



MODELLING CORAL REEFS TO SUPPORT THEIR LOCAL MANAGEMENT:

A CASE STUDY IN THE SPERMONDE ARCHIPELAGO, INDONESIA



Dissertation submitted by

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Dedicated to my grandmother –

Summary

The potential of simulation models to provide insights on ecological questions that are crucial for the management of marine resources has become more relevant in light of the apparent demise of coral reefs. Multiple coral reef stressors can interact in nonlinear ways, confounding ecological interpretation through field studies alone. Theoretical computer modelling offers a platform to test ecological hypotheses about multiple stressors and their systemic impacts. The main purpose of this thesis was to use coral reef ecological theory to create a model as a basis for a scientifically sound, user-friendly decision support tool for the local management of coral reefs. Four major objectives were established: (1) develop a local coral reef model representing the impacts of simultaneous stressors on key ecological groups, (2) turn it into a user-friendly decision-support tool to explore different management options, (3) collect qualitative and quantitative information on the artisanal fishery of Spermonde (Indonesia) to help understand its social drivers, and (4) apply the model to real case scenarios to project the trajectory of selected coral reef response variables.

Chapter two contains the description of SEAMANCORE (Spatially Explicit simulation model for Assisting the local MANagement of COral REefs) and its development. The model has two distinct compartments, benthos and fish, which run at different spatiotemporal scales and are affected by each other and by the three modelled stressors: fishing, bleaching and nutrients.

Chapter three outlines an assessment of the coral reef fishery in Spermonde, focusing on the role of the patron-client system in the fishing behaviour of individual fishermen. This study contributes to the body of scientific literature on social drivers influencing fishing behaviour by empirically showing catch and behavioural differences between fishermen within the patron-client system and independent fishermen. Quantitative data on catches obtained in this study were used to parameterize fishing scenarios in Spermonde for a real case application of the model.

Chapter four stems from the previous studies and adds ecological field collected data to parameterize SEAMANCORE. First, basic scenarios of nutrients and fishery were run under standardized conditions to appraise the stressors' effects on the modelled response variables. Fishery scenarios included a fishery ban, subsistence fishery, commercial fishery, and commercial combined with destructive fishing practices. In the second part, ten-year simulations were run for four sites in Spermonde (Indonesia) exposed to varying degrees of human impacts and different initial conditions to project their local coral reef's trajectories.

Chapter 5 summarizes the contributions of this dissertation, highlighting the limitations of the modelling approach, and provides recommendations on research directions for modelling local coral reefs and management of their associated artisanal fisheries.

Zusammenfassung

Angesichts des Verlusts von Korallenriffen hat das Potential von Simulationsmodellen an Relevanz gewonnen, Einblicke in ökologische Fragestellungen zu ermöglichen, die für das Management von marinen Ressourcen wichtig sind. Auf Korallenriffe einwirkende Stressfaktoren können auf nichtlineare Weise mit einander interagieren, wodurch Schlussfolgerungen aus ökologischen Feldstudien in ihrer Aussagekraft limitiert sind. Theoretische Computermodelle bieten die Möglichkeit ökologische Hypothesen zu mehreren Stressfaktoren und ihren systemischen Auswirkungen zu testen. Das Hauptziel dieser Doktorarbeit war deshalb die Entwicklung eines Modells als Grundlage für ein wissenschaftlich fundiertes, nutzerfreundliches Werkzeug zur Entscheidungshilfe für das lokale Management von Korallenriffen. Vier Hauptziele wurden verfolgt: 1) Entwicklung eines lokalen Korallenriff-Modells, das die Einflüsse simultaner Stressfaktoren auf ökologische Schlüsselgruppen repräsentiert, 2) Umwandlung des Modells in ein nutzerfreundliches Entscheidungswerkzeug zur Prüfung unterschiedlicher Managementoptionen, 3) Sammlung qualitativer und quantitativer Informationen über die traditionelle Fischerei in Spermonde (Indonesia), um soziale Einflüsse zu verstehen und 4) Anwendung des Modells auf reale Szenarien, um die Entwicklung ausgewählter Korallenriffkomponenten vorauszusagen.

Das zweite Kapitel beinhaltet die Beschreibung von SEAMANCORE (Spatially Explicit simulation model for Assisting the local MANagement of Coral Reefs – *räumlich explizites Simulationsmodell für lokales Korallenriffmanagement*) und seiner Entwicklung. Das Modell hat zwei separate Komponenten, Benthos und Fisch, die sich raumzeitlich unterschiedlich entwickeln, sich gegenseitig beeinflussen und von drei Modellstressoren beeinflusst werden: Fischerei, Korallenbleiche und Nährstoffe.

Das dritte Kapitel umfasst die Analyse der Korallenriff-Fischerei in Spermonde mit Fokus auf die Rolle von *patron-client* Systemen für das fischerei-bezogene Verhalten der individuellen Fischer. Durch die empirischen Ergebnisse, die Fang- und Verhaltensunterschiede zwischen in solchen *patron-client* Systemen arbeitenden und unabhängigen Fischern aufzeigen, trägt diese Studie zu der wissenschaftlichen Literatur bei die sich mit dem Einfluss von gesellschaftlich-bedingten Kräften auf die Fischerei beschäftigt. Quantitative Fangdaten dieser Studie wurden dafür verwendet, Fischerei-Szenarien für die Modellanwendung auf die realen Beispiele in Spermonde zu parametrisieren.

Das vierte Kapitel nimmt die vorhergehenden Studien als Grundlage und verwendet die im Untersuchungssystem gesammelten ökologische Daten für die Parametrisierung von SEAMANCORE. Zunächst wurden einfache Nährstoff- und Fischerei-Szenarien unter

standardisierten Bedingungen durchgeführt, um den Effekt der Stressfaktoren auf die simulierten Reaktionsvariablen des Modells zu bewerten. Fischereiszenarien beinhalteten Fischereiverbote, Subsistenz-Fischerei und kommerzielle Fischerei, sowie kommerzielle Fischerei in Verbindung mit zerstörerischen Fischereipraktiken. Im Zweiten Teil wurden vier Lokalitäten in Spermonde in 10-Jahres-Simulationen verschiedenen Niveaus anthropogenen Stresses ausgesetzt, um die Entwicklung der örtlichen Korallenriffe vorherzusagen.

Kapitel fünf fasst die Beiträge dieser Dissertation zusammen, diskutiert die Limitationen des verwendeten Modellierungsansatzes und erarbeitet Empfehlungen für zukünftige Forschungslinien für die Modellierung von Korallenriffen und des Managements der assoziierten Kleinstfischerei.

Paper outline

Paper 1

Sara Miñarro, Johannes Leins, Esteban Acevedo-Trejos, Elizabeth A. Fulton, Hauke Reuter (submitted to *Ecological Applications*)

SEAMANCORE: A Spatially Explicit simulation model for Assisting the local MANagement of COral Reefs.

Contributions: The project idea was conceived by Sara Miñarro and Hauke Reuter. Sara Miñarro designed the theoretical and applied framework of the model and software, with suggestions from Johannes Leins, Elizabeth A. Fulton and Hauke Reuter. Johannes Leins implemented the model in Java and contributed to its development. Esteban Acevedo-Trejos and Sara Miñarro designed the sensitivity exploration and its analysis. Sara Miñarro wrote the manuscript and appendices, with improvements by all co-authors.

Paper 2

Sara Miñarro, Gabriela Navarrete Forero, Hauke Reuter, and Ingrid E. van Putten (2016)

The role of patron-client relations on the fishing behaviour of artisanal fishermen in the Spermonde Archipelago (Indonesia). *Marine Policy*, vol. 69, pp. 73-83

Contributions: The project idea was conceived by Sara Miñarro and Hauke Reuter. Sara Miñarro, Hauke Reuter and Gabriela Navarrete planned the study. Sara Miñarro and Gabriela Navarrete designed the fieldwork questionnaires and data collection. Gabriela Navarrete collected the data. Sara Miñarro analysed the data with assistance from Ingrid E. van Putten and Gabriela Navarrete. Sara Miñarro wrote the manuscript with improvements from Ingrid E. van Putten.

Paper 3

Sara Miñarro, Jamaluddin Jompa, Jeremiah G. Plass-Johnson and Hauke Reuter (In preparation)

Modelling coral reefs in Indonesia: benthic cover, fish biomass and catch predictions under different fishing and eutrophication impacts.

Contributions: The project idea was conceived by Sara Miñarro, Hauke Reuter, and Jamaluddin Jompa. Sara Miñarro designed the study. Sara Miñarro and Jeremiah G. Plass-Johnson designed the fieldwork and collected the ecological field data, with logistical assistance from Jamaluddin Jompa. Sara Miñarro collected qualitative data for the fishery parameterization, and analysed the data. Sara Miñarro wrote the manuscript with improvements from Jeremiah G. Plass-Johnson and Hauke Reuter.

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Introduction

1. THE CORAL REEF CONUNDRUM

Coral reefs, covering a tiny surface of the ocean floor, are one of the most biologically diverse ecosystems on the planet and contain a greater number of species than any other shallow-water marine ecosystem, including more than 4000 species of fish (Spalding et al. 2001). The structural complexity created by reef building corals through calcification provides a unique living environment for numerous organisms in terms of habitat, refuge, and spawning, breeding or feeding grounds in otherwise unproductive waters. As a result of this exuberant productivity, coral reefs provide an array of goods and services to humans, particularly to the over 450 million people who live within close vicinity of these ecosystems, most of them directly or indirectly depending on them for food and income derived from fishing activities, dive tourism and coral protection among others (Pendleton 1995).

Despite their social and ecological relevance, 75% of the coral reefs are degraded to some extent (Burke et al., 2011). For the last decades, they have shown drastic declines in terms of biodiversity, biomass and structural complexity as a result of their high vulnerability to local and global impacts such as climate change (Hoegh-Guldberg et al. 1999), marine diseases (Harvell et al. 1999), coastal development (Mora, 2008), overfishing (Jackson et al. 2001), and watershed pollution (Fabricius 2005). These pressures, exacerbated by the fast increasing human population of coastal areas, have led scientists to conclude that complex coral-dominated reef ecosystems are likely to be rare by 2050 (Hoegh-Guldberg et al. 2010). Likewise, the projected scenarios are expected to have serious consequences for subsistence-dependent societies and wider regional economies through the loss of coastal protection, fisheries, and tourism (Hoegh-Guldberg et al. 2007).

The underlying causes driving the demise of coral reefs remain a matter of debate (Mora 2008), but their combined effects result in reduced functional redundancy, weakening and breaking of ecological linkages, seriously impairing ecosystem resilience (Hughes et al. 2003), or their ability to recover from natural and anthropogenic disturbances while remaining within the same ecosystem state (Holling 1973, Nyström et al. 2008). On the other hand, a few recent studies bring some hope to the grim picture of coral reefs and hint at the possibility of recovery. Gilmour et al. (2013) showed that an isolated reef recovered to former “pristine status” after a disturbance event when it was free from human impacts. Roff and Mumby (2012) suggest that research on coral reef resilience could have been biased by the fact that most of it has been undertaken in the Caribbean region, and that Indo-Pacific reefs might be, in fact, more resilient than was initially thought. However, the globalization of trade, combined with technological advances, is quickly changing the societal dynamics of Indo-Pacific island countries and exacerbating local impacts on their natural resources. An

extensive review of the status of coral reefs ranked overfishing, destructive fishing and watershed pollution as the strongest local threats faced by coral reefs around the world (Burke et al. 2011). Figure 1 displays a classification of the coral reefs of the world according to their level of threat by local activities. Indo-Pacific countries are especially exposed to the increasing demands of Asian markets such as Singapore or Hong Kong for marine products, with particular interest in a number of target species that are considered delicacies and can achieve a very high market value (e.g. tuna, sea cucumber, grouper, or napoleon wrasse). This has led to the development and widespread use of destructive fishing practices and overfishing in the Indo-Pacific seas, particularly impacting accessible coral reefs as a result of being located in shallow waters and close to coastal areas.

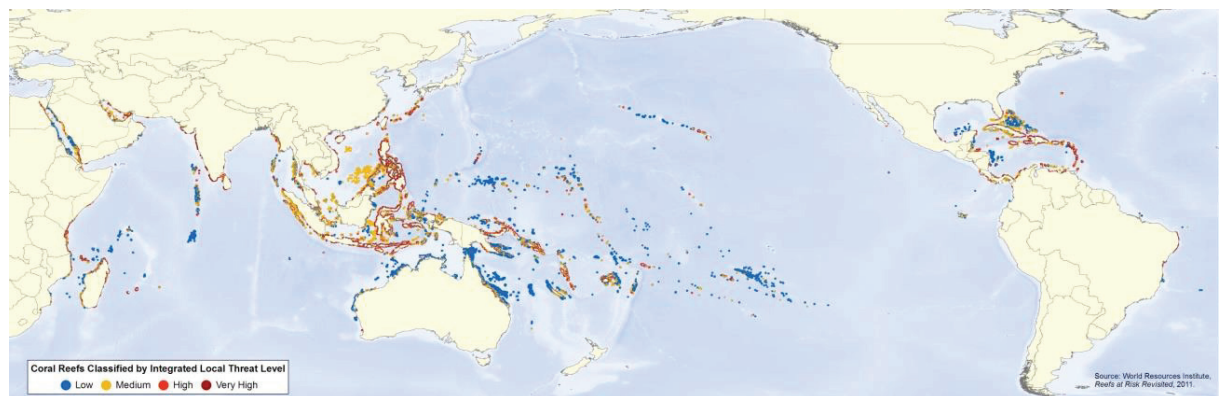


Figure 1. Coral reefs of the world classified by threat from local activities (Burke *et al.*, 2011).

Given the unimpressive trajectory of human attempts to mitigate CO₂ emissions to date, it has been argued that reducing the influence of local stressors such as declining water-quality, coastal pollution and overexploitation of key functional groups should become the primary goal of coastal resource management policies in order to assist coral reefs in the inevitable stress they will suffer in the following decades (Hoegh-Guldberg et al. 2007). To that end, it is important to further understand the feedbacks involved in providing greater ecosystem resilience. A review by Knowlton and Jackson (2008) highlights several pressing questions regarding the importance of local management to conserve coral reefs. One of them is to what extent do overfishing and eutrophication increase the vulnerability of corals to bleaching, disease and acidification caused by climate change; another one is to identify critical breakpoints and thresholds in the abundance and trophic composition of marine consumers below which coral populations will fail to recover. Individual-based models

(Huston et al. 1988, DeAngelis & Gross 1992) provide a tool to address those and other questions regarding combined effects of different stressors on the dynamics of these ecosystems.

The multiscale nature of coastal ecosystems complicates their understanding and management (Swaney et al. 2012). The last decades have brought a change in temporal and spatial scales associated with human activities over coastal ecosystems. The question of scale is a fundamental challenge for coastal research, as are the limitations in sampling, and the lack of a baseline for pristine coral reef ecosystems (Knowlton & Jackson, 2008). As complex adaptive systems (Nyström & Folke 2001), coral reef ecosystems are not easy to understand in their entirety. They are characterized by self-organization and co-evolutionary dynamics, presenting non-linearities, nested hierarchies, uncertainty, multidimensional interactions and emergent properties which require an integrated and interdisciplinary approach for their management (Rammel et al. 2007). Individual human decisions with little apparent impact can collectively have enormous consequences for coastal environmental quality, and success in managing the effects of these decisions will determine the quality of life in the coastal zone in the near future (Swaney et al. 2012). Many large-scale studies from the social sciences and ecological disciplines urge for novel and interdisciplinary combinations of existing tools to capture the adaptive dynamics and complex interactions inherent in those systems, which are impossible to capture by a reductive approach. Individual-based models present an opportunity to study these issues thanks to their ability to represent the behaviour of individual entities, feedbacks between individuals and compartments, and the properties emerging from their interactions and co-evolution (Rammel et al. 2007). They are a science-based tool for managers to explore the future outcome of possible environmental and conservation strategies. From medicinal to political predictions, cost-and-benefit economics, and risk assessment, models are increasingly and successfully being used to aid complex human challenges and decisions (Helbing 2012). The adequate management of coral reefs is a pressing issue under the current circumstances, and the only hope for preserving these ecosystems and the services they provide for future generations.

1.1. Coral reef stressors

Most coral reef stressors directly or indirectly reduce the coverage of coral as benthic substrate. If corals die or their carbonate accretion is reduced, the structural foundation of coral reefs is damaged and so is its habitat provision for the myriad of species dependent on

it (Graham et al. 2006). Sustained exposure to stressors has cumulative impacts which lower resilience thresholds and make reefs more vulnerable to further stress.

1.1.1. Global stressors

Global threats to coral reefs are worldwide phenomena caused mostly by the increased carbon dioxide concentration in the atmosphere and the subsequent consequences of that increase (e.g. global warming). As such, they are nearly impossible to manage at the local level and need to be tackled in international environmental political agreements. The best practice to protect coral reefs from those stressors is to keep local stressors to a minimum.

Warming oceans

In conjunction with El Niño Southern Oscillation influence, the progressive global ocean warming prompts periods of temperatures exceeding the maximum that corals, highly thermally sensitive organisms, are able to tolerate. If water temperature becomes too high, corals experience a stress response, bleaching, consisting of losing the symbiotic microalgae – zooxanthellae – contained in their tissue (Glynn 1991, Brown 1997). Without the zooxanthellae, most coral species struggle to meet their energy requirements, starving until they consume all their energy reserves and die. If the bleaching event is short-lived and the corals are healthy, they may survive, although their reproductive success can be impacted and they can be more vulnerable to diseases. Different coral species or growth forms have been shown to have different susceptibility to bleaching (Grimsditch & Salm 2006, Baldock et al. 2014), and corals located in upwelling or high current areas might be less impacted by bleaching. The frequency and severity of bleaching seems to be increasing, with 2016 having been a year of massive bleaching leaving some large coral reef areas with nearly 100% coral mortality (Hughes et al. 2016).

Storm intensification

Climate change is also thought to cause an increase in the frequency and intensity of tropical storms (Knutson et al. 2010). Storms are a natural perturbation that can drastically impact coral reefs in very short time scales (De'ath et al. 2012). They can break the coral reef structure and turn it into rubble, killing corals and impacting the entire habitat for its associated species. Large scale disturbances have mostly structural impacts, but they can

also cause changes in the human pressure on the ecosystem as part of the socio-ecological adaptation to new conditions (Hughes et al. 2005, Aswani et al. 2016).

Ocean acidification

Atmospheric CO₂ is partly absorbed by the ocean, reacting with water to form carbonic acid. This acidification increases the solubility of the mineral compounds –calcite and aragonite– necessary to form coral and other calcifying organisms' skeletons, such as crustose coralline algae (Anthony et al. 2008). Although ocean acidification does not currently seem to be having an immediate effect, it is likely to threaten coral calcification in the next decades. A precautionary approach is recommended by reducing local impacts to ensure coral reef health.

1.1.2. Local stressors

Local threats to coral reefs are the most severe in the Southeast Asia region, with Indonesia having the highest area of threatened reefs mostly from overfishing and destructive fishing followed by watershed-based pollution and coastal development (Burke et al. 2011).

Pollution and sedimentation

Coastal areas around the world have seen a decrease in water quality due to terrestrial run-off carrying fertilizers, sediments and pollutants from land clearing (Smith et al. 2003). A number of field studies have shown the degradation of coral reefs when water quality is reduced (reviewed by Fabribius 2005), generally characterized by a shift in the benthic community from nutrient-recycling photosynthetic organisms like hard corals into macroalgae, turf, and heterotrophic filter feeders. Coral larvae settlement rates are close to zero in sediment-covered areas. High sedimentation can kill coral tissue in a matter of days, and lower levels reduce photosynthetic yield in corals due to increased turbidity. Nutrification can also reduce coral growth as a result of higher planktonic standing stocks reducing light penetration and impairing zooxanthellae photosynthesis (D'Angelo & Wiedenmann 2014). Increased nutrients do not necessarily impair coral physiology directly (Szmant 2002, D'Angelo & Wiedenmann 2014), but it increases algae growth rates, giving them a competitive advantage over corals. Terrestrial nutrient input is suspected to enhance *Acanthaster planci* larval survival (Pratchett et al., 2014; Wooldridge, 2016), contributing to outbreaks of crown-of-thorns and other coral predators. Increased nutrients are also thought

to play a role in increasing the vulnerability of corals to thermal bleaching (Wooldridge and Brodie, 2015).

Coastal development and tourism

Increasing coastal populations - currently nearly 40% of the global population lives within 100km of coral reefs- mean a high pressure from development in the coastal zone (Burke et al. 2011). Direct impacts on near shore ecosystems can be caused by dredging, land reclamation, or construction work of airport and marinas. Indirect long term impacts include increased sedimentation from land clearing and construction, and pollution from poor waste management. Tourism often brings coastal development to isolated areas, increasing demand of seafood and production of sewage and waste. Poorly managed recreational diving can also damage coral reefs (e.g. Zakai & Chadwick-Furman 2002, Barker & Roberts 2004).

Fisheries

Millions of people depend on coastal fisheries for their livelihoods. Artisanal fisheries can serve subsistence or commercial purposes, providing for local consumption or export (FAO 2013). Fishing involves extracting biomass from the system through a variety of methods. Tropical fisheries are characterized by being very flexible and diverse in terms of fishing methods and target species (Pauly & Murphy 1982). In principle, well-managed fisheries can be sustainable and even leave coral reefs as healthy as those in areas where no fishing has taken place (Cinner et al. 2016). However, the globalization of trade has increased export market demand from commercial fisheries and the modernisation of even artisanal fleets (Pauly et al. 2002). Tropical fisheries are partly organised by patron-client relationships, where patrons provide the link between artisanal fishers (clients) and national and international buyers. Some fishing methods, such as bomb and cyanide fishing, have profound destructive effects on the ecosystem, but represent a cost-effective way to obtain high value catches (Pet-Soede and Erdmann 1998; Chozin 2008; Ferse et al. 2014; Hajramurni 2015). Figure 2 shows the areas where destructive fishing is mainly practiced.

Data on artisanal fisheries is often scarce, non-periodic or non-existent altogether, involving a high degree of uncertainty (Costello et al. 2012, Baigún 2013). In a historical study overfishing was found to be the major human disturbance to all coastal ecosystems examined (Jackson et al. 2001). It was correlated with major losses of biomass and

abundance of large animals which are now effectively absent from most coastal ecosystems. Ecological extinctions of entire trophic levels or functional groups make ecosystems more vulnerable to other natural and human disturbances such as nutrient input and eutrophication, hypoxia, diseases, storms, and climate change (Jackson et al. 2001; Hughes et al. 2003), and reduce biodiversity and ecological redundancy, which is one of the pillars of resilient ecosystems (Nyström et al. 2008).

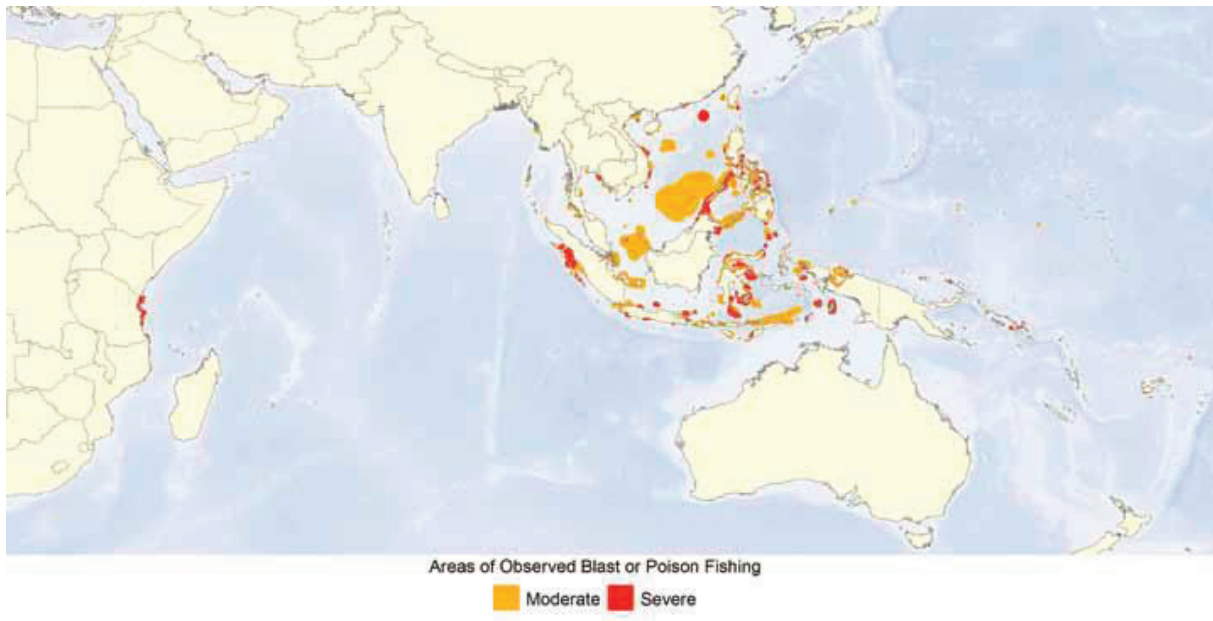


Figure 2. Main countries where destructive fishing – bomb and poison fishing- threatens coral reefs (Burke et al. 2011).

1.2. Management considerations

When aiming at successful management in a complex system with an amalgamation of actors and dependencies like coral reefs, a number of ecological, socioeconomic and institutional aspects must be taken into account.

Baselines and reference points

Defining a management plan relies on setting specific, realistic and measurable goals, but this is complicated by the lack of baseline data and reference points for coral reefs. First, marine coastal ecosystems have been influenced by humans for so long that accurately knowing what healthy biomass levels are is challenging. In the last decades ecological

changes are taking place at a very fast pace, and shifting baselines – the lack of a historical reference against which to compare a current ecological state (Pauly 1995)- can already be detected due to economic development (Swaney et al. 2012). Shifting baselines are a dangerous syndrome, as they impact the way that environmental policies are made by setting wrong or weaker conservation targets. This can be partly addressed by conducting studies in remote, pristine systems (e.g. Sandin et al. 2008 on Palmyra Atoll), by performing meta-analyses comparing fished and unfished areas (Edwards et al. 2014), or by looking at historical and geological records (Jackson et al. 2001, Rosenberg et al. 2005, McClanahan et al. 2007, Lotze & Worm 2009). However, as those are proxy studies with high uncertainty levels, a precautionary approach with more conservative targets is advisable. Second, logistic hurdles caused by coral reef remoteness and lack of infrastructure makes regular, uninterrupted monitoring a rare luxury. This lack of long term data makes reliable diagnosis and goal setting more difficult.

Local communities and stakeholders

In tropical island nations overexploitation of marine resources takes place in a decentralized manner and top down enforcement is challenged by the scattered natural landscape. In this situation community-based conservation has been shown to be a successful and desirable management strategy (White et al. 1994), but it needs to involve local community stakeholders, transparently, from the very onset (Ban et al. 2013) and incorporate community goals (McClanahan et al. 2006). Many conservation and management programs fail because they are unsuccessful in bringing local stakeholders on board, leading to a lack of support and compliance with management rules. Local communities may view conservation programs unfavorably (Bennet & Dearden 2014a), be it because they limit their livelihood options, because they are imposed on them, subtracting stakeholders' agency over their own resources, or because different stakeholders have conflicting interests. Thus involving marine resource users in the decision-making process is a critical factor (Johannes 2002), and integrating ideas of adaptive management guided by local traditional ecological knowledge, when available, might be beneficial (Berkes et al. 2000, Cinner et al. 2016). Detailed stakeholder assessments can further help to avoid the emergence of new issues by increasing our understanding of the socioeconomic trade-offs of implementation or noting the presence of outside agendas in conflict with local needs (Ban et al. 2013).

Economic opportunity is the leading indicator for harvest-related impacts in global fisheries (Sethi et al. 2010), highlighting the need for awareness and environmental education in tandem with economic alternatives when a decrease in resource exploitation is required.

Providing a number of reliable and diverse alternative livelihoods is needed, and it may work better when it is done by building upon and improving the efficiency of already existing practices (Bennet & Dearden 2014b). Successful management plans benefit from awareness and environmental education programs which increase the involvement of traditional fishermen (White & Vogt 2000). It is important that marine resource users understand the causal relationships leading to ecosystem degradation, and the effect it will have on their sustained livelihoods and health. Achieving this might be complicated by the presence of network power structures, such as patronage systems, in which the main decision makers are detached from the resource.

Context dependency

A nuanced and context dependent planning and follow up is recommended given the spatial and dynamic nature of human communities and the different vulnerability to the range of ecological and social factors involved (Arkema et al. 2006, Mumby & Steneck 2008, Long et al. 2016). Collection and analysis of site specific spatial data on human resource use (Ban et al. 2013), regular ecological monitoring (Kremen et al. 1994) and participatory diagnosis (Eriksson et al. 2016) are desirable actions that may lead to the improvement and fairness of coral reef management programs and to an increase of the adaptive capacity of coastal resource-dependent communities in the years to come (MCClanahan et al. 2008).

1.3. Case study: Spermonde Archipelago, Indonesia

This dissertation was focused on the Spermonde Archipelago as a case study. Spermonde, located in the Southwest corner of the larger Sulawesi Island (Indonesia), is home to a rich community of island dwellers who rely fundamentally on fishing activities to sustain their livelihoods (Ferse et al. 2014).

This area is of particular relevance for this study due to its gradient of human impacts, which go from highly impacted coral reefs in the near-shore, highly populated islands, to the off-shore, less impacted reefs (Edinger et al. 1998, Sawall et al. 2011). While historical records described the archipelago as a rich and diverse area for coral reef and fishery resources (Schwerdtner Máñez & Ferse 2010), the region has been profoundly deteriorated as a result of watershed and sewage pollution coming from the 1.3 million-inhabitant city of Makassar (Sawall et al. 2011), overfishing (Ferse et al. 2014), destructive fishing (Pet-Soede et al. 1999) and COTs outbreaks (Baird et al. 2013, Plass-Johnson et al. 2015). Blast fishing was

introduced in Indonesia during the Second World War (Galvez et al. 1989), and Spermonde is now classified as having moderate to severe destructive fishing (Fig. 2). Its abundant fringing, submerged, and patch coral reefs, located on a mostly shallow carbonate shelf in front of an important international port, provides easy access to fishing grounds and safe navigation protected from strong currents and weather events. These favourable conditions allow even the tiniest canoes to enter the fishery, making it nearly full open-access. The Indonesian government has a number of environmental protection laws and regulations in place to help exploit their fishery resources sustainably, but they are not regularly enforced or complied with (Radjawali 2012). Instead, some communities have local informal agreements over their marine jurisdiction, enforced by their own resource users, which define who has fishery access and which gears are approved in local zones (Glaser et al. 2010, Gorris 2016).

Hasanuddin University is located in the city of Makassar, and through a number of partnerships has provided continued support for long term marine ecological research in the area. The SPICE (Science for the Protection of Indonesian Coastal marine Ecosystems) program has been part of those research efforts for the past 14 years, with this dissertation being one of the final projects of the third SPICE round. As such, the relatively high number of publications available for this area compared with other coral reef ecosystems in developing countries provided a foundational background for the project.

2. MODELLING APPROACHES TO CORAL REEFS AND MARINE RESOURCE MANAGEMENT

Simulation models have been used to explore ecological questions and coral reef processes of a wide range of relevance and scale. From testing the adaptive bleaching hypothesis (Ware et al., 1996), exploring the growth patterns of macroalgae (Yniguez et al. 2008), assessing ecosystem-wide effects of pollution (Zhang et al., 2011), or detecting coral bleaching susceptibility by combining models with satellite data (Maina et al. 2008; Dadhich et al. 2012), the joint use of models with data or expert ecological knowledge has proven to be a valuable tool to widen our understanding of coral reef ecosystems functioning and responses to environmental changes. For instance, Zychaluk et al. (2012) used a data-driven model (i.e. using combined information from short time series to estimate parameters, and fitting the model to long-term data bases of benthic dynamics) with a flexible structure to explore coral reef benthic dynamics, and their results challenged the widely debated theory of alternative stable states. Simulation can be a powerful analytical tool for discovering

surprising consequences of simple assumptions (Axelrod 2003) and assessing the long-term dynamics of marine ecosystems as sort of virtual laboratories to test ecological hypotheses. The individual-based modelling approach is based on a thorough description of the processes, behaviour and ecology of the system individuals. Having a clear, mechanistic idea of how they react to change is a crucial requirement to have meaningful results. As complex hypotheses formulations, individual-based models (IBM) are part of the scientific method and serve to define research priorities. By synthesizing the current expert knowledge and modelling it, we can find the gaps in the explanations of causal relationships within the ecosystem. But as a simplification of the real world, they need to include the right level of accuracy to make them realistic, feasible, and tractable.

2.1. Individual-based models

Individual- or agent-based models simulate dynamic systems on the basis of the interaction of their components at the individual level. The IBM is a bottom-up, mechanistic approach that starts with the parts to recreate the emergent properties of a system (Grimm 1999). It does so by representing individuals of an ecosystem and their interactive behaviour to recreate the dynamics of that system as a whole. This approach has been gaining attention since May (1974) pointed out the chaotic dynamics displayed by simple nonlinear equations due to their strong dependency on initial conditions. Despite the eagerness to find general principles of ecology applicable to most cases, “the lessons of chaos are that simple principles will be the exception, incidents of history are important, and that, because predictions are impossible, the only way to find out what is going on in some dynamic systems is to simulate them exactly” (Judson 1994). This implies that a reductionist approach will not succeed in accurately representing an ecosystem. What is more, traditional deterministic models often do not reflect the very basic tenet of ecology: evolution. In evolution, individuals are the unit of selection, and IBM constitutes an advantageous method to explore the complex dynamics of ecological systems by acknowledging the universal facts that all individuals are different, and that interactions between them occur locally (Huston et al. 1988). Besides, an individual is easier to describe than a species or an ecosystem, and the boundaries between an individual and its environment are clearer as well (Judson 1994).

