ISSN 1198-6727

Fisheries Centre Research Reports

2020 Volume 28 Number 1

Ecosystem modelling to support fisheries management efforts in the Nyali-Mombasa area, coastal Kenya

Institute for the Oceans and Fisheries,
The University of British Columbia, Canada

Please cite as:

Wabnitz, Colette C.C., Omukoto, Johnstone O., Daw, Tim, Cheung, William W. L. (2018) Ecosystem modelling to support fisheries management efforts in the Nyali-Mombasa area, coastal Kenya. Fisheries Centre Research Report 28 (1): 76 pp

ISSN 1198-6727

Institute for the Oceans and Fisheries
University of British Columbia,
2202 Main Mall,
Vancouver, BC, V6T 1Z4.

This research report is indexed in Google Scholar, Research Gate, the UBC library archive (cIRcle).

TABLE OF CONTENTS

ACKNOWLEDGMENTS

The authors would like to thank F. Januchowski-Hartley for key data on the coral components of the model, detailed information about relevant communities at the modelled sites, and general expert feedback on different aspects of the ecosystem. We further acknowledge T. McClanahan for providing information on ecosystem components and general background for the modelling work; Joseph Maina for access to raw satellite habitat classification data for coastal Kenya; B. Crona, M. Thyresson, C. Cheupe and B. Gonzalez for data and information pertaining to the socio-economic context of the study. Other experts including, S. Zhou, M.-F. Racault, P. Erftemeijer, I. Bertram, M. Samoilys, B. Kaunda-Arara, C. Duarte, D. Obura, who provided data and helped complement and/or clarify existing information where relevant and necessary. S. Heymans is acknowledged for insightful and constructive comments that improved this report. This study was supported with funding through the project 'Sustainable Poverty Alleviation from Coastal Ecosystem Services (SPACES) NE-K010484-1', funded by the Ecosystem Services for Poverty Alleviation (ESPA) programme. The ESPA programme is funded by the Department for International Development (DFID), the Economic and Social Research Council (ESRC) and the Natural Environment Research Council (NERC).

DIRECTOR'S FOREWARD

UBC's Institute for the Oceans and Fisheries strives to contribute excellent research to help understand and effectively manage the world's changing oceans. Anthropogenic and ecological impacts affect not only the environment, but also the livelihoods of the fishers and communities reliant on them. It is, therefore, crucial to study the entire chain of well-being for an ecosystem, from changing environmental conditions, to the impacts of humans and social processes, to the effect of high-level policies and ecosystem services. As part of the Sustainable Poverty Alleviation from Costal Ecosystem Services project (SPACES), the present research addresses the important question: how can we best develop sustainable, effective fisheries decisions while preserving the livelihoods of fishers and their dependents?

This volume investigates the consequences from the effective ban of different fishing gears at Nyali-Mombasa, a site on the Kenyan coast. Using ecosystem modelling, it explores different scenarios for evaluating high-level impacts of various intervention or management decisions, as well as the resulting socio-economic consequences on relevant communities. The work has mapped various aspects of the Nyali-Mombasa ecosystem through the creation of a food web model, reproducing and quantifying main energy flows, and holistically investigating dominant food-web dynamics, and the role of fisheries on the system. With the exception of a simple Maputo Bay model (Silva et al. 1993), this research is the first to develop an Ecopath model for a coastal area in East Africa.

I congratulate the authors on their effort and this crucial research.

Dr. Evgeny Pakhomov
Director, Institute for the Oceans and Fisheries
The University of British Columbia

CONTEXT

The Sustainable Poverty Alleviation from Coastal Ecosystem Services project (SPACES) is supported by the UK Ecosystem Services for Poverty Alleviation (ESPA) programme to study the relationship between coastal ecosystems in Kenya and Mozambique and the wellbeing of poor people living along the coast. The project's activities look at how the condition of coral reefs and mangroves, and the ecological dynamics that determine this condition, affects the 'flow' of potentially useful services, how human inputs turn these into benefits and how social processes distribute these benefits to different members of society. The project analyses these 'ecosystem-wellbeing' chains and compares them across different kinds of ecosystem services in different contexts to understand how ecosystem services are linked to wellbeing and to identify potential policy levers that can enhance how poor people benefit from ecosystem services (www.espa-spaces.org).

This project component seeks to gain greater understanding of the feedbacks that exist between social and ecological system components that determine long-term trajectories, such as mutually reinforcing trends of environmental degradation and impoverishment (also called social-ecological traps by Cinner et al. (2011)) or where local empowerment creates synergistically beneficial outcomes for environmental governance and poverty (Daw et al. unpublished).

Specifically, the work described herein is intended as a preliminary step towards the estimation of the broad community, ecological, and economic effects of anthropogenic and ecological impacts on Kenyan coral reef ecosystems. Specifically, we sought to investigate the ramifications of the effective ban of different fishing gears at two specific locations along the coast of Kenya: Nyali-Mombasa (described here) and Vanga-Shimoni (described in a separate report). This initial step consists of the construction of a trophodynamic ecosystem model (using the freely available software Ecopath with Ecosim www.ecopath.org) for the locations of interest. Next steps will include simulations which might inform fisheries management decisions, as well as the identification of gaps in the data, and guidance for future research programmes.

ECOSYSTEM MODELLING TO SUPPORT FISHERIES MANAGEMENT EFFORTS IN THE NYALI-MOMBASA AREA, COASTAL KENYA

Colette C.C. Wabnitz[1],
Johnstone O. Omukoto[2], Tim Daw[3] and William W.L. Cheung[1]

[1]Changing Ocean Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, Canada
[2]Department of Fisheries Research, Kenya Marine and Fisheries Research Institute, Mombasa, Kenya
[3]Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, Sweden 10691

INTRODUCTION

Artisanal coral reef fisheries provide income, employment, and the main protein source to a large number of people, and therefore play a key role in food security in many developing countries throughout the tropics, including Kenya (Barnes-Mauthe et al. 2013, McClanahan et al. 2015). While marine fisheries contribute minimally to total landings in Kenya, they are important in socio-economic terms to a large number of coastal people (Malleret King et al. 2003, Matsue et al. 2014, Samoilys et al. 2017). The productivity of the Kenyan marine fishery is constrained by a number of biophysical factors including a narrow continental shelf, low productivity waters and seasonality (McClanahan 1988). This, combined with increasing fishing pressure as a result of increasing fisher density, increased demand and increased poverty (Ochiewo 2009, Cinner 2010, 2011, Waiyaki 2014), as well as poor governance (Japp 2011), has resulted in overexploitation and extensive degradation of coral reef ecosystems in many nearshore areas (Kaunda-Arara and Ntiba 2001, Mangi et al. 2007b, McClanahan and Hicks 2011, Hicks and McClanahan 2012).

Kenya enjoys a coastline of 640 km on the Western Indian Ocean, stretching from Somalia in the north to Tanzania in the south, with a narrow continental shelf estimated at 19,120 km^2 (or 6,500 km^2 to the 200 m depth contour (Ochumba 1983)). Generally, the shelf is narrow (< 5 km), with the exception of the area around the mouth of the Tana River and the Lamu area (~ 60 km) to the north. A fringing reef, which lies between a few hundred metres to a few kilometres from shore, fronts most of Kenya's coastal shoreline, enclosing a lagoon. The lagoon's depth varies between 0.2 and 10 m at mean low tide (Kenya has a 4 m tidal range) (McClanahan and Kaunda-Arara 1996). For most of the coastal area, important productive marine habitats such as coral reefs, seagrass and mangroves therefore are restricted, and resource use activities are concentrated close to shore. Artisanal fisheries in Kenya use various gears, including hand lines, traps, gill nets, seine nets and spearguns. Using these gears, fishers target a wide range of species, such snappers, octopus, parrotfish and rabbitfish. Fishing grounds are typically located between the shore and the outer reef edge, accessed by foot, swimming or using dug-out or outrigger canoes, with few fishers using motorized vessels - less than about 10% based on estimates from the Shimoni area, where a larger number of engine powered boats do exist (Malleret King 2000), and which is similar to the national level statistics produced in 1983 (Ochumba 1983).

Weather conditions in Kenya show strong seasonality in response to the movement of the Inter-Tropical Convergence Zone (ITCZ), a zone that influences the monsoon systems (Duing 1970). During the southeast monsoon (SE-*kusi*), which lasts from April to October, temperatures are cool, rains long and heavy (55-272 mm/month), seas rough and winds strong (0.5-0.75 m/s) (McClanahan 1988). The northeast monsoon (NW-*kaskazi*) on the other hand, lasting from November to March, is characterised by warmer temperatures, lower rainfall, calmer seas and steady and light winds (McClanahan 1988). The wind patterns prevailing during those seasons strongly affect local and regional currents, and in turn strongly influence local ecological processes and fisheries resource use. While catches have been reported to be lower during the SE monsoon, when winds are strongest and the conditions are often too rough for fishers (McClanahan 1988, Malleret King 2000), seasonality does not always seem to affect gear use or species exploited (McClanahan and Mangi 2001, Malleret King et al. 2003, Samoilys et al. 2017).

Most coastal communities are heavily reliant on marine resources for food security, income and their livelihoods, but the marine fisheries sector, mostly artisanal and multi-gear in nature, has registered important declines in recent years. A number of studies indicate that an increase in human population along the coast, damage to important fishery habitat such as coral and seagrass beds as a result of destructive fishing methods, and the harvesting of juveniles have led to several stocks being overfished (e.g., McClanahan and Shafir 1990, Mangi and Roberts 2006, Hicks and McClanahan 2012, Tuda and Wolff 2015, Samoilys et al. 2017). While the deployment of different gear types and catch distribution by gear vary along the Kenyan coast, the use of beach seines and spearguns, both of which have been prohibited through Fisheries Department legislation since 2001, is often widespread - in spite of the authorities' efforts to enforce beach seine bans (McClanahan et al. 2005) - and critical to catches in some areas (McClanahan and Kaunda-Arara 1996).

Seine nets

Seine nets are one of the most widely used destructive gears along the coast of Kenya (Glaesel 2000, McClanahan and Mangi 2001, Jiddawi and Ohman 2002, Mangi et al. 2007a). Pemba Island fishers are responsible for their introduction to Kenya in the 1960s when people fled Tanzania for political reasons (King 2000). Those fishers have since integrated through intermarriages and purchase of land, making the beach seine more acceptable (Signa et al. 2008). Beach seines are considered destructive mainly because of their small mesh size, which retains a large proportion of juvenile fish (McClanahan and Mangi 2004, Mangi and Roberts 2006), some of which are discarded (Mangi et al. 2007a), leading to recruitment overfishing (Cushing 1976, Sissenwine and Shepherd 1987). They are also considered destructive because they get dragged during deployment over fragile habitats such as seagrass beds and coral reefs, which additionally get trampled by fishers during use (Signa et al. 2008).

Based on the 2012 and 2014 frame surveys[1], and assuming an average of 15 fishers per net, between 2,895 and 3,255 fishers use beach seines – out of a total of between 11,000 and 18,000 estimated fishers (Signa et al. 2008). The activity is especially prevalent in Lamu and Gazi, as well as at Mtwapa/Marina, Msanakani, Reef and Nyali landing sites near Mombasa (see Figure 1). Beach seining is considered an important contributor to income generation and employment, leading also to food security, particularly for unemployed youth and women and especially among poor fishing households (Signa et al. 2008). Although a number of fishers would prefer utilising different gear, fishers often turn to beach seines due to the low/zero financial input or technical ability required for crew members as well as their efficiency in the short term (Obura 2001b, McClanahan et al. 2005). Thus, an effective ban of beach seines would likely have a very negative impact on many fishers' livelihoods leading to further increases in poverty levels. Ecosystem modelling combined with studies of the role of different value chain actors have shown that removal of beach seining would have disproportionate impacts on women traders who utilise the small, low-grade fish caught in large numbers by beach seining (Daw et al. 2015).

Studies at a number of locations have demonstrated significant drops in catches made using trap gear since the arrival of beach seines (McClanahan and Kaunda-Arara 1996). Aware of beach seine's negative impacts on stocks, associated resources and habitats, some communities have effectively banned their use, using traditional institutions or co-management approaches instead (McClanahan et al. 2008, Hicks et al. 2009). Sites where beach seines have been effectively banned by local communities, such as in Diani (McClanahan and Mangi 2001), clearly show increased total catches and CPUE of other gears (Mangi and Roberts 2007, McClanahan 2007, McClanahan et al. 2008). Beach seines are commonly disapproved of by elders (McClanahan and Mangi 2001), and are one of the main reasons for conflict between artisanal fishers (King 2000).

---

[1] Frame Surveys are assessments conducted to obtain information on the social amenities, facilities and services at the landing sites, the composition, magnitude and distribution of fishing effort that may guide the development and management of a fishery.

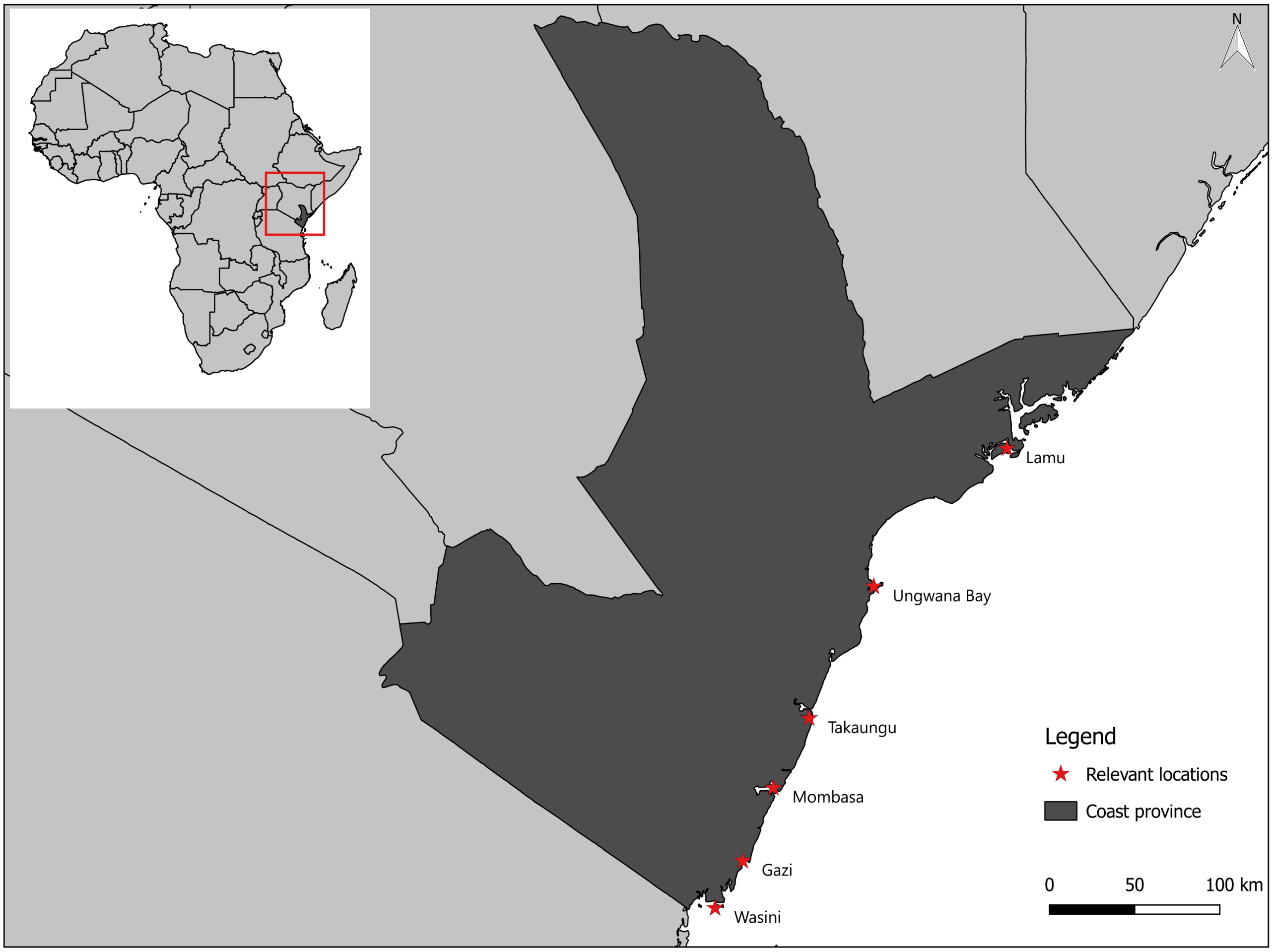


Figure 1 – Map of the Coast province highlighting the main locations (red stars) mentioned in this report. The inset highlights Kenya 's locations on the African continent.

Spearguns

Spearguns (spears/harpoons – see section 'Gears' below for definitions) can result in habitat damage as fishers tend to heavily trample on the reef flat or shallow lagoon areas while fishing (Mangi et al. 2007a). When using spearguns, fishers also tend to break corals or remove loose rubble to dislodge octopus from their hiding holes (Kivengea 2014) and/or when a fish target is missed. However, it could also be argued that it is in fact one of the most selective of all the gears, with lowest juvenile retention rates and studies indicating that it has maintained some of the highest CPUE over time (Samoilys et al. 2017). It therefore appears that with effective management it could be one of the better gears to use. Malleret King et al. (2003) suggest that the ban on spearguns was most likely targeted at relieving pressure on the fishery, with the intent of fishers then transferring to offshore fishing. However, as spearguns typically have the lowest monthly costs among fishing gears used (Mangi et al. 2007a), transfer to offshore fishing is unlikely given the lack of appropriate subsidies (Malleret King et al. 2003).

Domestic legal instruments are thorough enough and in theory should be sufficient to allow for the sustainable management of resources. The new Fisheries Management and Development Act of 2016 maintains the powers assigned to the Director of Fisheries in the Fisheries Act of 1989 to issue regulations promoting the proper management of specific fisheries, including closures, as well as gear and access limitations (Kamau et al. 2009). The Act also established the basis for the licensing of fishermen, and the enforcement of banned fishing gears in Kenya waters with the Wildlife (Conservation and Management) Act enforcing regulation only within MPAs (Kamau et al. 2009). However, the law is currently not effectively enforced (McClanahan et al. 2005; Signa et al. 2008).

The ban of both beach seines and spearguns, gears which are easy to use and comparatively cheap, would particularly affect young fishers who tend to be poor and lack capital to purchase other gears or use other fishing methods that may require access to a boat for example (Malleret King et al. 2003, Cinner 2010). It is clear that the successful ban of beach seine and speargun use will require a better understanding of the context in which these fishers operate and the development of programs that present viable alternatives to fishers, allowing them to break poverty traps (Cinner 2010). Successful sustainable fisheries management will need to consider all activities and strike a balance between strengthening livelihood opportunities by ensuring fisheries continue to provide economic and social benefits, while also enhancing the natural resilience and productive capacity of coastal habitats. Some of the recommendations put forth in Signa et al. (2008) for example, to be discussed with all stakeholders, may represent means to effect a slow phase out of beach seines and move towards effective marine resource management.

Effective management requires an integrated understanding of coral reefs as ecosystems (i.e., ecosystem-based (fisheries) management, Pikitch et al. 2004), with ecosystem models and indicators representing some of the most useful and powerful tools in this regard (Fulton 2010, Shin et al. 2010, Fulton et al. 2011). Ecosystem-based management (EBM), can be defined as “an integrated approach to management that considers the entire ecosystem, including humans. The goal of EBM is to maintain an ecosystem in a healthy, productive and resilient condition so that it can provide the services humans want and need. EBM, which forms part of the FAO sustainable fishing policy and other European and UN policies, differs from current approaches that usually focus on a single species, sector or activity or concern; it considers the cumulative impacts of different sectors” (McLeod et al. 2005, Acosta and Wintle 2016). Ecosystem models are useful in investigating biological interactions in natural communities; in allowing for the exploration of the complex and potential synergistic effects of different stressors where small changes can be magnified through nonlinear interactions, facilitating regime shifts and collapses; and in evaluating how such dynamics affect the sustainability of goods and services the modelled ecosystem provides. Beyond the direct effects of fishing on the fish themselves, fishing also causes a number of indirect effects. A large number of fish are important predators that mediate the competitive interactions of their prey, and the predators’ removal may have unexpected effects on ecological processes, community composition, and fishery yields. The primary role of models in ecosystem science is to permit controlled exploration of such a complex reality. They help elucidate patterns and processes that cannot necessarily be implemented, especially within sensible time scales, and/or that are not apparent from empirical data alone, thereby guiding research and management efforts. Within pre-defined temporal and spatial resolutions an ecosystem model must be able to describe the changes in a system based on the selected components that make up the system and generalities of how a system functions. Such models should ideally contribute to a greater understanding of how the system behaves and the driving forces and interactions of the system, as well as allow predictions of future states of the system based on ecological as well as socio-economic drivers impinging on the system. While ecosystem models are unlikely to quantitatively and accurately predict all ecosystem dynamics, they are useful in lending greater understanding of these dynamics, as well as in identifying robust management strategies and exposing trade-offs. Overall, their advantages trump their pitfalls (Fulton et al. 2003), and as such they represent a useful part of adaptive ecosystem-based management.

In this study, our main goal is to contribute to the scientific underpinning needed to advance ecosystem-based management at a key ecological site in Kenya, by developing an ecosystem model to represent a holistic perspective of dynamics and fluxes at Nyali-Mombasa. Specifically, we (i) describe the standardization, integration and analysis of the various datasets needed to establish the base ecological model; (ii) outline our findings with regards to catch data available for the area; and (iii) present, through the use of indicators, a summary of ecosystem state under current conditions. By running different scenarios, such a model would be useful for the evaluation of ecosystem-level impacts of various disturbances or management decisions, including an effective ban of beach seine and speargun use, and to explore the likely socio-economic impacts on fishers and their dependents of such interventions. The latter is particularly relevant given that poverty is pervasive among the local fishing communities, and management, therefore, requires the creation of inexpensive institutional interventions with the least likelihood of jeopardizing essential livelihoods. While models are intrinsically simplistic and present an averaged response that is ultimately unrealistic, especially in the face of environmental stochasticity (Walters and Martell 2004), we hope that the model developed here may prove a useful tool to evaluate the impact of management decisions and contextualize these to assist policy makers.

METHODS

This section is further divided into three segments presenting (i) an introduction to the study site; (ii) a description of the software utility Ecopath with Ecosim and some of the indicators that can be derived using this modelling tool; and (iii) the data utilised.

Study site

The study site itself stretches approximately from Nyali to Mtwapa, extending offshore just past the reef edge and encompassing a total of 29 km². The Mombasa area has long sandy beaches and low overhanging coral cliffs associated with scrubs and bushes, fringed by coral reefs. The seaward coast near Mombasa area is very flat, but around the island itself there are many creeks and mangrove swamps. While fishers predominantly use the area within the reef lagoon between shore and the outer reef edge, which is seldom deeper than 5 m at low tide, the "Fishers in Space" project showed that, weather allowing, around 50% of fishing trips crossed the reef crest. The average yearly mean sea surface temperature is 27°C.

Fishers rarely travel more than 100 m beyond the outer reef edge and, if they do so, only in the calmer northeast monsoon (McClanahan and Kaunda-Arara 1996). More than half of the lagoon is covered by a mixed-species seagrass community (dominated by *Thalassodendron ciliatum*) and associated seaweeds, as is common for such lagoons along the Kenyan coast (Ochieng and Erftemeijer 2003). The model area includes an important portion of the Mombasa Marine National Park and Reserve, specifically encompassing 4 km² of the no take zone.

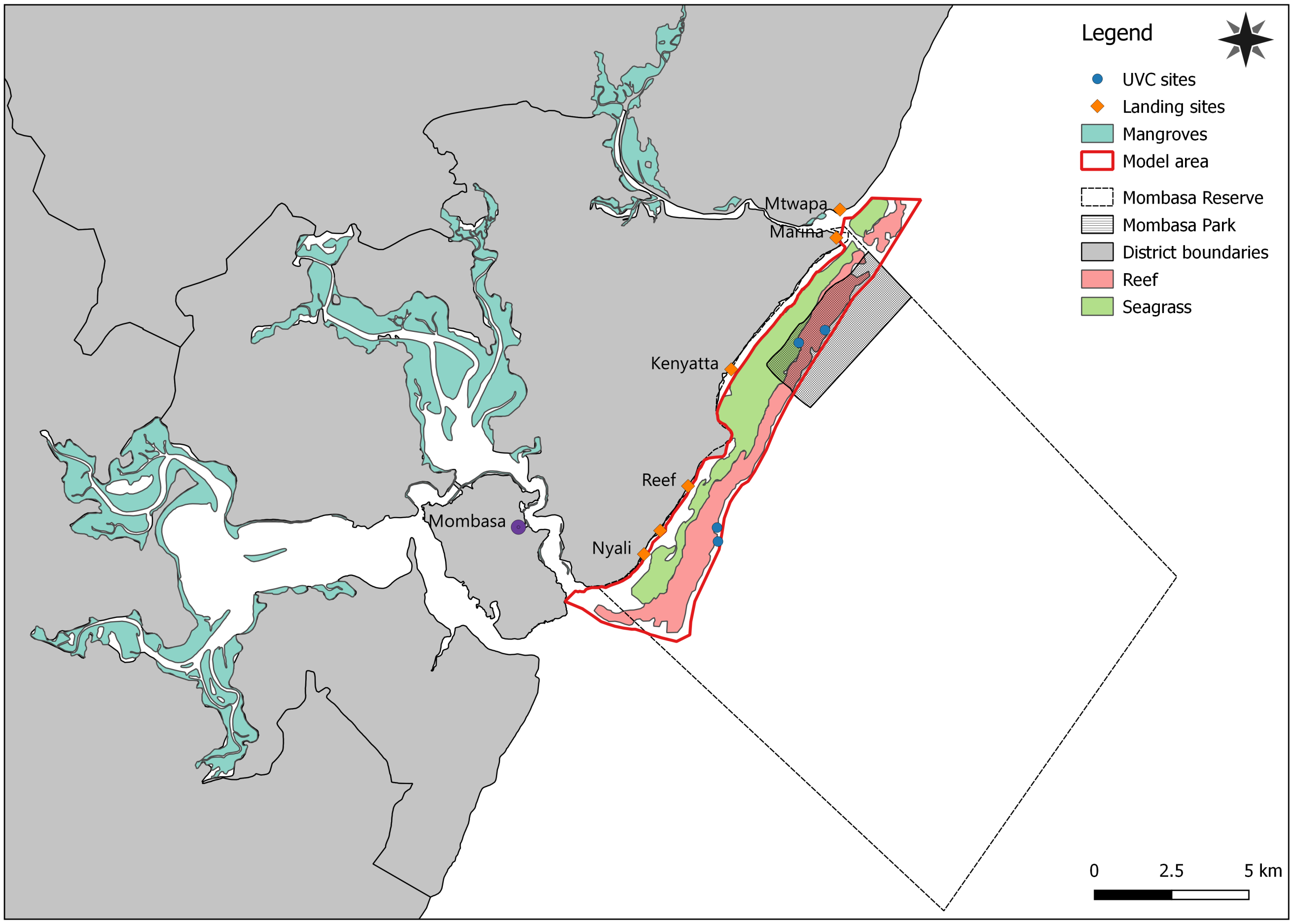


Figure 2 - Map of the study site including the model area bounded by a red line, the location of underwater visual survey (UVC) sites, the marine park (shaded box), the two main habitats within the park (seagrass and reef), and the six main landing sites (orange diamonds)

The Mombasa Marine National Park and Reserve (MMNPR) was established to protect the shallow fringing reef against threats arising from human activities, manage the various stakeholders that utilise the area, and derive revenues from tourist activities. The Mombasa Marine National Park and Reserve were gazetted for conservation purposes under The Wildlife Act Cap 376 of the Laws of Kenya through legal notices numbers 315 and 316 dated 9th December 1986, and supplement notice No. 88 of 11th December 1986, respectively. The reserve, which lies between Mtwapa creek and Tudor creek (northern and southern limits of model area – see Figure 2) and extends offshore, measures 200 km^2 and permits public access and controlled extractive use according to traditional methods of fishing (traps, gill nets, and hook and line). The park (10 km^2; see Figure 2), which is encompassed within the reserve, is a “no-take” zone (i.e., it is open to public recreation, but extractive uses are prohibited) and was legally gazetted in 1988. The area was heavily fished before protective management (McClanahan and Kaunda-Arara 1996, McClanahan and Mangi 2000) and total exclusion of fishers did not occur until mid-1991. Even thereafter sporadic poaching in the park at night was recorded until August 1992, at which point a night patrol was established (McClanahan and Kaunda-Arara 1996). Nevertheless, efforts to enforce park and reserve status resulted in a number of physical conflicts. In response, as part of an integrated coastal area management process, negotiations were undertaken with all stakeholders. By 1995 consensus was reached to eliminate beach seines and reduce park size; measures that were implemented in October of that same year (McClanahan and Mangi 2001). Since then, fishers-state relations have improved with fishers slowly adopting park management rules (Glaesel 1997). Reefs to the south of the park were demarcated as a marine reserve and, from 1995 onwards, officially, fishers were meant to fish using only traps, gill nets and hand lines. Tourist activities, such as snorkelling and SCUBA diving, are permitted within the park boundaries. The adjacent reef was declared a marine reserve in which artisanal fishing using traditional gears (traps, gillnets and handlines) is allowed. The conversion from an area with unregulated to traditional fishing at the park’s southern boundary, was also slow and not completed until around late 1994. Beach seine and speargunѕ were first effectively excluded in early 1994 (McClanahan and Kaunda-Arara 1996), but have been since, and are currently, recorded as an important gear in catches along the Nyali-Mombasa shoreline. In other words, the smaller closed area is functioning well, but not the reserve. Regulations that apply to the parks and reserves were originally described in the Kenyan Government Sessional Paper No. 3 of 1975 and formally in The Wildlife Act Cap 376 in 1989. This Act allows the minister to have discretionary powers to regulate areas in reserves. However, fisheries restrictions are not explicit and the lack of clarity and various interpretations of these limits have resulted in poor implementation (McClanahan 2007).

Mombasa has the largest population on the Kenyan coast, with significant land use practices around Mombasa contributing to the existing pressures on coastal resources. For example, poor land use practices around the creeks surrounding Mombasa (Figure 2), in part due to the clearing of vegetation to create space for informal settlements and subsistence farming, has led to increased sediment in the mangrove and towards the coast (Bosire et al. 2012). Raw sewage is known to run through the mangrove forest in canals and is discharged into the Tudor creek waters mainly from Mikindani, Tudor and the Old Town settlements (Bosire et al. 2012). Developments in industry and tourism have led to greater vulnerability of the shoreline to erosion and considerably add to the above listed pressures on coastal resources.

Habitats

The system modelled here covers a total area of 29 km^2 (Figure 2), 4.6 km^2 of which are in the park, with the remainder in the reserve. The surface area of the main habitat types were estimated based on a GIS habitat classification developed by Maina et al. (2015) from remotely sensed data. Surface areas were derived from shapefiles, with some of the polygons needing to be split and redrawn for the categories relevant to the present study. All calculations presented were conducted on the vector files, but calculations were also done on the raster files and yielded similar results for all habitat categories considered. The classification scheme included classes with mixed habitats (e.g., reef/seagrass), and classes that are likely to support both a different assemblage and different density of species than recorded during underwater visual surveys conducted on the forereef (e.g., rubble bank). Consequently, when estimating the total surface area of “reef”, we did not include the latter and made the informed decision also to include 25% of mixed classes. This yielded a total of 13.98 km^2 of seagrass, 1.29 km^2 of which was in the park, and 8.59 km^2 of reef (0.8 km^2 protected).

Table 1- Area included in the modelled system that is in the park and in the reserve and habitat coverage within each of these areas.

Habitat	**Reserve (fished) area (km²)**	**Park (unfished) area (km²)**
Coral	7.79	0.80
Seagrass	12.69	1.29
Other mixed habitats	3.92	2.51
Total	24.4	4.60

Modelling approach

The Ecopath with Ecosim (EwE) approach combines trophic mass-balance within a system with a dynamic modelling component (Christensen et al. 2008). Ecopath is the mass balance part of the modelling framework, providing a static description of an ecosystem through established species or species groupings, trophic connections between these, and catches that are taken from the system for a given time period, typically a year (Christensen and Walters 2004). Ecosim, the tropho-dynamic simulation module, allows for multispecies simulations to explore how given stressors (e.g., changes in primary production, increase in fishing pressure, changes in habitat) impact ecosystem structure and functioning, and policy exploration (e.g., fishing policies that would maximize a particular socio-economic or environmental goal for management) (Christensen and Walters 2004). A separate tool, Ecospace, also allows for the exploration of ecosystem dynamics established in Ecosim at a gridded spatial scale (Walters et al. 1999, Christensen et al. 2014). Polovina (1984) developed Ecopath to study coral reefs at French Frigate Shoals. The software itself has undergone a number of significant updates and modifications since its inception and a variety of dynamic capabilities have been added (Christensen et al. 2008, Coll et al. 2015, Scott et al. 2016, Steenbeek et al. 2016, Villasante et al. 2016).

The ecosystem modelling approach Ecopath with Ecosim is ideally suited to address the broader community and ecosystem implications of fishing for example, and is useful in the analysis of associated economic and social impact analyses. Indeed, this tool allows one to look at impacts and the development of management strategies in the context of the entire ecosystem and dependent communities. Ecopath model construction, the focus of the study carried out herein, highlights ecological relationships and describes an ecosystem over a specific period under the assumption that the mass balance in the production of any specific prey is equal to the biomass consumed by predators, in addition to any exploited biomass by local existing fisheries and any exports from the system. It is designed to include all biotic components of an ecosystem, and biomass expressed in t km^{-2} (equivalent to g m^{-2}) as wet-weight is typically the currency, and was used here.

Basic equations and input

The production P_i (t km^{-2} year^{-1}) of species *i* is the product of its biomass B_i (t km^{-2}) and its production per unit of biomass $(P/B)_i$ per year. The latter is equivalent to total mortality (Z) and is estimated as the sum of fishing (F_i year^{-1}) and natural (M_i year^{-1}) mortality rates. For each species or functional group, which can be made up of several species, the annual production is equal to the sum of catches (Y_i) the biomass consumed $B_i \cdot M2_i$, the net emigration (E_i), any biomass accumulation (BA_i), and the biomass lost to other mortality $B_i \cdot M0_i$.

$$P_i = B_i(P/B)_i = Y_i + B_i M2_i + E_i + BA_i + B_i M0_i$$

All these terms are expressed in t km^{-2} year^{-1}. The biomass consumed is defined as the sum of prey *i* consumed by all predators *j*:

$$B_i M2_i = \sum_{j=1}^{n} B_j\,(Q/B)_j DC_{ji}$$

where $M2_i$ is the predation mortality rate per year, DC_{ji} is the proportion of of prey *i* within the diet composition of predator *j*, and $(Q/B)_j$ is the consumption per unit of biomass for predator *j*. Q/B is typically derived from bioenergetics models or empirical relationships, often based on temperature, growth rate parameters and the aspect ratio of the caudal fin (see www.fishbase.org). The empirical relationships tend to overestimate Q/B, leading to very small production to consumption ratios (P/Q). P/Q is a dimensionless parameter that corresponds to the gross efficiency (GE). P/Q values typically range between 0.05 and 0.3. Exceptions include top predators, which can have lower P/Q values, and small fast-growing fish larvae or bacteria for example, which can have higher P/Q values. The other mortality $M0_i$ can also be expressed as the part of loss of production not used in the system $P_i(1\text{-}EE_i)$, where EE_i is termed the ecotrophic efficiency. EE thus represents the fraction of production that is used in the system (i.e., consumed by predators in the system, exported, or accumulated (see BA)). Ecotrophic efficiency is difficult to measure directly, which is why it is usually left to Ecopath to estimate. Its value ranges between 0 and 1 and is close to 1 for groups with high predation pressure.

Ecopath requires inputs regarding diet compositions and catches, and at least three of the four basic parameters (biomass, P/B, Q/B, and ecotrophic efficiency) for each functional group in the model. The missing parameter is then estimated by Ecopath (Pauly et al. 2000, Christensen et al. 2005).

It is important to recognise that a balanced Ecopath model is one representation of a given ecosystem and that it could be changed as new data or knowledge becomes available.

After gathering all initial data, the model was balanced and subsequently validated using the prebalance diagnostics (PREBAL) (Link 2010). PREBAL provides a set of guidelines presented as a “checklist” to ensure that potential problems are dealt with prior to model outputs being used for research or management questions (Link 2010) (see Appendix 1 for results). Balancing of the model was achieved by adjusting diets for those functional groups with EE values >1. Diet was the input parameter that we fine-tuned as prey proportions may have been overestimated, owing to inherent uncertainty in diet studies and the recognized flexibility in most predators’ diets based on prey composition in the system (Wootton 1990). The gross food conversion efficiency (P/Q) and the respiration over assimilation (R/A) estimates were generally within the expected ranges (Christensen et al., 2008). Exceptions included corals, which have characteristics of both auto and heterotrophs, as well as groups consisting of herbivores and detritivores (or groups to which herbivores or detritivores contribute the most to biomass). Once we assessed all data checks as satisfactory, various Ecopath output tools were used to calculate a number of indicators (see next section).

We also set confidence intervals around each input parameter to allow Ecopath to estimate a pedigree index indicative of the quality of the model. The pedigree is derived by allocating greater weight for locally collected or experimentally obtained data and lower weight to parameters derived from other models or extrapolated from other systems (Christensen et al. 2008). These confidence intervals (CI) are evaluated on a scale from 0 to 1, with 1 being the highest (Pauly et al. 2000). Confidence in data from field sampling was assumed to have the narrowest CI (10%–30%), and estimates derived from empirical relationships, adapted from other models or calculated by Ecopath were assumed to have the widest CI (50%–80%). Bar a few exceptions, most of the biomass data was obtained from locally conducted field surveys and other published field studies from Nyali-Mombasa specifically, or sites along the Kenyan coast. Therefore, they were defined as having relatively narrow CI. Biomass data obtained from similar sites further afield or adapted from other models were given wider CI. P/B and Q/B input parameters were defined as having 30%–60% CI, depending on whether they came from field studies (30%), empirical relationships (50%), or other models (60%). Diet data, which we derived mainly from the literature and Fishbase, were defined as having 20% CI when it came from quantitative field studies in Kenya/East Africa, 30% from expert opinion, and 50% from qualitative studies. Fishery data was assigned a 30% to 50% CI.

