, drag nets, trawl nets, fish fences, gill nets and more to collect fish (de la Torre-Castro et al., 2014; Jones et al., 2018a; Jones et al., 2018b; Unsworth et al., 2018; Exton et al., 2019; Jones and Unsworth, 2020). In many cases, these fishing gears are utilised simultaneously in the same fishery (Jones et al., 2018b), which in some ways make seagrass fisheries much more unique than coral reef fisheries which, depending on location, may only include one or two different gears (although some areas utilise many more). As a result, multiple actors engage with seagrass fisheries (e.g., de la Torre-Castro et al., 2014; Wallner-Hahn et al., 2022), but how these actors view seagrass systems, and whether views are similar across countries is relatively unknown.

Lastly, the conservation of seagrass meadows supports numerous Sustainable Development Goals (Unsworth et al., 2022) and this presents both opportunities and risks. Seagrass meadows exist at the land-sea interface where social and environmental development targets often collide, in part due to the multiple ecosystem functions and services that seagrass meadows provide (Nordlund et al., 2016). However, actions to protect or enhance certain ecosystem functions and services (e.g., carbon sequestration and storage), especially outside of a systems perspective, may disrupt or lessen the provision of other ecosystem functions or services, such as blue food production. There are few documented cases for seagrass systems, but risks have been highlighted for the blue economy in general (e.g., Bennett et al., 2021a) and numerous examples exist for terrestrial systems (for review see Muradian et al., 2013). Whether these colliding goals are indeed a risk, or opportunity for seagrass meadows is not apparent and warrants exploration.

Scope of the thesis

This thesis uses a social-ecological lens, that recognises human societies as part of the biosphere (Folke et al., 2016), to answer how seagrass meadows and their associated small-scale fisheries contribute to food security and poverty alleviation (**Figure 3**). Central to this thesis is the belief that social-ecological systems (SES) are categorised by two reciprocal interactions that act in tandem (conceptualised with an infinity symbol in **Figure 3,** and not to be confused with the Holling (1985) adaptive cycle). These include the flow of ecosystem goods and services to society, and society's impacts and modifying actions on the environment. With this in mind, this thesis has four broad objectives, which were to:

a) assess to what extent seagrass biota contributes to associated fauna in relation to blue food (**Paper I** and **III**),
b) assess the extent to which people depend on seagrass for blue food (**Paper II** and **III**),
c) assess how local people view seagrass social-ecological systems in the context of human use (**Paper IV**), and,
d) explore the external factors which influence reciprocal feedbacks within seagrass social-ecological systems (**Paper V**).

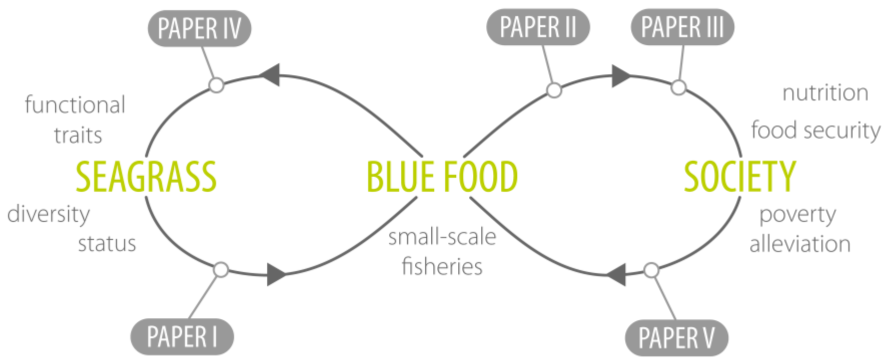

Figure 3. Seagrass social-ecological systems are comprised of reciprocal interactions that act in tandem; the flow of ecosystem services to people, and people's impact on seagrass meadows.

This thesis includes five papers. **Paper I** assesses the relationship between seagrass biodiversity (e.g., functional diversity, species diversity and structural diversity) and the production of associated fish in the context of SSF. **Paper II** identifies who uses seagrass meadows by examining a host of socio-economic drivers that influence use at the household level. **Paper III** examines two key elements of food security, food quantity and quality, and explores how seagrass meadows contribute to both in the context of micronutrients. **Paper IV** utilises local ecological knowledge to reveal change in seagrass SES and the causative factors that individuals attribute to this change. Finally, **Paper V** investigates how sustainable development interventions potentially result in unintended feedbacks that influence social-ecological reciprocity.

Methods

This thesis predominantly relies on a mixed-methods approach to understand seagrass SES, bridging traditional ecology and social science. The papers range in their dependence on empirical data (from empirical evidence to perspectives), their scale (from local to regional) as well as the methods employed (**Figure 4**). This thesis focuses on the Indo-Pacific seagrass bioregion, the most important in terms of seagrass richness and seagrass distribution (Short et al., 2007), where many seagrass associated SSF exist (Cullen-Unsworth et al., 2014; de la Torre-Castro et al., 2014; Quiros et al., 2018) and target either the same groups of species, or very closely related species (Unsworth et al., 2008; Pogoreutz et al., 2012; Honda et al., 2013).

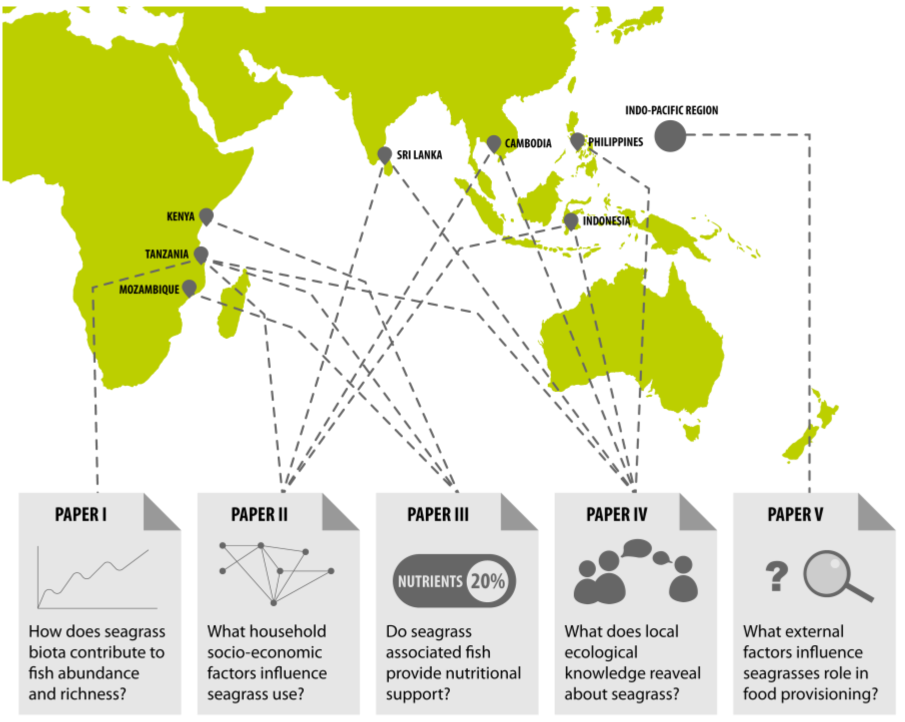

Figure 4. The Indo-Pacific seagrass bioregion hosts abundant seagrass meadows which was the setting of five papers included within this thesis.

Social-ecological systems

First coined by Ratzlaff (1969), the notion of social-ecological systems (SES) approach was turned into a framework by Berkes and Folke (1998) as an integrative and interdisciplinary way of understanding complex systems, such as tropical seagrass meadows. By merging analytical and empirical theory from ecology and social science it is suitably placed to help understand the diverse linkages that exist between the human-nature paradigm and in human-influenced seascapes (Turner et al., 2003; Walker et al., 2004; Liu et al., 2007). Several frameworks exist to analyse SES (Ashley and Carney, 1999; Limburg et al., 2002; Turner et al., 2003; Haberl et al., 2004; Carr et al., 2007; Pahl-Wostl, 2009) and such approaches have multiple names such the human-environment systems framework (Turner et al., 2003), the ecosystem services (ES) framework (Boumans et al., 2002), and earth systems analysis (Schellnhuber, 1999). Of these, the SES framework developed by Ostrom (2009) is one of few that addresses reciprocity between the social and ecological and gives both equal representation (Binder et al., 2013).

Because a SES approach integrates multiple disciplines, we can interpret the patterns and processes that drive seagrass meadow use by people (e.g., **Papers II** and **IV**). Additionally, rather than solely focusing on unidirectional relationships, we can identify links between seagrass meadow structure and function in the context of human use (e.g., **Paper I** and **III**). Lastly, because SES can also take a multi-scale approach (e.g., spatial, temporal, and organizational), we can interpret how changing drivers influence seagrass meadow use by people (e.g., **Paper V**). The SES approach is therefore a suitable tool to understand seagrass systems in the Indo-Pacific and consequently help in finding solutions to prevent further seagrass degradation by complex threats (e.g., eutrophication, over-fishing, coastal development, climate change) while simultaneously responding to growing human aspirations for improved quality of life and wellbeing (e.g., supply of fish, livelihoods).

