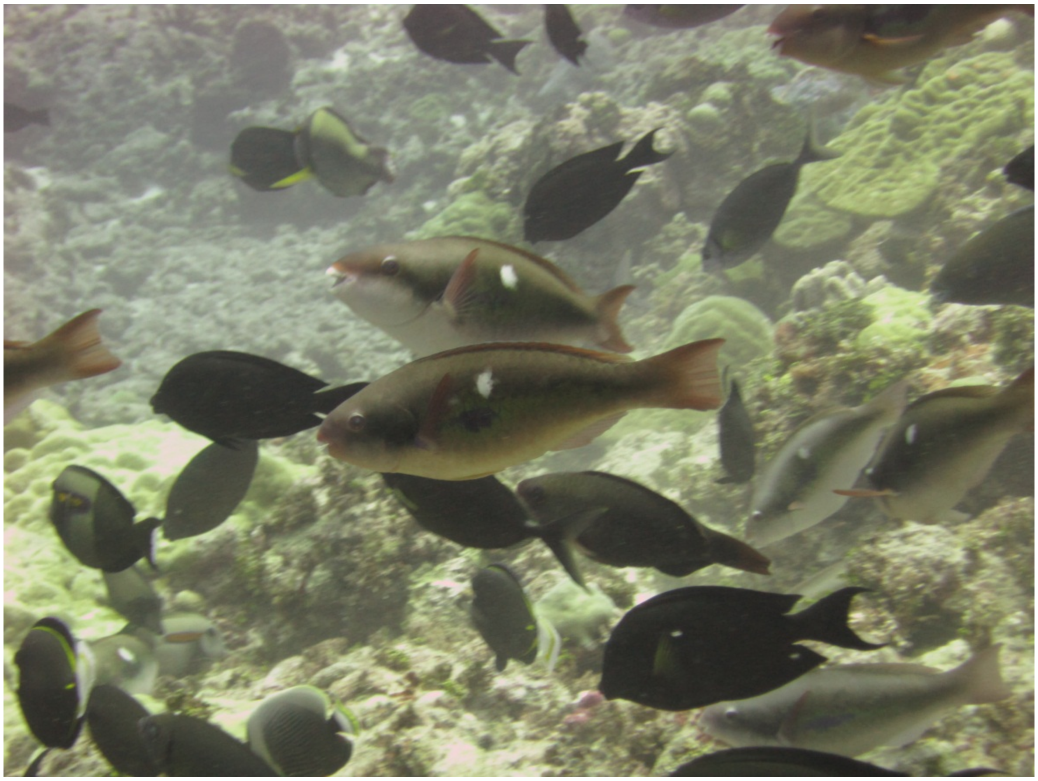
NOAA Technical Memorandum NMFS-PIFSC-43

doi:10.7289/V5B27S76

November 2014

Design and Parameterization of a Coral Reef Ecosystem Model for Guam



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Pacific Islands Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
U.S. Department of Commerce

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> Weijerman, M., I. Kaplan, E. Fulton, B. Gordon, 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, 113 p. + Appendices. doi:10.7289/V5B27S76

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Design and Parameterization of a Coral Reef Ecosystem Model for Guam

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doi:10.7289/V5B27S76

EXECUTIVE SUMMARY

Declines in the fish stocks and degradation of habitats around Guam have serious implications for the residents of Guam who depend on the ecosystem goods and services provided by coral reefs. The planned large relocation of military personnel, their dependents and contractors will have additional impacts on these marine resources. 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 modeling framework integrates physical, chemical, 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.

The Atlantis ecosystem model has successfully been applied to investigate ecosystem-based fisheries management scenario evaluations and ecological questions in Australia and North America. In this report we describe the construction of the Guam Atlantis Coral Reef Ecosystem Model. Atlantis incorporates various submodels that each have their own set of parameters and variables. Here we describe the details of each model component and present the parameterizations of the spatial and ecological submodels. The ultimate goal of the fully developed model is to provide a tool to evaluate management strategy scenarios against a backdrop of climate and ocean change.

The Guam Atlantis model is focused on the shallow (< 30 m) coral reefs fringing Guam and is predominantly based on biological data collected by the NOAA Pacific Islands Fisheries Science Center Coral Reef Ecosystem Division (CRED), fisheries data collected by Guam Division of Aquatic and Wildlife Resources, and water quality data collected by Guam Environmental Protection Agency and CRED. The physical model will be based on model output of a Delft3D model developed by the U.S. Geological Survey and Deltares and will be incorporated in 2015. 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. The physical model forces temperature and water fluxes, and the loading of sediments and nutrients into the shallow waters. We simulate food web dynamics of 42 functional groups: 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. We reconstructed biomass estimates of fish groups based on stock size in marine protected areas to guide the calibration of Guam Atlantis and to evaluate the model's ability to respond to a constant fishing pressure. 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 still under development and will be incorporated in the near future. After additional calibration with the fully developed Atlantis model, we will be able to evaluate alternative management scenarios.

ACKNOWLEDGEMENTS

This report was made possible with funding support from NOAA's Coral Reef Conservation Program and NOAA’s office of Habitat Conservation in support of NOAA’s Habitat Blueprint Initiative. Numerous people helped at various stages of the development of this ecosystem model. Gerry Davis, Jennifer Koss and Valerie Brown helped to get the initial funding. Data and feedback were provided by Ivor Williams, Terry Donaldson, Brett Taylor, Brent Tibbatts, Ed DeMartini, Laurie Raymundo, Dave Burdick, Valerie Brown, Roxanne Miller, Jesse Cruz, Annie Leon Guerrero, Jay Gutierrez, Joseph Cameron, Evangeline Lujan, Alex Kerr, Amanda Desvillers, Jade Delaveaux, Chuck Birkeland, Marc Nadon, Jon Brodziak, Carl Meyer, Adel Heenan, Oliver Vetter, Jamie Gove, Chip Young, Bernardo Vargas-Angel, Molly Timmers, Tomoko Acoba, Amanda Toperoff, Amanda Dillon, Darwina Griffin, Gerry Davis, Penglong Tao, Kimberly Lowe, Peter Houk, Tracey McDole, among others.

ABBREVIATIONS AND ACRONYMS

AFDW	ash-free dry weight
ARMS	Autonomous Reef Monitoring Structure
BGM	Box Geometry
CCA	crustose coralline algae
CNMI	Commonwealth of the Northern Mariana Islands
COTS	crown-of-thorns seastar
CPUE	catch per unit effort
CRED	Coral Reef Ecosystem Division
CSIRO	Commonwealth Scientific and Industrial Research Organisation
DAWR	Guam Department of Aquatic and Wildlife Resources
EPA	Guam Environmental Protection Agency
gh	gear hours
HYCOM	Hybrid Coordinate Ocean Model
IBM	Individual-Based Model
IUCN	International Union for Conservation of Nature
JIMAR	Joint Institute for Marine and Atmospheric Research
MPA	Marine Protected Areas
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmpspheric Administration
PAR	Photosynthetically Available Radiation
PIFSC	Pacific Islands Fisheries Science Center
REA	Rapid Ecological Assessment
SPC	Stationary Point-Count
SST	Sea Surface Temperature
WPacFIN	Western Pacific Fisheries Information Network
USGS	U.S. Geological Survey

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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 (e.g., Green et al., 2009; Jones et al., 2004). 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 (Alvarez-Filip et al., 2009; Graham et al., 2006; Green et al., 2009; Jones et al., 2004).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 (Perry et al., 2012; Graham et al, 2006).

Reef accretion requires energy and if the external aragonite or calcite saturation states decrease as a result of increased atmospheric CO_2, calcification will be reduced 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 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). Increases in water temperature lead to coral bleaching and disease epizootics and have already resulted in repeated mass coral bleaching and mortality events worldwide (reviewed in: Brainard et al., 2011). Current projections about 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-macroalgae competition, early life history development, and coral survival (Baskett et al., 2009; Gilmour et al., 2013). This approach can be met through the protection of a large and diverse herbivorous fish population (Bellwood et al., 2006; Pandolfi et al., 2003) 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 (reviewed in: Brainard et al., 2012). About half of the species that are very susceptible to bleaching are also heavily affected by disease and predation and recovery is slow or absent (Carpenter et al., 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 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 an increased 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, 2001; 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 (Edwards et al., 2010; Melbourne-Thomas et al., 2011; Mumby, 2006; Mumby et al., 2006). One model that integrates various disciplines and addresses agengy mandates is the Atlantis Ecosystem Model (Atlantis). Atlantis was developed by Dr. Beth Fulton at 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., 2004b). 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-modeling 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 report, will be novel.

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 with the military build-up. Ecosystem attributes were identified as "having a sustainable coral reef ecosystem that can recover from the current local

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

(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 trade-offs among ecosystem services of the alternative scenarios.

Objective

In this document, we present the basic formulations and parameterization of the Guam Atlantis Coral Reef Ecosystem Model (Guam Atlantis). 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 trade-offs of the identified alternative management scenarios once the model is fully developed. 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.

GUAM

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

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 2568 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 Hagatna, and between Tumon Bay and Anderson Air Force Base in the north (Fig. 1).

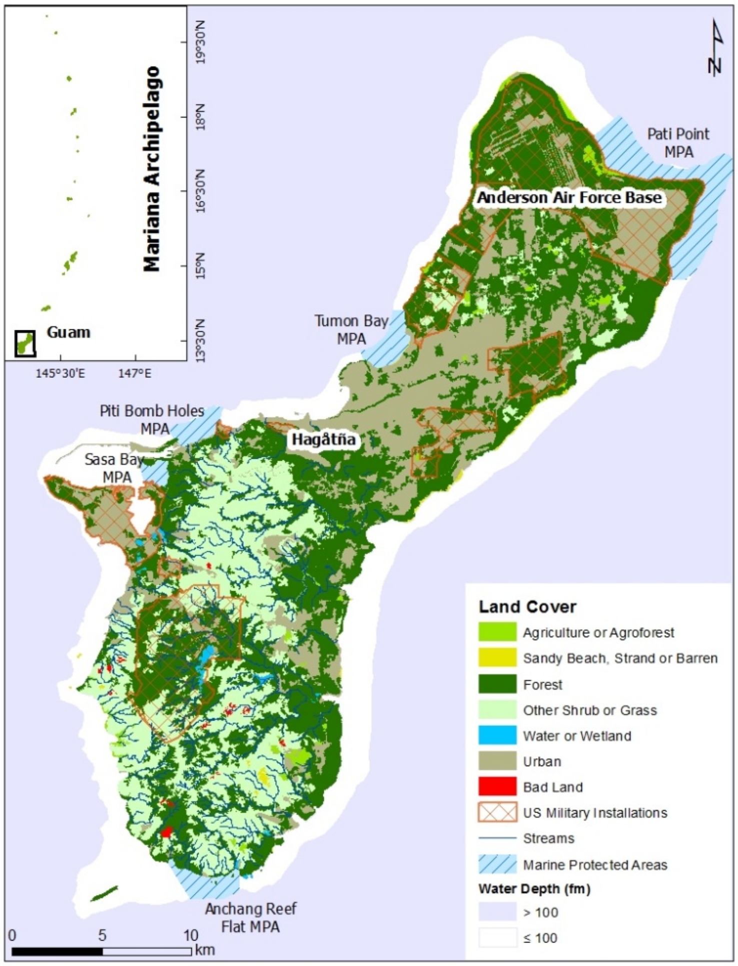


Figure 1.--Location of Guam in the Mariana Archipelago (inset) and land cover of Guam showing the main population centers in the central part of Guam, restricted access areas (military land), the many rivers in the southern part of Guam, and five marine protected areas.

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. 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. 2). Humidity is around 80% and the mean air temperature is 28°C.

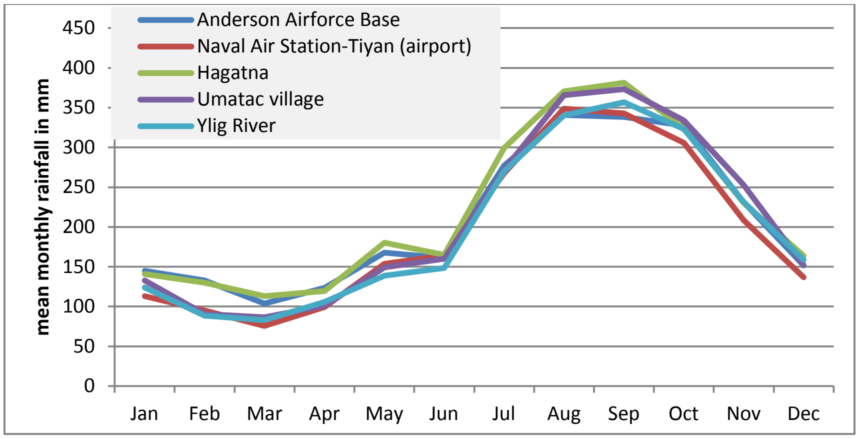


Figure 2.--Mean monthly rainfall at five stations in Guam (1970–2000 data from Lander and Guard 2003). Anderson Airforce Base is in the North of Guam, the airport in the center, Hagatna on the east coat in the center of the island (see Fig. 1), Umatac is on the southwest coast and Ylig is on the southeast coast just below Hagatna.

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. 3).

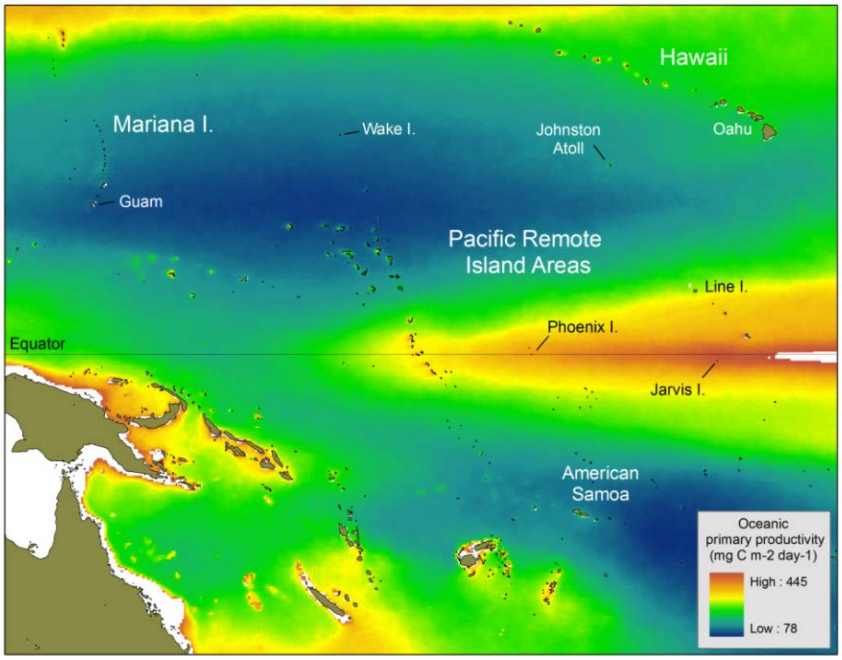
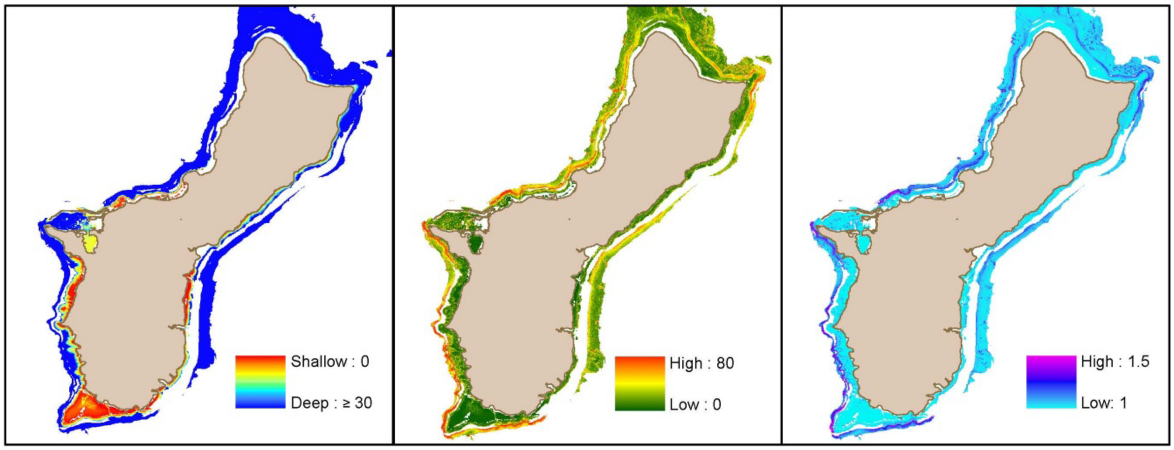


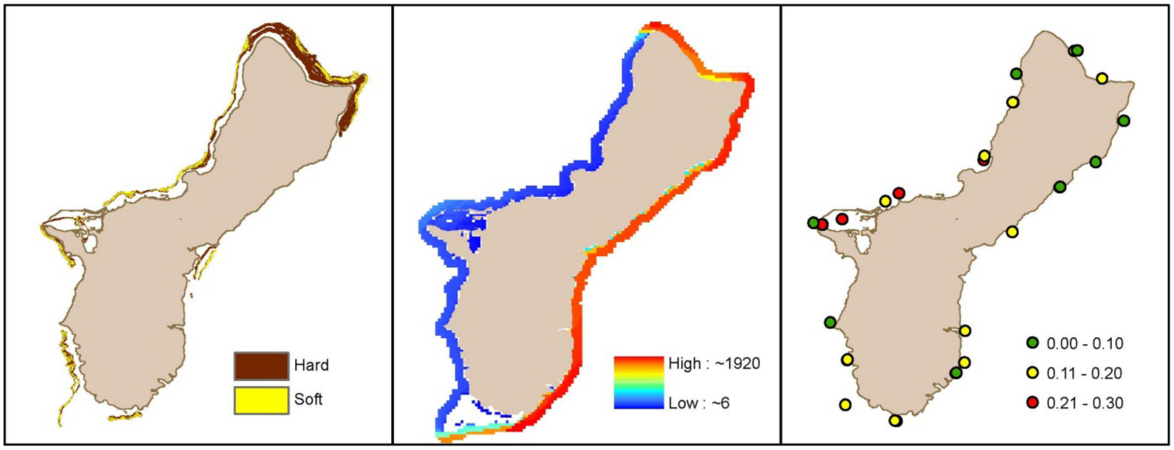
Figure 3.--Oceanic primary productivity derived from satellite imagery (average from 1999–2009). Figure taken with permission from Nadon et al (2012).

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., 2009).

Various environmental and geological variables influence the structure and composition of Guam’s reefs (Fig. 4).



Bathymetry (meter) Slope (degree angle) Rugosity (ratio complex to flat bottom)



Substrate (hard vs. soft bottom) Wave Energy (joule per meter³ (J/m³)) Surface Chlorophyll-a (microgram per liter (µg/L))

Figure 4.--Geological and environmental variables influencing Guam’s reef structure. Data from CRED, wave energy from Peter Houk, unpublished GIS layer. Figure created by Darwina Griffin, JIMAR.

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). These marine resources provide Guam with approximately $127 million per year of which revenues from tourism contributed more than 75% (van Beukering et al., 2007). 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 (Brainard et al., 2012; Burdick et al., 2008). 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 protected areas (MPAs; Fig. 1) and several watershed restoration projects are underway. In 2011, fish biomass in the MPAs 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 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."

CORAL REEF ECOSYSTEM MODELS

Models are an abstraction or conceptualization and simplification of simulated processes. They are not a perfect copy of the processes being modeled but instead are restricted to those properties that the modeler considers essential to represent the real processes or system as accurate as possible. The modeler can emphasize certain processes of a natural system and leave out those not deemed important to describe and influence the system under study. By selecting these particular parts of a natural system the model is, however, limited to what it can describe. A model is also restricted to the available data. For example, if data is collected to represent island-scale changes, one cannot accurately model processes on a smaller spatial scale.

There are various model structures (e.g., deterministic vs stochastic, continuous vs discreet, explanatory vs descriptive). Existing dynamic coral reef models can be grouped in (1) minimal models with few functional groups and dynamic processes, (2) individual or agent-based models (IBM) with more functional groups and dynamic process included than the minimal models, and (3) whole-of-system or end-to-end ecosystem models with multiple (e.g., > 10) functional groups and an integration of ecological, oceanographic, biochemical, and socioeconomic aspects. These model types differ in their main objective and, hence, include different components. A key

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

objective of minimal and IBM models is to increase understanding in specific reef processes, such as, algae-coral-grazer interactions with (Kubicek et al., 2012) and without environmental variables (Mumby et al., 2006), identification of key ecological processes responsible for reef degradation (Fung, 2009) or effects on coral cover as a result of different fishing regimes (Kramer, 2007; McClanahan, 1995). In general, these model types have limited functional groups and dynamic processes simulated and allow for the identification of the dominant stressors to a response of key states (e.g., coral or algal dominance), whether these responses are linear, catastrophic or hysteretic, and which feedback loops cause a particular type of response. The third category of coral reef models is the more complex end-to-end models where functional groups of all or most trophic levels and various dynamic processes are incorporated and which often also have a management component. These model structures allow for a multidimensional view on the interactive effects of multiple stressors on various management objectives but they lack in insight in the chains of interactions and feedback loops that link input and output. Examples are trophic models developed to investigate the fishing effects on coral reef ecosystems (e.g., Arias-González et al., 2004) and agent-based models coupled with difference equation models to represent key coral reef processes developed to evaluate the ecological and economic impacts of management scenarios for a generic reef (Melbourne-Thomas et al., 2011) and for Ningaloo Marine Park, northwest Australia (Gao and Hailu 2011).

Minimal models are usually designed to address research questions, are not always spatially explicit, and often lack the inclusion of socioeconomic components. Complex IBM and end-to-end models are difficult to parameterize, uncertainty and sensitivity analyses are limited, and they have a long development time. However, because they can include the whole ecosystem and socioeconomic components, they are designed to improve our understanding of the interactions and the vulnerabilities between human coastal communities and (coral reef) ecosystems and they can be instrumental for management scenario evaluations (Plagányi, 2007).

The main objectives for developing a coral reef ecosystem model for Guam are to support coral reef managers in selecting appropriate management strategies to reverse the ongoing degradation of the reef systems and the decreases in fish biomass whilst also taking into account the planned military buildup and change in climate and ocean chemistry and to evaluate the effects of these strategies on the socioeconomic factors of the local community. Although there are other model structures simpler in use and development (e.g., Ecopath with Ecosim and EcoSpace), we think that the Atlantis framework will give the best insight into our objectives based on its interdisciplinary set-up with various scales in time and space to allow for a more realistic representation of the dynamic processes and the inclusion of all steps in the adaptive management cycle.

Atlantis Model

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 (Fulton, 2001; Fulton et al., 2004a; Fulton et al., 2004b). A few years later a socioeconomic submodel was further advanced (Fulton et al., 2007). The Atlantis framework has not been applied to coral reef ecosystems and this novel approach is detailed further below.

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 (Fulton et al., 2004a; Fulton and Smith, 2004; Fulton et al., 2003b, 2004b, c; Fulton et al., 2005). 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). The Atlantis framework is very effective for evaluating management strategies as it includes key steps of an adaptive management cycle. It incorporates a range of submodels 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 (marine protected areas), individual quotas (bag limits), 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., Ainsworth et al., 2011; Brand et al., 2007; Fulton et al., 2007; Griffith et al., 2011; Horne et al., 2010; Kaplan et al., 2010; Link et al., 2010). To date Atlantis ecosystem models have been applied in Australia, the east and west coast of the United States, 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., 2011). Trade-offs, 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 stressors 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).

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 (Fulton et al., 2011). 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, 2001; Fulton et al., 2004a; Fulton and Smith, 2004; Fulton et al., 2003b, 2004b,c) 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., 2011). 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.

Modeled Coral Reef Ecosystem Threats

The fully developed Guam Atlantis Coral Reef Ecosystem Model will simulate aspects of the coastal physical oceanography, some of the key coral reef processes, the often synergistic effects of threats to Guam's corals and coral reefs, and the costs and revenues from tourism and fisheries. This integrated model can be a tool to improve management preparedness and for evaluation of response strategies to the main threats to Guam's reefs. As the fundamental component of the ecosystem, corals are the central groups in the Guam Atlantis model and we represent them by taking into account their life history, diet, habitat requirements, responses to threats, and resilience.

Corals provide substrate for colonization by benthic organisms, construct complex protective habitats for a high diversity of other reef-associated species, including commercially important invertebrates and fishes, and serve as food resources for a variety of animals. Massive and branching stony corals are the primary framework builders and a major source of calcium carbonate production of coral reefs. So without the coral colonies, coral reefs will likely cease to exist (Perry et al., 2012). Local resource managers can mitigate the effects of global changes to corals by reducing local threats and increasing resilience (Edwards et al., 2010; Kennedy et al., 2013; Mumby, 2006). Guam Atlantis can evaluate the simulated outcome, for example in terms of coral cover, of alternative management approaches to reversing the downward trend in coral cover and fish biomass, and estimate the economic and cultural effects to fishers.

In the method section 'Functional Group Descriptions and Biology' and 'Model Dynamics' we describe how we included corals and other functional groups simulated in the model and the main coral reef ecosystem processes. In Appendix A, we highlight the various threats to corals and briefly state their responses to these stressors and how we will incorporate them in the model when new code is developed to better represent those dynamics. Below we will describe how we included two key local threats to Guam's reef: reef fishing and land-based-sources of pollution.

Reef Fishing

Harvest of reef fishes alters trophic interactions that are particularly important on structuring coral reef ecosystems including corals-algae space competition and altering recruitment success of corals which is higher when larvae settle on crustose coralline algae than on macroalgae (Dulvy et al., 2004; Mumby et al., 2007). A high species richness of herbivorous species, which have complementary feeding behavior (Bellwood et al., 2006), can reduce the standing stock of macroalgae and increase the cover of crustose coralline algae and live coral cover (Burkepile and

Hay, 2008). These interactions between coral cover, macroalgal cover, and grazers can drive positive or negative feedbacks on the benthic composition (Mumby et al., 2006). Fish biomass on Guam is low compared with the unpopulated Northern Mariana Islands (Fig. 5).

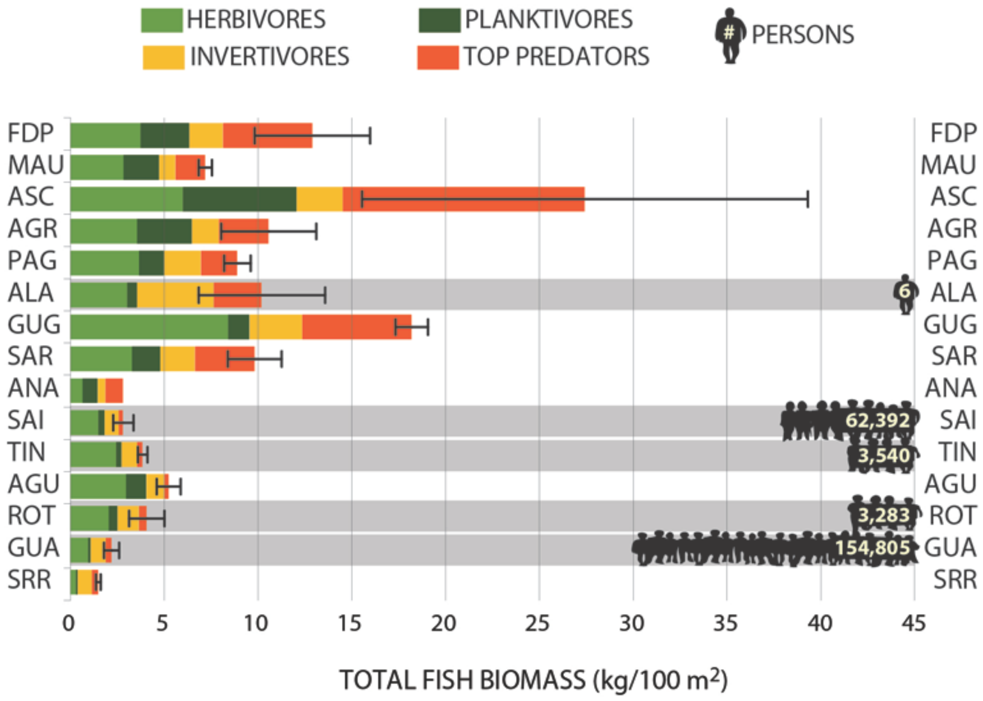

Figure 5.--Comparison of total fish biomass by consumer group around the islands in the Mariana Archipelago related to human population size. The islands are represented from north to south ending with Santa Rosa Bank (SRR), Guam is represented by the three letter code GUA. Data from CRED surveys in 2003, 2005, 2007, and U.S. Census 2010.

In the presented model corals are food for corallivorous, they provide shelter for juvenile fish lowering the availability of those prey fish to predators, and are suspension feeders. They are also habitat for various functional groups so those groups grow better in the presence of corals. The coral-algae-grazer interactions are, at the moment, only modeled through the inclusion of parameters of space competition and habitat dependency (e.g., corals depend on habitats with corals, crustose coralline algae [CCA] or hard substrate). In 2014, corals will be modeled as both suspension feeders and primary producers, and the corals-algae-grazer dynamics will be refined to simulate reef processes more accurately, following the formulations outlined in Melbourne-Thomas et al (Melbourne-Thomas et al., 2011) and Fulton et al (Fulton et al., 2006).

For the simple model version presented here, detailed representation of fishing is also not included. However, to test the productivity of the stocks as part of model calibration, we test a range of fixed fishing mortalities (see ‘Model Tuning and Diagnostics’ under ‘Methods’).

Land-based Sources of Pollution—Sediments and Nutrients

Guam's population has almost tripled since 1960 increasing the pressure on natural resources (Fig. 6). The population is likely to increase more steeply in the near future as a result of the planned military buildup (Kan, 2013).

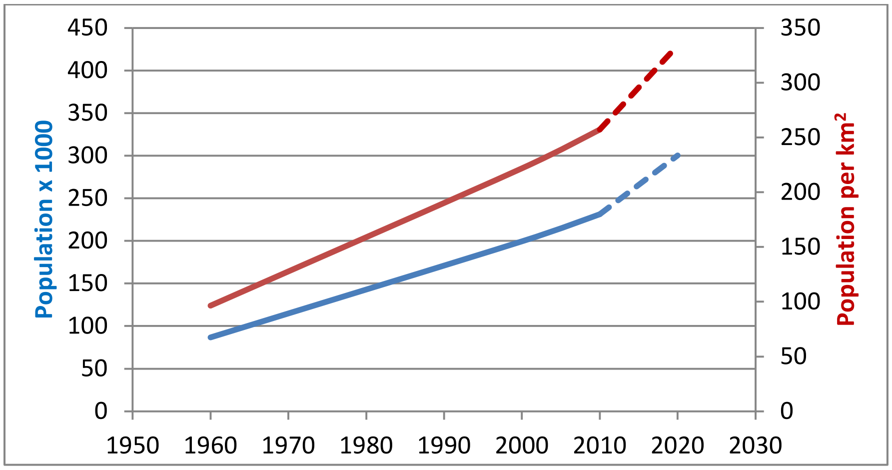

Figure 6.--Population growth in Guam in the last decades (US Census) and future estimated growth.

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 (Birkeland, 1997; Fabricius, 2005; Richmond and Hunter, 1990; Riegl and Branch, 1995). 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).

The main source of terrigenous nutrient and sediment inputs in southern Guam is through surface run-off and in northern Guam through underground seepage. All Guam sedimentation studies showed a sedimentation rate substantially higher than the amounts determined to impact corals elsewhere (Minton et al., 2006; Pastorok and Bilyard, 1985; Riegl and Branch, 1995; Rogers, 1990; Scheman et al., 2002; Storlazzi et al., 2009; Te, 2001; Tetra Tech, 2012; Wolanski et al., 2003a; Wolanski et al., 2003c) suggesting that the benthic community is under long term pressure with potential gradual and long-term declines and shifts in community structure.

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. In future versions of Guam Atlantis, their fate will be modeled with the oceanography submodel developed by Deltares and the U.S. Geological Survey (USGS) for Guam (see under 'Methods', 'Physical Model') and coral-specific code of the relationship between sediment and coral growth and recruitment will be incorporated. Presently, 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.

METHODS

Guam Atlantis Model Structure

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 1). In 2013, we started with the parameterization of the spatial and ecological submodels of Atlantis (Fig. 7). The model's start date is Jannuary 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.

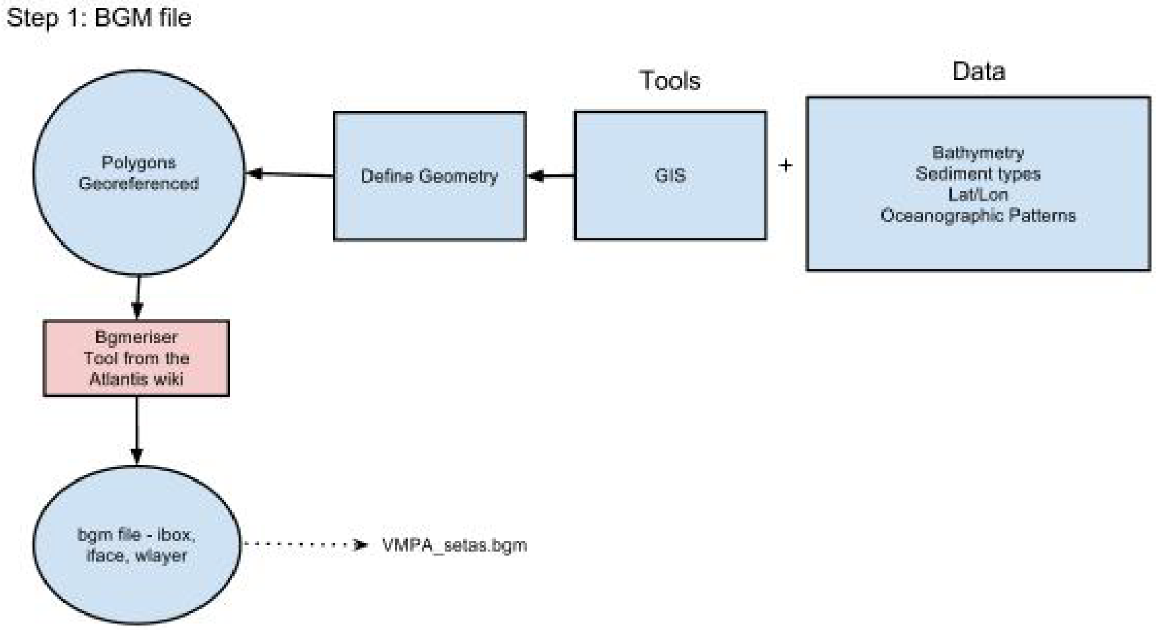

Figure 7.--Schematic overview of the Atlantis framework and requirements for the spatial submodel. BGM is box geometry (created by Carolina Parada and Bec Gorton).

Table 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 DAWR and WPacFIN.

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)
	Autonomous reef monitoring structure (ARMS) deployments for 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	Fishery characterization
	Catch statistics
	Effort statistics
	Catch-per-unit-effort
	Gear selectivity
	Species composition of the catch
	Reconstruction of 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 following 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 habitat area (e.g., coral, CCA, urchins, sea stars, coralivorous 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) and are included in the model (Friedlander and DeMartini, 2002).

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 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 (Marshell et al., 2011; Meyer and Holland, 2005; Meyer et al., 2010) 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 (Afonso et al., 2009; Meyer et al., 2007; Topping and Szedlmayer, 2011). Only oceanic plankton (including planktonic larval stages of coral reef species) and pelagic bacteria are influenced by the hydrology model as passive drifters and are advected by currents and could be exported out of our model boundary.

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; Kendall et al., 2013; Kool et al., 2011). Connectivity studies in the Indo-West Pacific showed that the oceanic conditions there 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. 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. 8). The nearest island in the Mariana Archipelago is Rota (CNMI) at 60 km northeast of Guam and 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 (Gilmour et al., 2013; Jones et al., 2009; Taylor et al., 2012). Genetic studies show that marine

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[3] www.esr.org

larvae are mostly retained within 20–30 km of their natal origin (Almany et al., 2013; Becker et al., 2007; Planes et al., 2009; Vollmer and Palumbi, 2007) 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, 2004]) (Bode et al., 2011; Geange and Stier, 2009).