Railsback & Grimm (2010) encourage the use of IBMs when one of the following is considered essential in the research question: (1) individual variability, (2) local interactions, and/or (3) adaptive behavior. Individual-based models simulate local interactions of autonomous dynamic entities in a complex system. The characteristics of each individual are tracked through time, providing large amounts of data similar to those yielded by long-term

monitoring of ecosystems. The difference with “natural” data is that, with this approach, the modeller can track the sources and processes that produce the observed results, because it is based on known parameters and procedures.

Object-Oriented Programming (OOP), the root of IBMs, provides a framework for structured programming based on communication between a set of modules or blocks of code. Independent objects are self-contained in the sense that they contain both their data and their controls. The same type of objects may present some of the same initial characteristics, but they also have the capacity to store their own information, which is then used to determine future behaviour based on their internal state and the environment. This way each virtual entity or individual is able to “evolve” throughout the simulation time. Through a property called inheritance, newly created objects can take the properties from an existing one and add its own properties on top. They too have the ability to show self-organization of the objects interacting in the model; schooling, trophic networks or regional distributions are just a few examples of properties emerging in ecological IBMs (Breckling et al. 2006). These and other characteristics of OOP make the way that objects relate and interact more biologically realistic. Furthermore, having field ecologists build their own models allows them to apply their knowledge directly without relying on programmers or pre-defined software tools that may restrict the optimal representation of the study system (Breckling et al. 2006; Reuter et al. 2011).

Structure and organization of IBMs

An individual-based model can be divided into three parts: (1) representation of the individual entities, (2) representation of the environment, and (3) scheduling (Reuter et al. 2011). Individual entities are represented by relatively short blocks of code called “classes”. Subclasses may be added with the purpose of creating a hierarchical structure, or simply to apply the same characteristics to all the objects in one class, and then defining specific ones for a subclass (e.g. class: animal; subclass: bird). A class is a storage unit containing three parts, two of structural nature, and one of dynamic character. First, it contains state variables that describe individual properties (e.g. biomass, size, age, sex, location, etc.). Second, it has statements and code blocks used to update the variables; these can be environment-dependent (including interactions with other entities) activity procedures such as movement, reproduction or feeding, or physiological procedures driven by the internal condition of the individual like aging or metabolism. Finally, a class must contain a scheduling mechanism to update its individual properties. This is usually accomplished by means of a Boolean variable “ALIVE”; when the variable is “true”, the “life loop” is active and iterated until the Boolean

status turns to “false”, in which the object will be considered dead and therefore no longer active. During program execution, each class is copied into individual objects which have the same code but their own information storage, allowing them to change (somehow evolving) throughout the simulation runs.

Typically, IBMs use either a grid-based representation of the environment, or vector maps. Vector maps may be more precise as they are scalable, and thus not dependent on grid resolution, which is usually fixed. In a grid-based environment, it is possible to depict a heterogeneous spatial organization or make the model spatially explicit by having specific information for each cell (e.g. depth, currents, light intensity, physical structures). Those attributes will affect the way individuals behave and how they relate to their environment. Furthermore, cells can be modified by the presence or absence, or the actions of, individuals; for instance, dense schooling in one area can deplete its resources, although this depletion can also be caused by a change in weather conditions. The environment representation can run updating routines such as reading-in weather data, or even coupling it to a Regional Oceanographic Model (ROM).

The effectiveness of IBMs to model complex systems with multiple interactions largely depends on agent organization (Chen et al. 2008). The scheduling process is responsible for the temporal organization of the model and the coordination of the different entities. Using a discrete event scheduling means that calculation results can be accessible at any time during simulation. It is important to choose the right unit of time according to the model’s purpose and the scale of the processes it represents. Scheduling is done by sequencing, or devising an event queue by which each object or action is invoked in a certain order. In many cases, it is advisable to store these changes and then apply them by synchronously updating the program. Reuter et al. (2011) advise to use a regularly updated approach in simple programs, switching to flexible scheduling in complex realistic representation so that the objects themselves control updating requests based on their internal state.

Using individual-based models is recommended in three situations: (1) when species habitat distribution has a large random element, (2) when biological or environmental discontinuities are frequent, and (3) when rare events are important (DeAngelis & Gross 1992). In coral reefs, these are exemplified by larval dispersal, habitat patchiness, or the influence of stressors like storms, destructive fishing, and bleaching. The number and biological variability of different species and functional groups, the interactions among them, the numerous spatio-temporal scales of the processes to be represented, or the increased complexity caused by the effects of fishing and the environment on each compartment are some of the challenges the IBM approach can overcome (Travers et al. 2007). Recent publications on fisheries management recommend using ecological risk assessments with a

hierarchical structure and precautionary approach to uncertainty, including a strong participation of stakeholders to help identify and evaluate important issues (Hobday et al. 2011). More and more social science studies encourage the integration of field ecological knowledge and socio-economic research by means of IBMs (e.g. Glaser 2012), in which case they are commonly referred to as agent-based models.

2.2. Review of previous models

Many models have been developed to study issues related to coral reefs. To inform the modelling approach taken in this dissertation, I will focus on those with the scope to assess ecosystem-wide effects of environmental changes and/or aid on environmental management issues at the community and the ecosystem level, going from models studying processes in one individual compartment of the coral reef (e.g. a school of fish, a section of substrate, etc.) to models giving a systemic overview of different ecosystem processes.

At the community level, IBMs have helped understand spatial processes of settlement and benthic competition between corals and macroalgae, in which cases different growth forms may be beneficial or disadvantageous, and how individual characteristics may influence community dynamics in coral reefs. Langmead and Sheppard (2004) developed a spatially explicit simulation model to assess the influence of background disturbance on the community dynamics of coral reefs. A cellular automaton-based model (a basic IBM where active units are represented as grid cells) was used to represent the basic colonial coral structure with very high resolution (1 cm² cells, for 10 single species of coral). This allowed assessing the role of spatial extent of disturbance in detail, represented as pseudo-randomly placed circular patches to bare substratum, and size of disturbed patches on the coral community structure. Differential probability of mortality was included based on colony size and tissue regeneration rates for each species. Percentage cover and population size structure of each coral species were the variables taken as model output. After rigorous testing, the model could predict accurately the coral population structure of 7 out of 10 species tested. Sleeman et al. (2005) used an 18x18m grid-based IBM to improve coral reef restoration techniques by representing the dynamic reef formation of *K*-selected and *R*-selected coral fragments, predicting what type of coral transplantation would work better for each category. They argue that spatial indices can be used as standardized measures for comparing different features of landscape structure, and emphasize the need to evaluate the ability of indices to identify differences in social, economic and ecological features as one of the future challenges of predictive modelling for coral reefs. Indices can provide a reliable, aggregated measure of such features while reducing the model's excessive complexity.

Tam & Ang (2012) created *ReefModel*, a 3-dimensional model simulating coral competition in a coral reef using object-oriented programming. In their model, functional groups were used instead of individual species, since the interactions between species are not yet fully understood (in the authors' opinion modelling at the species level could yield non-realistic results). The chosen functional groups have distinct biological characteristics, competition mechanisms and response to disturbances. The use of functional groups at low trophic levels and species at higher trophic levels has been encouraged for end-to-end models (Travers et al. 2007). Nevertheless, simulations with the *ReefModel* allowed identifying the most advantageous structural and growth habits for spatial competition, and the potential presence of alternative stable states in a coral reef under the same environmental regime. Kubicek et al. (2012) developed an IBM representing the dynamics of a coral reef community based on a combination between competition processes and disturbances. The community is composed of scleractinian corals and algae with their own life history characteristics (e.g. reproductive strategies, growth forms, response to changes in temperature, etc.), and the main perturbations considered are bleaching and physical disturbance at different degrees of intensity and frequency. The model reproduced major face shifts in community composition as a result of small changes in key parameters.

Individual-based models have also been used to study fish behaviour. For instance, Reuter & Breckling (1994) developed an IBM representing schooling behaviour of fish, successfully reproducing self-organization processes arising from a combination of fish speed and swimming direction based on the position of visible neighbours, as well as external obstacles. Shin and Cury (2004) used an IBM to assess the effects of changes in fishing on the size spectrum and the food web of fish communities.

Moving towards more ecosystemic approaches, it becomes useful to combine different model types and aggregate compartments and processes when suitable. McClanahan (1995) developed one of the first ecosystem models of coral reefs, summarizing the scientific ecological knowledge up to that moment. The model aimed at evaluating the effects of changes in fishing intensity and catch selection on two targeted ecological processes in a coral reef, benthic productivity and the calcium-carbonate balance. It considered the different relevant compartments of a shallow coral reef by representing two groups of primary producers (algae and corals, competing for sunlight), herbivores (sea urchins and fishes), and carnivores (piscivores and invertivores). Simulations were run to assess the effect of changes in fishermen abundance and catch preferences on fisheries yield, community structure and ecological processes. The model accounted for economic factors and the sustainability of the reef, and its results led to the compromise solution of protecting invertivorous fish to maintain sea urchins in check, while still fishing the other groups. This

paper proved that modelling of ecosystems can be a good tool for synthesizing current ecological knowledge, testing hypotheses and exposing areas where further research is needed.

Mumby (2006) used two models to explore the impact of fishing parrotfishes on the coral reef dynamics of Caribbean reefs. First, an analytical model was used to quantify the impact on grazing of depleting parrotfish biomass. Second, the outcome of this model was used to parameterize a simulation model representing ecosystem processes occurring on Caribbean fore reefs (i.e. hurricanes, coral-algal competition, and extinction of sea urchins), which was then used to test several hypotheses regarding the impact of hurricanes in reef trajectories, connectivity scenarios and the role of grazing by parrotfishes and sea urchins. In another study, Mumby et al. (2007) merged once more a simulation model and a simple analytical model to study whether algal-dominated reefs are an alternative stable state or a reversible result of environmental or ecological changes. Complex Caribbean fore reef habitat dynamics were simulated in detail making the minimum number of assumptions; coral recruitment and mortality, macroalgae and two classes of grazers (urchins and parrotfishes) were represented, corals and algae interacting at the colony scale, and all model parameters were derived from empirical studies in the region. The analytical model was used to determine equilibria and their stability.

Simulation of Infected Corals (SICO, Brandt & McManus 2009) is another spatially explicit IBM designed to assist the management of coral reefs. The model was developed as a tool to test hypotheses on the spread dynamics and impact of the white plague disease in different coral populations and different reef characteristics. With the obtained results, they were able to propose management strategies to prevent and deal with the disease once it had been introduced, based on the community composition that showed a higher resistance.

One of the most remarkable and widespread tools for modelling marine resources and fisheries impact, is Ecopath with Ecosim (EwE, Polovina 1984, Christensen & Pauly 1992, Christensen & Walters 2004). Ecopath is a steady-state mass-balanced model, based largely on trophodynamic links between functional groups. It has two main linear equations for each functional group: (1) Production, determined by catch, predation, accumulation, exports and other losses, and (2) Consumption, accounting for production, respiration and unassimilated food. Export and diet composition of each group are mandatory, and three of the four parameters—biomass (B), P/B, Q/B, and ecotrophic efficiency (EE)—also must be entered for each group. The linear equations are then solved and the unknown parameters are estimated (Weijerman et al. 2013). This approach can be used to study energy flows to gain insight into the ecosystem's maturity and functioning. Ecosim is the time dynamic option of Ecopath, which allows setting up simulations with applications such as fitting time series or

evaluating fisheries strategies. Ecospace is the application of the Ecosim model to each cell in a connected grid where fishing pressure is distributed according to the profitability and costs of fishing in each cell. As a result of the large amount of data required by EwE, its team was responsible of the creation of the largest free, online database of fish biological and ecological data, Fishbase (Froese & Pauly 2016).

Another widely used and highly complex model to aid management of marine resources is Atlantis (Fulton et al. 2004), a deterministic biogeochemical end-to-end regional model with an overall structure based on Management Strategy Evaluation (MSE). MSE is a simulation technique based on modelling each part of the adaptive management cycle to examine the implications of different management strategies of natural resources (Butterworth & Punt 1999, Sainsbury et al. 2000). Different management scenarios are tested across multiple candidate models to perform a robust evaluation of potential consequences.

Atlantis contains a submodel for each step of the adaptive management cycle. Its core component is a deterministic, 3D spatially resolved biophysical module which tracks the nutrient flows across biological groups in the system, typically resolved as functional groups. The environment is spatially explicit, with polygons matching relevant physical features of the modelled area. Consumption, production, waste production, migration, predation, recruitment, habitat dependency, and mortality are the main ecological processes represented. It also contains an exploitation submodel representing the impact of pollution, coastal development and broad-scale environmental change, focusing on fishing fleets dynamics. Fleets have their own characteristics of gear selectivity, habitat association, targeting, effort allocation and management structures. Explicit handling of economics, compliance decisions, exploratory fishing, etc. can also be included. An additional sampling submodel generates data with uncertainty levels from the simulations, which are then fed to real world assessment models. The output from those assessments is finally fed to the management submodel, which is in charge of making and implementing management decisions (e.g. gear restrictions, quotas, size limits, spatial and temporal zoning, etc.).

Fulton et al. (2005) used two Atlantis simulation models to test the performance of a set of ecological indicators in detecting the effects of fishing in two ecosystems in south-eastern Australia: one large marine embayment, and one Exclusive Economic Zone (EEZ)-scale regional marine ecosystem. This was done by first devising an operating model which represents the ecosystem functioning in a simplified version - a simulation including the main biological (invertebrates, primary producers, vertebrates) and three detritus groups incorporating the effect of fishing with different fishing gears- and afterwards applying a sampling model to generate the necessary data, including realistic measurement of uncertainty. This was a cost-effective method of providing large amounts of data from a well-

known system. Indicator performance was defined by their ability to track properties of interest from the ecosystem (i.e. biomass, diversity, size structure, spatial structure, food web structure, trophic level, size of nutrient pools, rates of nitrification and denitrification, etc.), whose desired values were known from the simulations. Results suggested that a combination of indicators from four biological groups (i.e. those with fast turnover rates, those targeted by fisheries, habitat-defining groups and charismatic or sensitive groups) would provide a balance of early detection and system characterization. Indicators at the community level should be the ones used for management purposes as they achieved the best compromise between data requirements, signal strength, sensitivity to natural variability, and responsiveness. Among those, fish biomass and size at maturity were proposed because they are easy to measure and perform consistently regardless of the level of exploitation intensity and ecosystem structure.

Weijerman et al. (2015) adapted the Atlantis model to represent a coral reef ecosystem in the tropical western Pacific in order to quantify the interactive effects of three main drivers, i.e. climate change, land-based pollution, and fishing. The study used six metrics as indicators of the ecosystem state: ratio of calcifying to non-calcifying benthic groups, community trophic level, biomass of apex predators, biomass of herbivorous fishes, total biomass of living groups, and end-to-start ratio of exploited fish groups.

Melbourne-Thomas et al. (2011) published CORSET, a regional scale simulation model of the effects of multiple stressors on the state of coral reefs. CORSET is a spatially explicit model coupling ecological dynamics from local (10^2 m) to regional scales (10^6 m) and parameterized for the Meso-American Reef region. Multiple instantiations of a local scale model of coral reef dynamics are linked through larval connectivity of corals, fish and urchins. At the local scale, benthic cover and consumer biomass are updated at weekly time steps, including nine functional groups (two coral, three algal, urchins and three reef-associated fish functional groups) with feedback relationships amongst them. Seasonality on ecological and biological processes is not included, but larval dispersal is simulated in detail by linking hydrodynamic (ROMS) and particle tracking models. Forcings of the system include changes in fishing pressure, hurricanes, disease and bleaching events, nitrification and sedimentation, and their scheduling is flexible. The model, despite being a “minimum realistic model” for portability purposes, is able to evaluate the consequences of larval connectivity at different spatial scales, and gives insights on drivers of fish stocks, vulnerability to hurricane events, and other important aspects for managers. Gurney et al (2013) used the model to investigate how the management of local stressors (i.e. low water quality and fishing) may influence the state of the coral reefs in Bolinao (Philippines) under different climate change scenarios relating to coral bleaching, generating several management recommendations.

3. MOTIVATION OF THE DOCTORAL DISSERTATION

The previous examples show the potential of simulation models to provide insights on ecological questions that are crucial for the management of marine resources. However, after this review of coral reef models, together with the preliminary fieldtrip data collection, it became apparent that no decision support tool at a local scale or the community level had been developed. Such a tool has the potential of contributing to enable and improve the community-based management of coral reefs. The idea was to bring together coral reef ecological theory to create a model as a basis for a scientifically sound, user-friendly decision support tool for the local management of coral reefs. As such, it needs to be computationally reasonable, user-friendly, and allow for input data that is easily collected.

Some of the aspects to consider included:

(a) Choice of represented processes:

For the model to be successful in aiding marine resource management, its structure needs to capture the mechanisms responsible for the ecosystem dynamics of interest. Aggregation and prioritization of processes needs to be made through inevitable assumptions, as well as a compromise between resolution and coverage of large spatio-temporal scales. In this dissertation, a focus on the feedbacks between the benthic habitat, the fish groups and the human external impacts should guide every step of the model development. A reasonably simple model following the Occam's razor (Blumer et al. 1987) and Medawar zone (Loehle 1999) principles with a limited number of parameters may be preferable to avoid scheduling issues, documentation and confounding effects, aiding in transparency and computational demand. This is not advocating for a too simple model which fails to capture the natural complexity existing in coral reefs, but to do it in a minimalistic way, including those agents and processes that are truly relevant in a manageable way, and aggregating or grouping processes or functional groups which do not benefit significantly from being individually represented.

(b) Flexible structure:

Ideally, a management model should be able to add new information on processes and characteristics as soon as it becomes available, so its design must be flexible, preferably with independent modules which can be added or subtracted and independently validated.

(c) Spatially explicit:

The model should be spatially explicit in order to capture the zonation of processes so that it provides information on where and how protective measures would be

beneficial. A detailed spatial description of the area of interest would be best for obtaining meaningful results.

(d) Challenges in model validation:

One of the limitations in the case of coral reefs is the lack of long-term baseline data for a reference ideal or pristine state (Knowlton & Jackson, 2008) to calibrate the model and contrast it against real-world patterns. This can be partly solved by comparing reefs with and without people, but the associated uncertainty must be considered. All areas are embedded in larger systems and are subject to different kinds of environmental conditions and human pressures (Knowlton & Jackson, 2008). Therefore, model structure or concept should not be entirely based on the available data, but on what the expert knowledge says about the processes (Sleeman et al. 2005), and model results should be skeptically examined and interpreted.

(e) Portability:

This model should be applicable to a wide range of coral reef sites. To accomplish that, the model general structure, choice of reef components and rules of interaction must follow general principles of coral reef ecological theory while the local conditions and parameters can be specified for particular case studies.

(f) Easily collected data for parameterization:

Selection of input and state variables should consider the usually isolated location of coral reefs and the lack of or limited logistical infrastructure. The data needed to parameterize the model case studies should be easy and inexpensive to measure, ideally not requiring highly specialized or numerous personnel.

(g) Detailed and transparent model description:

In order to be used in informing political and environmental decisions, models need to be clearly and understandably described. Sensitivity to parameters, uncertainty of model predictions, and the sources of parameterization need to be acknowledged, and a comprehensive validation must be done and documented.

3.1. Objectives

The specific objectives of this dissertation, stemming from the above are:

- I.) Develop a local coral reef simulation model that allows the representation of the impact of simultaneous stressors on key reef ecological groups.
- II.) Devise a user-friendly decision-support tool that allows the exploration of different management strategies and environmental scenarios on coral reefs.

- III.) Collect qualitative and quantitative information on the artisanal fishery of Spermonde, including gear types used on coral reefs, data on catch and CPUE, active fishermen population, spatial distribution of the fishery, and insight on the social structures affecting it.
- IV.) Apply the model with real field data and real case scenarios to the field site of Spermonde (Indonesia), to provide recommendations and test hypotheses on the predicted trajectories under various scenarios.

3.2. Publication outline

The objectives above were addressed in the three publications which form the core of this thesis, forming chapters 2, 3 and 4.

Chapter two contains the manuscript outlining the description of SEAMANCORE and its development. SEAMANCORE stands for spatially explicit simulation model for assisting the local management of coral reefs, and covers objectives I and II of this dissertation. The model has two distinct compartments, benthos and fish, which run at different spatiotemporal scales and are affected by each other and by the three modelled stressors: fishing, bleaching and nutrients. The chapter also includes the results of the sensitivity analyses and a user manual for the decision-support tool platform.

Chapter three is composed by the manuscript assessing the coral reef fishery in Spermonde and specifically the role of the patron-client system in the fishing behaviour of individual fishermen. This study also served to gather quantitative data on catches and is complemented by a companion paper under review on the spatial distribution of fishing effort (Navarrete-Forero et al. *Frontiers in Marine Science*). The two studies address objective III.

Chapter four stems from the previous studies and adds ecological field collected data to parameterize SEAMANCORE. First, basic scenarios of nutrients and fishery were run under standardized conditions to appraise the stressors' effects on the modelled response variables. Fishery scenarios included a fishery ban, subsistence fishery, commercial fishery, and commercial combined with destructive fishing practices. In the second part, ten-year simulations were run for four sites in Spermonde (Indonesia) exposed to varying degrees of human impacts and different initial conditions to project their local coral reef's trajectories.

Chapter five summarizes the contributions of this dissertation, highlighting the limitations of the modelling approach, and provides recommendations on research directions for modelling local coral reefs and management of their associated artisanal fisheries.

Finally, annexes 1 and 2 display the conferences and invited lectures where parts of this work were presented and secondary publications stemming from this PhD.

Chapter 1

SEAMANCORE: A Spatially Explicit simulation model for Assisting the local MANagement of CORal REefs

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Coral reef in Bone Tambung, Spermonde

Abstract

1. Management of coral reefs requires working with complex and multi-layered information. By providing user-friendly platforms with easily obtainable data requirements, models can help stakeholders explore likely outcomes of management strategies across a range of indicators.
2. SEAMANCORE is a free, open-source and user-friendly model application to assess the effects of simultaneous stressors on local coral reefs. It includes a detailed and customizable setup which allows users to apply the model to a range of tropical regions by inputting field data on benthic cover, fish biomass, and depth profile.
3. The model represents selected benthos and fish functional groups dynamics which interact with a fishery module under customizable scenarios of reef structure, nutrient levels, bleaching frequency and fishery management strategies.

Key-words: coral reefs, management, small scale fisheries, ecological modelling, destructive fishing, benthos dynamics, food web, cellular automaton.

1. INTRODUCTION

Coral reefs are important ecosystems both for their ecological and human services. Their structural complexity provides a unique living environment for numerous organisms, which in turn sustains the livelihoods of millions of people (Moberg & Folke 1999). Despite their social and ecological relevance, 75% of coral reefs are to some extent degraded (Burke et al. 2011). Their high vulnerability to local and global impacts (Hoegh-Guldberg et al. 1999), marine diseases (Harvell et al. 1999), coastal development (Mora 2008), overfishing (Jackson et al. 2001), and watershed pollution (Fabricius 2005) are highlighted as the main causes of their degradation. These pressures have led to conclude that coral reef ecosystems will probably be rare by 2050 (Hoegh-Guldberg et al. 2010), with serious consequences for subsistence dependent societies and regional economies through impacts on coastal protection, fisheries, and tourism (Hoegh-Guldberg et al. 2007).

Community-based conservation has been shown to be a successful and desirable management strategy (White et al. 1994, Cinner et al. 2016) particularly where overexploitation of marine resources takes place in a decentralized manner and top down enforcement is challenging. Successful management plans need to incorporate community goals (McClanahan et al. 2006), and they benefit from education programs which increase the involvement of traditional fishermen (White & Vogt 2000). Involving marine resource users in the decision-making process is a critical factor (Johannes 2002), as is developing case specific management strategies (Arkema et al. 2006, Mumby & Steneck 2008, Long et al. 2016).

Because of their ability to synthesise complex, multi-layered scientific information, models can improve our understanding and awareness of environmental issues by providing a mechanistic representation of ecological processes on the coastal zone. Models can help stakeholders explore the likely outcomes of management strategies across a range of variables by providing user-friendly platforms with easily obtainable data requirements. Building upon emerging initiatives of models developed to aid local coral reef management (e.g. Chang et al. 2008, Buddemeier et al. 2008, Weijerman et al. 2015), we propose SEAMACORE as a free, open-source and user-friendly application to assess the effects of simultaneous global and local stressors on coral reef communities. It includes a detailed and customizable setup which allows users to apply the model to a range of tropical regions. SEAMANCORE can be used to explore the potential trajectories of coral reefs under different scenarios of reef structure, nutrient levels, bleaching frequency and fishery management strategies.

2. THE MODEL

SEAMANCORE represents the spatial dynamics of a coral reef under the influence of local and global stressors. It focuses on the dynamics of selected fish and benthic functional groups, the ecological relationships amongst them and how they are affected by three stressors including climate change, fishing and eutrophication. The model domain is defined using a two-dimensional continuous cellular automaton (CA) grid, which represents the benthos of one coral reef patch of up to 1000 x 1000 m (1 km²) with a resolution of 10 x 10 cm. A second, lower resolution grid layer is superimposed describing the fish functional groups (i.e. Browsers and Grazers (BG), Scrapers (S), and Carnivores (Car)). Each fish cell represents an area of 400 m² containing 40000 benthos cells. The model is updated asynchronously to represent the different biological processes at suitable temporal scales. The fish grid is updated on a daily basis to account for the processes driving changes in fish biomass and their influence on the benthos. The benthos CA is updated every seven days, while the influence of disturbances including herbivorous feeding is computed daily. Each time step represents one day. The model features torus conditions to avoid boundary-born artefacts, except for the rules updating the benthos (e.g. vegetative growth), which use a “mirror approach” to avoid anomalous growth at undesired depths (*Appendix 1*). The model was developed using MASON multi-agent simulation toolkit (<http://cs.gmu.edu/~eclab/projects/mason>) and is written in the Java programming language. The program requires a greyscale bathymetric map of the field site (*Appendix 2*) to assign a depth category to each benthos cell. Depth categories influence the probability of occurrence of organisms and ecological processes, and determine whether the grid cells will be affected by stressors.

2.1. Benthos

Benthos grid cells belong to one of four categories at any given time step: *coral* (C), *macroalgae and turf* (MAT), *hard substrate* (HS) and *empty space* (E). Coral cells represent hard coral and compete for space with MAT. The category of hard substrate is used here *sensu* “cropped algae” category in Mumby (2006) and includes encrusting coralline algae, short grazed algal turf and rocky bottom, all of them likely to increase settlement of coral recruits (Vermeij 2005, Mumby 2006, Roth and Knowlton 2009). The “empty” category refers to bare substrate unsuitable for settlement of algal or coral recruits (e.g. sand).

Benthos dynamics are defined by (a) the rules of the cellular automaton and (b) disturbances applied to it (Fig. 1). The CA rules reflect the processes of coral-algae competition for space and the degree of connectivity from external reef sources. Coral and MAT cells turn into hard substrate by *Competition* with MAT and coral, respectively. A cell can only turn into coral or MAT by transitioning through the state of hard substrate. Hard substrate cells can turn into coral by *Coral colonization* and *External supply* of recruits, and into MAT when *Aging* or *MAT Colonization* rules apply. *Aging* and *Colonization* rules are affected by the selected nutrient scenario. Empty space cells can only turn into hard substrate by the *Global pre-colonization* rule. Disturbances include foraging from herbivorous fish groups, bleaching and destructive fishing. *Bomb fishing* turns every type of cell into empty space, and it resets the age of empty space cells. Disturbances that turn MAT cells into hard substrate include *BG foraging* and *Cyanide fishing*. *Scraper foraging* resets the age of HS cells. *Cyanide fishing* and *Bleaching* turn coral into hard substrate, while *Non-lethal bleaching* resets coral cells' age. As a result of the model's rules, realistic reef zonation patterns of the reef habitat emerge (Fig. 2).

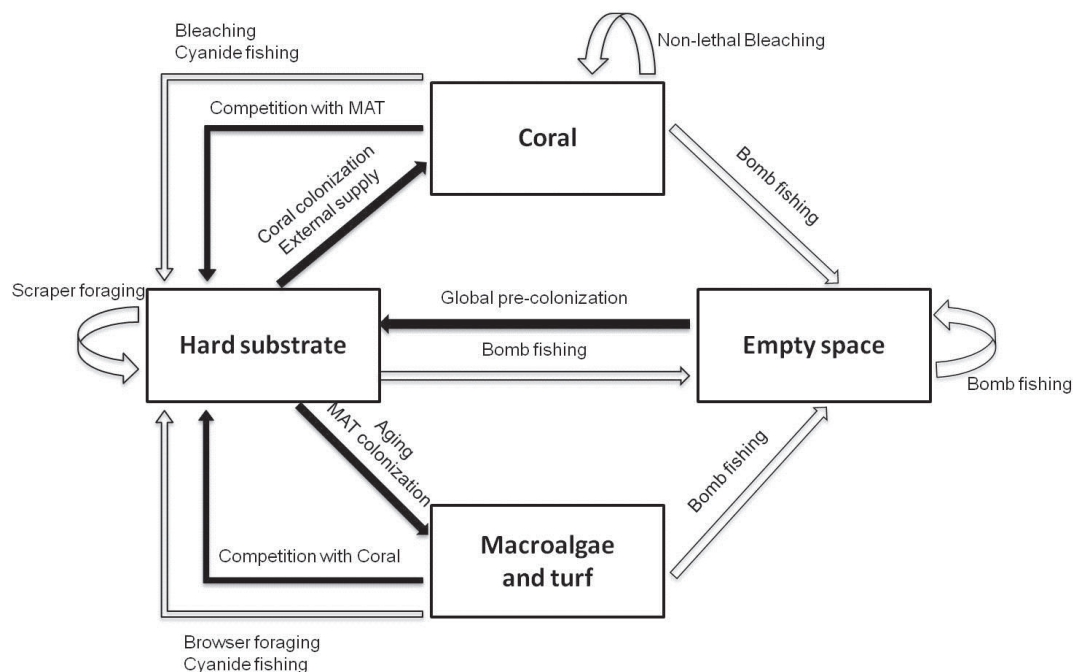


Figure 1. Diagram of the processes driving the benthos dynamics. Black arrows refer to cellular automaton rules; white arrows indicate disturbances.

2.2. Fish

Three functional groups of fish are considered in the model: browsers and grazers, scrapers, and carnivores. Fish cells (20 x 20 m) contain a biomass function which is updated every time step for each fish group. Fish biomass within a given fish cell is defined as:

$$B_{i,c}(t + 1) = B(t)_{i,c} [1 + F_{i,c}(B(t)_{i,c})] \quad (1)$$

where $B(t)_{i,c}$ is the biomass of the fish group i in cell c and $F_{i,c}(B(t)_{i,c})$ is a function of the net growth for each fish functional group i . The net growth function $F_{i,c}(B(t)_{i,c})$ accounts for the gains and losses of biomass for the functional group i and is given by:

$$F_{i,c}(B(t)_{i,c}) = (P_{i,c} + \Phi_{i,c}) - (M_{i,c} + \Pi_{i,c} + \Psi_{i,c}) + Y_{i,c} - E_{i,c} \quad (2)$$

where $P_{i,c}$ is the recruitment, $\Phi_{i,c}$ is the feeding, $M_{i,c}$ is the natural mortality, $\Pi_{i,c}$ is the predation, $\Psi_{i,c}$ is the fishing, $Y_{i,c}$ is the immigration, and $E_{i,c}$ is the emigration.

Recruitment within each cell has an external and an internal component:

$$P_{i,c} = P_{ext_{i,c}} + P_{int_{i,c}}(B_i, C_{cover_c}) \quad (3)$$

External recruitment $P_{ext_{i,c}}$ is a net biomass value representing larvae supply from neighbouring reefs, calculated by:

$$P_{ext_{i,c}} = \lambda_{i,c} \cdot C_{cover_c} \quad (4)$$

where $\lambda_{i,c}$ is the net amount divided amongst all grid cells and C_{cover_c} is the coral cover ratio calculated as the proportion of benthic cells within the fish cell, reflecting the increased probability of fish recruitment by the increased provision of refuge and food mediated by high coral cover (Jones et al. 2004, Gurney et al. 2013; Kerry & Bellwood 2015).

Internal recruitment $P_{int_{i,c}}$ occurs when the conditions for minimum reproductive biomass threshold (γ_i) and minimum biomass consumed through feeding (θ_i) are met, and is defined by:

$$P_{int_{i,c}} = \rho_i \cdot C_{cover_c} \cdot B(t)_{i,c} \cdot \left(1 - \frac{B(t)_{i,c}}{K_i}\right) \quad (5)$$

where ρ_i is the group's average reproduction rate and K_i is the carrying capacity, or the maximum biomass for the fish group. If the conditions are not met, $P_{int_{i,c}} = 0$.

Each fish group has a background mortality which decreases cell biomass linearly:

$$M_{i,c} = \delta_i \cdot B(t)_{i,c} \quad (6)$$

where δ_i is the group's average death rate.

The feeding process has different dynamics for each fish group. The amount of prey consumed is calculated by group-specific feeding equations, and the result is transformed to obtain the biomass gained by the predator by:

$$\Phi_{i,c} = C_i \cdot \sum_p \Pi_{p,i,c} \quad (7)$$

where $\sum_p \Pi_{p,i,c}$ is the summed amount of food consumed for all preys p , and C_i is a constant of the group's conversion factor.

Scrapers typically remove portions of the underlying carbonate substratum, feeding on HS cells in the model. Scrapers predation on HS is given by the standard Holling type II equation (Holling 1959):

$$\Pi_{HS,S,c} = \frac{\alpha_{HS} \cdot B(t)_{HS,c}}{1 + \alpha_{HS} \cdot \tau_{HS} \cdot B(t)_{HS,c}} \cdot B(t)_{S,c} \quad (8)$$

where α_{HS} is the attack rate, τ_{HS} is the handling time, $B(t)_{HS,c}$ is the biomass of hard substrate, and $B(t)_{S,c}$ is the biomass of scrapers.

