An integrated ecosystem model for coral reef management

where oceanography, ecology and socio-economics meet

Mariska Weijerman

Photo on front cover is Tumon Bay in Guam, *photo NOAA*

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An integrated ecosystem model for coral reef management

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Mariska Weijerman

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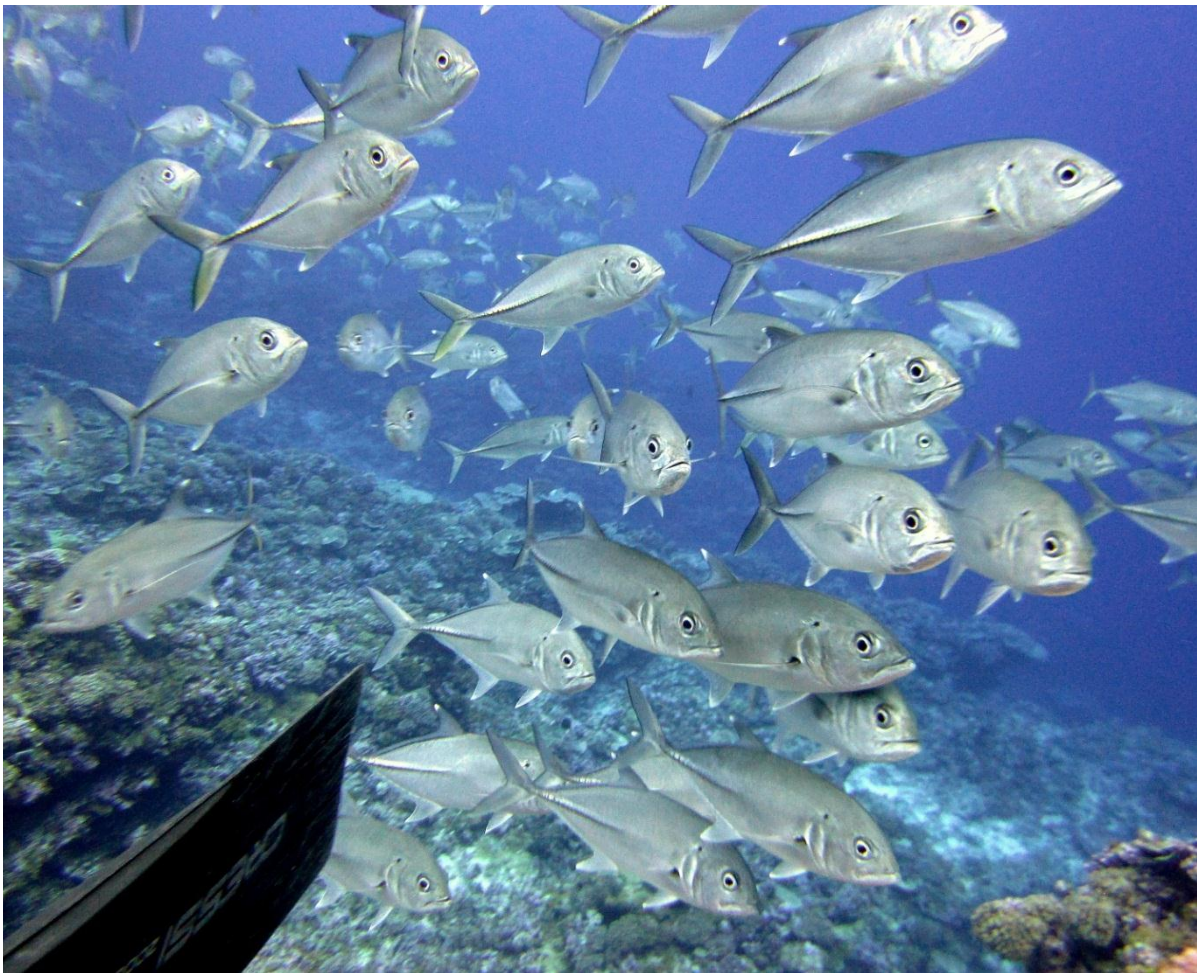
Table of Contents



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Chapter 1

General introduction

1.1 Background

Human well-being is linked to natural resources and the increase in human population and their activities leads to multiple users vying for the same resources. These uses can be of monetary benefits, for example, commercial and recreational fisheries, oil and gas mining, coastal development and aquaculture or of non-monetary benefits, such as cultural and spiritual values, and of ecosystem services (Costanza et al. 1998). Humans have now affected many of the earth's ecosystems and their services (Birkeland 2004, Doney et al. 2012, McCauley et al. 2015). These affected services include regulating services (e.g., the biogenic structure of reefs mediating extreme weather and the recycling of nutrients and detoxification of pollutants), provisioning services (e.g., food and medicines) and cultural services (e.g., cultural and spiritual values) upon which people and societies depend. Managing multiple uses are challenges confronting resource managers responsible for maintaining sustainable use of natural resources and preventing or mitigating the degradation of ecosystem services.

Coral reef ecosystems are especially vulnerable to climate change and worldwide a third of reef-building coral cover is projected to be lost by 2050 (Carpenter et al. 2008, Jackson 2008). Already live coral cover has declined since the seventies, with an estimated decline of 20% worldwide (Wilkinson 2008), 40% in the Indian and southwest Pacific Ocean (Bruno and Selig 2007), 50% in the Great Barrier Reef, Australia (De'ath et al. 2009), 70% in the East Asia Seas (Yap and Gomez 1985) and 50% in the Caribbean (Jackson et al. 2014). These declines are attributed to land-based sources of pollution, including sedimentation and eutrophication, and destructive fishing practices, overfishing and mortality events related to elevated temperatures, with most noteworthy being the global mass 'bleaching' events in 1998 and 2005 (bleaching is the expulsion of the symbiotic microscopic algae in the coral tissue). With the decline in coral cover the species they harbor are likely to decline as well (Jones et al. 2004, Munday 2004b). The main objective of this thesis is to develop a model to quantify the effects of watershed and fishery management on ecosystem services in order to evaluate the economic and ecological tradeoffs of alternative management policies against a backdrop of climate change.

Vulnerability of coral reef ecosystems to natural and human-induced disturbances is a function of (1) exposure to present and future climate states and human activities; (2) sensitivity or resistance (species can avoid or adapt to exposure depending on genes, local environmental variability and surrounding environmental changes); and (3) the capacity to recover (which depends on the availability of resources that enhance resilience, such as ecological factors, species and functional diversity, spatial factors, reproduction and connectivity, and shifting geographic ranges [reviewed in Brainard et al. 2011]). Local drivers and changing climate threaten the ecosystem functions and services that coral reef ecosystems provide. Ocean warming (e.g., Donner et al. 2005, Donner 2009), ocean acidification (e.g., Guinotte et al. 2003) and their synergistic effects (Harvey et al. 2013) have been ranked as the top proximate threats in recent reviews (Brainard et al. 2011, Burke et al. 2011). Disease, often associated with bleaching events and local human impacts, was ranked as the next most important threat in those reviews. Some researchers, however, have identified grounds for optimism: vulnerability assessments of corals and coral reef fishes to ocean warming and fishing indicated that reduced fishing may enhance key ecosystem processes and this likely increases a reef's capacity to recover (e.g., McClanahan et al. 2014). Other studies also indicated that local management regulations in reducing sedimentation, nutrient input and fishing can mitigate the effects of the imminent global threats (Carilli et al. 2009, Hughes et al. 2010, Graham et al. 2011b, Kennedy et al. 2013).

Traditionally, fishing regulations were based on single species management but recently there has been a fundamental shift towards ecosystem-based management (EBM) or ecosystem-based fisheries management (EBFM) with research and management coming to focus on the advantages of EBM (Hilborn 2011), including the development of EBM indicators (Fulton et al. 2005, Coll et al. 2010) and studies on cumulative effects on ecosystems of various disturbances (Brown et al. 2010, Griffith et al. 2012). Although the concept of EBM was originally introduced in 1873 by Spencer Baird (1873), EBM is only now the dominant approach advocated by researchers (Pikitch et al. 2004, Levin et al. 2009) and increasingly mandated by national fisheries policies and international agreements, for example, the U.S. National Ocean Policy 2010 (Executive Order 13547 2010) and the European Common Fisheries Policy 2014 (http://ec.europa.eu/fisheries/cfp/index_nl.htm). However, implementing EBM is not straightforward, due to the many, frequently conflicting, objectives of the various stakeholders (Link 2002) and the lack of suitable operational tools (Arkema et al. 2006).

EBM can be supported by ecosystem models that can help disentangle the effects of consumer-resource dynamics, habitat and climate factors (Guerry et al. 2012, Samhouri et al. 2013). Models have thus become important tools for gaining insights in to system changes due to human (e.g., fishing) or environmental (e.g., hurricanes) disturbances, to further develop theories of system function and interconnection, to identify tipping points, to assess trends by indicators and to point out research gaps (Mumby et al. 2007a, Fulton et al. 2011b, Ainsworth and Mumby 2014). Additionally, ecosystem models can simulate policy scenarios and evaluate the tradeoffs among stakeholders' objectives (Smith et al. 2007, Fulton et al. 2014). For example, real-world experimentation of large-scale fishery regulations is not generally feasible but tradeoffs can be evaluated using ecosystem models. Multi-species or ecosystem models can also complement single-species stock-assessment models and provide a more integrated framework for system-wide decision-making by focusing on emergent properties at the community and ecosystem levels (Fogarty 2013).

For the judicious use of ecosystems models as a management tool we need to ensure that they capture the combination of the effects of external drivers and internal feedbacks that shape these systems and their resilience under environmental change. On coral reefs, and on other systems, local drivers often influence or reinforce feedback mechanisms (Nyström et al. 2012) and other interactions between functional species groups. Examples include the shift in the energy balance from macrobes to microbes due to fishing, pollution and/or coastal development (McDole et al. 2012); a disruption in alga-coral-grazer dynamics due to a reduction in grazers and/or an increase in nutrients causing a shift from coral-dominated reefs to algal-dominated reefs (Mumby 2006, Mumby and Steneck 2008); trophic cascades due to a take of apex predators (Williams et al. 2008); a loss of fish abundance due to fishing (Williams et al. 2015); and a decline in fish diversity and abundance due to a decline in structural complexity resulting from a loss in coral cover (DeMartini et al. 2013, Graham and

Nash 2013). The capacity of organisms and natural systems to 'bounce back' can be degraded by sequential, chronic and multiple disturbances, physiological stress and general environmental deterioration (Nyström et al. 2000) and by the reduction of large and diverse herbivorous fish populations (Pandolfi et al. 2003, Bellwood et al. 2006). These dynamics and their relationships need to be included correctly in a coral reef ecosystem model to ascertain that model simulations are representative of the real system so that model projections are accurate and reliable.

The deterministic, spatially-explicit coral reef model, developed in this thesis, is an integrated framework that focuses at the emergent properties at the community and ecosystem level and can be used for system-wide decision-making and management strategy evaluation (MSE). To give it this capacity the inclusion of the myriad coral reef ecosystem relationships was needed. The identity of these relationships was established from simulation outcomes of other coral reef models and empirical field studies on reef systems. The Atlantis ecosystem modelling framework, developed for temperate fisheries systems, provided a flexible platform for the coding of tropical reef functionality, as it already specifically supported ecosystem scale MSE (Plagányi 2007). Atlantis' modular framework allows parameterization to be as detailed per module as desired by the developer, and Atlantis incorporates dynamic two-way interactions between oceanographic, ecological, biochemical and socio-economic processes. In this thesis, I explain my step-wise approach to the development and application of the Atlantis Coral Reef Ecosystem model (Guam Atlantis) with a case study of the reefs around Guam in the western tropical Pacific Ocean.

1.2 Step-wise approach

Model development involves tradeoffs between realism and process detail (Fig. 1.1; Levins 1966). The modeler's dilemma is to choose an approach that balances simplicity, realism and accuracy, and achieves the overlapping, but not identical, goals of understanding natural and managed systems and projecting their responses to change (c.f. Levins 1966). Depending on the leading principle of the model development (Mooij et al. 2010), models can be categorized as minimal, intermediate and complex models, and all have been applied to coral reef ecosystems.

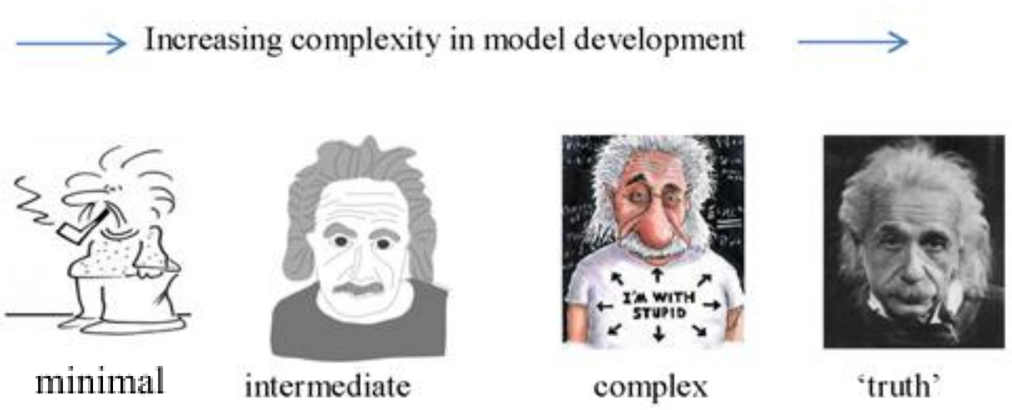


Figure 1.1. Schematic representation of model complexity and accuracy depending on the conceptualism of space, time and structure and the number of process details dynamically represented.

An ecosystem model can be seen as an abstract representation of a set of hypotheses that are either tested with empirical studies, theories or with minimal or intermediate models. The integration of system dynamics can be achieved through complementary use of models or through integrated models that combine many aspects of the system in one framework (Butterworth and Plaganyi 2004). Coral reef ecosystem models to date have generally focused on one or two external factors, such as, climate, nutrient and sediment inputs and fisheries (McClanahan 1995, Arias-González et al. 2004, Ainsworth et al. 2008b, Buddemeier et al. 2008, Riegl and Purkis 2009, Anthony et al. 2011b, Blackwood et al. 2011). Internal feedbacks have also been studied with coral reef models to provide insights into how these systems respond (e.g., linearly or non-linearly) to external factors and whether or not changes in system state lead to regime shifts or alternative stable states (Bellwood et al. 2004, Mumby 2006, Mumby et al. 2007a, Yñiguez et al. 2008, Renken and Mumby 2009, Tam and Ang 2012, Żychaluk et al. 2012).

For a full understanding, models need to capture how species- and ecosystem-level responses interact, as well as representing the link between species- and ecosystem-level processes accurately. Additionally, when attempting to understand the effects of human activities, these models need to capture the two-way dynamics between human use and ecological impacts and should be coupled with socio-economic models. Few models have included the various human activities that alter the coral reef dynamics and simultaneously the socioeconomic context in which they occur (Kramer 2007, Tsehaye and Nagelkerke 2008, Fung 2009, Melbourne-Thomas et al. 2011b). With the new insights provided by empirical studies and model results, a coral reef ecosystem model can now dynamically integrate the underlying biological processes that confer resilience and sustainability to reefs, with biochemical and hydrological dynamics and place those in the context of human activities.

To choose the appropriate model type and for proper model development, the objectives should be clear and upfront and stakeholders should be involved. I followed the guidelines for Integrated Ecosystem Assessments (Levin et al. 2009) for my ecosystem model development. The steps I took are presented in the following chapters in my thesis and include:

1. **Scoping**. In this step the specific ecosystem objectives and threats were identified. During a workshop that I organized together with the NOAA Pacific Islands Fisheries Science Center and the Pacific Islands Regional Office (PIRO), invited speakers presented the current status of Guam reefs, the main threats to those reefs, including a focus on the potential effects of the proposed military build-up in Guam. With that current context in place, I explained how ecosystem models in general, and the Atlantis model in particular, could serve as a decision-support tool in visualizing coral reef trajectories under alternative policy scenarios. Workshop participants discussed the overall goals of ecosystem metrics, identified ecological and economic indicators, and management strategies to assist resource managers in making educated decisions, based on evaluation of the economic and ecological tradeoffs highlighted by model simulations (Weijerman and Brown 2013 and unpublished results of meetings in July 2014).

2. **Indicator Development**. Ecosystem indicators that were identified during the workshop in 2012 (Weijerman and Brown 2013), are tested with an ECOPATH model (Christensen and Pauly 1992, Christensen et al., 2008). These indicators provide the basis for the assessment of status and trends in ecosystem state. Some of the selected indicators represent the abundance of key species while others serve as proxies for ecosystem attributes (e.g., maintenance of critical service functions, system maturity).

3. **Risk Analysis**. Having identified the leading principle for model development and the indicators, I evaluated the risk to these indicators posed by human activities and natural processes using a complex, end-to-end modelling framework, Atlantis (http://atlantis.cmar.csiro.au/). First I designed and parameterized the Atlantis model and then included key coral reef dynamics. From the literature, I identified the main drivers influencing the sustainability of ecosystem services (Brainard et al. 2011, Principe et al. 2012) (Table 1.1) and developed ways to incorporate the underlying response mechanisms, derived from published empirical relationships or from other coral reef models, into the Guam Atlantis model.

   A common maxim of model development is that ‘less is more’ (Levins 1966), i.e., one should only incorporate the key mechanisms and functional groups, balancing accuracy, complexity and realism of various dimensions, such as time, space, trophic components, process details, human activities, boundary conditions and forcings. Whole-of-system or end-to-end models are data intensive with high spatial and functional complexity compared to minimal or intermediate models but they can be robust when reasonable limits are set on their complexity (Fulton et al. 2003a, Fulton et al. 2003b, 2004c, Mitra and Davis 2010), the relevant biological groups and functions are considered and enough detail is incorporated to make accurate predictions (Travers et al. 2007).

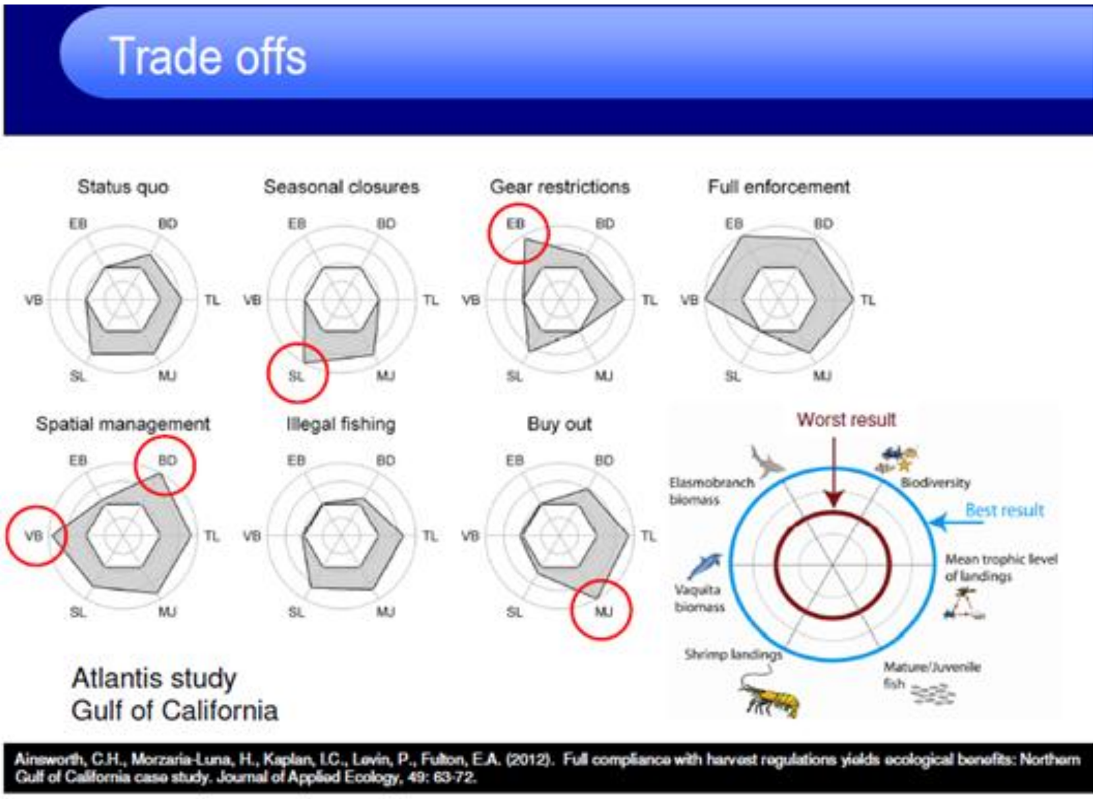
Table 1.1. Key drivers, pressures (proximate threats) and affected coral reef ecosystem variables.

Drivers	Pressures	Ecosystem Indicators
changing climate	ocean warming: elevated water temperatures	coral growth & mortality, coral recruitment, and benthic species composition
	ocean acidification: increasing atmospheric CO_2 concentrations and oceanic uptake	growth of corals and other calcifying species, benthic species composition, coral recruits; and survival rate of juveniles,
change in land use	sedimentation; non-point sources of pollution; nutrients; and disease	coral growth, cover, species composition, recruitment; turbidity; and algal cover
fishing activity	excessive fishing	coral and algal cover; fish biomass, abundance, size distribution and species composition; complexity; income/food for fisherman; and added value from fishing expenditures

After identifying the key dynamics and researching how to incorporate their relationship from empirical data and coral reef model simulations (see Chapter 6), the Atlantis code was modified to represent (a) coral growth in three dimensions; (b) coral-algal competition (e.g., space competition and macro-algal overgrowth); (c) negative effects of sediments on coral growth; (d) the positive feedback between the structural complexity of corals and fish (i.e., corals provide shelter to small and juveniles fishes while herbivorous fishes maintain coral reef algal assemblages in cropped states facilitating coral recruitment); (e) the 'bleaching' phenomenon, in which corals expel a portion of their symbionts (which causes the corals to lose color and appear 'bleached') when temperatures rise above a threshold; such bleaching event can results in total or partial mortality, with associated scope for short-term recovery; and (f) the negative effects of a decline in pH (i.e., 'acidification') on reef organisms including corals.

Criteria used for testing the validity of the model and to verify model outcomes were based on guidelines for Atlantis model development (Horne et al. 2010, Link et al. 2010, Ainsworth et al. 2011, Fulton et al. 2014) and include: 1) Predicted biomass matches observations or are plausible based on information from domain experts. In this case for many benthic groups this defaults to staying within a factor of two of initial conditions. For fish groups we expected predicted biomass (with no fishing or other drivers) to approximate those in marine reserves in Guam or from the unpopulated Northern Mariana Islands; 2) Weight-at-age stays stable and abundance of size classes decreases with increasing size classes (few large organisms and many small ones); and 3) Reproduced catch data has a plausible trajectory and magnitude of historical change without pushing any modeled group to extinction. Ecosystem relationships related to disturbances were validated by comparing model outcomes with empirical data and published literature. Based on the compliance with all three criteria and agreements between model outcome and expectations, I concluded that the Guam Atlantis model was stable with plausible biomass trajectories. With this model I then quantitatively compared the trajectories of the chosen indicators while simulating a range of anthropogenic drivers—land-based sources of pollution, fishing and climate change—separately and simultaneously.

4. **Management Strategy Evaluation**. Complex end-to-end models cannot be tractable evaluated using standard validation and sensitivity analyses (Stow et al. 2009). Consequently, this makes them unsuitable for tactical management, such as setting catch quotas or identify areas for protection from fishing. However, when MSE is justified, these end-to-end models are important strategic management tools to project how reefs will respond to the current global disturbances under alternative local management strategies. I will use the MSE approach to evaluate the potential of different management strategies to influence the status of natural and economic indicators (Fig. 1.2). By coupling this model to a Bayesian Network model framework, I was also able to identify the cultural and social-economic tradeoffs of the alternative management policies.



Trade offs

Atlantis study
Gulf of California

Ainsworth, C.H., Morzaria-Luna, H., Kaplan, I.C., Levin, P., Fulton, E.A. (2012). Full compliance with harvest regulations yields ecological benefits: Northern Gulf of California case study. Journal of Applied Ecology, 49: 63-72.

Figure 1.2. Example of the use of Atlantis for management strategy evaluation for the Gulf of California (as of Ainsworth et al. 2012). Various alternative management policies were simulated independently and all together (i.e., the full enforcement top right) to visualize and quantify the effects on the indicators.

1.3 Significance and novelty of thesis

In a wider context, this thesis forms part of the modelling work of the Atlantis ecosystem modelling community. Atlantis was developed by Dr. Elizabeth (Beth) Fulton (Commonwealth Scientific and Industrial Research Organisation) in 2001 and has since been applied to a range of temperate marine ecosystems in Australia, the US, South Africa and Europe, with tropical and polar examples under development (Fulton et al. 2011b). As EBM has become more prominent in national policies, so has the need for tools, such as ecosystem models, to inform EBM. Whole-of-system or end-to-end models, such as Atlantis, model the full suite of marine ecosystem dynamics, uses, management and feedbacks and synergies. Atlantis was designed as one of the very few modelling platforms that can handle “sunlight to fish markets and everything in between,” (http://atlantis.cmar.csiro.au/www/en/atlantis/Atlantis-Summit.html) particularly linking biophysical Regional Ocean Model Simulations (ROMS) to ecology with anthropogenic modules to interface with the various socio-economic facets of a marine ecosystem. The uniqueness of Atlantis is that it is multi-sector, modular, has multiple functional forms a user can choose, and it is designed specifically to address system-level management strategy evaluation. However, to maintain its usefulness Atlantis needs on-going development, refinement, testing and evaluation of the myriad modular approaches it provides in a variety of ecosystems.

All fully implemented and published applications of Atlantis to date have focused on temperate systems whereas Guam Atlantis, the model in this study, focuses on tropical coral reef ecosystems. Currently the University of South Florida is developing an Atlantis model for the Gulf of Mexico (including corals) and CSIRO is developing models for the Great Barrier Reef and Gladstone harbor (also including corals). The Guam Atlantis model differs from these models in its size of the spatial domain (e.g., 100 km^2 for Guam Atlantis compared to 1.6 million km^2 for the Gulf of Mexico). The Guam Atlantis model is likely more sensitive to benthic community processes and the dynamics that influence them. Parameterization of Guam Atlantis can aid these other more broad-scale models with details where needed.

Another novelty is the coupling of a Bayesian Network Model framework detailing the motivation and fishing activity of Guam's fisherman to Guam Atlantis. Since coral reef fisheries are considered to be more recreational than commercial in Guam (e.g., Van Beukering et al. 2007), economic 'rules' that govern the decision to go fishing for commercial reasons (which is the case when large areas are of concern) do not apply. Instead, the motivation to go fishing is driven by a desire to fish for fun, to put dinner on the table or for cultural reasons (Allen and Bartram 2008). Hence, the economic module of Atlantis, which was initially developed to represent the commercial fishery, does not fit well with the motivation for fisherman in Guam. A similar approach has also been used for a recreational lobster fishery by indigenous fisherman in the Torres Strait (van Putten et al. 2013), but has not previously been coupled to any Atlantis model. Marine tourism is of major economic importance in Guam (Van Beukering et al. 2007). I, therefore, also developed a Bayesian Network Model framework for dive tourism, which is coupled with the fishery motivation model to form the full Guam Atlantis ecosystem model (Chapter 8).

My thesis research also innovatively addresses the myriad threats that coral reefs face simultaneously. Many coral reef models have been developed, but only a few dynamically incorporate the oceanographic, ecological and biogeochemical processes, and none specifically include the spatial heterogeneity of a reef with a high-resolution daily time-step. Atlantis is generic enough in its dynamic processes to apply to other Pacific islands where there is sufficient data for quantifying the initial conditions (e.g., spatial model based on homogenous areas, biomass of all functional groups, spatial distribution of groups, life-history parameters if the biological communities differ greatly from the ones in Guam). The model-generated results aid in identifying the ecological and economic 'pros and cons' of alternative management policies, taking into account the current and future climate change threats. Resource managers can make more informed decisions based on those results.

This thesis investigates quantitatively the synergy of different drivers and the form of the relationships. First, the relationship (i.e., feedbacks, synergies and tradeoffs) between fishing, eutrophication and sedimentation (local drivers) was investigated. Secondly, the relationship between ocean acidification and ocean warming was investigated. And lastly, the interaction between both the local and global drivers was investigated. Simulations were performed with the reef system being exposed to one driver, than two and ultimately all three. Results showed only slight synergies but did suggest that fishing now (1985–2015) and climate change in the future (1985–2050) greatly impacted ecosystem metrics.

The thesis also advances coral reef modelling development in general and in particular for the Atlantis model community. The model described in this thesis also differs in its complexity from the many coral reef ecosystem models developed earlier. The model aims to include all functional species groups relevant in coral reef dynamics. Other studies have shown the importance of including the detrital pathways, which are very prominent in coral reefs (Paves and Gonzalez 2008) but have mostly been omitted in ecosystem models of reefs with the exception of the CAFFEE model (Ruiz Sebastián and McClanahan 2013). Bellwood et al. (2004) explained the importance of including the various groups of herbivores and their functional roles to properly account for changes in reef resilience and, although most coral reef models include herbivores, they are often lumped into one or a few functional groups whereas I group them by their functional role as grazers (preventing turf algae from growing into macroalgae), browsers (cropping down macro-algae), scrapers (scraping algae of the substrate opening up space for coral recruits), excavators (important bio-eroders and opening up substrate) and detritivores (recycling sediments). Moreover while structural complexity is recognized as greatly influencing fish diversity and abundance, it has only recently been given more prominence in coral reef models (Bozec et al. 2013, Bozec et al. 2014) and had not previously been combined with other disturbances or key reef dynamics in reef models. Similarly, the trophic role of apex predators had not generally been properly included into coral reef models. I included both (the influence of structural complexity via a derived relationship between complexity and prey vulnerability and trophic interactions), along with the main human-induced drivers to the reef. By representing this combination of socio-ecological processes the model can provide a more complete perspective on future reef trajectories.

1.4 Overall research objective and research questions

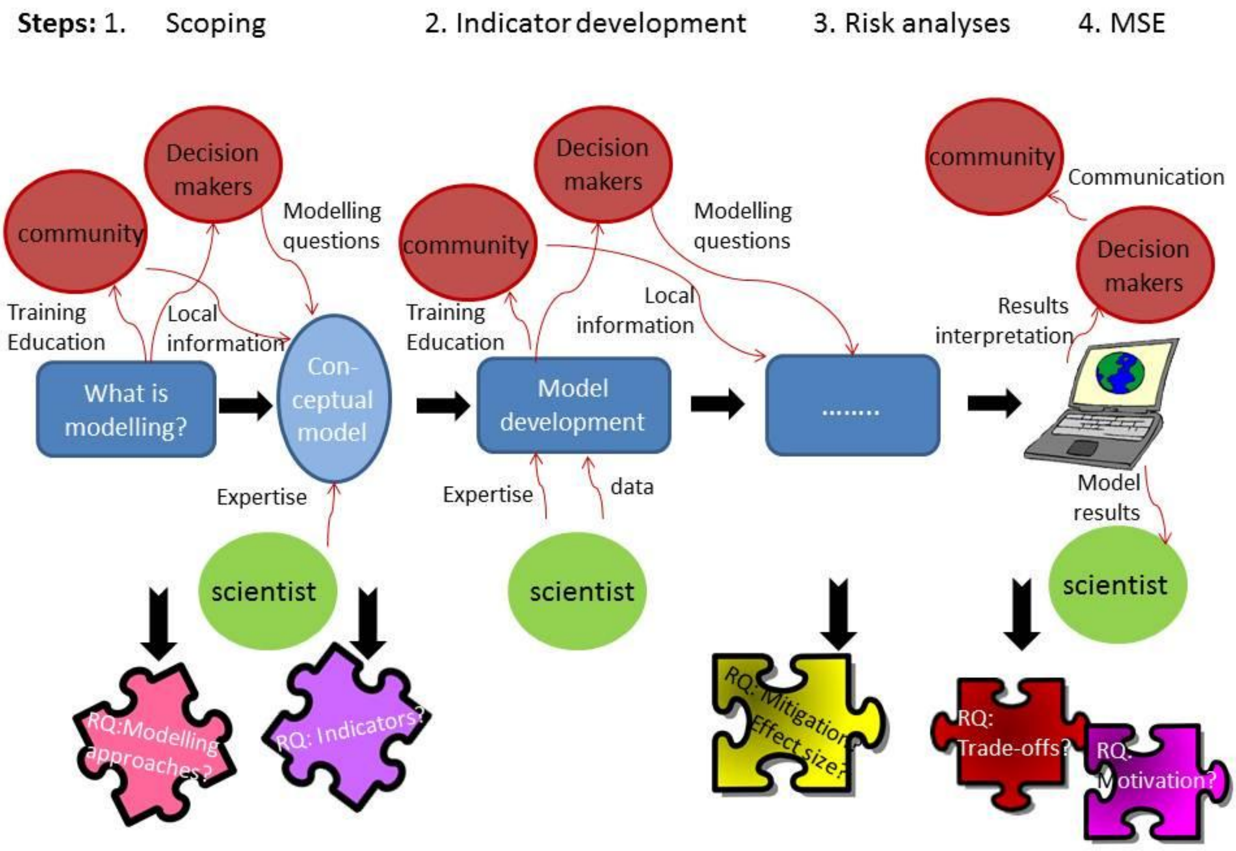
The overall research objective of this thesis is to quantify the effects of watershed and fishery management on ecosystem services using an ecosystem model in order to evaluate the economic and ecological tradeoffs of alternative management policies against a backdrop of climate change. To address this overall objective I explored the following research questions:

- What are the main goals of and differences between minimal, intermediate and complex models of coral reef ecosystems? Which approach(es) or combination of approaches obtain the most clarity and predictive capabilities if used in a management strategy evaluation framework?
- How does fishing affect ecosystems states? What are the most reliable indicators of fishing on coral reef ecosystem structure and function?
- Can local management strategies mitigate the impacts of climate change (ocean warming and acidification) on coral reef ecosystems? What is the effect size on performance metrics of key drivers to reefs when acting individually and concurrently?
- What are socio-economic and ecological tradeoffs of the existing rules and regulations governing reef fishery and conservation compared to the selected alternatives?

- What motivates Guam’s fishers to go fishing for reef fish and what determines the level of tourist participation in diving on coral reefs in Guam? How does the coral reef ecosystem state affect these participation rates and what are the effects of changes in these activities on the ecosystem?

1.5 Outline thesis

The step-wise approach (Section 1.2) and the research questions (Section 1.4) are combined and addressed in the various chapters in my thesis as indicated in Figure 1.3. By answering the research questions, parts of the puzzle are resolved, until at the end I can piece them all together and so achieve the general objective. This thesis consists of nine chapters including this introduction and a synthesis as the final chapter (Fig. 1.3). Chapters 2–8 are either already published or in various stages of the publication process. All chapters are written in collaboration with other scientists and I am the first author in all of them. A brief summary of each of the chapters follows.



Chapters: 2 3 4, 5, 6 7 and 8

Figure 1.3. Schematic representation of the steps taken to model development and implementation and how they are linked with various research questions (RQ: for full description see Section 1.4) addressed in the various chapters of this thesis and which, when pieced together, provide insight to the overall objective (figure adapted from Fulton et al. 2011a).

In Chapter 2, my co-authors and I reviewed the roles of three model types—classified based on their complexity as minimal, intermediate and complex models—in supporting sustainable coral reef ecosystem services. We highlighted the need to invest time in appreciating the identity and potential of each of the three model types in its own right and in concert. Minimal coral reef models are crucial to our understanding of ecosystem feedback loops and their response curves (e.g., linear, non-linear, modal). Understanding the drivers of change in a system's state will improve scope for effective management responses, reversing or preventing change. Intermediate models can assist managers with projections of ecosystem responses and indirect outcomes through the inclusion of the full spectra of trophic groups. These models can be used to answer many questions as they also include various environmental or anthropogenic forcings. For managers all-encompassing complex models may be the most informative decision-support tool for evaluating the economic and ecological tradeoffs of various management scenarios. These models are the ones that include all major dimensions (i.e., spatial, temporal, taxonomic, nutrient, human activities) in their simulations and, therefore, incorporate the often synergistic effects of various dynamic mechanisms and responses that may be omitted by minimal or intermediate models which sacrifice on these dimensions in return for transparency and ease of construction.

In Chapter 3, my co-authors and I assessed suitability of potential indicators of fishing pressure to coral reef ecosystem state. Despite the increase in number of modelling studies in coral reef areas, adequate information on appropriate indicators to quantify changes in these systems is still lacking. This chapter focuses on the quantitative description of characteristics of ecosystem attributes of three coral reef systems in Hawai`i along a fishing pressure gradient and identifies the most reliable indicators of ecosystem structure and function of coral reefs to support ecosystem-based fishery management. We also considered and compared our models with three other ecosystem models developed for Hawai`i: one concentrating on the role of herbivores in reef resilience at Kaloko-Honokohau National Historical Park; one characterizing the reef ecosystem structure along the Kona coast of Hawai`i; and the third one estimating the carrying capacity of monk seals at French Frigate Shoals in the Northwestern Hawaiian Islands. In contrast to those other studies, which focus on energy flows, our model and study uses the Ecopath model to assess key indicators related to fishing pressures.

Chapter 4 describes the design and parameterization of the Atlantis ecological module to make it suitable for coral reef ecosystems around Guam. This work, therefore, builds on the functionalities and deterministic relationships included in the base Atlantis model framework and already validated in Atlantis-related papers (e.g., Fulton et al. 2011b, Ainsworth et al. 2012, Griffith et al. 2012, Kaplan et al. 2012, Fulton et al. 2014). We give an overview of the separation of the species inhabiting a coral reef into functional groups and explain the data needs and sources of the various parameters used in this model. At this stage, coral reef dynamics and an oceanographic module were not yet implemented (see instead Chapter 6).

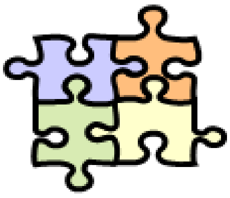
Chapter 5 describes an assessment of historic trends in the biomass of coral reef fish species around Guam from fishery-dependent and independent data. A core goal was to use catch time-series data to derive a reef-fish biomass time series that could be used to (later) test Atlantis model outputs. Although various studies have indicated that reef-fish stocks have declined around Guam, robust long-term time series data, based on actual survey data, are lacking. In this chapter, we modified an approach used to estimate time series of fish stocks based on single-species fishery data (Haddon 2010) and applied it to the multi-gear, multi-species inshore reef-fish fisheries in Guam.

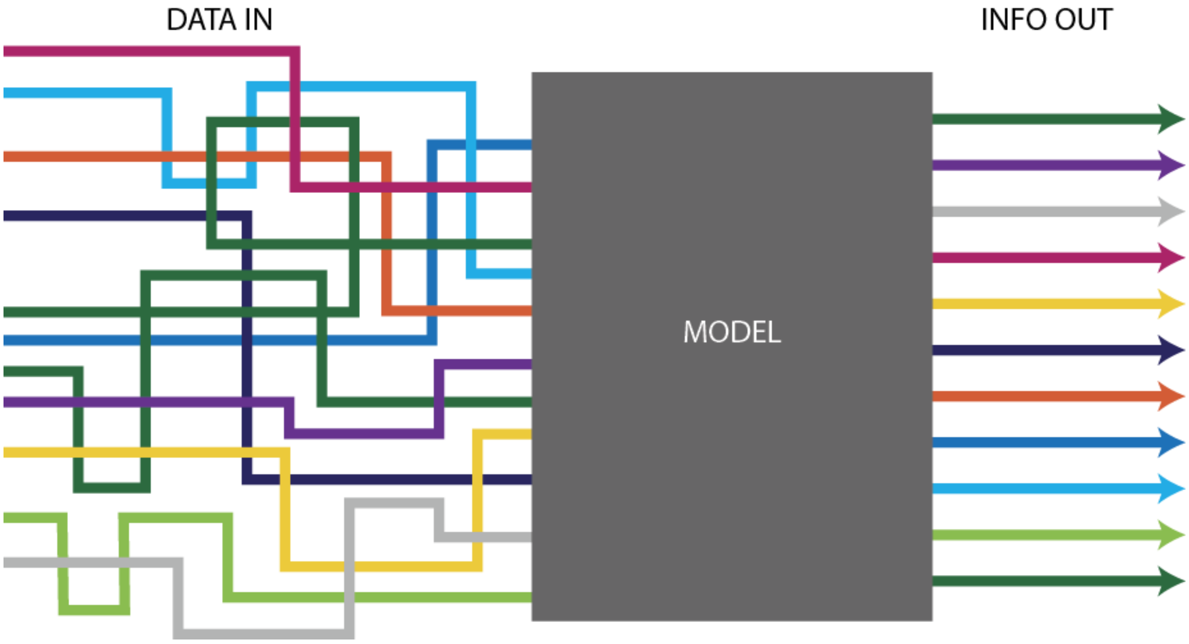
In Chapter 6, my co-authors and I assess the effect size of individual drivers (climate change, land-based sources of pollution and fishing) and concurrent effect size of these drivers on selected ecosystem metrics. We also assess the impact of local management on coral biomass trajectories under present climate change predictions. In Appendix F accompanying this chapter, we detail the modifications made to the Guam Atlantis ecosystem model developed under Chapter 4, through the inclusion of code for the relationships of key coral reef dynamics, with a particular focus on incorporating climate change impacts. This appendix also includes validation of the new code.

Chapter 7 describes the application of ecosystem modelling as a tool for exploring ecosystem level effects of changing environmental and management conditions. Policy scenarios identified by the local and federal resource managers in Guam were simulated with the Guam Atlantis model. Although Atlantis' applicability and suitability is limited for tactical management decisions (e.g., setting catch limits), it has value as a simulation technique to give insight in the ecosystem effects of alternative management approaches and to compare economic and ecological tradeoffs of each approach. Applying Atlantis to assess management options for coral reef ecosystems is a novel application.

Chapter 8 takes the results of Chapter 7 and combines them with socio-economic human behavior models to get insights into the socio-economic tradeoffs of the identified scenarios.

In Chapter 9 I reflect on the model development and discuss the challenges and limitations of the modelling approach and present a synthesis of the main findings and conclusions.




DATA IN
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Chapter 2

How models can support ecosystem-based management of coral reefs

Weijerman, M, EA Fulton, ABG Janssen, JJ Kuiper, R Leemans, BJ Robson, IA van de Leemput, WM Mooij. 2015. How models can support ecosystem-based management of coral reefs. Prog. in Oceanography, online.

Despite the importance of coral reef ecosystems to the social and economic welfare of coastal communities, the condition of these ecosystems have generally degraded over the past decades. With an increased knowledge of coral reef ecosystem processes and a rise in computer power, dynamic models are useful tools in assessing the synergistic effects of local and global stressors on ecosystem functions. We review representative approaches for dynamically modelling coral reef ecosystems and categorize them as minimal, intermediate and complex models. The categorization was based on the leading principle for model development and their level of realism and process detail. This review aims to improve the knowledge of concurrent approaches in coral reef ecosystem modelling and highlights the importance of choosing an appropriate approach based on the type of question(s) to be answered. We contend that minimal and intermediate models are generally valuable tools to assess the response of key states to main stressors and, hence, contribute to understanding ecological surprises. As has been shown in freshwater resources management, insight into these conceptual relations profoundly influences how natural resource managers perceive their systems and how they manage ecosystem recovery. We argue that adaptive resource management requires integrated thinking and decision support, which demands a diversity of modelling approaches. Integration can be achieved through complimentary use of models or through integrated models that systemically combine all relevant aspects in one model. Such whole-of-system models can be useful tools for quantitatively evaluating scenarios. These models allow an assessment of the interactive effects of multiple stressors on various, potentially conflicting, management objectives. All models simplify reality and, as such, have their weaknesses. While minimal models lack multidimensionality, system models are likely difficult to interpret as they require many efforts to decipher the numerous interactions and feedback loops. Given the breadth of questions to be tackled when dealing with coral reefs, the best practice approach uses multiple model types and thus benefits from the strength of these different models.

2.1 Introduction

Coral reefs are extremely important as habitats for a range of marine species, natural buffers to severe wave actions and sites for recreation and cultural practices. Additionally, they contribute to the national economy of countries with coral reef ecosystems. The economic annual net benefit of the world's coral reefs are estimated at US$29.8 billion from fisheries, tourism, coastal protection and biodiversity (Cesar et al. 2003). Moreover, coral reefs are important to the social and economic welfare of tropical coastal communities adjacent to reefs (Moberg and Folke 1999). Coral-reef related tourism and recreation account for US$9.6 billion globally and have also shown to be important contributors to the economy of Pacific islands (Cesar et al. 2003, Van Beukering et al. 2007). However, the functioning of coral reef ecosystems and their biodiversity is deteriorating around the world (Hoegh-Guldberg et al. 2007). In recent reviews on the extinction risks of corals, the most important global threats to the survival of corals and coral reefs were human-induced ocean warming and ocean acidification (Brainard et al. 2011, Burke et al. 2011). While local governments are limited in their capacity to reduce greenhouse gas emissions worldwide and so reduce the on-going ocean warming and acidification, they can play a pivotal role in enhancing the corals' capability to recover from impacts of these global threats by reducing additional local stressors caused by land-based sources of pollution and fishing (Carilli et al. 2009, Hughes et al. 2010, Kennedy et al. 2013, McClanahan et al. 2014).

The capacity of coral reef organisms and natural systems to 'bounce back' from disturbances can be degraded by sequential, chronic and multiple disturbance events, physiological stress and general environmental deterioration (Nyström et al. 2000), and through the reduction of large and diverse herbivorous fish populations (Pandolfi et al. 2003, Bellwood et al. 2006). These local stressors affect the coral-macroalgal dynamics and early life history development and survival of corals (Baskett et al. 2009b, Gilmour et al. 2013), but these stressors can be mitigated by proper management (Mumby et al. 2007b, Micheli et al. 2012, Graham et al. 2013). Ecosystem models can help managers in system understanding and in visualizing projections of realistic future scenarios to enable decision making (Evans et al. 2013). As has been shown in the management of freshwater resources, insight in the conceptual relations between key states and their response to stressors can have profound impacts on the way natural resource managers think about their systems and the options they have for ecosystem recovery (Carpenter et al. 1999).

Large-scale regime or phase-shifts have been identified in pelagic systems (Hare and Mantua 2000, Weijerman et al. 2005) and on coral reefs (Hughes 1994) and have influenced a new understanding in ecosystem dynamics that includes multiple-equilibria, nonlinearity and threshold effects (Nyström et al. 2000, Mumby et al. 2007a). The theory of alternative stable states implies, for example, that a stressed reef could not only fail to recover after a disturbance, but could shift into a new alternative stable state due to destabilizing feedbacks, such as a change in abiotic or biotic conditions (Mumby 2006, Mumby et al. 2013b). As a result, reversing undesirable states has become difficult for managers (Nyström et al. 2012, Hughes et al. 2013), even when stressors are being lowered (a phenomenon also known as hysteresis [Scheffer et al. 2001]).

The complexity of coral reef ecosystems with their myriad processes acting across a broad range of spatial (e.g., larval connectivity versus benthic community interactions) and temporal (e.g., turnover time of plankton versus maturity of sea turtles) scales makes modelling coral reef ecosystems for predictive assessments very challenging. The modeler's dilemma is to choose an approach that juggles simplicity, realism and accuracy, and reaches the overlapping but not identical goals of understanding natural systems and projecting their responses to change (Levins 1966).

Leading principles for ecosystem model development vary and include:

1) Interpolations to fill data gaps, for instance to provide information regarding what is happening between two observations in time or to fill in the three-dimensional picture of a system from two-dimensional data;
2) Forecasting or hindcasting approaches, i.e., to make predictions for operational management when a system is varying within historical bounds;
3) Enhancement of system understanding by quantification of a conceptual model (e.g., to calculate materials budgets) or to quantitatively test the plausibility of that conceptual model;
4) Developing ecological theory and generalizable ecological hypotheses;
5) Extrapolation and projection, i.e., to generate hypotheses regarding the function and likely responses of a particular system when perturbed beyond its previously observed state;
6) Scenario evaluations for operational or strategic management.

With regards to these principles, we believe that each circumstance is best suited by a different model approach (Table 2.1). Other authors, who have discussed the selection of appropriate modelling approaches, include Kelly et al. (2013), Fulton and Link (2014) and Robson (2014b). Robson (2014a) has further considered the implications of growing complexity in models of aquatic ecosystems.

Table 2.1. Leading principles for model development with a model approach suitable to reach the desired goal.

Leading principle	**Suitable model approach**
1) Interpolation	Data-driven (statistical) models Minimal models
2) Forecasting and hindcasting	Data-driven (statistical) models Physically-driven models
3) Quantification of a conceptual model	Complex models or intermediate models
4) Hypothesis generation—theory development or testing	Simple conceptual models (minimal models)
5) Extrapolation and projection	Complex, process realistic models, which capture the feedback processes that dictate longer term evolution of dynamics
6) Operational scenario evaluation	Targeted/refined (intermediate) mechanistic models

Models, suited for coral reef managers who need to define management strategies for the entire coral reef ecosystem, need to consider interactions among system components and management sectors as well as cumulative impacts of disturbances to the system (Rosenberg and McLeod 2005, Kroeker et al. 2013, Ban et al. 2014). Ecosystem understanding should include the human component in terms of their social and economic dependencies on these marine resources (Liu 2001, Nyström et al. 2012, Plagányi et al. 2013). Management scenarios that enhance the biological state might be unfavorable for the local economy, especially on short time scales. Responses of slow-reacting systems, such as coral reefs, could diminish community support for effective management. Still, they also give managers an opportunity to act before a new, less favorable, condition has established itself (Hughes et al. 2013). To date, few tools have been available that evaluate the socio-economic and ecological tradeoffs of management scenarios of an ecosystem-based approach to coral reef management. Coral reef ecosystem models that do include the human component are mostly focused on fisheries management with socio-economic impacts presented as changes in catches or landings (McClanahan 1995, Gribble 2003, Shafer 2007, Tsehaye and Nagelkerke 2008). Few models dynamically couple ecological dynamics to socio-economic drivers and these models also focus on fisheries management (Kramer 2007) with Melbourne-Thomas et al. (2011b) including a combination of fisheries, land-use and tourism.

The modelling approach most suitable to reach specific goals for ecosystem-based management depends on the type of governance (e.g., existing laws and enforcement), time and space scales under consideration, and data availability (e.g., data quantity, quality and accessibility; Tallis et al. 2010), as well as the maturity of scientific understanding of the system under consideration and the time and resources available for model refinement and validation (Kelly et al. 2013). The concepts encompassed by Management Strategy Evaluation (MSE) or Decision Support System (DSS) tools are a useful way of exploring management issues that can be applied to many model types. MSE involves simulation testing of alternative combinations of monitoring data, analytical procedures and decision rules to give insight in the implications for both the resource and the stakeholders, and can be used for evaluating the tradeoffs between socioeconomic and biological objectives (Smith et al. 2007). In situations when neither data nor time is a limiting factor for model development and site-specific management scenarios need to be simulated, ‘end-to-end’ or ‘whole-of-system’ models can be developed for the MSE. In more data-poor or time-limited situations or when less-specific scenarios with processes that are easily traced back are required, ‘minimum realistic’ models can be used as a basis of the MSE (Plagányi et al. 2013). Alternatively simple, even qualitative, models can be used to shed light on ecological (or other system) concepts, helping stakeholders to think about topics important in defining effective management strategies (Tallis et al. 2010) or these simpler models can be used as the logical basis of the MSE in their own right, as per Smith et al. (2004).

Drawing in all models of reef systems would be intractable, especially given the number of conceptual models that exist in the mainstream and grey literature. Consequently, we have put particular emphasis on their usefulness for evaluating the ecological implications of model applications for MSE (as that is where our expertise largely lies) and we constrain our review to the strengths and limitations of ‘dynamic’ coral reef ecosystem modelling approaches in their application to management scenario analyses. We define a 'dynamic' model of a given system as a set of mathematical formulations of the underlying processes in time and/or space with outputs for each time step over a specified period. With such a model, the development of the system in time and space can be simulated by means of numerical integration of the process formulations.

This review is not an exhaustive comparison of all dynamic coral reef ecosystem models but we have selected studies that employ commonly used or exemplar approaches that represent model types categorized as 'minimal', 'intermediate' and 'complex' models. This classification was based on a scoring system that combined (1) their level of realism (determined by the conceptualism of space, time and structure) and (2) the process details incorporated into the model (Table 2.2). Additionally, we looked at the leading principle for development of each model (Mooij et al. 2010). We contend that the leading principle of minimal dynamic models is understanding the type and shape of the response curve of ecosystems to disturbances. The leading principle of complex dynamic models is to predict the response of ecosystems to disturbances under different management regimes given the many feedbacks in the system. Intermediate dynamic models try to balance between these two objectives. They do so by expanding parts of the system to the full detail while deliberately keeping other components simple. In this way they can capture some key feedbacks while maintaining the tractability of simple models, meaning they can make use of analytical and formal fitting procedures (Plagányi et al. 2014). We highlight the differences between the model approaches, discuss their main goals and outline the approach to take the strength of the different modelling types to obtain clarity and predictive capabilities in a model.

2.2 Categorization of three coral reef model types: Minimal, intermediate and complex

The rationale for any model is the desire to capture the essence, and to remove or reduce the redundant aspects, of the system under study. What is essential and what is redundant and, thereby, what level of reduction is required, to a large degree depends on the questions being asked, the available information to base conceptualizations on and the way in which abstractions are formulated. The result is a 'model' that is realistic to varying degrees. It is not a clear cut recipe book approach as modelers need to define the tradeoffs between temporal and spatial resolutions, taxonomy and model structure, as well as model detail, i.e., between comprehensiveness and complexity. Using 27 published studies that we felt were representative of reef models in the literature, we classified the dynamic coral reef models along an axis of model type (Tables 2.3 and 2.4) to get a greater understanding of how differently sized models can be used in coral reef ecosystem management, particularly in the context of MSE. We first classified models primarily on basis of their leading principle. However, while categorizing models in terms of all of these facets separately is possible it is difficult to think in such hyper dimensional spaces, so to facilitate comparisons we then mapped models to a simple continuum of simple to complex via a scoring system (Table 2.2; for scoring results see Weijerman et al. 2015).

Table 2.2. Complexity scoring of various criteria to classify models or model applications.

Criteria/Score	1	2	3	4	Comments
Conceptualization of structure					
# plankton grps	0	1-2	3	> 3	groups can be individual species or aggregated species groups
# benthic grps	1	2	3-4	> 4	
# invertebrate grps	0	1-2	3-4	> 4	
# vertebrate grps	0	1-2	3-5	> 5	
Conceptualization of space					
	non-spatial	lumped	grid or cell based		lumped has a single output of entire modelled area; grid or cell based represents uniform or non-uniform grid or vectors
Process Details					
trophic interactions					
inter/intra species competition					
age structure					
biogeochemistry					
hydrodynamics					

2.2.1 Minimal models

With few mathematical equations, minimal dynamic models are often used as a toolkit for the development of ecological theory. Minimal models have proven to be a helpful tool in gaining fundamental insight into the complex dynamics of a specific system (i.e., chaos, cycles, regime shifts, etc.). In coral reefs, for example, they have played an important role in conceptualizing and understanding observed regime shifts (Hughes 1994, Mumby et al. 2013b). Generally, people do not intuitively consider nonlinear responses, i.e., we often assume that a small change in environmental conditions will lead to a small (or at least consistently proportional) change in the ecosystem. Minimal models have been used to show what kind of surprises could arise when nonlinear interactions between system variables (e.g., feedback mechanisms) are taken into consideration (#1 in Table 2.3). Using minimal models to simulate coral reef dynamics, fundamental insight into thresholds (#1), primary drivers of system dynamics (#2, 3), the type of system response to changing conditions and the effect of hysteresis can thus be gained (#4). Recently, the interaction between ocean acidification and warming and coral growth/cover has been examined with minimal models (#5). Some minimal models also incorporate local environmental changes (e.g., nutrient input, hurricanes and fishing) to study coral cover response and are able to forewarn whether current levels are precautionary or whether new challenges are coming (#6). Early minimal models examined the main drivers of reef accretion and erosion processes (#7–9). Gaining insight in these important aspects of a system's response to current or future perturbations can help managers to understand observed surprising dynamics, focus on the most relevant (sensitive) variables and to conservatively move away from tipping-point thresholds by increasing reef resilience. While, to the authors' knowledge, there is currently no published MSE using a simple reef model as a basis, the response curves derived from such models could be used as the basis of a qualitative MSE of the form undertaken in a temperate system by Smith et al. (2004).

One advantage of minimal models is their ability to thoroughly explore the behavior of the model in a multidimensional parameter space by using analytical or numerical methods. This way, the relative importance of specific processes or interactions can easily be traced back. However, minimal models ignore other potentially important phenomena that affect a system's behavior (Scheffer and Beets 1994). Moreover, they often assume spatially homogenous conditions and constant environments. Reefs have patchy distributions of corals and fish, often determined by environmental factors (Franklin et al. 2013), so including spatial dimensions explicitly in the model can greatly improve the realism of reef dynamics. However, explicit spatial representation is not automatically required, so long as careful thought is given to how to implicitly represent the spatial influences. Because minimal models lack the link between all trophic groups and the response of multiple stressors, they can be less suitable in a multispecies or multidisciplinary decision-making context. Minimal models have paved the way for the theory on generic early warning signals of tipping points (Scheffer et al. 2009). While minimal models themselves are likely to be too simplistic to precisely predict future behavior in systems that are not already well understood, early warning signals may be an important additional tool for ecosystem managers.

Based on the leading principle defined for minimal models, nine models could be classified as minimal models developed to enhance understanding of the type and shape of the response curve of ecosystems to disturbances (#1–9). According to our scoring system, the overall complexity score, based on the mean score of model structure, representation of space and process details, varied between 2.3 and 4.4 with a mean score of 3.3 (Weijerman et al. 2015) The box model (#7, 8) had an overall score of 4.4 and could also be placed in the intermediate category, whose overall score was between 3.0 and 5.0 with a mean of 4.1.

2.2.2 Intermediate models

Intermediate models are more focused than typical whole-of-system models; they try to marry the strengths of simple models (in terms of tractability) with a broader system perspective to selectively link the key drivers of the system. These models simulate species-specific behavior and age or size structure with a set of mathematical formulas, capturing the population dynamics of key functional groups and potentially their spatial heterogeneity if spatially explicit (Plagányi 2007). These kinds of models typically include at least one key ecological process (e.g., a link to lower trophic levels, interspecific interactions or habitat use) and potentially some representation of how the modelled components are affected by physical and anthropogenic drivers (Plagányi et al. 2014).

The leading principal for this type of model was defined as trying to find a balance between system understanding and predictive capabilities by expanding parts of the system to the full detail while deliberately keeping other components simple. For example, by including more details on process dynamics but limiting the functional groups (#15, 18), a greater understanding was reached of the population dynamics and perturbations (fishery [#15] and environmental factors [#18]) of that specific group. This more realistic and heterogeneous system representation provides information about a system that is not available from a minimal model. In pointing to a representative example of an intermediate complexity reef model there are a number of potential candidates. Two clear classes of questions have been tackled with these kinds of models. The first is around using multispecies or trophic models to explore the coral reef ecosystem impacts of fishing (Table 2.3, #10–16, 19) and the second uses models, often individual or agent-based models (Grimm et al. 2006), to consider how competing habitat defining groups respond to changing conditions (#17, 18, 20, 21).

The Ecopath and Ecosim (EwE) modelling platforms (Polovina 1984, Walters et al. 1997, Pauly et al. 2000) is one of the most commonly used model type for exploring trophic connections and responses to fishing pressure. Although the suite of EwE models can be considered complex based on our criteria (Table 2.2), the application of EwE models in the selected studies has been mostly to look at just one disturbance (fisheries) through expansion of that part of the model components while leaving the rest simple (e.g., few functional groups, no inclusion of Ecospace or life cycle (age-structured) processes) and, hence, the leading principle fits with our classification of 'intermediate'. Similarly while some agent-based models can be considered complex in terms of the elaboration of particular ecological mechanisms, in the context of their use in coral reef ecosystems they have often been used as intermediate complexity models. When EwE is used to explore reef dynamics it can give insight into a system's 'state' based on changes in energy flows as a response to perturbation (#10, 12 and 13) and multiple positive or negative feedback loops can be included with this model approach (#17, 21 and 22). The classification of EwE models also illustrates that modelling platforms often do not simply slot into one category but can be simple, intermediate or complex depending on the details of a particular application. For example, one application of EwE, for examining fishery scenarios for Indonesian reef systems, included 98 tropic groups and three of the five selected process dynamics (#14) and was used for evaluating management scenarios. Thus it was categorized as complex (Table 2.3) as its overall complexity score of 6.0 sits within the span of scores (5.3 to 6.8, mean 5.9; Weijerman et al. 2015) of complex models.

A disadvantage of intermediate models is that the software code often consists of linked models, which complicates the interpretation of results (Lorek and Sonnenschein 1999). Additionally, because of the need for more parameters, variables and model formulations, each with their own uncertainties, model output becomes less certain or robust (Pascual et al. 1997) and validation and sensitivity analyses are more cumbersome (Rykiel Jr 1996). Nevertheless these models are still simple enough that good use can be made of formal statistical estimation procedures originally developed for simpler models (Plagányi et al. 2014).

Management applications of intermediate models include the ability to inform managers where a system is on a gradient from 'pristine' to degraded/disturbed so that effective action can be identified and implemented (McClanahan 1995, Kramer 2007). Additionally, especially with respect to the suit of EwE models that have been used for fishery management strategy evaluation, this model approach gives valuable insight into ecosystem impacts of alternative fishery scenarios. However, spatial factors, nutrient dynamics, benthic processes and extrinsic forcing functions are not always included in intermediate models but can be important for projecting the effects of some perturbations on ecosystems (Robinson and Frid 2003).

2.2.3 Complex models

What we categorized as complex models are often called end-to-end models or whole-of-system models. These models typically include a food web spanning a set of trophic groups: detritus, primary producers, zooplankton ranging from small (µm) to large (m) animals, forage fish, invertebrates and apex predators, including humans. They also often explicitly simulate biogeochemical dynamics. For coral reefs that are surrounded by oligotrophic water, nutrients play a key role in ecosystem dynamics. Including biogeochemical processes in a coral reef ecosystem model is, therefore, essential to simulate these processes, especially since land-based sources of pollution have played an important role in the demise of many reef systems in the Caribbean (Lapointe 1997) and on the Great Barrier Reef (De'ath et al. 2012). In comparison with the other two model types, additional key ecosystem processes (e.g., trophodynamics and feedback loops) are represented to more comprehensively simulate a system's behavior. These complex models aim to provide quantitative projections of system changes in response to a set of changing abiotic and biotic conditions taking into account key components and their spatial heterogeneity (in some cases from microbes to whales and humans, and from sediment bioturbation to physical oceanography). Simplicity is sacrificed as these models are simultaneously complex in many dimensions (process details, number of functional groups, nutrients, spatial and temporal dimensions, see Table 2.3 #23–27). That is not to say every component or aspect is resolved in fine detail. Such an approach does not lead to useful outcomes; tradeoffs between the dimensions are nearly always required so as the scope or the number of scales extends sacrifices are likely required in other facets (such as using growth terms rather than very finely resolved physiological representations of each ecological process for each modelled group).

Representing a system in this way can be advantageous for capturing trophic cascades and synergistic effects of perturbations, as the model implementation explicit includes (1) key functional groups at each trophic level (Mitra and Davis 2010) and (2) model complexity varies with details where needed in terms of number of functional groups and compatibility between lower and upper trophic level formulations (Fulton et al. 2003a). These models can represent many more of the myriad nonlinear, two-way interactions than simple or intermediate models represent. Humans are an integral component of most complex models, both as users of ecosystem services and as drivers influencing ecosystem processes (Levin et al. 2009).

The major drawback of these model types is similar to that of intermediate models: the addition of complexity does not guarantee an improvement in the simulated output as uncertainty and error associated with the added components will be introduced to the model and can potentially degrade its performance. Uncertainty arises both from assumptions made in the model structure and from uncertainty around the values of parameters, amongst other sources (Draper 1995, Renard et al. 2010).

The difficulties of properly understanding the implementation of ecological and socio-economic processes in a complex model hamper straightforward validation and could lead to less reliable projections. To improve the performance of complex ecosystem models, studies have looked into the effects of trophic aggregations (Gardner et al. 1982, Fulton 2001), model structure (Ruiz Sebastián and McClanahan 2013), physiological detail (Fulton et al. 2004a, Allen and Polimene 2011), spatial representation (Fulton et al. 2004c), predator-prey relationships including age-structure (Botsford et al. 2011) and inter-predator competition (Walters and Christensen 2007). Best practice guidelines for developing complex models have been formulated (Fulton et al. 2004b, Flynn 2005, FAO 2007, Travers et al. 2007). Some of these recommendations are (1) the inclusion of functional groups at low trophic levels and species of higher trophic levels with an appropriate spatial dimension to represent organism dynamics more accurately; (2) inclusion of abiotic processes to simulate important drivers in structuring ecosystem communities; (3) the integration of physical and biological processes at different scales (relevant to the scales of key processes) to more realistically simulate those dynamics; (4) evaluating the model in terms of its ability to reproduce expected patterns from ecological theory and in terms of the degree to which it accords with current biophysical understanding of the system; and (5) two-way interactions between ecosystem components to allow dynamic feedback and nonlinear dynamics to emerge.

Most complex coral reef models are developed to assess the cumulative effects of climate change, fishing (#25, 26) and water quality (#27) on ecosystem dynamics and the resilience of coral reefs under simulated management scenarios (#23, 24). Through the inclusion of the breadth of the food web and many alternative interaction pathways, non-intuitive (and, therefore, unanticipated) outcomes in community structure can present themselves. It should be noted that unexpected, chaotic and non-linear system dynamics can be exhibited by simple models, again simply including more components does not guarantee revelations outside the purview of other approaches. Not only the number of groups represented, but also the number and types of interactions between them is important (Baird 2010, Takimoto et al. 2012). The main consideration is the inclusion of mechanisms of achieving alternative outcomes—multiple reaction pathways that can reach alternative stable states. The same logic is behind why the inclusion of humans and their activities in model simulations facilitates further evaluation of tradeoffs between ecosystem services and management goals. This information can then support the identification of policies and methods that have the potential to meet *a priori* stated objectives (Levin et al. 2009).

Although there is a continuous scale from minimal to complex model approaches, we differentiated between three categories (minimal, intermediate or complex) based on the leading principal for model development and on their overall complexity score related to the model conceptualism and process detail (Table 2.3). The mean complexity score reflects this continuous scale as model approaches overlap between the three categories. As we go from simple to complex models, a tendency in the leading principle is visible—from understanding towards prediction and projection. The desired balance between these two objectives in a given study could therefore give some indication of the appropriate level of model complexity.

Table 2.3. Selected dynamic coral reef ecosystem models and model applications categorized as minimal, intermediate and complex based on their system conceptualization and process detail (Table 2.2). For overall complexity score calculations, see (Weijerman et al. 2015).

#	Model	Source	Reef area	Leading principal	Suitable for MSE	Category based on leading principle	Overall Score
1	Caribbean reef model	Mumby et al. 2007a	Caribbean fore-reef	System understanding of coral-algae dynamics	Insight in benthic dynamics	Minimal	2.3
2	Bayesian Belief Network model	Renken and Mumby 2009	Caribbean fore reef	System understanding of macroalgal dynamics	Insight in benthic dynamics	Minimal	3.3
3	HOME model	Wolanski et al. 2004	Great Barrier Reef & Guam	System understanding of coral-algal dynamics	Insight in benthic dynamics	Minimal	4.3
4	Community model	Żychaluk et al. 2012	Kenya, Caribbean, Great Barrier Reef	System understanding of occurrence of alternative ecosystem states	Insight in benthic dynamics	Minimal	2.8
5	Community model	Anthony et al. 2011	Caribbean	System understanding in benthic dynamics under climate change	Insight in benthic dynamics	Minimal	3.4
6	Deterministic model	Blackwood et al. 2011	Caribbean	System understanding of coral-algal dynamics including reef complexity	Insight in reef resilience in relation to fishery	Minimal	2.9
7	Box model	Eakin 1996	25,308 m^2 Uva Island, Panama	System understanding of reef accretion/ erosion processes	Insight in reef complexity	Minimal	4.4
8	Box model	Eakin 2001	25,308 m^2 Uva Island, Panama	System understanding of reef accretion/ erosion processes	Insight in reef complexity	Minimal	4.4
9	ReefHab	Kleypas 1997	Generic reef (parameterized for Mesobarrier Reef Caribbean)	System understanding of reef accretion/erosion processes	Insight in environmental factors limiting reef habitat	Minimal	2.6
10	Energy-based model	McClanahan 1995	Generic local reef (parameter-ized for Kenyan reef)	System understanding of effect of fishing on ecosystem structure and fishery yield	Insight in tradeoffs of alternative fishery scenarios	Minimal/ Intermediate	5.0
11	Ecopath with Ecosim	Tsehaye and Nagelkerke 2008	6000 km^2 Red Sea	Fisheries effects on ecosystem - change in fishery scenarios	Insight in ecosystem impacts of alternative	Intermediate	4.1

#	Model	Source	Reef area	Leading principal	Suitable for MSE	Category based on leading principle	Overall Score
					fishery scenarios		
12	Ecopath with Ecosim	Weijerman et al. 2013	Hawaii	Identify indicators for fishery for management - change in fishing intensity	Insight in ecosystem impacts of increased fishing	Intermediate	4.5
13	Ecopath with Ecosim	Arias-González et al. 2004	Mexico	Fisheries effects on ecosystem - change in fishery scenarios	Insight in ecosystem impacts of alternative fishery scenarios	Intermediate	3.9
14	Ecopath with Ecosim	Ainsworth et al. 2008	Indonesia	Fisheries effects on ecosystem - change in fishery scenarios	Insight in ecosystem impacts of alternative fishery scenarios)	Complex	6.0
15	Effects of Line Fishing Simulator (ELFSim)	Little et al. 2007	Great Barrier Reef	Understanding of population dynamics of single species under alternative fishery scenarios	Evaluate tradeoffs on population dynamics of 1 species under alternative fishery scenarios	Intermediate	3.0
16	Individual-based model	Edwards et al. 2011	Caribbean mid-depth fore-reef	System understanding of disturbance impacts under alternative fishery scenarios	Insight in resilience of benthic community from disturbances under different fishery scenarios	Intermediate	4.6
17	Individual-based model	Wakeford et al. 2007	32 m^2 Lizard Island, Great Barrier Reef	System understanding (coral community dynamics after perturbations) and projected trajectory under future drivers	Insight in reef resilience in relation to disturbances	Intermediate	3.8
18	Spatially-explicit Reef Algae Dynamic (SPREAD) (individual-based)	Yñiguez et al. 2008	Florida, 3-D cells of 1x1 cm	System understanding (macroalgal growth and morphology)	Insight in environmental factors influencing macroalgal dynamics	Intermediate	4.4

#	Model	Source	Reef area	Leading principal	Suitable for MSE	Category based on leading principle	Overall Score
19	Lotka-Volterra model ~ adaptive behavior model	Kramer 2007	Generic Caribbean reef	Understanding in coupling between biological and fishery dynamics	Effects of fishery on ecosystem state and vice versa	Intermediate	5.0
20	Cellular automaton model	Langmead and Sheppard 2004	Caribbean	System understanding (coral community restructuring processes after disturbance)	Insight in reef resilience in relation to disturbances	Intermediate	4.1
21	Biogeochemical ~ hydrodynamic model	Faure et al. 2010	2066 km^2 lagoon, New Caledonia	System understanding (ecosystem variability under environmental disturbances)	Insight in biogeochemical response under different scenarios	Intermediate	3.4
22	Ordinary Differential Equation-based model	Riegl and Purkis 2009	Generic (parameterized for Arabian/Persian Gulf)	System understanding of coral community structure and recovery after multiple bleaching events)	Insight in coral community structure after repeated disturbances	Intermediate	3.8
23	Coral Reef Scenario Evaluation Tool (CORSET)	Melbourne-Thomas et al. 2011a	1342 km^2 (5-20 m depth) Generic reef ecosystem	Decision support tool with simulations based on 'what if' scenarios	Projecting reef futures under different scenarios	Complex	6.8
24	Ordinary Differential Equation-based model	Fung 2009	Generic local reef	System understanding (key ecological processes related to degradation) and scenario testing	Projecting reef futures under different scenarios	Complex	5.3
25	Integrated agent-based model	Gao and Hailu 2011	~6000 km^2, Ningaloo Marine Park, Australia	Decision support tool with simulations based on 'what if' scenarios	Site closure strategy analyses	Complex	5.4
26	Coral-Algae-Fish-Fisheries Ecosystem Energetics (CAFFEE)	Ruiz Sebastián and McClanahan 2013	Kenya	Model structure understanding, calibration methods	Insight in reef resilience related to fishery and environmental drivers	Complex	6.1
27	eReefs	Schiller et al., 2013; Wild-Allen et al., 2013; Mongin and Baird, 2014	300000 km^2, Great Barrier Reef, Australia	Support tool for rapid response and slow response management and system understanding	Projecting reef futures under different land management scenarios	Complex	6.8

2.3 Multiple model strategies in relation to coral reef management

2.3.1 Combining models of different complexity

Modelling is an art that balances simplicity, realism and accuracy of various dimensions (Levins 1966): time, space, trophic components, process details, human activities, boundary conditions and forcings. Considering coral reef management, all model formats have their pros and cons. However, insights gained by one model can be useful for the application of another (Mooij et al. 2009). Moreover, multiple model types can be combined. Their outcomes go beyond possible outcomes from a single model alone. Approaches combining models include:

- The ‘three-stage rocket approach’, in which first mini-models and then intermediate models can be used to identify the relevant variables or processes to steer on. The resulting intermediate model can then provide a basis for the complex model, with the aim of reaching a projection that is based on understanding. A variant of this approach is to couple models of different forms and origin to piece together a more complete representation of the system. Such approaches are becoming increasingly popular in the research community, but care must be taken to understand how to propagate error and deal with scale differences between the model types.
- The ‘build then refine approach’, in which a complex model is used to identify key drivers of system responses, which can then be used to develop simpler, faster models or statistical emulators, whose behavior can be more thoroughly characterized, providing more accurate predictions for a more limited range of scenarios (Robson 2014b).

But, as discussed in the following paragraphs, there are more ways in which we can benefit from combining modelling approaches, including the ‘peeling off complexity approach’, which is the opposite in form to the ‘three-stage rocket approach’.

2.3.2 From understanding to projecting

Minimal models are important for the development of concepts and theory; they examine how certain phenomena can be reproduced and so reveal general explanations. They are also helpful in identifying and getting insight into processes that cause nonlinear system behavior. As such, minimal models can provide a conceptual framework wherein management scenarios can be explored. They can help managers to address the right questions, i.e., which process details and variables to focus on. Intermediate models include enough detail to couple different concepts and test these concepts relative to each other and relative to other factors, such as external forcings (e.g., nutrient input, hurricane damage) and simplistic management scenarios. Improved understanding is still the main aim of this model type, although the increased complexity requires more effort to trace underlying mechanisms. When the understanding of key ecological or socioeconomic processes is sufficiently enhanced one can continue with making projections. However, some of the questions raised by ecosystem managers are beyond intermediate models, as they miss the necessary details in the model conceptualism or the full suite of key ecosystem processes.

Model complexity can arise either by increasing the detail at which particular compartments or processes are represented or by broadening the scope of the model, for instance, moving from a model of coral biology to a model of coral reef ecosystems to a model that also includes the human behaviors that affect those ecosystems. Many very complex biogeochemical models are narrowly focused, while broadly focused, integrated economic-ecological-biophysical models often represent their individual components with much less detail.

Well-formulated and comprehensive complex models are suitable for evaluating social, economic and ecological tradeoffs of alternative management scenarios but typically lack the straightforward validation needed to fully understand the model's projection capabilities. Very complex models may be too cumbersome to embed in end-user focused decision-support tools and may be too computationally intensive to allow large numbers of scenarios or optimization runs to be conducted. They may also lack transparency, which (when these models are used without also employing simpler models) can make it difficult for policy makers to develop confidence in the models and insight into the tradeoffs and processes represented in the models.

2.3.3 Including socio-economics

Intermediate and complex models are difficult to parameterize, analyze and validate and have a long development time. Because they often contain input from many experts, the model code may be less transparent and harder to maintain and debug, and the performance of these models is rarely thoroughly assessed. However, if these challenges can be overcome, they can include the whole ecosystem and socioeconomic components and so can be instrumental for management options and strategy evaluations (Plagányi 2007). For coral reef ecosystems such models are rare. From the 27 reviewed model studies, only three model approaches explicitly included human socioeconomic drivers (Table 2.3, EwE model [#14], coupled biological and Bayesian human behavior model [#18] and an integrated agent-based model [#25]), although in some models, fishing activity is implicit in the model parameterization (e.g., EwE models [#11–14]). The significance of a change in ecosystem state to fisherman or the feedback between fishing pressure and ecosystem state (Cinner et al. 2009, Cinner et al. 2011) are important components for successful management (Hughes et al. 2010, Plagányi et al. 2013).

2.3.4 'Peeling off' approach

As said above, a major criticism of complex models is the difficulty in understanding the underlying mechanisms of their outcomes. To improve our understanding of the way in which these models generate their results we need to peel off the many layers of complex models to effectively reduce their output to explore the key feedback mechanisms and their response to changes in conditions (van Minnen et al. 1995, Van Nes and Scheffer 2005b). Tools to do this include sensitivity analysis, network analysis of model output and construction of materials budgets to trace dominants pathways of carbon, energy or nutrients through the system. This approach helps to base complex models upon a proper understanding of the feedback mechanisms explored in minimal models and only those dynamic mechanism and responses that are key to the system's behavior should be incorporated (Fulton et al. 2005), keeping in mind that synergistic effects may occur. This resulting set of mechanisms and responses should then be augmented by incorporating spatial and environmental parameters that are thought to cause shifts in system states and for which these relationships between state variables were explored (van Nes and Scheffer 2005a). In this approach the results of complex model can be better validated using existing ecological theory and empirical data.

2.3.5 Stability versus complexity

Another recurring criticism of complex models is that community models (e.g., based on Lotka–Volterra equations) become increasingly unstable as complexity increases (May 1972). However, field and experimental observations have shown that ecosystem complexity enhances resilience and stability (Folke et al. 2004, Hughes et al. 2005, Friedrichs et al. 2007, Burgess et al. 2013, Pasari et al. 2013). Previous work has shown the critical role of space as a resource in marine systems, combating the complexity-stability conflict (Fulton et al. 2004c). Moreover, findings from food-web theory show that to improve a model's stability, the modelled food web should consist of multiple trophic levels and capture other food-web features, for example, weak links and mechanisms that weaken the interactions, such as, asymmetric feeding and non-feeding interactions (Fulton et al. 2003a, Rooney et al. 2006, Neutel et al. 2007, Travers et al. 2010). When models include sufficient interactions, simulated community stability increases rather than decreases with model complexity (Baird 2010).

Most dynamic ecosystem models include non-linear functional response curves that greatly contribute to system stability, for example, when predators are capped by a carrying capacity they can no longer drive prey to extinction. Also refugia, migration or dispersal terms and adaptive behavior or plasticity can be built into models to prevent species from dying out completely. However, particularly in more complex models, justifying the use of all these stabilizing mechanisms is difficult, as it is often challenging to obtain realistic parameter values and identify the actual shape of each response curve. The uncertainty of parameters and the complexity of the model makes it difficult to foresee the consequences of model behavior other than bringing stability, i.e., even if the model fit is good, it may be based on the wrong assumptions. Sensitivity analysis and peeling off complexity at the level of these stabilizing mechanisms could provide the required insights.

2.3.6 Ensemble modelling

A way to deal with limits on predictability is to run a complex model with different initial conditions and model formulations and explore the outcomes to assess the likelihood of certain events rather than give a single deterministic or tactical projection (Hannah et al. 2010). This approach is called ensemble modelling (another form of ensemble modelling is to compare the results of the application of different model frameworks to the same scenario, see below). Outcomes can then be compared with multiple minimal models for confirmation of results (Fulton et al. 2003a), with long term field data (Ruiz Sebastián and McClanahan 2013) or expert judgment (Mauser et al. 2013). Often, the most interesting and useful results are obtained when the model does not agree with expert judgment, as this indicates either (i) a fault in the conceptualization of the system as represented by the model, which indicates that further thought or research is needed, or (ii) the potential existence of an unforeseen system behavior that could have implications for management.

Another form of ensemble modelling is when different models are applied to a single system. The resulting bandwidth of outcomes can give insight in the 'structural uncertainty' of the inevitable artifacts in the model formulations (Trolle et al. 2014). This type of uncertainty can only be studied by concurrently applying multiple models and as this approach is rarely taken this type of uncertainty is often ignored. Despite the fact that handling and quantification of uncertainty in model output arising from uncertainty in the numerical inputs to the model (e.g., parameters, initial conditions, forcing functions, boundary conditions) is the typical focus of the published literature (e.g., Hoeke et al. 2011, Pandolfi et al. 2011, Yara et al. 2014 for uncertainties related to climate change and coral reef trajectories), structural uncertainty is often larger and has more significant implications for decision-makers.

2.4 Concluding remarks

This review of model types illustrates that much can be gained from investing time in appreciating the identity and potential of each of the three model types in its own right and in concert. Each of the discussed model types can be helpful, but each also has limitations, when used in a management-oriented context. Minimal coral reef models are crucial in our understanding of ecosystem feedback loops and their response curves. Understanding the drivers of change in a system's state will improve effective management responses—to reverse, prevent or mitigate this change. Intermediate models can assist managers with projections of ecosystem responses and indirect outcomes through the inclusion of a broad (but potentially still incomplete) set of key system components. Intermediate coral reef models can be used to answer many questions as they not only include key biological components, but also various environmental or anthropogenic drivers. For some questions (e.g., when there are multiple interacting drivers) more complex models are the most informative decision-support tools, as they include the major dimensions (i.e., spatial, temporal, taxonomic, nutrient, human activities) and, therefore, incorporate the often cumulative effects of various dynamic mechanisms and responses that are beyond what can be represented in minimal or intermediate models that sacrifice on these dimensions in return for tractability in understanding the model outcomes. For example, system-level models are useful for evaluating the economic and ecologic tradeoffs of various management scenarios, as these more complex models contain the extra detail that is required to capture the feedbacks of interest. However, complex models are not suitable in all situations; in many cases managers value the speed and transparency of simple models.

Nudibranch on crustose coralline algae. *Photo NOAA*

Chapter 3

Coral reef ecosystems and performance indicators

Weijerman, M, EA Fulton, FA Parrish. 2013. Comparison of coral reef ecosystems along a fishing pressure gradient. PLoS ONE 8:e63797.