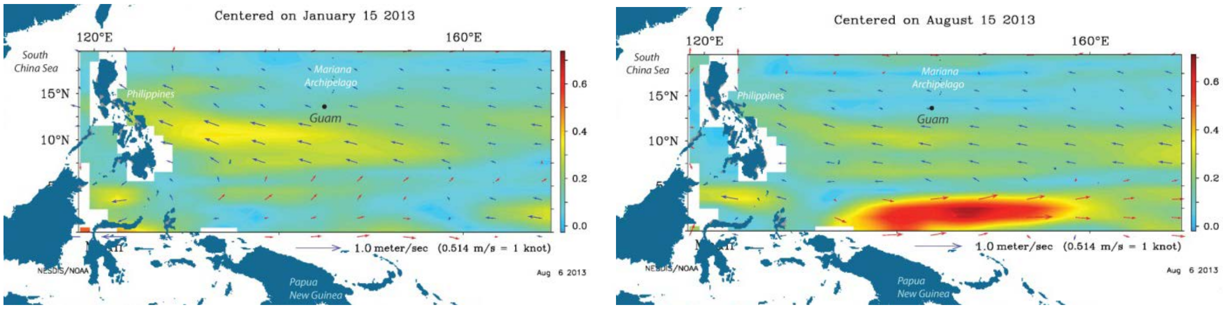

Figure 8.--Long-term (1993–2013) monthly mean large-scale oceanographic current patterns in the west Pacific Ocean (Bonjean and Lagerloef, 2002) for January (*left*) and August (*right*). Figure created by Amanda Dillon, PIFSC CRED

The coastal waters around Guam were divided into 55 polygons (Fig. 9). Polygons were based on similar characteristics of (1) the benthos defined by NOAA National Ocean Service (NOS) Biogeography Branch and updated by Guam DWAR and CRED data (NOAA NCCOS, 2005; Williams et al., 2012); (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 Division of Aquatic and Wildlife Resources 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 boxes (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 sandy bottom and some coral pinnacle clusters (e.g., Western Shoals). Additionally, we had seven static (i.e., biological processes not modeled) boundary boxes connecting all the deeper boxes, and the land mass of Guam as non-dynamic boxes. All boxes 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 boxes 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/

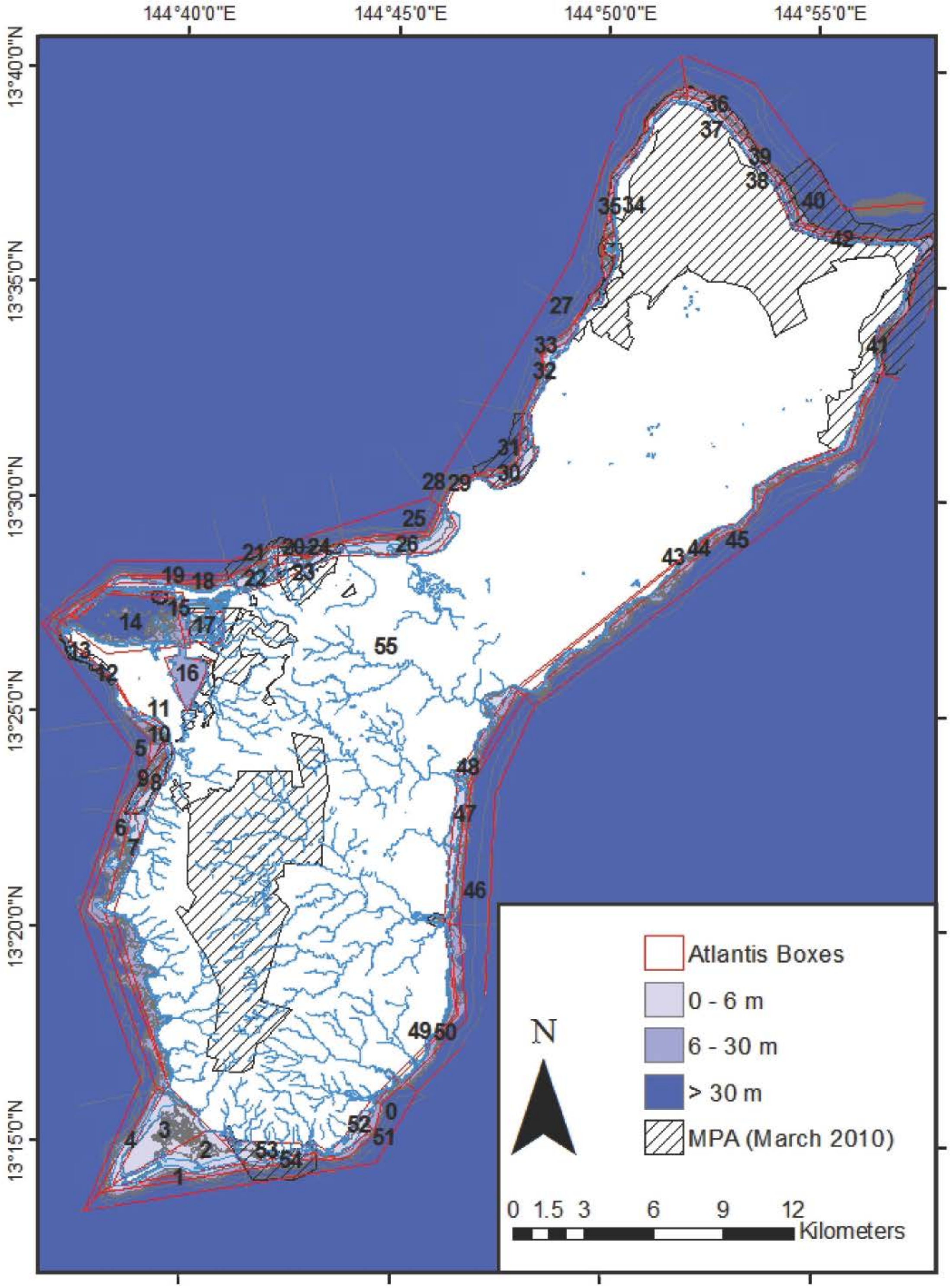

Figure 9.--Bathymetry, river flows, and location of protected areas overlayed with Atlantis polygons (boxes) representing areas with similar benthic and oceanographic conditions.

Physical Model

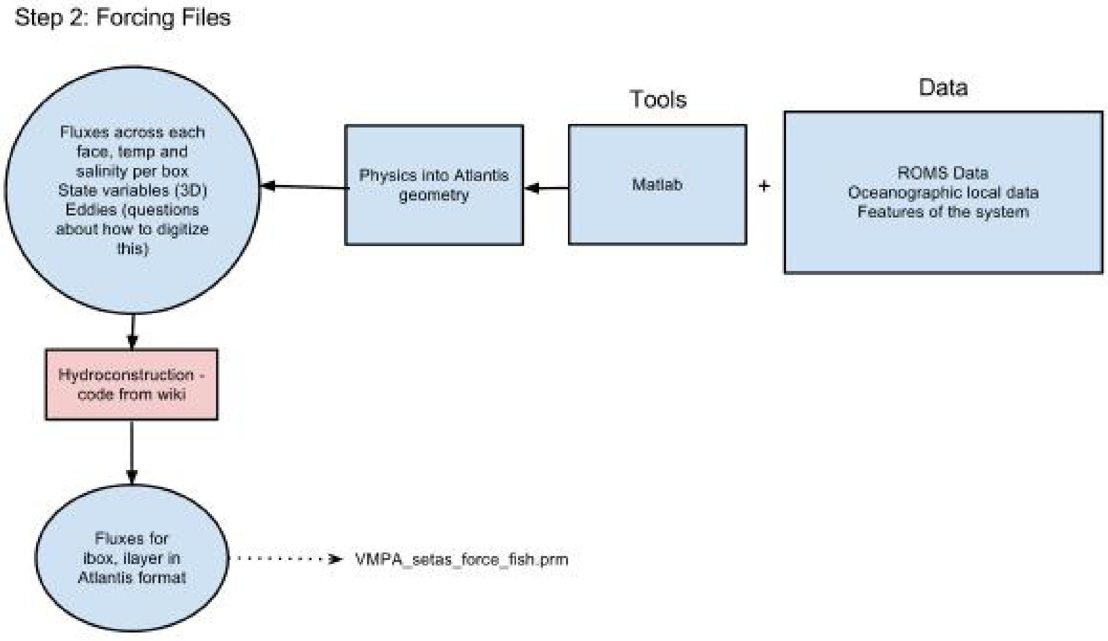

Figure 10.--Schematic overview of the Atlantis framework and requirements for the physical oceanography submodel (created by Carolina Parada and Bec Gorton).

Various data streams went into the physical submodel (Fig. 10); the physical oceanography as a dynamic file and solar radiation, sediment and nutrient inputs as impact files through time series.

Physical Oceanography

At this stage we use dummy data to keep fluxes stable but will incorporate a physical oceanography model once the Delft3D model is fully developed for Guam.

Solar Radiation

Solar radiation data for Guam was not available. However, modeled solar data calculated from January 1, 1991, to December 31, 2010, was 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. 11).

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

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

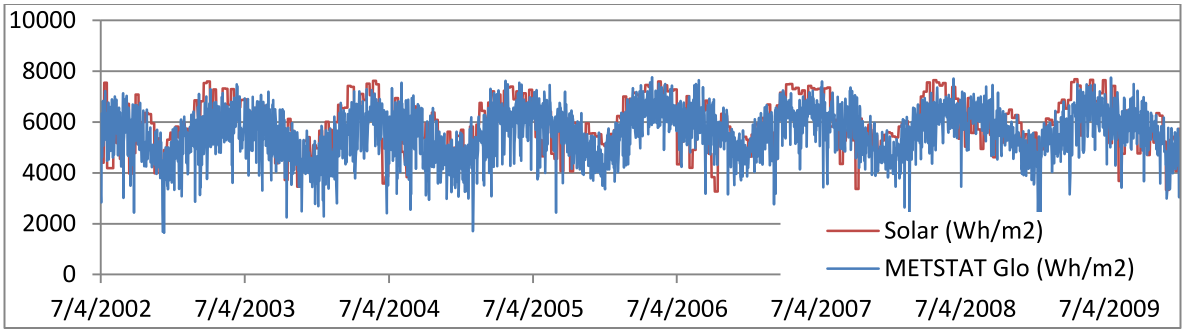

Figure 11.--Solar radiation data calculated from satellite derived photosynthetically active radiation data (red line: NOAA's Coast Watch)[7] and modeled data (blue line: National Solar Radiation Database)[8].

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 the physical oceanography submodel.

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 box (Table 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 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 2), it is noticeable that the slope was an order 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

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

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

[9] waterdata.usgs.gov/nwis

conducted on Guam which concluded that sediment rates in Guam are higher than any other reported values elsewhere (Minton et al., 2006; Storlazzi et al., 2009; Wolanski et al., 2003a).

To calculate the sediment discharge from the three rivers where we had flow rates for, we 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 2) and calculated the daily sediment discharge rate based on the flow rate of those rivers.

Table 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 BoxID**	**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 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.

River	**NOx g/s Slope**	**intercept**	**R^2**	**NH4 g/s 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 we further assumed a similar flow discharge rate as from the Pago, Ylig, and Inarajan River. For all rivers on the west coast with its steeper watersheds, we assume a similar flow discharge rate as from the Umatac, Ugum, and La Sa Fua rivers for the Atlantis boxes south of Apra Harbor and from the Antantano River in the Apra Inner Harbor and north of Apra Harbor (Table 4). Where necessary we reconstructed time series starting at January 1, 1991, and ending at December 31, 2012, by repeating the first or last years.

Table 4.--Summary information on the reconstruction of sediment and nutrient input data in Atlantis boxes along the southern part of Guam.

Atlantis Box Id	Correction (multiplication) factor from # point sources discharging into Atlantis box	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

[*] Two small rivers and cesspools.

Ecological Model

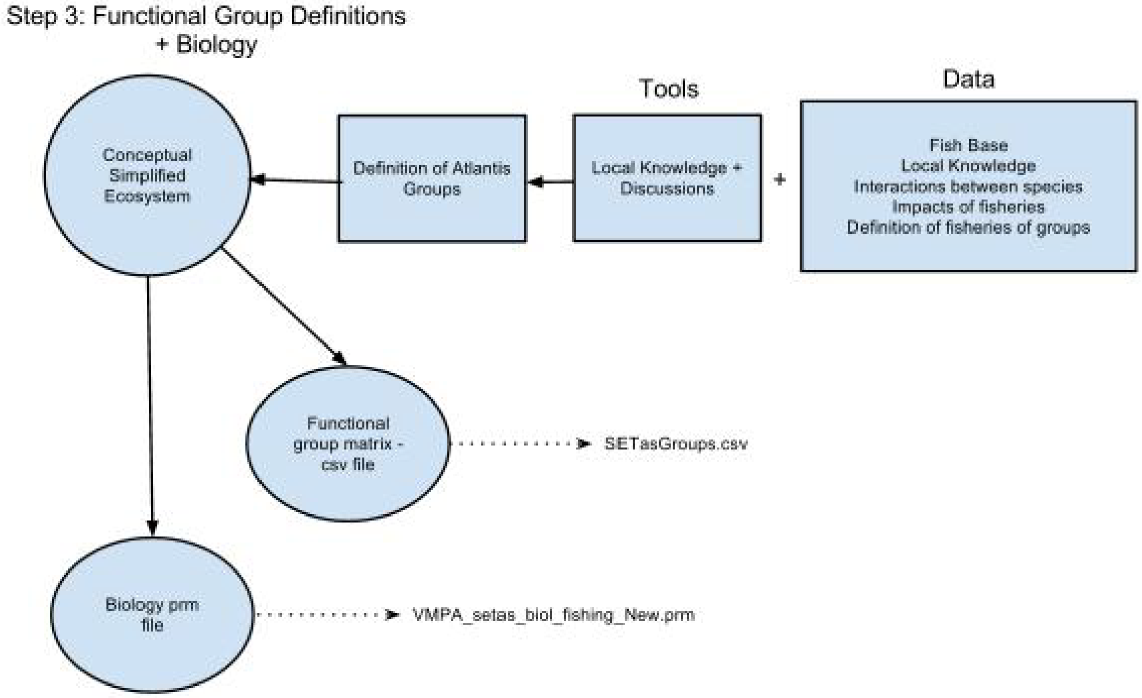

Figure 12.--Schematic overview of the Atlantis framework and requirements for the ecological submodel (created by Carolina Parada and Bec Gorton).

Rationale for Selection of Modeled Functional Groups

A large biological data set was needed for the ecological submodel (Fig. 12). Species and functional groups were included in the model with the aim of representing community dynamics of the nearshore reef, including predominant species sampled by NOAA PIFSC 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 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 (Table 5) 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 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
10	Crustose-coraline algae	CCA		primary producer		reef builder facilitates coral recruitment

No.	Functional groups	Atlantis Code	Species/description	Trophic level	Fishery target sp	Importance of inclusion
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
No.	**Functional groups**	**Atlantis Code**	**Species/description**	**Trophic level**		**Fishery target sp**
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
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

No.	Functional groups	Atlantis Code	Species/description	Trophic level	Fishery target sp	Importance of inclusion
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
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; Ribes et al., 2003). Corals and other filter feeding benthic organisms capture these small particles and so introduce nutrients to the food chain (Genin et al., 2009; Ribes et al., 2003). Phytoplankton make 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 (Genin et al., 2009; 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: 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: Max length, growth rate (k), max 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; Green et al., 2009; Jennings et al., 2001) and discussions with resource managers and coral reef fish specialists (Brett Taylor, University of Guam; Terry Donaldson, University of Guam; Ed DeMartini, PIFSC; Ivor Williams, PIFSC, and participants at the Guam workshop held in November 2012 [Weijerman and Brown, 2013]).

Coral reefs in Guam, as elsewhere in the world, exhibit phase shifts from coral to macroalgal dominance (Friedlander et al., 2008; Mumby et al., 2006). 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 (Bellwood et al., 2006; Steneck, 1988) 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 (Mumby, 2006; Williams et al., 2001), 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; Comeros-Raynal et al., 2012; Ong and Holland, 2010).

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 fisherman 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 (Donaldson and Dulvy, 2004) 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. Because of their 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 5) were checked based on various published sources (e.g., 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.

Data Sources

Data sources for the biological parameters and biomass and abundance data came predominantly from monitoring studies conducted by NOAA PIFSC CRED. These data were supplemented with data from Guam DAWR, Coastal Management Program, and University of Guam monitoring programs, peer-reviewed literature, technical reports, theses, and expert opinion. Below, for each functional group we provide the data sources and assumptions. Fish and benthic survey methods used by CRED are detailed in (Brainard et al., 2012; Richards et al., 2011; Williams et al., 2012) and are only briefly described here. The majority of data came from extensive fish and benthic surveys conducted by CRED in 2011 (Fig. 13) using a stratified random sampling design incorporating 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

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[10] www.fishbase.org

previous years were used to supplement data in Atlantis boxes not covered by 2011 surveys (Brainard et al., 2012).

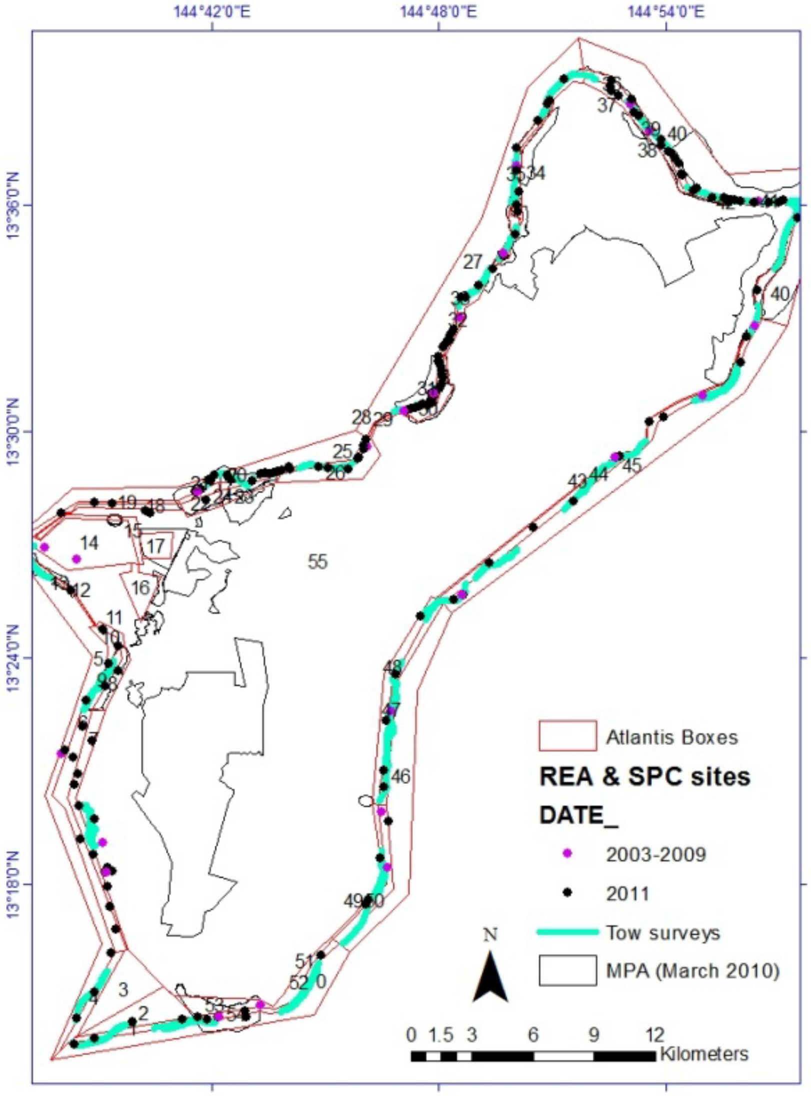

Figure 13.--NOAA’s Coral Reef Ecosystem Division conducts bi-triennial surveys around Guam. The black dots represent the 133 biological survey sites visited in 2011 whereas the red dots represent the survey sites visited in 2005, 2007, and 2009. The blue slugs indicate the trajectory of towed-diver surveys from 2005 to 2011.

Horizontal distribution of species among the Atlantis boxes came from the 2011 visual surveys 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 corrected those values by decreasing the numbers in the shallow boxes and scaling them based on the results from visual surveys. For instance, sharks were predominantly seen in boxes, 31, 47 and 51 so we increased the percentage for those boxes while decreasing it for others. Vertical distribution in the water column and habitat preference came from expert opinion (Dave Burdick, Coastal Management Program, Guam; Val Brown, NOAA Pacific Islands Regional Office, Guam; Terry Donaldson, University of Guam, Guam; Ivor Williams, NOAA Pacific Islands Fisheries Science Center, Hawaii) and literature on habitat affinity (Beukers and Jones, 1998; DeMartini and Anderson, 2007; DeMartini et al., 2010; Eriksson et al., 2012; Friedlander et al., 2007a; Gratwicke and Speight, 2005; Johansson et al., 2012).

Parameters for the dynamic files (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) (Table 6) and for vertebrates they are calculated as outlined in section “Biomass dynamics”.

Table 6.--Invertebrate functional groups and basic life history parameterization. Growth, clearance, and mortality rates are postcalibration values. Initial life history parameters were based on Weijerman et al. (2013).

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	0.06	0.006		
CRN	Massive Corals	0.03	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*), L_{inf}, age at first maturity, pelagic larval duration, maximum age) for fish and sharks were obtained from literature (Choat and Axe, 1996; Choat et al., 2006; Choat and Robertson, 2002; Gust et al., 2002; Hamilton et al., 2008; Hart and Russ, 1996; Ishihara and Tachihara, 2011; Longenecker and Langston, 2008; MacDonald, 1981; McIlwain et al., 2009; Rhodes et al., 2011; Sadovy et al., 2003; Schluessel, 2008; Sudekum et al., 1991; Taylor, 2012; Victor, 1986; Wellington and Victor, 1989; Wilson and McCormick, 1999), empirical formulas, FishBase, and expert opinion (Brett Taylor, Ed DeMartini, Terry Donaldson, Marc Nadon). In absence of data for natural mortality (*M*) we used an empirical relationship (Pauly, 1980):

$$log(M) = -0.066-0.279*LOG(L_{inf})+0.654*LOG(k)+0.463*LOG(T) \quad 2$$

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 degrees centigrade and was obtained from CRED 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:

$$t_{\max} = ln(0.01)/-M \quad 3$$

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 2 (table 7).

Table 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 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 B 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 C includes life history data of all abundant vertebrate species and 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.

Detritus (DL DR, C)

Detritus represents the pool of dead organic material, including particulate and dissolved organic matter. Detritus standing stock was estimated based on the suspended solid concentration monitored in marine waters around Guam by the Environmental Protection Agency and War in the Pacific National Historical Park (data obtained from Guam EPA). The wet weight (g/m^3) of the suspended solids was converted to mgN/m^3; 80% of the resulting value was allocated to refractory detritus (cohesive, small particles) and the remaining 20% to labile detritus (easily disassociated, small particles). Carrion was calculated by Atlantis. Total detritus in the sediment layer was assumed to be 100 g/m^3. Missing values for Atlantis boxes were assumed to be equal to adjacent boxes of the same depth range (either shallow or deep).

Pelagic and Benthic Bacteria (PB, BB)

Bacteria were divided into a pelagic functional group and a benthic functional group. Bacteria are amongst the most efficient consumers with a mean gross growth efficiency of approximately 40% (Cole et al., 1988). Bacteria remineralize organic materials and convert some organic material into bacterial biomass (Jennings et al., 2001).

From water samples taken at four sites around Guam the mean pelagic bacteria concentration was estimated and converted to mgN/m^3 resulting in 0.24 mgN/m^3 (SD 0.04) (CRED data). Estimates suggested that the concentration in Apra Harbor (Box 14) was 33% higher than along the northeast coast of Guam (Box 41) but because we only had samples from 1 time period, we assumed that the mean was a better representation of the concentration around the entire island and at both depth layers.

Data on benthic bacteria were not available for Guam so we used estimates from a reef system in Curaçao, Netherlands Antilles (Scheffers et al., 2004) which gave us 0.40 mgN/m^3. Again we assumed a uniform distribution and that they mainly occupied the sediment layer. For the two water layers we added an assumed concentration of 0.1 mgN/m^3. Both bacteria groups were assumed to consume refractory detritus.

Phytoplankton (PL, PS)

Phytoplankton data were calculated from chlorophyll-*a* data by applying a constant Redfield carbon to nitrogen ratio (7). This C:Chl ratio varies as a result of complex effects of changes in light, nutrients, and temperature (Wang et al., 2008). As our model domain only includes the euphotic zone and is generally well mixed, we assume a constant C:Chl ratio. Satelite-derived and in-situ data showed a strong seasonal pattern with higher values in the wet season (Jul-Dec) than in the dry season (Fig. 14).

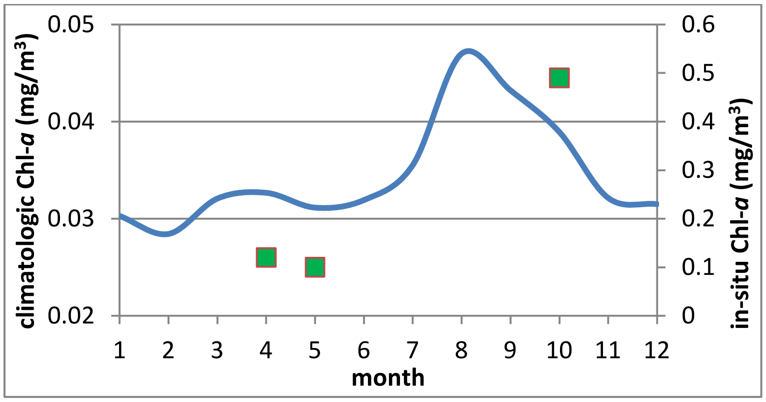

Figure 14.--Seasonal changes in chlorophyll concentration. Climatologic data is satellite derived encompassing 2002–2010 and in situ data came from surveys conducted by CRED in 2005, 2007, 2009, 2011.

We modeled two phytoplankton groups, large and small phytoplankton. Most studies use satellite derived time series of chlorophyll but we also had site-specific chlorophyll data from April, May, and October (CRED data). Satellite time series of chlorophyll-*a* concentration in open ocean water around Guam for 2002–2011 were obtained from the Moderate Resolution Imaging Spectroradiometer. Island-specific data sets were derived by taking all data pixels within an area bounded by 0.25° perpendicular to the island's 30 m isobaths to avoid the confounding effects of reflection in shallow water (Gove et al., 2013). These data showed annual mean chlorophyll-*a* concentration of 0.033 mg Chl-*a*/m^3 (SE 0.002) whereas in-situ water samples taken above a reef at the surface (1 m) resulted in an annual mean of 0.28 mg Chl-*a*/m^3 (SE 0.02) (CRED data, average of dry [April, May] and wet [October] season). We assumed that the in-situ samples were a better representation of the reef chlorophyll concentration and used those numbers in our further analyses of chlorophyll for all the Atlantis boxes.

Chlorophyll-*a* concentration at the surface (10 m) was 4 times higher during the wet season (0.42 mg Chl-*a*/m^3) compared to the dry season (0.10 mg Chl-*a*/m^3). At depths of 10–30 m this difference was slightly less with 0.35 mg Chl-*a*/m^3 in the wet season and 0.14 mg Chl-*a*/m^3 in the dry season (CRED data). For our calculation of phytoplankton, we used the annual surface mean chlorophyll-*a* values for the shallow Atlantis boxes and the 10-30 m averages for the deep boxes. We assumed that the proportion of large versus small phytoplankton biomass was 0.3:0.7 (Wang et al., 2008).

Zooplankton (ZC, ZH, ZD)

We divided zooplankton into three functional groups: carnivorous, herbivorous, and demersal or benthic zooplankton. Oceanic and demersal zooplankton data was difficult to obtain. For the oceanic carnivorous zooplankton, we used field data collected in April 2010, 33 km east of Guam (Suntsov and Domokos, 2013). These samples revealed a total micronekton concentration of 0.2-0.4 g/m^2 which was made up of fishes (0.06-0.1 g/m^2), euphausiid shrimps (0.08-0.16 g/m^2), myctophids (0.04-0.08 g/m^2), decapod shrimps (0.02-0.04 g/m^2), and predatory fishes (0.05 g/m^2) and a very low concentration of cephalopods (0.04 g/m^2). We used the mid-range of the total value as biomass concentration for our carnivorous zooplankton group assuming a mean depth to the reef of 10 m to get a biomass per volume concentration (0.03 g/m^3). However, since phytoplankton levels are 4 times higher in the wet (Aug-Dec) season compared to the dry season (based on CRED chlorophyll-*a* data), we assume that zooplankton levels will be four times higher as well giving us an annual mean biomass concentration of 0.08 g/m^3 or 0.70 mgN/m^3.

Zooplankton composition differs for the major zooplankton groups with herbivorous copepods making up the highest contribution in the total zooplankton abundance (93%-96%) but in biomass this contribution is 30%-36% (Heidelberg et al., 2010). Therefore, we assumed that the total oceanic zooplankton was 0.11 g/m^3 consisting of 0.08 g/m^3 carnivorous zooplankton and 0.036 g/m^3 herbivorous zooplankton (0.32 mgN/m^3). This estimate compares reasonably well with an estimate from oceanic zooplankton around Palau of 0.30 g/m^3 (Hamner et al., 2007) which is located in slightly more productive waters (Fig. 3, Palau is located southwest of Guam).

We then adjusted these values with the tenfold difference between open ocean and coastal water found for phytoplankton (based on CRED Chlorophyll-a data) resulting in a biomass of 7.0 mgN/m^3 for carnivorous zooplankton and 3.2 mgN/m^3 for herbivorous zooplankton.

Diet of carnivorous zooplankton consists mostly of herbivorous zooplankton, large and small phytoplankton, pelagic bacteria, and refractory detritus (Fauchald and Jumars, 1979). Diet of herbivorous zooplankton was assumed to be small phytoplankton, some large phytoplankton, pelagic bacteria, and refractory detritus. We further assumed that the distribution of herbivorous and carnivorous zooplankton was the same as that of phytoplankton.

Large-scale increases in zooplankton abundance over the reef are observed during the night, with many animals emerging from the substrate (Alldredge and King, 2009) and higher concentrations of zooplankton emergence per meter with increased substrate complexity (Porter and Porter, 1977). This demersal zooplankton consists of larvae or adult inverts (mainly crustaceans dominated in numbers by copepods) that reside on or within the reef during the day and migrate into the water column at night (with the highest density at first-quarter moon) and epibenthic zooplankton that spend part of their time in close proximity to or on reef surfaces and exhibit a swarming behavior (Heidelberg et al., 2004). Their biomass could be up to a factor 21 higher than that of the surrounding ocean (Alldredge and King, 1977). We assumed a demersal zooplankton biomass of 15 times the surrounding ocean or 14.5 mgN/m^3.

As the abundance of demersal zooplankton varies with the benthic substrate and increases with live coral cover (Grimm and Clayshulte, 1981), we assumed that the mean demersal zooplankton biomass (14.5 mgN/m^3) was associated to an area with a mean coral cover (12.8%, CRED data). We then adjusted the zooplankton biomass for each Atlantis box based on the deviation of mean coral cover; e.g., if coral cover in box A was half the mean coral cover (6.4%), demersal zooplankton was also half (7.2 mgN/m^3) and if coral cover was twice as much, we assumed the demersal zooplankton biomass was also twice as high. Our estimate was much higher than estimates in Discovery Bay, Jamaica (4.5 mgC/m^3, 0.8 mgN/m^3; Heidelberg 2004) and in Conch Reef, Florida (8.1–21.4 mgC/m^3, 1.4–3.8 mgN/m^3; Heidelberg et al., 2010) however, coral cover is much lower in the Caribbean (Aronson and Precht, 2000). Nevertheless, the model would greatly improve with better estimates for demersal zooplankton.

Diet of demersal zooplankton consists of herbivorous and carnivorous zooplankton, large phytoplankton, benthic bacteria, and refractory detritus (Alldredge and King, 1977; Chardy and Clavier, 1988; Genin et al., 2009).

Cephalopods (CEP)

This functional group includes all species of octopus (e.g., *Octopus cyanea*, *O. ornatus*, *O. teuthoides*) and squid. Biomass data from surveys were unavailable for Guam but we did have the annual landings from reef fishery statistics. Octopus is a sought after species both for bait and as food and the mean annual landing was 1422 kg/y for the 2001–2010 period.[11] By dividing the yield over the assumed fishing mortality (0.02/y) we got a standing stock of 71.1 metric tons in Guam or 1.001 g/m^2 (8.78 mgN/m^2). This estimate compares well with estimates from reef systems in Hawai`i (Weijerman et al., 2013) and Indonesia (Ainsworth et al., 2007). We assumed an equal distribution of cephalopods around Guam.

The diet of cephalopods consists of mainly crab larvae (Van Heukelem, 1976), other benthic mobile invertebrates, cephalopods, and juvenile and small fishes (Collins et al., 1994; Quetglas et al., 1999).

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[11] http://www.st.nmfs.noaa.gov/st1/recreational/queries/index.html

Benthic Substrate Cover Estimates: Macroalgae (MA), Turf algae (TRF), Crustose Coralline Algae (CCA)

Site-specific benthic cover was calculated through image analyses of photoquadrats along a 25-m long transect. Surveys were conducted at 133 random stratified sites around Guam in 2011 (Williams et al., 2012) and averaged per Atlantis box. For those boxes for which we did not have 2011 surveys, we used either towed-diver data (box 13) or data from prior years (box 14 and 52) or we assumed a similar benthic composition as another box (boxes 12, 15, 28, 29) based on the NOAA Habitat Map (NOAA NCCOS, 2005) or used the categories from the NOAA Habitat Map (box 16 and 17). To convert the cover data to biomass data for algae we used estimates from a reef system in Hawai'i (Smith et al., 2001). These estimates were subsequently corrected for their percentage cover and the proportion of hard substrate per Atlantis box. For macroalgae we used the "high turf" category from Smith et al. (2001) and multiplied that by 1.5 to adjust for the difference in height between high turf and macroalgae. For benthic filter feeders and corals, see the sections below.

Macroalgae include all species of macroalgae (including calicified macroalgae such as *Halimeda*) and cyanobacteria. Island-wide mean cover of macroalgae was estimated at 24.7%. Turf algae include all algae less than approximately 1 cm in length. Island-wide mean cover of turf algae was estimated at 39.4%. CCA include all species of crustose coralline algae. Island-wide mean cover of CCA was estimated at 8.9%.

Benthic Filter Feeders (BFF)

This functional group includes sessile filter feeders except for hard corals, such as, sponges, zooanthids, tunicates, hydroids, soft corals, and bivalves including giant clams. Spatial data on all these categories were very limited with island-wide survey data on soft coral cover from stratified random survey sites and giant clam densities from towed-diver data at one depth contour (approximately 10 m, both CRED data). As a proxy for this functional group we used the soft coral cover. To convert cover data to biomass we used the biomass of sponges from an inner reef in the Great Barrier Reef (Wilkinson and Cheshire, 1990) and corrected that for cover data and the proportion of hard substrate per Atlantis box. The resulted estimate was multiplied by 3 to account for the other categories of benthic filter feeders

Reef eroders (such as hetrotrophic endolithic sponges or other coelobites) are more prevalent in nutrient rich waters (Hallock 1988, Brock and Brock 1977). Opitz (1996) estimated the biomass of suspension feeders to be much larger than any other hetrotrophic group with a total wet weight of 1046 g/m^2 of which sponges made up 76%. So clearly, nutrient concentration has an immense impact on endolithic sponge biomass. In general, cryptic surface area is estimated to be 1.5–8 times the planar surface area of a reef (Richter et al., 2001; Scheffers et al., 2004) allowing for this high abundance. To account for these higher densities of filter feeders in nutrient rich areas, we assumed a cover of 9% in the harbor—slightly less than the estimated 12% in the Inner Harbor (Smith et al., 2009).

The diet of benthic filter feeders consists of mostly small phytoplankton, some large phytoplankton, all three groups of zooplankton, benthic and pelagic bacteria and refractory detritus (Fabricius and Dommisse, 2000; Ribes et al., 2003; Ribes et al., 2005; Wilkinson and Cheshire, 1990; Yahel et al., 2003).

Corals (CRS, CRN)

Although there are more than 375 coral species identified in Guam (Paulay, 2003), we only included the 107 species/genera that were observed during survey analyses. The majority of these coral species had a massive or encrusting growth form represented by massive *Porites* sp., *Leptastrea* sp. (particularly *L. purpurea*) *Montipora* sp., *Astreopora* sp. and *Favia* sp. (CRED and DAWR data). The most abundant branching or columnar species were *Porites rus*, *Pocillopora* sp. and *Acropora* sp. Branching species have overall a faster growth rate than the massive or encrusting growth forms which are important reef building species (Hughes et al., 2012). Branching corals also provide better protection for small fish species, recruits, and invertebrates (DeMartini et al., 2013; DeMartini et al., 2010; Enochs, 2010) whereas tabular corals are favored by larger fish (Kerry and Bellwood, 2012). Coral species also have different susceptibilities to ocean warming (Marshall and Baird, 2000; McClanahan et al., 2007), disease (Palmer et al., 2010; Ruiz-Moreno et al., 2012) and land-based sources of pollution (LBSP) (Fabricius, 2005; Raymundo et al., 2011). In general, species that invest highly in immunity have less energy for growth and reproduction. Based on these different characteristics, separating the corals into two functional groups reflects reality better than aggregating all corals into one group (Clancy et al., 2010).

In the model, we represent corals as coral holobiont being facultative producer/heterotroph; the holobiont is the collective community of coral host and its metazoan, protest, and microbial symbionts. We separated the corals based on their morphology and shelter capacity into branching or sheltering corals and massive/encrusting or non-sheltering corals (Appendix D). To convert the cover data to biomass data we used the mean value (30 g/m^2) of global reef estimates that ranged from 10 to 100 dry weight g/m^2 (Crossland et al., 1991) and converted that to mgN/m^2 by dividing it by 5.7 (adapted Redfield ratio). This estimate was subsequently corrected for coral cover and the proportion of hard substrate per Atlantis box.

Besides their phototrophic dependence, corals are also heterotrophs and have been shown to feed on a range of food types, e.g., zooplankton , microzooplankton, bacteria, sediment and suspended particulate matter, the latter comprising components from all particle types (Bak et al., 1999; Palardy et al., 2006; Palardy et al., 2008).