Browsers and grazers feed on MAT cells turning them into HS. Their feeding rate is a parabolic function which peaks at an optimal MAT cover to reflect the reduced herbivory observed in large algal patches in contrast to open space with small food patches (e.g. Ledlie et al. 2007, Hoey and Bellwood 2011). Browsers and grazers feeding is given by:

$$\Pi_{MAT,BG,c} = B(t)_{MAT,c} \cdot \left(\frac{-v \cdot (MATR(t)_c - MATR_{opt})^2}{(MATR_{min} - MATR_{opt})^2 + 1} + \varepsilon \right) \cdot B(t)_{BG,c} \quad (9)$$

where v and ε are fitted parameters; $MATR(t)_c$, $MATR_{opt}$ and $MATR_{min}$ are the current, optimal and minimum MAT cover ratio (number of MAT cells divided by the total number of benthos cells in current fish cell), $B(t)_{MAT,c}$ is the biomass of food and $B(t)_{BG,c}$ is the biomass of browsers and grazers.

Carnivores feed on both scrapers and BG by a reformulated Holling's disc equation to reflect multiple prey (Hollings 1959; Hilborn and Walters 1992; Moustahfid et al 2010). If the condition of minimum prey biomass ratio (μ) is met (minimum ratio of prey that carnivores are able to feed on), predation of BG prey is given by:

$$\Pi_{BG,Car,c} = \frac{\alpha_{BG} \cdot B(t)_{BG,c}}{1 + \sum_j \alpha_j \cdot \tau_j \cdot B(t)_{j,c}} \cdot B(t)_{Car,c} \quad (10)$$

where α_{BG} is the attack rate for browsers and grazers, $B(t)_{BG,c}$ is the biomass of browsers and grazers, and j refers to all the prey groups eaten by the carnivores (i.e. BG and scrapers). The biomass of prey caught per unit time increases slowly at low biomasses of BG with respect to the scrapers, and fast at lower scrapers biomass, representing the predator's behaviour of switching in response to prey relative abundance. The same equation is applied to obtain the consumed biomass of scrapers.

Fish movement occurs amongst neighbouring cells and is assumed to be driven by habitat quality, intraspecific density of the current and surrounding cells, and a permanence factor (ω_i). The net migration from cell a to b is given by:

$$E_{i(a,b)} = \frac{((1-\omega_i)/8) \cdot HQ_{i,b}}{\omega_i \cdot HQ_{i,a} + ((1-\omega_i)/8) \cdot \sum_{j=1}^8 HQ_{i,neighbour(j,a)}} \quad (11)$$

where ω_i is the permanence factor, and HQ is the cell's habitat quality.

Habitat quality for scrapers increases linearly with coral and with hard substrate cover, and decreases with algae cover:

$$HQ_{i,c} = \frac{CR(t)_c + (1-MATR(t)_c) + (HSR(t)_c)}{3} \quad (12)$$

where $CR(t)_c$, $MATR(t)_c$ and $HSR(t)_c$ are the coral, MAT and hard substrate cover ratio.

For BG, habitat preference increases linearly with coral and decreases with algae cover, and has a parabolic influence of algal cover:

$$HQ_{i,c} = \frac{CR(t)_c + (1-MATR(t)_c) + \left(\frac{-1 \cdot (MATR(t)_c - MATR_{opt})^2}{(MATR_{min} - MATR_{opt})^2 + 1} \right)}{3} \quad (13)$$

Habitat quality for carnivores is positively influenced by prey abundance (Wen et al. 2013) and negatively influenced by intraspecific competitors.

$$HQ_{i,c} = \frac{PREYR(t)_c + (1-PREDR(t)_c)}{2} \quad (14)$$

where $PREYR(t)_c$ and $PREDR(t)_c$ are the relative biomasses of fish prey (i.e. BG and scrapers) and the predator (i.e. carnivores), calculated by taking their standing biomass and dividing by their respective maximum biomasses.

The biomass lost to fishing $\Psi_{i,c}$ is calculated by the fishery module as explained in the next section.

2.3. Anthropogenic Impacts

Three types of anthropogenic stressors of different spatio-temporal scales can be specified in each simulation: bleaching frequency, nutrient levels, and fishing. Bleaching is the model's proxy for global ocean warming and has two effects on the benthos: *bleaching mortality* and *non-lethal bleaching* (Fig. 1). Each bleaching episode affects a proportion of the coral cells at each depth based on reported bleaching episodes in Indonesia (Sartin and Setiasih 2011; Bridge et al. 2014; *Appendix 1*). The user can specify the frequency of bleaching episodes changing parameter β .

The model observes three nutrient scenarios: low, medium, and high. The *low* nutrient scenario contains the standard parameterization with average algae growth rates obtained from the literature (*Appendix 1*). In the *medium* nutrient scenario, the benthos rules for *Aging* and *MAT Colonization* are changed by decreasing the time needed for a HS cell to become MAT by 20%. The *high* nutrient scenario affects the same rules decreasing the time by 40% and further increases the time for *Coral Colonization* by 20% (we assume coral growth is reduced as a result of higher planktonic standing stocks reducing light penetration and impairing zooxanthellae photosynthesis; D'Angelo & Wiedenmann 2014). We arbitrarily chose a 20% change in the growth rates because there was a high level of uncertainty in the literature due to the complexity of the processes involved. The times used in the *Colonization* and *Aging* rules can also be modified in the *advanced* mode of the user interface if more information becomes available or alternative plausible values are obtained for the model's application site.

The fishery module operates at the fish grid level and allocates fishing effort across the cells. The user can add an unlimited number of fishing techniques, which are defined by a customisable set of parameters including (a) number of fishing units (fleet), (b) time allocation, (c) maximum catch per unit of effort, (d) catchable proportion of the fish biomass per time step per cell, (e) maximum number of cells a fishing unit can visit per time step, (f) depth categories affected, (g) target fish groups susceptible to fishing mortality by the fishing technique, (h) minimum fishable biomass per fish cell, and (i) fishing style (i.e. non-destructive, cyanide, bomb fishing). The fishing style parameter defines the damage done to the reef habitat; non-destructive fishing does not affect the benthos grid; bomb fishing affects the benthos by turning a randomly selected 4 m² area of benthos into empty. Cyanide fishing turns an area of 1 m² randomly selected coral and MAT cells into HS. These effects are based on impacts reported by McManus et al. (1997) and Hlavacs (2008).

3. EXAMPLE APPLICATION

The user-friendly interface was developed with the aim of facilitating scenario testing of particular case studies and has two modes of use: standard and advanced. The *standard* mode allows the input of initial and boundary conditions (i.e. depth profile, initial benthos cover and aggregation ratios, initial fish biomass, and stressors), while the *advanced* mode allows for modification of the entire model parameterization, including biological rates and thresholds. The *standard* mode is currently parameterized to represent coral reefs of the Indo-Pacific (*Appendix*, tables 1-2), and input parameters and initial conditions can be changed according to case-specific abundance of functional groups, fishing pressure and biophysical conditions.

We ran one example application where we apply a daily fishing pressure of 5 fishing units at depth category 1 (0 – 5 m) with no fishing selectivity (targeting all fish groups) to a 300x300m map to display the graphic interface setup. The *nutrient scenario* is set to low and there is no bleaching. As shown in Figure II, fish groups in depth 1 repopulate thanks to migration from adjacent depth zones not affected by the fishery (spillover from not fished areas). Besides the visual real time output, the program can be set to print out the output as csv files. These files report for every time step and contain: (a) benthic cover by group, (b) benthic cover by depth and group, (c) fish biomass by group, (d) fish biomass by depth and group, (e) fishing yield (when applicable) by depth and fishing technique, and (f) spatial output at the interval specified.

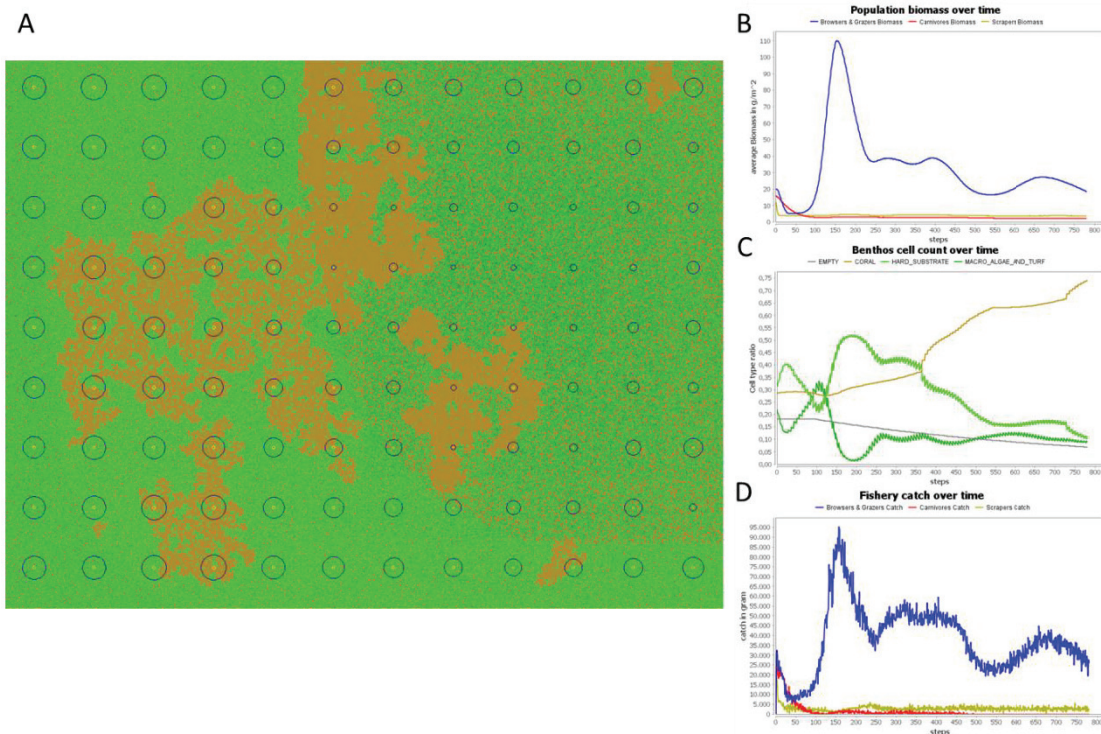


Figure II. Simulation display in the user interface for the example application. **(A)** is the spatial distribution of the reef in time step 210, representing the benthos habitat distribution (coral –orange-, macroalgae and turf –dark green-, hard substrate –light green-, and empty space –grey) and the fish groups in circles (browsers and grazers –blue-, scraper –brown-, and carnivores –red). The larger circles observed in two of the depths indicate higher biomass of fish in the areas not affected by fishing. The graphs represent the time series of fish biomass (B), benthos cover (C), and catch (D) of the on-going simulation.

4. PARAMETER SENSITIVITY

Sensitivity analyses were run for all parameters to assess their effect on the main response variables. First, a baseline scenario was parameterized with minimum stressors to focus on the ecological interactions in a “pristine” scenario. The baseline parameterization (*Appendix 1*) was based on available literature data and plausible estimation where needed. To measure parameter sensitivity we changed one parameter at a time to report the relative change in the response variables -namely coral cover, MAT cover, BG biomass, scrapers biomass and carnivores biomass- between time steps 500 and 2000. The choice of this time period was intended to allow the model to stabilise from the initial conditions. For fish parameters, we increased and decreased each of the baseline values by 25%. For

environmental parameters we gradually increased connectivity, bleaching and nutrients (as detailed in *Appendix 1*).

Under the model's premises, MAT cover is quantitatively the most sensitive variable to all the parameter types, while scrapers biomass and coral cover are the least affected. Fish parameters pertaining to the carnivore group were the most relevant (Fig. III), showing top-down control from predators. Changes in their death rate, prey minimum biomass ratio and conversion factor had the highest impact, as did browsers and grazers conversion factor producing an increase in MAT of 142% when reduced by 25%.

Changing the nutrient scenario – both to *medium* and *high*- affected the entire suite of response variables to the greatest degree (Fig. IV), as this changes three rules - two by 40% and one by 20% -.The *High* nutrients scenario caused a 291% increase in MAT, 170% in BG biomass, 157% carnivores, a 40% decrease in coral cover, and a 26% decrease in scrapers biomass. In contrast, yearly bleaching increased MAT cover by 113%. Parameters pertaining to the degree of connectivity with neighbouring reefs did not have as strong an effect as the parameters above, but it is noteworthy that a 25% decrease in coral larvae supply had double the effect on benthic cover variables than the equivalent increase.

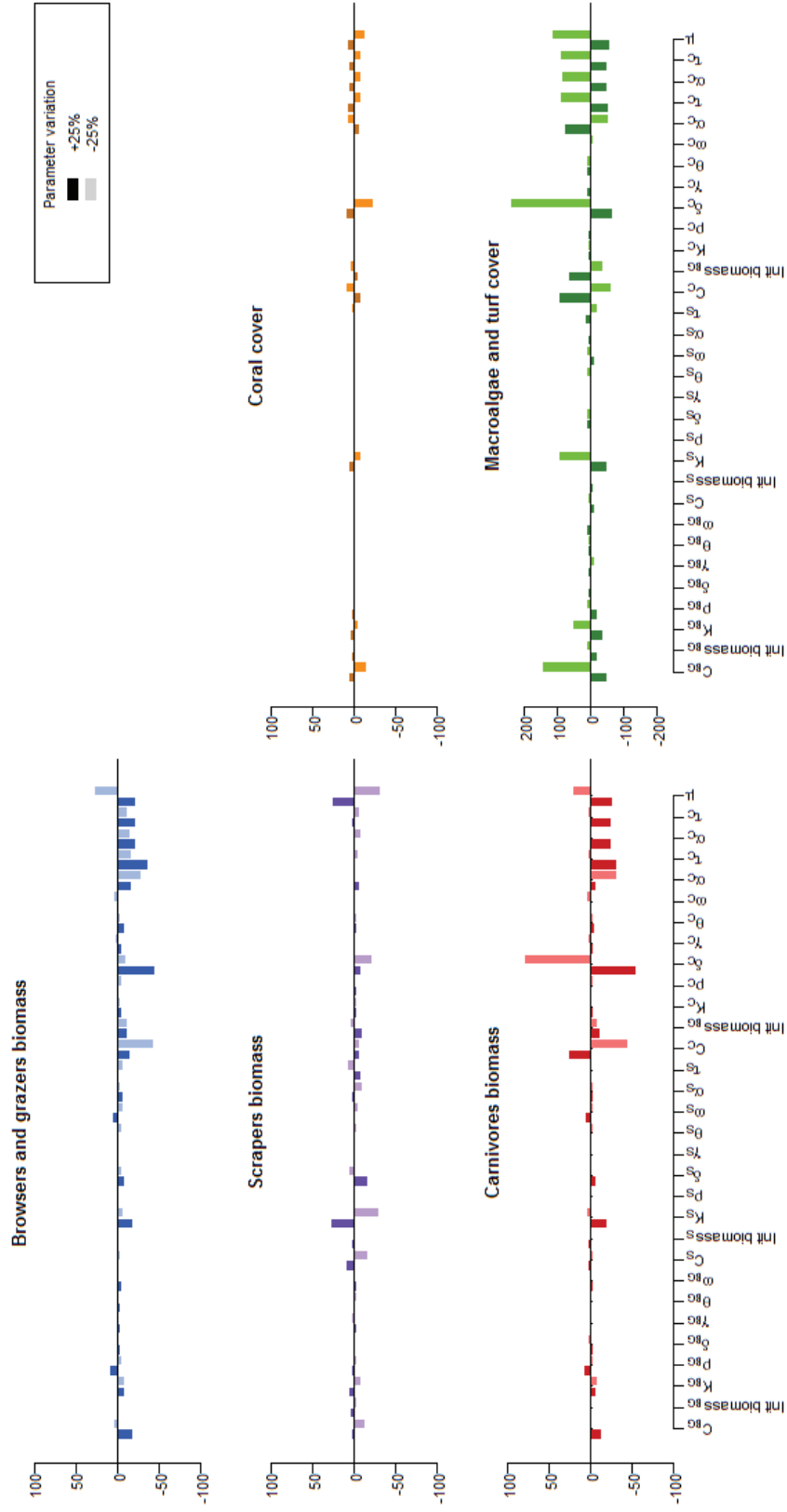


Figure III. Relative change in percentage on the response variables after individual variation of the fish parameters including conversion factor (C_i), initial biomass, maximum biomass (K_i), reproduction rate (ρ_i), death rate (δ_i), minimum reproductive biomass threshold (γ_i), consumed biomass factor (θ_i), permanence factor (ω_i), attack rate (α), handling time (τ), and prey minimum ratio (μ). Each parameter was increased and decreased by 25% from its value in the baseline scenario.

This sensitivity analysis provides information on the most important parameters under the current baseline setup. However, caution must be exercised when interpreting results from simulations with a different parameterization as changing one parameter could affect the influence of the rest on the the response variables.

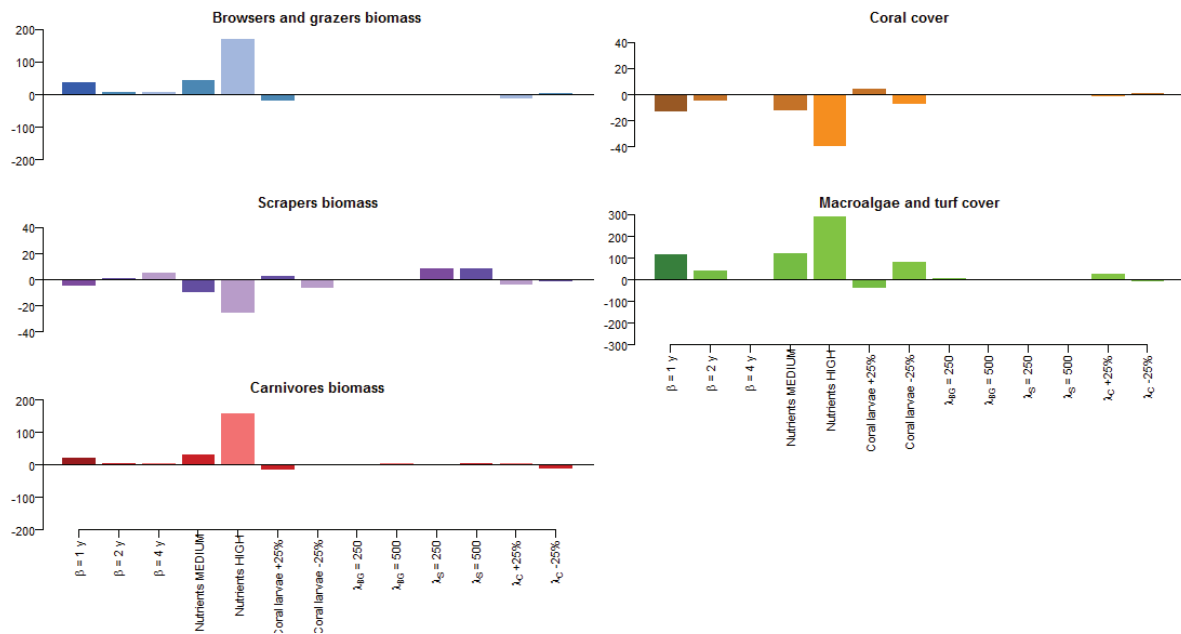


Figure IV. Relative change in percentage on the response variables after individual variation of environmental parameters from their value in the baseline scenario. These include bleaching interval β , nutrient scenarios, and external supply for coral and fish larvae (λ_i).

5. DISCUSSION

SEAMANCORE is a quantitative tool to explore potential outcomes of different resource management and environmental scenarios by simulating the dynamics of relevant coral reef functional groups. This user-friendly local coral reef model can be parameterized with limited field data, routinely collected in basic coral reef monitoring programs (Flower et al. 2017). These include a greyscale depth map image, benthic cover, and biomass of the three functional groups (*Appendix 2*).

The model brings together complex elements of a coral reef ecosystem in a spatially explicit setup. It can both be used as an exploration tool for local management and as a tool to

explore the influence of different pressures on the groups' population dynamics. It can be useful for testing potential synergies between stressors (Gurney et al. 2013), and can provide answers to whether one stressor is more detrimental than another (e.g. nutrification vs. fishing) in a case-specific assessment. It also provides a flexible menu display to test diverse fishing management strategies, including fishing selectivity, quotas, zonation and number of fishing units. It can be used to explore how a no-take area (fisheries closure) would affect the local reef. The large variety of settings allows for substantial case study customization.

One of the issues encountered was the increased computational demand with map size. From a size of 600x600m, more memory needs to be allocated to the program, and a powerful system is needed. Another challenge was the trade-off between model complexity and its usefulness as a tool for managers. We are aware that the model contains numerous assumptions that might prevent detailed questions being asked about specific processes, such as specific ecological questions about reef species not included in the choice of functional groups, or studies about net fishing yield as this model is concerned by one portion of the coral reef ecosystem. However, the focus of this project was to provide a tool to address human impact on ecosystem level dynamics and fishing yield, highlighting the feedbacks between the ecosystem and its human users. Future versions may refine the current equations, add more functional groups or even a dynamic fisheries module to further the scope of the application.

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Data accessibility

SEAMANCORE is a free, open source program written in Java which will be made accessible upon publication via the distribution program with several sample depth maps and

the baseline parameters hardcoded. This is the first version of this model. We look forward to further contributions from other parties who may want to build upon it.

Appendix 1: Description of SEAMANCORE

1. General information

This model was developed at the department of Theoretical Ecology and Modelling of the Leibniz center for Tropical Marine Ecology (ZMT Bremen) by Sara Miñarro with funding from BMBF (German Federal Ministry of Education and Research) and ZMT.

The purpose of the model is to provide a user-friendly exploration tool to assess likely outcomes of different resource management and environmental scenarios by simulating the population dynamics of a coral reef. SEAMANCORE represents the local spatial dynamics of a coral reef under the influence of local (fishing, eutrophication) and global (bleaching) stressors. It focuses on the dynamics of three fish and four benthic functional groups, the ecological relationships amongst them and how they are affected by external stressors. Fishing is explicitly modelled with parameters for intensity, depth ranges and selectivity, while the other stressors - bleaching and nutrification - are more broadly specified through scenario settings. This model is user-friendly and displays menus containing the changeable parameters. It can be used to explore the likely trajectories of a coral reef ecosystem under different scenarios of depth profile, nutrient regimes, connectivity, bleaching frequency and fishery management strategies.

2. Model assumptions and limitations

The model is a simplification of the ecosystem intended to represent the processes of benthos dynamics and trophic relationships relevant to fishing yield and habitat structure within one coral reef. As such, many assumptions were made and a number of important processes were left unrepresented, which means that model outcomes should be interpreted in the context of the represented components and processes.

First, the model does not account for natural erosion processes, which are likely to be important in fore reefs exposed to considerable wave action, and does not represent diverse habitats in terms of reef complexes (i.e. just the fore reef and reef crest and not the lagoon or back reef). Likewise, important benthic functional groups are left out, including benthic invertebrates with potential ecological implications such as urchins, or crown-of-thorns starfish, whose feeding rates can have strong control over the abundance of our benthos groups, and organisms which have been shown to dominate in certain phase-shifts such as soft corals and sponges (when using field data as initial conditions for the model, we include

soft corals and sponges within the algal group, and other benthic invertebrates as hard substrate). While the model could be expanded to include the specific dynamics of those organisms, its current purpose is to represent competition processes between corals and algae. Even within the model's functional groups, all corals are not equal ecologically, as branching corals are known to increase structural complexity and to be a preferred fish habitat, in comparison with massive corals (Wilson et al. 2008), while being more vulnerable to bleaching and mechanical damage (Grimsditch & Salm 2006, Baldock et al. 2014).

Numerous ecological factors can influence the functional response of predators in widely diverse ways (Hunsicker et al., 2011) that are hard to quantify and scale to entire functional groups. This model does not include the effect of high predator density or the influence of seasonality in terms of water temperature (Harborne 2012). Due to a lack of mechanistic understanding in the coral reef literature (Stier and White, 2014), we did not take into account shifts in foraging behaviour that may have been caused by predator abundance driving predator-predator interactions and/or antipredator behaviour in prey, and had to fit the predation behaviour parameters loosely based on freshwater studies. Predator interference takes place indirectly in the migration module, where habitat quality decreases for carnivorous fish with increasing predator density. We did not delve into the effects of high prey densities in feeding rates, which in some cases have been reported to decrease the feeding rate presenting a dome-shaped functional response (Harborne, 2012; Jeschke et al., 2004). This model may be used to evaluate scenarios with different functional response functions in the future.

Finally, the effect of land run-off and pollution introducing nutrients in the system is reflected in the model by an increase in algal growth rates but not in their interaction with coral, since there is no definitive evidence that nutrients increase the competitive advantage of algae (e.g. McCook 2001; Vermeij et al. 2010). Other reported effects of nutrification were not considered due to paucity in quantitative or mechanistic information available. For instance, terrestrial nutrients are suspected to enhance *Acanthaster planci* larval survival (Pratchett et al., 2014; Wooldridge, 2016) and to play a role in increasing the vulnerability of corals to thermal bleaching (Wooldridge and Brodie, 2015).

Overfishing, destructive fishing and watershed pollution have been ranked as the strongest local threats faced by coral reefs around the world (Burke et al. 2011). We chose to model them along with the largest perceived global threat, i.e. global ocean warming. However, other impacts such as ocean acidification or COTs outbreaks are not considered in the model.

3. Organisms

The benthos grid is composed of cells (10 x 10 cm) which belong to one of four categories: coral (C), macroalgae and turf (MAT), hard substrate (HS) and empty space (E). Benthos dynamics include the processes of coral-algal competition, growth, colonization, connectivity from external sources and disturbances. The three fish classes are: browsers and grazers (BG), scrapers, and carnivores. Fish cells (20 x 20 m) contain the biomass of each fish functional group, which is calculated every time step (i.e. one day). Each benthos and fish cell represents 10 x 10 cm (0.01 m²) and 20 x 20 m (400 m²), respectively. While the benthos grid operates as a cellular automaton, the fish grid cells contain a biomass function which is updated every time step.

3.1. Benthos

Benthos cells have three attributes at any given time step: type of cell, age, and depth. The cell's age - the time that a given cell has existed as a particular cell type- is used as a proxy to its density and is computed in the calculations for updating the CA. The age and number of surrounding cells from each type are used to calculate the outcomes of the benthic CA rules, plus a probability determined by depth. Cells use a Moore neighborhood (i.e. the 8 surrounding cells) for each CA calculation. If a cell is located in one of the boundaries, they use a mirror approach as schematized in figure 2.

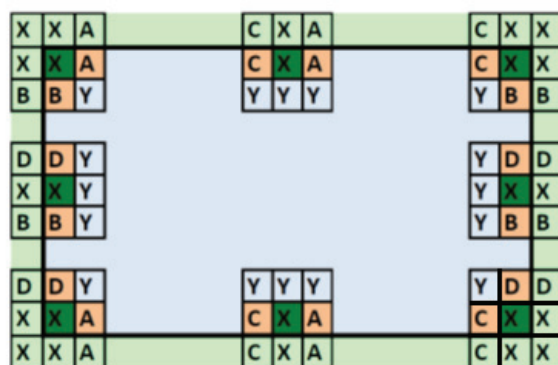


Figure 1. Diagram of the cells considered for computing the rules of the cellular automaton on the grid boundaries (A, B, C, D, X, Y denote arbitrary cell states).

CORAL:

Coral (C) cells have a higher probability than the other cell types of occurring next to each other to mimic their real life colonial behaviour. This is set up in the initialization by the aggregation level, and accounted for in the *Colonization rule*, by which coral cells have a higher probability of expansion when they are surrounded by coral neighbours. They grow more slowly than algae cells and are able to colonize hard substrate after a longer time, but are not affected by fish feeding. They also increase the probability of fish recruitment by providing refuge and food sources (e.g. Kerry & Bellwood, 2015; applied by Gurney *et al.*, 2013).

MACROALGAE AND TURF:

Macroalgae and turf (MAT) cells grow faster than coral cells, colonizing available hard substrate cells in their neighbourhood. Both coral and algae cells expand according to global averages extracted from published growth rates (Section 5). In the model's mechanistic approach, they can only colonize hard substrate cells, meaning that when another cell type is surrounded by C or MAT, it needs to become HS before turning into the colonizing cell type. Similarly, C and MAT cells compete for space. When one of either cell type is surrounded by competitors for a threshold number of time steps depending on the type and depth of the cells involved, it becomes a HS cell (*Pre-colonization rule*).

HARD SUBSTRATE:

The category of hard substrate is used here *sensu* "cropped algae" category in Mumby (2006), including also rocky bottom. When scrapers do not graze on hard substrate (HS) cells for a given number of time steps (resetting their age), they grow into a MAT cell (*Aging rule*). MAT cells spread laterally and colonize hard substrate cells at a higher pace than corals. If a hard substrate cell is surrounded by enough coral cells for a given amount of time steps, it becomes a coral cell by settlement of coral recruits, with a certain probability determined by its depth category. In order for a C cell to turn into MAT or vice versa, the cell needs to become HS first. If there continues to be the minimum required number of the colonizing cells in the neighbourhood for either C or MAT, the HS cell will switch to that cell type.

EMPTY SPACE:

The "empty" category refers to bare substrate unsuitable for settlement of algal or coral recruits (e.g. sand). This state is only reached as a result of specific disturbances upon a benthos cell (i.e. mechanical damage and blast fishing). Empty cells can change into hard substrate if the Global Pre-colonization rule is applied. The number of time steps needed

depends on the amount of ‘living cells’ (i.e. the other 3 cell types) versus empty cells in the entire model domain. The more living cells, the faster it will become hard substrate. Given that the model focuses on the hard reef area (reef crest and fore reef), sand is not a legitimate long term benthic state.

A. INITIALIZATION

The program requires three user input items to initialise the benthos: (a) a greyscale map representing the depth profile of the reef, (b) the initial cover ratio of each benthic category at each depth, and (c) the cell type aggregation levels (i.e. degree to which that habitat type is found in clumps). With this information, the model creates the initial benthic distribution of the reef. Benthos cells can be set up at a higher or lower aggregated form, computing coral cells first to give them greater priority of aggregation. The proportion P of cells of type c to be located inside an aggregation at a given depth d is given by:

$$P_{c,d} = CoverRatio_{c,d} \cdot AggrRatio_{c,d}$$

where $CoverRatio_{c,d}$ is the benthic cover and $AggrRatio_{c,d}$ is the aggregation level of cell type c .

An aggregation seed is placed at a randomly selected location and then grows until attaining a predefined size S given by:

$$S = MinAggrSize_c + r (UnplacedCells_{c,d} - MinAggrSize_c)$$

where $MinAggrSize_c$ is the minimum number of cells to form an aggregation, r is a random value between $[0, 1]$ and $UnplacedCells_{c,d}$ is the number of cells yet to be placed inside an aggregation. It is initially calculated multiplying $P_{c,d}$ with the total number of cells at depth d and reduced by S after building each aggregation. Seeds are placed until $UnplacedCells_{c,d} < MinAggrSize_c$. After that, the other cell types are distributed randomly.

B. RULES TO UPDATE THE BENTHOS CA.

When a benthos cell fulfils a specific set of rule conditions, the rule is applied and its cell type is changed accordingly. Otherwise, the cell age increases. If the cell changes to another type, its age is reset. Rules have a priority order of application detailed in Table 1. If the cell does not fulfil the first rule, then the second rule is checked for and so on. When a rule is fulfilled and applied (i.e. the cell type is changed or reset), the other rules are automatically

cancelled. The conditions for transformation are given by a set of parameters specified for each rule, including the depth of the cell, the current cell type, the potential transformed cell type (i.e. what would it turn into if the rule applies), the probability factor, the minimum number of neighbours, the minimum summed age of the neighbouring cells. The rules are as follows:

a) *Aging Rule (AgeThresholdRule)*

This rule turns a cell from hard substrate into macroalgae and turf, representing the growth of cropped algae or algal recruits into structurally emergent algae. It has a probability of happening which is subject to the specified nutrient scenario. The chosen nutrient scenario sets the minimum number of the time steps the cell type has been hard substrate as a condition to become a MAT (see section 5 for details on the parameterization).

b) *Pre-colonization Rule*

This rule applies to coral and MAT cell types and turns them into hard substrate cells. It represents the first step of a competition process. If one cell is surrounded by enough competitors of a minimum collective age (see conditions below), it will turn into HS before it can be colonized by the type outcompeting the current cell type. A coral cell cannot turn into MAT and vice versa without transitioning through HS first.

Conditions:

Case 1: if a MAT cell is (1) surrounded by ≥ 3 coral cells and (2) the coral cells' summed age is ≥ 50 , the rule applies and turns it into HS with a probability factor of 0.5.

Case 2: if a coral cell is (1) surrounded by ≥ 4 MAT cells and (2) the MAT cells' summed age is ≥ 100 , the rule applies and turns it into HS with a probability factor of 0.6.

c) *Colonization Rule*

This rule applies to HS cells and depending on the surrounding cells, turns them into coral or MAT cell type with the following conditions:

Conditions:

Case 1: if (1) the number of MAT surrounding cells ≥ 1 and (2) the minimum summed age of those MAT cells \geq number of time steps specified by the nutrient scenario, the rule applies and turns the HS cell into MAT with a probability factor depending on its depth category.

Case 2: if (1) the number of coral surrounding cells \geq a given number and (2) the minimum summed age of those MAT cells \geq number of time steps specified by the nutrient scenario,

the rule applies and turns the HS cell into coral with a certain probability. The 3 parameters change depending on the depth category and the season (wet or dry).

Both cases contain a probability factor which decreases with depth.

d) Global Pre-colonization Rule

This rule affects empty cells by turning them into hard substrate. It represents the turning of relatively “older” empty cells into “fertile” HS from successful settlement of larvae and recruits. The probability of this happening increases with higher proportions of C, MAT and HS subject to the conditions given below.