Indicators

Ecosystem models can be useful tools to develop robust and meaningful indicators capable of capturing the status of marine ecosystems’ structure and function against natural and/or anthropogenic changes and support decisions towards ecosystem-based management (Link 2005, Cury et al. 2008, Halpern et al. 2012, Rombouts et al. 2013, Coll et al. 2016). In this regard, the work undertaken by IndiSeas [“Indicators for the Seas” - www.indiseas.org; (Shannon et al. 2014, Coll et al. 2016)] is of particular interest. This international initiative has developed and assessed ecological indicators for comparisons across ecosystems to demonstrate predominantly fishing impacts on marine ecosystems worldwide and to inform meaningfully management actions towards sustainability. These indicators include fisheries and ecology-based indicators (e.g., Shin et al. 2010), biodiversity and conservation indicators (Coll et al. 2016), as well as socioeconomic and governance indicators (e.g., Bundy et al. 2016). Specifically, the EwE framework allows for the derivation of indicators that relate to the biomass of species or groups of species at different trophic levels of the food web; primary and secondary production; as well as energy flow through the food web and trophic efficiencies (notably through the Ecological Network Analysis (ENA) (Heymans and Baird 2000, Heymans et al. 2007). ENA is a modelling technique used for understanding the structure and flow of material between components of an ecosystem, as modelled (Ulanowicz 1997). It is descriptive in nature and is most commonly used for evaluating food webs (Wulff et al. 1989, Christensen and Pauly 1993). It is integrated into Ecopath and allows for the calculation of ecosystem macro-descriptors, which quantify trophic structure, organic matter recycling, and ecosystem size and organization.

We selected a suite of candidate indicators that we felt best described ecosystem structure and network flows (Table 2), based on the IndiSeas work mentioned above, the ENA tool, and a number of relevant publications (Fulton et al. 2005b, Samhouri et al. 2009, Shin et al. 2010). Specifically, ENA descriptors included total system throughput (T), Ascendency (A), and the overhead (O). Throughput is the sum of all flows in the model and thus describes the 'ecological size' of a system and represents a measure of its metabolism (Finn 1976, Ulanowicz 1986). Ascendency integrates both size and organization of a given system (Ulanowicz 1986). The system's overhead (O) is complementary to the Ascendency and measures to which degree particular links can be considered 'redundant' (Heymans 2003); it is an indicator of the ecosystem's strength in reserve (Ulanowicz 1986). ENA further allows the derivation of Transfer Efficiencies (TE), summarizing the proportion of consumption that is passed up a food web. The TE is obtained by calculating the ratio between the production of a given trophic level and the preceding trophic level (Pauly and Christensen 1995).

Trophic flows, trophic levels and biomasses of the modelled ecosystem are presented via two graphical representations: a flow diagram and a Lindeman spine (Field et al. 1989, Ulanowicz 1997). In the Lindeman spine, primary producers and detritus (both with TL = 1) were separated to better represent flows contributing to the different trophic levels.

Functional groups

The model developed represents average ecosystem state at Nyali-Mombasa for the year 2013. This time point was chosen because of: (1) data availability for both Mombasa and Vanga-Shimoni, as well as sites further along the East African coastline that could be included for comparative analyses in the future; and (2) household survey data that was collected in parallel to the ecological data used here, with a view i) to integrate these data into the ecosystem model under the value-chain analysis module, and ii) to form part of an integrated analysis of the socio-economic benefits derived from natural resources.

Biotic information for the Nyali-Mombasa model area was aggregated into 46 functional groups based on the best available data at the time of model development and applications indicated as of interest for model scenario runs. Functional groups are treated as a single biomass pool, although they can consist of a single or multiple species. The latter may in some cases, but typically does not, affect model dynamics. While individual functional groups can also be split into so-called stanzas according to life history stages, we did not apply this to any group here. Species were aggregated into groups mainly on the basis of similarities in habitat use, diet, feeding behaviour (i.e., roving, hunting, grazing), life-history characteristics and/or growth form in the case of corals. Due to their potentially important ecosystem role and impacts, sea urchins (key herbivores) were included as a distinct functional group. Fish, urchins and corals were all further separated based on whether data was recorded in reserve *versus* park (i.e., protected (P) or fished (F)). This partitioning was undertaken as these groups have been observed to follow differential trajectories following closure of areas to fisheries (McClanahan and Graham 2005, McClanahan et al. 2007). Such separation will also allow future model scenarios to test the impact of closures on ecosystem-level dynamics over time.

Fish data was obtained from underwater visual surveys conducted in 2013. All other data was derived from locally undertaken activities, where available and possible, or work carried out in similar reef ecosystems otherwise, along the East African coastline preferentially.

Ratios of production over biomass (P/B) and consumption over biomass (Q/B) came from published sources, or empirical relationships following Pauly (1980) and Palomares and Pauly (Palomares and Pauly 1998) for fish, and Brey (2001) for nonfish groups. The sections below provide details on the input parameters of all functional groups.

We did not factor in any immigration or emigration for any functional group.

About 80% of the consumption was assumed to be physiologically useful for consumer groups with non-assimilated food (20%, consisting of urine and faeces) directed to detritus (Christensen and Pauly 1992). Assimilation efficiency was adjusted to 70% for zooplankton and herbivores/detritivores (Welch 1968, Jarre-Teichmann 1996, Christensen et al. 2008).

Fisheries

The narrow continental shelf and ocean's low productivity constrains fishing activities mostly within a thin strip close to shore. Fishing is carried out by foot, or using simple boats, and can be dependent on the monsoon patterns. Mombasa county recorded a substantial reduction in the number of fishing crafts from 488 to 356 in 2012 and 2014 respectively (Department of Fisheries 2012, State Department of Fisheries 2014). Dugout canoes and dau boats are the fishing crafts that registered the greatest declines. Dugout canoes remain the main fishing craft. Overall, coastal inshore fisheries are being harvested beyond maximum sustainable yield (Kaunda-Arara et al. 2003, Hicks and McClanahan 2012, State Department of Fisheries 2013), with excessive and destructive fishing described as one of the major problems facing the local reefs (Welch 1969, McClanahan and Shafir 1990, McClanahan and Obura 1995).

Fish are caught using a variety of artisanal gears (sardine net, beach seines, spearguns, traps, gillnets, and handlines – see section below for more detailed description of gears) and mainly landed at one of six sites within the model area: Reef, Marina, Kenyatta, Nyali, Mtwapa, and Msanakani. Fishing takes place daily following seasonal and particularly tidal cycles. Fishing effort is high, and attributed to the relatively intense use of beach seines along the reserve (McClanahan and Mangi 2001, Mbaru 2012). The main species landed are coral reef/seagrass/sand associated demersal fish species. The most commonly caught demersal groups include lethrinidae, lutjanidae, scaridae, and siganidae. Spiny lobsters (Palinuridae) are also exploited, albeit they are commercially less important here than in Lamu County. Octopus (Octopodidae) also constitute an important fishery, together with squid and sea cucumber, although recent Fisheries Bulletin data indicate no catches of the latter for about the last ten years.

Gears

While a total of 8 gears were recorded by the Wildlife Conservation Society, who regularly conducts fish catch assessments at landing sites in Mombasa, ringnet were excluded from analyses as it is likely deployed further offshore, and sardine net was not used very much. It is a seasonally deployed gear only and the survey protocol may not be designed adequately to account for this gear's use and catch. Descriptions of the five main gears considered in the development of the Ecopath model for Mombasa presented below were mainly adapted from Samoilys et al. (2011). Sardine nets are not included as they mainly target the seasonal migration of small pelagic fish, vary in their make-up (McClanahan pers. comm.) and are only used at two landing sites (Mtwapa and Reef). Given the minimal amount of time that sardines spend in the area and based on survey data, sardine nets contributed 0.16 tonnes to total annual landings at Nyali Mombasa (equivalent to 0.1% of total catches).

Beach seine

A beach seine is a long multifilament nylon net with floats at the top and weights along the bottom, and a section of larger mesh netting on each wing and smaller-mesh in the centre. It is designed for use in coastal waters adjacent to the beach (or offshore from two boats when used as a reef seine). It is locally known as *buruta* or *juya* or *nyavu ya kukokota*. It is usually deployed in a semi-circle out from the beach, around a shoal of fish and then dragged in to shore by fishers pulling on both sides of the net. Since it is a long net, it usually takes a team of 8 to 25 fishers at a time to bring the net in. Target species include parrotfish (Scaridae), rabbitfish (Siganidae), emperor (Lethrinidae), sardines (Clupeidae) and halfbeaks (Hemiramphidae), with triggerfish (Balistidae) and surgeonfish (Acanthuridae) often caught incidentally. This gear was banned on November 9th 2001 (Kenya Gazette Notice no 7565 Vol CIII No 69), but the ban is being poorly enforced (see Introduction). As beach seines are dragged on the sea bed they cause direct physical damage to the reef/seagrass substratum (Carpenter and Alcala 1977) and their use has been associated with high rates of direct coral damage per unit catch and unit area. Beach seines are also associated with high incidental catch of juveniles (68%), and in some areas (e.g., Kiunga), but not Mombasa, high discard rates.

Basket trap

Traps, locally known as *malema,* are handmade with a split bamboo hexagonal frame and interwoven with split bamboo reeds to form hexagonal mesh. Bait is typically placed inside the trap to attract fish through a cone-shaped entrance on one side of the trap. The trap is weighed down with rock or pieces of coral and lowered onto the reef or seagrass beds, generally in the lagoon, with the use of ropes. Soak time is usually around 24 hours. Up to 4-6 traps are deployed from paddle canoes or outrigger sailboats by one or two fishers onboard. Common target species include rabbitfish, parrotfish and emperors. Traps are known to catch a high proportion of juvenile fish.

Hook and line

A single, generally weighted, monofilament line with one or more baited steel hooks. Lines are used off a stationary or drifting paddle or sailing canoe with 1-3 fishers onboard. Handlines are also used from shore. Fishers using handlines typically fish over rocky areas, coral reefs, reef edges/slopes and offshore areas down to a maximum of about 40m, targeting emperor, snapper, grouper, trevally and mackerel. Juvenile fish make up to 56% of the catch when using small hooks. This fishing method is locally referred to as *mshipi*.

Speargun

Bunduki are typically made out of wood with a separate steel harpoon finished by a sharpened tip and propelled by rubber strips. Speargun fishermen generally swim on the surface using a mask or small goggles, sometimes fins. The use of SCUBA has also been reported. Alternative similar gears include spear – a steel rod sharpened at one end with (*mkuki*) or without (*njoro*) a wooden handle – and harpoon – a wooden pole with (*mkondzo*) or without (*shomo*) a metallic tip. Although spearguns/spears/harpoons were declared illegal on November 9 2001 (Kenya Gazette Notice no 7565 Vol CIII No 69), they are still widely used. Spear fishers have a lot of contact with live corals and cause a high rate of trampling. Spearfishing at night gives sleeping fish a significant disadvantage. Speargun fishers typically target parrotfish, snapper, grouper, rabbitfish, octopus and lobster; while spear and harpoon fishers target mainly octopus and slow moving fish, such as rays and moray eels.

Gillnet

Gillnets can be used as stationary or drifting. The net is made of multifilament nylon string of varying thickness and mesh size. They are maintained uprights by floats along the top and weights along the bottom. Fish are caught by becoming entangled in the mesh. Stationary nets (*nyavu ya kutega*) are typically deployed by a team of at least 2 fishers from a canoe or a boat. They are deployed in reef lagoons and on outer reef slopes, can be set at the bottom, midwater or at the surface, and are generally left soaking overnight. Target species include emperor, rabbitfish, rays, sharks, kingfish, tuna, flounder, needlefish, halfbeak and lobster. Drift nets (*nyavu ya kuogelesha*) are deployed at the surface from boats or canoes, usually beyond the reef or in deeper lagoons, and let to drift freely with the current, or connected to the boat. The net is hauled in after several hours. Target species include sharks, tuna and kingfish. Turtle, dolphin and other marine mammals, as well as sea birds, are reported as bycatch.

Monofilament gillnet (*nyavu ya mkano*), which, as the name implies, are made of monofilament nylon, have small floats attached at the top of the net and small weights at the bottom. They are deployed a little differently to multifilament gillnets. One end of the net is anchored while the rest is then fed out into the water by two to four fishers from a canoe, or motorized boat, or fishers swimming (Tim Daw, pers. obs.). Fishers stay with the net, leaving it to soak for about 10 hours before hauling in the catch by pulling themselves back to the anchored end; they may also drive fish into the net with a team of swimmers. This type of net was banned under the same ordinance as beach seine and spearguns (Kenya Gazette Notice no 7565 Vol CIII No 69), because monofilament nets do not biodegrade and, therefore, if discarded or lost, continue to trap fish and other marine life (ghostfishing). Typical target species include halfbeak, mullets and rabbitfish. Birds and turtles are the most common bycaught species.

Catch and related fisheries data

The Kenya Marine Fisheries Research Institute (KMFRI) and the Wildlife Conservation Society (WCS) have been conducting independent dedicated surveys, so called catch assessment (CAS) surveys, of artisanal catches at select landing sites since September 2001. Data collection occurs over a subset of days each month and includes field observation in combination with structured questionnaire interviews focusing on catch (fish family/species, weights of total catch and the measured subset of the catch where applicable and, where possible, lengths) and effort (number of boats, gears used and number of crew). Due to staff capacity and funding constraints, data collection is not uniformly distributed among landing sites, or throughout the seasons.

Catch data was analysed by landing site (n=6), by gear (n=6) and by species/species groups, which we aggregated into model functional groups. For most individual species, or species groups in the catch dataset, there was only one matching Ecopath group (e.g., Rockcod = Serranidae). However, for a few, several catch names were attributed to a given Ecopath group. This was based on best available information gleaned from publications and communications with local experts at the time of model development. However, in some instances the supplied "catch name" may have been inconsistent over time resulting in data uncertainty. For example, while "scavengers" typically designate species within the family Lethrinidae, it is also sometimes used to designate species of the families Lutjanidae and Haemulidae (McClanahan and Mangi 2001). The attributions used here are highlighted in Table 2.

As surveys, conducted on a given number of days each month, only represent a subset of total annual catch, we estimated yearly landings by (i) calculating average daily catch by gear at each of the individual landing sites (total catch by group and gear/no. sampling days by gear at landing site), (ii) multiplying (i) by the ratio of number of days the gear was seen being deployed by the number of days scouts were out surveying, and (iii) multiplying (ii) by 220, the total number of estimated fishing days per year, which accounts for days when the tidal cycle does not encourage fishing (McClanahan and Mangi 2001, McClanahan et al. 2008, Maina et al. 2013)[2]. These values were then divided by the model area for input into Ecopath. Catch data for marlin (landed at Mtwapa) were not included as they are likely to have been fished outside of the model area. Some studies estimate total yield based on average daily catch, mean fishing effort (typically for artisanal fisheries the mean total number of active fishers), fishing days per year and area of fishing grounds (Samoilys et al. 2017). However, we felt that the inclusion of the ratio of the number of days over which the gear was observed actually being used to the total number of days surveyed was important, as the data, collected according to a relatively consistent monthly sampling protocol at Mombasa, clearly indicate that use varies among gears and not all gears are deployed on a daily basis. See Appendix 2 for range in values according to different assumptions.

---

[2] *Note that some other references (e.g., McClanahan and Mangi 2001, Signa et al. 2008) report fishers being active >24 days per month. Therefore, our estimates are likely to be conservative.*

Table 2 - Catch names and corresponding Ecopath group

Ecopath groups	Catch Name	Examples of families
Pelagics	Barracuda	Sphyraenidae
	Bonnito	Scombridae
	Cobia	Rachycentridae
	Fusilier	Caesionidae
	Halfbeak	Hemiramphidae
	Jack	Belonidae
	Kingfish	Trichiuridae
	Little mackerel	Clupeidae
	Mackerel	
	Needlefish	
	Queenfish	
	Ribbonfish	
	Sardines	
	Striated caesio	
	Travelly	
Reef fish	Brassychub	Kyphosidae
	Butterfly fish	Chaetodontidae
	Catfish	Gerreidae
	Eel fish	Monodactylidae
	Others	Acanthuridae
	Pursemouth	Balistidae
	Silver moony	Acanthuridae
	Surgeon	Sparidae
	Sweeper	
	Triggerfish	
	Unicornfish	
	Zebra fish	
Sweetlips and grunters	Blackskin	Haemulidae
	Grunter	
	Sweetlips	

As no size information was available for the catch data, yet “reef fish” and “parrotfish” model groups are split according to size categories (see functional group parameters below), we applied the proportions estimated for biomass data within each size class to catches. However, for parrotfish, biomass proportions were 74% and 26% for >30cm and <30cm respectively; which does not seem realistic for catches. A large proportion of parrotfish are harvested from the model area using beach seines deployed mostly over the seagrass beds from shore. Therefore, catches are predominantly likely to be composed of small bodied species such as *Leptoscarus vaigiensis* and *Calotomus spinidens* (Lugendo et al. 2005, Signa et al. 2008, Hicks and McClanahan 2012, Samoilys et al. 2017). As these species preferentially inhabit seagrass beds it is not surprising that they were not recorded from UVC surveys conducted over the reef. Consequently, in the absence of locally verified data we attributed a 50/50 split between the two size classes to the parrotfish catch data. Future efforts should attempt to address this uncertainty by including length-frequency data of catches into analyses.

As a function of effort, we estimated total catch per fisher per day by dividing total daily catch by the number of fishers that participated in fishing for that day, by gear.

Fishing mortalities for each group can be estimated by dividing catch by biomass for that group. With the exception of 4 groups, for which we calculated unrealistically high F/M ratios, fishing mortalities for a number of other key target groups were well below known stock status and/or reported values (e.g., Kaunda-Arara and Ntiba 2001, Kaunda-Arara et al. 2003, Hicks and McClanahan 2012). As most targeted fish groups are known to be fully exploited, F was set to 2•M and biomass adjusted accordingly. These adjustments appear realistic given that: (i) a large portion of the biomass for some of the target groups (including sweetlips & grunts as well as emperors) are known to utilise seagrass beds for forage. Whilst our calculations did augment UVC-derived biomass estimates to account for a proportion of the stock that would not have been included by reef-only transects (see below), it is likely that our method may have underestimated this stock proportion; (ii) some of the groups include more vagile species (e.g., sharks & rays and pelagics), which standard UVC surveys are not designed for and therefore cannot adequately take into account; and (iii) estimates fall within the range of values derived for the area from separate surveys (J. Omuhaya pers. obs.) .

The State Department of Fisheries (SDF) also regularly conducts catch assessments, which contribute to the publication of their annual Fisheries Statistics Bulletin (State Department of Fisheries 2013). The surveys essentially operate following the same principle as above, however, annual figures are produced according to a different set of assumptions based on frame assessment surveys conducted in parallel to the catch assessment surveys. These marine artisanal fisheries frame surveys have been carried out biennially since 2004, bar 2010, during different seasons (e.g., 2012 was carried out during the SEM while the 2014 survey was conducted during the NEM). The objective of these surveys is to collect, analyse and document critical data on present fishing effort, landing site facilities, services and infrastructure developments. The survey is a complete census of crafts, gears and fishers operating at the coast, and all landing site facilities and services. In addition to socio-economic information at the landing site, enumerators specifically collect information on the vessel type, length, propulsion, navigation aid on board, number of crew, gear type, gear size (mesh sizes, hook sizes), mode of operation for gillnets and the number of gears per craft. While useful and a commendable effort, such independent total census of fishers numbers tends to produce a fishing population that is larger than when accounting for fishers on actual sampling days, because some fishers do not report to the landing site during the regular incoming tide time, or because they fished during the night (McClanahan and Mangi 2001). Moreover, many fishers in the frame survey may not be active full-time. Originally, the SDF operated a routine fisheries data collection programme based on total enumeration, with all fishing trips detailed at all coastal landing sites. However, due to the logistics associated with operating such a programme, staff shortages and the costs involved, the SDF opted for a catch sampling approach instead. The new collection strategy focuses on targeting between 20 and 25 landing sites along the entire coast, where it is estimated that 70% of the total catch is landed. However, it is not entirely clear when this new protocol was implemented. In 2012, the survey was limited to three days (9th to 11th of July) (Department of Fisheries 2012), while in 2014 it was conducted over four days (25th to 28th of February).

Data obtained from the Fisheries Department (Statistics Fisheries Bulletin) for 2013 spanned January through November and included the following landing sites within the model area: Bamburi, Nyali and Marina. To account for a full year's worth of data, catch for December was estimated as the average from all other available months. Data in the Statistics Fisheries Bulletin report on groups landed at Bamburi, Nyali and Marina, while WCS data record fish and invertebrates landed at 6 sites: Kenyatta, Marina, Msanakani, Mtwapa, Nyali and Reef. Assuming that Bamburi describes the same landing site as Kenyatta, catch landed at Bamburi, Nyali and Marina account for 51% of WCS recorded landed catch overall. Further, assuming that the WCS dataset is more comprehensive and data collection more consistent than the programme led by the Fisheries State Department, we divided the available Fisheries Statistics Bulletin annual catch data by 0.51 to yield study-relevant annual landings data. These data were then processed according to the following steps before comparison with WCS obtained data:

1. Reporting for the Statistics Fisheries Bulletin was categorized according to a set of different groups. These were matched up with the previously defined Ecopath functional groups according to WCS/KMFRI catch data proportions as best we could:
    a. "Scavengers" were assumed to be emperors and "rock cod" groupers;
    b. "Black skin" were assumed to include species under the Haemulidae family (Anon 2015);
    c. "Unicornfish" were considered as part of the reef fish <30cm as Acanthuridae in the UVC data was all <30cm in the fished area;
    d. Total catch for "Other demersals" were split into Reef fish >60cm, Reef Fish 30-60cm, Reef Fish <30cm and wrasses according to WCS proportions; and
    e. Total "parrotfish" catch was evenly split between >60cm and <30cm.

Table 3 - Comparison of WCS and State Fisheries Department catch data (in tonnes)

Group	**Statistical Bulletin**	**Stats/0.51**	**WCS**	**% of Stats**	**% of (Stats/0.51)**
Rabbitfish	26.678	52.309	14.080	53%	**27%**
Emperors	9.276	18.188	11.754	127%	65%
Snappers	5.495	10.773	0.630	11%	6%
Parrotfish	28.800	56.470	62.917	218%	111%
Reef fish & wrasse	8.162	16.004	5.717	70%	36%
Sweetlips & grunts	4.056	7.953	1.452	36%	18%
Goatfish	8.545	16.756	0.305	4%	2%
Groupers	0.923	1.810	1.691	183%	93%
Lobsters	1.271	2.493	0.569	45%	23%
Sea cucumbers	0.000	0.000			
Octopus	5.707	11.190	10.501	184%	94%
Pelagics	30.056	58.933	21.036	70%	36%
Sharks/Rays	2.711	5.315	1.666	61%	31%
Non-Octopus Cephalopods			6.524		
Benthic crustacean			0.020		
TOTAL	**131.679**	**258.194**	**138.862**		

Diets

While research quantifying the abundance of reef fish in the Mombasa area has been ongoing for a number of years, few local data exist on their dietary composition and the abundance or diets of non-fish groups (e.g., lobsters, octopus), with the exception perhaps of sea urchins. Diet was informed as much as possible by published field data collected locally preferentially (e.g., Kamukuru and Mgaya 2004, Locham et al. 2015), derived from similar systems where such data was not available, and/or assembled from diet preferences and food items available from Fishbase. The diet matrix was developed for fish species and/or groups. In case of the latter, given that fish prey were often only labelled as finfish or unidentified fish, we relied on expert judgment/knowledge and other ancillary data for greater resolution. Unidentified fish were allocated to a group of prey using fish size, spatial co-occurrence and known behaviour, while proportions among a given prey category were allocated according to available biomass in the system.

For sharks & rays and pelagics we accounted for 40% of the diet originating from outside the modelled area, thus assuming that those species will move outside the studied system to feed (Christensen et al. 2008).

In the absence of detailed knowledge about proportionally how much each fish group from the protected area consumed prey from the fished area (and vice versa), we assumed that fish from the protected area had 10% of fished area fish they could prey on and vice versa.

Where relevant, further details are provided below for each individual group considered.

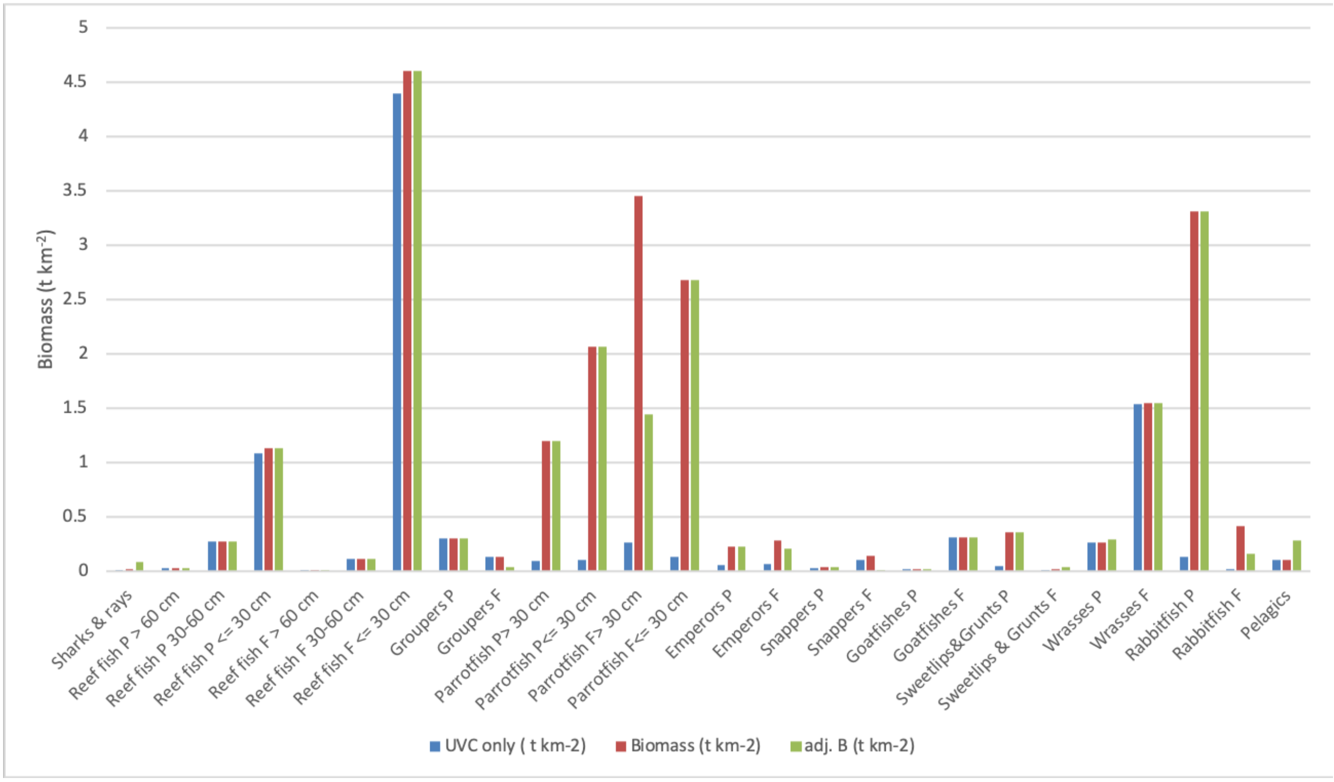


Figure 3 – Differences between UVC-derived biomass estimates (t km^{-2}; blue), augmented for relevant groups by the beach seine sweep method detailed in this report (red), and final adjusted biomass estimates (green) based on WCS fisheries data and literature derived F/M ratios for the study area.

Sea turtles

Five species of sea turtles have been documented within Kenyan waters (Frazier 1975): the green turtle (*Chelonia mydas*), hawksbill turtle (*Eretmochelys imbricata*), loggerhead turtle (*Caretta caretta*), olive ridley turtle (*Lepidochelys olivacea*) and the leatherback turtle (*Dermochelys coriacea*). Of these, green, hawksbill and olive ridley turtles are known to nest in Kenya (Okemwa et al. 2004). An aerial survey conducted in 1994 found that sea turtles are widely distributed along the coastline within the 20 m isobaths, in areas primarily associated with seagrass and coral reefs and identified as prime foraging areas (Wamukoya et al. 1996). Large numbers of turtles have been observed around Mpunguti/Wasini, Takaungu, Watamu, Ungwana Bay, Lamu and the adjacent offshore islands. Nzuki (2005) reports that green turtles account for 94% of recorded nesting activity based on monitoring along 31% of the Kenyan coastline. Increased sea turtle nesting and sightings were reported during the SEM in areas with important sea turtle foraging habitats and fishing grounds. We assumed 1 green turtle of 30 kg to be resident in Mombasa, yielding a biomass of 0.001 t km^{-2}.

Given the low incidence of hawksbill turtles along the coast, it is likely that they are fairly mobile and it would be difficult to determine the number of hawksbill that could be considered as resident in the Mombasa model area. As such, they are also likely to play a relatively minor role in the modelled ecosystem and this species has, for now, not been included.

Marine fisheries, the primary basis for coastal livelihoods is also the most immediate threat to sea turtles in Kenya. Sea turtle populations were shown to have declined in six sites by 25-75% due to habitat degradation, destructive fishing methods, demand for trade and consumption of marine turtle products, as well as growth of coastal population and tourism (Wamukota et al. 2006). Turtle bycatch in prawn trawlers is of greatest concern (Wamukoya and Mbendo 1995, Mueni and Mwangi 2002) and estimated to be responsible for up to 80% of all turtle mortality in Kenya (Okemwa et al. 2004), largely as a result of entrapment in fishing nets. Okemwa (2004) further reports that 54% and 6% of strandings reported involved green and hawksbill turtles, respectively. A trawler survey conducted by Mueni and Mwangi (2002) estimated that at least 3 turtles are caught in trawl nets per fishing day, although this varied greatly with season. Compliance with Turtle Exclusion Device usage was also found to be very low, due to complaints by trawler operators of a reduction in catch due to clogging of nets by debris. Poaching of adults and foraging juveniles is also known to occur, to supplement food and/or income (Nzuki 2005). In a study by Wamukota and Okemwa (2009), 85% of respondents indicated that the highest numbers of turtle mortalities are recorded during the NEM. While no bycatch or direct harvest was included in the current model given the small area of focus, the data presented here is relevant to mortality estimates. It also certainly can inform future efforts should such activities attempt to include areas further offshore and fisheries impacts on sea turtles.

Bjorndal et al. (2003) calculated true annual survival probability for green turtles protected from human induced mortality at Union Creek, Bahamas, to be equal to 0.891 year^{-1}. This decreased to 0.761 year^{-1} for individuals exposed to human-induced mortality. At Heron Island, Australia, sub-adults experienced an annual mortality rate of 0.1526 year^{-1} (Limpus 2009). At one of the largest foraging grounds for green turtles in the world, Nicaragua, where they are also directly targeted by fishermen for food, survival rate for large juvenile and sub-adult greens was estimated at 0.55 year^{-1} (Campbell and Lagueux 2005). We assumed for natural mortality to be similar to rates measured in Australia, and assumed for F = 0.75•M given the high occurrence of fishing mortality and incidental poaching reported in Kenya, yielding a P/B estimate of 0.263.

Little data is available on the natural consumption rates for green turtles. The Q/B ratio for green turtles was estimated at 8.869 year^{-1} based on daily intake measured in green turtles feeding on seagrass in the Bahamas (Bjorndal 1980) and a dry weight to wet weight ratio of 11.8% as estimated by Fourqurean and Schrlau (2003). Our estimate is slightly higher than the value used by Wabnitz et al. (2010) to reflect the greater rates of intake of seagrass compared to algae in Kenya (Nzuki and Muasa 2005). Data from a study conducted off the coast of Colombia suggests that consumption rates can be much lower (i.e., 1.9 year^{-1} (Amorocho and Reina 2008)). However, Amorocho and Reina's (2008) findings were based on an experimental set up that involved moving animals into the laboratory every three days to be fed the equivalent of 1-2% body mass, a ratio considered to be a maintenance diet (Higgins 2003). Therefore, these consumption estimates may not be consistent with feeding rates observed in the wild.

Green sea turtle sightings and capture by local fishers are typically strongly associated with areas dominated by dense seagrass beds and/or nearshore reefs. Observations and examination of gut contents of three stranded green turtles in the Vanga-Shimoni area revealed diets of mainly *Thalassia hemprichii* (50%), *Cymodocea* spp. (30%), *Syringodium isoetifolium* (12%) and Ulva spp. (4%) (Nzuki and Muasa 2005). The rest consisted of red and brown algae. The Mombasa model area includes a vast area of dense seagrass. Thus, we assumed for the diet of green sea turtles at Mombasa to be similar to that described for the Vanga-Shimoni area.

Sharks & rays

Carcharhinus macloti (hardnose shark), *Carcharhinus wheeleri/amblyrhynchos* (grey reef shark) and *Rhizoprionodon acutus* (mik shark) are species mentioned as being locally caught from inshore waters. (Schaeffer 2004). Fishing and trading for sharks, for both their meat and fins, has taken place along the East African coast for centuries. High catches of sharks are also reported in government statistics (State Department of Fisheries 2013). Shark meat is typically salted and dried and consumed locally. Fins are usually exported, with East-African traders well familiar with the value of shark fins in the Far East (Marshall 1997). In 2008, Kenya exported 10.984 tonnes of shark fin to Hong Kong (Oceana 2010), earning traders at least $6.6 million. In Mombasa, fishermen can earn up to $200 to $250 per kg of shark fin, although this depends on the quality and size of the fin. In 2013, a study designed to assess the extent of shark catches in artisanal tuna and the prawn trawl fisheries determined that shark bycatch is dominated by hammerhead sharks (*Sphyrna lewini*, 53.7%), blacktip reef sharks (*Carcharhinus melanopterus*, 33.7%), and grey reef sharks (*Carcharhinus amblyrhynchos*, 5.5%) (Kyalo and Ndegwa 2013). While most of the sharks landed are likely caught in fisheries targeting species off the reef in deeper waters, the latter two can often be found on coral reefs.

The species of rays most commonly encountered were *Taeniura lymma*, *Neotrygon kuhlii* and *Himantura uarnak* (F. Hartley-Januchowsky pers. comm). The meat of the rays' pectoral fins or wings is considered a delicacy among Kenyan coastal people (Ochumba 1988). They are typically caught by small-scale fishers in shallow coral reef areas using gillnets and sometimes spears at low tide (Ochumba 1988). *Himantura uarnak* are generally common and caught in deeper areas.

Natural mortality estimates for the representative shark species were obtained based on Pauly (1980). For rays, estimates were obtained from S. Zhou (pers. comm.) based on information published in Zhou (2011). Natural mortality estimates could not be weighted by species contribution to overall biomass as this data was lacking, and we therefore assumed M to be the mean of individual species' estimates (1.027 year^{-1}). F was assumed to be equal to 2•M given the known exploitation pressure on this group in the area and, together with landings data, the group's biomass was estimated at 0.084 t km^{-2}.

Q/B for this group was derived from Fishbase (3.237 year^{-1}).

Sharks were assumed to preferentially feed on fishes, but to also consume crustaceans, cephalopods and other mollusks (Cortés 1999, Last and Stevens 2009). All ray species are carnivorous, feeding on crustaceans, molluscs and fishes (Ochumba 1988).

Pelagic fish

UVC data for pelagic fish only included Carangidae, one of the most commonly spotted families on the reef. However, given that UVC surveys tend to focus on more closely reef-associated, often cryptic species, pelagics are likely to be underrepresented in this type of monitoring work. Moreover, given the high fishing pressure in the area, most pelagic fish are likely to be fairly shy of humans. Catch data indicate that Sphyraenidae (e.g., (*Sphyraena flavicauda, Sphyraena acutipinnis, Sphyraena barracuda, Sphyraena jello*), Carangidae (*Carangoides ferdau, Carangoides fulvoguttatus, Carangoides chrysophrys, Trachinotus blochii, Alectis indicus*), Belonidae, Hemiramphidae (e.g., *Hemiramphus far* and *Hyporhamphus affinis*) and Scombridae (e.g., *Scomberomorus commerson*) are known to occur, and are visibly targeted in the area.

Natural mortality rate estimates for the representative species were calculated based on Pauly (1980) and as these could not be weighted by species contribution to overall biomass, we set M equal to the mean of individual species' estimates (3.881 year^{-1}). F was assumed to be equal to 2•M given the known exploitation pressure on this group in the area and, together with landings data, the group's biomass was estimated at 0.280 t km^{-2}.

Q/B for this group was derived from Fishbase (13.82 year^{-1}).

The diet composition for this group reflected the group's species diversity. We set the majority of the prey to be fish, followed by invertebrates, zooplankton and primary producers.

Reef fish

Much of the data used to derive model parameters was based on an extensive monitoring database of coral reef fish developed and maintained by WCS since the 1990s. Biomass for all reef fish groups, with the exception of sharks & rays and pelagics, were estimated from an abundance of data obtained from UVC surveys conducted at depths between 6 m and 7.5 m along four 100 m x 5 m belt transects at four sites: two representative of the park (Mombasa park forereef and Mombasa) and the other two of the reserve (Nyali forereef and Ras Iwatine). These abundance data, categorized for 24 families in one of 9 size classes to the nearest 10 cm, were subsequently converted to biomass according to length-weight relationships developed over the course of many years by WCS and given for each family for each size class (McClanahan pers. comm.). Fish smaller than 3 cm were not counted to reduce errors in density comparisons (McClanahan and Kaunda-Arara 1996). Total biomass was then estimated as the average by family across transects at a site. Original data was recorded in kg ha^{-1} and converted into t km^{-2} for model purposes. As transects were conducted over coral reefs, with recorded abundances and biomass representative of such habitat, all estimates were standardized by multiplying UVC biomass values by total coral reef area and dividing these by total model area (but see section below). Relevant habitat areas for model development were estimated based on data in Maina et al. (2015) (see Table 1).