I conceptualize Indo-Pacific seagrass SES as a coupled system consisting of two main subsystems (McGinnis and Ostrom, 2014): the social and the ecological (**Figure 5**). For this purpose, the social subsystem is comprised of local communities and governance systems, and the ecological system is comprised of seagrass meadows and the biodiversity that is associated to them. Because of the interconnected nature of tropical marine seascapes, socio-economic and environmental interactions link the focal coupled system to other coupled systems such as coral reefs and mangrove forests (Ogden, 1988; Schlüter et al., 2019). While these are not specifically part of the seagrass system, the characteristics of these other systems are interrelated; seagrass meadows influence coral reefs and mangrove forests, and coral reefs and mangrove forests influence seagrass meadows (Dorenbosch et al., 2005a;

Dorenbosch et al., 2005b; Unsworth et al., 2008). For example, from an environmental perspective, collection of mangrove wood for fuel and building materials can change land cover composition and structure and disrupt the buffer that these systems provide to seagrass in terms of sediment retention or fish supply (Valiela and Cole, 2002; Honda et al., 2013).

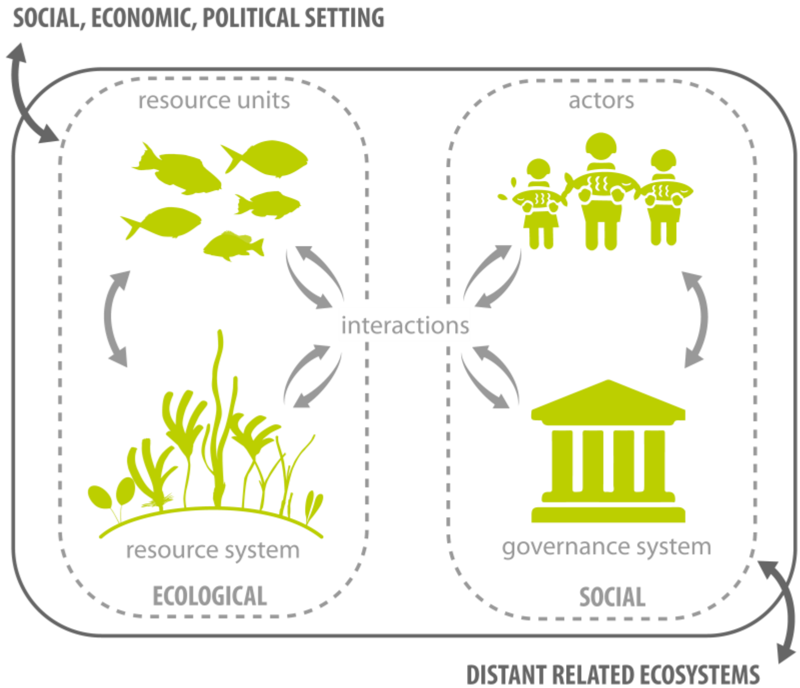

Figure 5. Conceptual seagrass social-ecological system inspired by, and adapted from, McGinnis and Ostrom (2014).

Social systems

The Indo-Pacific's human population is vast and incorporates a range of large and minority ethnic groups, with different cultures, languages and religions, an analysis of which is beyond the scope of this thesis (Williams, 2013). Countries within the region vary immensely by income, with around 11% of countries existing within the Low-Income category, 34% within the Low Middle-Income category, 25% within the Upper Middle-Income category and 30% in the High-Income category. However, population density within these income categories is hugely disproportionate, with nearly 90% of the Indo-Pacific's human population existing in Low and Low Middle-Income countries. To unravel the Indo-Pacific's social systems (**Papers II** and **IV**), I predominantly relied on qualitative methods in the form of household interviews.

Household interviews

Qualitative interviews are the most widely used methods employed in social science research and have been the basis of numerous studies across multiple disciplines, not least in marine social science (e.g., Daw, 2008; Cinner et al., 2009a; Lowitt, 2013; Sulu et al., 2015). Qualitative interviews can take numerous forms that include structured, semi-structured and unstructured interviews, each with their own merits. At one end of the scale, structured interviews typically involve collecting data through a set of predetermined questions; each interview uses the same set of questions allowing for simple comparisons between transcripts, but generally does not allow the discussion to evolve based on the respondents answers (St. John et al., 2014). Unstructured interviews sit at the other end of the scale, and generally ask questions based on the answer of the previous question (Drury et al., 2011). While such interviews allow for in-depth discussion centred around a certain key point, they often neglect other key points. Semi-structured interviews somewhat provide a best of both worlds in that a standard set of questions is employed, but there is also freedom to ask additional questions to elaborate and tease out further answers from the respondent (Young et al., 2014). **Papers II** and **IV** are underpinned by an extensive dataset comprising over 1000 semi-structured household interviews that were used to obtain broad scale data on demographics, household characteristics, marine and coastal resource use, diet, and seagrass knowledge.

Ecological system

Seagrasses form the basis of the ecological subsystem in the Indo-Pacific and are comprised of over 20 species often forming mixed and monospecific meadows (Short et al., 2007). These are characteristically comprised of mixed *Halodule uninervis*, *Halophila ovalis,* and *Cymodocea rotundata* areas towards the upper intertidal limits of meadows, shifting to mixed *Halodule* sp., *C. rotundata*, *Thalassia hemprichii* and *Halophila* sp. areas in the lower intertidal limits of meadows. Upper subtidal areas are comprised of *C. serrulata*, *T. hemprichii*, *Halophila* sp and *Syringodium isoetifolium*, shifting to *C. serrulata*, *T. hemprichii*, *Halophila* sp, *S. isoetifolium* and *Thalassodendron ciliatum* before being dominated by *T. ciliatum* or *Enhalus acorides*, often growing in monospecific strands. Each of these species provide different structural characteristics and complexity (**Figure 6**). As structurally complex habitats, seagrass meadows provide associated assemblages with food, shelter, nursery areas and feeding grounds (Parrish, 1989; Nakamura et al., 2003; Dorenbosch et al., 2005a). Seagrass plants are responsible for most organic production within the system followed by seagrass associated epiphytes. Faunal species associated to seagrass meadows have different food sources, with seagrasses often being marginally important for higher trophic levels. However, seagrass organic material is utilized by some fauna either through direct seagrass grazing or the consumption of detritus.

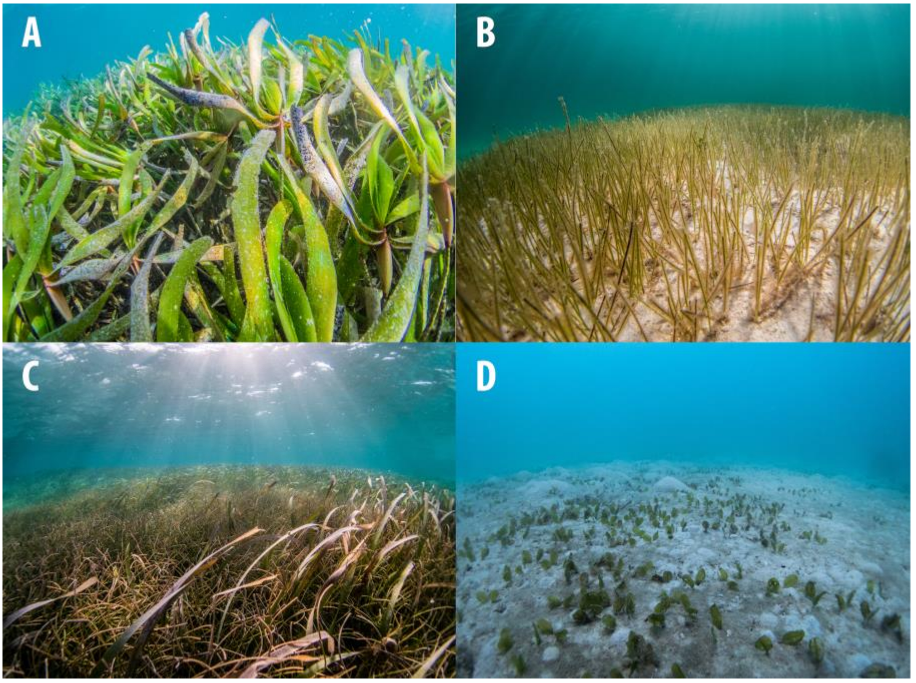

Figure 6. Seagrasses within the tropical Indo-Pacific seagrass bioregion are diverse. A) A dense monospecific meadow of the structurally complex species *Thalassadendron ciliatum*, B) A monospecific patch of the small, ribbon like species *Halodule uninervis*, C) multispecific meadow with variations in traits comprised of tall ribbon like *Thalassia hemprichii* and cylindrical *Syringodium isoetifolium,* and D) sparse patch of paddle shaped *Halophila ovalis*. Photos: Benjamin Jones.

As a result of their high productivity, seagrass meadows produce large amounts of detritus or litter. This can either be in the form of aboveground biomass (dead and decaying leaves), which are often deposited in sand patches and burrows found within seagrass meadows (Vonk et al., 2008), or be in the form of belowground biomass (roots and rhizomes), which are continuingly deposited within the sediment as a rich source of organic carbon (Tanaya et al., 2018). The decomposition of this detritus is of significant value for seagrass systems within the Indo-Pacific, where nutrients are generally limited (Nienhuis et al., 1989; Erftemeijer, 1994). This process is therefore key to regulate the supply of nitrogen and phosphorus to seagrass, and for seagrass to maintain its high productivity (Erftemeijer and Middelburg, 1993; Erftemeijer et al., 1993; Duarte and Chiscano, 1999).

Seagrass meadows within the Indo-Pacific are abundant with burrowing crustaceans, such as Thalassinidean and Alpheid shrimps, which use seagrass litter as a source of food and as material for building burrows (Abed-Navandi et al., 2005; Dworschak et al., 2006; Kneer et al., 2008). Similarly, a diverse array of Holothuriidae species are associated with seagrass meadows, most notable of which is *Holothuria scabra*, which shows preference to seagrass over coral habitats (Uthicke and Benzie, 1999; Hamel et al., 2001) and is commonly associated to *Thalassia hemprichii* and *Enhalus acoroides* (Long et al., 1996; Mercier et al., 2000).