In the model, corals not only provide food (see below), they also provide refuge for all juvenile fish and for all adult fishes except the piscivores and the large herbivores (humphead wrasse, large bodied-parrotfish, bumphead parrotfish).

Benthic Detritivores, Benthic Carnivores and Benthic Meiofauna

Cryptofauna associated with the reef framework are important components of the reef as they capture otherwise transient organic matter, efficiently recycle nutrients, and convert organic matter into readily available biomass for the trophic pathways and so support the high biomass accumulation (Froelich, 1983; Richter et al., 2001; Scheffers et al., 2004; Yahel et al., 2006). Paulay et al (2003) have reviewed the marine biota of Guam and identified more than 8000 species with almost a quarter belonging to the Mollusca (table 1 in Paulay et al., 2003).

The morphology of reef substrates is of paramount importance to organisms that intimately associate with them; in general, the surface area and porosity of coral rubble is a key factor in predicting infaunal density. For example, cryptic metazoans in *Porites damicornis* have been estimated at 4.2 g/l coral skeleton (Enochs and Hockensmith, 2008). Even though abundant cryptofauna can be found in dead coral substrates, in the absence of reef accretion, bioerosion will lead to framework destruction and ultimately to the collapse of the cryptofauna populations as the structures lose their sheltering capabilities.

Live corals provide food (tissue, mucus, fat-bodies, gametes) and shelter to crypto- and epifauna (Guest, 2008; Knudsen, 1967; Rotjan and Lewis, 2008; Stimson, 1990). The abundant food sources may be responsible for the high biomass of these communities (Enochs and Hockensmith, 2008). Larger size coral colonies harbor a disproportionally high abundance and biomass of crytofauna compared to the same colonies of smaller sizes making them very important in supporting cryptofauna communities. Massive corals support mostly endolithic fauna whilst branching corals are more often colonized by epilithic, mobile, and sessile invertebrates (Shirayama and Horikoshi, 1982). Richness and abundance of cryptic invertebrates are higher in substrates with greater structural complexity; this is especially true when a reef framework is compared with extremely eroded substrates such as sand (Bailey-Brock et al., 2007; Brander et al., 1971). However, on a gradient from lightly eroded to highly eroded substrate to rubble, diversity increased (Enochs and Hockensmith, 2008; Enochs, 2010), hence, degradation increases biodiversity up to a point. The lower diversity on live corals is understandable as live corals have effective defense mechanism resulting in a community that has adapted to survive and thrive in living corals. The majority (83%) of these animals were arthropods of which 77% were opportunistic omnivores (Enochs, 2010). The highly diverse community composition on dead coral substrate is more evenly spread between phyla—echinodermatids (36%), arthropods (33%) mollscs (25%)—and feeding guilds (Enochs 2010). This high diversity on dead coral substrate can also be explained by the fact that these substrates provide a greater diversity of food resources (algae, sessile suspension feeders) and retain more sediment (although too much sediment can clog up cavities or reduce light and could be detrimental to the cryptofaunal community (Choi and Ginsburg, 1983), which make them attractive to a diverse array of feeding guilds (Enochs, 2010).

Estimation of crytofaunal community composition

We analyzed the community composition and abundance data collected from four Autonomous Reef Monitoring Structures (ARMS) deployed around Guam from 2009 to 2011.[12] However, species that burrow into the calcium carbonate structure (such as polychaetes) are underrepresented in the ARMS data and sessile invertebrates were not yet analyzed. Therefore, all numbers are preliminary minimum numbers and will likely increase with additional analyses.

The average density was 918 individuals per ARMS unit with a community composition of 51.4% arthropods, 37.2 % mollusks, 5.9% echinioderms and 2.4 % annelids, which is comparable to that of dead coral substrate (see Fig 2.5 in (Enochs, 2010)). The biggest discrepancy between the ARMS data and the data from Enochs (2010) was in the annelids of which polychaetes can make up 12% of the infaunal biomass (Brock and Brock 1977) and can total 43,500 individuals/m^2 (Kohn and White 1977). Species collected from the ARMS units were grouped in the three functional groups (benthic carnivores, benthic detritivores, benthic meiofauna) according to their diet (Choy, 1986; Fauchald and Jumars, 1979; Hoover, 1999; Jernakoff et al., 1993; Malaquias et al., 2004; Mayfield et al., 2000; McLaughlin and Bailey-Brock, 1975; Monteforte, 1987; Stehlik, 1993; Uthicke et al., 2009; Yahel et al., 2006; Yonow, 1992). Final groups were checked by invertebrate experts (G. Paulay, University of Florida, S. Eberhardt, University of Hawai`i, M. Timmers, JIMAR) and compared with group compositions from Enochs (2010) and Enochs et al. (2011). Appendix E details the taxonomic organization of these invertebrates. When compared by feeding guild, the distribution was fairly even between main feeding guilds (Fig. 15) and similar to the composition in the East Pacific where omnivores comprised 28.78% of the community, detritivores 20.04%, herbivores 17.3% and carnivores 16.05% (Enochs, 2010).

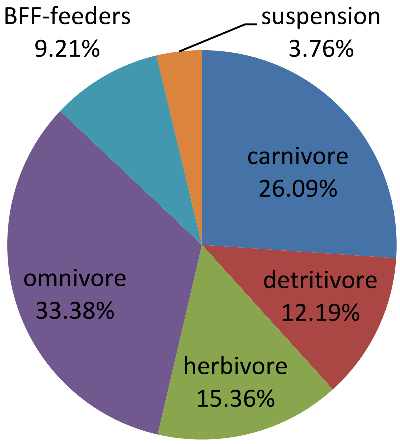

Figure 15.--Contribution of feeding guilds to the composition of invertebrates collected from ARMS units deployed at four locations around Guam.

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[12] http://www.pifsc.noaa.gov/cred/arms.php

We divided the omnivorous species equally between the herbivores, detritivores, and carnivores and assumed that the density of annelids (detritivores) was 10× higher, resulting in a cryptofaunal community composition of 39.8:38.1:22.1 (in terms of percentage) for carnivores, detritivores and herbivores on dead substrate. For live corals we assumed a community composition of 47.7:28.0:24.3 (in terms of percentage) based on Enochs and ARMS.

Estimation of total cryptofaunal biomass

The mean number of invertebrates was 918 (ranging between 1363 and 541) distributed over the ten plates of one ARMS unit (Appendix F). The area of one plate is 0.052 m^2, assuming animals inhabit the top and bottom of the plates, the total area is about 1 m^2, resulting in a density of 918 individuals/m^2 which is comparable to the abundance found by Enochs (2010) on the dense *Pocillopora* reefs of Panama. Crustaceans ranged in size between a few millimeters for amphipods to 2.5 cm for snapping shrimp with the most abundant group being the xantid crabs (16.7% of all organisms and 47.3% of all crustaceans) of which the hairy crab (Pilumnidae) were the most encountered (10.1%, 21.5%, resp.); polychaetes could reach as much as 10 cm for the spaghetti worms; gastropods ranged in size of 0.5 cm to 2 cm with the most abundant family the carnivorous dove shells (Columbellidae; 8.2% of all organisms and 19.5% of all mollusks). As the abundance was similar to the reef substrate of Panama (Enochs, 2010), we assumed that the biomass was similar as well. From Enoch's Fig. 3.8, we estimated the mean biomass of the four dead coral reef substrates to be 8.24 g AFDW/m^2, this corresponds to a total wet weight of 51.5 g/m^2 using a conversion factor of 16%. Using this value would imply that the mean weight per animal is 51 mg.

Biomass of cryptofauna on live coral is on average 1.6 times higher on live *Pocillopora* coral colonies compared to hard substrate (Enochs, 2010), however, in Guam the dominant coral genera are *Porites* sp., *Leptastrea* sp., and *Montipora* sp. which have massive and encrusting morphologies and do not have the dense branching morphology of *Pocillopora* colonies that can support a high abundance of cryptofauna. Overall complexity (i.e., three-dimensional structure) was estimated at 2.04 on a scale of 1 (no complexity) to 5 (high complexity) (CRED data). As a first approximation we assumed that live corals had 1.2 times the biomass of crypto fauna compared to dead coral substrate. For live coral areas we then estimated the total crypto fauna biomass to be 61.8 g/m^2.

For benthic detritivores we added the estimated biomass of sea cucumbers. Most sea cucumbers are nocturnal and those surveyed by CRED during day-time towed-diver and REA surveys are likely an underestimation. We used the data from REA surveys (CRED data) conducted in 2003, 2005 and 2009 and took the island-wide average density of 0.018 individuals/m^2. The most abundant species was *Sticopus chloronotus*. In a study on a reef in Mayotte in the western Indian Ocean, the average length of this species was 10.4 cm with a maximum length of 28 cm and a mean weight of 300 g (Eriksson et al., 2012). We used the mean abundance value to get a minimal estimate of the biomass of sea cucumbers in Guam of 5.4 g/m^2.

Estimation of biomass per cryptofaunal functional group

Using the community composition from ARMS for dead coral substrates and from Enochs (2010) for live corals, and the estimated total biomass value from Enochs corrected for difference in coral morphology, we estimated the biomass of the three benthic invertebrate groups. For areas with low complexity (complexity 1; complexity data for Guam came from CRED surveys) we used Enochs' category rubble, for complexity 2 we used the category highly degrade substrate (HDF), for complexity 3, medium degraded substrate (MDF) and for complexity 4 and 5 we used lightly degraded substrate(LDF) (Table 7). For example, on hard substrate with medium complexity (3), Enochs estimated a total biomass in dry weight of 10.95 gDW/m^2. This value corrected for difference in the reef composition between Panama and Guam resulted in an estimated biomass in wet weight of 68.44 gWW/m^2. From ARMS data we got a community composition of 39.8% benthic carnivores so the biomass of BC for medium complexity hard substrate was 27.23 gWW/m^2 (Table 7).

In Atlantis, these values were subsequently corrected for percentages hard substrate and coral cover for each Atlantis box around Guam.

Table 8.--Cryptic community composition and estimated biomass per functional group on Guam reefs. Community composition was based on ARMS data and biomass per feeding guild was based on Enochs (2010). We assumed that dry weight (DW) is 16% of wet weight (WW). BC = Benthic Carnivores; BD = Benthic Detritivores; BM = Benthic Meiofauna; HDF = highly degraded substrate; MDF = medium degraded substrate; LDF = lightly degraded substrate.

Dead substrate (gWW/m^2)	**BC benthic carnivores**	**BD benthic detritores**	**BM benthic meiofauna**	**Total biomass per complexity zone from Enochs in dry weight**	**Total biomass corrected for Guam's coral species composition in wet weight**
composition	*39.8%*	*38.1%*	*22.1%*	(gDW/m^2)	(gWW/m^2)
rubble	8.75	8.38	4.87	*3.52*	*22.0*
HDF	30.69	29.37	17.07	*12.34*	*77.13*
MDF	27.23	26.06	15.14	*10.95*	*68.44*
LDF	15.30	14.64	8.51	*6.15*	*38.44*
MEAN	**20.56**	**25.01**	**11.40**	***8.24***	***51.5***
Live (gWW/m^2)					
composition	*47.7%*	*28.0%*	*24.3%*	gDW/m^2	gWW/m^2
rubble	4.42	8.00	2.26	*4.42*	*9.28*
HDF	12.45	12.72	6.36	*12.45*	*26.13*
MDF	40.78	29.37	20.83	*40.78*	*85.57*
LDF	60.15	40.75	30.72	*60.15*	*126.22*
MEAN	**29.45**	**22.71**	**15.04**	***29.45***	***61.80***

Relatively few studies have estimated cryptofaunal biomass but these provide a comparison to our estimates in Guam Atlantis. One previous study by Ainsworth et al (2007) reported an infaunal biomass for a coral reef lagoon in Indonesia of 3.2 gC/m^2 (wet weight 27.4 t/km^2). Total epifaunal biomass was estimated to be 7.0 t/km^2 based on seastar abundance and this value was multiplied by five to account for other taxa. They then assumed a detritivorous to carnivorous invertebrate ratio of 1 to 5 and corrected the estimate to the total reef area resulting in a total in- and epifaunal biomass of 400 t/km^2. This estimate is much higher than our estimate of 51 t/km^2 but their reef area was much larger. Bustamante et al (2010) reported an infaunal invertebrate biomass of 5.5 t/km^2 and annelid biomass of 4.8 t/km^2. Total epifauna biomass excluding urchins, sea cucumbers and sea stars was estimated at 8.6 t/km^2 for a subtropical bay in Australia, which is much lower than our estimate.

Benthic Grazers (BG)

Echinoderms are conspicuous invertebrates on coral reefs and their booms and busts in abundances can have large-scale effects on reef community structure e.g., the loss of diadematids led to increase in macroalgae standing stock in the Caribbean (Lessios et al., 1984), an increase in *Acanthaster planci* changed coral community in Guam (Birkeland and Lucas, 1990) and both effects led to changes in higher trophic levels (Hay and Taylor, 1985; Williams, 1986).

On Guam, 52 species of sea urchins (Echinoidae) are identified (Paulay, 2003). Coral-reef echinoids decrease in abundance with depth, likely related to wave stress and food availability (Ebert, 1971). CRED (towed-diver surveys) and DAWR spatial survey results showed that boring urchins had an mean abundance of 0.16 individuals/m^2 and the larger urchins 0.004 ind./m^2. The boring urchin *Echinostrephus aciculatus*, was the most abundant species. Other species observed were the boring *Echinometra matthaei* and the larger diadematids, *Echinothrix diadema* and *E. calamaris*. We converted abundance to biomass values based on the mean test size derived from intensive surveys conducted by CRED in 2009 with 2.21 cm and 1 cm resp. for the two boring urchins and 10.5 cm and 6.0 cm rep. for the two diadematids (Muthiga and McClanahan, 1987; Russo, 1977). We calculated wet weight using the empirical formula of Russo: $W(g) = 0.247*D(cm)^{\wedge}2.66$; an alternate method by Muthiga and McClanahan had poor fits to data from Guam. For instance, mean weight for diadematids with mean test diameter of 8.25 cm was 552 g using Muthiga and McClanahan's relationship compared to 68 g using Russo's with the latter more realistic. We then took the weighted mean to calculate the overall biomass. For any Atlantis boxes for which we had no observational data, we assumed that a shallow box had twice as many urchins as the adjacent deeper box and vice versa, however, as the shallow areas harbor mostly juveniles we assumed the mean weight was halved (Ebert, 1971). If we did not have any data for the adjacent boxes we assumed a similar abundance as a box with a similar habitat based on the NOAA habitat map (NOAA NCCOS 2005**)**.

Diadematids' (*Echinothrix* spp) preferred diet is turf and filamentous algae but in absence or low abundance of that they feed on crustose coraline algae, some detritus, boring algae, and foraminiferans (Birkeland, 1989b). These shifts in diet make them very resilient to changes in environmental conditions that can lead to shifts in community composition. *Tripneustes* spp. are herbivorous and detritivorous and their feeding mode is grazing; the composition of their diet typically reflects the algal distribution found on the reef (Stimson et al., 2007). The short-spined *Echinometra* spp. eat boring cyanobacteria and in doing so, erode the reef substratum which explains why calcium carbonate sediments are usually the largest fraction of their gut content. They are often found in branching corals and in burrows in the reef substratum (Birkeland, 1989b). Drift algae can also be an important part of their diet. *Heterocentrotus* spp. are mostly herbivorous, grazing on filamentous or fleshy algae from bare substrate or the coral surface. Juvenile echinoids are too small to browse and tend to be detritivores or grazers of encrusting algae (Birkeland, 1989b).

Seastars (BSS)

Guam hosts 35 species of sea stars (Asteriodea) of which the crown-of-thorns seastar (COTS, *Acanthaster planci*) has received the most attention since the massive outbreak that devastated the reefs in 1967 (Paulay, 2003) as they are voracious coral predators (Glynn and Krupp, 1986; Kayal et al., 2012). This group is the only invertebrate group we separated into a juvenile (planktonic stage) and adult age class so as to represent this group more accurately. Although it is not totally clear why booms and busts occur, the hypothesis that nutrient runoff is a main factor in these outbreaks seems the most plausible explanation (Brodie et al., 2005). According to Birkeland (1982) COTS outbreaks occur on high islands and not or less so on low-lying atolls (e.g., Majuro and several other atolls did not have outbreaks in 1970s and in 2003–04 when high islands did have them). Birkeland also correlated large rain events after a dry period with outbreaks 3 years later. With a high concentration of nutrients in the water column after a seastar spawning event, it seems likely that more planktonic juveniles will survive as more food (> 2 µm phytoplankton) is available (Fabricius et al., 2010). A study on the Great Barrier Reef showed that the threshold level for COTS larvae development was Chl-*a* 0.8 µg /l and with every doubling of Chl-*a* concentrations up to 3 µg/l, COTS larvae survival increased approximately 8 fold (Fabricius et al., 2010).

Once COTS settle out of the plankton they hide in small crevices and eat coralline algae. They begin to come out at night to eat coral when they are 10 cm (Birkeland, 1982). When they are larger, they appear en masse. From CRED spatial towed-diver surveys conducted in 2003, 2005, 2007, 2009 and 2011, COTS were the most prevalent seastar species observed. Other seastars included *Culcita novaegineae*, *Linckia multifora*, and *L. laevigata*.

To convert abundance to biomass we assumed that the mean diameter was two-thirds of the maximum diameter and used the empirical relationship (Birkeland and Lucas, 1990):

$$WW\,(g) = 0.1609 * radius\,(cm)\,{}^\wedge\,2.893 \qquad 1$$

The weighted mean biomass for a density of 0.008 ind/m^2 was 0.31 g/m2. As towed-diver surveys are only conducted at 10–15 m depth we assumed that COTS densities were similar in the shallow reef compared with the adjacent deeper reef and we assumed that the shallow boxes harbor mostly juveniles so we halved the mean weight. For boxes with no data we assumed a biomass of an adjecent box with a similar habitat.

COTS and other coralivorous seastars consume *Acropora* sp., *Pocillopora* sp. and *Porites* sp. with the branching and table-shaped morphologies being the most preferred (Kayal et al., 2012). These species are also the most dominant branching corals in Guam (CRED, DAWR data). Because of this food preference, outbreaks of coralivorous seastars lead to a shift in the benthic community from branching coral dominated reefs to massive *Porites* and algal dominated reefs (Kayal et al., 2012).

Reef Fish

In Guam about 1100 fish species inhabit the 0–100 m coastal waters (Myers and Donaldson, 2003), however during daylight (scuba) dives many of them were never seen and, therefore, are not included in this model. The 328 included species are those seen during the day in 0–30 m water with some cryptic species and nocturnal species that hide in the shallow waters under overhangs or in rock crevices visible to divers (Appendix B). As all parameters are calculated as a weighted mean, the influence of the species never observed (and assumed rare) is assumed negligible.

Spatial fish abundance and size distribution data came from random surveys stratified by 3 depth strata (shallow < 6 m , mid 6–18 m, and deep >18 m) conducted by CRED in 2011. For apex predators, abundance and size distribution data came from towed-diver surveys as that is more accurate for these roving fish (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. Standard length was converted to TL by using published conversion factors and those from FishBase. Length-weight fitting parameters were available for 150 species commonly observed on visual fish transects in Hawaii (Hawaii Cooperative Fishery Research Unit unpubl. data). These parameters were supplemented with published sources, PIFSC data, and FishBase. In those cases where length-weight information did not exist for a given species, parameters from congeners were used. Site level biomass data was averaged to get a mean value per Atlantis box. For boxes with no data we assumed the same biomass values as a box with similar habitat characteristics and depth. Site level abundance data were used to estimate the species specific distribution among the boxes for adults and juveniles. Spatial recruit distribution was based on published literature on habitat preferences of recruits (DeMartini, 2004; DeMartini and Anderson, 2007; DeMartini et al., 2010; Man et al., 1995; Richards and Lindeman, 1987; Srinivasan, 2006; Taylor et al., 2012; Tupper, 2007).

Diet data came from literature (Bellwood and Choat, 1990; Bruggemann et al., 1994; Chen, 2002; Choat, 1991; Choat and Robertson, 2002; Crossman et al., 2005; Cvitanovic et al., 2007; Dierking, 2007; Ebert and Cowley, 2003; Guiasu and Winterbottom, 1998; Hobson, 1974; Karpouzi and Stergiou, 2003; Meyer et al., 2001; Myers, 1991; Paddack et al., 2006; Randall et al., 1978a; Sadovy et al., 2003; Schluessel et al., 2010; Sudekum et al., 1991; Young et al., 2003) and Fishbase. Using literature and Fishbase, diet items were allocated to the Atlantis functional groups (e.g. shrimp were split between BD (70%) and BC (30%); octopus was added under Cephalopods) per predator species. If unspecified bony fish were identified in a diet, we distributed that percentage equally among all non-piscivorous fish. For piscivorous fish, a small proportion of their diet was also attributed to piscivores. If data were available, diets of adults and juveniles were separated, if no data for juveniles were available we assumed they ate the same as the adults but proportions of some items were skewed towards smaller bodied prey. A weighted mean was computed per functional group and this was used as a base for the availability matrix that determines diets within Atlantis.

Marine Reptiles

The most abundant sea turtle in Guam is the green turtle, *Chelonia mydas*, with foraging green turtles along all coastlines but especially observed in a channel east of Cocos Lagoon (Atlantis boxes 2 and 53, DAWR data) and in Apra Harbor (boxes 14 and 15, D. Burdick pers. comm. not picked up by the DAWR aerial surveys; Fig. 16). Abundance data from aerial surveys conducted in 2007 by NOAA Fisheries and U.S. Fish and Wildlife Services, indicated 150–250 individuals in coastal area of 0–30 m depth (~ 95 km^2). This translates to a mean estimate of 2.1 individuals/km^2. Aerial surveys conducted for DAWR from 1989 to 2010 showed different numbers with a total of 603 turtles in 2007 and a mean annual sighting of 560 turtles which translates to 5.9 turtles/km^2 assuming the same stretch of coastal area. Turtle sightings differed little within a year (Fig. 17). As these data comprised a longer time-series, we used these data to estimate biomass and spatial distribution for the model. The survey areas of the aerial survey are from the coast until deep water (depth depending on visibility). For those aerial survey zones corresponding to a shallow and deep Atlantis box, we assumed an equal distribution. The average weight was assumed to be 136 kg which resulted in a biomass of 0.80 t/km^2.

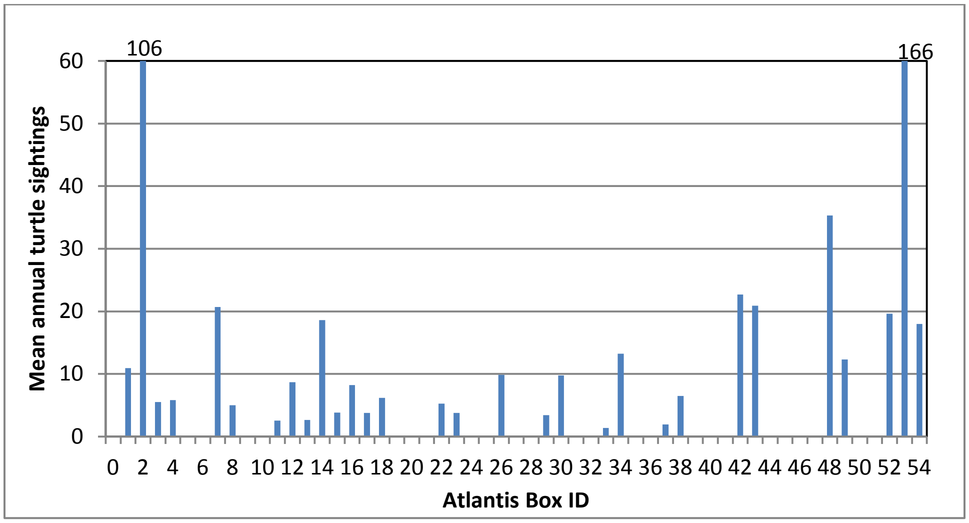

Figure 16.—Spatial distribution of sea turtles from aerial surveys conducted for DAWR from 1989 to 2010.

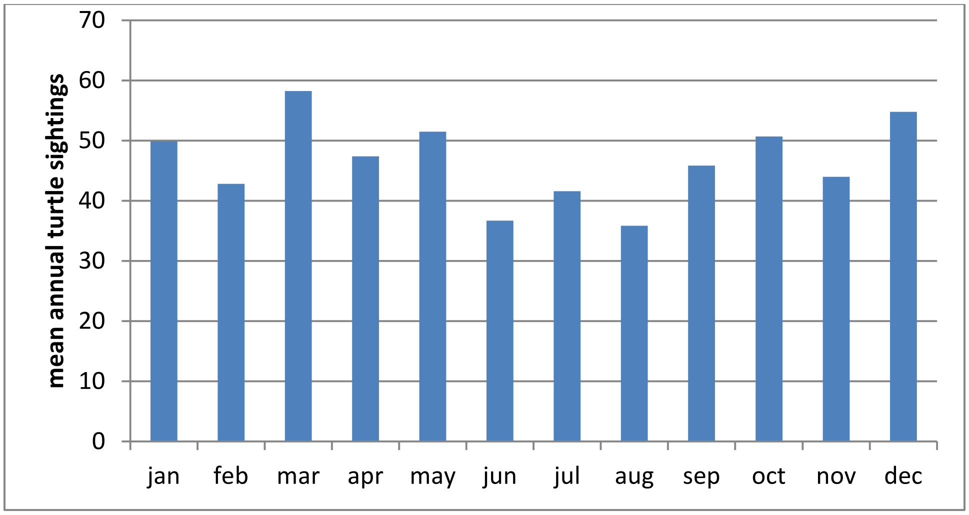

Figure 17.—Seasonal distribution of sea turtles with mean monthly sightings from aerial surveys conducted for DAWR from 1989 to 2010.

Model Dynamics

Biological Dynamics

Primary Production

Guam Atlantis uses the primary producer groups: macroalgae, turf algae, crustose coralline algae, and large and small phytoplankton. In a later version of the model, 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 nutrient, 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:

$$dB/dt = G - M_{lys} - M_{lin} - M_{quad} - \sum_{j=1}^{n} M_j - F \qquad 4$$

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:

$$G = \mu * \delta_{irr} * \delta_N * \delta_{space} * A \qquad 5$$

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. (Fulton et al., 2004a), as it varies between producers.

Growth rates were obtained from Weijerman et al. (2013) and during tuning of the model these initial growth rates were adapted (Table 9).

Table 9.--Growth rates for primary producers with alterations made during tuning in parentheses. Initial growth rate calculated from Weijerman et al 2013. Corals are not modeled as primary producers yet.

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:

$$d(NH)/dt = -\sum_{i=1}^{P} A_{NH,i} + \sum_{j=1}^{C} E_{NH,j} - S + R \qquad 6$$

$$d(NO)/dt = - \sum_{i=1}^{P} A_{NO,j} + S \qquad 7$$

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:

$$dB/dt = G - \sum_{i=1}^{n} M_i - M + I - E - F \qquad 8$$

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:

$$G = \sum_{i=1}^{n} P_i * \varepsilon_i * \delta_{O_2} * \delta_{space} \tag{9}$$

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 increasingly 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. (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 (Fulton et al., 2003b):

$$P_{ij} = \frac{B_i * a_{ij} * B_j * C_j}{1 + \frac{C_j}{g_j}\left(\sum_{i=1}^{n} B_i * a_{i,j} * E_{ij}\right)} \tag{10}$$

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:

$$g = G_{max} * \varepsilon \tag{11}$$

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 Weijerman et al. (2013) and were multiplied by 1.2 to reflect the maximum consumption rate which is used in Atlantis (Table 6).

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

$$G_{max} = CA * W^{CB} \qquad 12$$

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 + 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 we assumed that a predatory fish can eat a prey fish of 40% of its body length. We 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, mollusks, shrimp, and other benthic invertebrates, we 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 10). 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 10.--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	20.9	0.30
Roving piscivores	All fish species	153	70	0.46
Target Benthic piscivores	Invertivores	50.4	25.4	0.50
Benthic Piscivores	Invertivores	67.5	25.4	0.37

For planktivorous, corallivorous, detritivorous and herbivorous fish, turtles, and invertebrates which all do not eat age-structured prey, we defaulted to 0.2 for the upper gape limit. For invertivorous fish and rays we used 0.25. For all functional groups we used 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 or 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). We 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. We 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% (Cury and Christensen, 2005; Edward, 1986; Jobling, 1994).

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 13). 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 and Doonan, 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 Guam Atlantis steepness estimates, we used values derived for reef fish families by Myers et al. (1999) and interpolated other families based on their dependence on parental stock for recruitment.

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

$$\mathit{recruits} = \alpha * S / (\beta + S) \tag{13}$$

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.

To calculate the *alpha* and *beta* parameters for spawning fish species we made the following assumptions:

- stocks have an equal birthrate of females and males, i.e., $r = 0.5$;
- 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 a correction 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 (virgin) biomass in Guam (data from Williams et al., 2012).

These parameters are critical tuning parameters for Atlantis and were changed in adjusting model dynamics (Table 11).

Table11.--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 the 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, we 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. We assumed a fixed recruitment of 0.5. Growth rate is high for juveniles and declines to negligable when they reach sexual maturity (Limpus and Chaloupka, 1997)

Rays have 2–4 pups and sharks 1–6 and we 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.

Fisheries Characterization

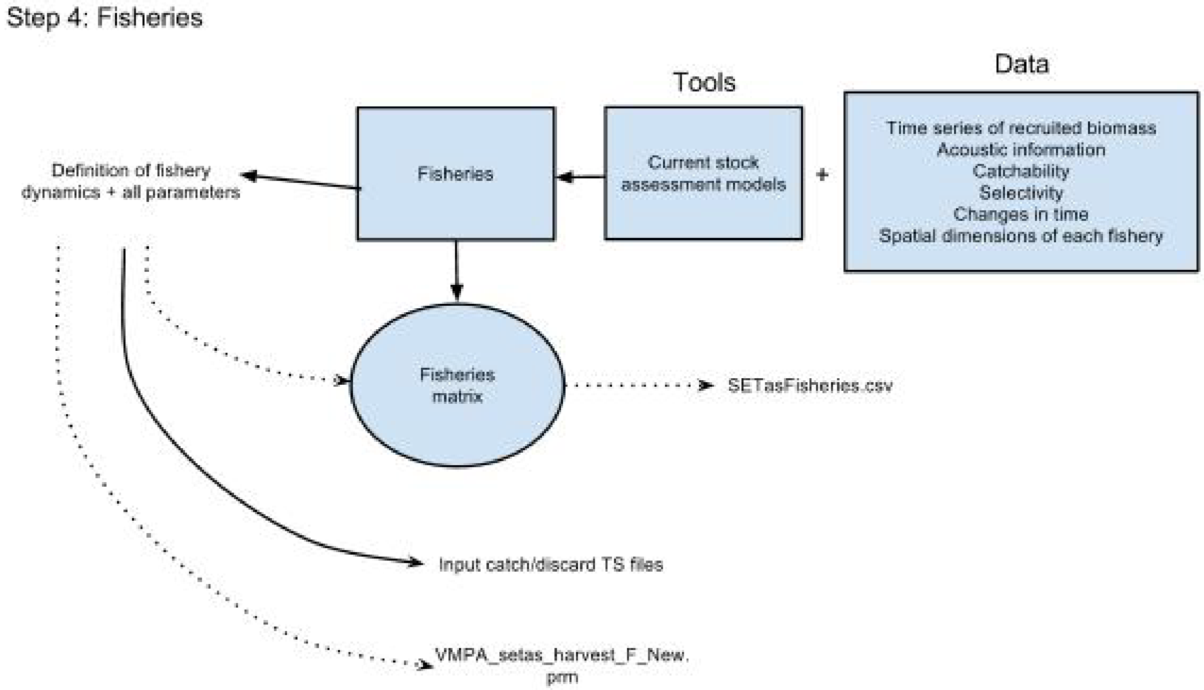

Figure 18.--Schematic overview of the Atlantis framework and requirements for the fishery submodel (created by Carolina Parada and Bec Gorton).

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). Agriculture was traditionally practiced as well, however, relatively frequent and intense typhoons and physical limitations on the amount of available land made large-scale agriculture impractical. It is estimated that at first contact with Europeans in 1521 there were fewer than 20,000 Chamorros on Guam (Amesbury and Hunter-Anderson, 2003). During the period of Spanish influence imported crops such as corn and introduced domestic animals such as cattle may have encouraged Chamorros to become less dependent on seafood. However, throughout this time the islands were still operating with a subsistence economy. After World War II a wage based economy developed in Guam, replacing subsistence agriculture and fishing (Amesbury and Hunter-Anderson, 2003). The forces of colonization, immigration, and cultural change have altered the needs of the island residents and have expanded dietary options far beyond what can be caught on the reef and grown in upland valleys. The most noticeable shift in the diet of Guam occurred after World War II from traditional foods such as fish, taro, yams, bananas, coconut and breadfruit to imported white rice and highly processed canned goods such as Vienna sausage and corned beef (Guerrero et al., 2008).

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 reef boundaries, while most local fishermen 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 fishery 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 12). Each method requires a varying degree of skill, and allows for different levels of species selectivity.

Table 12.--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.

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

gh = gear_hour.

Data source: DAWR and WPacFIN creel inshore fisheries survey data 1985–2012.

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 fishermen participating in pelagic fishing, almost all of the respondents reported “regularly giving fish to family, friends, or both” (Rubinstein, 2001). The DAWR survey results showed that only 1 fisherman sold his 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).

Guam Atlantis includes 7 fishery ‘fleets’ (including tourism as a non-extractive fishery) with fleets being based on gear types of shore-based fishery (Table 13). Recreational fishery data and socio-economic data came from creel surveys conducted by the Guam Department of Aquatic and Wildlife Resources (DAWR), the NOAA PIFSC Western Pacific Fisheries Information Network (WPacFIN) program, published creel and small-boat surveys, and from Guam partners (Department of Aquatic and Wildlife Resources, Guam Fisheries Cooperative).

Table 13.--Fishery fleets incorporated in the Guam Atlantis Coral Reef Ecosystem Model and the functional groups each gear type catches and the dominant (i.e., > 20% of catches per functional group) target species. See Table 5 and Appendix B for Functional Group definitions.

Fleet	Functional Group	Target Species
Tourism	SHR,RAY,REP,HHW,BHP,FHE,THG, FCO	Sharks, rays, turtles, humphead wrasse, parrotfishes, surgeonfish, corallivores
Hook and line	FPL, FIV, TIV, THB, FHG, FPB, TPB, FPR, FPM	Unicornfish, triggerfish, wrasse, snapper, surgeonfish, eel, grouper, jacks, houndfish
Net	FPL, FCO, FIV, TIV, HHW, FDE, FHB, THB, FHG, THG, FHS, FPB, TPB, FPR, FPM, BC, BD	Unicornfish, triggerfish, wrasse, snapper, surgeonfish, eel, grouper, parrotfish, jacks, houndfish, crab, lobster
Spearfishing SCUBA	TIV, THB	Wrasse, snapper, unicornfish
Spearfishing snorkel	FDE, HHW, FHB, THB, THG, FHS, FHE, BHP, TPB, CEP, BD	Surgeonfish, humphead wrasse, parrotfish, unicornfish, groupers, octopus, lobster
Hook and gaff	CEP	Octopus
Reef gleening	BD,BC,BM,MA,BFF,BG	Sea cucumbers, lobsters, crabs, mollusks (tritons), macroalgae, sea urchins

Catch and Biomass Reconstruction for 1985 Model

To verify the accuracy of ecosystem model simulations, it is necessary to compare the predicted biomass with historical time series of catch and relative abundance data. By tuning the dynamic parameters, these time series should overlap. Unfortunately, there were no time series available for biomass or abundance data from the past. However, time series of landings and efforts are well documented since 1985 by Guam Department of Aquatic and Wildlife Resources. These data sets include both boat-based surveys and shore-based surveys. Boat-based data include records from trolling (98% of trolling catch consisted of tuna and other pelagic species), bottom fishery (33% of catch consisted of non-reef-associated or deep species), and fishing trips outside of the model domain (e.g., Rota Bank, Eleven-mile Bank, etc.). As the model is limited to the shallow (< 30 m) coral reefs, we wanted to include only fishery data from this same area. From the boat-based fishery we could not exclude the data of the areas outside of our model domain, therefore, we only used the inshore fishery data for our calculations of the catch-per-unit-effort time series. We realize that this approach is not ideal as boat-based fisheries within the 30-m reef (e.g., spearfishing and hook and line) are now excluded. However, as we use the data to give us a relative indication of the fishery compared to 2011 and we are not interested in absolute numbers, we feel that this approach is justifiable.

Using the catch-per-unit-effort (CPUE) 1985–2012 data per gear type, we reconstructed the biomass of functional groups in 1985 relative to 2011 for which year we had both fishery independent and fishery dependent data. We based the change in relative abundance on these

CPUE series. We chose 1985 as a starting point for the historic model because we had the most complete record of catch and effort time series since then. Estimated total catches have declined since 1985 (Fig. 19; Appendix G). Moreover, in 1985 landings are estimated to have declined already by 84% compared to 1950 (Zeller et al., 2007), so for those species with already very low catch rates, 1985 biomass cannot be established. For example, 1985 was the last year the bumphead parrotfish appears in the catch records, with 515 kg reported by spearfishermen.