Conditions: if (1) the reference ratio (number of cells \neq EMPTY/number of EMPTY cells) \geq than the minimum reference ratio (= 0.8) and (2) applying EMPTY cell age \geq mutable minimum age (= [30, 100]) lower with higher reference ratio, the rule is applied.

This rule has a 0.01 probability of been applied, as empty cells are generally not colonisable substrate.

e) Connectivity Rule

This rule turns HS cells into coral, and it represents the level of connectivity of the simulated reef with other healthy reefs by means of external larval supply, subject to the following:

Condition: If the HS cell's age is \geq minimum age, the rule is applied with a probability parameter representing the degree of connectivity (changeable by the user).

f) Disturbance Rule

This rule can have different origins depending on the disturbance it represents: fishing, fish feeding, and bleaching. The affected depth category is the only general condition, and for each disturbance type a specific proportion of the cells are affected (Section 5).

Destructive fishing disturbance: (a) Blast fishing and damage (e.g. anchoring): it turns all affected benthos cells into EMPTY and resets the age of the cells; (b) Cyanide fishing: it turns all affected benthos cells into HS and resets the age of the cells.

Feeding disturbance: depending on the type of cell, it retrieves the number of affected cells from the food web module. It resets the age of HS cells to account for scrapers foraging, and turns MAT into HS to account for foraging by browsers and grazers.

Bleaching: it has two types, bleaching mortality and non-lethal bleaching. The frequency of bleaching β is a proxy for “climate change severity” chosen by the user. The *bleaching mortality* rule turns coral cells into HS, and the *non-lethal bleaching* rule resets the age of

coral cells (due to the expulsion of zooxanthellae, which stops their effective function as coral, but not their structure). These bleaching effects decrease with increasing depth (Section 5).

Table 1. Order of application of benthos rules.

Cell type	Rule name	Order
Empty	Disturbance: blast fishing	1
	Global pre-colonization	2
Hard substrate	Disturbance: blast fishing	1
	Disturbance: foraging	2
	Aging	3
	Colonization from MAT	4
	Colonization from CORAL	5
	Connectivity/external larval supply	6
Macroalgae and Turf	Disturbance: blast fishing	1
	Disturbance: cyanide fishing	2
	Disturbance: foraging	3
	Pre-colonization	4
Coral	Disturbance: blast fishing	1
	Disturbance: cyanide fishing	2
	Disturbance: bleaching mortality	3
	Disturbance: non-lethal bleaching	4
	Pre-colonization	5

3.2. Fish.

The three functional groups of reef fish (i.e. browsers and grazers, scrapers, and carnivores) were selected because of their trophic role and based on the classification by Edwards et al. (2014) for herbivorous fish. The fish grid contains information about the fish biomass in g m^{-2} and is updated daily, as is its influence on the benthos. The grid cells use a Moore neighbourhood (i.e. 8 surrounding cells) to calculate the biomass change in each time step.

Biomass changing processes include representations of the movement (migration), feeding (trophic relations), recruitment (reproduction), natural mortality and fishing. Each 20x20m cell

takes into account all the biomass variations in one time step and computes the net biomass change.

Figure 2 provides a flowchart of the model processes as they are computed by the application.

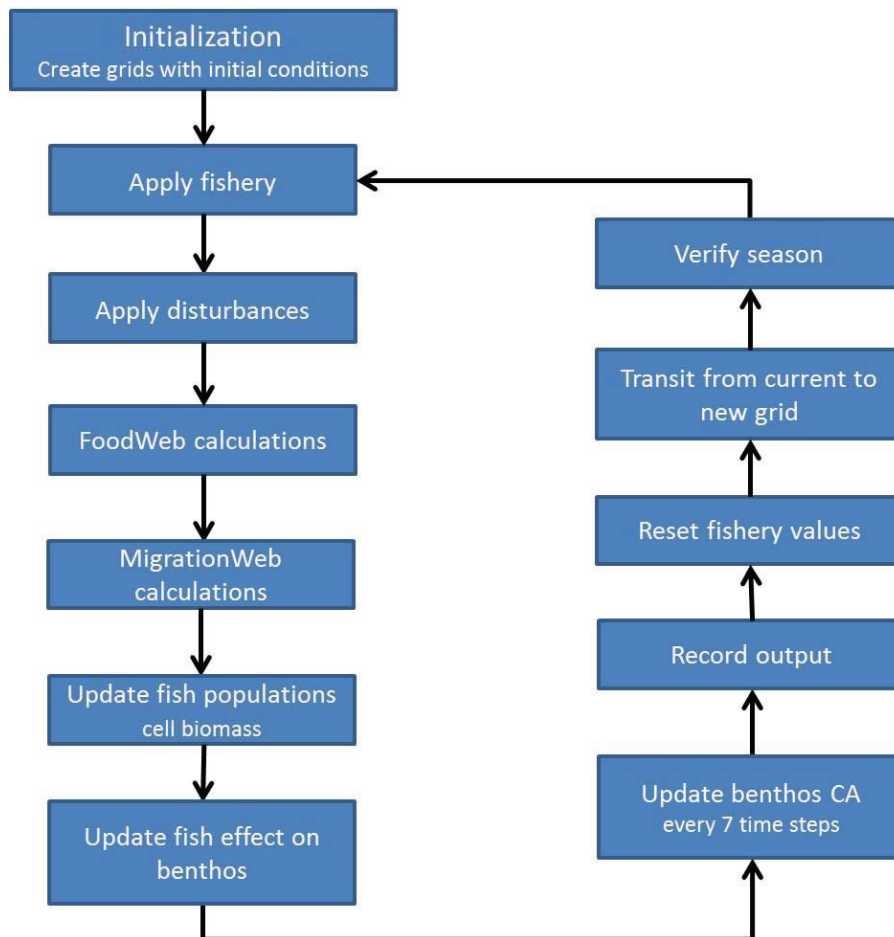


Figure 2. Flowchart of model processes.

A. FISH INITIALIZATION

Similarly to the benthos, the user is requested to input the initial biomass of the different fish functional groups. In this case, depth is not taken into account because fish can move and relocate fast according to benthic habitat. The program distributes these densities across the grid, taking into account each group's maximum biomass K_i (input by the user in g m^{-2} and transformed into grams per fish cell by the program). K_i is used as the carrying capacity

value in the recruitment equation and to calculate the minimum *prey* biomass for carnivores μ .

B. FISH UPDATING

The biomass of each fish group in each of the cells making up the grid is updated according a set of functions which take into account the processes affecting fish biomass – migration, recruitment, predation and feeding, natural mortality, and fishing. The more complex change behaviour processes are handled in three modules: the migration web, the food web, and the fishing module which calculate the biomass flow amongst compartments. Reproduction and natural mortality are handled by simpler equations applied to each fish cell.

(a) Feeding and predation

Feeding is handled by the Food Web module, which contains all the “predator-prey” relationships. The predator-prey relationships contain the predator biomass, prey biomass and their feeding function which allow the Food Web module to calculate and store the biomass lost by each fish group due to predation in a fish cell, as well as the number of benthos cells eaten. This information is accessed by the Change Behaviour calculator to update the gained or lost biomass, and by the benthos grid to reset or change affected cells, as described below:

- For the fish predator:
 $Gained_biomass = B_C * conversion\ factor$
- For the prey fish:
 $Lost_biomass = B_C$

where B_C is the biomass of the prey fish consumed by predation.

- For the benthos prey the number of cells affected by fish feeding (from the Food Web module) must be \leq number of cells of that type within the given fish cell (the foraging domain). The number of cells affected is calculated by the Food Web module as:

$$Affected\ cells = \frac{B_C}{B_{bcell} \cdot A_{bcell}}$$

Where B_{bcell} is the biomass contained in a benthos cell ($g\ m^{-2}$) and A_{bcell} is the area represented by one benthos cell, which is $0.01\ m^2$.

Once the number of cells is calculated, the benthos cells consumed are selected randomly within the fish cell. The feeding disturbance is applied to the selected

benthos cells depending on the predator-prey relationship taking place (i.e. for scrapers, HS cells' age is reset; for GB, MAT cells turn into HS).

(b) Fish movement

Fish movement occurs amongst neighbouring cells (distance = 1) and is handled by the Migration Web module, which identifies cells suitable of migration based on the relationships between available habitat and fish preferences. Fish movement to other cells is dependent on the habitat quality definitions for each functional group which are explained in the manuscript. The Migration Web module calculates the biomass flow amongst cells taking into account the habitat cell quality in terms of food abundance, benthos cover and/or biomass of the fish group (i.e. intraspecific competitors). Habitat quality values for each cell are then multiplied by the permanence factor, which is defined by the user for each fish group to give a probability of staying in the current cell and consequently saving the energy of moving. Once the Migration Web has calculated how much biomass is potentially flowing into a cell as immigration, it checks that the additional biomass does not surpass the maximum biomass allowed per cell per fish group. In the case of a cell receiving more immigrating biomass than the maximum allowed (immigration + resident biomass), the excess amount is returned to the cells of origin in the proportion that they contributed to the total immigration of the cell. The returned immigration biomass cannot surpass the maximum allowed because the reflux is calculated based on the previous biomass (the amount allowed to immigrate to a cell is the difference between the maximum biomass minus the previous biomass at the beginning of the time step). The actual biomass change is calculated after all the calculations are done and once the reflux has been applied.

4. Physical Properties

4.1. Depth.

A depth map can be uploaded by the user. It must be a greyscale map with depth categories every 5 (lower depths) and 10 m (higher depths). The model reads the map pixel values and assigns a depth category to each benthos cell (Table 2). Each pixel equals to 1 m². Processes using depth for their calculation include the benthos initialization, benthos rules, bleaching and fishing.

Table 2. Depth categories explanation and greyscale numbers assigned by the model.

Category	Real depth	Colour number
1	0 – 5	0 - 41 (black)
2	5 – 10	42 - 84
3	10 – 15	85 - 127
4	15 – 20	128 - 170
5	20 – 30	171 - 213
6	30 – 40	214 - 255 (white)

5. Fishing

The fishing module operates at the fish grid level, and Figure 3 shows a diagram of the fishery process as handled by the model. The program reads in the parameters defined by the user for each fishing technique, using depth to randomly select the cells where fishing can take place. If the cell's biomass of the affected fish groups \geq *BiomassThreshold*, the model calculates the biomass extracted according to the *CatchProportion*, and the benthos disturbance if applicable (i.e. if Cyanide or Bomb are selected as *FishingGear*). If *MaximumCatch* is reached, the fishery stops; otherwise, each fishing unit moves to the next cell and repeats the process until the maximum CpUE is achieved, or the maximum cell tries (*TryCount*) is reached.

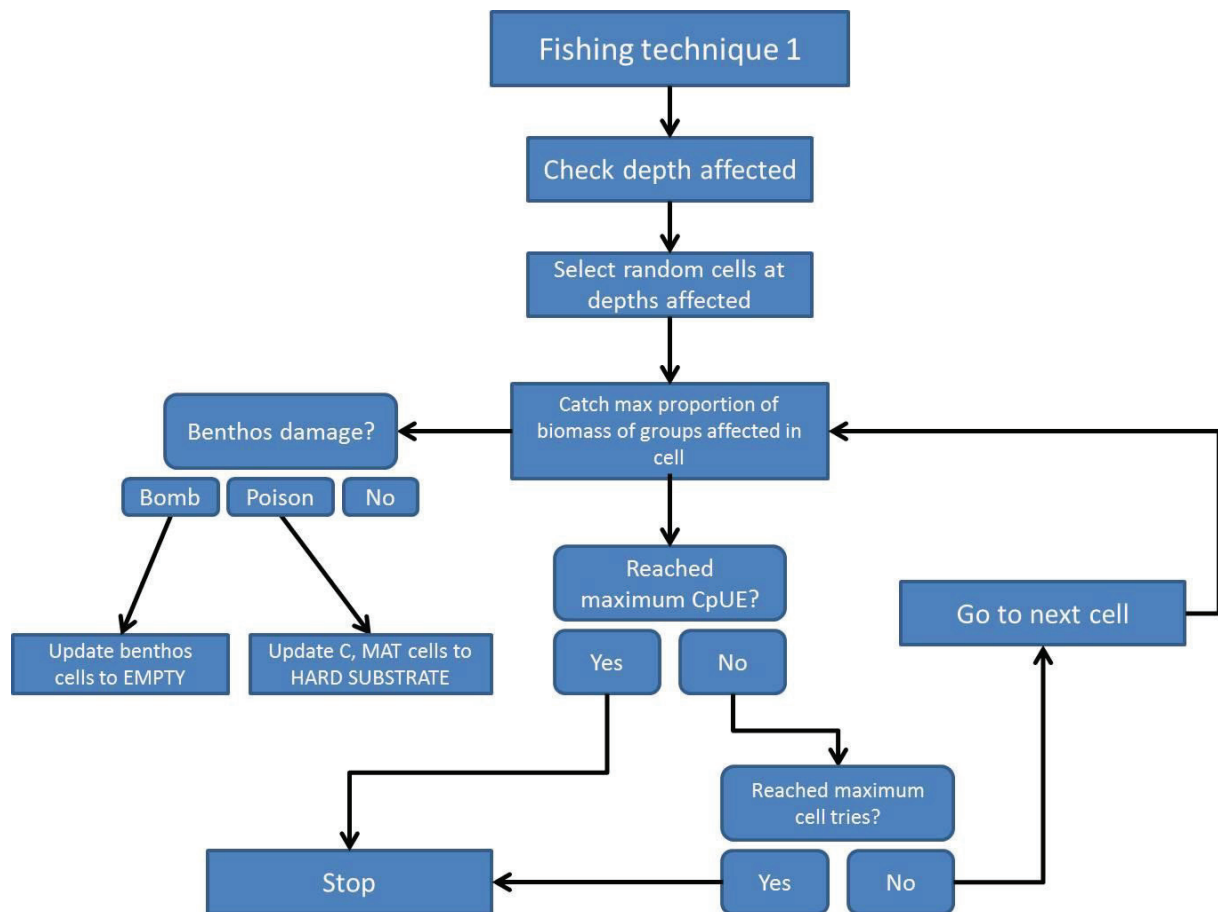


Figure 3. Overview of the fishing process.

6. Unit testing

Unit tests were performed to ensure the correct functioning of the program using the Junit framework (<http://junit.org/junit4/>). Table 3 displays a list of the implemented unit tests.

Table 3. List of unit tests performed on SEAMANCORE's program.

Test number	Tested process
1	Biomass threshold applicable to the fishery
2	Amount of biomass fished at each fishing ground
3	Limitation to a maximum catch amount
4	Calculation of external recruitment amount
5	Consideration of minimum prey biomass ratio for a default harvest function

6	Consideration of minimum prey biomass ratio for the HollingType 2 harvest function
7	Consideration of minimum prey biomass ratio for the OptimalForaging harvest function
8	Valid result from a default harvest function
9	Valid result from the HollingType 2 harvest function with one prey per predator
10	Valid result from the HollingType 2 harvest function with two preys per predator
11	Valid result from the OptimalForaging harvest function

7. Parameterization and sensitivity analyses

Whenever available, studies carried out in the Indo-Pacific were chosen to obtain the biological rates and other parameters; otherwise case studies from Australian reefs were used. The remaining parameters, notably the ones related to the feeding module, were fitted in order to represent the expected model behaviour through systematic iteration of uncertain parameter values and validation.

The hard coded parameters used for the benthos CA are detailed in Table 4. For coral growth rates, a weighted average was obtained based on Crabbe & Smith's (2002) study recording coral cover of branching and massive coral types in Wakatobi Marine National Park (South Sulawesi, Indonesia) at 5 m depth intervals. We chose the values corresponding to the site reported to be less affected by sedimentation to use as baseline. Based on those percentages, the skeletal linear extension rates of *Acropora* species and radial growth rates for non-branching coral species from Crabbe & Smith (2005) were averaged. We ensured that all the genres recorded by Best et al (1989) are represented by means of their growth rates. An exception is the genus *Fungia*, which we omitted because they do not create reef habitat and therefore their strategic function in the ecosystem is negligible for the purpose of this model. For each genus considered in the model, a weighted average of the growth rates was made for each depth and season. Season differentiation was deemed appropriate due to the significantly higher *Acropora*'s rates reported for the dry season in Crabbe & Smith's study (2005). The selected growth rates were the average for the reportedly mostly unimpacted site at Kaledupa. This gave: *Acropora* wet season= 142 mm/year; and *Acropora* dry season= 333 mm/year. Non-branching corals showed no significant differences in radial growth rates between seasons and their average growth rate was calculated from reported

values for *Porites lutea* (15 mm/year), *Montipora sp* (10 mm/year), and *Favia sp* (13 mm/year), resulting in an average growth rate of 13 mm/year. For simplicity's sake, and given that this model is largely based on theoretical assumptions, these growth rates were rounded up and standard deviations were not taken into consideration. The growth rates were converted in to cm/week, and this was then used as the benthos time steps needed to colonize a 10 cm patch; i.e. this is how long it takes for one HS cells to become a C cell if only one C cell is touching it. The time is divided among the number of coral cells surrounding a HS cell (i.e. the value used if there are two adjacent C cells is a half; a third if 3 adjacent C cells, etc.).

MAT growth rate was determined by directly averaging the growth rates used by Sandin & McNamara (2012) for their model (macroalgae growth rate= 0.5 m/year, turf growth rate= 1 m/year). For translating the values into the rules, the MAT growth rate (Table 4) was halved in the colonization rule in order to account for the environmental and biophysical surrounding factors not accounted for in the model rules. For coral colonization, the growth rate was divided by 1.5 (time multiplied by 1.5). This was found to produce more realistic benthic dynamics during calibration.

We could not find literature sources to estimate how many cells and how long it takes for the pre-colonization to happen, so *Pre-colonization* rule times were determined arbitrarily (50 days summed age of coral cells surrounding MAT, and 100 days summed age for MAT to turn a coral cells into HS). McCook et al. (2001) found limited evidence for algal overgrowth as the direct cause of coral mortality, and suggest that algal replacement may be confounded with algal competitive superiority. However, other studies found mechanisms by which algae can harm corals (Smith et al. 2006, Brooker et al. 2016), but there are confounding effects (Rasher & Hay 2014), and they do not apply in all cases as non-allelopathic algae occur more frequently next to corals (Bonaldo & Hay 2014). Thus the number of MAT cells required to "Pre-colonize" a coral cell as well as their summed age are higher than that of coral cells required to neutralize an algal cell.

Bleaching is the model's proxy for global ocean warming and has two effects: bleaching mortality and non-lethal bleaching, by which Coral cells turn into HS or their age is reset, respectively. The effect of bleaching decreases with increasing depth, and each bleaching episode affects a proportion of the coral cells based on well-documented bleaching episodes in Indonesia (Table 4). Destructive fishing was parameterized following reports from the Philippines (McManus et al. 1997) and Indonesia (Hlavacs, 2008). We considered the affected area for blast fishing to be an intermediate value between the worst and moderate effects, giving an area of 2 x 2 m, and for cyanide fishing an area of 1 x 1 m affected.

Table 4. Values and sources of the parameters utilised by the rules governing the benthos grid.

Parameter	Specification	Value	Units	Reference
Coral growth rate	0 – 5 m, wet season	60.73	mm year ⁻¹	Crabbe & Smith (2002) Crabbe & Smith (2005)
	0 – 5 m, dry season	131.4		
	5 – 10 m, wet season	40.09		
	5 – 10 m, dry season	80.2		
	10+ m, wet season	22.03		
	10+ m, dry season	35.4		
Algae growth rate (MAT average)		0.75	m year ⁻¹	Sandin & McNamara (2012)
Bleaching impact on coral cells	0 – 5 m, bleaching only	40	%	Sartin and Setiasih (2011)
	5 - 10 m, bleaching only	5		
	10 – 15 m, bleaching only	1		
	0 – 5 m, dead coral	47.5		
	5 – 10 m, dead coral	10		
	10 – 15 m, dead coral	0		
MAT density	Based on the average between maximum turf (160 g/m ²) and macroalgae (6230 g/m ²)	2000	g m ⁻²	Bonaldo & Bellwood (2011) Hoey & Bellwood (2011)
HS density		200	g m ⁻²	(fitted during model calibration)

Table 5 shows the benthos initial cover values chosen arbitrarily for all the analyses. Additionally, an aggregation level of 0.5 for coral cells was consistently used, while the other benthic groups had no aggregation. A *Connectivity* probability from neighbouring reefs of 0.01 was used as baseline.

Table 5. Benthos initial cover used throughout the baseline scenario and sensitivity analysis.

Depth	Empty	Coral	Hard Substrate	Macroalgae and Turf
1	0.15	0.3	0.35	0.2
2	0.13	0.3	0.42	0.15
3	0.08	0.35	0.39	0.18

Fish parameters were extracted from *fishbase.org* (Froese & Pauly 2016) or regional field studies whenever it was possible and averaged for the species encountered during a pilot field assessment during February 2013. Those were: for carnivores, *Anyperodon leucogrammicus*, *Aulostomus chinensis*, *Balistapus undulates*, *Cephalopholis argus*, *Cephalopholis boenak*, *Cephalopholis leopardus*, *Cephalopholis sexmaculata*, *Epinephelus fasciatus*, *Labracinus cyclophthalmus*, *Lutjanus carponotatus*, *Lutjanus decussatus*, *Plectropomus leopardus*, *Scolopsis bilineatus*, *Scolopsis monogramma*; for browsers and grazers, *Acanthurus leucocheilus*, *Acanthurus lineatus*, *Acanthurus nigrofuscus*, *Acanthurus pyroferus*, *Acanthurus thompsoni*, *Aluterus scriptus*, *Ctenochaetus binotatus*, *Ctenochaetus cyanocheilus*, *Ctenochaetus striatus*, *Siganus doliatus*, *Siganus canaliculatus*, *Siganus corallines*, *Siganus puellus*, *Siganus punctatus*, *Siganus vulpinus*, *Zebrasoma scopas*; and for scrapers, *Chlorurus bleekeri*, *Chlorurus microrhinos*, *Chlorurus sordidus*, *Scarus dimidiatus*, *Scarus flavipectoralis*, *Scarus niger*, *Scarus oviceps*, *Scarus frenatus*, *Scarus ghobban*, *Scarus globiceps*, *Scarus quoyi*, *Scarus scaber*.

For the parameters determining fish feeding behaviour, a dearth of quantitative studies in the coral reef literature (Stier and White, 2014), and no functional response studies produced for coral reef piscivorous fish (Harborne, 2012) made parameter estimation necessary. Death rate was calculated from the sum of the groups' average values for natural mortality and maintenance rates whenever available (Table 6). Maximum fish biomass was based on baseline and global values given by Sandin et al. (2008) and Edwards et al. (2014). While the maximum biomass is high in comparison with global averages, there have been very high reported densities of coral reef fish under favourable conditions such as settlement events

(Stier and White, 2014). We used the global average herbivorous fish biomass in unfished areas for the maximum biomass in the model reported by Edwards et al. (2014), grouping the browsers and grazers functional groups. Carnivore maximum biomass values were estimated under the premise that predatory fish can dominate accounting for up to 85 % of the total fish biomass in healthy coral reefs (Sandin et al. 2008).

Besides the sensitivity analyses reported in the manuscript, four different random seeds were tested showing no significant impact of stochastic effects. Environmental settings were changed from the baseline as follows: nutrient scenarios MEDIUM and HIGH; bleaching frequency every 1, 2, and 4 years; connectivity for coral and carnivores were modified $\pm 25\%$, and for browsers and grazers and scrapers the values of 250 and 500 g were tested (due to its value in the baseline being 0).

Table 6. Fish parameters used in the baseline scenario.

Parameter name	Units	Value
BG conversion factor C_{BG}	-	0.15
BG initial biomass	g m^{-2}	20
BG maximum biomass (K_{BG})	g m^{-2}	120
BG reproduction rate (ρ_{BG})	-	0.013
BG death rate (δ_{BG})	-	0.005
BG biomass threshold (Υ_{BG})	g m^{-2}	8
BG consumed biomass factor (θ_{BG})	-	0.1
BG permanence factor (ω_{BG})	-	0.3
BG external supply (λ_{BG})	g	0
S conversion factor C_S	-	0.18
S initial biomass	g m^{-2}	12
S maximum biomass (K_S)	g m^{-2}	100
S reproduction rate (ρ_S)	-	0.01
S death rate (δ_S)	-	0.005
S biomass threshold (Υ_S)	g m^{-2}	6

S consumed biomass factor (θ_s)	-	0.1
S permanence factor (ω_s)	-	0.3
S external supply (λ_s)	g	0
S attack rate (α_{HS})	-	0.0001
S handling time (τ_{HS})	s	10
C conversion factor C_C	-	0.10
C initial biomass	g m ⁻²	16
C maximum biomass (K_C)	g m ⁻²	600
C reproduction rate (ρ_C)	-	0.007
C death rate (δ_C)	-	0.0129
C biomass threshold (γ_C)	g m ⁻²	15
C consumed biomass factor (θ_C)	-	0.1
C permanence factor (ω_C)	-	0.1
C external supply (λ_C)	g	500
C prey 1 attack rate (α_{BG})	-	1
C prey 1 handling time (τ_{BG})	s	5
C prey 2 attack rate (α_S)	-	3
C prey 2 handling time (τ_S)	s	8
C prey minimum ratio (μ)	-	0.05

Appendix 2: Instructions manual

1. Downloading and launching SEAMANCORE

A zip version of the distribution file of SEAMANCORE will be made available upon publication which includes the java source code, a *resources* folder with sample greyscale depth maps, libraries required to run the model (*lib* folder), and a *parameters* folder with a sample *autoParams* file. An *autoParams* file is required to launch simulations on a server with different parameter combinations; the program runs simulations with all possible combinations of the parameters contained in the *autoParams* file.

The SEAMANCORE application is run directly on windows by clicking on the "run-with-gui.bat", or by running "run-with-gui" in a linux console, which opens the user interface.

2. Data requirements

The program requires four specific input data items to initialise the simulation: (a) a greyscale map representing the depth profile of the reef, (b) the initial percent cover of each benthos category at each depth, (c) the benthos aggregation levels (i.e. degree to which that habitat type is found in patches), and (d) the initial fish biomass for each group.

2.1. Depth map specifications

The program reads the colour number of the image and assigns a depth category to each pixel, which represents 1 m². Table 1 shows the range of colour equivalence for each depth, which go from black (shallower) to white (deeper). The map size should be divisible by 20 for the program to recognise it. If this condition is not met, the program will cut the extra pixels on the right side and bottom edge of the picture.

Table 1. Depth categories explanation and greyscale numbers assigned by the model.

Category	Real depth (m)	Colour number range
1	0 – 5	0 - 41 (black)
2	5 – 10	42 - 84
3	10 – 15	85 - 127
4	15 – 20	128 - 170
5	20 – 30	171 - 213
6	30 – 40	214 - 255 (white)

2.2. Benthos cover data

Benthos cover data can be collected with the usual monitoring methods - such as Line Point Intercept (LPI), benthic photographs and analysis with specialized software (e.g. CPCE (Kohler & Gill 2006)), etc. The benthic substrate should be classified in its entirety into the four benthic categories, i.e. Coral (including hard coral), Macroalgae and Turf, Hard Substrate (including shortly grazed algae, crustose coralline algae, dead coral, and rocky bottom), and Empty space (including sand, anthropogenic waste such as plastics and coral rubble). Other benthic organisms such as invertebrates are best classified as hard substrate, keeping in mind the assumption being made when assessing the results.

2.3. Fish biomass data

The model requires one value of fish biomass for each functional group in grams per square meter. This biomass value is assigned to each cell at the start so that all cells have the same biomass at time step 0. It is recommended to assume the first year (365 time steps) is a burn in period and so not to include this period in any consideration of results; in some instances it may be necessary to extend this burn in period to the point when the model achieves cyclical or steady dynamics. Since the model does not represent all coral reef fish functional groups, the user must choose the species included in the biomass estimation by means of their diets. A good source of diet information is Fishbase (Froese & Pauly 2016).

3. Menus

This section describes in detail how to use the menus in SEAMANCORE's user interface, including the meaning and units (when applicable) of the parameters. The user interface has a *Standard* and an *Advanced* mode depending on the number of parameters visible to the user. We will walk you through each mode's menus, talk about the visual output and finally display the common options at the task bar and other analytical tools. We recommend consulting the sensitivity analyses results in section 4 of the manuscript to inform the user's choice of parameter values.

3.1. Standard mode

The default GUI is in *Standard* mode, which features only parameters for specifying the initial conditions and environmental setup, excluding ecological parameters and biological rates used in the model's equations. Instead those parameters have their values taken from the baseline parameterization (detailed in *Appendix 1*, section 6).

Environment menu

This menu contains the environment and benthos settings.

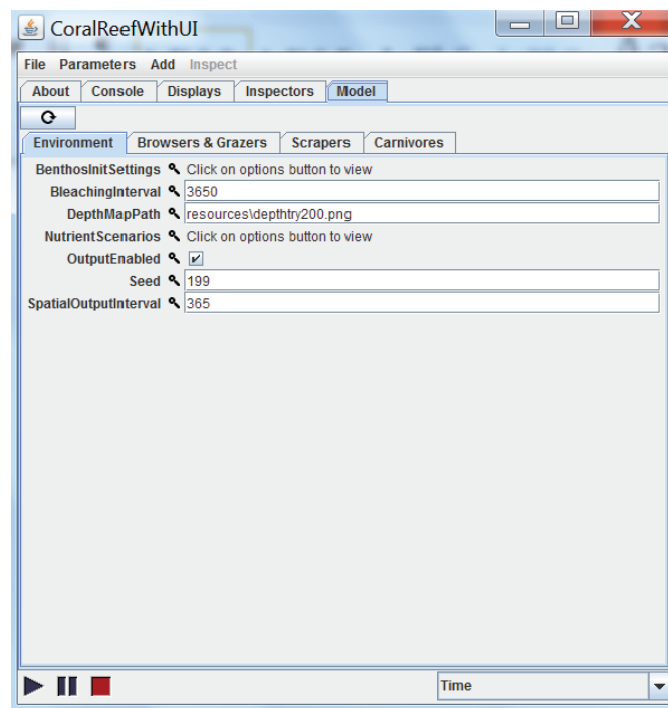


Figure 1. SEAMANCORE *Standard* environment menu.

Benthos initial settings: to specify the initial conditions of benthos cover and aggregation level, go to the first item on the menu and click *view* (figure 2). It will open the menu in figure 2, where the user can select the benthos cover and aggregation ratios at each depth category.

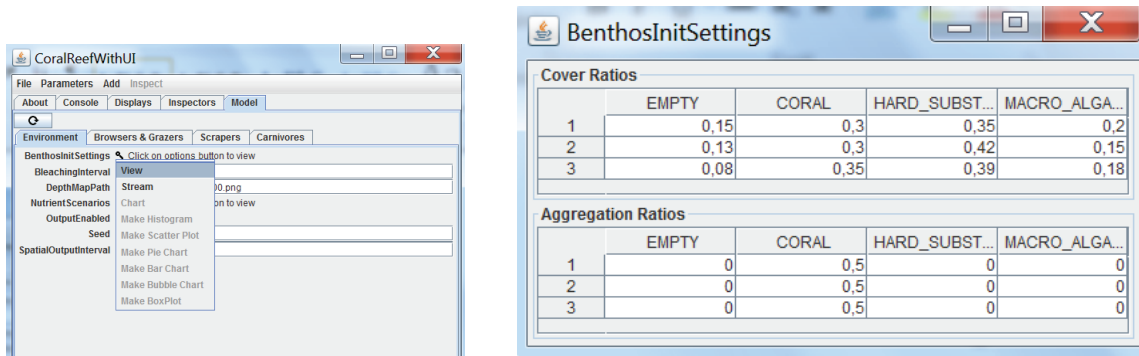


Figure 2. Transition to BenthosInitSettings menu, with the changeable benthos cover for each depth and the aggregation ratios for each depth.

Bleaching interval (β): the second item on the menu refers to the frequency at which bleaching episodes take place in the simulation. It is given in days, e.g. a yearly bleaching episode would be entered as 365. In the example of figure 1, bleaching occurs every ten years.

Depth map path: the third item requires the specific path for the depth map to be used in the simulation. We recommend placing your depth map in the 'resources' folder within the model's main directory **coralReef**.

Nutrient scenarios: *viewing* the fourth item of the menu opens another menu with two options (figure 3): SelectedScenarioLevel opens a drop down menu with the available scenarios, and NutrientScenarioDefinitions can be opened for each scenario to allow for the scenario's parameters to be changed. Those parameters refer to the summed age variable in the benthos rules as explained in *Appendix 1*, section 2.1.