While seagrasses co-evolved with herbivores, and thus adapted to grazing at a range of intensities (Heck and Valentine, 2006), herbivores influence seagrass meadows through top–down regulation of species diversity and biomass production (Scott et al., 2018). Seagrasses within the Indo-Pacific, and the tropics more broadly, are grazed by a diverse array of species, each with a range of feeding strategies (Carruthers et al., 2002). These include mesograzers, macroherbivores, and megaherbivores. Seagrass leaves provide a suitable substratum for macroalgal epiphytes (Duffy et al., 2003), which are an important food source for mesograzers (e.g. amphipods, isopods, and small gastropods) (Browne et al., 2013). Macroherbivores such as fish, sea urchins and larger gastropods ingest small amounts of seagrass leaf tissue (Alcoverro and Mariani, 2004; Eklöf et al., 2008), either to consume seagrass epiphytes (Pitt, 1997), or ingest seagrass tissue itself (Gullström et al., 2011). In terms of biomass, megaherbivores such as dugongs and green turtles consume the most seagrass tissue (Williams, 1988; Aragones, 1996). Herbivory within Indo-Pacific seagrass meadows plays a major part in the regulation of ecosystem structure and function, and this regulation can change with herbivore size and density (Scott et al., 2018).

Seagrass surveys

Given that seagrasses form the basis of the resource system, understanding their composition, structure and function are vital. Seagrass species composition, cover and shoot density are the most common metrics used to determine seagrass meadow state (McKenzie et al., 2012), but additional metrics are often also used such as nutrient content, total biomass, canopy height and epiphyte cover (Jones and Unsworth, 2016). The sampling for **Paper I** built on the Seagrass-Watch (a global seagrass monitoring network) methodology (McKenzie et al., 2000), which was used in a non-random manner to select plots across seagrass diversity gradients. Seagrass surveys for **Paper I** were conducted by snorkelling and placing 50cm x 50cm quadrats along a transect, although the same technique can be and is often utilised in the intertidal zone. By using quadrats, we are able to record seagrass metrics within a defined area such as percentage seagrass cover, shoot density, seagrass composition, canopy height, number of leaves per shoot, leaf length, leaf width and epiphyte cover.

Faunal surveys

Marine fauna – particularly fish and invertebrates – play a key role as resource units within seagrass SES. As many as 746 species of tropical fish are documented to utilise seagrass meadows during one part or all of their life cycle (Unsworth et al., 2019b), however, information on the number and diversity of invertebrate associates is unknown. As a result, this thesis predominantly focused on fish. Various methods are regularly used to survey shallow-water fish assemblages, including underwater visual census (e.g. line or point transects, underwater video) (Samoilys and Carlos, 1992; Darling et al., 2017), towed nets (Guest et al., 2003; Gullström et al., 2008), stationary nets (Acosta, 1997) and traps (Gell and Whittington, 2002; Bacheler et al., 2013). **Papers I** and **III** each used two different forms of underwater visual census (UVC); **Paper I** used Baited Remote Underwater Video (BRUV) systems (discussed in more detail below), whereas **Paper III** utilized a traditional UVC method. Traditional UVC can be conducted using a variety of methods, but characteristically reply on on-site visual counts of organisms whereby a snorkeler or diver remains in a stationary position or swims along a transect and counts observed organisms within a given area.

The use of camera-based methods for fish research is steadily growing (Whitmarsh et al., 2017; Lopez-Marcano et al., 2021). BRUVs have now been utilised in Antarctica (Smale et al., 2007), Oceania (Dunstan et al., 2011), Europe (Bloomfield et al., 2012), Africa (De Vos et al., 2015) (De Vos et al 2014), North America (Anderson and Bell, 2014), South America (Schmid et al., 2017) and Asia (Spaet et al., 2016). They have been utilised in multiple habitats such as rocky reefs (Colefax et al., 2016), coral reefs (Ghazilou et al., 2016), seagrass meadows (e.g. Peters et al., 2014), and soft sediments (e.g., Howarth et al., 2015), as well as pelagic (e.g. Rees et al., 2015) and deep-water environments (e.g. Collins et al., 2002). BRUVs have been used to answer a range of study questions. These include assessments of the effects of marine reserves and protected areas (e.g., Whitmarsh et al., 2014; Bornt et al., 2015; Coleman et al., 2015; Gilby et al., 2017). Such assessments focus on fish diversity as a response and not only focus on top predators, but numerous demersal fish species. In addition, there are numerous uses of BRUVs to study changes in faunal assemblages within and across the seascape where fish diversity is also important (e.g., Gomelyuk, 2009; Langlois et al., 2012; Rees et al., 2018; Swadling et al., 2019). BRUVs are also used to look at specific species, behaviours, and ecological functions like grazing (e.g., Denny et al., 2004; Gutteridge et al., 2011; Zintzen et al., 2011; Lefcheck et al., 2019).

Numerous studies have compared BRUV data with other methods, for which there have been both positive and negative findings (Cappo et al., 2004; Harvey et al., 2004; Langlois et al., 2006; Colton and Swearer, 2010; Ward-Paige et al., 2010; Tessier et al., 2013; Goetze et al., 2015). Many of the negatives have been down to poor visibility (which is also a factor for UVC) and the inability to detect more cryptic species (Watson et al., 2005).

While I appreciate that the BRUV method is not perfect, neither are more traditional methods; all methods will have individual strengths and weaknesses. For example, there is a consensus of the limitations of "diver-based" methodologies which relate to human-bias and many species being "diver aware" (Thresher and Gunn, 1986; Smith, 1988; Thompson and Mapstone, 1997; Kulbicki, 1998). These avoidance behaviours are more pronounced in areas with high fishing pressure (Kulbicki, 1998; Lindfield et al., 2014). Given that many species of fish utilise seagrass meadows as a nursery, a safe habitat to avoid predation, the presence of a large bodied individual snorkelling is enough to ensure that many species remain hidden. Studies suggest that BRUVs sample higher counts of fish that avoid contact with divers, recording more taxonomically distinct assemblages (Chapman et al., 1974; Chapman and Atkinson, 1986; Cappo et al., 2003; Watson et al., 2005; Watson and Harvey, 2007).

Statistical analysis

Univariate analysis

The use of mixed effects models was a common theme across **Papers I-III.** Mixed effects models have been developed under a range of names including random effects models, multilevel models, random coefficient models, mixed models, and random regression models, amongst others. In ecology, the popularity of using linear mixed effects models and generalized linear mixed effects models (GLMMs) has increased the last decade (Bolker et al., 2009; Zuur et al., 2009), and have extended upon traditional linear models to include both fixed and random effects as predictor variables.

Key to the use of mixed effect models is their use of random effects. Within **Papers I-III** I did not specifically test for differences between sites (**Paper I**) or countries (**Paper II** and **Paper III**), but instead accounted for potential differences through the incorporation of random effects. Such random intercepts allow the outcome to be higher or lower for each site, country, or region; random slopes allow fixed effects (e.g., structural straits, income, habitat) to vary for each site or country. Rather than focusing on them individually, I opted to use random effects as a source of variability. This allows us to make “broad level” inferences about the larger samples, which do not depend on a particular site or country. In other words, I was able to incorporate (instead of ignoring) site-to-site variability in order to improve the ability to describe how the fixed effects related to outcomes of studies.

In **Paper I**, I used linear mixed effects models (Zuur et al., 2009), fit with the *lmer()* function in the *lme4* package for R (Bates et al., 2015), to explore the relative importance of seagrass variables (e.g., meadow structure, seagrass cover, seagrass species richness), depth and land-use on fish abundance and fish species richness. **Paper II** used a combination of linear and generalised linear mixed effects models to understand drivers of seagrass dependence at the household scale and combined multiple models into a single causal network (see path analysis below). Finally, in **Paper III** I used a hurdle model approach (Cragg, 1971) to understand the influence of habitat, protection and depth on per capita micronutrient content in fish. The use of mixed effects models in this paper was underpinned by the realisation that in order for a fish to provide micronutrient support it has to pass two sequential hurdles, the first hurdle being whether or not the fish is present (probability of presence), and the second hurdle being the differences in micronutrient content when the fish are present. Such approaches have been used for numerous fisheries studies where zero inflated data is common (Amankwah et al., 2016; Cantoni et al., 2017; Mkuna and Baiyegunhi, 2019).

Structural equation modelling

In **Paper II** I relied on structural equation modelling (SEM) to investigate socio-economic drivers of seagrass dependence across households in a number of countries. SEM builds on path and confirmatory factor analysis that provides opportunities to assess both direct and indirect relationships between variables, where variables may be both predictors and responses (Grace, 2006). While over 100 years old (Wright, 1918), SEM has a long history within the social sciences, emerging in 1964 (Blalock, 1964) and rising with popularity in the 1970’s (Duncan, 2014). In the past 20 years, SEM has expanded into ecological research (Grace, 2006; Shipley, 2016), where it has been extensively used to test multiple hypotheses with numerous variables and the complex networks of causal relationships in ecosystems (van der Heide et al., 2011; Giacomazzo et al., 2020).