Three trophic mass-balance models representing coral reef ecosystems along a fisheries gradient were compared to evaluate ecosystem effects of fishing. The majority of the biomass estimates came directly from a large-scale visual survey program; therefore, data were collected in the same way for all three models, enhancing comparability. Model outputs—such as net system production, size structure of the community, total throughput, production, consumption, production-to-respiration ratio, and Finn's cycling index and mean path length—indicate that the systems around the unpopulated French Frigate Shoals and along the relatively lightly populated Kona Coast of Hawai`i Island are mature, stable systems with a high efficiency in recycling of biomass. In contrast, model results show that the reef system around the most populated island in the State of Hawai`i, O`ahu, is in a transitional state with reduced ecosystem resilience and appears to be shifting to an algal-dominated system. Evaluation of the candidate indicators for fishing pressure showed that indicators at the community level (e.g., total biomass, community size structure, trophic level of the community) were most robust (i.e., showed the clearest trend) and that multiple indicators are necessary to identify fishing perturbations. These indicators could be used as performance indicators when compared to a baseline for management purposes. This study shows that ecosystem models can be valuable tools in identification of the system state in terms of complexity, stability and resilience and, therefore, can complement biological metrics currently used by monitoring programs as indicators for coral reef status. Moreover, ecosystem models can improve our understanding of a system's internal structure that can be used to support management in identification of approaches to reverse unfavorable states.

3.1 Introduction

Resource managers are confronted with a range of challenges in their mission to sustain and restore coral reef services that humans desire. Reductions in fishery harvests, whether a result of the degradation of fish habitat, following declines of target fish population or increased regulation, will have substantial cultural, economic, and social implications for resource users. Effective management requires an understanding of coral reefs as ecosystems and of the complex and potential synergistic effects of different drivers (McLeod et al. 2005, Levin et al. 2009). Globally, about three-quarters of all coral reefs are threatened by increased stress from pollution, extensive fishing and climate change (Burke et al. 2011). About half of the coral species that are very susceptible to bleaching are also heavily vulnerable to disease and predation, and recovery can be slow or absent (Carpenter et al. 2008). At the Great Barrier Reef, coral cover has halved in the last three decades (De'ath et al. 2009). Ecological processes will interact with effects of global environmental change. For instance, herbivores (e.g., herbivorous fishes and sea urchins) can control the growth of algae and, therefore, facilitate coralline algal and coral settlement and growth, and they have been identified as a keystone group for their important role in structuring coral communities and improving reef resilience, i.e., the ability of a reef to absorb shock, resist phase shifts, and regenerate after natural and human-induced disturbances (Smith et al. 2001, Graham et al. 2006, McClanahan 1995, Nyström et al. 2000, Green et al. 2009). Reductions in herbivorous fish biomass also may affect the microbial diversity with a shift to more pathogenic microbes and reduced microbial species richness, ultimately affecting the condition of the reef (Bruce et al. 2012). Areas protected from fishing or with less fishing pressure generally have higher live coral cover than do unprotected areas, and fish communities have more large-bodied fishes (Selig and Bruno 2010, Wilson et al. 2010). It is our opinion that management should focus on assessment and improvement of reef resilience to maximize the capacity of corals to respond to the imminent threats of global climate change (Hoegh-Guldberg and Bruno 2010, Graham et al. 2011b).

Resource managers and users can benefit from an evaluation of the system's present status in terms of complexity, stability, and resilience—features that support biodiversity (Odum 1971) and ecosystem 'health' (health used in terms of high diversity, energy recycling, resilience) (Jørgensen et al. 2005). Fishing, habitat degradation, land-based sources of pollution and global environmental changes all affect the health of coral reef ecosystems. Coral reef models have been constructed to investigate ecosystem effects of fishing and alternative fishery management scenarios (Walters et al. 1997, Arias-González et al. 2004, Mumby 2006) habitat degradation (Gribble 2003, Ainsworth et al. 2008b), climate change (Hoeke et al. 2011, Pandolfi et al. 2011) and land-based pollution (Wolanski et al. 2003a, Mumby 2006). Despite the increase in number of modelling studies in coral reef areas, there is still little information on the most appropriate indicators for changes in these systems (Link 2005). Outcomes from ecosystem-based models can identify quantifiable metrics that reflect features of ecosystem's structure and function, indicative for a system's health under its level and type of perturbations (Jørgensen et al. 2005, Link 2005). Establishing these indicators is among the first steps scientists can take to support the implementation of ecosystem-based management (Levin et al. 2009, Shin et al. 2010a). Once these indicators are identified, the next step is to link them to criteria for management decisions; for example, indicator values X, Y, and Z that fall below a priori established threshold values will trigger a specified management action (Hall and Mainprize 2004). However, quantitative approaches for selection of ecosystem-level indicators are only beginning to emerge and, so far, mostly for pelagic systems (Fulton et al. 2005, Link 2005, Samhouri et al. 2009). These indicators might not be suitable for coral reef ecosystems because reef systems differ in structure and energy flow (e.g., more complex food webs, including the microbial food web, for effective recycling of the limited nutrients in reef systems) and in fisheries (e.g., more diversified on reefs).

Empirical studies on coral reef structure and function have generally used spatial patterns or temporal trends in benthic cover and fish biomass and assemblages as indicators for perturbations to reefs from terrestrial runoff (Stimson and Larned 2000, Fabricius 2005, Storlazzi et al. 2009a), climate change (Eakin 2001, Anthony et al. 2008, McClanahan et al. 2011b) and fisheries (Friedlander and DeMartini 2002, Williams et al. 2008, DeMartini et al. 2010, Williams et al. 2011). These parameters are usually used as performance indicators for reef health in monitoring programs. However, they target only direct effects of fishing and do so mostly on small scales (e.g., fish biomass and size structure inside and outside marien protected areas), and no indicators exist for indirect ecosystem effects. Such indicators are crucial to an assessment of the overall ecosystem effects of target species removal and to allow holistic fisheries management (Metcalf et al. 2011). Trophic mass-balanced models represent an analytical approach that could help evaluate ecosystem effects of fishing perturbations and identify optimal management scenarios (Walters et al. 1997, Arreguin-Sanchez et al. 2004, Fulton et al. 2005, Diaz-Uribe et al. 2007, Smith et al. 2007, Xu et al. 2011).

This study focuses on the quantitative description of the characteristics of ecosystem attributes of three coral reef systems along a fishing pressure gradient in Hawai`i, located in the middle of the Pacific Ocean (Fig. 3.1). We attempt to identify the most reliable indicators of ecosystem structure and function of coral reefs to support ecosystem-based fishery management. This comparative approach along an exploitation gradient is used to identify a range of indicators against which each system is assessed in relative terms. The model used is validated with empirical assessments from field data, and the suitability of performance indicators presently used for coral reef management in Hawai`i is discussed.

3.2 Methods

3.2.1 Study sites

We selected three systems along a gradient of fishing pressure on the basis of human population and commercial catch statistics (www.pifsc.noaa.gov/wpacfin/hi/dar/Pages/hi_data_3.php. Accessed 2011 Jan): (1) French Frigate Shoals (FFS) in the Northwestern Hawaiian Islands—no fishing, (2) Kona Coast of Hawai`i Island—medium fishing, and (3) O`ahu—heavy fishing (Fig. 3.1, Table 3.1).

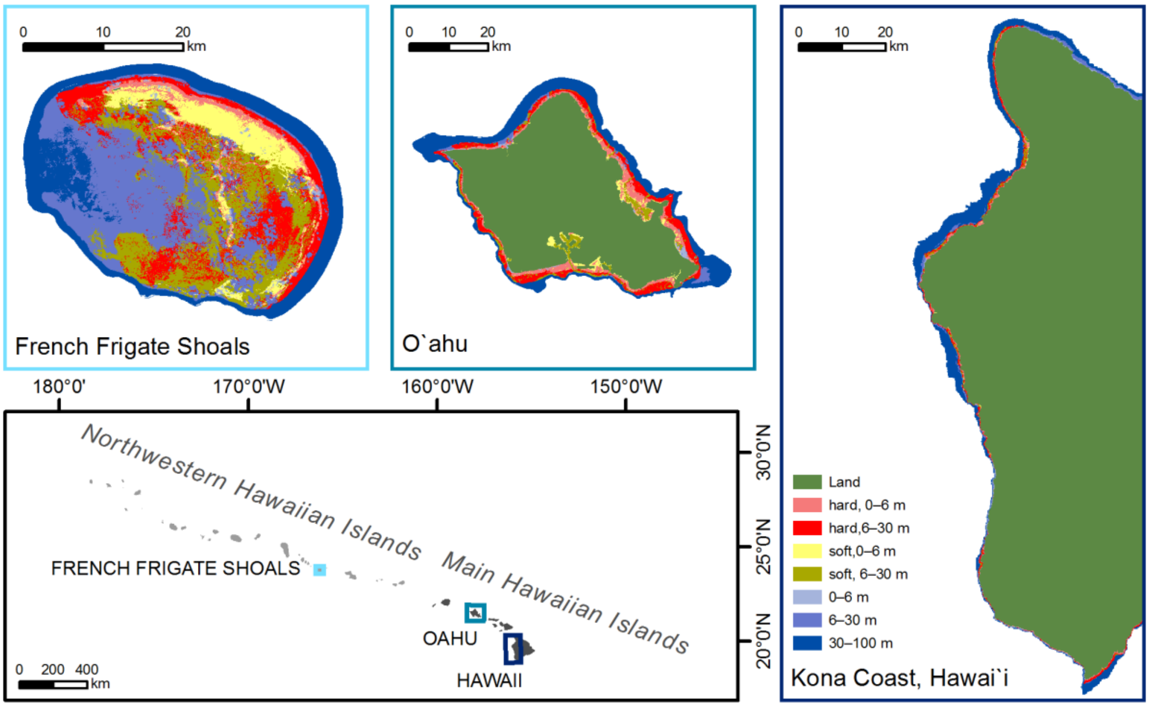

Figure 3.1. Habitat maps of the three modeled coral reef areas and their location in the Hawaiian Archipelago. Hard and soft in the legend indicate bottom type.

Table 3.1. Characteristics of the three coral reef areas included in this study. Exploitation indicates fishery exploitation. FFS = French Frigate Shoals.

Reef system	**Lat.**	**Long.**	**0-30 m area (km^2)**	**% Hard-bottom habitat**	**Human population[1]**	**Population/km^2 reef**	**Exploitation (% of total state catch)**
FFS	166.21	23.79	163	54	0	0	0
Kona	155.42	19.53	90	76	47,705	530	5
O`ahu	158.00	21.49	423	72	953,207	2,253	50

[1] US Census Bureau 2010 estimate

Models represent the status of the shallow-water (< 30 m), hard-bottom, forereef ecosystems in 2010. Total forereef area is 88 km^2 around FFS, 68 km^2 along the Kona Coast, and 307 km^2 around O`ahu (NOAA Fisheries Coral Reef Ecosystem Division [CRED] unpublished data). The monthly mean sea-surface temperatures vary between 24°C in winter and 27°C in summer (Friedlander et al. 2008). Situated in the middle of the North Pacific Ocean, the reefs are exposed to large winter swells that pound on the coastline from the northwest, summer swells from the south, and strong trade winds from the northeast. Hawai`i is located in the North Pacific Subtropical Gyre, which is characterized by low upwelling (Xie and Hsieh 1995) and low plankton standing stock (Longhurst et al. 1995). Climatologic chlorophyll-*a* standing stock from the open ocean were similar between the three areas with annual averages between 2004 and 2010 of 0.057 mg/m^3 (SE 0.003) for Hawai`i and 0.066 mg/$m^3$ (SE 0.004) and 0.067 mg/$m^3$ (SE 0.005) for O`ahu and FFS, respectively (CRED unpublished in-situ data).

3.2.2 Data

This study used data on coral reef fish assemblages, benthic cover, invertebrate assemblages, insular microbe and phytoplankton biomass all collected with the same suite of methods for each study site by the CRED as part of the Pacific Reef Assessment and Monitoring Program (Pacific RAMP). Benthic and fish surveys were conducted between 2001 and 2010 using Rapid Ecological Assessment (REA) surveys at long-term sites. In the earlier years (2001–2007) belt-transect surveys were conducted at fixed mid-depth (12–15 m) forereef sites. Since 2007, for Pacific RAMP, CRED implemented a stratified random survey design in forereef, hard-bottom habitats < 30 m using belt-transect visual surveys for benthic cover and invertebrates and stationary-point-count (SPC) visual surveys for fish data (for details on SPC surveys, see Williams et al. 2011). Fish length estimates from visual censuses were converted to weight using the allometric length-weight formula: $W=aTL^b$, where parameters *a* and *b* are constants, TL is total length in millimeters, and *W* is weight in grams.

Length-weight fitting parameters were available for 150 species (68% of all species included in the model) commonly observed on visual fish transects in Hawai`i (Hawai`i Cooperative Fishery Research Unit unpubl. data). These data were supplemented with information from other published sources and from studies reported on FishBase (www.fishbase.org) that were conducted in other tropical regions on the same species. The Kona Coast model also included fish and echinoid data collected using belt-transect surveys between 2002 and 2010 on mid-depth forereef habitats by the Division of Aquatic Resources (DAR). Towed-diver survey results for roving predatory fishes were used for all three models because that method appears most suitable for fishes that are highly mobile and heavily clumped or for rare fishes (Richards et al. 2011). Echinoderms often have a patchy distribution, and data from towed-diver surveys that cover a large area (~ 2000 m^2 vs. ~ 50 m^2 for REA surveys) are likely more accurate for conspicuous species (e.g., crown-of-thorns sea stars, large urchins, sea cucumbers). However, for boring urchins, it is difficult to obtain a reliable count by towed divers; therefore, we used a combination of belt-transect and towed-diver surveys for echinoderms. Phytoplankton and microbe data were derived from water samples taken at the surface and at ~ 1 m above the reef. Phytoplankton biomass was calculated from the chlorophyll-*a* concentration measured in the water samples, and insular bacteria biomass was calculated from the counted numbers of cells per milliliter. Ratios of production over biomass (P/B) and consumption over biomass (Q/B) came from published sources or empirical relationships following Pauly (1980) and Palomares and Pauly (1998) for fish and Brey (2001) for nonfish groups. Details on the input parameters of all functional groups and the diet composition matrices are in Weijerman et al. (2013).

3.2.3 Model

We constructed a mass-balance ecosystem model using the Ecopath with Ecosim v.6 software (www.ecopath.org). Ecopath is a steady-state mass-balanced model, determined largely by trophic interactions and fishery removals, can be used to describe and examine the energy flows in ecosystems, and provides insight into ecosystem maturity and functioning (Christensen et al. 2008). Ecopath was first developed by Polovina (1984) and further advanced by Christensen and Pauly (1992). This modelling approach is based on a set of simultaneous linear equations for each functional group (state variable) in the system, where the production of a given group is equal to the sum of all predation, nonpredatory losses, and exports. Each functional group in the model is represented by one balanced equation and requires five input parameters. 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. The most robust approach is to enter B, P/B, and Q/B and allow the model to estimate EE. This approach also provides a check for the mass balance because EE cannot be greater than 1.

We included in the model 33 functional groups representing 2 detritus groups (detritus and carrion), 6 microbial food-web groups (phytoplankton, 2 groups of bacteria, 3 groups of zooplankton), 3 benthic primary producers, 9 invertebrate groups, 11 fish groups, 1 marine reptile, and 1 marine mammal group (Weijerman et al. 2013). Species were aggregated into those groups on the basis of similarities in habitat use, diet, feeding behavior (i.e., roving, hunting, grazing), life-history characteristics (e.g., max age, growth constant, length at first maturity), and ecological role (i.e., excavators, bioeroders, scrapers, grazers, detritivores, browsers). Because of their potentially important ecosystem roles and impacts, sea urchins (key herbivores) and sea stars (coral predator) were included as distinct functional groups.

We added constraints on the EE, to range between 0 and 0.95, and used the default value for the assimilation efficiency of 80% for all groups. About 80% of the consumption was assumed to be physiologically useful for consumer groups, and the nonassimilated food (20%, consisting of urine and feces) was directed to detritus (Christensen and Pauly 1992). However, that default value tends to underestimate egestion by herbivores and detritivores. Thus, assimilation efficiency was adjusted to 70% for herbivorous fish groups, to 70% for demersal and carnivorous zooplankton, and to 60% for bacteria, herbivorous zooplankton and benthic deposit feeders (Chardy and Clavier 1988, Cole et al. 1988, Hassett and Boehlert 1999, Christensen et al. 2008).

To achieve mass-balance in the model, we modified the diet data slightly because these data were the most uncertain parts of the four main input values (B, P/B, Q/B, and diet) (Weijerman et al. 2013). After mass-balancing, the trophic level for each functional group was calculated by the model as were various network flow indices that measure the ecosystem maturity following Odum (1969) and Ulanowicz (1986). In the Kona Coast model EE was greater than unity for some invertebrate groups, indicating that the lower trophic levels had insufficient biomass or production to support the consumption of the higher trophic levels. To address this problem, the EE was set to the default value 0.95 to allow Ecopath to calculate the biomass. This approach is considered valid because this Ecopath model is a top-down model and scales the flows to the food required to maintain the biomass at the top of the food web (Bundy and Pauly 2001, Tsehaye and Nagelkerke 2008), and we are confident in the comparison of our estimates of the biomass for these higher trophic levels between the three models because they were all obtained through the same visual survey methods. Plankton biomass needed to be increased for the FFS and Kona models to ascertain enough biomass to sustain the total consumption. In coral reef systems, phytoplankton grazing is a principal pathway that allows allothonous nutrients (Genin et al. 2009) and suspended particulate matter (Fabricius and Dommisse 2000) to import to a reef community through the flowing water. Feeding rates increase when water flows over the reef (Fabricius 1995, Ribes et al. 2003, Genin et al. 2009), and the shape of the benthic community structure on a reef developed by the currents and waves increases capture efficiencies (Bilger and Atkinson 1992, Sebens et al. 1996). Therefore, it is believed an increase in plankton biomass from flows over the reef is valid (Morato et al. 2009).

Validation of the model structure was conducted through comparison of Ecopath's pedigree index with other Ecopath models. Ecopath estimated the pedigree index, on the basis of the confidence intervals (CI) of each input parameter, which describes how well rooted the model is in local data on a scale of 0 to 1, with 1 being the best (Pauly et al. 2000). Confidence in data from field sampling was assumed to have the narrowest CI (10%–30%), and estimates from other models or calculated by Ecopath were assumed to have the widest CI (40%–60%). Most of the biomass data were obtained from Pacific RAMP field surveys and other published field studies from Hawai`i. Therefore, they were defined as having a 10%–30% CI of the mean; whereas, P/B and Q/B input parameters were defined as having 20%–60% CI, depending on whether they came from field studies (~ 20%), empirical relationships (~ 40%) or other models (~ 60%). Diet data (from literature and Fishbase) were defined as having 40% CI when it came from qualitative studies in Hawai`i, 50% from expert opinion, and 80% from quantitative studies. Fishery data were assigned a 50% CI.

Sensitivity analyses were conducted using manual substitution of values (+ 25% , + 50%, – 25%, – 50% of original number) for biomass, P/B, and Q/B for cryptic or small invertebrate groups, because these were the groups with the most limited survey data, and examination of the effect of these changes on the basic input parameters.

3.2.4 Fishery

We defined two fishery "fleets": recreational and commercial. Commercial fishery data were compiled from records of the State of Hawai`i commercial fish landings using the NOAA PIFSC's Fishing Ecosystem Analysis Tool (FEAT; www.pifsc.noaa.gov/human_dimensions/fishing_ecosystem_analysis_tool.php. Accessed 2011 January), a geospatial tool that summarizes commercial fisheries landing statistics per species and fishery region. These fisheries data include coastal and pelagic fisheries. The Ecopath models in this study were limited to the shallow (0–30 m) reef areas with fish biomass estimated only from this area. We assumed that the coastal fishery data captured the extraction of top predators in the modeled area sufficiently, and, therefore, we excluded the pelagic fishery data. We also included landings from the aquarium trade in the commercial fishery fleet using data from Walsh et al. (2010). The aquarium trade is concentrated on the Kona Coast of Hawai`i, where 75% of the total state reported landings originate; therefore, this fishery is included only in the Kona Coast model. Recreational catch data came from the DAR Hawai`i Marine Recreational Fishery Statistics program (www.st.nmfs.noaa.gov/st1/recreational/index.html. Accessed 2011 January). Again, we excluded pelagic species. We compared the results of the recreational fishery with published creel surveys conducted in Hanalei, Kaua`i, Kane`ohe Bay, O`ahu (Friedlander and Parrish 1997, Everson and Friedlander 2004), and Puako, Hawai`i (J. Giddens pers. comm. October

2011). Because of the large discrepancy between results from creel surveys and the reported commercial and recreational landings, we calculated ‘correction’ factors using these values for some fish groups (Weijerman et al. 2013).

To calculate the fishing mortality, we divided the yield ($t/km^2/y$) by the estimated standing stock per functional group (t/km^2). The standing stock estimates used the Pacific RAMP daytime visual surveys. Because these surveys omit cryptic and nighttime species, values likely underestimate actual stock size. However, yield likely is underestimated as well because the nighttime fishery is not accounted for in the recreational landings or creel surveys; therefore, we believe that estimated fishing mortalities are still conservative estimates. Recreational fishery is reported for the entire state. For this fishery, we assumed the same proportion of statewide landings to landings per fishery region as retrieved from the FEAT model for commercial landings of reef fish. In other words, 50% of the total reef fish landings were from O`ahu and 5% from Kona.

3.2.5 Candidate indicators for ecosystem status under fisheries exploitation

We selected a suite of candidate indicators for ecosystem structure and network flows (Table 3.2) based mostly on the robust indicators identified by Fulton et al. (2005), who evaluated 31 ecological indicators with potential to detect effects of fishing between aggregation levels, two model types and four fishing pressure scenarios. We supplemented those indicators with reliable indicators identified by Arias et al. (2004), Samhouri et al. (2009), Shin et al. (2010b), and Xu et al. (2011) and with indicators used by the State of Hawai`i for coral reef monitoring. We used the following criteria to select ecosystem indicators: (1) indicators reflect well-defined ecological processes occurring under fishing pressure, (2) trends in the indicators are expected to be closely correlated with trends in fishing pressure; (3) indicators are easily measurable or estimated in monitoring programs. Included in Table 3.2 are criteria for mature and, in general, more resilient systems.

Table 3.2. Selected candidate indicators for coral reef ecosystem effects of fishery. These indicators were selected from literature reviews and a brief description (explanation) and expected response to fishery is given.

#	Candidate Indicator	Explanation	Expectation with increased fishery exploitation
1	Net primary production (NPP)	Activity index for lower trophic levels.	increase (zero for mature ecosystems)
2	Net system production	Sum of biomass accumulation, biomass lost to mortality, and biomass lost to migration of all benthic species.	Increase (close to zero for mature systems)
3	Total Biomass (B)	Sum of biomass for all ecosystem species.	decrease
4	B - sharks and jacks	Biomass of apex predators.	decrease
5	B - planktivores	Biomass of planktivorous fish.	increase

#	Candidate Indicator	Explanation	Expectation with increased fishery exploitation
6	B/P – size structure	Biomass to productivity ratio as an indication of the size structure of the organisms in the system.	Decrease (higher value indicates more mature system)
7	Piscivores:planktivores biomass ratio	Biomass ratio of piscivorous and planktivorous fish groups.	decrease
8	Total catch	The biomass of functional groups targeted by fisheries.	increase
9	Trophic level of catch	Biomass-weighted average of trophic level of all species caught.	decrease
10	Fishery gross efficiency	Indicates the importance of fishery in structuring the system structure (0.00002 is global average).	increase
11	Mean trophic level of community	Biomass-weighted average trophic level of all species in the ecosystem.	decrease (higher value indicates more mature system)
12	Total consumption	The sum of somatic and gonadal growth, metabolic costs, and waste products for all modeled species.	decrease (higher value indicates more mature system)
13	Total respiration	The portion of consumed energy that is not used for production or recycled as metabolic waste indicative for the systems activity of the higher trophic levels.	decrease (higher value indicates more mature system)
14	System's omnivory index (SOI)	The variance of the trophic level of a consumer's prey group (i.e., specialist, such as coralivorous fish, vs. generalist, such as omnivorous hermit crabs). This index characterizes the extent to which a system displays web-like features.	decrease
15	Ratio of primary production to respiration (PP/R)	The ratio of total production relative to total respiration.	increase (one for mature ecosystems)
16	Primary production required (PPR) for sustaining fish biomass consumption	Calculated primary production required by the system to sustain the level of fishery.	increase
17	Finn's mean path length	The average number of functional groups that a unit of energy flows through in the system before being lost (food chain length).	decrease (higher value indicates more mature system)
18	Finn's cycling index	The fraction of all flows in the ecosystem that is recycled.	decrease (higher value indicates more mature system)

#	Candidate Indicator	Explanation	Expectation with increased fishery exploitation
19	Predator cycling index	The fraction of all flows in the ecosystem recycled through non-detrital pathways indicates the importance of predation in the structure and functioning of the system at higher trophic levels.	decrease
20	Total system throughput (TST)	Represents all of the biomass flows and is the summation of consumption, respiration, export and flows to detritus.	decrease (higher value indicates more mature system)
21	Capacity	Measurement of size and complexity of the system, calculated as the product of TST and the maximum degree of specialization.	decrease (higher value indicates more mature system)

3.3 Results

3.3.1 Model structure and sensitivity

The Hawai`i Ecopath models' pedigree index values were 0.50 for FFS, 0.59 for O`ahu and 0.62 for Kona; all values fell in the medium–high range compared to 50 other Ecopath models, 48% of which had a pedigree from 0.40 to 0.59 and only 10% of which had a pedigree higher than 0.60 (Morissette 2007). These results suggest that the model is well rooted in local data and, therefore, robust.

Sensitivity analyses showed that the model was least sensitive to a change in Q/B ratio for the meiobenthos (e.g., benthic filter feeders, benthic carnivores, benthic deposit feeders and crustaceans), with only crustacean biomass changing more than 10% with a 50% applied increase or decrease of their Q/B ratio. However, decreasing the Q/B by 50% resulted in an unrealistically ratio of production over consumption (P/Q) of > 1 for benthic filter feeders. Benthic carnivores were the least sensitive group to changes in P/B ratio compared to the other small invertebrate groups (Fig. 3.2). Exploration of the sensitivity of the Q/B ratio with a decreasing biomass or P/B ratio (–25% and –50%) resulted in failure of the Ecopath model to calculate the EE. In comparison, elevation of these values resulted in a very high increase in the Q/B ratio, especially for benthic filter feeders as a response to a biomass increase and for benthic detritivores as a response to a P/B ratio increase. P/Q ratio values were unrealistically low (< 0.05) for all groups when biomass was changed and for all groups except the benthic carnivores when P/B changed. In contrast, biomass and the P/B ratio were not very sensitive to increasing P/B ratio or biomass, respectively, but more so to decreasing those values except for the biomass of benthic carnivores. Clearly, more study needs to be devoted to these invertebrate groups to obtain a better estimate of their biomass and P/B ratio for model improvement.

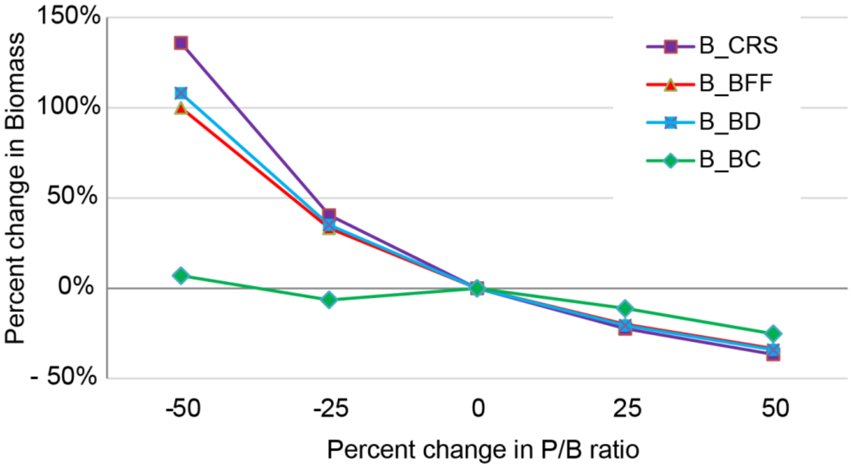

Figure 3.2. Results of sensitivity analysis of four invertebrate groups to changing the P/B ratio on the biomass. CRS=corals, BFF=benthic filter feeders, BD=benthic detritivores, BC=benthic carnivores.

3.3.2 General description of the three systems

Ecopath aggregates an entire system into distinct trophic levels sensu Lindeman (Christensen et al. 2008). FFS showed a higher overall biomass with the main differences in the higher trophic groups (Fig. 3.3). The models estimated that the majority (57%–64%) of the energy flows originated from detritus rather than from primary productivity, indicating that secondary production is based mainly on detritus and net primary production enters the coral reef food chain through heterotrophic benthic organisms. Transfer efficiency was highest from trophic level I to II, especially for the energy flow from detritus, suggesting high energy efficiency at the lower trophic levels. Although the total biomass values for the Kona system and the FFS system were similar, the transfer efficiency for the higher trophic levels (5 and up) was 1.5 to 2.5 times higher in FFS compared to both O`ahu and Kona. The importance of detritus and high efficiency in recycling also was corroborated by the high values for Finn’s cycling index, especially in the models with no (FFS) or intermediate (Kona) fishing perturbation.

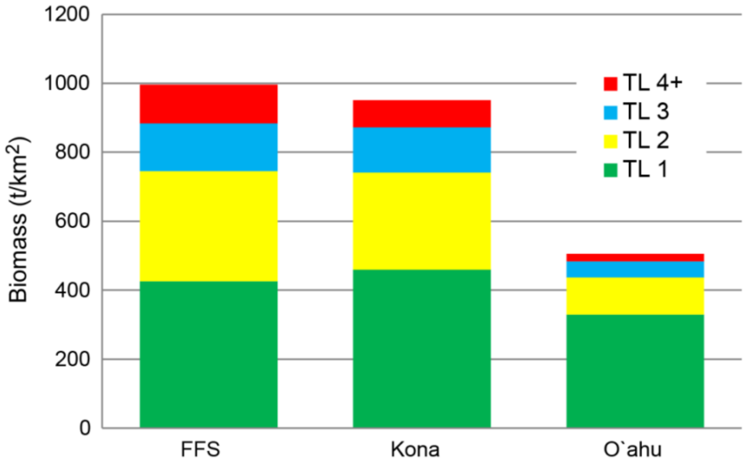

Figure 3.3. Composition of biomass (t/km^2) per trophic level (TL) for the three systems studied in Hawai`i. FFS is French Frigate Shoals; Kona represents the Kona Coast of Big Island.

3.3.3 Evaluation of indicators based on analyses of survey data

Benthic indicators derived by field surveys did not show any clear relationship with fishing pressure (Table 3.3); thus, habitat parameters alone cannot be used as fishery indicators. However, fish indicators did reflect the fishing pressure gradient. Direct effects of fishing were reflected in the increase in total catch and decrease in biomass of apex predators (roving piscivores and sharks) and of large-sized (≥ 50 cm) fishes with increasing fishing pressure (Table 3.3). Also, total fish biomass showed high values at FFS, intermediate values at Kona, and low values at the most populated (highest fishing pressure) island of O`ahu. The disparity in biomass of large fishes and apex predators between FFS and Kona is noteworthy in that it is much greater than the disparity between Kona and O`ahu, indicating that these indicators are quite crude and that the effect of fishing is almost binary (populated/unpopulated).

Against expectations, results show that biomass of planktivores (e.g., *Melichthys niger*, *Naso hexacanthus*, *Myripristis* sp., *Chromis* sp.) strongly declined with an increase in fishing pressure (Table 3.3). Planktivorous fishes are mostly prey fishes, and their biomass was expected to go up with a release of predation pressure (Fulton et al. 2005).

Table 3.3. Benthic (B) and fish (F) related indicators for coral reef health from survey data (unnumbered; NOAA Fisheries Coral Reef Ecosystem Division and Hawai`i Department of Aquatic Resources indicators) and candidate indicators (numbered) for fishery effects. The numbers correspond to the numbers in Table 3.2 for details on these indicators. Standard error given in parenthesis. FFS is French Frigate Shoals; Kona is the Kona Coast of Big Island.

No	B/F	(Candidate) Indicators	FFS	Kona	O`ahu
	B	Total biomass benthic algae (g/m^2)	281	225	307
	B	Total cover macroalgae (%)	12.5 (6.44)	2.3 (0.92)	17.7 (2.24)
	B	Total cover crustose coralline algae (%)	8.0 (5.01)	8.9 (0.94)	6.8 (0.88)
	B	Coral cover (%)	20.3 (6.61)	24.6	11.3 (1.36)
	B	Habitat complexity (towed-diver surveys 2008–2010; 1 is low, 5 is high)	2.2	2.9	1.9
	F	Total fish biomass (Rapid Ecosystem Assessment surveys 2005–2010) (g/m^2)	92	68	20
	F	Large (≥ 50 cm) fish biomass (towed-diver surveys 2006–2010) (g/m^2)	6.9	1.4	0.8
4	F	Biomass apex predators (sharks and roving piscivores) (g/m^2)	4.86	0.30	0.26
5	F	Biomass planktivores (g/m^2)	19.09	12.94	4.50
6	F	Piscivores:planktivores biomass ratio (g/m^2)	0.33	0.52	0.23

3.3.4 Evaluation of the candidate indicators on the basis of ecosystem structure and network analyses

Various candidate indicators showed a strong trend with increasing fishing pressure (Tables 3.3 and 3.4). Sequential ecosystem structure effects along the fishing pressure gradient were most clearly reflected by fishery-related indicators, net system production, size structure of the community and biomass of planktivores (Tables 3.3 and 3.4). The relatively high fishery gross efficiency for O`ahu suggests that that system structure is strongly influenced by fishing. The negative value for the system production at FFS indicates large import. Import is expected to be much higher at the forereef habitat of FFS because it is adjacent to a large lagoonal area, compared with the steep drop-off at the Kona Coast and the limited, shallow, lagoonal bays around O`ahu (Fig. 3.1). In our ecosystem network analyses, similar clear patterns were shown by Finn's mean path length, Finn's cycling index, and the primary production required to sustain the fishery (Table 3.4).

Table 3.4. Ecopath derived values for candidate indicators of fishery effects on coral reef ecosystems. The numbers correspond to the numbers in Table 3.2. FFS=French Frigate Shoals; Kona=Kona Coast of Hawai`i.

No.	Candidate Indicators	FFS	Kona	O`ahu	units
1	Net primary production (NPP)	7,057	8,739	6,403	t/km^2
2	Net system production	-158	517	3175	t/km^2
3	Total Biomass (B) exl. detritus	996	951	539	t/km^2
7	B/P – size structure	0.069	0.061	0.057	
8	Total catch	-	0.76	1.31	t/km^2/y
9	Mean trophic level of catch	-	2.96	3.11	
10	Fishery gross efficiency	-	0.000087	0.000205	
11	Mean trophic level of community	1.93	1.82	1.54	
12	Total consumption	21,056	21,715	9,187	t/km^2
13	Total respiration	7,215	8,223	3,228	t/km^2
14	System's omnivory index (SOI)	0.291	0.236	0.241	
15	Ratio of primary production to respiration (PP/R)	0.98	1.06	1.98	
16	Primary production required (PPR) to sustain fishery	0	26	142	t/km^2
17	Finn's mean path length (Food chain length)	5.11	4.45	3.57	
18	Finn's cycling index	28.42	22.92	16.01	% of TST
19	Predator cycling index	3.97	4.01	3.75	% of TST without detritus
20	Total system throughput (TST)	37,817	40,352	23,493	t/km^2
21	Capacity	207,484	226,151	119,837	flowbits

The remaining candidate indicators did not show a clear sequential pattern with increases in fishing pressure, but many indicators pertaining to the system's stability or maturity sensu Odum (1969) showed a binary pattern, with a minimal difference between FFS and Kona (Table 3.4). For example, mature, stable systems have a close coupling between production and respiration (P/R ~ 1) and, therefore, have no or little excess production, a high system throughput and capacity and high overall biomass. Other indicators that showed the same binary pattern were total biomass, mean trophic level of the community and biomass of roving piscivores. On the basis of the indicators for system maturity (Table 3.4), it appears that the reef system around O`ahu is in a more transitional state compared to the reef systems around FFS and along the Kona Coast. This difference could be a result of higher fishing perturbations as habitat (benthic indicators) did not show this trend.

Candidate indicators that did not show a simple linear pattern with an increase in fishing pressure were the piscivore:planktivore ratio and the net primary production. The system's omnivory index showed minimal to no differences among the three systems, indicating that the complexity of the food webs was similar. The trophic level of the catch was also similar between Kona and O`ahu.

3.4 Discussion

The results should be regarded as trends as it is impossible to make rigorous statements on the basis of only three points. Ideally, more Ecopath models will be developed for other islands in the Hawaiian Archipelago to get a better understanding of which combination of variables are most indicative for fishing pressure.

3.4.1 Model structure and sensitivity

In coral reefs, roughly 50% of the net primary production (NPP) produced offshore and on the reefs is channeled through the microbial loop (Azam et al. 1983, Pernthaler 2005, Zöllner et al. 2009). This high efficiency in reefs was successfully simulated in the model on the basis of the high detritus dependence and the high value of Finn's cycling index, especially for the Kona and FFS models. Including the microbial food web in the model increased total energy throughput and energy transfer efficiency (TE) from detritus but decreased the TE from primary productivity (PP). These effects could be caused by enhanced recycling of materials and energy by the microbes; therefore, including the microbial loop simulates the system behavior more appropriately (Paves and Gonzalez 2008). In all three models, TE was 1.4 to 1.8 times higher from detritus than from primary production, corroborating the importance of the microbial loop in coral reef ecosystems. On the basis of the pedigree, it was clear that all three models are highly rooted in local data enhancing the robustness.

Area is an important variable that influences model results. Comparison of our model results with results from other regional models was difficult because study area, survey methods and functional groups varied between models. The FFS Ecopath model of Parrish et al. (2011) also has a shallow (0–30 m) reef component, and, when comparable areas were derived, the fish biomass in Parrish et al's model was 94.3 g/m^2, which compared very well with our 91.6 g/m^2. It was not possible to compare any other functional groups. A Kona coast model (Wabnitz unpubl. data) includes the same shallow reef area that was used in this study but extends to a depth of 100 m and includes all habitat types for a total study area of 90 km$^{2.}$ In our study, we only used the forereef area at depths of 0–30 m for a total area of 68 km^2. Wabnitz (unpubl. data) used shallow (0–30 m) fish biomass values from Friedlander et al. (2006), and our estimate of 67.7 t/km^2 for our Kona coast model is very comparable with their hard-bottom estimates (ranging between 40 and 85 t/km^2) for their four Kona sites. We feel, therefore, confident that our fish biomass numbers are realistic.

The lower trophic groups have been considered mostly as biomass pools in other reported reef models and are the groups of greatest uncertainty; hence, variation can be expected. Urchin biomass in this study was 19 t/km^2, which was 5 times lower than values from Wabnitz (unpubl. data). Another discrepancy between Wabnitz (unpubl. data) and this study was the biomass of corals. Coral biomass in this study adjusted for the sand habitat (no corals) was 194 t/km^2 and in Wabnitz et al. 82 t/km^2. This large difference in coral biomass could be caused by the (assumingly) low coral cover in the mesophotic depth included in the Wabnitz (unpubl. data) study area. Clearly, more research on invertebrates would greatly enhance the model. Sensitivity analyses of the meiobenthos showed that changes in the Q/B ratio had little effect on the biomass or P/B ratio, but decreasing the biomass by 50% resulted in a change in P/B of 80%–100% for all four invertebrate groups and decreasing the P/B ratio resulted in a change in biomass of 100% for benthic filter feeders and deposit feeders and 136% for crustaceans. Our biomass estimates for these groups came from studies of the Kona Coast of Hawai`i supplemented by visual observations at hard-bottom sites in each system, and the P/B (and Q/B) ratios were weighted according to the species composition at each system and are in the range of values reported in other reef systems (Weijerman et al. 2013). Because these lower trophic functional groups play an important role in the transfer efficiency of energy, better estimates are highly recommended to improve the model.

3.4.2 Evaluation of indicators derived by monitoring programs

Coral and macroalgal cover are variables that are widely used as metrics in evaluating reef health and are also included in DAR’s monitoring program and the Pacific RAMP. Solely on the basis of these habitat indicators, reefs along the Kona Coast of Hawai`i (intermediate fishing) would be categorized as being in a better health than are reefs in FFS (no fishing; Table 3.3). Therefore, these variables are not directly indicative for fishery effects. Fishing does not necessarily degrade reefs, high macroalgal cover does not necessarily indicate a degraded reef (Parrish and Boland 2004, Vroom and Braun 2010) and high coral cover does not necessarily indicate a reef with high fishable biomass (McClanahan et al. 2011a).

In contrast, large-fish biomass and the candidate indicator, biomass of apex predators, showed a strong relation with fishing pressure; albeit, not a sequential relation, it was more a binary pattern where intermediate fishing pressure resulted in a sharp decline in biomass of these species. The piscivore:planktivore ratio was one of the indicators that was most robust in other system studies (Fulton et al. 2005) but was not an effective indicator of fishing pressure on the Hawaiian reef systems. This result could be because the biomass estimates for apex predators from towed-diver surveys were used. If biomass estimates from REA (small-scale) surveys were used, the piscivore:planktivore ratio would be 3.34 for FFS, 0.52 for Kona, and 0.19 for O`ahu, where shark and jack encounters in REA surveys are rare. This deceasing trend is what you would expect along a gradient of increasing fishing mortality with target species declining and planktivorous species contributing a larger part to fish assemblages (Fulton et al. 2005). However, in fished areas, jacks and sharks are likely wary of divers and swim away, and their numbers can be underestimated; whereas, in protected areas (such as FFS), jacks and sharks might be more curious and approach divers, hence, their numbers are likely to be overestimated at REA sites. Therefore, the biomass estimates from towed-diver surveys are believed to be more accurate (Richards et al. 2011). The same holds true for the biomass of planktivores, which, against expectations, decreased with increasing fishing pressure. This phenomenon could be explained by fishing mortality; according to the Hawai`i fishery statistics, planktivorous soldierfishes (*Myripristis* sp.), unicorn fish (*Naso breviosis*) and some sergeant fishes (*Abudefduf* sp.) are targeted in the fishery and could drive their numbers down in the populated areas. Although the exact drivers of this phenomenon are unknown, this trend of high planktivorous biomass in remote areas compared to populated areas also is observed elsewhere in the Pacific (Williams et al. 2011).

3.4.4 Evaluation of candidate indicators derived by Ecopath

Evaluation of the candidate indicators across a fishing pressure gradient showed that indicators at the community level were most robust (i.e., clearest trend) and that multiple indicators are necessary to identify fishing perturbation. Candidate indicators related to the system's community, such as total biomass, community size structure and trophic level of the community, were indicative of fishing pressure and could be used as performance indicators compared to a baseline (e.g., a 1950 system).

Community and ecosystem attributes deal with energy flows and ecosystem functioning and are not readily measurable from field studies. Throughput, production, and consumption—along with the internal state (i.e., Finn's cycling index, mean path length)—reflect a system's ability to support its current state and level of exploitation in the long term (Vasconcellos et al. 1997, Fulton et al. 2005). On the basis of the statistics of metrics indicative of a system's maturity sensu Odum (1969), reefs around FFS and along the Kona Coast were in a stable, mature state and the observed level of fishing along the Kona Coast was supported by the system. However, the coral reef ecosystem around O`ahu appears to be in a transitional state and fishing mortality is assumed to have played an important role in the current structure and functioning of this ecosystem. The mean trophic level of the community was an indicator that showed a clear decreasing trend with an increase in fishing pressure across the three study areas as did the biomass/production ratio, the mean food chain length and Finn's cycling index. The low EE for benthic algae (0.16–0.33) indicates a lack of herbivorous grazing pressure that could drive the transitional state (i.e., moving from a coral dominated system to an algal dominated system). Results from 7 out of 10 long-term (> 10 year) monitoring programs in O`ahu showed a coral cover decline of 4% to 35%, corroborating this hypothesis (Friedlander et al. 2008). Naturally, fishing mortality is not the only perturbation that affects the status of coral reef ecosystems. We used human population as an indicator for fishing intensity; however, with an increased population, other stressors to reef ecosystems, such as sedimentation, nitrification, and other land-based sources of pollution, also augment. Notwithstanding, the results from the Ecopath models in our study do show that fishing-related indicators did indicate a clear decreasing trend with an increase in fishing mortality and benthic indicators did not.

3.5 Conclusions

Candidate indicators for fishing pressure showed that indicators at the community level (e.g., total biomass, community size structure, trophic level of the community) showed the clearest trend with increased fishing mortality. Results also showed that multiple indicators are necessary to identify fishing perturbations. These indicators could be used as performance indicators when compared to a baseline for management purposes. Currently, collected data from monitoring programs in Hawai`i of fish biomass and fish assemblages and size structure clearly show a strong relation to fishing mortality, with higher fishing mortalities resulting in a shift in fish communities (decrease in number of large fishes and in biomass of piscivores), unlike data of benthic parameters (e.g., coral or algal cover). Ecopath statistics of the structure and functioning of ecosystems can supplement these metrics with insights into the stability of the system. Stable, mature systems are more likely to recover from perturbations, such as global change or local stressors to reefs (e.g., land-based sources of pollution, fishing). Understanding the processes that structure a reef is important in supporting marine resource managers to reverse transitional states to stable systems that yield high fishable biomass. On the basis of the results of this study, it is clear that the reefs around O`ahu are in a transitional state. The low EE for benthic algae around O`ahu, compared to around Kona and FFS, indicates that grazing pressure was minimal. Reduced grazing of (especially) macroalgae by herbivores could result in a shift to a system that is dominated by algae instead of corals; the latter is economically and aesthetically more desirable as it supports a higher fishable biomass and dive tourism. In follow-up studies, it would be beneficial to use Ecosim, a simulation model that uses Ecopath for input parameters, to evaluate management scenarios that are most likely to succeed in reversing the current transitional state of the coral reefs around O`ahu.

Branching *Acropora* coral. *Photo Dave Burdick*

Chapter 4

Design and parametrization of a coral reef ecosystem model for Guam

Weijerman, M, IC Kaplan, EA Fulton, R Gorten, S Grafeld, and R Brainard. 2014. Design and parameterization of a coral reef ecosystem model for Guam. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-43. 133 + Appendices

Declines in the fish stocks and degradation of habitats around Guam have serious implications for the residents of Guam who depend on the ecosystem services provided by coral reefs. Management on an ecosystem scale has proven to be a useful strategy to conserve, manage and restore marine systems. Implementing ecosystem-based management requires an understanding of the complex and often synergistic dynamics of coral reefs, including the role of humans in the ecosystem. The Atlantis modelling framework integrates physical, biogeochemical, ecological, and anthropogenic processes in a three-dimensional, spatially explicit domain and can serve as an useful decision-support tool for ecosystem-based coral reef management. We describe the details of each model component and present the parameterizations of the spatial and ecological modules in Atlantis.

The Guam Atlantis model is focused on the shallow (< 30 m) coral reefs fringing Guam and is predominantly based on biological data collected in Guam. The Atlantis model uses polygons as its 'grids' which were drawn to represent areas of similar ecological and oceanographic characteristics while also taking into account the spatial strata of fisheries catch data and existing spatial management areas. In the ecological module food-web dynamics of 42 functional groups are simulated: 3 detritus, 2 bacteria, 5 plankton, 3 algae, 2 corals, 7 invertebrate, and 20 vertebrate groups. We gathered and analyzed environmental, habitat, biological, and fishery data from diverse sources. These data helped us identify information gaps, such as, near-shore habitat data, biomass and abundance data of invertebrate species, chlorophyll-a data at different depths and certain life history parameters for invertebrates and fish.

After calibration and testing we believe that the model produces an adequate representation of Guam's coral reef ecosystems. However, there still is a need for the incorporation of coral-reef-specific dynamics and improved physical oceanography to better simulate coral reef processes around Guam. These aspects are described in Chapter six.

4.1 Introduction

Coral reef ecosystems are important as habitats, natural buffers, sites for recreation and cultural practices and as a key component of the marine economy. Coral reefs generate millions annually from marine tourism (Cesar et al. 2003, Van Beukering et al. 2007) and are important to the social and economic welfare of coastal communities (Moberg and Folke 1999). Commercial and recreational fisheries support many jobs and fishing expenditures generate millions of dollars in sales revenues and value-added benefits. Furthermore, in many Pacific islands, fisheries serve vital non-market functions, such as building social and community networks, perpetuating fishing traditions and providing fish to local communities. Yet, compared to pelagic fisheries, reef-associated fisheries have received little attention (Sadovy 2005). However, it is well established that there is a positive feedback between coral cover and reef-fish biomass (Jones et al. 2004, Green et al. 2009). When reef-building corals are lost, the subsequent reduction in structural complexity results in reduced species diversity and a loss of fish species that fulfill important ecological roles in the resilience of coral reefs (Jones et al. 2004, Graham et al. 2006, Alvarez-Filip et al. 2009). There is a general consensus among scientists that coral reefs are in trouble (Bruno and Selig 2007, Carpenter et al. 2008, Wilkinson 2008). In recent reviews on the extinction risks of corals, two of the most important threats to the survival of corals and especially coral reefs were identified as being human-induced ocean warming and ocean acidification (Brainard et al. 2011, Burke et al. 2011).

Massive and branching stony corals are the primary framework builders and a major source of calcium carbonate production of coral reefs. Two main processes regulate the abundance or growth of corals and other calcifiers: (1) accretion determined by the narrow range of suitable environmental conditions that allows the deposition of calcium carbonate, and (2) erosion resulting from physical, chemical, and biological processes. Reef structures are built by combining calcium and carbonate ions derived from the seawater into aragonite (or calcite) crystals that form the corals' skeletons. These coral skeletons and crustose-coralline algae are often cemented together with aragonite and high-magnesium calcite to form reefs. Natural ongoing bioeroding processes of this carbonate substrate influence the net structural growth (Perry et al. 2012). It is ultimately the maintenance of these three-dimensional structures rather than the corals themselves that provide the reef's functions and ecosystem services (Graham et al. 2006, Perry et al. 2012).

Reef accretion requires energy and if the external aragonite or calcite saturation states decrease as a result of increased atmospheric CO_2, calcification will reduce or stop altogether (Langdon and Atkinson 2005). Atmospheric CO_2 has increased rapidly from its pre-industrial level of 280 ppm to over 400 ppm today and the earth's system has already warmed, on average, close to 0.74°C globally over the last century primarily as a result of greenhouse gas emissions (IPCC 2007). Elevated water temperature can lead to coral bleaching (the expulsion of symbionts that give corals their color) and disease epizootics and have already resulted in repeated mass coral bleaching and mortality events worldwide (reviewed in Brainard et al. 2011). Current projections on global increases in atmospheric carbon dioxide concentrations, water temperatures and ocean acidification have led to predictions of a significant loss of corals and other calcifying marine organisms, resulting in reduced diversity of reef communities and a reduced resilience of corals to local stressors (Hoegh-Guldberg et al. 2007, Kennedy et al. 2013).

While local governments are limited in their capacity to reduce greenhouse gas emissions and so reduce the ongoing ocean warming and acidification, they can play a pivotal role in enhancing the corals' capability to recover from impacts of these global threats by reducing additional local stressors caused by land-based sources of pollution and excessive fishing (Carilli et al. 2009, Hughes et al. 2010, Kennedy et al. 2013). Based on their high biological diversity, coral reef ecosystems likely have increased functional redundancy, which is expected to provide increased resilience (resilience defined as the capacity to 'bounce' back from a disturbance) compared with less-diverse ecosystems. However, this capacity of organisms and natural systems to bounce back can by degraded by sequential, chronic, and multiple disturbances, physiological stress and general environmental deterioration (Nyström et al. 2000). Loss of resilience may take many forms, including increased disease susceptibility, impaired reproduction and recruitment, loss of functional diversity/redundancy in communities and reduced individual growth rates.

A critical part of any local management approach to enhance coral recovery from global threats is the mitigation of local stressors that affect coral-macroalga competition, early life history development and coral survival (Baskett et al. 2009b, Gilmour et al. 2013). This approach can be met through the protection of a large and diverse herbivorous fish population (Pandolfi et al. 2003, Bellwood et al. 2006) and through the reduction of nutrient input which favors algal growth above coral growth (Fabricius 2005). While some reefs are still in fair to good condition, many near-shore ecosystems adjacent to urban areas and popular destinations have suffered from land-based sources of pollution, fishing pressure, recreational overuse, crown-of-thorns seastar outbreaks and ocean warming (Wilkinson 2008).

As reefs provide a wealth of benefits to adjacent local communities, protecting these reefs from deterioration is a major endeavor for governments. Limits to fishing through the degradation of fish habitat, declines in important fish populations or increased regulations have the potential for important cultural, economic, and social implications to the residents of near-shore communities. Despite the importance of reefs and near-shore habitats to Guam's economy and culture, the condition of marine resources has generally degraded over the past 20 years (Burdick et al. 2008, Richmond et al. 2008). In recent years, additional development and construction have begun to accommodate the translocation of about 40,000–60,000 military personnel and civilians (Kan 2013). Naturally, this new infrastructure will likely result in increases in impermeable surfaces, demand on wastewater treatment and solid waste facilities, and use of marine resources.

Effective local management must be based on proper understanding of coral reefs as ecosystems and of the complex and sometimes synergistic impacts of different stressors while also taking into account social and economic dependencies on these marine resources. As a first step, resource managers and users can benefit from forecasts of the ecological, economic and social impacts of alternative management strategies and of an increase in human population. Secondly, state and federal agencies have specific mandates to choose actions to mitigate impacts on coastal ecosystems and economies. For example, NOAA Fisheries plays a supportive and advisory role in the management of living marine resources in coastal areas of Guam, and ecosystem-based management is an important component of NOAA’s Habitat Blueprint Initiative (http://www.habitat.noaa.gov/habitatblueprint/) and Next Generation Strategic Plan (http://www.ppi.noaa.gov/ngsp/), as well as in the U.S. National Ocean Policy 2010 (http://www.doi.gov/pmb/ocean/policy/index.cfm). To date, however, few tools have been available to support effective implementation of ecosystem-based management.

Models, as simplistic representations of ecosystems, can serve as useful tools to support decision making. Coral reefs models have been developed to investigate various aspects of the ecology of coral reefs with or without the predicted effects of global change, such as erosion and accretion (Eakin 1996, Kennedy et al. 2013), coral growth (Hoeke et al. 2011), larval connectivity (Mumby et al. 2011), space competition (Mumby 2006), influence of light on coral growth (Kleypas 1997), existence of alternative stable states (Żychaluk et al. 2012), effects of environmental perturbations on benthic community dynamics (Kubicek et al. 2012), and evaluation of management strategies that would improve reef resilience mostly focusing on fishing regulations (Mumby 2006, Edwards et al. 2011, Melbourne-Thomas et al. 2011a). One model that integrates various disciplines and addresses agency mandates is the Atlantis Ecosystem Model (Atlantis) developed by Dr. Elizabeth Fulton at the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Marine and Atmospheric Research in Hobart, Australia[1] and can simulate the complex ecosystem processes that link the physical environment with the associated biological and human communities (Fulton 2001, Fulton et al. 2004a, Fulton et al. 2004c). It also includes the main steps in an adaptive management cycle (including feedback from resource managers on performance indicators) and can be used as a decision-support tool allowing for the evaluation of ecological and economical cost-benefits of alternative management strategies. A 2007 United Nations Food and Agriculture Organization report, which reviewed the world’s leading 20 ecosystem-modelling platforms, rated CSIRO's Atlantis ecosystem model as the best in the world for evaluating management strategies at an ecosystem level (Plagányi 2007). However, to date the Atlantis framework has not been developed for a coral reef ecosystem so this approach, outlined in this chapter and chapter six, will be novel.

4.1.1 Stakeholder Participation

A requirement for effective ecosystem-based management is that local and federal stakeholders and resource managers identify and agree on common goals and objectives, such as clean water, sustainable coastal habitats and fisheries and conservation of biodiversity. To measure progress towards these agreed-upon goals, identifiable ecological and socioeconomic indicators need to be established. In November 2012, a workshop was held in Guam where local and federal resource managers, scientists, the fisheries cooperative, nongovernmental organizations and the Navy were invited to participate (Weijerman and Brown 2013). That workshop resulted in the common goal to identify management strategies that would reverse the downward trend in coral cover and fish biomass and mitigate the effects of the expected increase in human population associated

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[1] http://atlantis.cmar.csiro.au/

with the military build-up. Ecosystem attributes were identified as “having a sustainable coral reef ecosystem that can recover from the current local (e.g., fishery, land-based sources of pollution, crown-of-thorns seastar predation) and global (ocean acidification and warming) threats” (Weijerman and Brown 2013). Additionally, ecological and socioeconomic indicators to track progress and management scenarios were identified so that model simulations could help understand the tradeoffs among ecosystem services of the alternative scenarios. These management scenarios were further developed in a follow-up workshop in June 2014.

4.1.2 Objective

In this chapter, we present the basic formulations and parameterization of the Guam Atlantis Model. We describe the spatial delineation of the model extent, the aggregations of species into functional groups and the data processes and sources used for all biological parameterizations. Additionally, we describe the physical forcing files that are used in the model and briefly mention the fishery characteristics of Guam. We intend to apply the model to explore ecological and socioeconomic tradeoffs of the identified alternative management scenarios once the model is fully developed (Chapters seven and eight). At this stage we have initialized the model to represent the present day (2011) ecosystem status of Guam’s reefs, to (1) simulate the expected shift to a quasi-equilibrium state of a reef system assuming an absence of human stressors or natural disturbances; and (2) examine the modeled response to a range of fishing mortalities.

4.2 Guam

A summary overview of Guam is given here but for more detailed information see e.g., Burdick et al. 2008, Richmond et al. 2008, Brainard et al. 2012.

Guam is one of the largest and most populated islands in Micronesia with a total land area of 544 km^2 and a coastline of 244 km. It is about 48 km long and between 6 and 19 km wide. Guam is located at the southern tip of the Mariana Archipelago at 13°28’ N and 144°45’ E. The nearest island in the archipelago is Rota which is part of the Commonwealth of the Northern Mariana Islands (CNMI) located 60 km northeast of Guam and the Philippines located 2,568 km west of Guam. Guam’s population is around 160,000 (U.S. Census 2010) and it is a popular tourist destination with around 800,000 visitors every year mainly concentrated in Tumon Bay on the west coast (Brainard et al. 2012). Guam’s population is expected to increase with another roughly 60,000 people as a result of the planned relocation of U.S. military personnel, their dependents, and support staff (Kan 2013). Major population centers are in Tumon Bay, the capital Hagåtña, and between Tumon Bay and Anderson Air Force Base in the north (Fig. 4.1).

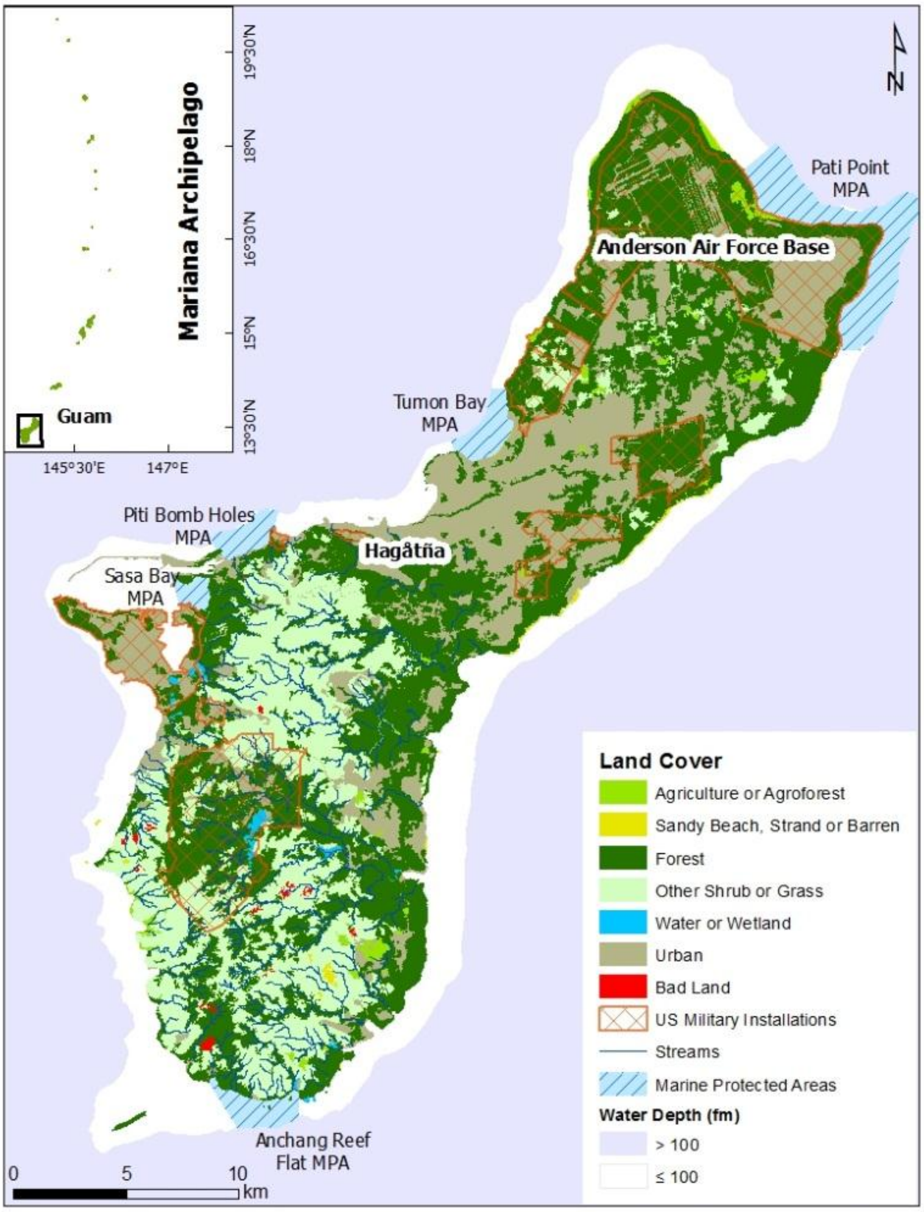

Figure 4.1. Location of Guam in the Mariana Archipelago (inset) and land cover of Guam showing the main population centers in the central part of Guam, restricted access areas (military land), the many rivers in the southern part of Guam, and five marine protected areas.

The northern part of Guam is relatively flat and primarily comprised of uplifted limestone whereas the southern part is of volcanic origin with steep hills and over 40 rivers draining into the coastal waters (Fig. 4.1). Guam has distinct wet and dry seasons with the dry season extending from January to June and a mean rainfall of 79 cm (SD 42), and a wet season from July to December with a mean rainfall of 176 cm (SD 25) (Lander and Guard 2003; Fig. 4.2). Humidity is around 80% and the mean air temperature is 28°C.

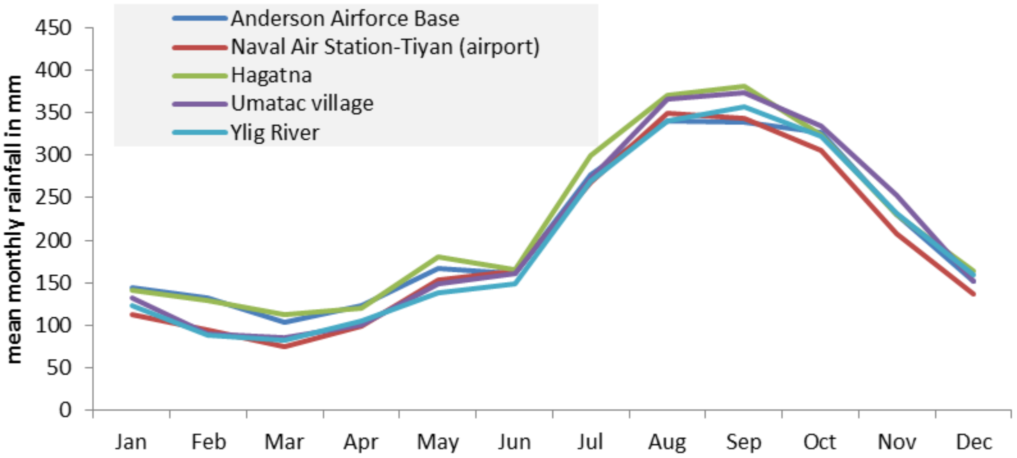

Figure 4.2. Mean monthly rainfall at five stations in Guam (1970–2000 data from Lander and Guard 2003). Anderson Airforce Base is in the North of Guam, the airport in the center, Hagåtña on the east coat in the center of the island (see Fig. 4.1), Umatac is on the southwest coast and Ylig is on the southeast coast just south of Hagåtña.

The major sea current influencing Guam is the North Equatorial Current bringing oligotrophic waters to Guam (Suntsov and Domokos 2013). Oceanic primary productivity is low around Guam compared to other islands in the Pacific especially compared to the Line Islands close to the equator (Nadon et al. 2012; Fig. 4.3).

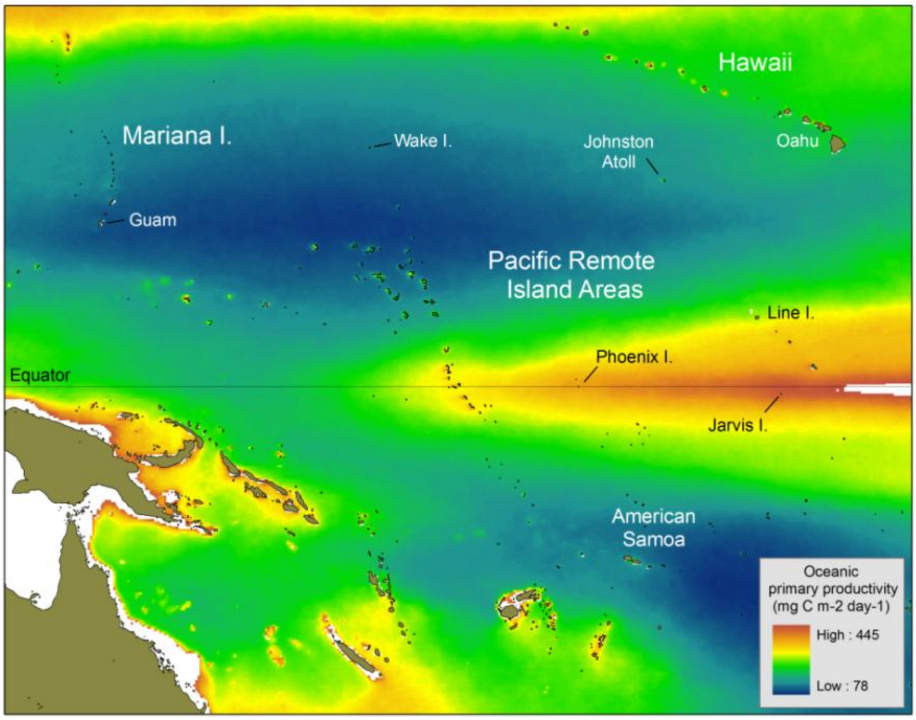

Figure 4.3. Oceanic primary productivity derived from satellite imagery (average from 1999–2009). Figure taken with permission from Nadon et al. (2012).

Historically, Guam experiences many typhones. Guam's typhoon season is during the humid summer months and four major typhoons have impacted Guam since 1994 (Burdick et al. 2008). There has been a decrease in the number and intensity of typhoons in the west Pacific in the past decade compared with earlier decades. Additionally, on average every year three tropical storms pass Guam (Storlazzi et al. 2009b).

Various environmental and geological variables influence the structure and composition of Guam's reefs (Fig. 4.4).

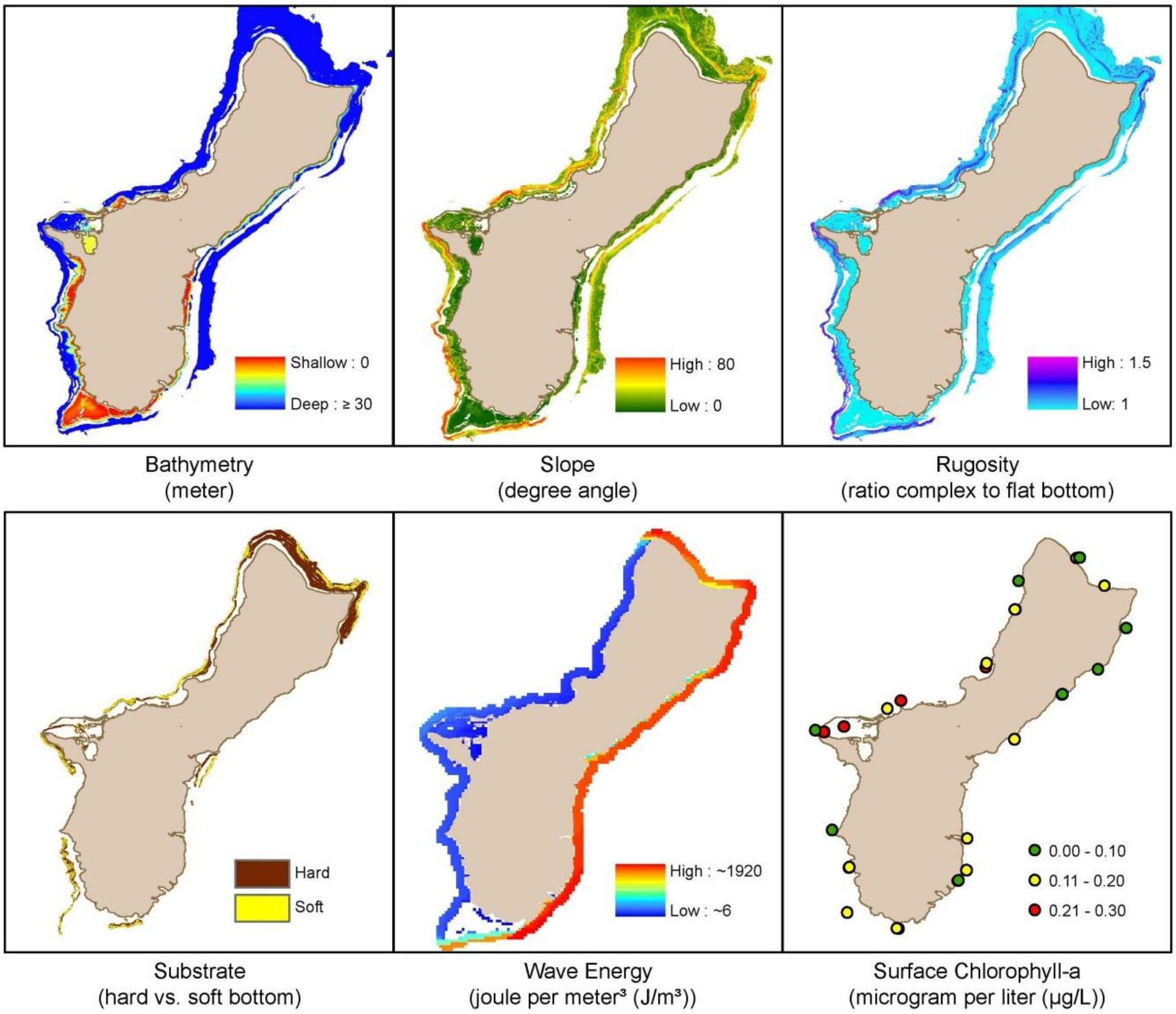

Figure 4.4. Geological and environmental variables influencing Guam's reef structure. Data from NOAA Coral Reef Ecosystem Division, wave energy from Peter Houk, unpublished GIS layer.

Guam is surrounded by fringing reefs with some reef flats along the windward areas. It is located close to the high-diversity region of the Coral Triangle and boasts more than 5100 known marine species including more than 1000 nearshore fish species and more than 375 species of stony, scleractinian corals (Paulay 2003). Fish biomass on Guam is low compared with the unpopulated Northern Mariana Islands (Fig. 4.5).

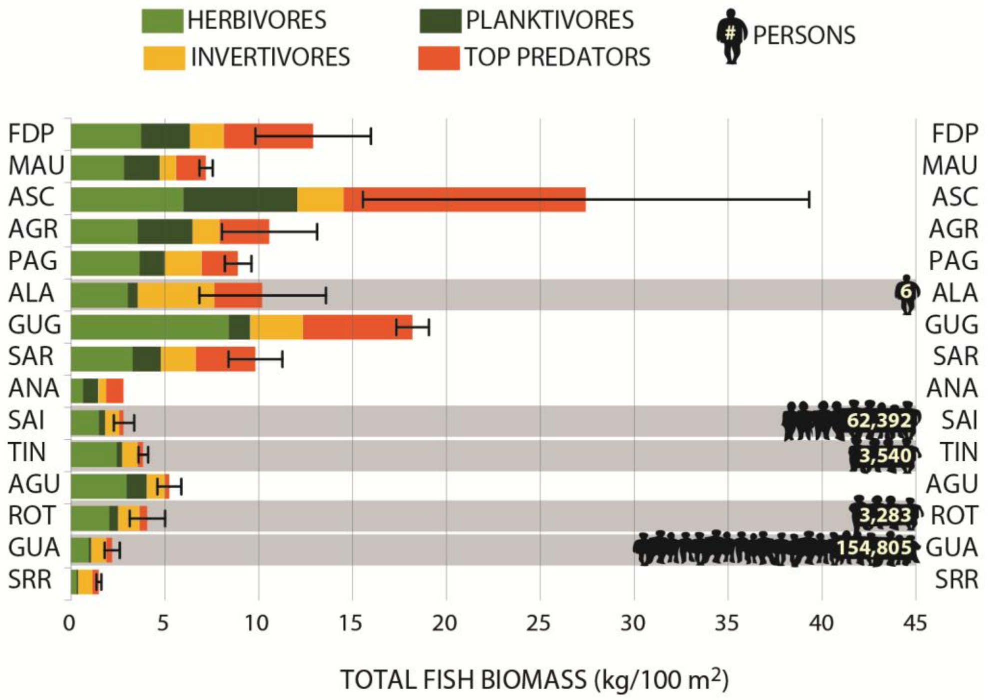

Figure 4.5. Comparison of total fish biomass by consumer group around the islands in the Mariana Archipelago related to human population size. The islands are represented from north to south ending with Santa Rosa Bank (SRR), Guam is represented by the three letter code GUA. Data from CRED surveys in 2003, 2005, 2007, and U.S. Census 2010.

Participation in reef fishery by the local population is seldom for economic reasons but it plays an important role in strengthening social bonds and is a chief source of enjoyment to Guam's residents (Van Beukering et al. 2007). Fish catches and coral cover have declined significantly over the last few decades. Small-scale fishery catches have declined by 84% since 1950 (Zeller et al. 2007). Coral cover has decreased from 50% in the 1960s to 25% in the 1990 to 15% in 2010, a 70% decline in the last 50 years (Burdick et al. 2008, Brainard et al. 2012). The main threats to the corals of Guam are river run-offs including heavy sediment loads that smother the corals in the southern reefs, ocean warming that leads to bleaching often followed by coral mortality, crown-of-thorns seastar outbreaks that can decimate coral populations and excessive fishing that leads to a disruption of ecosystem processes. In response to these declines, the government of Guam has created five marine preserves (MPAs; Fig. 4.1) and several watershed restoration projects are underway. In 2011, fish biomass in the preserves was 2.4 times higher than in the open areas around Guam (Williams et al. 2012). Additionally, the government of Guam participates in the Micronesia Challenge which was launched in 2006.[2] This initiative is a commitment between Micronesian governments to balance between the need to use their natural resources today and to sustain those resources for future generations. The five Micronesian governments of the Republic of Palau, the Federated States of Micronesia, the Republic of the Marshall Islands, the U.S. Territory of Guam, and the Commonwealth of the

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[2] http://www.micronesiachallenge.org/

Northern Mariana Islands all committed to "effectively conserve at least 30% of the near-shore marine resources and 20% of the terrestrial resources across Micronesia by 2020[2]."

Guam's population has almost tripled since 1960 increasing the pressure on natural resources (Fig. 4.6). The population is likely to increase more steeply in the near future as a result of the planned military buildup (Kan, 2013).

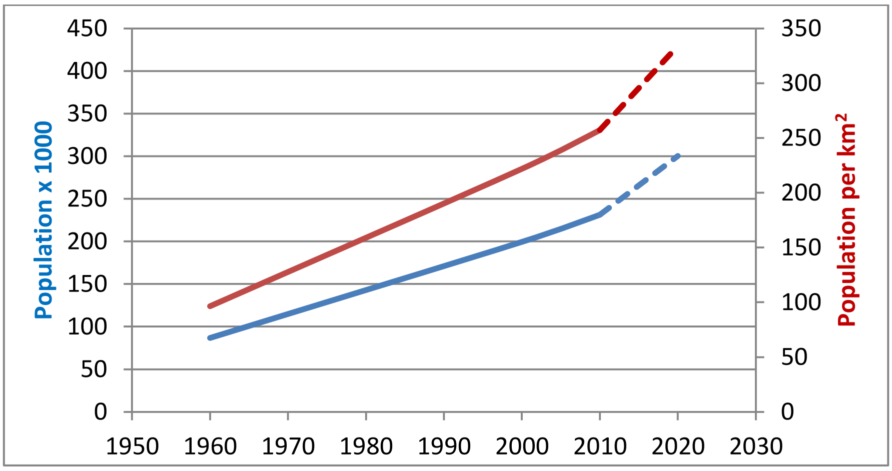

Figure 4.6. Population growth in Guam in the last decades (US Census) and future estimated growth.

The main source of terrigenous nutrient and sediment inputs in southern Guam is through surface run-off and in northern Guam through underground seepage. Guam sedimentation studies showed a sedimentation rate substantially higher than the amounts determined to impact corals elsewhere (Pastorok and Bilyard 1985, Rogers 1990, Riegl and Branch 1995, Te 2001, Scheman et al. 2002, Minton et al. 2006, Storlazzi et al. 2009a) suggesting that the benthic community is under long-term pressure with potential gradual and long-term declines and shifts in community structure. Sediments can smoother reefs, reduce light in the water column, induce sublethal effects, impede fertilization and reduce recruitment with the overall effect of reduced coral growth and shifts towards more sediment–tolerant species assemblages depending on the duration and load of the sedimentation (Richmond and Hunter 1990, Riegl and Branch 1995, Birkeland 1997, Fabricius 2005). A primary effect of increased nutrients into the oligotrophic marine waters is an increase in phytoplankton and benthic algae which are better in taking up these nutrients and grow faster compared to corals (Lapointe 1997, Szmant 2002). Nutrients can impact directly on coral physiology (increase zooxanthellae density) which disrupts the symbiosis and affects metabolic processes, coral growth and reproductive success (Fabricius 2005) and indirectly on space competition with other benthic organisms, such as filter feeders and algae (Koop et al. 2001).

4.3 Methods

4.3.1 Guam Atlantis Ecosystem Model

Atlantis model framework

The Atlantis framework was developed and refined in the early part of the 21st century simulating the ecosystems of Port Phillip Bay and, later, the southeast open coast of Australia. Atlantis is a three-dimensional, deterministic (differential equations), spatially-explicit model based on nitrogen-flows through main trophic groups with primary processes being consumption, production, migration, recruitment, waste production, and (natural and fishing) mortality. The model incorporates spatially differentiated habitats (as polygons) and vertical stratification (as water layers) allowing for the representation of hydrodynamic and biological processes (e.g., vertical migration of fish to different habitat types in their lifecycles, larval connectivity between reef areas). It incorporates a range of modules and levels of detail that encompass most options for management actions available in coastal waters. For instance, fishery options available at the fleet or species level include catch quotas, gear restrictions, spatial closures, individual quotas, seasonal closures and effort reductions. Nutrient/runoff management options include altering inputs of specific forms of nitrogen or sediment concentrations in any model polygon. Model simulations can be used to see if any of these scenarios consistently produce better outcomes in terms of improved habitat and increased target fish stocks, productivity, and fecundity, over defined time periods and to predict fisheries response to management of the fisheries.

Applications of Atlantis

Applications of Atlantis models have increased understanding of system dynamics; identified major processes, drivers and responses; highlighted major gaps in knowledge; and provided a mechanism to ‘road test’ management strategies before implementing them in reality (e.g., (Fulton et al. 2007, Kaplan et al. 2010, Griffith et al. 2011, Ainsworth et al. 2012). To date Atlantis ecosystem models have been applied in Australia, the east and west coast of the United States, the Gulf of Mexico, South Africa, and various models are in development in Europe. One of the key findings from these applications is that there is no single management application that provides a ‘silver bullet’ solution to ecosystem-based management (Fulton et al. 2011b). Tradeoffs, especially between conservation and industry, are complex as ecological, economic and social objectives vary greatly making it difficult to meet them all. Another important finding is that because cumulative drivers are included in the application of an Atlantis model, the resulting modifications in the ecosystem (e.g., water quality, habitat suitability, productivity) can undermine or counteract the effects of fisheries management (Fulton and Smith 2004, Kaplan et al. 2010, Fulton et al. 2014).

Limitations of Atlantis

As the Atlantis framework includes a wide range of complex options it can be tempting to use them all resulting in a high spatial and trophic resolution. However, not placing emphasis on the key dynamic processes and biological groups can lead to an unstable model that fails to represent realistic trophic structures and ecosystem dynamics. At the other extreme, very low spatial resolution or inappropriate trophic aggregation (e.g., across trophic roles) can lead to misleading model behavior that also does not resemble reality. Because Atlantis includes so many different data sets and processes, each associated with its own set of errors, Atlantis should not be used for tactical management questions (e.g., fisheries stock assessments, spatial allocation) but is more suitable for strategic direction settings in combination with other model types. Another limitation of Atlantis and other complex end-to-end models is handling uncertainty. Structural uncertainty can be explored (Fulton et al. 2003a, Fulton et al. 2004a, Fulton et al. 2004c) but uncertainty in parameters and data are more challenging, since long simulation time preclude brute-force Monte Carlo approaches. Instead, these uncertainties are handled by bounded parameterizations, multimodel inference and scenario uncertainty (Fulton et al. 2011b). The strength of the Atlantis approach lies in ranking different management actions based on defined objectives and potential scenarios for human and ecological behavior, rather than in the estimation of statistical uncertainty.

Guam Atlantis Model development

In 2012, we began with the development of the Guam Atlantis Coral Reef Ecosystem Model using the Atlantis framework. This approach is the first application of Atlantis to a coral reef ecosystem. The first year was mainly to discuss the model objectives with stakeholders (Weijerman and Brown, 2013) and collect and analyze the necessary data (Table 4.1). In 2013, we started with the parameterization of the spatial and ecological modules of Atlantis (Fig. 4.7). The model's start date is January 1, 2011 and this represents annual average conditions. For some groups (e.g., roving piscivores, sharks, rays) with more limited data, this date represents annual average conditions for approximately 2008–2011.