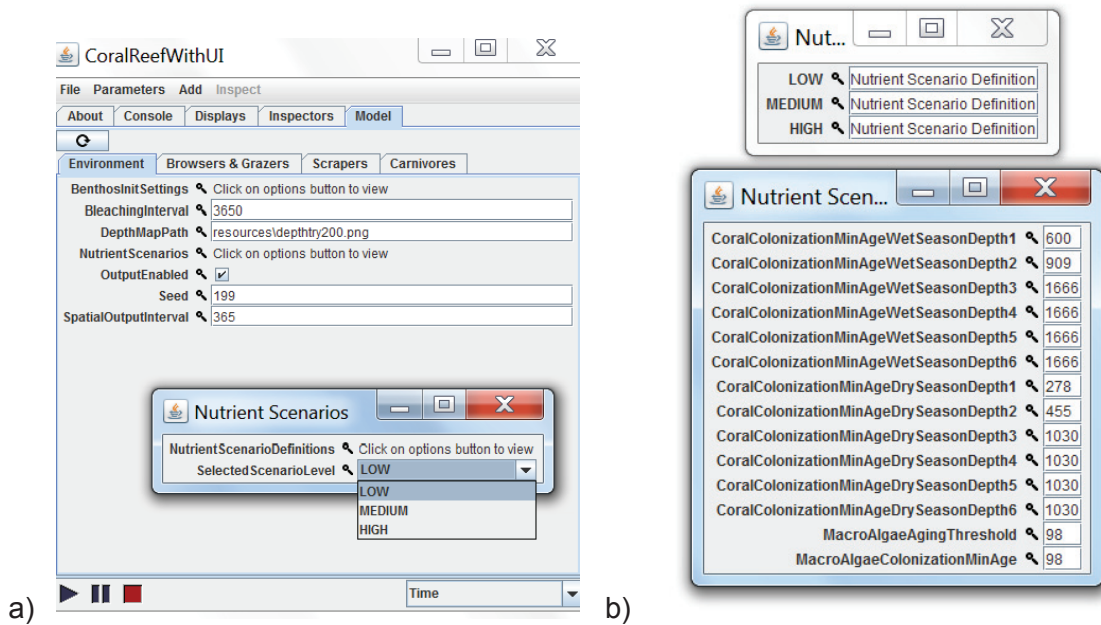


Figure 3. (a) Nutrient scenarios menu with the scenario level selection drop down menu, and (b) Nutrient scenario definitions with changing parameters for the relevant benthos rules.

OutputEnabled: this is a Boolean option which prints out the output as csv files when it is selected. If the option is unselected, it runs the simulations in the user interface without producing the output files. This may be convenient for exploratory runs intended to test different parameters or for just display purposes.

Seed: this is the random seed. When changed, model output could change as a result of using a different seed for the random processes. However, sensitivity analyses showed no remarkable variation caused by different seeds (see *Manuscript*).

SpatialOutputInterval: this item refers to the number of time steps between spatial output printings. Output is explained in detail in section 4.4.

Fish menus

The fish menus in Standard mode only contain the parameter for initial biomass (figure 4), which needs to be given in g m^{-2} .

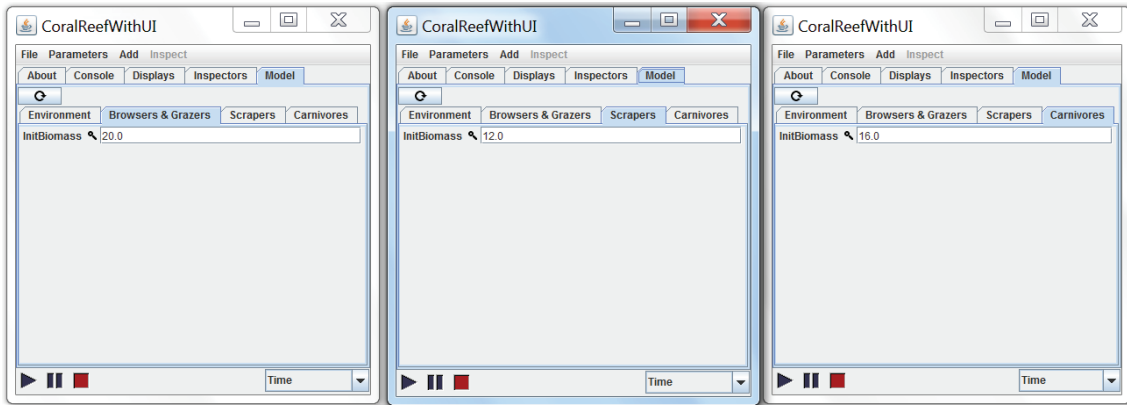


Figure 4. Fish menus in *Standard* mode.

3.2. Advanced mode

The Advanced mode features the same parameters as the Standard, plus additional ones that are detailed below.

Environment menu

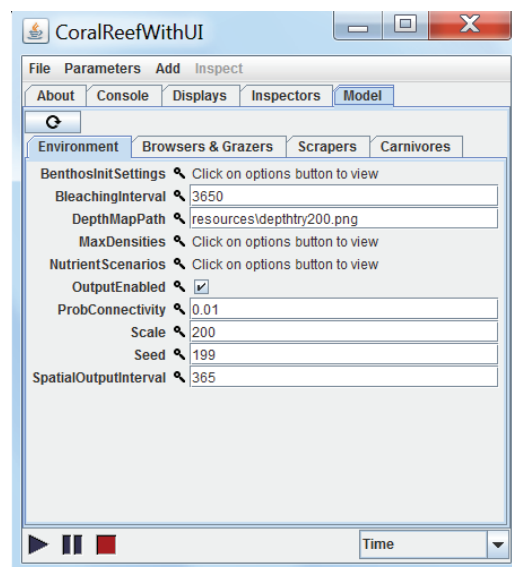


Figure 5. SEAMANCORE *Advanced* environment menu.

MaxDensities (K_i): this item opens a menu where the user can specify the maximum biomass for each functional group in $g\ m^{-2}$. For fish, the maximum biomass is the carrying capacity of each fish cell; for hard substrate and MAT benthos cells it is the effective value of a benthos cell, used by the model as the biomass that a fish eats if feeding on a benthos cell.

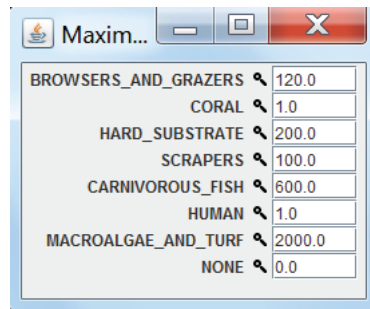


Figure 6. Maximum densities menu.

ProbConnectivity: this item requires an input between 0 and 1, and states the probability of connectivity in terms of coral larval supply.

Fish menus

The fish menus do not have inside menus, but present a list of cells where the parameters can be changed by typing the desired values. Besides initial biomass, they list all the parameters that may be modified for each fish group.

Browsers and grazers

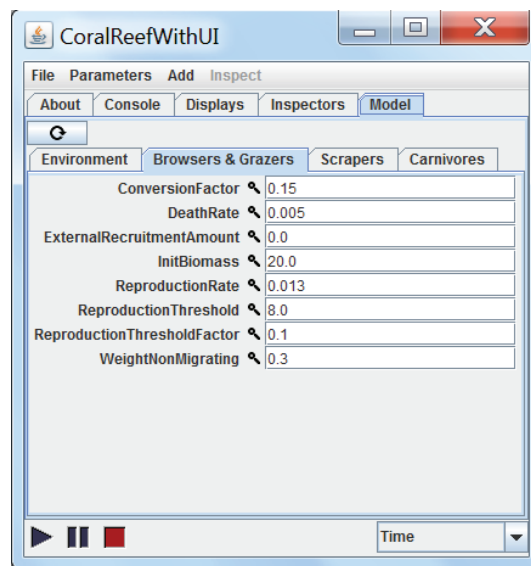


Figure 7. Browsers and grazers advanced menu.

Conversion factor (C_i): this item is the proportion of biomass consumed that is added to the current biomass (aka feeding efficiency). It requires a value between 0 and 1.

Death rate (δ_i): it is the group's average death rate, which decreases fish biomass linearly. It should include the background natural mortality plus a maintenance rate. It also requires a value between 0 and 1.

ExternalRecruitmentAmount (P_{ext_i}): it is a net biomass value added to the current biomass representing larval supply from neighbouring reefs. The net amount is divided amongst all grid cells and multiplied by the coral cover ratio, with the resulting amount being added to the current biomass.

ReproductionRate (ρ_i): is the group's average reproduction rate used in the internal recruitment calculation (see *Manuscript*).

ReproductionThreshold (v_i): it is the minimum biomass necessary for internal recruitment to take place, and is assessed individually for each cell. It is given in grams per square meter.

ReproductionThresholdFactor (θ_i): this is the minimum biomass that has to be consumed in order for recruitment to take place. It is given as a factor between 0 and 1 of the prey maximum biomass.

WeightNonMigrating (ω_i): this is the permanence factor, or the proportion of biomass which stays in the same cell. It requires a value between 0 and 1.

Scrapers

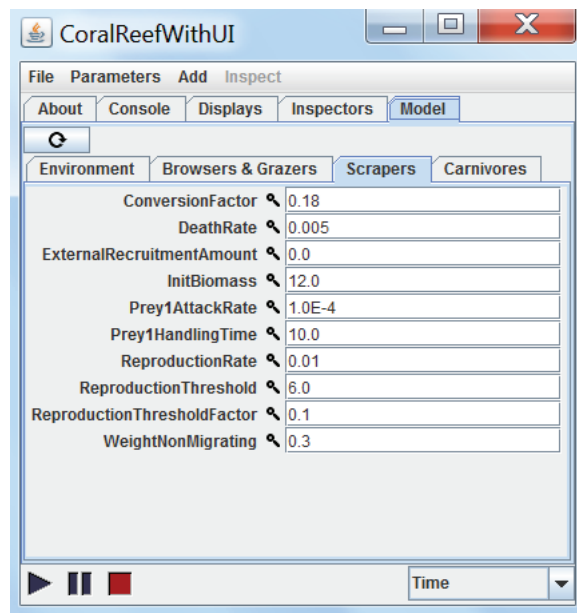


Figure 8. Scrapers advanced menu.

Prey1AttackRate (α_{HS}): it is the attack rate at hard substrate from scrapers used in the Holling type II equation (see *Manuscript*).

Prey1HandlingTime (τ_{HS}): it is the handling time at hard substrate from scrapers used in the Holling type II equation (see *Manuscript*).

Carnivores

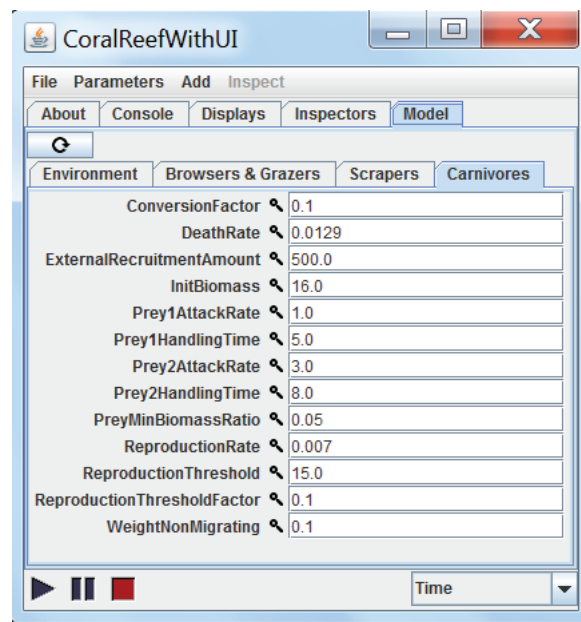


Figure 9. Carnivores advanced menu.

Prey1AttackRate (α_{BG}): it is the attack rate on browsers and grazers from carnivores used in the carnivores feeding equation (see *Manuscript*).

Prey2AttackRate (α_S): it is the attack rate on scrapers from carnivores used in the carnivores feeding equation.

Prey1HandlingTime (τ_{BG}): it is the handling time for carnivores feeding on browsers and grazers used in the carnivores feeding equation (see *Manuscript*).

Prey1HandlingTime (τ_S): it is the handling time for carnivores feeding on scrapers used in the carnivores feeding equation.

PreyMinBiomassRatio (μ): this is the minimum ratio of prey that carnivores are able to feed on. If the prey is below that ratio, we assume they are not accessible to the predator due to hiding, etc. The minimum biomass ratio is the same for both preys.

4. Common options and analytics

4.1. Parameters

The default Parameters mode is the *Standard* mode, but this can be easily modified by changing the mode to *Advanced* in the parameters menu (top bar, figure 10).

The user can change the parameters and save them as a new parameterization setup by going in the top menu: parameters --> save (figure 10). If you save them within the main **coralReef** folder as "params.xml", the program will load the parameterization in the file.

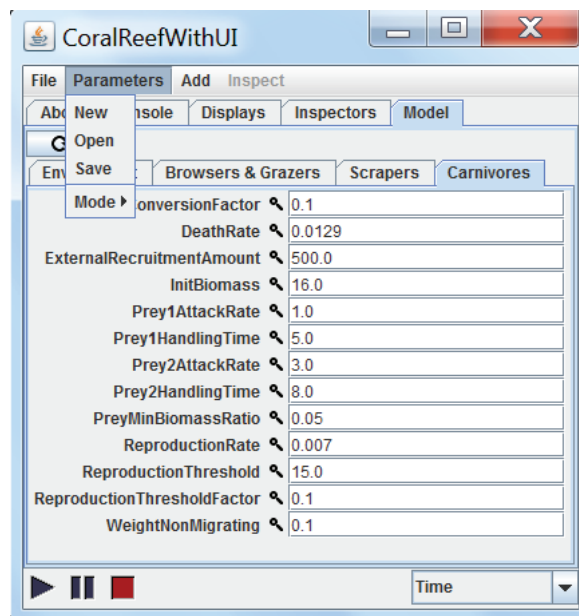


Figure 10. Display of the *Parameters* menu at the common top bar.

4.2. Fishery

To add a fishery influence, go to Add --> fishing technique and then specify the fishing gear characteristics. You can add as many fishing techniques as you like. However, caution is recommended with regard to fishing intensity in relation to map size, as small areas are easily overfished. The fishing parameters are detailed below.

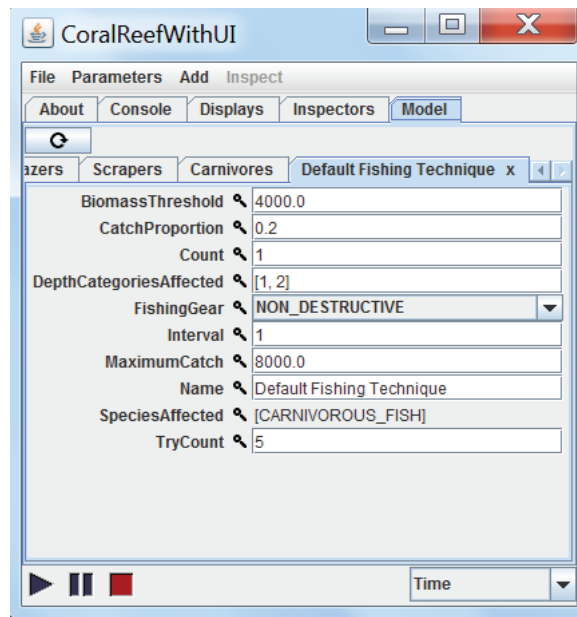


Figure 11. Display of the *Fishing Technique* menu. The user can add as many fishing techniques as they wish to simulate.

BiomassThreshold: it is the minimum fishable biomass in grams per fish cell. If the current cell biomass is less than this value, there is no catch.

CatchProportion: catchable proportion of the fish biomass per time step per cell. It requires a value between 0 and 1.

Count: it is the number of fishing units (fleet), which act independently but according to the fishing technique parameters.

DepthCategoriesAffected: depth categories subject to fishing by the fishing technique. A menu with the current depth categories is provided where the user can select the desired depths by ticking the boxes.

FishingGear: it is the type of fishing gear, which can be one of three: non-destructive, cyanide, bomb fishing (figure 12). The FishingGear parameter dictates the kind of damage done to the reef habitat: non-destructive fishing does not affect the benthos grid; bomb fishing affects the benthos by turning a randomly selected 4 m² area of benthos into Empty; and cyanide fishing turns an area of 1 m² randomly selected Coral and MAT cells into HS.

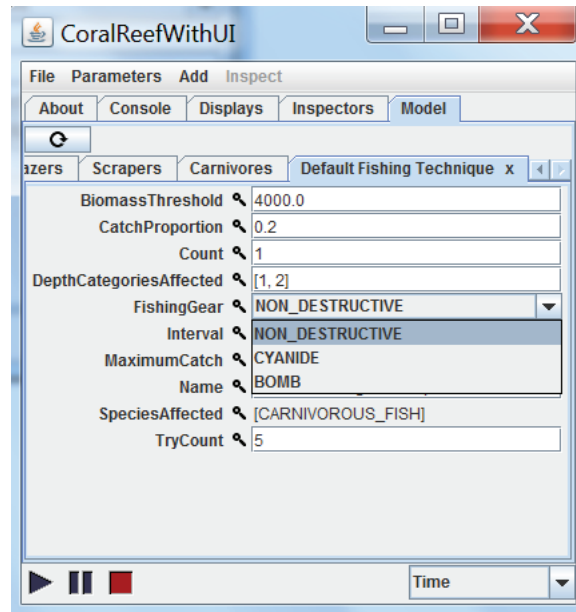


Figure 12. *Fishing Technique* menu with the dropdown choice for the fishing gear type.

Interval: this item refers to the frequency at which the fishing technique is carried out (i.e. time allocation), e.g. if the interval is 1, fishing takes place every day; if the value is 7, it takes place once a week, and so on.

MaximumCatch: maximum catch per unit of effort (in $\text{g unit}^{-1} \text{day}^{-1}$)

Name: giving a name to each fishing technique is optional but recommended when there is more than one, as the name will be printed in output files.

SpeciesAffected: target fish groups susceptible to fishing mortality by the fishing technique. Figure 13 shows the display of the SpeciesAffected menu, which can include all or none of the species (for instance if one wants to simulate damage to benthos from anchor dragging, or even COTs, it is possible to represent this by “fishing” simply setting the parameters appropriately).

TryCount: maximum number of cells a fishing unit can visit per time step

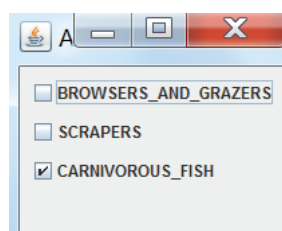


Figure 13. Selection menu for the SpeciesAffected parameter.

4.3. Inspectors

Opening the CoralReefwithUI display in the "Display" menu allows seeing the spatial simulation map in real time. Double clicking in the center of any fish cell (inside the circles representing the fish) will open the inspectors menu detailing the biomass gained or lost by each process within the chosen cell.

4.4. Output

The program can be set to print out the output by enabling the option on the *Environment* menu. This will print the output in several files in a "coralreef_output_gui" folder within the **coralReef** folder. These files report for every time step and contain: (a) benthic cover by group, (b) benthic cover by depth and group, (c) fish biomass by group, (d) fish biomass by depth and group, (e) fishing yield (if applicable) by depth and fishing technique. A spatial output can be printed at the interval specified in the *Environment* menu.

Chapter 2

The role of patron-client relations on the fishing behaviour of artisanal fishermen in the Spermonde Archipelago (Indonesia)

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Young fishermen from Badi, February 2013.

Abstract

Patron-client systems are ubiquitous in small-scale fisheries and are thought to have an important role on the way marine resources are exploited. With the aim of identifying key differences between fishermen with a patron and independent fishermen, questionnaires were used to obtain individual socio-demographic characteristics and perceptions of fishing behaviour of fishermen in Spermonde (Indonesia). Catch assessments of landings were carried out and differences between dependent and independent fishermen evaluated. Fishermen with patrons had more valuable catch with a higher portion of live fish while independent fishermen were more engaged in subsistence fishing. Fishermen with patrons had higher turnovers than independent fishermen, but this result was contested after accounting for additional costs resulting from their indebtedness. Comparison between perceived and empirically measured data showed that fishermen with patrons underestimated their expected daily catch. The results suggest that belonging to the patron-client system affects fishing behaviour by making fishermen use less diversified gears and increase their focus on commercial fishing. The consequence of this is an apparent reduced amount of seafood provision for the household and possibly greater ecological impact due to the use of cyanide, a destructive fishing method. While the patron-client system has gained attention as a potential institution to promote sustainable exploitation practices, the data analysed here suggest that the patron-client relationship indirectly causes a worse environmental impact by encouraging higher exploitation rates. The implications are that bringing the patron-client system on board sustainable fishing policies may require context-dependent considerations of cultural obstacles and social complexities.

Keywords: reef fisheries, socio-ecological systems, patron-client, marine resources, Indonesia

1. INTRODUCTION

Wild catch fisheries are the most important sector contributing to food security and nutrition for seafood-dependent countries (Hall et al. 2013). Indonesia has the second largest marine capture fishery in the world with more than 8 million people depending on marine-based economic activities (Harvey 2007). While Indonesia hosts more than 2.7 million fishers and produces 7 million tons of fish and seafood (FAO 2014), its fish stocks are overexploited (UNEP 2013). Overexploitation is the leading cause of extinction of marine species, followed by habitat loss (Dulvy et al. 2003). Even “low pressure” artisanal fishing methods have been shown to modify the trophic structure of coral reef ecosystems through cascading effects as a result of sequential depletion of keystone species (Bellwood et al. 2004, Berkes et al. 2006, Campbell & Pardele 2006, Dulvy et al. 2004, McClanahan & Mangi 2004). Challenges posed by enforcing fishing regulatory laws in such a widespread and decentralized archipelago and the fragmented nature of authority in Indonesia have facilitated the rise of illegal fishing (Dee et al. 2014, Heazle & Butcher 2007, Schwerdtner Máñez & Ferse 2010). Instead, local actors, especially the patron-client system, play a large role in structuring fishery dynamics and the flows of marine products through the reef fish food trade (Bailey et al. 2016). Small scale, reef-based fisheries contribute to most of the total catch in Indonesia, and make it one of the top exporters of coral reef wildlife (Dee et al. 2014). However, cumulative impacts such as overexploitation, pollution and structural damage mean that only 6% of coral reefs in Indonesia are considered to be in good condition (Harvey 2007). Depleted fishery resources and the high dependence on goods and services provided by coral reefs (Burke et al. 2011, Moberg & Folke 1999) lead to risks for the sustainability of the reef fishery, the livelihoods of coastal communities and the conservation of the remarkable marine biodiversity of the region. Understanding the complex drivers of fishery dynamics and targeting its central actors is essential to develop effective management initiatives aiming at an all-round sustainability of marine resources.

In Spermonde, the local fishery is temporally and spatially diverse employing a wide array of fishing methods and target species across its islands (Ferse et al. 2014). The fishery is partly organised by patron-client relationships, where patrons provide the link between artisanal fishers (clients) and national and international buyers. Patron-client systems are widespread throughout tropical small scale fisheries in India (Johnson 2010), Southeast Asia (Ruddle 2011), East Africa (Crona et al. 2010, Ferrol-Schulte et al. 2014), Mexico (Basurto et al. 2013) or Brazil (Seixas 2006, Weber et al. 2012). They are informal credit systems that bond powerful individuals with numerous subordinates in a reciprocal agreement; in exchange for favours ranging from loans to protection, patrons receive labour and other benefits such as

political support (Johnson 2010). Fisheries patronage has detractors and defenders. While some studies point out patrons' instrumental instigation of destructive fishing (Lowe 2002; Nurdin & Grydehoj 2014) and the asymmetric relation that potentially traps fishermen in a perpetual debt situation (summary in Idrus 2009, Adhuri et al. 2016), others regard the arrangement as a pseudo social security system which provides fishermen and their families with readily available resources to cope with, for instance, bad fishing seasons (Johnson 2010, Ferse et al. 2012). The relational ties between patrons and clients are not only economic but also family and neighbourhood-based, and they reinforce each other generating a feeling of "moral duty" from fishermen to their patrons (Adhuri et al. 2016).

In the Spermonde fishery, networks established between fishermen and patrons are flexible and diverse, and their structure varies according to the logistics of the fishing activity. For instance, in purse-seiners there are various levels of patronage, starting with one patron on board (the captain), a second patron staying on the island (the boat owner), and finally a patron in the city (the fish exporter). This is not a rule, as the boat owner can be the captain, and more middlemen can act as patrons in the city or in other cities in large networks (Deswandi 2012). This paper focuses on the relationship between fishermen and their direct patrons, the fish collectors on the island. In our case study, some fishermen have patrons while others are independent. Fishermen with a patron – also referred to as dependent (Figure 1) - are those indebted to a seafood collector or patron on the island (referred to as patrons hereafter), with the relationship typically starting with a loan for the fisherman to purchase a boat. The fisherman agrees to sell his fish exclusively to this collector (Radjawali 2011), who becomes his patron. On days when the catch is large enough, part of the income is used to pay off part of the debt (Figure 1). When the outstanding amount is paid in full the fisherman becomes independent, although this is not common because the debt relationship produces certainty for both fishermen and patrons (Adhuri et al. 2016). Not all independent fishermen were once dependent as some are able to enter the fishery using their own savings or borrowing from relatives. Independent fishermen do not have long-term debts and can sell their fish to a collector of their choosing. Fish collectors sell the products in the city to their own patrons (also called *Punggawa*) to whom they often owe money (Navarrete Forero 2015). The patrons in the city have no direct relation to the fishermen and this study did not cover their activities.

The fishery in Spermonde is mainly artisanal and has become more export-oriented following a "fashion-driven" preference for specific marine species (Schwerdtner Mnez & Ferse 2010). Destructive fisheries and overfishing have been fuelled by increasing export market demand, passed down to the fishermen by middlemen and patrons. Fish are taken from the islands to Makassar and from there exported to Malaysia, Singapore, Taiwan, and Hong

Kong (Sustainable Fisheries Partnership 2014). Patrons respond to market fluctuations by providing their clients with the necessary equipment for fishing and by buying the most marketable species from the fishermen, or alternatively, the species in which they specialize (Chozin et al. 2008, Ferse et al. 2014, Nurdin & Grydehoj 2014). In the latter case, fishermen working for a patron are expected to specialize in catching the fish that the patron specialises in selling (Adhuri et al. 2016). The heterogeneous distribution of patrons across the archipelago produces a diversification of the target species amongst the islands (Ferse et al. 2014) with potentially different local ecological impacts. For instance, the island of Barang Lompo is famous for its sea cucumber or *trepang* fishery (Schwerdtner Máñez & Ferse 2010) while fishermen on the islands of our study focus on groupers and the seasonal octopus fishery. Not only do patrons influence the fish species caught and sold but they also determine fishing techniques. Destructive fishing practices are widespread in Spermonde. For instance, Nurdin and Grydehoj (2014) report that 65% of the fishermen on the island of Karanrang use destructive fishing tactics - bombs and poison- on coral reefs. They also found evidence that the patrons were involved in distributing the illegal materials needed for these activities amongst their client fishermen.

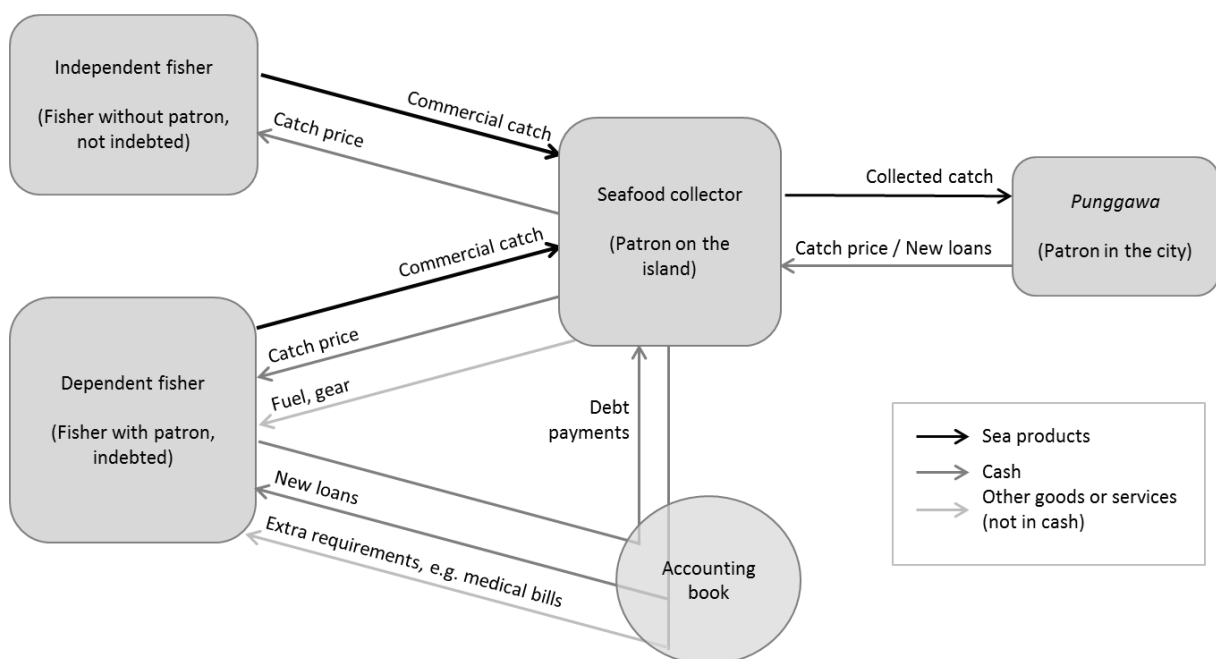


Figure 1. Diagram of the cash and good flows between actors of the Spermonde reef fishery value chain: the two groups of fishermen, the seafood collectors and the patrons in the city.

In sum, informal patron-client relationships have been referred to as a *de facto* governance system in Spermonde and recognised as an important driver of fishery dynamics (Deswandi 2012, Ferse et al. 2012, Ferse et al. 2014, Nurdin and Grydehoj 2014). But despite their potentially notable role in ecological sustainability and fisher wellbeing, the impact of patron-client relations on resource exploitation has been given limited attention in the fisheries literature (Johnson 2010), particularly in Indonesia. This paper aims at identifying key differences between fishermen with a patron and independent fishermen focusing on three questions:

- (1) Which socio-demographic individual variables (e.g. level of education, age, experience, number of people in the household) influence the likelihood of engaging in patronage?
- (2) How do dependent and independent fishermen differ in their fishing behaviour in terms of target species, time allocation and catch composition?
- (3) Is the patron-client system economically beneficial to fishermen?

First, the fact that some fishermen engage in patronage and other remain independent suggests that certain socioeconomic characteristics could make fishermen prone to get a first loan from a patron. As this may be the only way for some fishermen to enter the fishery, it was hypothesised that dependent fishermen would have more economic needs than independent ones, e.g. be younger and more inexperienced, or have larger households. This kind of information can be used for implementing policies aimed at increasing fishers' return from their fishing activity, reduce poverty and limit overfishing. Second, differences in fishing behaviour and catch composition were expected as dependent fishermen strive to fulfil their obligations to their patrons. Such differences provide insights into the indirect ecological impact of the patron-client system. Fishermen were interviewed to obtain socio-demographic data, economic information and perceptions of fishing behaviour variables using structured questionnaires. Empirical data on the catch and characteristics of individual fishing trips were collected. Finally, the actual revenue from the daily fishing trips was calculated and compared to the reported data in terms of daily catches and income to test the level of consistency between perceptions and empirical data.

2. METHODS

2.1. Study site

The Spermonde archipelago is located off the coast of South West Sulawesi, Indonesia (Figure 2). It comprises up to 150 coral cays and reef islands (of which 54 are inhabited) with submerged reefs on a shallow limestone shelf which extends about 60km offshore (Yusuf & Jompa 2012). There are two distinct seasons; the north-western monsoon or wet season with plentiful rainfall and storms typically from December to March, and the south-eastern monsoon or dry season from June to September. As a result of this monsoonal weather, South Sulawesi is the region with the highest precipitation seasonality in Southeast Asia (Moore 1995). Makassar (1.4 million inhabitants) is the main city of the South Sulawesi province and acts as one of the main commodity exporting hubs of Indonesia.

Spermonde supports a multi-species, multi-gear coral reef fishery which is exposed to a cross-shelf gradient of biophysical conditions and anthropogenic impacts. Fishing is the main source of livelihood, with over 70% of the men self-reporting as fishermen, and most households depend directly on selling their catch for income with little or no alternative livelihood options (Deswandi 2012, Ferse et al. 2014). The supply chain has two main endpoints in Spermonde's reef fishery; fishermen sell their catch to fish collectors (their patrons) usually working for one of the various *punggawas* operating in the region and the seafood is then taken to Makassar where it is either sold to international traders for exporting, or sold in the main fish market (Deswandi 2012). A recent survey on several Spermonde islands reflected that overall about half of the fishermen are independent and the other half work within a patron-client arrangement (Ferrol-Schulte *unpublished data*). However, in the same study virtually all the fishermen interviewed on Barrang Caddi worked for a patron (97%, N=29) while on Laia island they were mostly independent (90%, N=29), showing that the proportion is highly variable at the local level.

2.2. Data collection

Interviews were undertaken on the islands of Kodingareng Lompo (population: 4463, *pers comm* office of Kodingareng Lompo's community leader) and Badi (1944 inhabitants, *pers comm* office of Badi's community leader), and assessments of landings took place only on Badi. The islands are located approximately at 16 and 22 km from Makassar, respectively. The study was restricted to fishermen using small fibreglass boats (*lepa lepa*) with a small power engine and a stabilizing sidebar, called *Kapal katinting*. This boat type was chosen as

the sampling unit for three reasons: first, it is used to target coral reef species; second, it was the most common boat type (>30 units in both study sites); and third, the catch is landed on the island and could be recorded with precision (unlike other boat types which might sell it at sea or take it directly to Makassar [Deswandi 2012]). These boats usually carry one fisherman, going on daily fishing trips, and are combined with several types of hook-and-line gears, which make up 59% of the total fishing effort in the Spermonde reef fishery (Pet-Soede et al. 2001b). At all phases of the data collection, fishermen were asked to define their status as independent or indebted to a patron.