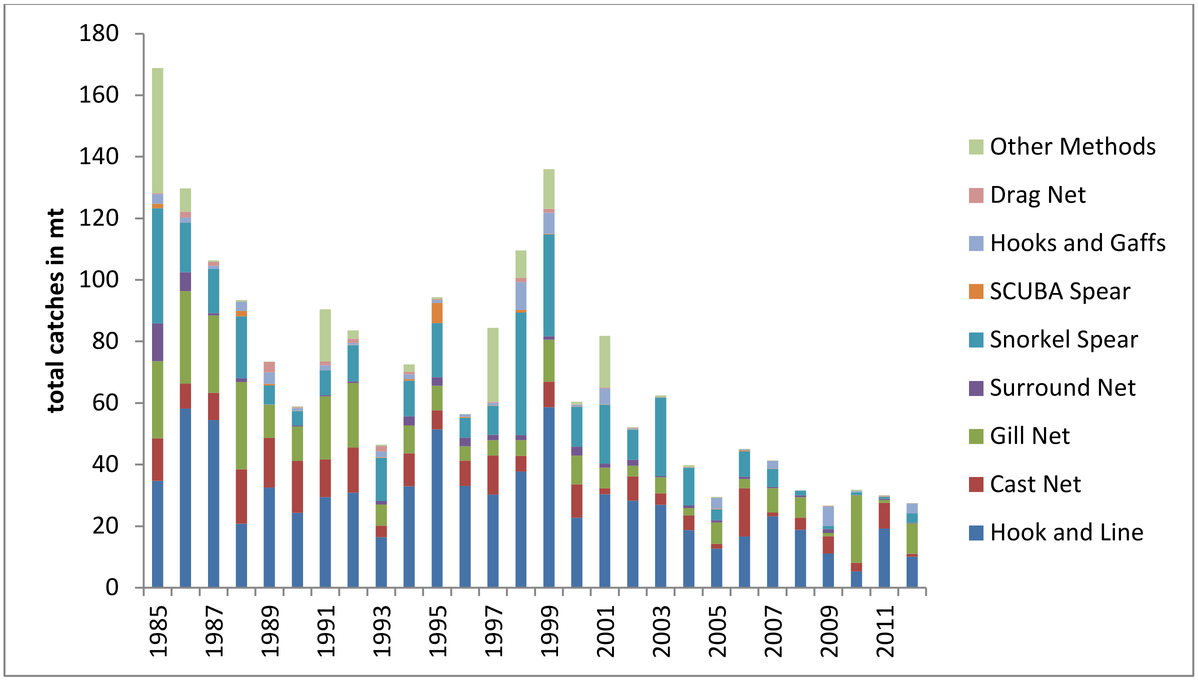

Figure19.--Time series of expanded inshore fishery landings per gear type. Pelagic baitfish landings are excluded from the hook and line catches. Data from Guam DAWR and WPacFIN.

We based our calculation of reconstructed fish biomass on the assumptions that annual CPUE (C/E) is linearly related to the annual biomass (B):

$$C_t/E_t = q * B_t \quad 14$$

and that the catchability coefficient, q, depends on the fishing gear and the experience of the fisher, i.e., different fishing operations can extract a different portion of the catch. The effort was calculated as number of gear-hours for the entire area of Guam.

Fishing is reported per zone per day type (i.e., weekday or weekend) so first we compare the CPUE per zone and day type with a simple 2-tail Student t-test on the paired annual CPUE values for which we had at least 6 years of CPUE data with at least 3 observations per year. For zone 4 we only had < 3 observations per gear type per day type so we could not compare between weekday and weekend. Only gill net fishing in zone 1 (from north of Tumon Bay to south Agana Bay) and snorkel spear fishing in zone 3 (south coast and southeast coast till Pago

Bay) showed a significant difference in CPUE between weekday and weekend fishing (Table 14). When combining all zones, there were not enough data to compare surround net or scuba spear fishing, and the other methods did not show a significant difference at $p = 0.05$. As most gear types did not show a difference between weekday and weekend, we pooled the data up to both day types and with ananalysis of variance (ANOVA) looked for differences between zones. Gil net fishing was the only gear with a significant difference between zones, with zone 1 having a higher CPUE (Table 14; Appendix H).

Table14. Comparison of CPUE per gear type between weekday and weekend with a Student t-test and between zones with ANOVA. Values are means (standard deviation) of 1985–2012. Zone 0 is the combination of zone 1, 2, 3 and 4. Bold numbers reflect a significant difference at $p = 0.05$.

Method	zone	Mean CPUE		student t test		ANOVA		
		weekday	weekend	*p*	n	Mean CPUE	p	n
Hook and line	1	0.13 (0.12)	0.09 (0.06)	0.11	27	0.11 (0.06)	0.78	27
	2	0.14 (0.11)	0.10 (0.07)	0.12	27	0.11 (0.06)		
	3	0.14 (0.12)	0.12 (0.07)	0.24	27	0.12 (0.05)		
Cast Net	1	0.42 (0.36)	0.46 (0.70)	0.79	27	0.40 (0.30)	0.70	27
	2	0.35 (0.23)	0.28 (0.24)	0.38	21	0.36 (0.22)		
	3	0.40 (0.26)	0.46 (0.49)	0.52	27	0.42 (0.27)		
Gill Net	**1**	**0.75 (0.44)**	**1.19 (0.74)**	**0.03**	**21**	**1.06 (0.64)**	**0.01**	**26**
	2	0.62 (0.32)	0.65 (0.63)	0.88	14	0.18 (0.43)		
	3	0.75 (0.47)	0.76 (0.49)	0.95	22	0.15 (0.39)		
Snorkel spear	1	0.69 (0.42)	0.86 (0.59)	0.38	6	0.93 (0.53)		
	2	1.05 (0.58)	0.77 (0.43)	0.26	9	0.87 (0.40)		
	3	**1.36 (0.71)**	**0.84 (0.38)**	**0.01**	**17**	0.93 (0.46)	0.88	22
Hook and Gaff	0	0.43 (0.37)	0.62 (0.81)	0.43	14			
Drag net	0	2.53 (1.41)	2.97 (2.43)	0.71	6			
Other	0	0.55 (0.73)	0.71 (1.03)	0.53	16			

For 2011, we have both CPUE data (from DAWR and WPacFIN fishery statistics) and biomass data (for fin fish from visual surveys conducted by CRED) so we could calculate the catchability coefficient for each gear type used in 2011 for catching fin fish. However, because of the large differences in catch and effort data between years (Appendix G), we decided to use the mean of the 2010, 2011, and 2012 data to calculate the CPUE. Also, as cast nets are predominantly used to catch juvenile fish (rabbit fish, goat fish, jacks) that come en masse to the shallow bays of Guam and are not included in the visual surveys, we excluded cast net catches and effort from further analyses. Based on the species composition of the remaining total landings, we calculated the proportion of catches of each functional group per gear type (e.g., 77% of the browsers are caught by gill net and 23% by spearfishing) and multiplied those proportions with the biomass estimates for that particular functional group from 2011 visual surveys. We then calculated q by taking the geometric mean of 2010–2012 of observed catch and effort values associated with the 2011 biomass per gear type using equation 15:

$$q = e^{\frac{1}{n}\sum Ln\left(\frac{I_t}{B_t}\right)} \tag{15}$$

This method is well established for pelagic fisheries (Haddon 2010) and we further assumed that it is applicable for the complex reef fishery when parsed out catches and effort per gear type. For the reconstruction of the relative biomass for the period 1985–2012, we multiplied the CPUE per gear type for each year with the derived constant q using equation 14 rewritten as $B_t = I_t * q$.

Naturally, when a fish is not targeted it does not turn up in the catch records implying that their biomass is zero or very low based on these current calculations. Therefore, we could only estimate the biomass of target groups (Fig. 20) and assumed a 20% decrease in biomass of the nontargeted species. Spatial distribution among the Atlantis polygons was assumed to be the same as the 2011 model, only the absolute quantity in biomass differed.

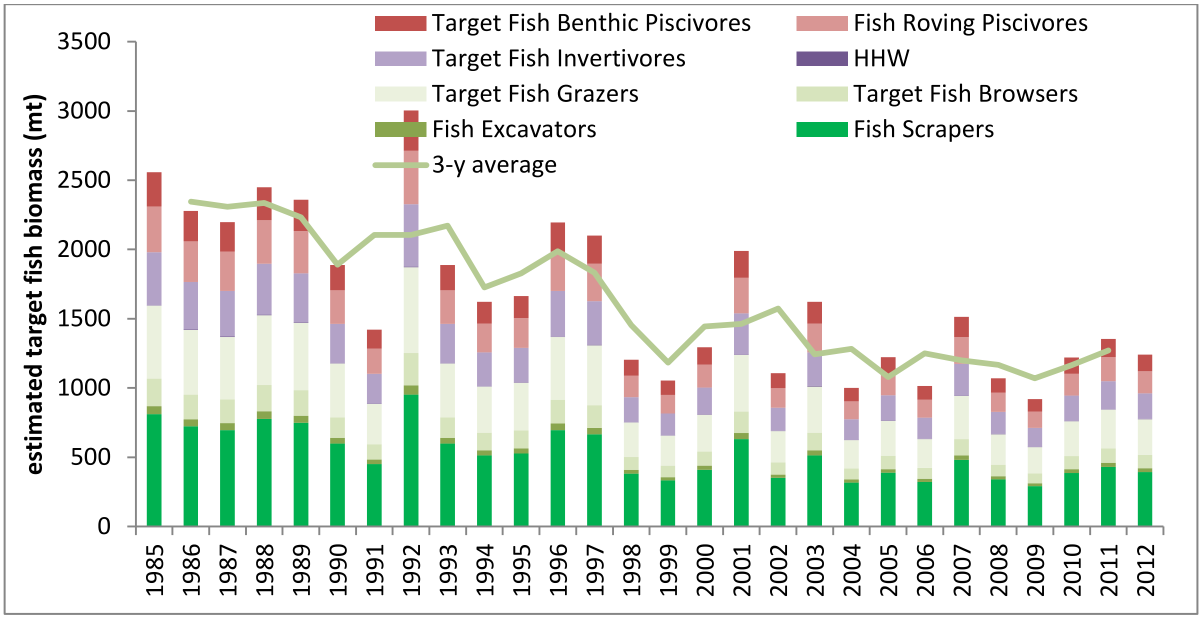

Figure 20.--Reconstruction of estimated biomass of target fish groups based on annual CPUE data, catch composition per gear type, and a constant gear catchability coefficient. CPUE data from DAWR and WPacFIN.

The reconstructed target fish biomass in 2011 was 1.67 times higher as the target fish biomass from the visual surveys. This discrepancy could be because the visual surveys are only from 0 to 30 m and reef fish can also be caught deeper. However, since we use it to identify trends and not for stock assessment purposes, it will be possible to use it for model calibration.

Historic benthic cover data were not available. Available older reports were mostly based on surveys from reef flats (Amesbury et al., 1993; Randall et al., 1978b; Randall and Sherwood, 1982). Also survey methods differed from those used by CRED making it impossible to compare values. In a comparative review of the benthic communities in Tumon Bay between 1977 and 1991, no major changes were found (Amesbury et al., 1993). The southern reef flats were already stressed by sedimentation and other land-based sources of pollution in 1977 (Randall et al., 1978b), indicating chronic stress for those coral communities. We assumed a stable cover for benthic communities. Spatial distribution was also assumed to be the same as for the 2011 initial conditions.

Using the present-day model as a template, we will construct a 1985 model for calibration purposes by evaluating the model's ability to represent the reconstructed fish biomass trends under historical fishing pressure and chronic habitat degration (i.e., reconstructed time series of sediment and nutrient inputs, see section: 'Sediment and nutrient forcing files') from 1985 to 2012.

Socio-economic Submodel and Visualization of Atlantis Model Output

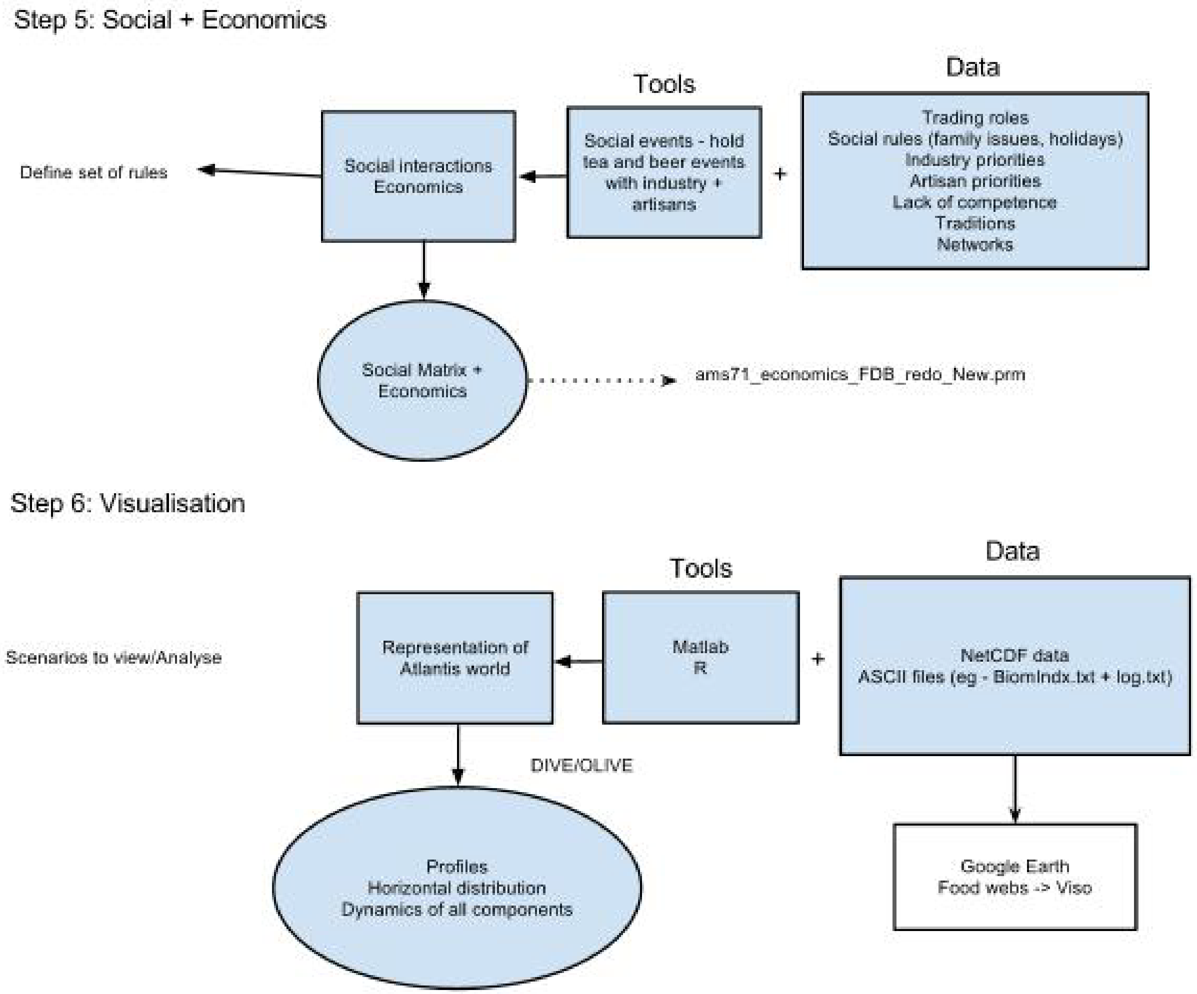

Figure 21.--Schematic overview of (*top*) the Atlantis framework and requirements for the socio-economic submodel and (*bottom*) how to visualize model output (created by Carolina Parada and Bec Gorton).

We have not yet included the socioeconomic submodel into Guam Atlantis but the visualization tools in Figure 21 are also suitable for the ecology submodel.

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. We followed the adjustment procedures as used in previous successful implementation of Atlantis (Ainsworth et al., 2011; Fulton et al., 2004b, c; Horne et al., 2010). We calibrated the dynamic behavior of Guam Atlantis in two phases.

In the first phase, we initialized the model with 2011 estimates of biomass and ran the model forward without fishing. Initial conditions represent approximately January 2011, and simulations were projected for 30 years. Our 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, we assumed that the system, beginning from an exploited ecosystem base in 2011, should return to conditions similar to those in marine protected areas (MPAs) around Guam or better (i.e., higher fish biomass values) as some forms of fishing are still allowed in the MPAs. We used mean estimates of (almost) unfished biomass (B_0) from underwater surveys conducted in MPAs around Guam in 2011 as calibration targets (CRED data). We acknowledge that this method is not ideal as species that are already locally rare (e.g., bumphead parrotfish, *Bolbometopon muricatum*) or at very low levels (apex predators) will not be represented accurately. Therefore, we also compared these estimates with biomass values from the relatively pristine reefs around the Northern Marianas (Fig. 5) and adjusted them when they differed more than 1.2 times. The benthic community structure did not vary greatly between inside and outside MPAs. For these groups and other7s for which we did not have unfished biomass estimates, our goal was merely to produce steady biomass through time time that fall within the range of current observations.

For these simulations we 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 (mum, *g* in eq. 11), clearance rate (*C* in eq. 10), and predation pressure dictated by the availability parameter (*a* in eq. 10). 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, we exercised the model with varying degrees of fishing pressure to evaluate responses of functional groups when perturbed. For these scenarios, we did not attempt to simulate fleet dynamics, but rather applied constant fishing on all fished groups (including only fishes) throughout the duration of the simulation. We expected biomass to decrease in response to fishing without going extinct at reasonable levels of fishing pressure. Generally, we expected highly productive stocks such as planktivores (Atlantis group FPL) to be able to withstand moderate amounts of fishing mortality, and unproductive, long-lived groups like large-bodied parrotfish (*Chlorurus* spp., Atlantis group FHE) and groupers (Atlantis group TPB) to decline under similar fishing rates. As a very approximate expectation, at fishing levels equal to the natural mortality rate (M), we 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 robust to additional fishing pressure usually pointed to problems with recruitment, and thus adjusting productivity via recruitment was generally the best solution.

RESULTS

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 (Figs 22 a–g). Some of the piscivore groups did not reach the expected unfished biomass level, most notably the roving piscivores and rays (Fig. 22c). 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, these trends, at least for corals, which in future versions of the model 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 (Figs. 23a–d). 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 (Figs. 24a–d). 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 (Fig. 24c).

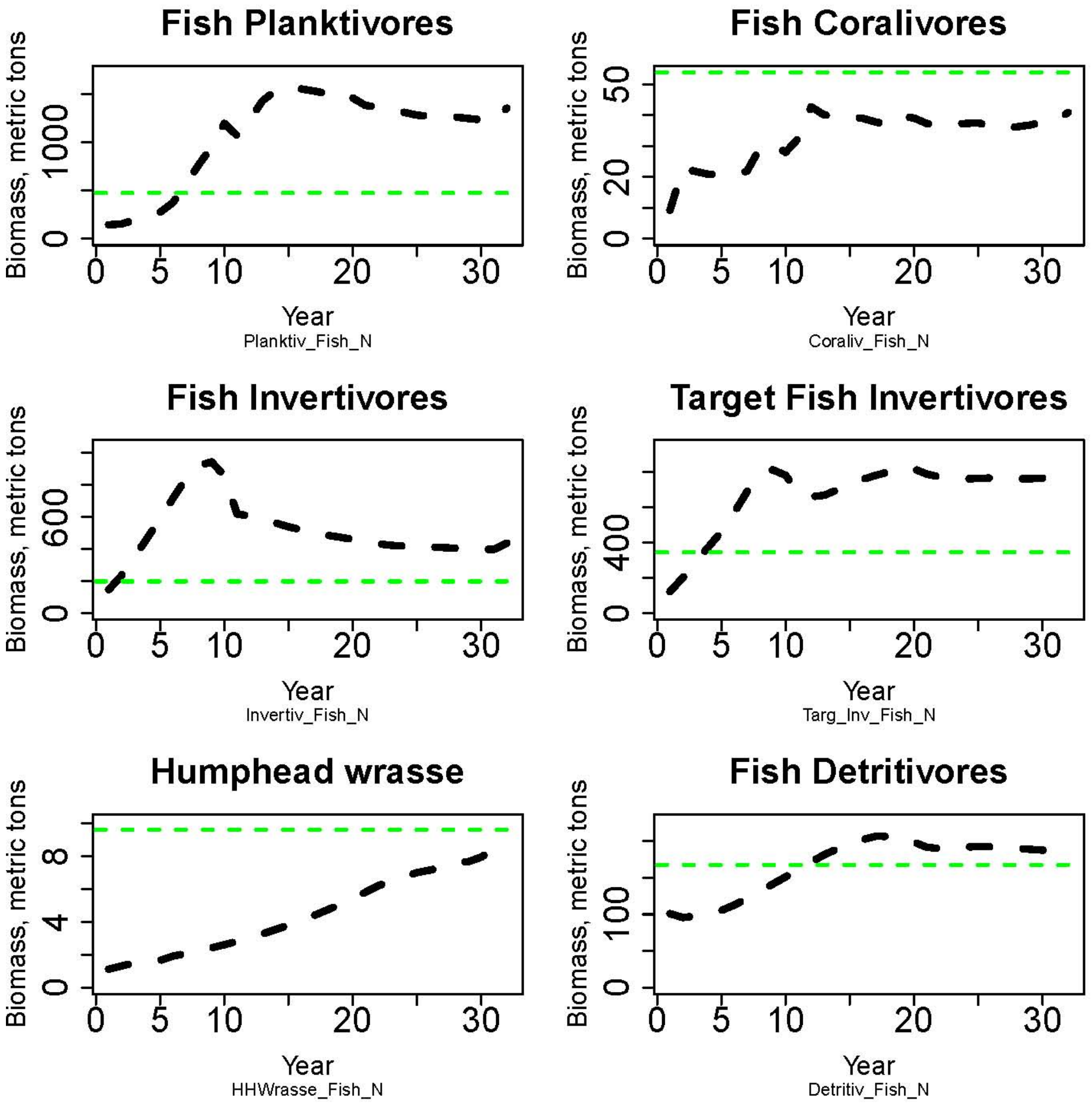

Figure 22a.--Biomass results for each functional group after initial tuning phase. Biomass is represented in metric tons summed over the entire model extent. Dotted green lines indicate mean biomass estimates for functional groups in marine protected areas where available (19 groups). *X*-axis shows number of years after start of simulation (2011).

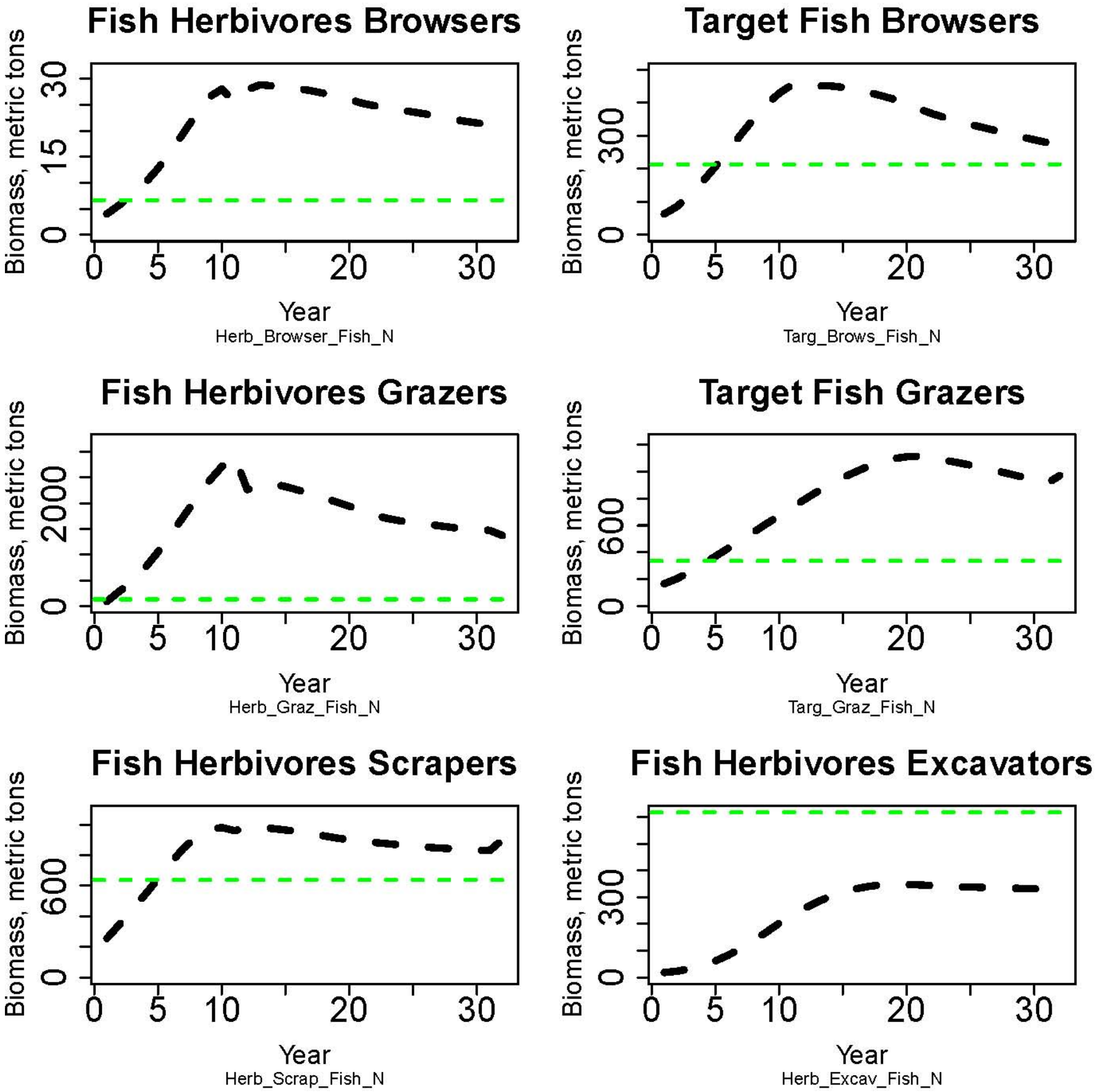

Figure 22b.--Biomass results for each functional group after initial tuning phase. Biomass is represented in metric tons summed over the entire model extent. Dotted green lines indicate mean biomass estimates for functional groups in marine protected areas where available (19 groups). *X*-axis shows number of years after start of simulation (2011).

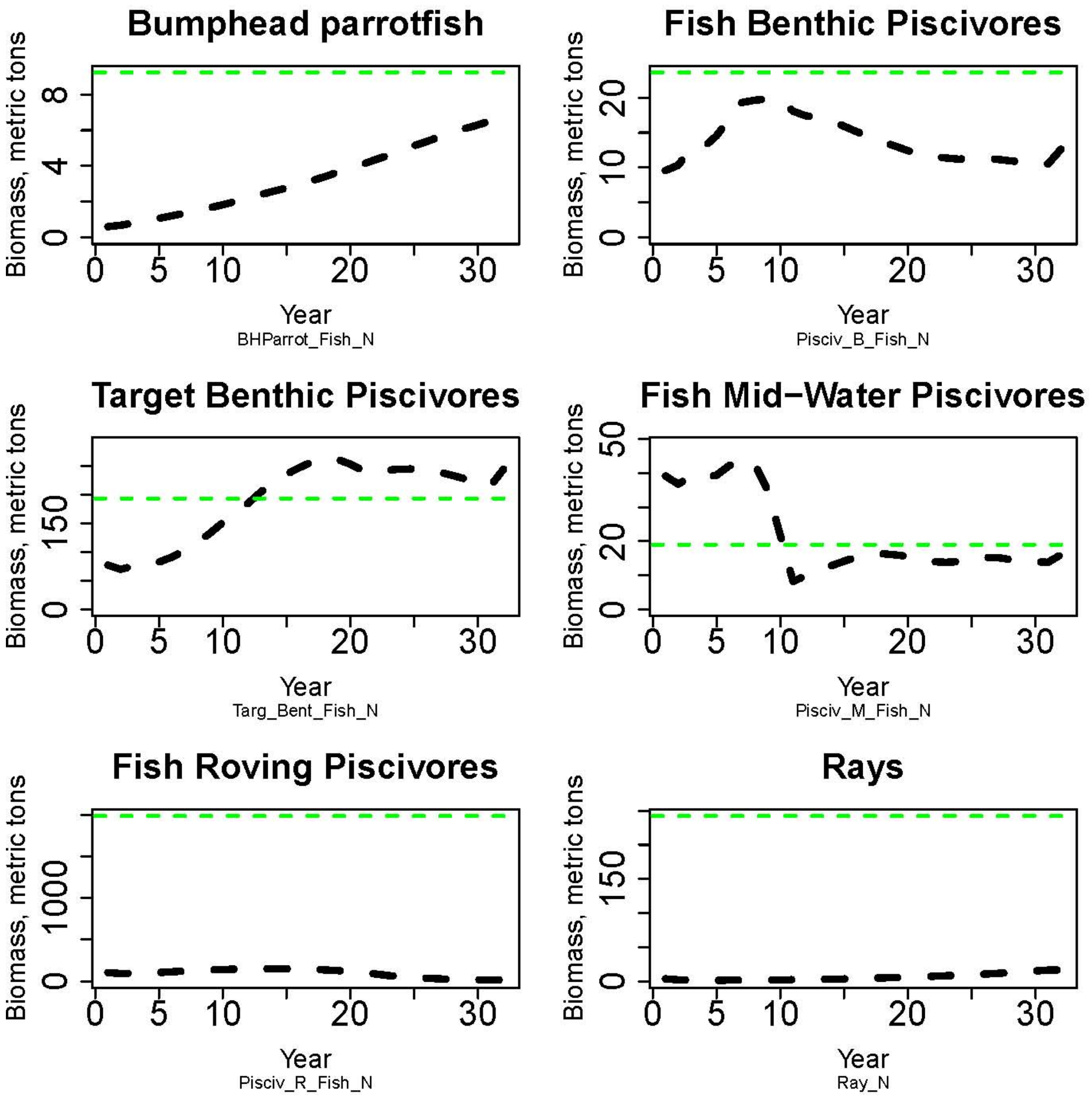

Figure 22c.--Biomass results for each functional group after initial tuning phase. Biomass is represented in metric tons summed over the entire model extent. Dotted green lines indicate mean biomass estimates for functional groups in marine protected areas where available (19 groups). *X*-axis shows number of years after start of simulation (2011).

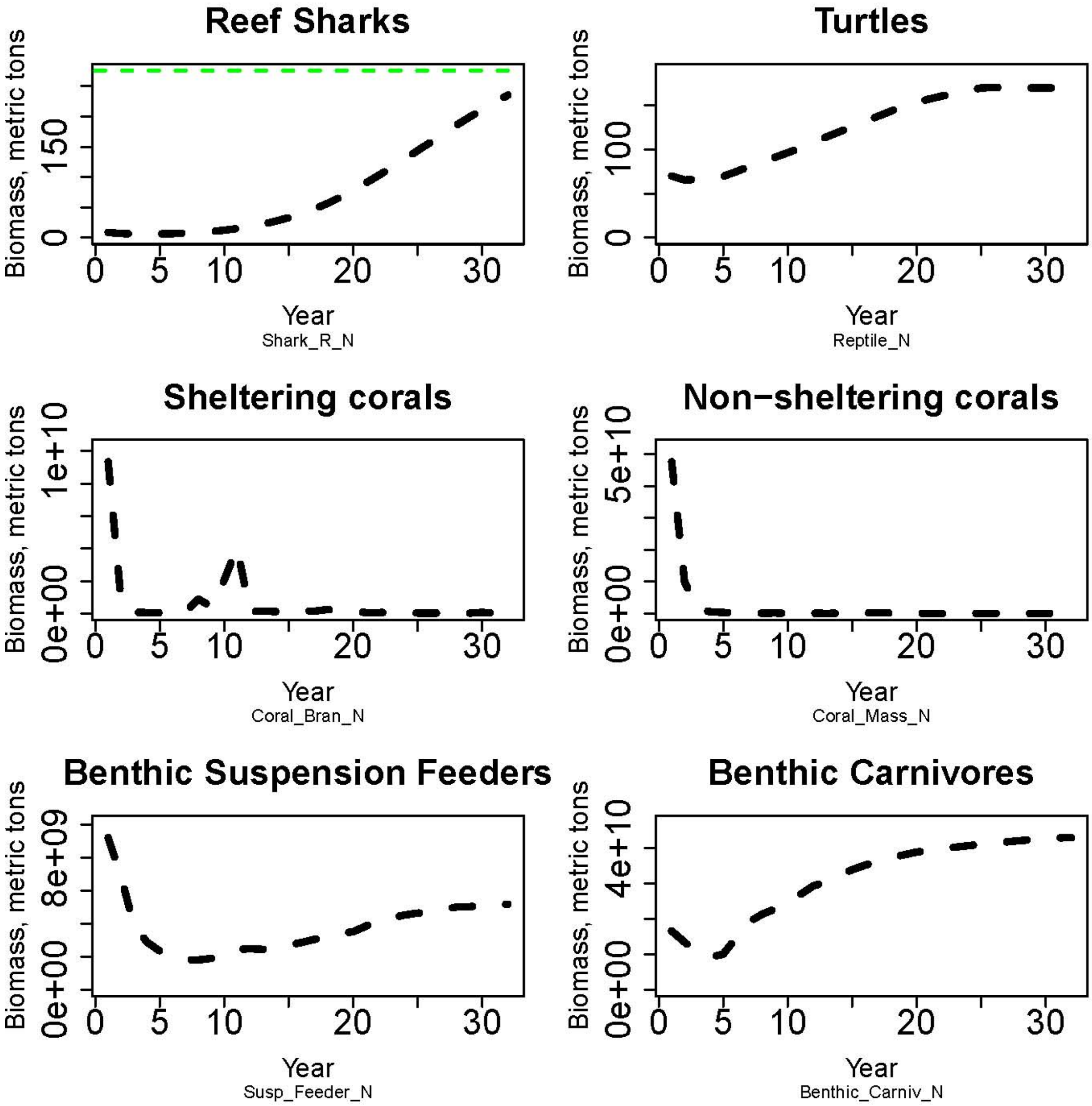

Figure 22d.--Biomass results for each functional group after initial tuning phase. Biomass is represented in metric tons summed over the entire model extent. Dotted green lines indicate mean biomass estimates for functional groups in marine protected areas where available (19 groups). *X*-axis shows number of years after start of simulation (2011).

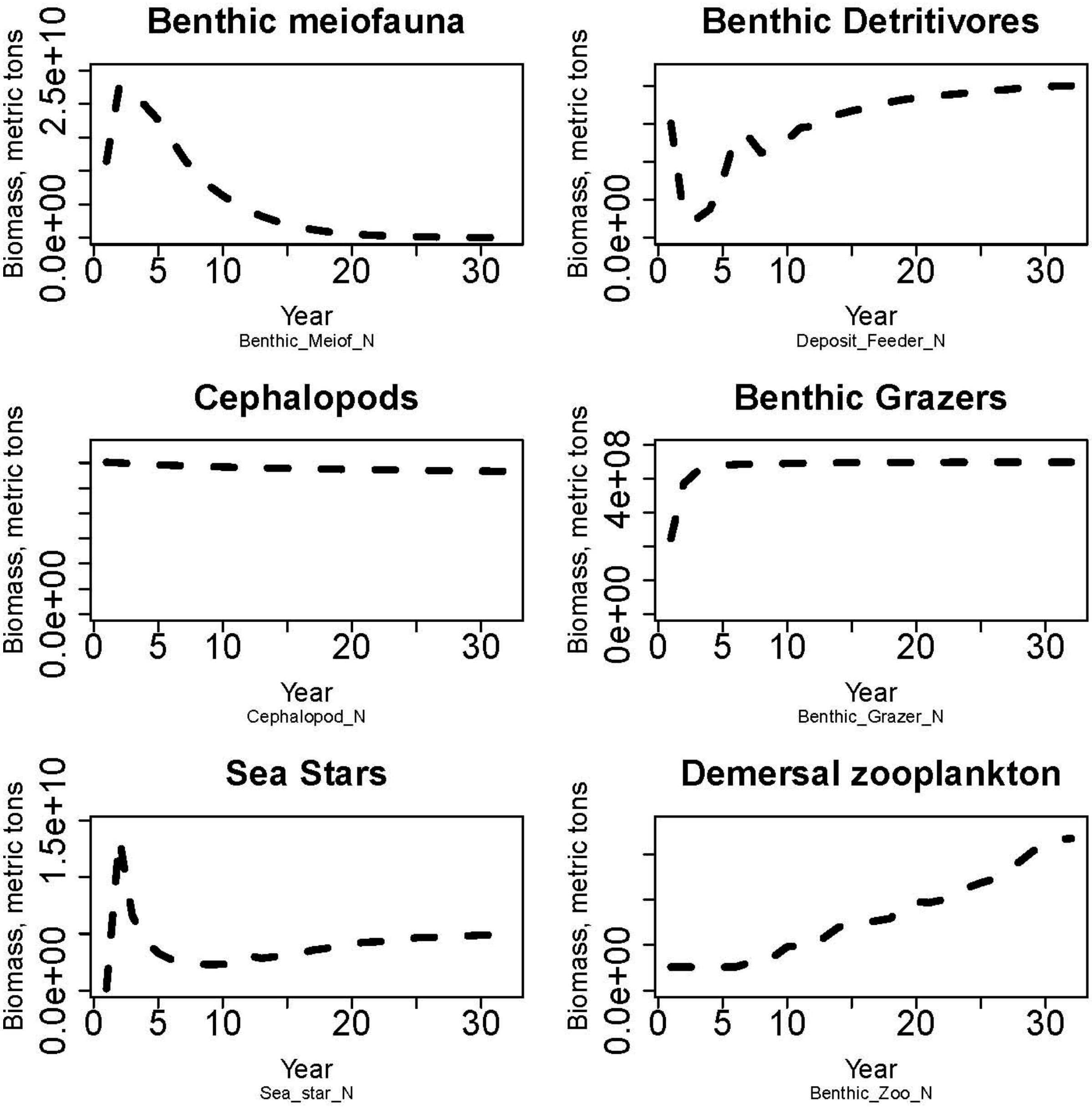

Figure 22e.--Biomass results for each functional group after initial tuning phase. Biomass is represented in metric tons summed over the entire model extent. *X*-axis shows number of years after start of simulation (2011).