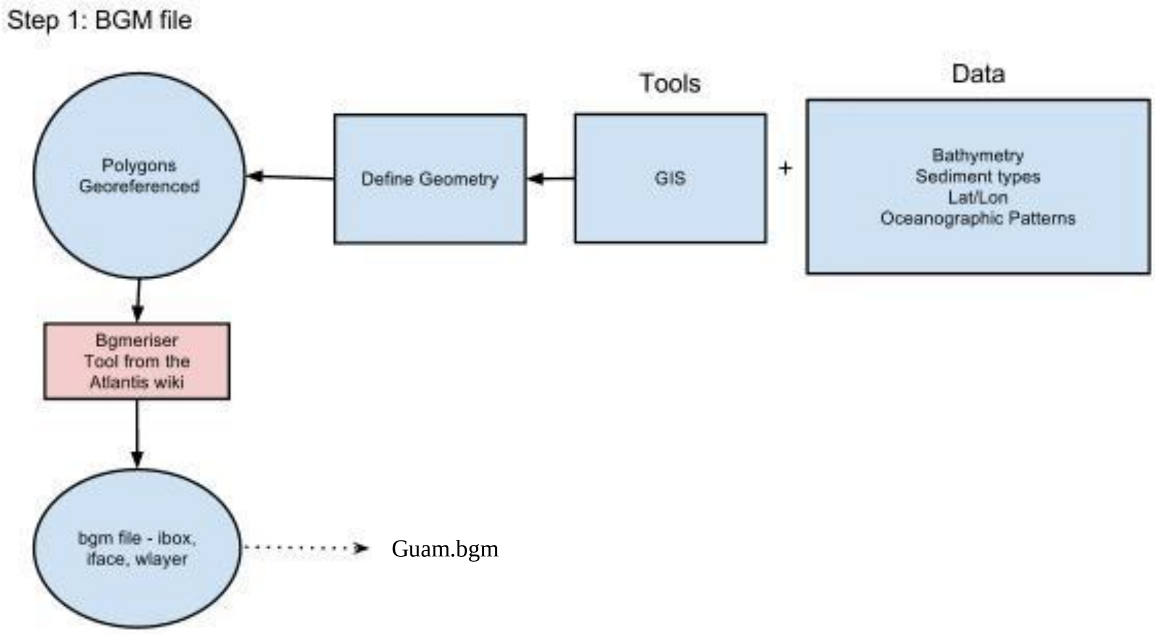

Figure 4.7. Schematic overview of the Atlantis framework and requirements for the spatial module and resulting bgm file. BGM=box geometry.

Table 4.1. Summary of data streams used in the Guam Atlantis Coral Reef Ecosystem Model. Many of these data are available as a GIS layer and available upon request from the first author. Fishery data came from Guam Division of Aquatic and Wildlife Resources (DAWR) and NOAA's Western Pacific Fisheries Information Network (WestPacFIN).

Location	Marianas, Guam
Oceanography	Currents Sea surface temperature (SST) Waves Chlorophyll-a
Near-shore mapping	Bathymetry Hard-soft bottom Slope & Aspect Rugosity Habitat
Land cover & anthropogenic influences	Land cover Roads Population density Watersheds Streams USGS flow rates and rainfall Waste water treatment plants Harbor (anthropogenic sites) Injection wells EPA water quality survey sites Impaired water
Biological data	Survey sites (DAWR, CRED) Cryptic invertebrate species composition and abundance Sea star and urchins biomass and spatial distribution Pelagic bacteria sample sites & biomass Coral, turf algae, macroalgae cover and biomass Fish biomass (total biomass; size distribution, species composition, spatial distribution) Sea turtle numbers, biomass, and spatial distribution Life history parameters, diet, migration, habitat dependency for all modeled groups
Fishery data	Catch and effort statistics Catch-per-unit-effort Gear selectivity Species composition of the catch Reconstruction of fish biomass for 1985-2012 Dive preference study results

Spatial Model

The boundary of Guam Atlantis is the 30-m isobath with a total 0-30-m depth area of 95 km^2 bordered by the coordinates: 13°39' N, 144°57' E, 13°14' S, and 144°37' W. Some coral-reef- associated species are confined to hard substrate which is present in 73% of the total 0–30 m area (e.g., coral, CCA, urchins, sea stars, corallivorous fish). Fish need a variety of habitats and depth zones; shallow coastal habitat for recruit settlement and juvenile survival and deeper habitats for foraging, sheltering and spawning sites for adults (Friedlander et al. 2007a, McMahon et al. 2012). These habitats include consolidated hard-bottom substrate (live coral cover >10%) with low macroalgal cover (< 10%), high topographical complexity (rugosity > 1.5 on a scale from 0 no rugosity to 5 high rugosity), access to unconsolidated (sand) habitats and a wide range of depths (e.g., 0–30 m) (Friedlander and DeMartini 2002), these habitats are included in the model.

Corals and marine species extend to below our 30-m model boundary. However, available data are limited to safe diving depths of approximately 30 m for underwater survey work. Notwithstanding, we believe that the population dynamics of the included marine species are mostly within the model boundary. Home range studies show that most reef fish have a strong site fidelity with movements of up to 1.6 km of coastline with continuous reef and some degree of diel habitat shift (Meyer and Holland 2005, Meyer et al. 2010, Marshell et al. 2011) although species can cross bare soft bottoms and travel over longer distances to spawning aggregation sites or to establish a new home range (Chateau and Wantiez 2009).

The larger reef-associated piscivores also stay close (< 30 m) to the reef but roam over larger areas with home ranges and mean distance from the reef increasing with fish size and they show diel habitat shifts and movement to spawning aggregation sites during specific times (Meyer et al. 2007, Afonso et al. 2009, Topping and Szedlmayer 2011). Only oceanic plankton (including planktonic larval stages of coral reef species) and pelagic bacteria could be exported out of our model boundary as they are influenced by the hydrology model as passive drifters and are advected by currents.

Larval connectivity is difficult to estimate. Most models combine ocean current data with a species' life history characteristics to simulate larval dispersal from discrete habitat patches in different seascapes (Cowen et al. 2006, Kool et al. 2011, Kendall et al. 2013). Connectivity studies in the Indo-West Pacific showed that the oceanic conditions lead to a transport of larvae from the South China Sea and from northern Papua New Guinea into the Coral Triangle (Kool et al. 2011, Treml and Halpin 2012). The large-scale oceanic circulation around Guam is controlled by the North Equatorial Current flowing northwestward fluctuating in speed and direction (Fig. 4.8)[3] (Bonjean and Lagerloef 2002). This directionality could indicate that Guam is a stepping zone for larval dispersal from species with a long pelagic larval duration from the outlying islands located southeast of the Mariana Archipelago or from Papua New Guinea (Fig. 4.8). The nearest island Rota, at 60 km northeast of Guam, could be another source of larvae. These potential larval supplies are important for the development and maintenance of the biogeography, genetic variability and biodiversity, however, it is likely less important for community recovery on short (< 50 years) time scales (Jones et al. 2009, Gilmour et al. 2013). Genetic studies show that marine larvae are mostly retained within 20–30 km of their natal origin (Becker et al. 2007, Vollmer and Palumbi 2007, Planes et al. 2009, Almany et al. 2013) which is supported by a near-surface current study around Guam (Wolanski et al. 2003b). For larvae to find the right microhabitat at the right time determines their success for establishment, i.e., lottery hypothesis (Munday 2004a) (Geange and Stier 2009, Bode et al. 2011).

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[3] www.esr.org

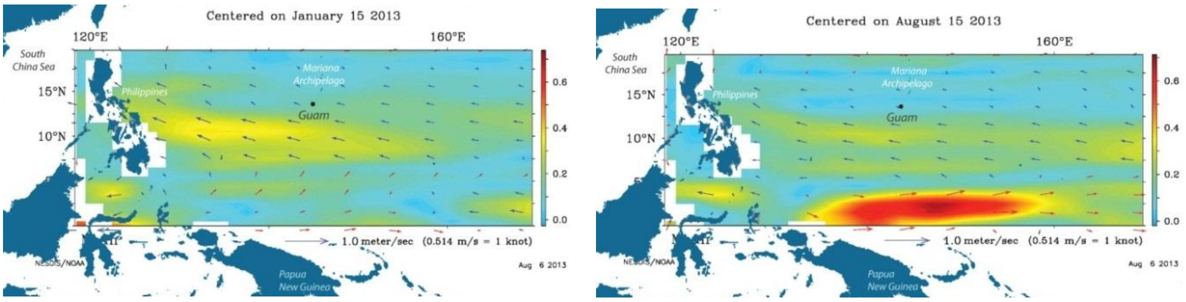

Figure 4.8. Long-term (1993–2013) monthly mean large-scale oceanographic current patterns in the west Pacific Ocean (Bonjean and Lagerloef 2002) for January (*left*) and August (*right*).

The coastal waters around Guam were divided into 55 polygons (Fig. 4.9). Polygon delineations were based on similar characteristics (Fig. 4.4) of (1) the benthos defined by NOAA National Ocean Service (NOS) Biogeography Branch (NOAA NCCOS 2005) and updated by Guam Division of Aquatic and Wildlife Resources (DAWR) and CRED data; (2) oceanographic conditions (CRED data; Peter Houk unpubl GIS layer); (3) bathymetry and substrate type (CRED data); (4) existing protected areas (National Marine Protected Areas Center)[4] and (5) fishing use (Guam DWAR creel survey data). Fishing in the near-shore shallow reef areas includes gleaning invertebrates, throw netting for mostly juvenile fish, spear fishing, hook and line fishing and gill net fishing. This set of characteristics resulted in near-shore shallow water polygons (0–6 m) characterized by reef flats, the deeper forereef zone from 6 to 30 m and Apra Harbor divided into Apra Inner Harbor, Sasa Bay, the shallow reefs bordering Apra Harbor and the deeper Harbor itself with mostly a sandy bottom and some coral pinnacle clusters (e.g., Western Shoals). Additionally, we had seven static (i.e., biological processes not modeled) boundary polygons connecting all the deeper polygons and the land mass of Guam as non-dynamic polygons. All polygons were further vertically divided into a shallow-water depth layer (0–6 m), a deepwater layer (6–30 m) and a sediment layer. Naturally, for the nearshore polygons that only reach to maximum of 6 m, there was only one water column layer and one sediment layer.

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[4] http://www.mpa.gov/

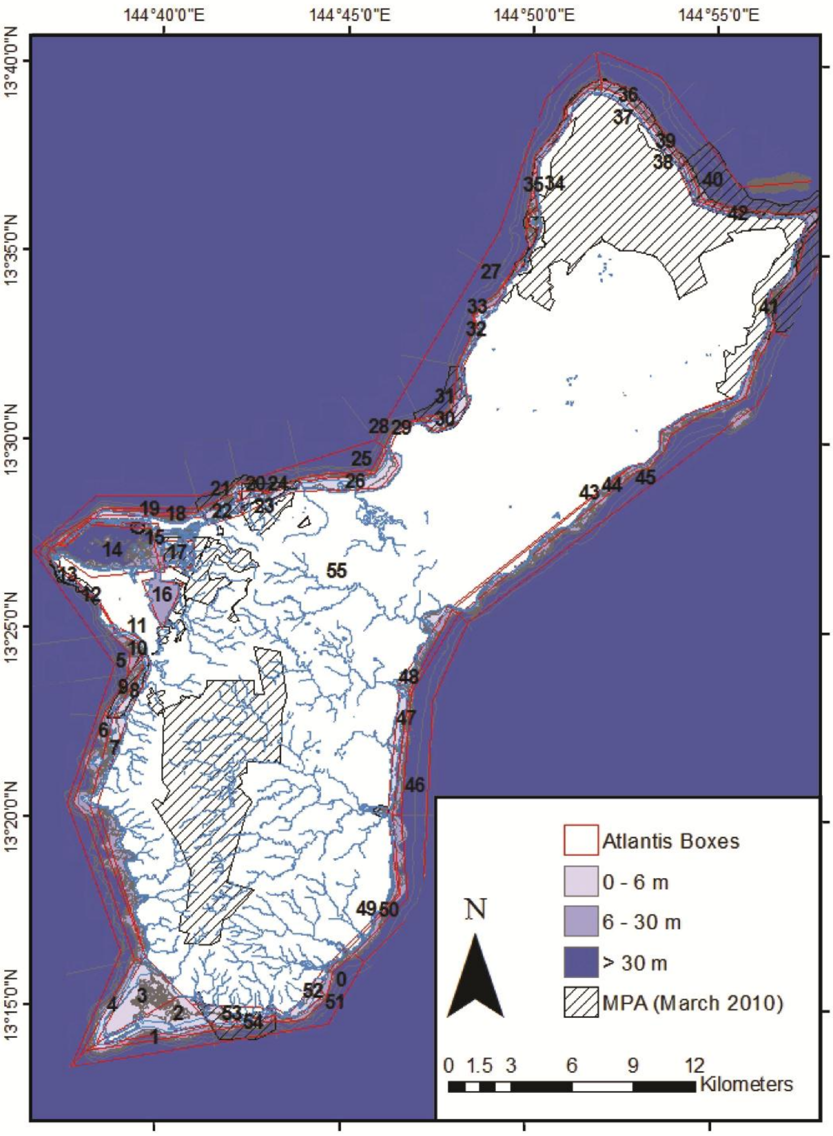

Figure 4.9. Bathymetry, rivers and location of protected areas overlayed with Atlantis polygons representing areas with similar benthic and oceanographic conditions.

Physical Model

Various data streams went into the physical module (Fig. 4.10): the physical oceanography as a dynamic file and solar radiation, sediment and nutrient inputs as impact files through time series.

Physical oceanography

In this Guam Atlantis version we use dummy data to keep fluxes stable. In the next version (Chapter 6) we will incorporate a physical oceanography model.

Solar radiation

Solar radiation data for Guam were not available. However, modeled solar data calculated from January 1, 1991, to December 31, 2010, were available from the National Solar

Radiation Database.[5] Photosynthetically Available Radiation (PAR in Einstein/m^2/day) was available for Guam from satellite data and obtained from NOAA's Coast Watch for 2002–2010.[6] This dataset was corrected for the influence of islands and the average for an eight-day interval was computed. We then converted the values to solar data in W/m^2 to compare it with the modeled data output. As the seasonality was similar between the two datasets and because the modeled time series comprised a much longer time span we used those data for the Atlantis model (Fig. 4.11).

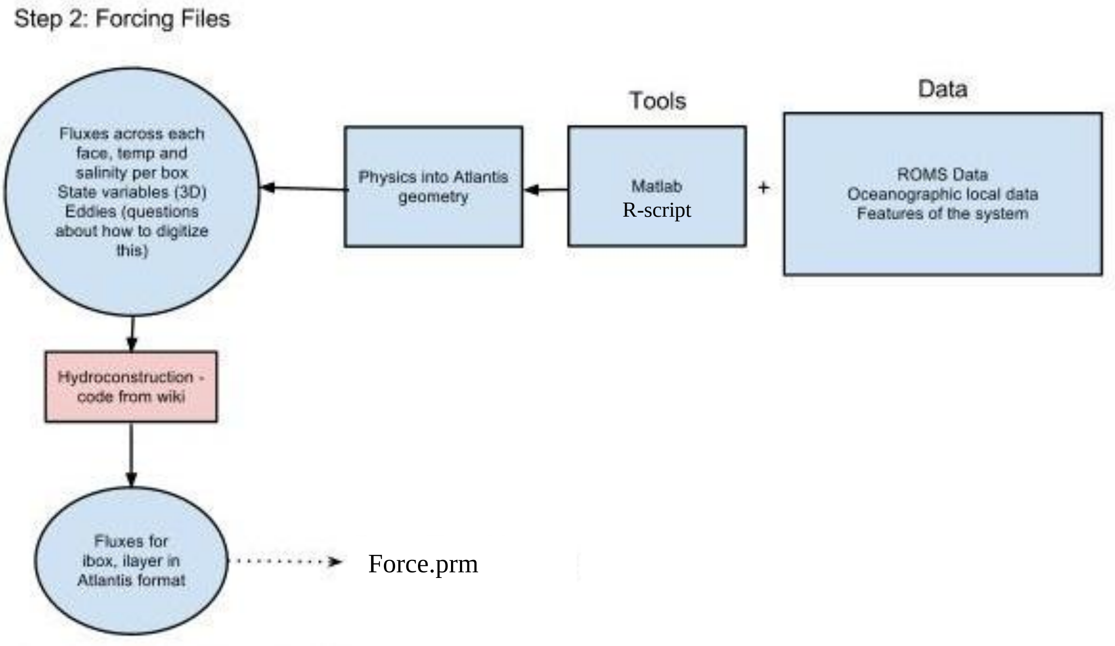

Figure 4.10. Schematic overview of the Atlantis framework and requirements for the physical oceanography module and resulting force.prm file.

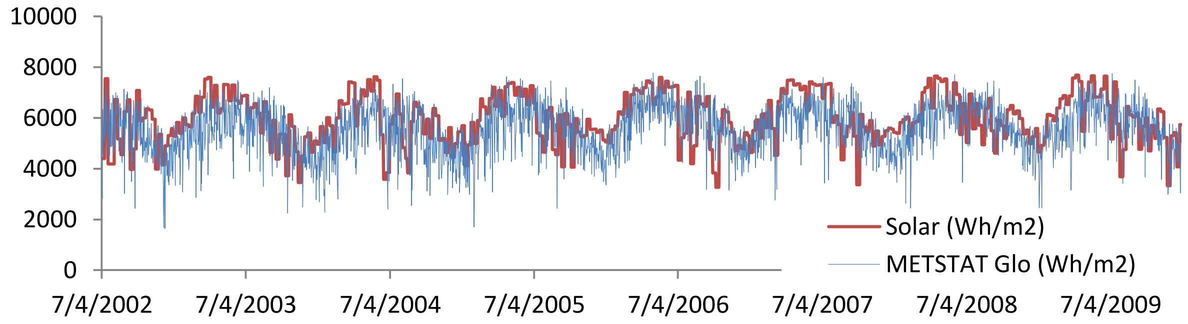

Figure 4.11. Solar radiation data calculated from satellite derived photosynthetically active radiation data (red line: NOAA's Coast Watch)[7] and modeled data (blue line: National Solar Radiation Database)[8].

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[5] rredc.nrel.gov/solar/old_data/nsrdb/

[6] coastwatch.pfeg.noaa.gov/erddap/griddap/erdMHpar01day.html

[7] coastwatch.pfeg.noaa.gov/erddap/griddap/erdMHpar01day.html

[8] rredc.nrel.gov/solar/old_data/nsrdb/

Salinity and temperature

Salinity and temperature time series were populated with an average value from 9 to 19 conductivity-temperature-depth casts per depth range (surface, 10, 20, 30 m) of surveys conducted in the dry (April and May) and wet (October) season around Guam. These values will be updated by the salinity and temperature values from a oceanography model (Chapter 6).

Sediment and nutrient input—forcing files

A flow discharge model has been developed for two watersheds in central Guam, one that discharges in the Apra Inner Harbor on the west coast and one that discharges in Pago Bay on the east coast (Tetra Tech 2012). Time series of daily flow discharge rates are available from five rivers (La Sa Fua, Ugum, Umatac, Inarajan, and Ylig) all in the southern part of Guam and suspended sediment discharge time series from the La Sa Fua, Ugum, and Ylig River.[9] We used these data to estimate sediment input per Atlantis polygon (Table 4.2).

A direct relation between flow rate and nutrient input is not available for Guam. Therefore, we reconstructed the nutrient input from a watershed with 4 rivers discharging into Hanalei Bay on the north coast of Kauai, Hawai'i (Table 4.3, data from Tetra Tech). This watershed shares many characteristics with Guam on their volcanic origin, steep slopes, vegetation cover, human population size and feral ungulate population. Although far from ideal, this data set was the closest data set we could find to represent point-source pollution in bays. Moreover, both flow rates on Guam as from Hanalai Bay were estimated using the same methods (Tetra Tech 2012). When comparing the slope and intercept of the relationship of flow rate and sediment discharge from the Hanalei Bay watersheds with the three watersheds with sediment data from Guam (Table 4.2), it is noticeable that the slope was orders of magnitude higher for Guam watersheds indicating a much higher sediment discharge rate compared to Hanalei Bay. This high sediment load can also been seen when comparing the mean sediment discharge of the watersheds on the two islands. These high sediment discharge rates are in correspondence with sediment studies conducted on Guam which concluded that sediment rates in Guam are higher than any other reported values elsewhere (Wolanski et al. 2003a, Minton et al. 2006, Storlazzi et al. 2009b). To calculate the sediment discharge from the three rivers where we had flow rates for, I used the mean slope and intercept of the flow rate and sediment discharge relationship from the Ugum, La Sa Fua and Ylig River (in red in Table 4.2) and calculated the daily sediment discharge rate based on the flow rate of those rivers.

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[9] waterdata.usgs.gov/nwis

Table 4.2. Characteristics of four rivers in the Hanalei Bay watershed, Island of Kauai, and seven rivers in central Guam and the slope and intercept of the linear relationship between flow rate (in m^3 per second) and sediment discharge rate (in grams per second). Calculated values for Guam in red.

Island	**River**	**Watershed area km^2**	**Atlantis Polygon ID**	**Mean flow rate m/s**	**Mean sediment discharge g/s**	**Slope**	**intercept**	**R^2**	**Data period mm/yy–mm/yy**
Kauai	Hanalei	0.89	NA	7.65	0.18	0.1376	1.6279	0.86	06/00–06/06
Kauai	Waioli	0.81	NA	1.58	0.23	0.0073	-0.1893	0.71	06/00–06/06
Kauai	Waipa	0.17	NA	0.67	0.05	0.0074	-0.1144	0.80	06/00–06/06
Kauai	Waikoko	0.060	NA	0.17	1.63	0.5095	-1.4283	0.95	06/00–06/06
Guam	Atantano	0.11	16	0.41		1.4934	-10.519		01/91–01/12
Guam	Ugum	5.92	7	0.71	219	1.5446	-17.309	0.71	08/80–07/81; 08/06–08/11
Guam	La Sa Fua	1.03	7	0.13	44	1.5937	-1.7681	0.64	10/06–10/11
Guam	Umatac	2.08	7	0.24		1.4934	-10.519		10/52–12/76; 10/01–10/11
Guam	Pago	8.42	48	0.83		1.4934	-10.519		01/91–01/12
Guam	Ylig	6.53	48	0.76	355	1.342	-12.479	0.64	08/80–10/81
Guam	Inarajan	4.34	52	0.50		1.4934	-10.519		10/52–12/82

Table 4.3. Slope, intercept and R^2 of the relationship between NO_x and flow discharge rate and NH_4 and flow discharge rate for four discharge points in the Hanalei Bay. g/s is grams per second, flow was in cubic square feet. The mean is from Waipa and Waikoko which have similar flow rates as Guam’s watersheds (Table 4.2).

	NOx g/s			**NH4 g/s**		
River	**Slope**	**intercept**	**R^2**	**Slope**	**intercept**	**R^2**
Hanalei	0.000009	-0.0013	0.76	0.000004	-0.0006	0.75
Waioli	0.0003	-0.0069	0.93	0.0007	-0.0173	0.94
Waipa	0.0001	-0.0015	0.95	0.0004	-0.0038	0.95
Waikoko	0.0003	-0.0007	0.95	0.0007	-0.0019	0.96
mean	*0.0002*	*-0.0011*		*0.00055*	*-0.0029*	

For all rivers on the east coast of Guam I further assumed a similar flow discharge rate as from the Pago, Ylig, and Inarajan rivers. For all rivers on the west coast with its steeper watersheds, I assumed a similar flow discharge rate as from the Umatac, Ugum and La Sa Fua rivers for the Atlantis polygons south of Apra Harbor and from the Antantano River in the Apra Inner Harbor and north of Apra Harbor (Table 4.4). Where necessary I reconstructed time series starting at January 1, 1991, and ending at December 31, 2012, by repeating the first or last years. Because of the large discrepancy in the sediment load between Hanalei Bay and the watersheds in Guam, I multiplied the calculated nutrient concentrations by 257 (the difference in sediment concentration).

In the version of the model presented here, sediment and nutrient inputs are modeled as inputs to coastal model cells adjacent to land with river mouths and sewage pipes. Guam Atlantis includes half saturation constants for each primary producer for their growth on dissolved organic nitrogen to account for the difference in productivity and nutrient limitation effects on the physiology of growth. The effects of sediments on corals are not incorporated in this version.

Table 4.4. Summary information on the reconstruction of sediment and nutrient input data in Atlantis polygons along the southern part of Guam.

Atlantis Polygon Id	Correction factor for number of point sources discharging into Atlantis polygon	Sediment discharge relationship with flow rate	River used to calculate nutrient and sediment discharge based on flow rate	Source empirical relationship between nutrients / sediments and flow rate	Source flow rate
7, 8, 10	6, 2, 0.5	Ugum, La Sa Fua, Ylig	Umatac, La Sa Fua, Ugum	USGS (SED) & Tetra Tech (NUT)	USGS
16, 17, 22, 23, 24, 26, 30, 32	1, 1, 1, 1, 0.5, 1 1, 0.5	Antantano	Antantano	USGS (SED) & Tetra Tech (NUT)	USGS
48, 49	3, 1.5	Ylig	Pago, Ylig	USGS (SED) & Tetra Tech (NUT)	USGS
52	1	Ylig	Inarajan	USGS (SED) & Tetra Tech (NUT)	USGS

Ecological Model

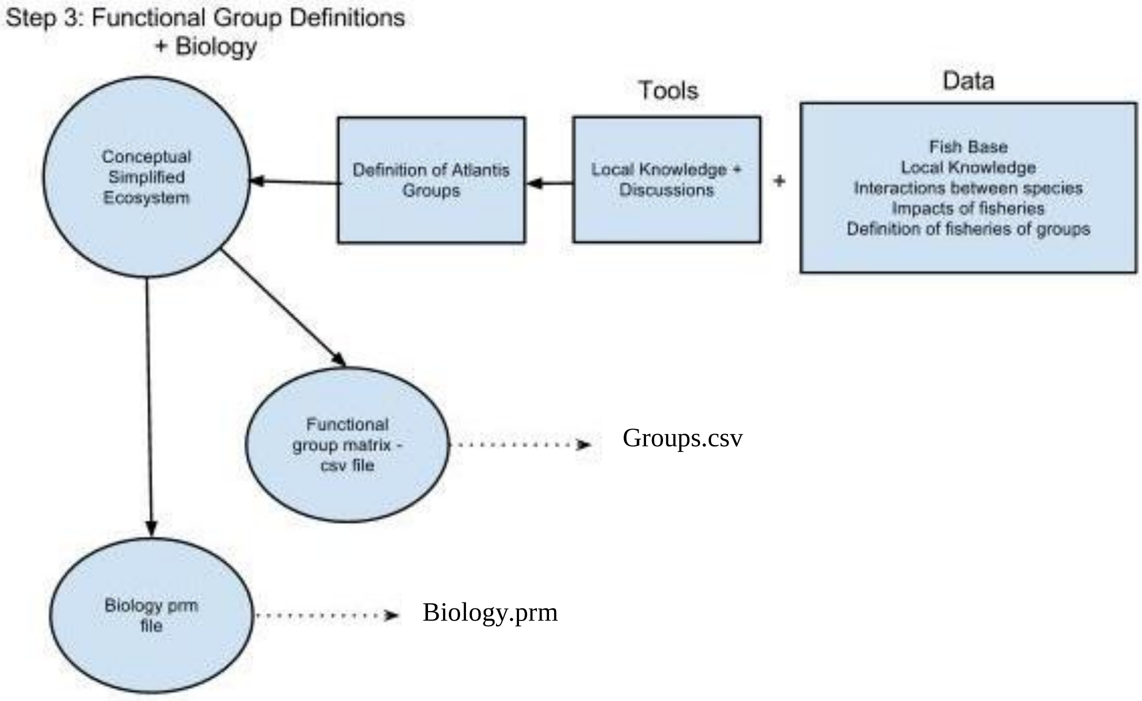

Figure 4.12. Schematic overview of the Atlantis framework and requirements for the ecological module with resulting functional groups and biological related parameter files.

Rationale for Selection of Modeled Functional Groups

A large biological data set was needed for the ecological module (Fig. 4.12). Species and functional groups were included in the model with the aim of representing community dynamics of the nearshore reef, including dominant species sampled by NOAA CRED and Guam monitoring programs. The number of trophic links and functional groups are important for the robustness of the model with, in general, more links and less groups leading to a greater recovery after a disturbance (Pinnegar et al. 2005). Additionally, omission of species or groups can be preferable to inclusion based on tenuous understanding and arguments (Fulton et al. 2003a, Johnson et al. 2009). Atlantis requires three detritus groups and the remaining functional groups are defined by the user. Guam Atlantis includes 42 functional groups: 3 detritus groups, 2 bacteria groups, 5 plankton groups, 3 benthic algal group, 3 sessile and 6 mobile invertebrate groups, and 20 vertebrate groups (Table 4.5). Species were aggregated into functional groups on the basis of diet, life-history characteristics, habitat preferences, ecological role in coral reef processes and whether they were targeted in reef fishery. Overall the functional groups selected are a compromise, intended to capture the major ecological responses (at the guild level) and responses to fishing, terrestrial inputs and climate change, at a taxonomic resolution relevant for fisheries and management decisions.

Table 4.5. Categorization of species data. Trophic level and functional group categorization of the coral reef ecosystem species based on their diet, habitat, life-history characteristics, ecological role, and interest to fishers and managers.

No	**Functional groups**	**Atlantis Code**	**Species/description**	**Trophic level**	**Fishery target sp**	**Importance of inclusion**
1	Carrion	DC	dead	detritus		nutrient recycling, part of microbial food loop
2	Refractory detritus	DR	long 'life' time	detritus		nutrient recycling, part of microbial food loop
3	Labile detritus	DL	easily degraded	detritus		nutrient recycling, part of microbial food loop
4	Pelagic Bacteria	PB	hetrotrophic bacteria (0.2-1 um)	bottom food web		nutrient recycling, part of microbial food loop, consume DOM/EOC from phytoplankton and macroalgae
5	Benthic bacteria	BB	hetrotrophic bacteria (0.2-1 um)	bottom food web		nutrient recycling, part of microbial food loop, consume DOM/EOC from phytoplankton and macroalgae
6	Small phytoplankton	PS	picoeukaryotes, cyanobacteria, < 1um	primary producer		part of microbial food loop, release DOM/EOC for uptake by hetrotrophic bacteria
7	Large phytoplankton	PL	incl. diatoms	primary producer		main food for benthic filter feeders
8	Turf algae	TURF	algae < 1cm	primary producer		nutrient exchange between sediment and water column, facilitates coral and CCA recruitment
9	Macroalgae	MA	algae > 1cm	primary producer		space competitor with corals, decreases coral and CCA recruitment

No	Functional groups	Atlantis Code	Species/description	Trophic level	Fishery target sp	Importance of inclusion
10	Crustose-coraline algae	CCA		primary producer		reef builder facilitates coral recruitment
11	Zooplankton - herbivores	ZH	copepods, appendingularias	bottom food web		most abundant herbivore, part of microbial food loop, consume hetrotrophic bacteria and small phytoplankton, 'sloppy' predation leads to remineralization (NH4, dissolved free amino acids, etc)
12	Zooplankton - carnivores	ZC	chaetognath, euphausiids, amphipods, crab larvae, isopods, mysids, polychaetes	bottom food web		main food for benthic filter feeders, consume small zooplantkon (prefer ciliates), small phytos up to 200 um
13	Demersal zooplankton	ZD	pelagic fish & invert larvae, copepods, polychaetes, foraminiferas	bottom food web		vertical migration, important food source for benthic filter feeders
14	Benthic carnivores	BC	e.g., polycheates, swimming crabs, cones, tritons, burrowing crustaceans, flatworm, sea snail, nudibranch, mantis shrimp	bottom food web		nutrient recycling, bottom foodweb, carnivorous diet
15	Benthic detritivores	BD	e.g., brittle stars, detritivorous polychaetes, peanut worms, crabs, shrimps, lobsters	bottom food web		nutrient recycling, bottom foodweb, detritivorous diet
16	Benthic meiofauna	BM	e.g., squat lobsters, limpets, top snails, chitons, snapping shrimps, hermit crabs, abalones, cowries	bottom food web		nutrient recycling, bottom foodweb, mostly herbivorous diet
17	Benthic suspension feeders	BFF	octocoral, sponges, tunicates, zooanthids, giant clams, bivalves, polychaetes, foraminifera, bryzoans, brittle stars	bottom food web		suspension feeders - important source of carbon uptake
18	Branching (sheltering) corals	CRS	corals that provide shelter: e.g., *Pocillopora*, *Acropora*, branching *Porites*, *Heliopora*, *Echinopora*.	bottom food web		frame builders of reef ecosystem, important primary producers and suspension feeders, less susceptible to disease, predation, acidicification & ocean temperature increase
19	Massive/Encrusting (non-sheltering) corals	CRN	corals that provide less or no shelter: e.g., massive *Porites*, *Leptastrea*. *Favia*, *Astreopora*, *Montipora*, *Goniastrea*, *Cyphastrea*	bottom food web		frame builders of reef ecosystem, important primary producers and suspension feeders, susceptible to disease, predation, acidicification & ocean temperature increase
20	Cephalopods	CEP	octopus, squids	invertebrate	x	important diet component
21	Benthic Grazers	BG	urchins (helmet collectors, pencil, boring urchin, diadema)	invertebrate	x	grazer, keeps algal biomass low promoting coral cover and coral recruitment
22	Sea Stars	BSS	including crown-of-thorns seastar	invertebrate		coral predator

No	Functional groups	Atlantis Code	Species/description	Trophic level	Fishery target sp	Importance of inclusion
23	Sharks	SHR	reef-associated sharks (gray reef, whitetip reef, Galapagos, blacktip reef, tawnry nurse shark)	apex predator	x	controls lower trophic groups, fast swimming roving, long life span
24	Rays	RAY	stingrays	apex predator		important to keep urchins & sea stars population size in control
25	Roving piscivores	FPR	jacks, snappers, barracudas	apex predator	x	controls lower trophic groups, fast swimming, roving, shorter life span than sharks
26	Mid-water piscivores	FPM	cornetfish, trumpet fish, houndfish, needlefish	apex predator		controls lower trophic groups, mid-water and surface water habitat
27	Benthic piscivores	FPB	eels, scorpionfish, lizardfish	apex predator		controls lower trophic groups, benthic habitat (sedentary)
28	Targer benthic piscivores	TPB	groupers	apex predator	x	controls lower trophic groups, benthic habitat (sedentary)
29	Bumphead parrotfish	BHP	*Bolbometopon muricatum*	herbivore	x	species of special interest, major agents of bioerosion on reefs, removing dead coral and exposing hard, reef matrix for colonization by coralline algae and corals
30	Herbivores—excavators/bioeroders	FHE	large-bodied parrotfish	herbivore	x	major agents of bioerosion on reefs, removing dead coral and exposing hard, reef matrix for colonization by coralline algae and corals, target species of reef fishery
31	Herbivores—scrapers	FHS	small-bodied parrotfish	herbivore	x	limiting the establishment and growth of macroalgae while intensely grazing epilithic algal turf, and providing areas of clean substratum for coral recruitment; < 35 cm
32	Herbivores—grazers	FHG	schooling;small angelfishes (all *Centropyge* species), and many species of surgeonfishes (all *Zebrasoma* and *Acanthurus* species except those that feed exclusively on plankton or are grazers / detritivores)	herbivore		intensely grazing epilithic algal turfs, decreasing the establishment and growth of macroalgae
33	Target herbivore—grazers	TGR	rabbitfishes, surgeonfish	herbivore	x	intensely grazing epilithic algal turfs, decreasing the establishment and growth of macroalgae

No	Functional groups	Atlantis Code	Species/description	Trophic level	Fishery target sp	Importance of inclusion
34	Herbivores—browsers	FHB	batfishes and parrotfishes of the genus *Calotomus* and *Leptoscarus*	herbivore		selecting individual algal components and remove only algae and associated epiphytic material, thus reducing coral overgrowth and shading by macroalgae, and can play a critical role in reversing coral-algal phase shifts
35	Target herbivore—browser	THB	unicornfishes, rudderfishes,	herbivore	x	selecting individual algal components and remove only algae and associated epiphytic material, thus reducing coral overgrowth and shading by macroalgae, and can play a critical role in reversing coral-algal phase shifts
36	Detritivores	FDE	Surgeonfish (mostly *Ctenochaetus* sp),	detritivore		important for recycling nutrients, feed on decomposing plant and animals parts
37	Invertivores	FIV	triggerfish, hawkfish, filefish	invertivore		important to keep urchins & sea stars population size in control
38	Target invertivore	TIV	wrasse, emperor, snapper, goatfish, squirrelfish, sweetlips	invertivore	x	important to keep urchins & sea stars population size in control
39	Humphead wrasse	HHW	Napolean wrasse, *Cheilinus undulates*	invertivore	x	species of special interest, important to keep urchins & sea stars population size in control
40	Coralivores	FCO	most butterflyfishes	invertivore		coral predator, also coral disease vector
41	Planktivores	FPL	soldierfish, cardinalfish, some unicornfish, fusiliers, chromis	planktivore		Feed on plankton and detritus (algal material), important in recycling nutrients and importing allochtonous carbon, nitrogen
42	Turtles	REP	green turtle, *Chelonia mydas*	herbivore	x	herbivore, crop macroalgae, keep turf low

Inclusion of Microbial Foodweb

Including the microbial foodweb increases total energy throughput and energy transfer efficiency (TE) from detritus but decreases the TE from primary productivity; this phenomenon could be a result of enhanced recycling of materials and energy by microbes and represent the system behavior better than excluding this foodweb (Paves and Gonzalez 2008). Various studies have searched for significant sources of nutrients that could explain the high reef productivity, such as, groundwater discharge in highly porous volcanic islands (Street et al. 2008) and pelagic bacterial uptake by suspension feeders (Bak et al. 1999). In pelagic eutrophic regions, large (> 5 μm) phytoplankton is grazed on by zooplankton which is eaten by planktivorous fish resulting in a short food chain. However, in oligotrophic regions a longer food chain that includes a microbial loop, dominates. In these systems, pico and nano-sized auto- and heterotrophic organisms dominate the planktonic biomass and production

(Campbell et al. 2003). Corals and other filter feeding benthic organisms capture these small particles and so introduce nutrients to the food chain (Ribes et al. 2003, Genin et al. 2009). Phytoplankton makes a small contribution to primary production on an area-specific basis, but if currents flow over the reef then much of their production may pass into the reef-food webs (Jennings et al. 2001). This grazing is a principal pathway through which allochtonous nutrients and suspended particulate matter are imported to a reef community from the flowing water (Fabricius and Dommisse 2000). The close coupling between primary production and heterotrophs (respiration) ensures efficient nutrient recycling (Duarte and Cebrian 1996) and small (< 20% net primary production) allochtonous carbon input can cause shifts to a net heterotrophic state (Odum and Odum 1955). In coral reefs roughly 50% of the net primary production produced offshore and on the reefs is channeled through the microbial loop (Azam et al. 1983, Pernthaler 2005, Zöllner et al. 2009). This high efficiency sustains the fish and invertebrate populations on the reef. The majority of algal production (20%–90%) is grazed and much of this leads directly to the production of fished biomass (Polunin and Roberts 1996).

Inclusion of 19 Functional Groups of Fishes

The trophic structure of tropical fish assemblages encompasses a larger trophic spectrum than temperate assemblages. In addition to invertivores and piscivores, tropical communities include various herbivores, sessile and mobile invertivores and zooplanktivores. These additional trophic groups ensure a better use of low-quality food resources, such as algae, seagrasses and sessile invertebrates compared to temperate systems (Harmelin-Vivien 2002). Coral reef fish have also been able to reach a speciation rate that is much higher than in temperate waters. For example, surgeon fishes of the genus *Ctenochaetus* are highly derived, they ingest about 85% of $CaCO_3$ and only exist in the Indo-Pacific; the obligate corallivorous butterflyfishes are also absent from temperate waters and found mostly in the western Pacific; parrotfishes have evolved to various genera that ingest a high percentage of $CaCO_3$ in the Indo-Pacific whereas in the Atlantic these species only browse on algae (Harmelin-Vivien 2002).

For the Atlantis model, coral reef fish were grouped into functional groups based on:

1. Diet: main (> 50%) food item is plants/plankton/inverts/coral/detritus/fish based on literature, Fishbase (www.fishbase.org) and expert opinion;
2. Feeding habit (ecological role): grazing/browsing/excavating/scraping/hunting/plankton feeding based on literature, Fishbase and expert opinion;
3. Habitat: within 1 m above substrate, in water column, mid-water and on surface, roving based on literature and expert opinion;
4. Life history parameters: maximum length, growth rate (k), maximum age (e.g., sharks are classified separately from other large roving piscivores such as jacks; large bodied and small bodied parrotfish are separated);
5. Commercial, cultural, ecological or management interest (e.g., humphead wrasse and bumphead parrotfish are both species of concern).

These important specializations were determined based on ecological literature available for coral reef fish (e.g., Bellwood et al. 2004, Cvitanovic et al. 2007, Friedlander et al. 2007b, Jennings et al. 2001, Green et al. 2009), discussions with resource managers and coral reef fish specialists (Brett Taylor, Terry Donaldson, University of Guam; Ed DeMartini, Ivor Williams, PIFSC) and participants at the November 2012 Guam workshop (Weijerman and Brown 2013).

Coral reefs in Guam, as elsewhere, exhibit phase shifts from coral to macroalgal dominance (Mumby 2006, Friedlander et al. 2008). Therefore, we further split up the herbivore fish group based on their role in preventing this phase shift from happening and in promoting resilience of the reef in order to better model reef processes (Green et al. 2009). Surgeonfish and some damselfish species (denuders or grazers) and parrotfish and urchins (scrapers and excavators) play a crucial role in preventing macroalgae (defined here as all foliose algal species > 1 cm standing stock) from emerging from algal turf (defined as all foliose algal species ≤ 1 cm) by their high feeding rate on turf algae (Steneck 1988, Bellwood et al. 2006) and so prevent coral overgrowth and shading by macroalgae (Bellwood et al. 2004). Yet they can only maintain the reef in a cropped state if coral cover does not decrease substantially (Williams et al. 2001, Mumby 2006), and they are not very effective in the reversal of a phase shift (Bellwood et al. 2006). Browsers are species that prefer to feed on macroalgal stands and could play a crucial role in the reversal of a phase shift. Excavators, and to a lesser degree scrapers, are those species that have a functional role in bioerosion, by scraping off (dead) coral and sediment and so facilitate coral and coralline algal recruitment (Bellwood et al. 2004). These last two groups consist entirely of parrotfishes and the bigger they are, the larger are their bites so the higher their effectiveness (Bruggemann et al. 1996, Ong and Holland 2010, Comeros-Raynal et al. 2012).

The world's largest parrotfish, the bumphead parrotfish, *Bolbometopon muricatum*, is an important bioeroder on a reef and a coral predator. They bite the substratum, shaping the corals and the coral reefs and remove up to five metric tons of calcium carbonate (half of which is live coral) annually (Bellwood and Choat 2011). Hence, their ecological role as bioeroders and facilitators of coral recruitment by preventing algal overgrowth is very important to the well-being of a reef (Bellwood and Choat 2011). However, because they can grow so large, sleep in groups in shallow water and spawn in large aggregations they are easily targeted by fishers and vulnerable to extinction (Comeros-Raynal et al. 2012). Visual sightings of the *B. muricatum* in Guam are nowadays rare and they could be locally extinct (Bellwood et al. 2003, Fenner 2012). Just like the bumphead parrotfish, the humphead wrasse, *Cheilinus undulates,* is also an iconic species and shares many of its life-history characteristics with the bumphead parrotfish (Donaldson and Dulvy 2004). Both species are listed as threatened on the IUCN red list and as a species of concern (SOC) to NOAA Fisheries. As iconic reef inhabitants, they could be a very important component to the dive industry making them not only ecologically important but also economically (see Chapter 8). Because of these important role, we included *B. muricatum* and *C. undulates* in the model as their own functional groups.

Our species assignments to the 19 functional groups (Table 4.5) were further checked based on various published sources (Bellwood and Choat 1990, Choat and Robertson 2002, Friedlander and DeMartini 2002, Green et al. 2009, Sandin and Williams 2010), FishBase[10] and expert opinion.

Seabirds and Marine Mammals

We did not include any seabirds or marine mammals in Guam Atlantis as we assume that their contribution in terms of production or extraction to the coral reef ecosystem is small as they either forage on the intertidal habitats or offshore on small pelagics. The same holds true for the resident dolphins that rest in some of Guam's shallow bays but feed offshore.

4.3.2 Data Sources

Data sources for the biological parameters and biomass and abundance data came predominantly from monitoring studies conducted by NOAA PIFSC CRED in 2011. These data were supplemented with data from Guam DAWR, Coastal Management Program and University of Guam marine Laboratory monitoring programs, peer-reviewed literature, technical reports, theses and expert opinion. Fish and benthic survey methods used by CRED are detailed in Richards et al. (2011), Brainard et al. (2012) and Williams et al. (2012) and are only briefly described here. Extensive fish and benthic surveys conducted by CRED in 2011 (Fig. 4.13) used a stratified random sampling design and incorporated shallow (0–6 m), mid-depth (6–18 m) and deep (18–30 m) sites (Williams et al. 2012). Fish surveys were conducted using a stationary point-count method (SPC) and the benthos was surveyed by analyzing images from photo-transects along the diameter of the 15 m cylinder. For Guam Atlantis we combined the results of the two deeper sites for our deep (6–30 m) polygons. Towed-diver surveys were conducted following a mid-depth (approximately 12–15 m) contour. Data from the towed-diver surveys were used for biomass estimates of apex predators as these data represent their biomass better than data from SPC surveys conducted at stratified random sites (Richards et al. 2011) and for the clustered distribution of seastars. Towed-diver and rapid ecological assessment (REA) survey data from previous years supplemented data in Atlantis polygons not covered by 2011 surveys.

Horizontal distribution of species among the Atlantis polygons came from the 2011 data supplemented with expert opinion (e.g., for green turtles and urchins). For apex predator and roaming species (e.g., jacks, sharks, rays) we assumed an even distribution as these large, faster swimming species will move more compared to the smaller-sized reef fishes. However, we adjusted those values by decreasing the numbers in the shallow polygons and scaling them based on the results from visual surveys. For instance, sharks were predominantly seen in polygons, 31, 47 and 51 so we increased the percentage for those polygons while decreasing it for others. Vertical distribution in the water column and habitat preference came from expert opinion (D. Burdick, Guam Coastal Management Program; V. Brown, NOAA Pacific Islands Regional Office, Guam; T. Donaldson, University of Guam; I. Williams, CRED) and literature on habitat affinity (Beukers and Jones 1998, DeMartini and Anderson 2007, Friedlander et al. 2007a, DeMartini et al. 2010, Eriksson et al. 2012, Gratwicke and Speight 2005, Johansson et al. 2012).

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[10] www.fishbase.org

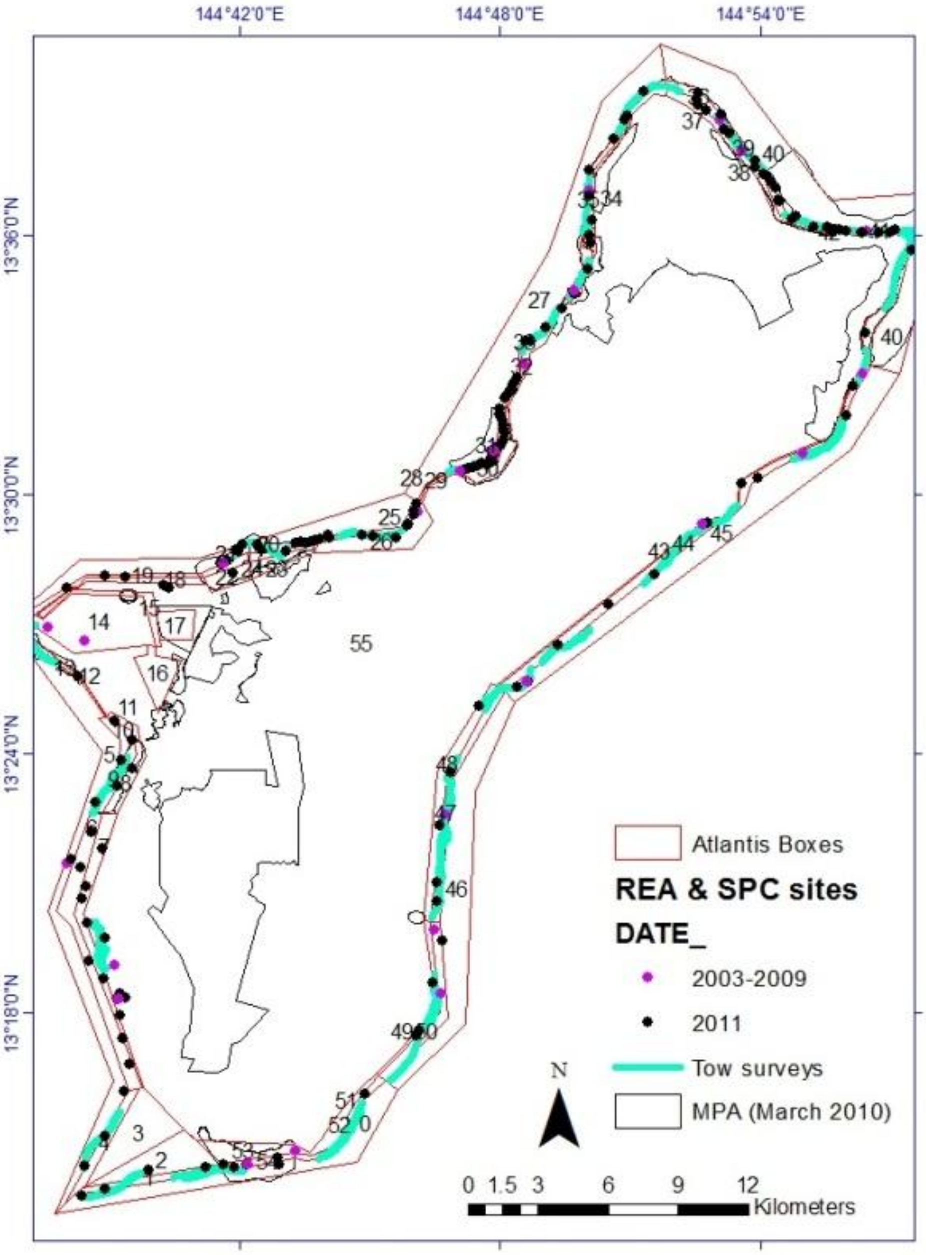


Figure 4.13. Survey sites around Guam. NOAA’s Coral Reef Ecosystem Division conducts bi-triennial surveys around Guam. The black dots represent the 133 biological survey sites visited in 2011 whereas the red dots represent the survey sites visited in 2005, 2007, and 2009. The blue slugs indicate the trajectory of towed-diver surveys from 2005 to 2011.

Parameters for the dynamic files (e.g., growth rate, clearance rate; see section ‘Biomass dynamics’) for invertebrates came from an Ecopath coral reef ecosystem model developed for Hawai’i (Weijerman et al. 2013; Chapter 3) (Table 4.6) and for vertebrates they are calculated as outlined in section “Biomass dynamics”.

Table 4.6. Invertebrate functional groups and basic life history parameterization. Growth, clearance, and mortality rates are postcalibration values. Initial life history parameters were based on Chapter 3.

Code	**Group**	**Maximum growth rate (mgN/day)**	**Clearance (mg^3/mgN/day)**	**Linear mortality (/day)**	**Quadratic mortality (/day)**
CEP	Cephalopods	0.022	0.002		
BSS	Sea Stars	0.013	0.001	0.00001	0.00001
BG	Sea Urchins	0.014	0.001	0.0001	0.005
CRS	Branching Corals	0.006	0.006		
CRN	Massive Corals	0.003	0.003		
BFF	Benthic Suspension Feeders	0.007	0.001		
BD	Benthic Deposit Feeders (Meiofauna)	0.033	0.003		
BC	Benthic Carnivores	0.023	0.002		
BM	Benthic Meiofauna	0.022	0.002		
ZD	Demersal Zooplankton	0.366	0.037		0.000001
ZC	Carnivorous Zooplankton	0.323	0.032		0.000001
ZH	Herbivorous Zooplankton	0.409	0.041		0.000001

Life history parameters (mortality, growth constant (k), infinite length (L_{inf}), age at first maturity, pelagic larval duration, maximum age) for fish and sharks were obtained from literature (MacDonald 1981, Victor 1986, Wellington and Victor 1989, Sudekum et al. 1991, Choat and Axe 1996, Hart and Russ 1996, Wilson and McCormick 1999, Choat and Robertson 2002, Gust et al. 2002, Sadovy et al. 2003, Choat et al. 2006, Hamilton et al. 2008, Longenecker and Langston 2008, Schluessel 2008, McIlwain et al. 2009, Ishihara and Tachihara 2011, Rhodes et al. 2011, Taylor et al. 2012), empirical formulas, FishBase and expert opinion (Brett Taylor, Terry Donaldson, University of Guam; Ed DeMartini, Marc Nadon, PIFSC). In absence of data on natural mortality (M) I used an empirical relationship (Pauly, 1980):

$$log(M) = -0.066-0.279*LOG(L_{inf})+0.654*LOG(k)+0.463*LOG(T) \qquad \text{Eq. 1}$$

where L_{inf} is asymptotic total length in cm, k is the growth constant from the Von Bertalanffy equation (both from literature or FishBase), and T is the mean temperature on the reef in °C and was obtained from CRED in situ data.

If, based on the calculated M, the chance that a species would reach its maximum age was less than 0.01%, we recalculated the maximum age ($t_{\max}$) based on the mortality-longevity assumption:

$$t_{\max} = ln(0.01)/-M \qquad \text{Eq. 2}$$

We then checked the chance that the functional group would reach its (weighted mean) maximum age and if this chance was < 0.01% we used the natural mortality based on the mortality-longevity assumption. For all the functional groups targeted in the reef fishery we used $t_{\max}$ to calculate M as fishing affects L_{inf} used in Equation 1 (Table 4.7).

Table 4.7. Natural mortality estimates used in the model (see text for calculation).

Functional Group	M in Years	Functional Group	M in Years
Sharks	0.21	Target herbivore—grazers	0.19
Rays	0.17	Herbivores—browsers	1.06
Roving piscivores	0.16	Target herbivore—browser	0.32
Mid-water piscivores	0.51	Detritivores	0.26
Benthic piscivores	0.53	Invertivores	0.61
Targer benthic piscivores	0.29	Target invertivore	0.49
Bumphead parrotfish	0.14	Humphead wrasse	0.15
Herbivores—excavators/bioeroders	0.41	Coralivores	1.05
Herbivores—scrapers	0.53	Planktivores	1.24
Herbivores—grazers	0.70	Turtles	0.07

Life history information for sea turtles came from literature: the von Bertalanffy growth constant k = 0.089 yr^{-1} (SD 0.015) and L_{inf} = 108.9 cm were based on Caribbean green sea turtles (Frazer and Ehrhart 1985); length-weight parameters were based on green turtles from Hawai'i (Balazs and Chaloupka 2004), age at sexual maturity was estimated at 18–27 y for a 99 cm carapace length with a comment that the upper estimate is more realistic (Frazer and Ehrhart 1985) and between 35 and 40 y for main Hawaiian Islands and > 50 y for Midway Atoll in the Northwestern Hawaiian Islands (Balazs and Chaloupka 2004). We used 37.5 y for the Guam Atlantis model. Juvenile green turtles leave their pelagic habitats at a carapace length of 35 cm (5 kg) when they are approximately 6 years old.

Appendix A includes all fish species per functional group with their scientific and common names, family, trophic level, the CRED method used for biomass estimate, biomass estimate and the average annual catch (DAWR, WPacFIN). Appendix B includes life history data as a weighted mean value per functional group.

Primary producers and invertebrates are modeled as biomass pools per area (mgN/m^2) for benthic organisms and per volume (mgN/m^3) for pelagic organisms. Vertebrate groups are divided into 10 age classes each tracked by the abundance and weight at age to allow for ontogentic shifts. Weights are measured through structural (bones and other hard parts) and reserve (muscles, fat, reproductive organs, and other soft tissue) weight (mgN/m^2).

Most available biological data were reported in grams wet weight per area or per volume. As the currency of Atlantis is nitrogen we converted wet weight to nitrogen by dividing it by 5.7 (based on the Redfield ratio) and by assuming dry weight equals to 5% of wet weight. We used a mean depth of 15 m to convert area specific data to volume specific data where needed. Weijerman et al. (2014a) gives general information about each functional group, their diet and biomass with data sources.

4.3.3 Model Dynamics

Biological Dynamics

Primary Production

Guam Atlantis includes the primary producer groups: macroalgae, turf algae, crustose coralline algae,and large and small phytoplankton. In a later version of the model (Chapter 6), code will be adapted for corals to make them both filter feeders (as such included in the present model) and primary producers. Growth is driven by Michaelis-Menten dynamics and varies with nutrients, light and space availability. Biomass is lost to predation, lysis, linear and quadratic mortality and harvesting. The rate of change in biomass B for a primary producer group is:

$$dB/dt = G - M_{lys} - M_{lin} - M_{quad} - \sum_{j=1}^{n} M_j - F \qquad \text{Eq. 3}$$

in which G is the growth rate of autotrophs, M is loss as a result of lysis (M_{lys}), linear mortality (M_{lin}) or quadratic mortality (M_{quad}), Mj is predation mortality as a result of grazer j, n is number of grazers, and F is mortality from harvesting. The rate of growth is defined as:

$$G = \mu * \delta_{irr} * \delta_N * \delta_{space} * A \qquad \text{Eq. 4}$$

where μ is maximum growth rate, δ_{irr} is light limitation factor, δ_N is nutrient limitation factor, δ_{space} is space limitation factor, and A is rate of catabolism. For formulation of the limitation factors, see Fulton et al. (2004a), as it varies between producers.

Growth rates were obtained from Chapter 3 and assumed to be similar between Hawai’i and Guam. During tuning of the model these initial growth rates were adapted (Table 4.8).

Table 4.8. Growth rates for primary producers with alterations made during tuning in parentheses. Initial growth rate calculated from Chapter 3.

Functional Group Name	Growth Rate
Large phytoplankton	0.410 (1.0)
Small phytoplankton	0.410
Macroalgae	0.018
CCA	0.010
Turf algae	0.030

Nutrient Dynamics

Nitrogen is the currency of Guam Atlantis and changes in ammonia (NH) and nitrate/nitrite (NO) are modeled. Nutrient concentrations effect the growth of primary producers and are governed by uptake by autotrophs, excretion by consumers, nitrification and denitrification:

$$d(NH)/dt = -\sum_{i=1}^{P} A_{NH,i} + \sum_{j=1}^{C} E_{NH,j} - S + R \qquad \text{Eq. 5}$$

$$d(NO)/dt = - \sum_{i=1}^{P} A_{NO,j} + S \qquad \text{Eq. 6}$$

where A is rate of uptake of NH or NO from the water column by autotroph i, P is set of all autotrophs, E is excretion of NH by consumer j, C is set of all consumers, S is amount of NH converted to NO by bacteria (nitrification) and R is amount of NH produced by denitrification.

Biomass Dynamics

Changes in biomass for vertebrate and invertebrate consumers are influenced by growth, predation, mortality, migration and harvesting:

$$dB/dt = G - \sum_{i=1}^{n} M_i - M + I - E - F \qquad \text{Eq. 7}$$

where biomass (B) is substituted for abundance per age-class for the vertebrates, G is growth, M_i is predation by predator i, n is the number of predators, M is mortality not captured by predator-prey dynamics, I is immigration into the model which is set to zero for Guam Atlantis, E is emigration out of the model which is also set to zero for Guam and F is fishing mortality.

Growth dependents on predation, assimilation efficiency and oxygen and space availability:

$$G = \sum_{i=1}^{n} P_i * \varepsilon_i * \delta_{O_2} * \delta_{space} \qquad \text{Eq. 8}$$

where P_i is predation by consumer on prey i, ε_i is the assimilation efficiency on prey i, and δ_{O_2} and δ_{space} are the oxygen and space limitation factors. Oxygen and space limitation apply to benthic invertebrates living on or in the sediment layer and is governed by a Michaelis-Menten relationship: oxygen limitation increases with depth and growth is inhibited by increases in the density of an invertebrate group until a threshold is passed where the maximum density is reached. Half saturation constants, depth of oxygen horizon, lower density thresholds, maximum densities and half saturation constant for space limitation were all adapted from Fulton et al. (2004c). For vertebrates growth is allocated further into structural and reserve nitrogen pools (Fulton et al. 2004b).

Mortality not captured by the predator-prey dynamics is composed of linear mortality, quadratic mortality and species-specific mortality (e.g., fouling by epiphytes on macroalgae, starvation) for each functional group.

Spawning and recruitment also affect biomass dynamics of vertebrates and these processes are described below.

Predation

In the Atlantis framework, predation can be modeled using various formulas. Fulton et al. (2003b) concluded that the Holling Type II functional response may predict ecosystem responses equally well as more complex models, therefore, for Guam Atlantis we implemented a modified version of the Holling Type II response to model predation:

$$P_{ij} = \frac{B_i * a_{ij} * B_j * C_j}{1 + \frac{C_j}{gj}\left(\sum_{i=1}^{n} B_i * a_{i,j} * E_{ij}\right)} \qquad \text{Eq. 9}$$

where P_{ij} is ingestion of prey i by predator j (mgN), B_i is biomass of prey i (mgN/m^3), a_{ij} is availability of prey i to predator j (unitless), B_j is biomass of predator j (mgN/m^3), C_j is the clearance rate of predator *j* (m^3/mgN/d), g_j is the growth rate of predator *j* (/d) and E_{ij} is the growth efficiency of predator *j* eating prey *i* (unitless).

The maximum ingestion rate (G_{max}) is the asymptote of this function when prey is abundant. Multiplying this maximum ingestion rate by an assimilation efficiency over all food types:

$$g = G_{max} * \varepsilon \qquad \text{Eq. 10}$$

gives us the maximum growth rate (*g*) in mgN/d/individual. We assume that the assimilation efficiency (ε) is 10% for vertebrates and 50% for invertebrates. Ingestion rates for invertebrates came from Chapter 3 and were multiplied by 1.2 to reflect the maximum consumption rate which is used in Atlantis.

For fish group, the maximum consumption rate depends on the weight of the predator:

$$G_{max} = CA * W^{CB} \qquad \text{Eq. 11}$$

with the constants *CA* and *CB* set to 0.3 and 0.7 respectively and units m^3/mgN/d (Hanson et al., 1997). We used weight estimates from Von Bertalanffy curves (structural and reserve nitrogen) to obtain maximum consumption for an average individual per age class.

Clearance is a measure of feeding efficiency when prey is scarce, i.e., at the origin of the predator-prey functional response. It reflects the rate at which growth increases with increased food abundance. Atlantis considers clearance as filter feeding a volume of water or swept-volume predation with units m^3/mgN/d. We assumed clearance rates to be 10% of the maximum growth rates.

The availability parameter (*a*) is a combined measure of prey preference and the relative availability of the prey to the predator. To derive these parameters we constructed a diet matrix to define the relative contribution of each prey group to each predator's diet, and set the *a* parameters equal to represent these binary predator/prey links and to qualitatively capture the strength of these links. During model tuning we calibrated these values, attempting to match realized diets (predicted by Atlantis) to observed diet fractions from field studies and to match realized growth (size-at-age) to expected size-at-age.

The amount a predator eats not only depends on the availability of its prey but also on the gape size for age structured predator/prey relationships (Karpouzi and Stergiou 2003). In general I assumed that a predatory fish can eat a prey fish of 40% of its body length. I used the weighted means of the morphometric data per functional group to calculate the upper limits of gape size as the largest prey body length to the maximum predator body length ratio. For example for jacks that eat fish, molluscs, shrimp and other benthic invertebrates, I divide the maximum length of the largest prey based on its diet composition, in this case invertivorous fish (25 cm) by the mean length for roving piscivores (the functional group of jacks; 73.5 cm) and so calculate the upper limit as 0.46 (Table 4.9). For species that take bites of their prey, size of the prey is not important. Therefore, for the functional group sharks we set the upper limit to 3.

Table 4.9. Estimation of gape size per Guam Atlantis functional group that preys upon age-structured groups.

Predator Functional Group	Dominant Prey Functional Group	Weighted Max Length Predator (cm)	Weighted Max Length Prey (cm)	Upper Gape Limit
Mid-water piscivores	Planktivores	70	21	0.30
Roving piscivores	All fish species	153	70	0.46
Target Benthic piscivores	Invertivores	50	25	0.50
Benthic Piscivores	Invertivores	67	25	0.37

For planktivorous, corallivorous, detritivorous and herbivorous fish, turtles and invertebrates which do not eat age-structured prey, I defaulted to 0.2 for the upper gape limit. For invertivorous fish and rays I used 0.25. All functional groups had 0.0001 as the lower gape limit.

Assimilation

Gross growth efficiency (GGE) is the ratio of production to consumption and for most groups has values between 10% and 30% (Christensen and Pauly 1992). Exceptions are top predators, such as marine mammals and seabirds, which can have lower GGE (between 0.1% and 1.0%), and small, fast-growing fish larvae, nauplii and bacteria, which can have higher GGE (between 25% and 50%). For example, copepods, the most abundant pelagic grazers, have a fairly high efficiency to assimilate carbon: the mean GGE is 25% but can exceed to 60% in places with high food concentrations (Hassett and Boehlert 1999); pelagic bacteria have a GCE of 40% (Cole et al. 1988) but larger invertebrates, such as sedentary octopus, can also have high GGE of 40%–60% (Jennings et al. 2001). I constrained the assimilation efficiency to be 80% for most carnivorous groups, i.e., ~ 80% of the consumption is assumed to be physiologically useful for consumer groups while the nonassimilated food (20%, consisting of urine and feces) is directed to detritus. Of this 80%, the majority of energy is used in respiration and a small fraction (e.g., one-eighth) might be translated into growth of the individual (e.g., an overall 10% GGE). However, for herbivores and detritivores this default value of 80% often underestimates egestion. I have, therefore, adjusted assimilation efficiency for detritivorous and herbivorous fish groups to 20%–35%, for demersal and carnivorous zooplankton to 30%–45%, for herbivorous zooplankton to 50%–55% and for in- and epifauna to 30%–50% (Edward 1986, Jobling 1994, Cury and Christensen 2005).

Spawning and Recruitment

The *alpha* and *beta* parameters in the Beverton-Holt stock recruitment relationship (Beverton and Holt 1957, 1993) are related, respectively, to unfished level of recruitment and productivity of the stock at low stock sizes (Equation 12). The steepness of this relationship is defined as the fraction of recruitment from an unfished population obtained when the spawning biomass is 20% of its unfished level (Mace et al. 1988). However, setting these parameters is a challenge (Mangel et al. 2010). For stocks where environmental drivers rather than the parental stocks are important to recruitment the steepness is often set to 1 and for stocks where the number of recruits are dependent on the parental stock the steepness approaches 0.2; in general the steepness depends on the demography of the stock (Mangel et al. 2010). For an age-structured population without fishing the steepness depends on the schedule of survival and fecundity at age and maximum per capita productivity.

From meta-analyses of stock-recruitment data for several pelagic species, a family-level median steepness has been estimated that varied between 0.28 for Anoplopomatidae (*Anplopoma fimbria*) and 0.95 for Lujanidae (*Lutjanus campechanus*) (Myers et al. 1999). For the Guam Atlantis model steepness estimates were used for reef-fish families from Myers et al. (1999) and interpolated for other families based on their dependence on parental stock for recruitment.

In Atlantis I used the Beverton-Holt stock recruitment model defined as:

$$recruits = \alpha * S / (\beta + S) \qquad \text{Eq. 12}$$

where recruits is the number of recruits in the whole system and a recruit is typically a ~ 30–90 day old post-settlement fish, S is the spawning biomass of mature adults of both sexes in mgN, α is the maximum number of recruits that can be produced, and β is the level of S that produces one half of the maximum number of recruits.

The *alpha* and *beta* parameters for spawning fish species are critical for tuning the model and were changed in adjusting model dynamics (Table 4.10). To calculate these parameters, we made the following assumptions:

- stocks have an equal birthrate of females and males;
- species or families where genetic results show that they are predominantly self-seeding, have a great dependency on the parental stock and, therefore, a low steepness;
- the biomass in the MPAs multiplied by an adjustment factor of 1.5 (total fish biomass around unfished northern Mariana islands is approximately 1.5 times higher than from MPAs in Guam) is equal to the unfished biomass in Guam (Williams et al. 2012).

Table 4.10. Beverton and Holt alpha and beta recruitment parameters for fish groups. Only when values changed during tuning are they given in the post-tuning columns.

Functional Group	**Calculated values**		**Post-tuning values**	
	alpha	beta	alpha	beta
Planktivores	2.28E+06	2.45E+08	2.28E+07	
Coralivores	2.10E+05	6.74E+07	2.10E+07	
Invertivores	4.50E+05	4.72E+08	4.50E+06	
Target invertivores	1.88E+05	8.22E+08	4.00E+06	
Humphead wrasse	1.13E+01	2.30E+09	1.13E+03	
Detritivores	9.99E+04	5.42E+08	5.00E+06	
Browsers	1.18E+04	8.33E+06	2.00E+05	
Target browsers	1.97E+04	2.67E+08	1.00E+06	
Grazers	6.31E+05	2.29E+08	5.31E+07	
Target grazers	1.67E+05	5.89E+08	4.67E+06	
Scrapers	9.09E+05	1.53E+09	1.80E+07	
Excavators	8.51E+03	1.48E+09	9.01E+05	
Bumphead parrotfish	1.97E+01	1.16E+09	4.00E+03	
Mid-water piscivores	9.01E+03	4.51E+06	1.35E+05	
Roving piscivores	9.66E+03	1.68E+09	1.66E+04	1.68E+07
Target benthic piscivores	6.27E+04	2.20E+07	3.03E+05	
Benthic piscivores	9.40E+03	6.76E+07	5.40E+04	
Rays	Fixed recruit = 1		1.5	
Sharks	Fixed recruit = 1.5		1.0	
Turtles	Fixed recruit = 0.5			

The functional groups sharks and rays have live young and sea turtles lay eggs, so their recruitment is modeled using a fixed number of offspring produced per adult. For sea turtles, recruit per adult is the product of hatch success, nests per year and clutch size; for sharks and rays, it is a product of number of off spring per female, pregnancy rate, proportion of females in a population and pregnancy interval. Female turtles lay approximately 120 eggs per nest with a hatching percentage of 77% (Schouten et al. 1997). They can lay up to 5 clutches per nesting season and females return to their nesting beaches approximately once every 4 years (Limpus and Nicholls 1988). Nesting season is from April to July with hatchlings emerging between June and September (Valerie Brown, Dave Burdick pers. comm.). Mortality rate of hatchlings on the beach and in the shallow coastal area is very high with estimates of 75% (Burgess et al. 2006). Although the juvenile pelagic stage is about 6 years, I used recruit age of 1 year and truncated the smallest age classes that have high levels of mortality and diets different from the larger individuals found around Guam. I assumed a fixed recruitment of 0.5. Growth rate is high for juveniles and declines to negligible when they reach sexual maturity (Limpus and Chaloupka 1997).

Rays have 2–4 pups and sharks 1–6 and I assumed that both have a pregnancy interval of 2 years (Braccini et al. 2006, Schluessel et al. 2010). These parameters translate to a maximum production of offspring of 1 and 1.5 per adult for respectively rays and sharks assuming an equal sex distribution.

4.3.4 Fisheries Module

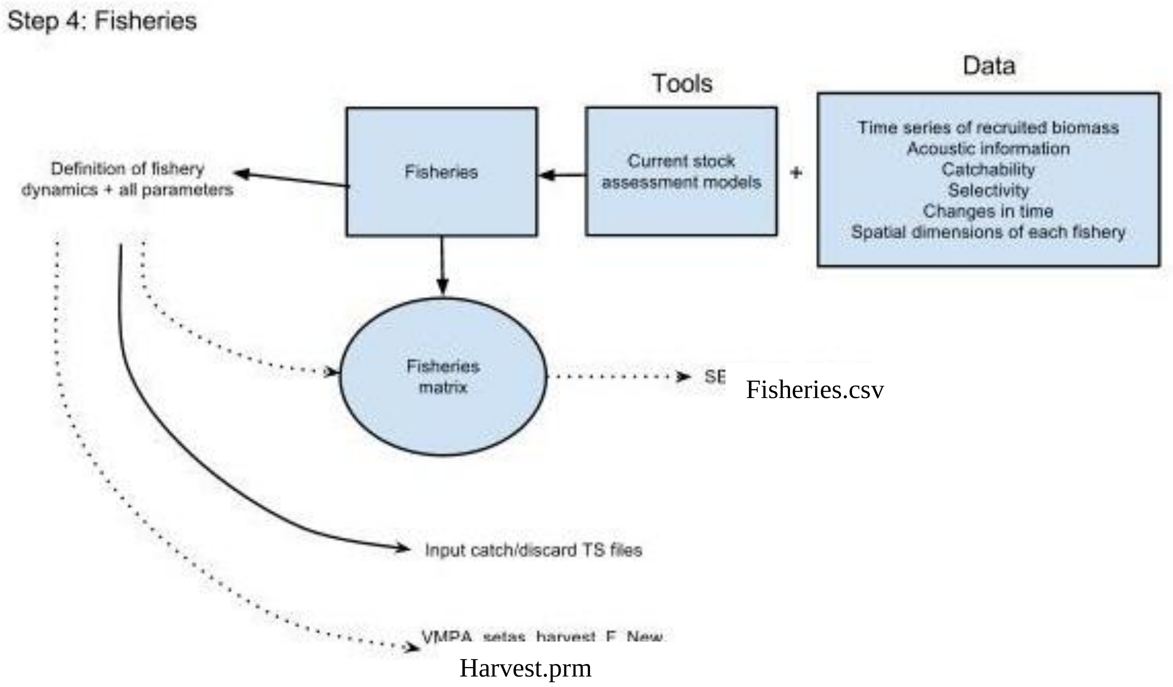


Figure 4.14. Schematic overview of the Atlantis framework and requirements for the fisheries module with resulting files including a fishery fleet file, catch time serie, and a harvest file.

A good understanding of the fishery is necessary to be able to simplify it in a model (Fig. 4.14). The fishing community in Guam includes individuals from a diverse set of cultures, such as indigenous Chamorro as well as introduced Anglo-American and Micronesian fishers (Allen and Bartram 2008). The island’s indigenous Chamorro people were highly skilled fishermen and archeological evidence suggests both reef and pelagic fish were caught using hooks, spears and nets (Amesbury and Hunter-Anderson 2003). Fishing on Guam is best considered a subsistence fishery, as commercial fisheries have had negligible effects on Guam’s economy. Commercial fishers target primarily pelagic species beyond the 0–30-m reef boundaries, while most local fishers target both reef and a few pelagic species. Both traditional and modern fishing techniques are currently in use on Guam (Hensley and Sherwood 1993). Common fishing methods include hook-and-line, spearfishing (both snorkel and scuba), gill nets, drag nets, and cast (or throw) nets; with hook-and-line being the most commonly used method (DAWR and WPacFIN 1985–2012 fisheries data); the highest catches were obtained from gill nets, hook-and-line and snorkel spearfishing and the highest catch-per-unit-effort obtained with surround nets and drag nets (Table 4.11). Each method requires a varying degree of skill, and allows for different levels of species selectivity.

Table 4.11. Relative effort based on annual mean number of hours that a gear type was used for shore-based fishery and the obtained catch and corresponding catch-per-unit-effort (CPUE) per gear type. Data source: DAWR and WPacFIN creel inshore fisheries survey data 1985–2012. gh = gear-hour.

Fishing method	Relative effort (%)	Relative catch (%)	Mean CPUE in kg/gh
Cast Net	7.1	9.1	0.39
Drag Net	0.4	3.3	2.64
Gill Net	13.7	29.2	0.65
Hook and Line	64.0	21.9	0.10
Hooks and Gaffs	2.3	3.0	0.39
Other Methods	4.4	5.3	0.37
Scuba Spear	0.4	1.8	1.55
Snorkel Spear	7.5	24.0	0.98
Surround Net	0.2	2.4	3.12

Fishing in Guam is also of cultural significance, as it is tightly woven with the identity of the islands' residents and the tradition of sharing catch with friends and family is a continuation of the Chamorro culture (Allen and Bartram 2008). In a survey conducted on fishers participating in pelagic fishing, almost all of the respondents reported 'regularly giving fish to family, friends or both' (Rubinstein 2001). DAWR survey results showed that only 1 fisher sold the fish at one time, indicating the subsistence or recreational goal of inshore fishing activities. Fishing also contributes to food security, with households reporting that 24% of fish consumed was caught by an immediate family member and an additional 14% of fish consumed was caught by a friend or extended family member (Van Beukering et al. 2007). Fish is an especially important source of food for large cultural events such baptisms, weddings and village fiestas (Rubinstein 2001).

Chapter 5 explains how we used catch-per-unit-effort data to reconstruct historic fish biomass trends used for model testing.

4.3.5 Socio-economic Module and Visualization of Atlantis Model Output

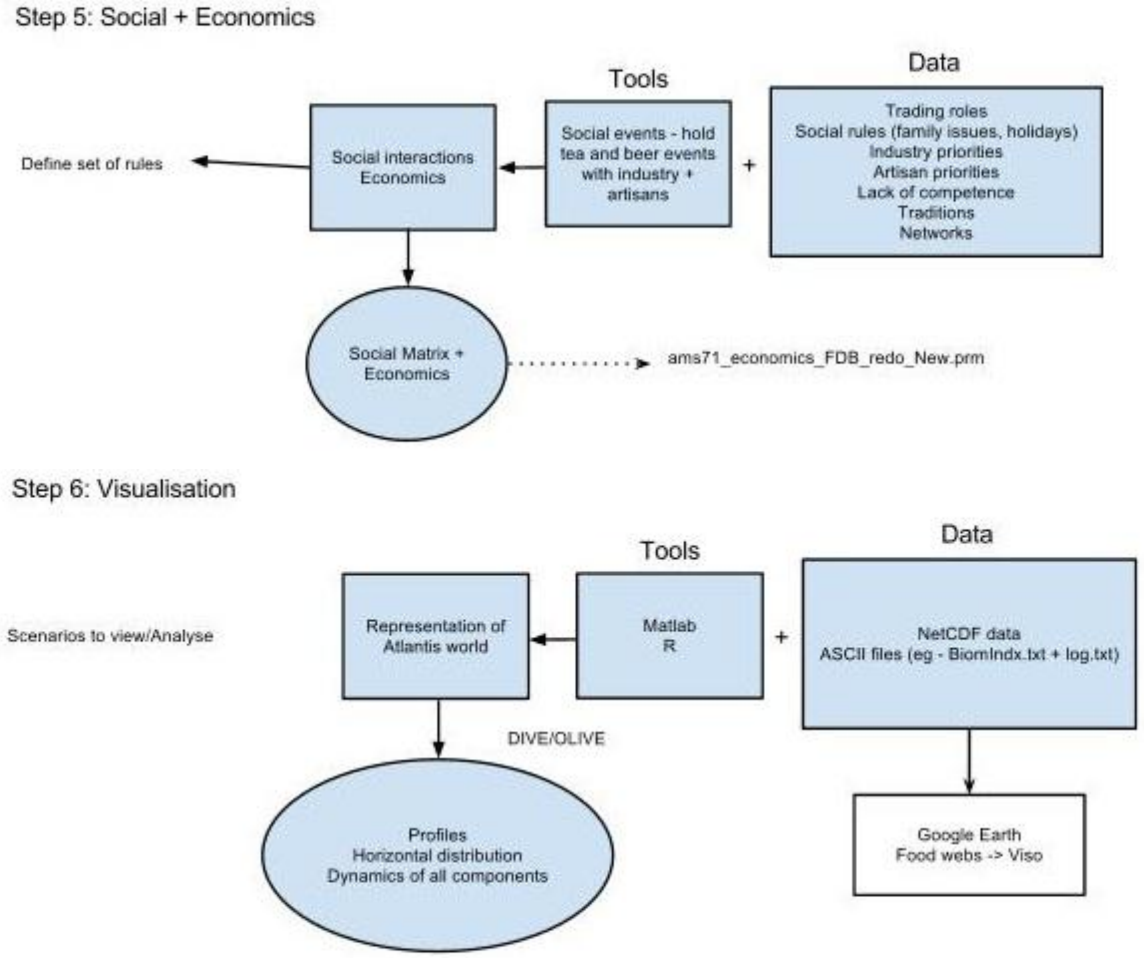


Figure 4.15. Schematic overview of (*top*) the Atlantis framework and requirements for the socio-economic module and (*bottom*) how to visualize model output.

We have not yet included the socioeconomic module into Guam Atlantis but the visualization tools in Figure 4.15 are also suitable for the ecology and fishery modules.

4.3.6 Model Tuning and Diagnostics

Adjusting input parameters is an iterative process in which current state (i.e., biomass, abundance, cover) and rate parameters are adjusted to generate realistic system behavior and fit model predictions qualitatively to observations. This process is made cumbersome by the slow run-time of Atlantis which also prohibits any automated estimations of model parameters. I followed the adjustment procedures as used in previous successful applications of Atlantis (Horne et al. 2010, Link et al. 2010, Ainsworth et al. 2011a). I calibrated the dynamic behavior of Guam Atlantis in two phases. In the first phase, I initialized the model with 2011 estimates of biomass and ran the model forward without fishing. Initial conditions represent approximately 2011, and simulations were projected for 30 years. Goals for this phase were to keep functional groups from going extinct and achieve weights-at-age (structural and reserve weight) within 0.5 and 1.5 and ideally between 0.8 and 1.2 times their initial biomass (Horne et al. 2010). In the absence of fishing, I assumed that the system, beginning from an exploited ecosystem base in 2011, should return to conditions similar to those in marine preserves around Guam or better (i.e., higher fish biomass values) as some forms of fishing are still allowed in the preserves. I used mean estimates from underwater surveys conducted in preserves around Guam in 2011 as calibration targets (CRED data). I acknowledge that this method is not ideal as species that are already locally rare (e.g., bumphead parrotfish) or at very low levels (apex predators) will not be represented accurately. Therefore, I also compared these estimates with biomass values from the relatively pristine reefs around the Northern Marianas (Fig. 4.5) and adjusted them when they differed more than 1.2 times. The benthic community structure did not vary greatly between inside and outside marine preserves. For these groups and others for which we did not have unfished biomass estimates, the goal was merely to produce steady biomass through time that fall within the range of current observations.

For these simulations I did not include large scale trends in climate or environmental forcing. Extinctions typically point to excessively high predation levels or extremely low productivity of the stock. The primary parameters involved with resolving these problems included growth rates (g in eqs. 9 and 10), clearance rate (C in eq. 9), and predation pressure dictated by the availability parameter (a in eq. 9). Tuning vertebrate weights-at-age involved adjusting growth rates, recruit weights, and assimilation efficiencies (ε in eq. 11). When weight-at-age was stable, vertebrate biomass could be adjusted further by manipulating Beverton and Holt recruitment parameters and the number of recruits for the non-fish vertebrates, and linear and quadratic mortality.

In the second phase of calibration, I exercised the model with varying degrees of fishing pressure to evaluate responses of functional groups when perturbed. For these scenarios, I did not attempt to simulate fleet dynamics, but rather applied constant fishing on all fished fish groups throughout the duration of the simulation. I expected biomass to decrease in response to fishing without going extinct at reasonable levels of fishing pressure. Generally, I expected highly productive stocks, such as, planktivores to be able to withstand moderate amounts of fishing mortality, and unproductive, long-lived groups like large-bodied parrotfish (*Chlorurus* spp.) and groupers to decline under similar fishing rates. As a very approximate expectation, at fishing levels equal to the natural mortality rate (M), I expected functional group biomass to decline by 50% compared to a no-fishing scenario (roughly assuming that the level of fishing mortality that results in the maximum sustainable yield [FMSY] = M and biomass at maximum sustainable yield [BMSY] = 50% B_0, Gulland 1970). Cases where biomass was too sensitive or too robust to additional fishing pressure usually pointed to problems with recruitment, and thus adjusting productivity via recruitment was generally the best solution.

4.4 Results

4.4.1 Initial Calibration: No Fishing Scenario

Our goal in this initial tuning phase was to produce steady biomass and, for vertebrates, stable weight and density in each age class.