Fish (non-pelagics) were grouped into 26 functional categories according to similar ecological characteristics, for some groups according to size, and to account for whether they are protected or not. These were: reef fish, groupers, parrotfish, emperors, snappers, goatfish, sweetlips & grunts, wrasses and rabbitfish. Species-level information is summarized in Table 5 for those families for which discrete group sampling (DGS) surveys were conducted. For families Lethrinidae, Lutjanidae and Mullidae no such data was available, therefore, we assumed species composition to be similar to data available for transects conducted in the early 2000s. For emperors, this included: *Lethrinus harak, Lethrinus mahsena, Lethrinus lentjan* and *Lethrinus nebulosus*; for snappers, surveys recorded *Lutjanus fulviflamma, Lutjanus gibbus, Lutjanus kasmira, Lutjanus boha,r and Lutjanus ehrenbergii;* while for goatfish, *Parupeneus macronema* and *Parupeneus barberinus* were the two most commonly encountered species.

Specifically for "Reef fish", UVC data collected by Tim McClanahan on coral reef habitat for the families Acanthuridae, Aulostomidae, Balistidae, Chaetodontidae, Holocentridae, Diodontidae, Monocanthidae, Pomacanthidae, Pomacentridae, Scorpaenidae, Muraenidae, Pempheridae and "others" were aggregated into 6 groups according to size (< 30 cm, 30-60 cm, >60 cm) and their level of protection (protected and fished) (Table 4). Parrotfish were also separated by size (<30 cm and > 30 cm).

Table 4 - Biomass estimates for all fish families recorded during underwater visual census (UVC) surveys in 2013 in the park (2 sites) and in the reserve (2 sites)

	Park			**Reserve**		
	Biomass according to size (t km^{-2})					
Family	< 30 cm	30 - 60 cm	> 60 cm	< 30 cm	30 - 60 cm	> 60 cm
Acanthuridae	24.126	5.830	-	9.630	-	-
Aulostomidae	-	0.400	0.460	0.020	0.060	-
Balistidae	2.07	1.150	-	0.840	-	-
Chaetodontidae	1.209	-	-	0.900	-	-
Holocentridae	6.286	-	-	1.410	-	-
Muraenidae	-	-	0.42	-	-	0.180
Pomacanthidae	1.367	0.370	-	0.570	0.370	-
Pomacentridae	2.628	-	-	2.160	-	-
Others	1.160	1.960	-	0.7690	-	-
Pempheridae	0.280	-	-	-	-	-
Scorpaenidae	0.050	-	-	0.05	-	-
Total biomass	**39.190**	**9.717**	**0.877**	**16.360**	**0.430**	**0.180**

Reef-specific biomass values for each of the groups were estimated by calculating an area-weighted value relative to the proportion of reef within the park and reserve. Values for input into Ecopath also included, for relevant groups, an estimated biomass proportion over seagrass beds (see section and textbox below).

Few studies have derived natural mortality rate estimates based on locally available data, therefore M values were mostly calculated based on empirical relationships following Pauly (1980). Notable exceptions include estimates for Lutjanidae, parrotfish < 30cm and Lethrinidae that were informed by the following publications: Kaunda-Arara and Ntiba (2001), Kaunda-Arara et al. (2003) and Hicks and McClanahan (2012). Functional group natural mortality estimates were weighted by individual species biomass contribution within their respective group, when possible. While the weighting procedure should ideally be conducted using biomass contributions by species to a functional group, as these were not available, weighting was based on species' abundances recorded during separate Discrete Group Sampling (DGS) surveys at the same sites. As fish within protected areas were not targeted by fisheries, P/B was set equal to M. For all other functional groups, fishing mortality rate was approximated from the ratio of known total annual catch to biomass.

Consumption rates were derived from Fishbase and Q/B estimates for a given guild were weighted according to individual species' DGS contributions within their respective groups. Species under the Acanthuridae family were classified as grazers or detritivores in line with their classification in Cinner et al. (2009) and Kruse et al. (2016).

A diet matrix was developed from a detailed analysis of food habits of relevant reef fish species along the Kenyan coast, as well as from information gleaned from Fishbase and available published studies (e.g., De Troch et al.

1998, Kamukuru and Mgaya 2004, Randall 2004, Lugendo et al. 2006, de la Torre-Castro et al. 2008, Unsworth et al. 2009b, Berkström et al. 2013a).

Relevant additional information for specific groups is included further below.

Importance of seagrass beds

In Kenya, as is characteristic of tropical systems, the area between the reef and the shore often includes a complex mosaic of diverse habitats, such as mangroves, seagrass beds, patch reefs and sand, with adults of many economically and ecologically important species typically found between the reef crest and deeper areas of the fore-reef (Adams et al. 2006). These habitats are functionally linked by the movement of organisms across their boundaries (Webster et al. 2002, Baguette et al. 2013). Dispersing individuals influence many ecological processes in recipient habitats, such as food web structure, organic matter/energy/nutrient exchange between habitat patches, species' population replenishment, and ecosystem resilience (Polis et al. 1997, Hyndes et al. 2014). Extensive movement of organisms between seagrass beds and reef systems is well documented, and includes foraging migrations (e.g. Ogden and Ehrlich 1977, Weinstein and Heck 1979, Robblee and Zieman 1984, Meyer and Schultz 1985, Nagelkerken et al. 2000a, Kruse et al. 2016) as well as ontogenetic migrations (i.e., habitat shift with changing life phase (e.g. Acosta and Butler 1997, Cocheret de la Moriniere et al. 2002, Dorenbosch et al. 2004b, Gratwicke et al. 2006, Burke et al. 2009)). Diurnally active herbivores forage in seagrass beds during the day and migrate to find shelter on coral reefs at night (Tribble 1981, Macia and Robinson 2005).

Conversely, at night, some zoo-benthivores move from daytime resting areas on coral reefs to feed in seagrass beds and/or sand flats (Nagelkerken and van der Velde 2004, Verweij et al. 2006, Nagelkerken et al. 2008). The absence of such habitats is correlated with a significantly lower density and diversity of adults on nearby coral reefs (Nagelkerken et al. 2001, Mumby et al. 2004, Dorenbosch et al. 2005). Both mangroves and seagrass beds have been highlighted as playing an important role in the assemblage composition of fish communities on reefs, with mangroves playing a particularly important role in the Caribbean (Acosta and Butler 1997, Nagelkerken et al. 2000b, Nagelkerken et al. 2001, Mumby et al. 2004). A recent meta-analysis suggests that for the Indo-Pacific, including eastern Africa, seagrass beds are the preferred juvenile habitat for many nursery species (Igulu et al. 2015), thereby positively influencing adult densities of many reef fish species on adjacent coral reefs (Gullström et al. 2002, Dorenbosch et al. 2004a, Dorenbosch et al. 2005).

Based on studies available for Kenya and other east African coastal areas with comparable habitat landscapes (e.g. Papadopoulos 1995, Kimani et al. 1996, De Troch et al. 2001, Gell and Whittington 2002, Gullström et al. 2002, Dorenbosch et al. 2005, Lugendo et al. 2006, de la Torre-Castro et al. 2008, Gullström et al. 2008, Nyunja et al. 2009, Unsworth et al. 2009a, Gullström et al. 2011, Berkström et al. 2012, Bosire et al. 2012, Berkström et al. 2013b) we assumed that: (i) a number of species also derive significant benefits from seagrass beds as juveniles (i.e., nursery species *sensu* Nagelkerken (2000b) - e.g, *Siganus sutor, Hipposcarus harid, Lutjanus monostigma, Mulloidichthys flavolineatus, Plectorhinchus flavomaculatus*); and (ii) others perform migrations in and out of the seagrass beds (e.g., *Cheilio inermis*, *Lethrinus harak, Lutjanus argentimaculatus, L. ehrenbergi*) to feed and/or in search of refuge from predation, with some probably spending more time in seagrass beds than over reefs (e.g., *Siganus sutor*, *Leptoscarus vaigiensis*, and *Calotomus spinidens*). These considerations therefore imply that total biomass estimates are higher than those derived from reef-based underwater visual census surveys alone (see text box below for method details used to account for this). However, some resulting biomass values were too low or too high based on landings data and known harvest rates for the area. In these instances, final group biomass values were derived by assuming $F = \alpha M$, where α is a multiplier based on known exploitation levels

Table 5 - Species-level information for all groups for which Discrete Group Sampling (DGS) surveys were conducted

	Park	**Reserve**
	Species recorded	
Groupers	*Cephalopholis nigripinnis*	*Cephalopholis argus*
	Cephalopholis argus	*Cephalopholis nigripinnis*
	Epinephelus merra	*Cephalopholis spiloparaea*
	Epinephelus punctatus	
	Epinephelus fuscoguttatus	
Parrotfish	*Scarus sordidus*	*Scarus sordidus*
	Calotomus carolinus	*Scarus atrilunula*
	Scarus atrilunula	*Calotomus carolinus*
	Scarus psittacus	*Scarus frenatus*
	Scarus rubroviolaceus	*Scarus japanensis*
	Scarus falcipinnis	*Scarus psittacus*
	Hipposcarus harid	*Scarus rubroviolaceus*
	Leptoscarus vaigiensis	
	Scarus tricolor	
Emperors	*Lethrinus harak*	*Lethrinus harak*
	Lethrinus mahsena	*Lethrinus mahsena*
	Lethrinus lentjan	*Lethrinus lentjan*
	Lethrinus nebulosus	*Lethrinus nebulosus*
Snappers	*Lutjanus fulviflamma*	*Lutjanus fulviflamma*
	Lutjanus gibbus	*Lutjanus gibbus*
	Lutjanus kasmira	*Lutjanus kasmira*
	Lutjanus bohar	*Lutjanus bohar*
	Lutjanus ehrenbergii	*Lutjanus ehrenbergii*
Goatfish	*Parupeneus macronema*	*Parupeneus macronemus*
	Parupeneus barberinus	*Parupeneus barberinus*
	Parupeneus indicus	*Parupeneus indicus*
	Parupeneus rubescens	*Parupeneus rubescens*
	Mulloidichthys flavolineatus	*Mulloidichthys flavolineatus*
	Mulloidichthys vanicolensis	*Mulloidichthys vanicolensis*
Sweetlips & grunts	*Plectorhinchus flamaculatus*	*Plectorhinchus gaterinus*
Wrasses	*Anampses caeruleopunctatus*	*Anampses meleagrides*
	Anampses meleagrides	*Bodianus axillaris*
	Anampses twistii	*Cheilinus trilobatus*
	Bodianus anthioides	*Cheilio inermis*
	Bodianus axillaris	*Cirrhilabrus exquisitus*
	Cheilinus trilobatus	*Coris caudimacula*
	Cheilio inermis	*Gomphosus coeruleus*
	Coris aygula	*Halichoeres cosmetus*
	Coris caudimacula	*Halichoeres hortulanus*
	Coris formosa	*Halichoeres scapularis*
	Coris gaimard/africana	*Labrichthys unilineatus*
	Gomphosus coeruleus	*Labroides dimidiatus*
	Halichoeres cosmetus	*Oxycheilinus bimaculatus*
	Halichoeres hortulanus	*Pseudocheilinus hexataenia*
	Hemigymnus fasciatus	*Stethojulis albovittata*
	Hologymnosus doliatus	*Thalassoma amblycephalum*
	Labroides bicolor	*Thalassoma hebraicum*
	Labroides dimidiatus	
	Macropharyngodon bipartitus	
	Pseudocheilinus hexataenia	
	Stethojulis albovittata	
	Thalassoma amblycephalum	
	Thalassoma hardwicke	
	Thalassoma hebraicum	
	Thalassoma lunare	

Parrotfish

In 2013, *Scarus sordidus* made up 37% and 52% of fish recorded on transects within the park and the fished area, respectively. Interestingly, in the early 2000s, *Leptoscarus vaigiensis* was commonly recorded on transects at both protected and fished sites, while one single individual was present in UVC data from 2013, in the park. *Scarus atriluna*, relatively common at both locations in 2013, did not feature on transects in the early 2000s. Part of these differences may be attributable to differences in the locations at which transects were conducted between these two time frames. *Leptoscarus vaigiensis*, commonly known as the marbled parrotfish, is a less mobile species that displays high site fidelity, being mostly found in seagrass meadows and sometimes on hard substrates with high macroalgal cover. As transects conducted in 2013 are some distance from the seagrass beds, this may explain their absence in the UVC data. However, given their importance in artisanal fisheries (Gell and Whittington 2002, Davies et al. 2009, Hicks and McClanahan 2012, Samoilys et al. 2017) we assumed that this species contributed to the overall biomass of parrotfish accounted for in the model and this is reflected in the final P/B and Q/B model estimates. A similar consideration was extended to *Calotomus spinidens*, the spinytooth parrotfish, a species that inhabits seagrass beds or dense beds of algae (Kuiter and Tonozuka 2001) and accounts for a large proportion of artisanal catches (Signa et al. 2008).This species is well-camouflaged and easily overlooked (Kuiter and Tonozuka 2001).

Scarus sordidus and all other species of parrotfish recorded during UVC surveys (Table 5) typically graze on a variety of benthic algae.

Stomach content analysis and direct field observations show that *L. vaigiensis* is an efficient grazer, feeding almost exclusively on seagrass leaves (Almeida et al. 1999, Gell and Whittington 2002, Gullström et al. 2011, Locham et al. 2015). Analysis of the guts of 15 individuals showed that 95% of measured contents consisted of seagrass plant material (Gullström et al. 2011). Together with other parrotfish species such as *Calotomus spinidens* they are considered to play a key functional role within seagrass beds (and on reefs) (Kirsch et al. 2002, Alcoverro and Mariani 2004, Goecker et al. 2005), and can significantly contribute to ecosystem dynamics and ecological stability (Valentine and Duffy 2006). While also feeding on seagrass *Calotomus spinidens* is also known to selectively feed on seagrass-associated epiphytes (Bruce and Randall 1985).

Small parrotfish predators were informed by known predators on *L. vaigiensis*, as listed in Gullström et al. (2011).

Rabbitfish

Rabbitfish are an important fish resource along the East African coast. *Siganus sutor* in particular is one of the most widely targeted and heavily fished species on the Kenyan coast (McClanahan and Mangi 2004, Samoilys et al. 2013). While rabbitfish were recorded on UVC transects, no species-level information was available. Data from previous years show *Siganus sutor* to be most frequently recorded, with occasional sightings of *Siganus stellatus* and *Siganus argenteus*. All rabbitfish are known to strongly associate with seagrass beds (Lugendo et al. 2005, Kimirei et al. 2011, Hicks and McClanahan 2012) and to be rarely observed on corals reefs (Kruse et al. 2016). Therefore, their biomass is likely to be considerably underestimated from reef-focused surveys alone.

Rabbitfish are herbivorous and browse on seagrass, often also consuming epiphytes growing on seagrass fronds (Almeida et al. 1999, de la Torre-Castro et al. 2008, Nyunja et al. 2009), with feeding activities appearing to take place mostly during the day (de la Torre-Castro et al. 2008).

Squid

This functional group includes species of the Sepiidae and Loligonidae families; mainly *Sepia latimanus, Sepioteuthis lessoniana* and *Urotweuthis duvaucelii* (Anam and Mostarda 2012). Other species may be common off the coast of Kenya but are likely to be mostly caught further offshore using bottom trawls.

As no data was available with regard to biomass, we let the model estimate B assuming an EE of 0.8. This assumes that the majority of the group's production is used in the system, reducing possibilities to overestimate its abundance and effects (Christensen and Pauly 1998).

Biomass calculations for species that associate with seagrass beds

Some species, notably *Leptoscarus vaigiensis*, *Calotomus spinidens* and *Siganus sutor*, strongly associate with seagrass beds. Other species or families, such as Lethrinidae and Lutjanidae, while typically being found on coral reefs and therefore commonly classified as reef fish, are known to extensively utilise seagrass beds for forage and as nursery grounds for their younger life-history stages (Papadopoulos 1995, Kimani et al. 1996, Kaunda-Arara and Ntiba 1997, De Troch et al. 1998, Gullström et al. 2002, Bosire et al. 2012), with seagrasses therefore supporting local fisheries on these species. For these groups, an additional biomass component to that derived from UVC surveys on coral reefs was estimated from beach seine catches, as this fishing gear is predominantly deployed over seagrass beds. This biomass proportion was calculated as:

$$B_i = \frac{C_i}{Aq_i}$$

where C_i = catch (in kg) of species/functional group *i, A* represents the area swept by a beach seine and q_i = the catchability of species/functional group *i*. Catchability is defined as the proportion of fish available to be captured that is caught by a defined unit of fishing effort (Ricker 1975). Catchability can also be defined as the efficiency of the fishing gear. Catchability (q_i) values were assigned to different species/functional groups depending on overall size, swimming ability, behaviour and morphology as: 0.5 for fish that are typically small (< 300 mm) and demersal or seeking cover within seagrass beds; and 0.4 for larger (>300 mm), faster swimming fish groups (Pierce et al. 1990, Jackson and Noble 1995, Bayley and Herendeen 2000). Catchability values were also informed by Blaber (1990) and Hahn et al. (2007). For the same functional groups located within the protected area, an additional biomass component was estimated according to the following equation:

$$B_{iP} = \frac{B_{iP-UVC} * B_{iF-bs}}{B_{iF-UVC}}$$

where B_{iP} = additional biomass of species/functional group *i* within the protected area, B_{iP-UVC} =biomass of species/functional group *i* from UVC surveys, B_{iF-bs} = biomass for species/functional group *i* within fished areas estimated from beach seine catches and B_{iF-UVC} = biomass for species/functional group *i* on fishing grounds based on UVC surveys.

An initial P/B value of 4.922 year^{-1} was calculated as the average of the P/B values derived for the three above listed species using the empirical relationship established in Brey (1999). Maximum age and weights were derived from Sealifebase (www.sealifebase.org), Clyde et al. (1984) and information listed under www.animaldiversity.org. However, based on the estimate of Q/B below, this yielded P/Q values greater than 0.3. Consequently, we reduced P/B to 4.4 year^{-1}. Opitz (1996) reports P/B ranges between 0.9 and 1.6 year^{-1} depending on species, with Gasalla et al. (2004) estimating P/B at 1.95 year^{-1}. Ainsworth (2007) estimated P/B based on the average of seven species at 4.348 year^{-1}.

In the absence of species-specific information, the Q/B value derived by Ainsworth et al. (2007) of 14.79 year^{-1} for three species (*Sepioteuthis lessoniana*, *Sepia officinalis* and *Sepiola affinis*) was used here. This value is similar to that derived by Pauly et al. (1993) based on an average daily consumption of 4.56% BW. It also falls within the range reported by Abolmasova (1985) for captive *Stenoteuthis oualaniensis* of between 5.7% and 13.8% BW per day. Gasalla et al. (2004) used much lower rates, setting Q/B at 3.9 year^{-1}.

Cuttlefish are known to prey on crustaceans, including zooplankton, and small fish. Cannibalism is common.

Jellyfish

The species specifically referenced as found along the shores of Kenya and Mozambique are *Physalia physalis* (Briggs 2013) and *Pelagia noctiluca* (Briggs and Connolly 2014), probably due to reports of tourists and locals being stung and warnings associated with such injuries (Anon 2014).

Pauly and Christensen (1993), modelling tropical waters in the South China Sea, used a P/B value of 5.01 and a Q/B ratio of 25.05; values that were then used in later models (Buchary et al. 2002). Data in Venier (1997) suggest a higher P/B (10.23 year^{-1}) than estimated here.

While jellyfish diet will vary based on species, given the lack of information available, the diet was kept purposefully broad (i.e., zooplankton and detritus). Cannibalism is common.

Octopus

Four species of octopus have been recorded in Kenyan waters: *Callistoctopus macropus*, *Octopus aegina*, *Octopus cyanea* and *Octopus vulgaris* (Anam and Mostarda 2012). All species of octopus are benthic cephalopods that are primarily found on muddy, rocky and sandy bottoms from the coastline to the edge of the continental shelf (Mangold 1983).

In the West Indian Ocean (WIO) region, octopus is extensively exploited by artisanal fishers as it is an important subsistence and economic activity for many coastal communities (Guard and Mgaya 2002, Guard 2003, Humber et al. 2006, Guard 2009). Fisheries in Kenya target both *Octopus vulgaris* and *Octopus cyanea*. As in other parts of the WIO, the octopus fishery in Kenya has been transitioning from one of local consumption to one of international export over the last 20 years (Wamukota et al. 2014). Kivengea (2014) found the selling price of common octopus to fluctuate between Ksh 80.00 per kg to Ksh 160.00 per kg for artisanal fishers and between Ksh 160.00 per kg to Ksh 280.00 per kg for middlemen. Prices for octopus products processed for overseas exports vary according to grade ranging between Ksh 382 and 722 per kg. Tanzania, Madagascar and Kenya are the largest exporters of octopus in the WIO and target primarily European markets, particularly Portugal, Italy, France and Spain (Rocliffe and Harris 2016). Despite increasing exports, octopus remains an important target species for domestic consumption. Octopus is targeted from intertidal reef flats and subtidal reefs, typically during low tide, using spearguns and variations thereof (hooked stick, harpoon, pointed stick). It is an easily targeted commodity, with women and children often engaged in the fishery. However, men are increasingly active in this fishery due to the high demand and price.

We derived biomass estimates for the model area based on octopus densities recorded on Kenyan reefs (Church and Obura 2006) and the average weight of a medium-sized individual *Octopus vulgaris*. From size frequency distributions of body weight, of both male and female individuals at Vanga and Shimoni, an average weight of 0.7 kg was used (Kivengea 2014). Prorating these values by reef habitat area over the model area yielded an estimate of 0.083 t km^{-2}. However, based on catch data, this yielded an unrealistic F/M. Given the importance of this fishery as an economic activity, octopus is heavily targeted (Otieno 2011). Octopus is assumed to be fully exploited in Kenyan waters (Rocliffe and Harris 2016). We therefore assumed F = 2M raising biomass to 0.183 t km^{-2}.

Octopus are considered fast growing, probably in part due to their lack of a complex skeletal system, high food intake, efficient digestion and assimilation. P/B was obtained by an empirical model established by Brey (1999):

$$\log P/B = 1.672 + 0.993 \cdot \log(1/A_{max}) - 0.035 \cdot \log(M_{max}) - 300.447 \cdot 1/(T+273)$$

where A_{max} is the maximum age in years, M_{max} is the maximum individual body mass in kJ (g_{DM}) and T is the bottom water temperature in degrees Celsius.

Octopus lifespan varies among species, but is typically short, and for *Octopus vulgaris* has been estimated at between 12 and 18 months (Van Heukelem 1983, Katsanevakis and Verriopoulos 2006). Maximum age was based on Perales-Raya et al. (2014). Maximum mass was estimated at 6 kg wet weight (Branch et al. 2008) and reported as 10 kg by Clyde et al. (1984). We used conversion rates of WM:AFDM of 0.2 and of 22.03 J/mgAFDM for benthic cephalopods as listed by Brey (2004). Using Brey's equation and values detailed above P/B was estimated at 3.28 year^{-1}. This value is comparable to estimates made by Weijerman et al. (2013) of 3.313 year^{-1}, Guénette and Hill (2009) of 3.02 year^{-1} and slightly higher than the one used by Ainsworth et al. (2007) of 2.327 year^{-1}. It is also similar to the one arrived at by Smale and Buchan (1981) and Buchan and Smale (1981) of 3.06 year^{-1}, Chagaris et al. (2015) of 3.1 year^{-1} and Tsehaye & Nagelkerken (2008) of 3.5 year^{-1}. Guerra estimated natural mortality for octopus at 1.09 year^{-1} (Guerra 1979), which assuming F=2M yield a P/B value of 3.27 year^{-1}.

Using Brey's relationship and food intake studies for *Octopus vulgaris* by Aguado-Giménez and García (Giménez and García 2002) yielded a Q/B estimate 8.76 year^{-1}. However, the authors acknowledge some caveats to the study, notably the poor performance of individuals at higher temperatures, known to occur in Kenya and other tropical reef environments. Van Heukelem (1976) indicated that ingestion rates of octopus typically average between 2 and 6% of body weight per day, in line with studies by Mangold and Boletzky (1973) who estimated a 5% rate, yielding a P/B value of 18.25 year^{-1}. Buchan and Smale (1981) estimated Q/B at 10.7 year^{-1}, comparable to the value used in an Ecopath model of the Kimberley area in Australia (12.5 year^{-1}) and that used by Ainsworth (2007) of 13.24 year^{-1}. We here set Q/B at 12.5 year^{-1}.

Octopus are carnivorous predators, known to forage on crabs, bivalves and gastropods, as well as polychaetes, other crustaceans, cephalopods and various species of small fish (Hanlon and Messenger 1996, Fiorito and Gherardi 1999, Smith 2003, McConnell and Scott 2010). Kivengea (2014) who studied octopus in Kenya found predominantly crustaceans in animals' stomachs, followed by molluscs, echinoderms and teleosts. These findings were corroborated by a study conducted in Foul Bay, South Africa, which found crustaceans to be the most frequently found prey group in octopus stomachs, followed by molluscs, teleosts and polychaetes (Smith 2003). This may in part reflect the availability of prey in the sampled area, with other studies in South Africa for example indicating that octopus preferentially foraged on bivalves (Buchan and Smale 1981, Smale and Buchan 1981). Similarly, Hanlon and Messenger (1996), explained that there are geographical differences in the diet of *Octopus vulgaris*: In the Mediterranean Sea off the coast of Catalonia (Spain), for example, the diet of *Octopus vulgaris* consisted to 80% of crustaceans, while in the Algarve (Portugal), they were found to feed to 80% on bivalves. Octopus are mostly nocturnal feeders. The most common predators of octopus include large predatory fish such as barracuda and eels (Hanlon and Messenger 1996).

Lobsters

In the Western Indian Ocean, there are 47 species from five families. Spiny lobsters (*Panulirus* spp.) occur throughout the Indo-Pacific and are common along the Eastern African coastline (Kulmiye and Mavuti 2005). While fishers have reported landing 9 species, fishery activities in Kenya focus chiefly on six: *P. ornatus*, *P. longipes*, *P. penicillatus*, *P. versicolor*, *P. homarus* and *P. dasypus*, *Panulirus ornatus* and *P. longipes* together account for over 75% of Kenya's lobster catch (Maina and Samoilys 2011).

A study focusing on the lobster fishery in Kenya in the late 1990s found that it is an activity carried out exclusively by men, with a large proportion of them engaged full-time as lobster fishermen and landing between 10 and 15 kg of lobsters per day (Marshall et al. 1999). In Lamu, fishermen report a dramatic decline in lobster catches at the rate of 8 kg per decade, from a maximum of 28 kg per trip per fisherman 30 years ago to less than 2.5 kg per trip per fisherman in 2011 (Maina and Samoilys 2011). Methods of catch include traps, bottom set gillnets, or diving to frighten a lobster out of its lair (Marshall et al. 1999).

In 1971, the main fishing areas for lobster included Lamu, Mombasa and Vanga-Shimoni, with Lamu alone accounting for 60% of total catches (Mutagyera 1978). These trends still hold today (Maina and Samoilys 2011). Reports indicate that many lobster fishermen do not land their catch at official landing sites, but instead sell lobsters directly to individuals, restaurants or traders (Marshall et al. 1999). Lobsters are sold as whole live animals or are frozen for domestic and export markets. While Kenya consumes an important proportion of its lobster catches, exports have increased in importance, especially to the EU, but also Singapore, Hong Kong and the United Arab Emirates (Maina and Samoilys 2011). Declines in sizes and number of lobsters encountered have been reported for a number of years, with the lobster resource generally considered overexploited at sites other than Lamu. Maina and Samoilys (2011), who conducted stock assessments in the area, concluded that the resource in the archipelago is still healthy and at sustainable levels. The fishery is currently under review for certification by the Marine Stewardship Council (Mwakio 2013).

Compared to other species of commercial importance such as *Octopus vulgaris, Siganus sutor* or *Lutjanus fulviflamma* for example, relatively little information is available on the status of key lobster species.

Lobster densities were derived from Church and Obura (2006), who conducted counts in 45-60 minute sample periods and estimated 0.2 individuals per 250 m^2. The average mass of lobster was taken from Okechi and Polovina (1995) and set at 0.27 kg. Prorating this biomass estimate by reef habitat area considered in the model area yielded a value of 0.064 t km^{-2}. However, when combined with catch data and known exploitation levels, biomass was reduced to 0.0309 t km^{-2}.

Natural mortality rates for lobsters were here set at 0.35 year^{-1}, the same rate estimated for *P. argus* in Nicaragua, a species common and heavily exploited throughout its range in the Caribbean/Atlantic, and which is likely to be similar to that of other Panulirus species (Butler et al. 2011). As lobster species are heavily targeted and considered overexploited in waters around Mombasa, we set F=2M. Thus P/B was estimated at 1.05 year^{-1}. P/B for *P. argus* was 0.67 year^{-1} in Guénette and Hill (2009), with natural mortality estimated at 0.22 year^{-1}. Opitz (1996) estimated P/B for lobsters to range between 0.35 and 1.03 year^{-1}, while it was set at 0.9 year^{-1} in a model for a reef system in Mexico with an important lobster fishery (Arreguín-Sánchez et al. 1993). Other published P/B estimates include that for two species of spiny lobsters in the Galapagos, *P. gracilis* and *P. penicillatus* (0.45 year^{-1} ; Okey et al. 2004) and for *P. argus* off South Africa (0.42 year^{-1}; Berry and Smale 1980).

Consumption rates were estimated at 2% body weight per day, equivalent to 7.3 year^{-1} (Perera et al. 2005). Other published Q/B rates range from 7.4 year^{-1} for a general model of the Caribbean (Opitz 1996) and Galapagos (Okey et al. 2004), to 8.2 year^{-1} for Mexico (Arreguín-Sánchez et al. 1993) and 9.5 year^{-1} for South Africa (Berry and Smale 1980).

Panuliridae are primarily considered carnivores. Spiny lobsters prey upon a diverse assemblage of benthic organisms, usually calcareous, and infaunal species, including molluscs (e.g., snails and clams), echinoid and asteroid echinoderms, smaller crustaceans, polychaetes, as well as algae and possibly fish (Lipcius and Eggleston 2008, Kanciruk 2012). Feeding habits of *P. homarus* off the south coast of Iran showed that lobster preferentially fed on crabs, bivalves and gastropods, with bivalves as the main food, crabs, gastropods and algae as secondary food, and polychaetes, fish and echinoderms as incidental food (Mashaii et al. 2011). Off the south coast of India, studies have shown that the abundance of *P. homarus*, particularly large individuals, seems to relate directly to the observed abundance of sea urchins (Thangaraja and Radhakrishnan 2012). Other species of lobsters are known to exert similar top-down control over urchins (Mayfield et al. 2001, Shears and Babcock 2002). Lobsters likely forage at night on seagrass beds and return to the reef for refuge during the day. *Panulirus argus* in the Caribbean has been observed handling seagrass fronds, in all likelihood feeding on the epiphytic organisms attached to the blades (Kanciruk 2012). Recorded predators include various species of larger reef fish, such as triggerfish (Kanciruk 2012), and sharks as well as octopus (Lipcius and Eggleston 2008).

Benthic invertebrates

With the exception of sea urchins, given the absence of data pertaining to different benthic invertebrate groups such as mollusks, echinoderms and crustaceans, a single benthic invertebrate group was considered here. It represents a wide array of benthic organisms, including crabs, ophiuroids, shrimps, worms, starfish, amphipods and bivalves. As such, this group also includes a diversity of behaviours and feeding habits. Many of these species are harvested for food. Several of them play a crucial role within the ecosystem, because, for example, they represent an important forage for a variety of commercially important food fish (Hobson 1974) and they effectively clean and aerate bottom sediments by scavenging dead organisms and/or filtering particles.

Biomass data for benthic invertebrates is difficult to obtain. Uncertainty in estimates of invertebrate biomass is likely, as these groups are the least studied and the most under-represented in the coral reef literature. The cryptic nature and nocturnal patterns of many benthic invertebrates, as well as the rugosity of benthic cover on coral reefs, combine to make accurate sampling of many benthic invertebrates extremely difficult (Klumpp and Pulfrich 1989, Sorokin 1993). Given the absence of quantitative data for benthic invertebrates in Kenya, Ecopath was allowed to estimate the biomass of this group based on the assumption that EE ~0.95. This assumes that most of the group's production is used in the system, reducing possibilities to overestimate its abundance and effects (Christensen and Pauly 1998).

In the absence of more detailed information, the P/B and Q/B ratios were adapted from Tudman (2001) and estimated at 3.261 year^{-1} and 11.62 year^{-1}, respectively. Ultimately, precise P/B and Q/B values will depend on the exact composition of the benthic invertebrate community, as an average, throughout the model area, and the contribution from crustaceans versus benthic carnivores versus detritivores to the overall group as well as the species or family composition within these clusters.

The diet of this group was set to consist chiefly of detritus, zooplankton and algae (Brey 2004).

Urchins

Sea urchins are highly abundant on coral reefs in Kenya (McClanahan 1998) and play a fundamental role as grazers on coral reef ecosystems; a function that has been recognized in both tropical and temperate ecosystems. They were therefore examined separately from benthic invertebrates.

There are 9 species of sea urchin species observed on southern Kenyan reefs/lagoons. *Diadema savignyi, Diadema setosum, Echinometra mathaei, Echinostrephus molaris, Echinothrix calamaris, Echinotrix diadema, Toxopneustes pileolus* and *Stomopneustes variolaris* are commonly found on reefs, while *Tripneustes gratilla* is the most common sea urchin in seagrass beds. Seagrass overgrazing episodes have been attributed to temporary population explosions of this species (Alcoverro and Mariani 2002). However, McClanahan et al. (1994) have shown that parrotfish and the sea urchin *Echinothrix diadema* appear to favour seagrass beds dominated by *Thalassodendoron ciliatum*, while *Diadema setosum, Diadema savignyi* and *Echinometra mathaei* favour areas high in *Thalassia hemprichii*.

Average mass for each of the species was obtained from local sampling studies (McClanahan unpublished data) (Table 6) and these were utilised to calculate biomass.

Table 6 – Average mass for sea urchins in Kenya (McClanahan unpublished data)

Species	*D. savignyi*	*D. setosum*	*E. mathaei*	*E. molaris*	*E. calamaris*	*E. diadema*	*T. pileolus*	*T. gratilla*
Mass (g)	125	150	33	2.5	347	347	100	109

As surveys have shown that urchin densities and the species present vary significantly between protected and open access areas (e.g.,McClanahan et al. 1999, McClanahan 2000), two separate groups were included (Urchins P and Urchins F) to allow for representation of observed differences between these management regimes.

As surveys were conducted over coral reef substrate only, biomass estimates were initially extrapolated to the entire modelled area by calculating a “reef” area-weighted biomass for all species. Given that the recorded species are also known to forage in seagrass beds, particularly *T. gratilla*, the biomass of the latter was augmented based on data from Alcoverro and Mariani (2000, 2002, 2004) who conducted urchin surveys at a number of fished and protected locations along the Kenyan coast, including Mombasa National Marine Park and Ras Iwatine.

Published P/B ratios, as well as available relationships to derive P/B, vary greatly (e.g., 1.08 year^{-1} in the Philippines (Regalado et al. 2011) to 0.58 year^{-1} for *E. mathaei*, 1.7 year^{-1} for *T. gratilla* in Pauly (1993)). Here we estimated P/B for each species based on information published in Ebert (1982), Ebert (1975), Drummond (1993), Regalado et al. (2011) and the assumption that K ~ M based on Pauly et al. (1993). All species were assumed not to be targeted by fishing, except for *T. gratilla*, known to be commonly used by fishers in Kenya as bait (Muthiga 2005) and for which we assumed F=0.25M.

While a number of studies have published rates of $CaCo_3$ loss per year (Glynn 1988, McClanahan and Muthiga 1988, Peyrot-Clausade et al. 2000), generally demonstrating that rates were higher on overfished reefs, these rates can be misleading when applied to Q/B estimates as they do not account for the proportion of reworked material in the urchins’ guts. Bronstein and Loya (2014) present results from their research on reefs around Zanzibar for four species of urchins, accounting for this important difference. Consequently, our Q/B estimates were based on this most recent study for *D. savignyi*, *D. setosum*, *E. mathaei* and *E. diadema*. As the authors do not present results for *E. molaris*, we used the average of all species, except *E. diadema* that is much larger and displays significantly greater Q/B rates than the other species and would not seem adapted to its feeding mode (see below). For *T. gratilla,* estimates were informed by previous calculations in Wabnitz et al. (2010) and estimated at 13.73 year^{-1}. As no data was available for *Toxopneustes pileolus*, we used the average of values for *D. savignyi* and *D. setosum* based on the comparable test size of the animal. Where necessary, conversion rates between dry mass (DM) and wet weight (WW) were taken from Atkinson and Grigg (1984). Diet proportions were also based on Bronstein and Loya (2014).

Q/B for *E. mathaei* was evaluated at 4.44 year^{-1} based on data from Carreiro-Silva and McClanahan (2001) and McClanahan and Kurtis (1991). Using information from ingestion rates by Bronstein and Loya (2014) led to an estimate of 35.66 year^{-1}. However, just using herbivory rates from that latter study yielded a Q/B value of 7.48 year^{-1}. Ingestion rates based on lab trials feeding sea urchins *ad libitum* a diet prepared from turf algae and agar over a 7-day period yielded estimates of 16.51 year^{-1} for the same species (Hiratsuka and Uehara 2007). Other published Q/B rates range between 3.58 year^{-1} on average for a reef system in the Philippines (Pauly et al. 1993) to 9.423 year^{-1} for a reef system in Raja Ampat (Ainsworth et al. 2007).

Urchins are generally considered to be herbivores, as their diets mostly consists of algae and seaweed (Klumpp et al. 1993). Although echinoids can show feeding preferences, they are also known to be opportunistic feeders with their diets comprising animal tissue, including live coral tissue (Bak and van Eys 1975), and varying according to habitat and season. While grazing on the hard substrate to feed on algae, urchins break down the reef substratum itself, leading at moderate densities to increased biodiversity (Johnson et al. 2003) and enhanced coral recruitment survival (Edmunds and Carpenter 2001, O'Leary et al. 2013). At higher densities they have been shown to limit reef growth and lead to reef degradation (Glynn and Manzello 2015).

Echinothrix diadema is known to forage on algae and encrusting organisms (Mortensen, 1940 in De Ridder and Lawrence 1982). *Echinometra mathaei* is a generalized herbivore feeding on a variety of macrophytes (McClanahan et al. 2007), and preferentially on turf growing on the surface of dead coral or pavement, which explains why calcium carbonate sediments are usually the largest fraction of the species' gut content (Odum and Odum 1955, McClanahan and Kurtis 1991). These findings were corroborated by results in Black et al. (1984) and Mills et al. (2000) who found that inorganic material constituted 73% of gut contents.