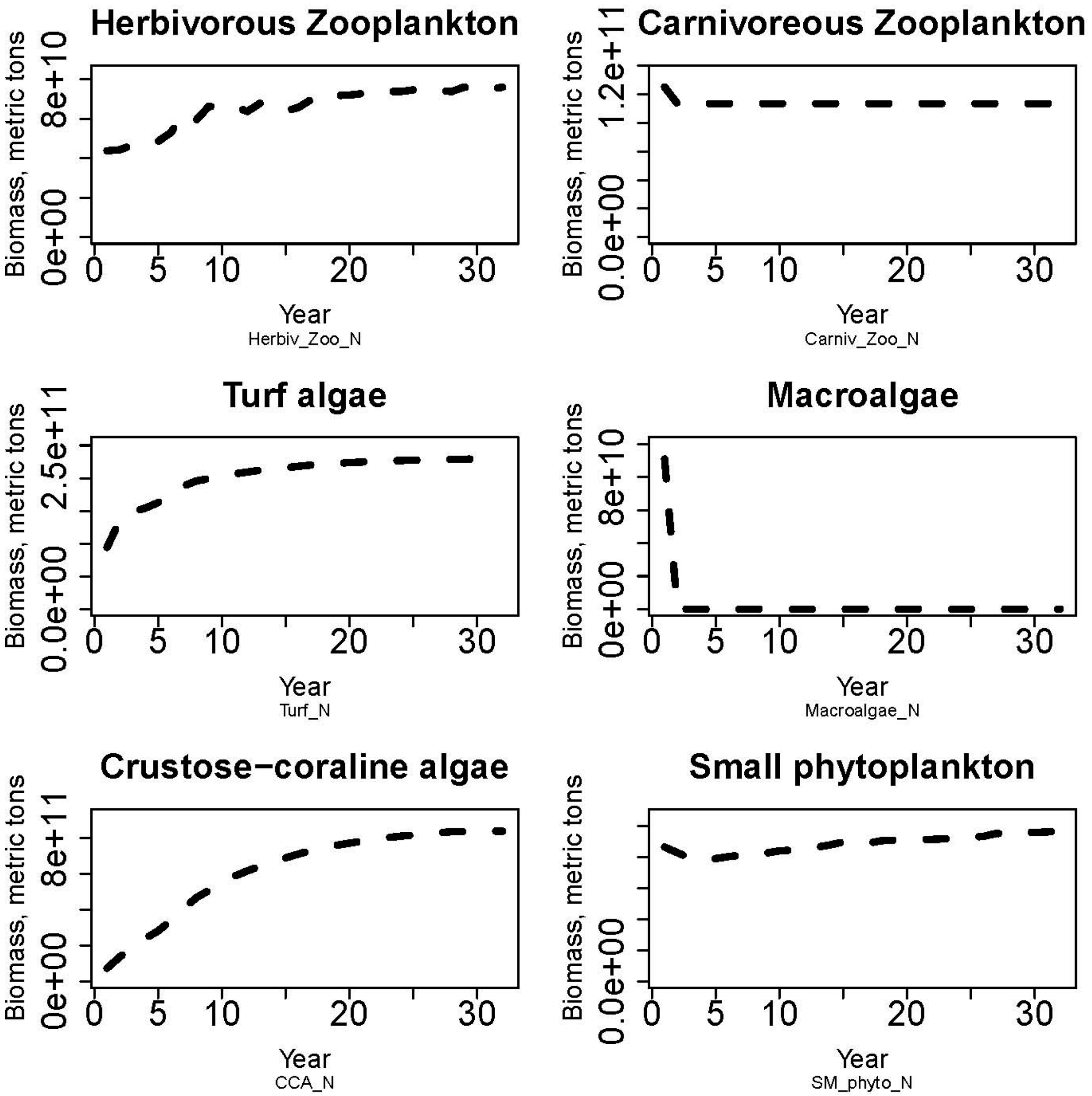

Figure 22f.--Biomass results for each functional group after initial tuning phase. Biomass is represented in metric tons summed over the entire model extent. *X*-axis shows number of years after start of simulation (2011).

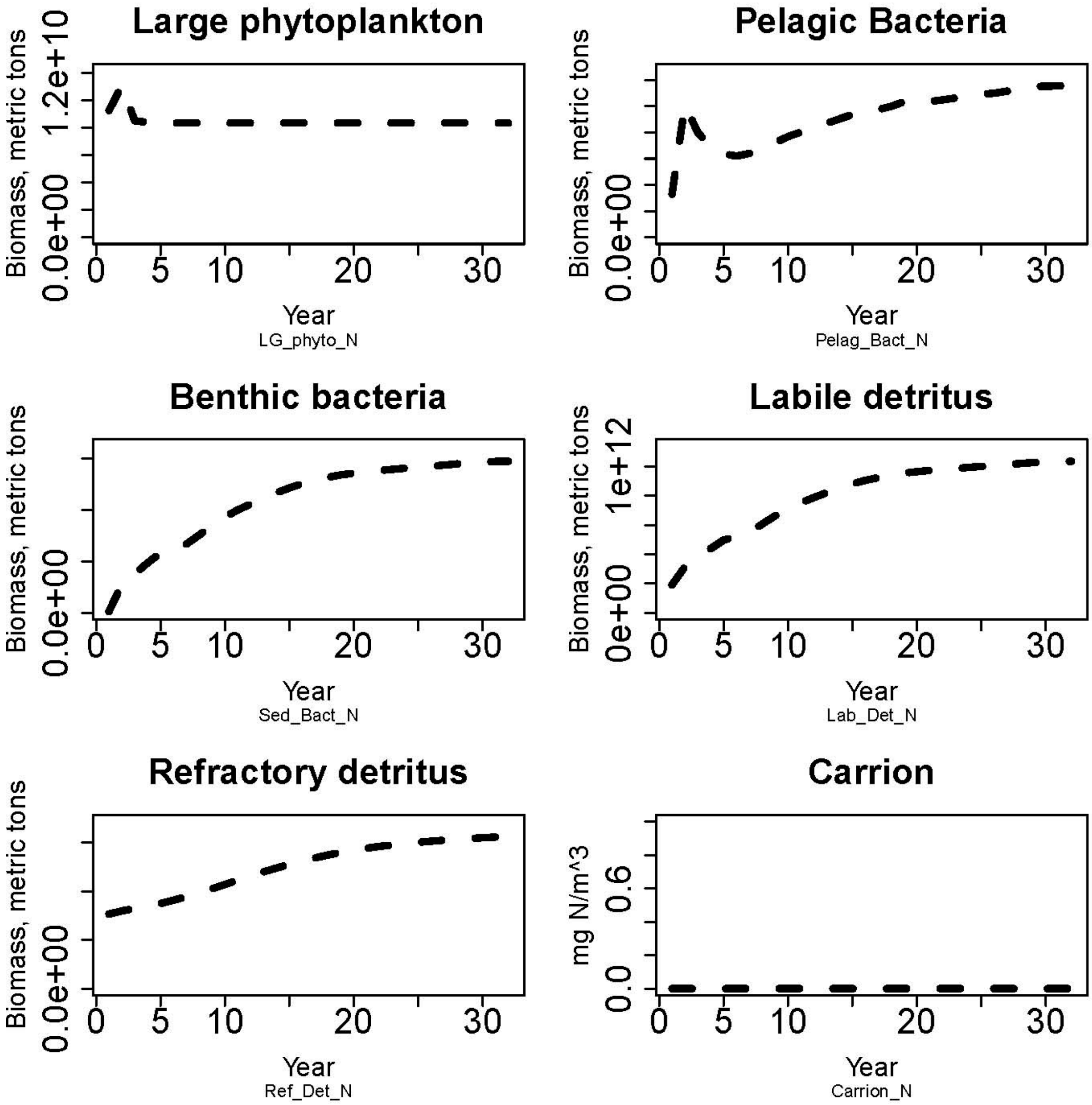

Figure 22g.--Biomass results for each functional group after initial tuning phase. Biomass is represented in metric tons summed over the entire model extent. *X*-axis shows number of years after start of simulation (2011).

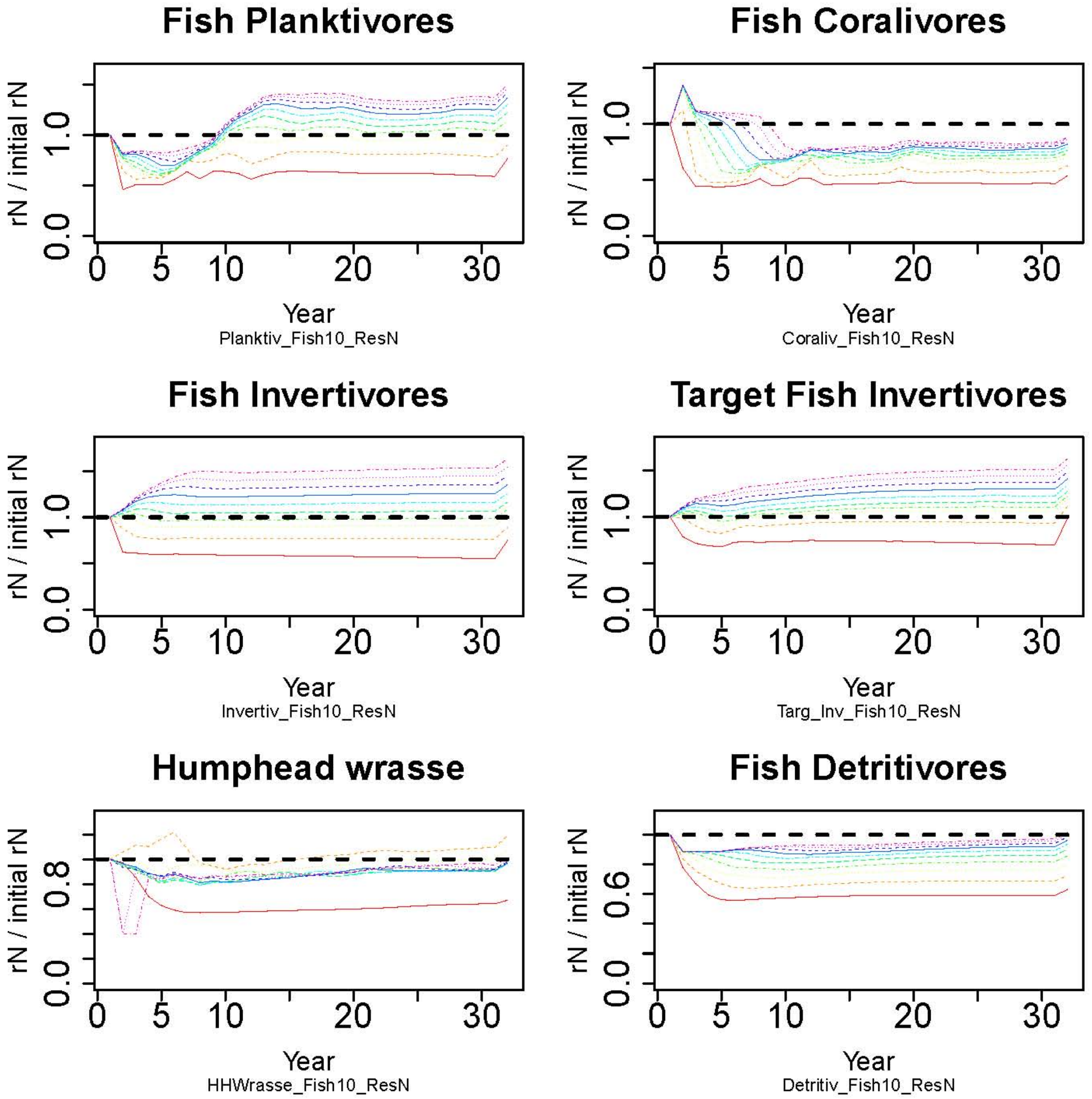

Figure 23a.--Ratio of reserve nitrogen to initial reserve nitrogen for each age class per vertebrate functional group after initial tuning phase. Age classes are plotted using a rainbow color scale, with red representing the youngest age class and violet the oldest. Reserve nitrogen represents weight at age that is related to muscle, fat, reproductive parts, and other soft tissue. As the ratio increases above 1, individuals become fat; as the ratio declines below 1, individuals begin to starve. *X*-axis shows number of years after start of simulation (2011).

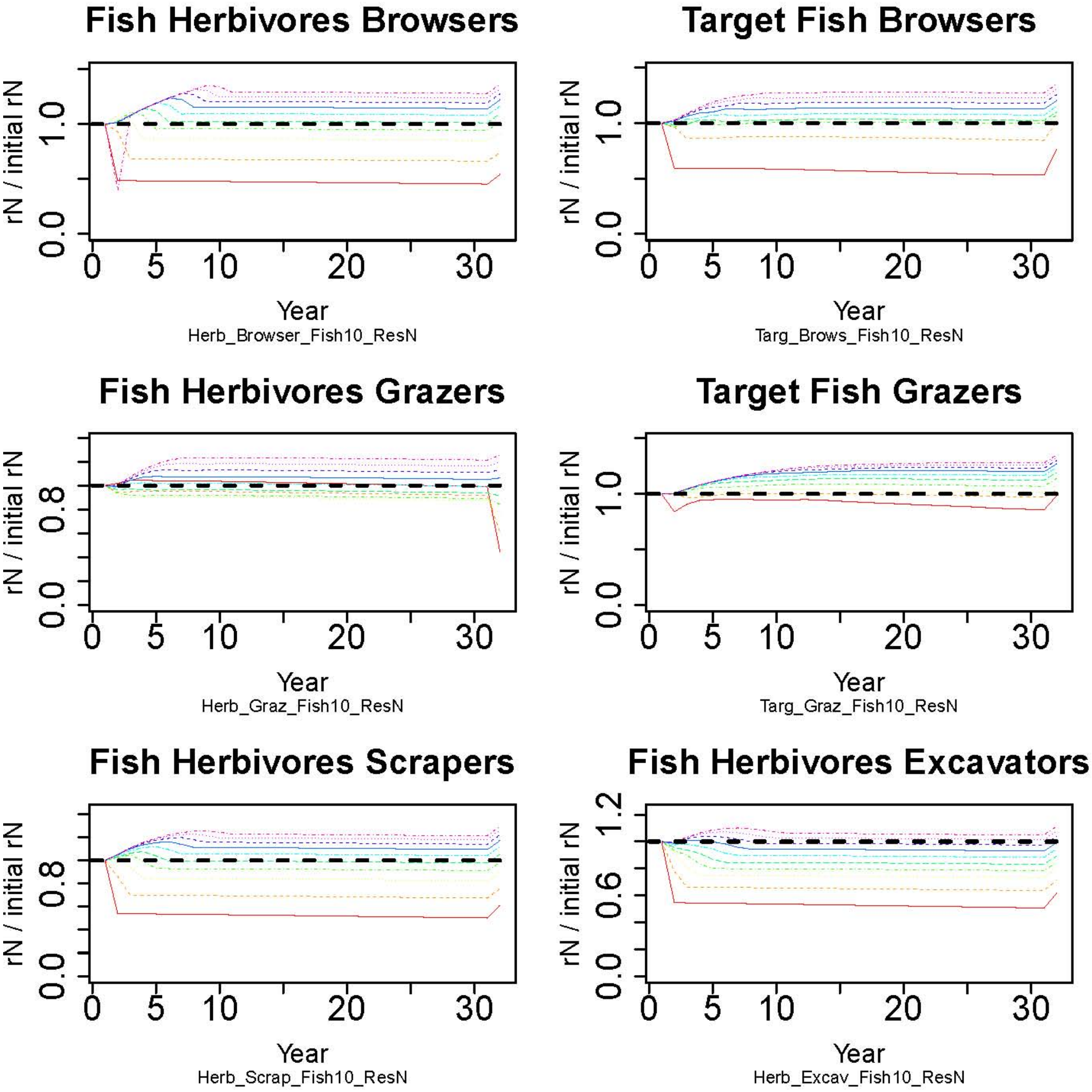

Figure 23b.--Ratio of reserve nitrogen to initial reserve nitrogen for each age class per vertebrate functional group after initial tuning phase. Age classes are plotted using a rainbow color scale, with red representing the youngest age class and violet the oldest. Reserve nitrogen represents weight at age that is related to muscle, fat, reproductive parts, and other soft tissue. As the ratio increases above 1, individuals become fat; as the ratio declines below 1, individuals begin to starve. *X*-axis shows number of years after start of simulation (2011).

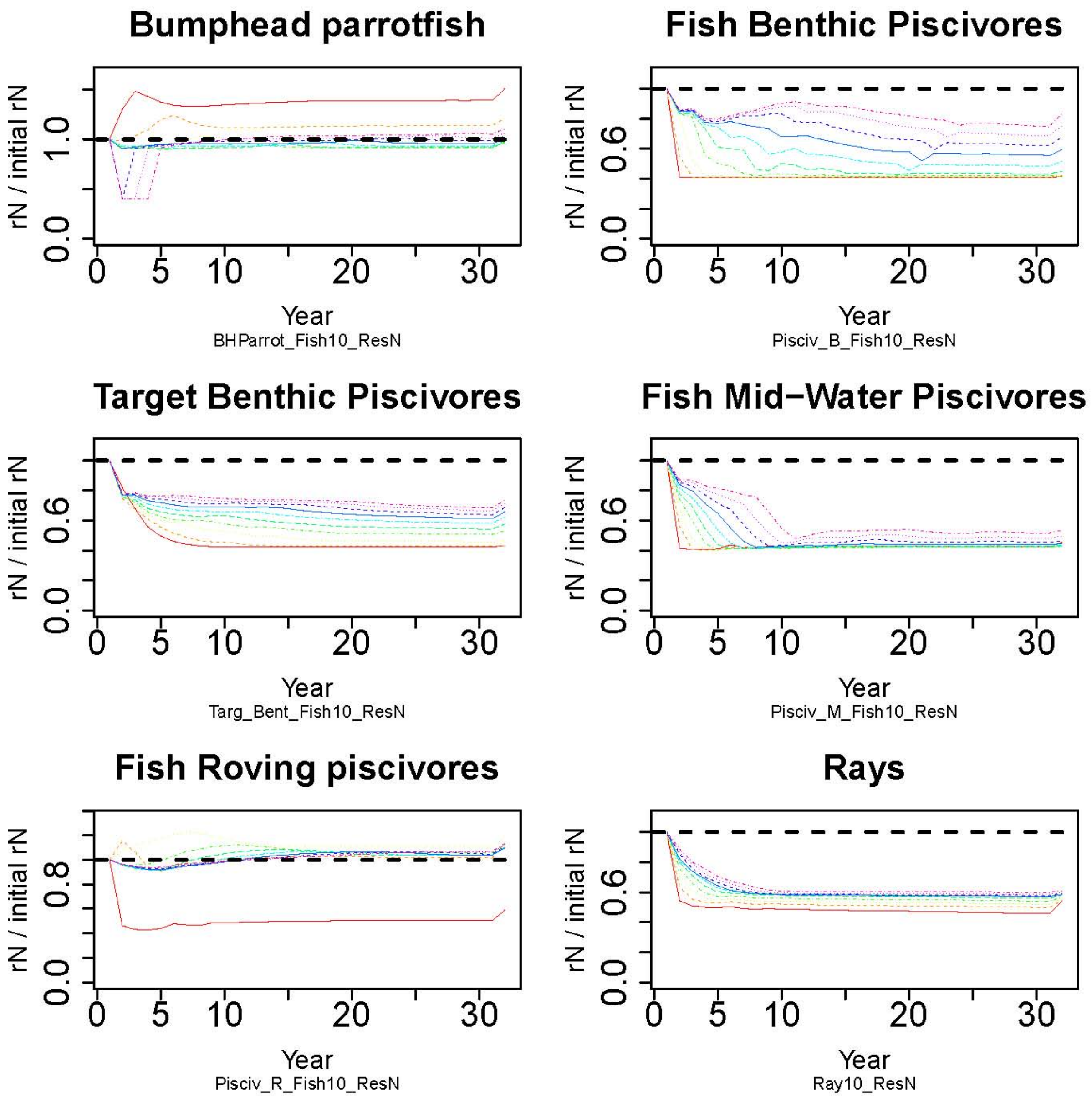

Figure 23c.--Ratio of reserve nitrogen to initial reserve nitrogen for each age class per vertebrate functional group after initial tuning phase. Age classes are plotted using a rainbow color scale, with red representing the youngest age class and violet the oldest. Reserve nitrogen represents weight at age that is related to muscle, fat, reproductive parts, and other soft tissue. As the ratio increases above 1, individuals become fat; as the ratio declines below 1, individuals begin to starve. *X*-axis shows number of years after start of simulation (2011).

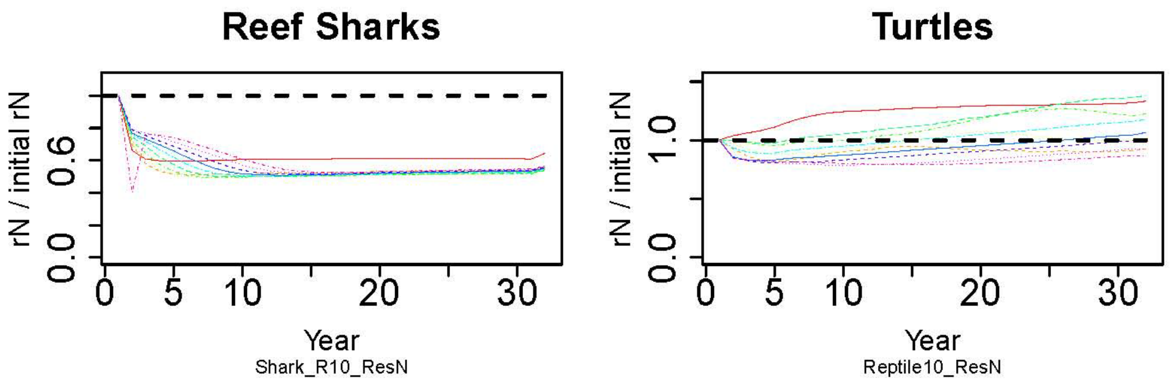

Figure 23d.--Ratio of reserve nitrogen to initial reserve nitrogen for each age class per vertebrate functional group after initial tuning phase. Age classes are plotted using a rainbow color scale, with red representing the youngest age class and violet the oldest. Reserve nitrogen represents weight at age that is related to muscle, fat, reproductive parts, and other soft tissue. As the ratio increases above 1, individuals become fat; as the ratio declines below 1, individuals begin to starve. *X*-axis shows number of years after start of simulation (2011).

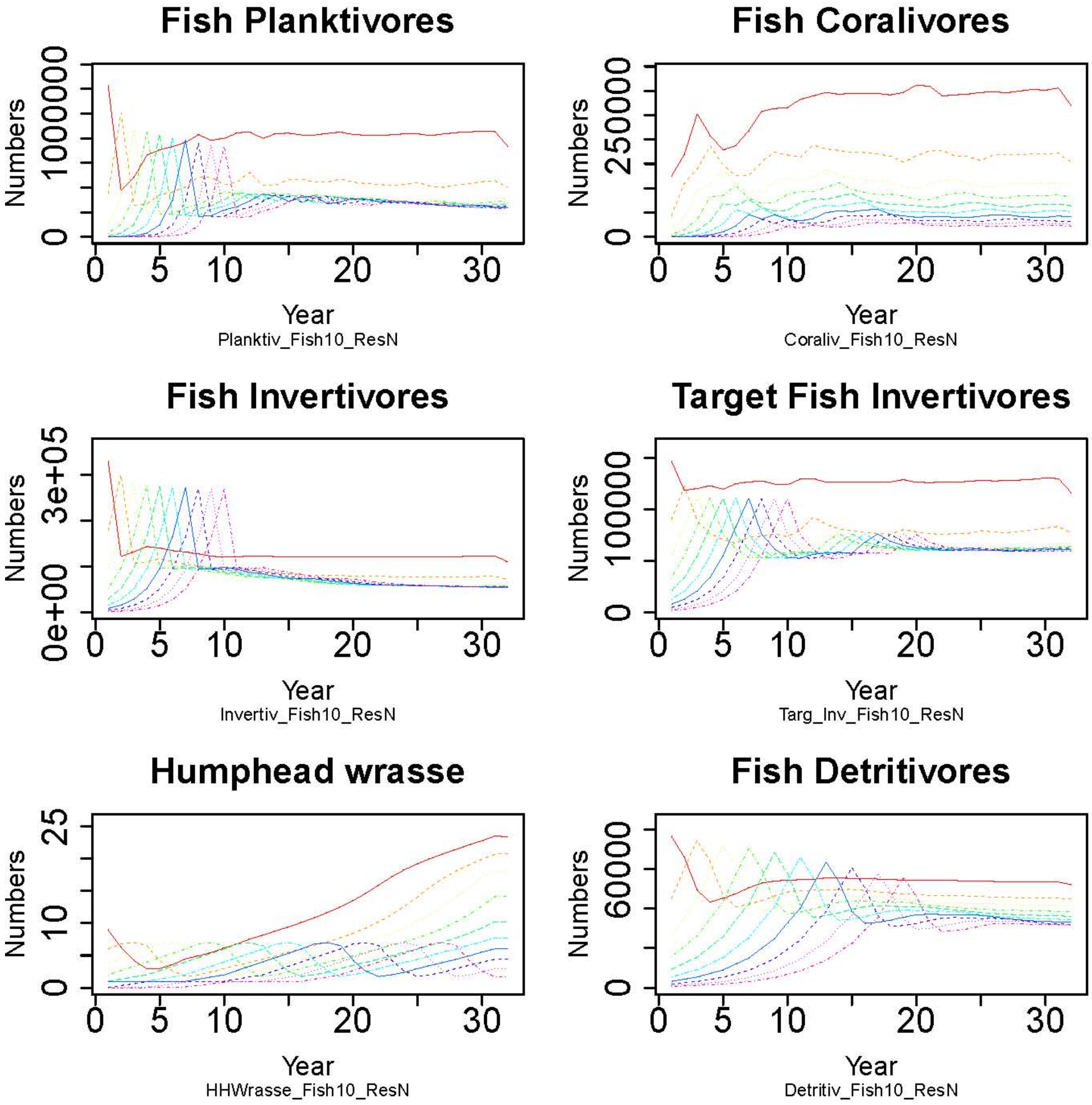

Figure 24a.--Total numbers for each age class per vertebrate functional group after initial tuning phase. Numbers are summed over the entire model extent. Age classes are plotted using a rainbow scale, with red representing the youngest class and the violet representing the oldest class. *X*-axis shows number of years after start of simulation (2011).

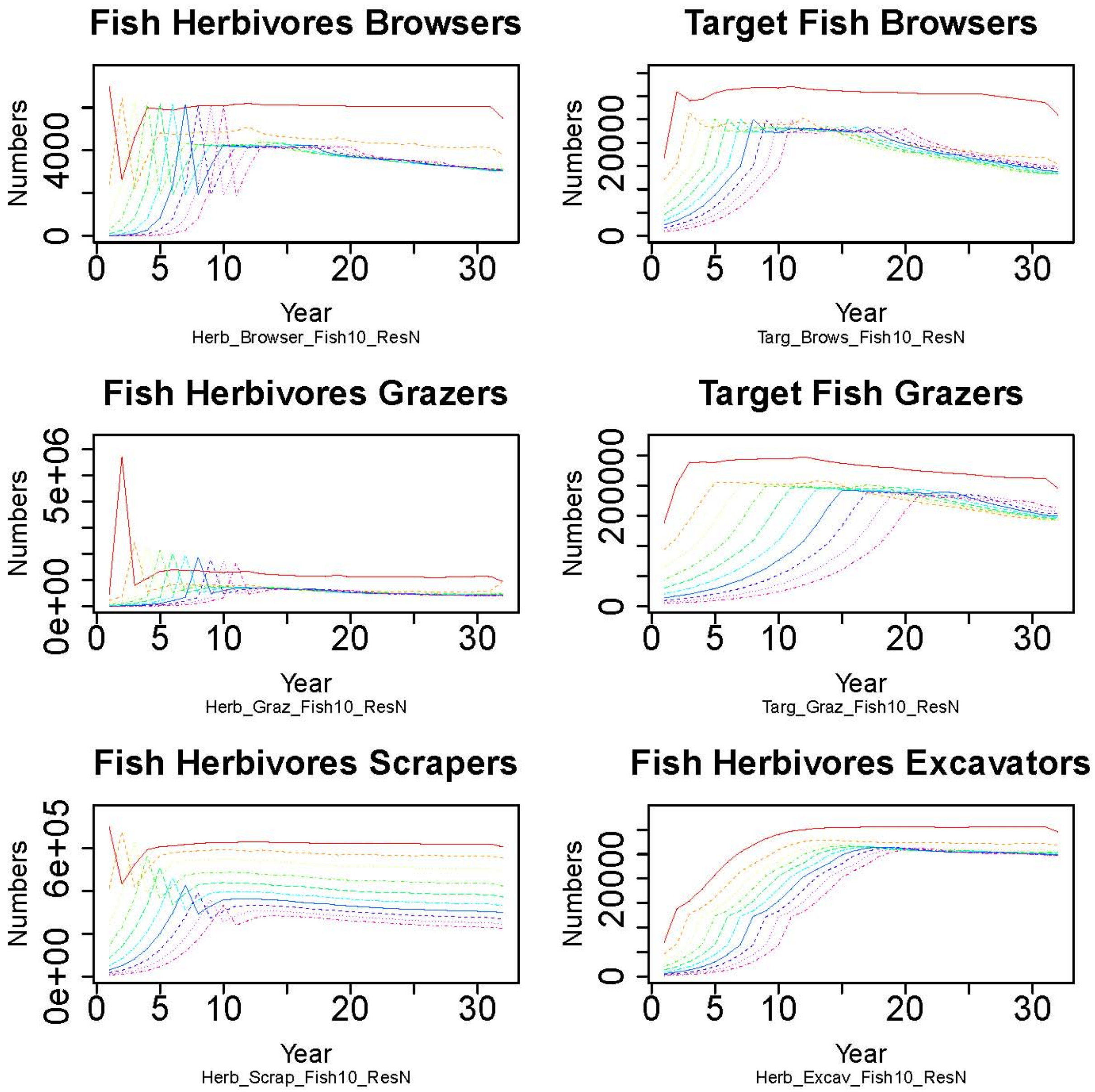

Figure 24b.--Total numbers for each age class per vertebrate functional group after initial tuning phase. Numbers are summed over the entire model extent. Age classes are plotted using a rainbow scale, with red representing the youngest class and the violet representing the oldest class. *X*-axis shows number of years after start of simulation (2011).

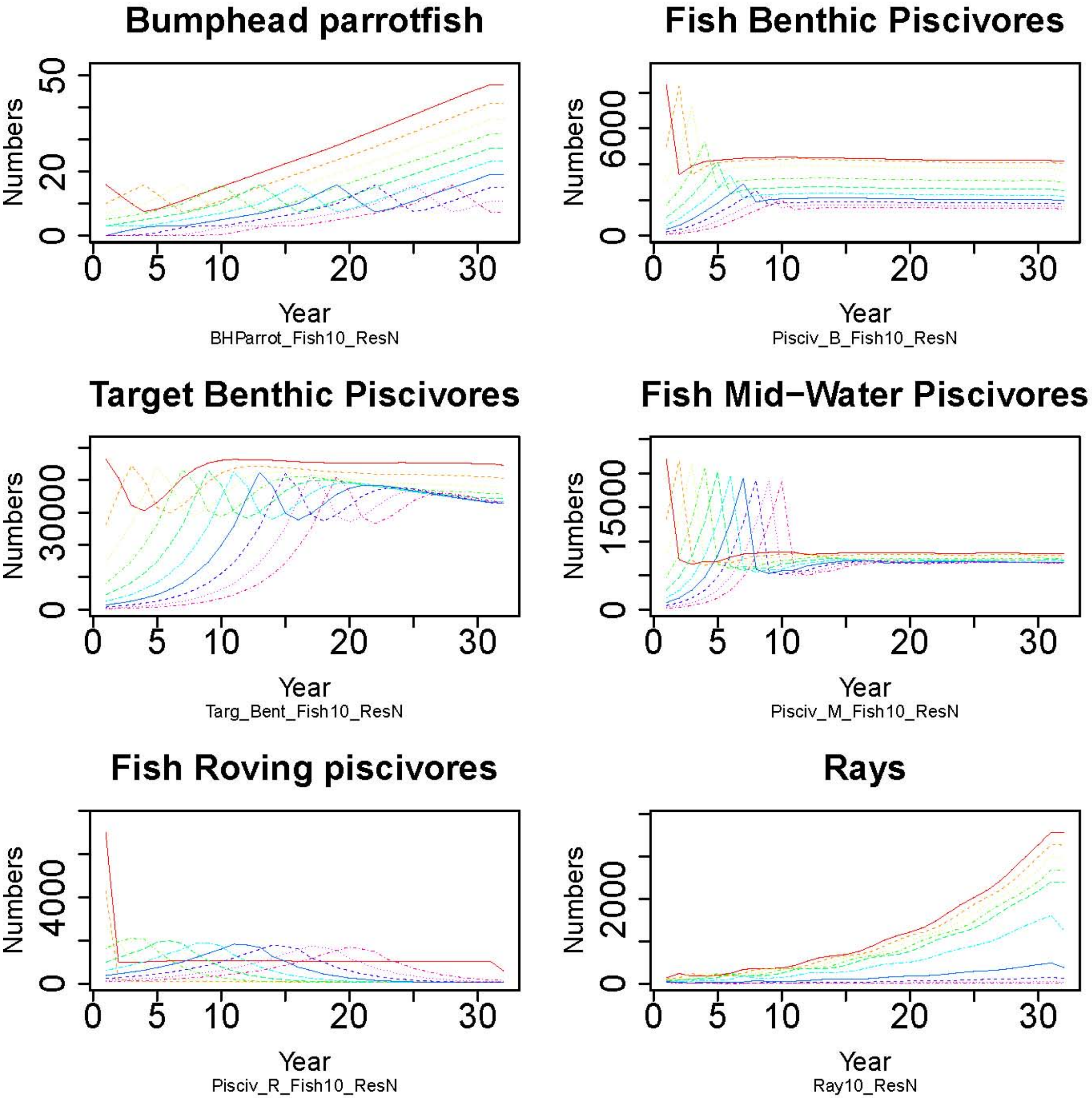

Figure 24c.--Total numbers for each age class per vertebrate functional group after initial tuning phase. Numbers are summed over the entire model extent. Age classes are plotted using a rainbow scale, with red representing the youngest class and the violet representing the oldest class. *X*-axis shows number of years after start of simulation (2011).

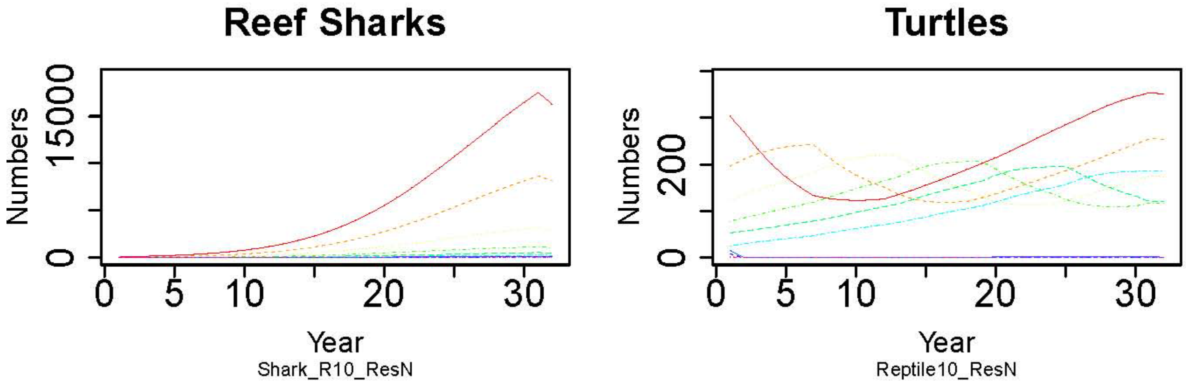

Figure 24d.--Total numbers for each age class per vertebrate functional group after initial tuning phase. Numbers are summed over the entire model extent. Age classes are plotted using a rainbow scale, with red representing the youngest class and the violet representing the oldest class. *X*-axis shows number of years after start of simulation (2011).