Biomass

Approximate values of unfished or lightly fished biomass in MPAs were available for all fish groups. In the absence of fishing, most fish groups in the simulations reached that biomass within 5–10 years after being released from environmental perturbation and fishing pressure. Some of the piscivore groups did not reach the expected unfished biomass level, most notably the roving piscivores and rays. In general, long-lived species (e.g., bumphead parrotfish and sharks) took longer to recover as expected from their life-history characteristics. Our goal for the invertebrate and primary producer groups was to keep them alive and stable through time, similar to mass balance procedures in Ecopath models (Polovina 1984). This goal was reached for the majority of these groups but not for benthic meiofauna, macroalgae or corals which all died after a few years. Most of the groups stabilized after about 20 years except for demersal zooplankton that continued to increase. As corals are the focus of our model, further tuning efforts are necessary. We expect that when the model code is updated with coral reef specific code (Chapter 6), these trends, at least for corals, which will be both predator and primary producer, will improve.

Weight-at-age for Vertebrate Groups

Results for weight-at-age (reserve weight) for most age classes were relatively stable and between the 0.5 and 1.5 of the initial weight as desired with some groups (all the herbivores: grazers, browsers, scrapers, excavators) remaining close to initial values. The exception was for the youngest juveniles of many groups, for which weight-at-age dropped immediately to 50% of their initial values. For mature age classes dropping to 50% of initial size-at-age (i.e., getting very skinny) hampers the reproduction, so it is important for them to keep their weight. For juveniles this weight loss is less important, especially since growth at later ages compensated for this, but in future tuning exercises this should be investigated further.

Density-at-age for Vertebrate Groups

Vertebrate densities maintained an age structure that roughly followed an exponential decline in abundance with age. The piscivores proved most difficult to tune with only the benthic piscivores and target benthic piscivores showing a final (year 10–30 and year 30 respectively) age structure with abundance declining smoothly with age.

4.4.2 Secondary Calibration: Constant Fishing Pressure

In the second calibration, I applied constant fishing mortalities to evaluate biomass response to these harvest rates for each functional fish group. I exerted an increasing fishing pressure on all vertebrate functional these groups except Fish Invertivores, Fish Herbivore Browsers, Fish Herbivore Grazers and Fish Benthic Piscivores as these groups are not targeted in reef fisheries. Biomass declined to half the initial biomass when fishing rates where equal to or exceeded natural mortality rates except for a few groups, such as, Corallivores, Target Fish Invertivores, Herbivore Excavators and Target Benthic Piscivores. These latter groups all showed an increase in biomass possibly as a result of a decrease in intra competition and inter-specific predation pressure. Results show that slow-maturing groups (Sharks, Turtles and Bumphead parrotfish) could sustain fishing mortality rates substantially higher than their natural mortality. For the non-harvested fish groups, the biomass stayed similar to the initial biomass or increased likely as a result of reduced predation pressure.

4.5 Discussion

Human-induced drivers on the natural resources of Guam have intensified and diversified. Tourism is a main factor contributing to the island’s economy and the number of tourists visiting Guam and the island’s resident population has increased steadily over the last few decades. Furthermore, as a result of the military buildup, military personnel and civilians are scheduled to move to Guam in the next few years. These changes are projected to have a profound effect on the island’s land cover (e.g., more surfaced roads, housing), land-based sources of pollution (e.g., increase in sewage, off roading related runoff) and natural resources (e.g., through recreational fishing, jet skiing, scuba diving). The resulting competition for space and resources suggests the need for improved quantitative tools to evaluate competing socioeconomic costs and benefits. There is also growing recognition that climate and ocean change affects the coral reef ecosystem and should be taken into account in management strategies. Coral reef ecosystem management has therefore become increasingly complex. However, with the improvement in computer power and the maturity of ecosystem models, such as Atlantis, new tools are now available for management scenario analyses.

The objective of this chapter was to detail the design of the model framework and the parameterization of the spatial and ecological module. Improvements as described below, especially for coral dynamics and oceanography, are explained in Chapter 6. With these improvements, the model is used to tests simple management strategies related to fishing effort, fishing areas and closures, simple ocean acidification scenarios and changes in nutrient and sediment loading (Chapter 7). These scenario analyses have been investigated with Atlantis previously. For instance, Kaplan et al. (2012) tested a series of fishing closures and gear switches using a California Current Atlantis model, and Griffith (2011) and Kaplan et al. (2010) considered scenarios for ocean acidification. Fulton et al. (2006) and Fulton and Smith (2004) tested effects of nutrient loading in Atlantis models in Australia. Finally, even with relatively simple fishing dynamics, results can be linked to economic models, such as, those of Arita et al. (Arita et al. 2011, Arita et al. 2013) and Kaplan and Leonard (2012).

The development of the Guam Atlantis model has been useful in integrating available data streams and identifying data gaps. Shallow (0–30 m) benthic mapping data still remains absent for large stretches of Guam. While data on fish and coral and algal cover are available through monitoring programs, data on other benthic filter feeders, epifauna (invertebrates living on top of the benthos), infauna (also called cryptic fauna, invertebrates living in the sediment or associated with benthic groups) and macroinvertebrates are sparse (e.g., just for one depth range or one bay) or absent. Additionally, in-situ data on chlorophyll-*a* are sparse. Both CRED and Guam Environmental Protection Agency (EPA) collect these data but CRED only as a snapshot in time every 3 years and EPA only for shallow surface waters and mostly for impacted bays. As chlorophyll-*a* is a useful proxy for phytoplankton biomass and, therefore, represents the bottom of the food chain, better estimates are needed. Furthermore, stock assessments for coral reef fish are rare and life-history parameters for most species are very sparse. For example, we needed to extrapolate Beverton and Holt recruitment parameters from a few species to many of the modeled fish groups.

In this chapter, Guam Atlantis does not include code specific to coral reef dynamics. The inclusion of coral-algal-grazer dynamics, important in shaping the benthic community, and factors that influence coral recruitment (sediment, CCA cover, excavators) will greatly enhance simulations of coral reef ecosystem processes. Furthermore, corals play an important role not only as a food source but also as refuge for juvenile fish and in the current model version corals died in the first few years; having corals better represented will likely stimulate fish biomass and the biomass of benthic invertebrates depending on corals.

The physical oceanography is currently simulated with mean values for temperature and salinity and stable fluxes. Despite the lack of coral specific code and the oceanic model, the results of the first two calibration phases show that the model can simulate main dynamics for most functional groups. Calibration results of no fishing or land-based sources of pollution showed that the biomass of fish groups reached unfished or lightly fished conditions. Long-lived species with slow reproduction took longer to recover (e.g., sharks, humphead wrasse, bumphead parrotfish, and rays) than species with a shorter life cycle, such as, planktivores, coralivores and detritivores. For some groups (e.g., roving piscivores) the tuning is still not ideal and better parameters are needed for subsequent calibrations. Calibration results of constant fishing pressure showed that, as can be expected, most groups decline in biomass once fishing pressure is equal to or exceeds their natural mortality. Further calibration to evaluate the model's ability to replicate historical biomass trends under historical fishing pressure and environmental changes are described in Chapter 6.


Guam Division of Aquatic and Wildlife Resources, Department of Agriculture

A fisherman throwing a cast net to catch juvenile fish in Tumon Bay

Chapter 5

Coral reef-fish biomass trends based onshore-based creel surveys in Guam

Weijerman, M, ID Williams, J Gutierrez, S. Grafeld, B Tibbatts, G Davis. *In review*. Coral reef-fish biomass trends based on shore-based creel surveys in Guam. Fisheries Bulletin

Coral reef fisheries play important roles in the social and economic welfare of coastal communities and provide vital non-market functions. The complexities of these multi-species, multi-gear fisheries pose challenges for fisheries management. The Guam Division of Aquatic and Wildlife Resources has a detailed creel survey program that attempts to capture the trends in inshore fishing activities. In this paper we focus on the Guam shore-based coral reef fishery (1) to evaluate the past and present fishery characteristics in terms of catch composition and effort per gear type, and (2) to reconstruct the standing stock of reef fishes in the shallow (< 30m) coral reef ecosystems for the period of 1985–2012. Total estimated effort of all gear types used has stayed more or less stable; however, estimated total catches have dropped from an annual mean of 100 metric tons (t) in the 1985–1990 time period to 36 t in the 2007–2012 period. Issues with survey consistency and bias undermine standard statistical methods in analysis of these data and qualify inferences from these data as tentative, yet interest in them is high due to the lack of alternative information. Reconstruction of historical target fish biomass showed a steep decrease in biomass from 1985 to around 1990, a leveling off from 1990 to 2005 before a subsequent decline more recently. Present stock size in Guam is very low compared with reef-fish biomass near unpopulated islands in the Mariana Archipelago. Given the cultural, economic, and ecological importance of reef fishes to Guam's residents, these low fish stocks are cause for concern.

5.1 Introduction

Coral reef fishing is an important activity for the social and economic welfare of many coastal communities (Dalzell et al. 1996, Moberg and Folke 1999). Commercial and recreational fishing supports various jobs and fishing expenditures generate millions of dollars in sales revenues and value-added benefits to the U.S. states and territories that have coral reefs (Craig 2008). Furthermore, in many Pacific islands, fisheries serve vital non-market functions such as building social and community networks, perpetuating fishing traditions and providing food to local communities (Dalzell et al. 1996, Plagányi et al. 2013).

In Guam, as a result of the frequency and intensity of typhoons as well as the limitations of available agricultural land, the people have traditionally been highly dependent on marine resources (Amesbury and Hunter-Anderson 2008). Only after World War II has a wage-based economy developed, replacing subsistence agriculture and fishing as the primary economic drivers (Amesbury and Hunter-Anderson 2008). A recent household study estimated that 35%–45% of respondents were active fishers (Van Beukering et al. 2007) which, if applied to Guam's estimated current population (2010 US census data available at www.bsp.guam.gov), indicates a potential fisher population of between 56,000 and 72,000 individuals.

From prehistoric to present times, there have been at least 52 different fishing methods used on Guam (Kerr 2011) and some of these traditional practices are still in use, such as the seasonal catching of bigeye scad, *Selar crumenopthalmus*, with surround nets (atulai) and throw/cast net fishing (talaya) (Hensley and Sherwood 1993). Modern reef-fish fishing on Guam is still best considered as primarily a subsistence or recreational fishery as commercial fisheries have had negligible effects on Guam's economy (Rubinstein 2001, Allen and Bartram 2008). Fishing also provides a key source of protein, with households reporting that 28% of fish consumed were caught by family members or friends (Van Beukering et al. 2007). Fish is an especially important source of food for large cultural events such baptisms, weddings and village fiestas (Rubinstein 2001). Apart from their cultural and socioeconomic significance, reef-fish populations also play an important ecological role in enhancing the resilience of Guam's shallow coral reef ecosystems (McClanahan 1997, Mumby et al. 2007b, Mumby and Harborne 2010, Graham et al. 2011b, Graham et al. 2013).

Despite their ecological and socioeconomic importance, reef-associated fisheries have received little attention compared to pelagic fisheries (Sadovy 2005) and suitable reliable data are often scarce (Warren-Rhodes et al. 2003, Houk et al. 2012). Furthermore, reef fisheries tend to be considerably more complex than pelagic fisheries, with a wide variety of motivations and participants using multiple gears, each with its own selectivity and targeting multiple species, and with overlap in the species caught among gears (Dalzell 1996, Maypa et al. 2002, Kuster et al. 2005, McClanahan and Cinner 2008). Publications on the reef-fish fishery around Guam report a decline in fish populations since the 1980s (Burdick et al. 2008) and a low fish biomass and a scarcity of larger individuals (Porter et al. 2005, Brainard et al. 2012). Other studies showed that Guam has a low fishery yield compared to other Pacific islands (Dalzell 1996), with an 86% decline in fish catches over the last 50 years (Zeller et al. 2007) and a 70% reduction in catch-per-unit-effort (CPUE) from 1985 to 1998 (Amesbury and Hunter-Anderson 2003).

Furthermore it is reported that the iconic humphead wrasse (*Cheilinus undulates*) and bumphead parrotfish (*Bolbometopon muricatum*) are increasingly rare (Amesbury and Hunter-Anderson 2003, Fenner 2012, D. Burdick unpubl data). Fish catches showed a decrease in the mean size-at-capture through time reducing overall biomass, reproductive potential and ecosystem function (McIlwain et al. 2009, Houk et al. 2012, Lindfield et al. 2014). The data used in most of these publications included both boat and shore-based fishery catch statistics where boat-based fisheries include trolling for pelagic species and bottom fishing for deep water (> 30 m) species. Shallow reef-associated fish landings—the focus of this report—accounted for 26% of the total fish catch for the boat-based fishery from 1985 to 2013 (Guam's Division of Aquatic and Wildlife Resources [DAWR] boat-based fishery data). In the last three years with complete data (2010-2012), average annual reef-fish catches from shore-based fisheries were 63 metric tons (t) of which reef fish comprised 43.5% and bigeye scad 50.2% (Table). During the same time period, average annual catches from boat-based fisheries were 213 t, with pelagic fish comprising 76.1% of the catch composition and reef fish making up 13.8%. Even though reef-fish landings from shore-based fishing activities accounted for just 34% of the total (boat-based and shore-based combined) reef-fish landings, the shallow-reef fish populations exploited in the shore-based fishery are potentially very important for subsistence or cultural reasons. Interview data from the shore-based creel program reported that only one fisher sold the catch, on one occasion, in the period from 1985 to 2012 (DAWR data).

Table 5.1. Composition of catches from the boat-based fishery and shore-based fishery in Guam during 2010–2012. *Other* includes invertebrates and unknown. Data came from Guam's Division of Aquatic and Wildlife Resources and the Western Pacific Fisheries Information Network.

	Boat-based fishery		**Shore-based fishery**	
Species	**% of catches**	**average annual catches (kg)**	**% of catches**	**average annual catches (kg)**
reef fish	13.8%	53,982	43.5%	27,465
pelagics	76.1%	119,179	0.6%	395
bottom fish	3.0%	11,650	0.0%	5
bigeye scad	6.6%	25,770	50.2%	31,714
other	0.5%	1,949	5.7%	3,614
total	100.0%	212,530	100.0%	63,193

Stock size over time can be estimated from a CPUE time series and a gear-specific catchability coefficient. Usually it is assumed that catch rates are linearly related to stock biomass and that the catchability coefficient is constant (Haddon 2010). This approach requires that the CPUE data are from a representative sample of the fish populations, where the catch is taken in a consistent way by one or more fishing methods. In addressing federal management via annual catch limits (ACLs) the CPUE time series available from the DAWR creel surveys have been rejected as uninformative for reef fish stock assessment (Sabater and Kleiber, 2014). The CPUE data for taxa infrequently encountered by any gear type in the survey are not reliable, and this includes most reef fish except some carangids (Bak-Hospital, 2015). Nevertheless, this has not inhibited use of the creel survey data on reef fish for investigations of this fishery's history by other authors (e.g., Zeller et al. 2007, Lindfield et al. 2014). In the mid-1980s, DAWR adapted their initial creel surveys into the current, more comprehensive creel survey methodology, which includes both boat-based fisheries and shore-based fisheries (Hensley and Sherwood 1993, Bak 2012). These survey results include effort and landings by gear type, location, and time of day and report catches at a species or family level (Hensley and Sherwood 1993).

Using the shore-based creel surveys from 1985–2012, we evaluated past (1985–1990) and present (2007–2012) fishery characteristics in terms of catch composition and effort per gear type to examine possible shifts in fishing activities and CPUE. We estimate the relationship between CPUE and stock biomass by incorporating a fishery-independent estimate of biomass obtained in 2011. While bearing in mind the limitations of the CPUE data for use in stock assessment, we then estimate the historical trend in reef-fish biomass relative to present stock size to see if these stocks appear to have been decreasing as indicated by previous studies.

5.2 Methods

5.2.1 Categorization of species into functional groups

We analyzed records in the catch database of the shore-based creel survey program for Guam (DAWR data; see metadata at https://inport.nmfs.noaa.gov/inport/item/5621). A total of 580 species or families appeared in the records. For some taxa there were very little data so we categorized them into groups based on their taxonomy, ecological function and importance to fisheries:

- 'baitfish' which includes all sardine-like species that periodically come to nearshore waters in large numbers (e.g., *Selar crumenophthalmus*, *Ellochelon vaigiensis*, *Gerres acinaces*, *Crenimugil crenilabis*);
- 'invertebrates' including crabs, lobsters, sea cucumbers, molluscs, octopus, urchins, and clams. The top shell (*Trochus niloticus*) was the dominant component in the invertebrate total catch as a result of very high landings in 1985 and 1991 (30 and 16 t respectively);
- 'non-reef' including the species that are pelagic (e.g., tuna), deep-water (e.g.,*Lethrinus rubrioperculatus*), freshwater (e.g., *Kuhlia rupestris*) or associated with sandy bottoms (e.g., *Moolgarda engeli*);
- 'macroalgae'; and,
- all reef-associated species that we further categorized in functional groups based on their ecological role, namely:
    - 'planktivores', including soldierfish (Holocentridae), some unicornfishes (e.g., *Naso annulatus*), chromises (*Chromis* sp), cardinalfish (*Apogon* sp)
    - 'corallivores', mostly butterflyfishes (*Chaetodon* sp)
    - 'detritivores', mostly surgeonfish (*Ctenochaetus* sp)

- ‘invertebrate feeders’ separated into exploited species (e.g., emperors *Lethrinus* sp., snappers *Lutjanus* sp., goatfish Mullidae, wrasses *Cheilinus* sp.) and non-exploited species (e.g., porcupinefish *Diodon* sp., file fish *Aluterus* sp.)
- ‘herbivore-browsers’, separated into exploited species (e.g., chubs *Kyphosus* sp., rabbitfish *Siganus* sp., unicornfishes *Naso unicornis*) and non-exploited species (e.g., milkfish *Chanos chanos*),
- ‘herbivore-grazers’, separated into exploited species (surgeonfishes *Acanthurus* sp.) and non-exploited species (sergeants *Abudefduf* sp)
- ‘herbivore-scrapers’, small-bodies parrotfishes (*Scarus* sp), all exploited species
- ‘herbivore-excavators’, large-bodied parrotfishes (*Chlorurus* sp, *Scarus rubroviolaceus*), all exploited species
- ‘bumphead parrotfish’, *Bolbometopon muricatum,* a exploited species
- ‘humphead wrasse’, *Cheilinus undulates*, a exploited species
- ‘benthic piscivores’, separated into exploited species (e.g., groupers *Epinephelus* sp.) and non- exploited species (e.g., moray eels *Gymnothorax* sp)
- ‘mid-water piscivores’, including mackerel (*Scomberoides* sp), needlefish (Belonidae), cornetfish (*Fistularia commersoni*), all exploited species
- ‘roving piscivores’, including jacks (Carangidae), barracudas (*Sphyraena* sp), all exploited species
- ‘rays’, stingrays, all exploited species
- ‘sharks’, including reef associated sharks (e.g., blacktip reef shark *Carcharhinus melanopterus*, grey reef shark *C. amblyrhynchos*, and whitetip reef shark *Triaenodon obesus*), all exploited species.

5.2.3 Guam creel inshore fishery survey program – collection of catch and effort data

The shore-based surveys of DAWR are designed to capture information on effort and catches of all shore-based fishing activities including non-motorized boat fishing launched from the shore-line (PIFSC 2015). There are two components in the program: (1) participation surveys to collect data on the type of fishing activities observed (effort data), and (2) fisher interviews to collect data on the duration of the fishing activities and the numbers and sizes of fish caught (catch and effort data). Guam has been divided into 92 fishing locations that are grouped into four coastal regions (Fig. 5.1):

- Region I - the northwestern portion of Guam from Gun Beach to Adelup (sites 1–11).
- Region II - the southwestern portion of Guam from Adelup to Agat (sites 12–34 excluding inaccessible sites 35–41).
- Region III - the central-eastern to southern portion of Guam from Pago Bay to Merizo (sites 42–71 excluding inaccessible sites 57–60).
- Region IV - the northern part of Guam, which is restricted to access (military base; sites 72–92).

Survey days were randomly selected twice per month and participation surveys were conducted between 5:30 am and midnight in the first three regions (Bak 2012). Interviews were conducted 4 times per month, once in regions 1 and 2 and twice (one week day and one weekend) in region 3. Data from restricted areas were collected through aerial surveys conducted on the same two days as the participation surveys. All aerial surveys began and ended at the same place (site #11 Adelup in Fig. 5.1). They began at a random time between 8 am and noon and were conducted for approximately 2 hours (Bak 2012). Effort was recorded as hours fishing per gear type and catch was recorded as the number and weights of fishes caught per fishing hour per gear type (PIFSC 2015). For our analyses we defined effort in units of gear-hours (gh), e.g., three fishing rods (hook and lines) used by a fisher for 2 hours corresponds to 6 gear-hours.

When comparing any fishery-derived value, we can only compare reported catches, and reporting was on a voluntary basis. Effort is mostly based on the visual participation surveys although details on the actual hours of fishing depend on the interviews. DAWR attempted to interview some fishers for each type of gear seen during the participation surveys. However, interviewers were not always able to collect information on all types of gear for varying reasons (Appendix C). For example, in recent years, scuba-spear fishers have shifted efforts from day-time fishing to night-time fishing, making it very difficult to acquire interviews (B. Tibbatts pers. comm. 25 Nov. 2013). Snorkel-spear, gill net, surround net and other gears are all inadequately interviewed by the DAWR creel surveys, even though participation counts indicate that spear fishing represents one of the largest components of the fishery in terms of fishing effort (K. Lowe, PIFSC pers. comm. 27 Nov., 2013, Bak-Hospital, 2015). Unfortunately, the number of snorkel-spear interviews has declined from an average of 30 a year in 1985–90 to an average of below 8 interviews a year in 2007–12 (Appendix C). Even for gear types with the most interviews, such as hook and line which had CPUE sample sizes of over 100 interviews per year in most years of the survey, only a few roving carnivores (carangids) and rabbitfish were encountered in CPUE interviews more than a dozen times per year from 2007–12 (Bak-Hospital, 2015). Because collecting data on CPUE for most of the taxa in most of the gears was difficult and infrequent, results dependent on the CPUE statistics are, at best, indicative relative measures and are presented by grouping families.

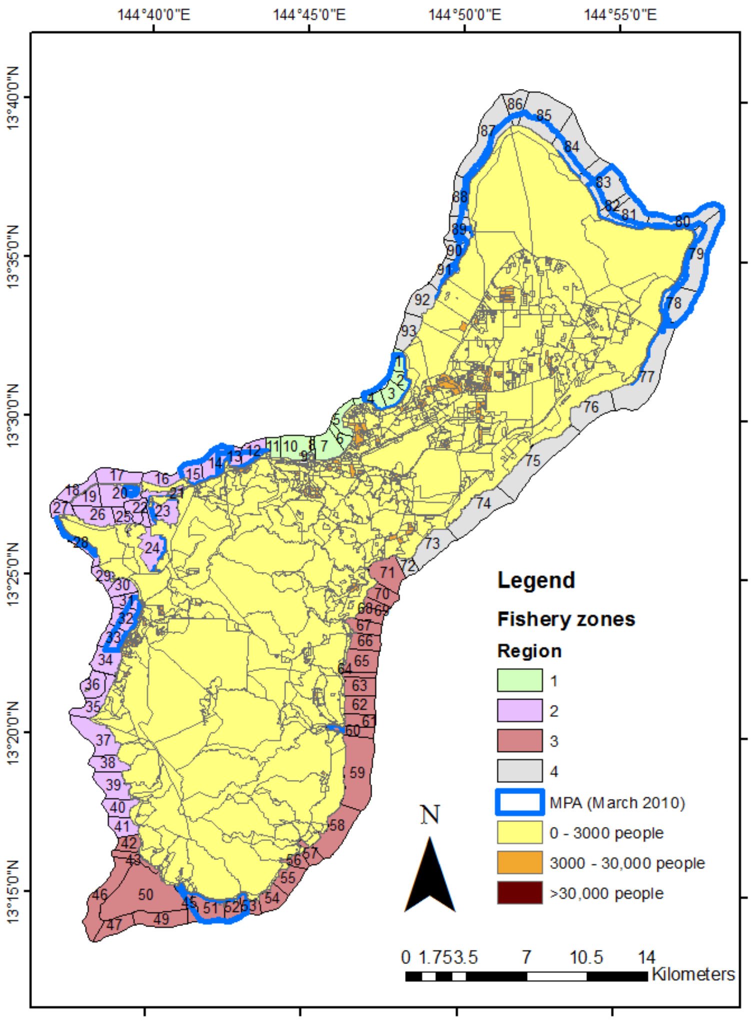


Figure 5.1. Guam shore-based creel survey fishing reporting regions (fisheries zones file from DAWR).

5.2.3 Estimates of total catch, total effort and CPUE

The staff of NOAA’s Western Pacific Fisheries Information Network (WPacFIN) program provides assistance to their partners in DAWR with fishery statistics and developed an expansion algorithm to extrapolate results of the shore-based sample surveys into estimates of island-wide catch and effort. When comparing the fishery characteristics of the late 1980s with recent years, we used these WPacFIN estimates of aggregate effort and catch to examine possible shifts in fishing activities and catch composition. WPacFIN estimated annual fishing effort (measured in gear-hours [gh]) per gear type per region by multiplying the total number of fishing gear-hours observed in the participation survey by two correction factors (1) the ratio of the number of days in a year to a total scheduled survey days and (2) the number of available fishing hours in the morning and in the evening (Bak 2012). WPacFIN estimated total annual catch per gear per region as the product of total annual effort and the gear- and region-specific average CPUE, the latter derived within each stratum as total sampled catch divided by total sampled effort. The estimated total catch per species within each stratum was calculated by multiplying aggregate annual catch by the ratio of that particular species in the catch from the sample surveys (Bak 2012). Missing CPUE data was substituted with a moving average of the previous 10 years of CPUE data.

When we discuss gear-specific CPUE time series, compare CPUE between the two 6-year time periods, estimate gear-specific catchability, and reconstruct biomass we use the sample interview CPUE data.

5.2.5 Fishery independent surveys – calculation of biomass (B)

In 2011, the Coral Reef Ecosystem Division (CRED) of NOAA's Pacific Islands Fisheries Science Center (PIFSC) conducted an intensive short-term stationary point-count survey (133 sample sites) of shallow (< 30 m), hard-bottom, coral reef areas around Guam. Methods are described in detail in Williams et al. (2012) and briefly outlined here. Fish abundance and size distribution data came from random surveys stratified into 3 depth strata (< 6 m; 6–18 m; and 18-30 m). As roving apex predators, such as sharks and jacks, are generally not well sampled by divers in small-area surveys, information on abundance and size distribution of these species came from towed-diver surveys conducted around Guam in 2007, 2009 and 2011 by CRED (Richards et al. 2011). Length estimates of fish from visual censuses were converted to weight using the allometric length-weight conversion: $W = a*TL^b$, where parameters a and b are constants, TL is total length in mm, and W is wet weight in grams. Length-weight parameters came from published sources, PIFSC data and FishBase (www.fishbase.org). In cases where length-weight information did not exist for a given species, parameters from congeners were used. For each taxon, trophic classification was based on diet information from FishBase. Using biomass density from diver surveys, and known areas of habitat from CRED GIS maps (described in Williams et al. 2012), we estimated biomass per functional group and for all fishes combined; these were minimum estimates as cryptic and nocturnal fishes are excluded from the day-time visual surveys.

5.2.6 Estimation of catchability and reconstructing historical fish biomass

We used the fishery-independent estimate of biomass in 2011, time series of annual CPUE by gear type, and estimates of catchability by gear type to reconstruct a time series of reef-fish biomass for 1985–2012. Nine gear types are differentiated in the shore-based surveys (Table 5.1). The gear type 'hooks and gaffs' was mainly used to catch octopus (98% of hook and gaff landings for period 1985–2012) and 'other' mostly includes gleaning for invertebrates and algae (60% and 16% of total landings per respective gear type; DAWR data) (Hensley and Sherwood 1993). For the historical reconstruction of the reef-fish biomass we excluded the gear types 'hooks and gaffs' and 'other' from the analyses. Additionally, cast nets were primarily used to catch juvenile fish (rabbitfish, goatfish, jacks) that can be hyper abundant in shallow (generally sandy) bays, which are habitats that were not sampled in the fishery-independent visual surveys; therefore, we also excluded cast nets in the reconstruction of historical biomass. Appendix D tabulates the number of times fish groups (as defined in methods) exploited by fishers were recorded per gear type for 3-year time periods (data aggregated over years to preserve fishers' confidentiality).

Fishing is reported per region per day type (i.e., weekday or weekend) so first we compared annual average CPUE by region and day type using a Welch two sample t-test for cases in which we had at least 6 years of CPUE data with at least 3 observations per year. For region 4 we had < 3 observations per gear type per day type in all years so we could not make meaningful comparisons between weekday and weekend day types for that region. Based on the results of these tests (see results section) we decided to aggregate CPUE data over regions and day types for further analyses. Even with such treatment, for some gear types interview data were sparse especially for surround net fishing, scuba spearfishing and drag net fishing (Appendix C). Moreover, for drag net and scuba spearfishing, there were some missing values–we calculated the CPUE for the missing data as the average of three previous years (Appendix C).

We based our estimation (reconstruction) of historical relative fish biomass on the assumption that CPUE (catch, C, divided by effort, E) or I is linearly related to biomass (B) in year t:

$$C_t/E_t = I_t = q * B_t \qquad \text{Eq. 1}$$

We further assumed that the gear-specific catchability coefficient, q, which likely depends on the experience of the fisher and other factors, i.e., different fishing operations can extract a different portion of the biomass, was constant. We also assumed that the observational errors of CPUE (I) are lognormal, multiplicative, and have a constant variance. Although these conditions are unlikely, given the infrequency of actual interview data for many taxa and strata, with the resulting high incidence of zeros and Poisson-like distributions with outliers, the assumptions were adopted to allow a simple approximation. If there are n years in the analysis, then the best estimate of the constant q is the geometric average of the time series of ratios of CPUE and biomass, I_t/B_t , and can be calculated with (Haddon 2010):

$$q = e^{\frac{1}{n}\sum Ln\left(\frac{I_t}{B_t}\right)} \qquad \text{Eq. 2}$$

This method is well established for pelagic fisheries (Haddon 2010) and we further assumed that it is applicable for the complex reef fishery when we parsed out catches and effort per gear type. We used the fishery-dependent statistics to estimate I per gear type per year and fishery-independent data to estimate biomass (as detailed above). However, we only have reliable biomass estimates for 2011. Since we wanted a n of at least 3, we assumed that the biomass was the same in the years around 2011 given by the 2011 SPC results. For each gear type, we derived smoothed estimates of q in accordance with equation 2 with n=3, I equal to the gear-specific annual CPUE values for 2010–2012 and B equal to the summed biomass of functional groups exploited by the gear type. Information on which functional groups were taken by the various gear types was derived from the catch composition of total landings from 1985–2012 (e.g., over this time span 23% of the browsers [e.g., unicornfish] and 32% of the roving piscivores [jacks] were caught by gill net).

To reconstruct the annual total biomass for the period 1985–2012, we divided the gear-specific CPUE for each year by the estimated gear-specific catchability q using equation 1 rewritten as $B_t = I_t / q$. Within each year we then calculated the reconstructed biomass for each functional group by multiplying the annual total biomass estimate by the 2011 species composition. For example, in 1985 the total biomass was estimated at 10,025 t, and excavators (large-bodied parrotfish) comprised 1.3% of the species composition in 2011 so the biomass of excavators in 1985 was estimated at 10,025 * 0.013 = 130 t. It is important to note, however, that the 2011 stock size estimate is conservative since it is based on only day-time visual surveys; nocturnal and cryptic species are undercounted by those surveys. Hence, these results can be treated as minimal estimates of biomass but are suitable to indicate trends in relative fish stock size over time, assuming the catchabilities have been constant.

5.3 Results

5.3.1 Comparing total catch, effort, CPUE between the past (1985–1990) and the present (2007–2012)

Examining the total estimated catch and effort data calculated with the expansion algorithm and including all gear types, showed that during two 6-yr time periods, 1985–1990 and 2007–2012, separated by a 17-yr interval, hook and line fishing was the most frequently used gear type in terms of effort, accounting for 59% of total estimated annual effort in the past and 71% in the recent time period (Table 5.2). Fishing with cast nets (which we did include in this comparison but excluded in our analyses of historical trends in reef-fish biomass) was the second most used gear type, accounting for ~14% of total annual estimated effort in both time periods. All other gear types were reported less often in recent years with declines in fishing effort ranging from 16% for drag net to 87% for hook and gaff (Table 5.2). Because hook and line fishing effort increased by 14% in the recent time period, the overall reported fishing effort was nearly the same in the two periods: an annual mean 217,420 gear hours for 1985–1990 vs. an annual mean 205,850 gear hours for 2007–2012.

Reported catches, however, were considerably higher in the 1985–1990 time period, at an estimated mean annual total catch of 100 t, compared to the 2007–2012 time period when they averaged 36 t (Fig. 5.2, Table 5.2). In comparing these two time periods, most noteworthy are the 74% decrease in catches for cast net fishing despite little change in effort and a 27% decrease in the hook and line fishing catches despite a 14% increase in effort. The largest decline in catches was for spearfishing, where reported catches of snorkel-spearfishing dropped 87% (reported effort declined by 36%) and for scuba spearfishing with a drop of 94% (reported effort declined by 90%). However, the decline in scuba-spearfishing effort is likely an artifact of the change in recent years of scuba spearfishing switching to a night time activity (B. Tibbatts, DAWR, 25 Nov. 2013), meaning that it is not recorded during shoreline surveys conducted in the morning (6:30 AM till noon) and only sporadically during the evening shift (7 PM till midnight). Similarly, recordings of cast net fishing are also difficult to obtain because of the intermittent nature of that fishery.

Hook and line fishing was the most represented gear type in the catch and effort records and, therefore, we assumed the most reliable. Using the fishery data for this gear type only showed relatively stable overall landings albeit with large annual fluctuations (Fig. 5.3). However, when we removed the baitfish landings, the landings of all other species showed a slow downward trend. The mean annual CPUE (based on the un-expanded interview data) for hook and line fishing varied in correspondence with the large fluctuation in landings of bait fishes but overall decreased between the two time periods with an annual mean of 0.15 kg/gear-hour (SE 0.02) for 1985–1990 and 0.08 kg/gear-hour (SE 0.02) for 2007–2012, a decrease of 49% (Table 5.2; Fig. 5.3). We used Welsh's two-sample t-test to compare mean CPUE between time periods. Where comparisons between the two time periods were meaningful (i.e., where we had more than 3 interviews per year per gear type), the CPUE was significantly lower in the later time period except for the ‘other’ method, i.e., reef gleaning (Table 5.2). Mean annual CPUE for other gear types are shown in Appendix C.

Table 5.2. Comparison of annual mean fishing effort, catch and catch-per-unit-effort (CPUE) between 1985–1990 and 2007–2012. Catch and effort are based on expanded data. CPUE (with the standard error in parentheses) is based on un-expanded interview data (not ratio of tabled catch and effort). *P*-value is for Welch’s two-sample *t*-test (allowing unequal variances) comparing CPUE between the two periods. NA represents less than 3 interviews per year per gear type (see Appendix C). Data from DAWR and WPacFIN.

	1985–1990			**2007–2012**			
Gear types	**mean effort gear-hours (% of total)**	**mean catch kg**	**CPUE (SE) kg/gear-hour**	**mean effort gear-hours (% of total)**	**mean catch kg**	**CPUE (SE) kg/gear-hour**	***P* value**
Hook & Line	127,219 (58.5%)	22,698	0.15 (0.02)	145,309 (70.6%)	16,589	0.08 (0.02)	0.015
Cast Net	31,913 (14.7%)	15,849	0.36 (0.04)	29,555 (14.4%)	4,143	0.10 (0.02)	< 0.001
Gill Net	22,647 (10.4%)	27,532	1.25 (0.11)	10,918 (5.3%)	10,022	0.56 (0.18)	0.01
Surround Net	1,470 (0.7%)	4,113	1.36 (0.67)	552 (0.3%)	417	0.67 (0.08)	NA
Snorkel Spear*	18,453 (2.9%)	16,508	0.76 (0.15)	11,736 (5.7%)	2,148	0.19 (0.06)	0.013
Scuba Spear*	1,553 (0.7%)	988	0.75 (0.10)	155 (0.1%)	58	0.34 (0.04)	NA
Hooks & Gaffs	6,396 (2.9%)	2,227	0.30 (0.05)	5,554 (2.7%)	2,134	0.36 (0.16)	NA
Drag Net	901 (0.4%)	1,378	1.18 (0.53)	141 (0.1%)	133	0.97 (0.35)	NA
Other Methods	6,868 (3.2%)	8,469	0.55 (0.29)	1,930 (0.9%)	181	0.07 (0.01)	0.10
Total	*217,420*	*99,761*		*205,850*	*35,825*		

*actual values for 2007–2012 higher as most spear fishing is now conducted at night and not captured in interviews

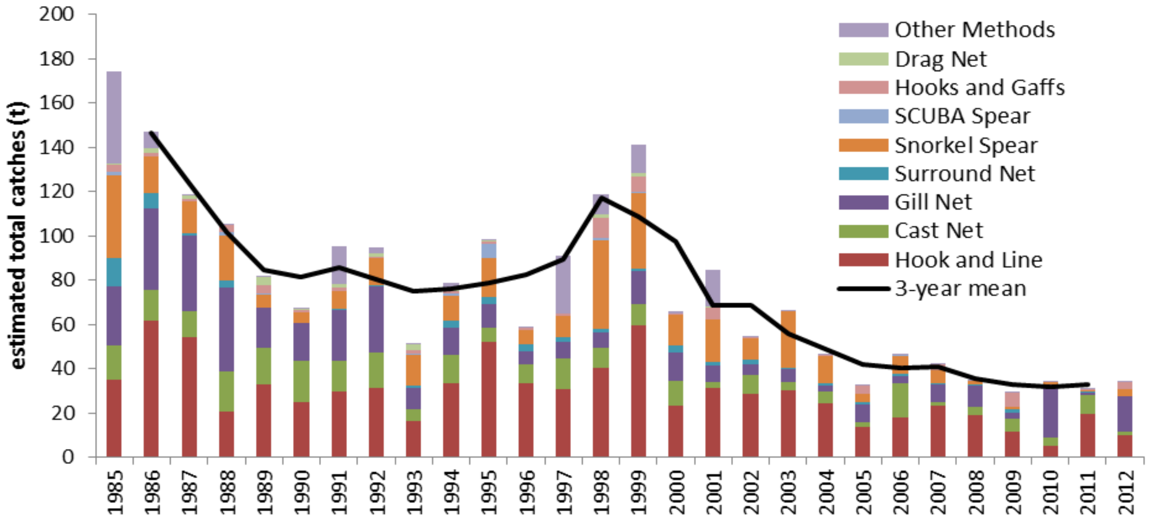


Figure 5.2. Time series of shore-based fishery landings in metric tons (t) per gear type based on data as provided by WPacFIN-expanded data. Pelagic baitfish landings are excluded from the hook and line catches. Black line represents 3-year mean of total catch.

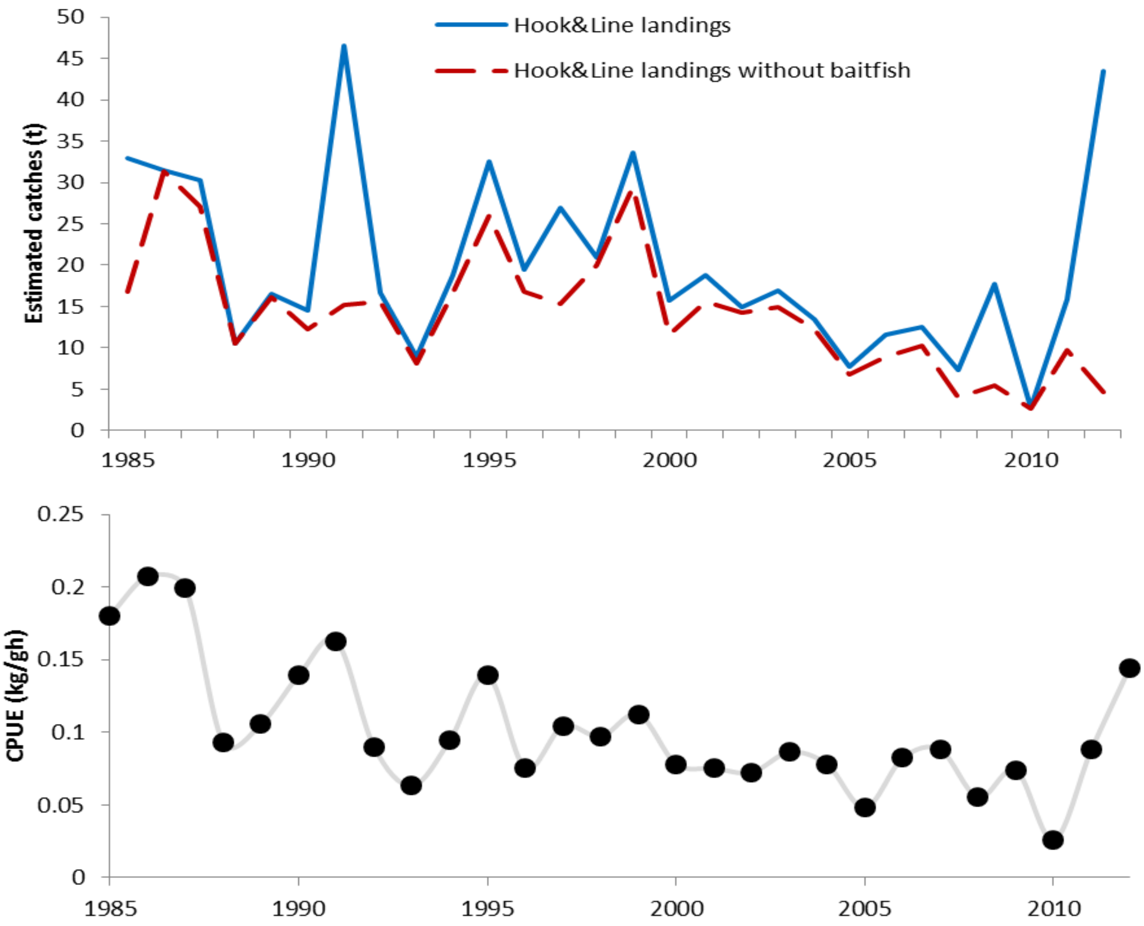


Figure 5.3. Time series of (*top panel*) shore-based hook and line fishery landings based on data as provided by WPacFIN-expanded data and (*bottom panel*) CPUE based on data from sample surveys. Pelagic baitfish landings are excluded from the red dashed line in top panel.

5.3.2 Species composition of landings

For each of the functional groups we calculated the relative contribution to the annual catch (Table 5.3). In all years, browsers (especially unicornfishes and rabbitfish) and invertebrate feeders (especially goatfish and emperors) made up about 50% of the total catches (Table 5.3). Comparing late 1980s catch data with recent years revealed a shift from a catch with the largest group (31%) of target browsers to a composition with 34% of pelagic bait fishes (e.g., bigeye scad, *Selar crumenophthalmus*). In 2012, baitfish made up 73% of the total catches.

Table 5.3. Relative contributions of functional groups to the total catch per year. Numbers in red indicate a contribution of > 10% to the total catch.

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Baitfish	16.4%	6.8%	7.2%	9.1%	9.8%	15.8%	42.2%	12.0%	9.9%	10.1%	13.9%	10.7%	23.6%	3.7%	6.5%
Invertebrates	22.0%	4.4%	3.1%	3.6%	6.8%	5.1%	12.2%	6.0%	8.9%	9.2%	4.8%	2.8%	12.8%	15.4%	9.2%
Non-reef	1.8%	5.2%	7.9%	2.1%	0.8%	1.8%	0.5%	1.8%	2.8%	2.5%	1.6%	0.8%	2.5%	5.3%	2.4%
Macroalgae	3.2%	3.2%	0.1%	0.1%	0.0%	0.0%	0.5%	0.1%	0.3%	0.8%	0.3%	0.0%	11.6%	3.4%	6.6%
Fish Invertivores	15.1%	20.3%	19.7%	24.1%	27.4%	19.0%	9.5%	21.8%	23.8%	18.4%	19.8%	22.6%	13.8%	18.9%	12.5%
Fish Planktivores	1.9%	0.7%	1.1%	0.7%	2.2%	1.5%	0.6%	1.2%	5.2%	1.8%	2.2%	2.5%	1.4%	3.0%	1.1%
Fish Corallivores	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%
Fish Detritivores	0.1%	0.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.2%	0.4%	0.3%	0.1%	0.1%	0.2%	0.1%
Fish Browsers	22.4%	30.8%	39.0%	40.4%	34.5%	26.3%	16.0%	35.8%	17.0%	29.4%	35.0%	36.2%	19.6%	30.7%	29.0%
Fish Grazers	3.9%	3.9%	9.3%	8.8%	7.7%	12.3%	3.9%	9.6%	7.4%	6.3%	7.6%	10.6%	4.4%	4.4%	4.4%
Fish Scrapers	1.3%	1.2%	0.5%	1.1%	0.2%	0.5%	2.5%	1.7%	2.2%	2.2%	1.7%	1.7%	1.6%	1.5%	4.3%
Fish Excavators	1.8%	0.0%	0.0%	0.2%	0.0%	0.5%	0.9%	0.9%	0.8%	0.7%	1.6%	1.0%	0.4%	2.7%	1.2%
Bumphead Parrotfish	0.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Humphead Wrasse	0.3%	0.1%	0.2%	0.6%	1.1%	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.5%	0.0%	0.0%	0.0%
Fish Benthic Piscivores	1.7%	2.5%	5.2%	2.2%	1.1%	5.4%	2.6%	3.2%	8.1%	4.5%	4.5%	2.3%	2.4%	4.0%	4.4%
Fish Mid-water Piscivores	3.0%	3.0%	0.0%	1.6%	3.0%	2.8%	1.6%	1.1%	2.2%	3.2%	2.1%	2.2%	0.2%	0.5%	3.4%
Fish Roving Piscivores	4.7%	3.3%	6.8%	5.2%	4.8%	8.9%	7.1%	4.3%	9.6%	3.6%	3.3%	5.9%	5.4%	6.0%	10.5%
Rays	0.0%	0.1%	0.0%	0.2%	0.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.0%
Sharks	0.0%	14.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.4%	1.6%	7.0%	1.4%	0.1%	0.4%	0.2%	4.2%

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Baitfish	16.5%	8.3%	5.5%	5.9%	6.0%	10.7%	11.2%	10.4%	21.1%	47.5%	3.4%	30.1%	72.6%
Invertebrates	6.1%	17.4%	3.8%	14.4%	6.9%	20.1%	5.5%	7.8%	2.2%	13.7%	2.9%	1.0%	4.8%
Non-reef	2.0%	1.9%	1.2%	5.5%	13.1%	3.5%	2.2%	0.4%	2.3%	2.6%	5.0%	0.6%	2.8%
Macroalgae	0.1%	10.3%	0.3%	0.2%	0.1%	0.0%	0.1%	0.1%	0.1%	0.1%	0.3%	0.1%	0.0%
Fish Invertivores	19.5%	19.7%	20.8%	17.8%	10.0%	20.5%	10.8%	16.2%	7.9%	6.5%	10.2%	15.3%	6.1%
Fish Planktivores	2.0%	0.8%	1.0%	0.9%	3.2%	0.5%	0.7%	0.3%	0.6%	1.4%	1.0%	0.2%	0.2%
Fish Corallivores	0.6%	0.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	3.9%
Fish Detritivores	0.3%	2.2%	0.0%	0.0%	0.0%	0.1%	0.3%	2.7%	0.0%	0.0%	0.0%	0.0%	0.0%
Fish Browsers	30.5%	16.8%	35.0%	26.1%	22.4%	12.1%	35.9%	25.7%	21.1%	7.4%	46.1%	10.3%	2.9%
Fish Grazers	7.8%	5.1%	5.6%	10.3%	9.8%	8.2%	8.4%	5.5%	8.7%	6.9%	20.3%	6.8%	0.3%
Fish Scrapers	1.6%	0.6%	1.1%	3.4%	0.9%	2.1%	2.6%	0.9%	4.8%	0.6%	1.3%	1.7%	0.5%
Fish Excavators	0.8%	0.7%	1.0%	3.5%	1.4%	0.5%	0.3%	0.1%	0.4%	0.2%	0.1%	0.6%	0.0%
Bumphead Parrotfish	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Humphead Wrasse	0.1%	0.0%	0.0%	0.2%	0.0%	0.0%	0.1%	0.4%	0.0%	0.0%	0.0%	0.0%	0.1%
Fish Benthic Piscivores	5.4%	2.3%	6.1%	3.1%	4.0%	3.5%	5.4%	6.4%	2.2%	1.2%	0.5%	0.8%	0.5%
Fish Mid-water Piscivores	1.3%	2.9%	1.3%	1.0%	2.8%	0.8%	0.9%	0.2%	1.8%	0.6%	0.9%	1.6%	0.0%
Fish Roving Piscivores	5.4%	10.1%	13.6%	6.0%	19.4%	17.2%	9.2%	22.9%	24.2%	11.3%	8.1%	30.9%	5.2%
Rays	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	2.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Sharks	0.1%	0.7%	3.5%	1.8%	0.0%	0.3%	4.3%	0.1%	2.4%	0.0%	0.0%	0.0%	0.0%

5.3.3 Reconstructing fish biomass per functional group

Using the sample interview data, we compared the CPUE between weekdays and weekends. Hook and line fishing in region 1 and 2 (Fig. 5.1) showed a significant difference between weekday and weekend fishing (Appendix E). Comparing CPUE per day type for all regions combined, cast net fishing, gill net fishing and snorkel spear fishing did not show a significant difference at p=0.05 between weekday and weekend. There were not enough data to compare weekday vs weekend CPUE for the remaining gear type fisheries. Since we are interested in daily fisheries, we pooled the data from day types and used ANOVA to look for differences between regions for hook and line fishing (the only gear type with enough information to conduct an ANOVA). There was no significant difference between regions (Appendix E). Since we focus on island-wide CPUE, data was pooled up to island level.

Including the data for all regions and day types we calculated the catchability coefficient of each gear type (Table 5.4) and the total reconstructed relative biomass (Fig. 5.4). There appeared to be a steep downward trend in fish biomass from 1985 to around late-1990s during which biomass almost halved, and from then onwards biomass appeared to level off for a decade before declining again more recently (Fig. 5.4).

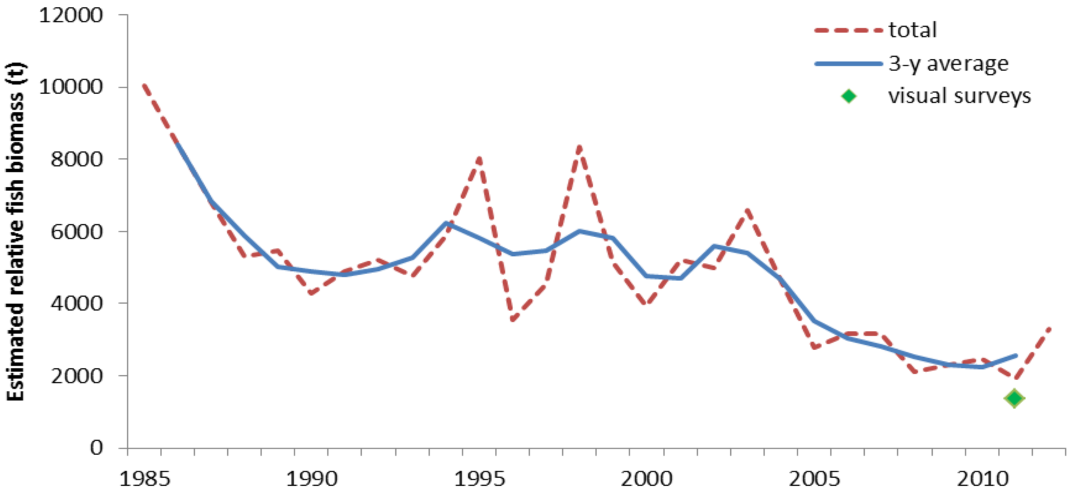


Figure 5.4. Reconstructed total reef fish biomass relative to 2011, excluding pelagic species and baitfish, based on annual catch composition per gear type and assuming a constant catchability coefficient for each gear type. The green diamond is the estimated biomass for 2011 computed by multiplying biomass density from CRED surveys by hard-bottom 0–30-m reef area (71 km^2) around Guam.

Table 5.4. Mean 2010–2012 CPUE (data from DAWR shore-based creel surveys) and estimated biomass in 2011 (data from visual surveys conducted by CRED) were used to calculate the catchability coefficient *q* for each gear type. Cast net data were excluded from the analysis (see "Methods").

	CPUE (kg/gh)			**Biomass**	***q***
gear type	**2010**	**2011**	**2012**	**(t)**	**(1000 gh)$^{-1}$**
Drag net	0.99	0.91	0.31	157	0.0042
Gill net	1.26	0.09	0.77	386	0.0012
Hook and Line	0.03	0.09	0.14	324	0.0002
Scuba	0.37	0.40	0.24	544	0.0006
Snorkel Spear	0.06	0.06	0.38	386	0.0003
Surround net	0.51	0.93	0.51	220	0.0028

Based on the catchability coefficient and the total reconstructed fish biomass (Fig. 5.4), we were able to estimate relative biomass of the functional groups targeted in the shore-based reef fisheries (Fig. 5.5).

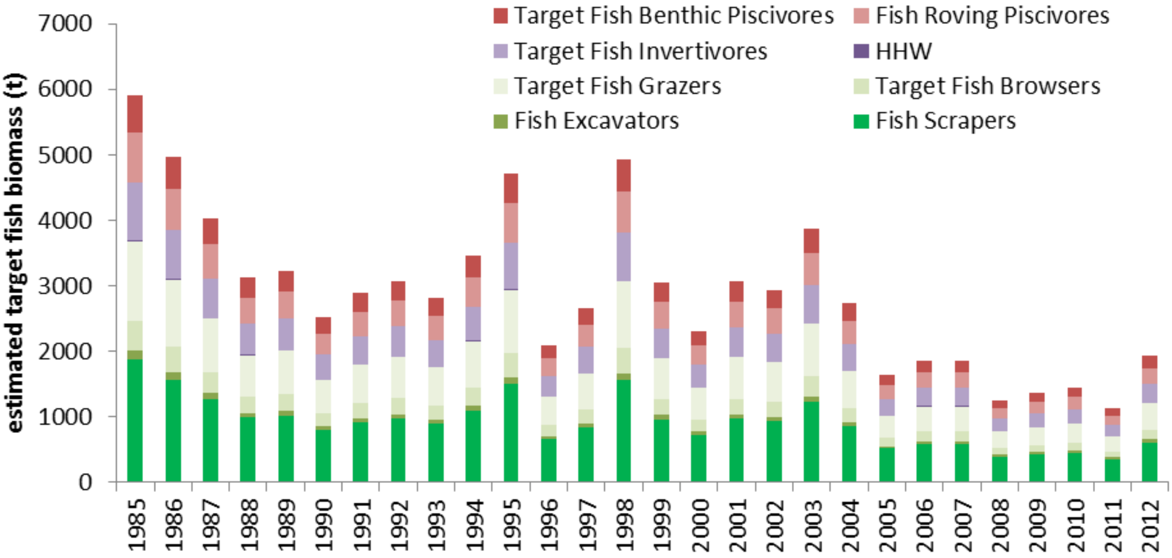


Figure 5. Reconstruction of biomass relative to 2011 of target fish groups based on a constant gear catchability coefficient per gear type and the reconstructed biomass from CPUE data and the 2011 fishery-independent surveys. CPUE data from sampled surveys conducted by DAWR. HHW is humphead wrasse.

5.4 Discussion

Calculating the CPUE for a multi-species, multi-gear reef fishery is not straight forward. Furthermore, there are many factors influencing the decision of reef fishers about when to fish (tide, rainfall, wind), where to fish (bay, reef edge, shore line) and which gear to use (speargun, hook and line, small meshed gillnet, larger meshed gillnet). As a result, the selectivity or catchability of a specific gear type can change and accurately capturing all these fishers in the surveys has proven difficult. Cast net and spearfishing were not captured well so the WPacFIN-expanded data are not an accurate representation of the total catch and effort.

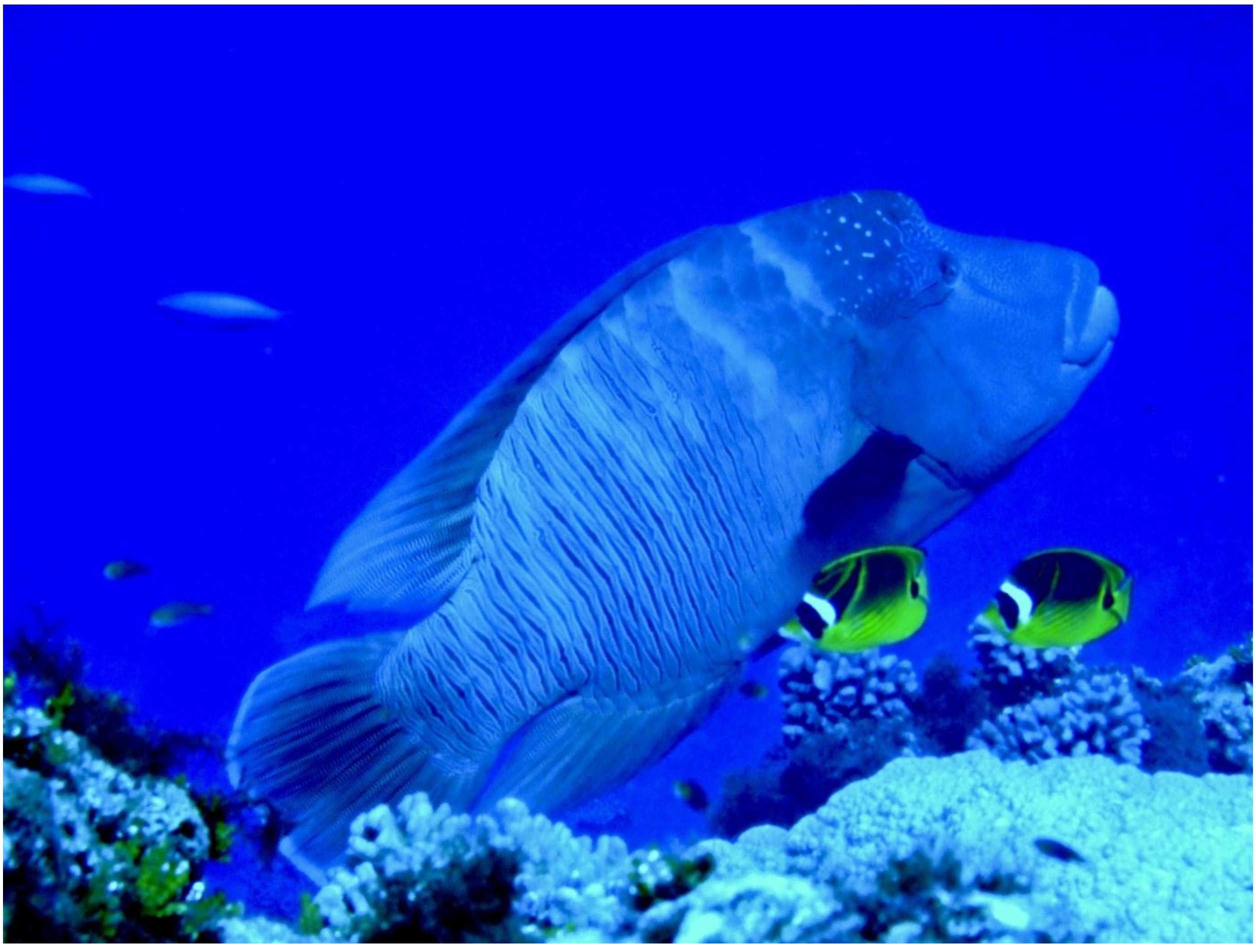
When just using the hook and line fishery data as an indication for the overall fishery, the trend shows a decrease in catches and CPUE over the 1985–2012 time period ($p<0.1$) (Fig. 3). These CPUE values (0.18 kg/line-hour for 1985–1990 and 0.11 kg/line-hour for 2007–2012) are lower than the CPUE recorded in the early 1980s for the hook and line fishery for shallow reef fish species which had a mean of 0.55 kg/line-hour (Katnik 1982 cited in Dalzell et al. 1996) and could indicate this downward trend started earlier.

Coral reef fishery yields worldwide range from 0.2–44 t/km^2/y (Dalzell 1996), but comparison among areas is confounded by differences in effort and in the species included in the catch data (e.g., with or without invertebrates or seasonal runs of juveniles), as well as in the assumptions about what constitutes ‘reef area’. Yields on Guam dropped from 1.30 t/km^2/y in the 1985–1990 time period to 0.58 t/km^2/y in the 2007–2012 time period when looking at the total catches of the expanded data of the shore-based fishery and using 95 km^2 as the 0–30 m reef area around Guam (NOAA Habitat Map including sandy areas, NOAA NCCOS 2005). When we only look at the reef-associated fishes (i.e., excluding all pelagics, non-reef associated fish and invertebrates), yield was 1.59 t/km^2/y and 0.74 t/km^2/y respectively, using 71 km^2 for hard-bottom reef area around Guam (NOAA NCCOS 2005); both estimates are at the lower end of the published global ranges.

Spear fishing is one gear type inadequately captured by the creel survey program. Main target species for spear fishers are surgeonfishes and parrotfishes (Appendix D). Parrotfishes can grow large, sleep in groups in shallow water, and spawn in large aggregations making them relatively easy targets for fishers and therefore vulnerable to depletion (Comeros-Raynal et al. 2012). From 1986 onwards, the bumphead parrotfish was absent from inshore catch records and since 2001 also from boat-based catch records (DAWR data) and could now be locally functionally extinct (Fenner 2012). Parrotfishes were caught by hook and line fishing (33%) and by spearfishing (40%) with landings slightly lower in recent years. However, as spearfishing is not adequately captured in the creel shore-based survey program, the CPUE data used to estimate biomass is suspect, and actual landings could be much larger. A study including parrotfish landings from the shore- and boat-based fishery showed a decrease in size of fish caught (Houk et al. 2012). Assuming there has been no upward trend in recruitment and that size composition of the catch reflects size structure of the population, this indicates a reduction in adult biomass and reproductive potential of the stock. Reduced biomass has ecological consequences as parrotfishes are important grazers and bioeroders (McIlwain et al. 2009, Lindfield et al. 2014). Spearfishing can have rapid and substantial negative effects on target fish populations (Meyer 2007, Lloret et al. 2008, Frisch et al. 2012). Pooling data over longer intervals than a year might improve the statistical power of the existing data to answer questions about the early and later period of the survey. Improving the shore-based creel survey program for spearfishing will give better insight on the impacts of this fishery

The estimated relative stock biomass (Fig. 5.4) results indicate a steep drop from 1985 until the late-1990s after which the standing stock appeared to have leveled off for a decade before declining again more recently. Abundance and size distribution data from the 2011 CRED visual surveys showed a lack of large fishes around Guam relative to the unpopulated Northern Mariana Islands (Williams et al. 2012). A paucity of large fishes is often taken to be an indication of fishing effects (Friedlander and DeMartini 2002, Fenner 2014). This reduction in abundance within the larger size classes can lead to a reduction in reproductive potential making it harder for the fish stocks to recover without the help of protective measures (Birkeland and Dayton 2005, McIlwain et al. 2009).

Keeping in mind all of the issues with the infrequent occurrence of many reef fish species, even in the gear types for which the survey produces relatively large samples of CPUE data, the results of this study suggest declines in biomass. If they are real, declines in stock biomass of the shallow coral reef fishes between 1985 and 2012 are causes for concern about the status of nearshore fishes and fisheries in Guam. The findings from our analysis of the shore-based creel survey data are broadly in agreement with a number of previous studies that focused on boat- and shore-based fisheries (Dalzell 1996, Zeller et al. 2007, Burdick et al. 2008) and on fish abundance and size distributions (McIlwain et al. 2009, Brainard et al. 2012, Houk et al. 2012).



Humphead wrasse and a pair of raccoon butterfly fish. *Photo NOAA*

Chapter 6

Applying the Atlantis model framework to coral reef ecosystems

Weijerman, M, EA Fulton, IC Kaplan, R Gorton, R Leemans, WM Mooij, RE Brainard. 2015. *Submitted to PlosOne.* An integrated coral reef ecosystem model to support adaptive management decisions under a changing climate.

Millions of people rely on the ecosystem services provided by coral reefs, but coral reefs are presently vulnerable to local human-induced disturbances and global climate change. Ecosystem-based management that considers the indirect and cumulative effects of multiple disturbances has been recommended and adopted in policies in many places around the globe. Ecosystem models that give insight into complex reef dynamics and their responses to multiple disturbances are useful tools to support planning and implementation of ecosystem-based management. We adapted the Atlantis Ecosystem Model to incorporate and predict key dynamics for a coral reef ecosystem around Guam in the tropical western Pacific. We used this model to quantify the effects of predicted climate and ocean changes, current land-based sources of pollution, and fishing. We used the following six ecosystem metrics as indicators of ecosystem state, resilience, and harvest potential: 1) ratio of calcifying to non-calcifying benthic groups, 2) the trophic level of the community, 3) the biomass of apex predators, 4) the biomass of herbivorous fishes, 5) total biomass of living groups, and 6) the end-to-start ratio of exploited fish groups. Simulation tests of the effects of each of the three drivers separately suggest that by mid-century climate change will have the largest overall effect on this suite of ecosystem metrics due to substantial negative effects on reef benthos (loss of coral cover). The effects of fishing were also important, negatively influencing five out of the six metrics. Moreover, LBSP exacerbates this effect for all metrics but not quite as badly as would be expected under additive assumptions, i.e., interaction is positive. Over longer time spans (i.e., 65 year simulations), climate change impacts have a slight positive interaction with other drivers, generally meaning that declines in ecosystem metrics are not quite as steep as the sum of individual effects of the drivers. These analyses offer one way to quantify impacts and interactions of particular stressors in an ecosystem context and to provide guidance to managers. For example, the model showed that improving water quality, rather than prohibiting fishing, appeared to extend the timescales over which corals can maintain high abundance by 5–8 years. This result, in turn, provides more scope for corals to adapt or for resilient species to become established and for local and global management efforts to reduce or reverse stressors.

6.1 Introduction

The future of coral reefs is uncertain. Reefs are threatened by local human-induced disturbances and climate change. Managing and understanding the consequences of these stressors and maintaining the reefs' high biodiversity and multitude of dynamic interactions necessitate an integrated ecosystem approach. This complexity also challenges assessing management outcomes (Nyström et al. 2012, McClanahan et al. 2014). Comprehensive, integrated ecosystem modelling is a useful tool to gain insight into reef dynamics while considering the multiple interacting stressors to these ecosystems (Pandolfi et al. 2011, Riegl et al. 2013). The utility of model projections depends on the model's ability to simulate key processes and components of the reef ecosystem and how these are influenced by and respond to different disturbances and management scenarios. To better address societal objectives, ecosystem models should also consider the socioeconomic consequences of changes in ecosystem state.

During an international coral reef stakeholder workshop (Principe et al. 2012, Yee et al. 2014), four economically important ecosystem services were identified: (1) shoreline protection, which is influenced by the structural complexity of a reef system; (2) tourism and recreational opportunities, which are influenced by turbidity (land-based sources of pollution) and algal and faunal communities; (3) production of fish; and (4) production of other natural products. Furthermore, stakeholders identified maximizing reef ecosystem integrity as a key objective (Carriger et al. 2013, Yee et al. 2014). Most existing coral reef models focus on biological feedback mechanisms (e.g., Mumby 2006, Edwards et al. 2011), though a smaller subset of ecosystem models include physical and biological disturbances (Wolanski et al. 2004, Baskett et al. 2009a, Hoeke et al. 2011) and human uses (fisheries) (Edwards et al. 2011, Ruiz Sebastián and McClanahan 2013, McClanahan 2014). Only a few models dynamically integrate socioeconomic and biophysical processes (Ainsworth et al. 2008b, Fung 2009, Melbourne-Thomas et al. 2011b, Ainsworth and Mumby 2014), which is necessary for exploring potential changes in the coral reef ecosystem services identified by stakeholders.

We adapted the Atlantis ecosystem model framework (http://atlantis.cmar.csiro.au/) developed initially for temperate fisheries systems (Fulton 2001, Fulton et al. 2005, Fulton et al. 2007) for application to the coral reef ecosystems around the island of Guam in the western tropical Pacific Ocean. Atlantis is suitable for testing management policies, conservation methods and assessments by simulating ecosystem dynamics and its complexities (Fulton et al. 2011b, Weijerman et al. 2015). Effective ecosystem-based management relies upon understanding the relative ecosystem effects of multiple disturbances acting concurrently (Balmford and Bond 2005). Ecosystem models, such as Atlantis, can simulate these disturbances simultaneously and allows for the exploration both of their impacts individually as well as their interactive and cumulative effects (Fulton et al. 2011b). By improving our understanding of these interacting influences on the ecosystem, we can gain insights into how better to manage human activities associated with coral reef ecosystems.

In this paper, we use the developed Guam Atlantis Coral Reef Ecosystem Model (Guam Atlantis; see Chapter 4 and Weijerman et al. 2014 Appendices) to explore the interactive effects of three drivers: climate change, land-based sources of pollution and fishing. We simulate the effects of two and three drivers simultaneously and looked at the interactive effects on the reef ecosystems surrounding Guam. Additionally, to make the model output more relevant to resource managers, we assess whether local management strategies can mitigate the effects of climate change as has been suggested in other studies (Hughes et al. 2010, Pandolfi et al. 2011, Kennedy et al. 2013, McClanahan et al. 2014).

The ecosystem metrics used to score the impacts of the drivers are based on performance indicators for reef resilience (Bascompte et al. 2005, Bellwood et al. 2011, Weijerman et al. 2013): (1) ratio of calcifiers to non-calcifiers in the benthic community (2) mean trophic level of the community; (3) biomass of apex predators; (4) biomass of herbivorous fishes; and (5) total system biomass excluding detritus (i.e., total biomass of living organisms). As a simple proxy for a socio-economic indicator, we also added: (6) the biomass at the end of a simulation (B_{Year30}) relative to the start (B_{Year0}) of fish groups exploited by recreational shore-based fishermen.

6.2 Methods

6.2.1 Modelling framework

The Atlantis framework consists of spatially explicit, three-dimensional irregular and, for each polygon and water layer, incorporates information on the biological, geochemical, and physical forcings (Fulton 2001, Fulton et al. 2007). Atlantis integrates these dynamics through two-way coupling and combines them with the effects of different human user groups (fisheries, oil extraction and mining or coastal development), and dynamically tracks the interaction of all these factors over time. Atlantis simulations use a simple forward difference integration scheme to solve a system of differential equations typically on a 12-h time step (finer adaptive substeps are executed for high turn-over rate groups such as plankton). The dynamic processes are user specific and many alternative model formulations can be selected to set complexity at a desired level. Fulton et al. (2011b) gives an overview of the modular structure of Atlantis and more information can be found at http://atlantis.cmar.csiro.au/ and in other publications of the application of Atlantis, such as, Griffith et al. (2012). Here we briefly discuss the spatial and oceanographic modules and the adaptations made to the ecological module.

In Appendix F the methods and assumptions made for the development of this innovative integrated coral reef ecosystem model are described in detail (Fig. 6.1). In previous applications of Atlantis models, corals were just modeled as benthic filter feeders (e.g., Brand et al. 2007, Kaplan et al. 2010, Link et al. 2010, Ainsworth et al. 2011a, Kaplan et al. 2012). We added code that addresses how corals are affected by (1) climate change (including ocean warming and acidification), (2) changes in land use (eutrophication and sedimentation) and (3) fishing activities. By including extensive empirical data collected from field studies in Guam, local-scale dynamics are projected over decades, and trends that will likely manifest themselves locally are identified. We carefully validated the model by examining the model behavior over 30–75 years without any disturbances, i.e., a ‘control’ system, following guidelines for Atlantis model development (Horne et al. 2010, Link et al. 2010, Ainsworth et al. 2011a). Model outcomes of scenarios with each of the disturbances were validated by comparing them with empirical studies from Guam or from regional studies if local information was not available (Appendix F).

6.2.2 Guam Atlantis model components

Spatial module

For detailed information on the model components and data sources see Weijerman et al. (2014b) or Chapter 4. We apply the Guam Atlantis model to represent the years 2015–2050, as well as a hindcast period of 1985–2015. Briefly, the Guam Atlantis model incorporates spatially-differentiated habitats (polygons) and vertical stratification (water layers) allowing for the representation of hydrodynamic and biological processes (e.g., migration of fish to different habitat types in their lifecycles, larval connectivity between reef areas). Preliminary discussions with ecologists and coral reef managers in Guam led to the use of two depth layers: 0–6 m and 6–30 m. We limited the model domain to this shallow (< 30 m) depth range of the reef system due to the availability of biomass and diversity data for species in these depth layers, and the relative paucity of data from deeper habitats. Biological data are primarily from NOAA's Pacific Islands Fisheries Science Center, Coral Reef Ecosystem Division (CRED) supplemented with data from Guam Coastal Zone Management Program, University of Guam Marine Lab, Guam Division of Aquatic and Wildlife Resources (DAWR) and Guam Environmental Protection Agency. Outer polygons (30–100 m) are included for oceanic forcing (nutrient import/export, larval connectivity, and water, heat and salinity fluxes). Based on the benthic habitat, fish assemblages, prevailing oceanographic conditions, fisheries reporting zones and the existing managed areas, we delineated 55 marine spatial units, 25 shallow, 23 deep and 7 outer boundary polygons (Fig. 6.1).

Oceanographic module

The oceanographic module consists of two main data inputs based on a Regional Ocean Modelling System (ROMS) developed for the Coral Triangle (CT) in the western Pacific Ocean (Castruccio et al. 2013) (downloaded October 24, 2014). The main focus of this CT-ROMS model was the larger Coral Triangle region, but the model domain includes Guam at its northern boundary. The data used from the CT-ROMS model includes: (1) horizontal fluxes (to estimate the magnitude and direction of the currents) that cross each face (or side) of the Atlantis polygons per daily time step, and (2) average vertical velocity, temperature and salinity per Atlantis polygon per daily time step. The available data were from 1957–2007 with a spatial resolution of 5 km. We extracted the grid points around Guam from 1985–2007 to calculate horizontal velocity, solar irradiance, temperature and salinity. The last year of data were repeated for years 2008–2050. Vertical velocity was not included in the CT-ROMS model output, hence, simulated values were created by taking random values with a mean of zero and standard deviation taken from field data (Vetter et al. 2010, Péquignet et al. 2011, Storlazzi et al. 2014).

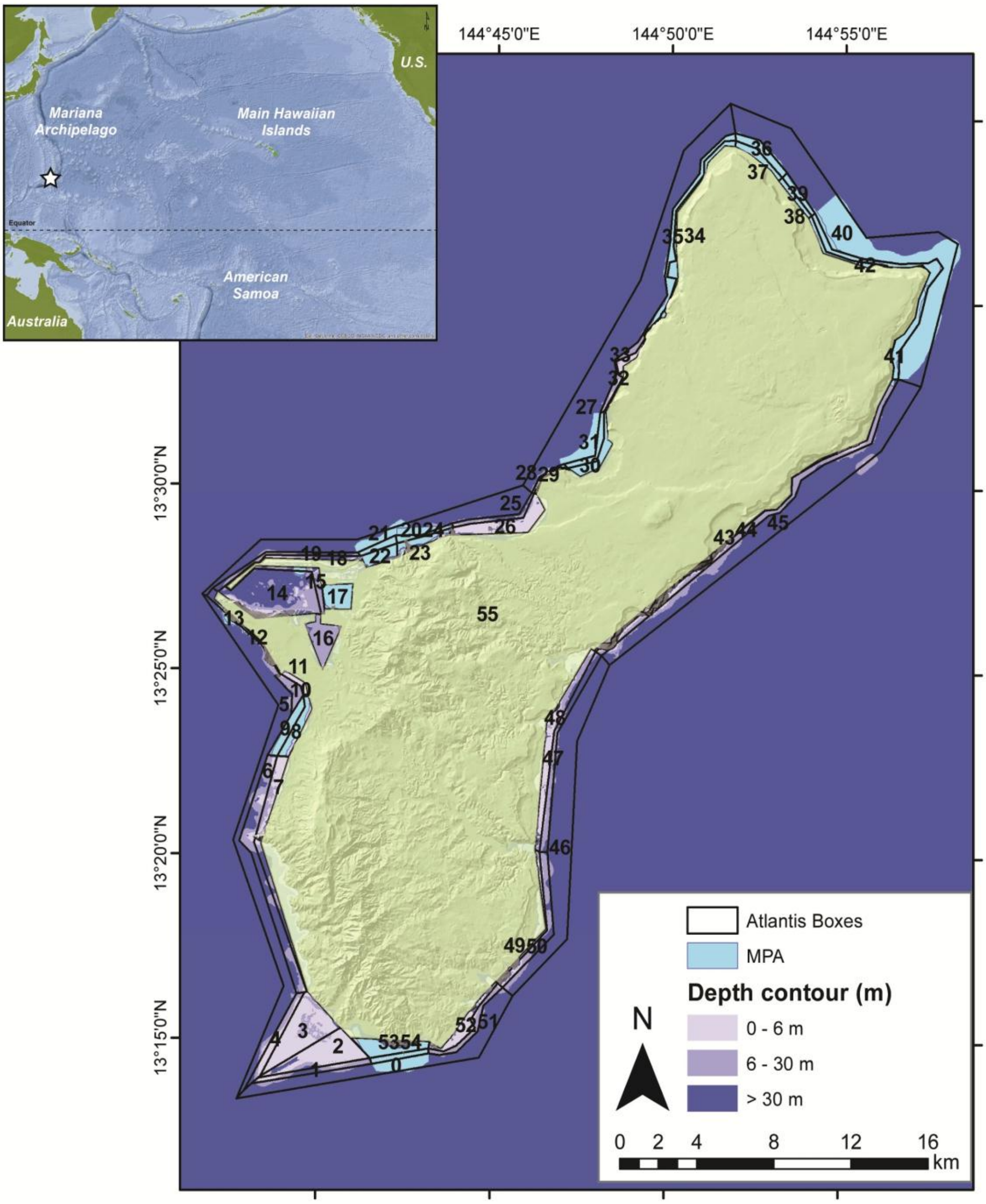


Figure 6.1. Spatial polygons of Guam Atlantis with 25 shallow (< 6 m) and 23 deep (6-30 m) dynamic polygons and 7 non-dynamic boundary polygons (outer-most 7 polygons) for the advection of nutrients and plankton and the island of Guam. The star in the inset map shows the location of Guam in the western Pacific Ocean. The polygons with nutrient and/or sediment inputs included numbers 3, 7, 8, 10, 16, 17, 22, 23, 24, 26, 30, 32, 48, 49, 52, and 53.

Ecological module

The reef's ecological module differs from most coral reef models developed to date, as it is process based and uses empirical parameterizations of basic metabolism (e.g., production, consumption, waste) and ecology instead of derived parameters, such as, productivity over biomass and consumption over biomass (Christensen et al. 2008). Furthermore, trophodynamic flows are fully coupled and the detrital pathways (both in the water column and in the sediment layer) are explicitly modeled. To represent those pathways, we included 42 functional groups consisting of 3 detrital, 5 plankton, 3 algal, 3 sessile invertebrate, 7 mobile invertebrate and 20 vertebrate groups (Appendix A). To accommodate improved understanding of reef resilience we grouped fishes by their life-history characteristics, habitat preferences and diet in the following functional groups: piscivores, corallivores, invertivores, planktivores, detritivores and herbivores. We have further classified the herbivores by their ecological roles as excavators/bioeroders, scrapers, grazers and browsers (Bellwood and Choat 1990, Paddack et al. 2006, Green et al. 2009, Hoey and Bellwood 2011, Heenan and Williams 2013). Based on the biomass of each species in 2011 (Williams et al. 2012), we took the weighted mean of species-specific data on diet and life-history parameters (e.g., growth rate, natural mortality, maximum age, age at maturity, size of recruits, length of pelagic larval development, von Bertalanffy growth coefficients, swim speed) for the overall estimation of those parameters for each functional group. Biomass estimates, spatial distribution, and fisheries data are detailed further in Weijerman et al. (2014b).

We avoided aggregating fished and unfished species into the same functional groups, and identified fishery target species based on shore-based creel surveys conducted since 1985 by Guam’s Division of Aquatic and Wildlife Resources (DAWR; Appendix A). We chose to limit the fishery data to shore-based creel surveys and not include the boat-based creel surveys as we assumed that the shore-based fishery took place entirely in our model domain while the boat-based fishery is mostly focused on trolling and demersal fishing in deeper waters. Appendix A has a complete list of the functional groups and their representative species, i.e., species accounting for ≥ 75% of biomass per group for the fish groups based on visual surveys conducted in 2011 by CRED (Williams et al. 2012). In addition to these living and detritus groups, ammonia, nitrate, and silica are represented dynamically. The model’s initial conditions represent 1985 (after a 10-year‘burn-in' phase) and we projected this forward for 30–65 years under the set of scenarios described below.

The coral framework is the foundation for coral reef ecosystems; hence, corals are integrally linked to most reef dynamics. Corals are consumers by night and photosynthesize by day, but are also a source of food to corallivorous invertebrates and fishes. Due to their three-dimensional structure, corals also provide habitat and shelter for many reef species (DeMartini and Anderson 2007, Enochs and Hockensmith 2008). Even dead corals continue to harbor diverse communities until erosion processes unbalanced by growth lead to the loss of three-dimensional structure (Alvarez-Filip et al. 2009).

Coral species have different life history dynamics and sensitivities to environmental factors (e.g., sediments, elevated temperature, disease) that influence mortality and growth. Hence, we grouped corals into massive and encrusting corals (‘massive’)—with lower growth rates and a lower sensitivity to stressors—and branching/tabular/columnar corals (‘branching’)—with higher growth rates and higher sensitivity to stressors (Marshall and Baird 2000, McClanahan et al. 2007).

After a literature review we identified key coral reef dynamics and the form of the relationships for those dynamics and added corresponding code (Appendix F; Table F-1). Coral specific parameters are included in Appendix G. We detailed the dynamics of coral growth (and growth-related complexity) and competition with benthic algae that are influenced by three main drivers (Fig. F-2): (1) climate change (a global stressor); (2) land-based sources of pollution (a local stressor); and fishing activities (also a local stressor). Table F-1 summarizes how these processes were simulated in the model and lists supporting literature for these relationships. We acknowledge that we have captured only the main processes, and that there are other processes which influence reefs that were either omitted or represented only in a simplified way (e.g., symbionts' dynamics [Baskett et al. 2009a], microbe-induced coral mortality [Smith et al. 2006], coral and algal diseases [Aeby et al. 2011, Williams et al. 2014], linear relationship between herbivore size and bioerosion [Mumby 2006] and others).