Tripneustes gratilla has been shown to feed continuously, day and night. They graze near the substrate and their diet consists predominantly of seagrass (*Thalassodendron ciliatum* and *Syringodium isoetifolium),* algae and periphyton (Herring 1972, de Loma et al. 2002, Lawrence and Agatsuma 2007).

Echinostrephus molaris lives in borings of its own making and is a member of the only echinoid genus that is adapted to 100% suspension feeding (Campbell et al. 1973). Detritus, plant remains and fragments of calcareous skeletons have been found in its gut.

All sea urchins are predated upon by pufferfish, wrasses, emperors, lobsters and octopus.

Table 7 – Food of echinoids considered in this study (adapted in part from table 1 p58 in deRidder and Lawrence (1982))

Species	Diet items
Diadema setosum	Algae; filamentous algae; algal films; turf algae; seagrass; some animal tissue; detritus
Diadema savignyi	All sorts of organisms on surface of coral; detritus
Echinothrix calamaris	Coraline algae; filamentous algae; brown algae; seagrass; diatoms; animal tissue; detritus
Echinothrix diadema	Algae and encrusting organisms
Echinometra mathaei	Calcareous mass; sponges; algae; calcareous algae; animal material; detritus
Tripneustes gratilla	Bits of plants and algae; seagrass; algae; detritus; animal material
Toxopneustes pileolus	Small calcareous balls
Echinostrephus molaris	Balls of coarse detritus, traces of plants and shells; algal particles; calcareous algae; algae; encrusting sponges

Sea cucumbers

Sea cucumbers typically inhabit tidal flats, seagrass beds and coral reefs (Marshall et al. 1999). They play crucial roles in the recycling of nutrients and bioturbation processes in marine benthic communities (Bruckner et al. 2003). Forty-four species from 10 genera have been recorded in Kenya (Muthiga and Conand 2014). Seventeen species are currently being harvested, with *H. fuscogilva* dominating the catch (Muthiga et al. 2010). Interestingly, however, targeted sea cucumber surveys on Kenyan reefs do not record *H. fuscogilva* (see table below).

Sea cucumber assemblages along the coast of Kenya are highly diverse and highly variable in species composition and density. While densities of individual species are generally low (0.01 to 1.5 ind. m^{-2}), overall they average ~3.5 ind. m^{-2} (Muthiga and Ndirangu, 2000 in Muthiga et al. 2007, Muthiga and Conand 2014) for a number of sites. Muthiga and Conand (2014) found abundances at a number of fringing reef sites to range between 1.08 to 1.25 indiv.400 m^{-2} for the most abundant species (*H. atra, H. leucospilota and S. chloronotus)*. Other common species that occurred in smaller numbers included *Actinopyga mauritiana*, *Bohadschia subrubra* and *B. atra*. Densities and diversity of sea cucumbers were found to be greatest in reef lagoons as well as in MPAs, but the factors controlling variability are currently poorly understood (Muthiga and Conand 2014).

For Mombasa, a total of 10 different species belonging to two orders (Aspidochirotida and Apodida) and three families (Holothuriidae, Stichopodidae and Synaptidae) were recorded (Orwa et al. 2009). The most abundant commercial species in the study area was the low value *H. leucospilota* (42.78%) that occurred at a density of 2.22 per 400 m^2 followed by the lollyfish (*H. atra*), the greenfish (*S. chloronotus*) and the yellow surffish (*A. mauritiana*). The overall density of commercial sea cucumbers in protected sites (11.00 /400 m^2) was higher than unprotected sites (2.29/400 m^2). The three most abundant species in protected sites were *H. leucospilota* (4.33/400 m^2; 39.39%), *H. atra* (3.33/400 m^2; 30.30%) and *S. chloronotus* (2.92/400 m^2; 26.52%), whereas the three most abundant species in unprotected sites were *H. leucospilota, H. atra* and *A. mauritiana*, at densities and relative abundance of 1.17/400 m^2 (50.91%), 0.54/400 m^2 (23.64%) and 0.30/400 m^2 (12.73%), respectively (Orwa et al. 2009). While abundance and diversity have been shown to be strongly correlated with the substrate cover (especially hard coral cover) and reef rugosity (Orwa et al. 2009), we did not have data separating densities between the reef and seagrass environments, and therefore assumed densities on seagrass beds to be half that recorded for reef environments. These densities were combined with average mass for each species sourced from the literature to derive biomass (1.354 t km^{-2}). Mass estimates were hard to come by and were often obtained from reef areas in other regions of the world where they may not be subject to the same pressure as in Kenya. The current biomass estimate may therefore be an overestimate and we recommend for this value to be revisited in the future based on locally collected species-specific mass information.

Ebert (1978) estimated a maximum age of 9 years for *H. atra* weighing 1,352 g. Using Brey's (1999) equation, a value of 7 years and Ebert's max weight, yielded a P/B value 0.524 $year^{-1}$. Values reported by Ainsworth et al. (2007) and Weijerman et al. (2013), 0.74 $year^{-1}$ and 0.8 $year^{-1}$, respectively, were comparable. A model for the Kimberley region in Australia also used a similar estimate of 0.6 $year^{-1}$ (Anon). Pauly et al. (1993) and Valls et al. (2012) suggested a higher value for sea cucumbers, 2.66 $year^{-1}$ and 11 $year^{-1}$, respectively.

Sea cucumbers have been harvested in Kenya since the 1900s, a pattern thought to be coincident with an influx of Asian nationals at that time (Mueni 2013). However, the fishery has experienced rapid changes in the last 15 years due to high demand for *bêche-de-mer* internationally, particularly Southeast Asia, and the higher prices offered (Muthiga and Ndirangu, 2000 in Muthiga and Conand 2014). Sea cucumbers were initially harvested in Malindi, Mombasa and Kipini through fisheries concessions (Muthiga et al. 2007). The introduction of SCUBA to the fishery in the early 1990s led to a peak in sea cucumber catches in 1992 at around 225 tonnes per year, declining to around 20 tonnes per year thereafter (Muthiga et al. 2007). The use of SCUBA for sea cucumber was prohibited at a departmental meeting in 1998, but its use continued until 2003 when a SCUBA ban was gazetted under the Legal Notice No. 214, Part 2 (c), Cap. (Muthiga et al. 2007).

The fishery is primarily artisanal, conducted by men, and sea cucumbers are collected and sold to be exported only, as holothurians do not form part of the Kenyan diet (Orwa et al. 2009). Collection is mainly done by hand either through walking or skin diving, and is concentrated in intertidal and subtidal (3 – 10 m) habitats depending on target species. Sea cucumbers are also landed as bycatch in the shrimp trawl fishery, and by speargun and ringnet fishers. Fishing is mainly carried out in the NEM season when the seas are calm and waters less turbulent (Ochiewo et al. 2010). While sea cucumbers are landed at a number of sites along the coast, including Nyali and Mombasa (Mueni 2013), sea cucumbers are mostly heavily targeted in Kwale districts (70% to 80% of the catch) (Muthiga and Conand 2014). Current catch statistics do not include sea cucumbers and local information seems to indicate that few fishermen target sea cucumbers in the area.

The Q/B value was calculated based on the following equation established by Cammen (1980) for the ingestion rate of aquatic deposit feeders and detritivores:

$$C = 0.381 \cdot W^{0.742}$$

where consumption (C) is in mg·day^{-1} and weight (W) is dry weight in mg. Assuming an average wet weight for all three key species of 500 g and a wet weight to dry weight conversion coefficient of 0.05 (I. Bertram, pers. comm.), Q/B was estimated at 10.2 year^{-1}. Sea cucumbers in the Kimberley model had a Q/B ratio set at a much lower value of 2.07 year^{-1}, while Ainsworth et al. (2007) estimated the Q/B for sea cucumbers at 8.25 year^{-1}. Pauly et al. (1993) estimated Q/B at between 3.2 and 3.8 year^{-1}, while Aliño et al. (1993) used a much higher Q/B value of 22.25 year^{-1}.

Holothurians are deposit feeders, with gut contents consisting predominantly of the surrounding substrate. At least nineteen species of fish including sharks and trigger-fish, gastropods, loggerhead turtles and starfish have been reported to prey on sea cucumbers (Marshall et al. 1999).

Corals

Some 55 coral genera and close to 200 species have been recorded from Kenya (Lawson 1969, Hamilton and Brakel 1984, Obura 2001a). The main species identified at Mombasa include those belonging to the massive and submasssive form of the following genera: *Porites, Astreopora, Favia, Favites*, *Leptoria*, *Platygyra Montipora, Galaxea and Pavona*; and the branching *Pocillopora, Stylophora, Acropora* and *Porites* (Muthiga 1996, McClanahan et al. 2001, Mangubhai et al. 2007). A number of species with encrusting forms (e.g., *Turbinaria, Coscinarea, Porites*) are also common. On the backreef, generally, Pavona Porites and Galaxea can be said to be the dominant genera. On the forereef coral diversity is much greater, with an increased abundance of branching *Acropora* spp. as well as encrusting forms of *Porites* spp.

Based on the published literature, a wide variety of means exist to calculate coral biomass from coral cover (Odum and Odum 1955, Martinez-Estalella and Alcolado 1990, Crossland et al. 1991, McClanahan 1995). Consequently, calculated coral biomass can vary markedly depending on the method applied and reflecting the immense range in actual coral tissue biomass between different species (M. Hardt, Blue Ocean institute, pers. comm., 2008). Moreover, while most studies seem to focus on tissue and/or zooxanthellae when referring to biomass (e.g., Fitt et al. 2000, Anthony et al. 2002, Thornhill et al. 2011), one may want to also consider the actual mass of calcium carbonate on a reef, particularly in light of climate change impacts. No such data was available for inclusion here, but this may be worthy of pursuit in the future. Estimates of coral cover were derived from 10 m transects in the lagoon and on the forereef within protected and fished areas, encompassing aspects of live coral cover as well as rugosity (F. Januchowski-Hartley, pers. comm.). Biomass was calculated taking these estimates of coral cover into account, as well as tissue biomass estimates in Fitt et al. (2000) and Anthony et al. (2002), and the percentage cover of reef habitat within the modelled area. Values were set at 0.067 t km^{-2} for *Acropora* spp., 0.497 t km^{-2} for massive and encrusting species and 0.045 t km^{-2} for other species within the no-take area. For the fished area, biomass was estimated at 0.365 t km^{-2}, 4.061 t km^{-2} and 3.805 t km^{-2} for each of the three groups, respectively.

It is generally accepted that the symbiotic association between corals and their algae (zooxanthellae) is central to the development of coral reefs in oligotrophic tropical oceans, because zooxanthellae transfer the majority of their production to the coral host (autotrophic nutrition) (Odum and Odum 1955). This symbiosis augments the carbon supply to the coral, with the symbionts benefitting from nutrient supply and the relatively stable environment provided by the coral host. In addition, an increasing number of studies have demonstrated that many species of corals acquire carbon and nutrients through heterotrophic feeding, ingesting organisms ranging from dissolved organic compounds to mesozooplankton (Muscatine et al. 1989b, Anthony et al. 2000, Godinot et al. 2011, Mills et al. 2004, Houlbrèque et al. 2004, Ferrier-Pagès et al. 2003, Palardy et al. 2008). Indeed, recent work indicates that heterotrophy accounts for up to 66% of the fixed carbon incorporated into coral skeletons and can meet from 15% to 35% of daily metabolic requirements in healthy corals, and up to 100% in bleached corals (Houlbrèque and Ferrier-Pagès 2009). Barnes and Hughes (2009) point out that in some corals, especially branching species, up to 95% of a coral's energy can be derived from autotrophy, down to around 50% for more heterotrophic species. Coral tissue growth appears to depend on the availability of energy provided through photosynthesis and feeding, with a number of studies showing that heterotrophy plays a particularly important role in tissue synthesis, while skeletal growth is mainly driven through photosynthesis (e.g., Dubinsky and Jokiel 1994, Anthony et al. 2002). Interestingly, a more recent study shows that despite among-species variation in physiology, and consistent effects of feeding on some monitored traits, energy allocation to tissue compared to skeleton growth did not depend on particle availability (Hoogenboom et al. 2015). Massive and encrusting corals typically have larger polyps, which we assumed are associated with greater ingestion rates of plankton and other particulate matter. *Acropora* are known as "poor" feeders, relying mainly on autotrophic pathways to derive the energy they need for growth and other metabolic processes (Muscatine et al. 1998, Houlbrèque et al. 2004). Based on the above, we assumed that autotrophic processes contributed 90% to animal coral production in *Acropora* spp., 75% for branching corals and 50% for massive and encrusting species.

Values derived by Crossland et al. (1991) (1.095 year^{-1}) and Arias Gonzalez et al. (1998) (21.68 year^{-1}), reflect large differences recorded in the turnover time for different species of corals (Chadwick-Furman et al. 2000, Goffredo and Chadwick-Furman 2003). *Porites* spp., *Pavona* spp. and *Galaxea* spp., some of the more dominant genera on the backreef (F. Januchowski-Hartley pers. comm.), tend to have massive hemispherical growth forms characterized by reproduction during a short period each year and slow growth. Wabnitz et al. (2010) derived a P/B of 0.14 year^{-1} based on information gleaned from Babcock (1991), who derived life history characteristics for three species of corals with relatively similar life characteristics to *Porites* spp. Weijerman et al. (2013) derived a P/B of 2.1 year^{-1} for a representative reef of the Hawaiian Islands where dominant genera would include *Pocillopora*, *Montipora* and *Porites*, by assuming a P/Q ratio of 0.6 and a Q/B of 3.25 year^{-1}.

Similar to P/B, consumption rates in the literature were found to vary widely between species, partly a reflection of location, depth, how much of a facultative consumer particular coral are, whether experiments were conducted *in situ* or in the laboratory, flow velocity and the abundance of food particles. Hence, the Q/B of individual groups is likely to differ markedly based on species composition and local conditions.

In the absence of locally derived parameters, P/B and Q/B values for input into Ecopath were adapted from the Coral-Algae-Fish-Fisheries Ecosystem Energetics (CAFFEE) model derived for a representative coral reef ecosystem in the Western Indian Ocean (Ruiz Sebastián and McClanahan 2013). Turnover rates were estimated at 2.53 year^{-1} for *Acropora* and branching species and 1.65 year^{-1} for massive and encrusting corals. Q/B values for branching species were set at 3.2 year^{-1}, lower than in Ruiz Sebastián and McClanahan (2013) to reflect their smaller polyps and lower feeding rates compared to massive species. *Acropora* spp. parameters were set equal to those for branching species.

While not used for model purposes, as we did not have data for the calcium carbonate biomass of the reef, estimates of calcium carbonate production derived from reef budget surveys are included here for information and possible future use (Perry et al. 2015). These are based on colony size and shape, and use basic geometric shapes to calculate the cross-sectional growth of coral per year based on different growth forms. Within the marine park, estimates averaged 532.86 t $CaCo_3$ km^{-2}, 1473.22 t $CaCo_3$ km^{-2}, and 210.79 t $CaCo_3$ km^{-2} for *Acropora* spp., massive/encrusting coral forms and other corals respectively (F. Januchowski-Hartley, unpublished data). In the reserve, estimates were calculated as 282.15t $CaCo_3$ km^{-2}, 979.16 t $CaCo_3$ km^{-2}, and 1520.94 t $CaCo_3$ km^{-2} for the same three groups.

As indicated, corals are primary producers, but also act as carnivores and consumers of detritus and dissolved organic carbon (Goreau et al. 1971, Muscatine et al. 1989a). Corals are known to ingest dissolved and particulate organic matter (DOM and POM) (Anthony 1999), picoplankton (Houlbrèque et al. 2004), nanoplankton (Houlbrèque et al. 2004), as well as meso-macrozooplankton (Rosenfeld et al. 1999, Ribes et al. 2003 , Palardy et al. 2006, Palardy et al. 2008). Sebens et al. (1996) showed that corals can ingest between 0.5 and two prey items per polyp per hour of ingestion, suggesting significant grazing capacity by corals on mesozooplankton over reefs.

Seagrass

Twelve seagrass species are found in Kenya in intertidal and sublittoral environments on sandy and muddy substrates down to 15 m, covering extensive areas of lagoons (Malleret King et al. 2003). Seagrasses play a variety of roles, including the binding of sediments to prevent erosion, the provision of habitat and nursery areas for juvenile fish and invertebrates such as prawns, the delivery of nutrients in the form of dead seagrass mats, and a source of food for green and hawksbill turtles, dugong and some fish species. Seagrass beds have been recognized for their importance in supporting local fisheries, particularly in relation to lethrinids (emperors), lutjanids (snappers), siganids (rabbitfish), scarids (parrotfish) and spiny lobsters.

Eight species have been recorded from the permanently submerged lagoon in the Mombasa Marine National Park (*Thalassia hemprichii, Thalassodendron ciliatum, Halophila stipulacea, H. ovalis, Halodule uninervis, Cymodocea rotundata, C. serrulata* and *Syringodium isoetifolium*) (Alcoverro and Mariani 2004). *Thalassodendron ciliatum* is the dominant seagrass species along the Kenyan coast (Kamermans et al. 2002b), spanning large areas of the reef flat, and covering the vast majority of the total surface of the MMNP lagoon. *Thalassodendron ciliatum* typically forms dense monospecific beds with high biomass, while the other species are present in mixed beds.

The biomass of seagrasses in the Mombasa model area varies by location and depth. Dense seagrass beds were found to cover 9.5 km^2 out of the 29 km^2 model area at Mombasa, with another 6 km^2 consisting of a mix of coral and seagrass (based on data from Maina et al. (2015)). We assumed 75% of the mixed habitat class to consist of seagrass (T. McClanahan pers. com.), yielding a total “seagrass” area of 13.98 km^2. Biomass values of *T. ciliatum* dominated beds were found to vary significantly between 33.7 g DW m^{-2} and 569.9 g DW m^{-2} for various locations surveyed in Kenya, Mozambique and Tanzania (Bandeira 1997, Ochieng and Erftemeijer 1999, Bandeira 2002, Kamermans et al. 2002a, Ochieng and Erftemeijer 2003, de Boer 2007, Gullström et al. 2008). We set the biomass estimate at 465.2 t km^{-2}, representing the average of two studies conducted over both the SEM and NEM (Gwada 2004, Uku and Björk 2005). These values were used as although the studies were conducted independently their findings were similar. Note however, that it is significantly lower than the value derived from data presented in Ochieng and Erftemeijer (1999) for Mombasa lagoon (1,446 t km^{-2}). No *T. ciliatum*-specific DW:WW conversion coefficient was found in the published literature; nor were we able to source one after contacting C. Duarte and P. Erftemeijer. Therefore, we applied the ratio commonly used for *Z. marina* of 0.19.

It is important to note that the above estimates are limited to the total leaf biomass. *Thalassodendron ciliatum* has a fairly unique morphology as, unlike most seagrasses, its vertical stems extend outside the sediments, raising the leaf bases considerably into the water column. Kay (1971) note “its erect flexuose stems with apical tufts of leaves to some extent resembling those of the tall *Laminaria* species of northern seas, though on a much smaller scale (its erect stems are usually 15-30 cm long, and its leaves 10-15 cm long)”. It has horizontal as well as vertical rhizomes, with the former showing a new vertical rhizome or shoot produced every fourth node. A cluster of leaves is then attached to the top of each living stem. Aboveground biomass therefore consists of both stems and leaves, with the ratio between the two ranging between 0.9 and 2.0 (Bandeira 2002, Uku and Björk 2005). As productivity seems to be typically estimated in terms of aerial or shoot production and herbivores are likely to chiefly consume leaves, we limited our biomass estimates to shoot biomass only.

Similar to biomass, productivity of *T. ciliatum* was found to vary widely, with values ranging between 4.5 and 36.8 g DW m^{-2} day^{-1} for sites along the coast of Kenya, Tanzania and Mozambique (Bandeira 1997, Ochieng and Erftemeijer 1999, Bandeira 2002, de Boer 2007). Values from Australia (Rasheed et al. 2008) fell towards the higher end of this range for monospecific as well as meadows dominated by *T. ciliatum*, but mixed in with *T. hemprichii*. P/B was estimated at 12.27 year^{-1} for the pseudo atoll of Tarupa Kecil, Indonesia (Brouns 1985) and at 8.317 year^{-1} for a mixed seagrass bed in the Philippines (Carlos et al. 1998). Ochieng and Erftemeijer (1999) estimated seagrass productivity and leaf biomass for the Mombasa lagoon over the course of one year in 1995/1996 to be 8.2 g DW m^{-2} day^{-1} and 569.9 g DW m^{-2}, respectively, yielding a P/B of 5.272 year^{-1}. A study conducted at Nyali yielded P/B estimates between 7.31 year^{-1} in the NE monsoon and 7.64 year^{-1} in the SE monsoon season, respectively (Uku and Björk 2005). An average of these latter two values was used here (7.475 year^{-1}).

Algae

Published detailed records of benthic algae from the Kenyan coast are rather scarce. Early reports (Knutzen and Jaasund 1979) indicate that seaweeds in the lagoon environment at the time were largely comprised of *Sargassum* spp. and *Halimeda* spp., while those of the reef flat were dominated by the genus Ulva, with at least three abundant species (*U. fasciata* Delile, *U. pulchra* Jaasund and *U. reticulata* Forsk.). *Laurencia papillosa*, *Graciliara* spp., *Padina* spp., *Halimeda* spp., *Turbinaria* spp. and *Hypnea* spp. were also found to be common but generally not abundant (Knutzen and Jaasund 1979). More recent surveys show varying cover of turf and macroalgae among sites within the MNPR, indicative of the abundance of urchins at those sites (Muthiga 1996). A detailed study of the littoral zonation pattern at Gazi Bay, which the authors highlight as generalizable to the Kenyan coast, show the rhizophytic algae *Udotea orientalis* and *Halimeda macroloba* to grow characteristically between the *T. ciliatum* stolons (Coppejans et al. 1992). Thus the “algae” functional group here is representative of a mix of turf, mostly present on the reef itself and with a cover of up to 40% (Mangubhai et al. 2007), and macroalgae, with the latter being present on both the reef and within seagrass beds.

In the absence of locally-sourced information, biomass values were based on data provided by T. Sauvage (pers. comm.) for turf and macroalgae in Hawaii and the following considerations: percentage substrate cover at UVC reef locations; proportion of reef habitat in the total model area; an additional estimated 5% cover of macroalgae within seagrass beds; and the proportion of seagrass bed cover within the area modelled. This yielded an estimate of 268.5 t km-^{2}.

Turf and macroalgae P/B show great variations between locations, between species and between sites on a given reef (Klumpp and McKinnon 1992, Payri 2000, Russ 2003), with values in the literature ranging between 6.375 year^{-1} and 37.640 year^{-1}. The estimate used here for turf (16.641 year^{-1}) was based on average values calculated for crest and reef flat areas at Myrmidon Reef, Great Barrier Reef (Russ 2003), which seems appropriate given the reef habitat categories included in the model area. Wabnitz et al. (2010) used a P/B value for turf of 19 year^{-1}. Weijerman et al. (2013) used a P/B estimate of 18.068 year^{-1} based on estimated daily turnover time for turf algae by Klumpp and McKinnon (1992). Miller et al. (2009) estimated a P/B ratio of 16.591 year^{-1}. P/B for macroalgae (9.824 year^{-1}) was based on an estimate derived by Payri (2000) and used in Wabnitz et al. (2010). Weijerman (2013) derived a comparable estimate of 11.963 year^{-1} for macroalgae. Ainsworth et al. (2007) estimated P/B for macroalgae at 10.5 year^{-1} and Carpenter et al. (1991) at 12.8 per year^{-1}. These values are also in line with estimates derived by Ruiz Sebastián and McClanahan (2013) using CAFFEE. The overall P/B was set at 12 year^{-1}.

Zooplankton

The composition of zooplankton over coral reefs is complex, patchy and highly dynamic. It typically consists of a mixture of pelagic plankton advected on to the reef (Heidelberg et al. 2004, Heidelberg et al. 2010), eggs spawned by reef fish (Hamner et al. 2007) and demersal plankton (Alldredge and King 1977). The latter consists of organisms that ascend from the substratum at night and contribute to a four to five-fold increase in demersal crustaceans and larger zooplankton, such as copepods (Heidelberg et al. 2004, Yahel et al. 2005a, Yahel et al. 2005b).

There is generally only limited information on zooplankton communities for East Africa, particularly for coastal waters (Okemwa 1990), and where these have been published they generally focus on descriptive parameters such as species composition and indices of diversity over time, for example (Mwaluma et al. 2003). Available information seems to indicate that copepods dominate the zooplankton community numerically, while data are contradictory in terms of biomass. A study conducted in Tudor Creek and including a station at the mouth of the Creek recorded 51 zooplankton taxa, representing 74% of the zooplankton abundance sampled (Okemwa 1990). Copepod were found to comprise 30-60% of total zooplankton biomass at Mida Creek (Mwaluma et al. 2003), and up to 92% at Gazi Bay (Osore 1992, Kitheka et al. 1996). Decapods, brachyurans, cnidarians, protozoans, amphipods, appendicularians, molluscs, chaetognaths, foraminifera, caridean larvae, and fish eggs as well as larvae were also present in samples at the locations mentioned above. Interestingly, around Inhaca Island, Paula et al. (1998) found gastropod larvae to be the most important organism in samples. Lugomela et al. (2001) showed that the diversity of copepods in waters off Unguja island, Tanzania, was high with calanoid copepods (*Acrocalanus gibber, Eucalanus spp, Temora stilifera, Temora turbida, Centrophages furcate* and *Acartia* spp.). The authors found appendicularians to be the only important non-copepod group in the mesozooplankton.

Overall, the same study found that protozooplankton (ciliates and heterotrophic dinoflagellates) contributed equally to heterotrophic plankton biomass. A study conducted over reefs in Florida showed that while copepods dominated samples numerically (93-96% of abundance), their contribution to total zooplankton biomass was only 35% (Heidelberg et al. 2010). Copepod abundance and species composition were also noted to vary according to season, presumably reflecting primary productivity patterns as a response to seasonal variations in temperature (Osore 1992, Paula et al. 1998) and precipitation levels (see below), with lowest numbers recorded during the dry season (Okera 1974, Okemwa 1990, Osore 1992, Mwaluma et al. 2003).

Given the disparity in focus on different size classes and in the absence of definitive data on the make-up and biomass contributions of individual groups to the overall zooplankton community at Nyali-Mombasa, we for now assumed “zooplankton” here to be primarily representative of the larger size fraction. We further assumed that while copepods generally are the most abundant zooplankton group, they would make up about 50% of the group’s biomass. Accordingly, biomass was calculated at 0.744 t km^{-2} based on data in Lugomela et al. (2001).

Published P/B values for zooplankton ranged between 40 year^{-1} (Polovina 1984) to 416 year^{-1} (Bozec et al. 2004), with Le Borgne (1982) estimating zooplankton P/B at 63.9 year^{-1} and 91.2 year^{-1} for carnivorous and herbivorous zooplankton respectively. It was here set at 90 year^{-1}.

Published Q/B values also show a wide range, spanning 196.28 year^{-1} for Raja Ampat (Ainsworth et al. 2007) to 1178.9 year^{-1} for a lagoon in the tropical South Pacific (Bozec et al. 2004). It was here set at 220 year^{-1}. Although within the range of previously published values, for both P/B and Q/B, estimates derived from data in Lugomela et al. (2001) appeared high (and average of 347.379 year^{-1} and 1112.62 year^{-1} across the entire community recorded). Messages sent to the lead author for clarification of some of the methods and values obtained were not answered.

While the importance of plankton in understanding food webs and their responses to natural and human-induced disturbance has increased in recent years, comparatively few studies on plankton community structure have been conducted in the Western Indian Ocean (but see Bryceson 1982, Lugomela 1995, Duineveld et al. 1997, Paula et al. 1998, Lugomela et al. 2001, Okuku et al. 2011, Limbu and Kyewalyanga 2015), specifically for coastal systems. Future studies should endeavour to derive better estimates for this poorly resolved, yet important functional group.

Diet data was primarily sourced from Heidelberg et al. (2004) and Alldredge et al. (2009).

Phytoplankton

Generally, unless situated in an upwelling area or off the mouth of a major river/estuary, coastal waters of the Western Indian Ocean are characterized by warm temperatures and low nutrients, low phytoplankton biomass (Kiteresi et al. 2011), and relatively low to moderate primary production with a distinct seasonal cycle.

A total of 75 phytoplankton taxa were found in the oceanic system around Vanga-Shimoni (Kiteresi et al. 2011). Diatoms were the most diverse group followed by dinoflagellates. A study conducted in 1999 during the rainy NEM season, off Ugunja island, Tanzania, found the phytoplankton community dominated by diatoms of the genus *Chaetoceros* spp, *Rhizosolenia* spp, *Bacteriastrim* spp, *Thalassiothrix* spp, *Leptocylindricus* spp and *Pseudonitszchia* spp. Common autotrophic dinoflagellates were *Ceratium* spp, *Protoperidinium* spp, and *Prorocentrum* spp. Dominance of diatoms in terms of biomass (84%) and production (73%), was also shown for another study conducted around Unguja Island in 1994 and 1996 during the rainy season (Wallberg and Andersson 2000). However, in contrast, during the dry season, pico-cyanobacteria accounted for 57% of the primary production and 51% of the biomass, while corresponding values for micro-plankton were 16% and 3%, respectively (Wallberg and Andersson 2000). Dominance of pico and nanoplankton is also described by Kyewalyanga (2015) as usual for the phytoplankton community of the Western Indian Ocean.

No published study is available detailing the phytoplankton biomass, community and primary production rates for Mombasa directly, but some data are available in the literature for surrounding areas. For example, Duineveld et al. (1997) estimated phytoplankton biomass for Gazi Bay at between 0.31 and 0.65 µg Chl*a* l^{-1}. These values are comparable to data also collected for Gazi Bay a few years prior by Lugomela (1995), which showed a value of 0.24 µg Chl*a* l^{-1} over the reef and 1.74 µg Chl*a* l^{-1} in the mangrove. The measurements also compare favourably with mean seasonal data collected around Unguja island, Tanzania (0.2 – 0.5 mg Chl*a* m^{-3}) (Bryceson

1982, Lugomela 1995, Lugomela et al. 2001, Limbu and Kyewalyanga 2015)[3] and Inhaca Island, Mozambique (0.34 mg Chl*a* m^{-3}) (Paula et al. 1998). In areas more heavily influenced by population, concentrations are typically higher, ranging between 0.95 mg Chl*a* m^{-3} for the less impacted Gazi Creek and 4.633 mg Chl*a* m^{-3} for the more polluted Makupa Creek (Okuku et al. 2011).

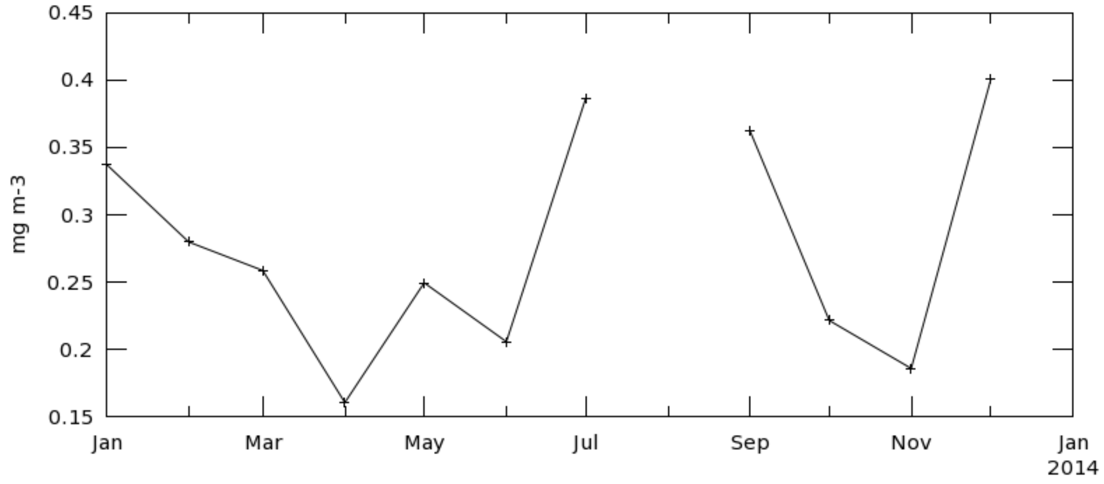


Figure 4 - Chlorophyll-a concentration in mg m^{-3} for the year 2013 for the area just off Mombasa from MODIS-Aqua

In-situ collected data also corroborate measurements taken from satellite. MODIS data for 2013 ranged between 0.16 and 0.4 mg Chl*a* m^{-3}, yielding an annual average of 0.277 mg Chl*a* m^{-3} (Figure 4), while data extracted from the European Space Agency's Ocean-Colour Climate Change Initiative (spatial resolution 4 km) ranged between 0.235 and 0.342 mg Chl*a* m^{-3}, with an annual average of 0.287 mg Chl*a* m^{-3} (Figure 5).

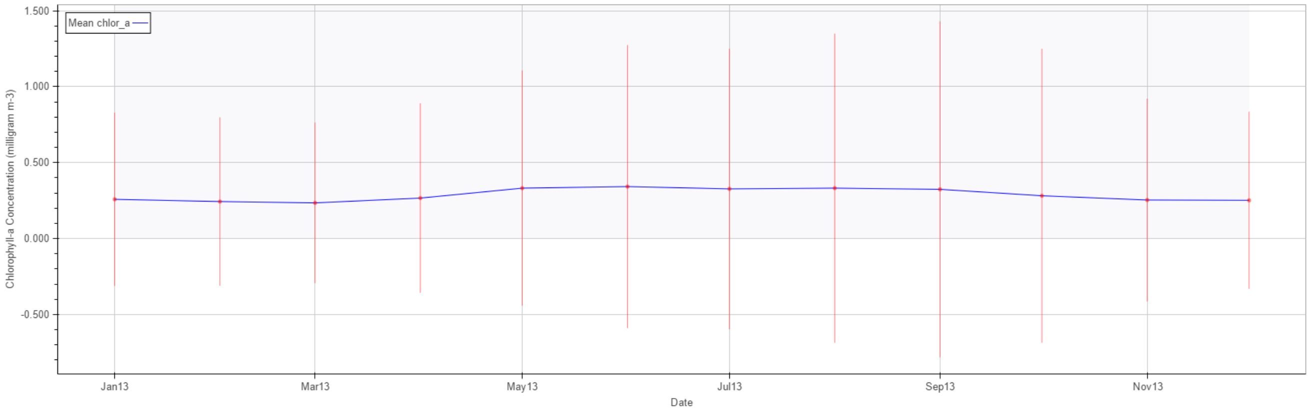


Figure 5 – Chlorophyll-a concentration in mg m^{-3} for the year 2013 for the area just off Mombasa from the European Space Agency's Ocean-Colour Climate Change Initiative

C: Chl a ratios in the literature are highly variable – 30 (Kromkamp et al. 1997), 84 (Charpy and Blanchot 1998), 60 (Yahel et al. 1998, Barbosa et al. 2001), 20 to 160 (Taylor et al. 1997) and 15 to 176 (Sathyendranath et al. 2009) - reflecting variations among phytoplankton groups and whether the measurements were conducted at the surface or at depth. Some authors have suggested that a higher ratio is more appropriate for generally low nutrient environments, with values as high as 200 applicable to open ocean oligotrophic environments (Gasol et

---

[3] In the case of Limbu (2015) and Paula et al. (1998) we assumed that the authors measured Chl-a concentrations as mg m^{-3} or µg l^{-1} and not as published (mg l^{-1} µg m^{-3}) as these would yield unrealistically low estimates.

al. 1997). As we do not have a locally estimated value, and in the absence of detailed information regarding phytoplankton composition in the area, an average C:Chl a ratio of 90 from the above reported values was applied here. Lugomela et al. (2001) use 100 in their study, but the references provided are for temperate and arctic conditions. We assumed 1 gC to be equal to 9 g WW (Pauly and Christensen 1995), although not a single other reference was found to corroborate this estimate, nor did contacted experts feel qualified to suggest whether this conversion factor appeared reasonable and/or to provide an alternate value. Deriving such a conversion ratio would be useful for future more reliable parameterisation. Based on these assumptions, an average estimated water column depth for the model area of 5 m, and available biomass data derived from the sources indicated above, phytoplankton biomass was set at 1.122 t km^{-2}. This value does not take into account the autotrophic components of the microbial pool that are notoriously difficult to measure and integrate given their diversity, but are an important part of autotrophic plankton. The Mombasa value is lower than the 3.29 t km^{-2} derived by Polovina (1984) for French Frigate Shoals, but higher than that calculated by Arias-González et al. (1997) for Moorea, French Polynesia (0.32 t·km^{-2}).

Rates of primary production in the region vary significantly, both in space and time. For values measured *in-situ*, primary production has been shown to range from less than 0.1 g C m^{-2} d^{-1} (Mitchell-Innes 1967) to more than 3.0 g C m^{-2} d^{-1}, especially in coastal embayments and along productive continental shelves. Most of the values determined in the Western Indian Ocean region fall between 0.5 and 2.0 g C m^{-2} d^{-1}. Lugomela et al. (2001) found integrated primary production, including bacterial production, to range from 204 to 4142 mg C m^{-2} day^{-1} off Unguja, Tanzania. Data extracted from the European Space Agency's Ocean-Colour Climate Change Initiative for the coastal waters off Mombasa for 2013 ranged between 329.467 and 425.789 mg C m^{-2} day^{-1}. These values correspond closely to measurements made at Gazi Bay, if values from the study are interpreted as g C m^{-2} day^{-1} rather than m^{-3} as published. While informative, as these values are water column integrated, they do not allow us to estimate the P/B for this area. The only P:B values (C turnover) we did come across came from a study in the northern Indian Ocean where Jochem et al. (1993) conducted transects in the open ocean, and another study conducted along the northern Kenyan coast, with transects also conducted offshore at depths ranging between 20 and 2000 m (Kromkamp et al. 1997). Based on the above findings, we used the average of net production values published by Lugomela et al. (2001) for cyanobacteria, nanoplankton and microplankton and the authors' standing stock estimates for these same groups to derive a P/B ratio of 207.37 year^{-1}. This value is similar to P/B derived for the autotrophic component of plankton samples (i.e., cyanobacteria, nanoplankton and microplankton) collected over both the dry and rainy season off Unguja Island. This ratio also falls within the range of other published estimates (e.g., Bienfang and Johnson 1980, Kromkamp et al. 1997, Bozec et al. 2004)[4], but is lower than the P/B of 475 year^{-1} derived for the Great Barrier Reef (Furnas et al. 1990), or of between 716 year^{-1} and 511 year^{-1} for Uvéa atoll, New Caledonia (Le Borgne et al. 1997) depending on the C: Chl a ratio used.