The growing popularity of SEM has resulted in new statistical tools for its implementation across a range of programmes and packages including the *lavaan* (Rosseel, 2012) and *piecewiseSEM* (Lefcheck, 2016) packages for R. Across the social sciences, *lavaan* is a popular statistical package given that it includes options for latent variables (hypothetical constructs), that is, variables that are not directly observed or measured but are inferred through other measurable variables. Unlike *lavaan*, *piecewiseSEM* was developed for ecological investigations, where, in relative terms, latent variables are far less common. However, the use of nested survey designs and random factors (discussed above in multivariate analysis) are far more common within natural sciences and the piecewise estimation approach used in *piecewiseSEM* allows for the computation of multiple linear or generalised linear mixed effects models into a single causal network (Lefcheck, 2016). While **Paper II** was predominantly a social study that included no ecological data, data was collected in multiple countries, and I wanted to make broad inferences about variables direct and indirect influences on seagrass dependence and therefore wanted to account for the country-to-country variability with the use of random effects.

Main results

From biodiversity to food

Foundation species play a key role in driving ecosystem functions (Angelini et al., 2011), not least in the production of food. Two ecological hypotheses are proposed to influence the effects of biota on ecosystem functions. The 'mass ratio' hypothesis proposes that ecosystem functions are determined by the functional traits of *dominant species* within the community (Grime, 1998), whereas the 'complementarity hypothesis' proposes that species and/or functional diversity instead drives ecosystem functions (Tilman et al., 1997). In **Paper I**, we tested whether the mass ratio hypothesis or the complementarity hypothesis best predicted the influence of tropical seagrass meadows on associated fish assemblages (**Figure 7**). In total, we examined the relative importance of seven seagrass indicators, which were either associated to the mass ratio (seagrass structure, seagrass cover, seagrass composition) or the diversity hypothesis (seagrass species richness, functional richness, functional dispersion).

In **Paper I** we found that seagrass structural traits and depth were the best predictors of fish abundance. In general, deeper meadows or meadows with higher canopy, longer and wider leaves, greater numbers of leaves per shoot, and lower overall shoot density exhibited greater fish biomass in terms of abundance. These findings conform with others from the region (Gullström et al., 2008), where structure provides greater habitat availability and reduces predation pressure (Hovel et al., 2002; Vonk et al., 2010). Deeper sites are also more likely to be closer to coral reefs where connectivity between the two habitats may influence abundance (Gullström et al., 2008; Gullström et al., 2011). In addition, we showed that an interaction between seagrass cover and land-use was the best predictor of fish species richness. Seagrass cover had strong positive effects on fish richness where human impacts were low, but weaker effects where human impacts were high. The most striking finding here was that the diversity of seagrass fish assemblages *closer* to human impacts remained high regardless of seagrass cover. While this needs further study, this potentially flips the human 'gravity' hypothesis that exists for coral reefs (Cinner et al., 2018b), where increasing human population size and accessibility to reefs diminishes gains in fish biomass and predators.

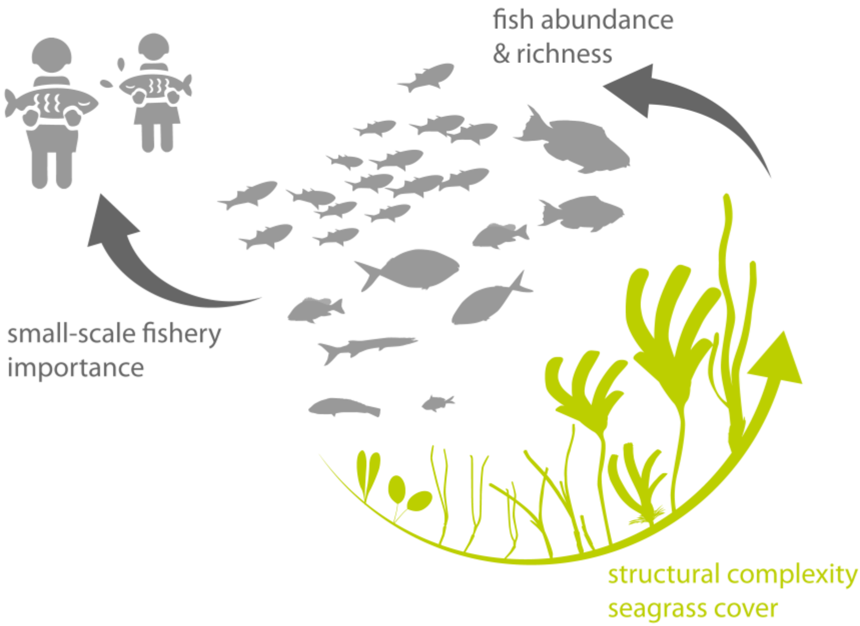

Figure 7. **Paper I**: Seagrass structural traits drive fish assemblages in small-scale fisheries. Green vectors loosely represent the key predictor variables used in the study and grey vectors represent the response variables.

Paper I found weak effects of species and functional diversity on total fish abundance and richness, so evidence for the 'complementarity hypothesis' in seagrass is poor in terms of fish production. A possible reason for this is that seagrass species compete, rather than complement each other, given that many are functionally identical in terms of their structural characteristics (e.g., leaf shape, height). When we looked at fish consumed in the household (grunts, snappers, and rabbitfish), our findings supplemented this. We found that the abundance of species like rabbitfish were negatively influenced by functional dispersion and positively influenced by land use. So, seagrass meadows that were functionally similar in terms of traits and closer to human populations had greater abundance of fish that are important for household consumption. It may be that an abundance of epiphytic algae was driving this, given that epiphytes are particularly important for generalist herbivores like rabbitfish (Ebrahim et al., 2020) and indirectly important for grunts and snappers (de la Moriniere et al., 2003), by supporting invertebrates (Belicka et al., 2012).

Reliable access to food for both poor and wealthy

In **Paper I**, we found that seagrass biota supported fauna that was important for food, namely fish like rabbitfish, snappers, and parrotfish. This supplements knowledge about the role that seagrass plays in supporting global fisheries production and food supply (Unsworth et al., 2019b). Seagrass is used as a fishing habitat across the Indo-Pacific region and likely sustains millions of households through food security and livelihood support (de la Torre-Castro and Rönnbäck, 2004; Cullen-Unsworth et al., 2014; Nordlund et al., 2018; McKenzie et al., 2021). However, the factors that govern the use of seagrass as a fishing habitat over other habitats are largely unknown, especially at the household scale. **Paper II** investigated the who, how and why of seagrass use across the Indo-Pacific region.

Across a range of different cultural, economic, and social settings, we found that seagrass meadows were the most common habitat used for fishing. Strikingly, nearly half of all households we talked to preferred to fish in seagrass over other habitats such as coral reefs, mangroves, the open ocean, or rocky reefs. Reliability was the primary reason for this preference (**Figure 8**); seagrass meadows reportedly provide large catches, and that target species are always found there in high abundance. Seagrass meadows are likely favoured due to the functional role they play for fish, providing valuable nursery habitats for example. This adds greater context to the findings of **Paper I**, suggesting that seagrass biota is important for household supply of food, but leaves open questions as to whether fishers specifically target seagrass areas with high structural complexity or certain desirable traits. This question was due to be answered in an additional paper, but due to the effects of the COVID-19 pandemic, fieldwork for this study could not be completed.

Paper II also revealed that roughly 3 in 20 people across the region were dependent on seagrass meadows as their *only* fishing ground, and therefore did not fish in any other habitats (**Figure 8**). Using path analysis, we revealed that dependence on seagrass was strongly influenced by household income and adaptive capacity. Our analysis revealed dual effects of household income that mediated through ownership of fishing assets that reflected a fisher's capacity to adapt and change. On one hand, poorer households were much less likely to own motorboats, instead owning traditional boats without an engine or no boat at all. Such households were reliant on seagrass as they were unable to fish elsewhere; seagrass is close to shore and easy to access without a motor. On the other hand, wealthier households were more likely to own certain types of fishing gear that incentivized them to use seagrass due to high rewards and low effort requirements. These were static fishing fences that don't require a fisherman to be present.

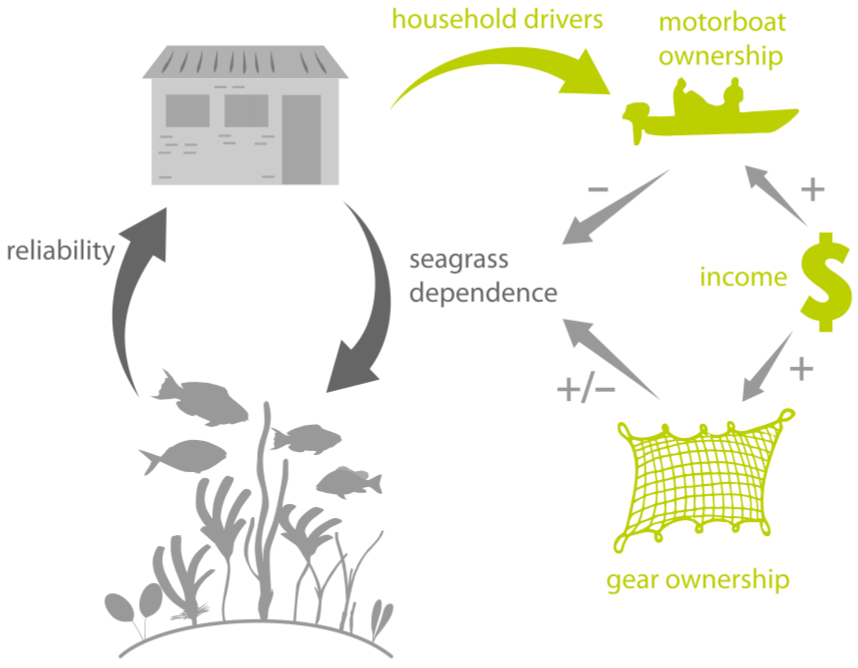

Figure 8. **Paper II**: Dependence on seagrass fisheries governed by household income and adaptive capacity. Green vectors loosely represent the key predictor variables used in the study and grey vectors loosely represent the response variables.