Model validation, verification and sensitivity analyses are discussed in Appendices H–J. Of importance to note is that the effects of acidification are likely underestimated with the model and coral biomass is sensitive to the growth rate of primary producers. Recently the role of phytoplankton in structuring fish communities has received more attention and helped explain the large regional (Pacific wide) differences in fish biomass between reefs close to populated and unpopulated areas (Williams et al. 2015), corroborating the importance of obtaining good estimates of these phytoplankton groups. Improving the relationship between reef organisms and acidification or obtaining more accurate downscaled time series of projected change in pCO_2 and getting better growth rates and biomass estimates of phytoplankton communities will likely enhance the model's capabilities to make projections. Additionally, the model skill in estimating fish biomass had a clear bias and overestimated a number of groups. More research is necessary to explain the bias and then correct for it (e.g., better fishery data, diet data of apex predators, recruitment data for the overestimated fish groups). However, with the current information available it is possible to make relative comparisons (Appendix F).

6.2.3 Model scenarios and model output

The outcome of a control run (Appendix H) that not included any of the identified stressors was compared with outcomes from runs with the various added drivers: climate change (i.e., ocean warming and acidification), land-based sources of pollution (LBSP) and fishing. Models were run for 30 years (1985–2015) to explore present conditions and for 65 years (1985–2050) to explore future conditions.

Predicted changes in atmospheric CO_2 concentrations came from the IPCC fifth Assessment Report using the highest emission scenario, Representative Concentration Pathway (RCP) 8.5 projection (Stocker et al. 2013). Predicted sea surface temperature data also came from the RCP 8.5 projection using the HadGEM-AO model output (data downloaded from the Coupled Model Intercomparison Project Phase5 [CMIP5]: http://apdrc.soest.hawaii.edu/las8/UI.vm), as the historical 1985–1990 modeled data corresponded well with satellite-derived SST data for Guam during the same time period. We overlaid this trend on the existing time series of temperature from the CT-ROMS model output (Castruccio et al. 2013) for each Atlantis polygon and created a projected temperature time series for each polygon out to 2050 while maintaining spatial differences around Guam.

These increased CO_2 concentrations for emission scenario RCP 8.5 led to a decrease in the oceanic pH which in turn led to a reduction in the aragonite saturation state of the ocean resulting in reduced calcification rates modeled as a reduced growth rate of corals (Appendix F which also explains relationships between pH and several other organisms).

Land-based sources of pollution were modeled as additional input of nitrogen and sediments into coastal polygons that had riverine runoff or sewage outflow pipes (Appendix F, Weijerman et al. 2014b). The sediment and nutrient loads were based on data collected from 2005–2007 (Guam Environmental Protection Agency, and CRED) and used as initial condition input data for the model. River flow and additional nutrient and sediment input data were based on time series from 1991 and 2011 and the last year was repeated for future projections. Hence, changes in land-use or the amount of rain were not taken into account. Fishing mortality was calculated for each functional group based on the historical catches from shore-based creel surveys conducted by DAWR. We assumed fishing mortality stayed constant at 2010–2012 levels for projections (Appendix F).

Ecosystem metrics used to score the effect size of the disturbances were based on performance indicators for reef resilience (Bascompte et al. 2005, Bellwood et al. 2011, Weijerman et al. 2013) plus one additional indicator: the ratio of biomass of targeted species in the recreational reef fishery at the end relative to the start of a simulation (Table 6.1). We used that metric as a proxy for one source of socio-economic benefits from the reef ecosystem—availability of preferred target fishery species.

Table 6.1. Ecosystem metrics used to determine effect size of simulation of scenario runs.

Metric	**Description**	**Rationale**
Ratio of benthic calcifiers to non-calcifiers	Ratio of total biomass of corals and crustose coralline algae (CCA), and total biomass of turf and fleshy macroalgae in the model domain	Corals form the framework of reef ecosystems and CCA is the ‘glue’ that cements the reef together a high ratio of calcifiers to non-calcifiers implies a more structurally complex system that provides more desirable ecosystem services than a macroalgal-dominated (flat) system (Weijerman et al. 2013)
Mean trophic level of the community	Biomass-weighted average of the trophic level of all functional groups in the ecosystem.	Indication of maturity for ecosystems; higher value represents more ecosystems (Weijerman et al. 2013)
Biomass of apex predators	Sum of biomass of apex predator groups (sharks, roving piscivores, benthic piscivores and mid-water piscivores).	Indication of ‘health’ for ecosystems; higher value represents ‘healthier’ ecosystem. In general, more apex predators decrease community susceptibility to perturbations (Bascompte et al. 2005).
Biomass of herbivorous fishes	Sum of biomass of all herbivorous fish groups.	Indication of resilience with more herbivores leading to less chance of ecosystem shifts to undesirable algal-dominated state (Bellwood et al. 2011).
Total biomass (excluding detritus)	Sum of biomass of all species.	Indication of maturity/stability of ecosystems; higher value represents more mature or stable ecosystem (Weijerman et al. 2013)
Ratio of biomass of target species at end to start of a run	Total biomass of all fish species that are targeted in the reef fishery at the end vs start of simulation run.	Indicator of socioeconomic condition; higher value means higher availability of target species to recreational fisherman

Ecosystem metrics were calculated as the average over the last three years of a simulation, to smooth over intra-and interannual variation, and results for each Atlantis polygon were summed to get results for the entire model domain for the island of Guam. For each of the six ecosystem metrics, the response ratio was calculated as the ratio of the metric under a scenario (e.g., climate change) relative to the value of that metric in the control run, following the methods in Kaplan et al. (2013). The interactive effects among the drivers were explored to see if their combined effect led to higher values (positive interaction) or lower values (negative interaction) than would be expected based on the sum of the impacts of the individual drivers (Kaplan et al. 2013). To determine the interactive effect size another two simulations were conducted: one with two drivers acting simultaneously (adding the two stressors with the largest effects individually), and the other with all three drivers. For instance, if two drivers individually caused a 2% and 3% decline in a metric, the additive expectation of combining both drivers is a 5% decline. If simultaneously applying the drivers actually led to only a 4% decline, the interaction is slightly positive; if simultaneously applying the drivers led to a 6% decline, the interaction is slightly negative. Based on the assumption that the sum of the individual effects is simply additive, the difference between the results of the simulation with concurrent drivers and the simulation results of the two or three individual drivers should be zero. To determine this interactive effect size, *d*, we added the relative control value (always 1 because results are standardized to the control) to the result of the scenario run with two or three drivers acting concurrently, and subtracted the individual effect sizes of the drivers according to:

$$d_{1,2,} = \mathrm{Y}_{\mathrm{AB}} + \mathrm{Y}_{\mathrm{control}} - \mathrm{Y}_{\mathrm{A}} - \mathrm{Y}_{\mathrm{B}}$$

$$d_{1,2,3} = \mathrm{Y}_{\mathrm{ABC}} + 2\mathrm{Y}_{\mathrm{control}} - \mathrm{Y}_{\mathrm{A}} - \mathrm{Y}_{\mathrm{B}} - \mathrm{Y}_{\mathrm{C}}$$

where Y_{AB} is the value of the ecosystem metric resulting from having two interactive drivers acting concurrently and $\mathrm{Y}_{\mathrm{ABC}}$ is the ecosystem metric resulting from three interacting drivers. A, B, and C are the three drivers (climate change, LBSP, and present day fishery). $\mathrm{Y}_{\mathrm{control}}$ is the relative control value (with the coefficient 2 to ensure that the expected interaction *d* is 0 if effects are simply additive), resulting from a simulation of the control run, and Y_{A}, Y_{B}, and Y_{C} indicate the value of the simulation of just the one driver.

6.3 Results

6.3.1 Individual drivers

Among the three 30-year (1985–2015) single stressor scenarios, fishing clearly had the largest overall ecosystem impacts based on the performance metrics used, mostly due to the large negative effect on the biomass of apex predators and the start-to-end ratio of biomass of fish groups targeted by recreational fisherman (Fig. 6.2). Global climate change almost exclusively affected the ratio of calcifiers to non-calcifiers resulting in a shift from coral and crustose coralline algae to turf and macroalgae (Fig. 6.2). LBSP had the largest effect on the ratio of calcifiers vs. non-calcifiers as well as clear effects on the biomass of apex predators. Trophic level was least affected of the ecosystem metrics, possibly because of the taxonomic resolution of the model; target and non-target groups had similar trophic levels and the biomass of apex predators was low in all simulations (e.g., 14% in the control scenario) compared to the biomass of the other fish groups, so even the 35% reduction in apex predator biomass due to fishing and 18% reduction due to land-based sources of pollution did not have a great influence on the overall trophic level of the community.

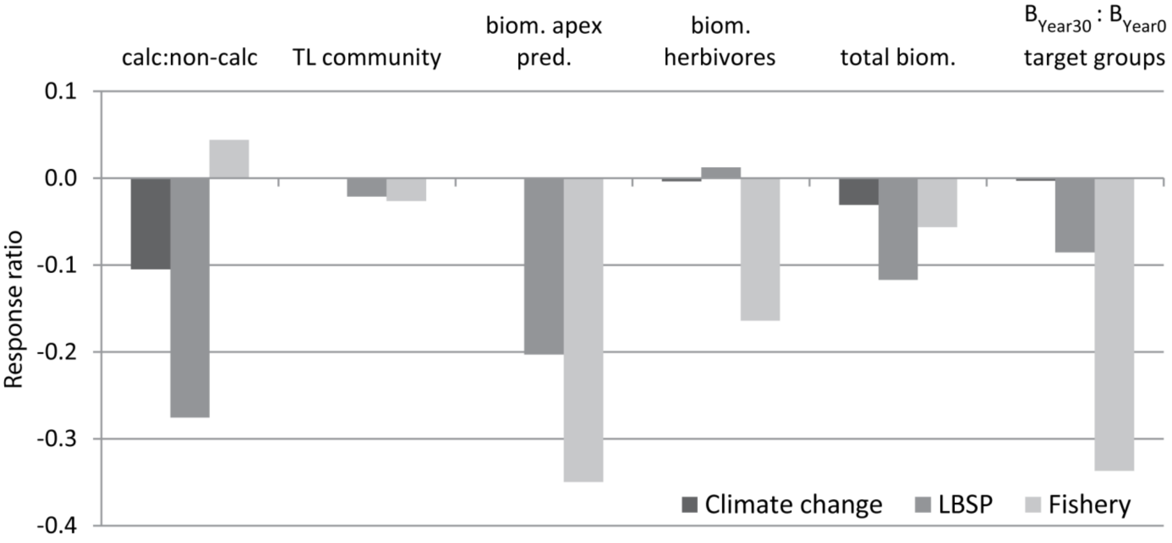


Figure 6.2. Response ratio of individual drivers' effect to control effect of the six ecosystem metrics after 30-year simulations. Responses greater than the control indicate a positive effect, and responses smaller than the control indicate a negative effect. The control simulation had no external drivers. LBSP is land-based sources of pollution. Climate change represents a simulation of both ocean warming and acidification. Fishing was simulated using a fixed fishing mortality based on 2010–2012 shore-based fishery landings.

Climate change effects dominate model dynamics at longer time scales (65 year simulations, 1985-2050). Using projected sea surface temperature rises, the bleaching threshold would be exceeded every year from 2023 onwards (Appendix F, year 48 in Fig. F-4). Therefore, it is not surprising that the effects of climate change are extremely high for the calcifiers to non-calcifiers ratio (ratio = 0.24 in climate change scenario versus 1.33 in control). In this longer simulation, climate change also had a negative effect on total biomass, including a decrease in most prey species other than some of the herbivorous fishes (Fig. 6.3). Similar to the 30-year simulation, fishing affected almost all ecosystem metrics negatively, but particularly the biomass of apex predators and target fishes (Figs. 6.3 and 6.4).

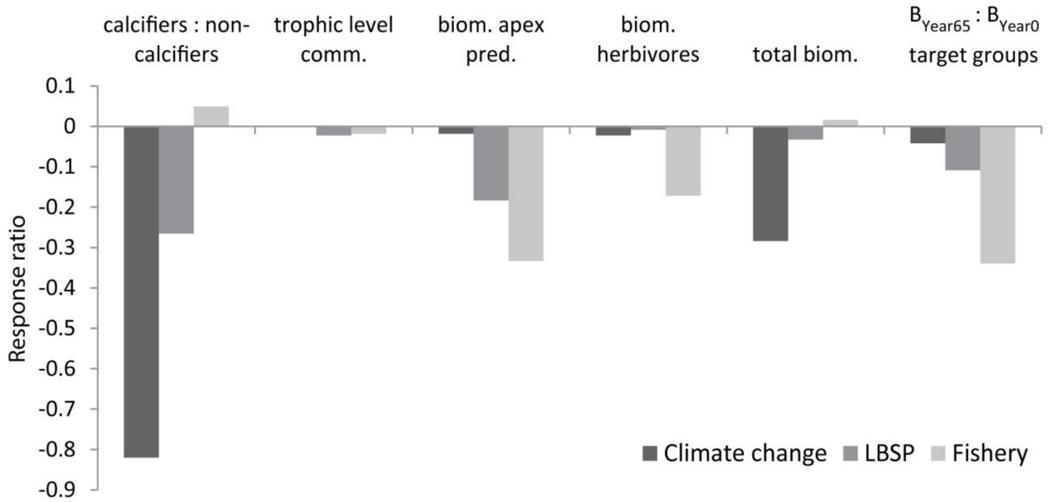


Figure 6.3. Response ratio of individual drivers' effect to control effect of the six ecosystem metrics after 65-year simulations. Responses greater than the control indicate a positive effect, and responses smaller than the control indicate a negative effect. The control simulation had no external drivers. LBSP is land-based sources of pollution. Climate change represents a simulation of both ocean warming and ocean acidification. Fishing was simulated using a fixed fishing mortality based on 2010–2012 reef-fish fishery landings.

Among the modeled vertebrate groups, turtles and mid-water piscivores came out as 'winners' under the fishing scenario (Fig. 6.4), as their predators, sharks, declined, and, in the case of turtles, competition for food (algae) also declined.

Averaging all metrics (Fig. 6.5) emphasizes that climate change is the dominant driver over the long term (65-year projections through year 2050), while fishing and LBSP appear to have influenced the performance of the system (as measured by our ecosystem metrics) most in the last 30 years (to 2015).

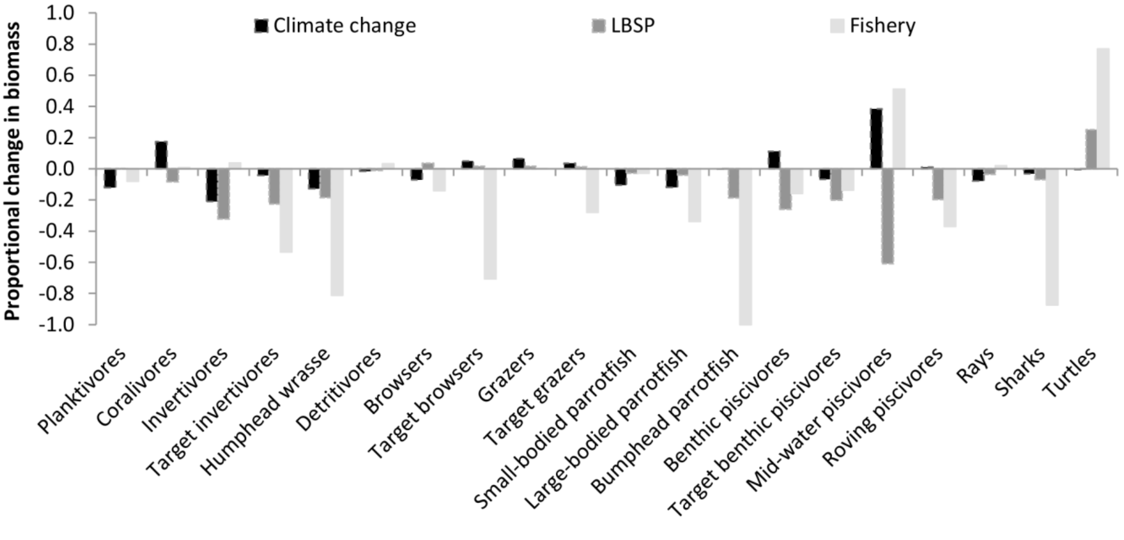


Figure 6.4. Vertebrate biomass response to each of the three simulated drivers, relative to the control biomass. Biomass responses are end values for year 2050 (65 year run). Control is a simulation with no external drivers. LBSP means land-based sources of pollution. Climate change represents a simulation of both ocean warming and ocean acidification. Fishing is simulated with fixed fishing mortality based on 2010–2012 shore-based fishery landings.

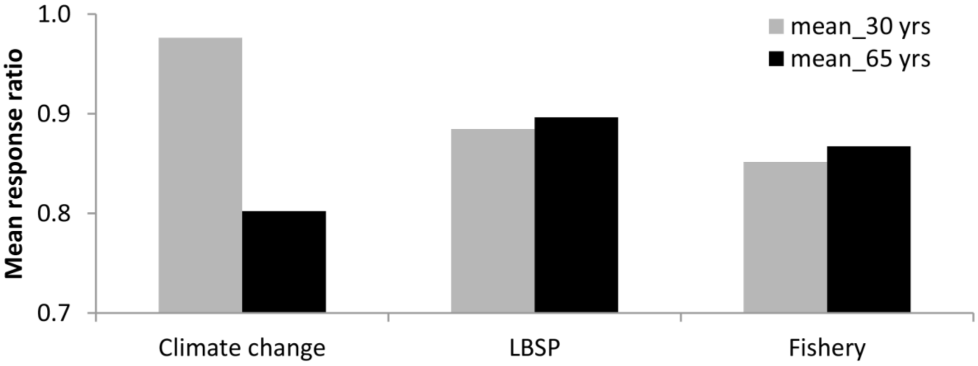


Figure 6.5. Average response ratio across all six ecosystem metrics of climate change, land-based sources of pollution (LBSP), and fishing after 30 (grey bars) and 65 (black bars) years. Values equal to one indicate no change relative to the control simulation and values lower than one indicate a negative effect. All six metrics were weighted equally.

6.3.2 Concurrent drivers

For the present-day conditions (30-year simulation), fishing appeared to have the greatest impact followed by LBSP (Fig. 6.5). Simulating those two drivers concurrently showed slight positive interactions for five out of six ecosystem metrics, i.e., the combined effects of concurrently simulating the two drivers were more positive than the additive effects of the two individual drivers. That was also true in simulations of all three drivers concurrently (Fig. 6.6), but in both cases these antagonistic effects were ≤0.10. Note that strong declines in the ecosystem metrics were still observed in scenarios with concurrent drivers, for instance the biomass of apex predators declined to only 55% of the value under the control scenario.

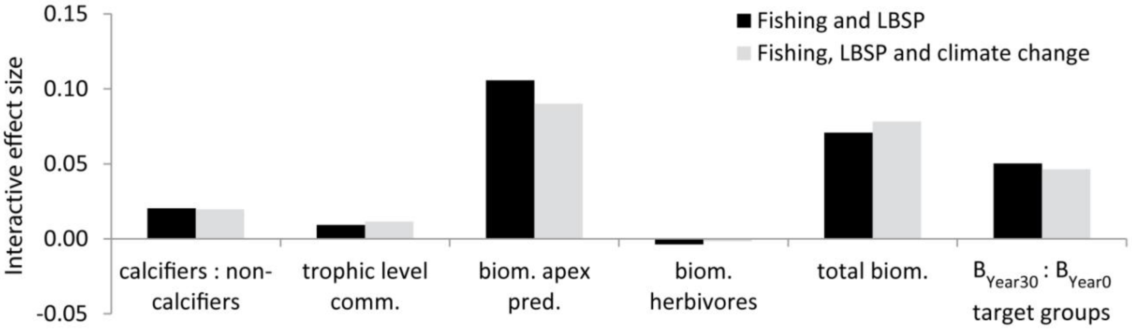


Figure 6.6. Interactive effect size on six ecosystem metrics (x-axis) when simulating fishing and LBSP concurrently (two drivers) and all three drivers (also including climate change) at the end of a 30-year run. The difference between the expected effect size, if these were simply additive, and the actual effect size of simulations with the two or three drivers concurrently is indicated by the black and grey bars respectively.

For the 65-year simulation, climate change had the largest individual effect followed by fishing and LBSP (Fig. 6.5), so we simulated those two drivers concurrently first, and then simulated all three drivers concurrently. Just as in the 30-year simulation, the interactive effect size was mostly positive, especially when all three drivers acted concurrently, i.e., a scenario with concurrent drivers led to slightly higher values of ecosystem metrics than could have been predicted from simply adding the individual driver effects (Fig. 6.7). As with the 30-year simulation, despite the slight positive interactions of the concurrent drivers, actual effects were negative, just not as extreme as might be expected by summing the individual driver effects. For instance, despite the 0.21 positive interaction of the ratio of calcifiers:non-calcifiers (Fig. 6.7), the combination of three drivers drove this ratio to only 19% of the control scenario result; the ratio of calcifiers to non-calcifiers was 0.24 if just climate change was simulated and 1.40 if just fishing was simulated, suggesting that the benefits of fishing for this metric were not fully realized when combined with climate change.

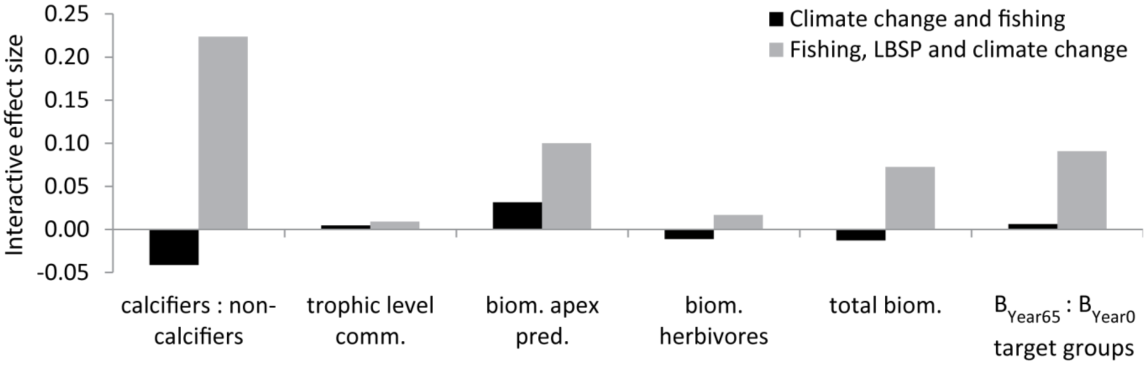


Figure 6.7. Interactive effect size on six ecosystem metrics (x-axis) when running simulation with climate change and fishery concurrently, and all three drivers at the end of a 65-year simulation. The difference between the expected effect size, if these were simply additive, and the actual effect size of simulations with the two or three drivers is indicated by the black and grey bars respectively.

In terms of management applications of these model results, reducing LBSP appears to have a noticeable effect on coral biomass, giving corals some additional capacity to deal with the early effects of climate change under the RCP 8.5 scenario for CO_2 emissions. However, when ocean temperature exceeds the bleaching threshold every year, the prognosis for corals is bleak (Fig. 6.8). Our study indicates that when just fishing is restricted, coral biomass follows the same trend as under a status quo scenario (Fig. 6.8).

The trend for the biomass of apex predators and of herbivores, showed, not too surprisingly, that the no-fishing scenarios (short dashed and dotted lines) resulted in the highest fish biomass. Similar results were obtained for the relative change in biomass of target species compared to the initial biomass: a declining and stabilizing trend at around 53% of initial biomass for status quo and at 55% for no LBSP scenarios and stabilizing at 80% for no fishing and at 85% for no fishing and no LBSP scenarios. What was surprising though, is that the herbivorous fish biomass stayed stable despite the reduction in coral biomass (and hence structural complexity and hiding places) in the last 15 years (Fig. 6.9). However, a 110-year simulation (only simulated for status quo scenario) does indicate that the biomass of the herbivorous prey fish slowly declines after coral cover has declined with a lag-time of about 15 years (Fig. 6.10). These 15 years correspond well to their mean generational age-span of 12.3 (SD 6.4) years.

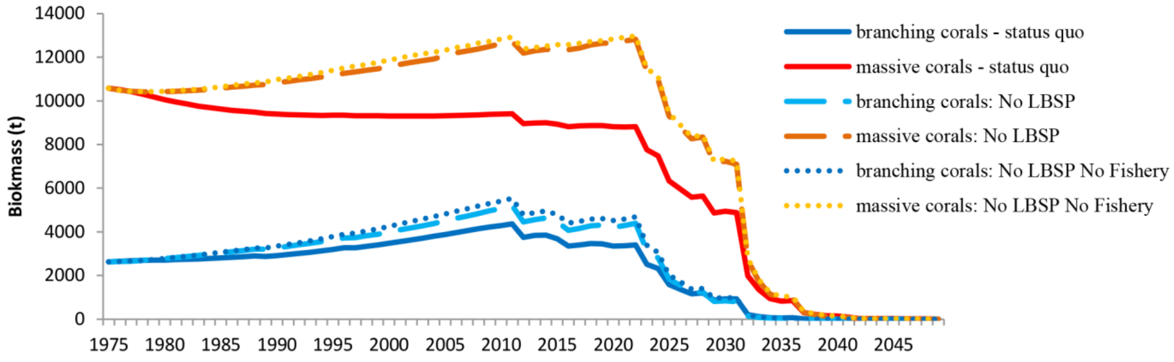


Figure 6.8. Projected effects of climate changes (RCP 8.5 scenario for pCO_2 emissions) concurrent with local threats (LBSP [land-based sources of pollution] and fishing) on massive (top red-shaded lines) and branching (bottom blue-shaded lines) coral biomass. The result of a no fishing scenario corresponded with the status quo scenario for both coral groups and was left out for clarity.

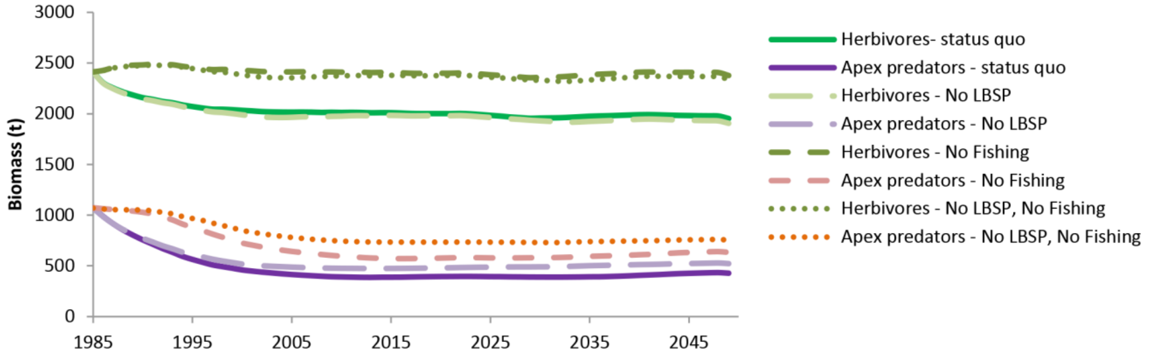


Figure 6.9. Projected effects of predicted climate changes (RCP 8.5 scenario for pCO_2 emissions) concurrent with local threats (LBSP [land-based sources of pollution] and fishing) on biomass of herbivorous fish (top green-shaded lines) and apex predators (bottom purple-shaded lines).

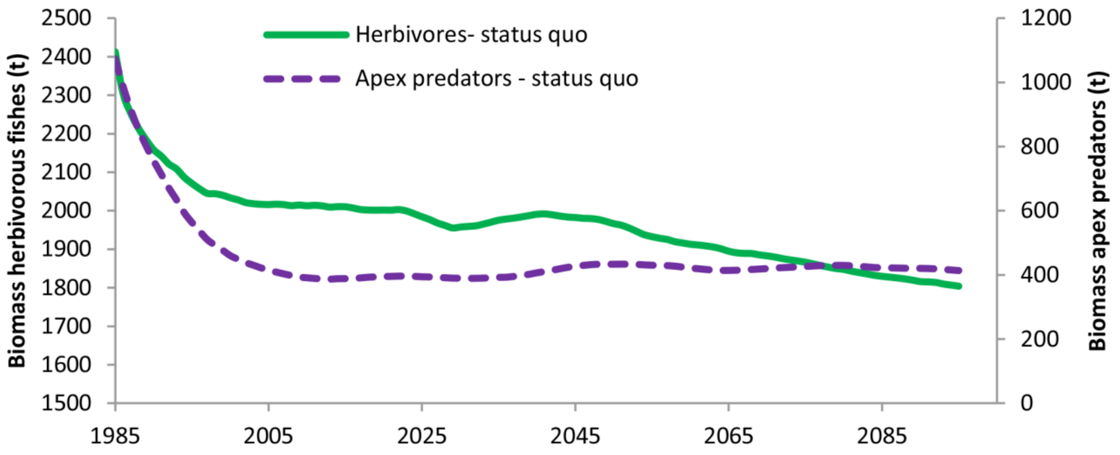
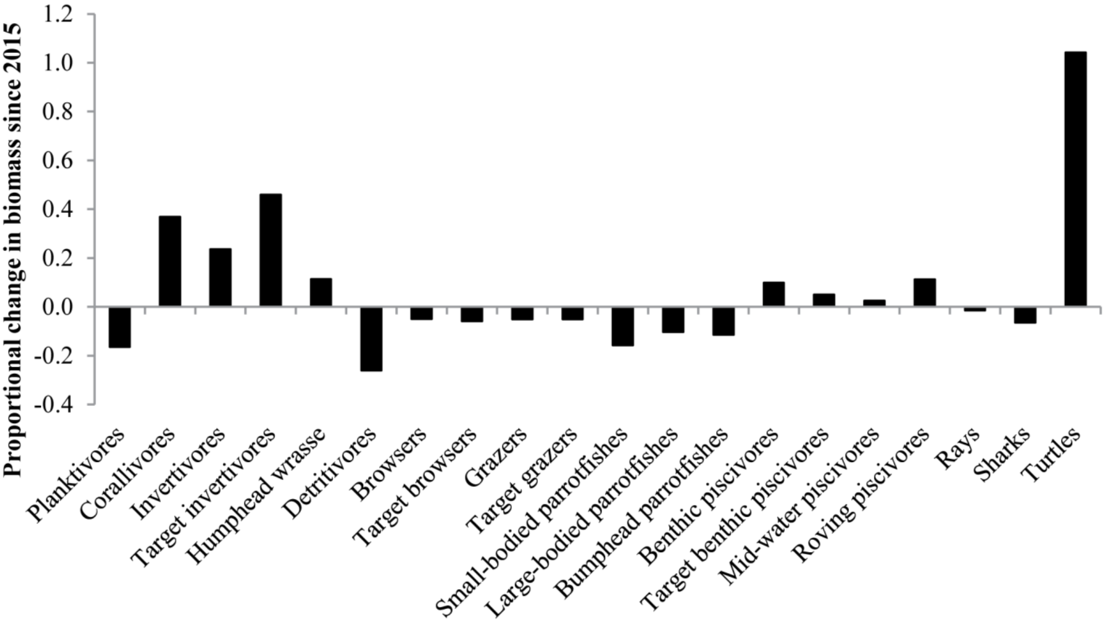


Figure 6.10. Projected effects of predicted climate changes (RCP 8.5 scenario for CO_2 emissions) concurrent with local threats on biomass of herbivorous fish (green line) and apex predators (purple dashed lines).

Main ‘winners’ projected by the model at the end of this century under a status quo scenario with climate change were turtles (100% increase), benthic filter feeders (600% increase) and detritivorous invertebrates (300% increase; Fig. 6.11).



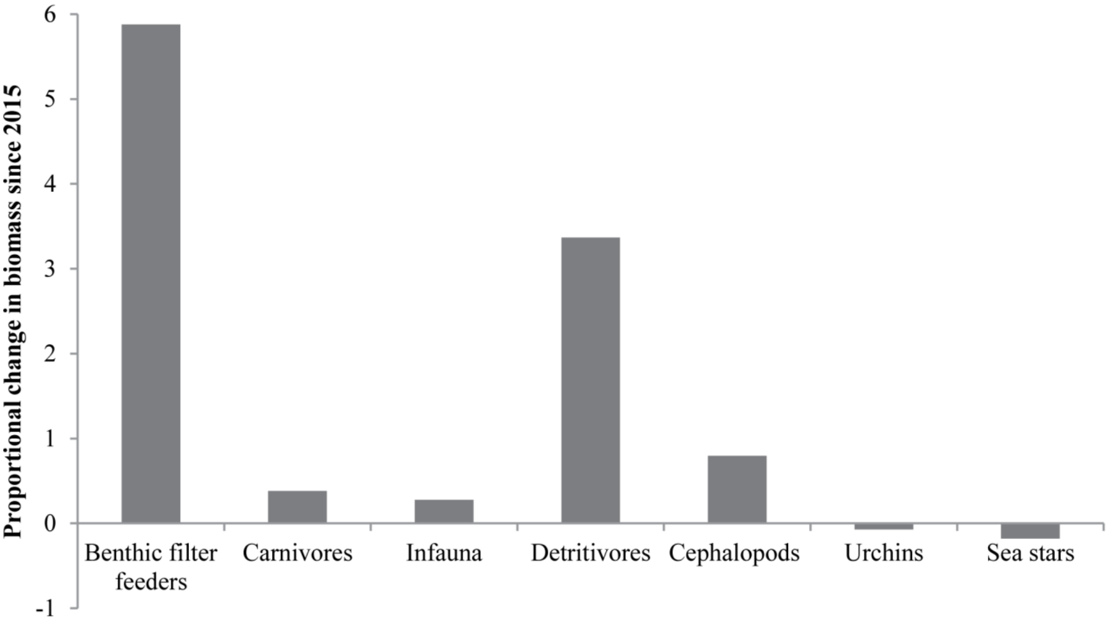


Figure 6.11. Projected relative biomass after a 110 year simulation comparing 2095 (end of simulation) to 2015 for (*top panel*) vertebrate and (*bottom panel*) invertebrate functional species groups.

6.4 Discussion

Ecosystem-based management considers the indirect and cumulative effects of multiple threats to a system. Ecosystems can frequently recover from short-term low-intensity disturbances, but when disturbances occur too frequently or when multiple disturbances impact the system in a short time span (i.e., before the system is recovered), recovery is limited or may not happen at all (Paine et al. 1998, Edwards et al. 2011, Ban et al. 2014). Quantifying the interactive effect size of disturbances is one way to gain insight into how these disturbances cumulatively affect the ecosystem. Looking first at the disturbances individually, ocean warming and acidification, had the largest effect on the ecosystem compared to LBSP and fishing, with fishing being a close second when looking at the end of 65-year simulations. Whereas ocean change primarily affected the benthic reef community, fishing impacted all ecosystem metrics, including four out of six, negatively. Fishing had the strongest negative effect on the biomass of target species and apex predators. This result is expected from any selective fishery (Jennings and Polunin 1996, Friedlander and DeMartini 2002). Surprising was the result that fishing actually had a beneficial effect on the ratio of calcifiers to non-calcifiers. This positive effect could be explained by the projected increase in turtle biomass, which were less preyed upon as the shark (main predator) populations had declined, and by less bioerosion, especially from large parrotfishes.

Results also suggest that presently (end of 30-year simulation) fishing affected almost all ecosystem metrics negatively and that LBSP exacerbated this effect, but not quite as badly as would be expected under additive assumptions. In the case herbivore biomass, fishing had a negative effect, but LBSP had a slight positive effect. The scenario with those concurrent drivers led to a slightly lower value of that ecosystem metric than could have been predicted from simply adding the individual driver effects. This result could indicate that the input of nutrients and sediments, which led to an increase in food abundance, offset the reduction in herbivore biomass through their extraction due to fishing. This pattern also held up after simulating concurrently the third driver, climate change. Despite the low interactive value, the combination of two and three drivers drove the herbivore biomass to 84% of the value in the control scenario.

Cumulative effects of combining all three drivers in the 65-year simulation were negative, in correspondence with temperate fisheries systems where the ecosystem was worse off once all three drivers came into play (Kirby et al. 2009, Ainsworth et al. 2011b). Estimated interactions were slightly positive, meaning that the combined effects were only slightly less than a null assumption of summing the individual effects of each of the three drivers.

As some studies speculated that mitigating local stressors to reefs increases the coral's resilience to climate change (Hughes et al. 2010, Edwards et al. 2011, Pandolfi et al. 2011, Kennedy et al. 2013), we simulated (1) a scenario with climate change and no input of LBSP, (2) a scenario with climate change and no fishing, and (3) a scenario with climate change and no local drivers (no fishing and no LBSP) and compared coral biomass trajectories with a status quo scenario (including climate change and local drivers). Model outcomes showed that when LBSP was stopped, coral biomass increased and stayed higher longer compared to the status quo scenario. In contrast to the idea that a fishing moratorium could mitigate the decline in coral biomass, our study suggests that this increasing trend in coral biomass was only slightly improved when fishing was also stopped. This result was also seen in a study in the Indian Ocean where fishery closures did not change hard coral cover (McClanahan 2014). Indeed, we showed that the biomass of herbivores and apex predators increases when fishing is stopped, however, despite the lower biomass of herbivores under the fishing scenario, coral biomass is higher and algal biomass is lower compared to the no fishing scenario.

Though studies (Mumby and Harborne 2010, Edwards et al. 2011) showed that high herbivore populations are important for the recovery of coral populations in some situations, our results do not suggest that this provides a substantial buffer against climate change for coral cover in Guam. Indeed, a study in the Caribbean (Edwards et al. 2011), the Great Barrier Reef (Thompson and Dolman 2010), and a global meta-analysis (Selig et al. 2012) showed a similar demise of coral cover when bleaching events were taken into account despite the establishment of MPAs. In the Caribbean study, depending on the location, a high presence of herbivores did postpone the most detrimental effects of ocean warming on coral cover by 18–50 years (Edwards et al. 2011). This discrepancy in the influence of herbivores could be caused by the way herbivore populations were modelled. In the Edwards et al. (2011) model, grazing intensity was fixed as 40% in the high grazing scenario and contrasted with a 10% grazing term in the low grazing scenario. In our model, although the total biomass of herbivores was lower in the status quo scenario, the grazing intensity appeared to still be high enough to keep the biomass of macroalgae down and of corals up. Model skill results (Appendix F) showed that the model over-estimates some herbivorous fish groups, most notably the small-bodied parrotfish. This over-estimation of small-bodied parrotfish may contribute to our projection of the relatively weak fishing effects on coral biomass.

Our results indicate that water quality is a key local threat in the decline of coral biomass. Improving the water quality might delay the coral's ultimate climate-driven decline by 5–8 years, which could buy time to acclimate to higher temperatures. A study on the coral genus *Pocillopora* from Guam suggested that corals can, at least in part, acclimate to temperatures of 32°C which would be sufficient for persistence under the RCP 8.5 scenario (Rowan 2004). If corals cannot acclimate over such short time spans (5–8 years) and we experience the RCP 8.5 pathway, our model suggests that reef-building corals will be severely impacted by 2035–2040 (Fig. 6.8). This result is similar to a more general modelling result from Pacific reefs where coral cover dropped to 5% by the year 2050 and close to zero in the year 2055 (Ortiz et al. 2014). Ortiz et al. (2014) suggested that corals in the Pacific could recover if we can reduce to the RCP 2.6 low CO_2 emission scenario.

With the reduction of the structural framework of a degraded coral reef, after a time lag of about 15 years, the biomass of herbivorous fish declined. This time lag is in between those observed in the western Indian Ocean (5–10 years; Graham et al. 2007) and the Caribbean (25–30 years; Paddack et al. 2009). In general, roving herbivores, such as, surgeonfishes and parrotfishes, can increase in abundance after mass bleaching events (Baker et al. 2008), but their recruits are dependent on coral habitat and are responsible for the lag-time effect in the ultimate decline in population size (Graham et al. 2007). Indirect effects of coral loss also include an abundance of sponges (Loh et al. 2015) and a decrease in reef fish, mostly obligate corallivorous species, pomacentridae and gobies (Coker et al. 2014). Our study showed that benthic filter feeders (including sponges) had doubled in biomass whereas sea stars (including the corallivorous crown-of-thorns seastars) declined. Corallivorous fish did not decline but, in fact, increased. This increase is likely because the modeled corallivorous fish functional group included species that also feed on soft coral and sponges. Similarly, the functional group planktivores (including pomacentrids) were not restricted to the small planktivores that are always associated with (mostly branching) corals, but also included large-bodied species, for example, unicorn fishes, resulting is less of a decline that would be expected from truly reef dependent species (Fig. 6.11; Wilson et al. 2006, Baker et al. 2008).

6.5 Concluding remarks

We successfully developed an integrated coral reef ecosystem model that takes into account the key reef dynamics and their relationship to disturbances. The model simulations of these dynamics corresponded well with empirical data from around Guam and regional studies. The model would, however, still benefit from further refinement. In particular, fishery data, and the nutrient, phytoplankton, and zooplankton dynamics could be improved, as should the handling of vertical mixing. Such refinements, however, would unlikely change our results on the short- and long-term importance of the different drivers examined.

Quantifying an ecosystem models' uncertainty and performing skill assessments are still an under-studied part of ecosystem modelling partly because of the complexity (and hence long run times and large number of parameters) of ecosystem models that computationally prohibits the use of well-established statistical analyses. Naturally, however, those results would greatly enhance the models' robustness and management applicability. By providing insights within a consistent setting, this version of the Guam Atlantis model can be used as a decision-support tool to quantify the relative tradeoffs of alternative ecosystem-based management scenarios. Guam Atlantis is capable of simulating the consequences of different management strategies (e.g., reduction in land-based sources of pollution or fishing), while simultaneously allowing for the expected effects of ocean warming and acidification, and therefore has utility for a range of regional (e.g., regulating pollution, land use and fisheries) and global (e.g., world-wide mitigations of CO_2 and other greenhouse gasses) management applications.

Simulating the main stressors on coral reef ecosystems suggests that the reefs around Guam are presently predominantly affected by fishing and secondarily by the input of nutrients and sediments. In the near future (20–30 years from now), the predicted climate change will have the most profound effect on coral reefs. Reducing additional nutrients and sediments could mitigate the loss of coral biomass for 5–8 years, but once the temperature exceeds the bleaching threshold annually, corals are unlikely to survive. A consequence of the loss of corals is the slow decline in fish abundance, particularly of those that use the corals as habitat during a part of their life cycle, and this decline could impact the reef-fish fishery negatively.

A sign advocating the stop of night-time spear fishing. *NOAA photo*

Chapter 7

Management Strategy Evaluation applied to coral reef ecosystems in support of Ecosystem-based Management

Weijerman, M, Fulton, EA, Brianard RE. 2015. *Submitted to Ecography*. Management Strategy Evaluation applied to coral reef ecosystems in support of Ecosystem-based Management.

Ecosystem modelling is increasingly widely used to explore ecosystem-level effects of changing environmental conditions and management actions. For coral reefs there has been a push in recent decades toward the use of ecosystem models to evaluate effects of fishing and the efficacy of marine protected areas as. We applied an ecosystem model to the coral reef ecosystem of Guam using a suite of management scenarios prioritized in consultation with local resource managers to review the ecological and socio-economic performance of the reef-fish fishery including secondary effects to coral habitat. Comparing tradeoffs across the selected scenarios showed that each scenario performed best for at least one of the selected performance indicators. The integrated 'full regulation' scenario (size limits, catch limits, marine preserves and no additional land-based sources of pollution) outperformed other scenarios with four out of the six performance metrics at the cost of reef-fish landings. When the effects of climate change were taken into account, several scenarios performed fairly equally well, but none prevented a collapse in coral biomass over the next few decades assuming a business-as-usual greenhouse gas emissions scenario.

7.1 Introduction

Sustainable use of environmental resources is inextricably linked to long-term human well-being. However, there is overwhelming evidence of anthropogenic loss or degradation of coral reef ecosystems worldwide (Gardner et al. 2003, Paddack et al. 2009, Brainard et al. 2011, Burke et al. 2011, De'ath et al. 2012). Coral reef managers are challenged with sustaining the ecosystem functions and services under changing environmental conditions and use patterns (Moberg and Folke 1999, Riegl et al. 2013, McClanahan et al. 2014). Management decisions intended to achieve desired outcomes for marine systems have cultural, social, and economic consequences for the many people who depend on or use those systems. Those consequences should be accounted for in ecosystem status assessments (Brewer et al. 2012, Plagányi et al. 2013, Cinner 2014, Pratchett et al. 2014). Over around the last decade there has been a movement toward ecosystem-based management (EBM) and ecosystem-based fisheries management (EBFM) and growing recognition that human dimensions are an integrated part of these ecosystems (Pikitch et al. 2004, Fulton et al. 2011c). This move towards EBM and EBFM has also been seen in ecosystem model-based applications for coral reef ecosystems, where coastal communities are often dependent on the reef's resources (Wilkinson 2008) making ecosystem models an important tool in evaluating ecological and socioeconomic tradeoffs of management policies (McClanahan et al. 2006, Ainsworth et al. 2008a, Brown and Mumby 2014).

A recent literature review showed there has been a steep increase in the number of peer-reviewed articles on artisanal coral reef fisheries in the last 30 years (Johnson et al. 2013). In 80% of 464 peer-reviewed articles on coral reef fisheries management implications of alternative management scenarios were discussed, but primarily in general conjectural terms (Johnson et al. 2013). Only 22% of these studies presented recommendations based on their own research. Studies on the effectiveness of different management actions and approaches, tradeoffs and trajectories under climate change are still lacking (Johnson et al. 2013) and this study contributes to filling that gap.

In this paper, we describe the application of an ecosystem model to a complex multispecies fishery with degraded habitats accounting for the effects of climate change. We apply the model using the island of Guam in the tropical west Pacific Ocean as a case study. We use the Atlantis ecosystem model (Fulton 2001, http://atlantis.cmar.csiro.au/) that has previously been applied to various, primarily temperate and polar, marine ecosystems around the world to explore ecological questions, impacts of ocean and climate change, spatially-explicit fishing efforts and to rank alternative management and policy scenarios (Fulton et al. 2011b). This is the first published application of Atlantis for a coral reef ecosystem (Weijerman et al. 2014b). Five management scenarios selected during workshops in Guam were compared against the status quo i.e., maintain existing Marine Protected Areas (MPAs) and current levels of land-based sources of pollution (LBSP): A) remove existing MPAs and implement catch limits (TAC), B) remove MPAs and implement minimum-size limits; C) remove MPAs and implement TAC and size limits; D) status quo with no LBSP; and E) size limits and TAC and no LBSP. For completeness we also examined an integrated scenario F) all regulations in place, i.e., scenario E with MPAs. Scenarios were simulated with and without including climate change predictions.

7.2 Methods

7.2.1 Study site

Over the last three decades coral cover and reef-fish biomass have declined in Guam (Burdick et al. 2008). To enhance conservation of fish stocks and habitat, the government of Guam established five marine preserves. MPAs have been shown to be effective at enhancing resilience to climate change (Micheli et al. 2012), increasing coral recovery in the Caribbean (Mumby and Harborne 2010), supporting larval supplies to other areas (Christie et al. 2010) and enhancing biomass and reproduction of fish species (Evans et al. 2008). The MPAs around Guam have increased fish abundance and reproduction of some fish species compared to the open access areas (Taylor et al. 2012, Williams et al. 2012). Managers are now interested in using ecosystem modelling to explore tradeoffs of alternative management approaches (Weijerman and Brown 2013). In two workshops held in Guam in November 2012 and June 2014, resource managers and other stakeholders were asked to select management approaches and objectives that were of interest. The resulting overarching goal for coral reef management was "to obtain a sustainable coral reef ecosystem that can achieve and maintain a more desirable state than the current state given local stressors (e.g., fishing, land-based sources of pollution, COTS predation) and climate-related stressors (ocean acidification and warming)." Specific objectives necessary to achieve that goal provide target outcomes that we used to assess the effectiveness of different modeled management scenarios. These were: (1) improved water quality (no additional LBSP), (2) increased reef resilience, (3) enhanced fish biomass, and (4) similar or improved fisheries landings (Weijerman and Brown 2013). These objectives have two somewhat contradictory elements: improved ecosystem status or condition (objectives #1–3) at the same time as sustained or increased levels of extraction (objective #4).

7.2.2 Atlantis ecosystem model

The Atlantis ecosystem modelling framework is a spatially-explicit dynamic model that couples biophysical processes with human-use dynamics and the adaptive management cycle. The biophysical module tracks nutrient flows (mainly nitrogen and silica) through the biological and detritus groups specified within the model domain (Fulton 2001). Production, consumption and growth, habitat dependency, reproduction, movement and large-scale migration are all handled explicitly. All vertebrates are represented as age-structured groups; invertebrates are handled as biomass pools. Apart from these living groups, ammonia, nitrate, silica, carrion, and labile and refractory detritus are also dynamically modeled in the water column and sediment. Human-use dynamics can be incorporated through the fishing, and management and assessment modules. For the purpose of our paper, fishing was represented by constant fishing mortality and we did not include the management and assessment module.

The Guam Atlantis model encompasses the shallow (< 30 m) reefs around Guam, spanning approximately 110 km^2 (Fig. 7.1). This model domain is divided into 55 marine spatial zones with one or two water layers and is forced with daily hydrodynamic flows, salinity, and temperature outputs from a 5-km resolution, three-dimensional Regional Ocean

Modelling System model (www.myroms.org) developed for the Coral Triangle region in the western Pacific Ocean (Castruccio et al. 2013).

Trophic dynamics are represented by 42 functional groups based on diet, life-history, ecological role, and habitat requirements. Where appropriate, functional groups were further divided into target and non-target taxa (Appendix A). Initial biomass estimates for all groups came from the Pacific Islands Fisheries Science Center, Coral Reef Ecosystem Division supplemented with data from the Guam Coastal Zone Management Program, Guam Division of Aquatic and Wildlife Resources (DAWR), Guam Environmental Protection Agency, and the University of Guam Marine Laboratory and represent the ecosystem status over the period 2009–2011 (Weijerman et al. 2014b).

Climate change effects, through ocean acidification and ocean warming, are included in the model (Chapter 6). Ocean acidification negatively affected growth rates of corals as well as echinoderms, molluscs, crustose coralline algae and copepods (modeled as herbivorous zooplankton), and increased the growth rates of phytoplankton and macroalgae (Langdon 2002, Cohen and Holcomb 2009, Kroeker et al. 2010, Shaw et al. 2012). Predicted atmospheric CO_2 data came from the Intergovernmental Panel on Climate Change Assessment Report 5 using the highest emission scenario Representative Concentration Pathway (RCP) 8.5 projection. These time series data were read into Atlantis to calculate the change in pH and aragonite saturation state and, ultimately, therefore calcification rates of corals and other calcifiers (Langdon and Atkinson 2005, Feely et al. 2009, Anthony et al. 2011b). Effects of ocean warming included coral bleaching (the expulsion of symbiotic algae in the coral tissue) leading to lower coral growth rates and higher mortality. Bleaching events were triggered when ocean temperature exceeded the local bleaching threshold (1°C above the maximum summer temperature in Guam) for more than specified periods of time (known as ‘degree heating weeks’ [DHW] that includes the magnitude and duration of elevated temperatures): 3 DHW for branching corals and 4 DHW for massive corals (Jokiel and Coles 1990, McClanahan 2004, Donner et al. 2005). Predicted sea surface temperature data came from the RCP 8.5 projection using the HadGEM-AO model output, which has been shown to perform well compared to 20 similar models from the Coupled Model Intercomparison Project Phase5 [CMIP5] (CRED unpublished data)(data downloaded from: http://apdrc.soest.hawaii.edu/las8/UI.vm). We overlaid this trend on the existing time series of temperature (Castruccio et al. 2013) for each Atlantis polygon to maintain spatial differences around Guam and create a time series out to 2047 (Fig. 7.2).

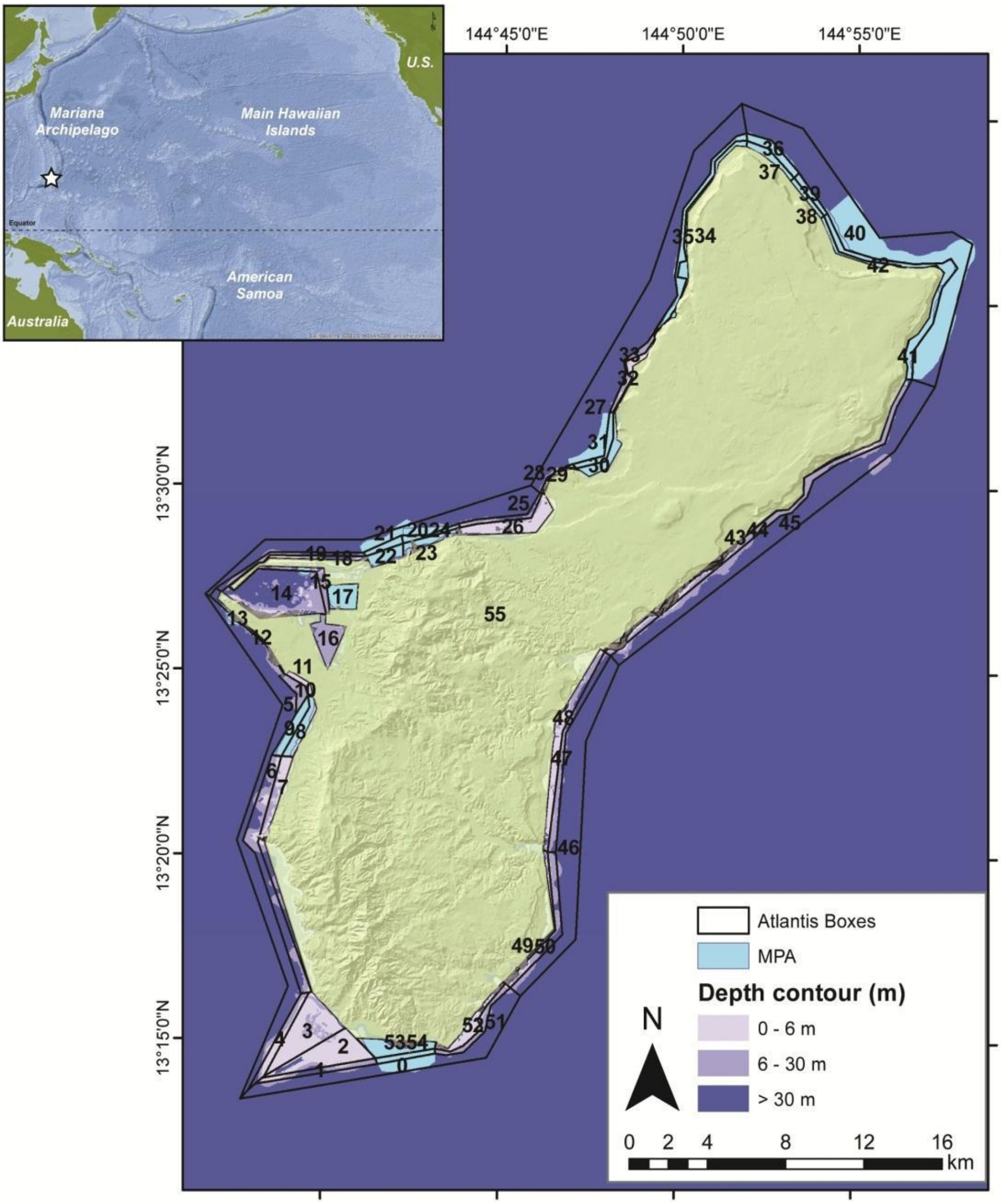


Figure 7.1. Spatial structure of the Guam Atlantis model based on homogeneous biophysical characteristics. Polygons closest to shore have one depth layer (0-6 m) and the others two (0–6 m and 6–30 m for the middle ones and 0–6m and 6–100 m for the 7 outer, boundary polygons). Blue polygons indicate marine preserves. The star in the inset map represents the location of Guam and the Mariana Archipelago in the Pacific Ocean. The polygons with nutrient and/or sediment inputs included numbers 3, 7, 8, 10, 16, 17, 22, 23, 24, 26, 30, 32, 48, 49, 52, and 53.

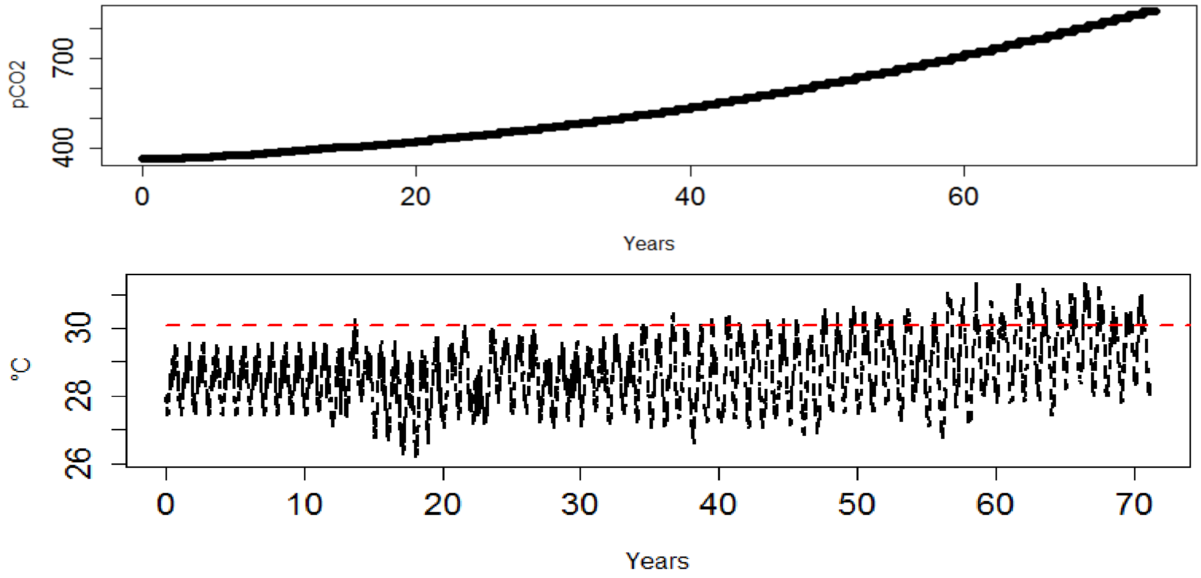


Figure 7.2. Trajectories of (*top*) predicted pCO_2 (IPCC AR5 RCP8.5) and (*bottom*) sea-surface temperature (HadGEM-AO) with bleaching threshold at 30.1°C (red dashed line). Time line is from 1975–2047. These time series were used as forcing factors for future climate and ocean change.

Initial conditions for the model and a detailed description of the model development and data sources are given in Chapters 4 and 6. The model was considered robust after passing three calibration tests (Horne et al. 2010, Link et al. 2010, Ainsworth et al. 2011a): (1) the model was able to reproduce unfished biomasses, i.e., the model reached and stabilized at similar biomass levels to those observed in marine reserves in Guam and at unpopulated Northern Mariana Islands; (2) weight-at-age stayed stable and abundance of size classes decreased with increasing size classes (few large organisms and many small ones), and (3) the model was able to fit historical catch time series which were derived from inshore creel fishery surveys conducted by DAWR. The model was further validated by comparing model output data for key coral reef dynamics (effect of LBSP, mitigating effect of structural complexity on fish predation, coral-algal competition) with empirical data from Guam and published relationships (Appendix F).

7.2.3 Simulated management scenarios

In total, seven scenarios were simulated with Guam Atlantis:

1) Status quo represented by five MPAs and existing levels of land-based sources of pollution. The status-quo simulation had constant fishing mortalities per functional group with no fishing in the MPAs. Fishing mortalities were calculated using shore-based creel surveys (DAWR) extrapolated to the whole of Guam by staff from the NOAA Western Pacific Fisheries Information Network (WPacFIN). Annual catches were compared to estimates of standing stocks for each functional group to give fishing mortality rates. We used a constant fishing mortality (F) per functional group (Table 1) with F=0 per year in the five MPAs. LBSP was modeled as the addition of nutrients and sediments to the coastal polygons with riverine run-off and/or sewage outfall pipes (Fig. 7.1), and estimated

loads were based on flow data and the related sediment and nutrient inputs per river for each Atlantis polygon (Weijerman et al. 2014b).

2) Remove existing MPAs and implement a weekly catch limit (TAC) with existing levels of LBSP. We estimated an annual limit as 75% of the average catches of the first five years of the status quo catches and then converted this value to a weekly TAC. We simulated the TAC scenario with the same fixed fishing mortalities as in the status quo simulation. Fishing was allowed in every polygon, when the TAC was reached, fishing stopped for that week.
3) Remove existing MPAs and implement size limits with existing levels of LBSP. For the size-limits based fishery simulations, we assumed a fishery that would leave all immature fishes. Based on the weight and age at first maturity, the fishery start age for each functional group differed (Table 7.1). Fishing was allowed in every polygon with fixed fishing mortalities equal to the status quo simulation.
4) Remove existing MPAs and implement TAC and size limits with existing levels of LBSP. In this scenario we combined the rules of scenarios 2 and 3.
5) Remove existing MPAs and implement TAC and size limits with no LBSP. This scenario differed only from scenario 4 by not simulating the delivery of additional nutrients and sediments to the coastal areas.
6) Status quo with no LBSP. In this scenario we used the same constant fishing mortalities as identified under scenario 1, but did not simulate any additional LBSP to the coastal areas.
7) Full regulations: keep existing MPAs and implement size limits and TAC with no LBSP. This scenario combines scenarios 5 and 6.

Each of the scenarios was first simulated for 30 years (1985–2015) without including climate change predictions. Then, based on performance evaluation (see Results section), the best three scenarios (#5–7) were also run for 45 years (1985–2030) under the current trajectories for climate change (RCP 8.5).

Table 7.1. Characteristics of reef-fisheries per functional fish group. Fishing was modeled as constant fishing mortality using mortality rates based on historical catches as shown in the first column. For the size-limited fishery scenario the age when fishing starts for each functional group was based on age and weight at first maturity.

Functional group	**Fishing mortality (per year)**	**Age at first maturity (years)**	**Length at first maturity (cm)**	**Weight at first maturity (g)**	**Age class fishery starts**	**Source life-history information (FishBase with additional data indicated by citation)**
Planktivores	0.026	1.2	13.9	162	2	Dee and Parrish 1994, Wilson and McCormick 1999
Coralivores	0.0001	1.2	10.7	177	2	MacDonald 1981
Invertivores	0.033	1.4	15.9	199	2	FishBase
Target invertivores	0.200	2.2	22.0	258	2	Taylor et al. 2012
Humphead wrasse	0.218	6.0	70	6,827	6	Choat et al. 2006
Detritivores	0.001	0.9	13.3	64	2	FishBase
Browsers	0.116	1.1	20.2	670	4	Taylor 2012
Target browsers	1.075	2.6	20.6	352	2	Taylor 2012
Grazers	0.004	1.7	14.0	193	3	FishBase
Target grazers	0.068	1.4	13.7	79	2	Hart and Russ 1996
Scrapers	0.018	1.4	17.9	84	2	Taylor 2012
Excavators	0.157	2.2	25.3	342	2	Taylor 2012
Bumphead parrotfish	1.50	8.0	61.0	4696	6	Hamilton et al. 2008
Benthic piscivores	0.096	2.0	76.5	996	2	FishBase
Target benthic piscivor	0.041	3.8	25.8	538	4	Rhodes et al. 201)
Mid-water piscivores	0.187	2.0	39.3	626	2	FishBase
Roving piscivores	0.104	5.6	77.1	2708	6	Sudekum et al. 1991, Longenecker and Langston 2008
Reef sharks	0.266	4.3	112.0	21,591	4	FishBase
Rays	0.003	5.4	150	38,196	4	Schluessel 2008
Turtles*	<0.0001	37.5	81	82,414	36	Frazer and Ehrhart 1985, Balazs and Chaloupka 2004

* turtles are not reported in catch data (take is prohibited) but anecdotal evidence suggests that they are served at large cultural events so we assumed a low harvest rate

7.2.4 Performance evaluation

The overarching goal that came out of the resource users and managers workshop was to improve reef ecosystem state while maintaining or increasing fisheries landings from current levels. The criteria we used to assess the performance of the scenarios are based on a model simulation with no external stressors for ecosystem state conditions and for the fishery the current landings, hence, ecosystem metrics reaching these values were considered best. Performance of each scenario was measured at the end of the simulation against criteria for six ecosystem metrics based on the management goals (Table 7.2):

1) *Improved water quality*. The metric used to assess the performance of this goal was benthic calcifiers to non-calcifiers ratio with calcifiers defined as corals and crustose-coralline algae (CCA) and non-calcifiers as turf and macroalgae. High concentrations of sediments and nutrients favor macroalgal growth over coral growth influencing the physical and ecological controls of coral-macroalgal dynamics (Hughes 1994, Lapointe 1997, Mumby et al. 2007a). Additionally, terrigenous sediment smothers corals and other substrate thereby lowering coral growth and recruitment (Marshell and Mumby 2012). Reefs in the southern part of Guam have experienced high sediment concentrations for around the last 30 years, because of clearing and burning of upslope watersheds, and the steep slopes wash large volumes of sediment into nearshore waters during heavy rainfall events (Wolanski et al. 2003a, Wolanski et al. 2004, Burdick et al. 2008). Over the same time period, severe recruitment failure has been observed (Minton et al. 2007). An important function of corals and crustose coralline algae is the three-dimensional structure they create through growth. This complexity gives refuge to numerous species and as such maintains diversity and enhances fisheries productivity (Coker et al. 2013, Rogers et al. 2014).
2) *Increased reef resilience*. Performance metrics for this goal were (a) biomass of apex predators and (b) biomass of herbivorous fishes, as these groups are critical for maintaining coral-reef habitat and the diverse assemblages dependent on these reefs (Jennings and Polunin 1996). The disappearance of apex predators from a reef can result in a shift towards smaller-bodied species in lower trophic levels and consequent loss of reef resilience (Stallings 2008, Mumby et al. 2012). Additionally, loss of apex predators increases the reef community's susceptibility to disturbances (Bascompte et al. 2005). Herbivores play a critical role in the maintenance of coral reef resilience by keeping algal communities in cropped states and thereby tipping the competitive balance towards corals (Mumby et al. 2007b, Hoey and Bellwood 2011, Bejarano et al. 2013). Large-bodied herbivores are believed to be particularly important in this regard (Lokrantz et al. 2008, Jayewardene 2009). Herbivorous urchins are not abundant in Guam (Brainard et al. 2012) and therefore we assumed are locally less important as grazers. Consequently, we focused on the various herbivorous fish species pooled into functional groups: browsers (e.g., unicorn fishes, *Naso lituratus*) reduce the biomass of upright algae, grazers (surgeonfishes, *Acanthurus sp*) maintain algal assemblages in cropped states, scrapers (small-bodies parrotfish, *Chlorurus sordidus*) eliminate algal growth on coral colonies, and they and excavators (large-bodied parrotfish, *Chlorurus frontalis*) open up space for coral recruitment (e.g., Bellwood and Choat 1990; Hoey and Bellwood 2011).
3) *Enhanced fish biomass*. High total fish biomass has been rated as important to ocean users (Williams and Polunin 2000). Additionally, a high biomass sustains the integrity of ecosystems as it incorporates a range of desirable characteristics (e.g., large breeding stock, diverse ecological functions, relatively intact ecosystem state including all trophic levels) and are, therefore, more likely to recover from disturbances and sustain extraction than low biomass systems (Jennings and Polunin 1997, Friedlander and DeMartini 2002, Dulvy et al. 2004, Marshell and Mumby 2012, Bejarano et al. 2013, Lindfield et al. 2014).

4) *Maintenance of or improved fishery landings*. Performance for this goal was measured by two fishery-related metrics: (a) the number of functional fish groups that are not overexploited, and (b) landings of reef fish. Recruitment overfishing (the reduction of a spawning stock past a point at which the stock can no longer replenish itself) can become an irreversible problem leading to fishery collapse (Taylor et al. 2012). We defined a functional group overexploited when the ratio of the spawning stock biomass (SSB) to the 'virgin' SSB was below 30% (Restrepo 1998). Landings of reef fishes are an important social metric. In Guam, many fishers fish for cultural or social reasons instead of economic reasons and the majority of fishers share their catches which makes fishing a social activity (Allen and Bartram 2008).

To account for interannual variability, we took the mean of the last five simulated years. For ease of interpretation and visualization, the 5-year mean values were normalized over all strategies so that the best result of an ecosystem metric is assigned the value of 1 and all other values scaled accordingly.

Table 7.2. Goals, ecosystem metrics and performance criteria. Performance of alternative strategies was based on reaching the criteria of conservation ecosystem metrics (#1-3) and extraction ecosystem metrics (#4a, b). Criteria were based on a simulation of no local (fishing and land-based sources of pollution) or global (climate change) disturbances. The criteria for landings are the landings of a status quo simulation.

Goal	**Ecosystem metric**	**Criteria without climate change (30 year)**	**Criteria with climate change (45 year)**
1. Improved water quality	Calcifiers:non-calcifiers ratio	0.94	1.15
2a. Increased reef resilience	Biomass of herbivores	2376 t	2,399 t
2b. Increased reef resilience	Biomass of apex predators	760 t	759 t
3. Enhanced fish biomass	Total reef-fish biomass	4967 t	5,447 t
4a. Maintain or improved fishery landings	Number of fish groups not overexploited	20	20
4b. Maintain or improved fishery landings	Biomass of reef-fish landings caught by shore-based fishers	130 t	130 t

Different weightings can be given to the ecosystem metrics in quantifying the overall performance of each management approach. Since managers identified 4 ecosystem goals and the identified ecosystem metrics are based on those goals, we weighted 1–4 equally and took the average of 2a (biomass herbivores) and 2b (biomass apex predators) for goal 2 and the average of 4a (number of fish groups not overexploited) and b (reef-fish landings) for goal 4. As the management goals can also be grouped into a conservation component, (goals 1–3) representing the functionality of the ecosystem and a socio-economic component (goal 4), we also evaluated the cost and benefit tradeoffs between the metrics #1–3 (all weighted equally) and metric #4 by taking the overall average of these two components (Table 7.2).

We wanted to take a realistic no-regrets approach to management strategy selection, so the better performing scenarios with no climate change were also re-run with climate drivers and effects included. For this approach we selected only scenarios where the performance evaluation with no climate change had an average across all goals > 0.50.

7.3. Results

No one management scenario was best for all goals. However, scenarios with improved water quality led to high ratios of calcifiers to non-calcifiers—all were 0.94 or above—which was a result of both increased coral cover and reduced algal biomass (Table 7.3, Fig. 7.3). Ecosystem effects of improved water quality included decreased biomass of planktivores (FPL), corallivores (FCO), benthic carnivores (BC), infauna (BM, e.g., polychaetes), benthic grazers (BG, urchins), and phytoplankton (PS, PL) and increased biomass of most apex predators (FPB, FPM, FPR, SHR), benthic filter feeders (BFF), benthic detritivores (BD, e.g., crabs, lobsters, molluscs), sea stars (BSS) and demersal (ZD) and herbivorous (ZH, copepods) zooplankton (Fig. 7.3).

Among fishery regulation scenarios, imposing a TAC led to more favorable outcomes than status quo and size limit scenarios. The TAC scenario led to higher biomass of herbivores and overall reef-fish biomass and fewer groups becoming overexploited compared to the status quo and size limit scenarios—only the bumphead parrotfish (*Bolbometopon muricatum*) was still overexploited in the TAC scenario. Ecosystem effects of the TAC scenario were less pronounced compared to the scenarios with improved water quality—with main effects being an increase in prey fish groups and in sharks (SHR). Response of invertebrate groups was similar in all fishery regulation and status-quo scenarios (Fig. 7.3). The tradeoff of the TAC scenario was a 20% reduction in fish landings.

For ecosystem state metrics (#1–3) the size-limit based fishery scored worse than status quo, but fish landings (goal #4) were 5% higher (Table 7.3). None of the ecosystem status metrics reached the criteria (Tables 7.2 and 7.3) and four fish groups were overexploited at the end of the simulation, compared to the status quos scenario. The small increase in fish catch, and switch towards larger size classes that is inherent to this scenario was reflected in the reduction in the abundance of large fishes (Fig. 7.4). Despite the overall reduction in predatory and invertivorous fish functional groups in this scenario, invertebrates themselves did not increase noticeably compared to the status quo scenario (Fig. 7.3).

The combined size limit and TAC and no LBSP scenario and the full regulation scenario (combined size limit and TAC, no LBSP and MPAs), had respectively two and three metrics that reached the criteria (Table 7.2) indicating improved ecosystem state compared to the status quo, but at the cost of 20% and 21%, respectively, reduction in fishery landings (Table 7.3). In all scenarios, the bumphead parrotfish was still overexploited. Under status quo scenarios with and without LBSP, and also in the size-limited fishery scenario, the humphead wrasse (*Cheilinus undulates*), target browsers (*Naso* sp.) and reef-associated sharks were also overexploited.

Table 7.3. Results of ecosystem metrics as mean values of last 5 years of a 30-year simulation of seven management scenarios. The criteria are the mean values of a 30-year simulation of no fishing and no land-based sources of pollution (LBSP). WQ is water quality and represents a simulation with no LBSP; calc is calcifiers (corals and crustose-coralline algae); non-calc is non-calcifiers (turf and macro-algae). Target fish groups are fish groups targeted by shore-based fishers (Appendix A).

	Status Quo	**Size-limit**	**TAC**	**Size limit &TAC**	**Status Quo & WQ**	**Size&Bag &WQ**	**Full regula -tions**	***Criteria***
ratio calc.: non-calc.	0.79	0.76	0.77	0.76	0.98	0.94	0.94	*0.94*
biomass herbivores (t)	2,007	1,834	2,160	2,122	1,986	2,075	2,086	*2,375*
biom. apex predators (t)	423	375	446	440	500	557	560	*760*
total reef-fish biom (t)	3,876	3,654	4,305	4,283	3,811	4,258	4,953	*4,966*
# of non-overexploited groups	16	16	19	19	16	19	19	*20*
landings targeted fish groups (t)	130	137	104	103	141	104	103	*130*

The management of complex ecosystems is influenced by the tradeoffs of the objectives related to different components of the reef system, i.e., the ecosystem goods (metrics #4) and ecosystem services (metrics #1–3). To show these tradeoffs we present an overall aggregate performance measure kite diagram for the average of the last 5 years of the simulation of each management scenario (Fig. 7.5). Comparing tradeoffs across these scenarios shows that each scenario neared the criteria of at least one of the ecosystem metrics (Fig. 7.5). When fishing is regulated according to the integrated ‘full regulation’ scenario (size limit and TAC, marine reserves, and no LBSP), landings were reduced by 21% but all other metrics increased between 4% (biomass herbivores) and 32% (biomass apex predators) compared to the status quo. The outcomes of this scenario were approaching the criteria for four out of the six metrics (Table 7.3, Fig. 7.5). Results were similar for the combined size limit and TAC with no LBSP but the total reef-fish biomass metric performed less well.

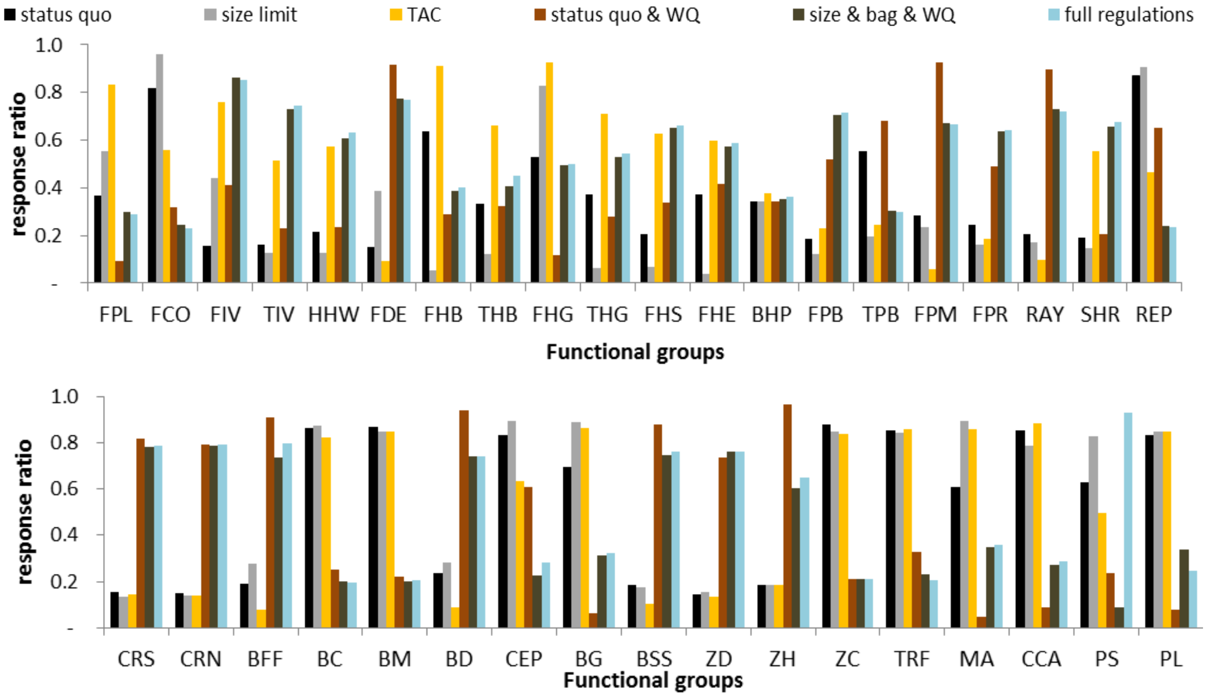


Figure 7.3. Ecosystem effects of alternative scenarios on (*top panel*) vertebrates and (*bottom panel*) invertebrates (values normalized so 1 = high and 0 = low biomass). Size limit and TAC results were very similar to only TAC results and left out for clarity. See appendix A for functional group codes.

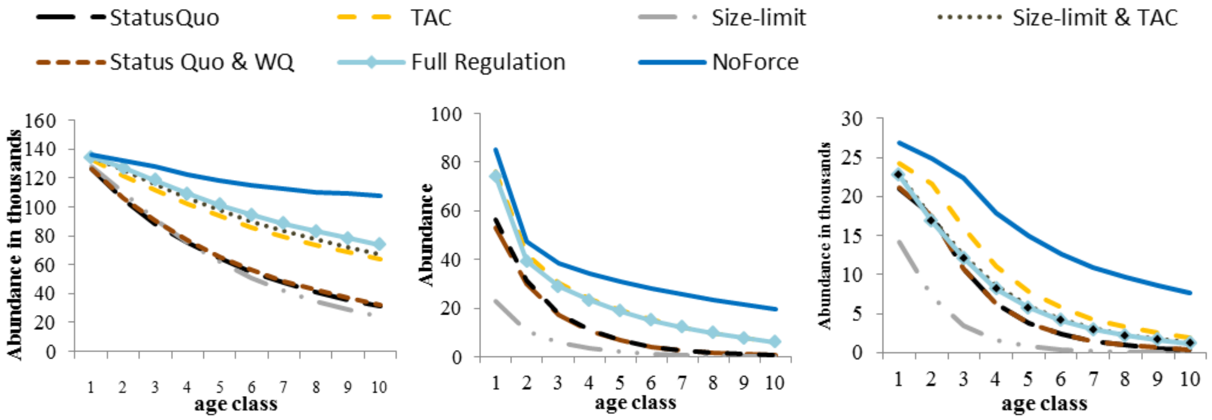


Figure 7.4. Size class distribution of (*left*) target invertivorous fish (e.g., goat fish, snapper, wrasse), (*middle*) humphead wrasse, and (*right*) target browsers (e.g., unicornfish) under different management scenarios. The “No Force” scenario indicates no fishing and no land-based sources of pollution. The scenario size limit & TAC and no LBSP led to very similar results as the size limit & TAC scenario and is therefore left out for clarity. WQ is water quality, indicating no LBSP. The full regulation scenario is size limit and TAC, MPAs and no LBSP.

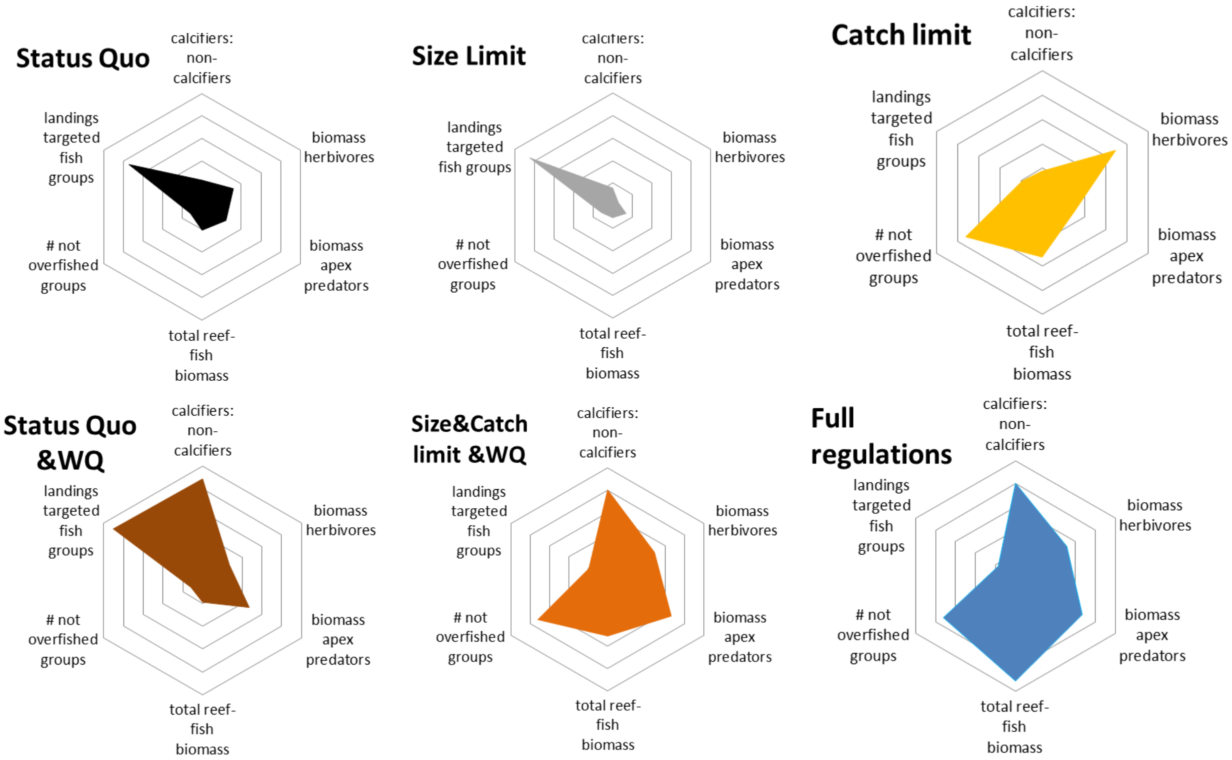


Figure 7.5. The overall performance of the management strategies for the scaled integrated (composite) performance measures (scaled so that best performance of any scenario in each metric is set to 1 (outer ring) and all other responses scaled to that). The performance of the size limit and catch limit (TAC) scenario was almost identical to the Catch limit scenario and is left out for simplicity.

Evaluating the overall performance of each management approach weighting the management goals 1–4 equally, the scenario with full regulations had the highest average value followed by the combined size limit and TAC and no LBSP (Table 7.4). Quantifying the performance of just the conservation components (goals 1–3), showed that the full regulation scenario again had the highest overall value (Table 7.4). With regard to the extraction or socioeconomic component (goal #4), two scenarios scored similar: status quo with no additional LBSP (0.51) and size limit (0.49; Table 7.4).

Table 7.4. Normalized results of ecosystem metrics used in performance evaluation of alternative management scenarios with regards to the ecosystem status (metrics # 1-3) and socio-economic conditions (metrics # 4a,b). WQ is water quality, indicating no land-based sources of pollution; calcifiers are corals and crustose coralline algae and non-calcifiers are turf and macroalgae.