RESULTS

Data collected along transects from underwater visual surveys on the coral reef habitat in the model area showed large differences in biomass among families and also show important differences between protected and fished areas (Figure 6).

For fished locations, Acanthuridae, Labridae and Pomacentridae made up most of the recorded biomass. At protected locations Acanthuridae, Serranidae, Labridae, Scaridae, Holocentridae and Siganidae comprised most of the biomass on the reef. Some of the largest differences among groups between fished and protected locations included Acanthuridae, Serranidae, Holocentridae, Scaridae and Siganidae (Figure 6).

---

[4] *Though the authors used a C:Chla ratio of 30 based on previous measurements conducted in the Netherlands*

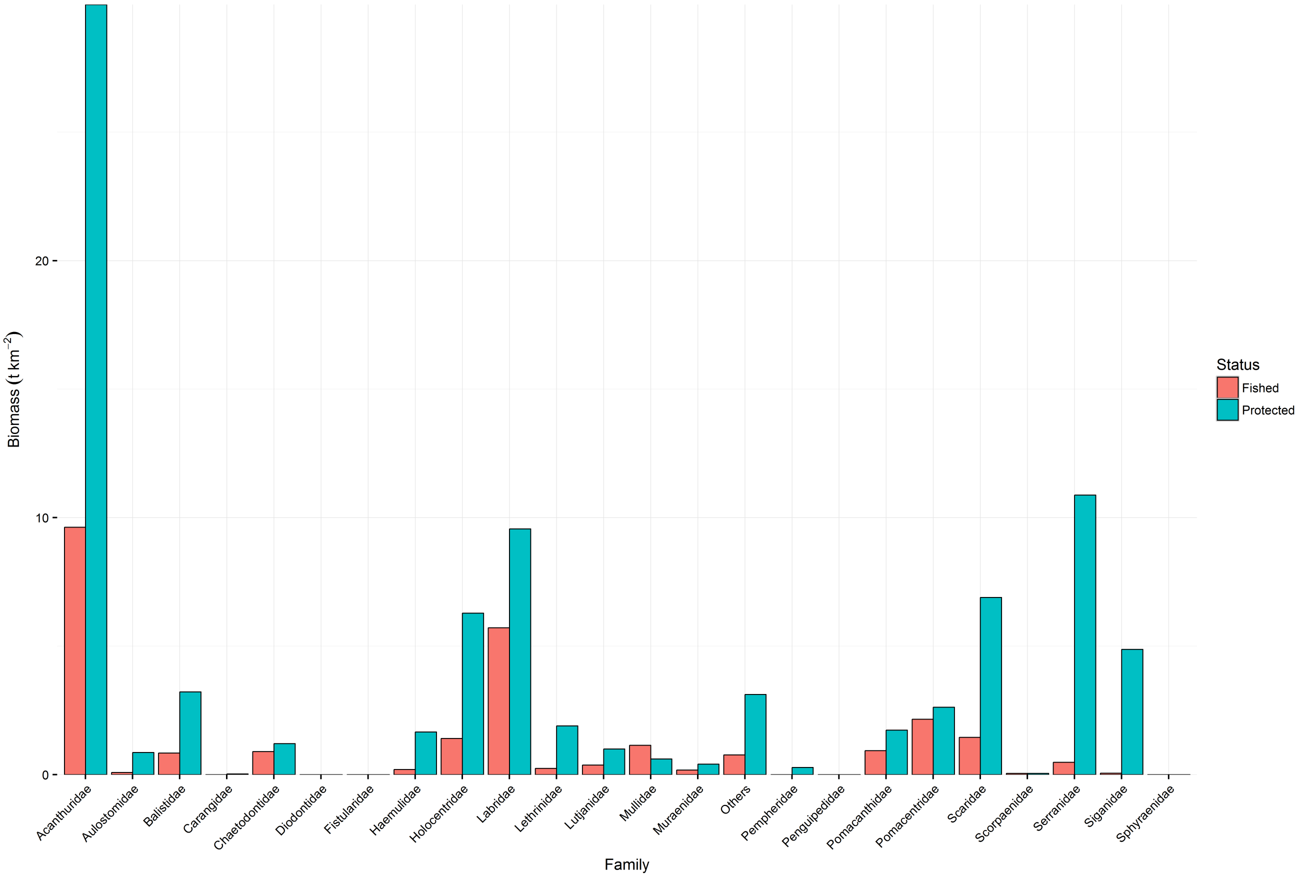


Figure 6 - Biomass by family as a result of data collected from underwater visual transects (UVC) on the coral reef (i.e., excluding seagrass) habitat only

Fisheries

Total catches from the five gear types included in the model were estimated at 5.02 t km^{-2}. The relative proportion of catches by the main gears employed in the near-shore fishery across all landing sites combined were estimated to be: beach seine (66%), speargun (14%), gillnet (10%), trap (7%), and handline (6%) (Table 8; Figure 7).

In terms of functional groups and across all gears, parrotfish dominated catches (45%), followed by pelagics (15%), rabbitfish (10%), emperors and octopus (both 8%). These groups were predominantly captured using different gears. Parrotfish were overwhelmingly captured using beach seines. Pelagics were landed using mostly beach seine and gillnet. Emperors were caught by fishers on handline and with gillnets; while the majority of rabbitfish were landed using traps followed by beach seine. Spearguns were by far the most common gear used to target octopus. Groupers, which only accounted for 1% of the overall catch, were mostly landed using handlines, followed by speargun. Based on landings data, herbivorous fish made up 58% of total catches at Nyali-Mombasa.

Small parrotfish (e.g., *Leptoscarus vaigiensis*) dominated beach seine catches, while barracuda, emperors, octopus and rabbitfish were the most commonly surveyed groups in catches landed using gillnet, handline, speargun and trap, respectively (Figure 7).

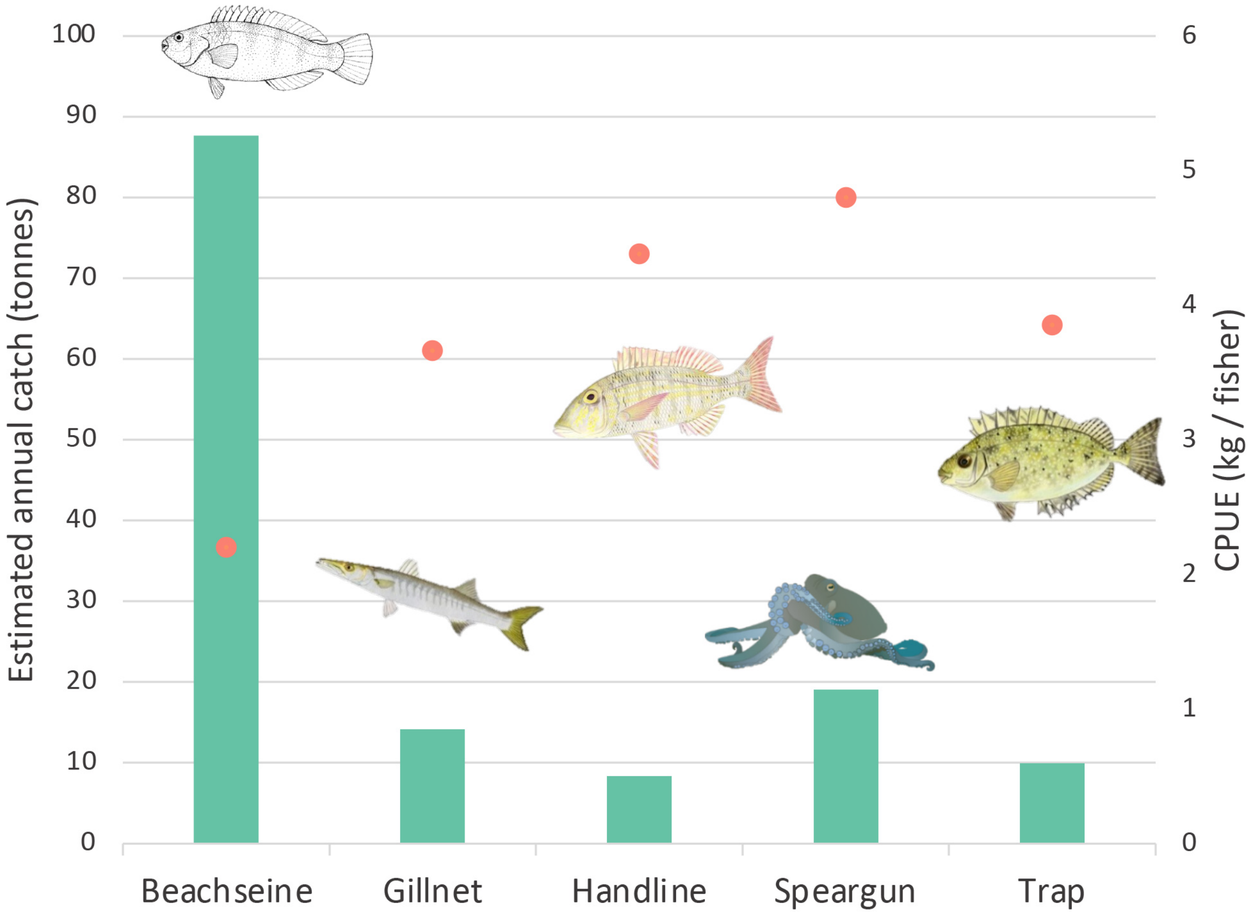


Figure 7 - Estimated annual catch (t km^{-2}; bar graph, left y-axis) landed using different gears for all landing sites combined at Nyali-Mombasa in 2013. Catch per unit effort (CPUE) is displayed as circles with units along the right y-axis. Species that dominate catches for each gear are displayed above the gear: from left to right, *L. vaigiensis*; *Sphyraena* spp; *Lethrinus* spp; *Octopus* spp; and *Siganus sutor*.

Gear use was not uniform among landing sites (Figure 9; Table 8) with total catch by gear landed at the individual sites contributing differentially to overall catch at Nyali-Mombasa. Most of the beach seine catch was landed at Marina and Reef. The majority of the catch landed with gillnets was recorded at Mtwapa, followed by Kenyatta, with these two landing sites also contributing most to catch landed using handline. Traps were mostly deployed at Kenyatta and Nyali, while speargun catches were mostly landed at Nyali, followed by Mtwapa and Kenyatta. At the level of individual landing sites dominant gears were: gillnet at Mtwapa; beach seine at Marina, Reef and Msanakani; speargun (gillnet and trap) at Kenyatta; and beach seine and speargun at Nyali (Figure 9).

Across all five landing sites, catch per unit effort (CPUE) was highest for speargun, followed by handline (Figure 7). CPUE was similar between trap and gillnet and lowest among all gears used for beach seine (Figure 7). CPUE varied across sites, with Kenyatta registering some of the highest values for gillnet, speargun and handline (Table 8). The highest trap CPUE was registered at Marina and Reef had the highest CPUE for beach seine (Table 8).

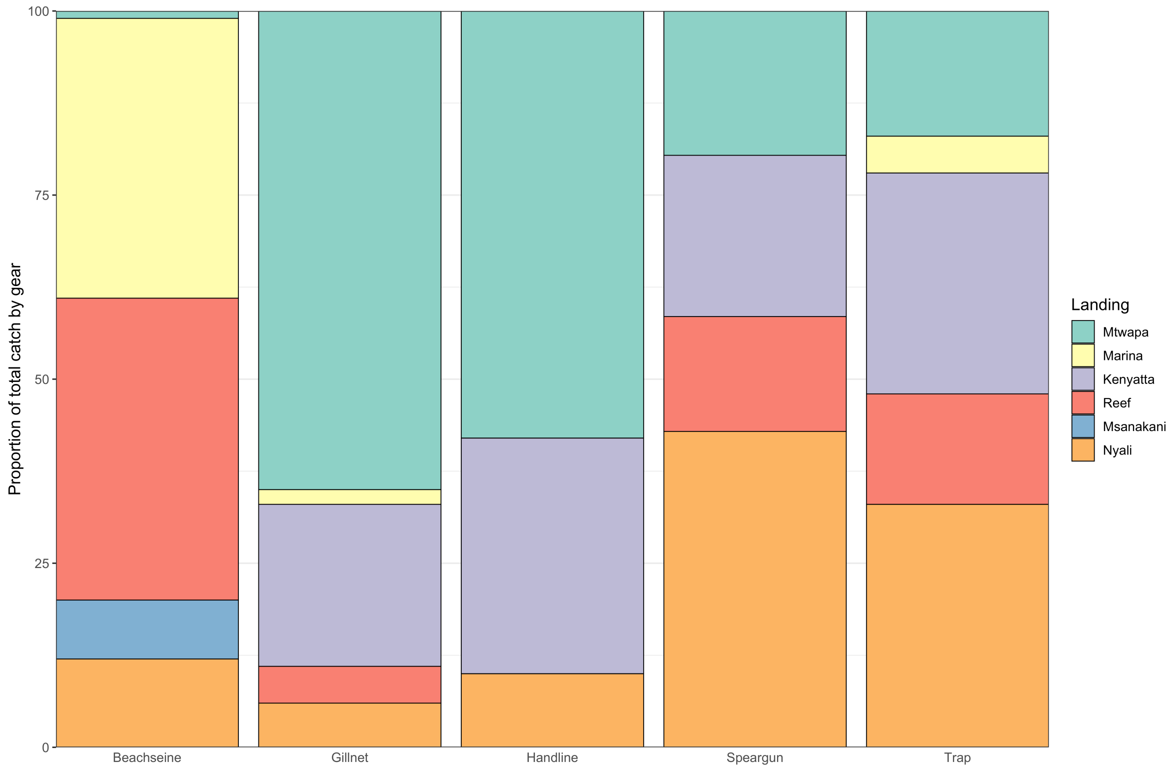


Figure 8 - Proportion of total catch landed by gear types at the different landing sites in Nyali-Mombasa

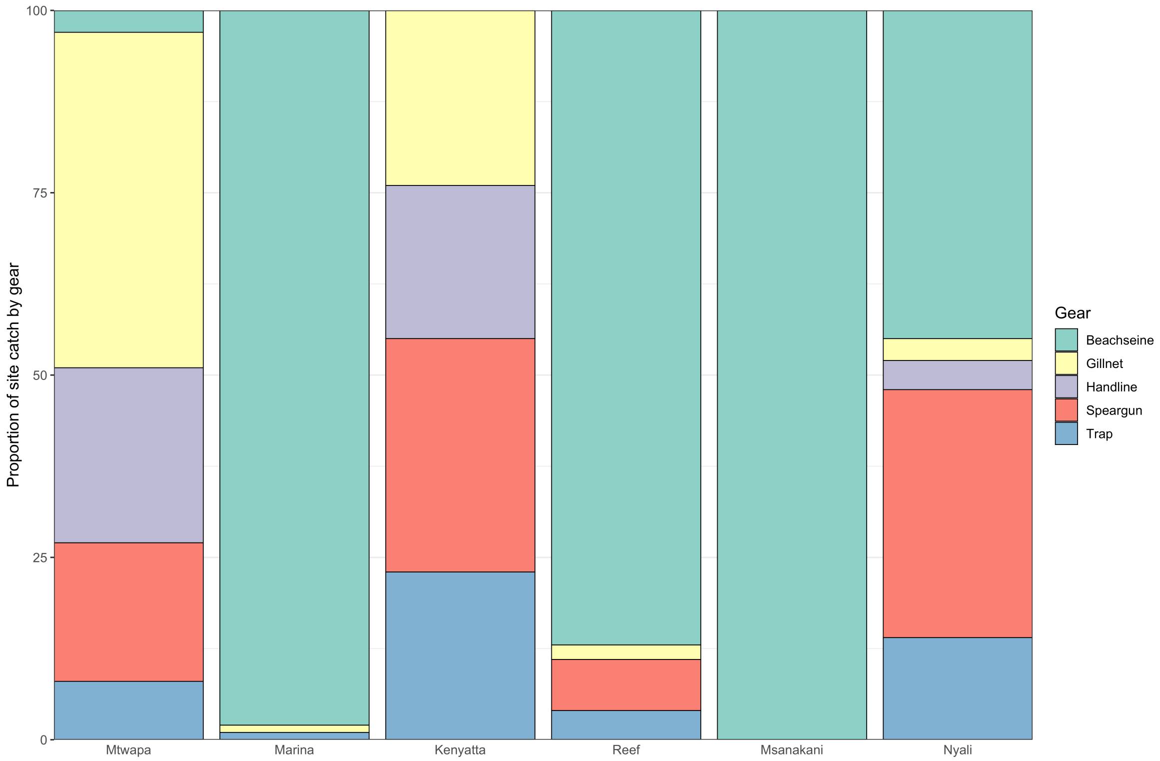


Figure 9 – Proportion of catch at a given landing site according to gear used at Nyali-Mombasa

General description of the system

Ecopath aggregates an entire system into distinct trophic levels *sensu* Lindeman (Christensen et al. 2008). Trophic levels, biomass and estimated flows between functional groups are represented graphically as a flow diagram and a Lindeman spine for Nyali-Mombasa in Figure 10 and Figure 11 respectively. Trophic parameters of the balanced model for all 46 groups are presented in Table 9 (outputs are in bold), while the diet matrix is available in Table 10.

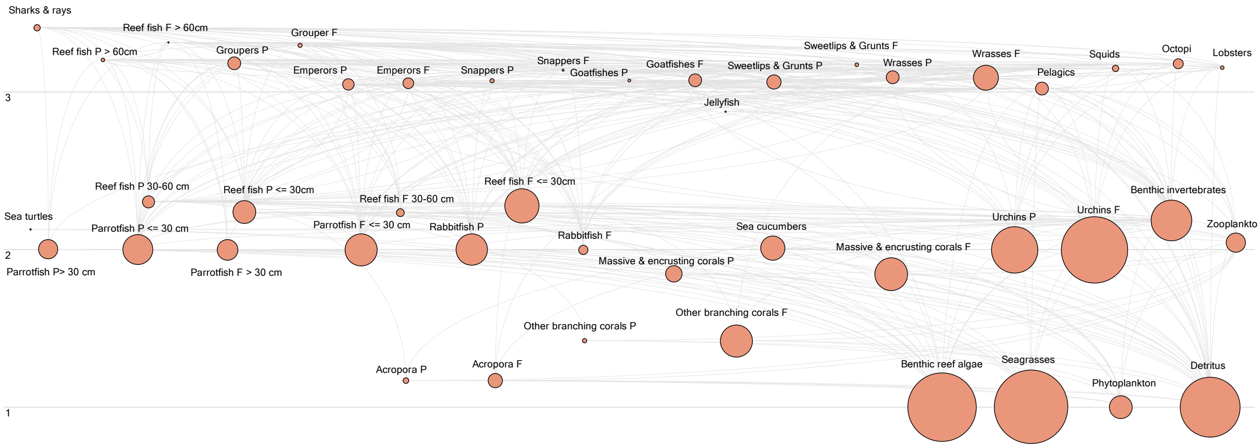


Figure 10 - Flow diagram of the Nyali-Mombasa ecosystem in 2013. Each functional group is shown as a circle of size approximately proportional to the log of the group's biomass. All functional groups are lined up against their trophic level (y-axis). Thin grey lines represent predator-prey relationships among groups.

Trophic levels ranged between 1 for primary producers and 3.41, 3.31 and 3.21 for top predators, here represented by sharks & rays, Reef Fish P >60 cm and Reef fish F >60cm, respectively. Generally, ecotrophic efficiency values were found to be high for all groups, with values lower for groups within protected areas. High EEs indicate that total mortality in the system is mainly driven by predation and fishing. The lower EE values of the protected guilds indicate that these groups generate a reasonable amount of surplus secondary production.

The primary producers, seagrass and benthic reef algae, accounted for 73% of total biomass (not including detritus) within the system. Animal consumers were dominated by herbivorous guilds, utilising that production (Figure 10). Sea urchins accounted for 24% of total living biomass. All protected reef fish groups made up just <1% of total biomass, while fished groups accounted for just >1% (mostly reef fish and parrotfish < 30cm in size). Small individuals dominated the reef fish functional groups. Consumption by sea urchins had the biggest impact on available resources.

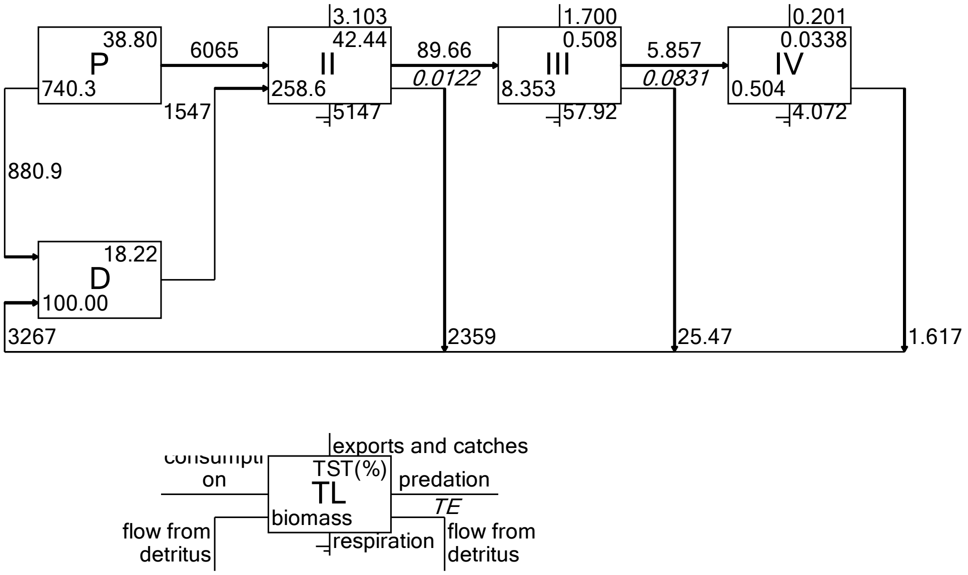


Figure 11 - A Lindeman spine representation of trophic flows (t·km^{-2}·year^{-1}) and biomasses (t km^{-2}) for the Nyali-Mombasa ecosystem.

Table 8 - Summary of WCS catch data by landing site and gear deployed, including total catch surveyed (kg); number of days sampled per site and number of days gear was recorded in use; average daily catch (kg); estimated annual catch (tonnes) and annual number of fishers; catch per unit effort (CPUE, kg/fisher/day); proportion of total overall catch by gear and proportion of each landing site's to overall catch.

	KENYATTA					**MTWAPA**						**MARINA**		
Gears		Gillnet	Handline	Speargun	Trap		Beach seine	Gillnet	Handline	Speargun	Trap	Beach seine	Gillnet	Trap
Total catch surveyed (kg)		779.500	657.000	1,023.000	742.000		59.500	789.800	414.500	322.500	143.000	3,337.500	34.000	50.500
Sampling days	54	40	41	49	48	19	1	14	12	17	5	22	3	10
Average daily catch (kg)		19.488	16.024	20.878	15.458		59.500	56.414	34.542	18.971	28.600	151.705	11.333	5.050
Estimated annual catch (tonnes)		3.176	2.677	4.168	3.023		0.689	9.145	4.799	3.734	1.656	33.375	0.340	0.505
Estimated annual no. of fishers		786	587	811	794		452	2,432	1,031	886	347	15,130	90	100
CPUE (kg/fisher)		4.039	4.563	5.141	3.805		1.526	3.761	4.657	4.216	4.767	2.206	3.778	5.050
Proportion of total overall catch by gear		22%	32%	22%	30%		1%	65%	58%	20%	17%	38%	2%	5%
Proportion of catch overall			9%						14%				25%	

	REEF				**NYALI**					**MSANAKANI**	**ALL LANDING SITES**
Gears	Beach seine	Gillnet	Speargun	Trap	Beach seine	Gillnet	Handline	Speargun	Trap	Beach seine	**Total**
Total catch surveyed (kg)	3,464.500	64.000	284.000	145.200	972.500	73.500	79.000	742.500	298.000	601.500	**15,092.500**
Sampling days	21	5	19	16	20	8	14	20	20	20	
Average daily catch (kg)	164.976	12.800	14.947	9.075	48.625	9.188	5.643	37.125	14.900	30.075	
Estimated annual catch (tonnes)	36.295	0.670	2.975	1.521	10.698	0.809	0.869	8.168	3.278	6.617	**139.348**
Estimated annual no. of fishers	13,085	199	639	346	6,138	352	286	1,628	1,001	4,983	**52,170**
CPUE (kg/fisher)	2.774	3.368	4.656	4.400	1.743	2.297	3.038	5.017	3.275	1.328	
Proportion of total overall catch by gear	41%	5%	16%	15%	12%	6%	10%	43%	33%	8%	
Proportion of catch overall		30%					17%			5%	

Including primary producers, the weighted trophic level of the community was 1.25, with seagrass and benthic reef algae as well as detritus, also given a trophic level of 1, keeping the mean low. Omitting primary producers, the mean trophic level was equal to 2.02, indicative of the large proportions of herbivores utilising the primary production within the area. This is also illustrated in the Lindeman spine analysis (Figure 11), with most of the biomass within the system represented by TL I and with flows occurring chiefly between primary producers and TL II. Trophic level II and I generated the most total system throughput (Figure 11). Not surprisingly based on these results, most catches originated from TL II.

Table 9 - Balanced Nyali-Mombasa model parameters. Values in bold are Ecopath outputs. TL = Trophic Level

No	**Group name**	**TL**	**Biomass (t/km²)**	**P/B (/year)**	**Q/B (/year)**	**EE**	**P/Q**	**Catch (t/km²)**
1	Sea turtles	2.13	0.001	0.263	8.869	**0.000**	0.030	
2	Sharks & rays	3.41	0.084	1.027	3.237	**0.667**	0.317	0.057
3	Reef fish P > 60cm	3.21	0.024	0.463	4.517	**0.231**	0.102	
4	Reef fish P 30-60 cm	2.30	0.268	1.000	20.000	**0.186**	0.050	
5	Reef fish P <= 30cm	2.24	1.131	1.200	22.000	**0.364**	0.055	
6	Reef fish F > 60cm	3.31	0.000	0.600	2.098	**0.776**	0.286	0.000
7	Reef fish F 30-60 cm	2.23	0.116	1.516	27.178	**0.092**	0.056	0.006
8	Reef fish F <= 30cm	2.28	4.608	1.188	23.000	**0.285**	0.052	0.177
9	Groupers P	3.18	0.300	0.420	5.050	**0.139**	0.083	
10	Grouper F	3.30	0.037	2.220	7.480	**0.740**	0.297	0.058
11	Parrotfish P> 30 cm	2.00	0.753	0.700	23.000	**0.091**	0.030	
12	Parrotfish P <= 30 cm	2.00	2.846	0.900	26.000	**0.457**	0.035	
13	Parrotfish F > 30 cm	2.00	0.868	1.500	25.000	**0.870**	0.060	1.085
14	Parrotfish F <= 30 cm	2.00	3.699	1.361	28.000	**0.474**	0.049	1.316
15	Emperors P	3.05	0.221	0.940	6.810	**0.508**	0.138	
16	Emperors F	3.05	0.213	2.940	9.800	**0.708**	0.300	0.405
17	Snappers P	3.07	0.038	1.070	10.243	**0.216**	0.104	
18	Snappers F	3.14	0.010	3.210	10.700	**0.695**	0.300	0.022
19	Goatfishes P	3.07	0.017	0.754	8.166	**0.479**	0.092	
20	Goatfishes F	3.07	0.308	0.788	8.166	**0.332**	0.097	0.011
21	Sweetlips & Grunts P	3.06	0.358	0.660	6.900	**0.459**	0.096	
22	Sweetlips & Grunts F	3.17	0.033	2.250	7.700	**0.722**	0.292	0.050
23	Wrasses P	3.09	0.292	1.432	13.126	**0.292**	0.109	
24	Wrasses F	3.09	1.541	1.440	12.799	**0.170**	0.113	0.014
25	Rabbitfish P	2.00	3.311	1.490	22.428	**0.240**	0.066	
26	Rabbitfish F	2.00	0.163	4.470	22.424	**0.706**	0.199	0.486
27	Pelagics	3.02	0.280	3.881	13.819	**0.681**	0.281	0.725
28	Squids	3.15	0.088	4.400	14.790	0.800	0.297	0.225
29	Jellyfish	2.88	0.001	5.010	25.050	**0.250**	0.200	
30	Octopi	3.18	0.183	3.280	12.500	**0.638**	0.262	0.362
31	Lobsters	3.16	0.031	1.050	7.300	**0.763**	0.144	0.020
32	Sea cucumbers	2.01	1.354	0.524	10.199	**0.000**	0.051	
33	Urchins P	2.00	20.150	0.430	27.937	**0.376**	0.015	
34	Urchins F	2.00	209.805	0.419	30.380	**0.304**	0.014	
35	Benthic invertebrates	2.19	10.270	3.261	11.620	0.950	0.281	0.001
36	Acropora P	1.17	0.067	2.530	3.200	**0.538**	0.791	
37	Acropora F	1.17	0.365	2.530	3.200	**0.310**	0.791	
38	Other branching corals P	1.42	0.045	2.530	3.200	**0.481**	0.791	
39	Other branching corals F	1.42	3.805	2.530	3.200	**0.310**	0.791	
40	Massive & encrusting corals P	1.84	0.497	1.650	3.500	**0.418**	0.471	
41	Massive & encrusting corals F	1.84	4.061	1.650	3.500	**0.452**	0.471	
42	Benthic reef algae	1.00	268.457	12.000		**0.973**		
43	Seagrasses	1.00	465.203	7.475		**0.801**		
44	Zooplankton	2.04	0.744	80.300	220	**0.844**	0.365	
45	Phytoplankton	1.00	1.122	207.369		**0.608**		
46	Detritus	1.00	100.000			**0.475**		

Table 10 - Diet matrix for the Nyali-Mombasa ecosystem. Predators are represented by numbers along the top edge of the table with prey group (and associated functional group number) on the left-hand side. Greyed cells represent diet proportions ≤ 0.001

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	44
1	Sea turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Sharks & rays	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Reef fish P > 60cm	-	▨	▨	-	-	-	-	-	▨	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Reef fish P 30-60 cm	-	0.005	0.023	▨	-	0.002	-	-	0.021	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Reef fish P <= 30cm	-	0.020	0.097	0.006	-	0.008	▨	▨	0.089	0.008	-	-	-	-	0.020	0.002	0.057	0.004	0.016	-	0.037	0.004	-	-	-	-	0.015	0.018	-	0.008	-	-	-	-	▨	-	-	-	-	-	-	-
6	Reef fish F > 60cm	-	-	▨	-	-	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Reef fish F 30-60 cm	-	0.002	▨	▨	-	0.008	-	-	▨	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Reef fish F <= 30cm	-	0.080	0.040	0.003	-	0.321	0.027	0.003	0.036	0.320	-	-	-	-	0.008	0.063	0.023	0.179	-	0.015	0.015	0.142	-	-	-	-	0.059	0.069	-	0.031	-	-	-	-		-	-	-	-	-	-	-
9	Groupers P	-	0.005	0.009	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Grouper F	-	▨	-	-	-	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Parrotfish P> 30 cm	-	0.013	0.065	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Parrotfish P <= 30 cm	-	0.049	0.244	0.015	-	0.020	0.002	▨	0.223	0.020	-	-	-	-	0.051	0.004	0.143	0.011	-	-	0.093	0.009	-	-	-	-	0.037	0.035	-	0.016	-	-	-	-	▨	-	-	-	-	-	-	-
13	Parrotfish F > 30 cm	-	0.015	0.007	-	-	0.060	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.011	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Parrotfish F <= 30 cm	-	0.064	0.032	0.002	-	0.258	0.021	0.002	0.029	0.257	-	-	-	-	0.007	0.050	0.019	0.144	-	-	0.012	0.114	-	-	-	-	0.048	0.052	-	0.023	-	-	-	-	▨	-	-	-	-	-	-	-
15	Emperors P	-	0.004	0.019	0.001	-	0.002	-	-	0.017	0.002	-	-	-	-	-	-	0.002	▨	-	-	0.007	▨	-	-	-	-	0.003	0.012	-	-	-	-	-	-	▨	-	-	-	-	-	-	-
16	Emperors F	-	0.004	0.002	▨	-	0.014	-	-	0.002	0.014	-	-	-	-	-	-	▨	0.008	-	-	▨	0.006	-	-	-	-	0.003	0.003	-	-	-	-	-	-	▨	-	-	-	-	-	-	-
17	Snappers P	-	▨	0.003	▨	-	▨	-	-	0.003	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Snappers F	-	▨	▨	-	-	▨	-	-	▨	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	Goatfishes P	-	▨	0.001	▨	-	▨	-	-	0.001	▨	-	-	-	-	▨	-	▨	▨	-	-	▨	▨	-	-	-	-	▨	▨	-	▨	-	-	-	-	-	-	-	-	-	-	-	-
20	Goatfishes F	-	0.005	0.003	▨	-	0.022	-	-	0.002	0.021	-	-	-	-	-	0.004	0.002	0.012	-	-	▨	0.010	-	-	-	-	0.004	0.006	-	0.003	-	-	-	-	▨	-	-	-	-	-	-	-
21	Sweetlips & Grunts P	-	0.006	0.031	0.002	-	0.003	-	-	0.028	0.003	-	-	-	-	-	-	0.004	▨	-	-	0.012	0.001	-	-	-	-	0.005	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22	Sweetlips & Grunts F	-	▨	▨	-	-	0.002	-	-	▨	0.002	-	-	-	-	-	-	-	0.001	-	-	▨	▨	-	-	-	-	▨	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	Wrasses P	-	0.005	0.025	0.002	-	0.002	-	-	0.023	0.002	-	-	-	-	0.005	-	0.015	0.001	0.004	-	0.010	▨	-	-	-	-	0.004	0.004	-	0.002	-	-	-	-	▨	-	-	-	-	-	-	-
24	Wrasses F	-	0.027	0.013	▨	-	0.107	-	-	0.012	0.107	-	-	-	-	-	0.021	0.008	0.060	-	0.005	0.005	0.047	-	-	-	-	0.020	0.028	-	0.012	-	-	-	-	▨	-	-	-	-	-	-	-
25	Rabbitfish P	-	0.057	0.284	0.018	-	0.023	-	-	0.260	0.023	-	-	-	-	0.059	0.005	0.167	0.013	-	-	0.108	0.010	-	-	-	-	0.043	0.009	-	0.004	-	-	-	-	▨	-	-	-	-	-	-	-
26	Rabbitfish F	-	0.003	0.001	▨	-	0.011	-	-	0.001	0.011	-	-	-	-	▨	0.002	▨	0.006	-	-	▨	0.005	-	-	-	-	0.002	0.002	-	▨	-	-	-	-	-	-	-	-	-	-	-	-
27	Pelagics	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28	Squids	-	0.073	0.010	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	0.049	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	Jellyfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.050	-	-	-	-	-	-	-	-	-	-	-	-	-
30	Octopi	-	0.065	0.020	-	-	0.020	-	-	-	-	-	-	-	-	-	-	-	-	▨	▨	-	-	-	-	-	-	▨	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31	Lobsters	-	0.006	▨	-	-	▨	-	-	▨	▨	-	-	-	-	▨	▨	▨	▨	-	-	-	-	-	-	-	-	-	-	-	▨	-	-	-	-	-	-	-	-	-	-	-	-
32	Sea cucumbers	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33	Urchins P	-	-	-	0.140	0.030	-	-	-	-	-	-	-	-	-	0.327	0.008	0.265	0.003	-	-	-	-	0.250	-	-	-	0.017	0.045	-	0.009	0.009	-	-	-	▨	-	-	-	-	-	-	-
34	Urchins F	-	-	-	-	-	-	-	0.166	-	-	-	-	-	-	0.341	0.800	0.138	0.520	-	-	-	-	-	0.250	-	-	0.177	0.469	-	0.091	0.091	-	-	-	0.003	-	-	-	-	-	-	-
35	Benthic invertebrates	0.099	0.055	0.070	0.078	0.085	0.100	0.140	0.009	0.249	0.199	-	-	-	-	0.182	0.043	0.147	0.028	0.880	0.880	0.600	0.600	0.570	0.650	-	-	0.009	0.025	-	0.800	0.890	0.008	-	-	0.049	-	-	-	-	-	-	-
36	Acropora P	-	-	-	-	0.003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	-	-	-	-	-	-	-
37	Acropora F	-	-	-	-	-	-	-	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	-	-	-	-	-	-	-	-	-	-	▨	-	-	-	-	-	-	-
38	Other branching corals P	-	-	-	-	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
39	Other branching corals F	-	-	-	-	-	-	-	0.023	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.009	-	-	-	-	-	-	-	-	-	-	0.003	-	-	-	-	-	-	-
40	Massive & encrusting corals P	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	▨	-	▨	-	-	-	-	-	-	-
41	Massive & encrusting corals F	-	-	-	-	-	-	0.010	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.003	-	-	-	-	-	-	-
42	Benthic reef algae	0.327	-	-	0.400	0.400	-	0.700	0.400	-	-	0.800	0.300	0.800	0.150	-	-	0.010	0.010	-	-	-	-	-	-	0.190	0.190	0.020	-	-	-	-	0.190	0.210	0.450	0.052	-	-	-	-	-	-	-
43	Seagrasses	0.564	-	-	-	-	-	-	-	-	-	0.050	0.550	0.050	0.700	-	-	-	-	-	-	-	-	-	-	0.800	0.800	0.033	-	-	-	-	-	0.650	0.350	0.088	-	-	-	-	-	-	-
44	Zooplankton	0.010	-	-	0.013	0.094	-	-	0.061	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.160	0.060	-	-	0.060	0.170	0.750	-	-	-	-	-	0.110	0.660	0.660	0.660	0.660	0.660	0.660	0.040
45	Phytoplankton	-	-	-	0.019	0.136	-	-	0.089	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.002	-	-	0.160	0.100	0.100	0.100	0.100	0.100	0.100	0.650
46	Detritus	-	0.030	-	0.300	0.240	-	0.100	0.220	-	-	0.150	0.150	0.150	0.150	-	-	-	-	0.100	0.100	0.100	0.050	0.020	0.030	0.010	0.010	0.007	-	0.200	-	0.010	0.800	0.140	0.200	0.526	0.240	0.240	0.240	0.240	0.240	0.240	0.310
47	Import	-	0.400	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.400	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Indicators

The system's overall summary statistics and selected indicators are presented in Table 11. The findings corroborate the results illustrated above, namely that the majority of trophic flows originated from primary producers. The high EEs attained for the main primary producers indicate that grazing is indeed central to the dynamics of the modelled system. The primary producers' high EEs were also reflected in the relatively low production to respiration ratio of 1.3 for the system overall. The mean transfer efficiency of the system as a whole was 3.67% for flows from primary producers, 4.64% from detritus and 3.91% overall. Transfer efficiencies were relatively low for the lower trophic levels, and increased moving up the food chain. The Finn's cycling index of 6.2%, showing that only a small fraction of the throughput (including detritus) gets recycled, corroborates the overall relatively low efficiency in recycling.