Seagrass for food quantity and quality

Paper II revealed that seagrass meadows were targeted as fishing grounds because they were reliable, and that low-income households were dependent on then for food and income, but whether seagrass meadows also provide nutritional support is an unknown. To advance this knowledge gap, I utilized a dataset where colleagues previously had surveyed fish communities at paired fished and protected sites across Kenya, Tanzania, and Mozambique, and surveyed fish communities within both seagrass meadows and coral reefs. We found that total fish biomass, abundance and species richness were higher on reefs than seagrass, both in protected and fished sites. However, while coral reefs harbour a greater number of individuals, and therefore total biomass, many of these are small fish that may not be as suitable for food. Since micronutrient values vary among fish species and trophic groups, we calculated the average values of six micronutrients across all fish species and found that on average, the two habitats provided similar micronutrient values, despite vast differences in fish species composition. However, when we assessed species in terms of their ability to meet several micronutrients needs in combination using a multifunctionality index, we found that, for any given species, micronutrient density was higher in protected seagrass than protected reefs, fished seagrass and fished reefs.

Sub-setting our data to include only target fish species (e.g., rabbitfish, emperor, parrotfish; **Paper I**) revealed even more striking findings. We found that key fishery species were rarely observed on reefs and were roughly five times more abundant in seagrass. This had knock-on effects to micronutrients showcasing seagrass as previously unrecognised reservoirs of micronutrients (**Figure 9**). The findings of **Paper III** underscore the value that SSF can play in providing nutritional security. Like others (Robinson et al., 2022), we indicate that coral reefs harbour large amounts of bioavailable micronutrients, driven by high biomass and diversity when compared with seagrass meadows. However, we found that contributing to this were large abundances of small fish (e.g., pomacentrids) that are routinely not harvested or potentially unfishable without further degrading reefs through use of destructive gears. Our findings strongly suggest that micronutrient export from seagrass meadows to communities is substantial and overlooked, and that seagrass meadows are not just reliable for quantity (**Paper II**) but also reliable for quality food and must be secured.

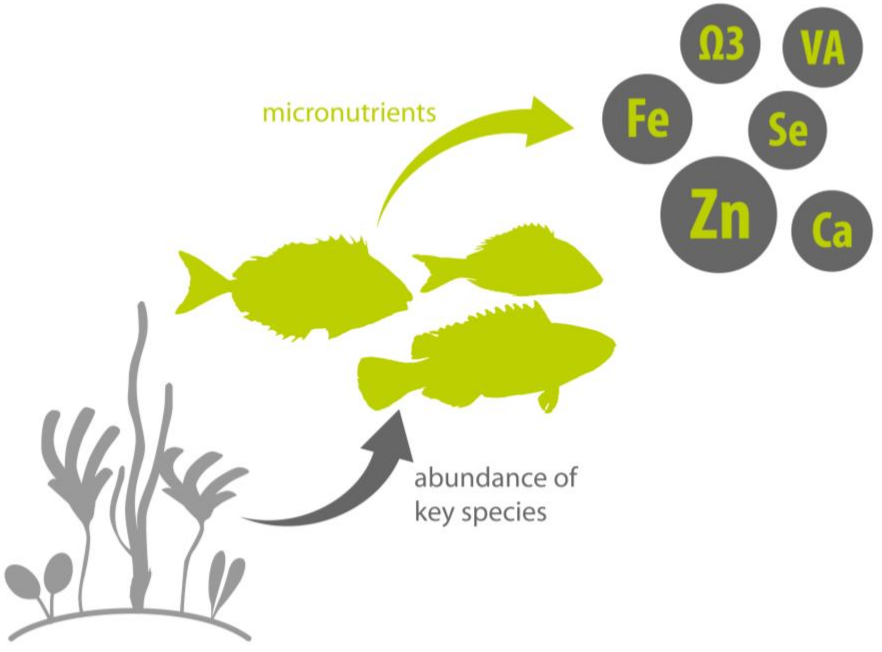

Figure 9. **Paper III**: Seagrass meadows as previously unrecognized reservoirs of micronutrients for human health. Green vectors loosely represent the key predictor variables used in the study and grey vectors represent the response variables.

Local interpretation of SES dynamics

Human behaviour is inherently variable, and views are influenced by a diverse range of values. To capitalise on this, **Paper IV** used local ecological knowledge (LEK) to investigate how different households and individuals viewed seagrass meadows, both ecologically and socially. Using a series of interviews to elicit LEK across Cambodia, Indonesia, the Philippines, Sri Lanka, and Tanzania, we supplemented information from **Paper II** and **Paper III** revealing that the majority of households agreed that seagrass meadows were an important place to find and collect food and that they were important for both people and fish. Moreover, households agreed that degradation of the marine environment significantly affected their lives into the future.

In the absence of long-term monitoring data, LEK can also be used to gain temporal information on the status of fauna in relation to seagrass systems (Unsworth et al., 2019a). Here we revealed ecological changes that were perceived locally over a five-year period, which included declines in the number and size of both fish and invertebrates across countries (**Figure 10**). However, **Paper IV** also exposed how dynamic LEK can be, especially in the context of the variability in human behaviour. Despite over half of respondents acknowledging that seagrass was threatened, and that local biota (fish and invertebrates) had declined in number and size, we found that respondents still believed that seagrass would persist into the future, and that certain activities (e.g., gleaning and seaweed farming) had no effect on seagrass or fauna.

We explored this contrasting LEK using *Attribution theory* (Heider, 2013). Attribution theory integrates cognitive dissonance and motivated reasoning to reveal how certain perceptions and values influence how individuals attribute causality (Lewandowsky et al., 2012). Since the generation of LEK is cognitive process, where individuals use past experiences and observations to inform current views, we suggest that cognitive dissonance may influence how individuals perceive threats to seagrass. For example, it could be that previous gleaning activity (often a regular family activity) potentially influences individuals to create new knowledge that the actions they participate in cannot be the reason for the decline that they themselves have observed. We suggest that previous experiences form the basis for individuals to acquire or invent new beliefs, that it must be something or someone else for example, to reduce internal conflict (i.e., we know invertebrates are declining but it can’t be from my activities).

Motivated reasoning (Kunda, 1990) explores how incentives influence beliefs and postulates that people are motivated to selectively use prior values to support the pre-desired suppositions. **Paper IV** showed that individuals believed that gleaning and seaweed farming were not a threat, and that seagrass will persist forever. Individuals are potentially incentivised to believe this due to the strong importance these habitats play for people, notably through food and income (**Paper II**, **Paper III,** and **Paper IV**). Here, individuals may be motivated by the value of seagrass as a place to find and collect food to support the desired conclusion that seagrass will be here forever. Simply put, people are driven to suppose that seagrass meadows have to endure because of the momentous value they have.

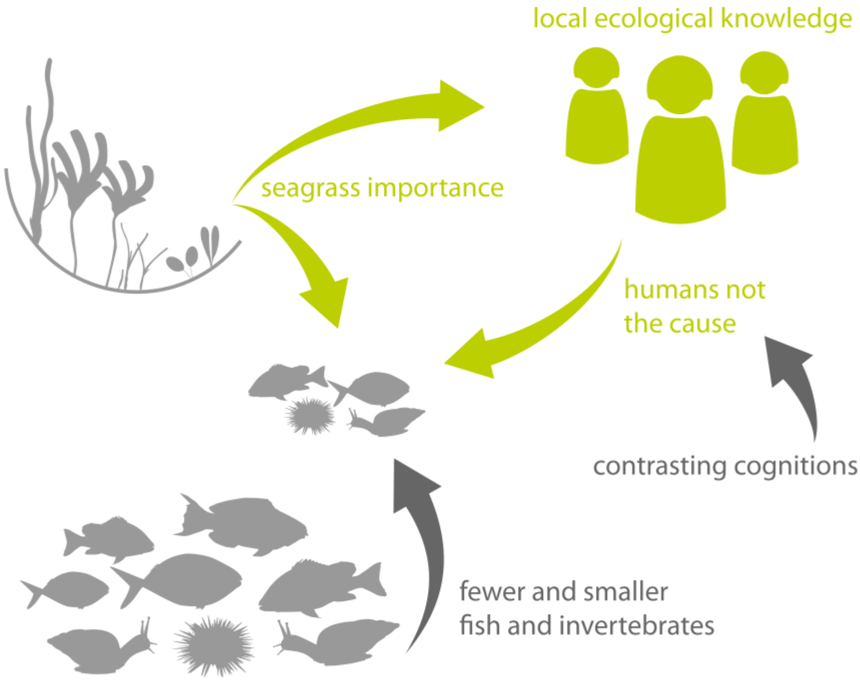

Figure 10. **Paper IV**: Local ecological knowledge reveals the importance of seagrass to human communities and reveals decline in fish and invertebrate communities over time. Contrasting psychological conditions influence how human communities interpret change in seagrass social-ecological systems. Green vectors loosely represent the primary study focus and grey vectors represent inferred information.