Goal	Ecosystem metric	Status Quo	Size-limit	TAC	Size limit & TAC	Size limit & TAC &WQ	Status Quo &WQ	Full Regula-tions
1	calcifiers:non-calcifiers	0.23	0.16	0.18	0.15	0.80	0.89	0.80
2a	biomass herbivores	0.32	0.06	0.70	0.60	0.48	0.27	0.51
2b	biomass apex predators	0.24	0.14	0.31	0.29	0.66	0.47	0.67
3	total reef-fish biomass	0.21	0.11	0.53	0.52	0.50	0.18	0.92
4a	number of non-overexploited groups	0.12	0.12	0.72	0.72	0.72	0.12	0.72
4b	landings targeted fish groups	0.75	0.85	0.19	0.16	0.19	0.90	0.17
	average goals 1-4	0.29	0.21	0.42	0.39	0.59	0.49	0.69
	conservation (#1–3)	*0.25*	*0.11*	*0.43*	*0.39*	*0.61*	*0.46*	*0.72*
	extraction (#4)	*0.43*	*0.48*	*0.46*	*0.44*	*0.46*	*0.51*	*0.45*

We also took into account the effects of predicted climate change (ocean acidification and ocean warming) on corals but only for the three management approaches that performed better overall (average effect size ecosystem metrics ≥ 0.5 when goals are weighted equally): status quo and no LBSP; size limit, TAC and no LBSP; and the full regulation scenarios. Absolute values for the ecosystem metrics varied only slightly between the three scenarios (Table 7.5). The major consequence of incorporating climate change was a large reduction in the ratio of calcifiers to non-calcifiers, to around half of the ratio in scenarios without climate change (Tables 7.3 and 7.5). The overall aggregate performance measure kite diagram shows the tradeoffs of the simulation of each management scenario with the full regulation and size limit and TAC and no LBSP scenarios being almost identical and scoring better overall than the status quo on four out of the six performance measures (Fig.7. 6). Comparison of outcomes with and without local stressors showed that coral biomass is greatly enhanced in the short-to-medium term (30 years) when local stressors are absent. However, the cumulative effects of climate change and local drivers resulted in a sharp reduction in all ecosystem metrics (Fig. 7.6), and corals decline dramatically after approximately 50 years, by which time projected ocean temperature regularly (almost annually) surpasses the bleaching threshold and pCO_2 > 500 ppm (Fig. 7.2). By that time, corals decline terminally irrespective of which management approach was implemented (Fig. 7.7).

Table 7.5. Results of ecosystem metrics as mean values of last 5 years of a 45-year simulation run of three management scenarios accounting for climate change. The criteria are the mean results of a simulation of no fishing, no land-based sources of pollution and no effects of climate change. WQ is water quality and represents no additional sediment and nutrient inputs, calcifiers are corals and crustose coralline algae; non-calcifiers are turf and macro-algae. t is metric tons.

	Size limit & TAC&WQ	**Status Quo & WQ**	**Full regulations**	***Criteria***
ratio calcifiers: non-calcifiers	0.58	0.61	0.58	*1.15*
biomass herbivores (t)	2,033	1,942	2,045	*2,399*
biomass apex predators (t)	550	513	555	*759*
total reef-fish biomass (t)	4,687	4,279	4,723	*5,447*
number of non-overexploited groups	18	16	18	*20*
landings targeted fish groups (t)	104	105	103	*130*

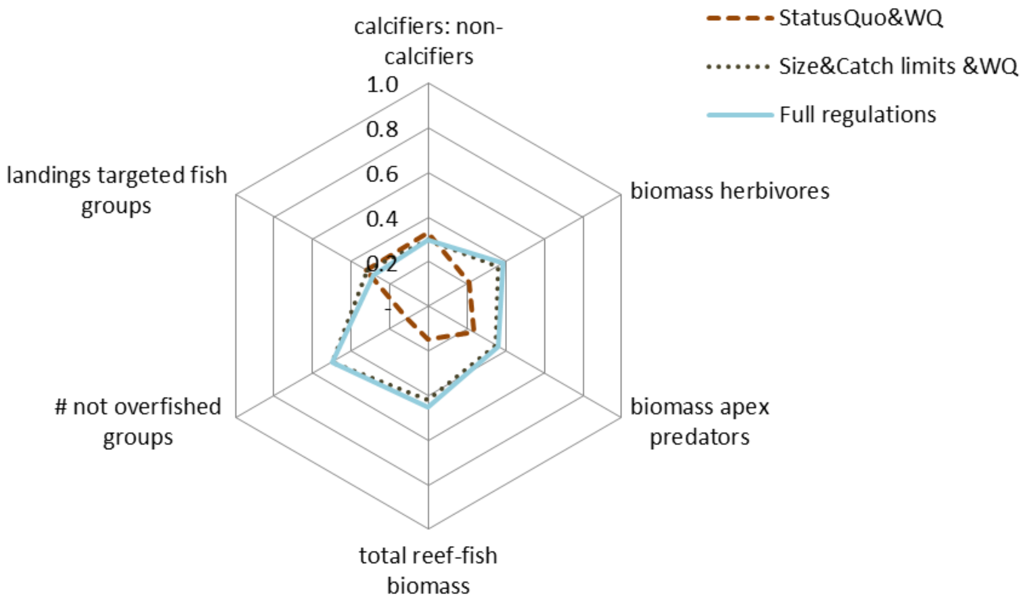


Figure 7.6. The overall performance of the management strategies for the scaled integrated performance measures (scaled so that best performance of any scenario in each metric is set to 1 and all other responses scaled to that). WQ is water quality and represents no additional sediment and nutrient inputs.

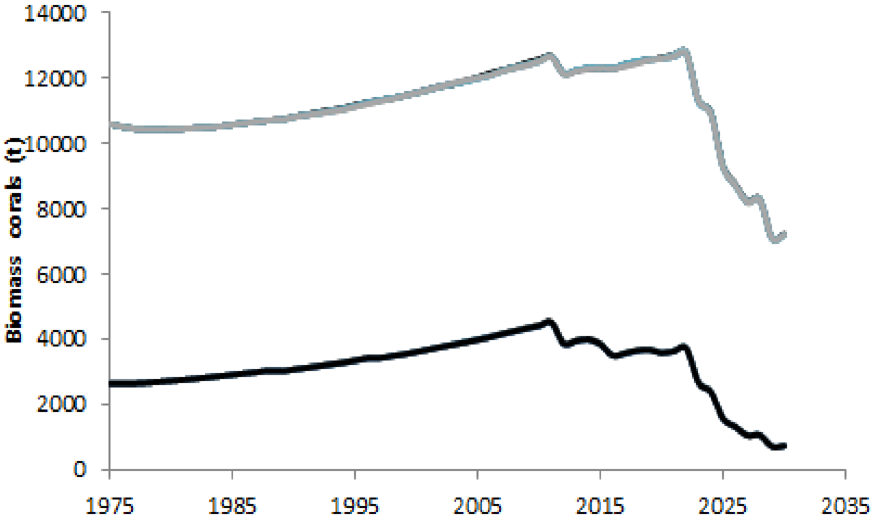


Figure 7.7. Biomass trajectories of (*grey line*) massive corals and (*black line*) branching corals under four management approaches simulating the effects of predicted climate change (ocean acidification and ocean warming) under the IPCC AR5 RCP 8.5 emission scenarios. The scenarios were status quo with no LBSP, size limit and TAC with no LBSP, full regulation scenario, no fishing and no LBSP scenario. All scenarios projected the same trend in coral biomass.

7.4 Discussion

A move toward resilience-based approaches to coral reef management, as an extension of EBM, has been promoted (Hughes et al. 2010, Pandolfi et al. 2011). Empirical evidence and modelling studies have improved understanding of reinforcing feedbacks, hysteresis, and the reversibility of phase-shifts (Hughes 1994, Scheffer et al. 2001, Bellwood et al. 2004, Mumby et al. 2007a). For example, local studies have shown that reversal of an alga-dominated state back to a coral-dominated state is possible on a small scale (Burkepile and Hay 2008, Stimson and Conklin 2008). Also, when local stressors are reduced, for example fishing is reduced (McClanahan et al. 2014) or the biomass of herbivores is enhanced (Edwards et al. 2011), corals appear to be more resilient to the effects of climate change and recover more quickly (Carilli et al. 2009). Evaluating selected management strategies in this study showed that each performance metric reached one or more of the criteria while performing less well on other criteria. Only the full regulation scenario, which integrated all management approaches, performed better (metrics closest to 1) overall with the main tradeoff being the landings of target reef-fish groups (Fig. 7.4, Table 7.4). However, when also taking into consideration the cumulative effects of climate change on coral reefs, all scenarios performed poorly (Fig. 7.6). Stricter regulations on size-limits and TAC with or without MPAs and no additional LBSP showed a slightly better performance than the status quo scenario in terms of fish biomass (total, herbivores, apex predators), but that did not correspond with clearly increased capacity for corals to deal with climate change. When the ocean temperature was consistently above the bleaching threshold in successive years and the atmospheric CO_2 concentration was above 500 ppm, all approaches showed a severe decline in coral biomass starting around 2023 (Fig. 7.7). This result corresponds with the findings of other studies that showed that corals will be in a rapid and terminal decline when the frequency of thermal events is too high for corals to recover (Thompson and Dolman 2010, Selig et al. 2012, Ortiz et al. 2014). Veron et al. (2009) showed that corals would be negatively affected by the combined effects of mass bleaching and ocean acidification once CO_2 concentration reaches above 450 ppm. While Silverman et al. (2009) suggests that when the CO_2 concentration surpasses 560 ppm, coral reefs will dissolve, and hence, fisheries management can have little impact on their survival at that point. The results from this case study can be used to draw more general conclusions about the range of management measures that are likely important in practical implementation of EBM in other tropical reefs.

MPAs, including no-take areas, are among the most studied management approaches for coral reef ecosystems (Johnson et al. 2013). Although MPAs tend to have higher diversity, density and biomass of exploited reef fishes and of some motile invertebrates compared with areas outside the MPAs, and can produce some benefits for reef-associated tourism (Graham et al. 2011a), there is limited evidence that MPAs can be expected to have large impacts outside their boundaries—such as on fisheries yields (Graham et al. 2011a). Therefore, it was perhaps not surprising that the status quo scenario (MPAs alone) did not come out as the ‘best’ overall approach for Guam as a whole. Only for goal 4, maintenance or improved fisheries landings, did status quo produce the ‘best’ result – particularly when water quality was improved.

While the full regulation scenario performed best for the ecosystem state, the cost of enforcement associated with the different management scenarios was not factored into our analysis. Enforcing TACs and/or size limits around the entire island is more labor intensive, and hence likely more costly, than the enforcement of fishery regulations in site-based marine preserves. Additionally, habitat damage inflicted by fishing gear, abandoned gear (e.g., ghost nets, fishing line), and trampling was also not taken into account. Fractured corals have a lower growth rate than entire colonies and small fragments have increased mortality rates in comparison with larger fragments (Rodgers et al. 2003). A study in Indonesia compared the effects of gear restriction on coral cover and reef-fish biomass and found that the prohibition of fishing nets led to less habitat degradation while maintaining fish biomass (Campbell et al. 2012). We did not include gear restrictions in our scenarios, but it seems safe to conclude that when no or limited gear types are allowed (such as in marine preserves) habitat will be less impacted. Managers and stakeholders need to agree on the weighting of the somewhat contradictory objectives and take into account these issues of gear use and enforcement when making a decision on which management approach would best suit their needs.

7.4.1 Caveats and model uncertainty

Corals’ response to ocean acidification is not fully understood (Mumby and van Woesik 2014) and their response to ocean warming is complex and depends on their thermal history and ability to acclimate or adapt (Maynard et al. 2008, Palumbi et al. 2014), not just the predicted level of greenhouse gas emissions (Baskett et al. 2009b). Resistance to coral disease, which often follows bleaching events, is predicted to change with some researchers predicting increased resistance (Yakob and Mumby 2011) and others expecting decreased resistance (Maynard et al. 2015). For that reason, we did not include that in the model, but clearly such changes would affect corals' future vulnerability to diseases. In our model we included the best available data for the effects of ocean warming and ocean acidification and modeled disease as a mortality factor after bleaching. However, these are fixed parameters that do not incorporate possible scope for adaptation or acclimatization to changing environmental conditions. We also omitted the effects of cyclones from all scenarios, which are predicted to become more frequent in the region in future years or changes in nutrient supply from deeper waters as a result of predicted increased stratification (IPCC 2007). Consequently, the results presented here should only be considered relative to each other rather than in absolute terms.

The model was validated based on its capability to reproduce expected coral reef dynamics for example between herbivore biomass, coral cover, and macroalgal cover, and between reef complexity and fish biomass (Chapter 6). The model was further deemed robust if it met accepted Atlantis modelling conventions (e.g., sizes of individual age classes not differing by more than 20% from initial conditions) as applied in other ecosystems (Horne et al. 2010, Link et al. 2010, Ainsworth et al. 2011a, Fulton et al. 2014). However, the lack of time series of any biological group made model skill assessment (Stow et al. 2009) impossible. Additionally, the physical state of the ecosystem contributed to the uncertainty of model outcomes as the oceanography module, used to force water flows and advect nutrients and plankton, was based on a ROMS model developed for the Coral Triangle (CT; Southwest of Guam) rather than targeted on Guam (Castruccio et al. 2013). This meant that Guam was on the 'edge' of the model domain, hence, not adequately incorporating all of the regional oceanographic initial conditions. Furthermore, the coastal polygons are small compared to the spatial resolution of the CT-ROMS model of 5 km, undermining the accuracy. However, in its current state, the model was capable of evaluating a range of potential management strategies and yielded results that (as described above) met various criteria for plausibility. Hence, we feel the current model is a fair representation of the ecosystem but it is only one implementation. Consequently, the analysis of management options here should only be considered a first step and subject to uncertainty that could be resolved (to some degree) in the future by checking the relative performance of the management options across multiple parameterizations of the model.

7.5 Conclusions

Management of coral reef ecosystem is transitioning toward an ecosystem-based management. The efficacy of marine protected areas has often been the key focus of ecosystem model-based analyses, but other scenarios and the effects of climate change remain understudied (Johnson et al. 2013). This paper showed that under the business as usual greenhouse-gas-emissions scenario (the RCP8.5 trajectory), with no adaptation or acclimation by reef organisms, the reefs around Guam will collapse in the next few decades. This conclusion corresponds with other recent studies of Pacific coral reef ecosystems (Thompson and Dolman 2010, Ortiz et al. 2014) and from a global meta-analysis (Selig et al. 2012). Model scenario evaluation for this study also indicate that without some form of biological adaptation by corals this collapse is likely to occur even with management scenarios in place to alleviate local stressor

Results showed that each of the identified scenarios had pros and cons and the combination of the various management approaches had the best results overall at the cost of a 21% loss in fish landings. The status quo scenario (with the established MPAs) with no LBSP had the best result for fish landings at the expense of reef functionality. Thus, choosing among management scenarios with conflicting goals requires a priori weighting of the importance of the various goals. For example, are the total fish landings equally or more important than the benthic condition of the reef or the functionality of the reef ecosystem? Ecosystem models can be an important tool for local management in visualizing and exploring the costs and benefits of the various approaches under consideration. Adoption of the approach that performed best can result in a more effective achievement of socio-economic and ecological goals.

Green sea turtle for culinary or visual pleasure. *Photo NOAA*

Chapter 8

Towards an Ecosystem-based approach of Guam’s coral reefs: the human dimension

Weijerman, M, Grace-McCaskey, C , Grafeld, S. Kotowicz, D, van Putten I. *Submitted to Marine Policy*. Towards an ecosystem-based approach of Guam’s coral reefs: the human dimension.

Management of tropical reef ecosystems under pressure from terrestrial and extractive marine activities is not straightforward, especially when the interests of extractive and non-extractive marine resource sectors compete. Before implementing management actions, potential outcomes of alternative management strategies can be evaluated in order to avoid adverse or unintended consequences. In tropical reef ecosystems the continued existence of the cultural and recreational fishing activities and the economically important dive-based tourism and recreation industry rest on sustainably managed marine resources. Through a case study of Guam, an ecosystem model was linked with human behavior models for participation in fishing and diving to evaluate future socio-ecological impacts of different management options. Ecosystem indices for reef status and resilience, and extraction potential were identified to evaluate the performance of alternative management scenarios. These marine ecosystem indices link the natural system to human uses (fishing and dive-based tourism and recreation). Evaluating management scenarios indicate that applying a single management tool, such as, input controls or marine preserves, without also managing the watershed, is suboptimal. Combining different management tools has negative near-term costs, particularly for the fishing sector, but these are likely to be outweighed by the long-term benefits obtained from greater species abundance. Adopting watershed management measures in addition to fishery regulations distributes the burden for improving the reef status across multiple sectors that contribute to reef pressures.

8.1 Background

Ecosystem-based management is increasingly advocated for marine fisheries around the world (Sainsbury and Sumaila 2003, Pikitch et al. 2004). Typically, different management strategies could be implemented to achieve the management objectives specified in an ecosystem approach. Management strategy evaluation (MSE), which compares and contrasts outcomes across multiple management objectives, is a tool implicit to an ecosystem approach (Smith 1994, Sainsbury et al. 2000). One MSE approach involves the development of integrated marine ecosystem models, which requires intimate knowledge of the biophysical as well as the socio-economic systems (Allen and Bartram 2008, Yee et al. 2014). Integrated models can simulate the ecological, social, and economic consequences of different management approaches (Smith et al. 1999, Smith et al. 2007, Fulton et al. 2014). Changing human behavior is the main management lever, and thus a critical component of integrated ecosystem modelling (Fulton et al. 2011c). However, human behavior models of non-commercial activities are seldom coupled to biophysical- economic models.

Typically, these integrated models depict economic behavioral drivers quantitatively through the use of metrics, such as, profit maximization (van Putten et al. 2012). Yet these models fail to capture the significant, non-commercial element of the fishery system, where fish might be taken for cultural or traditional celebrations, household consumption or barter (Everson and Friedlander 2004, Allen and Bartram 2008, Hospital and Beavers 2012). Moreover, this commercial focus on extraction ignores the significant economic importance of non-market and non-extractive uses of the marine system (Craig 2008).

Both reef-fish fisheries and reef-related tourism and recreation are dependent on the condition of the reefs, which are presently under heavy pressure in many parts of the world (Brainard et al. 2011, Burke et al. 2011). Effective management of coral reef resources must consider continued existence of these valuable extractive and non-extractive resource uses as well as the health of the marine ecosystem upon which they depend (Plagányi et al. 2013).

In this study, a dynamic reef biophysical model is linked with human behavior models for the coral reef ecosystem of Guam. In Guam, tourism is one of the major contributing economic activities to Guam's gross domestic product (Van Beukering et al. 2007) and reef-fish fishing is mainly conducted for social or cultural reasons (Allen and Bartram 2008). Despite the importance of a healthy reef system, the status of Guam's marine resources has deteriorated over the past few decades (Burdick et al. 2008, Williams et al. 2015). Guam's reefs have been stressed by poorly executed coastal development and high sediment load from fallow land burning in southern upstream watersheds (Wolanski et al. 2003a, Burdick et al. 2008). Inadequate sewage treatment systems and septic tanks have increased the nutrients and bacterial load in coastal waters (Guam EPA 2010, Raymundo et al. 2011). Crown-of-thorns seastar predation outbreaks, which can be connected with high nutrient concentrations in the waters (De'ath et al. 2012), have caused coral losses (Burdick et al. 2008). Fishing activities have caused a decline or loss of ecologically important fish species (Houk et al. 2012, Taylor et al. 2012, Bejarano et al. 2013). This combination of factors has led decision-makers to actively seek alternative management approaches and tools to guide them (Weijerman and Brown 2013).

The socio-ecological model developed in this study has three main components: a quantitative ecological component and qualitative fishery and tourism human behavior components. Combined, these three components can be used to simulate anthropogenic impact scenarios and their ecological effects and *vice versa*. The management scenarios considered were developed in consultation with local resource managers from three agencies in Guam, and include removing existing marine preserves (MPs) and implement catch and/or size limits and reducing land-based sources of pollution through improved watershed management. While coral reef quality increases under some management scenarios, indicators that are important to the dive industry, such as the biomass of charismatic species, remain low. A management scenario that trades off some reduction in reef-fish landings against an increase in the ecological attributes that are favored by divers could be preferable.

8.1.1 Case study location

Guam, which became an unincorporated territory of the United States in 1950, is the largest and southernmost island in the Mariana Archipelago of the western Pacific Ocean (between 13.2°N and 13.7°N and between 144.6°E and 145.0°E; Fig. 1). Guam in an volcanic island with an area of approximately 549 km^2 and a shoreline of about 187 km (129 km adjacent to coral reefs) (Burdick et al. 2008).

The human population of Guam is estimated at 159,358 individuals (U.S. Census Bureau 2014). Chamorros, the earliest inhabitants of Guam, comprise the largest ethnic group at 37.3% of the population (U.S. Census Bureau 2014), Filipinos make up 26.3%, followed by other Pacific Islanders (12.0%), whites (7.1%), and other Asians (6.0%). Nearly 10% of the population identify themselves as having two or more ethnicities (U.S. Census Bureau 2014).

Guam's Gross Domestic Product was $4.88 billion in 2013 (Bureau of Economic Analysis 2014), primarily based on tourism and the U.S. military. In 2013, Guam had approximately 1.3 million visitors of whom 70% were from Japan (Guam Visitors Bureau 2014). The tourism sector is estimated to contribute between 18% (Allen and Bartram 2008) and 35% (Laney 2006) of local employment. The U.S. military is the second largest contributor to Guam’s economy; its economic importance has increased in the last few years, and is expected to continue to grow with the relocation of thousands of US Marines and their dependents (Ruane 2013).

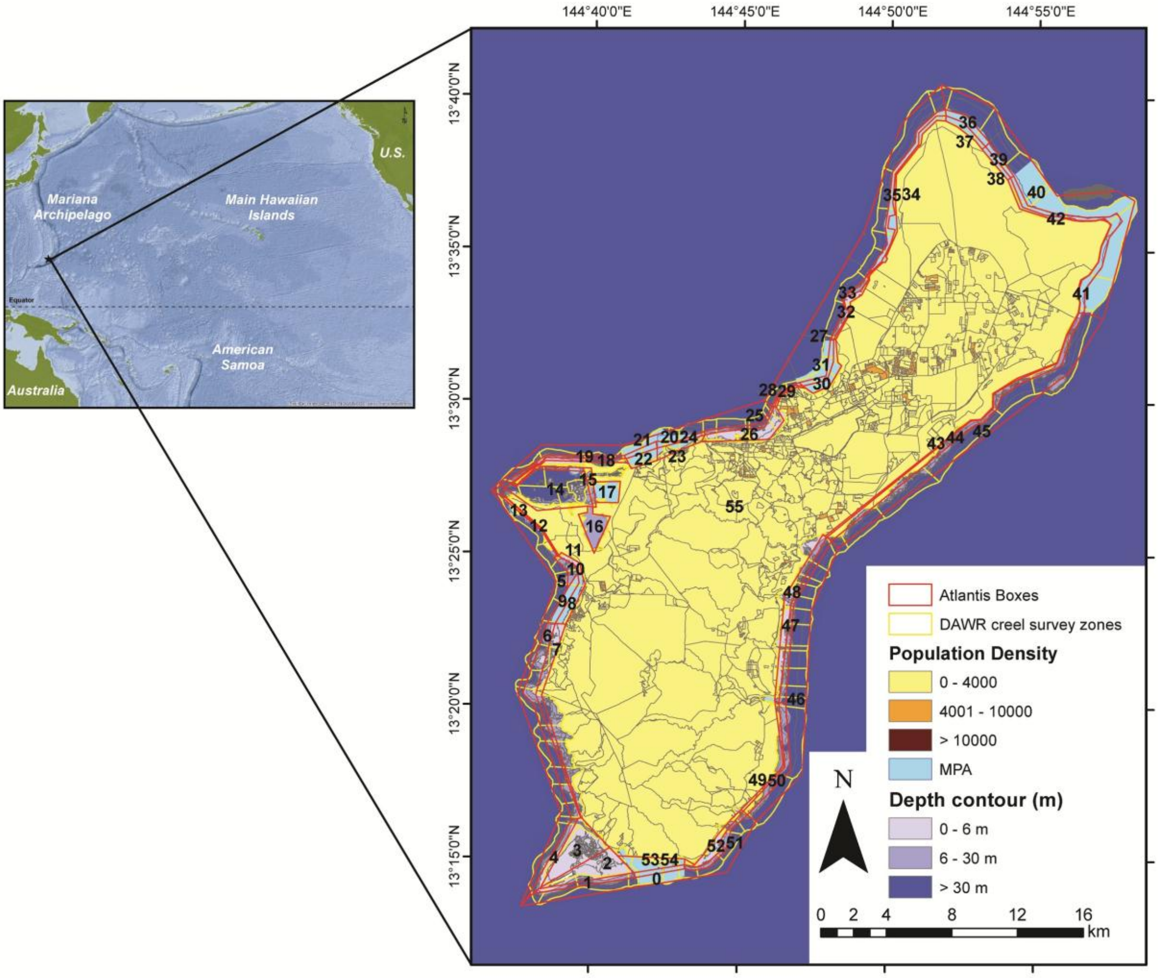


Figure 8.1. Location of Guam in the western Pacific Ocean (inset map) and the spatial model (Atlantis polygons) of the Guam Atlantis Coral Reef Ecosystem model showing human population density, creel survey zones and the depth contours.

8.1.2 Marine resource use in Guam

For Guam, fishing and diving are two important reef-based activities directly reliant on the status and ongoing sustainable use of Guam’s coral reef ecosystems.

Diving in Guam

Guam residents as well as tourists participate in between 256,000 and 340,000 dives on Guam’s reefs every year (Van Beukering et al. 2007). Thirteen legal dive outfitters operate on Guam and offer between one dive and up to four dives per day during peak seasons (Guam Visitors Bureau 2014). Additionally, there are anecdotal reports of some unregistered dive operators.

An estimated 6% of 1.34 million annual visitors go scuba diving while on Guam, and 3% of tourists visit Guam with scuba diving as the primary motivation for their trip (Guam Visitors Bureau 2013, dive shop owner pers. comm. November 2014). Although most tourists who visit Guam are from Japan, visitors from other Asian countries have significantly increased in recent years (Guam Visitors Bureau 2013). This shift in the demographics of tourism is particularly relevant as the participation in dive trips varies by country of origin, with tourists from Hong Kong and Taiwan being far more likely to participate in scuba diving than tourists from Japan, the US, and Korea (Table 8.1).

Table 8.1. Breakdown of visitors by country (Guam Visitors Bureau 2012) and the estimated number of people who went diving (Van Beukering et al. 2007)

Country	Arrivals (FY2012)	Dive participation (2002)	# Divers
Japan	901,683	5%	45,084
Korea	164,821	2%	3,296
Hong Kong	8,396	15%	1,259
Taiwan	49,851	14%	6,979
United States	50,967	8%	4,077

Fishing on Guam

While diving is a popular non-extractive use of Guam's coral reef resources, reef fishing is an important extractive use of marine resources (Van Beukering et al. 2007). Guam's near-shore reef fishery is a multi-species and multi-gear fishery. Fishing occurs from boats and from shore involving trawling (mostly for pelagic fish), net fishing (e.g., cast net, gillnet and surround net) and spearfishing (snorkel and scuba). Over the years gear methods have evolved and, new, more efficient catch methods used, some with detrimental impact. For instance, the relatively new practice of spearfishing on scuba has been linked to a decrease in large-size fishes leading to a targeting of smaller fish prior to reaching sexual maturity (Houk et al. 2012, Lindfield et al. 2014).

It is estimated that between 35% and 45% of Guam's households were involved in near-shore fishing (Van Beukering et al. 2007). Much of the fish caught on Guam is not traded in the market (and is not recorded in commercial statistics) but is instead eaten within the household or shared with family and friends. A 2005 survey of Guam households found that out of the fish consumed by households, nearly one-quarter (24%) was caught by the respondent or another member of the household, and an additional 14% was caught by a friend or extended family member (Van Beukering et al. 2007). The social obligation to share one's fish catch extends to all fishermen (Amesbury and Hunter-Anderson 2003). This cultural practice is particularly important among Guam's Chamorro residents, who often give a large proportion of their catch to family, friends and the local community (Pinhey et al. 2006, Kotowicz and Richmond 2013). Some of the other social reasons to go fishing include spending time with family and friends, to provide fish for a particular event or to teach members of the younger generation traditional fishing practices. These practices have non-market value as they can underpin social networks and cultural ties throughout the Pacific Islands region (Pinhey et al. 2006).

8.2 Methods

In this study a quantitative biophysical model of the coral reef ecosystems around Guam (Weijerman et al. 2014b, Chapter 6) was linked with qualitative behavior models of two reef-dependent sectors (coral reef fishing and dive tourism). The ecosystem model was based on the Atlantis framework and was developed in consultation with community experts (Appendix L) at workshops on Guam in November 2012 and June 2014. The aim of the Guam Atlantis model was to build a virtual coral reef ecosystem for managers and biologists to explore questions and provide a tool to undertake scenario analyses. The model integrates best available data from multiple disciplines, such as hydrology and ecology, at multiple scales. Details can be found in Weijerman et al. (2014b) and Chapter 6.

Atlantis is a deterministic model spatially resolved in three dimensions that tracks nutrient flows through the main biological groups in the ecosystem. For Guam Atlantis we parameterized two of four possible modules (Weijerman et al. 2014b). The first is an ecological module that simulates primary ecological processes (consumption, production, waste production, migration, predation, recruitment, habitat dependency, and mortality). The reef-fish species were aggregated in functional groups based on their diet, life history characteristics, and functional role (Chapter 4). The second is a physical oceanographic module that represents the bathymetry, major currents, salinity, and temperature and is based on the Regional Ocean Modelling System framework developed for the Coral Triangle (Castruccio et al. 2013). The third module simulates fisheries (or other human activities) and was simplified as a fixed fishing mortality per functional group based on historical catches from shore-based creel surveys conducted by the Guam Division of Aquatic and Wildlife Resources between 2010 and 2012 (DAWR). Due to a lack of data, this module did not include the effects of fishing gear on the benthic habitat and species (e.g., physical damage to corals, ghost net fishing and damage resulting from fish lines). Finally, the fourth Atlantis module simulates the socio-economic dynamics, which typically represents commercial fisheries governed by economic rules, and was replaced by the fisher and diver behavior models, outlined below.

The recently developed Atlantis model can correctly simulate key dynamics in coral reef ecosystems around Guam (Chapter 6). These dynamics include ocean acidification (Kleypas et al. 2006), ocean warming (Jokiel and Coles 1990), reef accretion and erosion (Eakin 2001), the relationship between the complexity of a reef ecosystem and its function to provide shelter for fish species (Graham and Nash 2013, Bozec et al. 2014), the effects of nutrient and sediment input on coral growth (Lapointe 1997, Wolanski et al. 2004) and coral-algal dynamics (i.e., macroalgae can overgrow corals, outcompete corals in nutrient-enriched waters, prevent coral recruit settlement, and crustose-coralline algae and, to a lesser extent, turf algae facilitate coral recruitment (Nugues and Bak 2006, Baskett and Salomon 2010, Marshell and Mumby 2012).

Modelled output ecosystem metrics of Guam Atlantis were based on a 30-year simulation and averaged over the last five years to account for interannual variation. Selected ecosystem metrics indicative of reef status and resilience (Bascompte et al. 2005, Bellwood et al. 2011, Weijerman et al. 2013) include: species abundance (measured as total reef-fish biomass), number of large fish (measured as the number of a slow growing species, represented by sharks, in the largest size class), and reef condition (measured as the ratio of calcifiers [corals and crustose-coralline algae] to non-calcifiers [turf and fleshy macroalgae]). Those metrics were augmented with two tourism-related metrics, abundance of charismatic species and reef-fish diversity (derived from species richness, i.e., the number of functional groups present, and the inverse of Pielou's Evenness: $J` = H`/H`_{max}$ where H` is the Shannon-Wiener diversity index), to link to the diver behavior model. For the link to the fishery behavior model two socio-economic metrics were added: landings of targeted fish species and landings of all species (including invertebrates; Fig. 8.2).

The qualitative human behavioral models leverage previously published information and expert knowledge from people who have worked with Guam's dive tourism sector or fishing sector (or both). The disciplinary background of the experts included anthropology, economics, resource science, sociology, and biological sciences. The two behavioral models focus on different aspects of the reef ecosystem; the tourism model focuses on reef condition while the fishery model focuses on the extraction of reef-fish species. For the tourism model, the selected ecosystem metrics are key to providing a high quality diving experience. For example, the presence or absence of charismatic species (Rudd and Tupper 2002), such as the humphead wrasse, *Cheilinus undulatus*, and bumphead parrotfish, *Bolbometopon muricatum*; coral cover (Barker and Roberts 2004) (indicated by the ecosystem metric reef condition), species abundance (Williams and Polunin 2000), and water clarity (Wielgus et al. 2003)(implicitly included in reef condition, i.e., with high nutrients and/or sediments in the water column, clarity decreases and algal growth is favored over coral growth reducing the reef condition ratio).

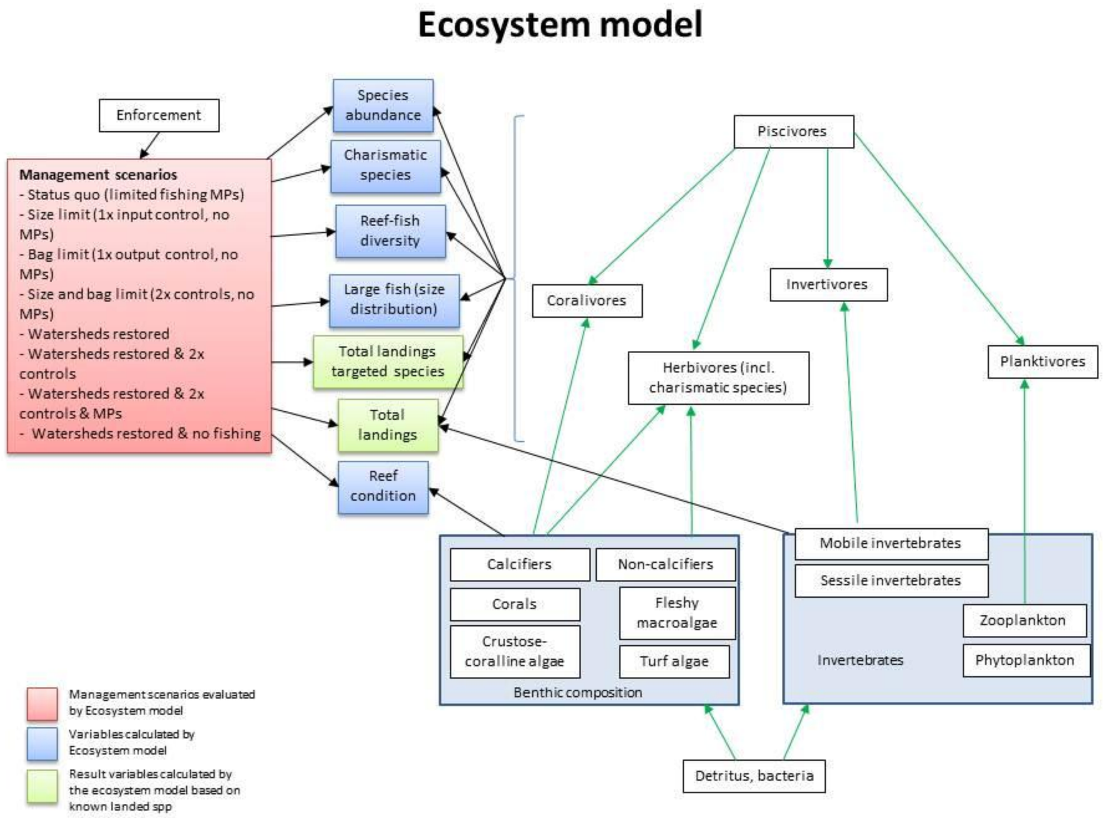


Figure 8.2. Conceptual representation of the Guam Atlantis Coral Reef Ecosystem Model. Foodweb connections between (simplified) functional groups are shown by green arrows. Black arrows indicate the linkages between the ecological model and the ecosystem metrics.

For the fishery model, species abundance was selected as the ecosystem metric that links the biophysical and human behavior models, which is expected to influence reef-fish fishery participation. The fisheries relevant ecosystem metrics, landings of targeted fish species and total landings, were used to discuss consequences of changes in expected fisher behavior. A species was assumed to be a target species when its representation in the landings of a particular gear type was greater than 20% (DAWR shore-based creel survey data).

We predicted quantitative change in the selected ecosystem metrics to qualitatively explore six management scenarios (B to F) simulated using the Guam Atlantis model and compared to the status quo scenario (A) (Table 8.2).

Table 8.2. Details of simulated management scenarios. LBSP = land-based sources of pollution.

Scenario	**Presence of marine preserves***	**Existing levels of LBSP**	**Fishing effort compared to status quo**	**Fishing of juvenile fish**
A: Status Quo	yes	yes	100%	goatfish, rabbitfish, jacks
Bi: Catch and size limits	no	yes	75%	no
Bii: Catch limits	no	yes	75%	goatfish, rabbit fish, jacks
Biii: Size limits	no	yes	100%	no
C: Restored watersheds	yes	no	100%	goatfish, rabbit fish, jacks
D: Catch and size limits, restored watersheds	no	no	75%	no
E: Full regulations	yes	no	75%	no
F: No coral reef fishing, restored watersheds	yes	no	0%	no

*preserves are simulated as no-take areas

As fisherman-specific catch data were not available, we could not use current estimates of daily or weekly catches to set a hypothetical ‘bag’ limit for scenarios Bi, Bii, D and E. Instead, we set annual allowable catch at 75% of the status quo landings at the end of a 30-year model run for each functional group. This allowable catch was then divided by 52 to get a weekly ‘bag’ limit. When this weekly limit was reached in the model run, fishing was stopped for the remainder of the week. For size limits, fishing of all fishes smaller than their size at maturity was stopped, including the seasonal runs on juvenile rabbitfish, goatfish and jacks.

For ease of interpretation and visualization, the 5-year mean values of the ecosystem metrics were normalized over all strategies resulting in values between zero (worst case) and one (best case).

8.3 Results

The results comprise two main components: 1) a description of the theoretical dive tourism and reef fishing participation behavior models; and 2) a description of the changes in the ecosystem metrics as predicted by Guam Atlantis for the different management scenarios. In the discussion we bring together these results by examining the socio-ecological implications of the different management approaches.

8.3.1 Dive behavior model

A qualitative model linking the ecological, economic and social factors that influence participation in dive trips in Guam is shown in Figure 8.3. A full description of nodes in the model is provided in Appendix M and a description of the relationship between nodes in Appendix N.

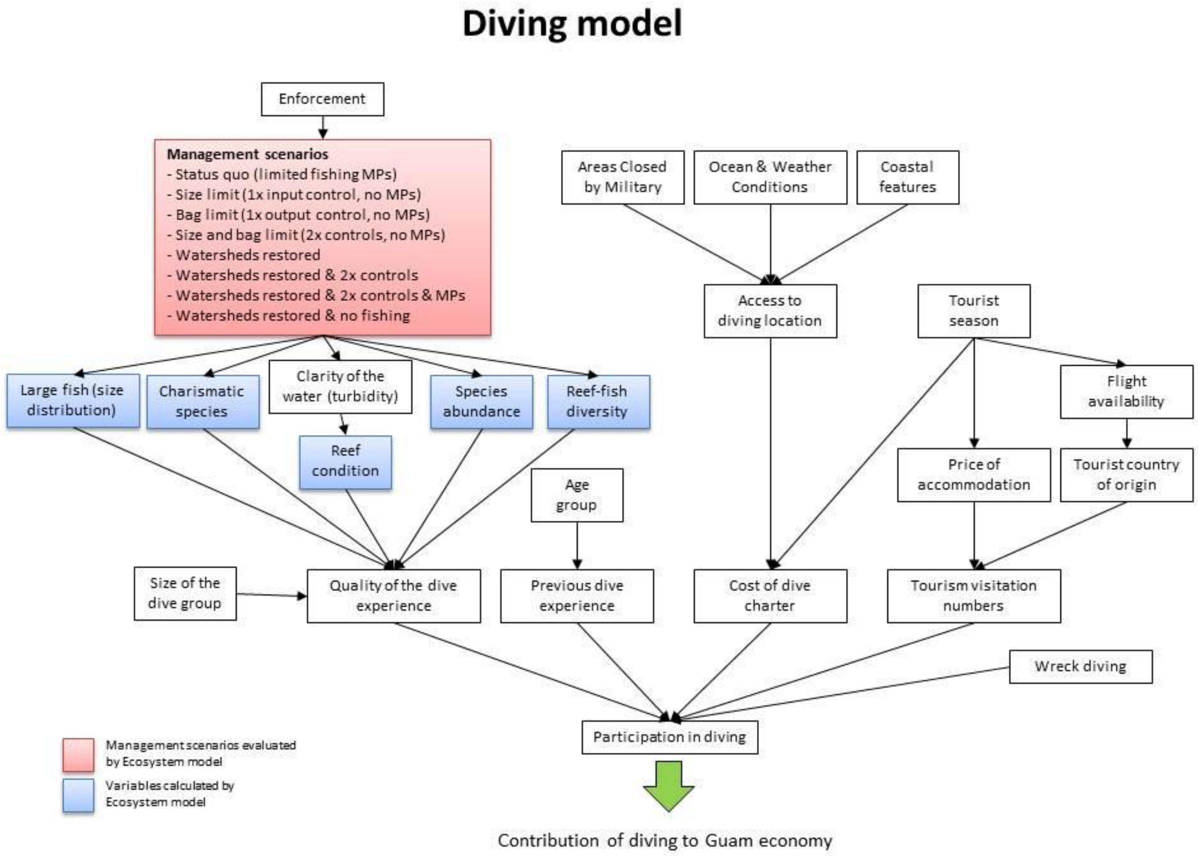


Figure 8.3. Influence of different environmental and socioeconomic factors on participation in dive trips in Guam.

Guam’s dive sector is heavily dependent on healthy coral reefs, and there is a clear connection between environmental attributes (i.e., the ecological indicators in the ecosystem model) and diver willingness to pay for diving on a reef (Grafeld et al. in prep). Management can indirectly influence diver participation and the dive experience by changing the ‘quality’ of the environment. For example, water clarity (turbidity), several areas around Guam have turbidity issues as a result of land-based pollution and changing water clarity could strongly influence the quality of the dive experience. However, it is acknowledged that other marine management not further explored here, can also influence the quality of a dive experience. These management approaches include, for instance, restricting diver behavior on the reef by placing limits on their autonomy (Sorice et al. 2007), controlling access to marine protected areas (Asafu-Adjaye and Tapsuwan 2008, Parsons and Thur 2008) or avoiding inter-sector conflict by spatially limiting contact with fishers or fishing gear (Gill et al. 2015).

Dive participation can be influenced by many other economic and social factors, some of which are outside the direct scope of influence of resource managers, such as tourist visitation numbers. Tourist visitation numbers and country of origin are of particular interest, as some tourists are more likely to go diving than others.

8.3.2 Reef fishing participation model

Similar to the diving model, a qualitative model describing the socio-demographic, economic and ecological factors influencing participation in Guam's reef fishery was developed (Fig. 8.4 and Appendices O and P).

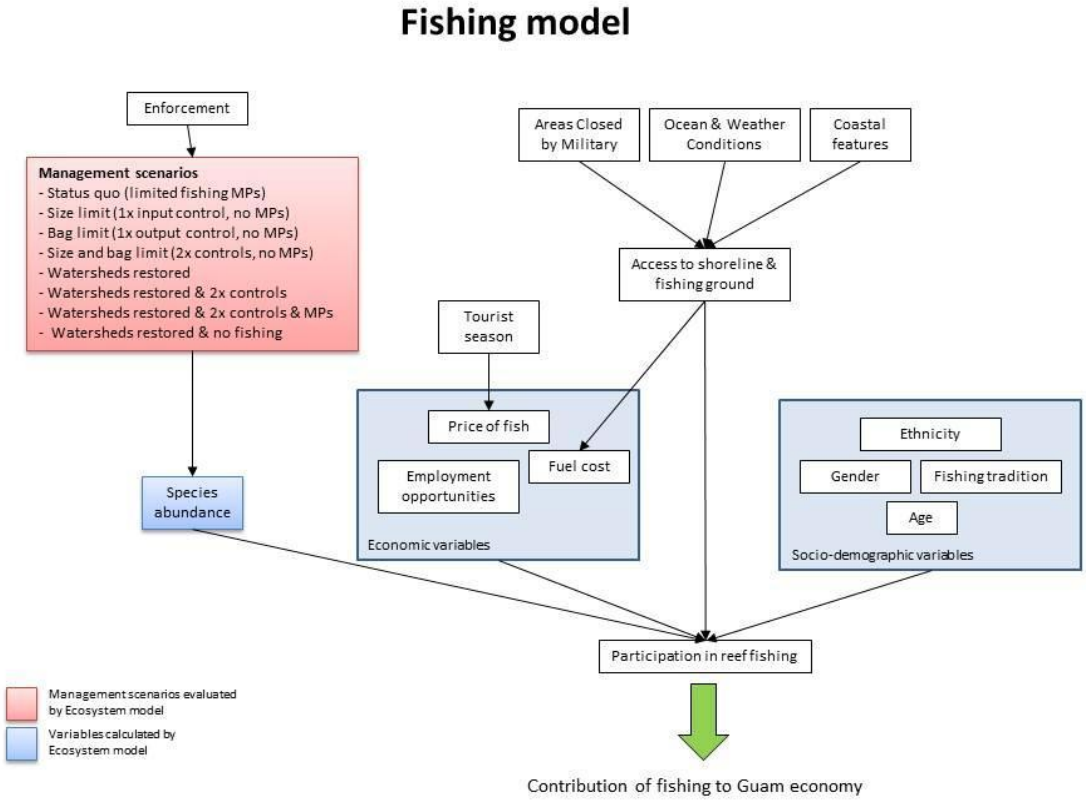


Figure 8.4. Influence of species abundance, economic and socio-demographic variables and participation in reef fishing on Guam.

Strategies for managing marine resource extraction and coral reef health can influence participation in reef fishing by affecting the abundance of exploited and non-exploited species, and by affecting where and when fishing can occur, what species (and sizes) can be taken, and the type of gear that can be used. Management scenarios introducing bag and size limits restrict the number and size of fish catch, which can influence how and where fishers choose to fish (Berkeley et al. 2004, Birkeland and Dayton 2005). Management of adjacent watersheds can decrease sedimentation and increase water quality, improving near-shore coral reef ecosystems that could lead to higher species abundance for reef fishing.

Spatial management of marine areas, such as marine preserves, can affect access to shoreline and nearshore fishing grounds (Mascia et al. 2010). Access to fishing grounds is also affected by environmental variables, including coastal features, such as, cliffs (Allen and Bartram 2008) and adverse ocean and weather conditions (Kotowicz and Allen, in review) and by military exercises (Kotowicz and Allen, in review).

Ethnicity (Allen and Bartram 2008), gender, age (Hospital and Beavers 2012) and whether one’s family has been traditionally engaged in fishing are socio-demographic variables that play a role in determining participation in reef fishing. Economic variables that affect a fisher’s decision to go reef fishing include the price of fish, which is partially determined by whether it is high tourist season, opportunities for employment and the cost of fuel (Hospital and Beavers 2012).

8.3.3 Changes in ecological indicators as a result of management

Performance of scenarios that include restored watersheds out-competed the other scenarios in terms of better reef condition and species evenness (Fig. 8.5). The full regulation (Scenario E) and no fishing & restored watershed (F) scenarios had a positive effect on the species abundance, but performed worst of all scenarios with regard to total landings (Fig. 8.5).

Compared to the status quo scenario (Scenario A), removing marine preserves while imposing bag and size limits (Scenario Bi) resulted in a 12% increase in species abundance and in 2.5 times the biomass of charismatic species (Table 8.3). However, fish landings were 79% of the status quo landings and total landings (including invertebrates) dropped to 53% of the status quo landings.

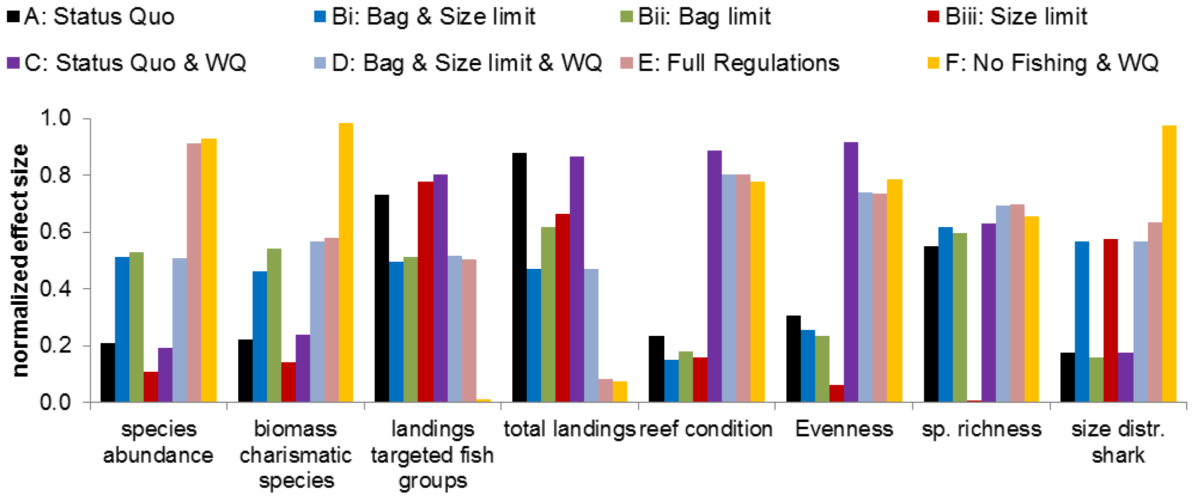


Figure 8.5. Effect size based on normalized values of ecosystem metrics at the end of a 30-year simulation to allow comparisons of alternative management scenarios. Modelled scenarios are explained in “Methods” section.

Table 8.3. Relative effect size of ecosystem metrics at the end of a 30-year simulation of the various management scenarios to the status quo scenario. Values are means of the last five years of simulations. WQ=water quality and represents improved watersheds. Overall effect size is the mean of the normalized ecosystem metric values as represented in Figure 8.5.

	Status Quo A	**Bag & Size limits Bi**	**Bag limit Bii**	**Size limit Biii**	**Status Quo & WQ C**	**Bag & Size & WQ D**	**Full Reg. E**	**No fishing & WQ F**
Total reef-fish biomass	1	1.12	1.13	0.94	0.99	1.12	1.31	1.33
Biomass iconic species	1	2.50	2.97	0.34	1.14	3.09	3.18	7.56
Landings targeted groups	1	0.79	0.80	1.05	1.08	0.80	0.79	0.0
Total landings	1	0.53	0.67	0.71	0.98	0.52	0.02	0.0
Reef condition	1	0.96	0.98	0.97	1.24	1.19	1.19	1.18
Evenness	1	1.00	1.00	0.98	1.04	1.02	1.02	1.03
Sp. richness	1	1.00	1.00	0.98	1.00	1.00	1.00	1.00
Size distribution sharks	1	12.32	0.37	12.54	1.00	12.32	14.10	31.01
Overall effect size	*0.41*	*0.44*	*0.42*	*0.31*	*0.59*	*0.61*	*0.62*	*0.65*

8.4 Discussion

Effective management of tropical reef ecosystems under pressure from terrestrial and extractive marine activities is not straightforward, especially with potentially competing reef-based activities. The shift towards ecosystem-based fisheries management (EBFM) demands quantitative tools to support policy and management decisions. Ecosystem modelling and management strategy evaluation (MSE) are widely used in single species management testing and are becoming increasingly used in support of EBFM (Fulton et al. 2011b). For EBFM evaluation, ecological models are coupled with socio-economic models to uncover societal linkages (Pikitch et al. 2004, Fulton et al. 2011c). Evaluation of the potential effect of different management approaches prior to implementation through modelling will reduce the chance of adverse or unexpected ecological or socio-economic outcomes in the future and likely improve performance and compliance (Fulton et al. 2014).

While the focus of this work was on a case study in Guam, the non-commercial reef-fish fishery and economic importance of diving also apply to many other tropical islands and coast lines making this approach generally applicable. EBFM that specifically includes the human dimension, has gained traction among scientists, politicians and resource managers in the last decade (Pikitch et al. 2004, Cinner et al. 2009). However, only a few models have attempted to couple biophysical and socio-economic dynamics for coral reef ecosystems (Gribble 2003, Shafer 2007, Melbourne-Thomas et al. 2011b). Human dimension-centered models have examined different coral reef ecosystem states and the links to socio-economic conditions and fishing participation (Cinner et al. 2009), as well as the effects of gear types on reef condition (McClanahan and Cinner 2008). Hence, the approach presented in this study is novel as it includes the entire ecosystem from plankton to humans and could be a valuable tool for EBFM.

Diminishing catches affecting the fishing sector have prompted a discussion on ways in which improved fishing and water quality outcomes may be achieved for Guam (Weijerman and Brown 2013, J. Cameron, POC Guam Coral Reef Conservation Program, pers. comm. July 2014). With the approach outlined in this case study, key human behavior models were linked with a biogeophysical model to gain insight into the key ecosystem metrics that link the two systems and evaluation of the consequences of management for socio-ecological effects in both the fishing and diving sector. The impacts of the management scenarios were quantified by means of ecosystem indices that could be meaningfully interpreted (although in a qualitative manner) in the context of the main marine activities in Guam.

8.4.1 Tradeoffs between marine sectors

At the heart of EBFM are the complex tradeoffs between objectives; these tradeoffs can be between ecological and socio-economic objectives (as in this study), but competing uses can also require tradeoffs between different socio-economic objectives. Both Guam's dive industry and reef fishing activities are inherently reliant on healthy coral reef ecosystems. The number of ecological indicators that the dive sector aims to maximize are more numerous (four in total) than the fishing sector, where species abundance (total reef fish biomass) is the only direct link to participation in reef fishing. In evaluating these tradeoffs, that discrepancy should be taken into account.

For the tourism and recreation sectors, local divers are important to Guam's economy and have demonstrated a willingness to make financial contributions towards marine management (Grafeld et al, in prep). While the dive model presented here does not allow for backwards interactions, it is important to note that given Guam's reliance on tourism, the ecological attributes that indicate coral reef quality may influence other factors, such as tourist visitation rates. Guam's high biodiversity reefs make it a very popular diving destination and a change in the perception as a lower quality dive location could negatively affect the tourism industry.

From the standpoint of the diving industry, a management scenario where there is no fishing and no land-based source pollution provides optimal results with the highest values for ecological indicators. However, this scenario eliminates all reef-fish fishing which may be impractical and infeasible politically, in addition to not being economically optimal as commercial fishing also contributes to the local economy, albeit a smaller amount than tourism. Importantly, the absence of fishing would counter the traditional use and identity of Guam's residents. Even though it is not easy to express the value of cultural fishing in monetary terms, the maintenance of cultural activities has important links to cultural identity and a healthy community and society (Kotowicz and Richmond 2013).

8.4.2 Interpreting alternative management scenarios

Alternative fisheries management scenarios will result in different ecological outcomes. Input and output controls, such as size and bag limits, will limit reef fishing by restricting the size and number of fishes that can be taken (Berkeley et al. 2004, Birkeland and Dayton 2005). Based on the ecosystem metrics for the management scenario, it is clear that imposing a simple input restriction (size limits) without any additional management measures will not improve the ecological outcomes for the reef; in fact, it may prove to worsen outcomes compared to the status quo, as fishing effort stays the same (so fishers will catch more larger individuals to make up the forgone catches of smaller fishes). Combined input and output controls in the form of size and bag limits or bag limits on their own will only marginally improve the ecological outcomes for the reefs' status compared to the status quo. In practice, input management tools are relatively easy to implement (Emery et al. 2012) and could mean a fast change in reef fishing behavior, but the net result on overall participation in fishing activities, compliance behavior and location choice is uncertain. For example, under size limits, fishers may choose to avoid areas where they know there are higher numbers of small fish, which in turn may lead to localized depletion in areas with larger fish. Similarly, fishers may choose to fish closer to shore to reduce fuel cost if there are bag limits – again causing localized effects. When areas are improving ecologically under the restored watershed management, fishers may choose to direct their effort to those areas. In other words, a transfer of effort as a consequence of the management scenarios is possible, which makes it difficult to determine with certainty the total effect of controls on fishing participation.

The ecological metrics indicate that restored watershed is an important contributor to a healthy marine ecosystem. However, watershed restoration on its own is not adequate to address the problems facing Guam's reefs and, in addition, may not achieve enough to provide the coral reef quality desired by the dive industry. While coral reef quality increases under the status quo and improved watershed scenario, total fish species biomass and the biomass of charismatic species remain low. Given the importance of these indicators for divers, selecting an alternative management scenario that allows for some reduction in fishery landings to be traded off against an increase in the ecological attributes that are favored by divers may be preferable to managers looking to balance the needs of both sectors.

Surprisingly, the scenarios with full regulations including size and bag limits and watershed restoration with retention of existing MPs (scenario E) and without the MPs (Scenario D) achieve similar ecological outcomes. The main difference is in the total reef fish biomass that is 17% higher when existing MPs are retained, most likely because fish can grow larger in MPs (Taylor et al. 2012). Removing MPs would increase shoreline and nearshore access to areas currently closed to fishers. It is likely that fishers will begin fishing in some of the areas that were common fishing grounds prior to being closed to fishing when MPs were established (Mascia et al. 2010). Fishers may also choose to fish with different gear and target different reef fish with the opening of MPs. The net result of reef-fishing participation in scenarios where MPs are opened cannot be determined. However, the potential for interactions between divers and fishers if MPs were opened may be concerning, as divers in other locations have expressed a preference to avoid such interactions (Gill et al. 2015).

Results show that there is little point in trying to manage the reef ecosystem and those who use it without also managing the watershed. Over a 30-year timeframe, the three management approaches with the most positive ecological impact all include restored watersheds. Three out of four ecosystem metrics important to the dive sector will improve if size and bag limits are imposed, the watershed is managed and existing marine preserves are maintained. In the short term there will be some negative impacts particularly on the fishing sector as a consequence of size and bag limits, but the long-term benefits for fishers and divers obtained from greater species abundance are likely to outweigh these short term costs. Adopting watershed measures in addition to input and output controls distributes the burden for improving the reef status across multiple entities responsible for reef pressures.

8.5 Next steps

Despite the difficulties in predicting the overall behavioral changes of fishers and divers under the different scenarios, the conceptual behavioral models (combined with the ecosystem model) provide a starting point for discussions with stakeholders. Effective resource management of coral reef systems is highly dependent on effective involvement of local communities (Cinner et al. 2012). The qualitative model of human behavioral drivers for reef fishing does not currently include probability distributions to enable a quantitative analysis. However, the behavioral models can be transformed into Bayesian Networks (BN), which would enable quantitative analyses of management approaches and the effects on the probability of participation in the dive and fishing sectors in Guam (Plagányi et al. 2013, van Putten et al. 2013). Even though the probability density function for a number of the variables was known, the conditional probabilities and relationships between mostly the social and cultural variables needs to be confirmed and tested by the local Guam community. Setting and testing the underlying probability distribution assumptions is an important component of developing a BN especially to promote local community ownership of the BN and modelling results.

8.6 Conclusion

Linking an ecological ecosystem model with socially and economically important human behavior gives us a better understanding of changes in ecological performance due to management of human-use activities. An integrated ecosystem model for Guam’s fringing reef ecosystem enabled us to simulate alternative management scenarios and assess the performance criteria on both dive participation and participation in reef-fisheries. When the objectives for reef ecosystems encompass conservation and extraction goals, an integrated ecosystem model can make the tradeoffs between different uses explicit. This allows managers to weigh the various performance measures and objectively consider the tradeoffs between resource users and determine a ‘best management solution’. From this study it is clear that the optimal management solution for the reef ecosystem in Guam (and the dive tourism and fishing sector) is to combine input and output controls, but most importantly, to restore the watershed and to thus improve ecological impacts.

Reefs at Adelup on west coast of Guam. *Photo Dave Burdick*

Chapter 9

Synthesis

9.1 Overview

The main objective of my thesis was to develop an integrated model to quantify the effects of watershed management and fishery regulations on coral reef ecosystem services against a backdrop of climate change impacts. Having developed and validated the model, I then applied it to evaluate socio-economic and ecological tradeoffs of alternative management strategies with and without taking the effects of climate change into consideration to also assess the cumulative effects of local and global drivers. Results of such modelling exercises can be used as one of the tools to support decisions in ecosystem-based management (EBM). This chapter starts with a reflection on the model development and its application for ecosystem modelling (Section 9.2). Next I discuss the complexity of coral reef modelling for management strategy evaluation (MSE) application often used in EBM (Section 9.3) and the challenges and limitation of this model development (Section 9.4). Finally I draw together conclusions for each of the research questions and the overall research findings and their implications for management (Section 9.5).

9.2 Reflections on model development and its application

The first step in any modelling study is to determine the modelling approach best suited to the main objective. In my case, I needed a modelling platform that could be applied to coral reef ecosystems and was suitable for MSE. By comparing and contrasting a range of coral reef ecosystem models, I settled on an end-to-end modelling framework that is complex enough in its conceptualism of space, time and structure and in process details to adequately represent the complexity of coral reef dynamic processes (Chapter 2). Reefs appear to be regulated by two trophic flows, one based on detritus and one based on phytoplankton (Chapter 3) hence, I wanted to dynamically capture the oceanographic forcings and biochemical processes. These options are already incorporated in the comprehensive Atlantis modelling framework (Fulton et al. 2011b, Griffith et al. 2011). Moreover, Atlantis was deemed most suitable for MSE (Plagányi 2007) compared to other intermediate and complex model frameworks (Chapter 2). Finally, its modular structure allows the user to make the modules as complex or simple as desired or to add additional dynamics (Chapter 4). As concluded in Chapter 2 no one model serves all needs. More often than not, the use of a range of models is needed to get to the desired outcomes (Fulton 2010, Mooij et al. 2010). This conclusion was also true for this study. Although I did use a complex model, relationships relevant to coral reef ecosystem dynamics came from various minimal and intermediate model outcomes. Examples are published relationships of algal-coral-grazer dynamics (Mumby et al. 2007b, Melbourne-Thomas et al. 2011a), effects of sediments of coral growth (Wolanski et al. 2004), relationship between structural complexity and fish biomass (Graham et al. 2006, DeMartini et al. 2013, Bozec et al. 2014) and effects of climate change on corals and other organisms (Chapter 6).

As the main goal of my thesis was to evaluate tradeoffs of alternative management strategies using the developed ecosystem model, I needed performance metrics that could indicate the effects of fishing on ecosystem status. These indicators were selected using the Ecopath modelling platform (Chapter 3). Building an Ecopath model also allowed me to investigate various parameters for invertebrate life history that are difficult to obtain from the literature but necessary as input parameters for Atlantis. Additionally, it gave me a better understanding of the energy flows within coral reef ecosystems and the amount of primary productivity necessary to sustain the upper trophic levels. For example, in Ecopath I had to greatly increase the amount of phytoplankton from values obtained by the literature, while in Atlantis I had to increase the growth rate to ensure that the phytoplankton groups did not become extinct. In Ecopath I justified the use of higher biomass by assuming that reefs receive a continuous supply due to the tidal forces and waves, bringing new phytoplankton to the reef community (Chapter 3). In Atlantis, where I model these dynamics, I had expected that the phytoplankton would be advected in enough supply. However, large phytoplankton quickly reduced to just 1% of its initial biomass despite the already increased growth rate. Sensitivity analyses showed that coral biomass is sensitive to the growth rates of phytoplankton (Chapter 6). Obviously, a better hydrological model is needed to regulate the nutrient-phytoplankton-zooplankton dynamics that influence changes in coral growth and biomass.

In general, for end-to-end models existing statistical tests for uncertainty analyses and model skill assessment (Stow et al. 2009) are impractical due to the many parameters involved and the long run time (Clancy et al. 2010, Fulton 2010, Link et al. 2012). In my case, additionally, one of the main complications for model development and model testing was the lack of time series data for any of the functional groups that were simulated in Atlantis. Using an assumption that is commonly used in single species fish stock assessments, namely that the catch-per-unit-effort is indicative of the relative biomass (Haddon 2010), I reconstructed the trend in biomass of the fish groups to be able to initialize my model in 1985 (Chapter 5) and to test the model with the reconstructed biomass time series and with the catch time series between 1985 and 2015 (Chapters 4 and 6). Initially, both the trend and the magnitude of these biomass time series did not overlap well with the modeled outcomes for some groups and I had to assess the reliability of the reported catches. After correcting for biases in reporting, I achieved reasonable fits of at least the trends. However, when I assessed the model skill, the regression between the observed and predicted data of 2011 showed a poor fit with a consistent bias (Chapter 6). This bias led to an overestimation of the tested fish groups and could be caused by inaccurate recruitment relationships or underestimation of mortality. Since I omitted the boat-based reef-fish fishery and the shore-based fishery data I did use underestimate the take from spear-fishers, a first step for improvement would thus be to better estimate the actual catches. Additionally, the catchability term, which I estimated based on only three data points (2010, 2011 and 2012) and used to estimate the historic biomass, can be improved. For example, through the use of age-structured fishery models, I could minimize the square root of the sum of the mean squared errors between reported catches and predicted abundance by solving for this catchability constant (i.e., changing this constant between a plausible minimum and maximum) using all historic data per gear type and adding a parameter to the reported catches to account for under-reporting and for missing the catches from the boat-based fishery (c.f. Haddon 2010). Alternatively or additionally, I could use biosampling results (if available) and derive better estimates of fishing mortality.

Despite these limitations, model validation based on general guidelines for Atlantis development (Horne et al. 2010, Link et al. 2010, Ainsworth et al. 2011a, Fulton et al. 2014) and by comparing model results with empirical data, published relationships and expert judgement (c.f. Tallis et al. 2010) indicated that simulated results corresponded reasonably well (Chapter 6).

9.3 Complexity of coral reef modelling for MSE application

Data needs for the complex Atlantis model are considerable, adding to the complexity of model development. Fortunately, most biological data was available through the Coral Reef Ecosystem Division of NOAA, Pacific Islands Fisheries Science Center, supplemented with data from the University of Guam Marine Laboratory, the Guam Environmental Protection Agency and the Guam Division of Wildlife and Aquatic Resources. However, long-term time series (i.e., longer than ten years) were not available or only available for selected small spatial areas (e.g., Tumon Bay, approximately five km^2) and not suitable for island-wide extrapolation. The absence of long-term data strongly limited model skill assessments and I had to rely on expert judgement for model validation (Uusitalo et al. 2015).

Even where data were available, the understanding and quantification of the relationships between drivers and ecological responses required considerable interdisciplinary effort. In model development, experts from disciplines ranging from physical oceanographers to biological oceanographers, and invertebrate experts to reef fish experts needed to be consulted to identify key functional groups and dynamics. Equally important for the application of the model in evaluating management options, was the input of experts from the human dimensions program (Pikitch et al. 2004, Fulton et al. 2011c). Throughout the model development and its application, the stakeholders (i.e., natural resource managers and other users) needed to stay involved as well (Levin et al. 2009, Tallis et al. 2010). Through two workshops, input was requested from these stakeholders to make sure that the work and the expectations were aligned. Preliminary results were shown at these workshops and model outcomes were validated by coral reef scientists, who have expert knowledge on Guam’s reefs, throughout the model development.

The interplay of managers (and other stakeholders) and modellers adds another layer of complexity. Often managers want to know the ‘best’ solution; however, in complex systems, such as coral reefs, and, hence, in using complex models that attempt to include all major processes in a single framework, there are always tradeoffs to be made between often competing goals and objectives (Smith et al. 2007). These tradeoffs need to be recognized and made by the managers themselves and the ecosystem modelling efforts can be used as a support tool in such decision making (Chapters 7 and 8). A successful example of this interplay between stakeholders and modellers is the overhaul of the complex multispecies fisheries in southeastern Australia based on an integrated management strategy evaluation process (using the Atlantis model) that was driven by stakeholders (Smith et al. 2004, Fulton et al. 2007). Ecological, economic and social performance of the fishery was evaluated by simulating various management scenarios, such as gear controls, quotas and spatial management. The strategy that performed best against a wide range of objectives was subsequently adopted and led to marked improvements in the fishery performance (Fulton et al. 2014).

9.4 Challenges and limitation of the model

A main challenge with complex end-to-end models is the numerous functional groups and relationships included, each with their own set of input parameters, assumptions and uncertainties (e.g., observation uncertainty, process uncertainty, uncertainty around natural variability and ignorance). Minimal models or single-species stock-assessment models can use a range of statistical techniques to estimate the uncertainties and quantify the final uncertainty around the projected values (Stow et al. 2009, Haddon 2010). However, for complex models with the myriad of parameters and relationships this approach is computationally infeasible. A pragmatic approach to handling uncertainty is the use of multiple models (Mooij et al. 2010, Trolle et al. 2014, Uusitalo et al. 2015). This ensemble of models can either consist of the same model structure but with different input parameters (Fulton et al. 2014) or can be of different model structures, for example, a food-web model and an age-structured model (Woodworth-Jefcoats et al. 2015), as long as the goal of the models' development is in agreement and hence results comparable. The results of these ensemble models can be used to quantify uncertainty, similar to the well-established practice in climate and weather projections. Clear communication and quantification of the uncertainty associated with ecosystem models and strategies to properly and consistently address them, are still challenging and is only just beginning to receive in-depth attention (Link et al. 2012). Unfortunately, I did not have the time to fully explore this route; however, this first version of Guam Atlantis does provide the possibility to be used in multiple model inference, either by comparing results with other model structures or by using various parameterizations of the Guam Atlantis model.

Due to these challenges and limitations, end-to-end models are best suited for strategic advice in EBM. For example, stock-assessment models that predict next years' quota basically use one term (i.e., epsilon) to capture the environmental variability and have one mortality parameter that theoretically encompasses the predator-prey and species-habitat interactions. When annual stock-assessment predictions vary from high to low or when stocks fail to recover, managers and fisherman will lose confidence in these stock assessments. Ecosystem models can help disentangle this 'epsilon' term and quantify the mortality term more realistically and so indicate what level of buffering is required for quotas set in an ecosystem context.

With this use of complex ecosystem models, expectations around quantifying uncertainties associated with model outcomes should be calibrated. In this context it is not the *magnitude* of the projection that is important but the emergent *patterns* (Grimm et al. 2005). In terms of informing on management alternatives, ecosystem models are best used relatively with the ecological and socio-economic performance measures compared across the alternative scenarios—in this way the scenarios can be evaluated in an internally consistent context. Nevertheless, the degree of rigor and the burden of proof should naturally be high when results are used for management, as management decisions not only affect the ecological system, but can also have substantial implications for human users and thus the socio-economic system. In my case, despite the poor model skill for fish biomass magnitude and the many assumptions that I needed to make, I argue that the developed model can be used for relative comparisons of the performance of alternative management (Chapter 6).

Model validation met the criteria of the general Atlantis guidelines and model outcomes of key dynamics generally corresponded with expert judgement and published and empirical relationships (Chapter 6). So, by comparing the model outcomes of alternative management strategies, outcomes that are all based on the same assumptions, relative trends and synergies could be explored and this led to expected and unexpected results. For example, fishing was identified as the greatest local threat to coral reefs, aggravated by land-based sources of pollution, and the greatest future threat is the predicted increase in mass coral bleaching caused by global warming (Chapter 7). This result is in line with current perceptions (e.g., Fenner 2012). However, comparing management scenarios, watershed improvement appeared of real importance for the overall ecosystem status in Guam, maybe even more so than to improve (herbivorous) fish stocks (Chapter 7). The latter being the current hypothesis, and makes sense intuitively. Model output that corroborates existing hypothesis, give more validity to the model. However, model output that differs, is very interesting and thought provocative, and leads to new research questions and a fresh look into the model development and the simulated dynamic processes.

9.5 Research findings

Ecosystem-based management that includes ecosystem services into integrated management strategies has gained increased traction with scientists and policymakers over the last few decades and ecosystem models can be useful tools in the various steps (scoping, indicator development, setting thresholds, risk analyses, MSE) in an EBM process (Tallis et al. 2010, Hassler et al. 2013, Kelble et al. 2013). With the predicted effects of climate change on coral reef ecosystem dynamics, more and more research focuses on how to mitigate or prepare for these effects and ecosystem models allow for these projections (Baker et al. 2008, Kennedy et al. 2013, McClanahan et al. 2014). However, current studies mostly focus on either one or a few aspects of climate change effects on coral reefs (e.g., structural complexity and fish biomass, fish biomass and coral cover, thermal stress and recovery of fish biomass or coral cover) and they mostly infer projections based on the assumed or found relationships (Baskett et al. 2009b, Graham et al. 2011b, Bozec et al. 2014, Rogers et al. 2014). This thesis integrated key dynamics and quantitatively assessed the relative trend of ecosystem changes in response to alternative management taking the effects of climate change into account. It therefore contributes to a knowledge gap in ecosystem understanding of multiple stressors to a reef ecosystem acting simultaneously. A current hypothesis is that if local management can increase (mainly herbivorous) fish biomass, corals will have a longer timespan to acclimate or recover from thermal stress (Carilli et al. 2009, Anthony et al. 2011b, Graham et al. 2011b, Kennedy et al. 2013, Palumbi et al. 2014). Based on my research presented in this thesis, I showed that when evaluating alternative management policies, while concurrently simulating the main other drivers on coral reef ecosystems, fishery regulations had little potential to mitigate the effects of thermal stress once the bleaching threshold was passed annually (Chapter 7). Moreover, with the current fishery regulations in Guam, the calcifier:non-calcifier ratio was actually higher despite the lower biomass of herbivorous fish. This result is perhaps in part because the model suggests that the number of herbivorous turtles would increase due to the decline in their predation by sharks. However, watershed management, that stops the additional input of nutrients and sediments, did offset the decline in coral biomass due to climate change. Naturally, this result does not mean that this is the case everywhere or that enhancing the herbivorous biomass is not beneficial for the functioning of a reef (McClanahan et al. 2014). This just shows that sometimes other factors can be more or equally important. With ecosystem modelling these unintuitive results can be recognized.

9.6 Conclusion

This thesis provides a novel application of the Atlantis ecosystem model for coral reefs since Atlantis, so far, had only been applied to temperate fisheries systems. This study also offers suggestions for choosing an appropriate model (or suite of models) depending on the leading principle of the study (Chapter 2). For adaptive resource management (or MSE) integrated thinking and decision support is required, which demands a diversity of modelling approaches. Integration can be achieved through complementary use of models or through integrated models that systematically combine all relevant aspects in one model. Such whole-of-system models can be useful tools for quantitatively evaluating scenarios as I did in this thesis. These models allow for an assessment of the interactive effects of multiple stressors on various, potentially conflicting, management objectives (such as conservation and extraction in the Guam case study).

This study also offers recommendations of ecosystem indicators for the effects of fishing on coral reef ecosystem structure and function (Chapter 3). Evaluation of the candidate indicators for fishing pressure showed that indicators at the community level (e.g., total biomass, community size structure, trophic level of the community) were most robust (i.e., showed the clearest trend) and that multiple indicators are necessary to identify fishing perturbations. Similar results were found for pelagic fisheries systems (Fulton et al. 2005).

Through the model development, guidelines (e.g., key coral reef dynamics, functionally important groups) and many details (e.g., relationship of reef dynamics, parameter estimations related to life history of many species) are provided (Chapters 4 and 6) that can be useful for the development of other coral reef models. It highlights an approach for data-limited situations with regard to time series when fishery data is present (Chapter 5). Although the application of this approach in my thesis leaves room for improvement, the already innovative approach itself is very useful for model tuning in data-limited systems (Chapters 5 and 6). The model application showed that by simulating separately the effects of land-based sources of pollution, fishing and ocean acidification and warming, climate change will have the largest overall effect on the ecosystem metrics by mid-century due to substantial negative effects on reef benthos (loss of coral cover) and that, to date, fishing has had the largest effect on the reef ecosystems around Guam (Chapter 6). Simultaneous modelling of the drivers showed that climate change impacts have a slight positive interaction with other drivers, generally meaning that declines in ecosystem metrics are not quite as steep as the sum of individual effects of the drivers. However, despite these synergistic effects, most ecosystem metrics did show strong declines in performance. The detrimental effect on corals of ocean warming under the current greenhouse gas emission scenarios is in correspondence with other studies (Thompson and Dolman 2010, Selig et al. 2012, Bozec et al. 2014). The study therefore, corroborates the urgency in reducing greenhouse gas emissions in order for coral reefs to survive.

Lastly, the thesis describes a novel approach to link outcomes of a quantitative biophysical model to qualitative human behavior or management models, which represent important socio-economic uses of the reef's resources, through the use of ecosystem metrics that are meaningful in both model types (Chapters 7 and 8). A better understanding of human behavior in relation to changes in ecosystem status or management strategies are needed for evaluating tradeoffs of those management strategies (Fulton et al. 2011c, van Putten et al. 2013, Brown and Mumby 2014). For Guam, tourism is of economic importance and reef condition influences the participation of divers while reef fishing is a cultural and recreational important activity and participation is influenced by fish abundance. Hence metrics that quantify the performance of management approaches are based on somewhat conflicting goals and this needs to be taken into account when tradeoffs are evaluated (Chapters 7 and 8).

Although not perfect, the Guam Atlantis coral reef ecosystem model is, to my knowledge, the first coral reef ecosystem model (1) with emergent properties of ecosystem processes and includes key dynamics and is, therefore, more realistic than other developed coral reef ecosystem models (Fogarty 2013), (2) integrates the main drivers simultaneously and so fulfills a research gap (Johnson et al. 2013) and (3) incorporates the entire ecosystem from hydrologic forcings to phytoplankton to apex predators and to humans and can, therefore, evaluate the socio-ecological tradeoffs of management scenarios (Fulton et al. 2014). Through model development, I also identified research gaps and can thus guide limited resources to areas most needed for ecosystem modelling. Moreover, now that it is developed, it can be used in multiple model inference for ecosystem-based management (Möllmann et al. 2014), to assess and quantify a range of research questions (Griffith et al. 2012, Kaplan et al. 2013, Smith et al.) and as a tool for resource managers in their MSE toolbox (Fulton et al. 2007, Ainsworth et al. 2012). With the current shift towards EBM and the many national and international policies now requiring it, this model could become a useful addition for coral reef EBM.

Marine invertebrates using the coral reef ecosystems as their home. *Photo NOAA*

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Appendices

Appendix A

This supplement provides additional information for chapter 4: "Design and parameterization of a coral reef ecosystem model for Guam". The information shows fish species observed during visual surveys conducted around Guam and categorized in a functional group based on diet, feeding mode, habitat, life history, and their ecological or economic importance. Rapid Ecological Assessments (REA) consist of stationary point counts at random, stratified sites, towed-diver surveys (TOW) are along a fixed depth (~10–15 m); catch is average annual catch from expanded inshore fishery data from 1985–2012. Species are sorted by decrease in biomass per functional group. Only those with a biomass > 0.05 g/m^2 or a recorded average annual catch > 10 kg are mentioned here, for a complete list see Weijerman et al. 2014.

Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Functional Group	**Fish Planktivores**	**FPL**				
Pomacentrus vaiuli	Pomacentridae	Ocellate damselfish	0.2	REA	0.33	3.1
Myripristis kuntee	Holocentridae	Shoulderbar soldierfish	61.0	REA	0.32	3.3
Plectroglyphidodon lacrymatus	Pomacentridae	Whitespotted devil	0.0	REA	0.18	2.2
Odonus niger	Balistidae	Redtoothed triggerfish	5.5	REA	0.16	3.2
Pomachromis guamensis	Pomacentridae	Guam damsel	0.0	REA	0.16	
Macolor macularis	Lutjanidae	Midnight snapper	0.0	REA	0.15	4.0
Macolor niger	Lutjanidae	Black and white snapper	2.5	REA	0.09	4.0
Blenniidae	Blenniidae	Blenny species	7.1	REA	0.07	
Myripristis berndti	Holocentridae	Blotcheye soldierfish	315.7	REA	0.06	3.7
Ptereleotris zebra	Microdesmidae	Chinese zebra goby	0.0	REA	0.05	3.4
Naso hexacanthus	Acanthuridae	Sleek unicornfish	30.9	REA	0.05	3.3
Dascyllus reticulatus	Pomacentridae	Reticulate dascyllus	0.0	REA	0.05	3.1
Naso vlamingii	Acanthuridae	Bignose unicornfish	32.3	REA	0.04	3.4
Pempheris oualensis	Pempheridae	Silver sweeper	91.6	REA	0.04	3.6
Abudefduf vaigiensis	Pomacentridae	Indo-Pacific sergeant	24.6	REA	0.02	2.6
A. sexfasciatus	Pomacentridae	Scissortail sergeant	37.9	REA	0.01	2.4
Myripristis amaena	Holocentridae	Brick soldierfish	21.5	REA	0	3.6
Apogon novemfasciatus	Apogonidae	Sevenstriped cardinalfish	18.7	REA	0	4.0
Functional Group	**Fish Coralivores**	**FCO**				
Chaetodon reticulatus	Chaetodontidae	Mailed butterflyfish	0.0	REA	0.07	2.6
Chaetodon citrinellus	Chaetodontidae	Speckled butterflyfish	0.3	REA	0.06	3.1
C. ornatissimus	Chaetodontidae	Ornate butterflyfish	157.5	REA	0.02	3.3
Arothron nigropunctatus	Tetraodontidae	Blackspotted puffer	22.1	REA	0	3.3
Functional Group	**Fish Detritivores**	**FDE**				
Ctenochaetus striatus	Acanthuridae	Striated surgeonfish	192.1	REA	1.34	2.0
C. *binotatus*	Acanthuridae	Twospot surgeonfish	3.8	REA	0.06	2.0

Functional Group	**Fish Browsers**	**FHB**				
Calotomus carolinus	Scaridae	Carolines parrotfish	69.5	REA	0.05	2.0
Chanos chanos	Chanidae	Milkfish	122.7	REA	0	2.0
Functional Group	**Target Fish Browsers**	**TFB**				
Naso lituratus	Acanthuridae	Orangespine unicornfish	2084.2	REA	0.58	2.3
Naso tonganus	Acanthuridae	Bulbnose unicornfish	143.6	REA	0.13	2.0
Kyphosus sp	Kyphosidae	Chubs	0.0	REA	0.12	
Naso unicornis	Acanthuridae	Bluespine unicornfish	10320.3	REA	0.04	2.0
Siganus argenteus	Siganidae	Streamlined spinefoot	684.6	REA	0.02	2.0
Functional Group	**Fish Grazers**	**FHG**				
Melichthys vidua	Balistidae	Pinktail triggerfish	5.6	REA	0.51	3.4
Stegastes fasciolatus	Pomacentridae	Pacific gregory	0.6	REA	0.3	2.2
Chrysiptera brownriggii	Pomacentridae	Surge damselfish	1.3	REA	0.22	2.7
Centropyge vrolikii	Pomacanthidae	Pearlscale angelfish	0.0	REA	0	2.8
Abudefduf septemfasciatus	Pomacentridae	Banded sergeant	191.3	REA	0	3.0
Abudefduf sordidus	Pomacentridae	Blackspot sergeant	37.5	REA	0	2.8
Functional Group	**Target Fish Grazers**	**THG**				
A. nigrofuscus	Acanthuridae	Brown surgeonfish	11.7	REA	0.96	2.0
Acanthurus lineatus	Acanthuridae	Lined surgeonfish	814.4	REA	0.74	2.0
Acanthurus nigricans	Acanthuridae	Whitecheek surgeonfish	7.1	REA	0.23	2.0
Acanthurus olivaceus	Acanthuridae	Orangespot surgeonfish	32	REA	0.16	2.2
Acanthurus blochii	Acanthuridae	Ringtail surgeonfish	37.5	REA	0.09	2.0
Zebrasoma veliferum	Acanthuridae	Sailfin tang	1.6	REA	0.06	2.0
Acanthurus pyroferus	Acanthuridae	Chocolate surgeonfish	0.1	REA	0.05	2.0
A. nigricauda	Acanthuridae	Epaulette surgeonfish	35.0	REA	0.02	3.0
A. xanthopterus	Acanthuridae	Yellowfin surgeonfish	764.2	REA	0	2.4
Acanthurus guttatus	Acanthuridae	Whitespotted surgeon	334.1	REA	0	2.0
Functional Group	**Fish Scrapers**	**FHS**				
Chlorurus sordidus	Scaridae	Daisy parrotfish	342.2	REA	2.29	2.0
Scarus psittacus	Scaridae	Common parrotfish	386.3	REA	0.61	2.0
Scarus forsteni	Scaridae	Forsten's parrotfish	8.8	REA	0.3	2.0
Scarus schlegeli	Scaridae	Yellowband parrotfish	279.6	REA	0.29	2.0
Scarus frenatus	Scaridae	Bridled parrotfish	0.2	REA	0.06	2.0
Scarus sp	Scaridae	Scarus genus	0.0	REA	0.06	
Scarus globiceps	Scaridae	Globehead parrotfish	10.5	REA	0.02	2.0
Chlorurus frontalis	Scaridae	Tan-faced parrotfish	181.0	REA	0.26	2.0
Functional Group	**Fish Excavators**	**FHE**				
Scarus altipinnis	Scaridae	Filament-finned parrotfish	62.1	REA	0.24	2.0
S. rubroviolaceus	Scaridae	Ember parrotfish	106.8	REA	0.12	2.0
Chlorurus sp	Scaridae	Large-bodies parrotfishes	0.0	REA	0.09	
Scarus festivus	Scaridae	Festive parrotfish	25.7	REA	0.03	2.0
Hipposcarus longiceps	Scaridae	Pacific longnoseparrotfish	114.5	REA	0.03	2.0
Scaridae	Scaridae	Parrotfish species	30.2	REA	0.01	
Chlorurus microrhinos	Scaridae	Steephead parrots	127	REA	0.01	

Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Functional Group	**Bumphead Parrotfish BHP**					
Bolbometopon muricatum	Scaridae	Green bumphead parrotfish	18.4	TOW	0.00	2.7
Functional Group	**Fish Invertivores FIV**					
Balistapus undulatus	Balistidae	Orange-lined triggerfish	17.0	REA	0.23	3.4
Paracirrhites arcatus	Cirrhitidae	Arc-eye hawkfish	0.0	REA	0.19	3.6
Sufflamen chrysopterum	Balistidae	Halfmoon triggerfish	0.0	REA	0.14	3.5
Sufflamen bursa	Balistidae	Boomerang triggerfish	3.4	REA	0.12	3.1
Valenciennea strigata	Gobiidae	Blueband goby	0.00	REA	0.08	4.0
Halichoeres biocellatus	Labridae	Red-lined wrasse	0.8	REA	0.07	3.4
Zanclus cornutus	Zanclidae	Moorish idol	15.9	REA	0.07	2.9
Pygoplites diacanthus	Pomacanthidae	Royal angelfish	0.00	REA	0.06	2.7
Chaetodon lunula	Chaetodontidae	Raccoon butterflyfish	1.9	REA	0.06	3.3
Balistoides viridescens	Balistidae	Titan triggerfish	148.7	REA	0.04	3.3
Diodon hystrix	Diodontidae	Spot-fin porcupinefish	235.7	REA	0.04	3.4
Rhinecanthus rectangulus	Balistidae	Wedge-tail triggerfish	33.1	REA	0.03	3.1
Chaetodon auriga	Chaetodontidae	Threadfin butterflyfish	24.1	REA	0.02	3.2
Plectorhinchus gibbosus	Haemulidae	Harry hotlips	78.6	REA	0.02	3.6
Bothus mancus	Bothidae	Flowery flounder	67.7	REA	0.01	4.4
Pseudobalistes flavimarginatus	Balistidae	Yellowmargin triggerfish	28.8	REA	0	
Cirrhitus pinnulatus	Cirrhitidae	Stocky hawkfish	43.5	REA	0	3.6
Aluterus scriptus	Monacanthidae	Scrawled filefish	210.9	REA	0	2.8
Functional Group	**Target Fish Invertivores TIV**					
Monotaxis grandoculis	Lethrinidae	Humpnose big-eye bream	0.0	REA	0.5	3.2
Thalassoma quinquevittatum	Labridae	Fivestripe wrasse	7.1	REA	0.41	3.6
Plectroglyphidodon dickii	Pomacentridae	Blackbar devil	0.0	REA	0.23	3.4
P. multifasciatus	Mullidae	Manybar goatfish	75.7	REA	0.16	3.5
Gnathodentex aureolineatus	Lethrinidae	Striped large-eye bream	0.0	REA	0.1	3.3
Sargocentron caudimaculatum	Holocentridae	Silverspot squirrelfish	0.9	REA	0.08	3.9
Lutjanus kasmira	Lutjanidae	Bluestripe snapper	9.7	REA	0.07	3.6
Halichoeres hortulanus	Labridae	Checkerboard wrasse	10.6	REA	0.07	3.4
Cheilinus sp	Labridae	Cheilinus wrasse	0.0	REA	0.06	
Lutjanus fulvus	Lutjanidae	Blacktail snapper	685.4	REA	0.06	4.1
Sargocentron tiere	Holocentridae	Blue lined squirrelfish	80.2	REA	0.05	3.5
Cheilinus trilobatus	Labridae	Tripletail wrasse	605.2	REA	0.05	3.5
Hologymnosus doliatus	Labridae	Pastel ringwrasse	18.6	REA	0.05	3.8
Neoniphon sammara	Holocentridae	Sammara squirrelfish	212	REA	0.05	3.6

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Parupeneus barberinus	Mullidae	Dash-and-dot goatfish	392.2	REA	0.04	3.2
Lethrinus harak	Lethrinidae	Thumbprint emperor	2192.6	REA	0.03	3.6
Mulloidichthys vanicolensis	Mullidae	Yellowfin goatfish	315.7	REA	0.03	3.6
Cheilinus fasciatus	Labridae	Redbreast wrasse	35.9	REA	0.03	3.4
Epibulus insidiator	Labridae	Slingjaw wrasse	31.7	REA	0.03	3.8
Lutjanus gibbus	Lutjanidae	Humpback red snapper	133	REA	0.02	3.6
Hemigymnus melapterus	Labridae	Blackeye thicklip	32.9	REA	0.02	3.3
Hemigymnus fasciatus	Labridae	Barred thicklip	12.5	REA	0.02	3.2
Parupeneus insularis	Mullidae	Twosaddle goatfish	118.4	REA	0.02	3.7
Novaculichthys taeniourus	Labridae	Rockmover wrasse	21.6	REA	0.01	3.3
Lethrinus olivaceus	Lethrinidae	Longface emperor	559.9	REA	0.01	3.8
Myripristis violacea	Holocentridae	Lattice soldierfish	20	REA	0.01	3.5
Thalassoma trilobatum	Labridae	Christmas wrasse	28.4	REA	0.01	3.6
Th. purpureum	Labridae	Surge wrasse	80.2	REA	0	3.6
Labridae	Labridae	wrasse family	12.5	REA	0	
Neoniphon opercularis	Holocentridae	Blackfin squirrelfish	38.2	REA	0	3.5
Sargocentron microstoma	Holocentridae	Smallmouth squirrelfish	11.1	REA	0	3.6
M. flavolineatus	Mullidae	Yellowstripe goatfish	3804.9	REA	0	3.3
H. trimaculatus	Labridae	Threespot wrasse	60.3	REA	0	3.5
Cheilio inermis	Labridae	Cigar wrasse	222.7	REA	0	4.0
Functional Group	**Humphead Wrasse**	**HHW**				
Cheilinus undulatus	Labridae	Humphead wrasse	124.0	REA	0.02	4.0
Functional Group	**Fish Benthic Piscivores**	**FPB**				
Paracirrhites forsteri	Cirrhitidae	Blackside hawkfish	0.0	REA	0.07	4.3
Gymnothorax javanicus	Muraenidae	Giant moray	156.3	REA	0.02	3.9
G. flavimarginatus	Muraenidae	Yellow-edged moray	11.2	REA	0.01	4.2
Aulostomus chinensis	Aulostomidae	Chinese trumpetfish	16.3	REA	0	4.2
G. undulatus	Muraenidae	Undulated moray	27.5	REA	0	4.3
Functional Group	**Target Benthic Piscivores**	**TPB**				
Cephalopholis urodeta	Serranidae	Darkfin hind	10.1	REA	0.34	4.0
Oxycheilinus unifasciatus	Labridae	Ringtail maori wrasse	23.7	REA	0.23	4.1
Cephalopholis argus	Serranidae	Peacock hind	36.8	REA	0.16	4.5
Epinephelus fasciatus	Serranidae	Blacktip grouper	1.3	REA	0.11	3.7
Lutjanus bohar	Lutjanidae	Two-spot red snapper	462.3	REA	0.1	4.1
Plectropomus laevis	Serranidae	Blacksaddled coralgrouper	68	REA	0.05	4.1
E. hexagonatus	Serranidae	Starspotted grouper	114.2	REA	0.02	4.1
Lutjanus monostigma	Lutjanidae	Onespot snapper	471.5	REA	0.02	4.3
P.s cyclostomus	Mullidae	Goldsaddle goatfish	17.7	REA	0.01	4.2
Epinephelus merra	Serranidae	Honeycomb grouper	992.7	REA	0.01	3.8

Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Epinephelus tauvina	Serranidae	Greasy grouper	12.3	REA	0.01	4.1
Functional Group	**Fish Mid-water Piscivores**	**FPM**				
Aphareus furca	Lutjanidae	Small toothed jobfish	22.0	REA	0.45	4.1
Scomberoides lysan	Carangidae	Doublespotted queenfish	303.7	TOW	0	4.5
Functional Group	**Fish Roving Piscivores**	**FPR**				
Sphyraena qenie	Sphyraenidae	Blackfin barracuda	27.8	TOW	1.04	4.5
Caranx melampygus	Carangidae	Bluefin trevally	3444.7	REA	0.02	4.5
Caranx papuensis	Carangidae	Brassy trevally	559.9	TOW	0.01	4.0
Caranx sexfasciatus	Carangidae	Bigeye trevally	929.6	TOW	0.01	4.5
Aprion virescens	Lutjanidae	Green jobfish	248.1	TOW	0.01	4.0
Sphyraena barracuda	Sphyraenidae	Great barracuda	557.3	TOW	0	4.5
Caranx ignobilis	Carangidae	Giant trevally	426.9	TOW	0	4.2
Carangoides ferdau	Carangidae	Blue trevally	12.9	TOW	0	4.5
Functional Group	**Rays**	**RAY**				
Aetobatus narinari	Myliobatidae	Spotted eagle ray	0.0	TOW	0.09	3.2
U. asperrimus	Dasyatidae	Porcupine ray	0.0	TOW	0.04	3.5
Functional Group	**Sharks**	**SHR**				
Nebrius ferrugineus	Ginglymostomatidae	Tawny nurse shark		TOW	0.09	4.1
Triaenodon obesus	Carcharhinidae	Whitetip reef shark		TOW	0.04	4.2
C. melanopterus	Carcharhinidae	Blacktip reef shark	9.0	TOW	0.02	3.9

Appendix B

This supplement provides additional information for chapter 4: "Design and parameterization of a coral reef ecosystem model for Guam". The detailed information shows marine vertebrate species per functional group, their proportion of the group, abundance from 2011 SPC and towed-diver surveys conducted by CRED, and life history characteristics. Mort. is mortality, k is the growth constant in the Von Bertalanffy growth curve, Linf is the infinite length, tmax is the maximum age in years, L-W is the length-weight relationship with the constants a and b, mat. is maturity and recruit age means recruitment from pelagic stage to reef habitat in days. The values are the weighted means per functional group. For values per species, see Weijerman et al. 2014. Additionally, invertebrate groups with descriptions are given.

Group	**Code**	**Perc. of group**	**Numbers per m^2**	**Mort. per y**	**k**	**Linf cm**	**tmax y**	**L-W a**	**L-W b**	**age at mat. y**	**Recruit age d**
1. Planktivores	FPL	1.00	0.04	1.24	0.58	25.32	6.70	0.02	3.05	1.39	23
2. Coralivores	FCO	1.00	0.00	1.71	0.98	18.56	4.37	0.05	2.95	1.17	37
3. Invertivores	FIV	1.00	0.01	1.01	0.57	25.37	7.51	0.03	3.07	1.38	49
4. Target Invertivores	TIV	1.00	1.59	0.77	0.38	39.53	9.38	0.02	2.99	2.21	27
5. Humphead wrasse	HHW	1.00	0.00	0.20	0.10	232.44	30.00	0.01	3.14	5.90	34
6. Detritivores	FDE	1.00	0.02	1.41	0.84	29.05	17.41	0.02	3.05	0.92	55
7. Browsers	FHB	1.00	0.00	2.14	1.43	29.82	4.35	0.01	3.16		15
8. Target Browsers	THB	1.00	0.00	1.25	0.68	36.27	14.18	0.03	3.09	2.58	70
9. Grazers	FHG	1.00	0.04	1.21	0.55	21.95	6.56	0.02	3.18	1.63	60
10. Target Grazers	THG	1.00	0.02	1.42	0.80	25.36	24.00	0.03	2.99	1.37	32
11. Scrapers	FHS	1.00	0.01	0.73	0.92	22.78	8.71	0.02	3.05	1.40	35
12. Excavators	FHE	1.00	0.00	1.08	0.65	44.69	11.14	0.02	3.08	2.19	35
13. Bumphead parrotfish	BHP	1.00	0.00	0.14	0.14	133.10	33.00	0.02	3.04	8.00	35
14. Benthic piscivores	FPB	1.00	0.02	0.53	0.21	72.11	8.00	0.01	3.03	2.00	60
15. Target Benthis piscivores	TPB	1.00	0.00	0.50	0.24	53.01	15.90	0.02	2.99	3.79	60
16. Mid-water piscivores	FPM	1.00	0.01	0.58	0.32	72.86	8.96	0.01	3.00	1.99	60
17. Roving piscivores	FPR	1.00	0.03	0.22	0.10	170.51	28.27	0.01	3.00	5.59	120
18. Reef-associated sharks	SHR	1.00	0.00	0.25	0.16	276.73	22.26	0.00	3.47	4.25	360
19. Rays	RAY	1.00		0.17	0.09	271.37	23.18	0.01	3.20	5.42	60
20. Sea Turtles	REP	1.00	0.0000059	0.14	0.09	108.90	62.00	0.05	3.30	37.5	2190

INVERTEBRATES

#	Code	Group	Description
21	BC	Benthic Carnivores	carnivorous epifauna invertebrates
22	BD	Benthic Detritivores	sea cucumbers, lobster, polycheates, detritivorous gastropods and crusteaceans (e.g.,crabs)
23	BO	Benthic Meiofauna	infauna: herbivorous polychaetes, gastropods and crustaceans
24	BFF	Benthic Suspension Feeders	octocoral, sponges, tunicates, zooanthids, giant clams, bivalves, polychaetes, foraminifera, bryzoans, brittle stars
25	CRS	Sheltering corals	corals species with a branching/tabular/columnar morphology
26	CRN	Non-sheltering corals	coral species with a massive/encrusting morphology
27	CEP	Cephalopods	octopus, squids
28	BG	Benthic Grazers	urchins (helmet, collectors, pencil, boring urchin, diadema)
29	BSS	Sea Stars	including crown-of-thorns seastar
	ALGAE		
30	TRF	Turf algae	< 1cm
31	MA	Macroalgae	> 1cm
32	CCA	Crustose-coraline algae	
	PLANKTON		
33	PS	Small phytoplankton	picoeukaryotes, cyanobacteria, < 1µm
34	PL	Large phytoplankton	> 1µm including diatoms
35	ZC	Zooplankton -carnivores	chaetognath, amphipods, crab larvae, isopods, mysid shrimps, polychaetes
36	ZD	Demersal zooplankton	pelagic fish & invert larvae, copepods, polychaetes, foraminiferas
37	ZH	Zooplankton - herbivores	copepods
	BACTERIA		
38	PB	Pelagic Bacteria	hetrotrophic bacteria (0.2-1 µm)
39	BB	Benthic bacteria	hetrotrophic bacteria (0.2-1 µm)
	DETRITUS		
40	DC	carrion	newly dead – in fishing discards
41	DR	refractory detritus	turnover time in order of years
42	DL	Labile detritus	easily degraded, turnover time in order of months

Appendix C

This supplement provides additional information for chapter 5: "Coral reef-fish biomass trends based on shore-based creel surveys in Guam. The detailed information shows:

The number of interviews per gear type per year. Total interviews between 1 and 4 are indicated as "<5".

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Hook and Line	53	46	32	38	45	59	63	66	61	83	78	76	87	84	85
Gill Net	38	34	28	28	25	41	35	40	33	36	49	31	50	48	51
Surround Net	7	< 5	< 5	5	0	< 5	0	< 5	0	< 5	< 5	0	0	0	0
Snorkel Spear	35	20	21	18	14	14	15	16	14	36	21	20	25	34	49
Scuba Spear	< 5	< 5	0	< 5	< 5	< 5	< 5	< 5	< 5	< 5	9	< 5	< 5	< 5	< 5
Drag Net	8	9	8	< 5	< 5	5	7	7	6	< 5	5	< 5	< 5	< 5	10

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Hook and Line	86	86	60	78	61	60	65	61	64	62	57	48	45
Gill Net	41	31	28	16	15	13	13	11	12	6	13	12	9
Surround Net	0	0	0	< 5	< 5	0	< 5	< 5	< 5	0	< 5	< 5	0
Snorkel Spear	28	27	19	14	10	8	9	5	6	5	7	< 5	11
Scuba Spear	< 5	< 5	< 5	< 5	0	0	0	0	0	0	< 5	0	0
Drag Net	4	< 5	0	0	0	< 5	< 5	0	0	0	0	0	0

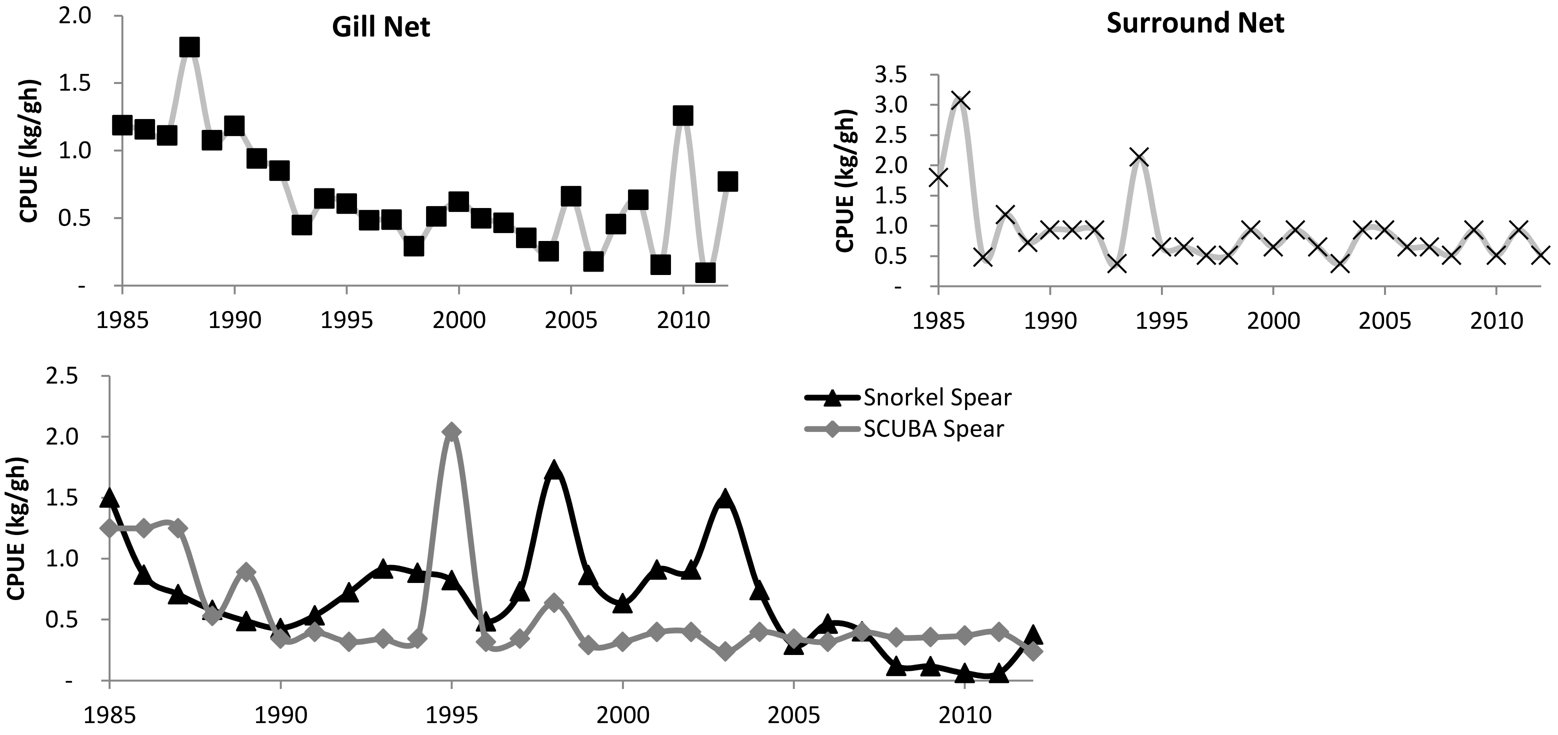
Annual CPUE values from sample data calculated by WPacFIN. Missing values in red are calculated as the mean of three previous years.

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Hook and Line	0.18	0.21	0.20	0.09	0.11	0.14	0.16	0.09	0.06	0.09	0.14	0.08	0.10	0.10	0.11
Gill Net	1.19	1.16	1.11	1.76	1.08	1.18	0.94	0.85	0.45	0.64	0.61	0.48	0.49	0.29	0.51
Surround Net	1.79	3.07	0.48	1.19	0.72	0.93	0.93	0.93	0.37	2.14	0.65	0.65	0.51	0.51	0.93
Snorkel Spear	1.50	0.87	0.71	0.58	0.49	0.43	0.53	0.72	0.92	0.88	0.82	0.49	0.73	1.73	0.87
Scuba Spear	1.25	1.25	1.25	0.53	0.89	0.34	0.40	0.32	0.34	0.34	2.04	0.32	0.34	0.64	0.29
Drag Net	1.11	1.23	0.95	0.20	2.66	0.91	2.06	2.96	0.91	2.11	1.54	1.52	1.42	1.83	1.66

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Hook and Line	0.31	1.21	0.91	0.81	2.11	0.31	1.08	0.31	0.56	2.11	0.99	0.91	0.31

Gill Net	0.08	0.08	0.07	0.09	0.08	0.05	0.08	0.09	0.06	0.07	0.03	0.09	0.14
Surround Net	0.62	0.50	0.46	0.35	0.25	0.66	0.18	0.45	0.63	0.15	1.26	0.09	0.77
Snorkel Spear	0.65	0.93	0.65	0.37	0.93	0.93	0.65	0.65	0.51	0.93	0.51	0.93	0.51
Scuba Spear	0.64	0.91	0.91	1.49	0.74	0.29	0.47	0.40	0.12	0.12	0.06	0.06	0.38
Drag Net	0.32	0.40	0.40	0.24	0.40	0.34	0.32	0.40	0.35	0.35	0.37	0.40	0.24

Time series of CPUE for various gear types.



Appendix D

This supplement provides additional information for chapter 5: "Coral reef-fish biomass trends based on shore-based creel surveys in Guam. The detailed information shows the number of times that landings from a fish group defined in text (see Methods) and Appendix A was recorded in interview data over 3-year periods (to conserve confidentiality of fishers). Blank indicates that no interview took place.

Scrapers (small-bodied parrotfishes)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	0	10	2	4	61	2
1988-90	0	7	0	0	18	0
1991-93	0	39	3	1	18	0
1994-96	0	34	5	6	53	5
1997-99	1	54	8	5	120	
2000-02	0	16	7	6	39	0
2003-05	0	7	1	3	20	0
2006-08	0	4	2		14	0
2009-11		3	0	2	5	0
2012-13		3	0		8	0

Excavators (large-bodied parrotfishes)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	0	3	0	0	24	0
1988-90	0	2	0	0	7	0
1991-93	0	8	2	4	8	0
1994-96	0	4	3	7	21	0
1997-99	0	6	6	5	39	
2000-02	0	1	2	2	25	0
2003-05	0	1	4	1	4	0
2006-08	0	1	2		1	0
2009-11		0	2	0	3	0
2012-13		0	0		3	0

Target browsers (unicorns, rabbitfishes)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	11	92	68	10	198	24
1988-90	6	112	85	1	137	2
1991-93	2	104	116	4	46	4
1994-96	3	80	114	20	129	4
1997-99	10	145	138	12	229	
2000-02	5	102	127	6	145	0
2003-05	0	28	47	7	51	2
2006-08	1	28	39		30	1
2009-11		23	24	1	20	2
2012-13		8	9		19	0

Target grazers (surgeonfishes)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	1	67	18	2	80	5
1988-90	2	90	14	0	72	2
1991-93	0	76	34	3	36	2
1994-96	0	76	28	9	84	2
1997-99	2	119	19	6	133	
2000-02	0	64	21	4	77	0
2003-05	0	25	26	1	29	1
2006-08	0	17	17		16	1
2009-11		10	9	0	8	3
2012-13		4	5		9	0

Target invertivores (goatfishes, emperors, snappers)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	60	258	46	2	151	32
1988-90	23	274	85	1	79	3
1991-93	44	337	203	6	62	2
1994-96	18	329	259	12	181	7
1997-99	64	469	329	3	307	
2000-02	14	305	255	13	163	0
2003-05	1	77	136	8	47	4
2006-08	1	29	117		28	0
2009-11		48	71	1	16	3
2012-13		33	29		29	0

Target benthic piscivores (groupers)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	1	10	8	1	31	1
1988-90	0	39	33	1	32	0
1991-93	0	55	93	2	26	1
1994-96	0	22	61	3	47	2
1997-99	0	32	68	1	71	
2000-02	0	24	72	2	40	0
2003-05	0	4	66	2	13	0
2006-08	0	4	46		10	0
2009-11		2	17	0	2	1
2012-13		2	6		6	0

Mid-water piscivores (barracudas)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	13	16	17	1	4	7
1988-90	6	9	25	0	1	0
1991-93	6	22	25	0	4	0
1994-96	4	20	29	0	6	1
1997-99	12	25	25	0	19	
2000-02	2	5	25	0	10	0
2003-05	2	4	23	0	4	0
2006-08	2	4	7		2	0
2009-11		5	14	0	1	1
2012-13		3	0		3	0

Roving piscivores (jacks)

	Drag Net	Gill Net	Hook & Line	Scuba Spear	Snorkel Spear	Surround Net
1985-87	27	76	71	1	9	5
1988-90	13	84	78	1	3	5
1991-93	9	63	139	0	5	0
1994-96	11	73	234	0	3	1
1997-99	14	98	303	0	3	
2000-02	6	66	236	0	5	0
2003-05	0	20	189	1	3	1
2006-08	0	10	190		1	2
2009-11		19	132	0	1	0
2012-13		13	89		1	0

Appendix E

This supplement provides additional information for chapter 5: "Coral reef-fish biomass trends based on shore-based creel surveys in Guam." The detailed information compares CPUE per gear type between weekday and weekend with a Welch two sample t-test (allowing unequal variances) and between regions with ANOVA for hook and line fishery. Values are means (standard deviation) over 1985–2012. Region 0 is the combination of region 1, 2, 3 and 4.

	region	**Mean CPUE**		**Welch two—sample t-test**		**ANOVA**		
Method		**weekday**	**weekend**	***p***	**n**	**Mean CPUE**	**p**	**n**
Hook and line	1	0.12 (0.09)	0.07 (0.05)	0.02	28	0.09 (0.06)	0.37	28
	2	0.10 (0.07)	0.07 (0.04)	0.04	28	0.09 (0.05)		
	3	0.12 (0.08)	0.09 (0.05)	0.10	28	0.11 (0.05)		
Cast Net	0	0.25 (0.18)	0.22 (0.14)	0.45	28			
Gill Net	0	0.65 (0.47)	0.71 (0.47)	0.62	28			
Snorkel spear	0	0.75 (0.57)	0.59 (0.37)	0.23	28			

Appendix F

This supplement provides additional information for chapter 6: "Applying the Atlantis model framework to coral reef ecosystems". It provides details on the application of Guam Atlantis to a coral reef ecosystem.

Table of Contents

Introduction
Added coral code: Coral biomass
  Recruitment
  Mortality
Model validation and verification
Added coral code: Coral related dynamics
  Driver 1: Climate change
    Climate change effects on coral reef ecosystems
  Driver 2: Land-based sources of pollution
    Land-based sources of pollution: Sedimentation and nutrient elevation effects on benthic composition and target fish biomass
  Driver 3: Fishing activity
    Effects of fishing of herbivores on corals-algae-grazers dynamics
Sensitivity and skill assessments
Conclusion

Introduction

In previous applications of Atlantis models, corals, if included at all, were modeled as benthic filter feeders (Brand et al. 2007, Kaplan et al. 2010, Link et al. 2010, Ainsworth et al. 2011a, Kaplan et al. 2012). We used that framework and parameterized it for the coral reef ecosystems around Guam. Details on the design, data sources and parameterization can be found in Weijerman et al. (2014) or Chapter 4. Here we describe the methods, assumptions, validation, and verification of added code to Atlantis that represent the relationships of key coral and coral reef dynamics (Fig. F-1). We organized the text per research topic rather than the traditional methods - results - discussion format. First we discuss the added code that addresses the growth of corals (change in coral biomass) and assess the adapted model's validation and verification process. We then validated these added dynamics by examining the model behavior over 30–75 years without any disturbances, i.e., a 'control' system, following the guidelines for Atlantis model development. Then we detail added code of key drivers, namely (1) climate change (ocean warming and acidification), (2) changes in land use (eutrophication and sedimentation), and (3) fishing activities. By including extensive empirical data collected from field studies in Guam, local dynamics are projected over time-scales of decades, and trends that manifest themselves are identified. Model outcomes of scenarios with each of the disturbances were compared with empirical studies from Guam or with regional studies, when local information was not available. Lastly we discuss how we conducted sensitivity analyses for the levels of primary productivity, structural complexity and the benthic algae-corals competition and present the results.

Added coral code: Coral biomass

Changes in coral biomass are modeled as the sum of growth and size-dependent recruitment, minus mortality (including predation; Eq. 1). Predation relates to the abundance of other system components including corals themselves and species that eat coral (Fig. F-1). Each of these processes is modeled as a series of functions based on empirical relationships taken from published studies.

$$\frac{\mathrm{d(Cx)}}{dt} = \mu_{Cx} - M_{lin\ Cx} - M_{quad\ Cx} - \sum\nolimits_{i=predator\ groups} P_{Cx,i} - F_{Cx} \qquad \text{Eq. 1}$$

where *Cx* is the invertebrate consumer (coral polyp), with μ_{Cx} the coral specific growth, $M_{lin\ Cx}$ and $M_{quad\ Cx}$ the linear and quadratic mortality of corals, P_i is predation by group *i*, and *F* is fishing or take of this group.

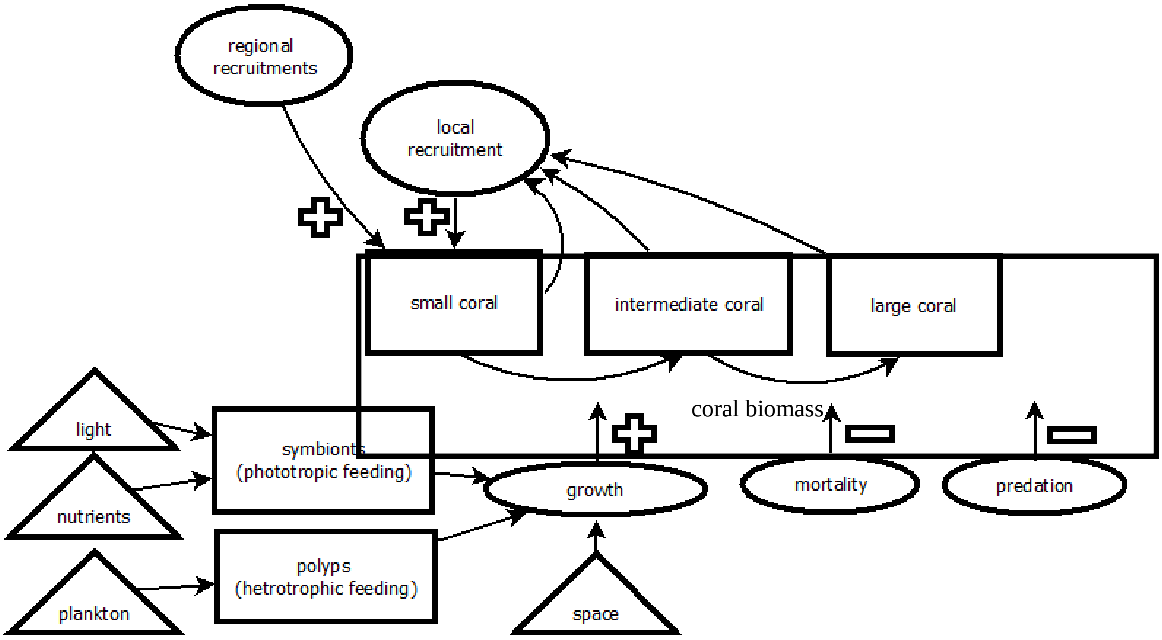


Figure F-1. Schematic representation of modeled changes in coral biomass due to growth (based on feeding), and recruitment minus mortality and coral predation (including bioerosion). Rectangles represent biomass, ovals processes, and triangles environmental properties. Other environmental conditions that influence growth and mortality (such as elevated temperature, sediments, overgrowth by macroalgae) are left out for clarity and included in figure F-2.

Growth is influenced by competition for food, light, space, and oxygen. Corals are heterotrophic at night and photosynthesize during daytime, and excess fixed carbon is converted to lipids for reserves (Rodrigues et al. 2008, Gustafsson 2013). Coral polyps can take up dissolved organic material for growth (Bythell 1990). At night, coral polyps extend their tentacles to capture zooplankton, particulate organic matter, and bacteria (Palardy et al. 2006, Palardy et al. 2008) that provide them with nitrogen and other nutrients. The coral code uses the standard Atlantis consumption routine with invertebrates modeled as biomass pools (Eq. 1, 2) and for vertebrates Atlantis tracks abundance, biomass, weight-at-age and condition (reserve weight versus structural weight) of each age class of each group through time. For coral polyps, change in biomass is modeled with:

$$\mu C = \left[\varepsilon_{Cx} \bullet \sum\nolimits_{i=living\ prey} P_{i,Cx} + \sum\nolimits_{j=detritus} P_{j,Cx} \bullet \varepsilon_{Cx,j}\right] \bullet hSp \bullet hO_2 \qquad \text{Eq. 2}$$

where ε_{Cx} is the growth efficiency of Cx when feeding on live prey, $\varepsilon_{Cx,j}$ the efficiency when feeding on detritus, hSp is space limitation, and hO_2 is oxygen limitation. Space limitation is determined by *min(1.0,max(0.0,(1.0 - B / (SPmax • area_hab))))* with B the combined coral polyp and symbiont biomass, *SPmax* the maximum biomass per area, and *area_hab* the species specific amount of habitat area available for settlement or growth.

The routine for primary producers was adjusted to allow for the symbionts-host representation (Eq. 3):

$$\frac{\mu C}{dt} = Bsymbiont \bullet \mu_C \bullet hN \bullet hI \bullet hSp \qquad \text{Eq. 3}$$

with μC the coral specific growth , *Bsymbiont* is the symbiotic zooxanthellae biomass, *hN* is nutrient limitation determined by the coral specific half saturation constant for growth on DIN and available nutrients, and *hI* is light limitation determined by the coral specific light saturation constant and the available light.

Coral growth is the sum of the heterotrophic and autotrophic growth. We further assumed that the photosynthesis threshold is 85% of noon daylight; proportion of corals feeding during daylight is 20%; translocation of energy from symbionts to host coral is 90% (Gustafsson 2013). Growth is also influenced by environmental factors (e.g., aragonite saturation state) and water quality (e.g., sediment load) as explained below in the section “Added coral code: Coral related dynamics”.

Recruitment

Recruitment is estimated as a function of supply and settlement survivorship, with supply being driven by the net import from Guam which we assume is relatively small, and local population fecundity which is affected by colony sizes and abundance with larger corals having a higher fecundity (Birkeland et al. 2013) (Eq. 4). To account for the difference in fecundity between size classes of corals they were modeled as three size/age classes each with three sub-bins. Corals can skip across sub-bins within size class but they cannot skip the next size class. Demographic coral data is sparse so we assumed an initial uniform distribution of size classes. These transitions are modeled according to:

$$T(i) = \frac{max\_accel\_transition}{1 + e^{(-3 \bullet (i - 1.5))}} \qquad \text{Eq. 4}$$

whereby $T(i)$=Transition to next size class for size class i, growth restriction is capped by the max_accel_transition parameter (0.1) and follows an exponential curve to mimic their 3D surface area (Edmunds et al. 2014).

Local recruitment is the sum of the recruitment of each size class according to:

$$local\ R = 1 - e^{-0.001 * B} \qquad \text{Eq. 5}$$

with R = recruitment and B = coral biomass for each size class.

Most Pacific corals are spawners (Baird et al. 2009) and with an increasing distance between coral colonies, chances of fertilization reduce due to Alleé effect (Birkeland et al. 2013). Survival of larvae until settlement is low (Graham et al. 2008) decreasing connectivity at regional scales (Birkeland et al. 2013). Settlement survivorship is modeled to be positively related to hard substrate, turf and crustose-coralline algae (CCA) and negatively to upright algae (Nugues and Bak 2006). As corals can only recruit to hard habitat, habitat is set as a potential facilitator for coral recruitment (Eq. 6). This relationship is a gross approximation and should ideally be replaced with a connectivity matrix if the appropriate data becomes available.

$$total\ R = localR + regionalR * (CCA\ cover + hard\ substrate + \partial * Turf\ cover) \qquad \text{Eq. 6}$$

with regional recruitment (regionalR) modeled as a constant and ∂ a correction factor (see assumptions), CCA is crustose-coralline algae.

We assumed that all modeled corals are spawners; coral recruits are the expected number of surviving larvae given current environmental conditions, i.e., we do not model the pelagic larval stage; contribution to recruitment follows an exponential relationship with coral biomass (Eq. 5) (Birkeland et al. 2013); recruitment is zero in macroalgal habitats, but is facilitated by crustose coralline algae and hard substrate, and by turf algae with a correction factor of 0.05–0.15 (Melbourne-Thomas et al. 2011a).

Mortality

Mortality is influenced by environmental factors (such as elevated temperatures) and by predation and competition (density-dependency, macroalgal overgrowth, fish bites, crown-of-thorns seastar predation, microeroders). These processes are discussed below.

Model validation and verification

Criteria used for testing the validity of the model and to verify model outcomes were based on guidelines for Atlantis model development (Horne et al. 2010, Link et al. 2010, Ainsworth et al. 2011a):

1) Predicted biomass matches observations or are plausible based on information from domain experts. In this case for many benthic groups this defaults to staying within a factor of two of initial conditions. For fish groups we expected predicted biomass (with no fishing or other disturbances) to approximate those in marine reserves in Guam or from the unpopulated Northern Mariana Islands (NOAA Pacific Islands Fisheries Science Centre, Coral Reef Ecosystem Division (CRED) data);
2) Weight-at-age stays stable and abundance of size classes decreases with increasing size classes (few large organisms and many small ones); and
3) Reproduced catch data has a plausible trajectory and magnitude of historical change without pushing any modeled group to extinction.

In control simulations (scenario with no disturbances) fish biomass reached a level between that seen in the marine reserves in Guam and in unfished areas around the Northern Mariana Islands and invertebrates reached a stable biomass (Appendix H-1) thereby complying with the first criteria for model development. For the vertebrates, the ratio of weight-at-age to initial weight-at-age stayed mostly between the desired values of 0.8 and 1.2, and in all cases between the acceptable levels of 0.5 and 1.5 (Appendix H-2). Additionally, the abundance of older age classes was lower than for younger age classes in all fish groups (Appendix H-3) resulting in an expected size-class distribution based on life-history information. These results satisfied the second criteria for model development. Simulating fixed fishing mortality showed that all groups were impacted by fishing pressure. Total fish biomass declined to half initial biomass when fishing mortality was between 0.4

and 1 times natural mortality for each functional group (Appendix H-4 for targeted functional groups). Testing to see if the model could reproduce the historic catches, we found that most of the groups were within 20% of the catch records from shore-based creel surveys conducted by DAWR (Appendix H-5; shown for selected functional groups) but the magnitude of biomass trends for functional groups targeted by spear fisherman did not agree with the estimated relative biomass trends (i.e., model declines were less than presumed actual biomass). For these groups we needed to increase the fishing effort in the latter half of 2000 to achieve a trend in the biomass trajectory that corresponded well with the estimated trajectory of relative historical fish biomass (Chapter 5, Appendix I).

This discrepancy is similarly to a retrospective model of the artisanal reef fisheries of Eritrea in which model trends only matched observed biomass trends when catches were increased to five-times reported catches (Tsehaye and Nagelkerke 2008). The disparity could be due to underreporting of catches or because we only used the shore-based fishery. It seems justified to increase the fishing effort as boat-based reef-fisheries landings show that in total these landings were twice as high as the landings from shore-based fishery (54.0 t vs 27.5 t; average of 2010–2012 DAWR data). However, it is unclear from the boat-based data from which depths or from which spatial zone these fish were taken but as the landings are that much higher it seems safe to assume that at least a part of these landings were taken from the 6–30-m depth zone, i.e., the deeper Atlantis polygons in this study. Simulations of increased levels of fixed fishing pressures corresponded well to the expected sensitivity of different groups to fishing pressure, even for the groups that did not show a similar magnitude in biomass after historic catches. This result suggests that the productivity and Beverton and Holt stock assessment parameters are parameterized adequately.

Adjusting the catches mainly from spear fisherman (Bak-Hospital 2015), resulted in better correspondence with the reconstructed time series of the biomass trajectories (Figs. I-1 and 2) and, therefore, also satisfied criteria three of model development. Obtaining improved fishery data for the boat-based fisheries, including allocating these catches spatially, could improve the model. Based on the compliance with all three criteria we concluded that the Atlantis model is stable with plausible biomass trajectories.

Added coral code: Coral related dynamics

After a literature review, we identified key coral reef dynamics and the form of the relationships for those dynamics and added corresponding code (Table F-1). These responses came from empirical data or from other modelling studies (Table F-1). Coral specific parameters are included in Appendix G. We detailed the dynamics of coral growth (and growth-related complexity) and competition with benthic algae that are influenced by three main drivers: (1) climate change (a global stressor indicated in blue in Fig. F-2); (2) land-based sources of pollution (a local stressor indicated in black in Fig. F-2); and fishing activities (also a local stressor indicated in black in Fig. F-2). The reasoning behind the inclusion of the processes and a brief description of how they were simulated in the model and the literature sources used are summarized in Table F-1. We acknowledge that we have captured only the main processes, and that there are other processes which influence reefs that were either omitted or represented only in a simplified way (e.g., symbionts' dynamics

(Baskett et al. 2009a), microbe-induced coral mortality (Smith et al. 2006), coral and algal diseases (Aeby et al. 2011, Williams et al. 2014), linear relationship between herbivore size and bioerosion (Mumby 2006) and others).

Table F-1. Summary of key coral reef ecosystem processes influenced by global and local drivers incorporated in Guam Atlantis based on a literature review. Equations of relationships are in the main text.

Drivers	**Rationale**	**Modeled As**	**Source**
GLOBAL-Ocean warming	Corals are both heterotrophic and, through their symbionts, autotrophic. Depending on the water temperature, duration of exposure to elevated temperatures and coral species sensitivity, symbionts may be expelled (bleaching). Bleached corals have higher mortality rates than healthy corals mostly through increased susceptibility to disease. Mortality and recovery are species specific.	Temperature induced expulsion of symbionts depending on the degree heating weeks, species-specific bleaching-related mortality and recovery depend on duration of elevated temperature.	(Jokiel and Coles 1990, Brown 1997, Hoegh-Guldberg 1999, Marshall and Baird 2000, McClanahan et al. 2004, Sotka and Thacker 2005, Hoegh-Guldberg et al. 2007, Eakin et al. 2009, Levas et al. 2013)
GLOBAL - Ocean Acidification	Reduced aragonite saturation results in reduced coral growth and increased bioerosion. It also has effects on other processes in their life history and on other calcifying organisms or organisms with a calcium skeleton.	Acidification was modeled to affect growth and/or fecundity of corals, plankton groups, crustose-coralline algae, macroalgae, bivalves and urchins.	(Berner 1965, Edmond and Gieskes 1970, Langdon 2002, Kleypas et al. 2006, Cohen and Holcomb 2009, Feely et al. 2009, Silverman et al. 2009, Zeebe and Wolf-Gladrow 2009, Hendriks et al. 2010, Kroeker et al. 2010, Anthony et al. 2011b, Harvey et al. 2013, Wittmann and Pörtner 2013)
LOCAL – change in framework complexity	Structural complexity is balanced by reef accretion through calcification and erosion through bioerosion, physical disturbances, and predation. For example, coral predation can reduce coral cover by 30% per year. Coral mortality can lead to a reduction in complexity as the balance between accretion and erosion is tipped towards erosion and hence leads to loss of shelter for fishes, which in turn leads to a loss of fish recruits, abundance and	Topographical complexity was based on a simplified conical shape of corals increasing in 3 dimensions and hence increasing the complexity. Bioerosion by cryptic invertebrates, loss of coral growth due to coral predation and destructive fishing practices are modeled as a reduction in complexity. We modelled the relationship between complexity and suitability for refuge for fish, leading to a change in predator availability according to a saturation function with the	(Eakin 1996, Glynn 1997, Eakin 2001, Jones et al. 2004, Alvarez-Filip et al. 2009, Ong and Holland 2010, Blackwood et al. 2011, Hixon et al. 2012, Perry et al. 2012, DeMartini et al. 2013, Graham and Nash 2013, Bozec et al. 2014)

Drivers	Rationale	Modeled As	Source
	diversity.	slope being dependent on a species-specific scalar. Both live and dead corals contribute to complexity.	
LOCAL - Land-based sources of pollution – nutrient increase	Nutrient enrichment favors macroalgal growth over the growth of other benthic groups. Increased macroalgal cover preempts space and increases sediment retention, reducing coral growth, preventing settlement of coral larvae, and causes mortality.	Change in coral biomass is related to species-specific coral growth, an inhibition factor from algal groups, an overgrowth factor of macroalgae, mortality of corals, and a facilitating factor of coral recruitment onto turf and crustose-coralline algae.	(McCook et al. 2001, Smith et al. 2006, Mumby et al. 2007b, Baskett et al. 2009b, Baskett and Salomon 2010, Melbourne-Thomas et al. 2011a, Gilmour et al. 2013)
LOCAL - Land-based sources of pollution – sediment increase	Sediment input hampers corals from growing as they divert energy into mucus production to allow them to slough off sediment particles. Sediment particles in the water column reduce light penetration thus decreasing growth of primary producers (including coral symbionts)	A “smothering effect” that reduces growth according to a linear relationship with the logarithm of sediment level.	(Wolanski et al. 2004)
LOCAL - Fishing - reduced herbivore population	Depletion of herbivores through fishing leads to reduced capacity to maintain turf algae in cropped states and thus leads to elevated standing stocks of macroalgae.	Modeled through trophodynamic relationships (availability matrix) and explicit fishing mortality or catch time series.	(Bellwood et al. 2006, Mumby et al. 2007a, Bellwood et al. 2011, Heenan and Williams 2013, Mumby et al. 2013a)

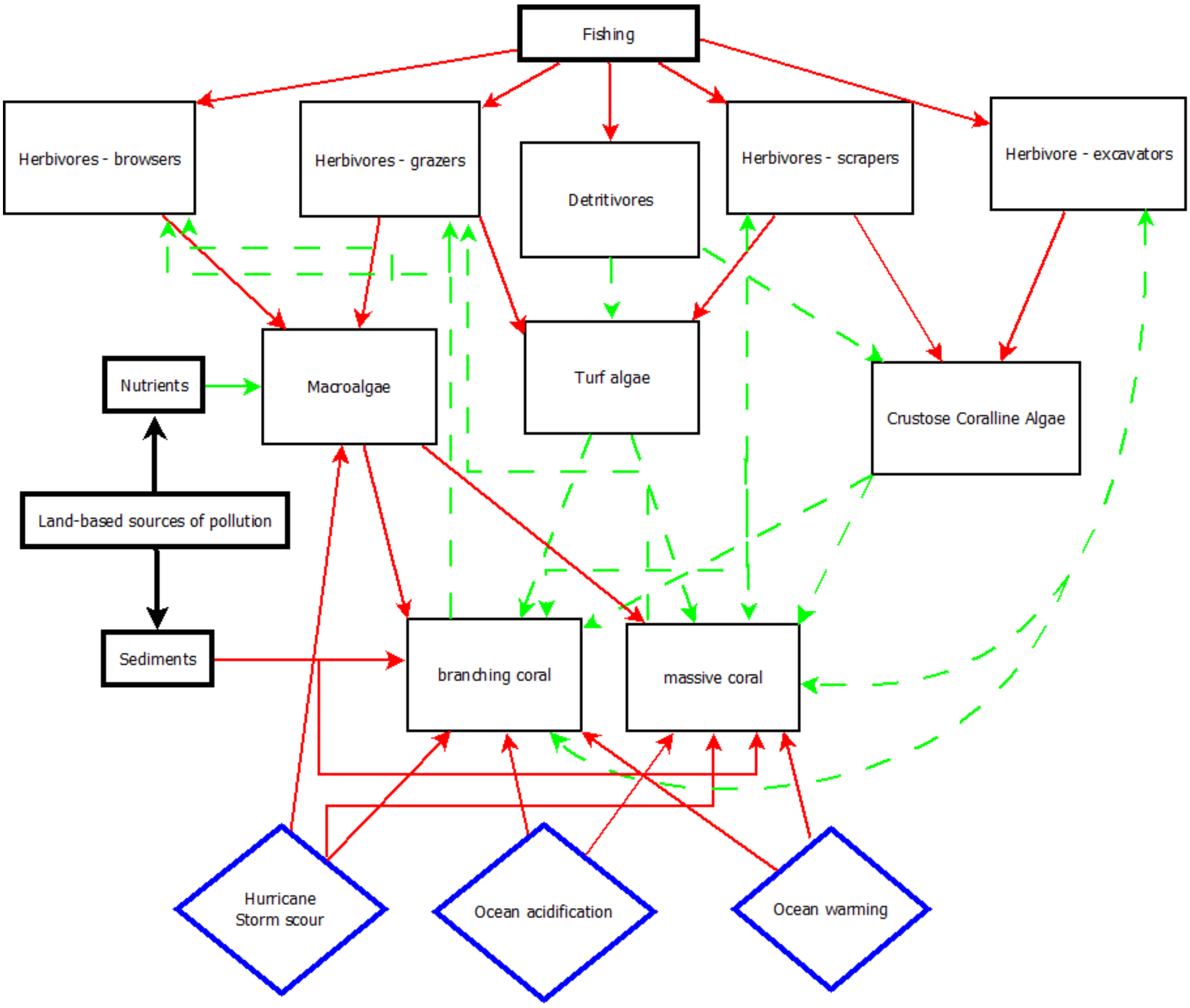


Figure F-2. Conceptual diagram simulating benthic space competition (macroalgae-coral overgrowth, turf and crustose-coralline algae facilitate coral recruit settlement) and the simplified feedback relation between algae and herbivores (herbivores crop algae facilitating coral recruitment and reducing macroalgal overgrowth, and corals provide shelter for fish) incorporated in the Guam Atlantis model. Red arrows indicate negative effects and green dashed arrows positive effects. Black rectangles are local stressors and blue diamonds are global stressors.

Driver 1: Climate change

Climate is predicted to change in many aspects but for this model application, we only look at the effects of ocean temperature and ocean acidification. Naturally, temperature induced stratification (leading to less nutrient in the upper water column) is also of importance but we assume that since we focus on the 0–30 m depth range that these impacts are less important. Hurricane damage, which are predicted to increase in intensity and frequency, is a natural phenomenon in Guam and can cause extensive damage to the reefs, however, in this version of Guam Atlantis we have not captured that effect.

Ocean warming

Corals have physiological processes that are optimized to the local long-term seasonal and inter-annual variations in temperature and an increase of only 1°C or 2°C above the normal local seasonal maximum can induce the expulsion of the symbiotic zooxanthellae (Jokiel and Coles 1990) leaving the coral looking ‘bleached’. Bleached corals are more prone to disease than healthy corals resulting in bleaching-related mortality. Bleaching can be predicted using an index of accumulated thermal stress above a locally established threshold, the Degree Heating Week (DHW) (Eakin et al. 2009). Corals can recover from bleaching episodes (Wilkinson 2004); however, at some point thermal stress events occur too frequently or for too prolonged a period for corals to be able to recover (we deemed corals to have recovered from a disturbance if their total biomass has reached the same level as before the onset of a disturbance). Projected increases in sea surface temperature for the Central Pacific for the period 2030–2039 vary between 0.6°C and 1.1°C depending on the IPCC scenario (Donner 2009). Two recent models of the long-term vulnerability of reefs to mortality from bleaching predicted a significant decline in coral reefs (Thompson and Dolman 2010, Edwards et al. 2011). However, other studies have shown that corals may have greater ability to adapt to higher temperature than previously believed (Eakin 2014, Palumbi et al. 2014), and also that reefs with high structural complexity and at greater depths (> 8 m) are less vulnerable to bleaching impacts (Graham et al. 2015).

In the model, when DHW > threshold, corals will bleach according to equations 7 and 8:

$$Ph_{t+1} = Ph_t - Pb \qquad \text{Eq. 7}$$

$$Pb = b \bullet (1 + DHW - threshold) \qquad \text{Eq. 8}$$

with *Ph* = 'healthy' or unbleached proportion and *Pb* the bleached proportion; *b* = bleaching rate and *DHW* the degree heating weeks. The threshold is set at 4 for massive corals and 3 for branching corals (Donner et al. 2005).

Of the bleached corals (*Pb* • *B*) some will die and others will survive. The overall coral biomass loss due to natural mortality and bleaching induced mortality at time step *i* is calculated as:

$$Mi = M \bullet Bcoral + ((Bzooxanth \bullet Pb) + (Bpolyp \bullet Pb \bullet Mb)) \qquad \text{Eq. 9}$$

with *M* = mortality rate due natural mortality, *Bcoral* is the sum of the symbiotic zooxanthellae biomass and the polyp biomass, *Bzooxanth* is the symbiotic zooxanthellae biomass and *Bpolyp* the coral polyp biomass, *Pb* the proportion of corals bleaching and *Mb* the bleaching induced coral mortality.

Simulating bleaching events, we assumed that the biomass of symbionts in unbleached corals is 30% of total coral biomass (Gustafsson 2013); the bleaching threshold temperature is 1°C above the summer maximum (threshold = 30.1°C) (Jokiel and Coles 1990); the proportion of corals bleaching is 20% for massive corals and 20%–40% for branching corals (Donner et al. 2005); coral mortality after a bleaching event is 42% for branching and 22.5% for massive corals (McClanahan 2004); recovery is believed to occur after 1 year for massive corals and after 4 months for branching corals (Lombardi et al. 2000, Sotka and Thacker 2005, Kvitt et al. 2011).

Predicted sea surface temperature data came from the Representative Concentration Pathway (RCP) 8.5 projection using the HadGEM-AO model output (data downloaded from the Coupled Model Intercomparison Project Phase5 [CMIP5]: http://apdrc.soest.hawaii.edu/las8/UI.vm), as the 1985–1990 modeled data corresponded well with satellite data from Guam in the same time period. We overlaid this trend on the time series of temperature (Castruccio et al. 2013) for each Atlantis polygon to maintain spatial differences around Guam, and thus created a projected temperature time series for each polygon out to 2050.

Ocean acidification

When calcium carbonate saturation state values are < 1, calcium carbonate tends to dissolve and at values > 20 calcium carbonate will spontaneously precipitate (reviewed in Brainard et al. 2011). However, at values between 1 and 20, calcifying organisms (such as corals) can create calcium carbonate shells or skeletons using a physiological calcifying mechanism. Increased atmospheric CO_2 leads to a lower pH, which in turn decreases calcification rates of adult and recruits at rates that vary among coral species (reviewed in Brainard et al. 2011). Evidence from numerous studies of calcifying organisms has suggested that corals affected by reduced saturation state may primarily experience reduced growth (Langdon 2002, Cohen and Holcomb 2009, Kroeker et al. 2010, Shaw et al. 2012), although many uncertainties remain especially since synergistic effects should be taken into account (Harvey et al. 2013, Kroeker et al. 2013), effects differ geographically (Comeau et al. 2014)and some corals still calcify when provided with sufficient food supplies (Holcomb et al. 2010).

Apart from the added code for the relationship between coral growth and pCO_2 (see below) we also parameterized the pCO_2 relationships (based on changes in pH) with various functional groups (Appendix G). Marine species most affected by ocean acidification are calcifying organisms (corals, echinoderms, molluscs), which exhibit negative relationships between ocean acidification, and growth and calcification rates (Hendriks et al. 2010, Kroeker et al. 2010, Wittmann and Pörtner 2013). Declines in growth rates of crustose coralline algae by 86% and rhodoliths by 100% have been reported (Langdon 2002, Kroeker et al. 2010)). In contrast, phytoplankton and fleshy macroalgae are likely to grow more rapidly in more acidic water (Hendriks et al. 2010, Harvey et al. 2013). Rates of herbivory necessary to maintain successful coral recruit settlement would have to increase as atmospheric CO_2 increases. Crustaceans did not show a significant negative effect of ocean acidification on growth or calcification (Kroeker et al. 2010, Harvey et al. 2013) or were reported to have a reduced sensitivity compared to corals, molluscs and echinoderms (Wittmann and Pörtner 2013). Reproduction rates declined for urchins and copepods with increasing pCO_2 (Kurihara and Ishimatsu 2008, Hendriks et al. 2010). We included nonlinear response relationships between growth and increased pCO_2 for phytoplankton and macroalgae, a linear decline of growth for benthic filter feeders (including bivalves) and crustose coralline algae, a linear decline in growth and fecundity for benthic grazers (urchins), and a monod response on growth and fecundity for herbivorous zooplankton groups (copepods; Wittmann and Pörtner 2013) (Fig. F-3).

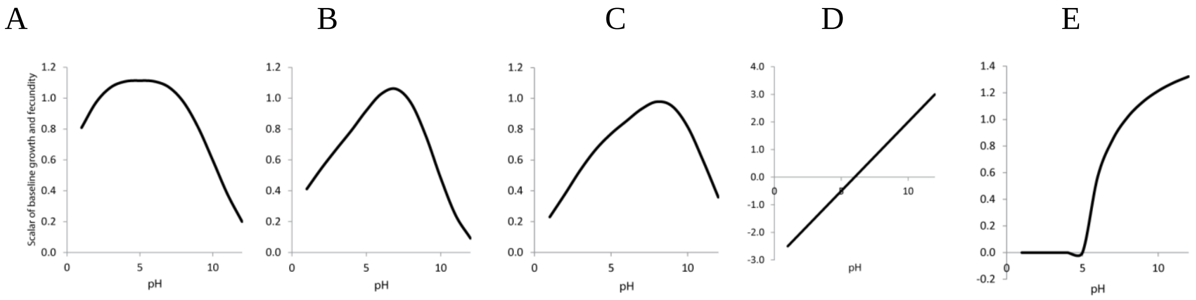


Figure F-3. Relative shape of the effect curve on from left to right (*A*) small phytoplankton, (*B*) large phytoplankton, (*C*) macroalgae, (*D*) benthic filter feeders, crustose-coralline algae and benthic grazers, and (*E*) herbivorous zooplankton. The growth rate and/or fecundity is multiplied with the scalar corresponding to the current pH at each time step in the model to account for the pH effects.

To approximate a range of qualitatively different functional responses of corals to the aragonite saturation state (Ω) and temperature (T) (Langdon and Atkinson 2005) we modeled the net calcification rate (*Gnet*) with equations 10–13:

$$Gnet = K_T \bullet (\Omega - 1)^{\lambda t * T/T_{opt}} \qquad \text{Eq. 10}$$

where T is the current temperature and T_{opt} the optimum temperature and K_T and λ are temperature-dependent functions accounting for the strength and shape of the calcification response to variation in Ω and T. The temperature response of K_T was assumed to be symmetrical around the optimal temperature for calcification and is given by:

$$Kt = \alpha - \beta \bullet \frac{(T - Topt)^2}{Topt} \qquad \text{Eq. 11}$$

where α and β are regression parameters.

The aragonite saturation state is calculated as the product of the calcium and carbonate ions divided by the solubility constant (K_{sp}):

$$\Omega = \frac{\left[\mathrm{Ca}^{2+}\right]\left[\mathrm{CO}_3^{2-}\right]}{K_{sp}} \qquad \text{Eq. 12}$$

where the CO_3^2 concentration and pH change according to the Bjerrum plot (Zeebe and Wolf-Gladrow 2009) which we reproduced using 250 µmol/kg reported for modern day CO_2 concentration at 23°C and a pH of 8.068 for the midpoint of the curve (Feely et al. 2009).

The pCO_2 concentration we used comes from the IPCC AR5 report using the highest emission scenario (Representative Concentration Pathway [RCP] 8.5) projection.
Finally, relative coral growth is calculated as:

$$\mu_{CT} = \mu_C \bullet \frac{G_{net}}{G_{base}} \qquad \text{Eq. 13}$$

We assumed that T_{opt} is near the summer maximum non-bleaching temperature of 29.1°C (http://coralreefwatch.noaa.gov/satellite/vs/guamandcnmi.php#GuamEast). Values used for the parameters are given in Appendix G.

Climate change effects on coral reef ecosystems

Both ocean acidification and elevated temperatures had a negative effect on coral biomass with coral bleaching leading to abrupt mortalities and slow recovery until bleaching events were too frequent for corals to recover (after 48 years, i.e., from 2023 onwards). Acidification led to a more continuous gradual decline in coral biomass caused by reduced calcification (Fig. F-4). The declines caused by acidification were weaker than those due to bleaching, though as discussed below we may be underestimating acidification (modeled reduction of pH to 7.95 in 2050). Macroalgal biomass increased when space was opened due to bleaching induced coral mortality (solid lines Fig. F-4) and also increased when coral biomass was reduced due to ocean acidification. Crustose-coralline algae, which are negatively affected by ocean acidification, did not show a decline in biomass but instead increased in biomass when space became available after corals bleached and died.

Modeled recovery after a bleaching event took 2–9 years, which falls within recovery times seen in Palau (Golbuu et al. 2007) and what has been reported from Guam (Burdick et al. 2008). Our results fall within the spread found for model simulations of IPCC scenario AR8.5 for various Pacific reefs with coral decline predicted to occur between 2030 and 2050 based on bleaching related mortality alone (Ortiz et al. 2014). The first reported bleaching events in Guam with no coral mortality were in 1994 and 1996 (Burdick et al. 2008) and more frequent bleaching events were observed in the shallow bays in September 2006, August and September 2007 and wide-spread bleaching occurred in the summer of 2013 and 2014 (V. Brown, NOAA Pacific Islands Regional Office pers. comm. Nov. 2014). Elevated temperatures which led to those bleaching events are shown in the satellite time series data as peaks above the red dashed threshold line in figure F-4 top panel. The response difference between the branching and massive corals is due to the difference in susceptibility to elevated temperatures and mortality rate after bleaching with (branching corals being more susceptible to bleaching and have a higher mortality rate and hence, the drop in coral biomass in larger for the branching corals [Fig. F-4]).

The modified Atlantis model projected a reduction in coral biomass of 2%–4% as a result of ocean acidification which appear less than predicted in other published studies which show an expected reduction of 22%–39% in calcification and a 47% reduction in abundance of coral recruits (Kroeker et al. 2013). Since we report on total coral biomass in the model domain, direct comparison is difficult—a 25% reduction in calcification does not automatically translate to a decrease in coral biomass, the coral skeleton is likely less robust due to decreased calcification but the actual live coral tissue could be similar. However, the IPCC scenario and algorithms we used led to a decrease in aragonite saturation of only 0.3 units corresponding to a pH decrease from 8.19 in 1975 to 7.95 in 2050, whereas most laboratory studies assume a pH decrease of at least 0.5 units. Aragonite saturation states are predicted to decrease by approximately 1.0 unit by the end of the century (100 years; Kleypas et al. 1999) so we likely underestimated the reduction in aragonite saturation.

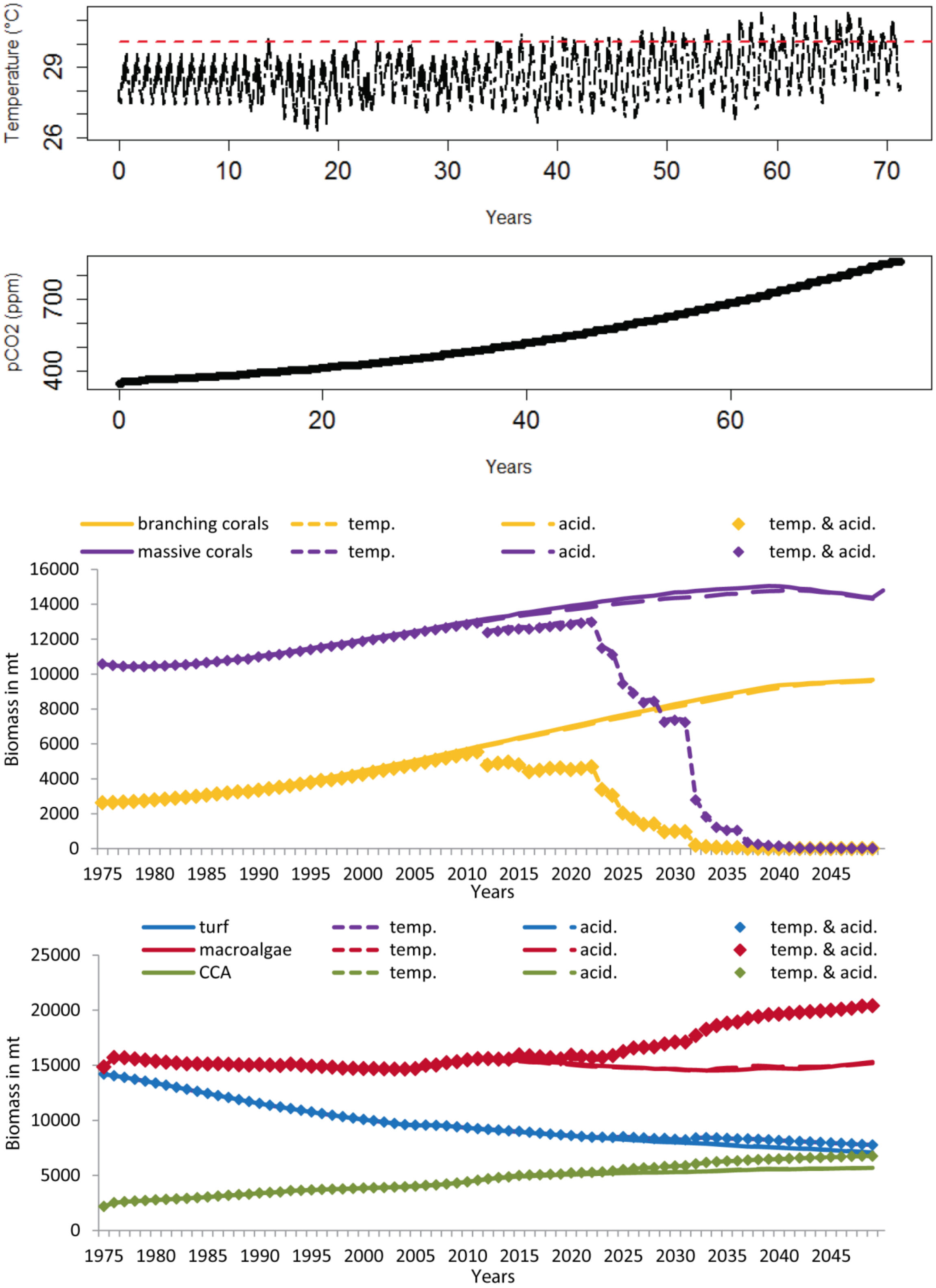


Figure F-4. (*Top panel*) Predicted sea-surface temperature (HadGEM-AO) with bleaching threshold at 30.1°C (red dashed line) and (*second panel*) pCO_2 trajectories (IPCC AR8.5), both time series used to force the model with. (*Bottom two panels*) Effects of elevated temperature (dashed lines), ocean acidification (long-short dashed lines), and the combined effects of ocean warming and acidification (diamonds) on the benthic communities compared to control run (solid lines) with effects on algae shown in third panel and on corals in bottom panel. Year 0 = 1975.

The combined effect of temperature and ocean acidification did not differ markedly from the (only) elevated temperature scenario (Fig. F-4 bottom panels). Laboratory studies have shown that elevated temperature increases calcium carbonate precipitation and could therefore offset the effects of reduced calcification (Kroeker et al. 2013). Certainly, temperature differences can confound the relationship between pCO_2 and calcification (Reynaud et al. 2003). In our model the average summer temperature of 29.4°C in Guam was very close to the modeled optimum calcification rate at 29°C (Jokiel and Coles 1977, Silverman et al. 2009) (Appendix G) which could be a reason why the coral biomass trajectory of only elevated temperature is similar to the trajectory of the combined effects of ocean acidification and elevated temperature. Also nutrients influence the calcification rate (Cohen and Holcomb 2009, Holcomb et al. 2010) and Guam was modeled to have quite high concentrations of nutrients in the shallow polygons so their growth due to filter feeding could also have offset the negative impact of ocean acidification. In future versions of the Guam Atlantis model, alternative time series of predicted pH and/or aragonite saturation states could be used as input values to get a better understanding of the variance in the effects size of calcification and coral growth and the synergistic effects of ocean acidification and ocean warming. For the application of the current model, we are confident that the predicted effects of ocean warming are well captured and since current knowledge suggests that they are acting as a primary course of coral decline in the near future (Pandolfi et al. 2011) we think that future trajectories are reasonably projected.

Driver 2: Land-based sources of pollution

Changes in land use can alter runoff of nutrients and sediments into coastal waters. The combined effects of elevated nutrients (bottom-up processes) and grazing (top-down processes) influence the physical and ecological controls of macroalgal dynamics (Hughes 1994, Lapointe et al. 1997). Higher concentrations of sediments and nutrients favor macroalgal growth over coral growth (Mumby et al. 2007a) and enhance coral disease (Aeby et al. 2011) resulting in decreased coral cover (Table F-1). Sediments are also detrimental for the settlement of calcifiers (corals and CCA) (Marshell and Mumby 2012). When substrate sediment load is low, coral recruits have a higher survival rate (Mumby et al. 2007a, Marshell and Mumby 2012). Time series of sediment and nutrient input to the marine coastal areas around Guam were based on river flow rates and sewage outfall pipes (Chapter 4).

For the benthic groups included in this model—corals (C), macroalgae (MA), crustose coralline algae (CCA) and turf algae (T)—biomass is associated with the physical space they occupy in the reef. The biomass dynamics of these groups are determined by trophic interactions and metabolic processes and are density dependent. We defined turf cover as all hard substrate that is not any other benthic category (Eq. 14):

$$T=1-MA-CCA-C \qquad \text{Eq. 14}$$

Coral-algal dynamics were simulated by changes in biomass with macroalgae overgrowing corals with a rate of α and hampering growth of corals with a rate of β and corals recruiting to turf and CCA with rate γ (Melbourne-Thomas et al. 2011a) and no recruitment in macroalgal habitats (Albright et al. 2008):

$$dC/dt = \mu \bullet C - M_{lin\text{-}C} - M_{quar\text{-}C} - Predation - \alpha \bullet MA - \beta \bullet MA + \gamma \bullet (CCA+T) \qquad \text{Eq. 15}$$

$$dMA/dt = \mu \bullet MA - M_{lin\text{-}MA} - M_{quar\text{-}MA} - Predation + \alpha \bullet MA + \beta \bullet MA \qquad \text{Eq. 16}$$

where μ is the growth rate, C is the biomass of corals, *MA* is the biomass of macroalgae, CCA the biomass of crustose coralline algae, T the biomass of turf algae and M_{lin} and M_{quar} are the linear and quadratic species-specific mortality rates. Furthermore, growth of primary producers is dependent on light, space and nutrient limitation (full description of these dynamics is detailed in (Fulton et al. 2004b)). We allowed for vertical growth, for example, on the base of branching corals, under or at the sides of overhangs and boulders, by setting the total benthic space available to 135% of planar area.

Coral growth can be further hampered by sediment. High sediment concentration in the water column not only limits the light available for photosynthesis (captured in Atlantis under light limitation), when sediment settles on the reef, corals have to divert some energy to producing mucus to slough off those sediments. This energy is then not available for growth. Using the empirical relationship derived from a study of sediment concentration and change in coral abundance conducted in Guam (derived from Equation 1 in (Wolanski et al. 2004)) we included a function to capture this 'smothering effect':

$$S = Sa \bullet \ln(sed\_level) + Sb \qquad \text{Eq. 17}$$

where *S* is the smothering effect, *Sa* the smothering coefficient and *Sb* the smothering constant. The *sed_level* is the concentration of sediments in the water column and changes over time mostly depending on riverine runoff.

We simulated two scenarios: (1) with estimated time series of river and sewage outflow that contained sediments and nutrients (Weijerman et al. 2014b), and (2) no inputs. Parameter estimates are given in Appendix G.

Land-based sources of pollution: Sedimentation and nutrient elevation effects on benthic composition and target fish biomass

Point source and non-point source pollution and accompanying elevated nutrient and sediment input into nearshore waters led to a rapid increase in phytoplankton and suspended solids followed by an increase in macroalgae and CCA and a decrease massive corals (Fig. F-5).

Increased sediment led to reductions in coral growth rates compared to the control scenario (Fig. F-5). Consistent with nutrient enrichment experiments (Smith et al. 2001, Brian et al. 2004) we had expected algal biomass to positively respond to nutrient input and that to lead to reductions in coral cover, the effects of which were shown by our model (Fig. F-5). The effect of sediments on the growth rate of corals and the competition between corals and algae are modeled using the same parameters, since massive corals have a lower growth rate, the effect is larger on massive corals.

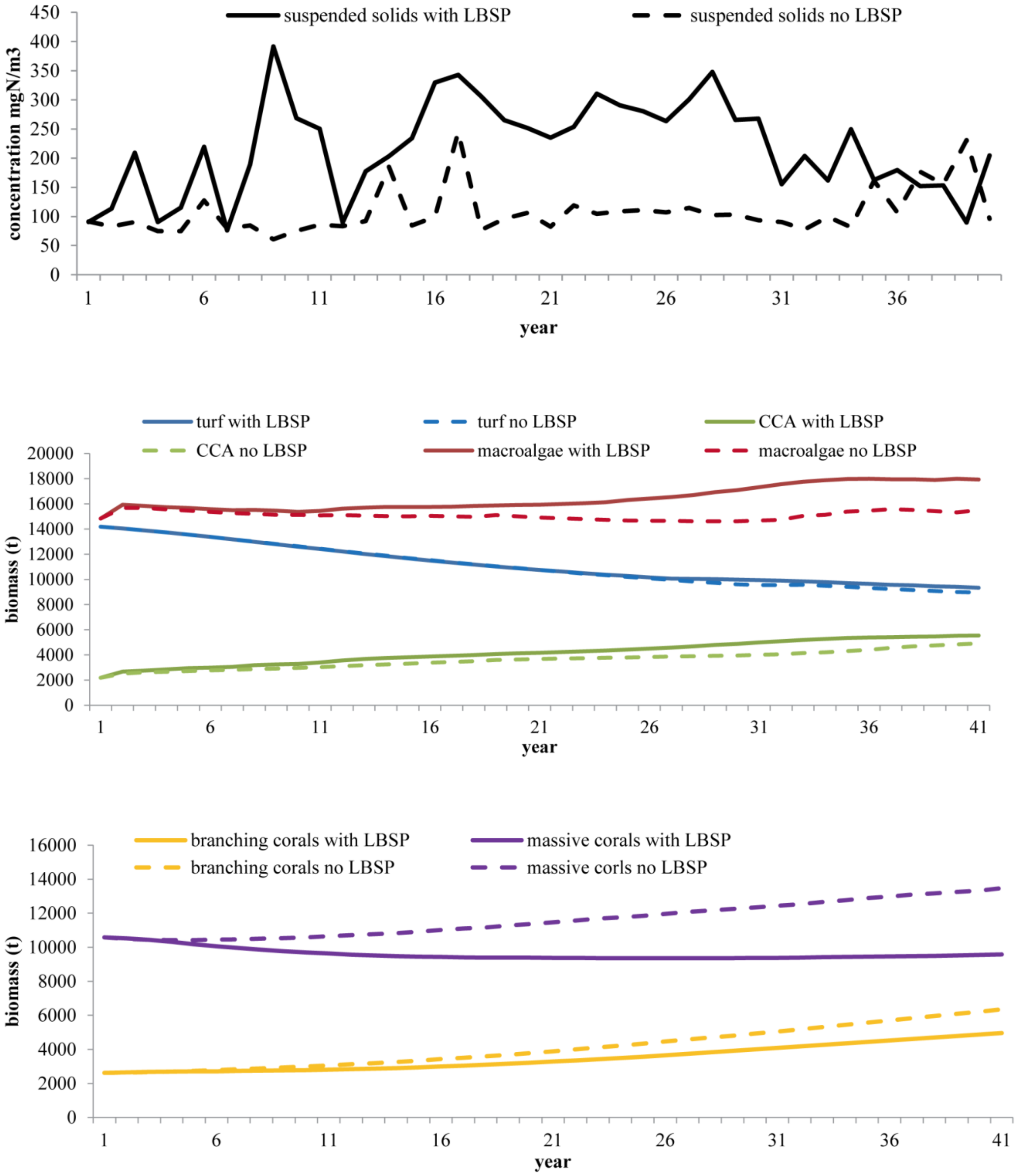


Figure F-5. Simulation of point source pollution into the shallow nearshore waters of Guam. Results contrast the concentration of (*top*) suspended solids, (*middle*) and biomass of algae, and (*bottom*) corals between two simulation runs of 40 years: (dashed lines) no land-based sources of pollution (LBSP) and (solid lines) with LBSP. Year 0 = 1975.

Results from surveys of reef flats in Guam along a gradient away from sewage outfall pipes showed reduced coral cover close to the outfall pipes (0.13 km) between 2009 and 2010 and no significant difference in percent coral cover away from the outfall pipes (1.13–11.3 km, Raymundo et al. 2011). In correspondence with those local results, the model appears to capture the effects of LBSP well with low coral cover in the southern polygons relative to the north and east of Guam.

Driver 3: Fishing activity

Parrotfish, grouped in large excavators and scrapers, fulfil an important ecological role by opening up substrate for coral recruitment (Table F-1). The feedback loop between corals, algae and grazers is possibly the most examined reef dynamic with minimal models, exploring the existence and thresholds of stable states (Hughes 1994, Mumby 2006). Cover of macroalgae on reefs is linearly negatively related to the biomass of herbivorous fishes (Mumby 2006, Bellwood et al. 2011). However, studies in the Caribbean have shown that herbivorous fishes can only maintain a maximum of 30%–40% of a reef structure in a cropped state (Williams et al. 2001). Large parrotfishes are more effective grazers than small ones (Ong and Holland 2010), for example, 75 small (< 15 cm) parrotfishes maintain the same area of substrate in grazed states as one single individual of 35 cm (Lokrantz et al. 2008). In locations with high fishing pressure, large parrotfish are removed and, although small parrotfishes will tend to increase in abundance due to predator release (Bellwood et al. 2011), the net effect of fishing pressure leads to reductions in grazing pressure potentially leading to phase shifts.

Corals have a positive effect on fish abundance by providing shelter (McClanahan 1995, Wilson et al. 2008, Blackwood et al. 2011, Kerry and Bellwood 2012, Ainsworth and Mumby 2014). Several studies have also demonstrated a positive relationship between coral complexity and fish diversity (Friedlander and Parrish 1998, Jones et al. 2004, Paddack et al. 2009), especially for corallivores and planktivores (Graham et al. 2006). This positive feedback appears to be driven by the increased survival of fish recruits and other small-bodied fishes (Jones et al. 2004, Graham et al. 2006, Coker et al. 2013, DeMartini et al. 2013, Rogers et al. 2014). Coral reef complexity is partly dependent on the topography of the reef substrate itself (e.g., boulders provide complexity) and partly by coral growth (e.g., large branching corals provide more shelter than small coral colonies). Benthic complexity values ranging between 1 (flat) and 5 (high structural complexity) were taken from CRED survey data and serve as a baseline. We then assume that changes in complexity reflect net coral growth (i.e., the balance between accretion and erosion). We used the topographical complexity model developed by Bozec et al. (2014) to calculate rugosity.

$$R = rug\_constant \bullet SI \qquad \text{Eq. 18}$$

where R = rugosity, *rug_constant* is the ratio of the vertical contour of a colony and the surface-to-area ratio of a colony, SI is the deformation of the reef surface and is calculated as the surface area of the reef (depending on height and diameter of coral colonies) divided by the planimetric area of the reef which depends on the maximum diameter and coral cover (Bozec et al. 2014).

Rugosity in turn affects the availability of prey to predators, according to the inferred relation of the habitat scalar at time i based on (Graham et al. 2006, DeMartini et al. 2013):

$$hab\_scalar_i = hab\_scalar \bullet (Rcoefft \bullet \ln(R) + Rconst) \qquad \text{Eq. 19}$$

In other words, rugosity affects the availability of prey fish to predators according to the inverse of the habitat scalar relationship with a maximum capacity set at 4 and a scalar coefficient depending on the species (varying between 0.6 for small species to 8.0 for unaffected species). For parameter estimates see Appendix G.

To determine the adapted model's capability to simulate the effects of the coral-algae-grazer relationships with the added code, we simulated two scenarios: (1) intensive fishing on herbivores (fishing mortality (F) of 0.8 per year), and (2) no fishing of herbivores. In both scenarios we kept fishing on other groups low (F=0.05 per year). Similarly for the relationship between complexity and fish biomass, we ran two 30-year simulations, one with this relationship included and one without, assuming a low fixed fishing mortality of 0.05 for all groups.