Table 11 - Summary statistics derived from the Ecological Network Analysis and other select system indicators.

Indicator	Abbreviation	Definition	Value	Units
Sum of all consumption			7740	t/km²/year
Sum of all exports			1728	t/km²/year
Sum of all respiratory flows			5204	t/km²/year
Sum of all flows into detritus			3274	t/km²/year
Total system throughput	TST	Sum of all flows (consumption, export, respiration, detritus). TST is indicative of whole ecosystem size (Christensen et al. 2008).	17947	t/km²/year
Mean trophic level of the catch		Weighted average of the TL of fisheries target species (Pauly et al. 1998)	2.44	
Gross efficiency (catch/net p.p.)			0.001	
Total primary production			6944	t/km²/year
Total primary production/total respiration	TPP/TR	Indicator of community energetic attributes and ecosystem maturity. In the early stages of ecosystem development primary production (TPP) is expected to exceed respiration (TR) (values greater than 1). As the system matures the ratio is expected to move towards 1 (Christensen et al. 2008).	1.3	
Total primary production/total biomass	TPP/TB	Indicator of community energy attributes and ecosystem maturity. As a system matures, biomass accumulates, therefore the TPP/TB ratio is expected to be high in developing systems and lower in more mature systems (Christensen et al. 2008).	6.9	
Total biomass (excluding detritus)			1007.8	t/km²/year
Total catch			5.02	t/km²/year
System omnivory index		Weighted average of the variance in the TL of consumers' prey groups. Indicator representative of trophic specialization and of how feeding interactions are distributed among trophic levels (Libralato 2008).	0.12	
Finn's cycling index		Percentage of flows that are recycled in the food web (Finn 1976).	7.30	% of TST
Relative ascendency (A/C)		Ascendency represents the organised power within a system and density of network linkages; Development Capacity is the upper limit of Ascendency (Ulanowicz 1986). The ratio is an index of organisation of the food web (Heymans et al. 2014).	31.44	%
Relative Overhead (O/C)		Energy that an ecosystem has in reserve; indicative of a system's strength when subjected to unexpected perturbations (Ulanowicz 1986).	68.56	%
Mean transfer efficiency		Efficiency with which energy is transferred between TLs. It is calculated as the geometric mean of TE for each of the integer trophic levels II to IV (Christensen et al. 2008).	3.9	%
Pedigree			0.422	
Proportion of primary production required to sustain fisheries	PPR	Calculated as primary production required divided by the total primary production of the system to sustain catches. Indicator of the sustainability of fisheries (Pauly and Christensen 1995; Tudela et al. 2005).	26.50	%

Ecological state indicators derived by Ecopath showed that the main flows in the system were consumption (45%) and respiration (35%), followed by flows to detritus (15%) and exports (6%) (Table 11). The low flow levels into detritus are also reflected in the low Finn Cycling index value and the low proportion of flows originating from the detritus (0.27%).

Ascendency was estimated at 31.44% of capacity and overhead at 68.56%, 78% of which was attributable to internal flows indicating that the system contains a high number of 'redundant' trophic linkages. These observations are consistent with a system exhibiting relatively high resilience to perturbation with respect to energy flows, or a high system stability *sensu* Odum (1971). However, it is important to note that such network indicators depend on both data and model construction as well as on reliable knowledge of ecosystem structure. Therefore, such indicators are most useful in well-studied systems (Fulton et al. 2005a, Heymans et al. 2014).

Calculated total net primary production was 6943.59 t·km^{-2}·year^{-1} and was equal to 6.8 times the system's total biomass.

The model's pedigree index was estimated at 0.375; falling in the medium range of existing Ecopath models (Morissette 2007).

The overall trophic level of the catch was low (2.44), indicative of a fishery that is mainly targeting herbivores and where higher trophic levels (and large fish) represent only a small proportion of the overall catch. The high abundance of small fish, which represent mostly prey fish for higher trophic levels, are an indicator of the fishing pressure exerted on predators in the system (Fulton et al. 2005b). The primary production required to sustain the catch was relatively high at 28.57%.

DISCUSSION

In this study, we developed a food web model for the Nyali-Mombasa ecosystem to reproduce and quantify the main energy flows in the system, the dominant food–web dynamics, and identify the role of fisheries. The current model complements initial work to understand ecosystem dynamics in coastal systems of East Africa (Silva et al. 1993, Tuda and Wolff 2018). The current model integrates available data and information for the study area and appears to adequately represent system dynamics. Its development has also highlighted existing gaps in information, and some of the remaining uncertainties as well as suggestions for future development are highlighted below.

Fisheries

Sixty-six per cent of total catch was landed using beach seines and 14% using spears. Thus, based on current legislation, 80% of the catch at Nyali-Mombasa was landed using illegal gears. This is likely an underestimate as the category "gillnet" under gears does not differentiate between legal multifilament gillnets and illegal monofilament nets.

The majority of the catch was dominated by herbivores, such as parrotfish and rabbitfish. While data collected are not resolved at the species level, published studies indicate that those groups are typically dominated by *L. vaigiensis* and *S. sutor*, respectively (McClanahan and Mangi 2004, Signa et al. 2008, Samoilys et al. 2017). Both are small bodied, marbled or mottled species that are known to inhabit, and are well camouflaged in, seagrass beds (Kuiter and Tonozuka 2001, Gullström et al. 2011) and predominantly feed on seagrass leaves (McClanahan et al. 1994, Almeida et al. 1999, Gell and Whittington 2002, Gullström et al. 2011, Locham et al. 2015). *Leptoscarus vaigiensis* is even commonly sometimes called the seagrass parrotfish.

Importance of seagrass beds

Much attention in terms of scientific research and management action has been placed on coral reefs and associated fisheries, with very little emphasis placed on seagrasses (Orth et al. 2006). Yet, previous studies have shown that seagrass systems play a critical socio-ecological role (de la Torre-Castro and Rönnbäck 2004, de la Torre-Castro et al. 2008, Cullen-Unsworth et al. 2014), an assessment further strengthened by our findings.

Seagrasses are typically associated with, and support, a wide array of fauna (e.g., gastropods, bivalves, echinoids, fish, dugong, sea turtles) through their capacity as nursery, breeding and feeding grounds, thereby also making a significant contribution to fisheries (de la Torre-Castro et al. 2014). In using seagrass beds as nursery and/or foraging grounds, coral reef fish influence food-web dynamics and transfer energy and nutrients across habitats. Seagrass beds therefore have a fundamental role in maintaining populations of commercially exploited reef fish and invertebrates (Nagelkerken et al. 2002, Mumby et al. 2004, Dorenbosch et al. 2005) and in supporting the resilience of reef systems through the connectivity of functional groups (Nystrom and Folke 2001, Olds et al. 2012). A number of commercially important vagile species from the families Scaridae, Sphyraenidae, and Siganidae were found by Kruse et al. (2016) to dominate coral and seagrass habitats off Chumbe island, Tanzania, supporting findings by others that these and other assemblages migrate between habitats (Unsworth et al. 2008), and underlining the importance of seagrass beds to reef fisheries.

In Chwaka Bay, Tanzania, where artisanal fisheries are very similar to those that operate along the Kenyan coastline, de la Torre-Castro and Rönnbäck (2004) found that seagrass-associated fish constituted the primary source of animal protein for the local people and seagrass-associated fisheries in the form of trap fisheries ("dema") provided the highest daily average income per fisherman.

Assuming that gears get deployed over seagrass beds according to the proportions laid out in Table 12 (F. Hartley-Januchowsky, pers. comm.), the estimated annual catch contributed by seagrass beds amounts to 93.738 tonnes, or 67% of total annual catch. This is likely a conservative estimate, as based on catch composition (e.g., high proportion of rabbitfish in traps) some gears are likely to be used in seagrass more frequently than indicated. For example, in Chwaka Bay, Tanzania, fishing with traps, handline and spear was found to take place over seagrass beds 30%, 22%, and 13% of the time, respectively (de la Torre-Castro et al. 2014).

The importance of parrotfish and rabbitfish, both in terms of biomass and landings (

Table 9) underscores the importance of these groups as key conduits for the transfer of energy between primary producers and predatory consumers (Valentine and Duffy 2006), thereby shaping community structure and ecosystem processes. This is all the more noteworthy as seagrass is of poor nutritional value (Bjorndal 1980), partly due to its high C/N ratio and cellulose content (Duarte 1990), and is therefore considered a rather unattractive as a food source. While *L. vaigiensis* are known to preferentially feed on seagrass blades (Almeida et al. 1999, Gullström et al. 2011), given that a high epiphytic cover characterises the shoots of *Thalassodendron ciliatum* at Nyali (Uku and Björk 2005), and that epiphytes have a much higher nutritional value than seagrasses themselves, the effect of epiphytes on the food choice of this species cannot be entirely discounted.

Table 12 - Estimated annual catch derived from seagrass beds based on informed proportion of time gears will be deployed over seagrass

	Beach seine	**Gillnet**	**Handline**	**Speargun**	**Trap**
Annual estimated catch (tonnes)	87.673	14.140	8.345	19.045	9.983
Proportion of time gear deployed on seagrass	95%	20%	50%	5%	25%
Estimated annual catch from seagrass (tonnes)	83.289	2.828	4.173	0.952	2.496

Model structure and uncertainty

Quantitative descriptions of the flux of matter and energy can provide significant insights into the fundamental structure of ecosystems. Results presented here show that the Nyali-Mombasa ecosystem is dominated, in terms of biomass, by primary producers, particularly 'seagrass' and 'benthic reef algae'. The trophic networks at Nyali-Mombasa were dominated by grazing, with herbivores accounting for >25% of all living biomass within the system, of which close to 95% was sea urchins. Eighty-seven per cent of the total herbivorous biomass was accounted for by urchins in the fished area alone. The fact that their biomass is much higher than that registered for urchins in the protected area is likely in part due to a lack of predators as a result of fishing, as documented in a number of case studies from the area (e.g., McClanahan and Muthiga 1988, McClanahan and Shafir 1990, McClanahan et al. 1994). The low biomass of higher trophic levels, particularly in the reserve, indicates that herbivores are not limited by predation pressure.

While reef fish biomass and catches were derived from local survey data, both datasets still suffer from some deficiencies, reducing the pedigree index. While underwater visual census surveys were conducted in the model area, they focused solely on the reef habitat. However, seagrass cover the majority of the Mombasa reserve/park

(Alcoverro and Mariani 2004). Consequently, UVC-derived biomass estimates are therefore likely to be conservative and were here augmented based on available local data, where available (e.g., urchin biomass on seagrass beds (Alcoverro and Mariani 2002)), informed assumptions according to published data for the area, and/or by adjusting biomass of target groups based on existing catch data and known exploitation levels. Future studies should aim to derive estimates of fish as well as sea urchin biomass over the seagrass bed using UVC and/or other means. Such surveys would also help determine appropriate species abundance and diversity for groups showing high residency in seagrass beds. Attempts at quantifying the proportional contribution of individual species weights, rather than abundance, to overall group biomass would also be beneficial to deriving estimates of group's P/B and Q/B ratios as well as diets with greater confidence. While catch data was collected locally, for a number of functional groups, when compared with fish biomass data, the resultant fish mortalities did not match known exploitation levels for the area (Kaunda-Arara et al. 2003, Hicks and McClanahan 2012). Moreover, while WCS catches are very similar to government-derived fish statistics for some groups, they under or overestimate landings compared to official statistics for others (Table 3). Note that the data provided by the State Fisheries Department for 2013 only spanned January through November. Therefore, to estimate total yearly catch, values for December were assumed to be equal to the average catch of available months. Moreover, WCS catch data was collected at six landing sites (Kenyatta, Marina, Mtwapa, Nyali, Reef, and Msanakani); while the Fisheries Department obtained data from three landing sites (Bamburi, Marina and Nyali). Those three sites (assuming Bamburi = Kenyatta) account for about 51% of catches from all six landing sites considered here. Hence, landings for comparative purposes presented in Table 3 include both estimates. Given these large and inconsistent differences between groups, it would be useful for a focus group to attempt to reconcile some of these discrepancies, and it is expected that based on expert advice some informed decisions could be made to (i) inform, which data should be used for modelling purposes; as well as (ii) guide both catch data collection more effectively and (iii) streamline their use.

Lower trophic levels, especially zooplankton, are currently poorly resolved due to lack of information and data to parameterise them. In coral reefs, roughly 50% of the net primary production (NPP) produced offshore and on reefs is channelled through the microbial loop (Ferrier-Pagès and Gattuso 1998, Zöllner et al. 2009). Future efforts should seek to derive concentrations, production rates and grazing rates, if applicable, of autotrophic and heterotrophic planktonic (micro) organisms in the water over the coral reef and seagrass bed of this system. Such additions, and the greater resolution of these lower trophic levels, would likely allow to simulate the system's behaviour more appropriately. Similarly, because these lower trophic functional groups play an important role in the transfer efficiency and recycling of energy through the food web, the model would also benefit from greater resolution among invertebrate groups, replacing for example the general "benthic invertebrate" category with "benthic gastropods", "benthic crustaceans", and "polychaetes" or by dividing them up according to "crustaceans", "carnivores", and "detritivores". However, this greater resolution among prey groups would only benefit model development if it can be matched by sufficiently resolved information in the predators' diets.

The biomass of corals included here, as mentioned earlier, only focuses on the "live" component. However, this area benefits from the unique opportunity to include data on the calcium carbonate portion of the coral reef framework (F. Januchowski-Hartley unpubl. data). Inclusion of this data would allow us to simulate the erosive behaviour of sea urchins and parrotfish, and the likely effects of ocean acidification and/or increased bleaching events with projected increasing sea surface temperature on the reef more appropriately. While the biomass values inclusive of the calcium component are available, no appropriate corresponding P/B values currently exist. Efforts to derive these for the species representative of the shallow coastal zone at Nyali-Mombasa therefore would be highly relevant.

Future efforts may also want to consider splitting the reef fish groups according to their functional role on the reef, therefore, for example, according to "planktivores", "detritivores", "corallivores", "excavators", "browsers", "scrapers", etc. This would allow for greater insights into how the reef ecosystem's function may change under different pressures and scenarios. It would also allow for the derivation of group-specific indicators such as predator:planktivore ratio, which is assumed to decline with increasing fishing pressure exerted on a system, and is here obscured by planktivores being aggregated under the general size-structured reef fish groups.

While comparison with other models can be useful, such an exercise needs to ensure that survey methods, general system characteristics (e.g., shallow coastal vs. pelagic) and functional groups are indeed comparable. Similarly, it is important to remember that yields (t km^{-2}) were estimated as input into the model and, as such, weight of the catch was divided by total model area. Comparison with catch data from other areas need to take this into account.

Developing a quantitative model of a marine ecosystem is, by its very nature, associated with a number of uncertainties. Different procedures to evaluate and refine model structure and outputs exist and were applied after initial balancing. Uncertainties persist because of empirical data limitations, particularly with regards to fisheries. The model should continue to be refined as further data are collected to improve upon certain group's parameters and stakeholders gain greater understanding of the system's dynamics as well as provide further specific management questions they would like to see addressed. In regard to the fisheries catch dataset, while changes were made to the available data and in the balancing process to roughly calibrate the model with known resource status and observed changes, it has not been rigorously calibrated utilising the software's fitting procedure (i.e., by adjusting the vulnerabilities of predator-prey interactions to allow for maximum congruence between modelled and observed time series of biomass using time series of fishing effort to drive simulations). Fitting the model and testing it under a variety of scenarios is a key step in its validation and the evaluation of its strengths and weaknesses. In follow up studies, therefore, it would be beneficial to (i) establish a model for an earlier time step, for example early 2000s, with studies indicating that by then reefs had generally recovered from the 1998 El Nino bleaching event; (ii) use Ecosim, the simulation component of the Ecopath with Ecosim software which uses Ecopath's results as input parameters, to fit the model to time series data of fish biomass and/or catch data to ensure the model is able to replicate observed trends and lend greater confidence to projections ; and (iii) evaluate management scenarios such as a ban on beach seine and speargun on the ecological communities as well as a number of socio-economic factors. These next steps are outside of the scope of the present project, but the model is still valuable to consider qualitatively for management considerations and policy-making decisions.

Thus, we recognize that further discussion with relevant experts and further data collection/validation should be conducted to fill knowledge gaps, increase parameter reliability, thereby increasing model accuracy. Nevertheless, based on the data currently available, our model represents the best approximation of an integrated understanding of the Nyali-Mombasa coastal ecosystem in 2013.

Indicators

Community and ecosystem indicators look at energy flows and ecosystem functioning, and are not readily measurable from field studies. Total throughput, production and internal state indices (i.e., Finn's cycling index, mean path length) reflect a system's ability to support its current state and level of exploitation in the long term (Vasconcellos et al. 1997). According to the statistics evaluating a system's stability and maturity (Odum 1969), fishing mortality plays an important role in the structure and functioning of the coral reef ecosystem at Nyali-Mombasa. There are also other human pressures impinging on the coral reef ecosystem in the study area. Given the high and increasing population density of Mombasa, the number of existing and planned developments along the coast, mostly for tourism, other stressors such as sedimentation, nitrification due to lack of or poorly treated effluents, and other land-based sources of pollution, are also on the rise. For example, Uku (2005) found bacterial epiphytes on *T. ciliatum* and *Thalassia hemprichii* in Nyali, that are characteristic of waste water, particularly from livestock farming areas, thus confirming seepage of groundwater from surrounding catchment areas into the local seagrass bed. While the measured nitrate levels at Nyali were higher than those recorded at a low nutrient site in Kenya, or those of average water column estimates worldwide, the residence time of those nutrients was low due to tidal variations (Uku 2005), thereby probably limiting their impact. While such nutrient loading certainly contributes to higher primary production rates and the dominance of higher turnover species in the system, based on available data, the relative contribution of these different factors cannot be elucidated at this time.

The low mean trophic level of the catch clearly underlines the current importance of herbivores in local catches, especially small parrotfish and rabbitfish. While these groups make up a considerable proportion of total catches, lethrinids, snappers and other large-bodied fish used to be caught in greater numbers across all gears (Kaunda-Arara et al. 2003, McClanahan et al. 2008, Samoilys et al. 2017). The rise in the proportion of small parrotfish and rabbitfish in catches are indicative of the intense fishing pressure that has been applied to the system, and also seem to underline these groups capacity to tolerate intense levels of fishing (Hicks and McClanahan 2012), lending the system "resilience". The system's overhead (68.56%) supports this notion. The system's ability to sustain high levels of fishing pressure is likely also largely supported by production from the protected area. These findings corroborate the results from a study conducted in Tanzania, for example, on a fishery specifically targeting blackspot snapper, which clearly showed that a protected area plays a vital role in sustaining the fishery on Mafia Island (Kamukuru et al. 2005). While incursions by predators into the fished areas may yield higher mortalities of some species, such behaviour may also help control urchin densities for example. Moreover, during such incursions fish may also contribute to catch levels.

The indicators targeting community energetics and cycling of nutrients, such as the ratio between total primary production (PP) and total respiration (R) (Odum 1969, Christensen 1995), primary production/biomass ratio (PP/B) both suggested that the system is at a relatively low level of development. This finding was corroborated by the low Finn's cycling index, showing that only a small fraction of the throughput (including detritus) gets recycled (6%).

CONCLUSION

By developing an ecological model, the work presented herein sought to represent a holistic perspective of ecosystem dynamics and fluxes at Nyali-Mombasa. Findings show that the system is mainly driven by bottom-up processes, with most biomass and energy flows encompassed within the lowest two trophic levels. The high proportion of parrotfish and rabbitfish, for both biomass and landings, underscores the importance of these groups as key conduits for the transfer of energy between primary producers and predatory consumers, thereby shaping community structure and ecosystem processes. They also underscore the importance of seagrass beds to reef fisheries at Nyali-Mombasa.

By running different scenarios, such a model would be useful for the evaluation of ecosystem-level impacts of various disturbances or management decisions, including an effective ban of beach seine and speargun use, and to explore the likely socio-economic impacts on fishers and their dependents of such interventions. The latter is particularly relevant given that poverty is pervasive among the local fishing communities, and management, therefore, requires the creation of inexpensive institutional interventions with the least likelihood of jeopardizing essential livelihoods. While models are intrinsically simplistic and present an averaged response, we hope that the model developed here may prove a useful tool to evaluate the possible impact of management decisions and contextualize these to assist policy makers in the future.

REFERENCES

Abolmasova, G. 1985. Energy metabolism and food requirements in captive squid Sthenoteuthis oualaniensis (Lesson) from the Indian Ocean. Ecologiya morya **19**:104-110.

Acosta, C. A., and M. J. Butler. 1997. Role of mangrove habitat as a nursery for juvenile spiny lobster, Panulirus argus, in Belize. Marine and Freshwater Research **48**:721-727.

Acosta, L. A., and B. A. Wintle. 2016. Using scenarios and models to inform decision making in policy design and implementation. Pages 37-80 *in* S. Ferrier, K. N. Ninan, P. Leadley, R. Alkemade, L. A. Acosta, H. R. Akçakaya, L. Brotons, W. W. L. Cheung, V. Christensen, K. A. Harhash, J. Kabubo-Mariara, C. Lundquist, M. Obersteiner, H. M. Pereira, G. Peterson, R. Pichs-Madruga, N. Ravindranath, C. Rondinini, and B. A. Wintle, editors. Methodological assessment of scenarios and models of biodiversity and ecosystem services. Secretariat of the Intergovernmental Platform for Biodiversity and Ecosystem Services, Bonn, Germany.

Adams, A. J., C. P. Dahlgren, G. T. Kellison, M. S. Kendall, C. A. Layman, J. A. Ley, I. Nagelkerken, and J. E. Serafy. 2006. Nursery function of tropical back-reef systems. Marine Ecology Progress Series **318**:287-301.

Ainsworth, C., D. Varkey, and T. Pitcher. 2007. Ecosystem simulation models for the Bird's Head Seascape, Papua, fitted to field data. Pages 1-174 *in* T. J. Pitcher, C. Ainsworth, and M. Bailey, editors. Ecological and economic analyses of marine ecosystems in the Bird's Head Seascape, Paupa, Indonesia: I. Fisheries Centre Research Report. Volume 15 Number 5.

Alcoverro, T., and S. Mariani. 2000. Effects of sea urchin grazing over a Kenyan mixed seagrass bed. Biologia Marina Mediterranea 7:195-198.

Alcoverro, T., and S. Mariani. 2002. The effects of the sea urchin grazing on the Thalassodendron ciliatum seagrass beds of a Kenyan lagoon. Marine Ecology Progress Series **226**:255-263.

Alcoverro, T., and S. Mariani. 2004. Patterns of fish and sea urchin grazing on tropical Indo-Pacific seagrass beds. Ecography **27**:361-365.

Aliño, P. M., L. T. McManus, J. W. McManus, C. L. Nañola, M. D. Fortes, G. C. Trono, and G. S. Jacinto. 1993. Initial parameter estimations of a coral reef flat ecosystem in Bolinao, Pagasinan, Northwestern Philippines. Pages 252-258 *in* Trophic Models of Aquatic Ecosystems. V. Christensen and D. Pauly (eds.) ICLARM Conference Proceedings.

Alldredge, A. L., and J. M. King. 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Marine Biology **41**:317-333.

Alldredge, A. L., and J. M. King. 2009. Near-surface enrichment of zooplankton over a shallow back reef: implications for coral reef food webs. Coral Reefs **28**:895-908.

Almeida, A. J., A. Marques, and L. Saldanha. 1999. Some aspects of the biology of three fish species from the seagrass beds at Inhaca Island, Mozambique. Cybium **23**:369-376.

Amorocho, D. F., and R. D. Reina. 2008. Intake passage time, digesta composition and digestibility in East Pacific green turtles (Chelonia mydas agassizii) at Gorgona National Park, Colombian Pacific. Journal of Experimental Marine Biology and Ecology **360**:117-124.

Anam, R., and E. Mostarda. 2012. Field identification guide to the living marine resources of Kenya. FAO Species Identification Guide for Fishery Purposes., FAO, Rome, Italy.

Anon. Knowledge integration and Management Strategy Evaluation modelling. https://www.alces.ca/files/KimberleyMSE/EwE.htm.

Anon. 2014. Medical file: jellyfish stings need the right care, immediately. http://kenyakidz.com/index.php?option=com_content&view=article&id=513:medical-file-jellyfish-stings-need-the-right-care-immediately&catid=17:health&Itemid=232

Anon. 2015. Uwezo fish shop: Operational manual for fish.

Anthony, K.R.N., S. R. Connolly, and B. L. Willis. 2002. Comparative analysis of energy allocation to tissue and skeletal growth in corals. Limnology and Oceanography **47**:1417-1429.

Anthony, K. R. N., and K. E. Fabricius. 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. Journal of Experimental Marine Biology and Ecology **252**:221-253.

Anthony, K. R. N. 1999. Coral suspension feeding on fine particulate matter. Journal of Experimental Marine Biology and Ecology **232**:85-106.

Arias-González, J. E. 1998. Trophic models of semi-protected and unprotected coral reef ecosystems in the South of the Mexican Caribbean. Journal of Fish Biology **53**:236-255.

Arias-González, J. E., B. Delesalle, B. Salvat, and R. Galzin. 1997. Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. Coral Reefs **16**:231-246.

Arreguín-Sánchez, F., J. Seijo, and E. Valero-Pacheco. 1993. An application of ECOPATH II to the north continental shelf ecosystem of Yucatan, Mexico. Pages 269-278 *in* Trophic models of aquatic ecosystems. ICLARM Conference Proceedings.

Atkinson, M. J., and R. W. Grigg. 1984. Model of a coral reef ecosystem. II. Gross and net benthic primary production at French Frigate Shoals, Hawaii. Coral Reefs **3**:13-22.

Babcock, R. C. 1991. Comparative demography of 3 species of scleractinian corals using age-dependent and size-dependent classifications. Ecological Monographs **61**:225-244.

Baguette, M., S. Blanchet, D. Legrand, V. M. Stevens, and C. Turlure. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews **88**:310-326.

Bak, R. P., and G. van Eys. 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia **20**:111-115.

Bandeira, S. O. 1997. Dynamics, biomass and total rhizome length of the seagrass Thalassodendron ciliatum at Inhaca Island, Mozambique. Plant Ecology **130**:133-141.

Bandeira, S. O. 2002. Leaf production rates of Thalassodendron ciliatum from rocky and sandy habitats. Aquatic Botany **72**:13-24.

Barbosa, A. B., H. M. Galvao, P. A. Mendes, X. A. Alvarez-Salgado, F. G. Figueiras, and I. Joint. 2001. Short-term variability of heterotrophic bacterioplankton during upwelling off the NW Iberian margin. Progress In Oceanography **51**:339-359.

Barnes-Mauthe, M., K. L. L. Oleson, and B. Zafindrasilivonona. 2013. The total economic value of small-scale fisheries with a characterization of post-landing trends: An application in Madagascar with global relevance. Fisheries Research **147**:175-185.

Barnes, R. S. K., and R. N. Hughes. 2009. An introduction to marine ecology. John Wiley & Sons.

Bayley, P. B., and R. A. Herendeen. 2000. The Efficiency of a Seine Net. Transactions of the American Fisheries Society **129**:901-923.

Berkström, C., M. Gullström, R. Lindborg, A. W. Mwandya, S. A. S. Yahya, N. Kautsky, and M. Nyström. 2012. Exploring 'knowns' and 'unknowns' in tropical seascape connectivity with insights from East African coral reefs. Estuarine, Coastal and Shelf Science **107**:1-21.

Berkström, C., T. L. Jörgensen, and M. Hellström. 2013a. Ecological connectivity and niche differentiation between two closely related fish species in the mangrove-seagrass-coral reef continuum. Marine Ecology Progress Series **477**:201-215.

Berkström, C., R. Lindborg, M. Thyresson, and M. Gullström. 2013b. Assessing connectivity in a tropical embayment: Fish migrations and seascape ecology. Biological Conservation **166**:43-53.

Berry, P., and M. Smale. 1980. An estimate of production and consumption rates in the spiny lobster Panulirus homarus on a shallow littoral reef off the Natal Coast, South Africa. Marine Ecology Progress Series **2**:337-343.

Bienfang, P., and W. Johnson. 1980. Planktonic properties of Honokōhau harbor: A nutrient enriched subtropical embayment. Pacific Science **34**:293-300.

Bjorndal, K. A. 1980. Nutrition and grazing behavior of the green turtle Chelonia mydas. Marine Biology **56**:147-154.

Bjorndal, K. A., A. B. Bolten, and M. Y. Chaloupka. 2003. Survival probability estimates for immature green turtles Chelonia mydas in the Bahamas. Marine Ecology Progress Series **252**:273-281.

Blaber, S. J. M., D. T. Brewer, J. P. Salini, and J. Kerr. 1990. Biomasses, catch rates and abundances of demersal fishes, particularly predators of prawns, in a tropical bay in the Gulf of Carpentaria, Australia. Marine Biology **107**:397-408.

Black, R., C. Codd, D. Hebbert, S. Vink, and J. Burt. 1984. The functional significance of the relative size of Aristotle's lantern in the sea urchin *Echinometra mathaei* (de Blanville). Journal of Experimental Biology and Ecology 77:81-97.

Bosire, J. O., G. Okemwa, and J. Ochiewo. 2012. Mangrove linkages to coral reef and seagrass ecosystem services in Mombasa and Takaungu, Kenya -- Participatory Modelling Frameworks to Understand Wellbeing Trade-offs in Coastal Ecosystem Services: Mangrove sub-component. Kenya Marine and Fisheries Research Institute (KMFRI) for Ecosystem Services for Poverty Alleviation (ESPA). Mombasa, Kenya.

Bozec, Y.-M., D. Gascuel, and M. Kulbicki. 2004. Trophic model of lagoonal communities in a large open atoll (Uvea, Loyalty islands, New Caledonia). Aquatic Living Resources **17**:151-162.

Branch, G., C. L. Griffiths, M. L. Branch, and L. E. Beckley. 2008. Two oceans: A guide to the marine life of southern Africa. Struik.

Brey, T. 1999. Growth performance and mortality in aquatic benthic invertebrates. Advances in Marine Biology **35**:153-223.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2.

Brey, T. 2004. Empirical relations in aquatic populations.*in* T. Brey, editor. Population dynamics in benthic invertebrates. A virtual handbook. Alfred Wegener Institute, Bremerhaven. Availableat: www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html.

Briggs, P. 2013. DK eyewitness travel guide: Kenya. Penguin publishers.

Briggs, P., and S. Connolly. 2014. Mozambique. Bradt Travel Guides.

Bronstein, O., and Y. Loya. 2014. Echinoid community structure and rates of herbivory and bioerosion on exposed and sheltered reefs. Journal of Experimental Marine Biology and Ecology **456**:8-17.

Brouns, J. J. W. M. 1985. A preliminary study of the seagrass Thalassodendron ciliatum (Forssk.) den hartog from Eastern Indonesia. Biological results of the snellius II expedition. Aquatic Botany **23**:249-260.

Bruce, R. W., and J. E. Randall. 1985. A revision of the Indo-West Pacific parrotfish genera Calotomus and Leptoscarus (Scaridae: Sparisomatinae). . Indo-Pacific Fishes **5**:32.

Bruckner, A. W., K. A. Johnson, and J. D. Field. 2003. Conservation strategies for sea cucumbers: can a CITES Appendix II listing promote sustainable international trade? SPC Beche-de-mer Information Bulletin **18**:24-33.

Bryceson, I. 1982. Seasonality of oceanographic conditions and phytoplankton in Dar es Salaam waters. University Science Journal **8**:66-76.

Buchan, P. R., and M. J. Smale. 1981. Estimates of biomass, consumption and production of *Octopus vulgaris* Cuvier off the east coast of South Africa. Oceanographic Research Institute, Investigational Report, 50.

Buchary, E., T. Pitcher, W. Cheung, and T. Hutton. 2002. New ecopath models of the Hong Kong marine ecosystem. Pages 6-16 Spatial Simulations of Hong Kong's Marine Ecosystem. Fisheries Centre Research Reports.

Bundy, A., R. Chuenpagdee, J. L. Boldt, M. de Fatima Borges, M. L. Camara, M. Coll, I. Diallo, C. Fox, E. A. Fulton, A. Gazihan, A. Jarre, D. Jouffre, K. M. Kleisner, B. Knight, J. Link, P. P. Matiku, H. Masski, D. K. Moutopoulos, C. Piroddi, T. Raid, I. Sobrino, J. Tam, D. Thiao, M. A. Torres, K. Tsagarakis, G. I. van der Meeren, and Y.-J. Shin. 2016. Strong fisheries management and governance positively impact ecosystem status. Fish and Fisheries:n/a-n/a.

Burke, J. S., W. J. Kenworthy, and L. L. Wood. 2009. Ontogenetic patterns of concentration indicate lagoon nurseries are essential to common grunts stocks in a Puerto Rican bay. Estuarine, Coastal and Shelf Science **81**:533-543.

Butler, M., A. Cockcroft, A. MacDiarmid, and R. Wahle. 2011. Panulirus argus. The IUCN Red List of Threatened Species 2011: e.T169976A6697254. http://dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T169976A6697254.en. .

Cammen, L. M. 1980. Ingestion Rate: An Empirical Model for Aquatic Deposit Feeders and Detritivores. Oecologia **44**:303-310.

Campbell, A. C., J. K. G. Dart, S. M. Head, and R. F. G. Ormond. 1973. The feeding activity of Echinostrephus molaris (de Blainville) in the central Red Sea. Marine Behaviour and Physiology **2**:155-169.

Campbell, C. L., and C. J. Lagueux. 2005. Survival probability estimates for large juvenile and adult green turtles (*Chelonia mydas*) exposed to an artisanal marine turtle fishery in the Western Caribbean. Herpetologica **61**:91-103.

Carlos, M. D., M. MartÃƒÂ-n, S. R. A. Nona, U. Janet, D. F. Miguel, E. G. Margarita, M. Â. NÃƒÂ¹ria, and A. H. Marten. 1998. Root production and belowground seagrass biomass. Marine Ecology Progress Series **171**:97-108.

Carpenter, K. E., and A. C. Alcala. 1977. Philippine coral reef fisheries resources. Part II. Muro-ami and kayaks reef fisheries, benefit or bane? Philippine Journal of Fisheries **15**:217-235.

Carpenter, R. C., J. M. Hackney, and W. H. Adey. 1991. Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnology and Oceanography **36**:40-49.

Carreiro-Silva, M., and T. R. McClanahan. 2001. Echinoid bioerosion and herbivory on Kenyan coral reefs: the role of protection from fishing. Journal of Experimental Marine Biology and Ecology **262**:133-153.

Chadwick-Furman, N. E., S. Goffredo, and Y. Loya. 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. Journal of Experimental Marine Biology and Ecology **249**:199-218.

Chagaris, D. D., B. Mahmoudi, C. J. Walters, and M. S. Allen. 2015. Simulating the Trophic Impacts of Fishery Policy Options on the West Florida Shelf Using Ecopath with Ecosim. Marine and Coastal Fisheries **7**:44-58.

Charpy, L., and J. Blanchot. 1998. Photosynthetic picoplankton in French Polynesian atoll lagoons: estimation of taxa contribution to biomass and production by flow cytometry. Marine Ecology Progress Series **162**:57-70.

Christensen, V. 1995. Ecosystem maturity - towards quantification. Ecological Modelling **77**:3-32.

Christensen, V., M. Coll, C. Piroddi, J. Steenbeek, J. Buszowski, and D. Pauly. 2014. A century of fish biomass decline in the ocean. Marine Ecology Progress Series **512**:155-166.

Christensen, V., and D. Pauly. 1992. ECOPATH II - A software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling **61**:169-185.

Christensen, V., and D. Pauly. 1993. Flow characteristics of aquatic ecosystems. Pages 338-352 *in* V. Christensen and D. Pauly, editors. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings 26, 390.

Christensen, V., and D. Pauly. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecological Applications **8**:S104-S109.

Christensen, V., and C. Walters. 2004. Ecopath with Ecosim: Methods, capabilities and limitations. Ecological Modelling **72**:109-139.

Christensen, V., C. J. Walters, and D. Pauly. 2005. Ecopath with Ecosim: A user's guide. Fisheries Centre, University of British Columbia, Vancouver (BC), Canada.

Christensen, V., C. J. Walters, D. Pauly, and R. Forrest. 2008. Ecopath with Ecosim version 6 -User Guide. Fisheries Centre, Vancouver (B.C.), Canada.

Church, J., and D. Obura. 2006. Sustaining coral reef ecosystems and their fisheries in the Kiunga Marine National Reserve, Lamu, Kenya. Pages 1381-1390 *in* Proceedings of the 10th International Coral Reef Symposium. Japanese Coral Reef Society Tokyo, Japan.

Cinner, J. E. 2010. Poverty and the use of destructive fishing gear near east African marine protected areas. Environmental Conservation **36**:321-326.

Cinner, J. E. 2011. Social-ecological traps in reef fisheries. Global Environmental Change **21**:835-839.

Cinner, J. E., C. Folke, T. Daw, and C. C. Hicks. 2011. Responding to change: Using scenarios to understand how socioeconomic factors may influence amplifying or dampening exploitation feedbacks among Tanzanian fishers. Global Environmental Change **21**:7-12.