Secondary Calibration: Constant Fishing Pressure

In the second calibration, we applied constant fishing mortalities to evaluate biomass response to these harvest rates for each functional group of fish (Figs. 25a–d). We exerted an increasing fishing pressure on all vertebrate functional groups except Fish Invertivores, Fish Herbivore Browsers, Fish Herbivore Grazers, and Fish Benthic Piscivores. Biomass declined to half the initial biomass when fishing rates where equal to or exceeded natural mortality rates (Figs 25a–d) 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 in a decrease in intra competition and inter specific predation presure. Our results show that slow-maturing groups (Sharks, Turtles and Bumphead parrotfish) could sustain fishing mortality rates substantially higher than their natural mortality. In future calibrations we will explore how the low initial biomass of these groups influences these results. For the non-harvested fish groups, the biomass stayed similar to the initial biomass or increased likely as a result of reduced predation pressure.

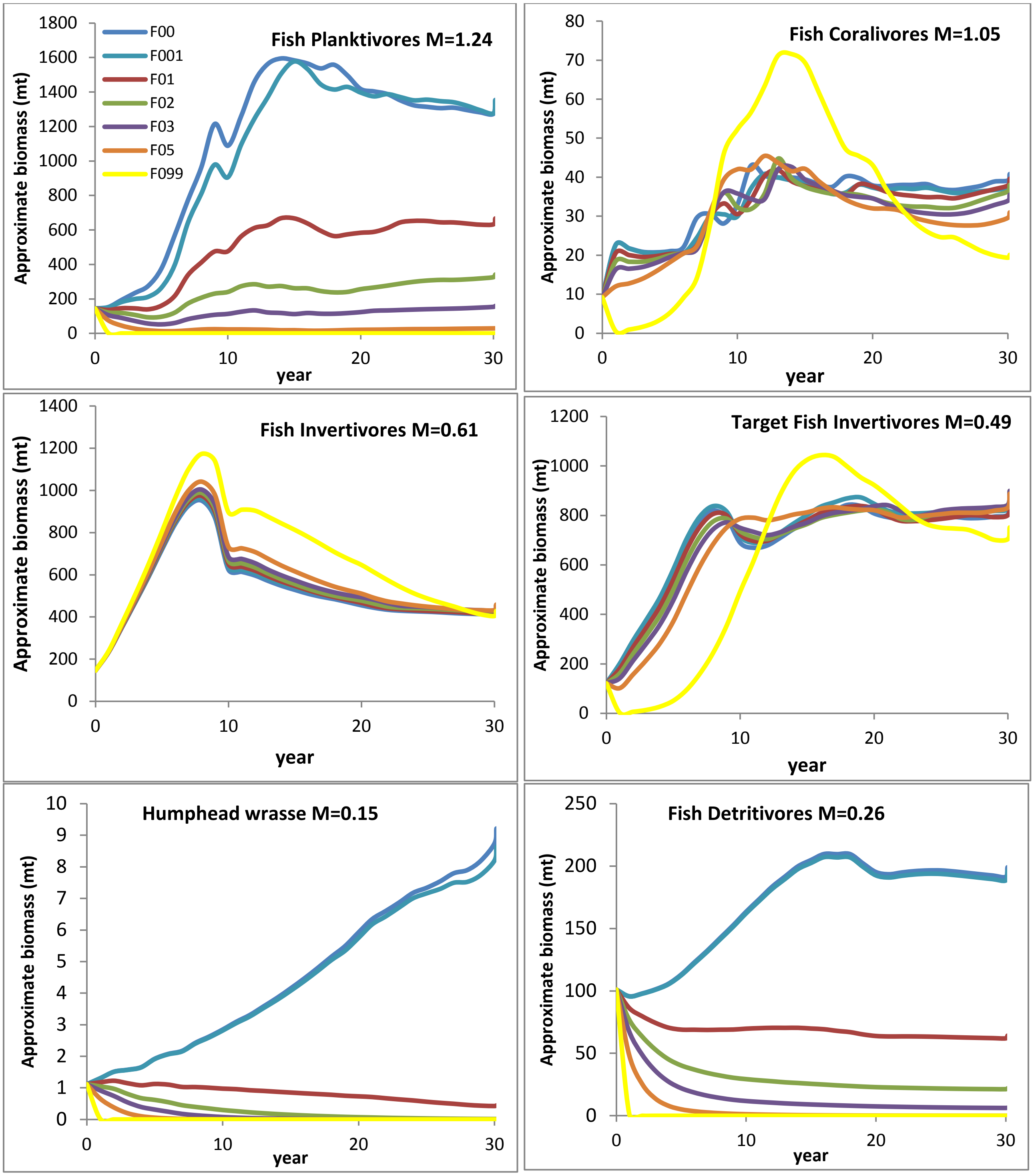

Figure 25a.--Biomass response of each functional group after secondary tuning phase exerting various levels of fishing pressures (F). Biomass is represented in metric tons summed over the entire model extent. *X*-axis shows number of years after start of simulation (2011). M is natural mortality. F00 is no fishing; F001 is a fishing pressure of 0.01; F01-F05 represents a fishing pressure of 0.1-0.5 and F099 is a fishing pressure of 0.99.

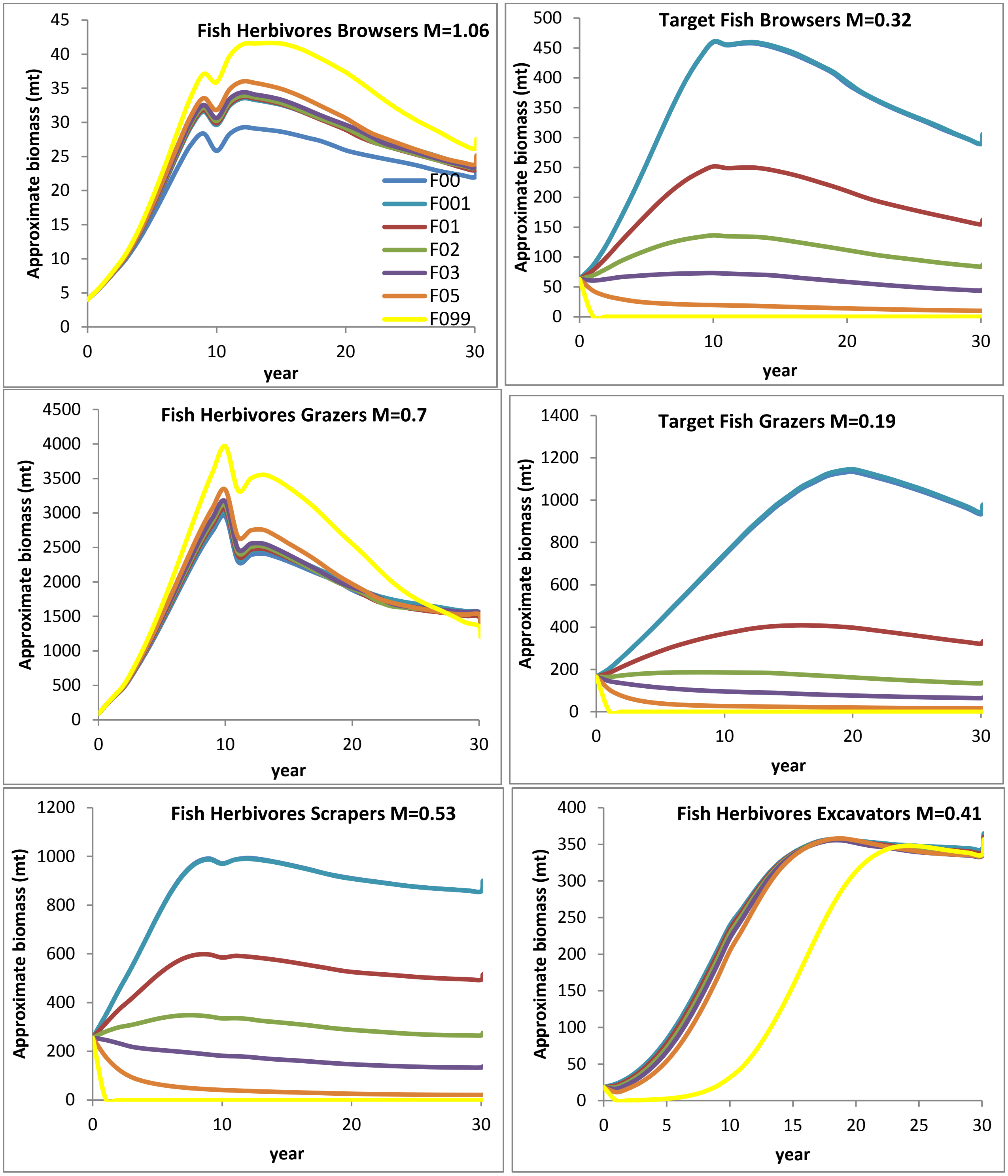

Figure 25b.--Biomass response of each functional group after secondary tuning phase exerting various levels of fishing pressures (F). Biomass is represented in metric tons summed over the entire model extent. *X*-axis shows number of years after start of simulation (2011). M is natural mortality. F00 is no fishing; F001 is a fishing pressure of 0.01; F01-F05 represents a fishing pressure of 0.1-0.5 and F099 is a fishing pressure of 0.99.

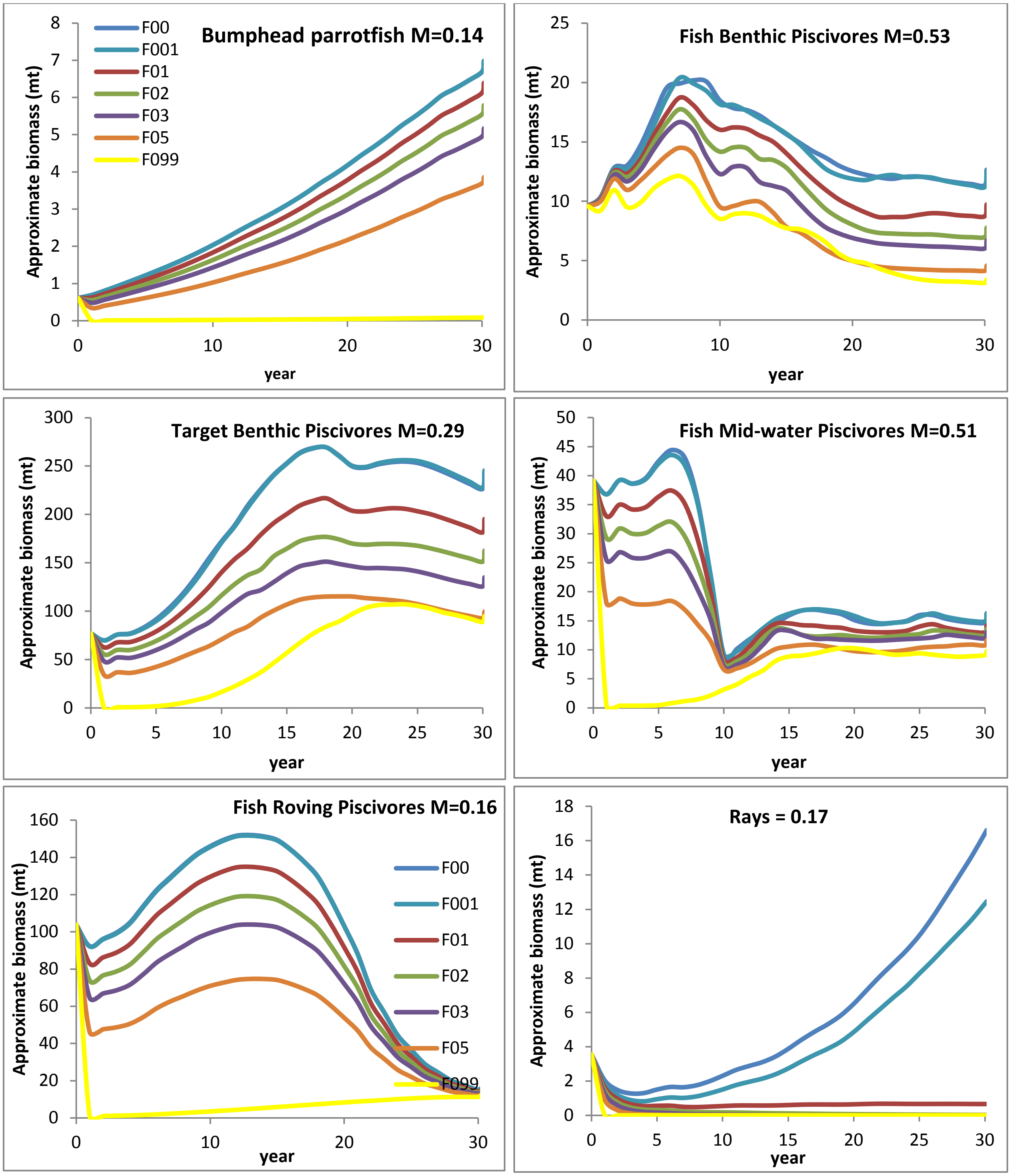

Figure 25c.--Biomass response of each functional group after secondary tuning phase exerting various levels of fishing pressures (F). Biomass is represented in metric tons summed over the entire model extent. *X*-axis shows number of years after start of simulation (2011). M is natural mortality. F00 is no fishing; F001 is a fishing pressure of 0.01; F01-F05 represents a fishing pressure of 0.1-0.5 and F099 is a fishing pressure of 0.99.

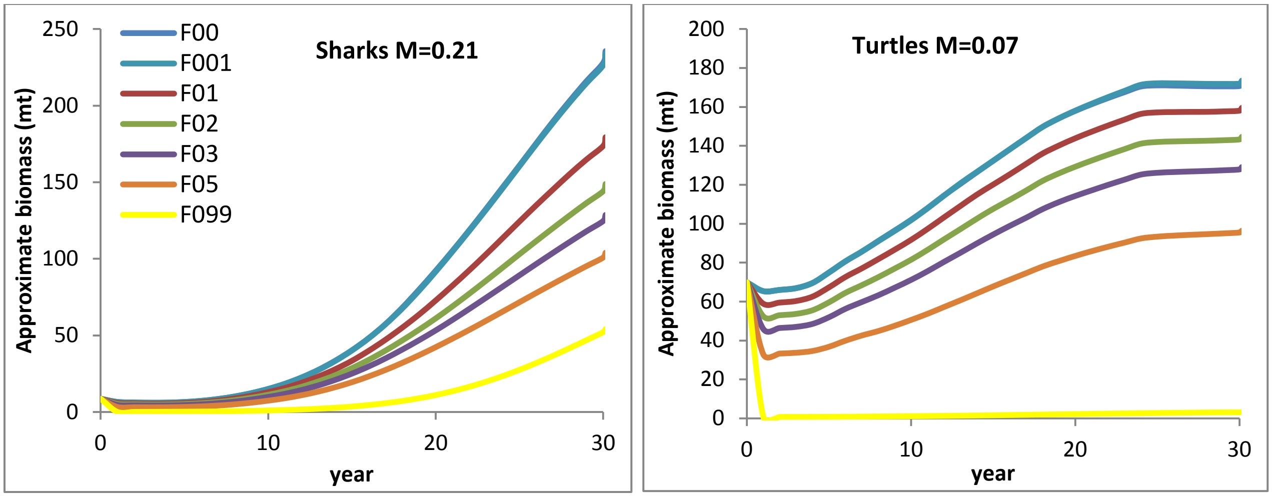

Figure 25d.--Biomass response of each functional group after secondary tuning phase exerting various levels of fishing pressures (F). Biomass is represented in metric tons summed over the entire model extent. *X*-axis shows number of years after start of simulation (2011). M is natural mortality. F00 is no fishing; F001 is a fishing pressure of 0.01; F01-F05 represents a fishing pressure of 0.1-0.5 and F099 is a fishing pressure of 0.99.

DISCUSSION

Human-induced pressures 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 personel 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, 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 technical memorandum was to report on the design of the model framework and the parameterization of the spatial and ecological submodel. Improvements described below, especially for coral dynamics and oceanography, are planned in the short term. Following these, the model may be used to tests simple management strategies related to fishing effort, fishing areas and closures, simple ocean acidification scenarios, and potentially nutrient and sediment loading. 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. (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 (2011; 2013) and Kaplan and Leonard (2012).

The development of the Guam Atlantis Coral Reef Ecosystem model has been useful in integrating available data streams and identifing 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 (invertebrates living in the sediment or benthic groups also called cryptic fauna), 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 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.

At this moment, Guam Atlantis does not include code specific to coral reef dynamics. This updating is still a work in progress. 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 simultions 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 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. This submodel will be based on the Delft3D modeling framework which uses the global Hybrid Coordinate Ocean Model (HYCOM)[13] to provide boundary conditions and is under development by Deltares[14] and the U.S. Geological Survey[15]. The Delft3D model has highly detailed flows and transport patterns along west-central Guam (grid size 0.5 km) and coarser grid sizes (2 km) for the rest of Guam. HYCOM has a high vertical resolution in coastal regions as it follows the terrain but constrains vertical grid points geometrically to remain at a fixed depth instead of joining and flowing them to close-by grid points with the same reference density. Output data from the Delf3D model will be integrated at 12-hour time steps across horizontal and vertical polygon boundaries. For projections lasting longer than the modeled time series, the data will be looped. Including the Delft3D model output will greatly enhance the model's ability to reflect Guam's reef dynamics, especially in southern Guam where sediment input is a major stressor to reefs.

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[13] See hycom.org for details.
[14] www.deltares.nl
[15] walrus.wr.usgs.gov/index.html

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 (e.g., historical bleaching events, COTS outbreaks, typhoons) will be performed in future versions of Guam Atlantis.

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APPENDIX A—BRIEF REVIEW OF PROXIMATE THREATS TO CORALS AND HOW THEY ARE INCORPORATED INTO THE GUAM ATLANTIS MODEL

We categorized the threats to coral, ordered by their importance for detrimental effects on corals following Brainard et al. (2011) (Table A1).

Table A-1.--Summary of identified threats to corals (Brainard et al., 2011), physiological response of corals and likely effect and how these effects are incorporated in the model. See text for details.

Scale	Proximate Threat	Physiological Response	Likely Effect	Modeled
Global	Ocean Warming	Expulsion of zooxanthellae; increased susceptibility to pathogens	Increased mortality; impaired recruitment; increased disease rate; decrease in productivity	Effects will be included in the final model but as yet only are represented via temperature dependency of baseline rates.
Local	Disease	Change in microbial community within coral symbiont	Mortality high for branching, low for massive corals, and exacerbated by temperature increase	Will be incorporated in the final model.
Global	Ocean Acidification	Reduced calcification and reef cementation; reduced juvenile survival; reduced fertilization success	Reduced growth in calcifying organisms; increased porosity; decreased survival juveniles; decreased number of recruits	Represented via pH-dependency of baseline rates in the final model
Local	Reef Fishing—Trophic Effects	More energy available for growth as a result of decreased space competition with algae	Parrotfish, especially large (> 35 cm) ones, can maintain 30% of reef area in a cropped state, this increases the coral growth rate and recruitment; large-bodied parrotfishes can also crop down macroalgae, small-bodied parrotfish can only keep turf algae in a cropped state. Apex predators will have a beneficial effect on coral growth as they control coralivores.	Space competition between benthic functional groups; habitat dependency of corals on hard substrate, coral and crustose coralline algal cover. Trophic effects are captured through the diet matrix.

Scale	Proximate Threat	Physiological Response	Likely Effect	Modeled
Local	Sedimentation	Energy investment in removal of sediment particles, reduced growth rate, reduced recruitment	Reduced growth rate with a higher reduction for massive than branching corals	Included as impact with time series where sedimentation increases turbidity which decreases light attenuation which reduces primary productivity. Coral specific dynamics in relation to sedimentation will be incorporated in final model
Local	Nutrients	Increase zooxanthellae density	Reduced growth rate and recruitment of corals. Increase in phytoplankton and macroalgal growth.	Growth is controlled by half saturation constant for each primary producer. At present coral recruitment is only represented by biomass of corals. In final model coral recruitment processes will be more realistic.
Local	Toxins	Disruption of metabolisms	Reduced growth rate and recruitment	Not modeled
Global & Local	Changing Storm Tracks/Intensities & Natural Physical Damage	Breakage in response to storm of especially branching	Episodic coral fragmentation with low survival rate, opening up of substrate which will be filled in by fast growing species.	Disturbances are not included in the present model but will be in the final model.
Local	Predation of corals	Energy shift to healing lesions, reduced larval survivalship	Increased coral mortality when coral cover is < 5%/increased coral mortality with episodic predator outbreaks	Predation modeled through prey availability (diet) matrix so more piscivores, less coralivores, less predation on corals
Local	Ornamental Trade	Removal of corals, reef fish and invertebrates	Depending on collection methods, destruction of habitat	Included in Fishery submodel to be developed in 2014

Global Threats

The present model is parameterized without the impacts of global threats. In 2014, we will include the effects of these important threats, especially ocean warming and acidification to corals by representing those threats via temperature and pH dependency of the baseline rates.

Local Threats

Reef Fishing

Harvest of reef fishes alters trophic interactions that are particularly important on structuring coral reef ecosystems including altering recruitment success of corals which is higher when larvae settle on crustose coralline algae than on macroalgae (Dulvy et al., 2004; Mumby et al., 2007). Fishing has indirect effects via trophic cascades on space competition with algae and coral mortality from predators and through transmission of disease (Brainard et al., 2011).

Resilience of reefs can be enhanced or maintained by healthy herbivore populations, especially by herbivorous wrasses and large (> 35 cm) parrotfishes (Bellwood et al., 2011; Ong and Holland, 2010). A high species richness of herbivorous species, which have complementary feeding behavior (Bellwood et al., 2006), can reduce the standing stock of macroalgae and increase the cover of crustose coralline algae and live coral cover (Burkepile and Hay, 2008). These interactions between coral cover, macroalgal cover, and grazers can drive positive or negative feedbacks on the benthic composition (Mumby et al., 2006).

The coral-algae-grazer interactions are, at the moment, only modeled through the inclusion of parameters of space competition and habitat dependency (e.g., corals depend on habitats with corals, crustose coralline algae [CCA] or hard substrate). In 2014, these dynamics will be refined to simulate reef processes more accurately, following the formulations outlined in Melbourne-Thomas et al (Melbourne-Thomas et al., 2011) and Fulton et al (Fulton et al., 2006).

Corallivorous fish and invertebrates are controlled by their predators. When these predatory fish are removed from reefs, corals will be more predated upon and will be more likely exposed to disease through transmission by corallivores. Predation is modeled through the prey availability matrix.

In Guam, the largest component of reef fish landings is unicorn fish (*Naso* sp) making up 38% of the total reef fish landings in the last decade (Fig. A-1).[16] Unicorn fishes can be either planktivorous (e.g. *Naso annulatus*, *N. brevirostris*, *N. hexacanthus*) or herbivorous (e.g. *Naso brachycentron*, *N. tonganus*, *N. lituratus*, *N. unicornis*). In Guam, 88% of the total biomass of *Naso* sp. are herbivores (CRED unpubl data) which crop macroalgae and are, therefore, important in keeping these algae under control.

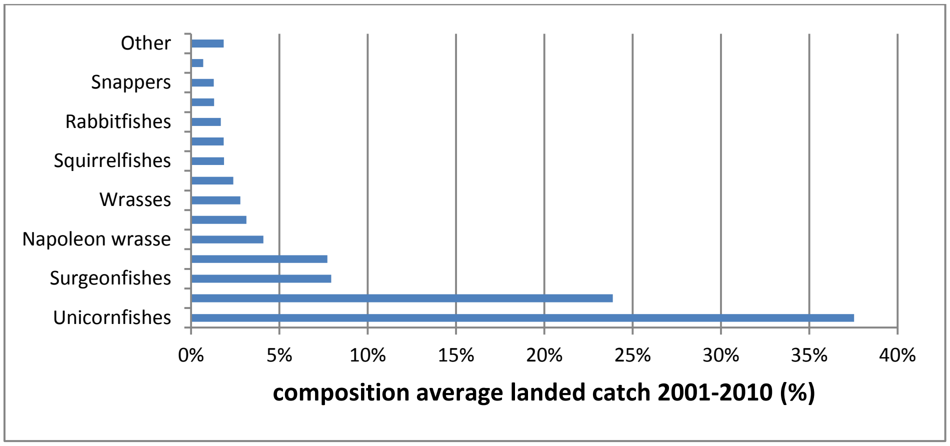

Figure A-1.--Composition of the average reef fish landings from 2001 to 2010 including both boat-based and shore-based fisheries.[16]

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[1] **www.pifsc.noaa.gov/wpacfin/guam/dawr/Pages/gdawr_data_4.php**

For the simple model version presented here, detailed representation of fishing is not included. However, to test the productivity of the stocks as part of model calibration, we test a range of fixed fishing mortalities (see 'Model Tuning and Diagnostics' under 'Methods').

Destructive Fishing Practices

Fishing activities that degrade the habitat by destroying the three-dimensional reef structure greatly reduce the long-term recovery of reef fish stocks (DeMartini and Anderson, 2007). Derelict fishing gear and various passive fishing practices can also destroy benthic structure and habitats, kill reef-building organisms, and entangle benthic and mobile fauna (Donohue et al., 2001). The extent to which it damages coral reef ecosystem is region dependent, with substantial habitat destruction as a result of blast fishing in southeast Asia. In Guam, as in many other parts of the world, derelict fishing gear is a problem but because we have no quantitative data on the damage it does, we decided not to include this threat into the model.

Land-based Sources of Pollution

Human activities in coastal watersheds introduce sediment, nutrients, chemical contaminants, and other pollutants into the ocean by various mechanisms, including river discharge, surface runoff, groundwater seeps, and atmospheric deposition. Coastal human populations and their collective consumption of natural resources have continued to increase unabated, as has human impacts on reef ecosystems (Burke et al., 2011).

Land-based sources of pollution cause various stresses to corals as summarized below (reviewed in Brainard et al., 2011).

Sediments—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 toward more sediment–tolerant species assemblages depending on the duration and load of the sedimentation. Soil erosion is a serious problem in the southern part of Guam affecting soil quality, water quality, and the coral reef ecosystem (Burdick et al., 2008; Kottermair et al., 2011; Porter et al., 2005). This part of the island is of volcanic origin with steep hills, 14 major watersheds and over 40 streams discharging in the coastal waters (Fig. 1).

Various studies have been conducted to characterize the flow discharge rates (Tetra Tech, 2012) and sediment dynamics (Minton et al., 2006; Scheman et al., 2002; Storlazzi et al., 2009; Wolanski et al., 2003a; Wolanski et al., 2003c). Soil erosion was estimated to be between 480 and 1200 t/km^2/y depending on the steepness of the slopes, the area of badlands (exposed patches of earth) and the amount of rainfall (Scheman et al., 2002). The sediment-laden river discharges are highest after large storm events and at the start of the wet season when the river beds have accumulated sediments from the small rain events during the dry season (Minton et al., 2006; Storlazzi et al., 2009; Wolanski et al., 2003a). Erosion increases as a result of wildfires, off-roading, upslope construction and agriculture, and runoff is exacerbated when these activities take place in the wet season (Kottermair et al., 2011; Minton et al., 2006). When the main roads were upgraded along the southwest coast in the early 1980s, erosion from this construction project was responsible for a complete burial of the coral communities adjacent to the construction (Birkeland, 1997) and the reefs appear not to have fully recovered (Wolanski et al., 2003a; D. Minton pers. comm 12/18/12). Erosion of burned land or badlands (Fig. A-2) results in six times as much sediment runoff than erosion of vegetated (savannah) land in the wet season and 18 months later erosion of these badlands is still twice as high as from vegetated lands (Minton et al., 2006).

Tetra Tech in collaboration with the Environmental Protection Agency has developed models to predict the amount of discharge for two watersheds in the central part of Guam (Tetra Tech, 2012). Additionally, the U.S. Geological Society (USGS) has continuous flow meters in three locations that measure sediment loads.

Figure A-2.--Orange bad land and steep hills in a watershed on the south coast of Guam (NOAA photo).

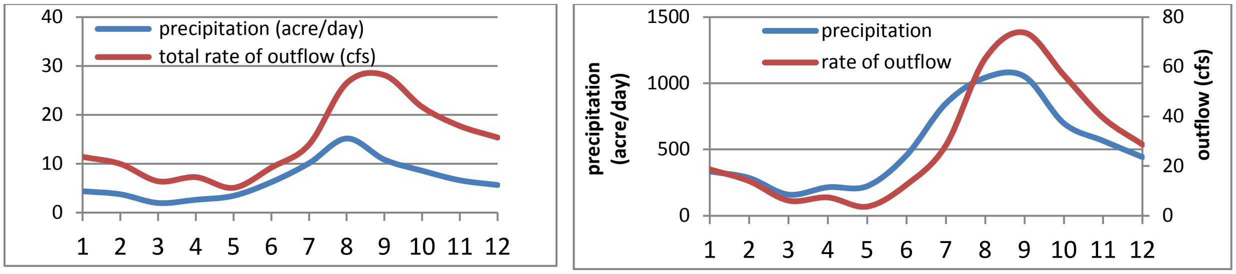

Figure A-3.--Average seasonal precipitation and modeled outflow volume into (*left*) Apra Inner Harbor from the Atantano River with a watershed area of 0.11 km^2 and (*right*) Pago Bay from the Pago River with a watershed area of 8.42 km^2. X-axis represents months of the year. (Tetra Tech, 2012)

These model outputs show that discharge rates are up to three times as high in the wet season (August to December) compared with the dry season, and that discharge rates are strongly related to precipitation (Fig. A-3). It is also clear that precipitation varies enormously by region around Guam with the central-southern part receiving the highest (292 cm/y) amount of rain (Lander and Guard, 2003). In northern Guam nonpoint sources of pollution through underground seepage is an important source for terrigenous nutrient input and in southern Guam surface runoff is a key source. There are also two sewage treatment plants with primary treatment and outfall pipes discharging in the coastal waters. Additionally, 41% of the households are still on septic tanks resulting in the untreated sewage entering coastal waters. Guam's Environmental Protection Agency (EPA) listed 11 out of 24 assessed bays as 'impaired' in 2010 (Guam EPA, 2010).

Sediment discharge has been modeled for two watersheds in Guam but nutrient discharge has not been modeled. However, for a watershed in Hawai'i with similar characteristics (volcanic, steep slopes, high rain fall) and upslope activities (e.g., feral population, vegetation type, human coastal population size) such a model was developed and we use those model outputs for nutrients corrected for flow rate conditions on Guam for Guam Atlantis input (see section in main text 'Forcing files,' 'Flow, nutrient and sediment input').

The fate of the pollutants in the discharge depends on coastal hydrodynamic conditions (Storlazzi et al., 2009; Wolanski et al., 2003a). Flows in and around the coral reefs influence the residence time of sediments, nutrients, and contaminants and, therefore, affect the amount of deposition of sediment on corals and other benthic organisms, that could potentially stimulate algal growth and trigger coral diseases and determine the duration and amount of light that is available for photosynthesis. Waves influence the vertical mixing and, therefore, the amount of freshwater that reaches the corals and re-suspension and transport of settled sediments. All these aspects are unfavorable for coral growth through the hampering of coral productivity as a result of lower light availability caused by the more turbid waters and the diversion of energy from growth to clearing sediments or to competing for space with algae that benefit from elevated nutrient concentrations (Fabricius, 2005; Riegl and Branch, 1995).

Additional consequences of sediment input and land-based sources of pollution are a decrease in coral reproduction, a decrease in coral recruitment, and a decrease in coral juvenile survival (Birkeland, 1997; Fabricius, 2005; Richmond and Hunter, 1990). Already, on the west coast of Guam, recruitment has dramatically declined from 503 recruits/m^2 in 1976 to 1 recruit/m^2 in 2006 (Minton et al., 2007). Impacts of sediments on mature corals vary enormously with some species of coral being effective in sediment removal in one area but ineffective in another (Rogers, 1990). Rogers (1990) determined that a sediment collection rate of > 0.01 g/cm^2/d is likely to have negative impacts on coral growth. Te (2001) found no difference in growth rates of *Montipora verrucosa* or *Porites compressa* with an increase in sediment collection rates of up to 0.07 g/cm^2/d. Pastorak and Bilyard (1985) found that chronic sedimentation rates of > 0.05 g/cm^2/d lead to severe or catastrophic impacts for corals. Riegl and Branch (1995) concluded that corals die if sedimentation rates of > 0.1 g/cm^2 persist for a few days. Monthly average sedimentation rates in Asan Bay and Agat Bay on the west coast of Guam were estimated between 0.005 and 0.36 g/cm^2/d (Minton et al., 2006, NPS unpubl data; Storlazzi et al., 2009). In Fouha Bay, sedimentation rates were as high as 1.3–3.3 g/cm^2/d. All Guam sedimentation studies showed a sedimentation rate substantially higher than the amounts determined to impact corals elsewhere, suggesting that the benthic community is under a long term pressure as a result of sedimentation with potential gradual and long-term declines and shifts in community structure. Sediments get flushed out of bays by strong tidal water currents, periodic storms, and typhoons (Wolanski et al., 2003a). However, these oceanographic conditions are mostly prevalent in the dry season when sediment input is lower. The calm seas during the wet season allow for the transport and settlement of the fine sediments to the corals at 20-m depth (NPS unpubl. data). In Fouha Bay, on the spouthwest coast of Guam, typhoon- and storm-event-driven swells with wave heights up to 4 m, led to resuspension and transport of the settled sediments and created surface plumes of 7 m thick with suspended solid concentrations of 1000–5000 g/m^3 blocking most to all light for benthic communities. Under these high swell conditions, sediments got flushed out in 1–2 days. These storm-driven swells occur typically 2–5 times per year (Wolanski et al., 2003a). Salinity was seldom less than 30 ppm in the plume and, hence, had no influence on the benthic community. Mean residence time of riverine fine sediment was 4.3 yrs (Wolanski et al., 2003a). It will take typhoon-driven waves 30 days to flush the bay if no new sediments enter the bay (Wolanski et al., 2003a).

In ther version of the model presented here, sediment and nutrient inputs are modeled as inputs to coastal model cells adjacent to land with river outflows or sewage pipes. In future versions of Guam Atlantis, their fate will be modeled with the oceanography submodel developed by Deltares and USGS for Guam (see in main text under ‘Methods’, ‘Physical Model’).

At present, coral recruitment is related to the overall biomass of corals. Coral specific code of the relationship between sediment and coral growth and recruitment is under development and will be incorporated to simulate more realistic dynamics.

Nutrients—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) and indirectly on space competition with other benthic organisms, such as filter feeders and algae (Koop et al., 2001). However, algal growth is also controlled by herbivores and nutrient effects are more prominent under conditions of reduced herbivory. 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.

A secondary effect of nutrient increase is the occurrence of coral disease (Bruno et al., 2003). Coral disease has become more prevalent in recent decades and affects most or all coral species in various life stages (reviewed in Brainard et al., 2011). The exact cause of disease is still unclear but could be related to low water quality (Kaczmarsky, 2006) or organic matter leached from macroalgae (Smith, 2006). Reductions in herbivorous fish biomass may also affect the microbial diversity with a shift to more pathogenic microbes and a reduced microbial species richness, likely increasing the likelihood of coral disease occurrences (Bruce et al., 2012). There is increasing evidence that ocean warming and coral bleaching are linked with disease outbreaks (Bruno et al., 2007; McClanahan et al., 2009; Raymundo et al., 2011) possibly because the coral's integrity is compromised by physiological stress or immune suppression resulting in damaging opportunistic pathogens (Lesser et al., 2007). In general, branching acroporids and pocilloporids had low immunity whereas the solitary fungids and massive poritids had high immunity (Palmer et al., 2010; Raymundo et al., 2011). As disease seems to be a secondary effect from bleaching and possibly from sewage we included the occurrence of partial mortality for the sheltering corals to reflect the disease. The dominant disease in Guam was White Syndrome which results in tissue loss that is rapidly colonized by turf algae (Raymundo et al., 2011). We will model disease as a decrease in coral cover and a subsequent increase in turf algae as a result of bleaching and assumed that 50% of bleached branching corals die. Bleaching events are caused by the magnitude and duration of thermal stress (e.g., degrees heating weeks) and are modeled as a climate change option in the final model but has not been incorporated in the present model.

Toxins—Additional land-based sources of pollution include toxins and contaminants which can reduce coral growth and reproduction and salinity changes which can cause behavioral responses (polyp retraction, mucus production, osmoregulation), mortality (primarily in shallow waters), bleaching, and reduced photosynthesis and fertilization success. All these stressors often act simultaneously with the overall effect of reduced coral growth, reduced reproduction success and a shift towards more tolerant species. As we do not have any time series on toxins entering Guam's shallow waters or empirical relationships of how it affects the coral growth and reproduction, we were not able to include these effects.