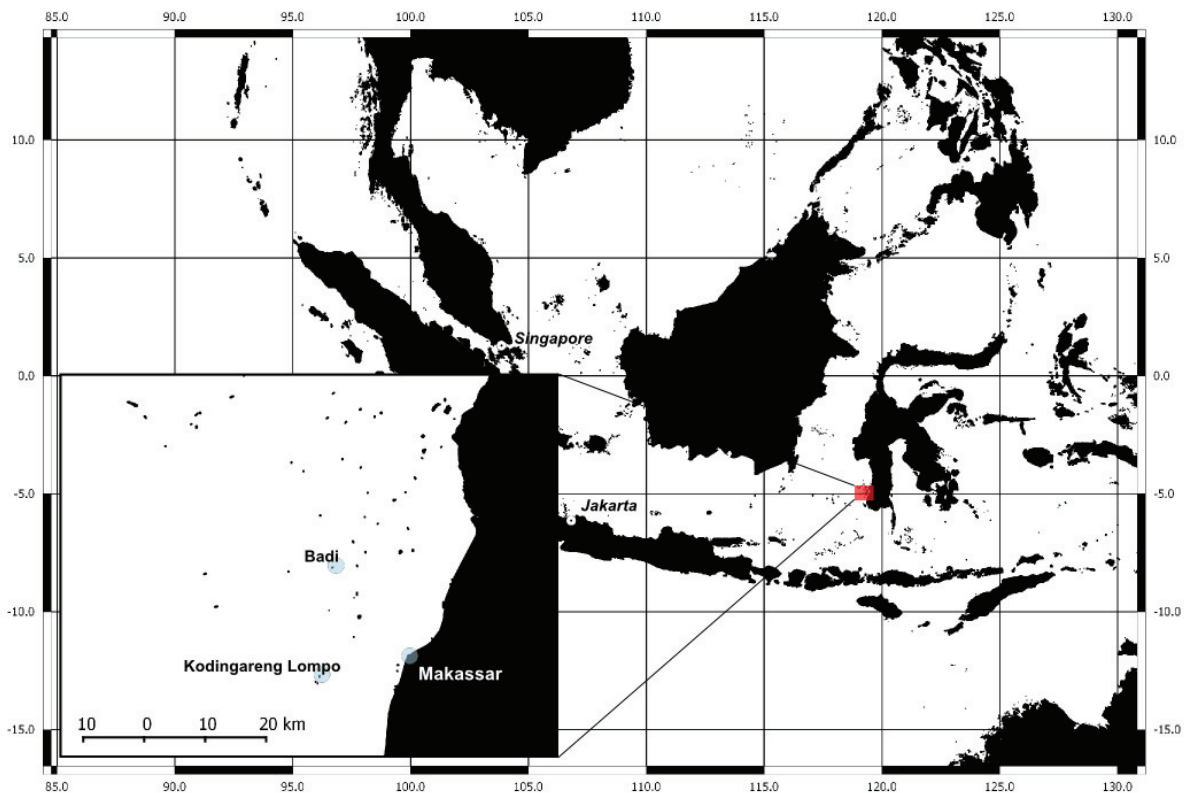


Figure 2. Regional map of Indonesia indicating the location of the Spermonde archipelago, the city of Makassar and the study sites, the islands of Badi and Kodingareng Lompo.

2.2.1. Surveys

A total of 63 households were interviewed by trained Indonesian assistants from the Hasanuddin University of Makassar, unrelated to the fishing industry, on the islands of Badi (N=33) and Kodingareng Lompo (N=30) between November 2014 and March 2015. Respondents were selected via random sampling of the fishermen list provided by the village representatives of the citizens' associations and interviewed based on availability and

willingness to participate in the study. Prior to each interview, they were briefed on the study purpose and the statement of Prior Informed Consent emphasizing their anonymity and voluntary participation. The structured interviews consisted of a series of questions designed to characterize fishermen's sociodemographic situation, livelihoods and income, the gear they used and target species, perceptions regarding their daily catch and propensity to fish in bad weather. Bad weather propensity was estimated with a score ranging from 0 – 4, with 0 reflecting the avoidance of fishing in any bad weather condition, and 4 indicating that they went out fishing in all bad weather scenarios: heavy rain, strong winds, storm, big waves.

Additionally, fishermen were asked to report the market prices for the commonly targeted species at the time of the study. Some prices undergo seasonal fluctuations; for instance, during the sampling period the main target species, coral trout or *Sunu (Plectropomus leopardus)*, experienced a two-fold gradual increase in price peaking in February for the Chinese New Year celebrations.

In addition, key informants - fish collectors and voluntary fishermen selected by snowball sampling- were interviewed about the functioning of the patron-client system and the steps and actors involved in the seafood supply chain in Spermonde.

2.2.2. Assessment of fishing trips

For a total of 180 fishing trips made by 63 fishermen, a catch sampling survey was applied to establish fished biomass directly after landing in the afternoon. The objective of this assessment was to measure selected fishing behaviour variables in dependent and independent fishermen. A minimum of one and a maximum of 8 daytrip's catch per fishermen were recorded. During the catch sampling survey, fishermen were asked details about their trip, e.g. duration, fishing gear, number of fishing grounds, weather conditions, whether they were satisfied with the catch. The catch was identified to species level using Allen's (2009) field guide for fishes and expert consultation for invertebrates. The number of individuals per species, weight in kg per species, mortality status of the fished item (dead or alive) and whether these items were sold or kept for local consumption were recorded. Weighing was done at the collector's place for the commercial part of the catch and directly at the landing site for the non-commercial items. In cases where it was not possible to assess the catch due to time limitations of the fishermen, data was collected by interviewing them in the evening.

The catch sampling surveys were all completed on Badi and linked to questionnaire data from the same fisherman when possible. If the fishermen had not participated in the

questionnaire, basic census information (i.e. age, education level, people in household, whether they owned the boat and whether they had a patron) was recorded while measuring the catch.

2.3. Data analysis.

2.3.1. Prices

An average of the current price of each commercial seafood item was obtained from the fishermen who targeted the particular species. The mean of the reported prices was derived for each species and standardized per kg or per fish depending on the unit of purchase used by fish collectors. Whenever a price for a species was not available, the price of the taxonomically closest species was used as assigned by the fishermen. All prices were reported in Indonesian rupiah and the amounts resulting from the calculations were transformed to US dollars.

2.3.2. Fishermen revealed income

The total turnover (amount of money fishermen obtained for the catch sold) for each fishing trip was calculated as the sum of the sold catch of each species multiplied by the reported prices. The revealed weekly income was estimated by multiplying individual fishermen's mean turnover per trip by the fishermen's reported number of fishing trips (day trips) during the wet season, which was then compared to the weekly income the fishermen stated in the interviews.

2.3.3. Statistical tests

All the statistical tests were aimed at identifying differences between dependent and independent fishermen in the means of individual variables and their significance. For comparing categorical data, Pearson's chi-square (χ^2) tests were used to test for differences between the two groups of fishermen. Where counts dropped to ≤ 5 , p-values were estimated based on 50000 replicated simulations by means of a Monte Carlo test significance test (Hope 1968). If significant, the contribution of each category to the differences was calculated. Numerical variables were tested for differences between the

groups using linear models (LM) with Gaussian error distributions. Data were log-transformed to meet the assumptions of normal distribution and homogeneous variance of the residuals, and the qqplots and plots of the residuals against the fitted values were visually inspected to verify there were no deviations from these assumptions (Quinn & Keough 2002). After testing for overdispersion, count data were tested for differences using a generalized linear model (GLM) with Poisson distributed error term and log-link function. Finally, reported and revealed catch and income data were compared both for dependent and independent fishermen to account for any perceptual inconsistencies by means of two-sample t-tests, previously checking data's fulfillment of assumptions of normality and homogeneity of variance.

All the statistical analyses and graphs were performed using R, version 3.1.1 (CoreTeam 2013). Results are presented as mean \pm standard deviation (SD) throughout the manuscript and considered statistically significant when $p < 0.05$.

3. RESULTS

3.1. Respondent characteristics

During the wet season, some of the fishermen depart for several months on fishing trips to other Indonesian regions with more favourable weather conditions. However, this depends on the island: in Kodingareng Lompo, none of the *kapal katinting* fishermen had migrated for the wet season; while in Badi 38.5% had left (60 out of 156 fishing boats). Fishermen who did not travel to other islands reported being too old to travel or being told by their patron not to go as the most common reasons. Table 1 displays the averages and proportions for general fishermen characteristics obtained from the interviews.

Out of the 100 fishermen that participated in the study (both the interviews and catch sampling survey), 37% were independent fishermen and 53% worked for a patron (with 10 % missing this information). These percentages were consistent across both Badi and Kodingareng Lompo. Out of the 63 fishermen from whom catch data was collected, 19 (30%) were independent fishermen, 34 (54%) worked for a patron and this information was not obtained from 10 (16%) individuals. From the interviewed fishermen, the 60% that had a patron (table 1) reported selling on average "almost all" of their daily catch to the patron as part of their agreement.

Fishermen reported consuming a mean of 1.08 kg of fish household⁻¹ day⁻¹ which scaled to the number of people in the household translates to almost 200g person⁻¹ day⁻¹ (table 1), twice as much as the average seafood consumption for the whole of Indonesia (78 g per capita per day, FAO Statistics Division 2011). However, it can be expected that communities living on small islands will have above average consumption of seafood as alternative sources of food are difficult to procure; almost 90% of the interviewees reported catching their own fish.

Table 1. Summary of respondents according to their stated characteristics.

Fishermen characteristics	Mean/Proportion	Standard deviation	N
Age (years)	39.57	12.1	88
Education level	Primary school	-	58
People in household	5.79	1.75	58
Proportion of fishermen with patron	0.60	-	89
Fishermen's experience (years)	23.48	12.47	63
Proportion catching own consumed fish	0.89	-	63
Number of fishes consumed day⁻¹ household⁻¹	9.28	9.27	63
kg of fish consumed day⁻¹ household⁻¹	1.08	0.85	60
g of fish consumed day⁻¹ capita⁻¹	197.82	187.52	27
Proportion of boat owners	0.81	-	58
Boat length (m)	6.31	1.68	60
Boat engine (HP)	7.89	3	60
Number of target species	3.69	2.54	75
Number of gears used	1.57	1.05	75
Fishing days per week (wet season)	4.76	1.76	63
Fishing days per week (dry season)	6.08	0.41	63
Num. of types of reef (shallow and/or deep)	1.68	0.47	62
Num. of reef zones (up to 3)	1.29	0.52	63
Fishing in bad weather	0.63	0.99	60
Kg caught day⁻¹ (wet season)	4.77	4.54	62
Kg caught day⁻¹ (dry season)	6.44	5.73	62
Approximate weekly income (wet season, USD)	54.52	74.60	63
Approximate weekly income (dry season, USD)	68.82	72.06	63

The mean weekly income reported for the wet season was of 54.52 USD, which corresponds to a mean salary of 218 USD per month. This value lies between the 2015 minimum wage for the South Sulawesi province (150 USD, [Wage Indicator Foundation]) and the average income for that province (304.2 USD per month, as calculated from GNI per capita, [World

Bank 2015]). The overall education level was primary school, with some fishermen having completed middle school.

Fishermen reported targeting between three and four different marine species and using between one and two different gears (table 1). Most of the fishermen use octopus bait and *kedo-kedo* (trolling hand line) interchangeably in their fishing trips during the wet season, with just a few free-diving for lobster or Napoleon wrasse (*pers obs*). With regard to reef zones, most of the fishermen reported fishing at the edge of the reef (92%), with few reporting fishing at the lagoon (27%) and almost none going to deep waters (0.1%). Although the data analysed here are specific to the wet season, it is worth noting that there are important differences between the wet and dry season in terms of reported fishing days per week, biomass caught, and weekly income, all being higher during the dry season. This is relevant because the sampling period represents the less productive part of the year for fishermen that, like the ones sampled, lack alternative sources of income.

3.2. Price of target species

The average prices for the reported target species paid to the fishermen by seafood collectors are shown in table 2. Minor species or small specimens not wanted by the collectors are generally consumed by the household or sold locally on the island, usually at a low price of around 0.15-0.37 USD (2000-5000 IDR) per fish or basket, and were not included in the turnover calculation.

The highest fish prices were for fish which were sold alive, used for live food fish trade. The highest prices reported were for Sunu or coral trout (*Plectropomus leopardus*). The price was about 3.5 times higher for live individuals of more than 1 kg (sizes *super* and *ekor*, Table 2), and twice as high for individuals of less weight. Live *Angke* or Napoleon wrasse also fetched a high price of nearly 20 USD kg⁻¹. The rest of the (dead) fish had significantly lower prices, none of them exceeding 3 USD kg⁻¹. Prices obtained for the live fish target species were very similar to those reported by Radjawali (2012); Napoleon wrasse had the same price, and coral trout showed a small variation caused by the proximity of the Chinese New Year celebrations at the time of the data collection.

Invertebrates were less lucrative with the exception of lobster (*Palinurus sp*). Only one fisherman reported the price for live lobster, 50.82 USD kg⁻¹. However, these are not caught very often as they have become rare in the region (Damora 2015, Junianto 2015) and few fishermen target them actively (Pet-Soede et al. 2001b). Octopus and squid are seasonal species which can fetch a relatively high price as they are easy to catch with the appropriate

gear. Octopus prices increase with individual size. Interestingly, squid was very popular on Kodingareng Lompo but no octopus was actively targeted, while octopus accounted for the largest part of the catch biomass on Badi. No squid was recorded in the catch assessments on that island, most likely because the assessment of fishing trips accounted only for daylight fishing and squid is typically fished at night.

Table 2. Prices reported by fishermen for species - and size categories when applicable- sold to seafood collectors on the island. The price is given per kg or per fish depending on the unit of purchase. **Size categories:** **Sunu** baby (0.3-1 kg), super (1-1.3 kg), ekor (> 1.3 kg); **Octopus** A (2 kg), B (1-2 kg), C (0.5-1 kg), D (< 0.5 kg). The family refers to family for fish and order for invertebrates.

Local name	English name	Family/Order	Size category	Mean price (USD/kg)	Mean price (IDR/fish)	Standard deviation	N
Sunu (live)	Coral trout	Serranidae	Baby	5.88		3.92	11
			Super	41.73		13.40	29
			Ekor	42.32		9.23	14
Sunu (dead)	Coral trout	Serranidae	Baby	2.73		1.75	9
			Super	11.85		7.99	23
			Ekor	12.09		6.20	18
Kerapu	Rockcod	Serranidae		1.27	0.18	4	
Cambang	Coralgrouper	Serranidae	Big		2.90	0.00	1
			Small		3.63	0.00	1
Mosso		Serranidae		1.81		0.36	2
Angke (live)	Napoleon wrasse	Labridae		19.96		0.00	1
Katamba	Emperor fish	Lethrinidae		1.44		0.25	4
Masidung		Carangidae		0.90		0.18	2
Cepa		Carangidae	Big		1.81	1.28	3
			Small		0.72	0.51	3
Ikan Putih	Trevally	Carangidae			1.44	0.72	2
Banyara	Mackerel	Scombridae			0.41	0.52	24
Tenggiri	Spanish mackerel	Scombridae		3.51		1.29	32
Tongkol	Mackerel tuna	Scombridae		1.81		0.90	3
Cakalang	Tuna	Scombridae			1.60	0.73	6
Bambangan	Squirrelfish	Holocentridae		2.90		0.00	2
Lobster	Lobster	Nephropidae		50.82		0.00	1

(live)						
Gurita	Octopus	Octopoda	A	2.28	0.33	18
			B	1.92	0.15	18
			C	1.31	0.22	18
			D	0.92	0.27	8
Cumi-cumi	Squid	Teuthida		2.32	0.31	41
Sotong	Cuttlefish	Sepiida		1.58	0.00	1

3.3. Differences between fishermen

3.3.1. Differences in reported characteristics

Selected characteristics reported during the interviews to represent sociodemographic, household economics and consumption patterns did not yield statistically significant differences between dependent and independent fishermen (table S1, appendix). Only the reported daily seafood catches were different between the fisher groups (table 3). Catches reported by independent fishermen ($5.81 \pm 5.26 \text{ kg day}^{-1}$) were significantly higher than those reported by fishermen with a patron ($3.96 \pm 3.78 \text{ kg day}^{-1}$) by almost 2 kg day^{-1} . However, standard deviation values suggest a high variation in the daily catch within groups.

3.3.2. Differences in revealed characteristics

Variables obtained from the catch sampling survey yielded no differences between fisher groups in terms of investment (i.e. time fishing, number of gears, and number of fishing grounds visited), total catch or level of satisfaction (Table 3). The average daily catch values of between 5.27 and 5.89 kg day^{-1} obtained are in the range of those estimated by Pet-Soede et al. (2001a) as the mean catch rates of 5.8 kg per daytrip for the combined reef fisheries in Spermonde.

The fishermen groups were different in terms of the proportion of fished items sold and amount in kg of catch consumed— i.e. not sold to a fish collector - (Table 3), which may have implications for food security. Fish collectors bought every commercial seafood item available independently of the fishermen status, and the amount of catch sold by weight did not show significant differences between patron and independent fishermen. In fact, both groups sold the same amount of commercial fish to the collector, and the statistical

difference between them is mainly due to the amount of subsistence fish (table 3). Post-hoc tests show that 73% of the difference in the proportion of sold fish items is explained by the amount of fish items that stayed on Badi, which were lower for fishermen indebted to a patron ($p = 0.002$). These subsistence species e.g. barracuda, longtom, fusiliers or sardines are mostly not a by-catch of the gears used for commercial species, but require specific gears such as *rinta* (multiple hooks in a vertical line) for small pelagics, or *bulu-bulu*, a particular bait for longtoms. The amount of catch consumed (i.e. not sold to a fish collector) was also significantly higher for independent fishermen ($p = 0.041$). Additionally, the proportion of live seafood items in the catch was significantly higher for fishermen with patron (table 3); 72% of the difference in the status of the fish at landing between the two groups is explained by the amount of live fish.

Fishermen with a patron earned 11.31 USD more per trip on average than independent fishermen, and the difference was statistically significant ($p = 0.027$). However, for fishermen with a patron the real earnings are probably lower than the figures obtained as payment of the debt needs to be deducted from this gross amount. For instance, a turnover for the total catch of 70 USD may be subject to a withdrawal of 10 USD for borrowed operational costs (fuel, gear), and 30 USD to write off part of their “real” debt (i.e. boat and other large purchases), as reported by interviewed fishermen and fish collectors (Navarrete-Forero 2015). In sum, fishermen with a patron are likely to get less money for their seafood items than the normal market price as part of their agreement with the patron (Ferse et al. 2014).

Despite not being statistically significant, the level of satisfaction for fishermen with a patron was 50% while independent fishermen were satisfied on 64% of the trips sampled (table 3). The catch composition of independent fishermen showed higher evenness in terms of functional groups and had a higher proportion of lower trophic groups (figure 3). In both fishermen groups the major part of the catch was composed of piscivores of the trophic level 4, corresponding to second tier carnivores. Those were mainly groupers (Serranidae), mackerels (Scombridae), trevallies (Carangidae), barracudas (Sphyraenidae) and longtoms (Belonidae). The cumulative fished biomass recorded in the study shows that fishermen with patrons fished more than double the amount of fish from the highest trophic level in absolute terms (figure 3).

Table 3. Means of the reported catch per day (from the interviews) and of the revealed variables from the fishing trips for dependent and independent fishermen, and results from the tests comparing the variables between the two groups (significant p-values are marked with *).

Variable	Mean/proportion for dependent	Mean/proportion for independent	N	Statistical value	p-value
Reported kg fished/day	3.96 ± 3.78	5.81 ± 5.26	62	F(1,60) = 4.688	0.03437*
Num of fishing grounds	2.46 ± 1.29	2.97 ± 1.96	91	z = -1.431	0.152
Num of gears used	1.15 ± 0.41	1.31 ± 0.59	91	z = -0.662	0.508
Time fishing (hours)	6.82 ± 2.52	7.92 ± 3.46	86	F(1,81) = 1.951	0.166
Total catch (kg)	5.89 ± 8.09	5.27 ± 5.28	167	F(1,165) = 0.3114	0.5776
Catch sold (kg)	5.42 ± 8.14	4.54 ± 5.36	166	F(1,164) = 0.02917	0.8646
Catch consumed (kg)	0.47 ± 1.41	0.81 ± 1.44	167	F(1,165) = 4.258	0.0406*
Proportion of live seafood items in catch	0.32	0.19	572	χ^2 (1, N= 572) = 9.7783	0.001767*
Proportion of fished items sold	0.77	0.64	572	χ^2 (1, N= 572) = 9.9215	0.001634*
Proportion of fish vs invertebrates	0.63	0.61	547	χ^2 (1, N= 547) = 0.21774	0.6408
Aggregated trophic level	3.78 ± 0.53	3.61 ± 0.72	362	z = 0.775	0.439
Turnover (USD)	27.87 ± 41.85	16.56 ± 21.84	133	F(1,131) = 5.033	0.02655*
Proportion of satisfactory trips	0.5	0.64	101	z = -1.441	0.150

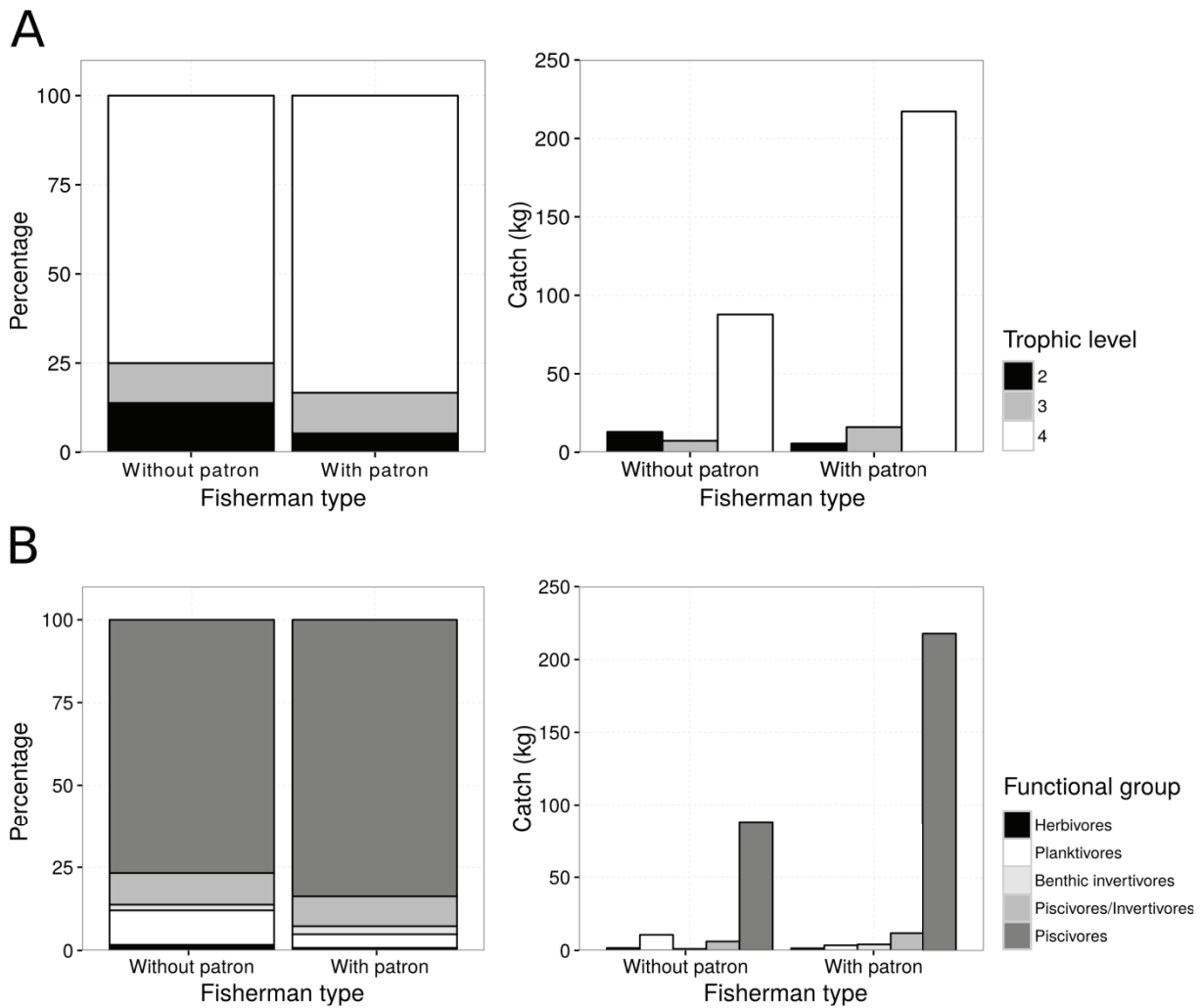


Figure 3. Aggregated trophic level (A) and functional group (B) of the individual seafood items in the catch and of the cumulative biomass fished during the duration of the study for independent fishermen (N = 116) and fishermen with patrons (N = 246).

3.3.3. Differences between stated and revealed variables

Incomes and catch were compared for consistency between the stated (reported in the interviews) and revealed (measured and derived from the trips assessments) values. Independent fishermen displayed a realistic perception of their catch and income with no differences between expectations and revealed data (Table 4). However, fishermen with patron reported significantly lower catches than measured in the catch assessment by less than half (reported catch = 2.82 ± 3.01 ; revealed catch = 6.46 ± 7.68 ; $p = 0.019$).

Table 4. Mean of the catch and gross income variables for dependent and independent fishermen, and results from the tests comparing their stated and revealed values (significant p-values are marked with *).

Variable	Mean for stated	Mean for revealed	N	t	p-value
Catch (kg day⁻¹, with patron)	2.82 ± 3.01	6.46 ± 7.68	17	2.420	0.01941*
Catch (kg day⁻¹, independent)	5.67 ± 5.20	5.58 ± 5.07	11	-0.046	0.9636
Income (USD, with patron)	56.45 ± 53.19	39.14 ± 34.14	34	-1.630	0.1084
Income (USD, independent)	59.13 ± 101.92	46.79 ± 48.21	19	-0.548	0.5868

4. DISCUSSION

Patron-client systems are a social configuration expected to have an effect on the way marine resources are exploited, and their role in the fishery value chain is getting increased attention as new regulations and management policies are implemented (Bailey et al. 2016). In order to grasp their socioecological influence in an artisanal coral reef fishery, differences in selected sociodemographic, economic and fishing behaviour variables were evaluated between independent fishermen and fishermen within the patron-client system. Perceptual interview data were coupled with individual-scale empirical data to ensure an accurate analysis of specific drivers in a complex socio-ecological system (Aswani et al. 2015), and to detect erroneous conceptions about causal relationships related to fisheries, which occur even among actors deeply engaged in the fishery (Wamukota et al. 2015).

The study was able to highlight differences in the quality of the catch between the two groups, and, interestingly, a distorted perception of catch rates by fishermen with patrons. First, fishermen with patrons caught more valuable seafood items -notably live fish- while independent fishermen landed more non-commercial items. Second, fishermen with patrons had higher turnovers than independent fishermen, but after accounting for the additional costs resulting from the fishermen's indebtedness, this result might actually be the reverse.

Third, fishermen with patron underestimated their expected daily catch when empirical catch data was compared to what they had reported in the interviews. These findings and their possible implications are discussed below.

4.1. Differences in fishing

The analysis of landing data from daily fishing trips yielded two important differences in the type of catch between the two groups of fishermen. First, independent fishermen had a larger amount of their catch not sold. Given that fish collectors bought all commercial seafood items both from their clients and from independent fishermen, the reason for the lower portion of catch sold is that a substantial part of the independent fishermen's catch was made up of non-commercial items. Non-commercial or subsistence species -i.e. non-commercial species or commercial species below market size- have to be targeted directly as they require different gears than those used for commercial species, so it can be assumed that fishermen actively engaged in subsistence fishing. This part of the catch is retained on the island as food for the fisher's household, sold at very low prices or given for free to other villagers, contributing to food security on the island. This scenario resembles what happens in other export-oriented activities in Sulawesi, such as shrimp farming, where the engagement in a food-production activity does not contribute to local food security (Idrus 2009). The reason fishermen with patrons focus on marketable target species is possibly due to the pressure of repaying their debts.

Second, fishermen with a patron landed substantially more live fish items from their trips. As shown by the price analysis, live fish is much more valuable than dead, incentivizing entering the live reef fish trade that is prevalent in the region. But live fish is hard to catch with traditional methods and its harvesting is linked to destructive fishing (Barber & Pratt 1997, Bruckner & Roberts 2008) and overexploitation of sensitive populations (Scales et al. 2007, Sadovy et al. 2013). Albeit illegal in Indonesia, using cyanide to stun the fishes is the most prevalent method for catching live fish due to its effectiveness and high catch (Erdman & Pet-Soede 1996, Radjawali 2011). Cyanide fishing poses environmental risks for coral reef ecosystems (Johannes & Riepen 1995) and liability risks for the fishermen using those methods. However, patrons are known to protect their client fishermen from prosecution through their connections to government officials (Radjawali 2011, Ferse et al. 2014), which makes the expected benefits of using illegal fishing methods far exceed the expected costs of being apprehended (Sumaila et al. 2006). Considering our results and others (Nurdin & Grydehoj 2014) it may be argued that belonging to the patron-client system in Spermonde makes fishermen more prone to practice destructive fishing. Given the limited alternative

options and their high dependency on marine resources, fishermen with a patron could find themselves in a poverty trap. A poverty trap is a situation where the poor are unable to overcome a low-income situation and engage in behaviours that reinforce their own poverty, in this case exhausting their own food and income source (Cinner 2010).

4.2. Differences in turnover

Although the higher turnovers suggest higher incomes in dependent fishermen of this study, qualitative information obtained in the informal interviews indicates that their true income level is much less. Considerable debt charges being deducted from the daily turnover as part of their patron agreement would explain why independent fishermen report higher expected incomes, and are more often satisfied after a fishing trip. It may constitute yet another reason to compel dependent fishermen to concentrate on the most profitable species in order to make enough money for meeting both debt repayment and household livelihood needs. Reported prices for the target species were consistent with those reported previously (Radjawali 2012) and did not differ between the groups. Since their catch per trip did not differ, the higher turnover must be explained by dependent fishermen focusing on more lucrative species. This preference is stimulated by having better, newer equipment, and economic and legal protection by the patron.

4.3. Differences in perception

Fishermen with a patron underestimated how much they fish. The reported daily catch was the only perceptual difference between the groups and it corresponded to half of the real catch. When compared to empirical data from the measured catches, both groups fished the same amount. This incongruence is hard to explain, but the potential consequences may pose issues for overexploitation. One explanation could be that the low or inexistent part of their catch that is kept for consumption has affected their perception of how much they fish. Yet it is unlikely that seasoned fishermen fail to assess their daily product with such a large margin of error. They could be trying to cover up for or mask illegal fishing by reporting lower catches, a behaviour that is observed in many different types of fisheries (e.g. Metzuzals et al. 2008) - especially if they are suspicious about interviewers' neutrality. Regardless of what causes this phenomenon, perceptions and expectations influence human behaviour, in this case fishing. If a group of fishermen, who arguably have a larger ecological impact, underestimate their daily catch they may be prone to increase fishing effort, escalating the problem of overfishing and sequential depletion of seafood species.

Returning to the initial study questions, the selected sociodemographic variables did not provide evidence that a particular portion of the fishermen population was more likely to engage in a patron-client relationship. Getting a patron-client agreement may be the only way for some fishermen to enter the fishery; thus fishermen with patron were expected to be younger and more inexperienced, or to have larger households. But those indicators were not noticeable in the study, which suggests other motivations unrelated to the social factors examined here.

The fact that both fishermen types sell their products to the same seafood collectors and there are no apparent sociodemographic differences explains why the differences in fishing effort and behaviour were small and hard to detect. Our results suggest that belonging to the patron-client system affects fishing behaviour by making the indebted fishermen use less diversified gears and focus on commercial fishing. The consequence of this is an apparent reduced amount of seafood provision for the household, and possibly a more damaging impact on coral reef ecosystems by virtue of their fishing method. The proportion of dependent fishermen on the islands is likely to be larger in the dry season. In the case of Badi, almost 40% of the *kapal katinting* fishermen had left the island at the time of sampling to fish in regions with more favourable weather conditions. Interviewed fishermen stated that many of them left as required by their patron (Navarrete-Forero 2015), who sponsors the trip during the entire wet season (Radjawali, 2011). Therefore, the influence of belonging to the patron-client system on the coupled socio-ecological system may be exacerbated during the dry season.

Finally, the study did not yield sufficient evidence to support either that the patron relationship is beneficial or detrimental for the fishermen in the long term. While patron fishermen might get benefits in terms of investment in the fishing trips, the costs of repaying their debts can be high. In addition, the perceptual data indicate that if the debt repayments were considered, their income levels may not equal that of their independent peers. Twenty years ago, fishermen in the live food fish trade were estimated to earn between 3-10 times more than artisanal fishermen (Erdman & Pet-Soede 1996). Although the patron fishermen sampled here engaged partly in artisanal fishing, their income was not significantly different from independent fishermen, even without subtracting the debt payment. The variables measured in this study indicate that, if debts were incorporated, the patron-client system may not bring economic advantages to fishermen and their households, but this would need to be confirmed in a follow up study of debt levels and repayments which is currently missing.

5. CONCLUSION

While no sociodemographic differences were found between dependent and independent fishermen in the study area that hint at the reasons why they might decide to engage in patronage, the groups displayed different fishing behaviour. The empirical data presented seem to reflect a more profit-driven fishing style in fishermen with patrons, possibly including destructive fishing practices. This market-driven fishing behaviour may threaten the long-term usability of their marine resources, risking a poverty trap. On the other hand, despite engaging in an asymmetric relationship in which they have little decision-making opportunities, fishermen may value the livelihood safety net that the patron-client system confers in scarce times (Ferse et al. 2012, Johnson 2010, Bailey et al. 2016) and feel a sense of loyalty to their patrons (Adhuri et al. 2016). The extent of the benefits conferred by the patron-client relationship has not been studied in this research and is needed to form a complete socioecological picture of such arrangements.