System change

In **Paper V**, we sought to place findings of the rest of this thesis (**Papers I-IV**) in the context of social-ecological change. Combining expert elicitation and a literature review, we investigated a number of sustainable development initiatives, such as those to preserve biodiversity, foster human health and provide poverty alleviation, and addressed the impact these have on ecosystem function and service provision (e.g., nursery function and fisheries). Using a SES framework (McGinnis and Ostrom, 2014) we demonstrate how certain interventions may feedback to result in unintended consequences for both people and nature (**Figure 11**). To explore unintended consequences we were inspired by feedbacks presented by Larrosa et al. (2016), which draw upon work by Schoon and Cox (2012). These resulted in the use of three types of unintended effects; *Flow effects* occur due to changes in the strength of linkages within the SES, *deletion effects* occur when linkages within the system are lost, and *addition effects* occur when sustainable development interventions introduce new elements to the system.

Paper V primarily showed that the reviewed sustainable development interventions were too narrow, focusing either on ecological or social goals instead of broader social-ecological goals. For example, we demonstrated how turtle conservation in areas of the Indo-Pacific has resulted in *flow effects* with detrimental impacts to seagrass meadows (Lal et al., 2010; Kelkar et al., 2013; Christianen et al., 2014). Through overgrazing, the important ecological functions that seagrass provides to fish (**Paper I**) is reduced (Arthur et al., 2013), with "knock-on" effects to communities who utilise seagrass as fishing grounds (**Paper II**), thus increasing a human-wildlife conflict (Arthur et al., 2013). We show that such interventions, while fundamentally well intentioned, ultimately risk failing with positive effects having limited long term sustainability.

Notably, initiatives to conserve turtles and promote seaweed farming actually may lead to greater food insecurity and nutritional inequality by reducing seagrass productivity (**Paper II and III**). Both initiatives across a range of locations have led to widespread loss of seagrass, or reductions in canopy height and cover (Eklöf et al., 2006; Arthur et al., 2013; Christianen et al., 2014). As we found in **Paper I**, canopy complexity and seagrass cover are fundamental for high fish production. Given that **Paper II** revealed that households prefer seagrass for large and reliable catches, such sustainable development initiatives place those at the lower end of the income scale at risk, who were often dependent on the habitat for food and/or income. Moreover, **Paper III** revealed that seagrass fisheries are unacknowledged reservoirs of micronutrients that support human health that may be undermined by sustainable development initiatives.

A key caveat to this analysis is the use of expert elicitation, which may have resulted in only picking case studies that suited our theory. While we first sought to find cases within the peer-reviewed and grey literature and also within the Regime Shifts Database (https://www.regimeshifts.org/), we found few examples of unintended consequences within seagrass SES. This potentially suggests that most Sustainable Development Initiatives do not actually have unintended consequences of this magnitude. However, there are two lines of evidence to suggest that this may not be the case. First, published literature linking sustainable development initiatives and seagrass meadows is sparse, despite the fact that multiple projects and programmes exist across the world (e.g., payment for ecosystem services programmes, seagrass restoration projects). Second, most programmes or projects fail to monitor both social and ecological indicators, suggesting that unintended consequences may remain hidden or go unnoticed.

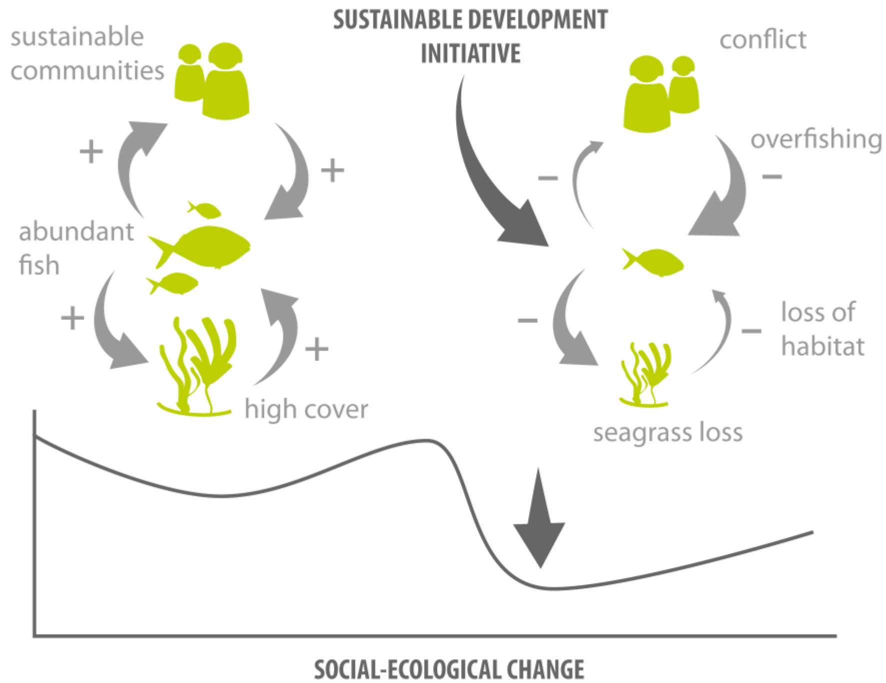

Figure 11. **Paper V**: The introduction of sustainable development initiatives induce unintended consequences (both risks and opportunities) that alter seagrass social-ecological systems and the supply of ecosystem services.

Synthesis and future perspectives

To the question *'how do seagrass meadows and their associated fisheries contribute to food security and poverty alleviation?'* **Papers I-IV** collectively reveal that seagrass meadows are an important cog in tropical blue food systems, while **Papers IV and V** reveal how this cog is potentially at risk. Within the introduction to this thesis, I asked whether the same characteristics that drive terrestrial food production (e.g., plant diversity) were applicable to the aquatic environment, or whether other characteristics matter more (e.g., certain traits). Current knowledge of biodiversity–ecosystem functioning (BEF) is underpinned mostly by theory or experimental studies, and whether predicted relationships exist in natural settings has been a topic of debate (Srivastava and Vellend, 2005; Duffy, 2009). Previous research from across the Indo-Pacific region had already highlighted the role of seagrass structure and complexity in driving fish community composition (Gullström et al., 2008), knowledge which that extends beyond the Indo-Pacific region to multiple seagrass systems (Heck and Orth, 1980b; Gratwicke and Speight, 2005; Henderson et al., 2017; Staveley et al., 2017). However, much of our previous understanding has come from studies where the focus has been on just one or two seagrass species. Unlike any previous work, **Paper I** tested the importance of all seagrass genera (*Thalassia*, *Enhalus*, *Halophila*, *Thalassodendron*, *Cymodocea*, *Halodule* and *Syringodium*) that constitute tropical seagrass meadows in the Indo-Pacific bioregion and found that structural traits composition was far more important for driving production of fish important for food than any diversity metric. Notably, **Paper I** revealed that the key traits (e.g., tall canopy, long and wide leaves) were primarily driven by dominant seagrass species rather than by seagrass species richness (Grime, 1998; Díaz et al., 2007). In the context of BEF research then, **Paper I** found that ecosystem functioning, represented by seagrass structural diversity, was unrelated to species richness—the most frequently used diversity metric in BEF studies, conforming with research on forested sites (LaRue et al., 2019).

I also questioned whether all habitats were equal, or whether some (e.g., seagrass meadows) mattered more for individuals in poverty. **Paper II** revealed that seagrasses (and likely their traits i.e., **Paper I**) were important for households for both food and income. While this information was not new, previous analyses had been highly context specific, focusing on one bay or island region (de la Torre-Castro and Rönnbäck, 2004; Unsworth et al., 2014). By using interviews from nearly 150 distinct villages across multiple countries, **Paper II** (and **Paper IV**) revealed this to be a pattern that existed wherever people existed within close proximity to seagrass. Thinking back to the safety-net function of SSF (Machena and Kwaramba, 1997; Béné, 2003), this paper also revealed that seagrass meadows were valued by people for their reliability and provided access for low-income households lacking adaptive capacity (i.e., ability to travel and fish elsewhere). I found that people preferred to fish on seagrass meadows over other habitats, and that links to household income were unique to households entirely dependent on seagrass. So, linking back to previous SSF literature (Teh et al., 2011), **Paper II** suggested not all habitats are equal in terms of *who* they support and that seagrass fisheries potentially help to alleviate poverty at the household level – they do not reduce poverty, but instead prevent further poverty. Furthermore, not all habitats are equal in terms of the food they supply. **Paper III** revealed that seagrass meadows harbour abundant micronutrient dense fish. While coral reefs harbour more fish, seagrass meadows harbour more nutritious fish – an average seagrass associated fish had greater micronutrient multifunctionality than an average reef associated fish. Such fish have the potential to contribute to curbing food insecurity, including nutritional deficiencies (Hicks et al., 2019), especially when combined with notions that smaller fish contain large quantities of micronutrients (Kawarazuka and Bene, 2011). Linking to contemporary works on the value of SSF for meeting nutrient demands (Bernhardt and O'Connor, 2021; Golden et al., 2021; Maire et al., 2021; Robinson et al., 2022), **Paper III** suggests that seagrass associated fish are *too nutritious to ignore*, and in the face of coral reef decline, these fish may become even more important.