Predation

Predation occurs mostly on *Acropora*, *Montipora*, *Pocillopora* and *Porites* by many corallivorous species of fish and invertebrates and is a chronic energy drain and threat to corals (Cole et al., 2008). Bite rates of 400–700 per hour are inflicted by butterflyfishes that eat coral polyps (Gochfeld, 2004), the bumphead parrotfish (largest parrotfish in the ocean) that also eat the coral skeleton can consume 12.7–15 kg coral per m^2 per year (Bellwood et al., 2003) whereas smaller parrotfish consume about 4 kg coral per m^2 per year (Bruggemann et al., 1994). Acute predation comes from crown-of-thorns seastar outbreaks; these large aggregations can reduce coral cover to less than 1% (Birkeland and Lucas, 1990). Causative mechanisms that drive outbreaks remain unknown, though two potential causes may be phytoplankton blooms caused by increased nutrient runoff and fishing of predators of corallivores (Birkeland, 1989a). Corals can recover from predation but only when the coral population is > 5% and healing is slowed by environmental stress (Jayewardene et al., 2009). Consumption of coral larvae is high mostly by planktonic fish species that benefit from the mass spawning events. As human population densities in coastal areas increase, it is likely that nutrient runoff and fishing increases resulting in an increase of corallivores. At the same time, with warming of ocean waters, corals will likely bleach more frequently and disease outbreaks will occur more frequently, decreasing coral cover. If coral cover is reduced below a threshold, predation can have depensatory effects in which the impacts of predator increase exponentially and inversely to the population density of corals (Mattio et al., 2008).

Predation is modeled through the diet matrix with higher predation on branching corals compared to massive corals by both corallivorous fishes and sea stars. Parrotfishes are assumed to eat both branching and massive corals equally.

Ornamental Trade

In Guam trade in coral is prohibited but collection for local use does occur especially for the aquarium trade (Burdick et al., 2008). Collection of reef fish species is incorporated in the fishery submodel through landings.

Natural Physical Damage

Guam is located in a zone with tropical storms (wind speed > 33 m/s) passing at a frequency of 10–15 typhoons per year (Webster et al., 2005). Typhoon damage includes partial mortality in especially branching corals with some recovery and some fragments stabilizing on the substrate. Typhones also lead to the opening up of substrate which is filled in by fast growing benthic species, such as algae.

Disturbances are not included in the present model but at a later stage we will include tropical storms by assuming a mortality of 10% for macroalgae, 25% for massive corals and 35% for branching corals after the passing of a hurricane. We will further assume that the opened up space will be occupied directly by turf algae.

APPENDIX B—FISH SPECIES OBSERVED DURING VISUAL SURVEYS CONDUCTED AROUND GUAM AND CATEGORIZED IN A FUNCTIONAL GROUP BASED ON DIET, FEEDING MODE, HABITAT, LIFE-HISTORY CHARACTERISTICS, AND OF ECOLOGICAL OR ECONOMIC IMPORTANCE

REA method was stationary point counts at random, stratified sites, TOW is survey results from towed-divers; catch is average annual catch from expanded inshore fishery data from 1985 to 2012. Species are sorted by decrease in biomass per functional group.

Functional Group:	**Fish Planktivores**	**FPL**				
Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Pomacentrus vaiuli	Pomacentridae	Ocellate damselfish	0.2	REA	0.332	3.1
Myripristis kuntee	Holocentridae	Shoulderbar soldierfish	61.0	REA	0.321	3.3
Plectroglyphidodon lacrymatus	Pomacentridae	Whitespotted devil	0.0	REA	0.180	2.2
Odonus niger	Balistidae	Redtoothed triggerfish	5.5	REA	0.160	3.2
Pomachromis guamensis	Pomacentridae	Guam damsel	0.0	REA	0.158	
Macolor macularis	Lutjanidae	Midnight snapper	0.0	REA	0.147	4
Macolor niger	Lutjanidae	Black and white snapper	2.5	REA	0.087	4
Blenniidae	Blenniidae	Blenny species	7.1	REA	0.066	
Myripristis berndti	Holocentridae	Blotcheye soldierfish	315.7	REA	0.060	3.7
Ptereleotris zebra	Microdesmidae	Chinese zebra goby	0.0	REA	0.048	3.4
Naso hexacanthus	Acanthuridae	Sleek unicornfish	30.9	REA	0.045	3.3
Dascyllus reticulatus	Pomacentridae	Reticulate dascyllus	0.0	REA	0.045	3.1
Chromis acares	Pomacentridae	Midget chromis	0.0	REA	0.044	3
Stethojulis bandanensis	Labridae	Red shoulder wrasse	0.8	REA	0.043	3.2
Pterocaesio marri	Caesionidae	Marr's fusilier	0.3	REA	0.042	3.4
Naso vlamingii	Acanthuridae	Bignose unicornfish	32.3	REA	0.041	3.4
Pterocaesio tile	Caesionidae	Dark-banded fusilier	8.7	REA	0.040	3.3
Ptereleotris evides	Microdesmidae	Blackfin dartfish	0.0	REA	0.037	3
Pempheris oualensis	Pempheridae	Silver sweeper	91.6	REA	0.036	3.6
Cirrhilabrus katherinae	Labridae	Katherine's wrasse	0.0	REA	0.035	
Hemitaurichthys polylepis	Chaetodontidae	Pyramid butterflyfish	0.0	REA	0.034	3.1
Chromis margaritifer	Pomacentridae	Bicolor chromis	0.4	REA	0.032	3
Melichthys niger	Balistidae	Black triggerfish	3.5	REA	0.032	2.4
Thalassoma amblycephalum	Labridae	Bluntheaded wrasse	0.0	REA	0.030	3.1
Acanthurus thompsoni	Acanthuridae	Thompson's surgeonfish	0.0	REA	0.029	3.4
Dascyllus trimaculatus	Pomacentridae	Threespot dascyllus	0.7	REA	0.028	2.8
Abudefduf vaigiensis	Pomacentridae	Indo-Pacific sergeant	24.6	REA	0.019	2.59
Chromis xanthura	Pomacentridae	Paletail chromis	0.0	REA	0.016	3.4
Thalassoma hardwicke	Labridae	Sixbar wrasse	0.0	REA	0.015	3.6

Functional Group: Fish Planktivores FPL

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Naso brevirostris	Acanthuridae	Spotted unicornfish	2.6	REA	0.012	2.7
Ptereleotris heteroptera	Microdesmidae	Blacktail goby	0.0	REA	0.011	3.4
Abudefduf sexfasciatus	Pomacentridae	Scissortail sergeant	37.9	REA	0.011	2.37
Myripristinae	Holocentridae	Soldierfishes	0.0	REA	0.009	
Amphiprion chrysopterus	Pomacentridae	Orangefin anemonefish	0.0	REA	0.009	2.8
Pseudanthias pascalus	Serranidae	Amethyst anthias	0.0	REA	0.008	3.3
Chromis alpha	Pomacentridae	Yellow-speckled chromis	0.0	REA	0.007	3
Nemateleotris magnifica	Microdesmidae	Fire goby	0.0	REA	0.007	3.1
Ecsenius bicolor	Blenniidae	Bicolor blenny	0.0	REA	0.005	2
Naso sp	Acanthuridae	Unicornfishes	0.0	REA	0.004	
Meiacanthus atrodorsalis	Blenniidae	Forktail blenny	0.0	REA	0.003	3.5
Chromis agilis	Pomacentridae	Agile chromis	0.0	REA	0.003	3
Chromis amboinensis	Pomacentridae	Ambon chromis	0.0	REA	0.002	2.7
Apogon sp	Apogonidae	Apogon species	0.0	REA	0.002	
Apogonidae	Apogonidae	Apogonidae species	7.1	REA	0.002	
Blenniella chrysospilos	Blenniidae	Red-spotted blenny	0.0	REA	0.002	2.5
Ecsenius opsifrontalis	Blenniidae	Comical blenny	0.0	REA	0.001	2
Xanthichthys auromarginatus	Balistidae	Gilded triggerfish	0.0	REA	0.001	3
Pseudocoris yamashiroi	Labridae	Redspot wrasse	0.0	REA	0.001	3.4
Ptereleotris microlepis	Microdesmidae	Blue gudgeon	0.0	REA	0.001	3.4
Acanthurus nubilus	Acanthuridae	Bluelinedsurgeon	0.0	REA	0.001	3.4
Amphiprion melanopus	Pomacentridae	Fire clownfish	0.0	REA	0.001	2.8
Amphiprion clarkii	Pomacentridae	Yellowtail clownfish	0.0	REA	0.001	2.9
Chromis vanderbilti	Pomacentridae	Vanderbilt's chromis	0.0	REA	0.000	3.2
Hoplolatilus starcki	Malacanthidae	Bluehead tilefish	0.0	REA	0.000	3.5
Myripristis amaena	Holocentridae	Brick soldierfish	21.5	REA	0.000	3.6
Amphiprion perideraion	Pomacentridae	Pink anemonefish	0.0	REA	0.000	2.6
Apogon angustatus	Apogonidae	Broadstriped cardinalfish	8.6	REA	0.000	3.3
Apogon novemfasciatus	Apogonidae	Sevenstriped cardinalfish	18.7	REA	0.000	4
Apogon fraenatus	Apogonidae	Bridled cardinalfish	0.0	REA	0.000	3.5

Functional Group Fish Coralivores FCO

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Plectroglyphidodon dickii	Pomacentridae	Blackbar devil	0.0	REA	0.226	3.4
Chaetodon reticulatus	Chaetodontidae	Mailed butterflyfish	0.0	REA	0.074	2.6
Chaetodon citrinellus	Chaetodontidae	Speckled butterflyfish	0.3	REA	0.055	3.1
Heniochus chrysostomus	Chaetodontidae	Threeband pennantfish	0.0	REA	0.030	3.3

Functional Group Fish Coralivores FCO

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Plectroglyphidodon johnstonianus	Pomacentridae	Johnston Island damsel	0.0	REA	0.030	3.3
Chaetodon lunulatus	Chaetodontidae	Oval butterflyfish	3.1	REA	0.028	3.3
Chaetodon ornatissimus	Chaetodontidae	Ornate butterflyfish	157.5	REA	0.018	3.3
Arothron meleagris	Tetraodontidae	Guineafowl puffer	0.0	REA	0.011	3.4
Chaetodon quadrimaculatus	Chaetodontidae	Fourspot butterflyfish	0.2	REA	0.008	3.3
Chaetodon unimaculatus	Chaetodontidae	Teardrop butterflyfish	0.0	REA	0.007	3.1
Chaetodon melannotus	Chaetodontidae	Blackback butterflyfish	0.0	REA	0.007	3.3
Heniochus singularius	Chaetodontidae	Singular bannerfish	0.0	REA	0.005	3.5
Chaetodon trifascialis	Chaetodontidae	Chevron butterflyfish	0.2	REA	0.004	3.3
Arothron nigropunctatus	Tetraodontidae	Blackspotted puffer	22.1	REA	0.004	3.3
Chaetodon mertensii	Chaetodontidae	Atoll butterflyfish	0.0	REA	0.003	3
Exallias brevis	Blenniidae	Leopard blenny	0.0	REA	0.002	3
Amanses scopas	Monacanthidae	Broom filefish	0.0	REA	0.002	2.9
Chaetodon meyeri	Chaetodontidae	Scrawled butterflyfish	0.0	REA	0.000	3.3

Functional Group Fish Detritivores FDE

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Ctenochaetus striatus	Acanthuridae	Striated surgeonfish	192.1	REA	1.336	2
Ctenochaetus binotatus	Acanthuridae	Twospot surgeonfish	3.8	REA	0.061	2
Ctenochaetus hawaiiensis	Acanthuridae	Chevron tang	0	REA	0.016	2
Ctenochaetus cyanocheilus	Acanthuridae	Bluelip bristletooth	0	REA	0.006	2.1
Amblygobius phalaena	Gobiidae	Banded goby	0.1	REA	0.004	2.7

Functional Group Fish Browsers FHB

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Calotomus carolinus	Scaridae	Carolines parrotfish	69.5	REA	0.053	2
Chanos chanos	Chanidae	Milkfish	122.7	REA	0.003	2
Chrysiptera biocellata	Pomacentridae	Twinspot damselfish	0.4	REA	0.000	2

Functional Group Target Fish Browsers THB

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Naso lituratus	Acanthuridae	Orangespine unicornfish	2084.2	REA	0.583	2.3
Naso tonganus	Acanthuridae	Bulbnose unicornfish	143.6	REA	0.126	2
Kyphosus sp	Kyphosidae	Chubs	0.0	REA	0.116	
Naso unicornis	Acanthuridae	Bluespine unicornfish	10320.3	REA	0.037	2
Siganus argenteus	Siganidae	Streamlined spinefoot	684.6	REA	0.023	2
Naso brachycentron	Acanthuridae	Humpback unicornfish	0.0	REA	0.003	2.7

Functional Group Fish Scrapers FHS

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Chlorurus sordidus	Scaridae	Daisy parrotfish	342.2	REA	2.286	2
Scarus psittacus	Scaridae	Common parrotfish	386.3	REA	0.608	2
Scarus forsteni	Scaridae	Forsten's parrotfish	8.8	REA	0.298	2
Scarus schlegeli	Scaridae	Yellowband parrotfish	279.6	REA	0.290	2
Scarus frenatus	Scaridae	Bridled parrotfish	0.2	REA	0.061	2
Scarus sp	Scaridae	Scarus genus	0.0	REA	0.056	
Scarus dimidiatus	Scaridae	Yellowbarred parrotfish	0.0	REA	0.023	2
Scarus globiceps	Scaridae	Globehead parrotfish	10.5	REA	0.018	2
Scarus oviceps	Scaridae	Dark capped parrotfish	0.0	REA	0.012	2
Scarus fuscocaudalis	Scaridae	Darktail parrotfish	0.0	REA	0.005	

Functional Group Fish Excavators FHE

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Chlorurus frontalis	Scaridae	Tan-faced parrotfish	181.0	REA	0.264	2
Scarus altipinnis	Scaridae	Filament-finned parrotfish	62.1	REA	0.240	2
Scarus rubroviolaceus	Scaridae	Ember parrotfish	106.8	REA	0.118	2
Chlorurus sp	Scaridae	Large-bodies parrotfishes	0.0	REA	0.087	
Scarus festivus	Scaridae	Festive parrotfish	25.7	REA	0.028	2
Hipposcarus longiceps	Scaridae	Pacific longnoseparrotfish	114.5	REA	0.026	2
Scaridae	Scaridae	Parrotfish species	30.2	REA	0.010	
Chlorurus microrhinos	Scaridae	Steephead parrots	127.0	REA	0.007	
Cetoscarus ocellatus	Scaridae	Bicolour parrotfish	0.0	REA	0.000	2

Functional Group Bumphead Parrotfish BHP

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Bolbometopon muricatum	Scaridae	Green bumphead parrotfish	18.4	TOW	0	2.7

Functional Group Fish Invertivores FIV

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Balistapus undulatus	Balistidae	Orange-lined triggerfish	17.0	REA	0.227	3.4
Paracirrhites arcatus	Cirrhitidae	Arc-eye hawkfish	0	REA	0.185	3.6
Sufflamen chrysopterum	Balistidae	Halfmoon triggerfish	0	REA	0.138	3.5
Sufflamen bursa	Balistidae	Boomerang triggerfish	3.4	REA	0.118	3.1
Valenciennea strigata	Gobiidae	Blueband goby	0	REA	0.076	4
Halichoeres biocellatus	Labridae	Red-lined wrasse	0.8	REA	0.074	3.4
Zanclus cornutus	Zanclidae	Moorish idol	15.9	REA	0.066	2.9
Pygoplites diacanthus	Pomacanthidae	Royal angelfish	0.0	REA	0.063	2.7
Chaetodon lunula	Chaetodontidae	Raccoon butterflyfish	1.9	REA	0.059	3.3
Parapercis clathrata	Pinguipedidae	Latticed sandperch	0.3	REA	0.037	3.6

Functional Group	Fish Invertivores	FIV				
Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Balistoides viridescens	Balistidae	Titan triggerfish	148.7	REA	0.036	3.3
Diodon hystrix	Diodontidae	Spot-fin porcupinefish	235.7	REA	0.036	3.4
Scolopsis lineata	Nemipteridae	Striped monocle bream	0	REA	0.033	3.2
Rhinecanthus rectangulus	Balistidae	Wedge-tail triggerfish	33.1	REA	0.032	3.1
Pomacanthus imperator	Pomacanthidae	Emperor angelfish	5.1	REA	0.032	2.7
Halichoeres margaritaceus	Labridae	Pink-belly wrasse	2.5	REA	0.026	3.7
Cantherhines pardalis	Monacanthidae	Honeycomb filefish	0.1	REA	0.024	3.5
Cantherhines dumerilii	Monacanthidae	Whitespotted filefish	7.5	REA	0.021	3.1
Chaetodon auriga	Chaetodontidae	Threadfin butterflyfish	24.1	REA	0.020	3.2
Heniochus monoceros	Chaetodontidae	Masked bannerfish	0.9	REA	0.018	3.5
Chaetodon ephippium	Chaetodontidae	Saddle butterflyfish	4.9	REA	0.017	3.1
Labroides dimidiatus	Labridae	Bluestreak cleaner wrasse	0.0	REA	0.016	3.5
Taeniura meyeni	Dasyatidae	Blotched fantail ray	0.0	REA	0.015	4.2
Plectorhinchus gibbosus	Haemulidae	Harry hotlips	78.6	REA	0.015	3.6
Malacanthus latovittatus	Malacanthidae	Blue blanquillo	0.5	REA	0.012	3.5
Forcipiger flavissimus	Chaetodontidae	Longnose butterfly fish	0	REA	0.011	3.1
Chaetodon ulietensis	Chaetodontidae	Pacific double-saddlebutterflyfish	3.5	REA	0.010	3.3
Chaetodon punctatofasciatus	Chaetodontidae	Spotband butterflyfish	0.0	REA	0.010	3.3
Pseudocheilinus evanidus	Labridae	Striated wrasse	0.0	REA	0.010	3.5
Apolemichthys trimaculatus	Pomacanthidae	Threespot angelfish	0.0	REA	0.008	2.6
Ostracion meleagris	Ostraciidae	Whitespotted boxfish	0.0	REA	0.008	2.9
Arothron stellatus	Tetraodontidae	Starry toadfish	5.7	REA	0.006	3.3
Plectroglyphidodon imparipennis	Pomacentridae	Brighteye damselfish	0.0	REA	0.006	3.2
Cirrhitichthys falco	Cirrhitidae	Dwarf hawkfish	0.0	REA	0.006	4
Bothus mancus	Bothidae	Flowery flounder	67.7	REA	0.006	4.4
Platax teira	Ephippidae	Tiera batfish	1.0	REA	0.005	4
Pseudobalistes flavimarginatus	Balistidae	Yellowmargin triggerfish	28.8	REA	0.004	
Forcipiger longirostris	Chaetodontidae	Longnose butterflyfish	0.0	REA	0.004	3.5
Plectorhinchus picus	Haemulidae	Painted sweetlip	3.4	REA	0.003	3.8
Plectorhinchus albovittatus	Haemulidae	Two-striped sweetlips	6.0	REA	0.003	3.9
Cheilodipterus quinquelineatus	Apogonidae	Five-lined cardinalfish	0.0	REA	0.003	
Neocirrhites armatus	Cirrhitidae	Flame hawkfish	0.0	REA	0.002	3.5
Cirrhitus pinnulatus	Cirrhitidae	Stocky hawkfish	43.5	REA	0.002	3.6
Chaetodon lineolatus	Chaetodontidae	Lined butterflyfish	1.1	REA	0.002	3.3
Plagiotremus tapeinosoma	Blenniidae	Piano fangblenny	0.0	REA	0.002	3.8

Functional Group	**Fish Invertivores**	**FIV**				
Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Pseudocheilinus tetrataenia	Labridae	Four-lined wrasse	0.0	REA	0.002	3.2
Labroides bicolor	Labridae	Bicolor cleaner wrasse	0.0	REA	0.002	4
Malacanthus brevirostris	Malacanthidae	Quakerfish	0.0	REA	0.002	3.5
Balistoides conspicillum	Balistidae	Clown triggerfish	0.0	REA	0.002	3.3
Amblycirrhitus bimacula	Cirrhitidae	Twospot hawkfish	0.0	REA	0.002	3.5
Cheilodipterus artus	Apogonidae	Wolf cardinalfish	2.6	REA	0.001	4.1
Pseudocheilinus octotaenia	Labridae	Eight-lined wrasse	0.0	REA	0.001	3.4
Canthigaster coronata	Tetraodontidae	Crowned puffer	0.0	REA	0.001	3.1
Canthigaster janthinoptera	Tetraodontidae	Honeycomb toby	0.0	REA	0.001	3.1
Pseudojuloides cerasinus	Labridae	Smalltail wrasse	0.0	REA	0.001	3.3
Pterois antennata	Scorpaenidae	Broadbarred firefish	0.0	REA	0.001	3.5
Gobiidae	Gobiidae	Goby family	0.5	REA	0.001	
Chaetodon bennetti	Chaetodontidae	Bluelashed butterflyfish	0.2	REA	0.001	3.3
Parapercis millepunctata	Pinguipedidae	Black dotted sand perch	0.0	REA	0.001	3.5
Aspidontus taeniatus	Blenniidae	False cleanerfish	0.0	REA	0.001	3.8
Amblyglyphidodon curacao	Pomacentridae	Staghorn damselfish	0.0	REA	0.000	2.6
Labropsis xanthonota	Labridae	Yellowback tubelip	0.0	REA	0.000	2.9
Eviota sp	Gobiidae	Gobys5	0.0	REA	0.000	
Pervagor janthinosoma	Monacanthidae	Blackbar filefish	0.0	REA	0.000	2.9
Plagiotremus laudandus laudandus	Blenniidae	Bicolour fangblenny	0.0	REA	0.000	4.4
Pervagor sp	Monacanthidae	filefishes	0.0	REA	0.000	
Centropyge multifasciata	Pomacanthidae	Barred angelfish	0.0	REA	0.000	2.8
Aluterus scriptus	Monacanthidae	Scrawled filefish	210.9	REA	0.000	2.8
Pseudocheilinus hexataenia	Labridae	Sixline wrasse	0.0	REA	0.000	3.2
Pomacentridae	Pomacentridae	damselfishes	0.2	REA	0.000	
Caracanthus maculatus	Caracanthidae	Spotted coral croucher	0.0	REA	0.000	3.2
Labroides pectoralis	Labridae	Blackspot cleaner wrasse	0.0	REA	0.000	4
Paraluteres prionurus	Monacanthidae	Blacksaddle filefish	0.0	REA	0.000	2.7
Pseudojuloides atavai	Labridae	Polynesianwrasse	0.0	REA	0.000	
Canthigaster epilampra	Tetraodontidae	Lantern toby	0.0	REA	0.000	3.1

Functional Group Target Fish Invertivores TIV

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Monotaxis grandoculis	Lethrinidae	Humpnose big-eye bream	0.0	REA	0.502	3.2
Thalassoma quinquevittatum	Labridae	Fivestripe wrasse	7.1	REA	0.407	3.6
Parupeneus multifasciatus	Mullidae	Manybar goatfish	75.7	REA	0.162	3.5
Gnathodentex aureolineatus	Lethrinidae	Striped large-eye bream	0.0	REA	0.102	3.3
Sargocentron caudimaculatum	Holocentridae	Silverspot squirrelfish	0.9	REA	0.084	3.9
Lutjanus kasmira	Lutjanidae	Common bluestripe snapper	9.7	REA	0.066	3.6
Halichoeres hortulanus	Labridae	Checkerboard wrasse	10.6	REA	0.066	3.4
Cheilinus sp	Labridae	Cheilinus wrasse	0.0	REA	0.056	
Lutjanus fulvus	Lutjanidae	Blacktail snapper	685.4	REA	0.055	4.1
Sargocentron tiere	Holocentridae	Blue lined squirrelfish	80.2	REA	0.053	3.5
Cheilinus trilobatus	Labridae	Tripletail wrasse	605.2	REA	0.048	3.5
Hologymnosus doliatus	Labridae	Pastel ringwrasse	18.6	REA	0.047	3.8
Neoniphon sammara	Holocentridae	Sammara squirrelfish	212.0	REA	0.046	3.6
Parupeneus barberinus	Mullidae	Dash-and-dot goatfish	392.2	REA	0.041	3.2
Lethrinus harak	Lethrinidae	Thumbprint emperor	2192.6	REA	0.034	3.6
Mulloidichthys vanicolensis	Mullidae	Yellowfin goatfish	315.7	REA	0.030	3.6
Macropharyngodon meleagris	Labridae	Blackspotted wrasse	1.0	REA	0.029	2.9
Cheilinus fasciatus	Labridae	Redbreast wrasse	35.9	REA	0.029	3.4
Coris aygula	Labridae	Clown coris	8.9	REA	0.028	3.4
Epibulus insidiator	Labridae	Slingjaw wrasse	31.7	REA	0.026	3.8
Lutjanus gibbus	Lutjanidae	Humpback red snapper	133.0	REA	0.024	3.6
Hemigymnus melapterus	Labridae	Blackeye thicklip	32.9	REA	0.024	3.3
Hemigymnus fasciatus	Labridae	Barred thicklip	12.5	REA	0.023	3.2
Parupeneus insularis	Mullidae	Twosaddle goatfish	118.4	REA	0.023	3.7
Sargocentron diadema	Holocentridae	Crown squirrelfish	8.0	REA	0.019	3.4
Coris gaimard	Labridae	Yellowtail coris	0.0	REA	0.018	3.5
Thalassoma lutescens	Labridae	Yellow-brown wrasse	1.2	REA	0.017	3.4
Cheilinus chlorourus	Labridae	Floral wrasse	61.5	REA	0.016	3.4
Cheilinus oxycephalus	Labridae	Snooty wrasse	0.0	REA	0.015	3.3
Sargocentron spiniferum	Holocentridae	Sabre squirrelfish	297.6	REA	0.013	3.5
Gomphosus varius	Labridae	Bird wrasse	3.6	REA	0.012	3.6
Anampses caeruleopunctatus	Labridae	Bluespotted wrasse	4.5	REA	0.011	3.3
Halichoeres marginatus	Labridae	Dusky wrasse	0.1	REA	0.011	3.3
Novaculichthys taeniourus	Labridae	Rockmover wrasse	21.6	REA	0.009	3.3
Lethrinus olivaceus	Lethrinidae	Longface emperor	559.9	REA	0.008	3.8
Myripristis violacea	Holocentridae	Lattice soldierfish	20.0	REA	0.008	3.5
Anampses twistii	Labridae	Yellowbreasted wrasse	0.0	REA	0.007	3.5
Stethojulis strigiventer	Labridae	Stripebelly wrasse	0.0	REA	0.006	

Functional Group **Target Fish Invertivores** **TIV**

Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Thalassoma trilobatum	Labridae	Christmas wrasse	28.4	REA	0.005	3.6
Halichoeres ornatissimus	Labridae	Ornamented wrasse	0.0	REA	0.005	3.1
Thalassoma purpureum	Labridae	Surge wrasse	80.2	REA	0.004	3.6
Labridae	Labridae	wrasse family	12.5	REA	0.004	
Halichoeres sp	Labridae	Halicoeres wrasse	0.0	REA	0.003	
Neoniphon opercularis	Holocentridae	Blackfin squirrelfish	38.2	REA	0.003	3.5
Bodianus axillaris	Labridae	Axilspot hogfish	3.4	REA	0.003	3.4
Lethrinus sp	Lethrinidae	emperors	0.0	REA	0.002	
Hologymnosus annulatus	Labridae	Ring wrasse	0.0	REA	0.002	4.2
Sargocentron sp	Holocentridae	Sargocentron fishes	0.0	REA	0.002	
Parupeneus pleurostigma	Mullidae	Sidespot goatfish	0.1	REA	0.001	3.4
Anampses meleagrides	Labridae	Spotted wrasse	0.0	REA	0.001	3.5
Grammistes sexlineatus	Serranidae	Sixline soapfish	0.2	REA	0.001	4
Oxycheilinus sp	Labridae	Oxycheilin wrasse	0.0	REA	0.001	
Pseudodax moluccanus	Labridae	Chiseltooth wrasse	0.0	REA	0.001	2.8
Sargocentron microstoma	Holocentridae	Smallmouth squirrelfish	11.1	REA	0.001	3.6
Oxycheilinus bimaculatus	Labridae	Two-spot wrasse	0.0	REA	0.000	3.5
Mulloidichthys flavolineatus	Mullidae	Yellowstripe goatfish	3804.9	REA	0.000	3.3
Belonoperca chabanaudi	Serranidae	Arrowhead soapfish	0.0	REA	0.000	4
Halichoeres trimaculatus	Labridae	Threespot wrasse	60.3	REA	0.000	3.5
Cheilio inermis	Labridae	Cigar wrasse	222.7	REA	0.000	4

Functional Group **Humphead Wrasse** **HHW**

Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Cheilinus undulatus	Labridae	Humphead/Napolean wrasse	124.0	REA	0.017	4

Functional Group **Fish Benthic Piscivores** **FPB**

Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Paracirrhites forsteri	Cirrhitidae	Blackside hawkfish	0.0	REA	0.072	4.3
Paracirrhites hemistictus	Cirrhitidae	Whitespot hawkfish	0.0	REA	0.034	3.8
Gymnothorax javanicus	Muraenidae	Giant moray	156.3	REA	0.016	3.9
Gymnothorax flavimarginatus	Muraenidae	Yellow-edged moray	11.2	REA	0.007	4.2
Gymnothorax sp	Muraenidae	morays	0.0	REA	0.001	
Aulostomus chinensis	Aulostomidae	Chinese trumpetfish	16.3	REA	0.001	4.2
Gymnothorax meleagris	Muraenidae	Turkey moray	0.4	REA	0.001	4.5
Gymnothorax undulatus	Muraenidae	Undulated moray	27.5	REA	0.001	4.3
Scientific name	**Family**	**Common name**	**Catch (kg)**	**survey method**	**biomass (g/m^2)**	**Trophic level**
Synodus variegatus	Synodontidae	Variegated lizardfish	1.2	REA	0.000	4.4

Functional Group **Fish Benthic Piscivores** **FPB**

Scorpaenopsis diabolus	Scorpaenidae	False stonefish	2.5	REA	0.000	4.2
Synodontidae	Synodontidae	Lizardfish species	0.8	REA	0.000	
Synodus binotatus	Synodontidae	Two-spot lizard fish	4.3	REA	0.000	4

Functional Group **Target Benthic Piscivores** **TPB**

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Cephalopholis urodeta	Serranidae	Darkfin hind	10.1	REA	0.338	4
Oxycheilinus unifasciatus	Labridae	Ringtail maori wrasse	23.7	REA	0.231	4.1
Cephalopholis argus	Serranidae	Peacock hind	36.8	REA	0.158	4.5
Epinephelus fasciatus	Serranidae	Blacktip grouper	1.3	REA	0.113	3.7
Lutjanus bohar	Lutjanidae	Two-spot red snapper	462.3	REA	0.100	4.1
Plectropomus laevis	Serranidae	Blacksaddled coralgrouper	68.0	REA	0.050	4.1
Variola louti	Serranidae	Yellow-edged lyretail	0.6	REA	0.022	4.3
Epinephelus hexagonatus	Serranidae	Starspotted grouper	114.2	REA	0.017	4.1
Lutjanus monostigma	Lutjanidae	Onespot snapper	471.5	REA	0.016	4.3
Parupeneus cyclostomus	Mullidae	Goldsaddle goatfish	17.7	REA	0.013	4.2
Epinephelus merra	Serranidae	Honeycomb grouper	992.7	REA	0.012	3.8
Cephalopholis spiloparaea	Serranidae	Strawberry hind	0.0	REA	0.011	4.1
Epinephelus tauvina	Serranidae	Greasy grouper	12.3	REA	0.008	4.1
Epinephelus sp	Serranidae	Groupers	0.0	REA	0.003	
Serranidae	Serranidae	Grouper family	4.4	REA	0.002	
Oxycheilinus digramma	Labridae	Cheeklined wrasse	0.0	REA	0.001	3.7
Cephalopholis sonnerati	Serranidae	Tomato hind	0.0	REA	0.000	3.8
Cephalopholis leopardus	Serranidae	Leopard hind	2.0	REA	0.000	4

Functional Group **Fish Mid-water Piscivores** **FPM**

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Elagatis bipinnulata	Carangidae	Rainbow runner	0	TOW	0.000	3.6
Aphareus furca	Lutjanidae	Small toothed jobfish	22.0	REA	0.453	4.1
Fistularia commersonii	Fistulariidae	Bluespotted cornetfish	0.0	TOW	0.002	4.3
Scomberoides lysan	Carangidae	Doublespotted queenfish	303.7	TOW	0.001	4.5

Functional Group **Fish Roving Piscivores** **FPR**

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Sphyraena qenie	Sphyraenidae	Blackfin barracuda	27.8	TOW	1.036	4.5
Caranx melampygus	Carangidae	Bluefin trevally	3444.7	REA	0.023	4.5
Caranx papuensis	Carangidae	Brassy trevally	559.9	TOW	0.008	4
Caranx sexfasciatus	Carangidae	Bigeye trevally	929.6	TOW	0.008	4.5
Aprion virescens	Lutjanidae	Green jobfish	248.1	TOW	0.007	4
Sphyraena barracuda	Sphyraenidae	Great barracuda	557.3	TOW	0.003	4.5
Caranx ignobilis	Carangidae	Giant trevally	426.9	TOW	0.003	4.2
Caranx lugubris	Carangidae	Black jack	0.4	REA	0.002	4.5
Carangoides ferdau	Carangidae	Blue trevally	12.9	TOW	0.001	4.5

Functional Group **Rays** **RAY**

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Aetobatus narinari	Myliobatidae	Spotted eagle ray	0	TOW	0.087	3.2
Urogymnus asperrimus	Dasyatidae	Porcupine ray	0	TOW	0.044	3.5

Functional Group **Sharks** **SHR**

Scientific name	Family	Common name	Catch (kg)	survey method	biomass (g/m^2)	Trophic level
Nebrius ferrugineus	Ginglymostomatidae	Tawny nurse shark	0	TOW	0.086	4.1
Triaenodon obesus	Carcharhinidae	Whitetip reef shark	365.7	TOW	0.038	4.2
Carcharhinus melanopterus	Carcharhinidae	Blacktip reef shark	622.1	TOW	0.022	3.9
Carcharhinus amblyrhynchos	Carcharhinidae	Grey reef shark	422.3	TOW	0.001	4.1

APPENDIX C—TABLE WITH 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*, *TL* is total length and *recruit age* means recruitment from pelagic stage to the reef in days. The rows highlighted in yellow are the weighted means per functional group. See text for data sources.