Effects of fishing of herbivores on corals-algae-grazers dynamics

The strong link between herbivorous fishes and the benthic community composition (high herbivore biomass resulted in low macroalgal cover and high coral and CCA cover) is clearly demonstrated in the scenarios with high (F=0.8) and no (F=0) fishing of herbivorous fishes while keeping fishing on all other targeted groups to F = 0.05. Compared to no fishing of herbivores (F=0), when herbivore fishing mortality was set to 0.8, biomass of turf and macroalgae is 6% higher, and biomass of calcifiers is 7% lower at the end of a 30-year simulation.

Scenarios with and without refuge effects from structural complexity showed the importance of incorporating the effects of complexity into coral reef ecosystem models. Fish biomass of most prey groups was enhanced by the three-dimensional complexity (Fig. F-6). Planktivores in particular were dependent on refuge associated with structural complexity, as their biomass was 6.6 times more in models with the complexity-refuge relationship enabled. In contrast, predatory fish groups had a 0.1–0.5 times lower biomass when habitat refugia relationships were included in models (Fig. F-6). Modeled increase in biomass of prey fish with increased structural complexity was in correspondence with empirical relationships from Guam (Appendix K).

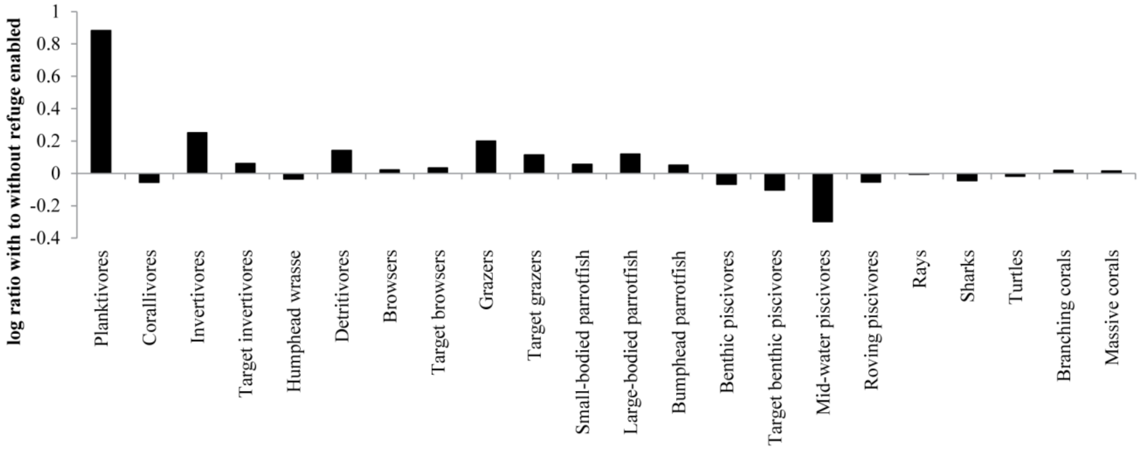


Figure F-6. Ratio of biomass with refuge enabled versus no refuge enabled for each functional vertebrate group and corals at the end of 40 year simulation run. Ratios are represented as logarithmic values of the actual ratio.

Simulations demonstrated strong links between herbivorous fish biomass and the benthic community, with herbivore biomass associated with low macroalgal cover and high cover of coral and CCA, as has been shown on reef in American Samoa (Heenan and Williams 2013), the Caribbean (Mumby et al. 2007a), the Great Barrier Reef (Wismer et al. 2009), Fiji (Rasher et al. 2012), but also in spatial surveys conducted around Guam (Williams et al. 2012).

Additionally, model outcomes show the importance of reef structure as refuge for fish species, by making them less vulnerable to predators. We parameterized this part of the model based on the study of Bozec et al. (2014), but those relationships could potentially be improved with site-specific data. Also the parameters used for erosion caused by fish, urchins and boring sponges that affect the reef's structural complexity should be updated with data from Guam when such data becomes available to improve the model.

Sensitivity and skill assessments

We performed sensitivity assessments on primary productivity (growth rate of primary producers), the structural complexity input parameters (diameter of corals), and the parameter for direct coral-algal competition (the β in equation 15). From the literature we derived plausible values for these parameters (Appendix G) and ran the model with the minimum and maximum estimates to get boundaries for plausible trajectories. We then visually inspected the derived cone of uncertainty (i.e., range of trajectories) to see which of the groups are sensitive to the parameters and if the trajectory of the control run fitted into this cone.

To assess the model skill, we compared 2011 projected biomass of each fish group against the observed biomass from CRED fish surveys conducted in 2011 using the root mean squared error (RMSE) according to:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(P_i - O_i)^2}{n}} \qquad \text{Eq. 20}$$

where n = the number of observations (fish groups), O_i = the ith of n observations, P_i = the ith of n projections, and O and P are the observation and projected annual averages, respectively (Stow et al. 2009).

Out of the three sets of parameters analyzed with a sensitivity assessment, only the growth rates of plankton showed substantial variation in outcomes of selected fish groups and coral biomass (Appendix J). For the rugosity (or structural complexity) sensitivity (the parameter inputs being the mean diameter for branching and massive coral colonies) the outcomes varied a little (mostly for the rugosity; Fig J-2), and target fish groups and corals were not sensitive to the parameter for coral-algal competition (Fig. J-3). When varying the growth rates of phytoplankton, most vertebrate groups showed a narrow cone of uncertainty, i.e., they are not sensitive to changes in these growth rates (Fig. J-1). Our control run estimates were in the middle of the cone for 10 out of the 13 target fish species, giving more confidence in the model results with regard to fish groups. However, coral cover and, hence, rugosity are much more sensitive to these changes making it important to get good estimates of the growth rates of these groups. Since we did not run the control scenario with the mean of the primary producers' growth rates, but rather the maximum of large phytoplankton and lower than the average for small phytoplankton, the projected biomass (red line in Fig. J-1) does not necessarily need to be in the middle of the cone. Future versions of Guam Atlantis should look more into the effect of the predicted variation in coral biomass as a response to the changes in growth rates of primary producers to help explain the high biomass trajectory in corals (top or above the cone) and the odd shape of the relationship between planktivores and plankton (where one could expect a linear relation).

Formal skill assessment of the Guam Atlantis model is impossible due to the lack of time-series of observed data. Instead we compared the observed biomass estimates from 2011 visual surveys conducted by CRED with the projected biomass in 2015 after simulating the status quo scenario for 30 years. Skill assessment results show that for fish groups with lower abundance (less than 50 t) model predictions at the end of a 30-year simulation corresponded reasonably well (RMSE = 14) with observations from visual surveys. For the more abundant species, model predictions were consistently above the observed estimates resulting in a very high value of RMSE (198) suggesting that the model has a bias (Fig. F-7). The largest discrepancy was for scrapers (parrotfish) and grazers (triggerfish, gregory, damselfish), and to a lesser extend for invertivores, planktivores and target grazers (surgeon fish). This result implies that either those fish groups are too productive in our model or that we underestimated the mortality. Since fish productivity responded reasonably to increased fishing mortality (Fig. H-4), it seems more likely that we underestimated fishing mortality, particularly because the fishery data did not capture all gear types equally well (K. Lowe, NOAA-PIFSC, pers. comm.). Fishing mortality is based on voluntary creel surveys and we did not take into account the boat-based fishery, for a future version of this Guam Atlantis model better fishery estimates are necessary to account for this difference.

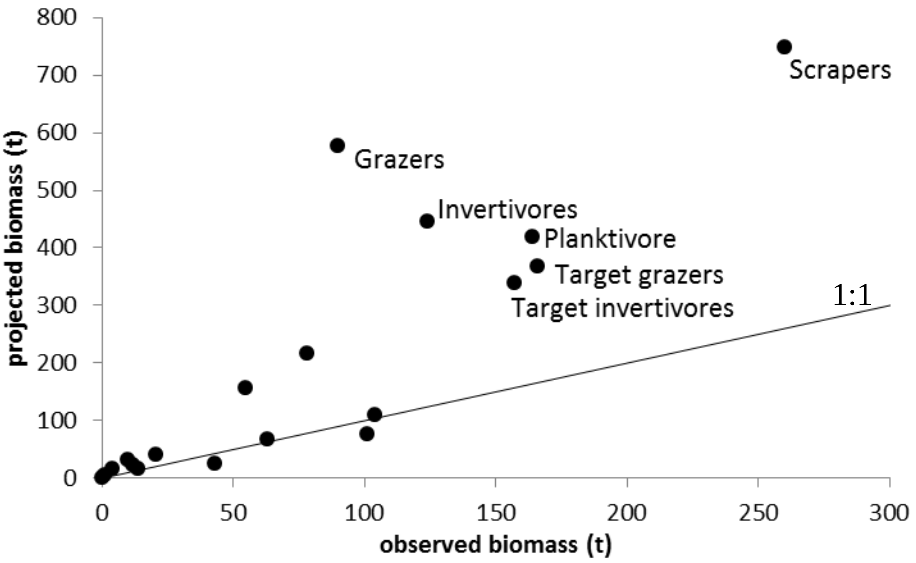


Figure F-7. Observed versus projected biomass of fish groups in 2011. Observations are from visual surveys conducted by NOAA Coral Reef Ecosystem Division in 2011, projected values are the mean of the last five years at the end of a 30-year run representing 2010–2015.

Conclusion

The adapted Guam Atlantis model met the three main criteria for Atlantis model development and is stable with plausible biomass trajectories. The paucity of time series of observational data prevented a formal skill assessment, but the model was able to reproduce biomass trajectories after disturbances (e.g., effects of climate change and sediment and nutrient inputs) that corresponded with expectations based on published relationships giving us confidence in the model validity. Additionally, the coral-algae-grazer dynamics are well simulated by the model with model outcomes comparable to expectations in response to low herbivorous biomass as well as the relationship between reef's structural complexity and its ability to provide refuge for prey fishes. Despite room for improvement (e.g., on historical fisheries catches and alternative predictions of pH and aragonite saturation) the model simulates the complex dynamics within a coral reef ecosystem well. However, in the future uncertainty in model outcome would be better captured by comparing model predictions across a range of parameterizations of the model.

Appendix G

This supplement provides additional information for chapter 6: "Applying the Atlantis model framework to coral reef ecosystems". It details the coral code related parameters.

Parameter	value	minimum	maximum	unit	source
Growth related:					
Autotrophic feeding					
light threshold for feeding	700			W/m^2	assuming 15% of noon sunlight
corals feeding during day	20			%	
translocation of nutrients to host	90			%	Gustafsson 2013
Sediment smothering effects					
Ksmother coefftient;	0.054			nd	Wolanski et al. 2003a
Ksmother_constant;	0.4622			nd	Wolanski et al. 2003a
Algal-coral competition					
max growth rate massive corals	0.0003	0.00011	0.019	d^{-1}	0.003 (Mumby); 0.003 (Weijerman et al. 2013); 0.0004-0.0194 (Ruiz Sebastián and McClanahan 2013); 0.00011-0.0055 (Melbourne-Thomas et al. 2011a)
max growth rate branching corals	0.0003	0.00011	0.059	d^{-1}	
max growth rate turf	0.075	0.027	0.4	d^{-1}	0.029 (Klumpp and McKinnon 1992); 0.027 (Miller et al. 2009); 0.04 (Ruiz Sebastián and McClanahan 2013); 0.05-0.4 (Melbourne-Thomas et al. 2011a)
max growth rate macroalgae	0.018	0.014	0.4	d^{-1}	0.018 (Klumpp and McKinnon 1992); 0.06 (Dailer et al. 2012) (*Kappaphycus*); 0.014 (Ruiz Sebastián and McClanahan 2013); 0.05-0.4 (Melbourne-Thomas et al. 2011a)
max growth rate CCA	0.01	0.01	0.026	d^{-1}	0.010 (Klumpp and McKinnon 1992, Weijerman and Brown 2013); 0.026 (Ruiz Sebastián and McClanahan 2013)
max growth rate small phytoplankton	0.41	0.41	3.2	d^{-1}	0.41 (Weijerman et al. 2013); 3.2 (Wang et al. 2008)
max growth rate large phytoplankton	4.1	0.41	6.4	d^{-1}	0.41 (Weijerman et al. 2013); 6.4 (Wang et al. 2008)
turf-coral overgrow (rate of growth suppression)	0				McCook et al. 2001

Parameter	value	minimum	maximum	unit	source
macroalgae-coral overgrow (rate of growth suppression)	0.0010	0.00014	0.0011	d^{-1}	McCook et al. 2001, Lirman 2003, Mumby and Dytham 2005, Melbourne-Thomas et al. 2011a
CCA-coral overgrow (rate of growth suppression)	0				(McCook 2001)
turf-coral facilitation (% facilitation of coral recruitment)	5	5	15	%	McCook et al. 2001, Melbourne-Thomas et al. 2011a
macroalgae-coral competition (% growth inhibition)	80	40	90	%	McCook et al. 2001, Melbourne-Thomas et al. 2011a
CCA-coral facilitation (% facilitation of coral recruitment)	5	5	15	%	McCook et al. 2001, Melbourne-Thomas et al. 2011a
half saturation constant for growth on DIN for massive corals	50	5.6	28	mgN/m^3	0.23-0.8 µM NO3 (Domotor and D'Elia 1984); 5-22µM NO3 (D'Elia et al. 1983)
half saturation constant for growth on DIN for branching corals	50	5.6	28	mgN/m^3	5.6-28 (0.4-2.0 µM); NO3 0.23-0.8 µM (Domotor and D'Elia 1984); 5-22uM (D'Elia et al. 1983)
half saturation constant for growth on DIN for turf algae	6			mgN/m^3	
half saturation constant for growth on DIN for macroalgae	6	1.4	11.2	mgN/m^3	0.1-0.8 mmol/m^3 (Lapointe 1997)
half saturation constant for growth on DIN for CCA	6			mgN/m^3	
half saturation constant for growth on DIN for small phytoplankton	0.35	0.0084	1.4	mgN/m^3	0.025 mmol/m^3 (Huisman et al. 2006); 0.6 nmol/m3 (Wang et al. 2008); 0.1 mmol/m^3 (Lapointe 1997)
half saturation constant for growth on DIN for large phytoplankton	0.35	0.0028	1.4	mgN/m^3	0.025 mmol/m^3 (Huisman et al. 2006); 0.2 nmol/m^3 at (Wang et al. 2008); 0.1 mmol/m^3 (Lapointe 1997)
light saturation branching corals	35	11	67	W/m^2	50-300 µE/m^2/s (Kleypas 1997)
light saturation massive corals	35	11	67	W/m^2	50-300 µE/m^2/s (Kleypas 1997)
light saturation turf	5			W/m^2	
light saturation macroalgae	5			W/m^2	Skagerrak & Baltic Sea ~ 100 µmol photons/m^2/s= 0.135 W/m^2
light saturation CCA	5			W/m^2	
light saturation small phytoplankton	20			W/m^2	Huisman et al. 2006
light saturation large phytoplankton	20			W/m^2	Huisman et al. 2006
Rugosity related:					
rugosity based habitat dependency coefficient	1.4613			nd	Shape of relationship inferred from Friedlander and Parrish 1998,

Parameter	value	minimum	maximum	unit	source
rugosity based habitat dependency constant	0.0475			nd	Graham et al. 2006, DeMartini et al. 2013
rugosity based habitat dependency cap	4			nd	
rugosity based habitat dependency scalar	8			nd	
rugosity constant	1.3			nd	adapted from Bozec et al. 2014
massive corals colony height parameter	0.715			cm	Bozec et al. 2014
branching corals colony height parameter	0.81			cm	average of slopes from *Porites* sp. (Bozec et al. 2014)
branching corals max. colony diameter	60	0-5	>300	cm	mean 26 cm L. Raymundo, unpublished data, 17 cm CRED data
massive corals max. colony diameter	30	0-5	>300	cm	mean 14 cm L. Raymundo, unpublished data, 15 cm CRED data
Ocean change related					
Aragonite saturation - CO_3 calculation					
Karag_A	0.9485			nd	Zeebe and Wolf-Gladrow 2009; Values for coefficients from proxy fitting exercise - from data given in Bjerrum plot
Karag_B	8.20416			nd	
Karag_C	2.3641			nd	
Karag_D	8			nd	
Karag_pH;	time series pCO_2			nd	IPCC AR5 RC8.5; for control simulation: pCO_2 =380 (~1985)
Kca_const;	0.0103				Berner 1965, Edmond and Gieskes 1970, Kleypas et al. 2006
K_Ks;	$6\ 10^{-9}$			nd	Kleypas et al. 2006
Calcification related parameters					
Reference baseline calcification rate	15.03	12.03	17.03	ppm	380 ppm (Silverman et al. 2009, Anthony et al. 2011a) needed to lower to get realistic rates of calcification
calcification T constant	9.7	9.03	10.37	nd	Silverman et al. 2009, Anthony et al. 2011a
calcification T coefficient	18.83	12.98	24.68	nd	Silverman et al. 2009, Anthony et al. 2011a
calcification optimum temperature	29			°C	close to summer ambient temperature (Jokiel and Coles 1977); summer solstice temp. (Silverman et al. 2009)
calcification Lambda	0.42	0.33	0.51	nd	Silverman et al. 2009, Anthony et al. 2011a
light threshold for autotrophic feeding	700			W/m^2	assumption 85% of noon irradiance

Parameter	**value**	**minimum**	**maximum**	**unit**	**source**
proportion feeding during light	20			%	assuming mostly feeding at night
host remineralization	90			%	Gustafsson 2013
Growth/fecundity relationship with pH					
CCA coeff. & const	-7.0, 1.0			nd	Langdon 2002, Kroeker et al. 2010
large phytoplankton coeff. & const	1.4, 1.1705			nd	Hendriks et al. 2010, Harvey et al. 2013
small phytoplankton coeff. & const	3.7, 1.0			nd	Hendriks et al. 2010, Harvey et al. 2013
macroalgae coeff. & const	1.6, 1.1			nd	Hendriks et al. 2010, Harvey et al. 2013
zooplankton coeff. & const	5.0, 1.7			nd	Kurihara and Ishimatsu 2008, Hendriks et al. 2010, Wittmann and Pörtner 2013
benthic grazers (urchins) coeff. & const	-3.0, 0.5			nd	Kurihara and Ishimatsu 2008, Hendriks et al. 2010, Wittmann and Pörtner 2013
benthic filter feeders (bivalves) coeff. & const	-7.0, 1.0			nd	Wittmann and Pörtner 2013
Bleaching parameters					
bleaching mortality massive corals	22.5	3.14	41.87	%	Jokiel and Coles 1990, McClanahan , Donner et al. 2005,
bleaching mortality branching corals	42	19.7	100	%	McClanahan et al. 2007
bleaching rate massive corals	25	9.8	40.2	%	
bleaching rate branching corals	24.2	6.9	41.5	%	
bleaching recovery rate massive corals	0.0027			d^{-1}	Lombardi et al. 2000
bleaching recovery rate branching corals	0.0822			d^{-1}	Kvitt et al. 2011 (0.2 degree /decade)
bleaching temperature corals	30.4			°C	1 degrees above summer max ambient, NOAA Coral Reef Watch
proportion of zooxanthellae in coral tissue	30	5	30	%	15% (Odum and Odum 1955); <5% (Thornhill et al. 2011); 30% (Gustafsson 2013)
degree heating weeks (DHW) threshold massive corals	4			DHW	Donner et al. 2005, McClanahan et al. 2007
degree heating weeks (DHW) threshold branching corals	3			DHW	Donner et al. 2005, McClanahan et al. 2007

Appendix H

This supplement provides additional information for chapter 6: “Applying the Atlantis model framework to coral reef ecosystems”. It shows example outputs from control simulations (i.e., a run with no external disturbances) of trajectories in fish biomass, invertebrate biomass, weight-at-age and numbers-at-age. The last figure (H-4) shows catch and biomass equilibrium plots.

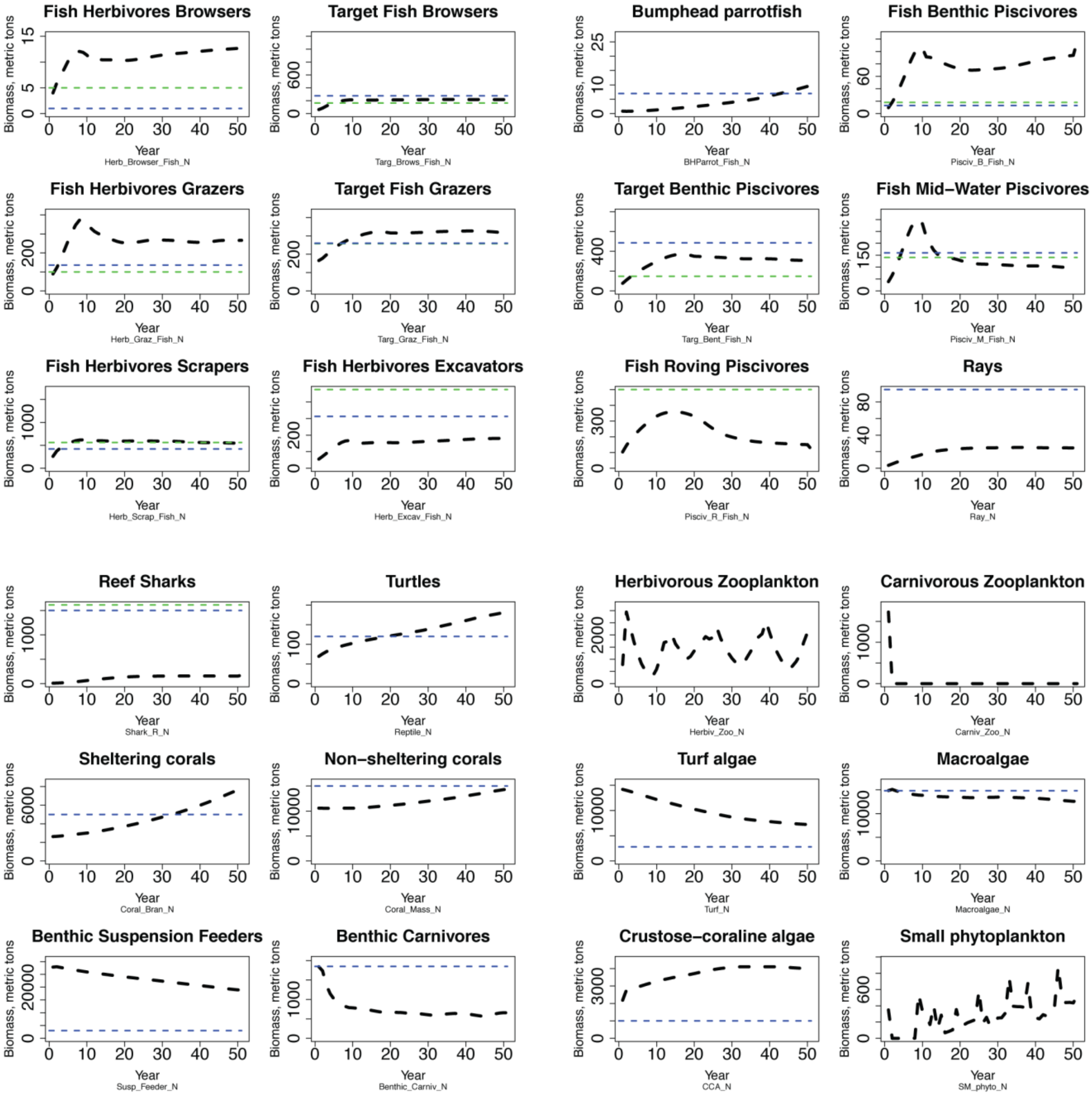


Figure H-1. Biomass trajectories of some fish, invertebrate, planktonic, and benthic functional groups of a scenario when no external disturbances were simulated. The green dashed line reflects the biomass in marine preserves in Guam (CRED surveys conducted in 2011). The blue dashed line represents the biomass calculated from surveys around the unpopulated Northern Mariana Islands.

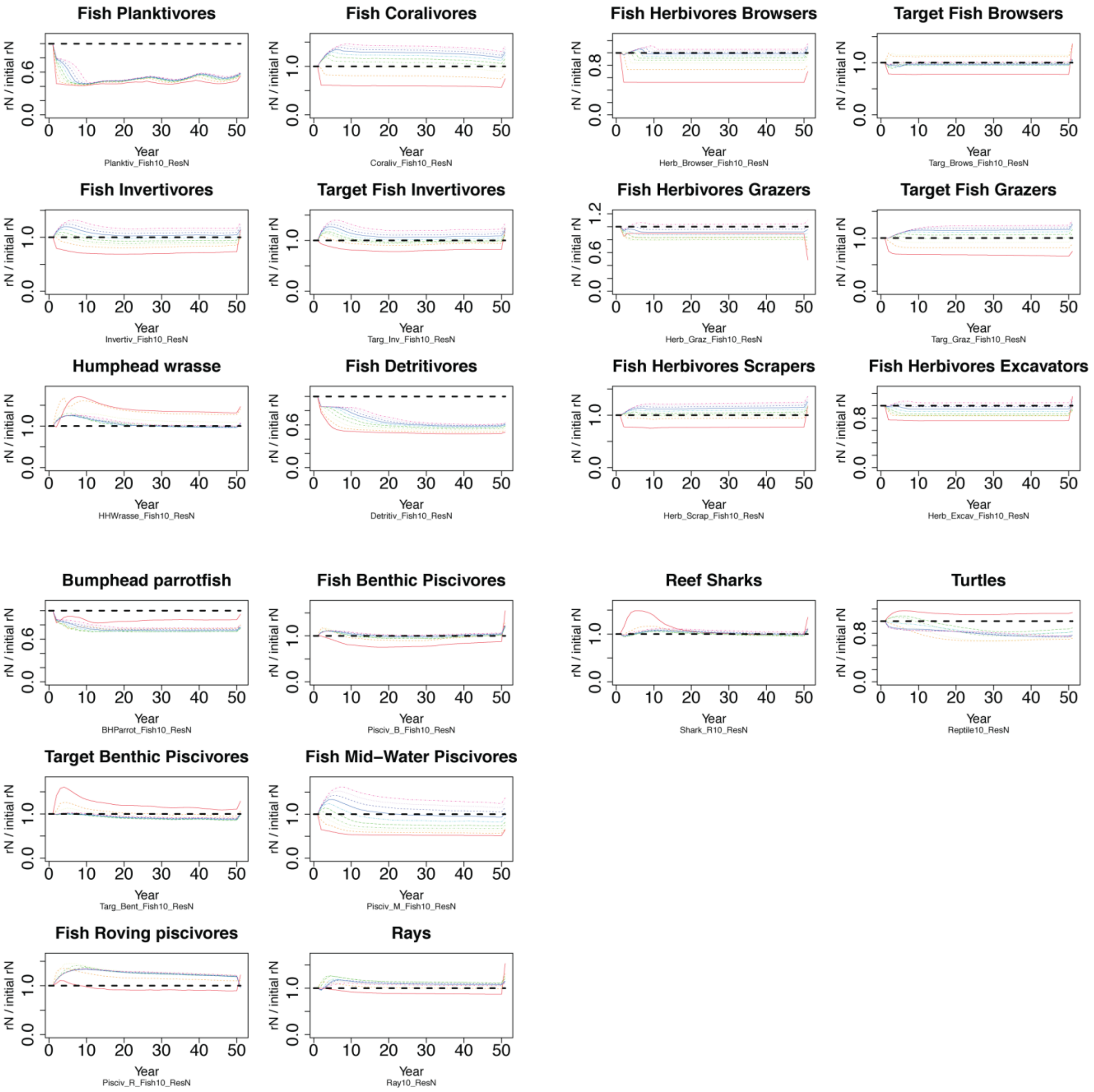


Figure H-2. The trajectory of the ratio of weight-at-age to initial weight-at-age of vertebrate functional groups of a scenario when no external disturbances were simulated. The rainbow colors represent the ten age classes with red being the youngest and violet being the oldest age class.

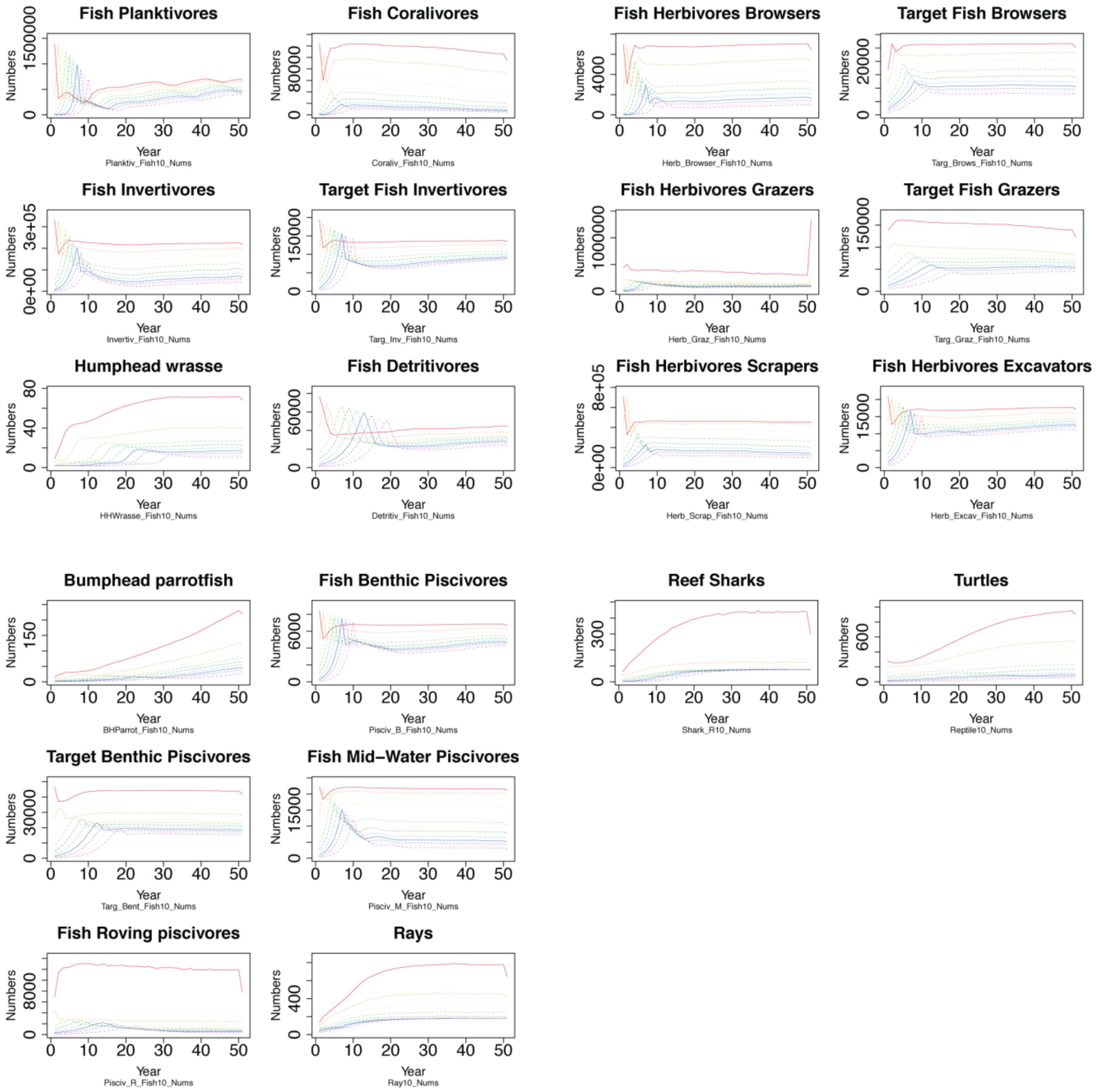


Figure H-3. The trajectory of abundance-at-age of vertebrate functional groups of a scenario when no external disturbances were simulated. The rainbow colors represent the ten age classes with red being the youngest and violet being the oldest age class.

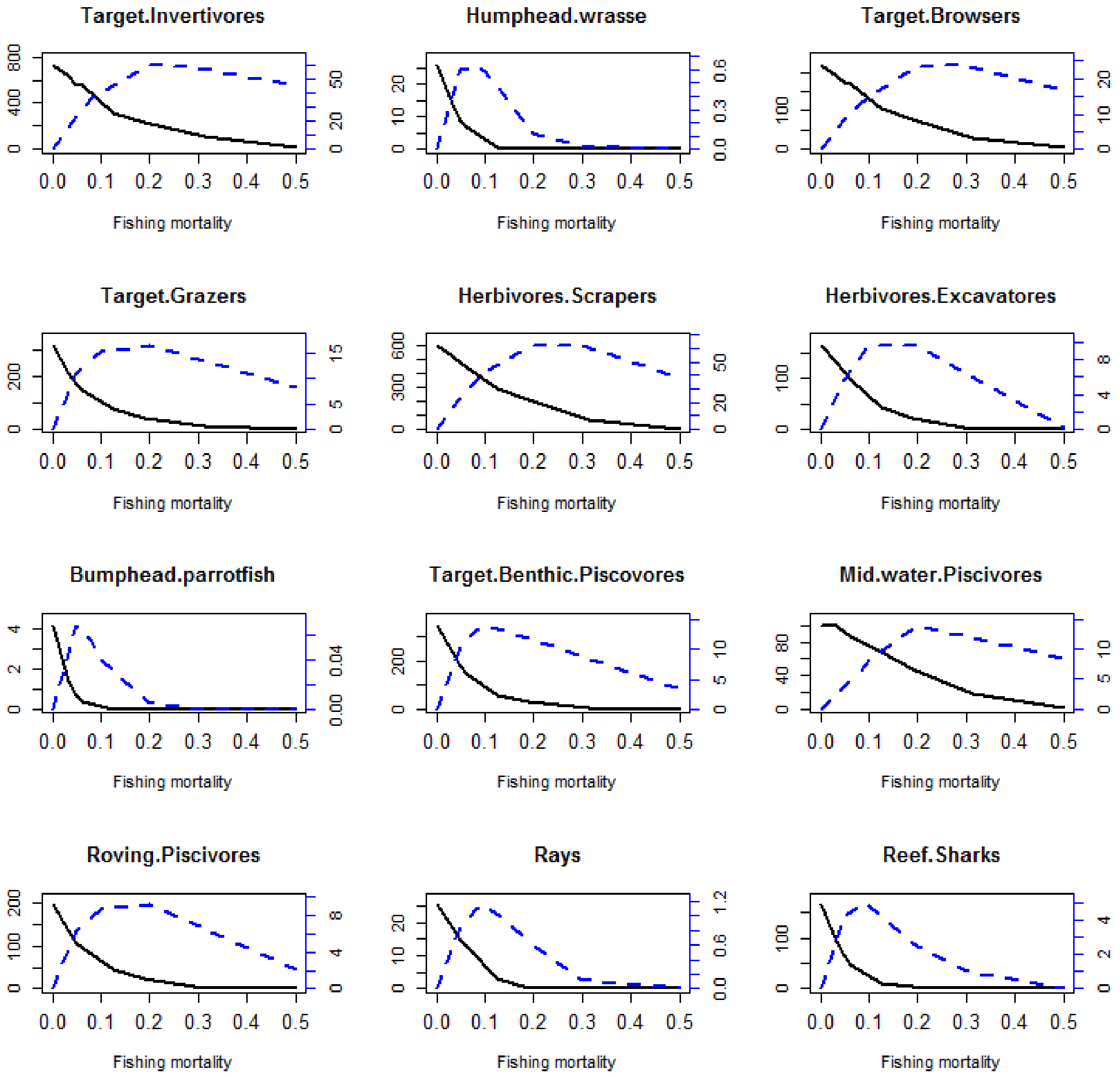


Figure H-4. Catch and biomass equilibrium plots for functional groups: catch (blue dashed line – right vertical axis) and biomass (black line – left vertical axis) against fishing mortality (F=0, 0.05, 0.08, 0.10, 0.20, 0.30, 0.50, 0.80). X-axis is fishing mortality per year, left y-axis is the biomass in tons, and right y-axis is the landings in tons. Both biomass and catches are shown at the end of a 30-year simulation. Natural mortality for target invertivores = 0.49/y; humphead wrasse = 0.15/y; target browsers = 0.32/y; target grazers = 0.19/y; scrapers = 0.53/y; excavators = 0.41/y; bunphead parrotfish = 0.14/y; target benthic piscivores = 0.29/y; mid-water piscivores = 0.51/y; roving piscivores = 0.16/y; rays = 0.17/y; sharks = 0.21/y.

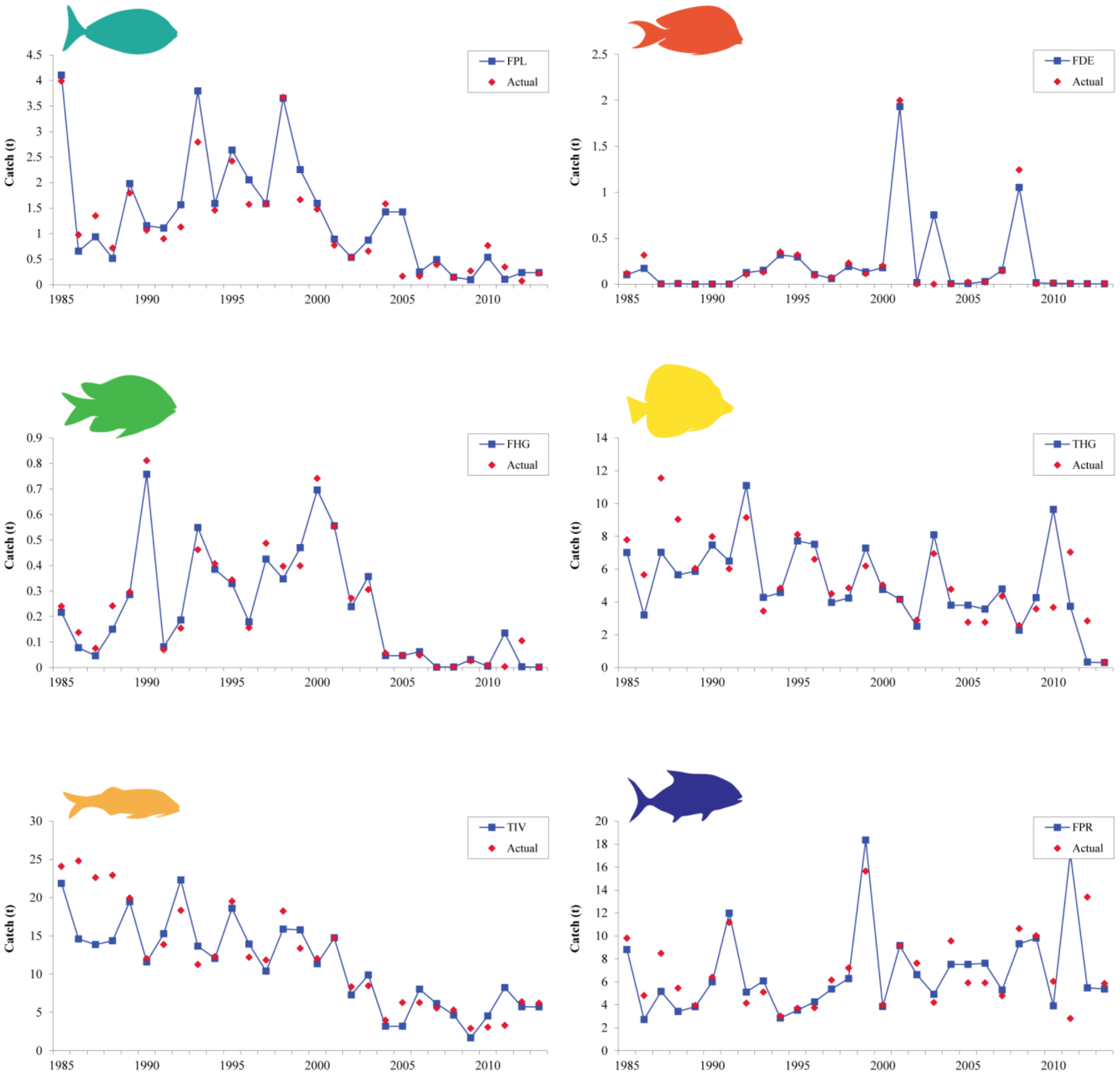


Figure H-5. Annual fish catches from a few functional groups. Blue squares are catches from the model output (forced with historical catches as far as possible given modelled ecosystem structure) and red diamonds are reported catches from creel survey data (Guam Division of Aquatic and Wildlife Resources).FPL=planktivores; FDE=detritivores; FHG=grazers; THG=target grazers; TIV=target invertivores; and FPR=roving piscivores.

Appendix I

This supplement provides additional information for chapter 6: "Applying the Atlantis model framework to coral reef ecosystems". Model predictions of biomass trajectories of the functional groups were compared to reconstructed time series from fishery-dependent (CPUE) and fishery-independent (visual survey) data of targeted fish species. There was a substantial discrepancy for the functional groups with low abundance data, such as the humphead wrasse, bumphead parrotfish, and sharks, but also for many of fish species targeted by spear fisherman (e.g., parrotfishes). Reported catch data (DAWR) showed a decline in catches in the last decade, this decline in landings (and effort) is reflected in an increase in fish biomass since 2005 (Fig. I-1 left bottom panel) which was not seen in reality (Brainard et al. 2012).

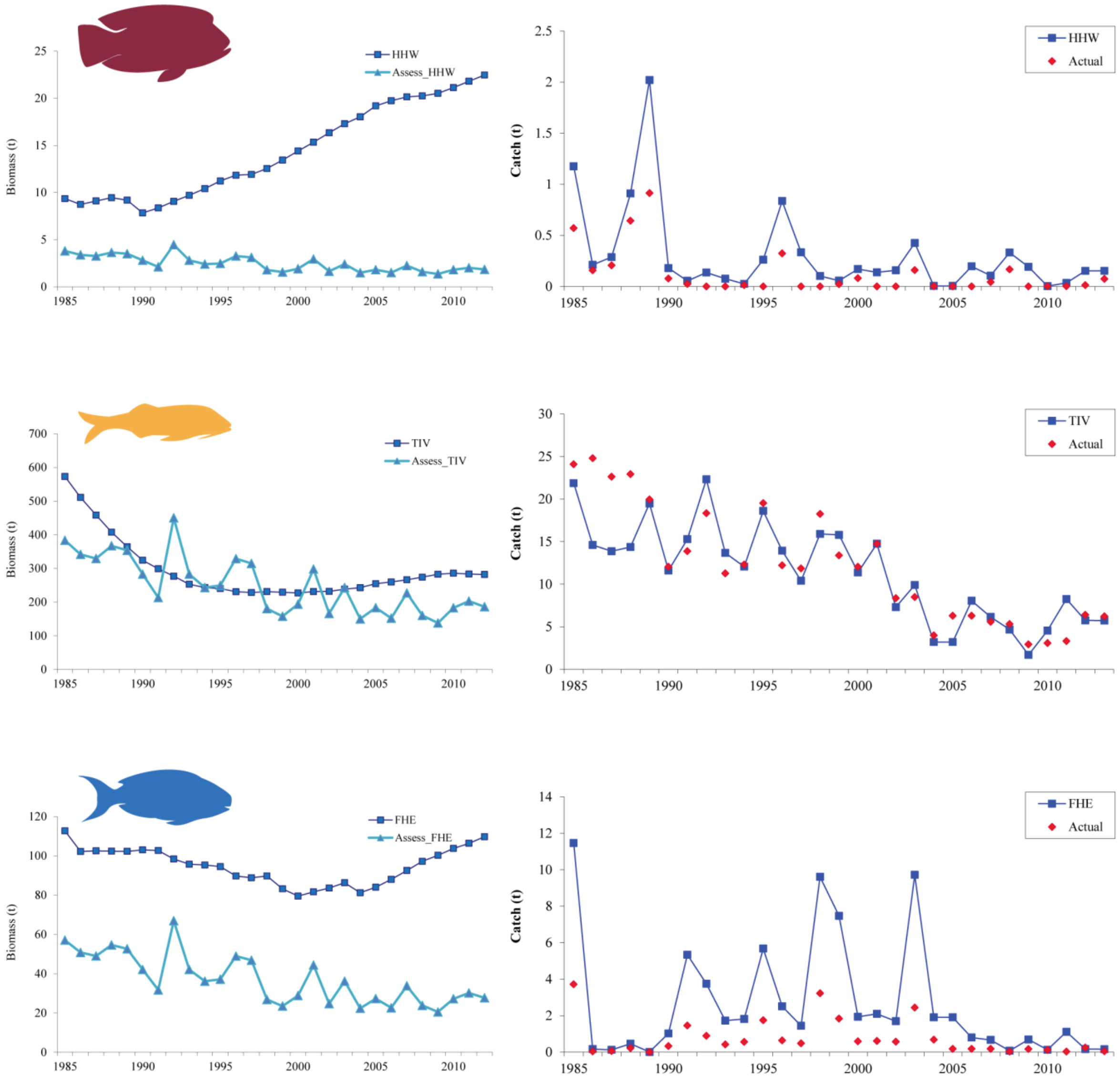


Figure I-1. Results from simulating historical catches with (*left panels*) biomass trajectory and (*right panels*) the catches (in blue) and estimated actual catches (in red; data from DAWR) of (*top*) humphead wrasse (HHW), (*middle*) targeted invertivores (e.g.,snappers, goatfish, emperor; TIV) and (*bottom*) large-bodied parrotfish (FHE)

When we assumed fish catches since 2005 stayed similar to fish catches between 2000 and 2004 for those species heavily targeted by spearfisherman i.e., for parrotfishes (FHE, FHS), goat fishes (TIV), humphead wrasse (HHW), and unicorn fishes (THB), the trend of the predicted biomass corresponded better with the estimated biomass based on the reconstructed time series (Fig. I-2).

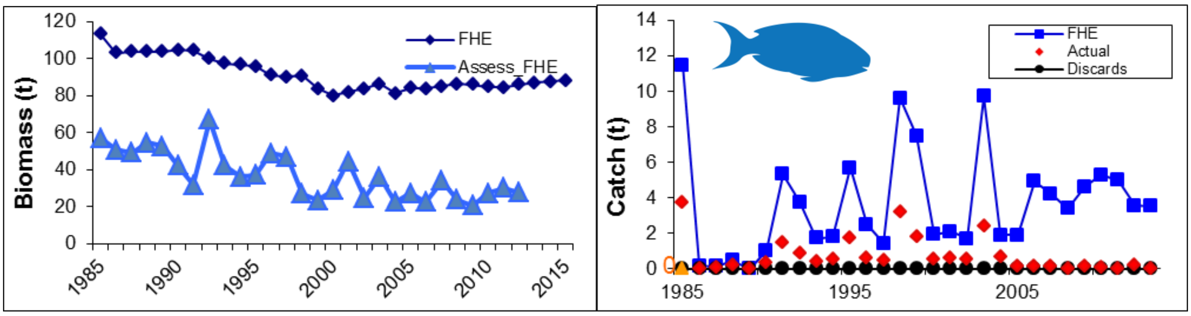


Figure I-2. Results from simulating historical catches with spearfish catches of the last decade of parrotfish at same levels as the average of 1999-2004. (*left panel*) Biomass trajectory (in diamonds) compared to reconstructed time series (in triangles) and (*right panel*) the catches (in blue) and estimated actual catches (in red) of (*top*) large-bodied parrotfish (FHE).

Appendix J

This supplement provides additional information for chapter 6: "Applying the Atlantis model framework to coral reef ecosystems". It shows the results of three sensitivity analyses.

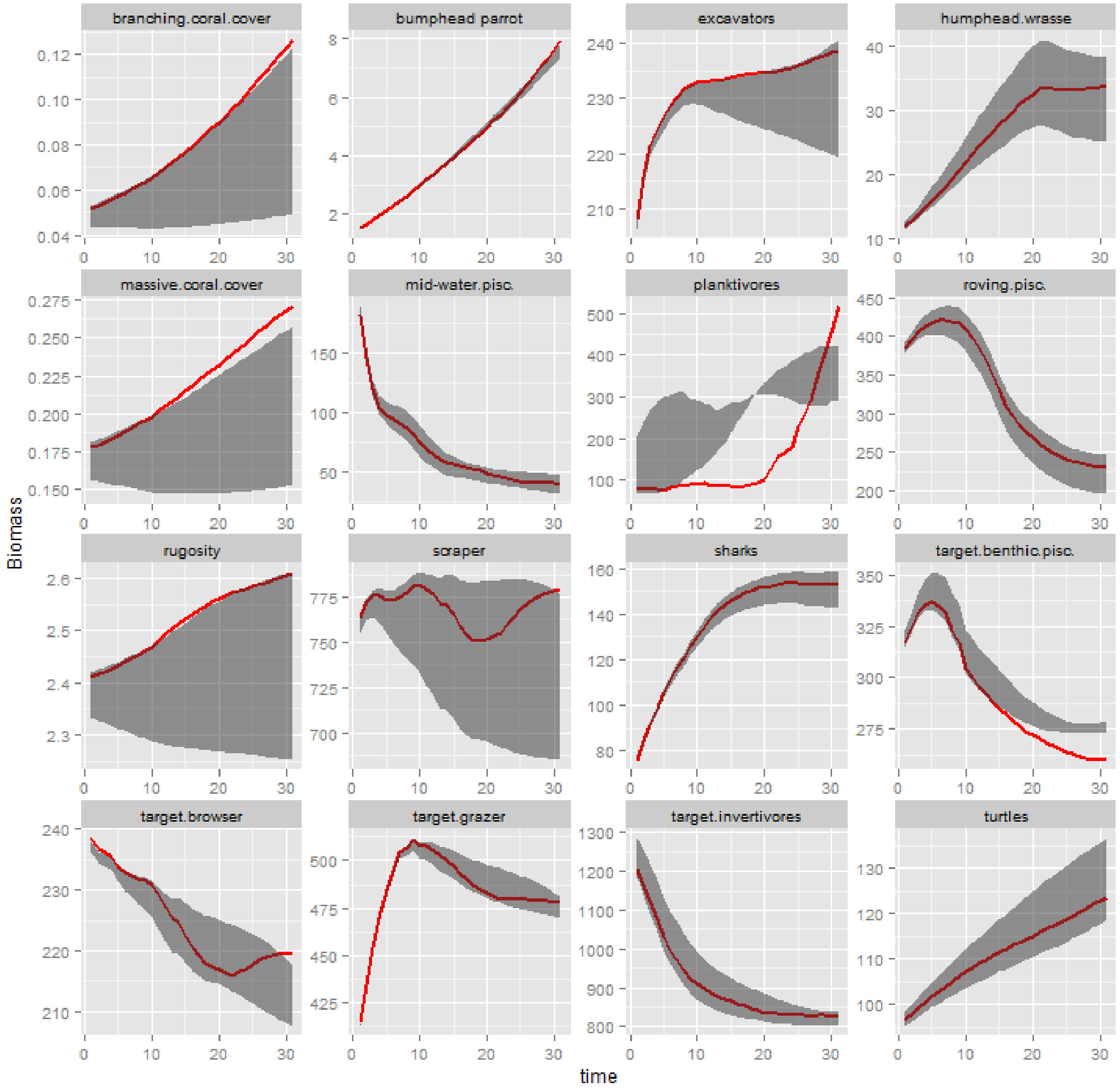


Figure J-1. Sensitivity of selected functional groups to growth rates of large and small phytoplankton. The shaded area represents the area between the minimum and maximum values used for these parameters (see Appendix G for parameter values). The red line is the trajectory of the control run.

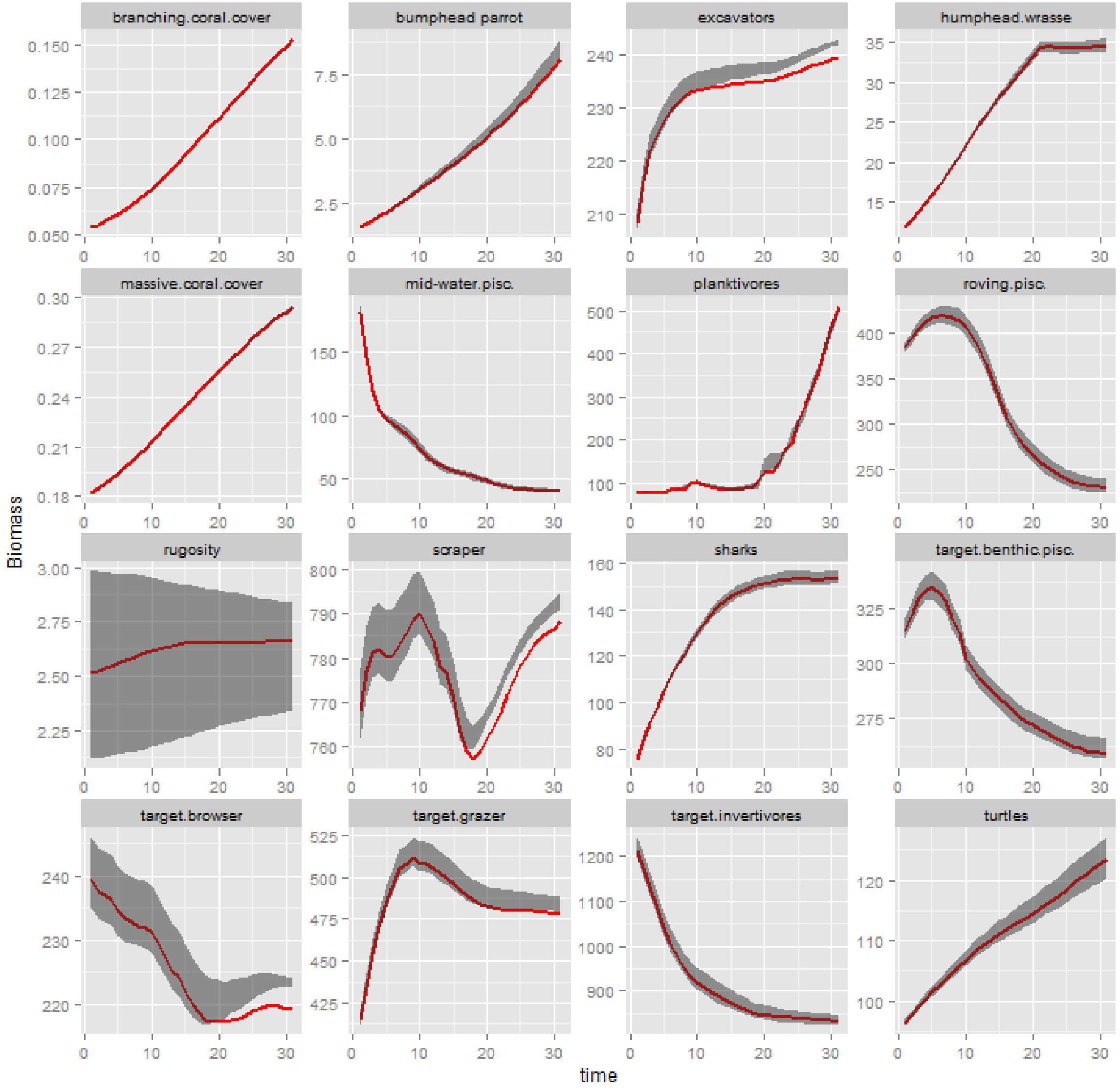


Figure J-2. Sensitivity of selected functional groups to rugosity estimations. The shaded area represents the area between the minimum and maximum values used for the mean coral diameter parameters (see Appendix G for parameter values). The red line is the trajectory of the control run.

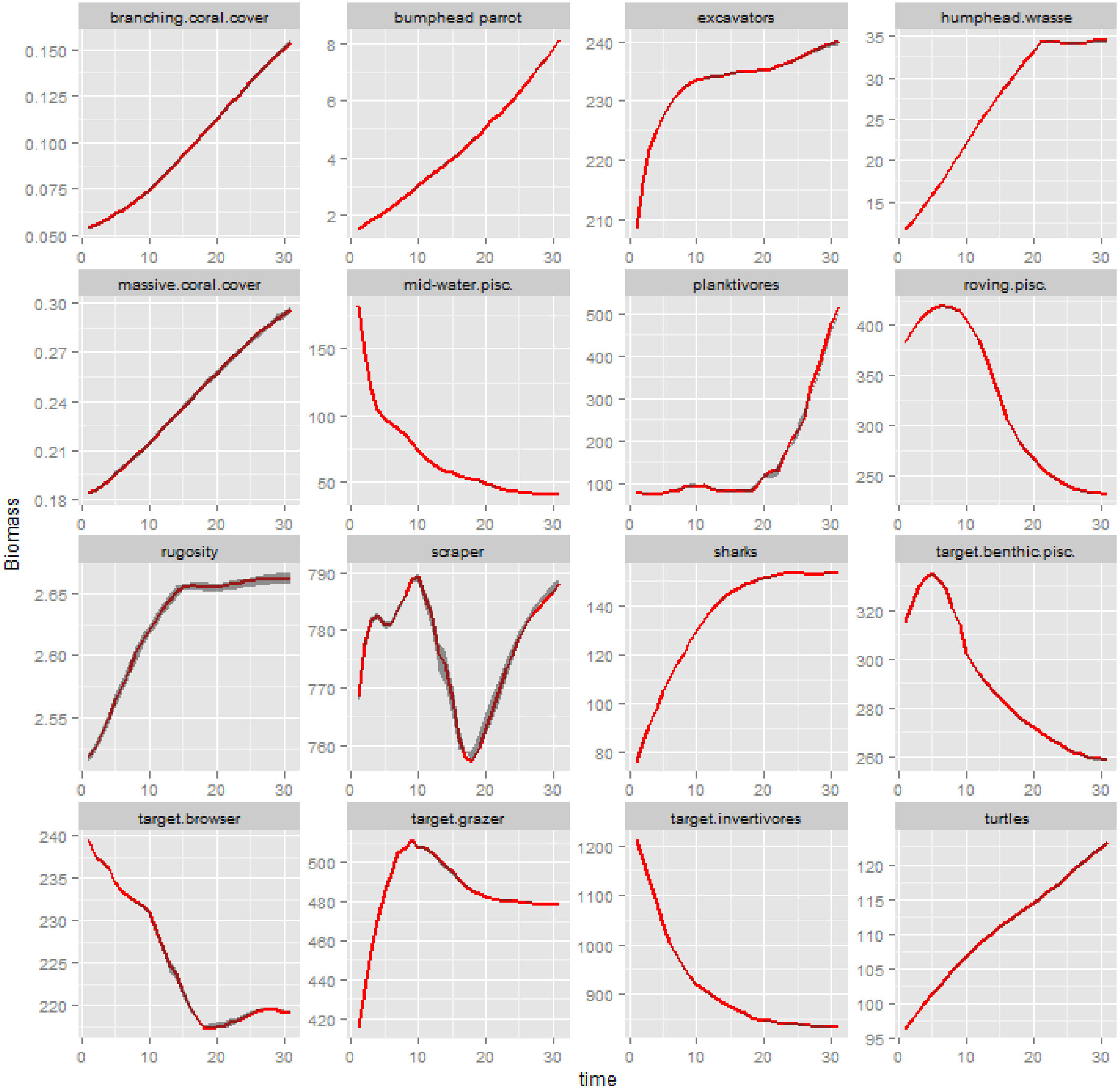


Figure J-3. Sensitivity of selected functional groups to relationship between coral and macroalgae. The shaded area represents the area between the minimum and maximum values used for this parameter (see Appendix G for parameter values). The red line is the trajectory of the control run.

Appendix K

This supplement provides additional information for chapter 6: “Applying the Atlantis model framework to coral reef ecosystems”. From reef-fish surveys around Guam conducted by CRED, the empirical relationship between structural complexity and fish biomass is apparent from all the upward trend lines in Figure K-1.

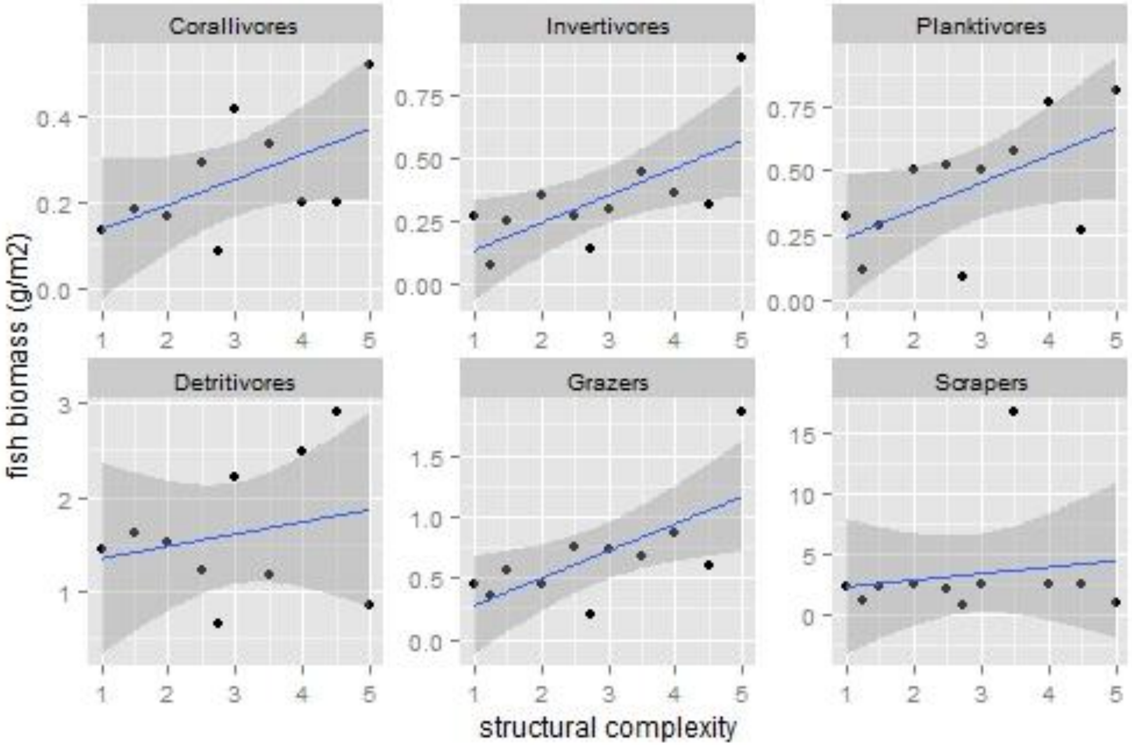


Figure K-1. Relationships between the structural complexity and the reef-fish biomass of six functional groups around Guam. Blue line is linear regression line with shaded area representing 95% confidence region. Data from visual surveys conducted by NOAA-PIFSC-CRED in 2011.

Appendix L

This supplement provides additional information for chapter 8: "Towards an ecosystem-based approach of Guam's coral reefs: the human dimension". It shows a list of participating organizations in the workshop and meetings conducted in Guam in 2011 and 2014

Organization
NOAA Fisheries Pacific Islands Regional Office (PIRO)
NOAA Pacific Islands Fisheries Science Center (PIFSC)
NOAA Coral Reef Conservation Program (CRCP)
NOAA-PIFSC – Coral Reef Ecosystem Division
JIMAR - University of Hawai'i
POC Coral Reef Conservation, Western Pacific Fishery Management Council, Director of Dept. of Chamorro Affairs
Guam Coastal Management Program (GCMP)
Guam Department of Agriculture
University of Guam Marine Laboratory
Humatåk Community Foundation
Guam Preservation Trust
Naval Facility Andersen Air Force Base (AAFB)
USDA Natural Resource Conservation Service
War in the Pacific National Park (NPS)
Guam Environmental Protection Agency

Appendix M

This supplement provides additional information for chapter 8: "Towards an ecosystem-based approach of Guam's coral reefs: the human dimension". It describes the nodes in the dive tourism behavior model. Starred (*) nodes connect directly to the ecological model.

Node	**Description of node**
Wreck diving	The presence or absence of a wreck at a dive site. Guam has several historic wrecks in Apra Harbor which are popular dive locations
Quality of dive experience	The combination of ecological and situational variables that influence overall satisfaction
Previous dive experience	The total number of dives an individual has previously completed
Cost of dive charter	The price paid to participate in a dive
Tourist visitation #	The number of tourists visiting the island
Tourist origin	Tourists from different countries do not all have the same preferences
Age group	The age of an individual (in years)
Price of accommodation	Price paid for hotel accommodations can vary throughout the year
Charismatic species*	The presence or absence of charismatic species, such as, bumpead parrotfish, Napoleon wrasse, sharks, turtles
Coral cover*	The average of coral cover in the entire model domain
Species abundance*	Species abundance is the standing stock biomass of the main species that comprise the fishery target groups (e.g., jacks, parrotfish, groupers, surgeonfish, goatfish, invertebrates) and non-target groups. The standing stock biomass changes over time due to habitat degradation and extraction.
Clarity of the water	Sediments and algal blooms can reduce the clarity of the water, and thus visibility.
Tourist season	Peak: January to May; Off season: July to November; June and December are shoulder months.
Flight availability	The number of flights arriving in Guam per month
Access to diving locations	Access to coastline areas and potential dive sites is restricted by the natural features of the coastline in Guam, ocean and weather conditions, and military/security access controls.
Watershed condition	A description of the watershed as degraded or not. Degraded watersheds are assumed to have the same run off of sediments and nutrients as present conditions. When watersheds are restored, we assume no additional sediment and nutrient inputs.
Marine preserves	Guam has 5 marine preserves: Tumon Bay MP, Piti Bomb Holes MP, Pati Point MP, Sasa Bay MP, and Achang MP. There are specific rules regulating fishing and other activities for each one. They cover approximately 16.3% of Guam's coral reef habitat from 0 to 30-m depth.
Ocean and weather conditions	Ocean and weather conditions that may change on a daily or seasonal basis, such as wind speed and direction, wave height, tides, and visibility; Waters in some areas around the island are too rough for diving during much of the year.
Coastal features	Access to Guam's coastline areas and potential dive sites is restricted by natural features
Access areas closed by military	Areas of the shoreline, territorial waters (out to 3 nm), and federal waters (3 - 200 nm) that are closed to fishing activities by the U.S. military and/or territorial and federal security agencies (e.g., the U.S. Department of Homeland Security).
Enforcement of marine preserves	The effectiveness of enforcement of rules regulating fishing and boating activities.

Appendix N

This supplement provides additional information for chapter 8: "Towards an ecosystem-based approach of Guam's coral reefs: the human dimension". It describes connection between nodes of dive tourism behavior model

Variable A	Variable B	Connection between variables	Reference
Enforcement	Marine preserves	The effectiveness of enforcement can determine if dive charters respect the rules regulating fishing and other activities within marine preserves.	Expert opinion
Marine preserves	Species abundance	The establishment (and enforcement) of marine preserves may influence the overall abundance of species and in particular in species that complete their life cycle within the marine preserve boundaries. Moreover, spillover effects may lead to a greater biomass or fish abundance of species just outside of the marine preserve boundaries.	Tupper 2007
Marine preserves	Charismatic species	The establishment (and enforcement) of marine preserves influences the overall abundance of charismatic species and in particular in species that complete their life cycle within the marine preserve boundaries.	Tupper 2007
Marine preserves	Coral cover	There is little evidence that marine preserves increase coral cover, as coral cover increase is related to herbivore biomass. However, herbivore biomass increases within marine preserves.	Gilmour et al. 2013
Watershed conditions	Turbidity	Different types of land use will have a different effect on runoff and thus ocean turbidity. Turbidity created by different land uses can be a problem in some areas of Guam. If the watershed is in good condition this will decrease runoff and thus turbidity.	Burdick et al. 2008
Oceans and weather conditions	Turbidity	Windy and stormy conditions can increase ocean turbidity.	Wolanski et al. 2003a
Oceans and weather conditions	Access to diving locations	Changes in ocean and weather conditions occur on a daily basis. Some weather conditions will not allow dive activities to take place. In addition, near shore waters on the east side of the island are too rough for diving.	Expert opinion

Variable A	Variable B	Connection between variables	Reference
Coastline features	Access to diving locations	Cliff lines make up a significant portion of the coastline and prevent coastal access for dive charters, particularly on the east side. The most popular dive destinations are on the west side of the island due to the presence of fringing reefs and bays and are accessible for dive charter for most of the year.	http://www.mdaguam.com/content/guam-beach-dives
Areas closed by military	Access to diving locations	Military areas are off limits and no access can be gained for dive charters. Further, construction in preparation for the military buildup has also inhibited access to municipal boat ramps, limiting the number of boat access points.	Expert opinion
Access to diving locations	Cost of dive charter	Decreased access to dive grounds from the shoreline can increase the distance boats need to travel, in turn, increases fuel use. With higher fuel prices are likely to be passed on to the customers.	Expert opinion
Tourist season	Cost of dive charter	In peak tourist season the cost of dive charters is higher as demand for charters is relatively higher.	Expert opinion
Tourist season	Price of accommodation	In the peak tourist season the price of accommodation is higher.	Expert opinion
Tourist season	Flight availability	In peak seasons there are more flights available to bring tourists to Guam.	Expert opinion
Price of accommodation	Tourist visitation numbers	If prices of accommodation are comparatively high this means that tourism visitation is likely to be negatively affected.	Expert opinion
Flight availability	Tourist visitation numbers	If more flights are available this is likely to increase the number of tourist visiting Guam.	Expert opinion
Flight availability	Tourist country of origin	There are more flights to Guam from some countries thus influencing the country of origin of the tourists.	Expert opinion
Wreck diving	Participation in dive trips	There are a number of popular wreck dives with historical significance in Apra Harbor, so the presence/absence of a wreck could also influence participation in dive trips.	http://www.nps.gov/submerged/Parks/WAPA.html
Tourist visitation #	Participation in dive trips	With higher tourist number the demand for dive trips is also likely to increase.	Expert opinion
Cost of dive charter	Participation in dive trips	More expensive dive trip costs is likely to negatively affect participation in dive trips.	Rudd and Tupper 2002
Previous dive	Participation in	People with previous dive experience are more likely to participate in new	Expert opinion

Variable A	Variable B	Connection between variables	Reference
experience	dive trips	dive experiences and partake in dive trips on their holidays.	
Age	Previous dive experience	Age group influences previous dive experience with older divers generally having completed more dives.	Grafeld et. al. (in prep)
Quality of the dive experience	Participation in dive trips	Positive dive experiences will mean that it is more likely that the tourist will participate in a dive trip.	Expert opinion
Size of dive group	Quality of the dive experience	Previous studies have included the size of the group on a dive charter as a measure of the quality of the dive experience (with a higher WTP for smaller groups).	Rudd and Tupper 2002, Schuhmann et al. 2013
Charismatic species	Quality of the dive experience	Charismatic species are important contributors to a dive experience. Some divers will value the sighting of charismatic species most as part of the dive trip.	$5.40 more/per ive to see more Napoleon wrasse (Grafeld et al. in prep)
Coral cover	Quality of the dive experience	The condition and extent of coral cover will increase the aesthetic quality of the reef and thus increase the quality of the dive experience.	Parsons and Thur 2008
Species abundance	Quality of the dive experience	The more species are visible and present on a dive – the more divers are likely to enjoy the experience.	$6.45 more per dive for a change from low to high fish biomass; $6.23 more per dive for a change from low to high fish species diversity (Grafeld et al. in prep)
Turbidity	Quality of the dive experience	If turbidity is high- visibility is low and likely to decrease the quality of the dive experience.	$10 on average (± $5) towards sediment reduction projects (Grafeld et al. in prep)
Tourist country of origin	Tourist visitation numbers	There are more tourists from some countries than others (i.e., Japanese tourists make up the largest group).	https://www.fhb.com/en/assets/File/Marketing/FHB_2013-14_GuamEconForecast.pdf

Appendix O

This supplement provides additional information for chapter 8: "Towards an ecosystem-based approach of Guam's coral reefs: the human dimension". It describes the nodes in the fishery behavior model. Starred (*) node connects to ecological model.

Node	**Description of node**
Enforcement	The effectiveness of enforcement of rules regulating fishing and boating activities.
Areas closed by military/security	Areas of the shoreline, territorial waters (out to 3 nm), and federal waters (3–200 nm) that are closed to fishing activities by the U.S. military and/or territorial and federal security agencies.
Ocean and weather conditions	Ocean and weather conditions may change on a daily or seasonal basis, such as wind speed and direction, wave height, tides, and visibility; waters in some areas around the island are too rough for fishing from small boats during much of the year.
Coastline features	Access to Guam's coastline areas and nearshore fishing areas is restricted by the natural features.
Access to shoreline and fishing grounds	Whether or not fishers can enter and/or utilize coastal and marine areas for fishing. Types of areas include coastal access roads, beaches, boat ramps, docks/piers and marine areas.
Tourist season	Peak: January to May; Off season: July to November; June and December are shoulder months.
Price of fish	The price for which fish are bought and sold on Guam. This depends on several factors, including seasonal availability of fish, time of year/tourist season, and outlet to which fish is being sold (Guam Fishermen's Co-op versus restaurants versus other markets).
Fuel cost	The cost of fuel. This is the main operating cost incurred in boat-based fishing on Guam.
Employment opportunities	1) Whether or not fishers earn income from non-fishing employment, 2) Whether or not that employment provides them with money beyond what is needed to meet regular expenses, allowing them to have "free time" and extra income.
Age	Age of fisher (in years)
Gender	Gender of fisher
Fishing tradition	Whether or not one comes from a "fishing family"; whether one's family members (especially older family members) are fishers.
Ethnicity	Ethnicity of fishers; people of some ethnicities are more likely to be engaged in fishing in Guam.
Species abundance	Species abundance is the standing stock biomass of the main species that comprise the fishery target groups (e.g., jacks, parrotfish, groupers, surgeonfish, goatfish, invertebrates) and others. The standing stock biomass changes over time due to habitat degradation and extraction.
Participation in reef fishing	Any activity that involves the collection of reef species. On Guam, this includes commercial fishing and non-commercial fishing. Fishers often use multiple fishing gears and target multiple marine species during a single fishing trip. Fish may be used for subsistence, given away or sold depending on a variety of trip-based factors. When and where one fishes, which methods are used, and which species are targeted depends on several factors, including the experience level of fishers and access to resources required to fish (e.g., boat, gear, fuel).

Appendix P

This supplement provides additional information for chapter 8: "Towards an exosystem-based approach of Guam's coral reefs: the human dimension". It describes connections between nodes in the fishery behavior model. Starred (*) node connects to ecological model.

Variable A	Variable B	Connection between variables	Reference
Enforcement	Management scenarios	The effectiveness of enforcement can determine if fishers respect and observe the rules regulating fishing activities.	Charles et al. 1999, Sutinen and Kuperan 1999, Hatcher et al. 2000
Management scenarios	Species abundance	Alternative management scenarios will affect species abundance differently. For example, the existence (and enforcement) of marine preserves may influence the overall abundance of species, particularly for species that complete their life cycle within the marine preserve boundaries. Size-based controls influence the overall abundance by limiting the fish allowed to be landed to those of a specific size. With a build-up of larger (older) individuals, larval quality and survivorship increases. Leaving the small, immature fish will increase the spawning biomass.	(Berkeley et al. 2004, Birkeland and Dayton 2005, Taylor et al. 2012, Williams et al. 2012)
Management scenarios	Access to shoreline and fishing grounds	Some management scenarios (such as the existence/expansion of MPs) may prevent fishers from accessing certain shoreline and nearshore areas, sometimes restricting access to common or traditional fishing grounds.	Expert opinion and personal observation
Areas closed by military/security	Access to shoreline and fishing grounds	Closed areas limit the ability of fishers to access fishing grounds. Further, construction, in preparation for the military buildup, has also inhibited access to municipal boat ramps, restricting boat access to nearshore fishing grounds. Fishers have to make longer boat trips to get to their fishing locations.	Expert opinion and personal observation
Ocean and weather conditions	Access to shoreline and fishing grounds	Changes in ocean and weather conditions occur on a daily and seasonal basis and contribute to fishers' decisions regarding whether to go fishing and where they will fish. Some nearshore waters on the east side of the island are too rough for fishing from small boats for approximately 9 months of the year, on average.	Expert opinion

Variable A	**Variable B**	**Connection between variables**	**Reference**
Coastline features	Access to shoreline and fishing grounds	Coastline features determine the extent of coastal access for fishers. For example, cliff lines make up a significant portion of the coastline and prevent access to adjacent fishing grounds.	Allen and Bartram 2008
Access to shoreline and fishing grounds	Fuel cost	Decreased access to shoreline and fishing grounds can increase the distance boats need to travel to preferred fishing grounds; this, in turn, increases fuel use. With higher fuel prices, the cost to travel further distances increases. Fuel is the main operating cost incurred in fishing on Guam. Increased fuel costs influence where and how often fishermen decide to fish.	Hospital and Beavers 2012 Expert opinion
Access to shoreline and fishing grounds	Participation in reef fishing	Access to fishing grounds can affect fishers' decision to fish via expectations for: financial profit, catching fish as food, and/or passing on fishing tradition. Access also affects decisions regarding when and where to fish, which gear to use, and which species to target. Further, restrictions to access may focus fishing in smaller areas, encouraging competition and local depletion in remaining open areas.	Halpern et al. 2004, Allen and Bartram 2008
Tourist season	Price of fish	Tourist season affects the price of fish because prices tend to be higher during high season when the demand is high for certain species.	Expert opinion
Price of fish	Participation in reef fishing	The current price of fish may determine: 1) whether one decides to go fishing, 2) the fishing method used (including location, gear used, and species targeted), and 3) what is done with the catch once landed (kept, given away/shared, sold).	Expert opinion
Employment opportunities	Participation in reef fishing	Fishing activities can be affected by: 1) whether fishers earn income from non-fishing employment, and 2) whether that employment provides them with money above and beyond what is needed to meet regular expenses. Fishers who hold jobs that provide them with extra income, and who have "free time," are able to buy and maintain a fishing boat and fishing gear, and afford the expenses of fishing trips. The fish they catch may be used for household consumption, given away, or sold for extra income to recoup fishing trip costs. Fishers who do not earn sufficient income may have a greater incentive to fish to provide food for their households.	Expert opinion

Variable A	Variable B	Connection between variables	Reference
Fuel cost	Participation in reef fishing	Fuel is the main operating cost incurred in boat fishing on Guam. As fuel prices increase, less of the fuel cost is recovered either when selling fish or when used as food. Above some price for fuel, fishers may decide not to go out fishing because it is not worth the investment in fuel. Therefore, increased fuel costs influence where and how often fishers decide to fish, which gear to use, and which species to target.	Hospital and Beavers 2012
Age	Participation in reef fishing	In general, younger people are more likely to fish than older people, especially physically-demanding activities such as spear fishing.	Expert opinion
Gender	Participation in reef fishing	Men are much more likely to fish than women.	Expert opinion and personal observation
Fishing tradition	Participation in reef fishing	Individuals are more likely to fish if they come from a "fishing family," and/or if other members of their families are fishers.	Expert opinion
Ethnicity	Participation in reef fishing	Individuals are more likely to fish if their ethnicity has been historically engaged in fishing.	Allen and Bartram 2008
Species abundance*	Participation in reef fishing	The overall abundance of marine species may determine: 1) whether one decides to go fishing, 2) the fishing method used (including location, gear, species targeted), and 3) what is done with the catch once landed (kept, given away/shared, sold).	Expert opinion

Summary

Widespread coral reef decline, including decline in reef fish populations upon which many coastal human populations depend, have led to phase-shifts from the coral-dominated systems, found desirable by humans, to algal-dominated systems that provide less ecosystem services, and the loss of functionally important species. Marine resource managers are challenged with providing strategies that can mitigate or prevent such phase shifts and losses and promote the sustainable use of marine resources. Additionally, managers need to take into account the impacts of these strategies on the socioeconomic conditions of the many resource users. To respond to these challenges scientists, managers and policy makers have advocated for an ecosystem-based approach instead of the traditional focus on individual (economically important) species. Ecosystem-based management includes the various dynamic processes that influence an ecosystem, such as hydrology, ecology, biogeochemistry, and human activities.

The management strategy evaluation (MSE) tool commonly used in single species stock assessments for evaluating socioeconomic and ecological tradeoffs of alternative management strategies, has now become more widely applied in multi-species or ecosystem assessments. Ecosystem modelling can include more of the key dynamic processes that drive ecosystems and by using that in an MSE framework provides a better understanding of the socio-ecological consequences of management options and quantifies these tradeoffs.

In this thesis, I review the use of minimal, intermediate and complex coral reef ecosystem models for their suitability of MSE applications. I conclude that complex models can integrate the myriad dynamic processes that govern coral reef ecosystems and are most suitable for MSE, but that minimal and intermediate models are needed to provide the relationships relevant to these dynamics. The main objective of this thesis was to develop a complex model and quantify the effects of watershed management and fishery regulations on coral reef ecosystem services against a backdrop of climate change impacts. For this model development, I selected the Atlantis ecosystem model framework and applied it to a case study of the coral reef ecosystems around Guam to evaluate the performance of alternative management strategies against identified ecosystem metrics..

Following the step-wise approach recommended for Integrated Ecosystem Assessments, I started with a workshop involving local stakeholders (including resource managers and other coral reef users) to identify the (1) overarching goal of coral reef management, (2) ecological indicators of reef status, and (3) socioeconomic indicators of reef users. Using an Ecopath model I identified additional ecosystem indicators of fishing impacts that could also be used as performance metrics in the ecosystem modelling of alternative strategies. Published relationships for key coral reef dynamics were used to apply the Atlantis framework to coral reef ecosystems. I then developed and parameterized the Guam Atlantis

model including 42 functional species groups and the system impacts of eutrophication, sedimentation, fishing and ocean warming and acidification. I validated the model simulations of no local or global stressors, a ‘control run’, following common guidelines for Atlantis development and I validated the added dynamics with published and empirical data or with expert judgement. Due to the absence of time series, model skill assessment was difficult but I could compare biomass of included fish groups after a 1985–2015 simulation with observational data in 2011. These results showed that the model is biased and overestimates various fish groups. However, because the origin of the bias is unknown, rectifying the bias at this point was not possible. Despite this, based on the model validations I concluded that the model was ‘scenario ready’ and suitable for use as a basis of *relative* comparisons of management strategies, allowing for evaluations to be conducted in an internally consistent context.

I applied the model to evaluate the relative performance of management strategies against a set of criteria based on the overall goals identified by local resource managers. These included: (1) improved water quality, (2) increased reef resilience, (3) enhanced fish biomass, and (4) similar or improved fishery landings. Comparing tradeoffs across the selected scenarios showed that each scenario performed ‘best’ for at least one of the performance indicators. The integrated ‘full regulation’ scenario (size and bag limits, marine preserves and no land-based sources of pollution) outperformed other scenarios with two thirds of the performance metrics approaching the criteria at the cost of reef-fish landings. When the effects of climate change were taken into account, the selected scenarios performed fairly equally, but none could prevent a collapse in coral biomass by mid-century under a business-as-usual greenhouse gas emission scenario. To get a better understanding of how these same management scenarios influence the economically important tourism sector and the socially important reef-fishing sector, I coupled the Guam Atlantis model to two human behavior models, one representing divers and the other fishers.

Ecosystem modelling also allows for the comparison of cumulative impacts. Assessments of individual and cumulative impacts of three stressors to reef ecosystems: land-based sources of pollution, fishing and climate change, showed that, to-date, fishing has had the most negative influence on ecosystem metrics that represent reef status, resilience and functioning, and climate change will have the most negative effect in the future most noticeably on the benthic community structure. Cumulative simulations generally showed that the actual effect was slightly less than could be expected based on the sum of their individual effects, keeping in mind that the actual effect size was negative.

With this model now developed, it provides a tool for assessing and quantifying a range of questions in support for EBM for coral reef ecosystems.

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