Thinking back to the key question of this thesis, **Papers I-III** revealed numerous mechanisms in reference to the *how*. Tropical seagrass meadows are diverse, both in terms of species and traits, but it is the latter that drives fish abundance and richness – the resources that lie at the heart of the capture fisheries. Tropical seagrass meadows are reliable, providing an abundance of easy-access resources for multiple actors without means to fish elsewhere – a safety-net for those with low household income. And lastly, tropical seagrass meadows are rich in micronutrients that are vital to curb malnutrition. Utilising local ecological knowledge, **Paper IV** revealed that local communities were highly aware of the importance of seagrass, both as a place to find and collect food and as an important habitat for fish – the *how*. However, **Paper IV** also implied that this local ecological knowledge of the *how* strongly influenced cognitive behaviour (cognitive dissonance and motivated reasoning), changing belief systems and attribution to threats. Cognitive dissonance is based on the cognitive consistency of the human mind (Heider, 1958), specifically that people avoid contradicting thoughts and actions, and is fairly common within the food and nutrition literature (Ong et al., 2017; Rothgerber and Rosenfeld, 2021), the conservation literature (Thøgersen, 2004; Balcetis and Dunning, 2007). It is either likely that such cognitions are far more common than we think, or that they do not exist at all – what we scientists perceive as threats to seagrass systems are not the key drivers of loss.

Jointly, **Papers I-IV** advance our knowledge of seagrass SES and reveal how seagrass meadows contribute to food security and poverty alleviation. That said, we still know much less about seagrass SES than we do about other archetypical blue food systems like coral reefs, despite the fact that the two are intricately linked. Between the two systems are flows of information from governance systems and actors, movements of organisms, energy and matter, and exchanges of people. However, our knowledge of seagrass SES is increasing and has expanded from a handful of early studies (e.g., de la Torre-Castro and Rönnbäck, 2004; de la Torre-Castro, 2006; Nordlund et al., 2011; Cullen-Unsworth et al., 2014) to a growing literature linking seagrass and society (e.g., Wawo, 2017; Wahyudin et al., 2018; Furkon et al., 2020; Nessa et al., 2020; Sjafrie et al., 2021; Wallner-Hahn et al., 2022) – this thesis and the papers included add to this growing literature.

Climate change is projected to have knock on effects to food production sectors such as fisheries and agriculture, not least across the tropics (Cinner et al., 2022). Rising to the challenge of improving global access to food while simultaneously conserving biodiversity (Tscharntke et al., 2012) demands that we engage with multiple food systems (IPBES, 2022), especially those that may persist the effects of climate change. While blue food habitats like coral reefs are projected to suffer greatly under current climate scenarios (Frieler et al., 2013; Cornwall et al., 2021; Dixon et al., 2022), there is evidence to suggest that seagrass meadows will persist, and may even benefit from a high CO_2 world (Zimmerman, 2021). This suggests that these blue food providers may grow in their importance for society, and that conserving them not only contributes to reducing food insecurity but host of other societal goals as well (Unsworth et al., 2022). **Paper V** attempted to place many of the thoughts and findings of **Papers I-IV** in the context of meeting multiple societal goals – in the context of ongoing sustainable development initiatives designed conserve biodiversity (SDG 14: Life below water), provide livelihoods (SDG 10: Reduced inequalities) and foster human health (SDG 3: Good health and well-being). **Paper V** showed that sustainable development initiatives have the potential to disrupt the food provisioning service of seagrass meadows when certain system links are influenced either on purpose or unintentionally. Such unintended consequences present both risks and opportunities for sustainable development, but must be acknowledged in policy and development, rather than being ignored.

The introduction to this thesis started with society's challenge of conserving biodiversity while reducing food insecurity (Tscharntke et al., 2012). I noted that production-oriented perspectives often fail to address the multiple reinforcing triggers of food insecurity (Koning et al., 2008), given that food insecurity is driven by inequality, access, and poverty, rather than scarcity. In this sense, conserving seagrass meadows represents many of the qualities we hope for in a food system – a system that provides sufficient (**Paper I**), safe (**Paper II**) and nutritious (**Paper III**) food for multiple individuals across society. But such a food system can only prosper if we acknowledge its existence and manage its threats (**Papers IV and V**).

Emerging questions

While this thesis has advanced our understanding of seagrass meadows and how they link to food, it has also presented numerous questions, both narrow (within field of seagrass research) and broad (across multiple topics). Interestingly, **Paper I** revealed that the effects of certain seagrass variables (e.g., seagrass cover, structural complexity) on fish assemblages were diminished in areas closer to human populations, but that abundance and richness were just as high as meadows further from human populations. The mechanisms of this need further study, but it may be that land-use (and perception of dirty and polluted waters) actually serves to buffer fishing pressure in some locations across the tropics, revealing urban seagrass meadows as hitherto unrecognised fish reservoirs in the tropics.

We know that seagrass meadows are an important place to find and collect food globally (Nordlund et al., 2018), more so within SSF across the Indo-Pacific (**Paper II** and **IV**), but we know almost nothing about what makes a seagrass meadow good for fishing, especially in relation to the seascape. While **Paper I** revealed that certain traits are important for certain fish, whether this information is held within local ecological knowledge is unknown. We need to understand whether seagrass meadows are simply targeted because they are easy to access, because other areas are unavailable (or at certain times of the year), or whether certain types of seagrass meadows are specifically targeted because they are better fishing grounds. Additionally, **Paper II** and **IV** revealed that communities show strong preference for seagrass and are dependent on the habitat for food and income. Whether this has always been the case or is a new phenomenon in response to decline of other habitats is undetermined. Simply put, have we just been ignoring this for the last 40+ years of research into SSF in the tropics?

Paper III found that key fishery species were much more likely to be observed in seagrass meadows than on coral reefs which, coupled with the "reliability" revealed in **Paper II**, poses multiple questions for coastal SSF across the tropics. Firstly, are these key fish species actually the favoured fish for food, or is their high catch rate just an artefact of where people fish? Effectively, are these fish species the key fishery species simply because they occur in the most fished habitat – seagrass meadows (**Paper II**)? Given that key food fish species are far more common in seagrass meadows than on coral reefs, is this just a result of people fishing more on seagrass than on reefs for the reasons identified in **Paper II** (e.g., lack of capital, reliability, accessibility)?

Paper III also revealed that micronutrient support from seagrass meadows is high when looking at an individual fish, but the pathway from meadow-to-plate remains unknown. We know that seagrass associated fish are caught, end up in markets and are sold for household consumption, but what next? How much is eaten, what are the portion sizes like, what does a typical meal comprise of? In order to answer such questions, we also need information on micronutrient support from invertebrates, which remain a hidden harvest. We know that invertebrate individuals are gleaned, often in quantity (Furkon et al., 2020; Chitará-Nhandimo et al., 2022; Stiepani et al., 2022), and consumed at the household level (De Guzman et al., 2019; Furkon et al., 2020; Chitará-Nhandimo et al., 2022), but what support in terms of nutrition do such fisheries provide?

While **Papers I-III** were mainly placed in the context of household consumption of fish, seagrass food systems potentially contribute to national economic growth through foreign exchange. For example, in Sri Lanka (a study location in **Papers II** & **IV**), most lagoonal SSF are focused on shrimp harvests (Silva et al., 2013). While shrimp farming was once highly important to export markets, due to environmental problems many actors transitioned back to collecting shrimp, either by hand or using nets and traps from seagrass meadows (Jones et al., 2018b). For a country with a GDP of nearly $90 billion, shrimp collected from seagrass, with an export value of $20 billion provides great potential for economic growth (Jones et al., 2018b). Yet these contributions are difficult to estimate (Béné et al., 2007), especially given the limited data on seagrass associated SSF.

We do not know how common unintended consequences stemming from sustainable development initiatives are for any systems, or how frequently social-ecological monitoring is employed within such initiatives. In **Paper V** we highlighted that mangrove planting has a strong potential for unintended consequences for seagrass meadows when conducted in an inappropriate manner (e.g., wrong species, wrong place), but that currently there is not sufficient data available to understand this. Aside from the obvious mangrove restoration failure, it would be useful to understand whether there are effects or feedbacks that influence seagrass meadows and their fisheries. In a somewhat similar vein, Blue Carbon habitats are being hailed as solutions to the climate crisis (Macreadie et al., 2021; Stankovic et al., 2021). While there are indeed positives, governance of such habitats also present risks to people that are not part of the conversation. Protection of Blue Carbon habitats must not disenfranchise communities that utilise them for food (Barbesgaard, 2016; Morrissey, 2021; Seddon et al., 2021). We must therefore seek to understand whether there are negative consequences of protection and payment for ecosystem services schemes (e.g., to avoid unintended consequences) for production of blue food.

Lastly, the UN Decade of Ecosystem Restoration provides numerous positives for our ocean. Restoration is an emerging frontier, not just within the seagrass research and conservation community, but across multiple blue food habitats such as reefs and mangroves (Duarte et al., 2020), and while research has been ongoing for decades, there is now significant interest from outside of academia. While we must seek to utilise this decade to mobilise restoration of blue food habitats for fisheries support, not least in the Indo-Pacific, we must also consider potential challenges, risks, and feedbacks. For example, how long after restoration can we expect to see benefits for people who depend on coastal resources on a daily basis, and does restoration as a “buzzword” detract attention and finances away from measures to invest in social and urban infrastructure that may facilitate (or even be needed for) natural recovery of blue food systems (e.g., Saunders et al., 2017).

Moving forward

Managing systems for both people and planet, whether this be for biodiversity and food provisioning or other ecosystem services, is a challenge that is not unique to the seagrass community. We are not alone in trying to rise to such challenges and key to this thesis is the use of a SES framework to understand seagrass meadows and their associated fisheries. In doing so, this thesis has explored how resource systems (seagrass meadows) influence the supply of resource units (fish) (**Paper I**) and how system actors depend on ecological resources (resource systems and units) for food and nutrients (**Paper II** and **III**). This thesis also explored how system actors view the system they use (**Paper IV**) and how certain actions can change and disrupt these systems further, placing people and nature at risk (**Paper V**). While I have used seagrass meadows as a model system, many of the same rules apply elsewhere.