Group	**Scientific Name**	**Perc. of**	**Numbers**	**Mort.**	**k**	**Linf**	**tmax**	**L-W**	**L-W**	**age at maturity**	**Recruit**
FISH		**group**	**per m^2**	**per y**		**cm**	**y**	**a**	**b**	**TL cm**	**age d**
Planktivores	**FPL**	**1.00**	**0.04**	**1.24**	**0.58**	**25.32**	**6.70**	**0.02**	**3.05**	**1.39**	**23**
	Pomacentrus vaiuli	0.14	0.15	1.53	0.62	10.67	4.50	0.05	2.78	1.40	16.8
	Myripristis kuntee	0.14	0.01	1.32	0.70	24.21	4.00	0.01	3.47	1.10	
	Plectroglyphidodon lacrymatus	0.08	0.03	1.62	0.68	10.67	4.10	0.06	2.64	1.20	20.4
	Odonus niger	0.07	0.00	0.58	0.25	41.74	11.40	0.01	3.00	2.70	121
	Pomachromis guamensis	0.07	0.14	2.69	1.19	6.45	2.30	0.02	3.19	0.80	21
	Macolor macularis	0.06	0.00	0.52	0.25	62.21	11.50	0.03	2.93	2.60	
	Macolor niger	0.04	0.00	0.43	0.21	77.49	13.70	0.02	3.05	3.00	
	Blenniidae	0.03	0.02	.		17.57		0.00	3.90		
	Myripristis berndti	0.03	0.00	1.10	0.62	34.54	4.60	0.03	3.00	1.20	
	Ptereleotris zebra	0.02	0.01	.		12.77		0.01	3.00		
	Naso hexacanthus	0.02	0.00	0.10	0.22	77.49	44.00	0.04	2.85		91
	Dascyllus reticulatus	0.02	0.01	0.87	0.52	8.57	5.30	0.03	3.13	1.70	20.6
	Chromis acares	0.02	0.07	2.88	1.32	6.45	2.10	0.03	3.00	0.80	25
	Stethojulis bandanensis	0.02	0.00	1.17	0.50	16.90	5.60	0.03	2.58	1.60	42.1
	Ptereleotris evides	0.02	0.01			12.80		0.01	3.00		
	Pterocaesio marri	0.02	0.00	0.98	0.53	36.60	5.40	0.01	3.15	1.30	

Group FISH	Scientific Name	Perc. of group	Numbers per m^2	Mort. per y	k	Linf cm	tmax y	L-W a	L-W b	age at maturity TL cm	Recruit age d
	Naso vlamingii	0.02	0.00	0.10	0.27	62.21	45.00	0.01	3.25	2.50	
	Pterocaesio tile	0.02	0.00	1.12	0.61	31.45	4.70	0.01	3.00	1.20	
	Pempheris oualensis	0.02	0.00	1.01	0.47	24.21	6.00	0.01	3.00	1.60	
	Cirrhilabrus katherinae	0.02	0.02	1.90	0.83	9.62	3.30	0.01	3.01	1.10	21
	Hemitaurichthys polylepis	0.01	0.00	1.80	1.02	19.02	2.80	0.03	3.00	0.80	
	Chromis margaritifer	0.01	0.01	1.78	0.75	9.60	3.70	0.03	3.00	1.20	33.2
	PL_other	0.12	0.04	1.48	0.73	17.78	4.56	0.02	3.06	1.32	
Coralivores	**FCO**	**1.00**	**0.00**	**1.71**	**0.98**	**18.56**	**4.37**	**0.05**	**2.95**	**1.17**	**36.90**
	Chaetodon reticulatus	0.26	0.00	1.80	1.02	19.02	2.80	0.03	2.99	0.80	40
	Chaetodon citrinellus	0.19	0.00	3.02	1.96	13.81	1.40	0.04	2.83	0.40	40
	Heniochus chrysostomus	0.10	0.00	1.80	1.02	19.02	2.80	0.02	3.26	0.80	40
	Plectroglyphidodon johnstonianus	0.10	0.01	1.26	0.50	12.77	5.60	0.06	2.64	1.00	25
	Chaetodon lunulatus	0.10	0.00	0.50	0.30	15.90	9.30	0.03	2.99	2.80	40
	Chaetodon ornatissimus	0.06	0.00	1.64	0.92	21.10	3.10	0.03	2.99	0.80	40
	Arothron meleagris	0.04	0.00	0.54	0.25	51.99	11.40	0.41	2.70	2.70	
	Chaetodon quadrimaculatus	0.03	0.00	1.99	1.13	16.94	2.50	0.03	2.99	0.70	40
	Chaetodon unimaculatus	0.03	0.00	1.64	0.92	21.10	3.10	0.05	2.83	0.80	40
	Chaetodon melannotus	0.02	0.00	0.23	0.14	15.90	20.10	0.03	3.05	5.60	40
	Heniochus singularius	0.02	0.00	1.14	0.63	31.45	4.50	0.03	3.00	1.20	40
	Cor_other	0.05	0.00	1.11	0.47	17.59	5.13	0.02	3.12	1.45	40
Invertivores	**FIV**	**1.00**	**0.01**	**1.01**	**0.57**	**25.37**	**7.51**	**0.03**	**3.07**	**1.38**	**49.12**
	Balistapus undulatus	0.13	0.00	0.85	0.40	31.45	7.10	0.01	3.55	1.80	121
	Plectroglyphidodon dickii	0.13	0.03	1.49	0.62	11.72	4.50	0.06	2.75	1.40	26.6
	Paracirrhites arcatus	0.11	0.02	0.87	0.30	14.86	11.00	0.02	3.13		30
	Sufflamen chrysopterum	0.08	0.00	0.92	0.40	23.18	7.10	0.02	3.15	1.80	121
	Sufflamen bursa	0.07	0.00	0.96	0.47	29.39	6.00	0.02	3.00	1.60	121
	Valenciennea strigata	0.04	0.01	0.92	2.84	16.94	5.00	0.01	3.05	0.30	

Group	Scientific Name	Perc. of	Numbers	Mort.	k	Linf	tmax	L-W	L-W	age at maturity	Recruit
FISH		**group**	**per m^2**	**per y**		**cm**	**y**	**a**	**b**	**TL cm**	**age d**
	Halichoeres biocellatus	0.04	0.02	1.45	0.62	12.77	4.50	0.01	3.00	1.30	24.8
	Zanclus cornutus	0.04	0.00	0.46	0.30	21.10	10.00	0.01	3.37		
	Pygoplites diacanthus	0.04	0.00	0.76	0.31	26.29	9.10	0.03	3.00	2.40	
	Chaetodon lunula	0.03	0.00	0.51	0.20	39.69	14.20	0.03	2.99	3.50	38
	Parapercis clathrata	0.02	0.00	1.16	0.52	19.00	5.40	0.01	3.05		
	Balistoides viridescens	0.02	0.00	0.38	0.17	77.49	16.90	0.02	3.02	3.70	121
	Dioton hysterix	0.02		0.46	0.20	93.73	10.00	0.19	2.47		
	Scolopsis lineata	0.02	0.00	2.08	1.33	21.10	2.10	0.02	2.98	0.60	
	Rhinecanthus rectangulus	0.02	0.00	0.89	0.40	26.29	7.10	0.05	2.64	1.80	121
	Pomacanthus imperator	0.02	0.00	0.47	0.19	46.87	15.00	0.03	3.00	3.60	
	Halichoeres margaritaceus	0.02	0.01	1.22	0.49	13.81	5.70	0.01	3.00	1.70	21.7
	Cantherhines pardalis	0.01	0.00	0.76	0.31	26.30	9.10	0.02	3.07		
	Cantherhines dumerilii	0.01	0.00	0.52	0.21	39.69	13.50	0.04	2.79	3.30	
	Chaetodon auriga	0.01	0.00	2.18	1.51	24.21	1.90	0.04	2.83	0.50	38
	Heniochus monoceros	0.01	0.00	1.41	0.78	24.21	3.60	0.02	3.21	1.00	38
	Chaetodon ephippium	0.01	0.00	1.23	0.63	24.21	4.50	0.02	3.06	1.20	38
	Labridae	0.01	0.01	1.33	0.54	12.80	5.20	0.01	3.23		50
	INV_other	0.10	0.02	1.15	0.58	25.30	6.71	0.03	3.02	1.72	
Target Invertivores	**TIV**	**1.00**	**1.59**	**0.77**	**0.38**	**39.53**	**9.38**	**0.02**	**2.99**	**2.21**	**27.10**
	Monotaxis grandoculis	0.23	0.12	0.47	0.22	65.27	13.00	0.04	2.84	3.00	30
	Thalassoma quinquevittatum	0.18	7.78	1.07	0.45	17.98	6.20	0.01	3.00	1.70	56.4
	Parupeneus multifasciatus	0.07	0.60	0.67	0.41	39.69	6.90	0.01	3.21	1.70	45
	Gnathodentex aureolineatus	0.05	0.17	0.88	0.42	31.45	6.80	0.03	3.06	1.70	
	Sargocentron caudimaculatum	0.04	0.42	1.32	0.73	26.29	3.90	0.02	2.96	1.00	
	Lutjanus kasmira	0.03	0.31	0.51	0.21	41.74	13.60	0.01	3.25	3.30	26
	Halichoeres hortulanus	0.03	0.40	1.28	0.72	28.35	3.90	0.01	3.06	1.00	32.5
	Cheilinus sp	0.03	0.18	0.30	0.22	34.00	15.30	0.02	3.05	3.70	27
	Lutjanus fulvus	0.02	0.05	1.13	0.72	44.82	4.00	0.02	2.97	1.00	26

Group FISH	Scientific Name	Perc. of group	Numbers per m^2	Mort. per y	k	Linf cm	tmax y	L-W a	L-W b	age at maturity TL cm	Recruit age d
	Sargocentron tiere	0.02	0.10	1.04	0.57	34.54	5.00	0.02	3.00	1.30	
	Cheilinus trilobatus	0.02	0.15	0.45	0.18	46.87	15.80	0.02	3.06	3.80	29.6
	Hologymnosus doliatus	0.02	0.00	0.26	0.16	41.70	17.80	0.01	3.01		
	Neoniphon sammara	0.02	0.20	0.99	0.52	33.51	5.40	0.03	2.89	1.40	
	Parupeneus barberinus	0.02	0.01	0.50	0.22	51.99	12.90	0.01	3.12	3.30	45
	Macropharyngodon meleagris	0.01	1.36	1.06	0.42	15.90	6.70	0.02	3.00	1.90	25
	Thalassoma lutescens	0.01	0.31	0.67	0.26	26.29	10.90	0.01	3.04	2.80	78
	Labridae	0.00	0.00	0.47	0.26	95.80	15.00	0.01	3.18		50
	Halichoeres sp	0.00	0.85	1.45	0.75	20.38	3.90	0.02	2.99		25
	Lethrinus harak	0.02	0.03	0.24	0.20	35.57	13.00	0.02	3.04	3.75	27
	Mulloidichthys vanicolensis	0.01	0.17	1.13	0.68	39.69	4.20	0.01	3.02	1.00	45
	Bodianus axillaris	0.00	0.00	0.82	0.32	21.10	8.80	0.02	3.00		23.5
	Target Inv other	0.16	0.01	0.78	0.38	36.43	10.24	0.02	2.99	2.53	
Humphead wrasse	**HHW**	**1.00**	**0.00**	**0.20**	**0.10**	**232.44**	**30.00**	**0.01**	**3.14**	**5.90**	**34**
	Cheilinus undulatus	0.01	0.00	0.20	0.10	232.44	30.00	0.01	3.14	5.90	34.3
Detritivores	**FDE**	**1.00**	**0.02**	**1.41**	**0.84**	**29.05**	**17.41**	**0.02**	**3.05**	**0.92**	**55**
	Ctenochaetus striatus	0.94	0.02	1.43	0.86	29.39	18.00	0.02	3.06	0.90	57
	Ctenochaetus binotatus	0.04	0.00	1.18	0.58	23.18	4.90	0.04	2.87	1.30	57
	Ctenochaetus hawaiiensis	0.01	0.00	1.03	0.52	29.39	18.00	0.02	3.01	1.40	57
	Ctenochaetus cyanocheilus	0.00	0.00	1.21	0.58	21.10	18.00	0.02	3.06		57
	Amblygobius phalaena	0.00	0.00	1.04	0.41	15.90	6.80	0.02	2.83	1.90	
Browsers	**FHB**	**1.00**	**0.00**	**2.14**	**1.43**	**29.82**	**4.35**	**0.01**	**3.16**		**15.2**
	Calotomus carolinus	0.95	0.00	2.25	1.51	21.46	3.00	0.01	3.15	0.84	15
	Chanos chanos	0.05		0.21	0.10	183.40	29.10	0.00	3.39	5.90	18
	Chrysiptera biocellata	0.00	0.00	1.63	0.75	13.29	3.70	0.02	3.00	1.10	18.2

Group	**Scientific Name**	**Perc. of**	**Numbers**	**Mort.**	**k**	**Linf**	**tmax**	**L-W**	**L-W**	**age at maturity**	**Recruit**
FISH		**group**	**per m^2**	**per y**		**cm**	**y**	**a**	**b**	**TL cm**	**age d**
Target Browsers	**THB**	**1.00**	**0.00**	**1.25**	**0.68**	**36.27**	**14.18**	**0.03**	**3.09**	**2.58**	**70**
	Naso lituratus	0.66	0.01	1.66	0.92	20.36	13.00	0.04	3.05	2.00	70
	Naso tonganus	0.14	0.00	0.43	0.19	65.27	15.10	0.01	3.25	3.50	70
	Kyphosus sp	0.13	0.00	0.38	0.18	77.49	17.90	0.01	3.15	4.08	
	Naso unicornis	0.04	0.00	0.51	0.22	49.31	23.00	0.03	2.92	4.60	71
	Siganus argenteus	0.03	0.00	1.17	0.75	43.80	3.80	0.01	3.15	0.90	
	Naso brachycentron	0.00	0.00	0.24	0.09	92.72	32.00	0.03	3.04	7.00	70
Grazers	**FHG**	**1.00**	**0.04**	**1.21**	**0.55**	**21.95**	**6.56**	**0.02**	**3.18**	**1.63**	**59.92**
	Melichthys vidua	0.40	0.00	0.69	0.31	35.57	9.20	0.01	3.55	2.20	121
	Stegastes fasciolatus	0.23	0.04	1.14	0.47	15.90	6.00	0.03	2.91	1.70	25
	Chrysiptera brownriggii	0.17	0.13	1.92	0.84	9.62	3.30	0.03	2.95	1.10	20
	Chrysiptera traceyi	0.03	0.11	2.92	1.19	4.86	2.30	0.03	2.93	0.80	23
	Stegastes sp	0.03	0.00	1.60	0.80	16.42	4.00	0.04	2.99	1.30	28
	Centropyge flavissima	0.03	0.00	0.42	0.64	14.86	11.00	0.03	2.80	1.20	
	Canthigaster solandri	0.02	0.00	2.00	0.97	11.72	2.90	0.03	2.98		
	Centropyge heraldi	0.02	0.00	1.92	0.88	10.67	3.20	0.03	3.00		
	Cirripectes variolosus	0.02	0.01	1.62	0.68	10.67	4.10	0.01	3.00	1.20	
	Centropyge shepardi	0.02	0.00	2.11	0.97	9.62	2.90	0.07	2.58	0.90	
	GRZ_other	0.01	0.00	1.52	0.70	14.63	4.64	0.04	2.93	1.33	
Target Grazers	**THG**	**1.00**	**0.02**	**1.42**	**0.80**	**25.36**	**24.00**	**0.03**	**2.99**	**1.37**	**32.06**
	Acanthurus nigrofuscus	0.41	0.04	1.66	1.00	24.21	25.00	0.03	3.03	0.80	31
	Acanthurus lineatus	0.32	0.00	1.72	0.97	19.54	16.00	0.03	3.03	1.10	30
	Acanthurus nigricans	0.10	0.00	0.72	0.28	24.21	34.00	0.07	2.67	2.80	25
	Acanthurus olivaceus	0.07	0.00	0.76	0.38	41.74	33.00	0.04	3.06	1.90	61
	Acanthurus blochii	0.04	0.00	0.57	0.25	44.82	35.00	0.03	3.03	2.80	25
	Zebrasoma veliferum	0.02	0.00	0.62	0.28	41.74	27.00	0.03	2.87	2.80	55
	Acanthurus pyroferus	0.02	0.00	0.92	0.42	26.29	28.00	0.02	3.00	1.80	25

Group FISH	Scientific Name	Perc. of group	Numbers per m^2	Mort. per y	k	Linf cm	tmax y	L-W a	L-W b	age at maturity TL cm	Recruit age d
	Zebrasoma flavescens	0.01	0.00	0.70	0.25	21.10	35.50	0.01	3.16	3.10	55
	THG_other	0.02	0.00	0.80	0.40	39.40	25.00	0.02	2.98	3.09	
Scrapers	**FHS**	**1.00**	**0.01**	**0.73**	**0.92**	**22.78**	**8.71**	**0.02**	**3.05**	**1.40**	**35**
	Chlorurus sordidus	0.62	0.02	0.25	0.95	21.79	9.00	0.02	3.11	1.30	
	Scarus psittacus	0.17	0.01	1.61	0.89	20.60	6.00	0.02	3.01	1.36	35
	Scarus forsteni	0.08	0.00	1.46	0.88	28.10	12.00	0.03	2.92	1.79	35
	Scarus schlegeli	0.08	0.00	1.65	1.01	25.29	8.00	0.03	2.84	1.99	35
	Scarus frenatus	0.02	0.00	1.48	0.84	24.42	19.00	0.03	3.06	0.90	35
	Scarus sp	0.02	0.00	1.04	0.55	32.89	5.15	0.02	2.98	1.33	35
		0.02	0.00	1.03	0.55	33.20	5.15	0.02	2.98	1.33	
Excavators	**FHE**	**1.00**	**0.00**	**1.08**	**0.65**	**44.69**	**11.14**	**0.02**	**3.08**	**2.19**	**35**
	Chlorurus frontalis	0.34	0.00	1.17	0.71	37.20	11.00	0.01	3.16	1.63	
	Scarus rubroviolaceus	0.15	0.00	1.12	0.66	37.63	6.00	0.02	3.02	1.91	35
	Chlorurus sp	0.11	0.00	0.79	0.59	103.00	11.00	0.02	2.97	2.07	
	Scarus festivus	0.04	0.00	0.75	0.39	46.87	14.00	0.02	2.97	1.80	35
	Hipposcarus longiceps	0.03	0.00	0.98	0.57	42.64	7.00	0.01	3.11	3.00	
	Scarus altipinnis	0.31	0.00	1.14	0.65	34.02	14.00	0.02	3.09	2.89	
	Scaridae	0.01	0.00	0.88	0.59	70.37	10.73	0.02	2.96	2.07	35
	Chlorurus microrhinos	0.01	0.00	0.63	0.30	45.73	11.00	0.02	3.02	3.59	
	Cetoscarus ocellatus	0.00	0.00	0.54	0.30	82.57	10.00	0.02	3.00		
Bumphead parrotfish	**BHP**	**1.00**	**0.00**	**0.14**	**0.14**	**133.10**	**33.00**	**0.02**	**3.04**	**8.00**	**35**
	Bolbometopon muricatum	1.00	0.00	0.14	0.14	133.10	33.00	0.02	3.04	8.00	
Benthic piscivores	**FPB**	**1.00**	**0.02**	**0.53**	**0.21**	**72.11**	**8.00**	**0.01**	**3.03**	**2.00**	**60**
	Paracirrhites forsteri	0.53	0.00	0.58	0.20	24.21	8.00	0.02	3.13	2.00	
	Paracirrhites hemistictus	0.25	0.00	0.55	0.20	29.39	8.00	0.02	3.13	2.00	

Group FISH	**Scientific Name**	**Perc. of group**	**Numbers per m^2**	**Mort. per y**	**k**	**Linf cm**	**tmax y**	**L-W a**	**L-W b**	**age at maturity TL cm**	**Recruit age d**
	Gymnothorax javanicus	0.12	0.00	0.29	0.20	303.20	8.00	0.00	3.30	2.00	
	Gymnothorax flavimarginatus	0.05	0.00	0.30	0.20	243.43	8.00	0.00	3.35	2.00	
	BenthP_other	0.04	0.00	0.77	0.47	65.43	8.03			2.06	
Target Benthis piscivores	**TPB**	**1.00**	**0.00**	**0.50**	**0.24**	**53.01**	**15.90**	**0.02**	**2.99**	**3.79**	**60**
	Cephalopholis urodeta	0.31	0.01	0.78	0.34	29.39	8.30	0.03	2.82	2.10	
	Oxycheilinus unifasciatus	0.21	0.00	0.45	0.18	47.90	15.80	0.02	3.00	3.80	
	Cephalopholis argus	0.14	0.00	0.42	0.18	62.21	15.90	0.01	3.18	3.60	
	Epinephelus fasciatus	0.10	0.00	0.14	0.25	44.70	22.00	0.01	3.04	6.00	41
	Lutjanus bohar	0.09	0.00	0.14	0.09	92.72	31.80	0.02	3.06	7.20	26
	Plectropomus laevis	0.05	0.00	0.22	0.09	128.11	32.00	0.01	3.24	6.60	
	Variola louti	0.02	0.00	0.38	0.18	85.62	15.90	0.01	3.08	3.60	
	Epinephelus hexagonatus	0.02	0.00	1.51	0.91	27.32	3.10	0.01	3.04	0.80	41
	Lutjanus monostigma	0.01	0.00	0.47	0.22	62.21	13.00	0.02	2.91	3.00	26
	Parupeneus cyclostomus	0.01	0.00	0.60	0.29	51.99	9.90	0.01	3.00	2.30	45
	Epinephelus merra	0.01	0.00	1.14	0.65	34.54	4.40	0.02	2.97	1.10	41
	TBP_other	0.02	0.00	0.31	0.28	82.56	15.00	0.01	3.06	3.37	
Mid-water piscivores	**FPM**	**1.00**	**0.01**	**0.58**	**0.32**	**72.86**	**8.96**	**0.01**	**3.00**	**1.99**	**60**
	Aphareus furca	0.99	0.01	0.58	0.32	72.40	9.00	0.01	3.00	2.00	
	Fistularia commersonii	0.00	0.00	0.44	0.30	163.33		0.00	3.05		
	Scomberoides lysan	0.00	0.00	0.59	0.33	72.40	8.70	0.01	2.92	1.90	
	Elagatis bipinnulata	0.00	0.00	0.68	0.60	183.41	4.80	0.02	2.24	1.00	
Roving piscivores	**FPR**	**1.00**	**0.03**	**0.22**	**0.10**	**170.51**	**28.27**	**0.01**	**3.00**	**5.59**	**120**
	Sphyraena qenie	0.95	0.03	0.21	0.10	173.37	28.90	0.01	3.00	5.70	
	Caranx melampygus	0.02	0.00	0.27	0.19	120.03	12.50	0.03	2.97	3.20	
	Caranx papuensis	0.01	0.00	0.44	0.21	72.40	13.70	0.04	2.85	3.00	
	Caranx sexfasciatus	0.01	0.00	0.37	0.19	102.85	15.20	0.02	2.99	3.20	

Group	Scientific Name	Perc. of group	Numbers per m^2	Mort. per y	k	Linf cm	tmax y	L-W a	L-W b	age at maturity TL cm	Recruit age d
FISH											
	Aprion virescens	0.01	0.00	0.30	0.14	114.98	20.60	0.02	2.89	4.30	120
	Sphyraena barracuda	0.00	0.00	0.19	0.09	203.44	32.10	0.01	3.01	6.40	
	Caranx ignobilis	0.00	0.00	0.19	0.08	168.35	26.30	0.02	2.98	3.50	
	Caranx lugubris	0.00	0.00	0.30	0.13	90.69	22.10	0.02	2.92	4.80	
	Carangoides ferdau	0.00	0.00	0.35	0.17	102.85	16.90	0.02	3.00	3.60	
SHARKS											
Reef-associated sharks	**SHR**	**1.00**	**0.00**	**0.25**	**0.16**	**276.73**	**22.26**	**0.00**	**3.47**	**4.25**	**360**
	Nebrius ferrugineus	0.58	0.00	0.27	0.19	323.09	15.30	0.00	3.57	2.80	
	Triaenodon obesus	0.26	0.00	0.16	0.07	216.45	41.60	0.00	3.34	8.20	
	Carcharhinus melanopterus	0.15	0.00	0.29	0.17	203.44	17.10	0.00	3.34	3.30	
	Carcharhinus amblyrhynchos	0.01	0.00	0.79	0.86	243.43	3.40	0.00	3.37	0.70	
Rays	**RAY**	**1.00**		**0.17**	**0.09**	**271.37**	**23.18**	**0.01**	**3.20**	**5.42**	**60**
	Aetobatus narinari	0.66	0.00	0.09	0.03	333.00	13.80	0.01	3.13	4.00	60
	Urogymnus asperrimus	0.34	0.00	0.35	0.20	150.30	41.60	0.01	3.35	8.20	
REPTILES											
Sea Turtles	**REP**	**1.00**	**0.0000059**	**0.14**	**0.089**	**108.9**	**62**	**0.05**	**3.3**	**37.5**	**2190**
	Chelonia mydas	1.00	0.00	0.14	0.09	108.90	62	0.16	3.00	37.50	2190

APPENDIX D—LIST OF CORAL SPECIES FROM GUAM GROUPED INTO MASSIVE/ENCRUSTING SPECIES AND BRANCHING/TABULAR CORAL SPECIES

CRS; Branching Corals	CRN; Massive/encrusting Corals	CRN; Massive/encrusting Corals
Pavona chiriquiensis	Porites sp	Psammocora nierstraszi
Pocillopora sp	Leptastrea sp	Pavona sp
Porites rus	Favia sp	Fungia sp
Acropora sp	Leptastrea purpurea	Hydnophora microconos
Porites vaughani	Astreopora sp	Millepora tuberosa
Porites cylindrica	Montipora sp	Lobophyllia sp
Heliopora coerulea	Goniastrea edwardsi	Montipora tuberculosa
Echinopora sp	Cyphastrea sp	Astreopora gracilis
Porites annae	Astreopora myriophthalma	Pavona explanulata
Pocillopora eydouxi	Psammocora haimeana	Favia helianthoides
Psammocora stellata	Cyphastrea serailia	Leptastrea transversa
Pocillopora verrucosa	Platygyra pini	Montastraea curta
Goniopora fruticosa	Goniastrea sp	Pavona duerdeni
Gardineroseris planulata	Acanthastrea sp	Coscinaraea columna
Pocillopora elegans	Pavona varians	Diploastrea heliopora
Acropora abrotanoides	Montipora verrucosa	Leptastrea pruinosa
Acropora humilis	Stylocoeniella armata	Montipora venosa
Acropora palifera	Favia favus	Turbinaria sp
Millepora sp	Favia stelligera	Turbinaria stellulata
Pocillopora danae	Astreopora listeri	Cycloseris sp
Favia stelligera	Favites sp	Leptoseris incrustans
Galaxea sp	Galaxea fascicularis	Lobophyllia/Symphyllia
Stylophora sp	Montipora caliculata	Oulophyllia sp
Pocillopora meandrina	Montipora foveolata	Platygyra sp
Pavona maldivensis	Goniastrea retiformis	Scolymia australis
Turbinaria reniformis	Montastraea sp	Psammocora sp
	Echinophyllia sp	Porites massive
	Goniastrea pectinata	Stylocoeniella sp
	Leptoria sp	Favia matthaii
	Leptoria phrygia	Platygyra daedalea
	Goniopora minor	Pocillopora damicornis
	Montipora verrilli	Herpolitha sp
	Stylophora pistillata	
	Goniopora sp	

APPENDIX E—TOTAL NUMBER OF ORGANISMS PER PHYLUM AND ORDER COLLECTED FROM 12 ARMS UNITS DEPLOYED IN 4 LOCATIONS (3 AT EACH LOCATION) BROKEN DOWN BY FUNCTIONAL GROUP

The omnivores were divided equally among the three functional groups BC, BD, and BM. Bold numbers are the totals per order and phylum.

TAXON	Benthic Carnivores (BC)	Benthic Detritivores (BD)	Benthic Meiofaun (BM)	omnivores	Benthic Filter Feeders (BFF)	Benthic Filter Feeders (BFF)	Grand Total
Annelida		**202**					**202**
unidentified		2					2
Polychaeta		200					200
Arthropoda	**684**		**308**	**3964**	**398**	**76**	**5430**
unidentified				114			114
Decapoda	**534**		**308**	**3850**	**398**	**76**	**5166**
Alpheidae				124			124
Brachyura				390			390
Caridae				60			60
Carupa	12						12
Chlorodiella			2	202			204
Cryptodromiopsis				12			12
Diogenidae				272			272
Dynomenidae						70	70
Epiactea				4			4
Galatheidae					296		296
Garthiella				18			18
Hippolytidae				202			202
Leucosidae	38						38
Liomera				272			272
Lophozozymus				2			2
Majidae			268				268
Medaeus	20						20
Palaemonidae				96			96
Palicidae				2			2
Parthenopidae				38			38
Penaeidae				38			38
Percnon			32				32
Perinea			6				6
Pilodius				148			148
Pilumnidae				1114			1114
Pilumnus				54			54
Platypodia				4			4
Porcellanidae					102		102

TAXON	Benthic Carnivores (BC)	Benthic Detritivores (BD)	Benthic Meiofaun (BM)	omnivores	Benthic Filter Feeders (BFF)	Benthic Filter Feeders (BFF)	Grand Total
Portunidae	108						108
Rhynchocinetidae				44			44
Stenopodidae				2			2
Thalamitoides	356						356
Trapezia						6	6
Tweedieia				16			16
Xanthias				8			8
Xanthidae				728			728
Stomatopoda	**150**						**150**
Echinodermata		**248**	**116**		**42**	**62**	**468**
Echinoida			**72**				**72**
Echinometra			40				40
Echinometridae			32				32
Ophiurida		**66**					**66**
Ophiurida		66					66
Asterozoa		**182**	**44**		**42**	**62**	**330**
Asteroidea						62	62
Echinoidea			44				44
Holothuroidea		76					76
Ophiuroidea		106			42		148
Mollusca	**2294**		**1400**		**654**	**308**	**4656**
Archaeogastropoda			**614**				**614**
Fissurellidae			48				48
Haliotidae			48				48
Patellidae			66				66
Pleurotamarioidea			36				36
Polychaeta			8				8
Trochidae			310				310
Turbinidae			98				98
Arcoida					**100**		**100**
Arcidae					100		100
Cephalaspedea	**2**						**2**
Cephalaspidea	**80**		**156**				**236**
Bullidae			154				154
Cephalaspidea	58						58
Chelidonura	22						22
Haminoeidae			2				2
Heterostropha						**94**	**94**
Limoida					**56**		**56**
Limidae					56		56
Mytiloida					**68**		**68**

TAXON	Benthic Carnivores (BC)	Benthic Detritivores (BD)	Benthic Meiofaun (BM)	omnivores	Benthic Filter Feeders (BFF)	Benthic Filter Feeders (BFF)	Grand Total
Mytilidae					68		68
Neogastropoda	**1816**					**2**	**1818**
Neoloricata			**124**				**124**
Chitonidae			124				124
Neotaenioglossa	**172**		**500**			**212**	**884**
Cerithioidea			186				186
Cypraea			8				8
Cypraeidae			284				284
Eulimidae	6						6
Ovulidae						2	2
Potamididae	124						124
Ranellidae	42						42
Triphoridae			22				22
Triviidae						210	210
Notaspidea	**14**						**14**
Nudibranchia	**208**						**208**
Octopoda	**2**						**2**
Octopus	2						2
Ostreoida					**100**		**100**
Pectinidae					42		42
Spondylidae					58		58
Veneroida					**206**		**206**
Carioidea					6		6
Lucinidae					94		94
Psammobiidae					32		32
Tellinidae					68		68
Veneridae					6		6
Bivalvia					124		124
Gastropoda			4				4
Mollusca			2				2
Nematoda		**2**					**2**
Nemertea	**30**						**30**
Platyhelminthes	**2**						**2**
Sipuncula		**142**					**142**
Sipunculidae		142					142
Grand Total	**3010**	**594**	**1824**	**3964**	**1094**	**446**	**10932**

APPENDIX F—MEAN NUMBERS PER PHYLUM OF THE CRYPTOFAUNA PER LOCATION FROM ARMS DEPLOYMENTS (3 ARMS AT EACH LOCATION) AROUND GUAM

SiteID	**GUA-02**		**GUA-05**		**GUA-08**		**GUA-12**	
Phyla	**No. Individuals**	**Rel. Abun**	**No. Individuals**	**Rel. Abun**	**No. Individuals**	**Rel. Abun**	**No. Individuals**	**Rel. Abun**
Annelida	138	7.9%	30	0.73%	32	0.90%	2	0.12%
Arthropoda	782	44.8 %	1232	30.14 %	2382	66.87 %	1034	63.67%
Chordata	32	1.8%	32	0.78%	14	0.39%	8	0.49%
Echinodermata	150	8.6%	102	2.50%	18	0.51%	198	12.19%
Mollusca	528	30.3 %	2684	65.66 %	1072	30.10 %	372	22.91%
Nematoda	0	0	2	0.05%				
Nemertea	0	0	2	0.05%	24	0.67%	4	0.25%
Platyhelminthes	0	0	2	0.05%				
Sipuncula	114	6.5%	2	0.05%	20	0.56%	6	0.37%
Grand Total	**1744**	**100%**	**4088**	**100%**	**3562**	**100%**	**1624**	**100%**
per ARMS	**581.3**		**1362.7**		**1187.3**		**541.33**	

APPENDIX G—EXPANDED ANNUAL LANDINGS PER FUNCTIONAL GROUP. DATA FROM DAWR AND WPACFIN

Functional Groups	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
BC	503	79	12	270	232	39	372	156	42	128	310	7	5,851
BD	2,840	1,917	1,624	1,635	1,718	1,750	1,702	1,742	1,658	1,929	2,272	1,615	1,743
BG		2,435	74	71		10	11	21	2	1	4	7	308
BM	29,901	385	211	212	3	263	15,805	76	98	433	96	19	322
CEP	9,806	2,433	1,982	3,189	4,189	2,366	2,211	2,044	2,852	5,334	3,683	1,139	2,848
BFF	2,443	0	29	27	28	2	295	615	11	3	1	2	12
MA	6,649	4,673	94	94	5	26	738	59	153	662	295	17	13,206
Fish Planktivores	3,988	976	1,346	715	1,792	1,066	899	1,126	2,791	1,457	2,421	1,574	1,581
Fish Coralivores				2		1	1	0	7	11	15	1	8
Fish Detritivores	116	316	1	11	0	2	1	106	130	349	319	94	71
Fish Browsers	374	1,105		545	46	17	238	184	5	97	52	93	14
Fish Grazers	240	137	75	242	296	809	70	154	462	407	344	156	487
Fish Invertivores	4,959	5,142	2,027	2,440	2,582	1,571	1,126	2,844	1,343	2,992	2,608	2,131	1,749
Fish Benthic Piscivores	842	447	1,010	87	88	609	277	172	756	1,023	784	332	544
HHW	571	158	206	641	913	76	22			11		323	
Fish Scrapers	2,766	1,801	564	1,158	204	362	3,954	1,627	1,169	1,786	1,933	1,109	1,837
Fish Excavators	3,716	37	61	216	1	321	1,455	896	417	562	1,742	637	479
BHP	515												
Target Browsers	45,928	44,349	48,845	42,032	28,319	18,702	25,008	34,546	9,072	24,269	39,099	22,969	22,338
Target Grazers	7,795	5,653	11,553	9,042	6,042	7,955	6,018	9,149	3,530	4,847	8,109	6,603	4,499
Target Invertivores	24,090	24,790	22,622	22,915	19,945	11,997	13,879	18,321	11,260	12,303	19,512	12,211	11,834
Fish Mid-water Piscivores	6,158	4,434	57	1,632	2,489	1,998	2,512	1,070	1,162	2,643	2,314	1,407	270
Fish Roving Piscivores	9,803	4,777	8,485	5,457	3,950	6,394	11,175	4,145	5,103	2,999	3,704	3,749	6,158
Target Benthic Piscivores	2,585	3,216	5,522	2,213	853	3,225	3,754	2,933	3,572	2,698	3,912	1,107	2,195
Rays		203		214	297								
Sharks		16,548				5	21	417	841	5,775	1,584	41	453

Functional Groups	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
BC	2,566	673	252	5,741	438	92	60	1,224	15	16	245	0	310	27	815
BD	3,171	1,788	2,011	1,835	1,674	1,757	1,638	1,689	1,621	1,618	1,619	1,613	1,621	1,619	1,617
BG	47	1,966	13	0	1	3	572	452	1,231	304	13	0	25	12	8
BM	1,010	294	444	233	75	8	19	597	37	34	19	0	52	23	17
CEP	12,555	9,508	2,060	7,947	1,099	7,819	2,339	4,322	1,048	3,169	312	0	500	284	4,139
BFF	5	67	388		0	0	1	3	2	4	6	0	6	4	2
MA	4,092	9,849	66	9,383	186	128	30	16	56	54	31		91	31	28
Fish Planktivores	3,669	1,659	1,476	772	534	654	1,582	162	389	140	70	0	343	70	223
Fish Coralivores	3	89	463	159	1	0	0	5	2	1	34	0	1	1	4,402
Fish Detritivores	229	115	196	1,999	1		1	22	143	1,243	5	0	7	5	4
Fish Browsers	91	865	187	61	567	896	60	29	3	2	3	0	3	12	2
Fish Grazers	397	398	742	553	272	305	56	49	1	2	26	0	4	105	2
Fish Invertivores	3,705	3,897	2,420	2,978	2,645	4,090	928	764	46	2,171	163	0	205	228	548
Fish Benthic Piscivores	974	4,613	419	148	134	6	199	26	231	1,653	250	0	11	13	95
HHW		21	79			159	0		42	166		0	0	12	73
Fish Scrapers	1,809	6,433	1,170	524	598	2,377	451	727	1,362	439	1,994	0	451	727	516
Fish Excavators	3,227	1,840	587	611	568	2,435	681	178	176	23	169	0	27	252	50
BHP															
Target Browsers	36,922	42,441	22,456	15,216	19,016	17,502	10,952	4,118	18,692	11,913	8,711	2	15,995	4,440	3,255
Target Grazers	4,853	6,194	5,035	4,144	2,892	6,946	4,776	2,760	4,355	2,566	3,561	1	7,032	2,846	331
Target Invertivores	18,237	13,374	12,046	14,733	8,356	8,477	3,978	6,274	5,573	5,308	1,393	1	3,315	6,396	6,216
Fish Mid-water Piscivores	624	5,128	985	2,638	745	677	1,400	262	474	110	696	0	326	713	25
Fish Roving Piscivores	7,203	15,632	3,969	9,170	7,626	4,191	9,558	5,910	4,786	10,634	8,182	0	2,812	13,377	5,852
Target Benthic Piscivores	3,845	1,953	3,548	1,990	3,299	2,179	1,791	1,184	2,587	1,297	112	0	151	352	493
Rays	62						0		1,055				0	0	0
Sharks	211	6,293	44	618	1,987	1,239	14	96	2,237	41	1,006		1	6	4

APPENDIX H—ANOVA RESULTS COMPARING CPUE BETWEEN ZONES PER GEAR TYPE

Hook and line

Zones	*Count*	*Sum*	*mean*	*Variance*	*SD*
1	27	2.93	0.11	0.004	0.06
2	27	3.02	0.11	0.004	0.06
3	27	3.24	0.12	0.003	0.05

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.002	2	0.00091	0.25	0.78	3.11
Within Groups	0.28	78	0.00363			

Cast Net

Zones	*Count*	*Sum*	*mean*	*Variance*	*SD*
1	27	10.93	0.40	0.088392	0.30
2	27	9.75	0.36	0.047269	0.22
3	27	11.31	0.42	0.07337	0.27

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.05	2	0.0245	0.35	0.70	3.11
Within Groups	5.43	78	0.0697			

Gill net

Zones	*Count*	*Sum*	*mean*	*Variance*	*SD*
1	26	27.49	1.06	0.41	0.64
2	26	17.73	0.68	0.18	0.43
3	26	18.70	0.72	0.15	0.39

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	2.22	2	1.11	4.45	**0.01**	3.12
Within Groups	18.76	75	0.25			

Snorkel spear fishing

Zones	*Count*	*Sum*	*mean*	*Variance*	*SD*
1	22	20.48	0.93	0.28	0.53
2	22	19.07	0.87	0.16	0.40
3	22	20.40	0.93	0.21	0.46

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.057	2	0.028411	0.129647	0.878639	3.142809
Within Groups	13.81	63	0.219142			

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