Cinner, J. E., T. R. McClanahan, N. A. J. Graham, M. S. Pratchett, S. K. Wilson, and J.-B. Raina. 2009. Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. Journal of Applied Ecology **46**:724-732.

Clyde, F. E. R., M. J. Sweeney, and C. E. Nauen. 1984. FAO species catalogue. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis No. 125, Volume 3, Rome, Italy.

Cocheret de la Moriniere, E., B. J. A. Pollux, I. Nagelkerken, and G. van der Velde. 2002. Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. Estuarine Coastal and Shelf Science **55**:309-321.

Coll, M., E. Akoglu, F. Arreguín-Sánchez, E. A. Fulton, D. Gascuel, J. J. Heymans, S. Libralato, S. Mackinson, I. Palomera, C. Piroddi, L. J. Shannon, J. Steenbeek, S. Villasante, and V. Christensen. 2015. Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. Reviews in Fish Biology and Fisheries **25**:413-424.

Coll, M., L. J. Shannon, K. M. Kleisner, M. J. Juan-Jordá, A. Bundy, A. G. Akoglu, D. Banaru, J. L. Boldt, M. F. Borges, A. Cook, I. Diallo, C. Fu, C. Fox, D. Gascuel, L. J. Gurney, T. Hattab, J. J. Heymans, D. Jouffre, B. R. Knight, S. Kucukavsar, S. I. Large, C. Lynam, A. Machias, K. N. Marshall, H. Masski, H. Ojaveer, C. Piroddi, J. Tam, D. Thiao, M. Thiaw, M. A. Torres, M. Travers-Trolet, K. Tsagarakis, I. Tuck, G. I. van der Meeren, D. Yemane, S. G. Zador, and Y. J. Shin. 2016. Ecological indicators to capture the effects of fishing on biodiversity and conservation status of marine ecosystems. Ecological Indicators **60**:947-962.

Coppejans, E., H. Beeckman, and M. De Wit. 1992. The seagrass and associated macroalgal vegetation of Gazi Bay (Kenya). Hydrobiologia **247**:59-75.

Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science: Journal du Conseil **56**:707-717.

Crossland, C. J., B. G. Hatcher, and S. V. Smith. 1991. Role of coral reefs in global ocean production. Coral Reefs **10**:55-64.

Cullen-Unsworth, L. C., L. M. Nordlund, J. Paddock, S. Baker, L. J. McKenzie, and R. K. F. Unsworth. 2014. Seagrass meadows globally as a coupled social–ecological system: Implications for human wellbeing. Marine Pollution Bulletin **83**:387-397.

Cury, P. M., Y.-J. Shin, B. Planque, J. M. Durant, J.-M. Fromentin, S. Kramer-Schadt, N. C. Stenseth, M. Travers, and V. Grimm. 2008. Ecosystem oceanography for global change in fisheries. Trends in Ecology & Evolution **23**:338-346.

Cushing, D. H. 1976. In praise of Petersen. ICES Journal of Marine Science **36**:277-281.

Davies, T., N. Beanjara, and T. Tregenza. 2009. A socio-economic perspective on gear-based management in an artisanal fishery in south-west Madagascar. Fisheries Management and Ecology **16**:279-289.

Daw, T. M., S. Coulthard, W. W. L. Cheung, K. Brown, C. Abunge, D. Galafassi, G. D. Peterson, T. R. McClanahan, J. O. Omukoto, and L. Munyi. 2015. Evaluating taboo trade-offs in ecosystems services and human well-being. Proceedings of the National Academy of Sciences of the United States of America **112**:6949-6954.

de Boer, W. F. 2007. Seagrass-sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. Hydrobiologia **591**:5-24.

de la Torre-Castro, M., M. Björk, J. Eklöf, and P. Rönnbäck. 2008. Seagrass importance in food provisioning services: fish stomach content as a link between seagrass meadows and local fisheries. Western Indian Ocean Journal of Marine Science 7:95-110.

de la Torre-Castro, M., G. Di Carlo, and N. S. Jiddawi. 2014. Seagrass importance for a small-scale fishery in the tropics: The need for seascape management. Marine Pollution Bulletin **83**:398-407.

de la Torre-Castro, M., and P. Rönnbäck. 2004. Links between humans and seagrasses—an example from tropical East Africa. Ocean & Coastal Management **47**:361-387.

de Loma, T. L., C. Conand, M. Harmelin-Vivien, and E. Ballesteros. 2002. Food selectivity of Tripneustes gratilla (L.) (Echinodermata: Echinoidea) in oligotrophic and nutrient-enriched coral reefs at La Réunion (Indian Ocean). Bulletin of Marine Science **70**:927-938.

De Ridder, C., and J. M. Lawrence. 1982. Food and feeding mechanisms: Echinoidea. Pages 499-519 *in* M. Jangoux and J. M. Lawrence, editors. Echinoderm nutrition. CRC Press, Rotterdam, The Netherlands.

De Troch, M., S. Gurdebeke, F. Fiers, and M. Vincx. 2001. Zonation and structuring factors of meiofauna communities in a tropical seagrass bed (Gazi Bay, Kenya). Journal of Sea Research **45**:45-61.

De Troch, M., J. Mees, and E. Wakwabi. 1998. Diets of abundant fishes from beach seine catches in seagrass beds of a tropical bay (Gazi Bay, Kenya). Belgian Journal of Zoology **128**:135-154.

Department of Fisheries. 2012. Marine water fisheries frame survey 2012 report. Ministry of Fisheries Development.

Dorenbosch, M., M. G. G. Grol, M. J. A. Christianen, I. Nagelkerken, and G. van der Velde. 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density coral and diversity on adjacent reefs. Marine Ecology Progress Series **302**:63-76.

Dorenbosch, M., M. C. van Riel, I. Nagelkerken, and G. van der Velde. 2004a. The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. Estuarine Coastal and Shelf Science **60**:37-48.

Dorenbosch, M., M. C. Verweij, I. Nagelkerken, N. Jiddawi, and G. van der Velde. 2004b. Homing and daytime tidal movements of juvenile snappers (Lutjanidae) between shallow-water nursery habitats in Zanzibar, western Indian Ocean. Environmental Biology of Fishes **70**:203-209.

Drummond, A. 1993. Studies on the biology of three species of sea urchin on the South African East Coast. University of Natal, Pietermaritzburg, South Africa.

Duarte, C. M. 1990. Seagrass Nutrient Content. Marine Ecology Progress Series **67**:201-207.

Dubinsky, Z., and P. L. Jokiel. 1994. Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. Pacific Science **48**:313-324.

Duineveld, G. C. A., P. A. W. J. De Wilde, E. M. Berghuis, A. Kok, T. Tahey, and J. Kromkamp. 1997. Benthic respiration and standing stock on two contrasting continental margins in the western Indian Ocean: the Yemen-Somali upwelling region and the margin off Kenya. Deep Sea Research Part II: Topical Studies in Oceanography **44**:1293-1317.

Duing, W. 1970. The monsoon regime of the currents in the Indian Ocean. DTIC Document.

Ebert, T. A. 1975. Growth and mortality of post-larval echinoids. American Zoologist **15**:755-775.

Ebert, T. A. 1978. Growth and size of the tropical sea cucumber Holothuria (Halodeima) atra Jager at Enewetak Atoll, Marshall Islands. Pacific Science **32**:183-191.

Ebert, T. A. 1982. Longevity, Life History, and Relative Body Wall Size in Sea Urchins. Ecological Monographs **52**:353-394.

Edmunds, P. J., and R. C. Carpenter. 2001. Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proceedings of the National Academy of Sciences **98**:5067-5071.

Ferrier-Pagès, C., J. Witting, E. Tambutté, and K. P. Sebens. 2003. Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral Stylophora pistillata. Coral Reefs **22**:229-240.

Ferrier-Pagès, C., and J.-P. Gattuso. 1998. Biomass, Production and Grazing Rates of Pico- and Nanoplankton in Coral Reef Waters (Miyako Island, Japan). Microbial Ecology **35**:46-57.

Field, J. G., F. Wulff, and K. H. Mann. 1989. The need to analyze ecological networks. Pages 3-12 Network analysis in marine ecology. Springer.

Finn, J. T. 1976. Measures of ecosystem structure and function derived from analysis of flows. Journal of Theroretical Biology **56**:363-380.

Fiorito, G., and F. Gherardi. 1999. Prey-handling behaviour of Octopus vulgaris (Mollusca, Cephalopoda) on Bivalve preys. Behavioural Processes **46**:75-88.

Fitt, W. K., F. K. McFarland, M. E. Warner, and G. C. Chilcoat. 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnology and Oceanography **45**:677-685.

Fourqurean, J. W., and J. E. Schrlau. 2003. Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. Chemistry and Ecology **19**:373-390.

Frazier, J. 1975. Marine turtles of the Western Indian Ocean. Oryx **13**:164-175.

Fulton, E. A. 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems **81**:171-183.

Fulton, E. A., J. S. Link, I. C. Kaplan, M. Savina-Rolland, P. Johnson, C. Ainsworth, P. Horne, R. Gorton, R. J. Gamble, A. D. M. Smith, and D. C. Smith. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries **12**:171-188.

Fulton, E. A., A. Smith, and A. E. Punt. 2005a. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science **62**:540-551.

Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2003. Effect of complexity on marine ecosystem models. Marine Ecology Progress Series **253**:1-16.

Fulton, E. A., A. D. M. Smith, and A. E. Punt. 2005b. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science: Journal du Conseil **62**:540-551.

Furnas, M. J., A. W. Mitchell, M. Gilmartin, and N. Revelante. 1990. Phytoplankton biomass and primary production in semienclosed reef lagoons of the central Great-Barrier-Reef, Australia. Coral Reefs **9**:1-10.

Gasalla, M., and C. Rossi-Wongtschowski. 2004. Contribution of ecosystem analysis to investigating the effects of changes in fishing strategies in the South Brazil Bight coastal ecosystem. Ecological Modelling **172**:283-306.

Gasol, J. M., P. A. del Giorgio, and C. M. Duarte. 1997. Biomass distribution in marine planktonic communities. Limnology and Oceanography **42**:1353-1363.

Gell, F. R., and M. W. Whittington. 2002. Diversity of fishes in seagrass beds in the Quirimba Archipelago, northern Mozambique. Marine and Freshwater Research **53**:115-121.

Giménez, F. A., and B. G. García. 2002. Growth and food intake models in Octopus vulgaris Cuvier (1797): influence of body weight, temperature, sex and diet. Aquaculture International **10**:361-377.

Glaesel, H. 1997. Fishers, Parks and Power: The socio-environmental dimensions of marine resource decline and protection on the Kenya Coast. Ph.D. thesis. University of Wisconsin, Madison.

Glaesel, H. 2000. State and Local Resistance to the Expansion of Two Environmentally Harmful Marine Fishing Techniques in Kenya. Society & Natural Resources **13**:321-338.

Glynn, P. W. 1988. El Nifio warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. Galaxea **7**:129-160.

Glynn, P. W., and D. P. Manzello. 2015. Bioerosion and coral reef growth: a dynamic balance. Pages 67-97 *in* C. Birkeland, editor. Coral Reefs in the Anthropocene. Springer.

Godinot, C., F. Houlbrèque, R. Grover, and C. Ferrier-Pagès. 2011. Coral Uptake of Inorganic Phosphorus and Nitrogen Negatively Affected by Simultaneous Changes in Temperature and pH. PloS One **6**:e25024.

Goecker, M. E., K. L. Heck, and J. F. Valentine. 2005. Effects of nitrogen concentrations in turtlegrass *Thalassia testudinum* on consumption by the bucktooth parrotfish *Sparisoma radians*. Marine Ecology Progress Series **286**:239-248.

Goffredo, S., and N. E. Chadwick-Furman. 2003. Comparative demography of mushroom corals (Scleractinia : Fungiidae) at Eilat, northern Red Sea. Marine Biology **142**:411-418.

Goreau, T. F., N. I. Goreau, and C. M. Yonge. 1971. Reef corals: autotrophs or heterotrophs? The Biological Bulletin **141**:247-260.

Gratwicke, B., C. Petrovic, and M. R. Speight. 2006. Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. Environmental Biology of Fishes **76**:191-210.

Guard, M. 2003. Assessment of the artisanal fishery of Octopus cyanea Gray, 1929 in Tanzania: Catch dynamics, fisheries biology, socio-economics and implications for management. University of Aberdeen, Scotland.

Guard, M. 2009. Biology and fisheries status of octopus in the Western Indian Ocean and the suitability for marine stewardship council certification. United Nations Environmental Programme.

Guard, M., and Y. D. Mgaya. 2002. The artisanal fishery for *Octopus cyanea* Gray in Tanzania. AMBIO:528-536.

Guénette, S., and R. L. Hill. 2009. A trophic model of the coral reef ecosystem of La Parguera, Puerto Rico: synthesizing fisheries and ecological data. Caribbean Journal of Science **45**:317-337.

Guerra, A. 1979. Edad y crecimiento de *Octopus vulgaris* del Atlantico centro-oriental (26°10'N-23°30'N) Committee for the Eastern Central Atlantic Fisheries Series **78**:113-126.

Gullström, M., C. Berkström, M. C. Öhman, M. Bodin, and M. Dahlberg. 2011. Scale-dependent patterns of variability of a grazing parrotfish (Leptoscarus vaigiensis) in a tropical seagrass-dominated seascape. Marine Biology **158**:1483-1495.

Gullström, M., M. Bodin, P. G. Nilsson, and M. C. Ohman. 2008. Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. Marine Ecology-Progress Series **363**:241-255.

Gullström, M., M. de la Torre Castro, S. O. Bandeira, M. Björk, M. Dahlberg, N. Kautsky, P. Rönnbäck, and M. C. Öhman. 2002. Seagrass Ecosystems in the Western Indian Ocean. AMBIO: A Journal of the Human Environment **31**:588-596.

Gwada, P. 2004. An assessment of seagrass survival and functioning in response to manipulations in sediment redox at Nyali Lagoon, Kenya., Report submitted to WIOMSA.

Hahn, P. K. J., R. E. Bailey, and A. Ritchie. 2007. Beach seining. Pages 267-323 *in* D. H. Johnson, B. M. Shrier, J. S. ONeal, J. A. Knutzen, X. Augerot, T. A. ONeil, and T. N. Pearsons, editors. Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. . American Fisheries Society, Bethesda, Maryland.

Halpern, B. S., C. Longo, D. Hardy, K. L. McLeod, J. F. Samhouri, S. K. Katona, K. Kleisner, S. E. Lester, J. O/'Leary, M. Ranelletti, A. A. Rosenberg, C. Scarborough, E. R. Selig, B. D. Best, D. R. Brumbaugh, F. S. Chapin, L. B. Crowder, K. L. Daly, S. C. Doney, C. Elfes, M. J. Fogarty, S. D. Gaines, K. I. Jacobsen, L. B. Karrer, H. M. Leslie, E. Neeley, D. Pauly, S. Polasky, B. Ris, K. St Martin, G. S. Stone, U. R. Sumaila, and D. Zeller. 2012. An index to assess the health and benefits of the global ocean. Nature **488**:615-620.

Hamilton, H. G. H., and W. H. Brakel. 1984. Structure and coral fauna of East African reefs. Bulletin of Marine Science **34**:248-266.

Hamner, W. M., P. L. Colin, and P. P. Hamner. 2007. Export-import dynamics of zooplankton on a coral reef in Palau. Marine Ecology-Progress Series **334**:83-92.

Hanlon, R. T., and J. B. Messenger. 1996. Cephalopod Behaviour. Cambridge University Press, Cambridge, United Kingdom

Heidelberg, K. B., K. L. O'Neil, J. C. Bythell, and K. P. Sebens. 2010. Vertical distribution and diel patterns of zooplankton abundance and biomass at Conch Reef, Florida Keys (USA). Journal of PLankton Research **32**:75-91.

Heidelberg, K. B., K. P. Sebens, and J. E. Purcell. 2004. Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. Coral Reefs **23**:263-276.

Herring, P. J. 1972. Observations on the distribution and feeding habits of some littoral echinoids from Zanzibar. Journal of Natural History **6**:169-175.

Heymans, J. J. 2003. Comparing the Newfoundland southern Labrador marine ecosystem models using information theory. Pages 62-71 *in* J. J. Heymans, editor. Ecosystem models of Newfoundland and southeastern Labrador: additional information and analyses for "back to the future". Vol. 11(5). Fisheries Centre Research Reports, Vancouver (BC), Canada.

Heymans, J. J., and D. Baird. 2000. Network analysis of the northern Benguela ecosystem by means of NETWRK and ECOPATH. Ecological Modelling **131**:97-119.

Heymans, J. J., M. Coll, S. Libralato, L. Morissette, and V. Christensen. 2014. Global Patterns in Ecological Indicators of Marine Food Webs: A Modelling Approach. PloS One **9**:e95845.

Heymans, J. J., S. Guenette, and V. Christensen. 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. Ecosystems **10**:488-502.

Hicks, C. C., and T. R. McClanahan. 2012. Assessing Gear Modifications Needed to Optimize Yields in a Heavily Exploited, Multi-Species, Seagrass and Coral Reef Fishery. PloS One **7**:e36022.

Hicks, C. C., T. R. McClanahan, J. E. Cinner, and J. M. Hills. 2009. Trade-offs in values assigned to ecological goods and services associated with different coral reef management strategies. Ecology and Society.

Higgins, B. M. 2003. Sea turtle husbandry. The biology of sea turtles **2**:411-440.

Hiratsuka, Y., and T. Uehara. 2007. Feeding ecology of four species of sea urchins (genus Echinometra) in Okinawa. Bulletin of Marine Science **81**:85-100.

Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fishery Bulletin **72**:915-1031.

Hoogenboom, M., C. Rottier, S. Sikorski, and C. Ferrier-Pagès. 2015. Among-species variation in the energy budgets of reef-building corals: scaling from coral polyps to communities. The Journal of Experimental Biology **218**:3866-3877.

Houlbrèque, F., and C. Ferrier-Pagès. 2009. Heterotrophy in Tropical Scleractinian Corals. Biological Reviews **84**:1-17.

Houlbrèque, F., E. Tambutté, C. Richard, and C. Ferrier-Pagès. 2004. Importance of a micro-diet for scleractinian corals. Marine Ecology Progress Series **282**:151-160.

Humber, F., A. Harris, D. Raberinary, and M. Nadon. 2006. Seasonal closures of no-take zones to promote a sustainable fishery for *Octopus cyanea* (Gray) in Southwest Madagascar. BlueVentures Conservation Report. London, United Kingdom.

Hyndes, G. A., I. Nagelkerken, R. J. McLeod, R. M. Connolly, P. S. Lavery, and M. A. Vanderklift. 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. Biological Reviews **89**:232-254.

Igulu, M. M., I. Nagelkerken, M. Dorenbosch, M. G. G. Grol, A. R. Harborne, I. A. Kimirei, P. J. Mumby, A. D. Olds, and Y. D. Mgaya. 2015. Mangrove Habitat Use by Juvenile Reef Fish: Meta-Analysis Reveals that Tidal Regime Matters More than Biogeographic Region. PloS One **9**:e114715.

Jackson, J. R., and R. L. Noble. 1995. Selectivity of Sampling Methods for Juvenile Largemouth Bass in Assessments of Recruitment Processes. North American Journal of Fisheries Management **15**:408-418.

Japp, D. 2011. Contribution to a comprehensive review of progress made to improve Governance of the marine fisheries sector in the ESA-IO region, and identification of priority areas for actions of regional significance that could be undertaken by the IRFS Program in relation to key principles of good governance., Prepared on behalf of: AGROTEC Consortium. Report/Rapport: SF/2012/9 IRFS Kenya fisheries governance.

Jarre-Teichmann, A. 1996. Initial estimates on krill. Page 20 *in* D. Pauly and V. Christensen, editors. Mass-balance models of North-Eastern Pacific ecosystems. Fisheries Centre Research Reports. Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.

Jiddawi, N. S., and M. Ohman, C. 2002. Marine Fisheries in Tanzania. AMBIO **31**:518-527.

Jochem, F. J., F. Pollehne, and B. Zeitzschel. 1993. Productivity regime and phytoplankton size structure in the Arabian Sea. Deep Sea Research Part II: Topical Studies in Oceanography **40**:711-735.

Johnson, M. P., N. J. Frost, M. W. Mosley, M. F. Roberts, and S. J. Hawkins. 2003. The area-independent effects of habitat complexity on biodiversity vary between regions. Ecology Letters **6**:126-132.

Kamau, E. C., A. Wamukota, and N. A. Muthiga. 2009. Promotion and management of marine fisheries in Kenya. Pages 83-138 *in* G. Winter, editor. Towards sustainable fisheries law: A comparative analysis. IUCN, Gland, Switzerland in collaboration with the IUCN Environmental Law Centre, Bonn, Germany.

Kamermans, P., M. A. Hemminga, J. F. Tack, M. A. Mateo, N. Marba, M. Mtolera, J. Stapel, A. Verheyden, and T. Van Daele. 2002a. Groundwater effects on diversity and abundance of lagoonal seagrasses in Kenya and on Zanzibar Island (East Africa). Marine Ecology Progress Series **231**:75-83.

Kamermans, P., M. A. Hemminga, J. F. Tack, M. Á. Mateo, N. Marbà, M. S. P. Mtolera, J. Stapel, A. Verheyen, and T. Van Daele. 2002b. Groundwater effects on diversity and abundance of lagoonal seagrasses in Kenya and on Zanzibar Island (East Africa). Marine Ecology - Progress Series **83**:75-83.

Kamukuru, A. T., T. Hecht, and Y. D. Mgaya. 2005. Effects of exploitation on age, growth and mortality of the blackspot snapper, Lutjanus fulviflamma, at Mafia Island, Tanzania. Fisheries Management and Ecology **12**:45-55.

Kamukuru, A. T., and Y. D. Mgaya. 2004. The food and feeding habits of blackspot snapper, Lutjanus fulviflamma (Pisces: Lutjanidae) in shallow waters of Mafia Island, Tanzania. African Journal of Ecology **42**:49-58.

Kanciruk, P. 2012. Ecology of juvenile and adult Panulirudae (spiny lobsters). Pages 59-92 *in* J. S. Cobb and B. F. Phillips, editors. The biology and management of lobsters: Ecology and Management. Elsevier.

Katsanevakis, S., and G. Verriopoulos. 2006. Seasonal population dynamics of Octopus vulgaris in the eastern Mediterranean. ICES Journal of Marine Science: Journal du Conseil **63**:151-160.

Kaunda-Arara, B., and M. Ntiba. 2001. Estimation of age, growth parameters and mortality indices in Lutjanus fulviflamma (Forsskal 1775)(Pisces: Lutjanidae) from Kenyan inshore marine waters. Journal of Agriculture, Science and Technology **3**:53-63.

Kaunda-Arara, B., and M. J. Ntiba. 1997. The reproductive biology of Lutjanus fulviflamma (Forsskål,1775) (Pisces: Lutjanidae) in Kenyan inshore marine waters. Hydrobiologia **353**:153-160.

Kaunda-Arara, B., G. A. Rose, M. S. Muchiri, and R. Kaka. 2003. Long-term trends in coral reef fish yields and exploitation rates of commercial species from coastal Kenya. Western Indian Ocean Journal of Marine Science **2**:105-116.

Kay, Q. O. N. 1971. Floral structure in the marine angiosperms Cymodocea serrulata and Thalassodendron ciliatum (Cymodocea ciliata). Botanical Journal of the Linnean Society **64**:423-429.

Kimani, E., G. Mwatha, E. Wakwabi, J. Ntiba, and B. Okoth. 1996. Fishes of a shallow tropical mangrove estuary, Gazi, Kenya. Marine and Freshwater Research **47**:857-868.

Kimirei, I. A., I. Nagelkerken, B. Griffioen, C. Wagner, and Y. D. Mgaya. 2011. Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. Estuarine, Coastal and Shelf Science **92**:47-58.

King, A. 2000. Managing without institutions: The role of communication networks in governing resource access and control. University of Warwick.

Kirsch, K. D., J. F. Valentine, and K. L. Heck. 2002. Parrotfish grazing on turtlegrass *Thalassia testudinum*: Evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. Marine Ecology Progress Series **227**:71-85.

Kiteresi, L. I., E. O. Okuku, S. N. Mwangi, B. Ohowa, V. O. Wanjeri, S. Okumu, and M. Mkono. 2011. The Influence of Land Based Activities on the Phytoplankton Communities of Shimoni-Vanga system, Kenya. International Journal of Environmental Research **6**:151-162.

Kitheka, J. U., B. O. Ohowa, B. M. Mwashote, W. S. Shimbira, J. M. Mwaluma, and J. M. Kazungu. 1996. Water circulation dynamics, water column nutrients and plankton productivity in a well-flushed tropical bay in Kenya. Journal of Sea Research **35**:257-268.

Kivengea, G. M. 2014. The biology and fishery of common octopus (*Octopus vulgaris*, Cuvier 1797) in the Kenyan south coast. University of Nairobi.

Klumpp, D. D., and D. A. McKinnon. 1992. Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. Marine Ecology Progress Series **86**:77-89.

Klumpp, D. W., and A. Pulfrich. 1989. Trophic significance of herbivorous macroinvertebrates on the central Great Barrier Reef. Coral Reefs **8**:135-144.

Klumpp, D. W., J. T. Salitaespinosa, and M. D. Fortes. 1993. Feeding ecology and trophic role of sea urchins in a tropical seagrass community. Aquatic Botany **45**:205-229.

Knutzen, J., and E. Jaasund. 1979. Note on littoral algae from Mombasa, Kenya. Journal of the Eeast African Natural History Society and National Museum **168**:1-4.

Kromkamp, J., M. De Bie, N. Goosen, J. Peene, P. Van Rijswijk, J. Sinke, and G. C. A. Duinevel. 1997. Primary production by phytoplankton along the Kenyan coast during the SE monsoon and November intermonsoon 1992, and the occurrence of Trichodesmium. Deep Sea Research Part II: Topical Studies in Oceanography **44**:1195-1212.

Kruse, M., M. Taylor, C. A. Muhando, and H. Reuter. 2016. Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve. Regional Studies in Marine Science **3**:49-57.

Kuiter, R. H., and T. Tonozuka. 2001. Pictorial guide to Indonesian reef fishes. Part 2. Fusiliers - Dragonets, Caesionidae - Callionymidae. Zoonetics, Australia.

Kulmiye, A. J., and K. M. Mavuti. 2005. Growth and moulting of captive Panulirus homarus homarus in Kenya, western Indian Ocean. New Zealand Journal of Marine and Freshwater Research **39**:539-549.

Kyewalyanga, M. 2015. Phytoplankton Primary Production. Pages 213-232 in UNEP-Nairobi Convention and WIOMSA, editor. The Regional State of the Coast Report: Western Indian Ocean. UNEP and WIOMSA, Nairobi, Kenya.

Kyalo, K. B., and S. Ndegwa. 2013. Shark bycatch - small scale tuna fishery interactions along the Kenyan coast. IOTC-2013-WPEB09-13.

Kyewalyanga, M. Phytoplankton Primary Production. Western Indian Ocean:213.

Last, P. R., and J. D. Stevens. 2009. Sharks and rays of Australia. CSIRO Publishing, Australia.

Lawrence, J. M., and Y. Agatsuma. 2007. Ecology of Tripneustes. Developments in Aquaculture and Fisheries Science **37**:499-520.

Lawson, G. W. 1969. Some observations on the littoral ecology of rocky shores in East Africa (Kenya and Tanzania). Transactions of the Royal Society of South Africa **38**:329-339.

Le Borgne, R. 1982. Zooplankton production in the eastern tropical Atlantic Ocean: Net growth efficiency and P:B in terms of carbon, nitrogen, and phosphorus. Limnology and Oceanography **27**:681-698.

Le Borgne, R., M. Rodier, A. LeBouteiller, and M. Kulbicki. 1997. Plankton biomass and production in an open atoll lagoon: Uvea, New Caledonia. Journal of Experimental Marine Biology and Ecology **212**:187-210.

Limbu, S. M., and M. S. Kyewalyanga. 2015. Spatial and temporal variations in environmental variables in relation to phytoplankton composition and biomass in coral reef areas around Unguja, Zanzibar, Tanzania. SpringerPlus **4**:646.

Limpus, C. J. 2009. A biological review of Australian marine turtles. 2. Green turtle *Chelonia mydas*. Environmental Protection Agency.

Link, J. S. 2005. Translating ecosystem indicators into decision criteria. ICES Journal of Marine Science: Journal du Conseil **62**:569-576.

Link, J. S. 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL. Ecological Modelling **221**:1580-1591.

Lipcius, R. N., and D. B. Eggleston. 2008. Introduction: Ecology and Fishery Biology of Spiny Lobsters. Pages 1-41 Spiny Lobsters. Blackwell Science Ltd.

Locham, A. G., B. Kaunda-Arara, J. G. Wakibia, and S. Muya. 2015. Diet and niche breadth variation in the marbled parrotfish, Leptoscarus vaigiensis, among coral reef sites in Kenya. African Journal of Ecology **53**:560-571.

Lugendo, B., I. Nagelkerken, G. Van Der Velde, and Y. Mgaya. 2006. The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: gut content and stable isotope analyses. Journal of Fish Biology **69**:1639-1661.

Lugendo, B. R., A. Pronker, I. Cornelissen, A. de Groene, I. Nagelkerken, M. Dorenbosch, G. van der Velde, and Y. D. Mgaya. 2005. Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. Aquatic Living Resources **18**:149-158.

Lugomela, C., P. Wallberg, and T. G. Nielsen. 2001. Plankton composition and cycling of carbon during the rainy season in a tropical coastal ecosystem, Zanzibar, Tanzania. Journal of PLankton Research **23**:1121-1136.

Lugomela, C. V. 1995. Spatial and temporal dynamics of phytoplankton biomass and species composition in Chwaka Bay, Zanzibar., Report EU TS3-CT92-01I4, NIOO, Yerseke.

Macia, S., and M. P. Robinson. 2005. Effects of habitat heterogeneity in seagrass beds on grazing patterns of parrotfishes. Marine Ecology Progress Series **303**:113-121.

Maina, G. W., and M. Samoilys. 2011. Lamu lobsters – a dwindling resource. East African Wildlife Society **35**:34-35.

Maina, G. W., M. Samoilys, H. Alidina, and K. Osuka. 2013. Targeted fishing of the shoemaker spinefoot rabbitfish, Siganus sutor, on potential spawning aggregation in southern Kenya. Reef fish spawning aggregations in the Western Indian Ocean: Research for management.

Maina, J., K. Jones, C. Hicks, T. McClanahan, J. Watson, A. Tuda, and S. Andréfouët. 2015. Designing Climate-Resilient Marine Protected Area Networks by Combining Remotely Sensed Coral Reef Habitat with Coastal Multi-Use Maps. Remote Sensing **7**:15849.

Malleret King, D. 2000. A Food Security Approach to Marine Protected Area Impacts on Surrounding Fishing Communities: : the case of Kisite Marine National Park in Kenya. University of Warwick.

Malleret King, D., A. King, S. Mangubhai, J. Tunje, J. Muturi, E. Mueni, and H. On'ganda. 2003. FMSP project R8196: Understanding fisheries associated livelihoods and the constraints to their development in Kenya and Tanzania. A review of marine fisheries resources for Kenya., DFID, unpublished project report.

Mangi, S. C., and C. M. Roberts. 2006. Quantifying the environmental impacts of artisanal fishing gear on Kenya's coral reef ecosystems. Marine Pollution Bulletin **52**:1646-1660.

Mangi, S. C., and C. M. Roberts. 2007. Factors influencing fish catch levels on Kenya's coral reefs. Fisheries Management and Ecology **14**:245-253.

Mangi, S. C., C. M. Roberts, and L. D. Rodwell. 2007a. Financial Comparisons of Fishing Gear Used in Kenya's Coral Reef Lagoons. AMBIO: A Journal of the Human Environment **36**:671-676.

Mangi, S. C., C. M. Roberts, and L. D. Rodwell. 2007b. Reef fisheries management in Kenya: Preliminary approach using the driver–pressure–state–impacts–response (DPSIR) scheme of indicators. Ocean & Coastal Management **50**:463-480.

Mangold, K. 1983. Octopus vulgaris. Pages 335-364 *in* P. R. Boyle, editor. Cephalopod Life Cycles. Species Accounts. Academic Press, London, United Kingdom.

Mangold, K., and S. von Boletzky. 1973. New data on reproductive biology and growth of Octopus vulgaris. Marine Biology **19**:7-12.

Mangubhai, S., P. L. Harrison, and D. O. Obura. 2007. Patterns of coral larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya. Marine Ecology Progress Series **348**:149-159.

Marshall, N. T. 1997. Trade in sharks and shark products in Kenyan waters. Pages 31-38 *in* N. T. Marshall and R. Barnett, editors. The trade in sharks and shark products in the western Indian and southeast Atlantic oceans. TRAFFIC East/Southern Africa,Nairobi, Kenya, .

Marshall, N. T., A. H. Milledge, and P. S. Afonso. 1999. Stormy Seas for Marine Invertebrate: Trade in Sea Cucumbers, Seashells and Lobsters in Kenya,Tanzania and Mozambique. Traffic East/Southern Africa, Nairobi, Kenya.

Martinez-Estalella, N., and P. M. Alcolado. 1990. Caracteristicas de las comunidades de corales petreos de la macrolaguna del Golfo de Batabano. Pages 25-32 *in* P. M. Alcolado, editor. El bentos de la macrolaguna del Golfo de Batabano. Editorial Academia, La Havana, Cuba.

Mashaii, N., F. Rajabipour, and A. Shakouri. 2011. Feeding Habits of the Scalloped Spiny Lobstrer, Panulirus homarus (Linnaeus, 1758)(Decapoda: Palinuridae) from the South East Coast of Iran. Turkish Journal of Fisheries and Aquatic Sciences **11**.

Matsue, N., T. Daw, and L. Garrett. 2014. Women Fish Traders on the Kenyan Coast: Livelihoods, Bargaining Power, and Participation in Management. Coastal Management **42**:531-554.

Mayfield, S., E. de Beer, and G. M. Branch. 2001. Prey preference and the consumption of sea urchins and juvenile abalone by captive rock lobsters (<emph type="2">Jasus lalandii)</emph>. Marine and Freshwater Research **52**:773-780.

Mbaru, E. K. 2012. An Assessment of the Kenyan Coastal Artisanal Fishery and Implications for the Introduction of FADs. Rhodes University, Grahamstown, South Africa.

McClanahan, T., E. H. Allison, and J. E. Cinner. 2015. Managing fisheries for human and food security. Fish and Fisheries **16**:78-103.

McClanahan, T., N. Muthiga, and S. Mangi. 2001. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. Coral Reefs **19**:380-391.

McClanahan, T. R. 1988. Seasonality in East Africa's coastal waters. Marine ecology progress series. Oldendorf **44**:191-199.

McClanahan, T. R. 1995. A coral reef ecosystem fisheries model:Impacts of fishing intensity and catch selection on reef structure and processes. Ecological Modelling **80**:1-19.

McClanahan, T. R. 1998. Predation and the distribution and abundance of tropical sea urchin populations. Journal of Experimental Marine Biology and Ecology **221**:231-255.

McClanahan, T. R. 2000. Recovery of a coral reef keystone predator, Balistapus undulatus, in East African marine parks. Biological Conservation **94**:191-198.

McClanahan, T. R. 2007. Management of Area and Gear in Kenyan Coral Reefs. Pages 166-185 Fisheries Management. Blackwell Publishing Ltd.

McClanahan, T. R., and N. A. J. Graham. 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Marine Ecology Progress Series **294**:241-248.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

McClanahan, T. R., and C. C. Hicks. 2011. Changes in life history and ecological characteristics of coral reef fish catch composition with increasing fishery management. Fisheries Management and Ecology **18**:50-60.

McClanahan, T. R., C. C. Hicks, and E. S. Darling. 2008. Malthusian Overfishing and Efforts to Overcome It on Kenyan Coral Reefs. Ecological Applications **18**:1516-1529.

McClanahan, T. R., and B. KaundaArara. 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conservation Biology **10**:1187-1199.

McClanahan, T. R., and J. D. Kurtis. 1991. Population regulation of the rock-boring sea urchin Echinometra mathaei (de Blainville). Journal of Experimental Marine Biology and Ecology **147**:121-146.

McClanahan, T. R., J. Maina, and J. Davies. 2005. Perceptions of resource users and managers towards fisheries management options in Kenyan coral reefs. Fisheries Management and Ecology **12**:105-112.

McClanahan, T. R., and S. Mangi. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecological Applications **10**:1792-1805.

McClanahan, T. R., and S. Mangi. 2001. The effect of a closed area and beach seine exclusion on coral reef fish catches. Fisheries Management and Ecology **8**:107-121.

McClanahan, T. R., and S. C. Mangi. 2004. Gear-based management of a tropical artisanal fishery based on species selectivity and capture size. Fisheries Management and Ecology **11**:51-60.

McClanahan, T. R., and N. A. Muthiga. 1988. Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia **166**:269-276.

McClanahan, T. R., N. A. Muthiga, A. T. Kamukuru, H. Machano, and R. W. Kiambo. 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. Biological Conservation **89**:161-182.

McClanahan, T. R., M. Nugues, and S. Mwachireya. 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. Journal of Experimental Marine Biology and Ecology **184**:237-254.

McClanahan, T. R., and D. Obura. 1995. Status of Kenyan Coral Reefs. Coastal Management **23**:57-76.

McClanahan, T. R., and S. H. Shafir. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia **83**:362-370.

McConnell, K. M., and K. Scott. 2010. Prey species preference and specialized feeding behavior in the Mediterranean *Octopus vulgaris*.

McLeod, K., J. Lubchenco, S. R. Palumbi, and A. A. Rosenberg. 2005. Scientific Consensus Statement on Marine Ecosystem-based Management.

Meyer, J. L., and E. T. Schultz. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnology and Oceanography **30**:146-156.

Miller, R. J., D. C. Reed, and M. A. Brzezinski. 2009. Community structure and productivity of subtidal turf and foliose algal assemblages. Marine Ecology Progress Series **388**:1-11.

Mills, M. M., F. Lipschultz, and K. P. Sebens. 2004. Particulate matter ingestion and associated nitrogen uptake by four species of scleractinian corals. Coral Reefs **23**:311-323.

Mills, S. C., M. Peyrot-Clausade, and M. F. Fontaine. 2000. Ingestion and transformation of algal turf by *Echinometra mathaei* on Tiahura fringing reef (French Polynesia). Journal of Experimental Marine Biology and Ecology **254**:71-84.