SES frameworks have been used to understand savannahs (Beale et al., 2013), farming systems (Özerol, 2013), forest landscapes (Auclair et al., 2011; Fischer, 2018; Gonzalez-Redin et al., 2019), mountain landscapes (Rescia et al., 2008), wetlands (Song et al., 2021), urban forests (Vogt et al., 2015), plantations (Shumi et al., 2019; Gonzalez-Redin et al., 2020) and various other natural resource management systems (Delgado-Serrano et al., 2015; Fischer et al., 2021). Yet, for the most part, lessons learnt in terrestrial systems are rarely carried over in the way that we manage marine systems, even though many of the challenges we face are not new (e.g., displacement of communities, multiple uses). For example, many forest systems are multi-use, where forest products are commercially harvested, ecosystem services are economically valued and communities gain a range of non-market cultural, economic, and subsistence goods and services (Gilmore et al., 2013). In such cases, multiple-use forest management has been highlighted as an equitable strategy to satisfy the demands of multiple stakeholders (García-Fernández et al., 2008), alongside calls to manage such systems for ecosystem services bundles (Raudsepp-Hearne et al., 2010; Yang et al., 2019; Orsi et al., 2020). Rarely are such approaches employed in management of seagrass meadows, which too have multiple non-market goods and services, as well as commercial services such as nutrient absorption and carbon sequestration. The role of seagrass meadows for blue food production adds even greater value to these habitats and highlights the need to manage these systems for ecosystem services bundles, rather than single ecosystem services alone.

I would argue that actors from terrestrial and marine systems simply do not talk enough, and with numerous calls for swathes of highly protected MPAs (Sala et al., 2021), it also seems that integrated coastal zone management has gone out of fashion. For seagrass systems at least, conservation efforts on land may have overwhelmingly greater impact on the resilience of seagrass systems than implementing highly protected MPA's; most threats associated to seagrass loss come from beyond the confines of an MPA – from the land (Eklöf et al., 2009; Quiros et al., 2017; Unsworth et al., 2018). It is very likely that working with small-holder farmers to restore riparian vegetation (Unsworth et al., 2019a), and improving infrastructure like sewage systems (Tuholske et al., 2021) would greatly reduce the primary stressors influencing seagrass condition and have knock-on effects for the people that use them.

Throughout this thesis, I have taken a holistic approach to explore seagrass SES. With particular emphasis on **Paper V**, such approaches need not only focus on seagrass meadows but can be applied more broadly across the conservation sphere. Using the evidence, frameworks, and toolkits available to us as researchers and practitioners is needed if we are to move forward and manage systems for biodiversity and people.

Reflections

COVID-19, resilience, and adaptive capacity

I see many parallels in how the COVID-19 pandemic has affected me personally, my thesis and how seagrass meadows are used by people, especially concerning the topics of resilience, adaptive capacity, and mobility. If the COVID-19 pandemic has taught me anything, it is that the social and environmental connections that you cultivate around you are key for resilience. I had many plans and desires for what my PhD was going to look like; months of traveling between human communities in the Indo-Pacific region to help unravel people's connection to seagrass meadows. I planned to have hundreds of conversations about what seagrass meadows mean to people, what they provide and the support they give. But the COVID-19 pandemic meant that much of this could not happen.

A key challenge of the COVID-19 pandemic was mobility – the lack of mobility in fact. An inability to travel made it difficult, or rather impossible, to answer and conduct the studies I had originally planned. I spent over a year in limbo, waiting to see if restrictions eased, before realising that the clock was ticking, and I needed to reassess what I have and how I was going to move forward. Here, social (or rather professional) networks were a source of adaptive capacity. Fortunately for me, work that I had conducted and been involved with prior to my PhD afforded me the opportunity to answer similar but different questions that still fit neatly within the scope of my original aims. Other networks provided scope to include new dimensions in my thesis that I had not even thought about previously. So, just as seagrass meadows offer a safety-net for people with reduced mobility (**Paper II**), my own social environment became a fallback when my mobility was reduced. That said, I note that I am privileged. I acknowledge that such challenges are dwarfed by the plight of people that depend on seagrass meadows (and other coastal habitats) for daily needs, but on reflection, COVID-19 has only increased my appreciation for the challenges that people face and strengthened my desire to do what I can to respond.

Ethics, equity, and final remarks

There is an abundance of literature on the role of ethics in social science research. Yet, for the most part, research ethics consider and focus on the actions of researchers (or institutions) in the context of the participants. Non-participants are very rarely considered, even though social and environmental science with practical applications overwhelmingly affect people. These non-participants are often the majority; in social science we often choose a subset of the population to allow us to make broad scale assumptions about the rest of the population. The findings of social and environmental science, especially in the context of food and poverty, will ultimately affect people's lives (either in a good way, or a bad way). I have often wondered how the ethics of research and conservation look to them. These murmurings were partly the reason for **Paper V**; to address the implications of certain actions on people that have not been considered – on non-participants.

Greater attention needs to be paid to social equity; that is impartiality, fairness, and justice for all people in both social and environmental policy. To that tune, Bennett et al. (2021b) recently highlighted how to better integrate social equity into marine conservation policy and practice, whereas the UN Decade of Ocean Science for Sustainable Development provides a unique opportunity to change the way we conduct ocean science. Its tagline, "The science we need for the ocean we want", reflects the need to generate science that supports both people and biodiversity. I feel that this thesis epitomises that tagline. This thesis has highlighted the important role that seagrass biodiversity plays for people in terms of supply of important fish harbouring rich micronutrients. It recognises the diverse and many peoples that use seagrass meadows and depend on its biodiversity for food and livelihoods. These people must be acknowledged and respected in future environmental policy to maintain and maximize benefits – to manage the ocean for the seagrass meadows we (all) want.

Sammanfattning

Att bevara den biologiska mångfalden och samtidigt föda en växande befolkning är en av antropocenens stora utmaningar. På senare tid har flera globala bedömningar lyft fram vikten av den marina miljön för tillgången på mat (ofta kallad ”blå mat”), samt den tillhörande mångfalden av försörjningsmöjligheter. Småskaligt fiske (SSF) med jakt på både fisk och evertebrater är här centralt. Om blå mat ska vara en del av lösningen för att ta itu med matosäkerhet behöver vi en djupare förståelse för hur kustnära livsmiljöer fungerar när det kommer till biologisk mångfald, människor och mat. Enkelt uttryckt behöver vi veta hur dessa livsmiljöer bidrar till matförsörjningen, både vad gäller ekologiska funktioner och socialekonomiska drivkrafter. Sjögräsängarna som sträcker ut sig över hela den indopacifiska regionen är ett av många kustnära ekosystem som ger mat och försörjningsmöjligheter. Genom att använda detta system som en ram, syftar denna avhandling till att utforska hur sjögräsängar och deras associerade SSF bidrar till födotillgång och fattigdomsbekämpning. Avhandlingen, som består av fem studier, bygger på blandade metoder för att förstå sjögräsängarna som ett social-ekologiskt system. De studierna varierar i användning av empiriska data, deras skala såväl som de metoder som används. **Studie I** använder teorier om den biologiska mångfaldens ekosystemfunktion för att undersöka relationen mellan sjögräs och produktionen av associerad fisk i samband med SSF i Tanzania. Resultaten pekar på att strukturella egenskaper hos sjögräset, snarare än artrikedom, driver den abundans och mångfald av arter som är nyckeln till ett produktivt fiske. **Studie II** undersöker de socioekonomiska drivkrafterna som påverkar sjögräsanvändningen på hushållsnivå. Studien visar att hushållens användning av sjögräsängar för mat och inkomst var högre än för alla andra studerade livsmiljöer, och att människor använder sjögräsängar för att de är pålitliga. Den visar också att hushållens inkomst är nyckeln till att förklara varför människor använder sjögräsängar som fiskevatten, där låginkomsthushåll var beroende av sjögräsängarna som skyddsnät, medan höginkomsthushåll använde sig av sjögräsängarna på grund av den höga avkastningen. **Studie III** undersöker två nyckelelement för livsmedelssäkerhet, matkvantitet och matkvalitet, och visar hur sjögräsängar bidrar till båda när det kommer till mikronäringsämnen, vilka är avgörande för människors hälsa. Data från hela Östafrika visade att sjögräsängar spelar en viktigare roll än andra studerade livsmiljöer för att tillhandahålla

mikronäringsrika fiskarter. **Studie IV** använder lokal ekologisk kunskap för att undersöka upplevd tidsmässig förändring i fiskars och evertebraters abundans och storlek, men identifierar samtidigt möjliga kontrasterande uppfattningar som sätter mänskliga samhällen i fara. Slutligen presenterar **Studie V** en syntes av tidigare studier som har undersökt hur vissa initiativ för hållbar utveckling resulterar i oavsiktliga konsekvenser som påverkar utbudet av blå mat. Studien identifierar ett antal oavsiktliga effekter som utsätter människor som använder sjögräsängar för risker och samtidigt minskar de positiva effekterna av själva initiativet för hållbar utveckling. Tillsammans beskriver de fem artiklarna det dynamiska samspelet mellan biologisk mångfald, människor och mat, och placerar sjögräsängar – vilka förekommer världen över – i framkanten av utvecklingen mot en hållbar produktion av blå mat. Det belyser hur sjögräsängar representerar många av de kvaliteter vi letar efter i ett livsmedelssystem - ett system som tillhandahåller en tillräcklig mängd säker och näringsrik mat för en mångfald av individer från alla samhällsgrupper.

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