With examples of failed formal efforts to engage the community in marine resource management in Spermonde (Glaser et al. 2010), and the low nature-based tourism in the archipelago, influential institutions with economic interests such as the patron-client system have gained attention as a critical link to convey management approaches for a more sustainable exploitation (Ferse et al. 2012, Crona et al. 2010). However, patron-client systems may discourage conservation because their major decision-makers - the patrons in the city- have neither knowledge nor direct dependency on the marine resources being exploited (Basurto et al. 2013). Fish collectors understand fishery dynamics and may be receptive to take part in endorsing more sustainable fishery practices - for instance, by not buying small sized groupers from fishermen- but it would require a unanimous effort, which seems unfeasible in Spermonde (Navarrete Forero 2015). In addition, rejecting the catch resulting from destructive fishing would be too costly for the patrons as they are the most profitable products, and they themselves face economic pressures from their indebtedness to a *Punggawa*. Economic opportunity is the leading indicator for harvest-related impacts in global fisheries (Sethi et al. 2010), highlighting difficulties in achieving the trade-offs that are necessary to maintain a sustainable fishery. To our knowledge, this is the first study that empirically assesses differences in fishing behaviour between fishermen within the patron-client system and independent fishermen. It seems to support the notion that such arrangements limit the potential of fishermen as effective managers of the resources they depend on, a pitfall for conservation (Cinner et al. 2009, Cinner et al. 2012, Frey & Berkes 2014). For instance, between 20-30% of the imported seafood in the USA - Indonesia being one of the top ten exporters- corresponds to illegal and unreported catch (Pramod et al.

2014). Illegal and unreported catch accounted for 40 million USD only in the Raja Ampat Regency, Indonesia (Varkey et al. 2010); did the patron-client system play a role in encouraging this kind of fishing? How much does illegal catch account for in Spermonde? Community-based conservation and management regimes aiming at meeting community goals can be successful (McClanahan et al. 2006, Govan 2009, Hamilton et al. 2011), but in cases like Indonesia where enforcement is low and alternatives to fishing are scarce, it seems that the only possible way to bring the patron-client system on board sustainable fisheries would be by targeting the *Punggawas*. They convey market demand down the value chain and have the means to buffer the short term economic losses. At the moment, the data analysed here suggests that the patron-client relationship indirectly causes a worse environmental impact by encouraging higher exploitation rates. The implications are that bringing the patron-client system on board sustainable fishing policies may require hard work, and context-dependent considerations with careful examination of cultural obstacles and social complexities.

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Appendix

Table A.1. Mean of the reported variables in the interviews for dependent and independent fishermen, and results from the tests comparing the variables between the two groups.

Variable	Mean for dependent	Mean for independent	N	Statistical value	p-value
Age (years)	38.11 ± 10.51	41.77 ± 14.05	88	F(1,86) = 1.599	0.2094
Island	-	-	99	χ^2 (1, N= 99) = 0.389	0.5328
Education level	-	-	58	χ^2 = 0.3473	1
Experience (years)	22.08 ± 10.0	25.33 ± 15.16	63	F(1,61) = 0.08675	0.7693
People in household	5.84 ± 1.59	5.71 ± 2.05	58	z = 0.188	0.851
Boat ownership (proportion)	0.73 ± 0.45	0.95 ± 0.22	58	z = -1.838	0.06605
Catches own fish	-	-	62	χ^2 = 3.6489	0.1702
Num of fishes consumed day ⁻¹ household ⁻¹	9.06 ± 6.34	9.57 ± 12.28	63	F(1,61) = 0.7975	0.3753
Kg of fish consumed day ⁻¹ household ⁻¹	1.16 ± 1.04	0.99 ± 0.60	54	F(1,52) = 0.02241	0.8816
Num of target species	3.95 ± 2.33	3.84 ± 2.62	75	z = 0.223	0.824
Num of gears	1.64 ± 0.84	1.69 ± 1.20	75	z = -0.151	0.8799
Bad weather score (higher = more risky behavior)	0.55 ± 0.87	0.74 ± 1.13	60	z = -0.942	0.346
Reef types (Shallow/Deep)	1.66 ± 0.486	1.706 ± 0.47	62	z = -0.389	0.6976
Reef zones (lagoon, edge, reef)	1.31 ± 0.52	1.26 ± 0.53	63	z = 0.160	0.873
Fishing days/week	4.53 ± 1.96	5.07 ± 1.41	63	z = -0.983	0.326
Reported Kg fished/day	3.96 ± 3.78	5.81 ± 5.26	62	F(1,60) = 4.688	0.03437*
Existing alternative income	0.14 ± 0.35	0.19 ± 0.40	63	z = -0.496	0.61977
Reported weekly income (USD)	55.46 ± 52.24	58.07 ± 100.15	63	F(1,61) = 1.599	0.2108

Chapter 3

Modelling coral reefs in Indonesia: benthic cover, fish biomass and catch predictions under different fishing and eutrophication impacts

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Drying fishing nets on Kapoposang, November 2014.

Abstract

In countries where heavy exploitation of coastal ecosystems occurs in a decentralized manner, involving marine resource users in the decision-making process is necessary to incorporate community goals. Equally as important is developing case-specific management strategies including specific stressors and environmental characteristics of the system of interest. With the aim of informing local management on the potential future trajectories of their marine resources, we applied a two-dimensional model to four neighbouring Indonesian coral reef systems exposed to varying degrees of water quality and fishing pressure. The model was spatially explicit and contained four benthic and three fish functional groups. To represent the effects of environmental factors on reef dynamics, the model included three water nutrient scenarios and ecological processes such as benthic competition and trophic interactions. The bathymetric profile, initial conditions for fish abundances and benthic cover at three depths, along with fishery characteristics were collected in-situ at each of the islands for model parameterization. Case-specific stressors were customized exploring how nutrients and fishing practices affect the ecological variables of interest (i.e. fish biomass, benthic cover and fishing yield).

1. INTRODUCTION

Millions of Indonesians depend on small-scale coral reef fisheries for subsistence or commercial purposes (i.e. local consumption or export, FAO 2013). Fishing can have negative impacts on coral reef communities by removing important ecological functions resulting in negative feedbacks (Mumby & Steneck 2008, Flower et al. 2017). Negative impacts can be highly emphasized at a very small scale when highly destructive fishing methods, such as bomb and cyanide fishing are utilized (Pet-Soede and Erdmann 1998; Chozin 2008; Ferse et al. 2014; Hajramurni 2015). Local stressors such as eutrophication interact with fishing in highly complex ways that can be ambiguous when trying to disentangle via observation alone. Nevertheless, most coral reef stressors directly or indirectly reduce the coverage of live coral as benthic substrate. If corals die or their carbonate accretion is reduced, the habitat and its provisions for the myriad of species become degraded, potentially resulting in undesirable ecological states (Graham et al. 2006). The complex dynamics and feedbacks between fish and their benthic habitat are considered to be essential in driving coral reef health. Sustained exposure to stressors has cumulative impacts which lower resilience thresholds and make reefs more vulnerable to further stress.

Multiple coral reef stressors can interact in nonlinear ways confounding ecological interpretation through field studies alone. Theoretical computer modelling can offer a platform to test ecological hypotheses about multiple stressors and their systemic impacts. A number of models have evaluated the cumulative impact of various stressors on coral reefs (Gurney et al. 2013, Weijerman et al. 2015), many of them concluding that local drivers are relatively more important for ecosystem health than global drivers. Although these models, simulated across large spatial scales (10s of kms), partition local and global drivers, they overlook the nuances that can determine community structure at a finer grain. Thus, modelling ecological dynamics at the reef scale may help to clarify among the many local disturbances and help determine their individual contributions, or detriments, to reef health.

In this study we used “Spatially Explicit simulation model for Assisting the local MANagement of COral Reefs” (SEAMANCORE), a model focused on the dynamic relationships between coral reef benthic habitat and fish. This model evaluates the effect of selected stressors and their interactions on (1) benthic cover, (2) fish abundance, and (3) fishing yields with standardized scenario settings altering nutrient levels and fishing pressure. The model was parameterized with real field data collected at four islands off southwest Sulawesi, Indonesia. Running on-shore to off-shore (7 to 55 kms), these four islands represent a gradient of disturbance driven my effluents from the mainland and fishing pressure. We projected ten

years in the response variables identifying variability in their ecological condition in comparison to their current condition.

2. METHODS

2.1. The model

SEAMANCORE (Miñarro et al. *submitted*) was developed using MASON multi-agent simulation toolkit (<http://cs.gmu.edu/~eclab/projects/mason>) and is written in Java programming language. The model simulates the spatial dynamics of selected coral reef functional groups under the influence of three stressors including: climate change, fishing and eutrophication. The model domain is defined using a two-dimensional continuous cellular automaton (CA) grid, which represents the benthos of a coral reef patch with a resolution of 10 x 10 cm. Benthos grid cells belong to one of the four categories at any given time step: coral, Macroalgae And Turf (MAT), hard substrate and empty space. A second, lower resolution grid layer is superimposed describing the fish functional groups which include: browsers and grazers (BG), scrapers, and carnivores. Each fish cell represents an area of 400 m² containing 40000 benthos cells, which are used by the fish module to calculate the cell biomass in the next step. Biomass transfer occurs through movement, and trophic relationships between groups. Each time step represents one day. Benthos dynamics are defined by CA rules and disturbances. The CA rules reflect the processes of coral-algae competition, colonization of free hard substrate space, and connectivity from external reef sources. If hard substrate cells are not grazed for a given amount of time, they grow into MAT cells. Aging and colonization rules are affected by the selected nutrient scenario. Disturbances include foraging from herbivores, bleaching and destructive fishing including bomb fishing and cyanide fishing. As a result of the model's rules, realistic reef zonation patterns of the reef habitat emerge. Fish biomass is updated for each functional group by means of a net growth function accounting for gains and losses from the processes of recruitment, feeding, natural mortality, predation, fishing and migration among grid cells. Most fish processes are affected by the proportions of benthic cover groups. A greyscale bathymetric map is used to specify local conditions by assigning a depth category to each benthos cell. Depth categories influence the probability of occurrence of ecological processes, and determine whether grid cells will be affected by stressors. Input variables for scenario definitions include the depth map, benthos groups cover by depth for the first 15 m,

initial fish biomass by functional group, nutrients and fishery specifications. A full model description is provided in Miñarro et al. (*submitted*).

2.2. Study area

The Spermonde Archipelago is located in southwest Sulawesi, Indonesia, on a carbonate coastal shelf extending about 60 km offshore (Yusuf & Jompa 2012). Data were collected at reefs from four islands located across a gradient of increasing distance from the mainland: Samalona (05° 07 S, 119° 20 E, 7-km distance) , Barrang Lompo (05° 02 S, 119° 19 E, 11-km distance), Badi (04° 57 S, 119° 16 E, 19-km distance), and Kapoposang (04° 41 S, 118° 57 E, 55-km distance). The Jene Berang river, heavy agricultural practices, and the sewage from the coastal city of Makassar (1.3 million-people) result in sediment plumes, nutrients and pollutants to various levels reaching the coral reef communities of the islands (Cleary et al. 2005). The four islands have differing populations that reflect in localized ecological impacts. Fishing is the main source of livelihood, with over 70% of the men self-reporting as fishermen, and most households depend directly on selling their catch for income with little or no alternative livelihood options (Deswandi 2012, Ferse et al. 2014). Commercial catch normally includes fish in the higher trophic levels, with the subsistence portion consisting of the unsold remainder of the catch including below market-sized carnivores and herbivorous fish (Miñarro et al. 2016).

The island of Samalona hosts a tourist resort. The touristic venue motivates a special interest in protecting the island's reefs, which are locally guarded to prevent destructive and other illegal fishing activities. This island is therefore categorised as having a low exploitation level (Madduppa et al. 2014). Samalona is recovering from a 2003 crown-of-thorns (COTs) outbreak which affected half of the reef surrounding the island and triggered high mortality in *Acropora* species (Baird et al. 2013). Barrang Lompo is densely populated and the reefs are exposed to considerable fishing pressure (Madduppa et al. 2014), including destructive fishing (*pers comm*). Sewage from the densely populated island and its near-shore location result in poor water quality (Kegler 2016). A recent, severe COTs outbreak was reported to have halved the live coral cover at this site (Plass-Johnson et al. 2015). Badi's mid-shelf location reduces exposure to effluents from the mainland resulting in relatively high water quality (Kegler 2016). Badi has low exploitation (Madduppa et al. 2014) facilitated by community-based conservation projects raising awareness about marine resources (Williams et al. 2014). This island was the focus of sister studies collecting more accurate data on the artisanal reef fishery (Miñarro et al. 2016, Navarrete Forero et al. *submitted*). Interviews with hook and line fishermen indicated that they fish six days per week on average, bringing in an

average catch of 6.4 kg day⁻¹ in the dry season, and almost five days per week and 4.77 kg day⁻¹ in the wet season (Miñarro et al. 2016). They also reported consuming an average of 1 kg of fish per day per household. The average measured catch was about 5.6 kg per day (Miñarro et al. 2016, Navarrete Forero et al. *submitted*). Kapoposang is inhabited by a small community of subsistence, gillnet fishers. Water quality at this site is high (Teichberg et al. *in prep*). Locals report witness to infrequent bomb fishing from fishermen coming from other islands. The reefs of the island are protected but have low enforcement (pers comm) thus being attractive to poachers.

2.3. Data collection

Data collecting surveys took place between November and December 2014, at the windward side (NW) of the islands with the exception of Kapoposang, where sampling occurred at the NE side of the island. Exposure to higher wave energy has resulted in high reef accretion. The three inshore islands are coral cays and Kapoposang is classified as a barrier island, located at the edge of the Spermonde shelf (Kneer 2013) and exposed to deep oceanic waters, and stronger waves and currents.

The start of sampling was standardized at 8:00 am. Three 50 m transects, separated by 10 m, were laid at three depths: (i) 1-3 m for the reef “crest” and flat (D1), (ii) 5m for the upper reef slope (D2), and (iii) 12m for the deeper part of the slope (D3). Note that the deep survey at Kapoposang belongs to a vertical wall, unlike the other sites in which 12 m falls on the reef slope. Benthic cover is substantially reduced below 15 m as a result of a decreased light availability for photosynthetic organisms. The maximum depth at the inshore islands is reportedly about 25 m, and 50 m at Kapoposang (Edinger et al. 1998). Data were collected via SCUBA. Underwater visual censuses of the fish were performed first and by the same diver. All fishes over 3 cm were counted when occurring 2.5 m either side of the transect tape. They were estimated to the nearest cm. Cryptic and transient, pelagic species were not recorded because accurate counts and identification could not be guaranteed, or when they had limited association with the reef as habitat.

Fish counts were followed by Line Point Intercept (LPI, Graham et al 2014) surveys every 0.5 m for a rapid assessment of the model’s functional groups. For each replicate, 50 benthic photographs were taken every other meter on one side of the transect tape. Benthic categories for the LPI included: live hard coral, sand (including sand and heavy sedimentation), hard substrate (including rock, rubble, crustose coralline algae and other encrusting organisms or hard bottom on which recruitment is possible), macroalgae, turf, sponge, soft coral, and others. A Eureka Manta logger (GEO Scientific Ltd.) was deployed at

every depth during sampling to collect environmental data. These data included: depth, date and time, Chlorophyll a, salinity, dissolved oxygen, pH, and turbidity.

2.4. Input data

Fish field data were divided into the model's functional groups by looking up their reported diet on Fishbase (Froese & Pauly 2016) and following Green & Bellwood's (2009) guide for herbivore classification. Species whose diet did not fall into the model's functional groups descriptions were excluded, such as planktivores and carnivores feeding on crustaceans. Carnivorous species were only included when reported to feed on herbivores or fish eggs, either as the totality of their diet or as a part of it. Browsers and grazers include herbivores feeding on algae, including macroalgae and turf, such as the Acanthuridae family. Butterflyfishes (Family Chaetodontidae) were categorised as BG because, although they are known corallivores, they are also reported to feed on algae (Pratchett 2005), soft corals and other organisms (Anderson et al. 1981) classified here within the algae category due to their competition with hard corals. Scrapers included mostly parrotfishes from the genus *Scarus* and *Chlorurus*. Fish biomass was calculated from individual size observations using length-weight relationships obtained from Kulbicki et al. (2005).

Data from benthic transects were divided into the four groups considered in the model. The coral category included only hard coral, and empty space included only sandy substrate. Macroalgae, turf, soft coral and sponges were included in the MAT category because they all compete with hard corals for space. Hard substrate includes rocky bottom, crustose coralline algae and other benthic organisms which do not compete with hard corals. A depth map was created for each island by converting raster geolocation data provided by the MaCSI centre (Hasanuddin University) into polygons using QGIS (QGIS Development Team 2014) and then into a greyscale image, ensuring the maintenance of scale so that one pixel equals 1 meter.

2.5. Scenario specification

2.5.1. Basic scenarios

A first analysis was done by simulating standard fishing and nutrient scenario combinations to assess the sensitivity of the model by using the same depth map and initial conditions

(Table S1). We used Barang Lompo's initial conditions because of its smaller sized (800 x 280), more easily computed, depth map, and we set bleaching frequency to three years (with mild bleaching episodes as described in Miñarro et al. (*submitted*)). The fishery scenarios are detailed in table 1 and were run for three nutrient scenarios: low, medium, and high. Fishing scenarios included: no fishing, subsistence, commercial, and destructive. The parameters which define the fishing technique in each time step are: (a) biomass threshold (also referred as vulnerability) - the minimum fishable biomass per fish cell; (b) catch proportion - the catchable portion of fish biomass per cell; (c) number of fishing units employing the fishing technique (fleet); (d) depth categories susceptible to fishing by the fishing technique; (e) type of fishing, which can be one of three: non-destructive, cyanide, or bomb fishing, dictating the kind of damage done to the reef habitat; (f) frequency at which the fishing technique is carried out (i.e. time allocation); (g) maximum catch per unit of effort (once the maximum catch is reached, the fishing unit will stop fishing for the day); (h) species affected - fish groups susceptible to fishing mortality by the fishing technique; and (i) try count - the maximum number of cells a fishing unit can visit per time step. Fishery parameter values were estimated based on Miñarro et al. (2016), Navarrete et al. (*submitted*), and personal observations during fieldwork. The commercial scenario includes both commercial and subsistence specifications, and the destructive scenario includes commercial and bomb fishing specifications. Each scenario was run with 3 different random seeds as replicates. Simulations were run for ten years.

Table 1. Parameters used for each fishing technique in the general scenarios.

Parameter	No fishery	Subsistence	Commercial	Destructive
Biomass threshold (g)	-	1000	1000	800
Catch proportion	-	0.5	0.5	0.7
Number of fishing units	-	10	10	4
Depth	-	1, 2	1,2,3	1, 2, 3, 4
Fishing Gear	-	Non-destructive	Non-destructive	Bomb
Frequency (days)	-	1	1	14
Maximum CPUE (g unit⁻¹ day⁻¹)	-	4000	10000	20000
Species affected	-	ALL	Carnivores	ALL
Try count	-	3	8	5

2.5.2 Spermonde islands

For each of the four islands, we ran a “business as usual” simulation with the data and estimates obtained in previous fieldwork and the underwater sampling described above. Each scenario was simulated three times with different random seeds and the mean \pm standard deviation was used in the results to account for possible stochastic effects. For Samalona, the stressors included high nutrients and commercial and subsistence fishing. For Barrang Lompo, high nutrients with commercial (the number fishing units was set higher to 15 to reflect the higher fishing pressure reported for this island), subsistence and bomb fishing every 30 days. The Badi simulations had medium nutrients with commercial, subsistence and cyanide fishing every 14 days. Kapoposang had low nutrients and subsistence and bomb fishing only as there is no commercial reef fishery to our knowledge.

2.6. Data analysis

For the basic simulations, average coral cover, algae cover, BG biomass, scraper biomass, carnivore biomass and catch were calculated for the last year of simulation for the three replicates and plotted with whiskers representing the standard deviation for each scenario. For the Spermonde scenarios, both the last year average and the average for the simulation time were calculated. For the total average, the first year was excluded as it was considered an adjustment period in which model behaviour is unstable (Miñarro et al. *submitted*). Values are given as mean \pm standard deviation throughout the document.

3. RESULTS

3.1. Distribution of benthic cover and fish biomass at different depths

Results from the field transects are shown in table 2. The highest coral cover was found in Badi (around 50%), with particularly high cover at 5 and 12 m, MAT cover was relatively high at 2-3 m. Barrang lompo had very high coral cover at 2-3 m but lower than 30% in deeper transects, and relatively low MAT cover. It also presented the highest proportions of hard substrate, which were mostly rubble. Kapoposang and Samalona had the highest MAT cover. Samalona had around 40% of MAT at all depths, with the largest portion being turf. Hard substrate was high at 5 m and mostly composed by rubble. During our sampling,

abundant sedimentation was observed covering corals, while some were being overgrown by turf algae. In the shallow transects a large area covered by juvenile *Acropora* coral heads was observed. Kapoposang had high levels of coral cover, but surprisingly also displayed high MAT; the MAT composition was different amongst depths: mainly turf at 2 m, 50% turf/50% macroalgae at 5 m, and mostly sponges at 12 m. The deep survey at Kapoposang belongs to a vertical wall, unlike the other sites in which at 12 m there is still the reef slope.

Fish biomass displays high variability and standard deviation likely due to high fish mobility. For this reason they were grouped together into one value for the initial conditions of the model (Table S2). The highest fish biomass was observed in Kapoposang, with 30.66 g m² of carnivores and 35.14 g m² of browsers and grazers. Browsers and grazers biomass was 34.06 g m² on average in Badi. The highest biomass of scrapers was observed in Badi (11.32 g m²) and Samalona (8.25 g m²).

Table 2. Mean \pm Standard deviation of the model's functional groups from the field transects (N=3 per depth). MAT includes macroalgae, turf, soft coral and sponges; hard substrate includes rocky bottom, crustose coralline algae and other benthic organisms which do not compete with hard corals.

	Samalona			Barrang Lompo			Badi			Kapoposang		
	D1	D2	D3	D1	D2	D3	D1	D2	D3	D1	D2	D3
Coral (%)	27.3 \pm 4.7	9.6 \pm 6.5	27.3 \pm 1.2	47.6 \pm 6.9	18.6 \pm 7.8	27.3 \pm 4.7	28.6 \pm 11.6	53.3 \pm 4.5	47 \pm 1.41	20.6 \pm 4.8	35.6 \pm 4.2	35.3 \pm 4.5
	33 \pm 1.4	39 \pm 6.5	41 \pm 2.2	10 \pm 2.2	12.3 \pm 8.5	18.7 \pm 4.1	31.3 \pm 8.6	5.7 \pm 1.2	17.7 \pm 6.6	36.4 \pm 10.7	26.3 \pm 4	45 \pm 3.3
Macroalgae and turf (%)	18.7 \pm 7.4	39 \pm 2.8	23.7 \pm 3.8	39.7 \pm 2.5	42.7 \pm 4.7	41 \pm 2.8	23 \pm 2.2	38 \pm 5	27 \pm 3.6	26.8 \pm 1.9	26.3 \pm 2.4	12.7 \pm 3.4
	22 \pm 7.3	12.3 \pm 4	8.7 \pm 3.1	4 \pm 3.6	26.3 \pm 6.2	13.3 \pm 1.2	17 \pm 3.6	3 \pm 1.4	7.3 \pm 2.5	15.5 \pm 3.9	11.7 \pm 1.7	2.7 \pm 0.5
Empty space (%)	0	4.3 \pm 2.1	33.1 \pm 18.9	6.3 \pm 7	1.9 \pm 0.8	3 \pm 1.7	18.7 \pm 2.7	15.8 \pm 2.6	67.7 \pm 76.1	46.7 \pm 26.1	48.3 \pm 12.1	10.5 \pm 1.1
	11.6 \pm 9	6.2 \pm 6.9	7 \pm 1.9	0	2.7 \pm 3.1	6.9 \pm 3.9	18.7 \pm 14.2	7.9 \pm 10.2	7.4 \pm 3.1	3.4 \pm 2.5	11.8 \pm 7.6	1.6 \pm 0.4
Scrapers (g m⁻²)	0.9 \pm 0.6	0.7 \pm 0.5	2.5 \pm 0.6	1.1 \pm 0.4	1.1 \pm 0.6	2 \pm 1.3	1.6 \pm 1.3	0.7 \pm 0.5	7.1 \pm 5.6	35.2 \pm 13.3	3.6 \pm 1	53.3 \pm 40.8
	0.9 \pm 0.6	0.7 \pm 0.5	2.5 \pm 0.6	1.1 \pm 0.4	1.1 \pm 0.6	2 \pm 1.3	1.6 \pm 1.3	0.7 \pm 0.5	7.1 \pm 5.6	35.2 \pm 13.3	3.6 \pm 1	53.3 \pm 40.8

3.2. Basic simulations

Results from the last year average of the general simulations, which included four fishing scenarios and three nutrient scenarios of increasing expected impact, are presented in Fig. 1. Benthic cover was dominated by coral for all scenarios, with values ranging between 75% and 97%, while algae cover ranged from 1 – 22% (Fig. 1-A). Coral cover was lower in the high nutrient scenarios, particularly with no fishing or subsistence fishing, while it remained above 90% in the commercial and destructive scenarios. In turn, MAT cover was highest in the high nutrient scenarios but with lower absolute values with increasing fishing destructiveness.

Fish biomass declined in relation to initial biomass, which was relatively low (BG = 3.45 g m², S = 3.18 g m², C = 1.4 g m²) for carnivores in all fishing scenarios, and increased only in the no fishing - high nutrient scenario (Fig. 1-B). Scrapers biomass declined only in the subsistence fishing scenario, likely because they were being fished along with the other fish groups, and increased gradually in the commercial and destructive fishing scenarios, up to a biomass of 5 g m². The population of scrapers decreased with increasing nutrients, with the most marked effect being shown in absence of fishing. Biomass of browsers and grazers doubled in the absence of fishing and increased slightly in the destructive fishing - high nutrient scenario, while it decreased in the remaining simulations. For each fishing scenario, BG biomass was higher with high nutrients, showing a strong trophic effect of increased macroalgae and turf.

The highest average catch after 9 years was produced by the subsistence scenario under high nutrients, followed by the commercial fishery and the subsistence fishery with low and medium nutrients (Fig. 1-C). Interestingly, the commercial fishing scenario's catch, which includes both commercial and subsistence fishing, is only less than 1 kg higher than subsistence only. When fishing took place, catch increased with higher nutrients, following the trophic pattern mentioned. The first fishery scenario – no fishing – naturally produced no catch. The fourth fishery scenario shows a very high standard deviation due to the lower frequency of the destructive fishing.

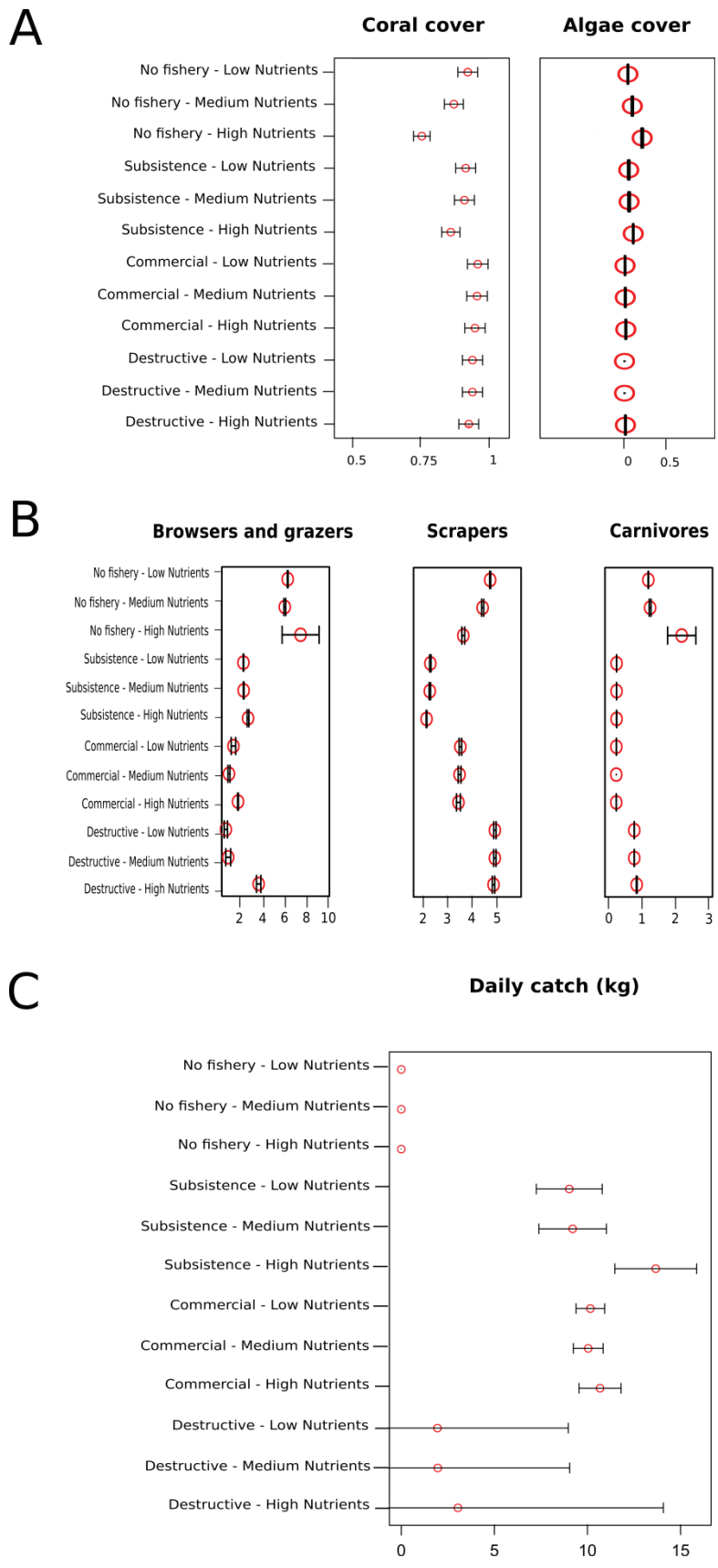


Figure1. Tenth year average of (A) coral and algae cover, (B) fish biomass in $g\ m^{-2}$, and (C) daily catch in kg for each of the basic scenarios.

3.3. Predictions for Spermonde case study

Last year averages of the response variables from the three simulation runs for each island are presented in Fig. 2. At the end of the simulation, coral dominated the benthos in all islands, with the lowest values occurring in Barrang Lompo (90%). Fish biomass was highest for islands with less fishing pressure, with Kapoposang (low nutrification) displaying almost double the total biomass, and with the highest biomass of browsers and grazers ($5.7 \pm 0.37 \text{ g m}^{-2}$). The lowest total biomass occurred in Badi. Samalona had the highest biomass of scrapers ($4.94 \pm 0.003 \text{ g m}^{-2}$), which dominated fish biomass also in Badi. Both islands had relatively low biomass of the other fish groups. Kapoposang produced the highest total yield, with 10 kg per day more on average than Badi (second highest) and 17 kg more than Samalona, which had the lowest catch. However, Barrang Lompo produced the same fishing yield as Kapoposang once scaled to reef area, with 0.06 g m^{-2} .

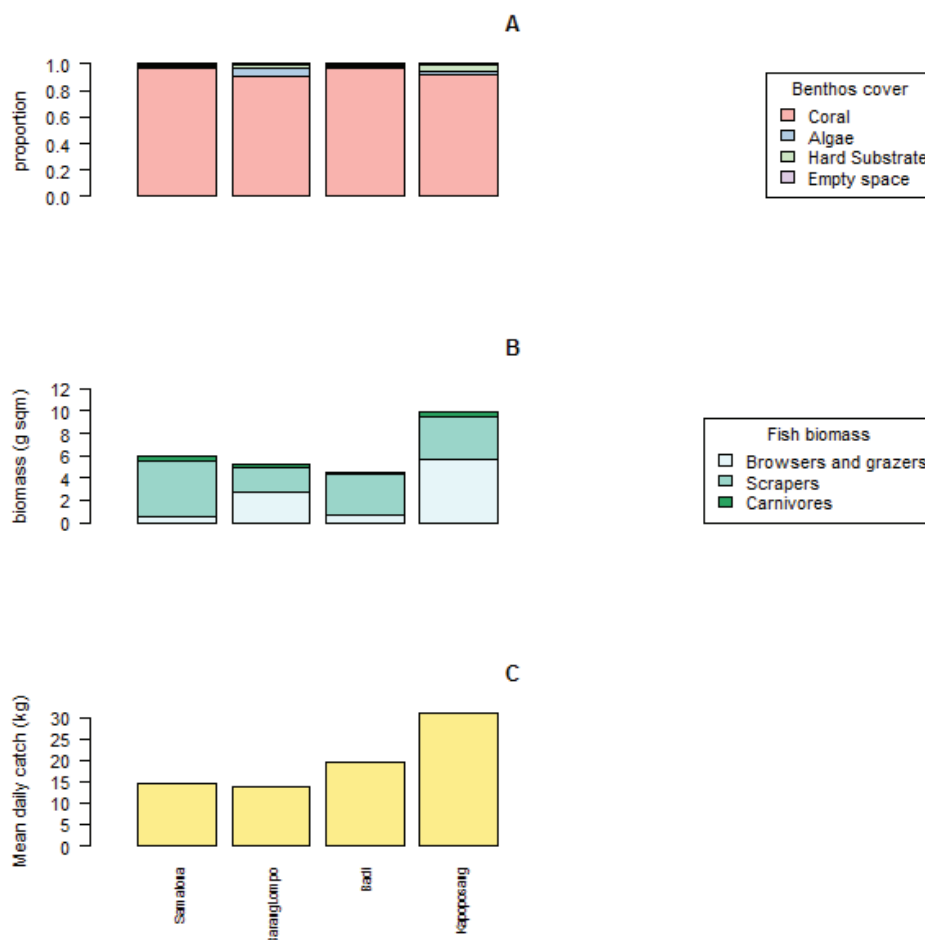


Figure 2. Results for the Spermonde simulations derived from the fieldwork data. Tenth year Spermonde simulations average.