Mitchell-Innes, B. A. 1967. Primary production studies in the south-west Indian Ocean, 1961-1963. Investigational Report 14. Oceanographic Research Institute, Durban, South Africa. .

Morissette, L. 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. University of British Columbia.

Mueni, E. 2013. SCEAM Indian Ocean country report – KENYA. Pages 55-57 Report of the FAO Workshop on Sea Cucumber Fisheries: An Ecosystem Approach to Management in the Indian Ocean (SCEAM Indian

Ocean). Mazizini, Zanzibar, the United Republic of Tanzania, 12–16 November 2012 FAO Fisheries and Aquaculture Report. No. 1038. Rome, Italy

Mueni, E., and J. Mwangi. 2002. Trawler survey along the Kenyan coast. KWS report.

Mumby, P. J., A. J. Edwards, J. E. Arias-Gonzalez, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorczynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature **427**:533-536.

Muscatine, L., P. G. Falkowski, Z. Dubinsky, P. A. Cook, and L. R. McCloskey. 1989a. The Effect of External Nutrient Resources on the Population Dynamics of Zooxanthellae in a Reef Coral. Proceedings of the Royal Society of London. B. Biological Sciences **236**:311.

Muscatine, L., C. Ferrier-Pagès, A. Blackburn, R. D. Gates, G. Baghdasarian, and D. Allemand. 1998. Cell-specific density of symbiotic dinoflagellates in tropical anthozoans. Coral Reefs **17**:329-337.

Muscatine, L., J. W. Porter, and I. R. Kaplan. 1989b. Resource partitioning by reef corals as determined from stable isotope composition. Marine Biology **100**:185-193.

Mutagyera, W. B. 1978. Some Observations on the Kenya Lobster Fishery. East African Agricultural and Forestry Journal **43**:401-407.

Muthiga, N. 1996. A Survey of the Coral Reef habitats of the Mombasa Marine Park and Reserve with a Review of the Existing Park Boundary.

Muthiga, N., J. Ochiewo, and J. Kawaka. 2007. Chapter 2: Sea cucumbers in Kenya. Commercial sea cucumbers: A review for the Western Indian Ocean. WIOMSA book Series:8-20.

Muthiga, N., J. Ochiewo, and J. Kawaka. 2010. Strengthening capacity to sustainably manage sea cucumber fisheries in the western Indian Ocean. SPC Beche-de-mer Information Bulletin **30**:3-10.

Muthiga, N. A. 2005. Testing for the Effects of Seasonal and Lunar Periodicity on the Reproduction of the Edible Sea Urchin Tripneustes gratilla (L) in Kenyan Coral Reef Lagoons. Hydrobiologia **549**:57-64.

Muthiga, N. A., and C. Conand, editors. 2014. Sea cucumbers in the western Indian Ocean: Improving management of an important but poorly understood resource. WIOMSA Book Series No. 13.

Mwakio, P. 2013. State moves to certify lobster fishing. Standard digital - http://www.standardmedia.co.ke/business/article/2000094430/state-moves-to-certify-lobster-fishing.

Mwaluma, J., M. Osore, J. Kamau, and P. Wawiye. 2003. Composition, abundance and seasonality of zooplankton in Mida Creek, Kenya. Western Indian Ocean Journal of Marine Science **2**:147-155.

Nagelkerken, I., J. Bothwell, R. S. Nemeth, J. M. Pitt, and G. van der Velde. 2008. Interlinkage between Caribbean coral reefs and seagrass beds through feeding migrations by grunts (Haemulidae) depends on habitat accessibility. Marine Ecology Progress Series **368**:155-164.

Nagelkerken, I., M. Dorenbosch, W. Verberk, E. C. de la Moriniere, and G. van der Velde. 2000a. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Marine Ecology Progress Series **194**:55-64.

Nagelkerken, I., S. Kleijnen, T. Klop, R. van den Brand, E. C. de la Moriniere, and G. van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Marine Ecology Progress Series **214**:225-235.

Nagelkerken, I., C. M. Roberts, G. van der Velde, M. Dorenbosch, M. C. van Riel, E. C. de la Morinere, and P. H. Nienhuis. 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Marine Ecology Progress Series **244**:299-305.

Nagelkerken, I., and G. van der Velde. 2004. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. Marine Ecology Progress Series **274**:153-159.

Nagelkerken, I., G. van der Velde, M. W. Gorissen, G. J. Meijer, T. van't Hof, and C. den Hartog. 2000b. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine Coastal and Shelf Science **51**:31-44.

Nystrom, M., and C. Folke. 2001. Spatial resilience of coral reefs. Ecosystems **4**:406-417.

Nyunja, J., M. Ntiba, J. Onyari, K. Mavuti, K. Soetaert, and S. Bouillon. 2009. Carbon sources supporting a diverse fish community in a tropical coastal ecosystem (Gazi Bay, Kenya). Estuarine, Coastal and Shelf Science **83**:333-341.

Nzuki, S. 2005. Enhancing the conservation and management of sea turtles in Kenya.

Nzuki, S., and J. Muasa. 2005. Participatory habitat characterization and GIS database development for the conservation and manahement of sea turtles in south coast Kenya. Report No: WIOMSA/MARG-I/2005 – 04

O’Leary, J. K., D. Potts, K. M. Schoenrock, and T. R. McClanahan. 2013. Fish and sea urchin grazing opens settlement space equally but urchins reduce survival of coral recruits. Marine Ecology Progress Series **493**:165-177.

Obura, D. O. 2001a. Can differential bleaching and mortality among coral species offer useful indicators for assessment and management of reefs under stress? Bulletin of Marine Science **69**:421-442.

Obura, D. O. 2001b. Participatory monitoring of shallow tropical marine fisheries by artisanal fishers in Diani, Kenya. Bulletin of Marine Science **69**:777-791.

Oceana. 2010. The international trade of shark fins: Endangering shark populations worldwide. Page 2.

Ochieng, C. A., and P. L. A. Erftemeijer. 1999. Accumulation of seagrass beach cast along the Kenyan coast: a quantitative assessment. Aquatic Botany **65**:221-238.

Ochieng, C. A., and P. L. A. Erftemeijer. 2003. Chapter 7. The seagrasses of Kenya and Tanzania. Pages 82-91 *in* E. P. Green and F. T. Short, editors. World Atlas of Seagrasses: Present Status and Future Conservation. University of California Press, Berkeley, USA.

Ochiewo, J. 2009. Small-Scale Fisheries. in Coastal livelihoods in the Republic of Kenya. ASCLME Coastal Livelihoods Assessments - Kenya http://www.asclme.org/reports2013/Coastal%20Livelihoods%20Assessments/41%20ASCLME%20CLA%20Kenya%20final%20draft%208-11-2010.pdf.

Ochiewo, J., M. de la Torre-Castro, C. Muthama, F. Munyi, and J. M. Nthuta. 2010. Socio-economic features of sea cucumber fisheries in southern coast of Kenya. Ocean & Coastal Management **53**:192-202.

Ochumba, P. B. O. 1983. Oceanographic Features Along the Kenyan Coast: Implications for Fisheries Management and Development. Marine Resource Management Program, School of Oceanography, Oregon State University.

Ochumba, P. B. O. 1988. The Distribution of Skates and Rays along the Kenyan Coast. Journal of the East Africa Natural History Society and National Museum **78**:25-45.

Odum, E. P. 1969. The strategy of ecosystem development. Science **104**:262-270.

Odum, E. P. 1971. Fundamentals of Ecology. Saunders, Philadelphia, PA (USA).

Odum, H. T., and E. P. Odum. 1955. Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll. Ecological Monographs **25**:291-320.

Ogden, J. C., and P. R. Ehrlich. 1977. Behavior of Heterotypic Resting Schools of Juvenile Grunts (Pomadasyidae). Marine Biology **42**:273-280.

Okechi, J. K., and J. J. Polovina. 1995. An evaluation of artificial shelters in the artisanal spiny lobster fishery in Gazi Bay, Kenya. South African Journal of Marine Science **16**:373-376.

Okemwa, E. 1990. A study of the pelagic copepods (Copepoda; Crustacea) in a tropical marine creek Tudor, Mombasa, Kenya, with a special reference to their community structure, biomass and productivity. Free University of Brussels.

Okemwa, G. M., S. Nzuki, and E. M. Mueni. 2004. The status and conservation of sea turtles in Kenya. Marine Turtle Newsletter **105**:1-6.

Okera, W. 1974. The zooplankton of the inshore waters of Dar es Salaam (Tanzania, S. E. Africa) with observations on reactions to artificial light. Marine Biology **26**:13-25.

Okey, T. A., S. Banks, A. F. Born, R. H. Bustamante, M. Calvopiña, G. J. Edgar, E. Espinoza, J. M. Fariña, L. E. Garske, and G. K. Reck. 2004. A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecological Modelling **172**:383-401.

Okuku, E. O., B. Ohowa, S. N. Mwangi, D. Munga, L. I. Kiteresi, V. O. Wanjeri, S. Okumu, and J. Kilonzo. 2011. Sewage pollution in the Coastal waters of Mombasa City, Kenya: A norm Rather than an Exception. International Journal of Environmental Research **5**:865-874.

Olds, A. D., R. M. Connolly, K. A. Pitt, and P. S. Maxwell. 2012. Habitat connectivity improves reserve performance. Conservation Letters **5**:56-63.

Opitz, S. 1996. Quantitative Models of Trophic Interactions in Caribbean Coral Reefs. ICLARM, Manila, Philippines.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott, and S. L. Williams. 2006. A global crisis for seagrass ecosystems. Bioscience **56**:987-996.

Orwa, P., M. Ntiba, N. Muthiga, and J. Kawaka. 2009. Holothurian population resource assessment: Mombasa Marine National Park and nearby unprotected reefs. Pages 162-177 *in* J. Hoorweg and N. A. Muthiga, editors. Advances in Coastal Ecology. African Studies Centre Leiden, Netherlands.

Osore, M. K. W. 1992. A note on the zooplankton distribution and diversity in a tropical mangrove creek system, Gazi, Kenya. Hydrobiologia **247**:119-120.

Otieno, M. J. 2011. Fishery Value Chain Analysis: Background Report–Kenya. FAO, Rome, Italy. IT 2–10.

Palardy, J. E., A. G. Grottoli, and K. A. Matthews. 2006. Effect of naturally changing zooplankton concentrations on feeding rates of two coral species in the Eastern Pacific. Journal of Experimental Marine Biology and Ecology **331**:99-107.

Palardy, J. E., L. J. Rodrigues, and A. G. Grottoli. 2008. The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. Journal of Experimental Marine Biology and Ecology **367**:180-188.

Palomares, M. L., and D. Pauly. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Marine and Freshwater Research **49**:447-453.

Papadopoulos, I. 1995. Kenyan seagrass fields as feeding grounds for the early life stages of important consumption fish (Gerreidae and Lutjanidae). . University of Gent, Zoology Institute, Marine Biology Section: Gent.

Paula, J., I. Pinto, I. Guambe, S. Monteiro, D. Gove, and J. Guerreiro. 1998. Seasonal cycle of planktonic communities at Inhaca Island, southern Mozambique. Journal of PLankton Research **20**:2165-2178.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil **39**:175-192.

Pauly, D., and V. Christensen. 1993. Stratified models of large marine ecosystems: a general approach and an application to the South China Sea. Large marine ecosystems: stress, mitigation and sustainability. AAAS Press, Washington, DC:148-174.

Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature **374**:255-257.

Pauly, D., V. Christensen, and C. J. Walters. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impacts of fisheries. ICES Journal of Marine Science **57**:697-706.

Pauly, D., V. Sambilay Jr, and S. Opitz. 1993. Estimates of relative food consumption by fish and invertebrate populations, required for modeling the Bolinao reef ecosystem, Philippines. Pages 236-251 *in* V. Christensen and D. Pauly, editors. Trophic models of aqautic ecosystems. ICLARM Conference Proceedings 26.

Payri, C. 2000. Production primaire et calcification des algues benthiques en milieu corallien. Oceanis **26**:427-463.

Perales-Raya, C., E. Almansa, A. Bartolomé, B. C. Felipe, J. Iglesias, F. J. Sánchez, J. F. Carrasco, and C. Rodríguez. 2014. Age Validation in Octopus vulgaris Beaks Across the Full Ontogenetic Range: Beaks as Recorders of Life Events in Octopuses. Journal of Shellfish Research **33**:481-493.

Perera, E., I. Fraga, O. Carrillo, E. Díaz-Iglesias, R. Cruz, M. Báez, and G. S. Galich. 2005. Evaluation of practical diets for the Caribbean spiny lobster *Panulirus argus* (Latreille, 1804): effects of protein sources on substrate metabolism and digestive proteases. Aquaculture (Amsterdam, Netherlands) **244**:251-262.

Perry, C. T., G. N. Murphy, N. A. J. Graham, S. K. Wilson, F. A. Januchowski-Hartley, and H. K. East. 2015. Remote coral reefs can sustain high growth potential and may match future sea-level trends. Scientific Reports **5**:18289.

Peyrot-Clausade, M., P. Chabanet, C. Conand, M. F. Fontaine, Y. Letourneur, and M. Harmelin-Vivien. 2000. Sea urchin and fish bioerosion on La Réunion and Moorea reefs. Bulletin of Marine Science **66**:477-485.

Pierce, C. L., J. B. Rasmussen, and W. C. Leggett. 1990. Sampling Littoral Fish with a Seine: Corrections for Variable Capture Efficiency. Canadian Journal of Fisheries and Aquatic Sciences **47**:1004-1010.

Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E. D. Houde, J. Link, P. A. Livingston, M. Mangel, M. K. McAllister, J. Pope, and K. J. Sainsbury. 2004. Ecosystem-Based Fishery Management. Science **305**:346-347.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics **28**:289-316.

Polovina, J. J. 1984. Model of a coral reef ecosystem. Coral Reefs **3**:1-11.

Randall, J. E. 2004. Revision of the Goatfish Genus Parupeneus (Perciformes: Mullidae) with Descriptions of Two New Species. Bishop Museum.

Rasheed, M. A., K. R. Dew, L. J. McKenzie, R. G. Coles, S. P. Kerville, and S. J. Campbell. 2008. Productivity, carbon assimilation and intra-annual change in tropical reef platform seagrass communities of the Torres Strait, north-eastern Australia. Continental Shelf Research **28**:2292-2303.

Regalado, J. M., W. L. Campos, and A. Santillan. 2011. Population biology of *Tripneustes gratilla* (Linnaeus)(Echinodermata) in seagrass beds of Southern Guimaras, Philippines. Science Diliman **22**.

Ribes, M., R. Coma, M. J. Atkinson, and R. A. Kinzie. 2003. Particle removal by coral reef communities: picoplankton is a major source of nitrogen. Marine Ecology Progress Series **257**:13-23.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191. Fisheries Research Board Canada.

Robblee, M. B., and J. C. Zieman. 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. Bulletin of Marine Science **34**:335-345.

Rocliffe, S., and A. Harris. 2016. The status of octopus fisheries in the Western Indian Ocean. Blue Ventures, London, United Kingdom.

Rombouts, I., G. Beaugrand, L. F. Artigas, J. C. Dauvin, F. Gevaert, E. Goberville, D. Kopp, S. Lefebvre, C. Luczak, N. Spilmont, M. Travers-Trolet, M. C. Villanueva, and R. R. Kirby. 2013. Evaluating marine ecosystem health: Case studies of indicators using direct observations and modelling methods. Ecological Indicators **24**:353-365.

Rosenfeld, M., V. Bresler, and A. Abelson. 1999. Sediment as a possible source of food for corals. Ecology Letters **2**:345-348.

Ruiz Sebastián, C., and T. R. McClanahan. 2013. Description and validation of production processes in the coral reef ecosystem model CAFFEE (Coral–Algae–Fish-Fisheries Ecosystem Energetics) with a fisheries closure and climatic disturbance. Ecological Modelling **263**:326-348.

Russ, G. R. 2003. Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. Coral Reefs **22**:63-67.

Samhouri, J. F., P. S. Levin, and C. J. Harvey. 2009. Quantitative evaluation of marine ecosystem indicator performance using food web models. Ecosystems **12**:1283-1298.

Samoilys, M., N. Kanyange, D. Macharia, G. W. Maina, and J. Robinson. 2013. Dynamics of rabbitfish (Siganus sutor) spawning aggregations in southern Kenya. Pages 33-45 *in* J. Robinson and M. Samoilys, editors. Reef Fish Spawning Aggregations in the Western Indian Ocean: Research for Management. WIOMSA/SIDA/SFA/CORDIO. WIOMSA Book Series 13.

Samoilys, M., G. W. Maina, and K. Osuka. 2011. Artisanal fishing gears of the Kenyan coast.

Samoilys, M. A., K. Osuka, G. W. Maina, and D. O. Obura. 2017. Artisanal fisheries on Kenya's coral reefs: Decadal trends reveal management needs. Fisheries Research **186, Part 1**:177-191.

Sathyendranath, S., V. Stuart, A. Nair, K. Oka, T. Nakane, H. Bouman, M. H. Forget, H. Maass, and T. Platt. 2009. Carbon-to-chlorophyll ratio and growth rate of phytoplankton in the sea. Marine Ecology Progress Series **383**:73-84.

Schaeffer, D. 2004. Assessment of the artisanal shark fishery and local shark fin trade on Unguja Island, Zanzibar.

Scott, E., N. Serpetti, J. Steenbeek, and J. J. Heymans. 2016. A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. SoftwareX **5**:25-30.

Sebens, K. P., K. S. Vandersall, L. A. Savina, and K. R. Graham. 1996. Zooplankton capture by two scleractinian corals,Madracis mirabilis andMontastrea cavernosa, in a field enclosure. Marine Biology **127**:303-317.

Shannon, L., M. Coll, A. Bundy, D. Gascuel, J. J. Heymans, K. Kleisner, C. P. Lynam, C. Piroddi, J. Tam, M. Travers-Trolet, and Y. Shin. 2014. Trophic level-based indicators to track fishing impacts across marine ecosystems. Marine Ecology Progress Series **512**:115-140.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia **132**:131-142.

Shin, Y.-J., L. J. Shannon, A. Bundy, M. Coll, K. Aydin, N. Bez, J. L. Blanchard, M. d. F. Borges, I. Diallo, E. Diaz, J. J. Heymans, L. Hill, E. Johannesen, D. Jouffre, S. Kifani, P. Labrosse, J. S. Link, S. Mackinson, H. Masski, C. Möllmann, S. Neira, H. Ojaveer, K. ould Mohammed Abdallahi, I. Perry, D. Thiao, D. Yemane, and P. M. Cury. 2010. Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. ICES Journal of Marine Science: Journal du Conseil **67**:692-716.

Signa, D., P. Tuda, and M. Samoilys. 2008. Social, Economic and Environmental Impacts of Beach Seining in Kenya an Information Review and Field Study, Final Report. East Africa. FAO and CORDIO.

Silva, R., M. Sousa, and A. Caramelo. 1993. The Maputo Bay ecosystem (Mozambique). Pages 214-223 *in* Trophic models of aquatic ecosystems. ICLARM Conference Proceedings.

Sissenwine, M. P., and J. G. Shepherd. 1987. An Alternative Perspective on Recruitment Overfishing and Biological Reference Points. Canadian Journal of Fisheries and Aquatic Sciences **44**:913-918.

Smale, M. J., and P. R. Buchan. 1981. Biology of Octopus vulgaris off the east coast of South Africa. Marine Biology **65**:1-12.

Smith, C. D. 2003. Diet of *Octopus vulgaris* in False Bay, South Africa. Marine Biology **143**:1127-1133.

Sorokin, Y. I. 1993. Coral reef ecology. Springer Verlag, Berlin, Germany.

State Department of Fisheries. 2013. Annual Fisheries Statistical Bulletin. Ministry of Agriculture, Livestock and Fisheries.

State Department of Fisheries. 2014. Marine artisanal fisheries frame survey 2014 report. Ministry of Agriculture, Livestock and Fisheries.

Steenbeek, J., J. Buszowski, V. Christensen, E. Akoglu, K. Aydin, N. Ellis, D. Felinto, J. Guitton, S. Lucey, K. Kearney, S. Mackinson, M. Pan, M. Platts, and C. Walters. 2016. Ecopath with Ecosim as a model-building toolbox: Source code capabilities, extensions, and variations. Ecological Modelling **319**:178-189.

Taylor, A. H., R. J. Geider, and F. J. H. Gilbert. 1997. Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll a ratios: Results of a modelling study. Marine Ecology Progress Series **152**:51-66.

Thangaraja, R., and E. Radhakrishnan. 2012. Fishery and ecology of the spiny lobster Panulirus homarus (Linnaeus, 1758) at Khadiyapatanam in the southwest coast of India. Journal of the Marine Biological Association of India **54**:69-79.

Thornhill, D. J., R. D. Rotjan, B. D. Todd, G. C. Chilcoat, R. Iglesias-Prieto, D. W. Kemp, T. C. LaJeunesse, J. M. Reynolds, G. W. Schmidt, T. Shannon, M. E. Warner, and W. K. Fitt. 2011. A Connection between Colony Biomass and Death in Caribbean Reef-Building Corals. PloS One **6**:e29535.

Tribble, G. W. 1981. Reef-based herbivores and the distribution of two seagrasses (*Syringodium filiforme* and *Thalassia testudinum*) in the San Blas Islands (Western Caribbean). Marine Biology **65**:277-281.

Tsehaye, Y., and L. A. J. Nagelkerke. 2008. Exploring optimal fishing scenarios for the multispecies artisanal fisheries of Eritrea using a trophic model. Ecological Modelling **212**:319-333.

Tuda, P. M., and Wolff, M. 2018. Comparing an ecosystem approach to single-species stock assessment: The case of Gazi Bay, Kenya. Journal of Marine Systems **184**:1-14.

Tuda, P. M., and M. Wolff. 2015. Evolving trends in the Kenyan artisanal reef fishery and its implications for fisheries management. Ocean & Coastal Management **104**:36-44.

Tudman, P. D. 2001. Modelling the trophic effects of fishing on a mid-shelf coral reef of the central Great Barrier Reef. Bachelor of Science with Honours thesis. James Cook University, Brisbane, Australia.

Uku, J., and M. Björk. 2005. Productivity aspects of three tropical seagrass species in areas of different nutrient levels in Kenya. Estuarine, Coastal and Shelf Science **63**:407-420.

Uku, J. N. 2005. Seagrasses and their Epiphytes: Characterization of abundance and productivity in tropical seagrass beds. Stockholm University, Sweden.

Ulanowicz, R. E. 1986. Growth and Development: Ecosystem Phenomenology. Springer Verlag, New York (NY), USA. Reprinted by iUniverse 2000.

Ulanowicz, R. E. 1997. Ecology: The Ascendent Perspective. Columbia University Press, New York (NY), USA.

Unsworth, R., P. S. De León, S. L. Garrard, D. J. Smith, and J. J. Bell. 2009a. Habitat Usage of the Thumbprint Emporer Lethrinus harak (Forsskål, 1775) in an Indo-Pacific Coastal Seascape. Open Marine Biology Journal **3**:16-20.

Unsworth, R. K., S. L. Garrard, P. S. De León, L. C. Cullen, D. J. Smith, K. A. Sloman, and J. J. Bell. 2009b. Structuring of Indo-Pacific fish assemblages along the mangrove–seagrass continuum. Aquatic Biology **5**:85-95.

Unsworth, R. K. F., P. S. De Leon, S. L. Garrard, J. Jompa, D. J. Smith, and J. J. Bell. 2008. High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. Marine Ecology-Progress Series **353**:213-224.

Valentine, J. F., and J. E. Duffy. 2006. The central role of grazing in seagrass ecology. Pages 463-501 *in* A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, The Netherlands.

Valls, A., D. Gascuel, S. Guénette, and P. Francour. 2012. Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Marine Ecology Progress Series **456**:201-214.

van Heukelem, W. F. 1976. Growth, bioenergetics and life span of *Octopus cyanea* and *Octopus maya*. University of Hawaii.

Van Heukelem, W. F. 1983. Octopus cyanea. Pages 267-276 *in* P. R. Boyle, editor. Cephalopod Life Cycles, Vol 1: Species Accounts. Academic Press, London, United Kingdom.

Vasconcellos, M., S. Mackinson, K. Sloman, and D. Pauly. 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecological Modelling **100**:125-134.

Venier, J. M., D. Pauly, and 1997. 1997. Trophic dynamics of a Florida Keys coral reef ecosystem.*in* Proceedings of the 8th International Coral Reef Symposium.

Verweij, M. C., I. Nagelkerken, S. L. J. Wartenbergh, I. R. Pen, and G. Velde. 2006. Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, *Haemulon flavolineatum*. Marine Biology **149**:1291-1299.

Villasante, S., F. Arreguín-Sánchez, J. J. Heymans, S. Libralato, C. Piroddi, V. Christensen, and M. Coll. 2016. Modelling marine ecosystems using the Ecopath with Ecosim food web approach: New insights to address complex dynamics after 30 years of developments. Ecological Modelling **331**:1-4.

Wabnitz, C. C. C., G. Balazs, S. Beavers, K. A. Bjorndal, A. B. Bolten, V. Christensen, S. Hargrove, and D. Pauly. 2010. Ecosystem structure and processes at Kaloko Honokōhau, focusing on the role of herbivores, including the green sea turtle Chelonia mydas, in reef resilience. Marine Ecology Progress Series **420**:27-44.

Waiyaki, E. 2014. Coping strategies of Kenya's coastal artisanal fishing house-holds against poverty: Do these strategies produce any sustained benefit? International Institute of Social Studies, The Hague, The Netherlands.

Wallberg, P., and A. Andersson. 2000. Transfer of carbon and a polychlorinated biphenyl through the pelagic microbial food web in a coastal ecosystem. Environmental Toxicology and Chemistry **19**:827-835.

Walters, C., D. Pauly, and V. Christensen. 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems **2**:539-554.

Walters, C. J., and S. J. D. Martell. 2004. Fisheries Ecology and Management. Princeton University Press, Princeton (NJ), USA.

Wamukota, A., T. D. Brewer, and B. Crona. 2014. Market integration and its relation to income distribution and inequality among fishers and traders: The case of two small-scale Kenyan reef fisheries. Marine Policy **48**:93-101.

Wamukota, A. W., S. Nzuki, and J. Muasa. 2006. Community participation in the conservation and management of sea turtles in Kenya. Page 351 *in* M. Frick, A. Panagopoulou, A. F. Rees, and K. Williams, editors. Book of asbtracts. 26th Annual Symposium on Sea Turtle Biology and Conservation Island of Crete, Greece, 3-8 April 2006. International Sea Turtle Society.

Wamukota, A. W., and G. Okemwa. 2009. Perceptions about trends and threats regarding sea turtles in Kenya. Pages 193-205 *in* J. Hoorweg and N. Muthiga editors. Advances in Coastal Ecology: People, processes and ecosystems in Kenya African Studies Centre, Leiden, The Netherlands.

Wamukoya, G. M., M. J.M., and W. K. Ottichillo. 1996. Marine aerial survey; marine mammals, sea turtles, sharks and rays. KWS Technical Series Report 1.

Wamukoya, G. M., and J. R. Mbendo. 1995. Incidental capture of sea turtles in Shrimp trawl fisheries in Kenya. KWS Technical Report Series.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution **17**:76-83.

Weijerman, M., E. A. Fulton, and F. A. Parrish. 2013. Comparison of Coral Reef Ecosystems along a Fishing Pressure Gradient. PloS One **8**:e63797.

Weinstein, M. P., and K. L. Heck. 1979. Ichthyofauna of Seagrass Meadows Along the Caribbean Coast of Panama and in the Gulf of Mexico - Composition, Structure and Community Ecology. Marine Biology **50**:97-107.

Welch, H. E. (1968). Relationships between assimiliation efficiencies and growth efficiencies for aquatic consumers. Ecology **49**(4):755-759.

Wootton, R. J. 1990. Feeding. Pages 32-72 *in* R. J. Wootton, editor. Ecology of Teleost Fishes. Springer Netherlands, Dordrecht.

Wulff, F., J. G. Field, and K. H. Mann, editors. 1989. Network Analysis in Marine Ecology: Methods and Applications Coastal and estuarine studies Vol. 32. Springer Verlag, Berlin, Germany.

Yahel, G., A. F. Post, K. Fabricius, D. Marie, D. Vaulot, and A. Genin. 1998. Phytoplankton distribution and grazing near coral reefs. Limnology and Oceanography **43**:551-563.

Yahel, R., G. Yahel, T. Berman, J. S. Jaffe, and A. Genin. 2005a. Diel pattern with abrupt crepuscular changes of zooplankton over a coral reef. Limnology and Oceanography **50**:930-944.

Yahel, R., G. Yahel, and A. Genin. 2005b. Near- bottom depletion of zooplankton over coral reefs: I: diurnal dynamics and size distribution. Coral Reefs **24**:75-85.

Zhou, S. 2011. Sustainability assessment of fish species potentially impacted in the Northern Prawn Fishery: 2007-2009. Report to the Australia Fisheries Management Authority, Canberra, Australia.

Zöllner, E., H.-G. Hoppe, U. Sommer, and K. Jürgens. 2009. Effect of zooplankton-mediated trophic cascades on marine microbial food web components (bacteria, nanoflagellates, ciliates). Limnology and Oceanography **54**:262-275.

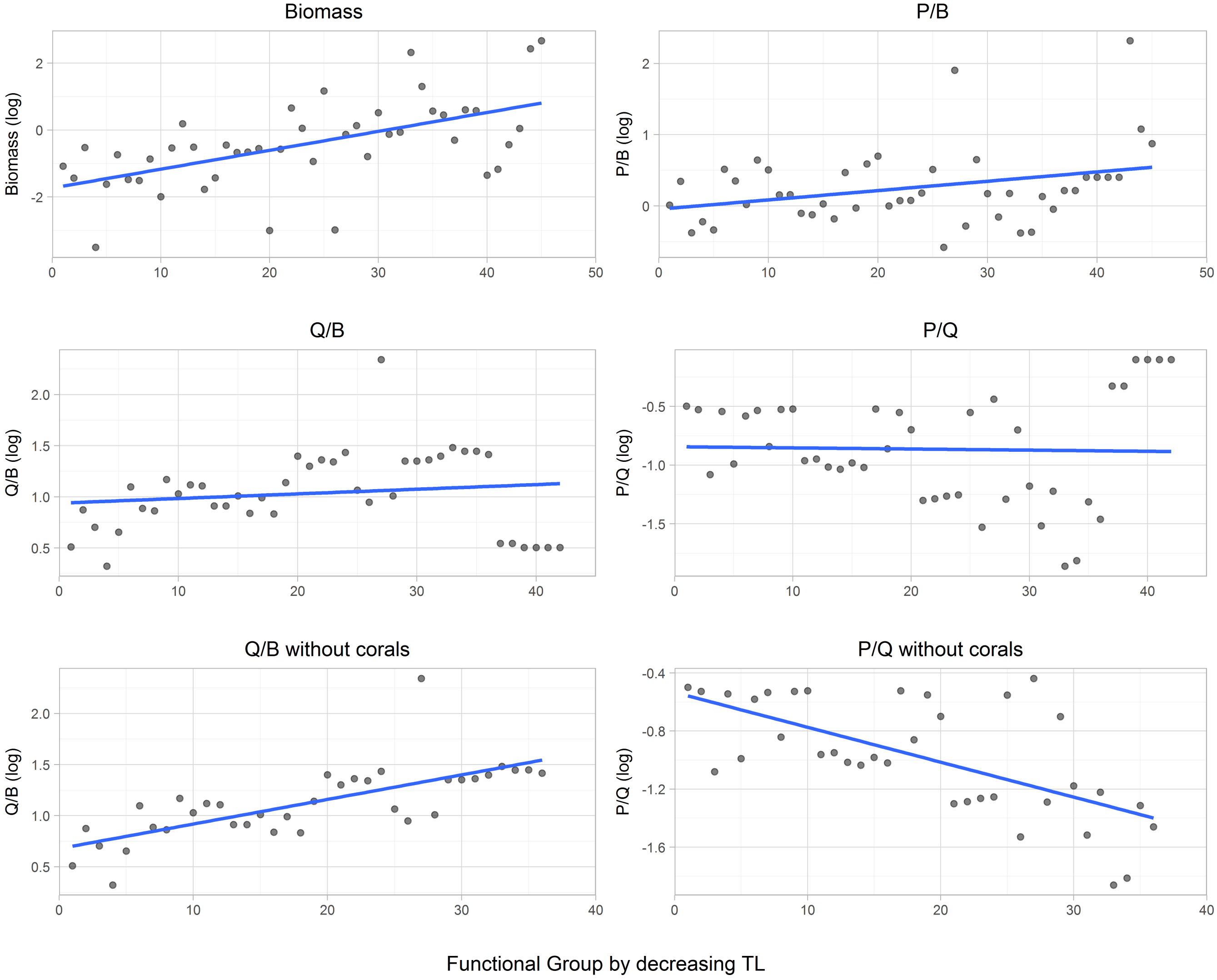
APPENDICES

Appendix 1

PREBAL results for log biomass, P/B and Q/B (with and without corals) for all groups organized by declining trophic level. The x-axis value in the graphs represent the groups as per the assigned Prebal value in the table below. The GroupNo refers to the original number they were assigned in model development and TL: trophic level.

PreBal	GroupNo	Group	TL
1	2	Sharks & rays	3.458885
2	10	Grouper F	3.336686
3	9	Groupers P	3.322349
4	6	Reef fish F > 60cm	3.320404
5	3	Reef fish P > 60cm	3.199592
6	30	Octopi	3.194557
7	22	Sweetlips & Grunts F	3.177474
8	31	Lobsters	3.15643
9	28	Squids	3.153078
10	16	Emperors F	3.055074
11	23	Wrasses P	3.106339
12	24	Wrasses F	3.094711
13	20	Goatfishes F	3.074505
14	19	Goatfishes P	3.072958
15	17	Snappers F	3.139073
16	21	Sweetlips & Grunts P	3.063859
17	16	Snappers P	3.072276
18	15	Emperors P	3.0505
19	27	Pelagics	3.0074
20	29	Jellyfish	2.873029
21	4	Reef fish P 30-60 cm	2.314152
22	8	Reef fish F <= 30cm	2.292731
23	5	Reef fish P <= 30cm	2.238599
24	7	Reef fish F 30-60 cm	2.232516
25	35	Benthic invertebrates	2.186965
26	1	Sea turtles	2.117987
27	44	Zooplankton	2.041667
28	32	Sea cucumbers	2.009298
29	26	Rabbitfish F	2.001187
30	25	Rabbitfish P	2.001187
31	11	Parrotfish P> 30 cm	2.000928
32	13	Parrotfish F > 30 cm	2.000928
33	34	Urchins F	2.000337
34	33	Urchins P	2.000084
35	14	Parrotfish F <= 30 cm	2
36	12	Parrotfish P <= 30 cm	2
37	40	Massive & encrusting corals P	1.84375
38	41	Massive & encrusting corals F	1.84375
39	39	Other branching corals F	1.421875
40	38	Other branching corals P	1.421875
41	36	Acropora P	1.16875
42	37	Acropora F	1.16875
43	45	Phytoplankton	1

44	42	Benthic reef algae	1
45	43	Seagrasses	1



Appendix 2

Summary table of catches by gear by landing site and the variation in total annual catches depending on assumptions.
Annual catch estimate A = average daily catch * 220 fishing days per year;
Annual catch estimate B = average daily catch * ratio of gear use * 220.
The bis refers to the same calculations but using 306 fishing days instead of 220.

	KENYATTA					**MTWAPA**						**MARINA**		
Gears		Gillnet	Handline	Speargun	Trap		Beachseine	Gillnet	Handline	Speargun	Trap		Beachseine	Gillnet	Trap
Total catch (kg)		779.500	657.000	1023.000	742.000		59.500	789.800	414.500	322.500	143.000		3337.500	34.000	50.500
Sampling days	54	40.000	41.000	49.000	48.000	19	1.000	14.000	12.000	17.000	5.000	22	22.000	3.000	10.000
Gear use / sampling days		0.741	0.759	0.907	0.889		0.053	0.737	0.632	0.895	0.263		1.000	0.136	0.455
Avg daily catch (kg)		19.488	16.024	20.878	15.458		59.500	56.414	34.542	18.971	28.600		151.705	11.333	5.050
Estimated annual catch (tonnes) - A		4.287	3.525	4.593	3.401		13.090	12.411	7.599	4.174	6.292		33.375	2.493	1.111
Estimated annual catch (tonnes) - B		3.176	2.677	4.168	3.023		0.689	9.145	4.799	3.734	1.656		33.375	0.340	0.505
Est. annual catch (tonnes) - A bis		5.963	4.903	6.389	4.730		18.207	17.263	10.570	5.805	8.752		46.422	3.468	1.545
Est. annual catch (tonnes) - B bis		4.417	3.723	5.797	4.205		0.958	12.720	6.676	5.194	2.303		46.422	0.473	0.702

	REEF					**NYALI**						**MSANAKANI**		
Gears		Beachseine	Gillnet	Speargun	Trap		Beachseine	Gillnet	Handline	Speargun	Trap		Beachseine	**TOTAL**
Total catch (kg)		3464.500	64.000	284.000	145.200		972.500	73.500	79.000	742.500	298.000		601.500	15092.500
Sampling days	21	21.000	5.000	19.000	16.000	20	20.000	8.000	14.000	20.000	20.000	20	20.000	
Gear use / sampling days		1.000	0.238	0.905	0.762		1.000	0.400	0.700	1.000	1.000		1.000	
Avg daily catch (kg)		164.976	12.800	14.947	9.075		48.625	9.188	5.643	37.125	14.900		30.075	
Estimated annual catch (tonnes) - A		36.295	2.816	3.288	1.997		10.698	2.021	1.241	8.168	3.278		6.617	176.070
Estimated annual catch (tonnes) - B		36.295	0.670	2.975	1.521		10.698	0.809	0.869	8.168	3.278		6.617	139.348
Est. annual catch (tonnes) - A bis		50.483	3.917	4.574	2.777		14.879	2.811	1.727	11.360	4.559		9.203	244.897
Est. annual catch (tonnes) - B bis		50.483	0.933	4.138	2.116		14.879	1.125	1.209	11.360	4.559		9.203	193.820