Response variables were also averaged for the entire simulation time, excluding the first adjustment year. Coral was again the dominating benthic group in all islands (Fig. 3-A), with the lowest values occurring in Kapoposang (84%) and Barrang Lompo (87%). The free benthic space was occupied mostly by macroalgae and turf in Barrang Lompo, and hard substrate in Kapoposang. Fish biomass was highest for islands with less fishing pressure, with Kapoposang (low nutrification) displaying the highest total biomass, biomass of carnivores ($1.65 \pm 1.11 \text{ g m}^{-2}$) and browsers and grazers biomass ($11.35 \pm 8.26 \text{ g m}^{-2}$). Samalona had the highest biomass of scrapers ($5.1 \pm 0.76 \text{ g m}^{-2}$). Badi had the lowest biomass of BG ($5.15 \pm 5.07 \text{ g m}^{-2}$), and Barrang Lompo had low biomass of scrapers and carnivores. Browsers and grazers values have a remarkably high standard deviation which indicates high fluctuation in the populations, which were particularly high for Samalona ($9.37 \pm 19.88 \text{ g m}^{-2}$) and Barrang Lompo ($7.42 \pm 14.7 \text{ g m}^{-2}$). Kapoposang produced the highest average yield for the entire time, maintaining 10 kg per day more on average than Badi (second highest) and 20kg more than Samalona, which had the lowest catch.

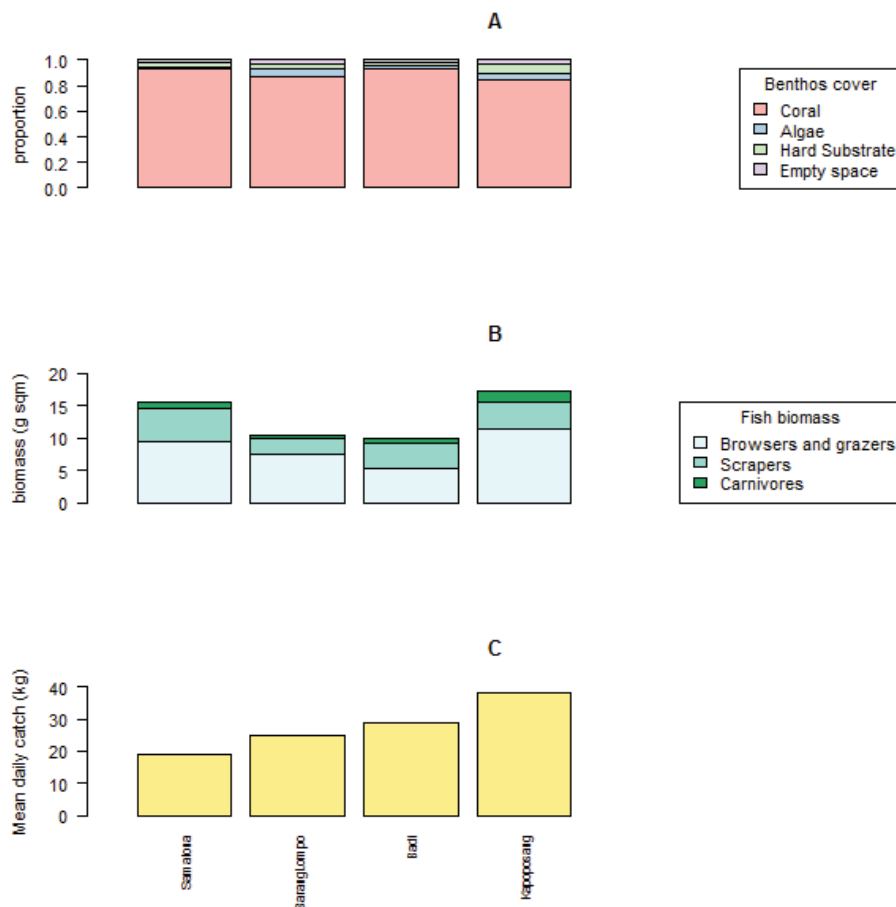


Figure 3. Results for the Spermonde simulations derived from the fieldwork data. “Business as usual” simulations total average excluding first year.

4. DISCUSSION

The aim of this study was to shed light on drivers of coral reef dynamics by simulating different scenarios of fishing and water nutrients on a newly developed model application (Miñarro et al. *submitted*). Additionally, we collected real field data to parameterize the initial conditions for four islands in Indonesia with the aim of predicting the likely coral reef state 10-years from now. The modelled response variables included coral and algae cover, fish abundance, and fishing yield.

4.1. Fieldwork results for input data

The rapid ecological field assessment was performed with the aim of collecting data to parameterize the model's initial conditions and does not allow for a reliable diagnosis of coral reef state to be made, so our findings should be considered with these limitations in mind. Particularly, schooling behaviour shown by many herbivorous fish species may influence the counts, and is common to find high variability in the relative proportion of fish functional groups amongst reefs (McNeil et al. 2015).

We expected to encounter a gradient of human impact from near to off-shore as supported by a number of studies (Edinger et al. 1998, Cleary et al. 2005, Sawall et al. 2011), and this was reflected in the fish biomass and mildly in the coral cover, but not in the algae cover. In general the average cover of hard coral was high compared to the average for Indo-Pacific reefs (Bruno & Selig 2007), but consistent with values reported for Spermonde during the same period (Teichberg et al. *in prep*). Samalona and Barrang Lompo's lower coral cover were close to the average values for East Indonesia of around 20% (Bruno & Selig 2007), while Badi and Kapoposang were well above this average. Macroalgae and turf cover displayed different patterns than expected, with some of the highest values appearing in the least impacted island. While both Samalona (near-shore) and Kapoposang (furthest from shore) had very high algae, in Kapoposang it was composed of a diverse group of organisms combining turf, sponges and macroalgae. This may indicate a more diverse benthos than the rest of the inner shelf island reefs, where the MAT category included mostly turf, and could partly be due to Kapoposang's remote location and geographical differences. On the other hand, macroalgae are rarely seen in remote, theoretically pristine reefs, where turf (8-22% cover) is commonplace (Williams et al. 2013). Some studies suggest that algae actually dominate healthy reefs (Vroom et al. 2006), and that turf algae colonization after disturbance can lead to a recovery of coral dominance (Adjeroud et al. 2009). Samalona's high turf cover and the high amount of sediment smothering corals presumably resulting from the river plume indicates that this may not be the case for highly polluted waters, potentially showing

that good local fishery management is not enough if your reef is located next to a large coastal city with poor waste treatment.

The measured biomass of browsers and grazers for Badi and Kapoposang was within the range of worldwide estimates for unfished areas (Edwards et al. 2014). BG biomass for Samalona was within normal range for fished areas, while Barrang Lompo showed lower than normal BG biomass. Biomass of scrapers was lower than the average estimate for fished areas (Edwards et al. 2014) for all the islands but Badi, which was within range. The biomass of piscivores was low for all the inner shelf reefs and consistent with values for the most densely human-populated islands in the Pacific, while Kapoposang had an average piscivore biomass comparable to that of uninhabited islands (Williams et al. 2015). According to McNeil et al. (2015), in terms of fish functional properties Kapoposang would be in the healthy end of the spectrum, with high biomass of piscivores and high browsers and grazers, and Badi might be transitioning towards a pristine state by first increasing the biomass of key low trophic levels that clear the reef to allow coral recruitment.

4.2. Basic simulations: Drivers of benthos cover, fish biomass, and catch

The general simulations yielded expected results in terms of increased fish biomass in the absence of fishing (Fig. 1-B), reduced catch after nine years of destructive fishing (Fig. 1-C), or relatively lower coral cover in the high nutrient scenarios - particularly with no fishing or subsistence fishing (Fig. 1-B). The latter effect may indicate that the impact of nutrients is diluted when more aggressive fishing behaviour is in place.

Unexpected feedbacks between fishing, nutrients, and the modelled fish and benthic functional groups were reflected by the relatively high fish biomass and catch under high nutrients and destructive fishing compared to the other scenarios of fishing. First, our results point to certain model limitations which produce an abnormally high coral cover. Coral cover was extremely high compared with reported values for the Indo-Pacific (Bruno & Selig 2007) and Spermonde in the same time frame (Teichberg et al. *submitted*). High coral benthic occupancy prevents MAT colonization, which causes a reduction of browsers and grazers due to a lack of food sources, reducing in turn the biomass of carnivores and ultimately the fishing yield, particularly for commercial and cyanide fishing which target carnivores exclusively. In this situation, destructive fishing and bleaching counterintuitively increase fish biomass and catch by freeing space to allow algae to expand, providing food for the herbivores which is transferred upwards the trophic chain. Additionally, due to commercial fishing selectivity for carnivores, herbivores in the model have reduced predatory pressure and their biomass increases, in synergy with higher MAT abundance driven by high nutrients.

Scrapers biomass remained low likely as a result of low hard substrate cover for them to feed on. Their lowest biomass was in the subsistence scenario, probably due to the compound effect of low food sources and high predation. Their low biomass likely contributed to a low carnivore biomass in the subsistence scenario. Under the current model assumptions, feeding is a more important driver of herbivore biomass than coral habitat provision especially with low biomass failing to meet the minimum reproductive threshold.

4.3. Spermonde scenarios

We simulated the current scenarios for the four islands in Spermonde. Last year averages show a consistent drop in fish biomass across islands (Fig. 2-B), particularly for BG and carnivores in reefs that started with high biomass. Despite a steep loss in biomass, Kapoposang produced the highest yield, probably owing to the herbivorous fish present in the catch, which had no selectivity. Results from the basic simulations showed a much lower catch for the destructive fishing scenario, but in that case it did not include subsistence fishing, instead having a commercial fishery and higher frequency of dynamite fishing. This suggests that low-pressure, continued, fishing throughout the fish groups is better both for the system (i.e. fish biomass) and for the obtained yield. Unfortunately, Kapoposang is an outlier here and on other islands and throughout the world fisheries the main driver of fishing pressure is economic (Miñarro et al. 2016; Sethi et al. 2010), making a catch composed by low trophic levels less valuable and thus less desirable. From the inner-shelf islands, Badi had the highest catch despite having lower fish biomass, likely owing it to its diversification of fishing techniques (subsistence, commercial, cyanide) with low numbers of fishing units.

A few noteworthy observations can be inferred from comparing the total average throughout the simulation time (Fig. 3) with the last year. First, fish biomass is more than double for all islands, and daily catch increases with distance from the shore. The catch in Barrang Lompo and Badi was reduced by more than 10 kg per day. Their common feature is a combination between commercial and destructive fishing, which is not present in the other islands. Second, fish biomass is more diversified with BG dominating in all reefs except for Badi. This changes in the last year of simulation, where scrapers is the leading group (except in Kapoposang where BG biomass is half the fish biomass).

5. CONCLUSIONS

The presented results seem to indicate that under “aggressive” fishery scenarios (i.e. highly selective, combination of destructive and commercial fishing), the dynamics of the reef are no longer affected by the nutrient scenarios, which had a mild negative effect under no fishing and subsistence fishing. Additionally, fishery combinations of destructive and commercial characteristics produced lower catch over time, and commercial fishery cases saw steeper relative biomass reduction and potential loss of diversity.

By means of its assumptions, our model indicates that some healthy levels of MAT are not only desirable but also necessary when kept in balance with herbivores, creating a positive feedback which eventually increases the overall fish biomass and catch. This is supported by our results from the Kapoposang benthic transects, where algae made up a third of the benthic substrate and the reef had some of the highest fish biomass values. Our simulation results also support the notion that disturbances are responsible for the high species diversity seen in coral reefs (Connell 1978) by creating space for other species – losers under current conditions – to expand.

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Appendix

Table S1. Parameter values used in the basic simulation runs.

Parameter name	Units	Value
Bleaching frequency	days	1095
BG conversion factor	-	0.15
BG initial biomass	g m ⁻²	3.75
BG maximum biomass	g m ⁻²	120
BG reproduction rate	-	0.013
BG death rate	-	0.005
BG biomass threshold	g m ⁻²	8
BG consumed biomass factor	-	0.1
BG permanence factor	-	0.3
BG external supply	g	0
S conversion factor	-	0.18
S initial biomass	g m ⁻²	3.18
S maximum biomass	g m ⁻²	100
S reproduction rate	-	0.01
S death rate	-	0.005
S biomass threshold	g m ⁻²	6
S consumed biomass factor	-	0.1
S permanence factor	-	0.3
S external supply	g	0
S attack rate	-	1
S handling time	s	10
C conversion factor	-	0.10
C initial biomass	g m ⁻²	1.4
C maximum biomass	g m ⁻²	600
C reproduction rate	-	0.007
C death rate	-	0.009

C biomass threshold	g m ⁻²	15
C consumed biomass factor	-	0.1
C permanence factor	-	0.1
C external supply	g	500
C prey 1 attack rate	-	1
C prey 1 handling time	s	5
C prey 2 attack rate	-	3
C prey 2 handling time	s	5
C prey minimum ratio	-	0.05
Coral cover	-	D1 = 47 D2 = 18.7 D3 = 27
MAT cover	-	D1 = 10 D2 = 12.3 D3 = 18.7
Hard Substrate cover	-	D1 = 39 D2 = 42.7 D3 = 41
Empty cover	-	D1 = 4 D2 = 26.3 D3 = 13.3

Table S2. Parameter values used in the Spermonde simulations.

Parameter \ Island	Samalona	Barrang Lompo	Badi	Kapoposang
Reef area (km²)	0.75	0.22	0.48	0.49
Nutrients	High	High	Medium	Low
Coral cover	D1 = 27.3 D2 = 9.7 D3 = 27.3	D1 = 47 D2 = 18.7 D3 = 27	D1=28.7 D2=53.3 D3 = 47	D1 = 21 D2 = 35.7 D3 = 35.3
MAT cover	D1 = 33 D2 = 39 D3 = 41	D1 = 10 D2 = 12.3 D3 = 18.7	D1=31.3 D2 =5.7 D3=17.7	D1 = 36.4 D2 = 26.3 D3 = 45
Hard substrate cover	D1 = 18.7 D2 = 39 D3 = 23.7	D1 = 39 D2 = 42.7 D3 = 41	D1 = 23 D2 = 38 D3 = 27	D1 = 27 D2 = 26.3 D3 = 12.7
Empty space cover	D1 = 22 D2 = 12.3 D3 = 8.7	D1 = 4 D2 = 26.3 D3 = 13.3	D1 = 17 D2 = 3 D3 = 8.3	D1 = 15.6 D2 = 11.7 D3 = 7
BG initial biomass (g m⁻²)	12.5	3.8	34.1	35.1
S initial biomass (g m⁻²)	8.3	3.2	11.3	5.6
C initial biomass (g m⁻²)	1.4	1.4	3.14	30.7

Synthesis and Discussion

The potential of simulation models to provide insights on ecological questions that are crucial for the management of marine resources has been recognised in the last decades (Plagányi et al. 2014). The main purpose of this thesis was to use coral reef ecological theory to create a model as a basis for a scientifically sound, user-friendly decision support tool for the local management of coral reefs. To accomplish that we devised four major objectives, namely (1) develop a local coral reef model representing the impact of simultaneous stressors on key reef ecological groups, (2) turn it into a user-friendly decision-support tool to explore different management options, (3) collect qualitative and quantitative information on the artisanal fishery of Spermonde to help understand its social drivers, and (4) apply the model to real case studies to project their coral reef trajectories. Below is a synthesis of this thesis contribution in relation to these objectives.

1. CRITICAL EVALUATION OF THE MODELLING FRAMEWORK

The core work of this thesis consisted in developing SEAMANCORE as an ecological model intended for assisting the local management of coral reefs. SEAMANCORE is a quantitative tool to explore potential outcomes of different resource management and environmental scenarios by simulating the dynamics of relevant coral reef functional groups.

1.1. Choice of processes

A model is an abstract representation of a system with the purpose of answering a research hypothesis. This means that trying to meticulously represent it is out of scope. One of the common issues a modeller faces is choosing the number of parameters and processes to include in their model. Including too few parameters may produce a biased model only providing obvious or expected results, while if it has too many, it may be over fitted to the data/observations of the sample system and not easily transferable to other similar systems. The question of a trade-off between bias and variance is discussed by Grimm et al. (2005) as “the Medawar zone”, term first coined by Loehle in 1990. The Medawar zone is described as the area of intermediate model complexity where its pay-off is high. There is an adequate number of parameters that will make a model useful; anything less will be too simple to produce independent predictions, and anything more will be too complicated to have useful applications. How this simplification is accomplished reflects the assumptions being made and will define whether the model is useful or not. Aggregation and prioritization of processes are necessary through inevitable assumptions, as is to achieve a compromise between

resolution and coverage of spatio-temporal scales. A reasonably simple model with a limited number of parameters may be preferable to reduce confounding effects, increase transparency and reduce the computational demand. However, for the model to be successful in addressing issues pertaining to marine resource management, its structure needs to capture the mechanisms responsible for the ecosystem dynamics of interest. Aggregating processes or functional groups and losing a certain amount of detail is an option when they perform the same function and there is no significant benefit in representing them individually (e.g. Fulton et al. 2004).

In this dissertation, a focus on the feedbacks between the benthic habitat, the fish groups and the human external impacts on ecosystem level dynamics and fishing yield guided every step of the model development. This means that this model is not suited to answer ecological questions about specific reef species or about net fishing yield, instead its outcomes need to be interpreted in the context of the represented components and processes. SEAMANCORE is innovative in its approach by connecting two distinct dynamic compartments, benthos and fish, which run at different spatiotemporal scales and are affected by each other and by the three modelled stressors: fishing, bleaching, and nutrients. Overfishing, destructive fishing and watershed pollution have been ranked as the strongest local threats to coral reefs around the world (Burke et al. 2011). They were thus selected for the model along with the largest perceived global threat - global ocean warming -, over other relevant impacts such as ocean acidification or crown-of-thorns outbreaks. This choice was deemed the best compromise to provide a tool to address human impact highlighting the feedbacks between the ecosystem and its human users, while following most of the theoretical definitions and consensus in coral reef literature, where benthos dynamics and trophic relationships were considered some of the most relevant to fishing yield and habitat structure within one coral reef. The functional group approach taken in SEAMANCORE meant that huge aggregations were made by grouping together all benthos into four categories, and selecting fish three functional groups which excluded many common coral reef species. This reduction was necessary as a trade-off to increase the benthos spatial resolution, which permitted the use of published data to parameterize the growth rates of corals and algae while keeping the computational requirements relatively low. The choice of fish feeding equations included the effect of prey abundance, but not confounding effects of high predator density (e.g. territoriality), or the influence of water temperature (Harborne 2012), due to a paucity of mechanistic information in the coral reef literature (Stier and White, 2014).

1.2. Achievements of SEAMANCORE

Bringing together complex elements of a coral reef ecosystem, the model set-up was able to reproduce explicit spatial dynamics and capture coral reef zonation patterns. This was one of the goals of the modelling effort due to its importance for spatial resilience, management, and conservation (Margules & Pressey 2000, Ban et al. 2013, Allen et al. 2016). The model was able to clearly reproduce basic ecological processes, including complex feeding relations for one and two preys based on resource abundance, recruitment, fish movement into more desirable areas, and the effect of stressor combinations. It can both be used as an exploration tool for local management and to study the influence of different stressors on reef population dynamics. It can be useful for testing potential synergies between stressors (e.g. Gurney et al. 2013), and for providing insights about the relative effects of stressors (e.g. eutrophication vs. fishing) in largely customizable case-specific simulations.

SEAMANCORE, as developed in this thesis, is a free, open access modelling tool with a flexible structure and user-friendly interface. Model portability was another guiding principle for its development. The model can be broadly applied to a wide range of coral reef sites by specifying initial conditions and environmental characteristics, and by modifying parameter values directly on the user interface. While the current version was made for the Indo-Pacific region, the model general structure and rules of interaction follow general principles of coral reef ecological theory. The model's flexible, modular structure, permits the relatively easy addition - or deletion- of processes and compartments. This way, the model can be modified to add characteristics pertaining to other study interests and could potentially be used for coral reefs in the Caribbean by, for instance, adding a new functional group to represent sea urchins, which are key grazers in the Caribbean (Williams & Polunin 2001). Future versions may refine the current equations, add more functional groups or even a dynamic fisheries module to further the scope of the application. SEAMANCORE strives to be as user-friendly as possible with an intuitive menu interface and easy-to-gather input data requirements. Simulations can be parameterized with limited field data which is routinely collected in basic coral reef monitoring programs (Flower et al. 2017), including rapid benthic cover and fish biomass assessments. The greyscale bathymetric map requires one *png* image, which can be easily produced from GIS data or even hand-drawn and digitalized.

1.3. Limitations of SEAMANCORE

Modelling any system constitutes a thorough test for the modeller's understanding of it. The task is more challenging in mechanistic or IBM approaches where a detailed description is needed. In the case of SEAMANCORE the rules developed for small scale benthic

processes did not yield the expected results in the larger scale simulations. The set-up was too advantageous for coral cells, which ended up overtaking the reef area under virtually every scenario. Despite having a design by which the global pre-colonization rule – turning empty cells into hard substrate – only had a 1% probability of occurring, the empty space state was not durable enough. This essentially triggered benthos colonization by coral or MAT. The cause of this problem going undetected during model development was using insufficient scenarios in the model calibration. To calibrate the model, a layered, hierarchical approach was used consisting on verifying the patterns in benthos cover (a) with the benthos compartment only under different initial cover proportions, nutrient and bleaching scenarios, and (b) with the benthos and fish compartments under different initial cover and biomass conditions, nutrient and bleaching scenarios. Because it was assumed that pristine reefs behave as described in the coral reef literature – based largely on studies made in coral reefs impacted to some degree- fishery scenarios were excluded from the benthos calibration. Furthermore, a smaller subset of the ordinarily used map (200 x 200 cells) was used to achieve faster calibration results. Including coral as part of scraper diet might overcome this limitation and make model dynamics more realistic.

Validation of SEAMANCORE with data was only possible with reference values obtained from global meta-analysis or individual studies. The lack of long term continued monitoring data of coral reefs and artisanal reef fisheries under clearly specified conditions made it impossible to compare the modelled trajectories with real data. As such, validation was based on reference points and qualitative descriptions of observed or expected patterns.

1.4. Ecological insights

Models contribute with the synthesis of qualitative and quantitative knowledge of ecosystems (Berger *et al.*, 2008). From hypothesis testing (e.g. by changing particular behavioural rules, modifying environmental parameters, etc.), to generation of data for future management scenarios, model simulations can show how complex interactions among human resource users, environmental and ecological factors shape life histories and the dynamics of coral reef ecosystems. However, the use of such complex approaches carries a number of complications with it, the first one being the task of disentangling model results. Despite the limitations described in section 1.3, the model reproduced expected benthic and fish relative dynamics, and was able to provide information on the potential efficiency of fishing technique combinations. Our results indicate that under combinations of destructive and commercial fishing, dynamics of the coral reefs were dominated by fishing with no apparent influence of

nutrient levels. Aggressive fishing behaviour produced reduced catch over time, steeper relative biomass reduction and potential loss of diversity.

By means of its assumptions, our model showed that some healthy levels of MAT were not only desirable but also necessary when kept in balance with herbivores, creating a positive feedback which eventually increased the overall fish biomass and catch. This was supported by our results from the Kapoposang benthic transects, where algae made up a third of the benthic substrate while the reef sustained the highest reported fish biomass values. Our simulation results also support the notion that disturbances are responsible for the high species diversity seen in coral reefs (Connell 1978) by creating space for other species – losers under current conditions – to expand. Although this behaviour was excessively stressed due to the model parameterization, it showed coral reefs under any given scenario gravitating towards one particular “stable state” – i.e. high coral cover–, a notion which is supported by studies on the coral reef fossil record showing a remarkable stability in coral reef communities (Pandolfi 1999).

2. INFLUENCE OF SOCIAL STRUCTURES ON FISHERMEN BEHAVIOR: THE CASE OF THE PATRON-CLIENT SYSTEM IN SPERMONDE

Unlike the fishery set-up in SEAMANCORE, fishing behaviour in tropical artisanal fisheries is not constant throughout weeks and years but exhibits high flexibility in effort, target species and fishing grounds (Pauly & Murphy 1982). Complex social networks linking local fisheries with local, regional and global seafood markets are an important driver of such variability. Patron-client systems are informal credit systems that bond powerful individuals with numerous subordinates in a reciprocal agreement by which patrons extend favours ranging from loans to protection to fishermen and receive labour in return (Johnson, 2010). Chapter three of this thesis contributed to untangle the role of the patron-client system on the fishing behaviour of individual fishermen in Spermonde by evaluating differences in selected sociodemographic, economic and fishing behaviour variables between independent fishermen and fishermen within the patron-client system. While the reasons that compel fishermen to engage in patronage were unclear, the groups displayed different fishing behaviour, with fishermen with patrons exhibiting a profit-driven fishing style by getting more valuable catch from higher trophic levels and possibly including destructive fishing practices, while independent fishermen had larger subsistence catch. This market-driven fishing

behaviour from dependent fishermen could threaten the long-term sustainability of the fishery and lead to a poverty trap. On the other hand, fishermen may value the safety net that the patron-client system confers in scarce times (Ferse et al, 2012a; Johnson, 2010; Bailey et al, 2016). Knowing that patronage has a strong influence in the fishermen catch, time allocation, etc. it is safe to assume that patrons may dictate which species to target following regional or global market trends (Schwerdtner Máñez & Ferse 2010). This makes them a powerful driver for the artisanal fishery in Spermonde, and potentially in other geographic areas where similar systems are in place.

3. CONCLUSIONS AND OUTLOOK

The work in this thesis successfully fulfilled its initial objectives. A coral reef model representing the impact of simultaneous stressors was produced and converted into a user-friendly decision-support tool to facilitate the assessment of different management options. Model limitations regarding benthic dynamics may be overcome by an additional modelling iteration loop in which corals are included as part of scraper fish diet and its parameters recalibrated. The study on the artisanal fishery of Spermonde contributed to the body of scientific literature on social drivers influencing fishing behaviour by empirically showing catch and behavioural differences between fishermen within the patron-client system and independent fishermen. It also provided quantitative information about daily catches, which was used to parameterize fishing scenarios in Spermonde for a real case application of the model to project coral reef trajectories under a gradient of anthropogenic stressors and initial conditions.

Some research recommendations to increase the usefulness and efficiency of modelling coral reef ecology and resource management stem from this work. While the choice of organisms and processes in SEAMANCORE could be enlarged, the complexity added would difficult the interpretation of results (Weijerman et al. 2015). Instead, a refinement of process description at adequate scales is advised. One particular gap encountered during this thesis was the paucity of detailed feeding equations for coral reef fish. We encourage the pursuit of more research focusing on developing functional responses of coral reef organisms, which may be quite different from those of pelagic fish (Hunsicker et al. 2011, Harborne 2012).

Human behaviour is the main source of uncertainty in fisheries management (Fulton et al. 2011), and it is widely accepted that only by linking the social and ecological systems around coral reefs will we be able to find solutions to their widespread degradation (e.g. McClanahan

et al. 2008). As shown by our research on the patron-client system, social networks play a crucial role in how stakeholders deal with marine resources. This includes cultural factors, knowledge distribution, social and religious pressures (Hviding & Baines 1994), awareness (White & Vogt 2000), and economic opportunity (Sethi et al. 2010), which guide fishers' objectives. The choice of fishing strategies and tactics is affected by fish availability, market demands, and social, technological and economic resources. Further advancement of resource management research may benefit from further modelling human behaviour in explicit ways. Developing dynamic human behavioural models requires more in-depth studies to understand decision-making mechanisms at the local, regional and global scales, along with transparent monitoring to prevent catch underreporting, and to increase data resolution. Small scale fishers show an adaptation process when confronted with different types of limitations and stimuli, which can lead to specialization, cooperative work and changes in behaviour in response to fishing efficiency (Salas & Gaertner 2004). Many island communities, such as those in Indonesia, display a combination of fishing vessels and gears that can be easily adapted to changes in species abundance by switching targets, or to different physical and organizational contexts. Ignoring such issues limits the ability to anticipate fishers' response to different resource regulation and management initiatives (Salas & Gaertner 2004). Demands of a globalized market, fishermen perceptions, preferences, abilities and resource access all play a crucial role in catch size and distribution of fishing effort. Including them in models targeting the study of better management and protection of coral reefs ecosystems is likely to increase their effectiveness and fairness for the human communities depending on them.

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Annex

ANNEX 1

Overview of active conference contributions presenting parts of the PhD work.

Number	Conference name, location	Date	Authors	Presentation title	Contribution type
1	International Conference of Marine Sciences, Bogor (Indonesia)	June 2013	Miñarro S, Reuter H.	Individual-based Models for the Management of Coral Reefs: Application to the case of Spermonde, Indonesia.	Oral presentation
2	Bremen PhD days in the Marine Sciences, Bremen (Germany)	April 2014	Miñarro S, Reuter H.	An integrated simulation model as a tool for managing coral reefs in Indonesia.	Oral presentation
3	IMBER Open Science Conference (Future Oceans), Bergen (Norway)	June 2014	Miñarro S, Reuter H.	An integrated individual-based model as a tool for socio-ecological management of coral reefs in Indonesia.	Oral presentation
4	Invited seminar at the Faculty of Marine Science and Fisheries, Hasanuddin University, Makassar (Indonesia)	December 2014	Miñarro S.	Introduction to ecological modelling and its application to the coral reefs of Spermonde.	Seminar
5	International Symposium on Sustainable Management of Coastal and Marine Resources in the Savu Sea Waters, Kupang (Indonesia)	May 2015	Miñarro S, Reuter H.	Why and how to use a model as a decision-support tool to sustainably manage marine resources.	Oral presentation
6	Conference on	September	Reuter H,	Coral reef	Oral

	Small Islands Research in Tropical Regions. Makassar (Indonesia)	2015	Miñarro S.	based marine resource use - Application of different modelling approaches.	presentation
7	Conference on Small Islands Research in Tropical Regions. Makassar (Indonesia)	September 2015	Navarrete-Forero G, Miñarro S , Breckwoldt A, Mutmainnah A, Putri A.P, Walyandra Z.Z, Sudirman, Reuter H.	Location, use and selection of fishing grounds in Spermonde: the case of hook and line fishers from Badi Island.	Oral presentation
8	International Conference on Science for the Protection of Indonesian Coastal Marine Ecosystems. Bali (Indonesia)	January 2016	Miñarro S , Leins J, Fulton E, Jompa J, Reuter H.	A user-friendly simulation model to assist in the local management of coral reefs exposed to multiple stressors.	Oral presentation
9	International Conference on Science for the Protection of Indonesian Coastal Marine Ecosystems. Bali (Indonesia)	January 2016	Navarrete-Forero G, Miñarro S , Breckwoldt A, Sudirman, Mildemberger T, Reuter H.	Where do fishers go? Mapping fishing grounds in the artisanal coral reef fishery of Badi Island, Spermonde.	Poster
10	International Coral Reef Symposium (ICRS). Honolulu, Hawai'i.	June 2016	Reuter H, Breckwoldt A, Glaser M, Teichberg M, Miñarro S , Lukman M, Jompa J.	Integrative analysis of sustainable trajectories in heavily used Indonesian coral reef systems.	Oral presentation

ANNEX 2

List of additional publications I have been part of as part of my PhD work.

1. Partelow S, Lukas MC, Rohe J, Nelson K, Borges R, **Miñarro S**, Tamatey E. Ocean and society: Integrating research in the environmental social sciences. *Youmares 7 conference proceedings*, September 2016, Hamburg, Germany.
2. Navarrete Forero G, **Miñarro S**, Mildenerger T, Breckwoldt A, Sudirman, Reuter H. Investigating spatial patterns of an artisanal fishery through participatory boat tracking in Spermonde (Indonesia). *Under Review in Frontiers in Marine Science*.
3. Teichberg M, Wild C, Bednarz VN, Kegler H, Lukman M, Gärdes A, Heiden JP, Weiland L, Abu N, Nasir A, **Miñarro S**, Ferse SCA, Reuter H, Plass-Johnson JG. Spatio-temporal patterns in coral reef communities of the Spermonde Archipelago, 2012-2014, I: Comprehensive reef monitoring reveals two indices that reflect changes in reef health. *In preparation for Frontiers in Marine Science*.
4. Plass-Johnson JG, Ferse SCA, Bednarz VN, Gärdes A, Heiden JP, Lukman M, **Miñarro S**, Kegler H, Weiland L, Wild C, Reuter H, Teichberg M. Spatio-temporal patterns in the coral reef communities of the Spermonde Archipelago, 2012-2014, II: Fish assemblages. *In preparation for Frontiers in Marine Science*.

ANNEX 3

Changes in the published version of the PhD dissertation.

Page ii- Correction in Prof. Dr. Wilhelm Hagen's affiliation.

Page 3- Summary in German.

Page 5- Addition of the paper outline including author contributions.

Page 7- Updated page numbers in table of contents.

Page 49, 71- Withdraw broken link for model download and clarification of its future publicly accessible location.

Page 125- Table readability improvements.

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Versicherung an Eides Statt

Ich, Miñarro Villanueva Sara (Matr.-Nr. 2950924)

versichere an Eides Statt durch meine Unterschrift, dass ich die vorstehende Arbeit selbständig und ohne fremde Hilfe angefertigt und alle Stellen, die ich wörtlich dem Sinne nach aus Veröffentlichungen entnommen habe, als solche kenntlich gemacht habe, mich auch keiner anderen als der angegebenen Literatur oder sonstiger Hilfsmittel bedient habe.

Ich versichere an Eides Statt, dass ich die vorgenannten Angaben nach bestem Wissen und Gewissen gemacht habe und dass die Angaben der Wahrheit entsprechen und ich nichts verschwiegen habe.

Die Strafbarkeit einer falschen eidesstattlichen Versicherung ist mir bekannt, namentlich die Strafandrohung gemäß § 156 StGB bis zu drei Jahren Freiheitsstrafe oder Geldstrafe bei vorsätzlicher Begehung der Tat bzw. gemäß § 161 Abs. 1 StGB bis zu einem Jahr Freiheitsstrafe oder Geldstrafe bei fahrlässiger Begehung.

Bremen, 8 February 2017

Sara Miñarro Villanueva

